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

2 **acidification experiments with natural communities**

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13 **Short summary**

14 Diatoms are a group of phytoplankton species responsible for ~20% of primary

15 production on Earth. Ocean acidification (OA) could influence diatoms but the key

16 question is if they become more or less important within marine food webs. Here we

17 synthesize OA experiments with natural communities and found: Diatoms are more likely

18 to be positively than negatively affected by OA and larger species may profit more than

19 smaller ones. This has important implications for ecosystem services diatoms provide.

21 **Abstract**

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

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

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

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

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

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

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

29   to elevated CO_2 with respect to abundance or biomass; 2) if shifts within the diatom

30   communities could be expected and how they are expressed with respect to taxonomic

31   affiliation and size structure. We found that bulk diatom communities responded to high

32   CO_2 in ~60 % of the experiments and in this case more often positively (56 %) than

33   negatively (32 %; 12 % did not report the direction of change). Shifts among different

34   diatom species were observed in 65 % of the experiments. Our synthesis supports the

35   hypothesis that high CO_2 particularly favors larger species as 12 out of 13 experiments

36   which investigated cell size found a shift towards larger species. Unraveling winners and

37   losers with respect to taxonomic affiliation was difficult due to a limited database. We

38   conclude that OA-induced changes in diatom competitiveness and assemblage structure

39   may alter key ecosystem services due to the pivotal role diatoms play in trophic transfer

40   and biogeochemical cycles.

41   **1. Introduction**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

59   2005).

60   Diatoms display an enormous species richness, with recent estimates accounting for so

61   far undiscovered diatoms (including freshwater) being in the range of 20,000 – 100,000

62   species (Guiry, 2012; Mann and Vanormelingen, 2013). Sournia et al. (1991) derive a

63   number between 1400 – 1800 of described marine diatoms based on microscopy while

64   *Tara* Oceans reported ~4700 operational taxonomic units from genetic samples

65   distributed over all major oceans except the North Atlantic and North Pacific (Malviya et

66   al., 2016). Known diatom taxa span a size range of several orders of magnitude (<5 µm

67   up to a few mm) with a wide range of morphologies and life strategies, e.g. single cells

68   and cell chains, pelagic and benthic habitats (Armbrust, 2009; Mann and Vanormelingen,

69   2013; Sournia et al., 1991). Accordingly, they should not be treated as one functional

70   group, but rather as a variety of subgroups occupying different niches.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

85 biogeochemical cycles and ecosystem services in the world oceans.

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

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

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

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

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

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

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

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

94 community composition under ocean acidification.

95 **2. Literature investigation**

96 **2.1. Approach**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

112   **2.2. Data compilation**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

138   sufficient data on morphological details to fully exclude this scenario. Furthermore, we

139   emphasize that CO_2 can also shift the temporal occurrence of a diatom response (Bach et

140   al., 2017). For example, a diatom bloom could occur earlier in a high CO_2 treatment than

141   in the control but with a similar bloom amplitude (Donahue et al., 2019). In this case we

142   assigned a "positive" response because an earlier bloom occurrence mirrors a higher net

143   growth rate under elevated CO_2.

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

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

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

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

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

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

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

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

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

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

154   community shifts, and metadata is compiled/described in Table 1 and most of it is self-

155   explanatory (e.g. incubation temperature). The coordinates from where the investigated

156   plankton communities originate are given in Table 1 and illustrated in Figure 2. Their

157   habitats were categorized according to water depth, salinity, or life style in the case of

158   benthic communities: "oceanic" = water depth > 200 m (unless the habitat lies within a

159   fjord or fjord-like strait), S > 30; "coastal" = water depth < 200 m, S > 30; "estuarine" =

160   water depth < 200 m, S < 30; "benthic" = benthic communities (diatoms growing on

161   plates) were investigated. We reconstructed the water depth in case it was not provided

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

163   some of the experiments conducted in land-based facilities were imprecise and marked

164   positions on land. In this case the habitats were set to coastal or estuarine depending on

165   salinity. If salinity was not given we checked the location on Google Earth for potential

166   fresh water sources and also checked the text for more cryptic indications (e.g.

167   "euryhaline" in a lagoon were strong indications for an estuarine habitat). The methods

168   with which responses of the bulk diatom communities to high OA were determined varied

169   greatly among studies and included light microscopy (LM), pigment analyses (PA), flow

170   cytometry (FC), genetic tools (PCR), and biogenic silica (BSi) analyses (Table 1).

171   **2.3. Accounting for different experimental setups to balance the influence of**

172 **individual studies on the outcome of the literature analysis**

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

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

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

176 Hall-Spencer et al., 2008; Johnson et al., 2011). However, pelagic communities are

177 advected with currents so that it is very difficult to simulate OA in open waters. Thus,

178 OA experiments where pelagic communities are exposed to increasing levels of CO_2 were

179 so far always performed in closed containers even though it is well known that

180 confinement causes experimental artefacts (Calvo-Díaz et al., 2011; Ferguson et al., 1984;

181 Guangao, 1990; Menzel and Case, 1977). The degree by which confinement causes

182 experimental artefacts will differ from study to study depending on factors such as the

183 incubation volume, the length of incubation, or the selective removal of certain size

184 classes from the incubation (Carpenter, 1996; Duarte et al., 1997; Nogueira et al., 2014).

185 In our literature synthesis we had to deal with a large variety of experimental setups and

186 there are very likely differences how well a given setup represents the natural

187 environment. Therefore, we aimed to develop a metric that allows us to estimate "how

188 well the natural system (which we are ultimately interested in) is represented by the

189 experimental setup". This metric – termed the "relative degree of realism (RDR)" – was

190 used to balance the influence of individual studies on the final outcomes of the literature

191 analysis. Most certainly, we do not mean to devalue any studies but think that the highly

192 different scales of experiments, ranging from 0.8 L lab incubations to 75 m^3 *in situ*

193 mesocosms, should not be ignored when evaluating the literature. In the following we

194 will first derive the equation for the RDR and introduce the underlying assumptions.

195 Afterwards we describe aspects that were considered while conceptualizing the RDR.

196 The incubation volume in the studies considered herein ranged from bottle experiments

197   to *in situ* mesocosm studies with considerably larger incubation volumes. Smaller

198   differences in incubation volumes (e.g. 0.5 vs. 2 L) were shown to have no, or a minor,

199   influence on physiological rates (Fogg and Calvario-Martinez, 1989; Hammes et al.,

200   2010; Nogueira et al., 2014; Robinson and Williams, 2005). However, they can influence

201   food web composition (Calvo-Díaz et al., 2011; Spencer and Warren, 1996), e.g. by

202   unrepresentatively including certain organism groups such as highly motile

203   mesozooplankton. Larger differences of incubation volumes (e.g. 10 vs. 10000 L) are

204   considered to have a major influence on the enclosed communities, with the larger volume

205   being more representative of natural processes (Carpenter, 1996; Duarte et al., 1997;

206   Sarnelle, 1997). Therefore, our first assumption to conceptualize the RDR was that larger

207   incubation volumes represent nature generally better than smaller ones.

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

209   patchily distributed organisms (e.g. copepods). This is a valid procedure to reduce noise

210   and to increase the likelihood to detect CO_2 effects but it also influences the development

211   of plankton communities since the selective removal of certain size classes can modify

212   trophic cascades within the food web (Ferguson et al., 1984; Nogueira et al., 2014). For

213   example, Nogueira et al. (2014) compared plankton successions of pre-filtered (100 µm)

214   and unfiltered communities and found that the removal of larger grazers and diatoms gave

215   room for green algae and picophytoplankton to grow. Such manipulations make the

216   experiment less representative for a natural food web which brought us to the second

217   assumption for the RDR: The smaller the mesh size during the pre-filtration treatment,

218   the less complete and thus the less realistic is the pelagic food web.

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

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

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

222   incubator and is indicative for the relation of open space to hard surfaces. Therefore we

223   first converted V into a radius (r) assuming spherical shape:

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

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

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

227   The assumption of spherical shape was necessary because it allowed us to calculate V/S

228   from only knowing V which is usually the only parameter provided with respect to

229   container characteristics. We are aware that this is a simplification because the majority

230   of containers used in experiments will likely have had cylindrical shape. However, the

231   conversion from volume to surface assuming cylindrical shape would have required

232   knowledge of two dimensions (radius and height of the cylinder). Although shape can

233   influence processes within the container (Pan et al., 2015), it is a less important factor to

234   consider in our study because sensitivity calculations assuming reasonable cylinder

235   dimensions showed that the V/S differences due to container shape will be small

236   compared to the V/S differences due to the range of container volumes compared here.

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

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

239   µm) so that the RDR is defined as:

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

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

242   less influential with increasing d_{mesh}. The rationale for the non-linear increase is that

243   incubations will still have an increasing bias even if they do not have any pre-filtration

244   treatment due to generally increasing organism motility with size. For example, when

245   collecting a plankton community with a Niskin bottle, more motile organisms can escape

246   from the approaching sampler so that the food web composure is still affected even

247   without subsequent pre-filtration. For this reason we also capped the maximum d_{mesh} to

248   10,000 μm when there was no pre-filtration treatment applied since none of the studies

249   included significantly larger organisms. The rationale for calculating the cube root of

250   d_{mesh} was that in this case the influence of V/S and d_{mesh} on RDR becomes roughly similar.

251   Figure 1 illustrates the change of RDR as a function of V and d_{mesh}. High RDRs are

252   calculated for large-scale *in situ* mesocosm studies (~50 – 190) while bottle experiments

253   yield RDRs between ~1 – 12.

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

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

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

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

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

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

260   experiments (Time). Time is reliably reported in all studies and therefore principally

261   suitable for the RDR. Our first thoughts were that a realistic community experiment

262   should be long enough to cover relevant ecological processes such as competitive

263   exclusion and therefore also parameterized Time in the first versions of the RDR

264   equation. However, we decided to not account for it in the final version because the

265   factors that define the optimal duration of an experiment are poorly constrained. For

266   example, a 1 day experiment in a 10 L container could indeed miss important CO_2 effects

267   caused by food web interactions. On the other hand, a 30 days experiment in the same

268   container could reveal such indirect effects but at the same time be associated with

269   profound bottle effects and make the study unrepresentative for simulated natural habitat.

270   Thus, too long and too short are both problematic and the optimum is hard to find. One

271   such attempt to find the optimum Time was made by (Duarte et al., 1997) who analyzed

272   the plankton ecology literature between 1990 – 1995. By correlating the experimental

273   duration with the incubation volume of published experiments they provided an optimal

274   length for any given volume. However, as noted by Duarte et al. (1997), their correlation

275   is based on publication success and therefore rather reflects common practice in plankton

276   ecology experiments and not necessarily a mechanistic understanding of bottle effects.

277   Thus, as there is no solid ground for a parameterization of Time we ultimately decided to

278   not consider it for the RDR.

279   Finally, we want to point out (and explicitly acknowledge) that the RDR approach to

280   balance the influence of studies on the final outcome of the literature analysis is of course

281   not the one perfect solution and most likely incomplete (see above). However, balancing

282   a literature analysis with the RDR score may still be an improvement relative to the other

283   case where each experiment is treated exactly equal despite huge differences in the

284   experimental setup. Nevertheless, to account for both views (i.e. the RDR is useless vs.

285   the RDR is useful) we will present the outcome of our literature analysis in two different

286   ways throughout the paper: 1) by simply counting the number of outcomes and adding

287   them to yield a cumulative score (N-based approach; left columns in Figs. 3 and 4); 2) by

288   adding the RDR score of the experiments with a certain outcome to yield a cumulative

289   ∑RDR score (RDR-based approach; right columns in Figs. 3 and 4).

290   **3. Results**

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

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

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

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

295 communities were investigated in 16 % and 6% of the studies, respectively. 4 % of the

296 studies did not provide coordinates where the samples were taken although the region

297 was reported (Table 1; Fig. 2).

298 Among the 69 experiments, 23 (33 %, $\sum$RDR = 595) revealed a positive influence of CO_2

299 on the "bulk diatom community" (see section 2.2), while 13 (19 %, $\sum$RDR = 266)

300 revealed a negative one. 5 experiments (7 %, $\sum$RDR = 21) found a CO_2 effect but did not

301 specify whether it is a positive or negative one. 28 experiments (41 %, $\sum$RDR = 706)

302 found no effect (Fig. 3A).

303 We also checked if the pCO_2 range tested in the experiments had an influence on whether

304 the bulk diatom community responded to changing carbonate chemistry. This was done

305 because we expected the likelihood to find an OA response to be higher when the pCO_2

306 difference between treatments and controls is larger. Thus, we calculated the investigated

307 pCO_2 range (highest pCO_2 – lowest pCO_2) for each experiment and categorized the range

308 into "small" ($\leq$300 µatm), "medium (300 – 600 µatm), and "large" ($\geq$600 µatm). Among

309 the 41 experiments that found a CO_2 effect on the bulk diatom community (positive,

310 negative, and unreported direction of change), 4 (10 %, $\sum$RDR = 106) found it within the

311 low range, 12 (32 %, $\sum$RDR = 123) in the medium range, and 25 experiments (68 %,

312 $\sum$RDR = 653) in the high range. Among the 28 experiments that found no CO_2 on the

313 bulk diatom community, 3 (12 %, $\sum$RDR = 12) tested within the low range, 8 (32 %,

314 $\sum$RDR = 230) within the medium range, and 17 experiments (68 %, $\sum$RDR = 465) within

315 the high range. According to this analysis, the likelihood of detecting a CO_2 effect on the

316 bulk diatom community does not depend on the investigated pCO_2 range.

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

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

319 investigated in a subset of 40 of the 69 experiments (Fig. 3B). Within this subset of 40

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

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

322 %, $\sum$RDR = 67) found no CO_2 effect on diatom community composition. 14 studies (35

323 %, $\sum$RDR = 141) reported a CO_2-dependent shift but did not further specify any changes

324 in the size-class distribution (Fig. 3C).

325 We also tested if the bulk diatom response to OA in coastal, estuarine, and benthic

326 environments was different from the bulk response in oceanic environments. The

327 rationale for this comparison was that carbonate chemistry conditions in oceanic

328 environments may generally be more stable than in the often more productive coastal,

329 estuarine, and benthic environments (Duarte et al., 2013; Hofmann et al., 2011).

330 Therefore, diatoms from oceanic environments may be more sensitive to OA (Duarte et

331 al., 2013). We found 47 experiments with coastal + estuarine + benthic diatom

332 communities. Within this subset, 15 experiments (32 %, $\sum$RDR = 557) revealed a positive

333 influence of CO_2 on the "bulk diatom community" while 6 (13 %, $\sum$RDR = 244) revealed

334 a negative one. 4 experiments (9 %, $\sum$RDR = 19) found a CO_2 effect but did not specify

335 whether it is a positive or negative one. 22 experiments (47 %, $\sum$RDR = 693) found no

336 effect (Fig. 4A). In contrast, we found 19 experiments with oceanic communities. Within

337 this subset, 5 experiments (26 %, $\sum$RDR = 17) revealed a positive influence of CO_2 on

338 the "bulk diatom community" while 7 (37 %, $\sum$RDR = 21) revealed a negative one. 1

339 experiment (5 %, $\sum$RDR = 2) found a CO_2 effect but did not specify whether it is a

340 positive or negative one. 6 experiments (32 %, $\sum RDR = 13$) found no effect (Fig. 4B).

341 Overall, we found a bulk diatom response to OA (positive, negative, and unreported

342 direction of change) in 53 % of the experiments in coastal + estuarine + benthic

343 environments as opposed to 68 % in oceanic environments. Thus, an OA response of the

344 bulk diatom community was more frequently observed in oceanic environments which

345 was mostly due to the higher frequency of negative OA responses (Fig. 4).

4. Discussion

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

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

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

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

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

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

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

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

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

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

357 investigated species composition (Fig. 3C). This is certainly a conservative outcome

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

359 experiments that investigated the diatom assemblage with higher taxonomical resolution

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

361 been overlooked in many other experiments.

362 The comparison of OA effects in different environments revealed that bulk diatom

363 communities responded more frequently to OA in oceanic than in coastal + estuarine +

benthic environments. Especially negative effects of OA were more frequent in oceanic

environments (Fig. 4). This result is not particularly surprising since communities found

near coasts may be adapted to larger carbonate chemistry variability and therefore be

better suited to deal with OA (Duarte et al., 2013). It should be kept in mind, however,

that this comparison is based on "only" 19 oceanic experiments in contrast to 47 coastal

+ estuarine + benthic experiments. Furthermore, our habitat characterization depends on

certain criteria (mainly water depth and salinity; see section 2.2) and these may be

insufficient for our habitat comparison. For example, plankton communities from near

oceanic islands such as the Azores were labelled as "coastal" although they may have

been moving within oceanic currents and just happened to be close to shore when they

were collected. Accordingly, this type of habitat comparison would be more robust if the

community had been characterized based on the prevailing carbonate chemistry they are

usually exposed to. Unfortunately, information on the background carbonate chemistry is

hardly ever provided.

4.1 CO_2 effects on diatom assemblages originating from (direct) physiological responses to high CO_2

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

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

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

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

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

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

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

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

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

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

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

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

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

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

394   1997). Accordingly, increasing seawater pCO_2 may increase the proportion of diffusive

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

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

397   for increased rates of photosynthesis and cell division.

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

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

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

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

402   (2014) who experimentally demonstrated a positive relationship between cell volume and

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

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

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

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

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

408   allometric concept (Fig. 3, Table 2). Twelve out of 13 experiments in which cell size was

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

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

411   towards smaller diatoms, Fig. 3C). An allometric scaling of CO_2 sensitivity is particularly

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

428   niche (i.e. being competitive at lower CO_2 due to an efficient CCM) is diminished under

429   high CO_2 conditions. Which of the scenarios occurs in nature would also depend on how

430   flexible species are in terms of switching carbon acquisition modes, as well as resource

431   allocation. In this regard, it is noteworthy that only few physiological studies on OA

432   effects have taken into account the role of changing nutrient concentrations or even a

433   transition to nutrient limitation. The available experimental evidence suggests that

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

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

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

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

438   experiments but not on the community-level.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

461   diatom communities.

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

463   modified by multiple other environmental drivers changing simultaneously. Climate

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

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

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

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

468   2012). Analogously, warming may have positive or negative effects on photosynthesis

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

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

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

472   will interact with the impacts of OA.

473   **4.2 Indirect CO_2 effects on diatom assemblages through food web interactions**

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

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

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

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

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

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

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

481   2015; Thor and Oliva, 2015). Nevertheless, much of the currently available empirical

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

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

484   phytoplankton community (Alvarez-Fernandez et al., 2018; Meunier et al., 2017).

485   However, bottom-up effects on zooplankton biomass, size structure, or species

486   composition may in turn trigger feedbacks on diatom communities, thereby leading to a

487   feedback loop that may reinforce until a new steady state is reached. Such considerations

488   illustrate that also second or third order effects need to be considered when assessing OA

489 effects on the level of ecological communities. Accounting for such indirect effects

490 requires a holistic approach considering all key players in of the food web (something

491 that is beyond the scope of this study). Therefore, interpretations about what the observed

492 responses could mean for entire plankton food webs or even biogeochemical element

493 cycles (section 4.3) should always be regarded with some healthy skepticism as they often

494 neglect the potential for indirect effects.

4.3 Implications of changes in diatom community structure for pelagic food webs and biogeochemical cycles

497 The taxonomic composition and size structure of phytoplankton communities influences

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

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

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

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

502 size shift at the bottom of a food web might eventually lead to higher production in higher

503 trophic levels such as fish. Indeed, recent experimental evidence indicated that fish

504 (including commercially important species) could under certain constellations benefit

505 from high CO_2 due to higher food availability, although it was not tested if this response

506 is somehow linked to the diatom size structure (Goldenberg et al., 2018; Sswat et al.,

507 2018).

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

509 influenced by the composition of diatom communities (Tréguer et al., 2018). This is

510 particularly well recognized in the context of organic carbon export to the deep ocean, for

511 which diatoms are considered to play a pivotal role (Smetacek, 1985). Given that high

512 CO_2 favours large and perhaps more silicified diatoms over smaller ones (section 4.1),

513   we might expect accelerated sinking and thus a positive feedback on the vertical carbon

514   flux. This classical hypothesis is supported by observational evidence from two

515   consecutive years of the North Atlantic spring bloom where, despite similar primary

516   production, particulate organic carbon sequestration into the deep ocean was much higher

517   in the year when the larger diatom species dominated (Boyd and Newton, 1995).

518   However, whether the positive relationship between size and carbon export holds under

519   all circumstances is by no means clear (Tréguer et al., 2018) . It is possible that shifts

520   towards larger sized species coincide with shifts in other traits that feed back negatively

521   on carbon export. For example, when the size shift is associated with decreasing C:Si

522   stoichiometry it may ultimately reduce carbon export (Assmy et al., 2013).

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

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

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

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

527   with our limited understanding we can currently not go further than classifying CO_2-

528   induced changes in diatom communities as "a potential risk" that may cause changes in

529   key ecosystem services.

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536   **References**

537   Alvarez-Fernandez, S., Bach, L. T., Taucher, J., Riebesell, U., Sommer, U., Aberle, N.,
538   Brussaard, C. P. D. and Boersma, M.: Plankton responses to ocean acidification: The
539   role of nutrient limitation, Prog. Oceanogr., 165, 11–18,
540   doi:10.1016/j.pocean.2018.04.006, 2018.

541   Armbrust, E. V.: The life of diatoms in the world's oceans, Nature, 459(7244), 185–
542   192, doi:10.1038/nature08057, 2009.

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

550   Azam, F., Fenchel, T., Field, J. G., Gray, J. S., Meyer-Reil, L. A. and Thingstad, F.: The
551   Ecological Role of Water-Column Microbes in the Sea, Mar. Ecol. Prog. Ser., 10, 257–
552   263, doi:10.3354/meps010257, 1983.

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

556   Bach, L. T., Riebesell, U., Gutowska, M. A., Federwisch, L. and Schulz, K. G.: A
557   unifying concept of coccolithophore sensitivity to changing carbonate chemistry
558   embedded in an ecological framework, Prog. Oceanogr., 135, 125–138,
559   doi:10.1016/j.pocean.2015.04.012, 2015.

560   Bach, L. T., Alvarez-Fernandez, S., Hornick, T., Stuhr, A. and Riebesell, U.: Simulated
561   ocean acidification reveals winners and losers in coastal phytoplankton, PLoS One,
562   12(11), e0188198, doi:10.1371/journal.pone.0188198, 2017.

563   Bach, L. T., Hernández-hernández, N., Taucher, J., Spisla, C., Sforna, C., Riebesell, U.
564   and Aristegui, J.: Effects of Elevated CO2 on a Natural Diatom Community in the
565   Subtropical NE Atlantic, Front. Mar. Sci., 6(March), 1–16,
566   doi:10.3389/fmars.2019.00075, 2019.

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

571   Biswas, H., Cros, A., Yadav, K., Ramana, V. V., Prasad, V. R., Acharyya, T. and Babu,
572   P. V. R.: The response of a natural phytoplankton community from the Godavari River
573   Estuary to increasing CO2 concentration during the pre-monsoon period, J. Exp. Mar.
574   Bio. Ecol., 407(2), 284–293, doi:10.1016/j.jembe.2011.06.027, 2011.

575   Biswas, H., Shaik, A. U. R., Bandyopadhyay, D. and Chowdhury, N.: CO2induced
576   growth response in a diatom dominated phytoplankton community from SW Bay of
577   Bengal coastal water, Estuar. Coast. Shelf Sci., 198, 29–42,
578   doi:10.1016/j.ecss.2017.07.022, 2017.

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

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

584 Boyd, P. W., Collins, S., Dupont, S., Fabricius, K., Gattuso, J. P., Havenhand, J.,
585 Hutchins, D. A., Riebesell, U., Rintoul, M. S., Vichi, M., Biswas, H., Ciotti, A., Gao,
586 K., Gehlen, M., Hurd, C. L., Kurihara, H., Mcgraw, C. M., Navarro, J. M., Nilsson, G.
587 E., Passow, U. and Pörtner, H. O.: Experimental strategies to assess the biological
588 ramifications of multiple drivers of global ocean change-A review, Glob. Chang. Biol.,
589 24, 2239–2261, doi:10.1111/gcb.14102, 2018.

590 Brzezinski, M. A. and Nelson, D. M.: Chronic substrate limitation of silicic acid uptake
591 rates in the western Sargasso Sea, Deep Sea Res. Part II Top. Stud. Oceanogr., 43(2–3),
592 437–453, doi:10.1016/0967-0645(95)00099-2, 1996.

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

595 Calvo-Díaz, A., Ðaz-Pérez, L., Suárez, L. Á., Morán, X. A. G., Teira, E. and Marañón,
596 E.: Decrease in the autotrophic-to-heterotrophic biomass ratio of picoplankton in
597 oligotrophic marine waters due to bottle enclosure, Appl. Environ. Microbiol., 77(16),
598 5739–5746, doi:10.1128/AEM.00066-11, 2011.

599 Carpenter, S. R.: Microcosm Experiments Have Limited Relevance for Community and
600 Ecosystem Ecology, Ecology, 77(3), 667–680, 1996.

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

604 Davidson, A., McKinlay, J., Westwood, K., Thomson, P., van den Enden, R., de Salas,
605 M., Wright, S., Johnson, R. and Berry, K.: Enhanced CO_2 concentrations change the
606 structure of Antarctic marine microbial communities, Mar. Ecol. Prog. Ser., 552, 93–
607 113, doi:10.3354/meps11742, 2016.

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

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

616 Duarte, C. M., Gasol, J. M. and Vaqué, D.: Role of experimental approaches in marine
617 microbial ecology, Aquat. Microb. Ecol., 13(1), 101–111, doi:10.3354/ame013101,
618 1997.

619 Duarte, C. M., Hendriks, I. E., Moore, T. S., Olsen, Y. S., Steckbauer, A., Ramajo, L.,
620 Carstensen, J., Trotter, J. A. and McCulloch, M.: Is Ocean Acidification an Open-Ocean
621 Syndrome? Understanding Anthropogenic Impacts on Seawater pH, Estuaries and
622 Coasts, 36(2), 221–236, doi:10.1007/s12237-013-9594-3, 2013.

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

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

630 Endo, H., Yoshimura, T., Kataoka, T. and Suzuki, K.: Effects of CO2and iron
631 availability on phytoplankton and eubacterial community compositions in the northwest
632 subarctic Pacific, J. Exp. Mar. Bio. Ecol., 439, 160–175,
633 doi:10.1016/j.jembe.2012.11.003, 2013.

634 Endo, H., Sugie, K., Yoshimura, T. and Suzuki, K.: Effects of CO2 and iron availability
635 on rbcL gene expression in Bering Sea diatoms, Biogeosciences, 12(7), 2247–2259,
636 doi:10.5194/bg-12-2247-2015, 2015.

637 Endo, H., Sugie, K., Yoshimura, T. and Suzuki, K.: Response of Spring Diatoms to
638 CO2 Availability in the Western North Pacific as Determined by Next-Generation
639 Sequencing, PLoS One, 11(4), e0154291, doi:10.1371/journal.pone.0154291, 2016.

640 Fabricius, K. E., Langdon, C., Uthicke, S., Humphrey, C., Noonan, S., De'ath, G.,
641 Okazaki, R., Muehllehner, N., Glas, M. S. and Lough, J. M.: Losers and winners in
642 coral reefs acclimatized to elevated carbon dioxide concentrations, Nat. Clim. Chang.,
643 1(6), 165–169, doi:10.1038/nclimate1122, 2011.

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

646 Feng, Y., Hare, C. E., Leblanc, K., Rose, J. M., Zhang, Y., DiTullio, G. R., Lee, P. A.,
647 Wilhelm, S. W., Rowe, J. M., Sun, J., Nemcek, N., Gueguen, C., Passow, U., Benner, I.,
648 Brown, C. and Hutchins, D. A.: Effects of increased pCO2 and temperature on the north
649 atlantic spring bloom. I. The phytoplankton community and biogeochemical response,
650 Mar. Ecol. Prog. Ser., 388, 13–25, doi:10.3354/meps08133, 2009.

651 Feng, Y., Hare, C. E., Rose, J. M., Handy, S. M., DiTullio, G. R., Lee, P. A., Smith, W.
652 O., Peloquin, J., Tozzi, S., Sun, J., Zhang, Y., Dunbar, R. B., Long, M. C., Sohst, B.,
653 Lohan, M. and Hutchins, D. A.: Interactive effects of iron, irradiance and CO2 on Ross
654 Sea phytoplankton, Deep. Res. Part I Oceanogr. Res. Pap., 57(3), 368–383,
655 doi:10.1016/j.dsr.2009.10.013, 2010.

656 Ferguson, R. L., Buckley, E. N. and Palumbo, A. V.: Response of marine
657 bacterioplankton to differential filtration and confinement., Appl. Environ. Microbiol.,
658 47(1), 49–55, doi:0099-2240/84/010049-07$02., 1984.

659 Field, C. B., Behrenfeld, M. J., Randerson, J. T. and Falkowski, P. G.: Primary

660 Production of the Biosphere: Integrating Terrestrial and Oceanic Components, Science
661 (80-.)., 281(5374), 237–240, doi:10.1126/science.281.5374.237, 1998.

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

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

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

672 Gao, K. and Campbell, D. A.: Photophysiological responses of marine diatoms to
673 elevated CO2 and decreased pH: A review, Funct. Plant Biol., 41(5), 449–459,
674 doi:10.1071/FP13247, 2014.

675 Gao, K., Xu, J., Gao, G., Li, Y., Hutchins, D. A., Huang, B., Wang, L., Zheng, Y., Jin,
676 P., Cai, X., Häder, D. P., Li, W., Xu, K., Liu, N. and Riebesell, U.: Rising CO2 and
677 increased light exposure synergistically reduce marine primary productivity, Nat. Clim.
678 Chang., 2(7), 519–523, doi:10.1038/nclimate1507, 2012.

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

684 Giordano, M., Beardall, J. and Raven, J. A.: CO2 concentrating mechanisms in algae:
685 mechanisms, environmental modulation, and evolution., Annu. Rev. Plant Biol., 56, 99–
686 131, doi:10.1146/annurev.arplant.56.032604.144052, 2005.

687 Goldenberg, S. U., Nagelkerken, I., Marangon, E., Bonnet, A. and Camilo, M.:
688 Ecological complexity buffers the impacts of future climate on marine animals
689 Corresponding author Keywords, Nat. Clim. Chang., 1–19, doi:10.1038/s41558-018-
690 0086-0, 2018.

691 Grear, J. S., Rynearson, T. A., Montalbano, A. L., Govenar, B. and Menden-Deuer, S.:
692 pCO2 effects on species composition and growth of an estuarine phytoplankton
693 community, Estuar. Coast. Shelf Sci., 190, 40–49, doi:10.1016/j.ecss.2017.03.016,
694 2017.

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

698 Guiry, M. D.: How many species of algae are there?, J. Phycol., 48(5), 1057–1063,
699 doi:10.1111/j.1529-8817.2012.01222.x, 2012.

700 Hall-Spencer, J. M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.
701 M., Rowley, S. J., Tedesco, D. and Buia, M.-C.: Volcanic carbon dioxide vents show
702 ecosystem effects of ocean acidification, Nature, 454, 96–99, doi:10.1038/nature07051,
703 2008.

704 Hama, T., Inoue, T., Suzuki, R., Kashiwazaki, H., Wada, S., Sasano, D., Kosugi, N. and
705 Ishii, M.: Response of a phytoplankton community to nutrient addition under different
706 CO2 and pH conditions, J. Oceanogr., 72(2), 207–223, doi:10.1007/s10872-015-0322-4,
707 2016.

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

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

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

717 Hare, C. E., Leblanc, K., DiTullio, G. R., Kudela, R. M., Zhang, Y., Lee, P. A.,
718 Riseman, S. and Hutchins, D. A.: Consequences of increased temperature and CO2 for
719 phytoplankton community structure in the Bering Sea, Mar. Ecol. Prog. Ser., 352, 9–16,
720 doi:10.3354/meps07182, 2007.

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

724 Hofmann, G. E., Smith, J. E., Johnson, K. S., Send, U., Levin, L. A., Micheli, F.,
725 Paytan, A., Price, N. N., Peterson, B., Takeshita, Y., Matson, P. G., de Crook, E.,
726 Kroeker, K. J., Gambi, M. C., Rivest, E. B., Frieder, C. A., Yu, P. C. and Martz, T. R.:
727 High-frequency dynamics of ocean pH: A multi-ecosystem comparison, PLoS One,
728 6(12), e28983, doi:10.1371/journal.pone.0028983, 2011.

729 Hopkins, F. E., Turner, S. M., Nightingale, P. D., Steinke, M., Bakker, D. and Liss, P.
730 S.: Ocean acidification and marine trace gas emissions, Proc. Natl. Acad. Sci. U. S. A.,
731 107, 760–765, doi:10.1073/pnas.0907163107, 2010.

732 Hoppe, C. J. M., Hassler, C. S., Payne, C. D., Tortell, P. D., Rost, B. R. and Trimborn,
733 S.: Iron limitation modulates ocean acidification effects on Southern Ocean
734 phytoplankton communities, PLoS One, 8(11), doi:10.1371/journal.pone.0079890,
735 2013.

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

740 Hoppe, C. J. M., Schuback, N., Semeniuk, D., Giesbrecht, K., Mol, J., Thomas, H.,

741 Maldonado, M. T., Rost, B., Varela, D. E. and Tortell, P. D.: Resistance of Arctic
742 phytoplankton to ocean acidification and enhanced irradiance, Polar Biol., 41(3), 399–
743 413, doi:10.1007/s00300-017-2186-0, 2017b.

744 Hussherr, R., Levasseur, M., Lizotte, M., Tremblay, J. É., Mol, J., Thomas, H.,
745 Gosselin, M., Starr, M., Miller, L. A., Jarniková, T., Schuback, N. and Mucci, A.:
746 Impact of ocean acidification on Arctic phytoplankton blooms and dimethyl sulfide
747 concentration under simulated ice-free and under-ice conditions, Biogeosciences, 14(9),
748 2407–2427, doi:10.5194/bg-14-2407-2017, 2017.

749 James, R. K., Hepburn, C. D., Cornwall, C. E., McGraw, C. M. and Hurd, C. L.:
750 Growth response of an early successional assemblage of coralline algae and benthic
751 diatoms to ocean acidification, Mar. Biol., 161(7), 1687–1696, doi:10.1007/s00227-
752 014-2453-3, 2014.

753 Johnson, V. R., Brownlee, C., Rickaby, R. E. M., Graziano, M., Milazzo, M. and Hall-
754 Spencer, J. M.: Responses of marine benthic microalgae to elevated CO_2, Mar. Biol.,
755 160(8), 1813–1824, doi:10.1007/s00227-011-1840-2, 2011.

756 Kim, J.-M., Lee, K., Shin, K., Kang, J.-H., Lee, H.-W., Kim, M., Jang, P.-G. and Jang,
757 M.-C.: The effect of seawater CO_2 concentration on growth of a natural phytoplankton
758 assemblage in a controlled mesocosm experiment, Limnol. Oceanogr., 51(4), 1629–
759 1636, doi:10.4319/lo.2006.51.4.1629, 2006.

760 Kim, J. M., Lee, K., Yang, E. J., Shin, K., Noh, J. H., Park, K. T., Hyun, B., Jeong, H.
761 J., Kim, J. H., Kim, K. Y., Kim, M., Kim, H. C., Jang, P. G. and Jang, M. C.: Enhanced
762 production of oceanic dimethylsulfide resulting from co2-induced grazing activity in a
763 high CO2world, Environ. Sci. Technol., 44(21), 8140–8143, doi:10.1021/es102028k,
764 2010.

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

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

771 Mallozzi, A. J., Errera, R. M., Bargu, S. and Herrmann, A. D.: Impacts of elevated
772 pCO2 on estuarine phytoplankton biomass and community structure in two
773 biogeochemically distinct systems in Louisiana, USA, J. Exp. Mar. Bio. Ecol.,
774 511(September 2018), 28–39, doi:10.1016/j.jembe.2018.09.008, 2019.

775 Malviya, S., Scalco, E., Audic, S., Vincent, F., Veluchamy, A., Poulain, J., Wincker, P.,
776 Iudicone, D., de Vargas, C., Bittner, L., Zingone, A. and Bowler, C.: Insights into
777 global diatom distribution and diversity in the world's ocean, Proc. Natl. Acad. Sci.,
778 113(11), E1516–E1525, doi:10.1073/pnas.1509523113, 2016.

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

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

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

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

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

795 Meunier, C. L., Algueró-Muñiz, M., Horn, H. G., Lange, J. A. F. and Boersma, M.:
796 Direct and indirect effects of near-future pCO2 levels on zooplankton dynamics, Mar.
797 Freshw. Res., 68(2), 373–380, doi:10.1071/MF15296, 2017.

798 Milligan, A. J., Varela, D. E., Brzezinski, M. A. and Morel, F. M. M.: Dynamics of
799 Silicon Metabolism and Silicon Isotopic Discrimination in a Marine Diatom as a
800 Function of pCO2, Limnol. Oceanogr., 49(2), 322–329, 2004.

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

805 Nielsen, L. T., Jakobsen, H. H. and Hansen, P. J.: High resilience of two coastal
806 plankton communities to twenty-first century seawater acidification: Evidence from
807 microcosm studies, Mar. Biol. Res., 6(6), 542–555, doi:10.1080/17451000903476941,
808 2010.

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

812 Nogueira, P., Domingues, R. B. and Barbosa, A. B.: Are microcosm volume and sample
813 pre-filtration relevant to evaluate phytoplankton growth?, J. Exp. Mar. Bio. Ecol., 461,
814 323–330, doi:10.1016/j.jembe.2014.09.006, 2014.

815 Pan, Y., Zhang, Y., Peng, Y., Zhao, Q. and Sun, S.: Increases of chamber height and
816 base diameter have contrasting effects on grazing rate of two cladoceran species:
817 Implications for microcosm studies, PLoS One, 10(8), 1–14,
818 doi:10.1371/journal.pone.0135786, 2015.

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

821 Park, K. T., Lee, K., Shin, K., Yang, E. J., Hyun, B., Kim, J. M., Noh, J. H., Kim, M.,

822 Kong, B., Choi, D. H., Choi, S. J., Jang, P. G. and Jeong, H. J.: Direct linkage between
823 dimethyl sulfide production and microzooplankton grazing, resulting from prey
824 composition change under high partial pressure of carbon dioxide conditions, Environ.
825 Sci. Technol., 48(9), 4750–4756, doi:10.1021/es403351h, 2014.

826 Paul, A. J., Bach, L. T., Schulz, K.-G., Boxhammer, T., Czerny, J., Achterberg, E. P.,
827 Hellemann, D., Trense, Y., Nausch, M., Sswat, M. and Riebesell, U.: Effect of elevated
828 CO2 on organic matter pools and fluxes in a summer Baltic Sea plankton community,
829 Biogeosciences, 12, 6181–6203, doi:10.5194/bg-12-6181/2015/, 2015.

830 Pomeroy, L. R.: The ocean food web - A changing paradigm, Bioscience, 24, 499–504,
831 1974.

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

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

838 Reul, A., Muñoz, M., Bautista, B., Neale, P. J., Sobrino, C., Mercado, J. M., Segovia,
839 M., Salles, S., Kulk, G., León, P., van de Poll, W. H. D., Pérez, E., Buma, A. and
840 Blanco, J. M.: Effect of CO2, nutrients and light on coastal plankton. III. Trophic
841 cascade, size structure and composition, Aquat. Biol., 22, 59–76, doi:10.3354/ab00585,
842 2014.

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

846 Roleda, M. Y., Cornwall, C. E., Feng, Y., McGraw, C. M., Smith, A. M. and Hurd, C.
847 L.: Effect of ocean acidification and pH fluctuations on the growth and development of
848 coralline algal recruits, and an associated benthic algal assemblage, PLoS One, 10(10),
849 1–19, doi:10.1371/journal.pone.0140394, 2015.

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

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

855 Sala, M. M., Aparicio, F. L., Balagué, V., Boras, J. A., Borrull, E., Cardelús, C., Cros,
856 L., Gomes, A., López-Sanz, A., Malits, A., Martínez, R. A., Mestre, M., Movilla, J.,
857 Sarmento, H., Vázquez-Domínguez, E., Vaqué, D., Pinhassi, J., Calbet, A., Calvo, E.,
858 Gasol, J. M., Pelejero, C. and Marrasé, C.: Contrasting effects of ocean acidification on
859 the microbial food web under different trophic conditions, Ices J. Mar. Sci., 73(3), 670–
860 679, doi:10.1093/icesjms/fsv130, 2015.

861 Sarmiento, J. L., Gruber, N., Brzezinski, M. A. and Dunne, J. P.: High-latitude controls
862 of thermocline nutrients and low latitude biological productivity, Nature, 427(6969),

863   56–60, doi:10.1038/nature10605, 2004.

864   Sarnelle, O.: Daphnia effects on microzooplankton: comparisons of enclosure and
865   whole-lake responses, Ecology, 78(3), 913–928, doi:10.1016/S0010-4655(02)00300-4,
866   1997.

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

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

874   Schulz, K. G., Bellerby, R. G. J., Brussaard, C. P. D., Büdenbender, J., Czerny, J.,
875   Engel, A., Fischer, M., Koch-Klavsen, S., Krug, S. A., Lischka, S., Ludwig, A.,
876   Meyerhöfer, M., Nondal, G., Silyakova, A., Stuhr, A. and Riebesell, U.: Temporal
877   biomass dynamics of an Arctic plankton bloom in response to increasing levels of
878   atmospheric carbon dioxide, Biogeosciences, 10, 161–180, doi:10.5194/bg-10-161-
879   2013, 2013.

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

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

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

893   Shaik, A. U. R., Biswas, H. and Pal, S.: Increased CO_2 availability promotes growth of
894   a tropical coastal diatom assemblage (Goa coast, Arabian Sea, India), Diatom Res.,
895   32(3), 325–339, doi:10.1080/0269249X.2017.1379443, 2017.

896   Shen, C. and Hopkinson, B. M.: Size scaling of extracellular carbonic anhydrase
897   activity in centric marine diatoms, J. Phycol., 51(2), 255–263, doi:10.1111/jpy.12269,
898   2015.

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

905   doi:10.1038/nature11229, 2012.

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

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

912   Sommer, U., Paul, C. and Moustaka-Gouni, M.: Warming and ocean acidification
913   effects on phytoplankton - From species shifts to size shifts within species in a
914   mesocosm experiment, PLoS One, 10(5), 1–17, doi:10.1371/journal.pone.0125239,
915   2015.

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

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

922   Sswat, M., Stiasny, M. H., Taucher, J., Algueró-Muñiz, M., Bach, L. T., Jutfelt, F.,
923   Riebesell, U. and Clemmesen, C.: Food web changes under ocean acidification promote
924   herring larvae survival, Nat. Ecol. Evol., 2(May), 1–5, doi:10.1038/s41559-018-0514-6,
925   2018.

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

930   Tatters, A. O., Schnetzer, A., Xu, K., Walworth, N. G., Fu, F., Spackeen, J. L., Sipler,
931   R. E., Bertrand, E. M., McQuaid, J. B., Allen, A. E., Bronk, D. A., Gao, K., Sun, J.,
932   Caron, D. A. and Hutchins, D. A.: Interactive effects of temperature, CO2 and nitrogen
933   source on a coastal California diatom assemblage, J. Plankton Res., 40(2), 151–164,
934   doi:10.1093/plankt/fbx074, 2018.

935   Taucher, J., Jones, J., James, A., Brzezinski, M. A., Carlson, C. A., Riebesell, U. and
936   Passow, U.: Combined effects of CO2 and temperature on carbon uptake and
937   partitioning by the marine diatoms Thalassiosira weissflogii and Dactyliosolen
938   fragilissimus, Limnol. Oceanogr., 60(3), 901–919, doi:10.1002/lno.10063, 2015.

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

944   Thoisen, C., Riisgaard, K., Lundholm, N., Nielsen, T. G. and Hansen, P. J.: Effect of
945   acidification on an Arctic phytoplankton community from Disko Bay, West Greenland,

946 Mar. Ecol. Prog. Ser., 520, 21–34, doi:10.3354/meps11123, 2015.

947 Thor, P. and Dupont, S.: Transgenerational effects alleviate severe fecundity loss during
948 ocean acidification in a ubiquitous planktonic copepod, Glob. Chang. Biol., 21(6),
949 2261–2271, doi:10.1111/gcb.12815, 2015.

950 Thor, P. and Oliva, E. O.: Ocean acidification elicits different energetic responses in an
951 Arctic and a boreal population of the copepod Pseudocalanus acuspes, Mar. Biol.,
952 162(4), 799–807, doi:10.1007/s00227-015-2625-9, 2015.

953 Tortell, P. D., DiTullio, G. R., Sigman, D. M. and Morel, F. M. M.: CO2 effects on
954 taxonomic composition and nutrient utilization in an Equatorial Pacific phytoplankton
955 assemblage, Mar. Ecol. Prog. Ser., 236, 37–43, doi:10.3354/meps236037, 2002.

956 Tortell, P. D., Payne, C. D., Li, Y., Trimborn, S., Rost, B., Smith, W. O., Riesselman,
957 C., Dunbar, R. B., Sedwick, P. and DiTullio, G. R.: CO2 sensitivity of Southern Ocean
958 phytoplankton, Geophys. Res. Lett., 35, L04605, doi:10.1029/2007GL032583, 2008.

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

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

965 Trimborn, S., Lundholm, N., Thoms, S., Richter, K.-U., Krock, B., Hansen, P. J. and
966 Rost, B.: Inorganic carbon acquisition in potentially toxic and non-toxic diatoms: the
967 effect of pH-induced changes in seawater carbonate chemistry., Physiol. Plant., 133(1),
968 92–105, doi:10.1111/j.1399-3054.2007.01038.x, 2008.

969 Trimborn, S., Brenneis, T., Hoppe, C. J. M., Laglera, L. M., Norman, L., Santos-
970 Echeandía, J., Völkner, C., Wolf-Gladrow, D. and Hassler, C. S.: Iron sources alter the
971 response of Southern Ocean phytoplankton to ocean acidification, Mar. Ecol. Prog. Ser.,
972 578, 35–50, doi:10.3354/meps12250, 2017.

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

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

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

983 Witt, V., Wild, C., Anthony, K. R. N., Diaz-Pulido, G. and Uthicke, S.: Effects of ocean
984 acidification on microbial community composition of, and oxygen fluxes through,
985 biofilms from the Great Barrier Reef, Environ. Microbiol., 13(11), 2976–2989,

986   doi:10.1111/j.1462-2920.2011.02571.x, 2011.

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

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

993   Wu, Y., Campbell, D. A., Irwin, A. J., Suggett, D. J. and Finkel, Z. V.: Ocean
994   acidification enhances the growth rate of larger diatoms, Limnol. Oceanogr., 59(3),
995   1027–1034, doi:10.4319/lo.2014.59.3.1027, 2014.

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

1000   Yoshimura, T., Suzuki, K., Kiyosawa, H., Ono, T., Hattori, H., Kuma, K. and Nishioka,
1001   J.: Impacts of elevated CO2 on particulate and dissolved organic matter production:
1002   Microcosm experiments using iron-deficient plankton communities in open subarctic
1003   waters, J. Oceanogr., 69(5), 601–618, doi:10.1007/s10872-013-0196-2, 2013.

1004   Young, J. N., Kranz, S. A., Goldman, J. A. L., Tortell, P. D. and Morel, F. M. M.:
1005   Antarctic phytoplankton down-regulate their carbon-concentrating mechanisms under
1006   high CO$_2$ with no change in growth rates, Mar. Ecol. Prog. Ser., 532, 13–
1007   28, doi:10.3354/meps11336, 2015.

1008   Zeebe, R. E. and Wolf-Gladrow, D. A.: CO2 in seawater: Equilibrium, kinetics,
1009   isotopes, Elsevier O., Elsevier, Amsterdam., 2001.

1010

1011   **Tables and Figures**

1012

1013   **Table 1**. Response of diatom communities to high CO_2. 69 experiments from 54

1014   publications were considered here. Location refers to the place where diatom

1015   communities were collected. The RDR is dimensionless (see methods). T is the average

1016   incubation temperature in °C. DoE are days of experiment with the number of samplings

1017   given as the second number. Pre-filt. gives the mesh size in case the collected plankton

1018   community was pre-filtered before incubation. Setup refers to the incubation style:

1019   undiluted volumes (batch), repeatedly diluted volumes (s.-cont.), flow-through setups

1020 (fl.-thr.; only benthos), chemostats (chem.; only pelagic), CO_2 vent sites (seep; only

1021 benthos). Incubations can either be performed on deck (e.g. shipboards), *in situ* (e.g. *in*

1022 *situ* mesocosms) or under laboratory conditions. V refers to the incubation volume.

1023 Nutrient ammendments were made in some but not all studies. The element indicates

1024 which nutrients were added. Asterisks indicate the presense of residual nutrients at the

1025 beginning of the study. Manipulations were done with: CO_2 saturated seawater (SWsat),

1026 acid additions (Acid), combined additions of acid and base (Comb.), CO_2 gas additions

1027 (CO_2), Aeration at target pCO_2 (Aer.), Passing CO_2 gas through a diffusive silicone tubing

1028 (Diff.). Meth. indicates the applied methodology to investigate diatom communities: light

1029 microscopy (LM), pigment analyses (PA), flow cytometry (FC), genetic tools (PCR),

1030 biogenic silica (BSi). The pCO_2 range of the experiment with the number of treatments

1031 given in brackets. The response of the bulk diatom community to CO_2: no effect (~),

1032 positive (p), negative (n), not reported (N/A). The pCO$_2$ response indicates approximately

1033 in between which treatments a CO_2 response was observed. Please note that this is based

1034 on visual inspection of the datasets and therefore involves subjectivity. Please also note

1035 that the range equals the treatment values in case only two treatments were set up. CO_2

1036 induced shifts between diatom species can be: shift to larger species (large), shift to

1037 smaller species (small), unspecified shift (shift), no species shift detected (~), not reported

1038 (N/A). Winners or losers of the diatom community comprise: *Chaetoceros* (Chae), large

1039 *Chaetoceros* (Chae I), medium *Chaetoceros* (Chae II), small *Chaetoceros* (Chae III),

1040 *Neosyndra* (Neos), *Rhabdonema* (Rhab), *Eucampia* (Euca), *Cerataulina* (Cera),

1041 *Thalassiosira* (Thals), *Proboscia* (Prob), *Pseudo-nitzschia* (Ps-n), *Thalassionema*

1042 (Thalns), *Cylindrotheca* (Cyli), *Guinardia* (Guin), *Synedropsis* (Syned), *Dactyliosolen*

1043 (Dact), *Toxarium* (Toxa), *Leptocylindrus* (Lept), *Grammatophora* (Gram), *Bacillaria*

1044 (Baci), *Navicula* (Navi).

Reference	lat	long	RDR	S	T (°C)	Habitat	DoE/ # of sampl.	Pre-filt. (µm)	Setup	Incub.	V (L)	Nutr.	Manip.	Meth.	pCO₂ range (µatm)	CO₂ effect	pCO₂ 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,Fe,(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,NH4	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	350 - 630	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		
(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	~		~		

Reference																				
(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		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	
(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/?		fl.-thr.	Lab	0.65	none	Comb.	PA	(2) 430, 1170	~		N/A		
(Rossoll et al., 2013)	54.329	10.149	8.1	18	18	est.	28/7	200	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	106.1	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	13.5	20	5	est.	44/26	200	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	~		

Reference																					
(Sommer et al., 2015)	54.329	10.149	49.8	20	9,15	est.	24/11	no	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		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	400 - 1000	~		
(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		
(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		

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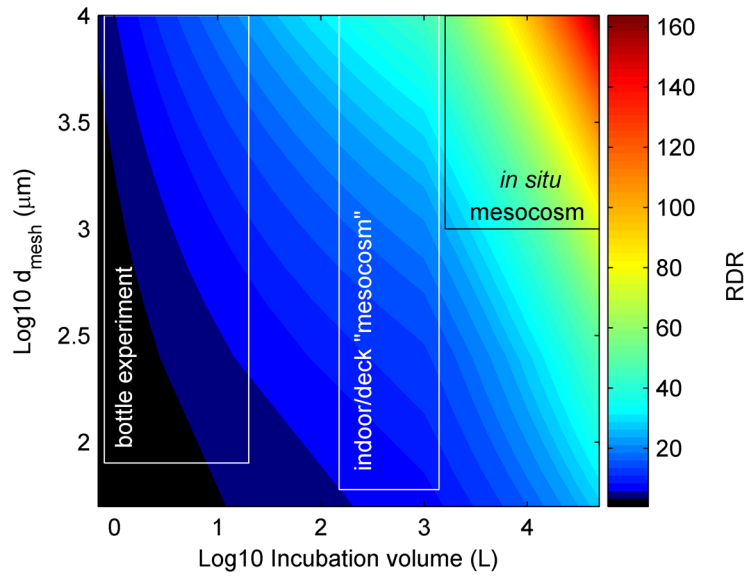

1048   **Figure 1**. RDR as a function of incubation volume and size of the mesh that was used

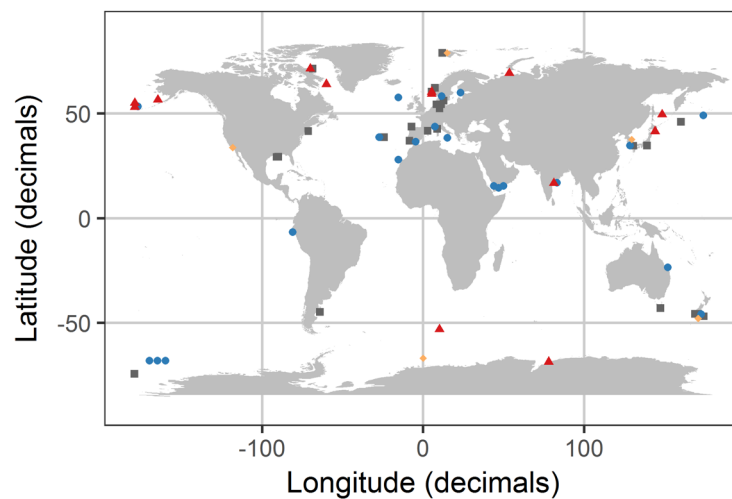
1049   while filling the incubation volumes (d_{mesh}). The black and white boxes illustrate

1050   approximate ranges of the three main types of containers used in experiments. Please note

1051   that the general definition for mesocosms are volumes >1000 L (Guangao, 1990) but

1052   since most authors also use this term for open batch incubations with volumes between

1053   150 – 1000 L we also stick to this term for the intermediate class.

1054

1055   **Figure 2.** Distribution of experiments with associated OA response of the bulk diatom

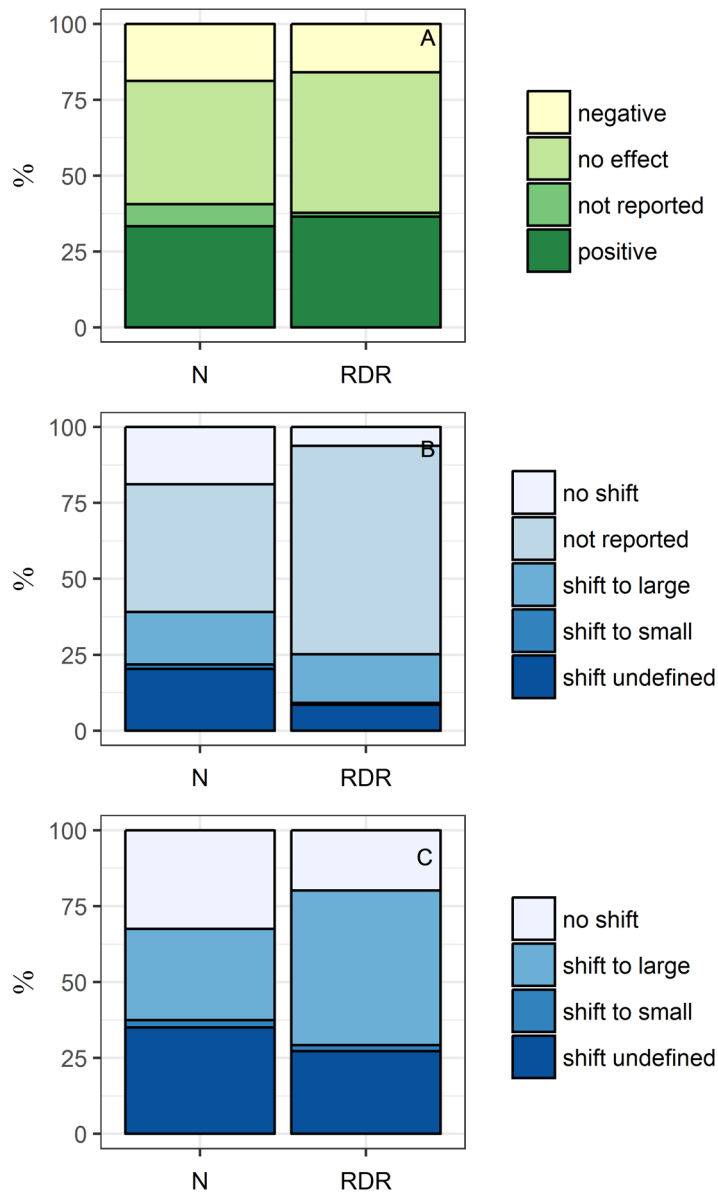
1056   communities as listed in Table 1. Blue circles = positive effect; red triangles = negative

1057   response; grey squares = no response; orange diamonds = response not reported.

1058   Locations were slightly modified in case of geospatial overlap to ensure visibility. Please

1059   note that the three blue points in the Ross Sea at about -68, -165 are approximate locations

1060   because the reference did not provide coordinates.

1061

1062   **Figure 3**. Summary of the literature analysis. (A) Response of the bulk diatom

1063   community to ocean acidification. (B) Shifts among different diatom species due to ocean

1064   acidification. 'Shift to large' and 'shift to small' indicate that the diatom community

1065   shifted towards the dominance of larger or smaller species, respectively. (C) Same data

1066   as in B but excluding studies where species shifts within the diatom community were not

1067   reported. This reduced the dataset from 69 to 40 studies. The left column is based on the

1068   number of studies. For example, the bulk diatom community was positively affected by

1069   OA in 29 out of 69 studies which is 33 %. The right column is based on the RDR values.

1070   For example, the ∑RDR value of all studies where the diatom community was positively

1071   affected by OA was 605 which is 36 % of the total ∑RDR.

1072

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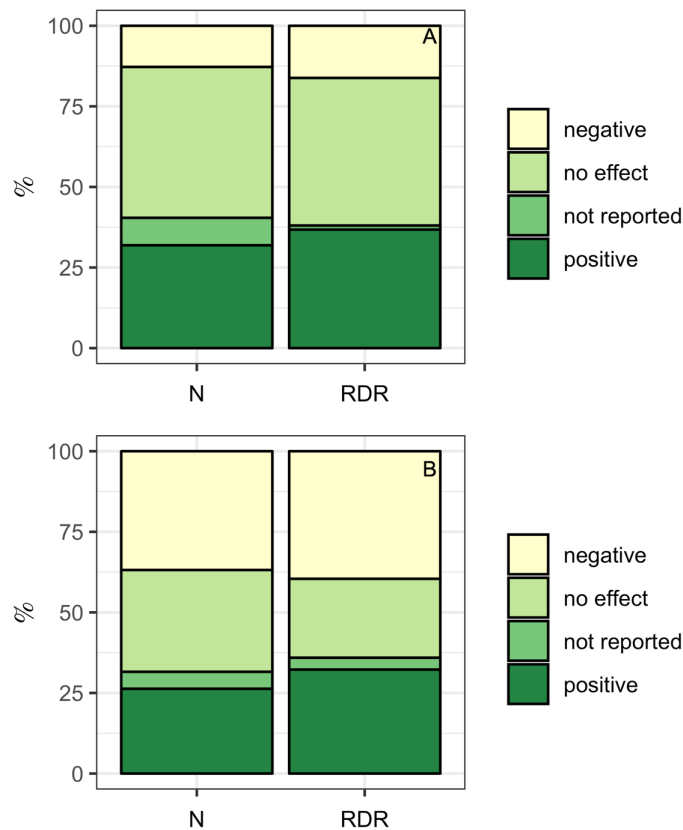
1074   **Figure 4**. Comparison of the diatom bulk response to OA in different environments. (A)

1075   coastal + estuarine + benthic environments with 47 experiments. (B) Oceanic

1076   environments with 19 experiments. The left column is based on the number of studies.

1077   For example, the bulk diatom community was positively affected by OA in 5 out of 19

1078   studies in oceanic environments which is 26 %. The right column is based on the RDR

1079   values. For example, the $\sum$RDR value of all studies where the oceanic diatom community

1080   was positively affected by OA was 17 which is 32 % of the total $\sum$RDR.

1081