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 high $CO_2$ and larger species may profit in

19  particular. This has important implications for ecosystem services diatoms provide.

21  **Abstract**

22  Diatoms account for up to 50% of marine primary production and are considered to be

23  key 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. The

38     OA-induced changes in diatom competitiveness and assemblage structure may alter key

39     ecosystem services due to the pivotal role diatoms play in trophic transfer and

40     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  (see section 2.3). While this approach excludes the determination of effect size, it

111  provides an unbiased insight on the direction of change of potential $CO_2$ effects.

112  Before going into the details of data compilation we want to emphasize once more that

113  the motivation for this study was not to investigate the physiological response of diatoms

114  to OA. Such meta analyses or reviews have already been made (Dutkiewicz et al., 2015;

115  Gao and Campbell, 2014). Instead our goal was to summarize how diatoms respond to

116  OA in their natural habitat. More generally, experiments with ecological communities (as

117  compiled in our study) do not so much aim for a mechanistic understanding of a certain

118  process (as e.g. in physiological experiments) but rather assess the general sensitivity of

119  more natural communities to environmental drivers. Therefore, it is important to have a

120  realistic setup because the net response of any player in the food web is composed of a

121  direct physiological response to $CO_2$ and by $CO_2$-induced alterations of interactions with

122  other species. From that point of view it is  desirable to include all important ecosystem

123    components, because when trophic cascades are represented incompletely then the

124    observed response in an experiment may not reflect the response that would occur in

125    nature which is what we are ultimately interested in (Carpenter, 1996). Clearly,

126    investigating OA effects on diatoms or any other group in complex communities has the

127    disadvantage that the actual cause for an observed response can hardly ever be determined

128    with high certainty (Bach et al., 2017, 2019). However, experiments compiled herein

129    investigated the development of initially similar plankton communities over time with the

130    only difference being carbonate chemistry conditions between control and the treatments.

131    Thus, we can at least be sure that the differences in diatom abundance or community

132    composition between control and treatment (which is the focus of our study) is caused by

133    simulated OA, even though the underlying mechanisms cannot be pinned down with

134    certainty.

135    **2.2. Data compilation**

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

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

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

139    OR "high $CO_2$" or "carbon dioxide" OR "elevated $CO_2$" OR "elevated carbon dioxide"

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

141    be relevant when they were published in peer-reviewed journals, contained a description

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

166     growth rate under elevated $CO_2$.

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

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

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

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

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

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

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

174    temperature), we considered only the control conditions with respect to the stressors other

175    than $CO_2$ (e.g. at control temperature). Furthermore, we extracted various metadata from

176    each study largely following the literature analysis of Schulz et al. (2017). All bulk diatom

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

178    it is self-explanatory (e.g. incubation temperature). The coordinates from where the

179    investigated plankton communities originate are given in Table 1 and illustrated in Figure

180    2. Their habitats were categorized according to water depth, salinity, or life style in the

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

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

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

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

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

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

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

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

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

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

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

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

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

194    analyses (Table 1).

195    **2.3. Accounting for different experimental setups to balance the influence of**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

224   2010; Nogueira et al., 2014; Robinson and Williams, 2005). However, they can influence

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

226   unrepresentatively  including  certain  organism  groups  such  as  highly  motile

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

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

229   generally being more representative of natural processes (Carpenter, 1996; Duarte et al.,

230   1997; Sarnelle, 1997). Therefore, our first assumption to conceptualize the RDR was that

231   larger incubation volumes represent nature generally better than smaller ones.

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

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

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

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

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

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

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

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

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

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

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

243   To parameterize the two abovementioned assumptions, we first converted the volume

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

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

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

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

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

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

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

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

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

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

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

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

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

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

258    consider in our study because sensitivity calculations assuming reasonable cylinder

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

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

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

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

263    µm) so that the RDR is defined as:

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

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

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

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

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

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

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

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

272    10,000 μm when there was no pre-filtration treatment applied since none of the studies

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

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

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

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

277    yield RDRs between ~1 – 12.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

302     not consider it for the RDR.

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

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

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

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

307     case where each experiment is treated exactly equally despite huge differences in the

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

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

310     ways throughout the paper: 1) by simply counting the number of outcomes (N) and adding

311     them to yield a cumulative $\sum$N score (N-based approach; left columns in Figs. 3 and 4);

312     2) by adding the RDR score of the experiments with a certain outcome to yield a

313     cumulative $\sum$RDR score (RDR-based approach; right columns in Figs. 3 and 4).

314     **3. Results**

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

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

317      considered hereafter (Table 1). Most were done with plankton communities from coastal

318      (46 %) and oceanic (28%) environments. Estuarine and benthic communities were

319      investigated in 16 % and 6% of the studies, respectively. 4 % of the studies did not provide

320      coordinates where the samples were taken although the region was reported (Table 1; Fig.

321      2).

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

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

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

325      specify whether it is a positive or negative one. 28 experiments (41 %, $\sum$RDR = 728)

326      found no effect (Fig. 3A).

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

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

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

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

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

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

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

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

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

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

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

338      $\sum$RDR = 230) within the medium range, and 17 experiments (68 %, $\sum$RDR = 487) within

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

359  whether it is a positive or negative one. 22 experiments (47 %, $\sum$RDR = 715) found no

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

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

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

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

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

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

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

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

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

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

**4. Discussion**

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

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

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

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

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

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

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

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

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

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

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

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

383 experiments that investigated the diatom assemblage with higher taxonomical resolution

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

385 been overlooked in many other experiments.

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

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

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

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

390    near coasts may be adapted to larger carbonate chemistry variability (Duarte et al., 2013)

391    and therefore be better suited to deal with OA. It should be kept in mind, however, that

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

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

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

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

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

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

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

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

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

401    hardly ever provided.

402    **4.1 $CO_2$ effects on diatom assemblages originating from (direct) physiological**

403    **responses to high $CO_2$**

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

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

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

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

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

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

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

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

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

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

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

proportion of $CO_2$ uptake vs. $HCO_3^-$ uptake for photosynthesis varies largely among diatoms (Burkhardt et al., 2001; Rost et al., 2003; Trimborn et al., 2008) and is theoretically also a function of cell size (Flynn et al., 2012; Wolf-Gladrow and Riebesell, 1997). Accordingly, increasing seawater $pCO_2$ may increase the proportion of diffusive carbon uptake and/or lower the energy and resource requirements for CCM operation (Raven et al., 2011). From a physiological point of view, these mechanisms could allow for increased rates of photosynthesis and cell division.

So how do these theoretical considerations align with (A) the variable and species-specific physiological responses of diatoms to increasing $CO_2$ (Dutkiewicz et al., 2015), and (B) the results from community-level experiments compiled in this study? Regarding the variability of physiological responses, progress has recently been made by Wu et al. (2014) who experimentally demonstrated a positive relationship between cell volume and the magnitude of the $CO_2$ fertilization effect on diatom growth rates. Their findings agree well with theoretical considerations, which predict that high $CO_2$ is particularly beneficial for carbon acquisition by larger species as they are more restricted by diffusion gradients due to lower surface-to-volume ratios than smaller cells (Flynn et al., 2012; Wolf-Gladrow and Riebesell, 1997). The outcome of our literature analysis supports this allometric concept (Fig. 3, Table 2). Twelve out of 13 experiments in which cell size was taken into account found a shift towards larger species. This is reflected in the $\sum$RDR score of 265 which is ~25 times higher than the opposite result (i.e. $CO_2$-induced shifts towards smaller diatoms, Fig. 3C). An allometric scaling of $CO_2$ sensitivity is particularly useful for modelling since cell size is a universal trait which is relatively easy to measure and therefore frequently available (Ward et al., 2012). Accordingly, it may lead to significant improvements of ecological and/or biogeochemical model projections under $CO_2$ forcing when more than one size class for diatoms is considered.

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

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

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

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

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

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

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

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

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

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

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

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

452  niche, i.e. being competitive at lower $CO_2$ due to an efficient CCM, is diminished under

453  high $CO_2$ conditions (a scenario that is neglected in the physiological literature). Which

454  of the scenarios occurs in nature would also depend on how flexible species are in terms

455  of switching carbon acquisition modes, as well as resource allocation. In this regard, it is

456  noteworthy that only few physiological studies on OA effects have taken into account the

457  role of changing nutrient concentrations or even a transition to nutrient limitation. The

458  available experimental evidence suggests that increasing $pCO_2$ may reduce cellular

459  nutrient requirements for CCM operations and therefore free resources for elevated

460  maximum diatom population densities, particularly when running into nutrient limitation

461  (Taucher et al., 2015). Unfortunately, however, the relevance of this mechanism has so

462  far only been investigated in monoclonal laboratory experiments but not on the

463  community-level.

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

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

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

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

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

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

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

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

472      observed in coccolithophores (Bach et al., 2011, 2015; Kottmeier et al., 2016).

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

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

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

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

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

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

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

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

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

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

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

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

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

486      diatom communities.

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

488      modified by multiple other environmental drivers changing simultaneously. Climate

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

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

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

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

493  2012). Analogously, warming may have positive or negative effects on photosynthesis

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

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

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

497  will interact with the impacts of OA.

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

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

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

501  the food web (Bach et al., 2017; Gaylord et al., 2015). For example, if a grazer of a diatom

502  species is negatively affected by OA then this may benefit the prey and indirectly promote

503  its abundance. Direct OA impacts on zooplankton communities are usually assumed to

504  play a minor role, although there is some experimental evidence that lower pH may have

505  physiological effects at least on some sensitive species or developmental stages (Cripps

506  et al., 2016; Thor and Dupont, 2015; Thor and Oliva, 2015). Nevertheless, much of the

507  currently available empirical evidence indicates that zooplankton communities are

508  affected by OA rather via bottom-up effects, e.g. via changes in primary production or

509  taxonomic composition of the phytoplankton community (Alvarez-Fernandez et al.,

510  2018; Meunier et al., 2017; Sswat et al., n.d.). However, bottom-up effects on

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

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

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

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

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

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

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

518     entire plankton food webs or even biogeochemical element cycles (section 4.3) should

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

520     indirect effects.

521     **4.3 Implications of changes in diatom community structure for pelagic food webs**

522     **and biogeochemical cycles**

523     The taxonomic composition and size structure of phytoplankton communities influences

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

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

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

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

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

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

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

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

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

533     2018).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

555    key ecosystem services.

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564

565	**Data availability**

566	All data used in this study is compiled in Table 1.

567	**Competing interests**

568	The authors declare no competing interests.

569	**Author contribution**

570	LTB did the literature analysis, conceptualized the RDR, and drafted the manuscript

571	except for parts of the introduction and discussion. JT drafted parts of the introduction

572	and discussion. Both authors interpreted the findings and revised the manuscript.

573

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1059

1060    **Tables and Figures**

1061

1062    **Table 1**. Response of diatom communities to high $CO_2$. 69 experiments from 54

1063    publications were considered. Location refers to the place where diatom communities

1064    were collected. The RDR is dimensionless (see section 2.3). T is the average incubation

1065    temperature in °C. DoE are days of experiment with the number of samplings given as

1066    the second number. Pre-filt. gives the mesh size in case the collected plankton community

1067    was pre-filtered before incubation. Setup refers to the incubation style: undiluted volumes

1068    (batch), repeatedly diluted volumes (s.-cont.), flow-through setups (fl.-thr.; only benthos),

1069    chemostats (chem.; only pelagic), $CO_2$ vent sites (seep; only benthos). Incubations

1070    (Incub.) can either be performed on deck (e.g. shipboards), *in situ* (e.g. *in situ* mesocosms)

1071    or under laboratory conditions. V refers to the incubation volume. Nutrient ammendments

1072 (Nutr.) were made in some but not all studies. The element indicates which nutrients were

1073 added. Asterisks indicate the presense of residual nutrients at the beginning of the study.

1074 Manipulations (Manip.) were done with: $CO_2$ saturated seawater (SWsat), acid additions

1075 (Acid), combined additions of acid and base (Comb.), $CO_2$ gas additions ($CO_2$), Aeration

1076 at target $pCO_2$ (Aer.), Passing $CO_2$ gas through a diffusive silicone tubing (Diff.). Meth.

1077 indicates the applied methodology to investigate diatom communities: light microscopy

1078 (LM), pigment analyses (PA), flow cytometry (FC), genetic tools (PCR), biogenic silica

1079 (BSi). The $pCO_2$ range of the experiment with the number of treatments given in brackets.

1080 The response of the bulk diatom community to $CO_2$: no effect (~), positive (p), negative

1081 (n), not reported (N/A). The $pCO_2$ response indicates approximately in between which

1082 treatments a $CO_2$ response was observed. Please note that this is based on visual

1083 inspection of the datasets and therefore involves subjectivity. Please also note that the

1084 range equals the treatment values in case only two treatments were set up. $CO_2$ induced

1085 shifts between diatom species can be: shift to larger species (large), shift to smaller

1086 species (small), unspecified shift (shift), no species shift detected (~), not reported (N/A).

1087 Winners or losers of the diatom community comprise: *Chaetoceros* (Chae), large

1088 *Chaetoceros* (Chae I), medium *Chaetoceros* (Chae II), small *Chaetoceros* (Chae III),

1089 *Neosyndra* (Neos), *Rhabdonema* (Rhab), *Eucampia* (Euca), *Cerataulina* (Cera),

1090 *Thalassiosira* (Thals), *Proboscia* (Prob), *Pseudo-nitzschia* (Ps-n), *Thalassionema*

1091 (Thalns), *Cylindrotheca* (Cyli), *Guinardia* (Guin), *Synedropsis* (Syned), *Dactyliosolen*

1092 (Dact), *Toxarium* (Toxa), *Leptocylindrus* (Lept), *Grammatophora* (Gram), *Bacillaria*

1093 (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 | ~ | | ~ | | |
| (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 | | |

| Reference | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| (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 | 29.8 | 18 | 18 | est. | 28/7 | no | batch | Lab | 300 | N,P,Si | Aer. | LM | (5) 390 - 4000 | ~ | | N/A | | |
| (Sala et al., 2015) | 41.667 | 2.800 | 26.1 | 38 | 14 | coastal | 9/2 | no | batch | Lab | 200 | none | CO2 | LM | (2) 400, 800 | ~ | | N/A | | |
| (Sala et al., 2015) | 41.667 | 2.800 | 26.1 | 38 | 22 | coastal | 9/2 | no | batch | Lab | 200 | none | CO2 | LM | (2) 400, 800 | ~ | | N/A | | |
| (Schulz et al., 2008) | 60.267 | 5.217 | 133.7 | 31 | 10.5 | coastal | 25/18-23 | no | batch | in situ | 27000 | N,P | Aer. | PA | (3) 350 - 1050 | ~ | | N/A | | |
| (Schulz et al., 2013) | 78.937 | 11.893 | 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 | ~ | | |
| (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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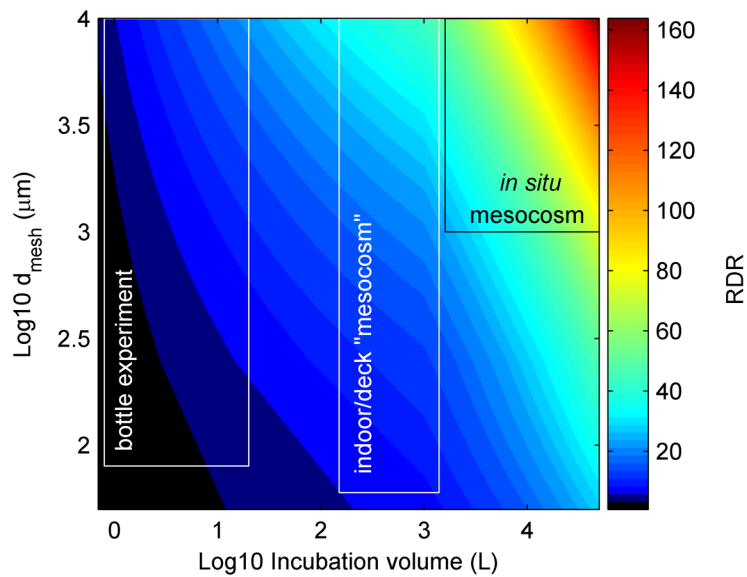

1096

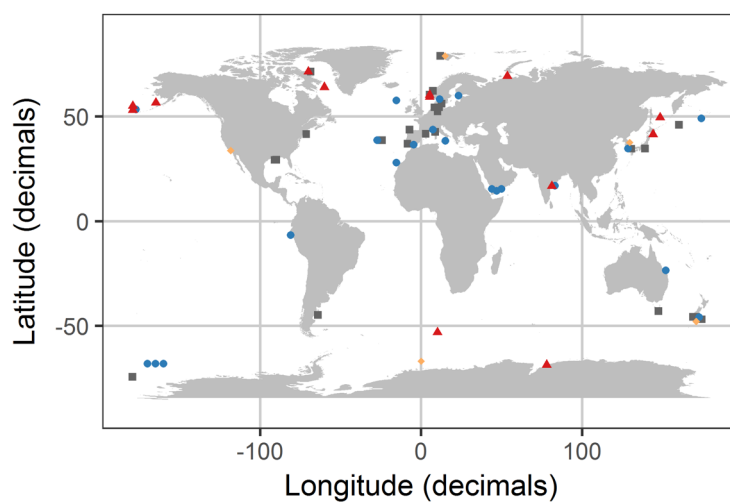
1097  **Figure 1**. RDR as a function of incubation volume and size of the mesh that was used

1098  while filling the incubation volumes ($d_{mesh}$). The black and white boxes illustrate

1099  approximate ranges of the three main types of containers used in experiments. Please note

1100  that the general definition for mesocosms are volumes $\geq 1000$ L (Guangao, 1990) but since

1101  most authors also use this term for open batch incubations with volumes between 150 –

1102  1000 L we also stick to this term for the intermediate class.

1103

1104  **Figure 2.** Distribution of experiments with associated OA response of the bulk diatom

1105  communities as listed in Table 1. Blue circles = positive effect; red triangles = negative

1106  response; grey squares = no response; orange diamonds = response not reported.

1107  Locations were slightly modified in case of geospatial overlap to ensure visibility. Please

1108  note that the three blue points in the Ross Sea at about -68, -165 are approximate locations

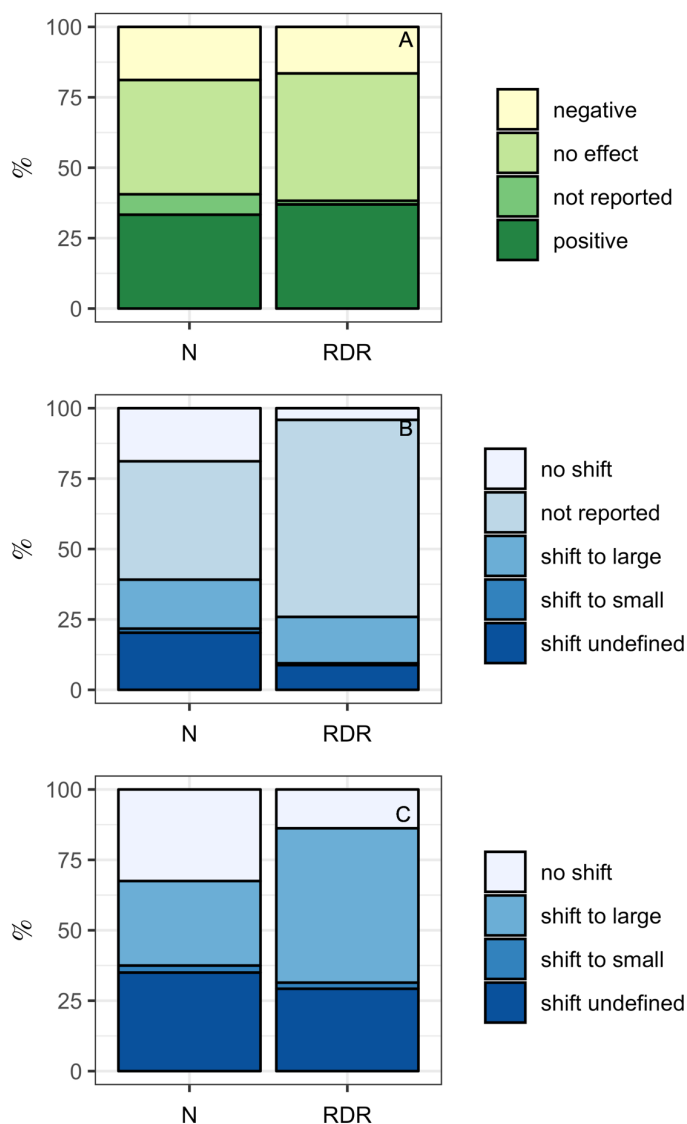
1109  because the reference did not provide coordinates.

1110

**Figure 3**. Summary of the literature analysis. (A) Response of the bulk diatom community to ocean acidification. (B) Shifts among different diatom species due to ocean acidification. 'Shift to large' and 'shift to small' indicate that the diatom community shifted towards the dominance of larger or smaller species, respectively. (C) Same data as in B but excluding studies where species shifts within the diatom community were not reported. This reduced the dataset from 69 to 40 studies. The left column is based on the number of studies. For example, the bulk diatom community was positively affected by OA in 23 out of 69 studies which is 33 %. The right column is based on the RDR values. For example, the ∑RDR value of all studies where the diatom community was positively

1120    affected by OA was 595 which is 37 % of the total $\sum$RDR. Please keep in mind that the

1121    RDR-based approach excludes benthic studies wheras the N-based approach includes

1122    them.

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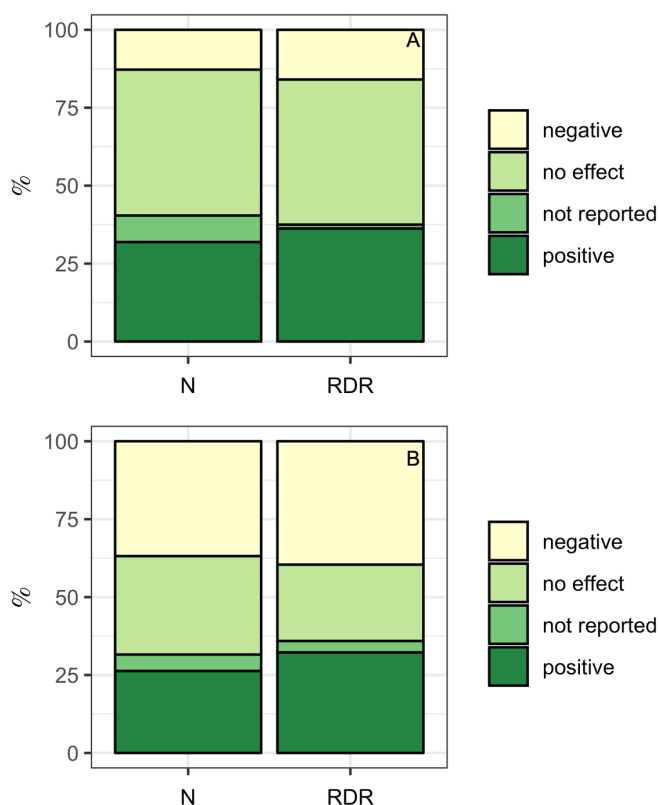
1124

1125    **Figure 4**. Comparison of the diatom bulk response to OA in different environments. (A)

1126    coastal + estuarine + benthic environments with 47 experiments. (B) Oceanic

1127    environments with 19 experiments. The left column is based on the number of studies.

1128    For example, the bulk diatom community was positively affected by OA in 5 out of 19

1129    studies in oceanic environments which is 26 %. The right column is based on the RDR

1130    values. For example, the $\sum$RDR value of all studies where the oceanic diatom community

1131    was positively affected by OA was 17 which is 32 % of the total $\sum$RDR. Please keep in

1132    mind that the RDR-based approach excludes benthic studies wheras the N-based

1133    approach includes them.

1134