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## Ocean acidification in the Mediterranean Sea: pelagic mesocosm experiments. A synthesis

L. Maugendre, Cecile Guieu, Jean-Pierre Gattuso, Frédéric Gazeau

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1 **Ocean acidification in the Mediterranean Sea: pelagic mesocosm experiments. A**  
2 **synthesis.**

3

4 L. Maugendre<sup>1,2</sup>, C. Guieu<sup>1,2</sup>, J.-P. Gattuso<sup>1,2,3</sup> and F. Gazeau<sup>1,2,\*</sup>

5

6 [1] Sorbonne Universités, UPMC Univ Paris 06, UMR 7093, LOV, Observatoire

7 Océanologique de Villefranche, 06230, Villefranche-sur-Mer, France

8 [2] CNRS-INSU, Laboratoire d'Océanographie de Villefranche, 06230 Villefranche-sur-Mer,

9 France

10 [3] Institute for Sustainable Development and International Relations (IDDRI), Sciences Po,

11 27 rue Saint Guillaume, F-75007 Paris, France

12

13 \*Corresponding author: f.gazeau@obs-vlfr.fr

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16 Mediterranean Sea.

## 17        **1. Introduction**

18        Planet Earth has entered a new geological era, the Anthropocene, in which geologically  
19        significant conditions and processes are profoundly altered by human activities (Waters et al.,  
20        2016). Among many impacts, human activities have released excessive amounts of carbon  
21        dioxide (CO<sub>2</sub>) in the atmosphere leading to warming and ocean acidification: a decrease in pH  
22        and CO<sub>3</sub><sup>2-</sup> concentration and an increase in CO<sub>2</sub> and HCO<sub>3</sub><sup>-</sup> concentrations (Gattuso and  
23        Hansson, 2011). On average, at the global scale, surface ocean pH has decreased by 0.1 units  
24        since the beginning of the industrial era, equivalent to an increased acidity of 26% (Ciais et  
25        al., 2013). An additional decrease of pH is expected by 2100, ranging from 0.07 to 0.33,  
26        depending on the CO<sub>2</sub> emission scenario considered (Gattuso et al., 2015).

27        Whilst the chemistry of ocean acidification is understood with a very high level of  
28        confidence, its impacts on ocean biology and biogeochemistry are known with much lower  
29        confidence levels. In the last 20 years or so, ocean acidification research has clearly made the  
30        greatest progress on the physiological responses of single species or strains (e.g. Andersson et  
31        al., 2011; Riebesell and Tortell, 2011). There is, however, a clear lack of knowledge regarding  
32        the response of communities or ecosystems (Riebesell and Gattuso, 2015).

33        Among the poorly known impacts is the effect of ocean acidification on the efficiency of  
34        the biological pump, the transport of organic matter from the surface to the deep sea and, in  
35        turn, on the global carbon cycle and climate regulation. About 50% of the global primary  
36        production occurs in the ocean (Field et al., 1998). Primary production converts CO<sub>2</sub> to  
37        organic matter through photosynthesis. As all organisms remineralise this organic matter  
38        through respiration in the surface mixed-layer, consuming O<sub>2</sub> and releasing CO<sub>2</sub> to seawater,  
39        only about 30% of the organic matter produced is exported to the deep sea (Falkowski et al.,  
40        1998) where it is partially remineralised by bacteria and 1 to 3% is buried in sediments (De  
41        La Rocha and Passow, 2007).

42 As changes in the efficiency of this biological pump have the capacity to alter the capacity  
43 of the ocean to store anthropogenic CO<sub>2</sub>, there is therefore a great need in projecting its future  
44 evolution. Ocean acidification experiments focussing on single plankton species do not allow  
45 assessing the impacts of ocean acidification on the CO<sub>2</sub> uptake capacity of the ocean. Since  
46 2000, a significant number of perturbation experiments have been performed to fill this  
47 knowledge gap by focusing on communities rather than on isolated species (Figure 1 and  
48 Table 1). Most have been performed in the northern hemisphere with a focus on coastal meso-  
49 and eutrophic sites, or following nutrient addition at the start or during the experiments.  
50 However, ocean provinces are very diverse (Longhurst et al., 1995) but around 60% of the  
51 ocean is oligotrophic, an area that is expected to expand in the future (Polovina et al., 2008;  
52 Irwin and Oliver, 2009). Yet, the impacts of ocean acidification on these regions are almost  
53 unknown. Past community perturbation experiments were performed using various  
54 approaches, from small bottle incubations ( $\leq 1$  L) to large mesocosms ( $> 50,000$  L), and over  
55 different time scales (a few days to a few weeks). Mesocosms allow for the maintenance of  
56 natural communities under close-to-natural conditions and the collection of sinking organic  
57 matter (Riebesell et al., 2008; Riebesell et al., 2013). They therefore are attractive tools to  
58 study the impact of ocean acidification on plankton community structure and functioning as  
59 well as on organic matter export.

60 The European MedSeA project (<http://medsea-project.eu>) was launched in 2011 with  
61 the objective to focus on the impacts of ocean acidification and warming in the Mediterranean  
62 Sea. In this semi-enclosed sea, pH has decreased by 0.055 to 0.156 units from pre-industrial  
63 to 2013, depending on the location (Hassoun et al., 2015). A further decrease of 0.24 to 0.46  
64 units is projected for the end of the century (Goyet et al., 2016). The Mediterranean Sea is  
65 characterised by low concentrations of nutrients and chlorophyll (The Mermex group, 2011).  
66 Based on satellite-derived estimates, chlorophyll *a* concentrations exhibit low values (less

67 than  $0.2 \mu\text{g L}^{-1}$ ) over most of the Mediterranean Sea, except for the Liguro-Provençal region  
68 where relatively large blooms can be observed in late winter-early spring (e.g. Mayot et al.,  
69 2016). These features make this region of Mediterranean Sea a perfect natural laboratory to  
70 study the effects of nutrient availability (oligotrophy vs. mesotrophy) on the response of  
71 plankton community to  $\text{CO}_2$  enrichment.

72 Two experiments were performed in the framework of the MedSeA project to  
73 investigate the effects of ocean acidification on plankton communities in the NW  
74 Mediterranean Sea during two seasons with contrasted environmental conditions (i.e. summer  
75 oligotrophic stratified waters vs. winter mesotrophic well-mixed waters). These experiments  
76 were performed using large mesocosms deployed in the field and using an interdisciplinary  
77 approach to study a large number of parameters and processes. This manuscript aims to  
78 briefly present the experiments and its main findings. It also highlights some issues while  
79 performing these experiments in the Mediterranean Sea and provides perspectives for future  
80 plankton community research in low-nutrient, low-chlorophyll areas.

## 81        2. Overview of the experimental set-up

82            Two experiments were conducted in the Northwestern Mediterranean Sea: the first  
83 one, in the Bay of Calvi (Corsica, France; Fig. 2) in summer (June-July 2012), and the second  
84 one in the Bay of Villefranche (France; Fig. 2) in winter (February-March 2013). The  
85 experimental set-up and mesocosm characteristics are described in Gazeau et al. (this issue-a).  
86 Briefly, for each experiment, nine 50 m<sup>3</sup> mesocosms (2.3 m in diameter and 15 m deep; Fig.  
87 3A) were deployed for 20 and 12 d in the Bay of Calvi and the Bay of Villefranche,  
88 respectively. Once the bottom of the mesocosms was closed, CO<sub>2</sub> saturated seawater was  
89 added to generate a *p*CO<sub>2</sub> gradient across mesocosms ranging from ambient level to 1,250  
90 µatm, with three control mesocosms (C1, C2 and C3) and six mesocosms with increasing  
91 *p*CO<sub>2</sub> (P1 to P6). In the Bay of Calvi, the six *p*CO<sub>2</sub> levels were P1: 550, P2: 650, P3: 750, P4:  
92 850, P5: 1000 and P6: 1250 µatm. In the Bay of Villefranche, the levels were P1: 450, P2:  
93 550, P3: 750, P4: 850, P5: 1000 and P6: 1250 µatm. Mesocosms were grouped in clusters of  
94 three with each cluster containing a control, a medium and a high *p*CO<sub>2</sub> level (cluster 1: C1,  
95 P1, P4; cluster 2: C2, P2, P5 and cluster 3: C3, P3, P6; Fig. 3B). Acidification of the  
96 mesocosms was performed over 4 d by addition of various volumes of CO<sub>2</sub>-saturated  
97 seawater. Once the target *p*CO<sub>2</sub> levels were reached, the experiments started (day 0; 24 June  
98 2012 and 22 February 2013 for the Bay of Calvi and the Bay of Villefranche, respectively).  
99 No further CO<sub>2</sub> addition was performed and *p*CO<sub>2</sub> levels evolved in mesocosms driven by air-  
100 sea fluxes, temperature changes and net community production. Weather permitting,  
101 conductivity-temperature-depth (CTD) casts were performed every day in each mesocosm as  
102 well as in the ambient environment with a Sea-Bird Electronics (SBE) 19plusV2. Depth-  
103 integrated (0-10 m) samplings from the mesocosms and from the ambient environment were  
104 performed daily using integrating water samplers, IWS (HYDRO-BIOS®). Sediment traps  
105 located at the bottom end of the mesocosms were collected by SCUBA diving (daily in the

106 Bay of Calvi and every 2-3 d in the Bay of Villefranche) and a zooplankton net haul (200  $\mu$ m  
107 mesh size) was performed in each mesocosm at the end of the experiment, only in the Bay of  
108 Calvi. While in the Bay of Calvi, the experiment lasted 20 d as scheduled, a storm irreversibly  
109 damaged the bags on March 7<sup>th</sup> in the Bay of Villefranche, and the experiment had to be  
110 interrupted after 12 d. All data collected during the two experiments are openly available on  
111 Pangaea, Bay of Calvi: <http://doi.pangaea.de/10.1594/PANGAEA.810331> and Bay of  
112 Villefranche: <http://doi.pangaea.de/10.1594/PANGAEA.835117>.

### 113 3. Main results

114 At both locations, the target  $p\text{CO}_2$  levels were successfully reached at the start of the  
115 experiments (Fig. 3C). As no further  $\text{CO}_2$  addition was performed to maintain  $\text{CO}_2$  levels at  
116 the target values, high  $p\text{CO}_2$  levels gradually declined. While the decrease was limited in  
117 summer,  $p\text{CO}_2$  dropped at a much larger rate in winter as a consequence of strong wind and a  
118 second  $\text{CO}_2$  addition would have been necessary (Gazeau et al., this issue-a) but was  
119 prevented by the storm which damaged almost all mesocosms.

120 The objective of our study was to conduct two experiments under contrasted  
121 conditions in terms of nutrient concentration and community composition. The summer  
122 experiment was performed in warm waters with very low concentrations of chlorophyll *a* and  
123 nutrients (Table 2). The molar ratio of inorganic N:P increased from 1.7 at the beginning of  
124 the experiment to ~4 on day 20, a value that is much lower than theoretical plankton  
125 requirements, suggesting, together with very low concentrations of these elements, a strong  
126 nitrate and phosphate co-limitation (Louis et al., this issue). The hydrological and weather  
127 conditions of the Bay of Villefranche were typical of winter conditions in the Northwestern  
128 Mediterranean Sea (low temperature and irradiance; Gazeau et al., this issue-a). However, as a  
129 consequence of very favourable weather conditions during the acidification phase (four sunny  
130 days prior to the start of the experiment), nutrients were rapidly consumed in all mesocosms.  
131 Most of the available nitrate was already consumed at the beginning of the experiment,  
132 reaching levels and a molar inorganic N:P ratio of 13 not usually encountered during this  
133 period of the year precluding the formation of a significant bloom (Louis et al., this issue).  
134 Long time series of chlorophyll *a* and nutrient concentrations are available in this area of the  
135 Mediterranean Sea, enabling to bring the experiments into a wider context and check for their  
136 representativeness. Conditions encountered during the summer experiment were typical of  
137 conditions in the Northwestern Mediterranean Sea between June and December as depicted

138 for the concentration of chlorophyll *a* (Fig. 4A) as well as nitrate, phosphate and silicate (Fig.  
139 4B). In contrast, winter conditions in the Northwestern Mediterranean Sea are much more  
140 variable depending on location and the year considered, with a large variability in nutrient  
141 concentrations and the formation or absence of a bloom. The analysis of these two long time  
142 series highlights the difficulty to catch a bloom following a winter-mixing event in this  
143 region. More importantly, these comparisons confirm that the nutrient concentrations  
144 encountered at the beginning of the winter experiment were clearly outside the range of  
145 values found in this area at this period of the year (Fig. 4B).

146         Although the concentration of total chlorophyll *a* was 20 times higher in winter than in  
147 summer, in both experiments plankton communities were clearly dominated by small  
148 phytoplankton cells such as Haptophyceae, Cyanobacteria and Chlorophyceae in the Bay of  
149 Calvi and Cryptophyceae, Haptophyceae and Pelagophyceae in the Bay of Villefranche  
150 (Gazeau et al., this issue-b; Table 2). Large species such as diatoms represented less than ~5%  
151 and ~11% of phytoplankton biomass respectively in summer and in winter. This is not  
152 surprising as it is well known that, in this region, diatoms dominate later in the spring during  
153 the transition period between mixed and stratified conditions (Claustre et al., 1994).

154         Both communities were close to metabolic balance with a tendency toward autotrophy  
155 during the winter experiment (Maugendre et al., this issue-a). In summer, both the abundance  
156 and the production of heterotrophic prokaryotes remained constant throughout the experiment  
157 (Celussi et al., this issue). In winter, although bacterial abundances increased significantly  
158 during the experimental period, bacterial production did not change significantly (Celussi et  
159 al., this issue). The addition of inorganic <sup>13</sup>C allowed following the transfer of carbon from  
160 inorganic via bulk particulate organic carbon and phytoplankton to bacteria by means of  
161 biomarkers as well as to zooplankton and settling particles. In summer, the community was  
162 slow-growing and based on regenerated production while in winter the fast-growing species at

163 the start of the experiment were replaced by slow-growing ones during the experiment as a  
164 consequence of nutrient limitation (Maugendre et al., this issue-b). Nitrogen fixation appeared  
165 to be an active metabolic process in summer (Rees et al., this issue) but no activity of  
166 nitrifiers could be detected in winter (Rees, unpublished data). During both experiments,  
167 export of carbon to the sediment traps was highest at the start of the experiments, and 5 times  
168 larger in winter than in summer (Gazeau et al., this issue-b).

169 The main results with respect to the observed effects of CO<sub>2</sub> enrichment are shown in  
170 Table 3. The vast majority of parameters and processes which were investigated suggest an  
171 overall resilience of the plankton community structure and function in both locations and  
172 season. Gazeau et al. (this issue-b) showed that although few phytoplankton groups were  
173 negatively or positively impacted by CO<sub>2</sub> enrichment in summer, their response remained  
174 small with no consequence on total chlorophyll *a* concentrations, transparent exopolymeric  
175 particle formation (data only available in the Bay of Villefranche; Bourdin et al., this issue)  
176 and organic matter export (Gazeau et al., this issue-b). Similarly, scanning electron  
177 microscopy reported by Oviedo et al. (this issue) did not highlight any change in the  
178 abundance of coccolithophores and siliceous phytoplankton, and no change in size structure  
179 which could have had an impact on sedimentation rates. As a result of such limited  
180 modifications in the phytoplankton community structure, gross and net primary production  
181 rates exhibited no apparent change in response to elevated *p*CO<sub>2</sub> (Maugendre et al., this issue-  
182 a; Maugendre et al. this issue-b). Bacterial production rates were negatively affected in  
183 summer and several bacterial enzymatic activities responded to CO<sub>2</sub> enrichment, either  
184 negatively or positively (Celussi et al., this issue). However, no consequences were observed  
185 on community mineralisation rates (Maugendre et al., this issue-a). In winter (no data in  
186 summer), viral abundances and replication cycles appeared uncorrelated to the imposed *p*CO<sub>2</sub>  
187 conditions. Although there was no clear association between specific abundances of nitrifiers

188 and changes in  $p\text{CO}_2$ , the summer experiment in the Bay of Calvi provided evidence of a  
189 stimulation in nitrogen fixation at  $p\text{CO}_2$  levels above  $1000 \mu\text{atm}$  (P5 and P6; Rees et al., this  
190 issue). Nevertheless, the mechanisms and diazotroph(s) responsible for  $\text{N}_2$  fixation remain  
191 unknown and this study strongly argues for a better characterization of diazotrophs and  
192 diazotrophy under fixed conditions of  $p\text{CO}_2$  (Rees et al., this issue). Zooplankton population  
193 structure and feeding rates were only investigated during the summer experiment in the Bay  
194 of Calvi and no effects in any of the studied parameters/processes could be detected  
195 (Zervoudaki et al., this issue). All these results converge in suggesting that elevated  $p\text{CO}_2$   
196 levels will not lead to important changes in plankton structure, metabolic rates and sea surface  
197 biological carbon fixation under conditions of strong limitation by nutrient availability.

198 As discussed in the papers brought together in the present special issue, these results  
199 stand in contrast to similar large *in situ* mesocosm experiments conducted in eutrophic areas  
200 (or following nutrient addition; see Table 1) as well as to very recent experiments performed  
201 under low nutrient conditions in the Baltic Sea (Paul et al., 2015; Bach et al., 2016). In the  
202 Northwestern Mediterranean Sea (Bay of Blanes), using indoor tanks, Sala et al. (2016)  
203 exposed coastal plankton communities to elevated  $\text{CO}_2$  levels under contrasting conditions: in  
204 winter, at the peak of the annual phytoplankton bloom, and in summer, under low nutrient  
205 conditions. These recent studies suggested that plankton communities will be more affected  
206 by ocean acidification under low nutrient conditions than in more productive waters. This is  
207 in contrast to the two experiments described here. There are two non-mutually exclusive  
208 reasons for these discrepancies. First, the experiment of Sala et al. (2016) was conducted in an  
209 area that is much less nutrient limited than the sites investigated in the present study. Even  
210 during their summer low-nutrient experiment, Sala et al. (2016) reported nitrate  
211 concentrations almost ten times higher than those observed in summer in the Bay of Calvi and  
212 four times higher than those observed in winter in the Bay of Villefranche at the start of the

213 experiment. Likewise, the concentration of chlorophyll during our summer experiment was  
214 three times lower than the one observed by Sala et al. (2016) in summer. The much lower  
215 nutrient availability during our experiments likely explains the contrasting responses of  
216 planktonic communities in these different environmental settings. The second potential  
217 explanation of the discrepancies is related to the duration of the experiments. The two large *in*  
218 *situ* mesocosm experiments performed in the Baltic Sea (Paul et al., 2015; Bach et al., 2016)  
219 were performed over significantly longer time scales (> 43 d). Impacts of elevated CO<sub>2</sub> were  
220 visible during the last phase when the plankton communities were relying on remineralised  
221 nutrients. Our experiments did not exceed ~20 d (12 days for the winter experiment) and it is  
222 likely that the build-up of remineralised nutrients did not reach concentrations large enough to  
223 significantly relieve nutrient limitation.

#### 224 4. Conclusion and perspectives

225 The Mediterranean Sea is a typical low-nutrient low-chlorophyll area which exhibits  
226 large changes in nutrient concentrations in the illuminated surface waters that depend strongly  
227 on the seasonal hydrological regime. Nutrients are severely depleted in the surface layer  
228 during summer oligotrophic conditions characterized by strong thermal stratification. During  
229 winter mixing events (January–February), nutrients are re-injected to the surface layer,  
230 providing favourable conditions for a bloom initiation. Superimposed to these well-known  
231 seasonal features is an important inter-annual variability (Marty et al., 2002; de Fommervault  
232 et al., 2015). Short events driven by the atmosphere such as strong short wind events (i.e.  
233 Andersen and Prieur, 2000) and sporadic atmospheric inputs (i.e. Pulido-Villena et al., 2010)  
234 can lead to transient increase in nutrient concentrations impacting nutrient stocks and thus  
235 likely biota and biogeochemical fluxes. Indeed, while a wind event can inject nutrients from  
236 below by rapidly deepening the mixed layer depth (Andersen and Prieur, 2000), atmospheric  
237 inputs such as Saharan dust events, biomass burning or intense rain events can bring new  
238 nutrients to the surface of the water-column on short-time scales (The Mermex group, 2011,  
239 and references therein). In some cases, both nutrients from below and above can also be  
240 responsible of profound transient changes in nutrient dynamics and impact biota (Guieu et al.,  
241 2010). Nutrient availability is therefore a main control of ecosystem condition in the  
242 Mediterranean Sea. The perturbation experiments reported in the present special issue show  
243 no or low impact of ocean acidification on key biogeochemical processes, both in summer  
244 and winter whereas the natural assemblage was highly dependent on nutrient availability. Our  
245 summer *in situ* ocean acidification mesocosm experiment was representative of summer  
246 conditions in the Northwestern Mediterranean Sea. The results appear solid regarding the  
247 impact of ocean acidification on short time scale on the biogeochemistry of such oligotrophic  
248 system. Caution should be exercised to interpret the results of the winter experiment because

249 the expected bloom conditions were not met, and important changes in nutrient availability  
250 were observed during the acidification step leading to conditions inside the mesocosms that  
251 were not representative of ambient conditions. Moreover, poor weather conditions at the  
252 beginning of the experiment (including variable and low light availability) prevented the  
253 stabilisation of blooming conditions in the bags. Yet, the time of the year to perform this  
254 experiment was carefully chosen according to the 18-year time series both at Point B and  
255 DYFAMED (Fig. 4). Unfortunately, this experiment is a good illustration that biological  
256 activity in the Mediterranean Sea exhibits a large interannual variability and specific short-  
257 term events, such as blooms, are difficult to capture.

258         The mesocosm approach was a good tool in the case of the summer experiment. Yet,  
259 considering the tenuous changes – or no change – observed at elevated  $p\text{CO}_2$ , a different  
260 strategy would have helped refining our results. Rather than using a  $p\text{CO}_2$  gradient over six  
261 mesocosms, a triplicate treatment strategy taking into account two ocean acidification  
262 scenarios could have been more appropriate to better quantify possible impacts. Based on  
263 these observations, it appears that a large mesocosm pelagic approach may not be the ideal  
264 strategy in the Mediterranean Sea – or any other truly oligotrophic system - since the impacts  
265 expected will likely be low or non-existent irrespective of ambient conditions when the  
266 mesocosms were filled. A land-based experimental device providing well controlled  
267 environmental conditions (including light and temperature) would be more appropriate.  
268 Indeed, as for the global ocean, the Mediterranean Sea has experienced a positive trend in  
269 both sea surface and deep-water temperature (The Mermex group, 2011) and yet specific  
270 studies assessing the combined effects of ocean warming and acidification on planktonic and  
271 benthic primary production are scarce. Moreover, as mentioned above, atmospheric  
272 deposition is an important source of new nutrients to the Mediterranean Sea which should also  
273 be considered as an additional driver. Changes in seawater pH and temperature may affect the

274 bioavailability of some nutrients by altering their speciation as well as the adsorption/release  
275 from/to particles.

276 A follow up of this project could thus be to work in very well controlled conditions of  
277  $p\text{CO}_2$ , light, temperature and atmospheric deposition in large clean indoor containers (a small  
278 version of the mesocosms currently under development at the Laboratoire d'Océanographie  
279 de Villefranche) to investigate the impacts of atmospheric deposition under present and future  
280  $p\text{CO}_2$  and temperature conditions.

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403 **Figure legends**

404 Figure 1. A: world map showing the localisation of ocean acidification perturbation  
405 experiments conducted on natural planktonic communities (see Table 1 and supplementary  
406 material for the full list). Experiments considering only the effects of ocean acidification are  
407 represented by a blue circle while experiments considering another stress (either ocean  
408 warming, nutrient concentrations or lights levels) as additional factors are represented as a  
409 pink triangle. B: cumulated number of studies focused on the effects of ocean acidification  
410 (and sometimes another stress: ocean warming, nutrient or lights levels) on natural planktonic  
411 communities. The years reported correspond to the date of the experiments.

412 Figure 2. Map showing the two study sites in France, the Bay of Calvi in Corsica and the Bay  
413 of Villefranche on the French Riviera. The station DYFAMED (doi: 10.17882/43749) where  
414 long-term data series are available is also show (see Fig. 4).

415 Figure 3. A: schematic view of the mesocosm used during these experiments. B: aerial view  
416 of the grouping of mesocosms showing the location of the ambient (OUT) sampling. C:  
417 measured and targeted  $p\text{CO}_2$  (in  $\mu\text{atm}$ ) during the experiments in summer 2012 in the Bay of  
418 Calvi and in winter 2013 in the Bay of Villefranche.

419 Figure 4. A: annual distribution of chlorophyll  $a$  concentrations (in  $\mu\text{g L}^{-1}$ ) at the point B  
420 station (BV: Bay of Villefranche;  $43^\circ 41' \text{N} - 7^\circ 19' \text{E}$ ; SOMLIT; [http://somlit.epoc.u-](http://somlit.epoc.u-bordeaux1.fr/)  
421 [bordeaux1.fr/](http://somlit.epoc.u-bordeaux1.fr/)), at the DYFAMED station (Dyf; see Fig. 2;  $43^\circ 25' \text{N} - 7^\circ 52' \text{E}$ ;  
422 doi: 10.17882/43749) and in the Bay of Calvi (BC;  $42^\circ 35' \text{N} - 08^\circ 44' \text{E}$ ; Goffart et al., 2015).  
423 The periods at which both experiments have been conducted are represented as white bars. B:  
424 box-and-whisker plots of annual evolution (1997-2014) of nutrient (nitrate:  $\text{NO}_3^-$ , phosphate:  
425  $\text{PO}_4^{3-}$  and silicate:  $\text{Si}(\text{OH})_4$ , all in  $\mu\text{mol L}^{-1}$ ) in the Bay of Villefranche (BV; point B station;  
426  $43^\circ 41' \text{N} - 7^\circ 19' \text{E}$ ; SOMLIT; <http://somlit.epoc.u-bordeaux1.fr/>) and at the DYFAMED

427 station (Dyf; see Fig. 2; 43°25'N - 7°52'E; doi: 10.17882/43749). Concentrations observed *in*  
428 *situ* (OUT; empty red circles) and in the mesocosms (full red circles; average  $\pm$  standard  
429 deviations) are also shown.

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430 Table 1. Literature survey on ocean acidification perturbation experiments conducted at the level of planktonic communities. Studies are grouped  
 431 by their geographical location (Indian, Pacific, Atlantic, Arctic and Southern Oceans) and further classified by their experimental year.  
 432 Indications are provided on the season covered, the type of incubation (Incub; M: *in situ* mesocosm (> 1000 L), (M): indoor mesocosms (> 1000  
 433 L), C: container (20-1000 L), B: bottle (< 20 L), B-SCC and B-CC: respectively semi-continuous and continuous cultures in bottles), the volume  
 434 of incubations (V; in L), the mesh-size on which sampled seawater was sieved (S; in  $\mu\text{m}$ , NS: not sieved), the duration of the experiment (D; in  
 435 days), the addition of nutrients or not (Add; W: with, Wo: without), the concentrations, at the start of the experiment, of nitrate and nitrite ( $\text{NO}_x$ ),  
 436 phosphate ( $\text{PO}_4^{3-}$ ) and silicate (Si(OH)) in  $\mu\text{mol L}^{-1}$  as well as chlorophyll *a* (Chl *a*; in  $\mu\text{g L}^{-1}$ ). References associated to each study are numbered  
 437 (Ref), the full bibliographic list can be found in the supplementary material. Studies considering another stress (either ocean warming, nutrient or  
 438 lights levels) are in bold. \* indicates addition of iron. <sup>1</sup>: experiment with addition of HCl without buffering with  $\text{NaHCO}_3$ . <sup>2</sup>: the experimental  
 439 control  $p\text{CO}_2$  lower than *in situ*  $p\text{CO}_2$  level.

Study location (year)	Season	Incub	V	S	D	Add	$\text{NO}_x$	$\text{PO}_4^{3-}$	Si(OH)	Chl <i>a</i>	Ref
Indian ocean											
Godavari river estuary, Bay of Bengal (2009)	Spring	B	5.6	200	5	W	7.6	3.2	14.8	2.3	[1]
				NS		Wo	6.9	0.6	5.2	1.2	
Pacific Ocean											

Peruvian coast (2000)	Fall	B-SCC	4	NA	11	Wo	25	2.3	26	2	[2]
<b>Bering Sea shelf (2003)</b>	<b>Summer</b>	<b>B-CC</b>	<b>2.5</b>	<b>NS</b>	<b>9-10</b>	<b>W</b>	<b>+4</b>	<b>+1</b>	<b>+8</b>	<b>1.2</b>	<b>[3]</b>
<b>Bering Sea offshore (2003)</b>							<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	
Southern coast of Korea (2004)	Fall	C	150	60	14	Wo	0.2	0.2	10	NA	[4]
						W	23	0.9			
Okhotsk Sea (2006)	Summer	B	9	200	14	Wo	0.05	0.25	1.06	0.31	[5]
Bering Sea (2007)	Summer	B	12	200	14	Wo	16	1.5	38	0.39	[6]
Northwestern Pacific (2007)	Summer	B	12	200	14	Wo	16	1.4	32	0.21	
<b>Southern coast of Korea (2008)</b>	<b>Fall</b>	<b>M</b>	<b>2,400</b>	<b>NS</b>	<b>20</b>	<b>W</b>	<b>41</b>	<b>2.5</b>	<b>40</b>	<b>1</b>	<b>[7-9]</b>
<b>California current (2008)</b>	<b>Fall</b>	<b>B</b>	<b>4</b>	<b>NS</b>	<b>3-4</b>	Wo	<b>&lt;0.05</b>	<b>10</b>	<b>14</b>	<b>NA</b>	<b>[10]</b>
						W	<b>10-20</b>				
Northwestern Pacific (2008)	Summer	B	12	200	14	Wo	13.4	1.2	13.4	0.34	[11, 12]
						W*					
Bering Sea (2009)	Summer	B	12	200	7	Wo	18.1	1.47	17	2	[11, 13, 14]
						W*					
Shimoda, Japan (2009)	Winter	C	500	100	15	W	12.6	0.77	12.4	0.06	[15]
Ocean Station Papa (2010)	Summer	B	5	200	4	Wo	8	0.88	14.2	0.39	[16]
Shimoda, Japan (2011)	Winter	C	400	100		W	4.4	0.4	12.8	1.2	[17]
Oyashio region (2011)	Spring	B	12	200	3	Wo	13.7	0.99	11.76	0.7	[18]

<b>Southern coast of Korea (2012)</b>	<b>Spring</b>	<b>M</b>	<b>2,400</b>	<b>100</b>	<b>19</b>	<b>W</b>	<b>15.6</b>	<b>0.93</b>	<b>13.4</b>	<b>15</b>	<b>[19, 20]</b>
Qingdao coast, Yellow Sea (NA)	NA	C	20	200	5	Wo	17.2	0.5	5.9	NA	[21]
Atlantic Ocean											
Norwegian fjord, North Sea (PeECE I, 2001)	Spring	M	11,000	NS	19	W	15	0.45	0.2	0.5	[22, 23]
Norwegian fjord, North Sea (PeECE II, 2003)	Spring	M	20,000	NS	19	W	8.6	0.4	12	0.5	[24-42]
Norwegian fjord, North Sea (PeECE III, 2005)	Spring	M	27,000	NS	22	W	15	0.6	3.2	2	
<b>North Atlantic (2005)</b>	<b>Spring</b>	<b>B-CC</b>	<b>2.7</b>	<b>200</b>	<b>14</b>	<b>W</b>	<b>5</b>	<b>0.31</b>	<b>0.7</b>	<b>1.5</b>	<b>[43, 44]</b>
Norwegian fjord, North Sea (2006)	Spring	M	11,000	NS	20	W	17	1	NA	0.5	[45-47]
Oresund strait, Baltic Sea (2007)	Spring	B	2.5	175	14	Wo	1.05	0.27	5.7	NA	[48] <sup>1</sup>
	Summer					Wo	0.65	0.18	5.2	NA	
<b>Sweden, Baltic Sea (2008)</b>	<b>Spring</b>	<b>C</b>	<b>100</b>	<b>NS</b>	<b>20</b>	<b>Wo</b>	<b>6.5</b>	<b>0.7</b>	<b>20.8</b>	<b>1</b>	<b>[49]</b>
Kiel fjord, Baltic Sea (2009)	Spring	M	50,000	3000	21	W	10	0.65	8	2	[50]
Kiel Bight, Baltic Sea (2009)	Summer	C	300	NS	28	W	35	2.2	40	5	[51]
						Wo	NA	NA	NA		
Subtropical North Atlantic (2009/2010)	Spring	B	NA	NS	1-3	W	+5	+0.5	+5	0.06-0.6	[52]
						Wo	NA	NA	NA		
<b>Blanes Bay, Mediterranean Sea (2010)</b>	<b>Winter</b>	<b>C</b>	<b>200</b>	<b>200</b>	<b>9</b>	<b>Wo</b>	<b>3.11</b>	<b>0.14</b>	<b>2.01</b>	<b>0.96</b>	[53-56]
<b>Blanes Bay, Mediterranean Sea (2011)</b>	<b>Summer</b>	<b>C</b>	<b>200</b>	<b>200</b>	<b>9</b>	<b>Wo</b>	<b>0.39</b>	<b>0.02</b>	<b>0.34</b>	<b>0.2</b>	
<b>Norwegian fjord, North Sea (2011)</b>	<b>Spring</b>	<b>(M)</b>	<b>2,500</b>	<b>NS</b>	<b>14</b>	<b>W</b>	<b>9.5</b>	<b>0.3</b>	<b>2.6</b>	<b>2</b>	<b>[57]</b>

Norwegian fjord, North Sea (2011)	Spring	M	75,000	3000	35	W	5	0.16	NA	1.2	[58-61]
Finland, Baltic Sea (2012)	Spring	M	50,000	3000	43	Wo	0.05	0.15	6.2	1.8	[58, 62-75]
<b>Kiel Bight, Baltic Sea (2012)</b>	<b>Fall</b>	<b>(M)</b>	<b>1,400</b>	<b>NS</b>	<b>21</b>	<b>Wo</b>	<b>3.7</b>	<b>1.52</b>	<b>20</b>	<b>&lt;1</b>	<b>[76-80]</b>
<b>Bay of Villefranche, Mediterranean Sea (2012)</b>	<b>Spring</b>	<b>B</b>	<b>4</b>	<b>200</b>	<b>12</b>	<b>Wo</b>	<b>0.2</b>	<b>0.02</b>	<b>1.2</b>	<b>0.8</b>	<b>[81]</b>
<b>Alboran Sea (2012)</b>	<b>Summer</b>	<b>C</b>	<b>20</b>	<b>200</b>	<b>7</b>	<b>Wo</b>	<b>0.6</b>	<b>0.14</b>	<b>1.2</b>	<b>0.85</b>	<b>[82-85]</b>
<b>Ria Formosa coastal lagoon (2012)</b>	<b>Winter</b>	<b>B</b>	<b>4.5</b>	<b>NS</b>	<b>2</b>	<b>Wo</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>0.9</b>	<b>[86]</b>
<b>Northwest European shelf (2012)</b>	<b>Spring</b>	<b>B</b>	<b>4.2</b>	<b>NS</b>	<b>4</b>	<b>Wo</b>	<b>0.3-1.1</b>	<b>&lt;0.02-0.14</b>	<b>&lt;0.2-2.1</b>	<b>0.25-3.5</b>	<b>[87-96]</b>
North Atlantic (2012)	Spring	B	5	200	9-10	W	8	0.5	6	NA	[97]
Bay of Calvi, Mediterranean Sea (2012)	Summer	M	50,000	5000	20	Wo	0.06	0.023	1.67	0.064	This study
Bay of Villefranche, Mediterranean Sea (2013)	Winter				12		0.13	0.01	1.145	1.147	
<b>Kiel Bight, Baltic Sea (2013)</b>	<b>Summer</b>	<b>(M)</b>	<b>1,400</b>	<b>NS</b>	<b>28</b>	<b>Wo</b>	<b>1</b>	<b>0.6</b>	<b>11</b>	<b>NA</b>	<b>[98]</b>
Sweden, Baltic Sea (2013)	Winter	M	55,000	3000	111	Wo	6.7	0.75	9.8	0.3	[99-101]
Arctic Ocean											
<b>Fram Strait (2009)</b>	<b>Summer</b>	<b>(M)</b>	<b>1,000</b>	<b>NA</b>	<b>9</b>	<b>W</b>	<b>6</b>	<b>0.09</b>	<b>6</b>	<b>2.6</b>	<b>[102]</b>
Svalbard (2010)	Spring	M	50,000	3000	30	Wo	0.1	0.07	0.2	0.2	[103-125]
						W	5.5	0.4	1.4		

<b>Svalbard offshore (2010)</b>	<b>Summer</b>	<b>C</b>	<b>20</b>	<b>100</b>	<b>15</b>	<b>Wo</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>0.6</b>	<b>[126]</b>
Disko Bay, West Greenland (2012)	Spring	B	1	250	11-17	Wo	9.3	0.8	7.5	<5	[127]
Arctic (2012)	Summer	B	1	NS	4	Wo	0.04-9.5	NA	1.6-10.3	0.8-3	[128-136]
<b>Southern Ocean</b>											
<b>Ross Sea (2005)</b>	<b>Summer</b>	<b>B-CC</b>	<b>2.7</b>	<b>200</b>	<b>13</b>	<b>Wo</b> <b>W*</b>	<b>23.6</b>	<b>1.53</b>	<b>66.3</b>	<b>6</b>	<b>[137]</b>
Ross Sea (2006)	Spring	B-SCC	4	NA	10 - 18	Wo	NA	NA	NA	NA	[138]
Derwent River estuary, Tasmania (2007)	Summer	B	2.5	250	14	Wo	<0.2	0.5-0.2	12	1.3	[139] <sup>1</sup>
	Spring						4.8	0.58	~70	0.4	
Davis Station (2008/2009)	Summer	C	650	200	10	Wo	<0.43	<0.29	~70	1.8	[140, 141]
	Summer						3	0.4	~70	3	
Weddel Sea (2010)	Summer	B	4	200	27-30 18-20	Wo W*	29	2	76	NA	[142] <sup>2</sup>
Tasmanian Sea (2010)	Summer	C	22	NS	5	Wo	NA	NA	NA	NA	[143]
New Zealand (2011)	Winter										
Western Antarctic Peninsula (2012/2013)	Spring	B	4	NA	15-21	Wo	10-23	<0.5-2	50	8-10	[144]
South Georgia and Sandwich Islands (2013)	Summer	B	1	NS	4	Wo	18-24	NA	1.2-1.6	4.2	[128-136]

440 Table 2. Environmental and experimental conditions observed in the mesocosms (average  $\pm$  standard deviation) and in ambient seawater (OUT)  
 441 at the start (day 0) and at the end of the experiment in the Bay of Calvi in summer 2012 (day 20) and in the Bay of Villefranche in winter 2013  
 442 (day 12). O<sub>2</sub>: dissolved oxygen concentration,  $p\text{CO}_2$ : partial pressure of CO<sub>2</sub> and  $\text{pH}_T$ : pH on the total scale estimated based on measured total  
 443 alkalinity ( $A_T$ ) and total inorganic carbon ( $C_T$ ) concentrations using the R package seacarb (Gattuso et al., 2016). NO<sub>3</sub><sup>-</sup>: nitrate, NH<sub>4</sub><sup>+</sup>:  
 444 ammonium, PO<sub>4</sub><sup>3-</sup>: phosphate, Si(OH): silicate. POC: particulate organic carbon, PON: particulate organic nitrogen, TEP-C: transparent  
 445 exopolymeric particles carbon content. Chl *a*: chlorophyll *a*. The percentage of contribution of the main taxonomic groups found during the  
 446 experiments and determined from high performance liquid chromatography (HPLC) measurements using modified CHEMTAX is also shown  
 447 (Prasino: Prasinophyceae, Dino: Dinophyceae, Crypto: Cryptophyceae, Hapto: Haptophyceae, Pelago: Pelagophyceae, Chloro: Chlorophyceae,  
 448 Cyano: Cyanophyceae).

	Bay of Calvi (summer 2012)				Bay of Villefranche (winter 2013)				
	Initial (day 0)		Final (day 20)		Initial (day 0)		Final (day 12)		
	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside	
<b>Hydrology</b>									
Temperature (°C)	22.16 $\pm$ 0.01	22.23	24.24 $\pm$	24.27	13.24 $\pm$ 0.01	13.24	13.17 $\pm$	13.19	
Salinity	37.98 $\pm$ 0.01	37.96	38.16 $\pm$	38.17	38.15 $\pm$ 0.01	38.11	38.18 $\pm$	38.19	
O <sub>2</sub> ( $\mu\text{mol L}^{-1}$ )	226 $\pm$ 1	226	208 $\pm$ 1	209	249 $\pm$ 1	243	251 $\pm$ 1	240	
<b>Carbonate chemistry</b>									
$p\text{CO}_2$ ( $\mu\text{atm}$ )	465 $\pm$ 6	458	473 $\pm$ 9	495	358 $\pm$ 17	354	373 $\pm$ 17	391	
$\text{pH}_T$	8.02 $\pm$ 0.01	8.02	8.01 $\pm$ 0.01	8.00	8.12 $\pm$ 0.02	8.12	8.11 $\pm$ 0.02	8.09	

$A_T$ ( $\mu\text{mol kg}^{-1}$ )	$2530 \pm 1$	2532	$2547 \pm 2$	2544	$2561 \pm 1$	2557	$2561 \pm 1$	2560
$C_T$ ( $\mu\text{mol kg}^{-1}$ )	$2227 \pm 4$	2225	$2225 \pm 4$	2232	$2275 \pm 9$	2269	$2284 \pm 10$	2293
<b>Inorganic nutrients (<math>\text{nmol L}^{-1}</math>)</b>								
$\text{NO}_3^-$	$60 \pm 8$	50	$66 \pm 10$	NA	$132 \pm 31$	1166	$238 \pm 139$	1307
$\text{NH}_4^+$	$400 \pm 200$	150	$210 \pm 20$	660	$72 \pm 14$	62	$35 \pm 12$	40
$\text{PO}_4^{3-}$	$23 \pm 3$	35	$6 \pm 2$	NA	$10 \pm 2$	12	$10 \pm 1$	120
Si(OH)	$1670 \pm 0$	1920	$1260 \pm 100$	1770	$1145 \pm 35$	1350	$1090 \pm 140$	1200
<b>Organic matter (<math>\text{mmol L}^{-1}</math>)</b>								
POC	$4.3 \pm 1.0$	5.6	$4.3 \pm 0.2$	5.4	$12.2 \pm 0.4$	8	$9.6 \pm 0.7$	NA
PON	$0.2 \pm 1.0$	0.7	$0.7 \pm 0.1$	0.7	$1.6 \pm 0.1$	0.8	$1.3 \pm 0.2$	NA
TEP-C	NA	NA	NA	NA				
<b>Phytoplankton</b>								
Chl <i>a</i> ( $\text{ng L}^{-1}$ )	$64 \pm 11$	124	$76 \pm 9$	115	$1147 \pm 62$	950	$908 \pm 82$	1170
Dominant species (%)	Hapto (33) Cyano (20) Chloro (17)	Hapto (38) Cyano (17) Chloro (16)	Chloro (34) Hapto (22) Cyano (21)	Hapto (28) Chloro (19) Cyano (18)	Cryo (26) Hapto (22) Pelago (18)	Cryo (21) Prasino (18) Diatoms (17)	Hapto (31) Pelago (23) Prasino (14)	Prasino (21) Diatoms (17) Cryo (16)
<b>Heterotrophic prokaryotes</b>								
Abundance ( $10^3 \text{ mL}^{-1}$ )	$385 \pm 70$	467	$465 \pm 35$	465	$719 \pm 19$	615	$1206 \pm 123$	669
<b>Viruses</b>								
Abundance ( $10^3 \text{ mL}^{-1}$ )	$9.2 \pm 0.7$	NA	$9.8 \pm 1.2$	NA	$12.8 \pm 4.3$	4.2	$11.6 \pm 2.0$	10.2



	<i>Synechococcus</i>				
	<i>Prochlorococcus</i>				
	Calcifying phytoplankton community				
	<i>Emiliana huxleyi</i> coccolith morphology				
	<i>Emiliana huxleyi</i> calcification degree				
Heterotrophic prokaryotes	Abundance				
	% highly active prokaryotes	■	■	<ul style="list-style-type: none"> <li>• Different trophic regimes revealed diverse effects of ocean acidification on prokaryotes</li> <li>• Ocean acidification and organic substrates were responsible for metabolic alterations</li> <li>• Viral and prokaryotic abundances were not affected by increased CO<sub>2</sub> levels</li> </ul>	Celussi et al. (this issue)
	Heterotrophic Production	■			
	β-glucosidase	■			
	Lipase				
	Chitinase		■		
	Alkaline phosphatase	■			
Viruses	Leucine aminopeptidase	■			
	Abundance			<ul style="list-style-type: none"> <li>• See above</li> </ul>	Celussi et al. (this issue)
	Activity	▨		<ul style="list-style-type: none"> <li>• No direct effect of elevated pCO<sub>2</sub> on viral replication cycles could be detected</li> <li>• Lysogeny was dependent on system productivity, as well as on phytoplankton dynamics</li> <li>• Lysis was not related to any of the measured environmental parameters</li> <li>• Mild differences in lysogeny in the most perturbed mesocosm were occasionally found, along with different phytoplankton dynamics</li> </ul>	Tsiola et al. (this issue)
Mesozooplankton	Abundance and composition			<ul style="list-style-type: none"> <li>• Ocean acidification does not have detectable effects on the studied parameters</li> <li>• Food limitation had more significant effect on copepods than ocean acidification</li> <li>• The experimental set-up for the oligotrophic conditions did not provide the information on the effect of acidification</li> </ul>	Zervoudaki et al. (this issue)
	Copepod eggs, nauplii stock and feeding rates		▨		
Metabolic rates	Oxygen metabolism (O <sub>2</sub> light-dark)			<ul style="list-style-type: none"> <li>• Summer conditions close to metabolic balance in the Bay of Calvi</li> <li>• Winter autotrophic conditions in the Bay of Villefranche, with no bloom</li> <li>• No effect of ocean acidification on plankton metabolic rates at both sites</li> <li>• Natural environmental limitations override a potential effect of ocean acidification</li> </ul>	Maugendre et al. (this issue-a)
	Gross phytoplankton production ( <sup>18</sup> O)				
	Organic carbon production (particulate and dissolved; <sup>14</sup> C)				
	Calcification rates ( <sup>14</sup> C)				

	Carbon flow ( $^{13}\text{C}$ and biomarkers)		<ul style="list-style-type: none"><li>• Inorganic <math>^{13}\text{C}</math> was added to follow carbon transfer in plankton communities using biomarkers</li><li>• Summer community production dominated by slow-growing species is representative of stratified nutrient limited conditions</li><li>• Winter community evolved from a dominance of fast-growing species to slow-growing species, due to nutrient limitation</li><li>• No detectable effect of ocean acidification on production and carbon transfer during both experiments</li></ul>	Maugendre et al. (this issue-b)
Nitrogen fixation	Diazotrophic community structure $\text{N}_2$ fixation rates		<ul style="list-style-type: none"><li>• First study of ocean acidification impacts on Mediterranean Sea <math>\text{N}_2</math> fixation</li><li>• Ocean acidification enhanced rates of <math>\text{N}_2</math> fixation in Mediterranean coastal waters</li><li>• <math>\text{N}_2</math>-fixing bacteria observed were not representative of the main marine <math>\text{N}_2</math>-fixers</li><li>• A diverse community of <math>\text{N}_2</math>-fixing bacteria changed in composition unrelated to ocean acidification</li></ul>	Rees et al. (this issue)

452 **Supplementary material: list of publications cited in Table 1**

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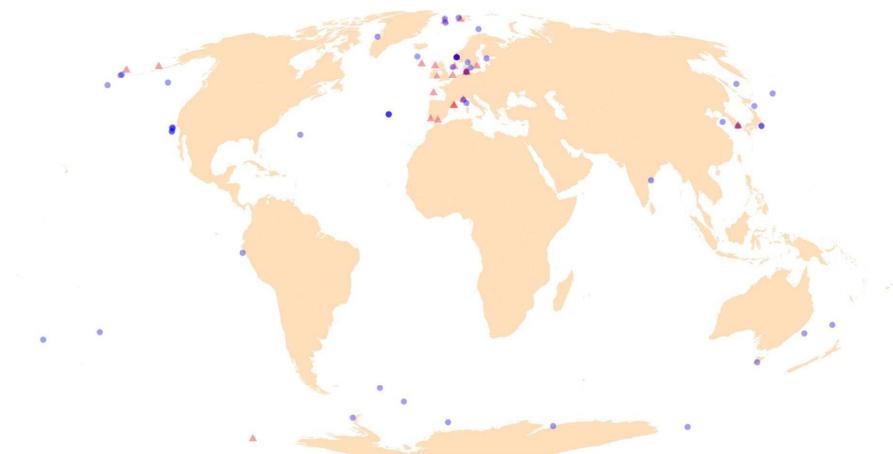
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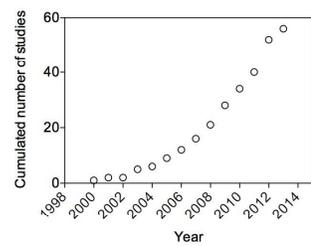
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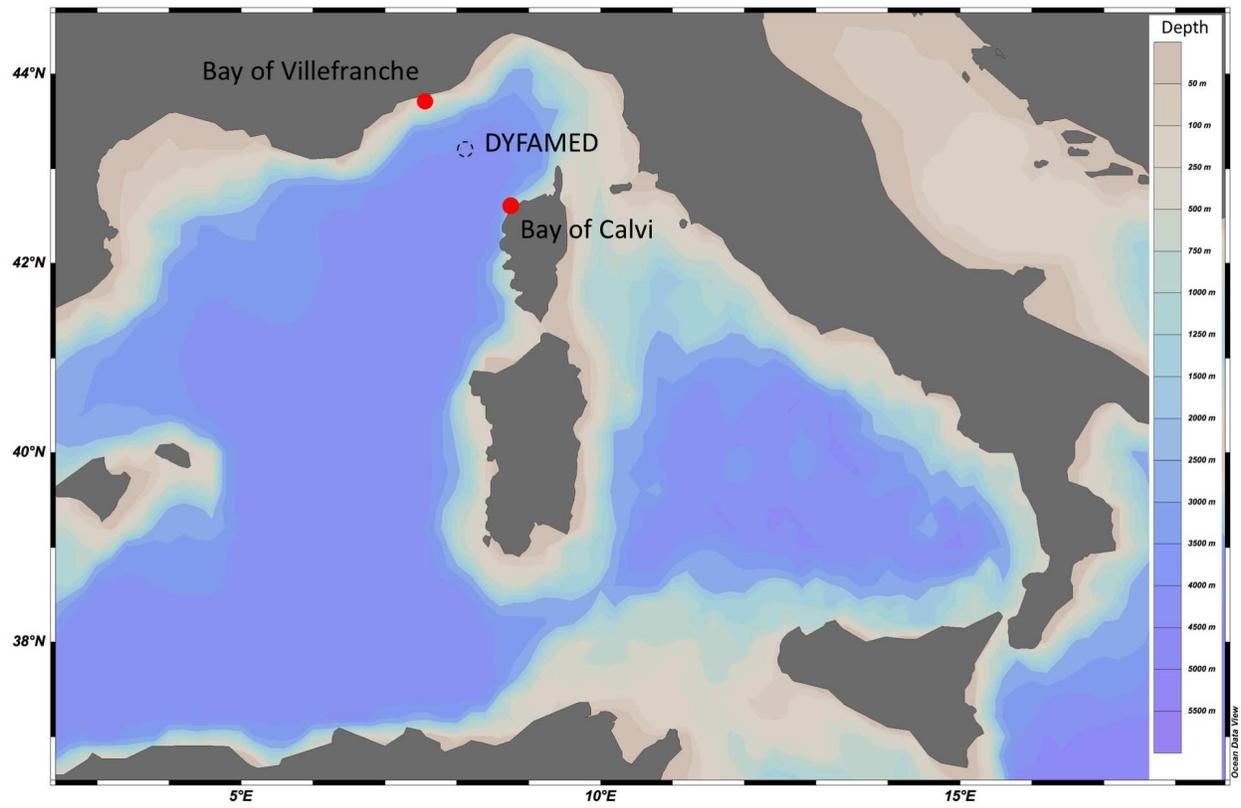
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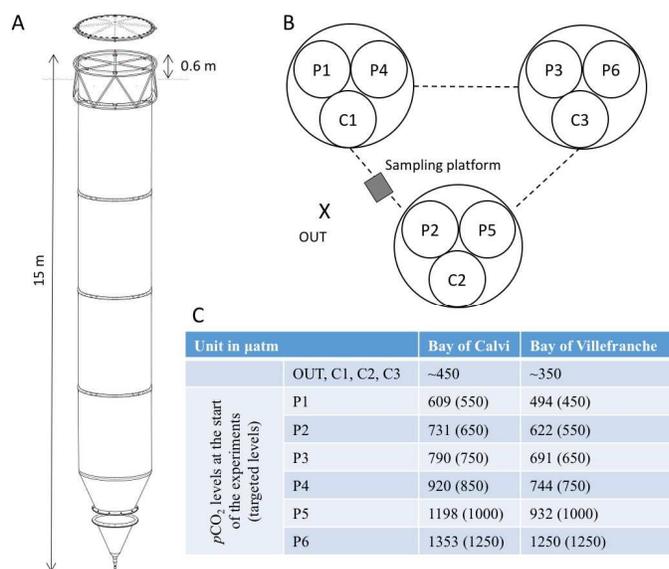


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