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1. Introduction

Planet Earth has entered a new geological era, the Anthropocene, in which geologically significant conditions and processes are profoundly altered by human activities (Waters et al., 2016). Among many impacts, human activities have released excessive amounts of carbon dioxide (CO_2) in the atmosphere leading to warming and ocean acidification: a decrease in pH and CO_3^{2-} concentration and an increase in CO_2 and HCO_3^- concentrations (Gattuso and Hansson, 2011). On average, at the global scale, surface ocean pH has decreased by 0.1 units since the beginning of the industrial era, equivalent to an increased acidity of 26% (Ciais et al., 2013). An additional decrease of pH is expected by 2100, ranging from 0.07 to 0.33, depending on the CO_2 emission scenario considered (Gattuso et al., 2015).

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

Among the poorly known impacts is the effect of ocean acidification on the efficiency of the biological pump, the transport of organic matter from the surface to the deep sea and, in turn, on the global carbon cycle and climate regulation. About 50% of the global primary production occurs in the ocean (Field et al., 1998). Primary production converts CO_2 to organic matter through photosynthesis. As all organisms remineralise this organic matter through respiration in the surface mixed-layer, consuming O_2 and releasing CO_2 to seawater, only about 30% of the organic matter produced is exported to the deep sea (Falkowski et al., 1998) where it is partially remineralised by bacteria and 1 to 3% is buried in sediments (De La Rocha and Passow, 2007).

As changes in the efficiency of this biological pump have the capacity to alter the capacity of the ocean to store anthropogenic CO_2, there is therefore a great need in projecting its future evolution. Ocean acidification experiments focussing on single plankton species do not allow assessing the impacts of ocean acidification on the CO_2 uptake capacity of the ocean. Since 2000, a significant number of perturbation experiments have been performed to fill this knowledge gap by focusing on communities rather than on isolated species (Figure 1 and Table 1). Most have been performed in the northern hemisphere with a focus on coastal meso- and eutrophic sites, or following nutrient addition at the start or during the experiments. However, ocean provinces are very diverse (Longhurst et al., 1995) but around 60% of the ocean is oligotrophic, an area that is expected to expand in the future (Polovina et al., 2008; Irwin and Oliver, 2009). Yet, the impacts of ocean acidification on these regions are almost unknown. Past community perturbation experiments were performed using various approaches, from small bottle incubations (≤ 1 L) to large mesocosms (> 50,000 L), and over different time scales (a few days to a few weeks). Mesocosms allow for the maintenance of natural communities under close-to-natural conditions and the collection of sinking organic matter (Riebesell et al., 2008; Riebesell et al., 2013). They therefore are attractive tools to study the impact of ocean acidification on plankton community structure and functioning as well as on organic matter export.

The European MedSeA project (http://medsea-project.eu) was launched in 2011 with the objective to focus on the impacts of ocean acidification and warming in the Mediterranean Sea. In this semi-enclosed sea, pH has decreased by 0.055 to 0.156 units from pre-industrial to 2013, depending on the location (Hassoun et al., 2015). A further decrease of 0.24 to 0.46 units is projected for the end of the century (Goyet et al., 2016). The Mediterranean Sea is characterised by low concentrations of nutrients and chlorophyll (The Mermex group, 2011). Based on satellite-derived estimates, chlorophyll *a* concentrations exhibit low values (less than 0.2 μg L^{-1}) over most of the Mediterranean Sea, except for the Liguro-Provençal region where relatively large blooms can be observed in late winter-early spring (e.g. Mayot et al., 2016). These features make this region of Mediterranean Sea a perfect natural laboratory to study the effects of nutrient availability (oligotrophy vs. mesotrophy) on the response of plankton community to CO_2 enrichment.

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

2. Overview of the experimental set-up

Two experiments were conducted in the Northwestern Mediterranean Sea: the first one, in the Bay of Calvi (Corsica, France; Fig. 2) in summer (June-July 2012), and the second one in the Bay of Villefranche (France; Fig. 2) in winter (February-March 2013). The experimental set-up and mesocosm characteristics are described in Gazeau et al. (this issue-a). Briefly, for each experiment, nine 50 m^3 mesocosms (2.3 m in diameter and 15 m deep; Fig. 3A) were deployed for 20 and 12 d in the Bay of Calvi and the Bay of Villefranche, respectively. Once the bottom of the mesocosms was closed, CO_2 saturated seawater was added to generate a pCO_2 gradient across mesocosms ranging from ambient level to 1,250 µatm, with three control mesocosms (C1, C2 and C3) and six mesocosms with increasing pCO_2 (P1 to P6). In the Bay of Calvi, the six pCO_2 levels were P1: 550, P2: 650, P3: 750, P4: 850, P5: 1000 and P6: 1250 µatm. In the Bay of Villefranche, the levels were P1: 450, P2: 550, P3: 750, P4: 850, P5: 1000 and P6: 1250 µatm. Mesocosms were grouped in clusters of three with each cluster containing a control, a medium and a high pCO_2 level (cluster 1: C1, P1, P4; cluster 2: C2, P2, P5 and cluster 3: C3, P3, P6; Fig. 3B). Acidification of the mesocosms was performed over 4 d by addition of various volumes of CO_2-saturated seawater. Once the target pCO_2 levels were reached, the experiments started (day 0; 24 June 2012 and 22 February 2013 for the Bay of Calvi and the Bay of Villefranche, respectively). No further CO_2 addition was performed and pCO_2 levels evolved in mesocosms driven by air-sea fluxes, temperature changes and net community production. Weather permitting, conductivity-temperature-depth (CTD) casts were performed every day in each mesocosm as well as in the ambient environment with a Sea-Bird Electronics (SBE) 19plusV2. Depth-integrated (0-10 m) samplings from the mesocosms and from the ambient environment were performed daily using integrating water samplers, IWS (HYDRO-BIOS©). Sediment traps located at the bottom end of the mesocosms were collected by SCUBA diving (daily in the

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

3. Main results

At both locations, the target pCO_2 levels were successfully reached at the start of the experiments (Fig. 3C). As no further CO_2 addition was performed to maintain CO_2 levels at the target values, high pCO_2 levels gradually declined. While the decrease was limited in summer, pCO_2 dropped at a much larger rate in winter as a consequence of strong wind and a second CO_2 addition would have been necessary (Gazeau et al., this issue-a) but was prevented by the storm which damaged almost all mesocosms.

The objective of our study was to conduct two experiments under contrasted conditions in terms of nutrient concentration and community composition. The summer experiment was performed in warm waters with very low concentrations of chlorophyll *a* and nutrients (Table 2). The molar ratio of inorganic N:P increased from 1.7 at the beginning of the experiment to ~4 on day 20, a value that is much lower than theoretical plankton requirements, suggesting, together with very low concentrations of these elements, a strong nitrate and phosphate co-limitation (Louis et al., this issue). The hydrological and weather conditions of the Bay of Villefranche were typical of winter conditions in the Northwestern Mediterranean Sea (low temperature and irradiance; Gazeau et al., this issue-a). However, as a consequence of very favourable weather conditions during the acidification phase (four sunny days prior to the start of the experiment), nutrients were rapidly consumed in all mesocosms. Most of the available nitrate was already consumed at the beginning of the experiment, reaching levels and a molar inorganic N:P ratio of 13 not usually encountered during this period of the year precluding the formation of a significant bloom (Louis et al., this issue). Long time series of chlorophyll *a* and nutrient concentrations are available in this area of the Mediterranean Sea, enabling to bring the experiments into a wider context and check for their representativeness. Conditions encountered during the summer experiment were typical of conditions in the Northwestern Mediterranean Sea between June and December as depicted for the concentration of chlorophyll *a* (Fig. 4A) as well as nitrate, phosphate and silicate (Fig. 4B). In contrast, winter conditions in the Northwestern Mediterranean Sea are much more variable depending on location and the year considered, with a large variability in nutrient concentrations and the formation or absence of a bloom. The analysis of these two long time series highlights the difficulty to catch a bloom following a winter-mixing event in this region. More importantly, these comparisons confirm that the nutrient concentrations encountered at the beginning of the winter experiment were clearly outside the range of values found in this area at this period of the year (Fig. 4B).

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

Both communities were close to metabolic balance with a tendency toward autotrophy during the winter experiment (Maugendre et al., this issue-a). In summer, both the abundance and the production of heterotrophic prokaryotes remained constant throughout the experiment (Celussi et al., this issue). In winter, although bacterial abundances increased significantly during the experimental period, bacterial production did not change significantly (Celussi et al., this issue). The addition of inorganic ^{13}C allowed following the transfer of carbon from inorganic via bulk particulate organic carbon and phytoplankton to bacteria by means of biomarkers as well as to zooplankton and settling particles. In summer, the community was slow-growing and based on regenerated production while in winter the fast-growing species at the start of the experiment were replaced by slow-growing ones during the experiment as a consequence of nutrient limitation (Maugendre et al., this issue-b). Nitrogen fixation appeared to be an active metabolic process in summer (Rees et al., this issue) but no activity of nitrifiers could be detected in winter (Rees, unpublished data). During both experiments, export of carbon to the sediment traps was highest at the start of the experiments, and 5 times larger in winter than in summer (Gazeau et al., this issue-b).

The main results with respect to the observed effects of CO_2 enrichment are shown in Table 3. The vast majority of parameters and processes which were investigated suggest an overall resilience of the plankton community structure and function in both locations and season. Gazeau et al. (this issue-b) showed that although few phytoplankton groups were negatively or positively impacted by CO_2 enrichment in summer, their response remained small with no consequence on total chlorophyll *a* concentrations, transparent exopolymeric particle formation (data only available in the Bay of Villefranche; Bourdin et al., this issue) and organic matter export (Gazeau et al., this issue-b). Similarly, scanning electron microscopy reported by Oviedo et al. (this issue) did not highlight any change in the abundance of coccolithophores and siliceous phytoplankton, and no change in size structure which could have had an impact on sedimentation rates. As a result of such limited modifications in the phytoplankton community structure, gross and net primary production rates exhibited no apparent change in response to elevated pCO_2 (Maugendre et al., this issue-a; Maugendre et al. this issue-b). Bacterial production rates were negatively affected in summer and several bacterial enzymatic activities responded to CO_2 enrichment, either negatively or positively (Celussi et al., this issue). However, no consequences were observed on community mineralisation rates (Maugendre et al., this issue-a). In winter (no data in summer), viral abundances and replication cycles appeared uncorrelated to the imposed pCO_2 conditions. Although there was no clear association between specific abundances of nitrifiers and changes in pCO_2, the summer experiment in the Bay of Calvi provided evidence of a stimulation in nitrogen fixation at pCO_2 levels above 1000 µatm (P5 and P6; Rees et al., this issue). Nevertheless, the mechanisms and diazotroph(s) responsible for N_2 fixation remain unknown and this study strongly argues for a better characterization of diazotrophs and diazotrophy under fixed conditions of pCO_2 (Rees et al., this issue). Zooplankton population structure and feeding rates were only investigated during the summer experiment in the Bay of Calvi and no effects in any of the studied parameters/processes could be detected (Zervoudaki et al., this issue). All these results converge in suggesting that elevated pCO_2 levels will not lead to important changes in plankton structure, metabolic rates and sea surface biological carbon fixation under conditions of strong limitation by nutrient availability.

As discussed in the papers brought together in the present special issue, these results stand in contrast to similar large *in situ* mesocosm experiments conducted in eutrophic areas (or following nutrient addition; see Table 1) as well as to very recent experiments performed under low nutrient conditions in the Baltic Sea (Paul et al., 2015; Bach et al., 2016). In the Northwestern Mediterranean Sea (Bay of Blanes), using indoor tanks, Sala et al. (2016) exposed coastal plankton communities to elevated CO_2 levels under contrasting conditions: in winter, at the peak of the annual phytoplankton bloom, and in summer, under low nutrient conditions. These recent studies suggested that plankton communities will be more affected by ocean acidification under low nutrient conditions than in more productive waters. This is in contrast to the two experiments described here. There are two non-mutually exclusive reasons for these discrepancies. First, the experiment of Sala et al. (2016) was conducted in an area that is much less nutrient limited than the sites investigated in the present study. Even during their summer low-nutrient experiment, Sala et al. (2016) reported nitrate concentrations almost ten times higher than those observed in summer in the Bay of Calvi and four times higher than those observed in winter in the Bay of Villefranche at the start of the experiment. Likewise, the concentration of chlorophyll during our summer experiment was three times lower than the one observed by Sala et al. (2016) in summer. The much lower nutrient availability during our experiments likely explains the contrasting responses of planktonic communities in these different environmental settings. The second potential explanation of the discrepancies is related to the duration of the experiments. The two large *in situ* mesocosm experiments performed in the Baltic Sea (Paul et al., 2015; Bach et al., 2016) were performed over significantly longer time scales (> 43 d). Impacts of elevated CO_2 were visible during the last phase when the plankton communities were relying on remineralised nutrients. Our experiments did not exceed ~20 d (12 days for the winter experiment) and it is likely that the build-up of remineralised nutrients did not reach concentrations large enough to significantly relieve nutrient limitation.

4. Conclusion and perspectives

The Mediterranean Sea is a typical low-nutrient low-chlorophyll area which exhibits large changes in nutrient concentrations in the illuminated surface waters that depend strongly on the seasonal hydrological regime. Nutrients are severely depleted in the surface layer during summer oligotrophic conditions characterized by strong thermal stratification. During winter mixing events (January–February), nutrients are re-injected to the surface layer, providing favourable conditions for a bloom initiation. Superimposed to these well-known seasonal features is an important inter-annual variability (Marty et al., 2002; de Fommervault et al., 2015). Short events driven by the atmosphere such as strong short wind events (i.e. Andersen and Prieur, 2000) and sporadic atmospheric inputs (i.e. Pulido-Villena et al., 2010) can lead to transient increase in nutrient concentrations impacting nutrient stocks and thus likely biota and biogeochemical fluxes. Indeed, while a wind event can inject nutrients from below by rapidly deepening the mixed layer depth (Andersen and Prieur, 2000), atmospheric inputs such as Saharan dust events, biomass burning or intense rain events can bring new nutrients to the surface of the water-column on short-time scales (The Mermex group, 2011, and references therein). In some cases, both nutrients from below and above can also be responsible of profound transient changes in nutrient dynamics and impact biota (Guieu et al., 2010). Nutrient availability is therefore a main control of ecosystem condition in the Mediterranean Sea. The perturbation experiments reported in the present special issue show no or low impact of ocean acidification on key biogeochemical processes, both in summer and winter whereas the natural assemblage was highly dependent on nutrient availability. Our summer *in situ* ocean acidification mesocosm experiment was representative of summer conditions in the Northwestern Mediterranean Sea. The results appear solid regarding the impact of ocean acidification on short time scale on the biogeochemistry of such oligotrophic system. Caution should be exercised to interpret the results of the winter experiment because the expected bloom conditions were not met, and important changes in nutrient availability were observed during the acidification step leading to conditions inside the mesocosms that were not representative of ambient conditions. Moreover, poor weather conditions at the beginning of the experiment (including variable and low light availability) prevented the stabilisation of blooming conditions in the bags. Yet, the time of the year to perform this experiment was carefully chosen according to the 18-year time series both at Point B and DYFAMED (Fig. 4). Unfortunately, this experiment is a good illustration that biological activity in the Mediterranean Sea exhibits a large interannual variability and specific short-term events, such as blooms, are difficult to capture.

The mesocosm approach was a good tool in the case of the summer experiment. Yet, considering the tenuous changes – or no change – observed at elevated pCO_2, a different strategy would have helped refining our results. Rather than using a pCO_2 gradient over six mesocosms, a triplicate treatment strategy taking into account two ocean acidification scenarios could have been more appropriate to better quantify possible impacts. Based on these observations, it appears that a large mesocosm pelagic approach may not be the ideal strategy in the Mediterranean Sea – or any other truly oligotrophic system - since the impacts expected will likely be low or non-existent irrespective of ambient conditions when the mesocosms were filled. A land-based experimental device providing well controlled environmental conditions (including light and temperature) would be more appropriate. Indeed, as for the global ocean, the Mediterranean Sea has experienced a positive trend in both sea surface and deep-water temperature (The Mermex group, 2011) and yet specific studies assessing the combined effects of ocean warming and acidification on planktonic and benthic primary production are scarce. Moreover, as mentioned above, atmospheric deposition is an important source of new nutrients to the Mediterranean Sea which should also be considered as an additional driver. Changes in seawater pH and temperature may affect the bioavailability of some nutrients by altering their speciation as well as the adsorption/release from/to particles.

A follow up of this project could thus be to work in very well controlled conditions of *p*CO_2, light, temperature and atmospheric deposition in large clean indoor containers (a small version of the mesocosms currently under development at the Laboratoire d'Océanographie de Villefranche) to investigate the impacts of atmospheric deposition under present and future *p*CO_2 and temperature conditions.

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Figure legends

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

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

Figure 3. A: schematic view of the mesocosm used during these experiments. B: aerial view of the grouping of mesocosms showing the location of the ambient (OUT) sampling. C: measured and targeted pCO_2 (in µatm) during the experiments in summer 2012 in the Bay of Calvi and in winter 2013 in the Bay of Villefranche.

Figure 4. A: annual distribution of chlorophyll *a* concentrations (in µg L^{-1}) at the point B station (BV: Bay of Villefranche; 43°41’N - 7°19’E; SOMLIT; http://somlit.epoc.u-bordeaux1.fr/), at the DYFAMED station (Dyf; see Fig. 2; 43°25’N - 7°52’E; doi: 10.17882/43749) and in the Bay of Calvi (BC; 42°35′N - 08°44′E; Goffart et al., 2015). The periods at which both experiments have been conducted are represented as white bars. B: box-and-whisker plots of annual evolution (1997-2014) of nutrient (nitrate: NO_3^-, phosphate: PO_4^{3-} and silicate: Si(OH), all in µmol L^{-1}) in the Bay of Villefranche (BV; point B station; 43°41’N - 7°19’E; SOMLIT; http://somlit.epoc.u-bordeaux1.fr/) and at the DYFAMED

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

Table 1. Literature survey on ocean acidification perturbation experiments conducted at the level of planktonic communities. Studies are grouped by their geographical location (Indian, Pacific, Atlantic, Arctic and Southern Oceans) and further classified by their experimental year. Indications are provided on the season covered, the type of incubation (Incub; M: *in situ* mesocosm (> 1000 L), (M): indoor mesocosms (> 1000 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 of incubations (V; in L), the mesh-size on which sampled seawater was sieved (S; in μm, NS: not sieved), the duration of the experiment (D; in days), the addition of nutrients or not (Add; W: with, Wo: without), the concentrations, at the start of the experiment, of nitrate and nitrite (NO_x), phosphate (PO_4^{3-}) and silicate (Si(OH)) in μmol L^{-1} as well as chlorophyll *a* (Chl *a*; in μg L^{-1}). References associated to each study are numbered (Ref), the full bibliographic list can be found in the supplementary material. Studies considering another stress (either ocean warming, nutrient or lights levels) are in bold. * indicates addition of iron. [1]: experiment with addition of HCl without buffering with $NaHCO_3$. [2]: the experimental control pCO_2 lower than *in situ* pCO_2 level.

Study location (year)	**Season**	**Incub**	**V**	**S**	**D**	**Add**	**NO_x**	**PO_4^{3-}**	**Si(OH)**	**Chl *a***	**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]
Bering Sea shelf (2003)	**Summer**	**B-CC**	**2.5**	**NS**	**9-10**	**W**	**+4**	**+1**	**+8**	**1.2**	**[3]**
Bering Sea offshore (2003)							**NA**	**NA**	**NA**	**NA**	
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	
Southern coast of Korea (2008)	**Fall**	**M**	**2,400**	**NS**	**20**	**W**	**41**	**2.5**	**40**	**1**	**[7-9]**
California current (2008)	**Fall**	**B**	**4**	**NS**	**3-4**	**Wo**	**<0.05**	**10**	**14**	**NA**	**[10]**
						W	**10-20**				
Northwestern Pacific (2008)	Summer	B	12	200	14	Wo W*	13.4	1.2	13.4	0.34	[11, 12]
Bering Sea (2009)	Summer	B	12	200	7	Wo W*	18.1	1.47	17	2	[11, 13, 14]
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]

Southern coast of Korea (2012)	**Spring**	**M**	**2,400**	**100**	**19**	**W**	**15.6**	**0.93**	**13.4**	**15**	**[19, 20]**
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	
North Atlantic (2005)	**Spring**	**B-CC**	**2.7**	**200**	**14**	**W**	**5**	**0.31**	**0.7**	**1.5**	**[43, 44]**
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][1]
	Summer					Wo	0.65	0.18	5.2	NA	
Sweden, Baltic Sea (2008)	**Spring**	**C**	**100**	**NS**	**20**	**Wo**	**6.5**	**0.7**	**20.8**	**1**	**[49]**
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]
Subtropical North Atlantic (2009/2010)	Spring	B	NA	NS	1-3	Wo	NA	NA	NA	0.06-0.6	[52]
						W	+5	+0.5	+5		
Blanes Bay, Mediterranean Sea (2010)	**Winter**	**C**	**200**	**200**	**9**	**Wo**	**3.11**	**0.14**	**2.01**	**0.96**	**[53-56]**
Blanes Bay, Mediterranean Sea (2011)	**Summer**	**C**	**200**	**200**	**9**	**Wo**	**0.39**	**0.02**	**0.34**	**0.2**	
Norwegian fjord, North Sea (2011)	**Spring**	**(M)**	**2,500**	**NS**	**14**	**W**	**9.5**	**0.3**	**2.6**	**2**	**[57]**

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]
Kiel Bight, Baltic Sea (2012)	**Fall**	**(M)**	**1,400**	**NS**	**21**	**Wo**	**3.7**	**1.52**	**20**	**<1**	**[76-80]**
Bay of Villefranche, Mediterranean Sea (2012)	**Spring**	**B**	**4**	**200**	**12**	**Wo**	**0.2**	**0.02**	**1.2**	**0.8**	**[81]**
Alboran Sea (2012)	**Summer**	**C**	**20**	**200**	**7**	**Wo**	**0.6**	**0.14**	**1.2**	**0.85**	**[82-85]**
						W	**3**	**0.5**			
Ria Formosa coastal lagoon (2012)	**Winter**	**B**	**4.5**	**NS**	**2**	**Wo**	**NA**	**NA**	**NA**	**0.9**	**[86]**
Northwest European shelf (2012)	**Spring**	**B**	**4.2**	**NS**	**4**	**Wo**	**0.3-1.1**	**<0.02-0.14**	**<0.2-2.1**	**0.25-3.5**	**[87-96]**
						W	**+2**	**+0.2**			
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	
Kiel Bight, Baltic Sea (2013)	**Summer**	**(M)**	**1,400**	**NS**	**28**	**Wo**	**1**	**0.6**	**11**	**NA**	**[98]**
Sweden, Baltic Sea (2013)	Winter	M	55,000	3000	111	Wo	6.7	0.75	9.8	0.3	[99-101]
Arctic Ocean											
Fram Strait (2009)	**Summer**	**(M)**	**1,000**	**NA**	**9**	**W**	**6**	**0.09**	**6**	**2.6**	**[102]**
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		

Svalbard offshore (2010)	**Summer**	**C**	**20**	**100**	**15**	**Wo**	**NA**	**NA**	**NA**	**0.6**	**[126]**
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]
Southern Ocean											
Ross Sea (2005)	**Summer**	**B-CC**	**2.7**	**200**	**13**	**Wo** W*	**23.6**	**1.53**	**66.3**	**6**	**[137]**
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][1]
	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][2]
Tasmanian Sea (2010) New Zealand (2011)	Summer Winter	C	22	NS	5	Wo	NA	NA	NA	NA	[143]
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]

Table 2. Environmental and experimental conditions observed in the mesocosms (average ± standard deviation) and in ambient seawater (OUT) 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 (day 12). O_2: dissolved oxygen concentration, pCO_2: partial pressure of CO_2 and pH_T: pH on the total scale estimated based on measured total alkalinity (A_T) and total inorganic carbon (C_T) concentrations using the R package seacarb (Gattuso et al., 2016). NO_3^-: nitrate, NH_4^+: ammonium, PO_4^{3-}: phosphate, Si(OH): silicate. POC: particulate organic carbon, PON: particulate organic nitrogen, TEP-C: transparent exopolymeric particles carbon content. Chl *a*: chlorophyll *a*. The percentage of contribution of the main taxonomic groups found during the experiments and determined from high performance liquid chromatography (HPLC) measurements using modified CHEMTAX is also shown (Prasino: Prasinophyceae, Dino: Dinophyceae, Crypto: Cryptophyceae, Hapto: Haptophyceae, Pelago: Pelagophyceae, Chloro: Chlorophyceae, 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
Hydrology								
Temperature (°C)	22.16 ± 0.01	22.23	24.24 ±	24.27	13.24 ± 0.01	13.24	13.17 ±	13.19
Salinity	37.98 ± 0.01	37.96	38.16 ±	38.17	38.15 ± 0.01	38.11	38.18 ±	38.19
O_2 (µmol L^{-1})	226 ± 1	226	208 ± 1	209	249 ± 1	243	251 ± 1	240
Carbonate chemistry								
pCO_2 (µatm)	465 ± 6	458	473 ± 9	495	358 ± 17	354	373 ± 17	391
pH_T	8.02 ± 0.01	8.02	8.01 ± 0.01	8.00	8.12 ± 0.02	8.12	8.11 ± 0.02	8.09

A_T (µmol kg^{-1})	2530 ± 1	2532	2547 ± 2	2544	2561 ± 1	2557	2561 ± 1	2560
C_T (µmol kg^{-1})	2227 ± 4	2225	2225 ± 4	2232	2275 ± 9	2269	2284 ± 10	2293
Inorganic nutrients (nmol L^{-1})								
NO_3^-	60 ± 8	50	66 ± 10	NA	132 ± 31	1166	238 ± 139	1307
NH_4^+	400 ± 200	150	210 ± 20	660	72 ± 14	62	35 ± 12	40
PO_4^{3-}	23 ± 3	35	6 ± 2	NA	10 ± 2	12	10 ± 1	120
Si(OH)	1670 ± 0	1920	1260 ± 100	1770	1145 ± 35	1350	1090 ± 140	1200
Organic matter (mmol L^{-1})								
POC	4.3 ± 1.0	5.6	4.3 ± 0.2	5.4	12.2 ± 0.4	8	9.6 ± 0.7	NA
PON	0.2 ± 1.0	0.7	0.7 ± 0.1	0.7	1.6 ± 0.1	0.8	1.3 ± 0.2	NA
TEP-C	NA	NA	NA	NA				
Phytoplankton								
Chl *a* (ng L^{-1})	64 ± 11	124	76 ± 9	115	1147 ± 62	950	908 ± 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)	Cryto (26) Hapto (22) Pelago (18)	Cryto (21) Prasino (18) Diatoms (17)	Hapto (31) Pelago (23) Prasino (14)	Prasino (21) Diatoms (17) Cryto (16)
Heterotrophic prokaryotes								
Abundance (10^3 mL^{-1})	385 ± 70	467	465 ± 35	465	719 ± 19	615	1206 ± 123	669
Viruses								
Abundance (10^3 mL^{-1})	9.2 ± 0.7	NA	9.8 ± 1.2	NA	12.8 ± 4.3	4.2	11.6 ± 2.0	10.2

Table 3. Summary of main results and highlights obtained during the two experiments in summer 2012 in the Bay of Calvi and in winter 2013 in the Bay of Villefranche. Green, red and grey boxes refer to, respectively, positive, negative and not detectable effects of CO_2 enrichment. Hatched boxes indicate that no data are available.

Parameters and processes		**CO_2 effect**		**Highlights**	**Related publication**
		Summer	**Winter**		
Hydrology and carbonate chemistry					Gazeau et al. (this issue-a)
Nutrients				• Contrasted nutrient stoichiometry in surface waters in summer and winter • Dissolved organic pool was a large stable fraction of N and P in summer and winter • CO_2 had no effect on nutrient dynamics that was mostly biologically controlled	Louis et al. (this issue)
Particulate organic matter	Concentration			• Organic matter export was not impacted by CO_2-enrichment	Gazeau et al. (this issue-b)
	Export to sediment traps				
Transparent exopolymeric particles (TEP)	TEP carbon content TEP precursors TEP densities TEP volume concentrations			• A large contribution of TEP to organic carbon • A substantial contribution of ultraphytoplankton to phytoplankton carbon pool • No effect of ocean acidification on TEP, TEP precursors and size distribution • Shift in ultraphytoplankton community during the experiment • Vast production of TEP precursors by Synechococcus and/or TEP degradation	Bourdin et al. (this issue)
Phytoplankton community	Total chlorophyll *a*			• Production limited by nutrient availability and community dominated by small species • In areas where nutrient availability exerts a strong pressure on phytoplankton growth, CO_2 addition will likely have very limited effects on phytoplankton diversity	Gazeau et al. (this issue-b)
	Haptophyceae				
	Cryptophyceae				
	Chlorophyceae				
	Bacilophyceae				
	Dinophyceae				
	Prasinophyceae				
	Pelagophyceae				
	Cyanophyceae				
	Diatoms				
	Nano-eukaryotes				
	Pico-eukaryotes				

	Synechoccocus				
	Prochlorococcus				
	Calcifying phytoplankton community			• A pCO_2 driven phytoplankton succession did not occur in these oligotrophic areas • Different species-specific sensitivities to pCO_2 were observed • Coccolithophore community structure changed with time, nutrients and temperature	Oviedo et al. (this issue)
	Emiliania huxleyi coccolith morphology				
	Emiliania huxleyi calcification degree				
Heterotrophic prokaryotes	Abundance			• Different trophic regimes revealed diverse effects of ocean acidification on prokaryotes • Ocean acidification and organic substrates were responsible for metabolic alterations • Viral and prokaryotic abundances were not affected by increased CO_2 levels	Celussi et al. (this issue)
	% highly active prokaryotes				
	Heterotrophic Production				
	ß-glucosidase				
	Lipase				
	Chitinase				
	Alkaline phosphatase				
	Leucine aminopeptidase				
Viruses	Abundance			• See above	Celussi et al. (this issue)
	Activity			• No direct effect of elevated pCO_2 on viral replication cycles could be detected • Lysogeny was dependent on system productivity, as well as on phytoplankton dynamics • Lysis was not related to any of the measured environmental parameters • Mild differences in lysogeny in the most perturbed mesocosm were occasionally found, along with different phytoplankton dynamics	Tsiola et al. (this issue)
Mesozooplankton	Abundance and composition			• Ocean acidification does not have detectable effects on the studied parameters • Food limitation had more significant effect on copepods than ocean acidification • The experimental set-up for the oligotrophic conditions did not provide the information on the effect of acidification	Zervoudaki et al. (this issue)
	Copepod eggs, nauplii stock and feeding rates				
Metabolic rates	Oxygen metabolism (O_2 light-dark)			• Summer conditions close to metabolic balance in the Bay of Calvi • Winter autotrophic conditions in the Bay of Villefranche, with no bloom • No effect of ocean acidification on plankton metabolic rates at both sites • Natural environmental limitations override a potential effect of ocean acidification	Maugendre et al. (this issue-a)
	Gross phytoplankton production (^{18}O)				
	Organic carbon production (particulate and dissolved; ^{14}C)				
	Calcification rates (^{14}C)				

	Carbon flow (^{13}C and biomarkers)		• Inorganic ^{13}C was added to follow carbon transfer in plankton communities using biomarkers • Summer community production dominated by slow-growing species is representative of stratified nutrient limited conditions • Winter community evolved from a dominance of fast-growing species to slow-growing species, due to nutrient limitation • No detectable effect of ocean acidification on production and carbon transfer during both experiments	Maugendre et al. (this issue-b)
Nitrogen fixation	Diazotrophic community structure		• First study of ocean acidification impacts on Mediterranean Sea N_2 fixation • Ocean acidification enhanced rates of N_2 fixation in Mediterranean coastal waters • N_2-fixing bacteria observed were not representative of the main marine N_2-fixers • A diverse community of N_2-fixing bacteria changed in composition unrelated to ocean acidification	Rees et al. (this issue)
	N_2 fixation rates			

Supplementary material: list of publications cited in Table 1

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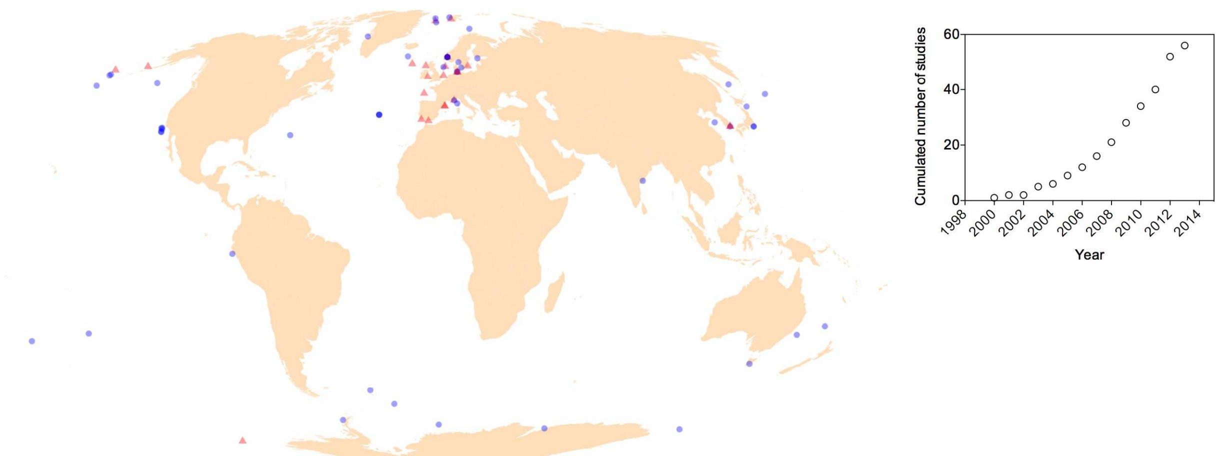
A

B


Cumulated number of studies
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40
20
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1998
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2002
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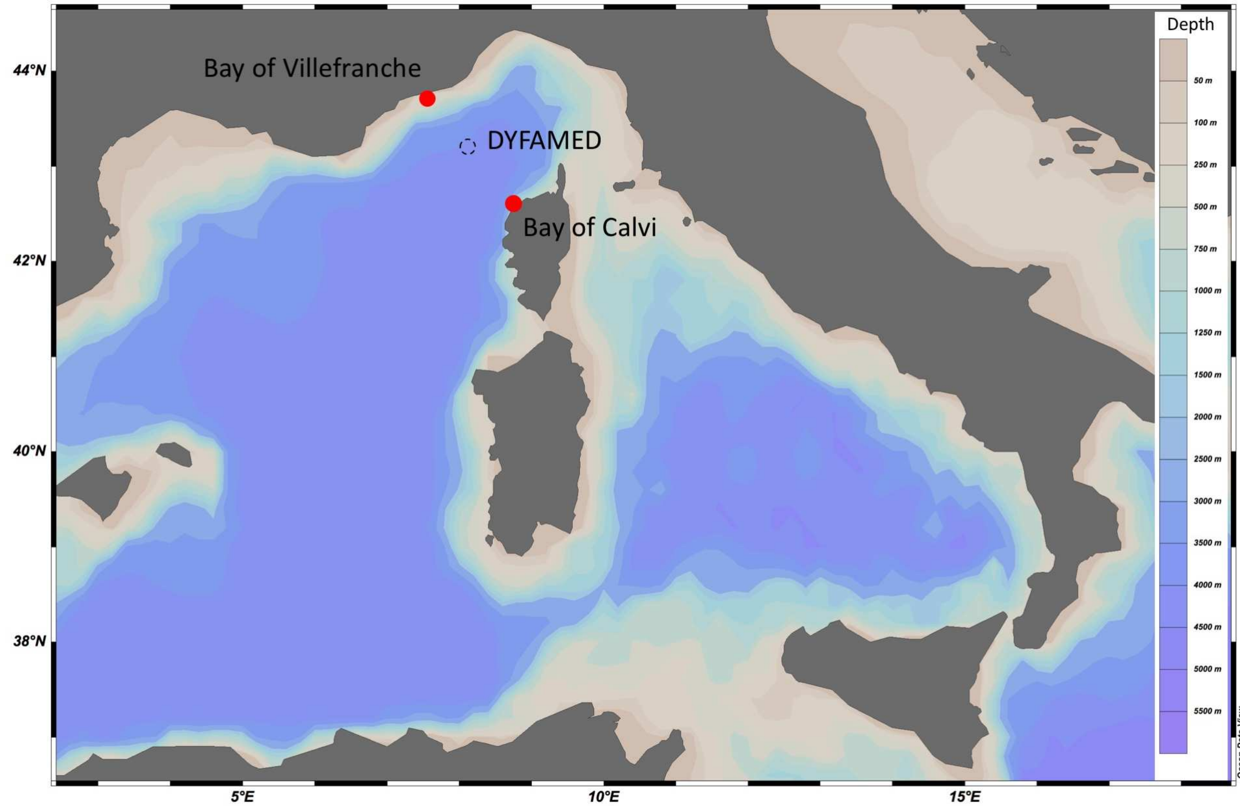
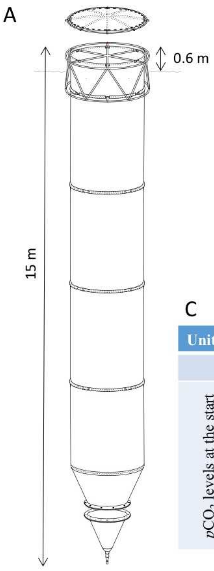


Bay of Villefranche
DYFAMED
Bay of Calvi
44°N
42°N
40°N
38°N
5°E
10°E
15°E
Depth
50 m
100 m
250 m
500 m
750 m
1000 m
1250 m
1500 m
2000 m
2500 m
3000 m
3500 m
4000 m
4500 m
5000 m
5500 m
Ocean Data View

A



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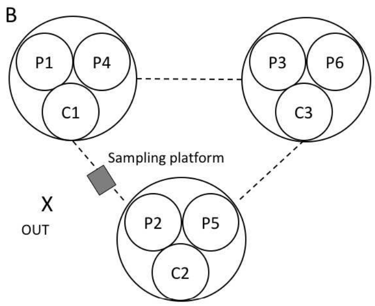
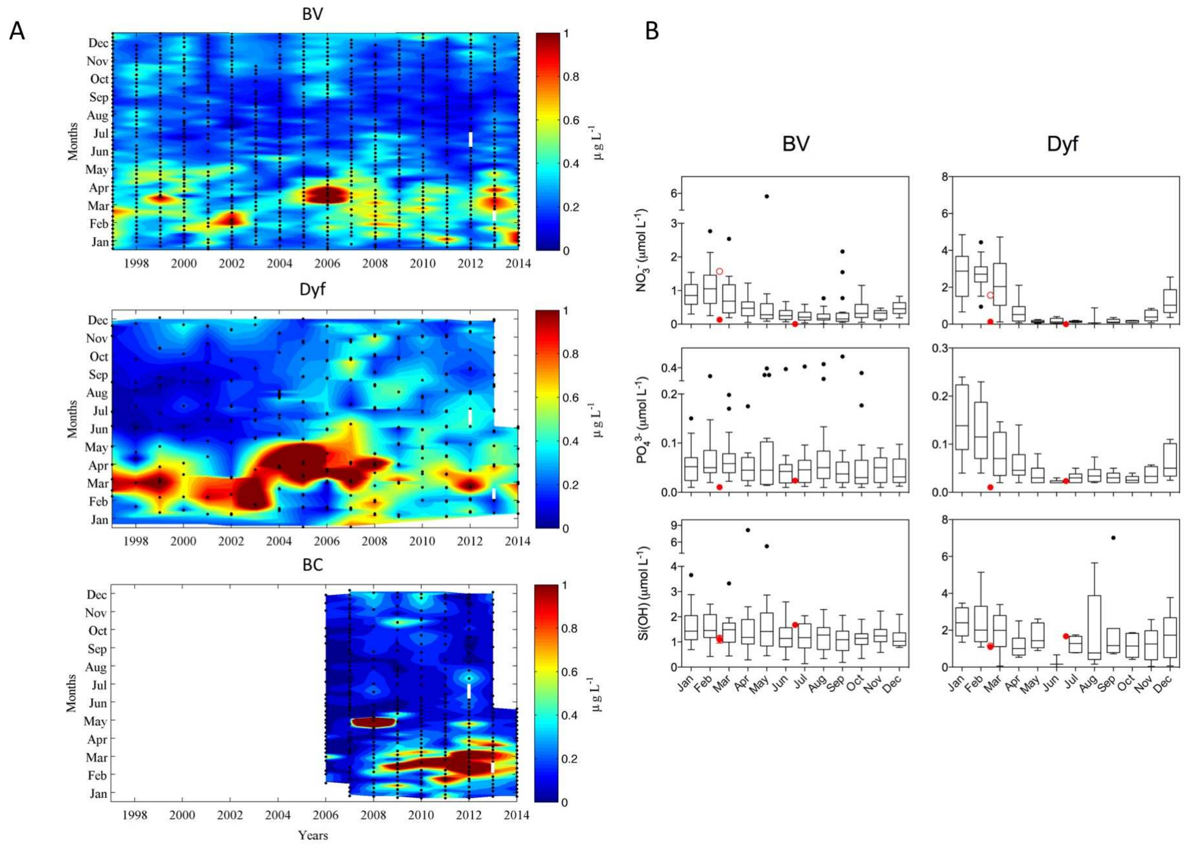


C

Unit in µatm		Bay of Calvi	Bay of Villefranche
	OUT, C1, C2, C3	~450	~350
pCO$_2$ levels at the start of the experiments (targeted levels)	P1	609 (550)	494 (450)
	P2	731 (650)	622 (550)
	P3	790 (750)	691 (650)
	P4	920 (850)	744 (750)
	P5	1198 (1000)	932 (1000)
	P6	1353 (1250)	1250 (1250)


A
BV
Dyf
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Months
Years
μg L-1
B
BV
Dyf
NO3- (μmol L-1)
PO43- (μmol L-1)
Si(OH) (μmol L-1)
Jan Feb Mar Apr May Jun Jul Aug Sep Oct Nov Dec