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High-resolution ocean pH dynamics in four subtropical Atlantic benthic habitats

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Abstract

Oscillations of ocean pH are largely unknown in coastal environments and ocean acidification studies often do not account for natural variability yet most of what is known about marine species and populations is found out via studies conducted in near shore environments. Most experiments designed to make predictions about future climate change scenarios are carried out in coastal environments with no research that takes into account the natural pH variability. In order to fill this knowledge gap and to provide reliable measures of pH oscillation, seawater pH was measured over time using moored pH sensors in four contrasting phytocenoses typical of the north Atlantic subtropical region. Each phytocenosis was characterized by its predominant engineer species: (1) *Cystoseira abies-marina*, (2) a mix of gelidiales and geniculate corallines, (3) *Lobophora variegata,* and (4) encrusting corallines. The autonomous pH measuring systems consisted of a pH sensor; a data logger and a battery encased in a waterproof container and allowed the acquisition of high-resolution continuous pH data at each of the study sites. The pH variation observed ranged by between 0.09 and 0.24 pH_{NBS} units. A clear daily variation in seawater pH was detected at all the studied sites (0.04–0.12 pH_{NBS} units). Significant differences in daily pH oscillations were also observed between phytocenoses, which shows that macroalgal communities influence the seawater pH in benthic habitats. Natural oscillations in pH must be taken into account in future ocean acidification studies to put findings in perspective and for any ecological recommendations to be realistic.

1 Introduction

Over the past 250 years, anthropogenic CO_2 emissions have caused an increase of atmospheric CO_2 concentration from 280 ppmv (parts per million volume) to 387 ppmv (Le Querè et al., 2009). It has been stated that this concentration will double by the end of the current century (Houghton et al., 2001). Oceans act as an important carbon sink:

from 2000 to 2006, the oceans absorbed approximately 24 % of total anthropogenic CO_2 emissions (Canadell et al., 2007) reducing CO_2 levels present in the atmosphere (IPCC, 2007; Sabine and Feely, 2007). However, when CO_2 dissolves in seawater the gas reacts and forms carbonic acid (H_2CO_3) which then can dissociate and lose hydrogen ions resulting in the formation of bicarbonate and carbonate ions. It is the increase in concentrations of bicarbonate and hydrogen ions that lower the pH of seawater and causes ocean acidification. Over the last 200 years ocean pH is thought to have decreased by approximately 0.1 units, from 8.21 to 8.10 (Royal Society, 2005; Kleypas, 2006). It is predicted that pH will decrease by a further 0.3–0.4 units by the end of the century (Orr et al., 2005; Doney et al., 2009).

Recently, the effects of ocean acidification on marine ecosystems have been an important research area. Numerous laboratory studies have been published showing evidence that ocean acidification influences development, growth, physiology and survival of marine organisms, especially calcifying species (Orr et al., 2005; Fine and Tchernov, 2007; Ries et al., 2009; Dupont et al., 2013). Studies have demonstrated a wide range of responses to seawater acidification by different taxonomic groups (Doney et al., 2009; Kroeker et al., 2013). However, most studies designed to identify the effects of ocean acidification use already available average values of carbon chemistry parameters (pH oscillation, total alkalinity, pCO$_2$ and dissolved inorganic carbon) instead of measuring them in situ (McElhany and Busch, 2012). Separate studies specifically measuring pH and carbonate levels in the same habitats often result in values that are inconsistent with pCO$_2$ averages used in studies. Experiments designed to assess the impact of ocean acidification should therefore also measure carbon chemistry within the studied habitats of the model species used. Laboratory experiments also tend to focus on testing responses to values of pH and pCO$_2$, and saturation states for calcite and aragonite, anticipated in the near future (see review by Dupont and Thorndyke, 2013). Yet it has also been reported that pH in the oceans is not constant; temporal and spatial variations do exist (Hoffman et al., 2011). Experimental studies often neglect local environmental pH variability as well as other important environmental parameters

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and stressors that have adaptive impacts on populations. The combined impacts of ocean acidification and multiple stressors and their natural variability are largely unknown but may have a large influence on our predictions of future climate change scenarios. In coastal environments in particular, variability may be amplified due to the ambient heterogeneity and biological activity (Middelboe and Hansen, 2007).

Little is known about the influence of different phytocenoses on pH. However, a pronounced 24 h cycle of pH has been documented in Pacific coastal environments around America, with pH values varying by ±0.24 units in a singleday (Wooton et al., 2008). In the open ocean diurnal variation is not as pronounced: an average pH range of 0.024 units is more typical (Hoffman et al., 2011). In shallow water coastal environments surface water pCO_2 is also significantly higher and pH levels lower than the values expected based on equilibrium with current atmospheric levels (Fagan and Mackenzie, 2007; Bates et al., 2010; Thomsen et al., 2010; Shamberger et al., 2011; Yu et al., 2011; Hofmann et al., 2011).

In this paper we studied temporal pH variation in four different shallow water phytocenoses common in the North Atlantic subtropical region. Our main objective was to assess natural in situ pH values and daily cycles in contrasting coastal habitats, in order to provide information of this geographic area that will inform future ocean acidification studies.

2 Material and methods

Four study sites, each with a contrasting dominant engineer species, were selected in shallow water coastal sites around the Canary Islands. The sites (four different phytocenoses) represent the most common rocky bottom ecosystems occurring in the Atlantic archipelagos (Azores, Madeira, Salvages and the Canary Islands): (1) *Cystoseira abies-marina* canopy-forming systems, (2) a mixed turf of Gelidiales and geniculate corallines (*Gelidium canariense*, *G. arbuscula*, *Pterocladiella capilacea*) and geniculate corallines (*Haliptilon virgatum*, *Ellisolandia elongata*, *Jania adhaerens*), (3) *Lobophora*

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variegata stands (Sangil et al., 2011) and (4) sea urchin barren grounds dominated by crustose algae due to the grazing activity of the sea urchin *Diadema africanum* (Hernández et al., 2008). The characteristics of each phytocenosis are summarized in Table 1.

A moored pH measuring system was deployed at each of the study sites (Table 2). Each system consisted of a Seabird SBE 18 pH sensor attached to a data logger and a lead battery protected inside a waterproof container. Each system was placed inside a plastic box with several openings to allow water circulation and this box was firmly attached to the rocky bottom using a pneumatic drill at about 5 to 10 m depth in each site (Fig. 1).

The pH sensors were previously calibrated against NIST buffer solutions (4, 7 and 10 pH ±0.02) using the software SEASOFT and its module pHfit. The loggers were programmed to take measurements once every 30 min and the systems were deployed for 15 days during two time periods at each site (see details in Table 1). The timing of deployment and retrieval of the pH systems was dependent on sea state and measurements could therefore not be made simultaneously at all four sites due to logistic restrictions. The study was also disrupted because the pH sensor located in the encrusting coralline algae site was subject to vandalism during the second sampling period – no data could be gathered for this particular time in this phytocenosis. The location and study periods for each different site are summarized in Table 1.

3 Results

All four sites displayed a clear 24 h pH cycle. The lowest pH values were recorded in the morning between 08:00 and 10:00 a.m., and values were highest between 15:00 and 19:00 p.m., though there were differences between phytocenoses (Fig. 2, Table 1). Overall pH_{NBS} values measured in this study ranged between 8.04 (*Cystoseira abies-marina* community, autumn) and 8.10 (gelidiales-geniculate corallines and *C. abies-marina*, spring). The greatest pH_{NBS} per period variation occurred in the

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C. abies-marina community during autumn 2011 (0.24, ranging from 8.04 to 8.28). The lowest pH_{NBS} variation was 0.09 recorded in the gelidiales-geniculate coralline community in autumn 2011. In the remaining sites and time periods pH_{NBS} varied by 0.12–0.16. The highest mean pH_{NBS} per time period was measured in the gelidiales-geniculate corallines and *Cystoseira* communities in spring 2012 (pH_{NBS} 8.23) and the lowest mean value was recorded in the gelidiales-geniculate corallines in autumn 2011 (pH_{NBS} 8.10).

Despite seasonal variations in pH_{NBS}, a daily pattern was still apparent though its range was relatively small in comparison. Based on mean pH_{NBS} per hour the diurnal cycle was clearest in the *C. abies-marina* site in autumn 2011, where daily pH_{NBS} values varied by; 0.12 units (Figs. 2 and 3). The same site in May 2012 still showed a clear daily pattern (Fig. 3) but the variation in values was smaller, just 0.08. Mean daily variation was lowest (0.04 pH_{NBS} units day^{-1}) in the gelidiales-geniculate coralline site in November 2011 and *Lobophora variegata* site in 2011 (Figs. 2 and 3). The crustose algae phytocenosis could only be examined in October 2011, due to vandalism of experimental equipment, and daily pH_{NBS} varied by 0.05 units at this site (Fig. 3).

The exact timing of daily pH_{NBS} maxima and minima was different in each phytocenoses (Figs. 2 and 3). The highest daily values were generally recorded in the afternoon, between 15:00 and 16:00 p.m. but at the *C. abies-marina* site these maxima occurred later in the day, between 18:00 and 19:00 p.m.

In the gelidiales-geniculate coralline site, daily variation and daily means differed between the two studied periods. In the gelidiales-geniculate phytocenosis, pH_{NBS} varied by 0.08 units over a 24 h cycle in March 2012 compared to 0.04 units variation in autumn 2011 (Fig. 2). At the same site mean pH_{NBS} was higher in the spring period (pH_{NBS} 8.23) compared to autumn (pH_{NBS} 8.10) (Table 3).

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4 Discussion

The data showed that daily pH variation differed between phytocenoses, and that the observed differences seem to be related to algae productivity. This suggests that in coastal environments the type of phytocenosis present influences the pH gradient inhabited by all organisms within that ecosystem. Continuous monitoring of pH in four contrasting habitats has revealed that the largest variation in pH throughout the sampling period and the highest daily variation in pH values occurred in the *Cystoseira abies-marina* phytocenesis in autumn 2011. Daily fluctuations in pH were clear at this site, where algal cover was higher compared to the three other studied phytocenoses (Table 3). *Cystoseira abies-marina* is a perennial species present throughout the whole year and tends to form large accumulations of drift algae along the edge of the seashore. The high algal biomass of *Cystoseira abies-marina* and associated high levels of primary production could be key to the large daily fluctuations in pH at this site; since high levels of CO_2 uptake during periods of photosynthesis and CO_2 release during non-photosynthetic periods could cause pH to vary more widely.

The diel patterns exhibited in the coastal ecosystems studied are similar to diel patterns observed in coral reef ecosystems in Hofmann et al. (2011). Daily variation was characterized by consistent and moderate fluctuations ranging from 0.1 to 0.25 pH units day^{-1}. Other comparable diurnal pH fluctuations measured elsewhere were 0.1 units day^{-1} in spring in the Bay of Calvi in the Mediterranean (Frankignoulle and Bouquegneau, 1990) and 0.15 day in autumn in the Bay of Bengal in the Indian Ocean (Subramanian and Mahadevan, 1999). In oligotrophic open ocean areas pH variation tends to be lower, for example daily variations in pH were between 0.02 to 0.10 units over a 30 days period (Hoffman et al., 2011). In comparison, diurnal variations up to 0.5 units day^{-1} were observed in a productive Kelp forest close to the Kerguelen Archipelago in the Southern Ocean in austral summer (Delille et al., 2009).

The daily pH cycle detected at all four sites in the present study can be explained by daily variations in photosynthesis, respiration and seawater temperature. Seawater pH increases when CO_2 is captured by photosynthetic organisms (macroalgae and phytoplankton) throughout the daytime, and decreases at night when CO_2 is respired and diffuses from the ocean to the atmosphere (Bensoussan and Gatuso, 2007).

Our data also shows that some seasonal variation in pH exists; mean pH values were higher in the winter–spring period compared to the autumn. The late winter–spring season is when the highest growth rates of engineer species occur in these phytocenosis in the Canary Islands (Medina and Haroun, 1994; Montañés et al., 2006). The spring growth of these engineer species is triggered by the breakdown of the seasonal thermocline when cold nutrient-rich deep waters mix with the upper, nutrient-depleted waters (De León and Braun, 1973; Barton et al., 1998), and by the availability of more daylight hours.

The highest seasonal pH variability, as much as 0.13 pH_{NBS} units, was recorded in the gelidiales-geniculIate coralline phytocenosis. The variation in pH recorded here was double that previously observed in the Canary Islands region; a value of 0.055 pH units from the European Station for Time Series in the Ocean (González-Dávila and Santana-Casiano, 2011). However, seawater samples from the European Station for Time Series in the Ocean were collected in an open ocean area, not in shallow coastal water sites such as we used in our study. The shallow coastal areas studied here, as well as others around the world, are subject to greater variation in a number of environmental parameters that influence spatial and temporal pH; both biotic factors (photosynthesis, respiration) and abiotic (freshwater input, nutrient concentration, local upwelling or volcanic activity). The organisms living in coastal areas are therefore continuously coping with relatively large oscillations in pH and these oscillations may increase in the future due to rising seawater CO_2 concentrations that will decrease the ocean's natural buffering capacity (Schulz and Riebsell, 2012).

Coastal regions have complex spatial and temporal variation in carbon chemistry. The results of our study suggest that local carbon chemistry should be measured and taken into consideration when designing ocean acidification experiments in preference to the use of regional averages. The existence of diurnal, seasonal and spatial variation in pH should also be incorporated into models of ocean pH and allowed for in studies with benthic species and populations that aim to assess the effect of ocean acidification.

Author contributions. C. A. Hernández and J. C. Hernández design the study and J. C. Hernández, C. Sangil and S. Clemente carried them out. C. A. Hernández and J. C. Hernández prepared the manuscript with contributions from all co-authors.

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Table 1. Characteristics of the four studied phytocenoses.

Phytocenosis	Growth form	Cover	Thalli lengh
Cystoseira abies-marina	Perennial	200–400 %	300–600 mm
Gelidiales and geniculate corallines	Perennial	40–80 %	100 mm
Lobophora variegata	Perennial	150–250 %	50–100 mm
Crustose algae	Perennial and annual	40–60 %	5 mm

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Table 2. Locations of study sites where pH sensors were deployed.

Phytocenosis	Site	Island	Latitude	Longitude
Cystoseira abies marina	Punta del Hidalgo	Tenerife	28°34′07.23″ N	16°20′00.12″ W
Gelidiales and geniculate corallines	Puerto de la Cruz	Tenerife	28°25′05.03″ N	16°32′44.71″ W
Lobophora variegata	Las Cabras	La Palma	28°27′54.02″ N	17°49′51.72″ W
Crustose coralline	Abades	Tenerife	28°08′27.73″ N	16°26′09.81″ W

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Table 3. Descriptive statistics for pH profiles at each site.

Phytocenosis	Time period	Range	Min	Max	Mean	SD
Cystoseira abies-marina	Autumn	0.24	8.04	8.28	8.15	0.05
	Spring	0.15	8.16	8.31	8.23	0.03
Gelidiales and geniculate corallines	Autumn	0.09	8.07	8.16	8.10	0.02
	Spring	0.14	8.17	8.31	8.23	0.03
Lobophora variegata	Autumn	0.12	8.08	8.20	8.15	0.02
	Winter	0.15	8.09	8.24	8.17	0.03
Crustose coralline	Autumn	0.16	8.08	8.24	8.14	0.03

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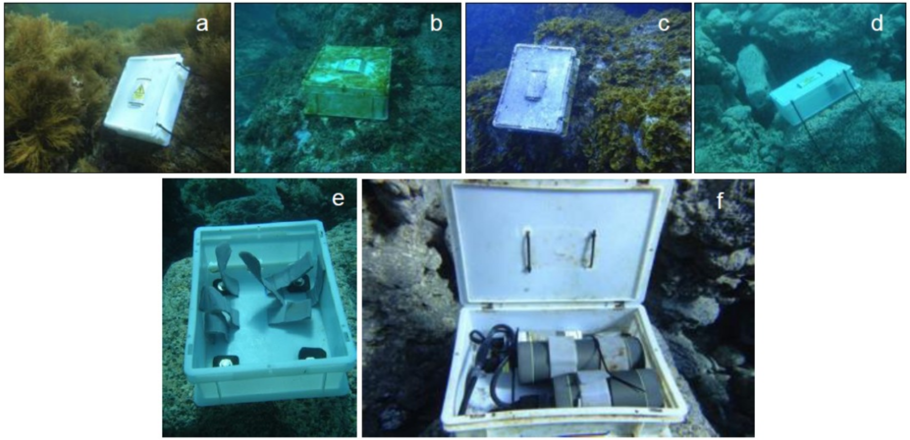

Figure 1. pH sensor cases deployed at each of the phytocenoses studied: **(a)** *Cystoseira abies-marina;* **(b)** Gelidiales and geniculate corallines; **(c)** *Lobophora variegata;* **(d)** Crustose algae. **(e)** Internal set up of the underwater case; and **(f)** pH sensor, data logger and lead battery.

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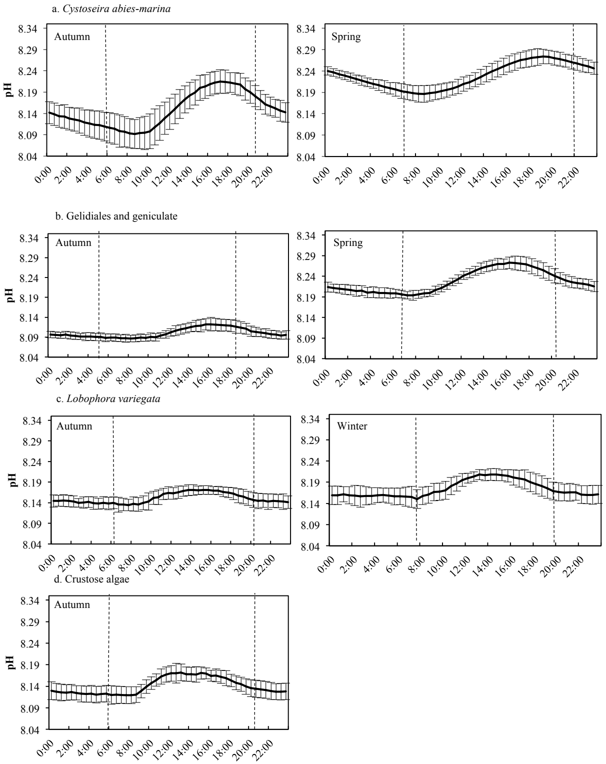

Figure 2. Mean pH per hour of the day at each site: **(a)** *Cystoseira abies-marina;* **(b)** Gelidiales and geniculate corallines; **(c)** *Lobophora variegata;* **(d)** Crustose algae. The vertical dotted lines indicate the time of sunrise and sunset.

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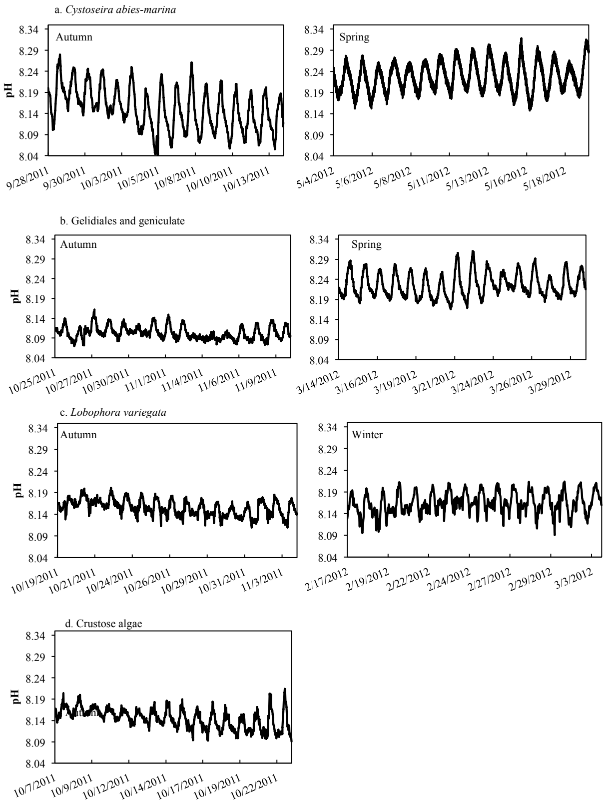

Figure 3. Variation in seawater pH at each site: **(a)** *Cystoseira abies-marina;* **(b)** Gelidiales and geniculate corallines; **(c)** *Lobophora variegata;* **(d)** Crustose algae.