Marine Environmental Research 136 (2018) 99–105

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Macroalgal response to a warmer ocean with higher CO_2 concentration

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ARTICLE INFO

Keywords:
Ocean acidification
Climate change
Primary production
Respiration
Macroalgae
Coastal ecosystem

ABSTRACT

Primary production and respiration rates were studied for six seaweed species (*Cystoseira abies-marina, Lobophora variegata, Pterocladiella capillacea, Canistrocarpus cervicornis, Padina pavonica and Corallina caespitosa*) from Subtropical North-East Atlantic, to estimate the combined effects of different pH and temperature levels. Macroalgal samples were cultured at temperature and pH combinations ranging from current levels to those predicted for the next century (19, 21, 23, 25 °C, pH: 8.1, 7.7 and 7.4). Decreased pH had a positive effect on short-term production of the studied species. Raised temperatures had a more varied and species dependent effect on short term primary production. Thermophilic algae increased their production at higher temperatures, while temperate species were more productive at lower or present temperature conditions. Temperature also affected algal respiration rates, which were higher at low temperature levels. The results suggest that biomass and productivity of the more tropical species in coastal ecosystems would be enhanced by future ocean conditions.

1. Introduction

Over the past 250 years, anthropogenic CO_2 emissions have caused an increase in atmospheric CO_2 concentration, from 280 ppmv (parts per million volume) (Le Quéré et al., 2009) to 404 ppmv (NOAA ESRL Global Monitoring Division, 2016). This is likely to exceed 1000 ppmv by the year 2100 (Meehl et al., 2007; Fabry et al., 2008) if anthropogenic CO_2 emissions are not significantly reduced. Based on this increase in CO_2 and other greenhouse gases, global circulation models predict a rise of 1.5 °C to > 5 °C in average global air temperature by the year 2100 (Houghton et al., 2001; IPCC, 2013). This warming is expected to raise the sea surface temperature (SST) of the oceans by 1 °C–7 °C (Houghton et al., 2001; IPCC, 2013). Furthermore, this increase in pCO_2 has caused the oceans to change from being a net source of CO_2 for the atmosphere to a CO_2 sink, since the industrial revolution. From 2000 to 2006, the oceans absorbed approximately 24% of total anthropogenic CO_2 emissions (Canadell et al., 2007), lowering CO_2 levels in the atmosphere (Sabine and Feely, 2007; IPCC, 2013). This seawater absorption of anthropogenic CO_2 is causing the Ocean Acidification (OA): mean surface ocean pH has decreased by approximately 0.1 units since pre-industrial times (Royal Society, 2005; Kleypas et al., 2006; Orr et al., 2005; Raven et al., 2005; Meehl et al., 2007). Current mean ocean pH is ~8.07 (Hall-Spencer et al., 2008) and a further decrease of approximately 0.3–0.5 units is predicted before the end of the 21st century (Gattuso and Hansson, 2011; Gruber et al., 2012).

Temperature increase and OA are expected to have profound impacts on marine ecosystems (Fabricius et al., 2013), such as food web changes and drastic shifts in marine communities (Vergés et al., 2014; Linares et al., 2015). Many organisms already suffer from their direct effects (Bartsch et al., 2012; Dupont and Pörtner, 2013; Wittmann and Pörtner, 2013).

OA especially affects calcifying species: it produces the diminution of the calcite and aragonite saturation states on seawater, so calcifying organisms experience a reduced availability of calcium carbonate, or even the dissolution of their structures. These effects can be particularly strong in coastal shallow-water ecosystems (Dupont and Pörtner, 2013; Wittmann and Pörtner, 2013).

Seaweeds have a great importance in these shallow-water ecosystems, where many of its species act as ecosystem engineers (Steneck et al., 2002) and carbon sinks. In these environments, benthic marine macroalgae play the most important role in the carbon cycle (Gao et al., 1999), having the photosynthesis/respiration cycle the ability to modulate seawater pH (Bensoussan and Gattuso, 2007).

Temperature is the main abiotic factor that controls the geographical distribution of macroalgae (Lüning, 1990; Bertocci et al., 2014). With continued warming, macroalgal species may be affected in different ways, depending on how important the temperature increase is. For example, the presence and abundance (survival and primary

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https://doi.org/10.1016/j.marenvres.2018.01.010
Received 7 November 2017; Received in revised form 16 January 2018; Accepted 16 January 2018
Available online 22 February 2018

production) of a species in a given location is influenced by the range of physiological tolerance to temperature during its life cycle. As a result, global warming has caused many organisms to shift their geographical range towards higher, cooler latitudes, especially those species that prefer lower water temperatures (e.g. Smale and Wernberg, 2013; Yesson et al., 2015).

Photosynthetic and growth rates of marine macro-autotrophs are likely to increase under elevated CO_2 concentration (Koch et al., 2013), due to the increased supply of dissolved inorganic carbon (DIC). This response depends on their carbon physiology and the presence and type of carbon concentration mechanisms (CCMs) within their cells: species with downregulating or low affinity for HCO^{3-} CCMs will be able to use the extra CO_2 present in seawater and consequently increase their photosynthetic rates (Cornwall et al., 2017). Predictive models and studies carried out on natural CO_2 vents predict that seagrasses and non-calcifying macroalgae will benefit by the lower pH (Hall-Spencer et al., 2008). However, the variety of responses to OA ranges from positive to negative responses, depending of the study and the species (e.g. Israel et al., 1999; Israel and Hophy, 2002; Connell and Russell, 2010; Porzio et al., 2011).

To increase the knowledge of the impact of ocean acidification on aquatic ecosystems, more studies showing the impact of elevated pCO_2 on both calcareous and non-calcareous macroalgae are needed (Hurd et al., 2009). Further research should also be conducted to examine the combined effects between raised temperatures and increased CO_2 concentration, as these effects may combine to affect algal species composition, abundance and productivity worldwide (Harley et al., 2012; Krumhansl and Scheibling, 2012; Koch et al., 2013). In this study, we assessed the combined effect of temperature (19, 21, 23 and 25 °C) and different predicted levels of pH (8.1, 7.7 and 7.4 pHNBS) on the short-term photosynthetic and respiration rates of different key or engineer seaweed species, so as to predict the impact of global change on their productivity. Six different species of macroalgae were sampled (*Corallina caespitosa, Pterocladiella capillacea, Padina pavonica, Cystoseira abies-marina, Lobophora variegata* and *Canistrocarpus cervicornis*). These are important components in shallow subtidal communities in the Canary Islands (Northeast Atlantic Ocean), constituting more than 70% percent of macroalgal cover (Sangil et al., 2014). The Canaries are located at the southern end of the Temperate Northern Atlantic Realm (Azores Canaries Madeira ecoregion, in the Lusitanian province) (Spalding et al., 2007), in a transition zone where macroalgae of warm temperate affinity coexist with macroalgae with tropical affinity (Sangil et al., 2011).

We hypothesized that the temperature increase may affect the studied species short-term response differently, favouring some species over others. At the same time, a higher pCO_2 in water would enhance short-term primary production of the selected macroalgae. We also hypothesized that an increase in CO_2 concentration and temperature would act synergistically in some of the species (those with tolerance for higher temperatures), enhancing short-term primary production, but in other species, more adapted to temperate characteristics, higher temperature levels would have an antagonist effect on the fertilization produced by the CO_2 concentration increase.

2. Material and methods

2.1. Sample collection

Six macroalgal species were selected based on their importance as components in shallow subtidal communities in the Canary Islands. The studied species for this work were: *Corallina caespitosa, Pterocladiella capillacea, Padina pavonica, Cystoseira abies-marina, Lobophora variega*ta and *Canistrocarpus cervicornis*.

Samples of the selected macroalgal species were collected from rocky coastal areas of the North of Tenerife, Canary Islands (29.40–27.63N and -18.16 to -13.33W) during June-July 2014 by scuba diving between 2 and 5 m depth. They were stored in plastic containers with seawater from the collection area and transported to the laboratory in less than 1 h. The pieces of the collected macroalgae with a wet mass of about 0.100–0.500 g with no epiphytes were selected, rinsed with filtered seawater and placed in 2 l plastic beakers under experimental conditions for acclimatization. The samples from each species were acclimated for 48 h before the experiments.

2.2. Experimental assembly

Experiments were conducted with filtered seawater (FSW) purified within a recirculating system provided with DRYDEN AQUA active filter media (AFM) bio-crystals, 10 and 50 μm UNICEL polyamide paper filters and a UV-C AQUAEL 11W filter. Salinity was kept at a constant value of about S = 37 by exchanging water when higher salinity values were measured. Light was provided by fluorescent lamps for plant growth and the light intensity was kept constant for all cultures. Light was measured in lux using a luxometer and energy in $\mu E\ s^{-1}\ m^{-2}$ (PAR) was calculated by multiplying by a conversion factor of 0.018 (Thimijan and Heins, 1982). The irradiance during light cycles was constant at approximately $60\ \mu E\ s^{-1}\ m^{-2}$.

Experiments combined different pH and temperature treatments. The selected pH treatments were the present seawater average pH_{NBS} 8.1, the predicted average 7.7 for the year 2100 (IPCC, 2013), and the expected 7.4 during extreme episodes by the year 2100 (Caldeira and Wickett, 2005). The temperature treatments were 19, 21, 23 and 25 °C. The mean annual temperature of Canary Islands waters is presently around 21.5 °C, with an interannual variation between 18 and 24 °C.

Four 200 l tanks, each with seawater at one target temperature level, were used as water baths. Temperature was controlled in these tanks by using a combination of heaters and chillers, and it was monitored (at least four times a day) along with salinity using a portable conductivity meter (WTW cond 315i). Target pH was controlled in smaller 2 l containers by bubbling pure CO_2 into the water using an automatic control system by AquaMedic. These containers were placed inside the larger temperature baths to control both pH and temperature. During acclimatization, each tank at a desired temperature level had three smaller 2 l containers, each at a desired pH level (pH: 8.1, 7.7 and 7.4). In order to do 6 replicates for each combined species x temperature x pH treatments, 12 samples of each species were place inside each of the 2 l containers for acclimatization (six to measure primary production and six to measure respiration). The experiment was conducted separately for each species.

The pH control system consisted of a pressurized CO_2 bottle connected to an electronic valve, which was controlled by a console that measured pH using an electrode. The console opened the valve to bubble CO_2 into the water when pH had to be lowered to reach the desired level.

2.3. Net primary production and respiration

After the acclimatization time, net primary production and respiration rates were measured using short incubations. Six replicates for each combined species x temperature x pH treatments were used. Replicate samples were placed in separate transparent plastic containers filled with seawater at the target pH treatment (100 ml). These containers were placed inside temperature baths previously set at the target temperature levels. Net primary production and respiration were measured by oxygen production and oxygen depletion after a set incubation time. Initial O_2 concentration was measured with an O_2 sensor (VWR OX 4000 H portable) and initial pH_{NBS} with a mobile pH meter (Metrohm 826, with a Primatrode NTC IP pH electrode and temperature sensor) before introducing the sample. The beakers were sealed and placed in the incubation tanks under the light sources, submerged in seawater at the desired set of temperature levels. Due to the small size of the plastic beakers used for these measurements, pH was not

kept constant during these incubations. Beakers for dark respiration measurements were covered with aluminium foil. An extra beaker with no samples was incubated as a blank for each combined pH–temperature treatment. Incubations lasted for 2 h; after each, the samples were removed from the beaker and final O_2 concentration and pH_{NBS} were measured. They were then stored for dry mass determination. Net primary production and respiration were calculated as mg O_2 g^{-1} dry mass $hour^{-1}$. The 2h incubation time was determined after several incubation tests previously performed with the studied species to asses an incubation time long enough to obtain measurable O_2 variation without reaching O_2 super-saturation.

2.4. Dry mass measurements

Seaweed samples were dried in the oven at 60 °C for 48 h, to finally assess the dissolved oxygen production per gram. Dry mass of the samples was measured using a precision balance.

2.5. Carbon system parameters

Seawater total alkalinity (T_A) was measured using an open cell potentiometric titration with a Metrohm Dosimat 665 titrator using 0.01 N HCl with a salinity of about S = 35 (Dickson et al., 2007). Measurements were made before the incubations for each combined treatment. The rest of the carbonate chemistry parameters were calculated from T_A and pH using the package seacarb 3.08 for R (https://cran.r-project.org/web/packages/seacarb/). Calculations were based on a set of constants, K_1 and K_2, taken from Lueker et al. (2000).

2.6. Data analysis

A three way permutational ANOVA (Anderson et al., 2008) was used to analyse net primary production and dark respiration rates (as dissolved oxygen variation per gram dry-mass and hour). All factors were treated as fixed, 'species' with six levels (*C. caespitosa*, *P. capillacea*, *P. pavonica*, *C. abies-marina*, *L. variegata* and *C. cervicornis*), 'temperature' with four levels (19 °C, 21 °C, 23 °C and 25 °C) and 'pH' with three levels (pH_{NBS} 7.4, pH_{NBS} 7.7 and pH_{NBS} 8.1). The analysis used Euclidean-distance similarity with 4999 permutations. Sums of squares type III were employed in the analysis design. *A posteriori* pairwise comparisons were used to explore significant terms. The software PRIMER 6 and PERMANOVA + were used for all analyses of variance (Anderson et al., 2008). Mean values were expressed with the standard error of the mean (mean ± se). A 5% significance level was applied.

3. Results

There were significant differences in production rates between species (Table 1a, Fig. 1): *C. cervicornis* was the most productive macroalga in this study, with production rates that almost doubled those of *L. variegata*, the second more productive species.

Analyses carried out on primary production showed a significant interaction between the factors 'Species x Temperature' and significant differences per factor 'pH' (Table 1a). The interaction 'Species x Temperature' indicated that there are different patterns of primary production in relation to temperature, for the macroalgal species considered. At the different temperatures, primary production was highest in *C. cervicornis* and *L. variegata*, while the lowest values were recorded in *C. caespitosa* and *C. abies-marina*. *P. capillacea* and *P. pavonica* showed intermediate values (Fig. 2). A posteriori analysis among species for each temperature found significant differences in most pairwise comparisons (Table 2). *C. caespitosa* production was highest at 19 °C and lowest at 25 °C, and pairwise comparisons found significant differences between 19 °C vs 25 °C and 21 °C vs 25 °C (Table 3). *P. capillacea* showed maximum values at 21 °C, and minimum at 19 °C, however no

Table 1
a) Three-way Permutational ANOVA showing the effect of temperature and pH on net primary production rates in six different macroalgae. **b**)Three-way Permutational ANOVA showing the effect of temperature and pH on respiration rates in six different macroalgae.

a) Source	df	MS	Pseudo-F	P(perm)
Species	5	28.252	104.00	0.0002
Temperature	3	0.752	2.771	0.0416
pH	2	0.938	3.455	0.0328
Species x Temperature	15	0.722	2.660	0.0012
Species x pH	10	0.341	1.256	0.2674
Temperature x pH	6	0.365	1.346	0.238
Species x temperatura x pH	30	0.061	0.758	0.8142
Res	352	0.271		
Total	423			

b) Source	df	MS	Pseudo-F	P(perm)
Species	5	3.305	96.287	0.0002
Temperature	3	0.198	5.769	0.0006
pH	2	1.209E-2	0.352	0.701
Species x Temperature	15	4.949E-2	1.441	0.1286
Species x pH	10	2.756E-2	0.803	0.639
Temperature x pH	6	8.377E-3	0.244	0.9666
Species x temperatura x pH	30	1.582E-2	0.460	0.9954
Res	350	3.433E-2		
Total	421			

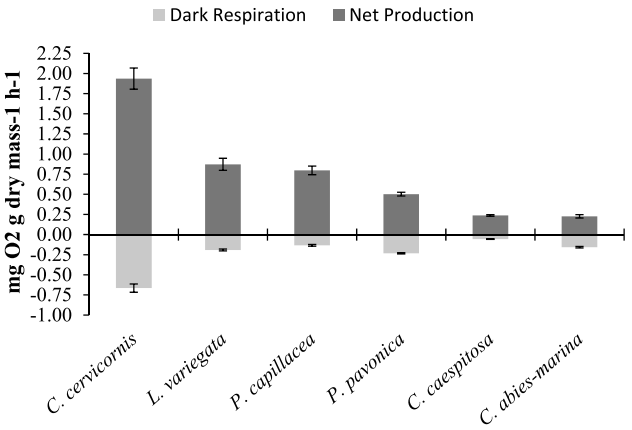

Fig. 1. Mean production and respiration rates per studied species. Error bars stand for SE.

significant differences were found between temperature pairs. *P. pavonica* production was highest at 21 °C and lowest at 23 °C. Significant differences were found between 19 °C vs 23 °C and between 21 °C vs 23 °C. *C. abies-marina* showed its maximum at 21 °C, and the minimum at 25, with significant differences between the pairs 19 °C *vs* 21 °C, 21° *vs* 23 °C and 21 °C *vs* 25 °C. *L. variegata* production was highest at 25 °C and lowest at 21 °C, with significant pairwise differences between 19 °C *vs* 21 °C and 21 °C vs 25 °C. *C. cervicornis* showed maximum production at 25 °C, and minimum at 21 °C, with a significant difference only between 23 °C *vs* 25 °C.

There was a significant effect of pH on algal productivity and this was consistent among the selected species of algae. Productivity was significantly greater at pHNBS 7.4 and 7.7 compared to pHNBS 8.1 (Fig. 3, Table 4).

Algal respiration varied significantly with temperature and among species (Table 1b) and was higher at 19 °C (Fig. 4). Algal respiration was significantly greater at the lowest temperature (19 °C) and similar amongst all the other temperatures tested (Table 5). *C.cervicornis* was the species that showed the highest respiration, followed by *P. pavonica*, *L. variegata*, *C. abies-marina* and *P. capillacea*. The alga with lowest respiration rates was *C. caespitosa* (Fig. 1). A posteriori comparisons found significant differences for all pairs of comparisons except *C. abies-*

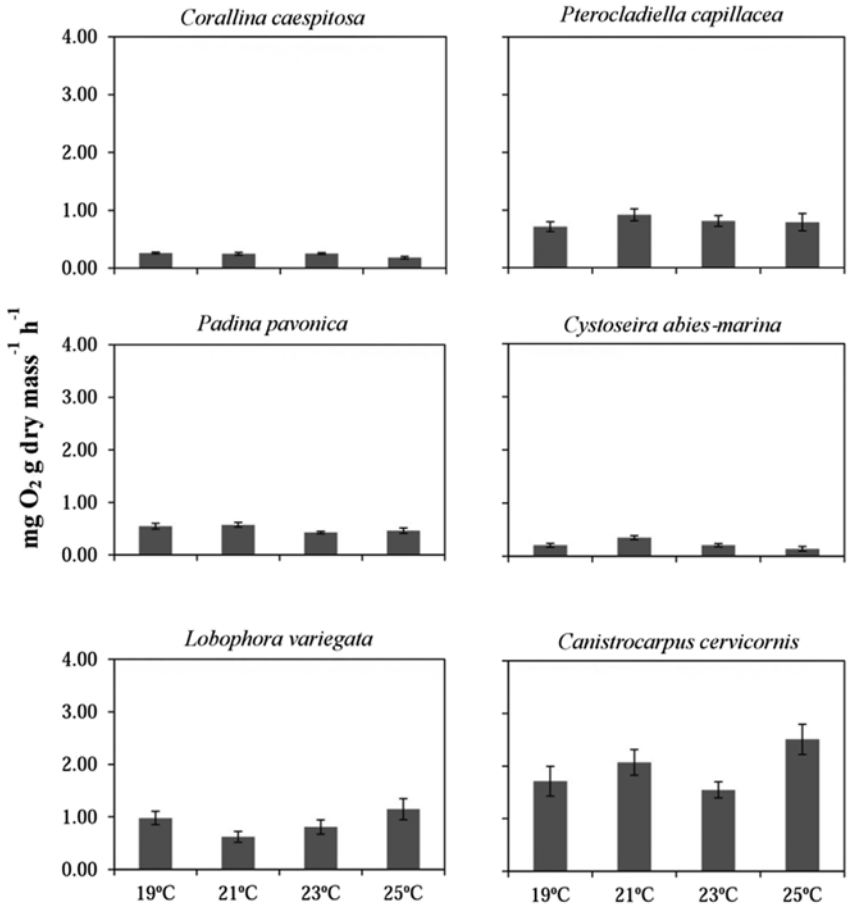

Fig. 2. Mean primary production of the studied algae species at the different temperature levels. Error bars stand for SE.

marina vs *P. capillacea* (Table 6).

4. Discussion

Our data show that an increase in temperature and a decrease in pH have significant effects on the primary production of the studied macroalgal species (Table 1; Figs. 2 and 3). As is generally understood, both are confirmed to be associated with a global change scenario in marine environments. Regarding the effects of OA, production rates were higher at the lower pH levels predicted for the next 100 years (pH_{NBS} 7.7 and pH_{NBS} 7.4 as an extreme value) than at current pH levels (pH_{NBS} 8.1 (Table 1; Fig. 3). This enhancement effect on primary production, added to the fact that many herbivore species are calcifying organisms that can be negatively affected by OA (Dupont and Pörtner, 2013; Wittmann and Pörtner, 2013), has the potential to alter the structure of the communities where these organisms are present, causing a shift towards autotrophy. Based only on the effects of OA, a dominance of fleshy macroalgae is expected in the studied region rocky coastal ecosystems. Species that use HCO_3^- or recur to CCMs may respond positively when more CO_2 is available at sub-saturating irradiance (Koch et al., 2013). Light conditions during the experiments were indeed below saturation. In addition, many autotrophs have a higher

Table 2
Results of pairwise analyses for 'Species x Temperature' interaction for pairs of level of the factor 'Temperature' in the net primary production rates.

Groups	19 °C		21 °C		23 °C		25 °C	
	t	P(perm)	t	P(perm)	t	P(perm)	t	P(perm)
C. abies-marina vs P. capillacea	57.363	0.0002	62.746	0.0002	61.951	0.0002	41.354	0.0004
C. abies-marina vs L. variegata	59.193	0.0002	23.362	0.022	40.764	0.0004	54.314	0.0002
C. abies-marina vs *C. cervicornis*	51.181	0.0002	76.149	0.0002	84.877	0.0002	83.678	0.0002
C. abies-marina vs P. pavonica	58.195	0.0002	38.139	0.0008	5.676	0.0002	47.143	0.0002
C. abies-marina vs C. caespitosa	14.783	0.149	20.936	0.043	0.468	0.659	12.203	0.248
P. capillacea vs L. variegata	17.965	0.083	21.607	0.041	0.015	0.987	14.451	0.163
P. capillacea vs C. cervicornis	33.061	0.001	47.307	0.0004	40.874	0.0004	49.881	0.0002
P. capillacea vs P. pavonica	17.824	0.082	36.512	0.0004	40.249	0.0006	20.083	0.058
P. capillacea vs C. caespitosa	53.181	0.0002	76.716	0.0002	62.627	0.0002	3.962	0.0006
L. variegata vs C. cervicornis	23.064	0.023	56.941	0.0002	34.792	0.0016	39.728	0.001
L. variegata vs P. pavonica	32.384	0.001	0.4019	0.695	26.142	0.011	36.351	0.0006
L. variegata vs C. caespitosa	55.801	0.0002	32.087	0.0014	40.329	0.0004	52.796	0.0002
C. cervicornis vs P. pavonica	39.489	0.0002	65.445	0.0002	71.681	0.0002	7.176	0.0002
C. cervicornis vs C. caespitosa	49.341	0.0002	8.103	0.0002	85.118	0.0002	82.639	0.0002
P. pavonica vs C. caespitosa	54.443	0.0002	61.724	0.0002	71.754	0.0002	48.797	0.0002

Table 3
Results of pairwise analyses for 'Species x Temperature' interaction for pairs of level of the factor 'Species' in the net primary production rates.

Groups	*C. caespitosa*		*P. capillacea*		*P. pavonica*		*C. abies-marina*		*L. variegata*		*C. cervicornis*	
	t	P(perm)	t	P(perm)	t	P(perm)	t	P(perm)	t	P(perm)	t	P(perm)
19°C *vs* 21°C	0.242	0.816	17.952	0.087	0.416	0.667	28.072	0.009	21.456	0.039	0.800	0.422
19°C *vs* 23°C	16.521	0.106	0.815	0.428	2.287	0.026	0.043	0.970	0.892	0.387	0.465	0.639
19°C *vs* 25°C	3.086	0.004	0.426	0.672	11.744	0.260	12.352	0.236	0.778	0.452	19.257	0.059
21°C *vs* 23°C	1.365	0.191	0.865	0.388	2.834	0.008	29.744	0.003	10.357	0.311	16.762	0.102
21°C *vs* 25°C	27.713	0.011	0.759	0.464	15.627	0.134	37.773	0.0008	24.831	0.017	13.012	0.203
23°C *vs* 25°C	16.877	0.110	0.142	0.888	0.597	0.555	13.517	0.188	14.667	0.163	28.961	0.005

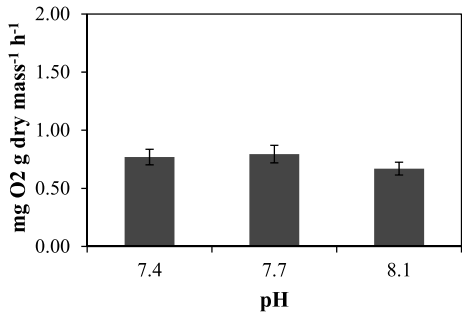

Fig. 3. Effect of seawater pH on algal productivity: mean primary production of the six studied species at each pH level. Error bars stand for SE.

Table 4
Results of pairwise analyses for 'pH' factor in the net primary production rates.

Groups	t	P(perm)
7.4 *vs* 7.7	7,03E-04	1
7.4 *vs* 8.1	2,3946	0,0174
7.7 *vs* 8.1	2343	0,0204

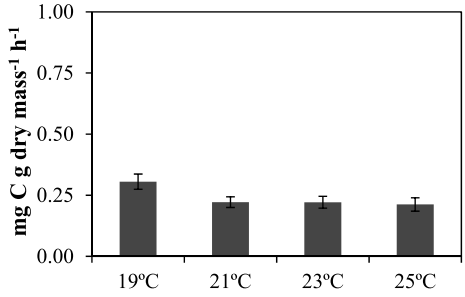

Fig. 4. Effect of seawater temperature treatments on algal respiration rates: mean algal respiration from the 6 studied species at each level of factor temperature. Error bars stand for SE.

Table 5
Results of pairwise analyses for 'Temperature' factor in the respiration rates.

Groups	t	P(perm)
19 °C *vs* 21 °C	3.458	0.0004
19 °C *vs* 23 °C	31.552	0.001
19 °C *vs* 25 °C	32.856	0.001
21 °C *vs* 23 °C	0.299	0.775
21 °C *vs* 25 °C	0.784	0.439
23 °C *vs* 25 °C	0.460	0.651

photosynthetic affinity for CO_2 than for HCO_3^- (Bowes, 1985; Madsen and Sand-Jensen, 1991; Durako, 1993), so an increase in CO_2 concentration related to OA can benefit these species. HCO_3^- also has an elevated concentration in seawater, although in a lesser proportion than CO_2, contributing more DIC available for seaweed production.

The influence of temperature on primary production showed varied results among the species. *L. variegata* and *C. cervicornis* would probably benefit from increasing mean seawater temperature (Fig. 2, Table 3). *L. variegata* is already an important engineer species in rocky bottom areas in the Canary Islands, while. C. cervicornis does not have such a role: it was present in the study areas, but with low biomass and cover. *L. variegata* and *C. cervicornis* show both tropical characteristics, such as higher optimal temperature that influences their biogeographical distribution, suggesting they would benefit from an increase in seawater temperature, as supported by the results of this work. The other macroalgal species are more adapted to temperate conditions and our results reflect how their primary production is not enhanced, or even decreases at higher temperature levels. *C. abies-marina* and some *Gelidium* species have been showing signs of recession in the Canary Islands region during the last three decades (Sansón at al. 2013; Valdazo et al., 2017), but its relationship with the seawater temperature rise requires more evidence. The Canary Islands are located in a transition zone between temperate and tropical regions and the results support the idea that seaweed communities in the Canary Islands can shift towards more tropical characteristics in the future. There are already signs of tropicalization in the marine communities of the Canary Islands: some fish species with tropical affinity have shown a population increase in the last few decades and others with temperate preferences have suffered a drop in population (Falcón, 2016). *Fucus guiryi,* a brown algae associated with temperate waters, has also shown a population decrease at its southern boundary in the islands (Anadón et al., 2014; Riera et al., 2015).

Respiration rates were not affected by pH levels, but were affected by temperature: carbon loss due to respiration in the samples was higher when tested at the lower temperature levels in this work (19 °C). This contradicts the known response of increased respiration rate with temperature, but it has been stated that tropical plants are known to acclimate to high temperatures by lowering their carbon loss due to respiration as temperature rises (Koch et al., 2013). This could be beneficial for the studied macroalgal communities in the future, especially for those with species that showed increased production with higher temperature. There was no effect of pH levels on respiration rates during the experiments, indicating that inorganic carbon availability in seawater has no influence on this metabolic process.

Production and respiration rates exhibited some notable differences between species *C. cervicornis* was significantly the algae with higher primary production and respiration rates (Fig. 1). On the other side, *C. caespitosa* and *C. abies-marina* were the species with lower production rates. In the case of *C. caespitosa,* this is attributable to the elevated mass of its calcareous structures. *C. abies-marina* also showed relatively high respiration rates (Production/Respiration was 1.44).

Among the studied species, two are calcifying species, the rhodophyte *C. caespitosa* and the brown alga *P. pavonica*. In the former species, temperature can affect net primary production and dark respiration, owing to the reduction in primary production registered at 25 °C, our highest temperature treatment. *P. pavonica* showed a higher primary production at 21 °C and lower values at higher temperatures. This suggests that these species will be negatively affected by the mean

Table 6
Results of pairwise analyses for 'Species' factor in the respiration rates.

Groups	t	P(perm)
C. abies-marina vs P. capillacea	19.651	0.053
C. abies-marina vs L. variegata	32.932	0.0022
C. abies-marina vs C. cervicornis	98.488	0.0002
C. abies-marina vs P. pavonica	75.582	0.0002
C. abies-marina vs C. caespitosa	12.541	0.0002
P. capillacea vs L. variegata	45.937	0.0002
P. capillacea vs C. cervicornis	10.119	0.0002
P. capillacea vs P. pavonica	82.829	0.0002
P. capillacea vs C. caespitosa	73.485	0.0002
L. variegata vs C. cervicornis	89.459	0.0002
L. variegata vs P. pavonica	29.374	0.0048
L. variegata vs C. caespitosa	13.626	0.0002
C. cervicornis vs P. pavonica	85.097	0.0002
C. cervicornis vs C. caespitosa	11.853	0.0002
P. pavonica vs C. caespitosa	22.965	0.0002

temperature rise accompanying global change.

According to Koch et al. (2013), it is uncertain if species from the genus *Corallina* are saturated at current dissolved inorganic carbon (DIC) levels. It seems that this alga can use HCO_3^- as a source of carbon. Bicarbonate use is more energetically demanding than direct CO_2 use (Kübler and Raven, 1994; Beardall et al., 2009), so at higher CO_2 concentrations (OA conditions) this species would be expected to switch to diffusive CO_2 use, with a consequent increase in primary production. The increase in primary production at high pCO_2/low pH in *P. pavonica* is consistent with previous knowledge of this species. However, *P. pavonica* is not believed to be carbon-saturated at current CO_2 levels and can use extra CO_2 when available (Einav et al., 1995). Johnson et al. (2012) found a raised *in situ* photosynthetic response of *P. pavonica* with CO_2 enrichment at natural pH gradients and at saturating light intensity. Since *P. pavonica* and *C. caespitosa* are calcifying species, the effect of pH on their calcification rates should be considered, as well as interactions with other species. The $CaCO_3$ content in *P. pavonica* has been shown to decrease in low pH with long term exposures (Johnson et al., 2012) and *C. caespitosa* has suffered dissolution of its $CaCO_3$ structures at pH below 7.9 in the dark (Egilsdottir et al., 2013). This structural loss could involve its defences being compromised by long exposure to low pH conditions, although low pH could also affect potential grazers, especially calcifying herbivores such as sea urchins.

Although *C. abies-marina* was in the low range of primary production among the species studied in this experiment, it acts as an ecosystem engineer and forms large canopies with high biomass in the shallow subtidal rocky benthos. It therefore has greater potential to alter the carbon system parameters than other more productive species. According to our experiments, this alga can take advantage of the lowest pH levels, but higher temperature negatively affects its production rate.

The results obtained for *L. variegata* highlight that this species benefits from the highest pH and temperature levels used in our study, with net primary production being enhanced by pH and temperature, its respiration decreasing with higher temperature. It has been shown that *L. variegata* can use HCO_3^- as carbon source and is not saturated at the present DIC levels (Holbrook et al., 1988; Enríquez and Rodríguez-Román, 2006). This means that this species can take advantage of future DIC levels due to OA, which agrees with our results. This species is an important ecosystem engineer and the second most productive alga in our study (Fig. 1), with relatively high net primary production and low dark respiration/gross production rates (R/Pg = 0.18). In an OA scenario with higher pCO_2 and temperature, *L. variegata* communities may thrive and perform an important role in mitigating OA impact.

5. Conclusions

In conclusion, our results suggest that a lower-pH ocean, according to current predictions (Gattuso and Hansson, 2011; IPCC, 2013), would enhance primary production in the studied algal species. However, the associated increase in temperature would have varied effects. These effects include an increase in production for those algae with tropical characteristics and a decrease in those species with temperate distribution. This means that in subtropical areas (warm-temperate regions), a future with more autotrophic coastal ecosystems is expected with a shift in ecosystem structures towards tropical characteristics, mainly due to the increase in temperature. Using these short-term experiments we aimed to simulate the effect of different future pH and temperature levels.

It must be considered that our results represent effects that were studied on a limited, though significant, number of species, and testing a limited number of parameters. Clearly, caution is required in extrapolating the results to the ecosystem level. In order to achieve that objective, longer experiments (preferable on natural acidified system as CO_2 vents) are needed, taking the effects of more variables and the interactions with herbivores and other primary producers into consideration. Also, possible acclimation of algal physiology to future conditions could alter these findings. In spite of the limitations of this kind of manipulative laboratory experiments, they are essential tools for the interpretation of the results that can be obtained from *in situ* experiments, where the number of involved variables is large.

Conflicts of interest

None.

Acknowledgements

Thanks to Valerio Chinea, who helped preparing the culture tanks for the experiments and kept the experimental conditions stable.

This work was supported by the Spanish Ministerio de Economía y Competitividad within the framework of the project Plan Nacional de Investigación, [grant number BLUEROCK, CGL17 2013_43908_R].

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