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Ecological characterization of intertidal rockpools: Seasonal and diurnal monitoring of physico-chemical parameters

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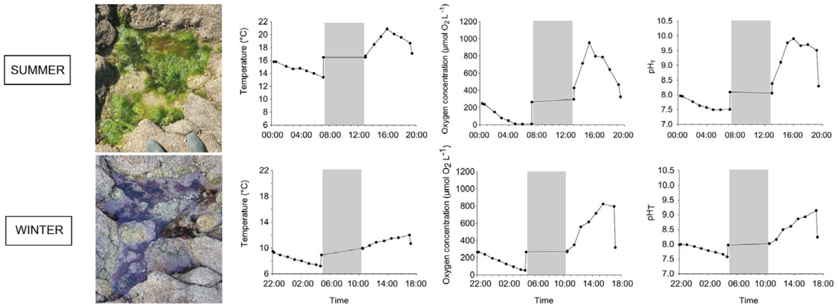
GRAPHICAL ABSTRACT



ABSTRACT

Keywords:
Rockpool
Seasonal variation
Diurnal variability
Coralline algae
Fleshy algae

Diurnal and seasonal variations in temperature, salinity, oxygen concentration, carbonate chemistry parameters and nutrient concentration were monitored within mid-tidal rockpools on the north-western coast of Brittany, France. We also examined the importance of rockpool physical characteristics (e.g. shore height, surface, volume and depth) on the physico-chemical variability. Rockpool shore height and depth appeared as the main physical factors driving physico-chemical variations. Shallow upper shore rockpools exhibited the largest diurnal and seasonal fluctuations of temperature, oxygen concentration and pH_T. Conversely, deeper and lower shore rockpools experienced weaker variations, excepted for salinity and nutrient concentrations. The physico-chemical environment was likely to be strongly influenced by rockpool community composition, especially in summer when rockpools were colonized by dense canopy-forming algae. During the day-time emersion, photosynthesis increased oxygen concentration and pH_Tbut decreased nutrient concentrations in upper shore rockpools. The increase in rockpool pH_T provided an alkaline environment conducive to coralline algal calcification. Conversely, at night, upper shore rockpools presented a strong decrease in oxygen concentration and pH_T due to the high community respiration, increasing the dissolution in coralline algae. Therefore, rockpools are characterized by complex interactions between physical and chemical parameters and biological processes. Rockpools appear as suitable environments to examine the physiological processes set up by species to face natural variability, especially in a context of climate change.

1. Introduction

Intertidal communities are exposed to a dynamic environment influenced by tidal flooding (Widdows and Brinsley, 2002). Organisms living at the interface between land and sea are exposed

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to consecutive periods of emersion and immersion. During low tides, organisms undergo harsh environmental conditions characterized by high temperature variations and solar radiation, low humidity and windy conditions (Martínez et al., 2012; Tomanek and Helmuth, 2002). These physical conditions take species close to their physiological thresholds (Fernández et al., 2015), through a rapid desiccation and damages to photosynthetic and cellular components (Collén and Davison, 1999; Hoffman et al., 2003).

On the sea shore, rockpools are patchy depressions which retain seawater during low tide. This intertidal marine environment acts as refuge for many intertidal species (Underwood and Jernakoff, 1984; Zander et al., 1999), due to the lower amplitude of physico-chemical fluctuations compared with emerging substrate (Metaxas and Scheibling, 1993). However, physico-chemical variations within rockpools remain much greater than those of nearshore seawater (Morris and Taylor, 1983). Strong diurnal and seasonal variations in rockpools have been recorded for temperature, oxygen concentration, pH and salinity (Daniel and Boyden, 1975; Morris and Taylor, 1983), but never in terms of whole carbonate chemistry and nutrients. In addition to temporal variations, rockpool physico-chemical parameters are highly variable in space, depending mainly on the wave exposure and the shore height (Firth et al., 2013; Martins et al., 2007).

Rockpools are also characterized by strong interactions between physico-chemical parameters and biological processes (Benedetti-Cecchi et al., 2000; Underwood and Jernakoff, 1984). In particular, species distribution and abundance are controlled by both abiotic factors (Huggett and Griffiths, 1986; Metaxas and Scheibling, 1993; Truchot and Duhamel-Jouve, 1980) and species interactions, such as herbivory, predation and competition (Metaxas and Scheibling, 1993). The high productivity observed in these habitats is mostly explained by the diversity of seaweeds (Araujo et al., 2006) and invertebrates (Ganning, 1971) which develop in rockpools (Firth et al., 2014).

In this context, the present study aims to (1) quantify diurnal and seasonal variations in multiple physico-chemical parameters (e.g. temperature, salinity, oxygen concentration, carbonate chemistry and nutrient concentration), which naturally occur within intertidal rockpools and (2) assess the importance of rockpool physical characteristics (e.g. shore height, surface, volume and depth) on the physico-chemical variability. Seasonal variations within rockpools were examined over a period of 14 months, during which two diurnal monitoring of physicochemical parameters were carried out, one in the winter and one in the summer. Finally, the composition of the community present in each rockpool was examined in the winter and the summer to better understand the influence exerted by biotic factors on the physico-chemical variability.

2. Materials and methods

2.1. Seasonal monitoring

From January 2015 to March 2016, 5 rockpools were monitored every 2 weeks during spring tides under fair weather conditions. Rockpools were situated in a rocky shore at the Bloscon site in Roscoff, Brittany, France (48°43′28N 03°58′08W). Rockpools monitored were distributed at different heights above chart datum (C.D., Table 1) in the mid-tidal zone and were colonized by coralline algae, non-calcareous algae and associated fauna (Fig. 1). All selected rockpools were filled with seawater at each high tide and were isolated from the sea at each low tide. Selected rockpools presented different volumes and depth to assess relationships between physical structure, physico-chemical variability and assemblage composition.

Measurements of temperature, dissolved oxygen concentration, pH_T (pH expressed on the total hydrogen ion concentration scale) and salinity were performed at different locations across of each rockpool, using a multimeter (HQ40D, Hach Lange, Ltd portable LDO). All measurements and samples were made at the end of the emersion of rockpools, just before they were covered by the tide. Throughout the year, measurements were made at the same positions and depth in each rockpool and seawater was homogenized before each measurement. Seawater pH and temperature measurements were realized using a probe associated with a temperature sensor with an accuracy of 0.3 °C and 0.02 pH units, respectively (PHC101, Hach Lange, IntelliCAL). The pH probe was calibrated using Tris/HCl and 2-aminopyridine/HCl buffers (Dickson et al., 2007). Dissolved oxygen concentrations (mg L^{-1}) were measured with a luminescent dissolved oxygen probe (LDO101, Hach Lange, IntelliCAL) with an accuracy of 0.02 mg L^{-1} and converted to oxygen concentrations in μmol L^{-1}. Salinity was determined using a conductivity probe (CDC401, Hach Lange, IntelliCAL, accuracy of 0.1). Seawater samples were also taken in the rockpools for total alkalinity (A_T) measurements. 60 mL seawater samples for A_T analyses were filtered through 0.7 μm Whatman GF/F filters and poisoned with a mercuric chloride solution to prevent biological activity (Dickson et al., 2007). A_T was determined by an open-cell titration on an automatic titrator (Titroline alpha, Schott SI Analytics, Mainz, Germany) according to the method developed by Dickson et al. (2007). A_T was calculated using a Gran function applied to pH values ranging from 3.5 to 3.0 (Dickson et al., 2007) and corrected using standard reference material provided by Andrew G. Dickson (CRM Batch 111). Saturation state of seawater with respect to aragonite (Ω_{Ar}) and saturation state of seawater with respect to calcite (Ω_{Ca}) were calculated from pH_T, A_T, temperature and salinity using the CO2SYS software (Lewis and Wallace, 1998), using constants from Mehrbach et al. (1973) refitted by Dickson and Millero (1987). Nitrite (NO_2^-, μmol L^{-1}), nitrate (NO_3^-, μmol L^{-1}), phosphate (PO_4^{3-}, μmol L^{-1}) and silicate ($Si(OH)_4$, μmol L^{-1}) concentrations were monitored once a month. For NO_2^-, NO_3^- and PO_4^{3-} measurements, 60 mL of seawater was sampled and filtered through 0.7 μm Whatman GF/F filters in 100 mL plastic containers. Then, samples were frozen (−20 °C) pending analyses. For $Si(OH)_4$, 60 mL seawater samples were filtered through 0.8 μm Millex cellulose ester filters in 100 mL plastic containers and were kept refrigerated pending analyses. Nutrient samples were measured using a AA3 auto-analyzer (Seal Analytical) according to the method of Aminot and Kérouel (2007), with an accuracy of 1 nmol L^{-1} for NO_2^-, 0.02 μmol L^{-1} for NO_3^-, 1 nmol L^{-1} for PO_4^{3-}, and 0.01 μmol L^{-1} for $Si(OH)_4$. Seasonal physico-chemical parameters were compared with those of near shore seawater (when available), obtained from SOMLIT (Service d'Observation en Milieu LITtoral, INSU-CNRS) station, located in the Estacade site in Roscoff.

2.2. Diurnal monitoring

Among the five rockpools chosen for the seasonal monitoring, three of them were selected for diurnal measurements (rockpools 2, 4 and 5, Table 1). Two 24-h monitoring were realized during spring tides, in summer (September 3rd, 2015) and in winter (March 10th, 2016). Measurements of temperature, pH_T, oxygen concentration, salinity and A_T were realized every hour during the emersion period, and Ω_{Ar} and Ω_{Ca} were calculated as described above. Near shore seawater was also monitored and sampled just before and after the emersion period. All samples were analyzed as described above.

2.3. Community composition

After the one-year monitoring, biomass sampling was realized in the 5 rockpools in summer and in winter. 10 × 10 cm quadrats were randomly placed in rockpools and all the seaweeds and

Table 1

Physical characterization of the five rockpools monitored for seasonal variations at the Bloscon site in Roscoff (Brittany, France). Mean emersion duration was calculated from the water height obtained from the "Service Hydrographique et Océanique de la Marine (SHOM)". Surface area is the surface of water measured at low tide from pictures. Min and max emersion duration were determined over January 2015 to March 2016.

Rockpool	Shore height (m)	Mean emersion duration (h)	Min emersion duration (h)	Max emersion duration (h)	Surface area (m^2)	Volume (m^3)	Maximum depth (cm)	Surface/volume ratio
1	6.4	7 h 40	7 h 01	10 h 13	2.58	0.294	23	8.77
2	6.2	7 h 20	6 h 51	9 h 22	0.54	0.063	25	8.56
3	5.8	6 h 40	6 h 33	8 h 02	0.79	0.175	31	4.50
4	4.9	5 h 30	5 h 25	5 h 47	0.57	0.087	32	6.51
5	4.4	4 h 40	3 h 55	5 h 23	1.16	0.234	46	4.95

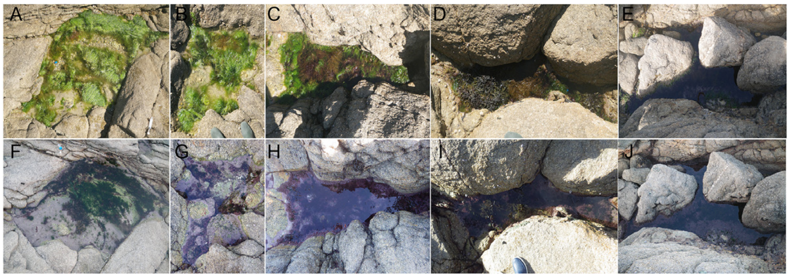

Fig. 1. Pictures of rockpools 1 to 5 in summer (A to E) and winter (F to J). All rockpools were located in the Estacade site in Roscoff (Brittany, France).

animals in the quadrats were sampled. The number of quadrats per rockpool depended on the size of the rockpools (4 quadrats for rockpools 2 and 4, 5 quadrats for rockpool 3 and 8 quadrats for rockpools 1 and 5). In the laboratory, macrofauna and seaweed species were sorted and the main species were identified. Species dry weight (DW) was determined after drying fresh samples at 60 °C for 48 h. Species were then burned for 6 h at 500 °C in a furnace to obtain ash-free dry weight (AFDW; Crisp, 1984). For the CCA *L. incrustans*, the biomass could not be determined precisely without deteriorating rockpools. Therefore, the cover percent was estimated for each quadrat and AFDW was obtained from previously established relationships between the surface covered by the alga and the AFDW.

2.4. Data analysis

Differences in physico-chemical parameters among rockpools were examined from seasonal data using a three-way permutational multivariate analysis of variance (PERMANOVA), based on Euclidian distance (Anderson, 2001). PERMANOVAs were run with 4999 permutations (Anderson, 2001). These statistical analyses were performed with the PRIMER 7 & PERMANOVA+ software package. The Principal component analysis (PCA) was completed using R 3.2.2 version from seasonal data. The PCA was performed using the "factoextra" package to test the correlation between environmental and physical variables and determine which variables explain most of the space–time variability observed between rockpools.

3. Results

3.1. Seasonal variations

The physico-chemical parameters exhibited significant differences between rockpools (PERMANOVA, $F = 44.9$, $p < 0.001$, $n = 29$) except between rockpools 3 and 4 (Table 2, Figs. 2 and 3). The rockpools 1 and 2 showed the largest amplitude for all physico-chemical parameters, except for salinity and nutrient concentrations. Conversely, the rockpool 5 presented weak seasonal variations for all parameters except for salinity and nutrient concentrations, which exhibited the largest variations. Physico-chemical parameters showed strong differences according to seasons. At the end of the emersion period, the seawater temperature within rockpools varied from 7.9 °C in February 2015 in rockpool 3 to 26.9 °C in July in rockpool 1. Minimum oxygen concentrations were recorded in the rockpool 5 in January 2016 (242 μmol O_2 L^{-1}), while maximum concentrations were obtained in the rockpool 1 in November, reaching 1040 μmol O_2 L^{-1}. The rockpool 5 showed the lowest salinity in January (33.4), while the highest values were recorded in rockpool 2 in May and August (36.6). The minimum pH_T was 7.79 and was measured in rockpool 5 in January 2016. The maximum pH_T value was 10.01, recorded in rockpool 1 in April. A_T varied from 1553 μmol L^{-1} in early September to 2588 μmol L^{-1} in late January 2016 in rockpools 2 and 5, respectively. Carbonate saturation states of seawater with respect to aragonite (Ω_{Ar}) and calcite (Ω_{Ca}) are the lowest in rockpool 5 in January 2016 (1.3 and 2.1, respectively) and the highest in rockpool 1 in May (11.5 and 17.9, respectively).

NO_2^- concentrations varied from 0.00 μmol L^{-1} in August in rockpool 1 to 0.65 μmol L^{-1} in early September in rockpool 5 (Fig. 3). The rockpool 1 also presented the lowest NO_3^- (0.06 μmol L^{-1}) and PO_4^{3-} (0.04 μmol L^{-1}) concentrations in May and June, respectively. The highest NO_3^- and PO_4^{3-} concentrations were measured in rockpool 5 in late January 2016 (19.65 μmol NO_3^- L^{-1}) and early March 2015 (1.07 μmol PO_4^{3-} L^{-1}), respectively. $Si(OH)_4$ concentrations reached minimum concentrations of 0.51 μmol L^{-1} in rockpool 3 in April and maximum concentrations of 7.41 μmol L^{-1} in rockpool 5 in September.

The first principal component (PC1) of the PCA was strongly positively correlated with depth, nutrients and A_T and negatively correlated with increasing shore height, pH_T, oxygen concentration and salinity (Fig. 4a). The second principal component (PC2) indicated an opposition between temperature and oxygen concentration. The different nutrients were clearly positively correlated between them and A_T, but negatively correlated with oxygen concentration, pH_T, temperature and salinity.

From the PCA, the within-rockpool seasonal variability appeared mainly driven by temperature (Fig. 4b). The rockpool 5 differed from the others through much higher nutrient concentrations and A_T, and lower pH_T, salinity and oxygen concentrations. Conversely, the rockpools 1 and 2 were characterized by high pH_T, salinity and oxygen concentrations, but low nutrient concentration and A_T.

Table 2
Results of PERMANOVA's post-hoc pairwise tests performed on the physico-chemical parameters obtained from the seasonal monitoring of the five rockpools ($n = 29$). Significant results are in bold ($p<0.05$).

	Rockpool 1		Rockpool 2		Rockpool 3		Rockpool 4	
	t	p	t	p	t	p	t	p
Rockpool 2	2.5	**0.004**	–	–	–	–	–	–
Rockpool 3	3.0	<**0.001**	3.7	<**0.001**	–	–	–	–
Rockpool 4	3.3	<**0.001**	2.9	<**0.001**	1.5	0.14	–	–
Rockpool 5	11.1	<**0.001**	12.3	<**0.001**	11.0	<**0.001**	13.1	<**0.001**

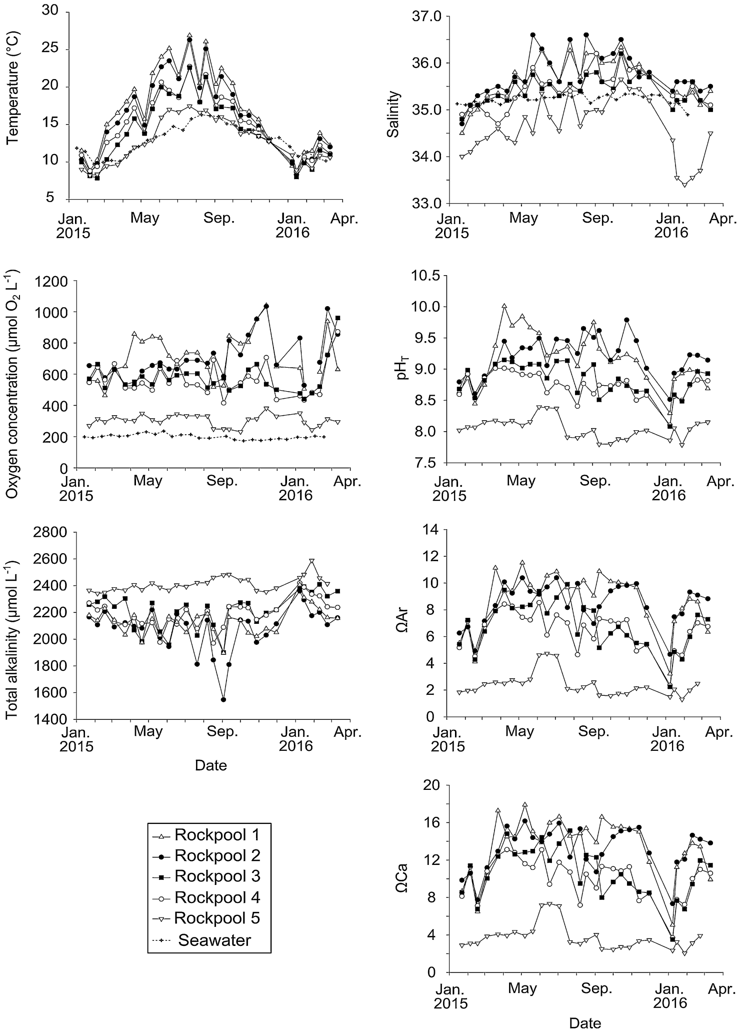

Fig. 2. Seasonal variations in physico-chemical parameters within 5 rockpools monitored every two weeks during spring tides from January 2015 to March 2016. Ω_{Ar} and Ω_{Ca} were calculated using the CO2SYS software. The near shore seawater parameters (dot line) were obtained from the SOMLIT station located in the Estacade site in Roscoff (Brittany, France).

3.2. Diurnal variations

Diurnal variations exhibited differences among the 3 rockpools monitored both in the summer 2015 (Fig. 5) and the winter 2016 (Fig. 6). While rockpool 1 presented high variations for all physico-chemical parameters, variations in rockpool 5 were close to those of nearshore seawater. Furthermore, higher diurnal amplitudes were observed in the summer for all parameters, except for salinity for which variations are greater in winter. In the winter, diurnal temperature in rockpool 2 varied from 7.2 °C to 12.0 °C at the end of night- and day-time emersion, respectively. In the summer, temperature ranged from 13.4 °C at night to 20.9 °C at the middle of day-time emersion.

The salinity in rockpools was higher in the summer than in the winter. In the summer, the rockpools 2 and 3 exhibited low salinity variations during night- and day-time emersion. Salinity fluctuations in these rockpools were close to the values of near-shore seawater. Conversely, the rockpool 5 presented higher variations, with a decrease in salinity until 35.0 at the end of the emersion period. Oxygen concentrations during night-time emersion reached minimum concentrations in rockpool 2, at 53 and 10 μmol O_2 L^{-1} in the winter and the summer, respectively. During the day-time emersion, maximum oxygen concentrations were measured in rockpool 3 in winter (913 μmol O_2 L^{-1} after 6 h of emersion) and rockpool 2 in summer (955 μmol O_2 L^{-1} after 2 h of emersion). In rockpool 5, variations in oxygen concentration were lower than in other rockpools. A reduction in oxygen concentration was observed during the day-time emersion in the summer. As for oxygen concentration, pH_T was constantly reduced at night down to a minimum value was reached in rockpool 2 at the end of the

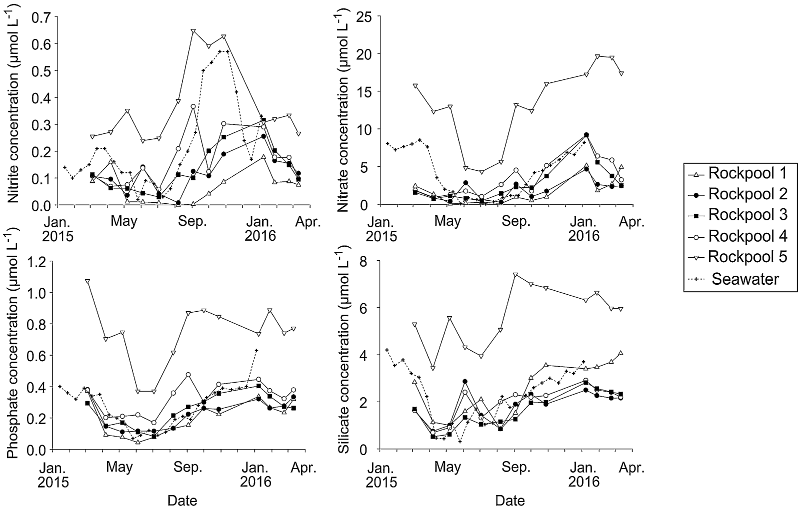

Fig. 3. Seasonal variations in nutrient concentrations within 5 rockpools monitored once a month during spring tides from January 2015 to March 2016. The near shore seawater parameters (dot line) were obtained from the SOMLIT station located in the Estacade site in Roscoff (Brittany, France).

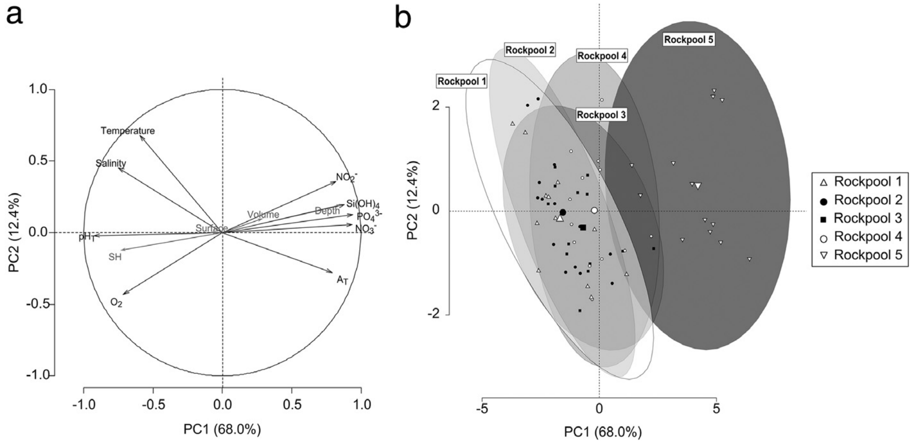

Fig. 4. Representation of (a) the correlation circle between physico-chemical variables measured within each rockpool (black arrows), the physical characteristics of rockpools (gray arrows; SH: shore height) and the two principal components and (b) contribution of the space–time measurements to the two principal components.

emersion period (7.57 and 7.49 in the winter and the summer, respectively). During the day, maximal pH$_T$ values of 9.14 in the winter and 9.90 in the summer were also reached in rockpool 2. Conversely, the rockpool 5 presented low diurnal pH$_T$ variations both in the winter and the summer. A pH$_T$ reduction was also observed during the day-time emersion in the summer. In the winter, A_T increased at night in rockpool 2 only (maximum of 2566 μmol L^{-1}), while in the summer the rise in A_T was observed within the 3 rockpools monitored. During the day-time emersion, A_T was strongly reduced in rockpools 2 and 3 for each season, with extremely low values reached in rockpool 2 in summer (1553 μmol L^{-1}). As for other parameters, A_T presented weak variations in rockpool 5. The carbonate saturation state with respect to aragonite (Ω_{Ar}) and calcite (Ω_{Ca}) decreased at night in the 3 rockpools monitored, for each season. During the night-time emersion, Ω_{Ar} declined below 1 within rockpools 2 and 3, both in the winter and the summer. Conversely, during the day-time emersion, Ω_{Ar} and Ω_{Ca} increased significantly in rockpools 2 and 3. Maximum values of 11 and 17 were reached in rockpool 2 in the summer, for Ω_{Ar} and Ω_{Ca}, respectively. Except in the rockpool 5, in which Ω variations were close to those of near-shore seawater.

3.3. Community composition

Regarding the floral composition, strong differences were observed between rockpools and according to the season (Table 3). *L. incrustans* attained the highest biomasses in rockpools 1 and 3 in winter and summer, respectively. Conversely, higher biomass of *E. elongata* was recorded within rockpool 5 both in summer and winter. Fleshy algae biomass ranged from 204.5 g AFDW m^{-2} to 712.3 g AFDW m^{-2} in summer (rockpools 2 and 4, respectively) and from 3.7 g AFDW m^{-2} to 228.0 g AFDW m^{-2} in winter (rockpools 2 and 5, respectively). In the summer, rockpool 1 was dominated by the green algae *Ulva intestinalis* and the brown seaweed *S. muticum* while the rockpool 2 was mainly composed by *Ulva* sp. In winter, fleshy algae were nearly absent in these two rockpools. *S. muticum* was the dominant fleshy alga within the rockpool 3 both in the summer and the winter, although winter biomass was only half that of summer biomass. In the rockpool 4, the fleshy algal biomass was lower in winter compared with summer being mainly composed by the brown alga *F. serratus*. The fleshy algal biomass of rockpool 5 consisted of more diverse and sparse seaweeds. Although *Ulva* sp. and *S. muticum* were still abundant in this rockpool, the greater part of summer biomass corresponded to a few small feet of *Laminaria digitata*. In winter, fleshy algae community was dominated by undetermined filamentous red algae which grew on *E. elongata*.

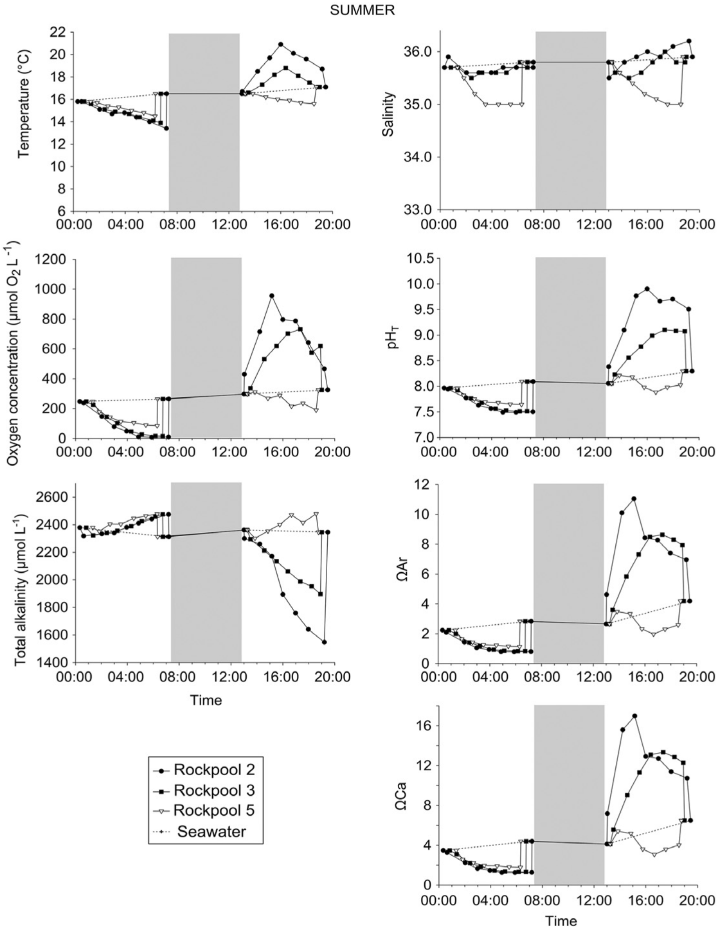

Fig. 5. Summer diurnal variations in physico-chemical parameters within 3 rockpools monitored every hours during emersion in September 2015. The near shore seawater parameters were measured at the beginning and at the end of the emersion. Ω_{Ar} and Ω_{Ca} were calculated using the CO2SYS software. The gray section represents the period during which all the rockpools were covered by the tide.

Table 3
Winter and summer biomasses (in grams of ash-free dry weight) of the dominant coralline and fleshy algae present in the five rockpools monitored for seasonal variations at the Bloscon site in Roscoff (Brittany, France).

	Rockpool 1	Rockpool 2	Rockpool 3	Rockpool 4	Rockpool 5
Summer					
Coralline algae biomass (g AFDW m^{-2})	**603.3**	**929.3**	**1058.6**	**327.6**	**510.1**
Lithophyllum incrustans	603.3	899.5	948.5	245.3	318.2
Ellisolandia elongata	0.08	29.7	82.3	110.1	191.6
Fleshy algae biomass (g AFDW m^{-2})	**584.2**	**204.5**	**260.2**	**712.3**	**573.3**
Ulva intestinalis	285.7	42.2	40.1	–	–
Sargassum muticum	250.8	7.7	79.6	105.4	123.5
Ulva sp.	28.8	136.9	29.1	85.2	69.8
Fucus serratus	–	2.2	–	379.5	18.8
Chondrus crispus	10.8	0.6	17.7	77.7	0.7
Laminaria digitata	–	–	–	–	200
Other red algae	5.1	14.2	55.6	28.0	79.1
Winter					
Coralline algae biomass (g AFDW m^{-2})	**674.9**	**599.9**	**695.7**	**183.1**	**338.6**
Lithophyllum incrustans	674.9	593.6	654.8	164.2	297.6
Ellisolandia elongata	–	6.3	40.4	18.8	40.7
Fleshy algae biomass (g AFDW m^{-2})	**11.4**	**3.7**	**108.4**	**121.1**	**228.0**
Sargassum muticum	10.9	1.0	38.0	–	–
Ulva sp.	0.2	0.3	1.3	2.4	2.8
Cladophora sp.	0.15	1.4	–	7.6	–
Gelidium spinosum	–	–	66.4	–	–
Fucus serratus	–	–	–	88.1	–
Chondrus crispus	0.1	–	0.5	21.3	1.5
Codium sp.	–	–	–	–	34.3
Dilsea carnosa	–	–	–	–	22.4
Other red algae	0.1	0.9	0.9	1.6	166.9

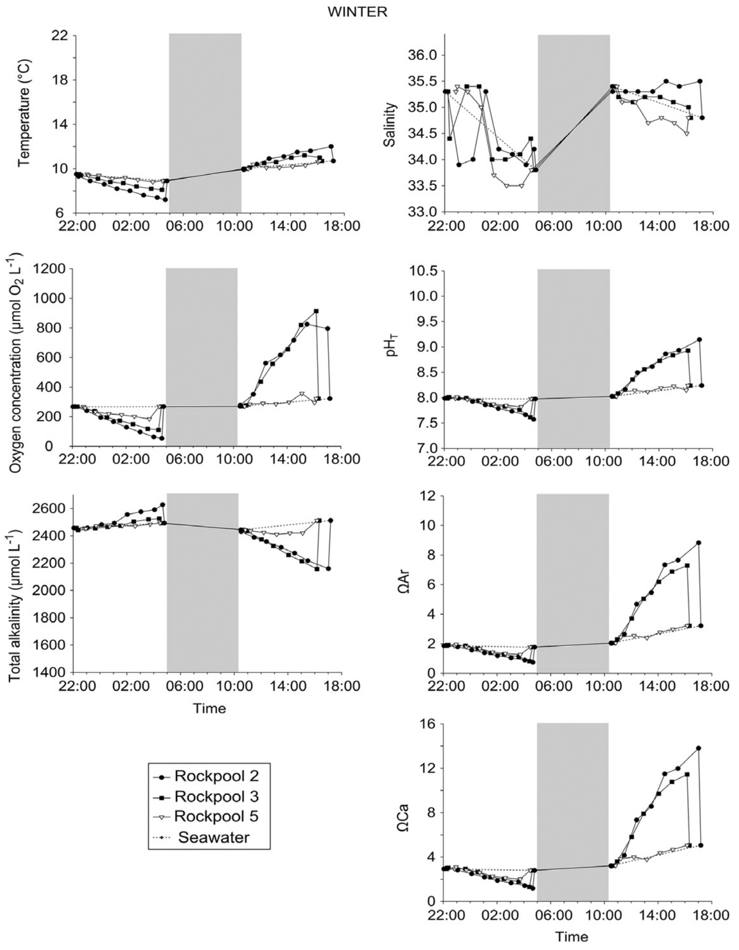

Fig. 6. Winter diurnal variations in physico-chemical parameters within 3 rockpools monitored every hours during emersion in March 2016. The near shore seawater parameters were measured at the beginning and at the end of the emersion. Ω_{Ar} and Ω_{Ca} were calculated using the CO2SYS software. The gray section represents the period during which all the rockpools were covered by the tide.

The total biomass of fauna ranged from 4.2 g AFDW m^{-2} (rockpool 5) to 11.8 g AFDW m^{-2} (rockpool 4) in summer and from 0.7 g AFDW m^{-2} (rockpool 1) to 12.4 g AFDW m^{-2} (rockpool 2) in winter. The gastropod *Gibbula umbilicalis* dominated the faunal species in all the rockpools both in winter and summer. The biomass of *G. umbilicalis* extended from 0.75 g AFDW m^{-2} to 4.14 g AFDW m^{-2} in summer (rockpools 5 and 3, respectively) and from 0 g AFDW m^{-2} to 6.1 g AFDW m^{-2} in winter (rockpools 4 and 2, respectively).

4. Discussion

Rockpool environment is governed by complex interactions between physical, chemical and biological parameters (Martins et al., 2007). Rockpools can be described by evaluating their shore height, surface, depth and volume. Among these characteristics, shore height appeared as one of the main physical factors controlling the physico-chemical variability within rockpools, as evidenced by Morris and Taylor (1983). Consistently with their findings, rockpools 1 and 2 located on the upper shore exhibited the largest diurnal and seasonal fluctuations of temperature, oxygen and pH_T. In contrast, the rockpool 5 was the lowest on the shore and the deepest and presented weaker variations in temperature, oxygen and pH_T but higher nutrient concentrations and total alkalinity. In accordance with the present results, Martins et al. (2007) suggested that rockpools depth was more important in controlling physico-chemical variability than surface and volume.

During the day, upper shore rockpools were directly exposed to incident light, increasing the seawater temperature. Moreover, rockpools higher on the shore zone are exposed to external conditions for longer than lower ones, increasing the duration of thermic exchange with the atmosphere (Martins et al., 2007). This results in larger diurnal and seasonal variations in temperature than in lower shore rockpools. Similarly at night, the temperature within rockpools was mainly driven by the atmospheric temperature and wind exposure. In both the winter and the summer, atmospheric temperature at night was lower than near-shore seawater. As a consequence, during the emersion period, the temperature decrease at night was more important in high shore rockpools. In contrast to the upper shore rockpools, lower shore rockpools presented lower seasonal and diurnal variations for all parameters, except for salinity and nutrients. The salinity showed seasonal variability, with higher values in the summer, when evaporation was maximal. However, freshwater seepage may occur within the rockpool 5, as the salinity in this rockpool was lower than near-shore seawater both for seasonal and diurnal measurements. This statement is in accordance with the higher nutrient values measured in this rockpool.

As for intertidal emerging substrate, light intensity and temperature exert a strong influence on biological processes (Fernández et al., 2015; Martínez et al., 2012). Indeed, rockpool communities undergo a wide range of irradiance, determined by the seasonal, daily and tide cycles, and the cloud cover (Figs. 7 and 8; Häder et al., 2003). In the present study, the CCA *L. incrustans* colonized all rockpools, but reached the highest biomass in shallow high shore rockpools, both in the winter and the summer. This suggested that this species was stress-tolerant and was able to withstand high

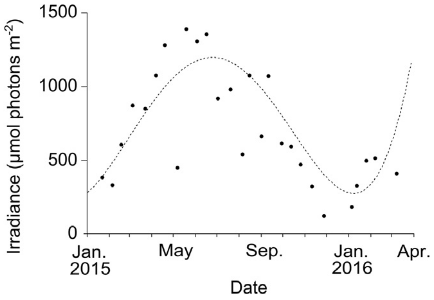

Fig. 7. Seasonal variations in light intensity measured at noon in air at the Station Biologique de Roscoff from January 2016 to April 2016 (dot line). Black dots represent the mean irradiance measured in air during day-time emersion for each seasonal measurement.

temperatures and light intensities (Dethier, 1994; Kooistra et al., 1989). Conversely, the articulated coralline algae *E. elongata* attained higher biomass within deeper and shaded rockpools. Egilsdottir et al. (2016) related a strong inhibition of photosynthesis and calcification in *E. elongata* under irradiances beyond 200 µmol photons m^{-2} s^{-1} in the summer. In the present study, *E. elongata* was almost absent from upper shore rockpools, where incident light intensity reached up to 800 and 1600 µmol photons m^{-2} s^{-1} in the winter and the summer, respectively (Fig. 8). Hence, conversely to *L. incrustans, E. elongata* may tolerate lower light intensities (Egilsdottir et al., 2016; Korbee et al., 2014) and may benefit from the shaded environment provided by deeper and sheltered rockpools.

In the summer, shallow upper shore rockpools were dominated by *Ulva intestinalis* and *Ulva* sp., respectively, although *Sargassum muticum* was co-dominant within the rockpool 1. *Ulva* is a cosmopolitan genus in intertidal environments, especially rockpools, and is characterized by a strong ability to cope with changing light conditions and tolerate high light intensities (Altamirano et al., 2000; Gómez et al., 2004; Ruangchuay et al., 2012). *S. muticum* was the dominant canopy-forming species in the rockpool 3. As for *Ulva* sp., Norton (1977) demonstrated that *S. muticum* have a broad tolerance for irradiance, salinity and temperature.

Within the rockpool 4, a dense canopy of the brown algae *Fucus serratus* was observed both in the winter and the summer. Thus, rockpools 1 to 4 are covered by a dense canopy of *U. intestinalis*, *S. muticum* and/or *F. serratus* from spring to late summer, when light intensities are high. Olabarria et al. (2013) highlighted the importance of canopy composition for understory species. For most intertidal seaweeds, the high light intensities in the summer often greatly exceed their needs for photosynthesis (Franklin and Forster, 1997). Although photoinhibition may affect these canopy-forming species, they are also likely to act as a protective layer for understory species, which may benefit from reduced light stress for their metabolic activity (Bordeyne et al., 2015; Tait and Schiel, 2011). In the summer, *L. incrustans* and *E. elongata* would thus be protected from photoinhibition by the dense canopy formed by *U. intestinalis*, *S. muticum* and *F. serratus*. This statement may be consistent with the bleaching observed in *E. elongata* when colonizing rockpool edges without canopy (personal observation). The bleaching in coralline algae under high irradiances has already been reported by Häder et al. (2003).

Communities inhabiting rockpools also exerted a strong influence on the physico-chemical variations. During the day-time emersion, a part of incident light was used by seaweeds for their photosynthesis, reducing inorganic carbon and nutrients in the seawater during the emersion period and increasing oxygen concentrations. *Ulva* spp. are known to have a high plasticity in utilizing different forms of inorganic carbon through the use of powerful carbon concentration mechanisms (CCM; Axelsson et al., 1999; Axelsson et al., 1995; Rautenberger et al., 2015). This process may confer a competitive advantage to *Ulva* spp., especially when CO_2 is limited (Axelsson et al., 1995; Larsson et al., 1997). Similarly, the ability of *S. muticum* to use bicarbonates (HCO_3^-) through CCM makes it unlikely to be limited in CO_2 for its photosynthesis (Thomas and Tregunna, 1968). Interestingly, no clear seasonal trend was measured in rockpools in terms of oxygen concentrations. Within upper shore rockpools, oxygen concentration varied greatly throughout the year with a peak detected in November, although light intensities were reduced compared with the summer. Several explanations could be provided: (1) the high light intensities in summer induce photoinhibition in seaweeds colonizing shallow and high shore rockpools, limiting oxygen concentration increase (Egilsdottir et al., 2016; Häder et al., 2003; Raven and Hurd, 2012). (2) The high photosynthetic rates combined with the important canopy biomass in summer severely reduced the nutrients which rapidly became limiting for seaweed primary production (Henley et al., 1991; Metaxas et al., 1994). In the autumn, the highest nutrient availability and the lowest light intensities may increase photosynthesis and oxygen release in rockpools. Oxygen concentration within the lower shore rockpool was more stable during the year than in other rockpools, with concentrations close to those of near-shore seawater. This rockpool was more shaded than other rockpools due to the presence of high surrounding rocks. Although nutrient concentrations were higher, the lower incident light may limit the community production.

During the night-time emersion, the community respiration decreased the oxygen concentration in the three rockpools monitored, both in the winter and the summer. However, the higher seaweed biomass in the summer reduced drastically oxygen concentrations, especially within rockpools 2 and 3. The higher temperature in the summer at night may increase the metabolic rates of rockpool communities (Tagliarolo et al., 2013; Zou et al., 2007) reducing oxygen concentration more severely. A plateau was reached from 4 am in these two rockpools, which became almost anoxic at the end of the night-time emersion. Conversely, in the winter, the decrease in oxygen concentration at night was more linear until the end of the night-time emersion. Temperature also influences gas solubility, and Truchot and Duhamel-Jouve (1980) suggested that the increase in oxygen concentration during the day and the decrease at night may be limited by diffusion process across the air–water interface.

By their photosynthesis, seaweeds also reduced the carbon dioxide (CO_2) concentration in the rockpools during the emersion period. As consequence, the pH_T of seawater increased, and reached 10 in spring in the rockpool 1, during the bloom of *Ulva intestinalis*, consistent with the results of Björk et al. (2004) for isolated rockpools in Sweden. A peak of pH_T was also observed in November in the rockpool 2, which corresponded to the maximum oxygen concentration in this rockpool. Conversely, at night, the community respiration during emersion increased the CO_2 concentrations and reduced the pH_T down to 7.5. The important seaweed biomass in the summer and the high respiration at night severely decreased the pH_T until a plateau was reached when oxygen has been consumed.

The variations in pH_T have a strong influence on the carbonate saturation state with respect to aragonite (Ω_{Ar}) and calcite (Ω_{Ca}). In marine systems, the equilibrium between the different inorganic carbon species is a major factor influencing the calcification process (Borowitzka and Larkum, 1987). Ω defines the ability of calcareous species to produce their skeleton, through the precipitation of calcium carbonate ($CaCO_3$) (Kleypas et al., 2006; Raven, 2011). The relationship between saturation state values and coralline calcification and growth is well known (Kuffner et al., 2008). Despite the presence of seasonal variations, Ω was much greater than 1 in upper shore rockpools during the day-time emersion, making the environment more conducive to calcification. In

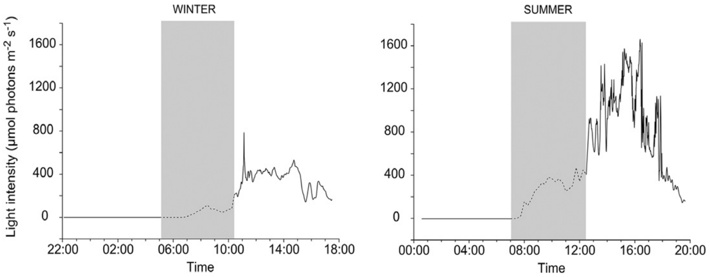

Fig. 8. Winter and summer diurnal variations in light measured in air in the Bloscon site in March 2016 and September 2015 respectively. The gray section represents the period during which all the rockpools were covered by the tide. Irradiance during immersion was estimated using extinction coefficient of light in seawater.

the lower shore rockpool, Ω_{Ar} and Ω_{Ca} reached values close to 1 in January which suggests a lower potential for calcareous species to calcify in winter during day-time emersion.

Several studies underlined the interaction between photosynthesis and calcification processes in coralline algae (Comeau et al., 2012; McCoy et al., 2016). The "*trans* calcification" process described by McConnaughey and Whelan (1997) suggests that calcareous algae may uptake seawater HCO_3^- and convert it to CO_2 thanks to proton transport through the organism. A part of this CO_2 would be used for algal photosynthesis while another part would be converted to produce CO_3^{2-} used for calcification. Although this process was evidenced in the freshwater alga *Chara corallina* (McConnaughey and Whelan, 1997), "*trans* calcification" may also occur in geniculate coralline algae (McCoy et al., 2016) and *L. incrustans*. Within rockpools, where CO_2 concentrations may be low during the day, this mechanism may provide sufficient inorganic carbon substrate to increase both photosynthetic and calcification rates. This statement would be consistent with the decrease in A_T observed during the day-time emersion in the summer within upper shore rockpools. Temperature increase in the summer may also have a positive effect on calcification and growth rates of coralline algae (Martin et al., 2006; Steller et al., 2007). Finally, a part of the calcification can also be attributed to calcareous fauna, since (Tagliarolo et al., 2013) highlighted an increase in calcification rates in summer in several intertidal gastropods, including *G. umbilicalis.*

E. elongata is known to have high calcification rates, with a light to dark ratio of 3.6 (El Haikali et al., 2004). In a recent study, Egilsdottir et al. (2016) estimated that calcification in *E. elongata* on the north coast of Brittany was 3.3 µmol $CaCO_3$ g DW^{-1} h^{-1} in the summer and 1.1 µmol $CaCO_3$ g DW^{-1} h^{-1} in the winter. During night-time emersion, the increase in A_T reflected the dissolution of coralline algae, explained by the decline of pH_T and Ω. This suggests that the increase in dissolution rates during night-time emersion would be offset by high calcification rates during the day-time emersion. In a Mediterranean shallow infralittoral ecosystem dominated by *E. elongata*, Bensoussan and Gattuso (2007) also evidenced strong diurnal variations, with higher calcification rates when light intensities were maximal. In the present study, biomass of *E. elongata* reached 982 g DW m^{-2} in rockpool 5. This value is lower than those reported for infralittoral communities on the Costa Brava (1110 to 4015 g DW m^{-2}; Ballesteros, 1988), but is close to the lower values reported by El Haikali et al. (2004) on the Gulf of Marseilles (820 to 2544 g DW m^{-2}). Moreover, in south-west Wales, Edyvean and Ford (1987) evidenced that $CaCO_3$ deposition rate for *L. incrustans* was 378.96 g m^{-2} plant surface area $year^{-1}$. Within rockpools, many factors may influence the calcification rates in coralline algae, such as rockpools exposition to incident light, the seawater physico-chemical parameters, but also the interaction with other species. However, the present results evidence that coralline algae colonizing rockpools can be considered as a key element of carbonate cycles in the shallow coastal waters.

This study provides evidence that although seaweeds were likely to strongly influence physico-chemical variations in rockpools, these variations were also governed by more complex interactions between physical parameters of rockpools (e.g. shore height, depth, light exposure, temperature…), chemical processes (gas exchange between the seawater and the atmosphere, interaction between physico-chemical parameters) and biotic factors (metabolic processes of species, nutrient/light limitation). Rockpools can thus be considered as complex dynamic environments, unique in their functioning due to the large number of interactions between physical, chemical and biological factors.

Within rockpools, physico-chemical variations mainly depend on their depth and the duration of their isolation from the sea during low tide. Seaweed species colonizing rockpools can thus survive harsh environmental conditions, such as low oxygen concentration and pH_T at night or high temperature and low nutrient concentrations during the day. However, species require a regular exchange of seawater for regulating physico-chemical parameters and recover from the emersion period. In coralline algae, low pH_T and carbonate saturation state at night may have deleterious consequences on their calcareous skeleton by increasing dissolution (Comeau et al., 2012; Egilsdottir et al., 2016).

The present study evidenced that rockpool organisms undergo physico-chemical variations that may greatly exceed those predicted with climate change for the end of the century (Gattuso et al., 2015). However, few studies took into account both emersion variability and inter-specific interactions (Olabarria et al., 2013). Regarding climate change experiments, particular attention should be paid to the natural variability that tested species undergo. Therefore, rockpools appear as suitable environments to examine the physiological processes set up by species to face natural variability.

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References

Altamirano, M., Flores-Moya, A., Figueroa, F.L., 2000. Long-term effects of natural sunlight under various ultraviolet radiation conditions on growth and photosynthesis of intertidal *Ulva rigida* (Chlorophyceae) cultivated in situ. Bot. Mar. 43, 119–126.

Aminot, A., Kérouel, R., 2007. Dosage automatique des nutriments dans les eaux marines: méthodes en flux continu. Ifremer, MEDD, Quae.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46.

Araujo, R., Sousa-Pinto, I., Barbara, I., Quintino, V., 2006. Macroalgal communities of intertidal rock pools in the northwest coast of Portugal. Acta Oecol. 30,192–202.

Axelsson, L., Larsson, C., Ryberg, H., 1999. Affinity, capacity and oxygen sensitivity of two different mechanisms for bicarbonate utilization in *Ulva lactuca* L. (Chlorophyta). Plant Cell Environ. 22, 969–978.

Axelsson, L., Ryberg, H., Beer, S., 1995. Two modes of bicarbonate utilization in the marine green macroalga *Ulva lactuca*. Plant Cell Environ. 18, 439–445.

Ballesteros, E., 1988. Composición y estructura de la comunidad infralitoral de *Corallina elongata* Ellis & Solander, 1786, de la Costa Brava (Mediterráneo occidental). Invest. Pesq. 52, 135–151.

Benedetti-Cecchi, L., Bulleri, F., Cinelli, F., 2000. The interplay of physical and biological factors in maintaining mid-shore and low-shore assemblages on rocky coasts in the north-west Mediterranean. Oecologia 123, 406–417.

Bensoussan, N., Gattuso, J.-P., 2007. Community primary production and calcification in a NW Mediterranean ecosystem dominated by calcareous macroalgae. Mar. Ecol. Prog. Ser. 334, 37–45.

Björk, M., Axelsson, L., Beer, S., 2004. Why is *Ulva intestinalis* the only macroalga inhabiting isolated rockpools along the Swedish Atlantic coast? Mar. Ecol. Prog. Ser. 284, 109–116.

Bordeyne, F., Migné, A., Davoult, D., 2015. Metabolic activity of intertidal *Fucus* spp. communities: evidence for high aerial carbon fluxes displaying seasonal variability. Mar. Biol. 162, 2119–2129.

Borowitzka, M.A., Larkum, A.W.D., 1987. Calcification in algae: Mechanisms and the role of metabolism. Crit. Rev. Plant Sci. 6, 1–45.

Collén, J., Davison, I.R., 1999. Reactive oxygen metabolism in intertidal *Fucus* spp. (Phaeophyceae). J. Phycol. 35, 62–69.

Comeau, S., Carpenter, R.C., Edmunds, P.J., 2012. Coral reef calcifiers buffer their response to ocean acidification using both bicarbonate and carbonate. Proc. Roy. Soc. B: Biol. Sci. 280, 20122374.

Crisp, D.J., 1984. Energy flow measurements. In: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the Study of Marine Benthos. Blackwell, Oxford, pp. 197–279.

Daniel, M., Boyden, C., 1975. Diurnal variations in physico-chemical conditions within intertidal rockpools. Field Stud. 4, 161–176.

Dethier, M.N., 1994. The ecology of intertidal algal crusts: Variation within a functional group. J. Exp. Mar. Biol. Ecol. 177, 37–71.

Dickson, A.G., Millero, F.J., 1987. A comparison of the equilibrium constants for the dissociation of carbonic acid in seawater media. Deep Sea Res. 34, 1733–1743.

Dickson, A.G., Sabine, C.L., Christian, J.R., 2007. Guide to Best Practices for Ocean CO_2 Measurements. In: PICES Special Publication, North Pacific Marine Science Organization, Sidney, British Columbia, p. 176.

Edyvean, R.G.J., Ford, H., 1987. Growth rates of *Lithophyllum incrustans* (Corallinales, Rhodophyta) from South West Wales. Br. Phycol. J. 22, 139–146.

Egilsdottir, H., Olafsson, J., Martin, S., 2016. Photosynthesis and calcification in the articulated coralline alga *Ellisolandia elongata* (Corallinales, Rhodophyta) from intertidal rock pools. Eur. J. Phycol. 51, 59–70.

El Haikali, B., Bensoussan, N., Romano, J.C., Bousquet, V., 2004. Estimation of photosynthesis and calcification rates of *Corallina elongata* Ellis and Solander, 1786, by measurements of dissolved oxygen, pH and total alkalinity. Sci. Mar. 68, 45–56.

Fernández, Á., Arenas, F., Trilla, A., Rodríguez, S., Rueda, L., Martínez, B., 2015. Additive effects of emersion stressors on the ecophysiological performance of two intertidal seaweeds. Mar. Ecol. Prog. Ser. 536, 135–147.

Firth, L.B., Schofield, M., White, F.J., Skov, M.W., Hawkins, S.J., 2014. Biodiversity in intertidal rock pools: Informing engineering criteria for artificial habitat enhancement in the built environment. Mar. Environ. Res. 102, 122–130.

Firth, L.B., Thompson, R.C., White, F.J., Schofield, M., Skov, M.W., Hoggart, S.P.G., Jackson, J., Knights, A.M., Hawkins, S.J., 2013. The importance of water-retaining features for biodiversity on artificial intertidal coastal defence structures. Divers. Distrib. 19, 1275–1283.

Franklin, L.A., Forster, R.M., 1997. The changing irradiance environment: consequences for marine macrophyte physiology, productivity and ecology. Eur. J. Phycol. 32, 207–232.

Ganning, B., 1971. Studies on chemical, physical and biological conditions in Swedish rockpool ecosystems. Ophelia 9, 51–105.

Gattuso, J.P., Magnan, A., Billé, R., Cheung, W.W.L., Howes, E.L., Joos, F., Allemand, D., Bopp, L., Cooley, S.R., Eakin, C.M., Hoegh-Guldberg, O., Kelly, R.P., Pörtner, H.O., Rogers, A.D., Baxter, J.M., Laffoley, D., Osborn, D., Rankovic, A., Rochette, J., Sumaila, U.R., Treyer, S., Turley, C., 2015. Contrasting futures for ocean and society from different anthropogenic CO_2 emissions scenarios. Science 349,1–10.

Gómez, I., López-Figueroa, F., Ulloa, N., Morales, V., Lovengreen, C., Huovinen, P., Hess, S., 2004. Patterns of photosynthesis in 18 species of intertidal macroalgae from southern Chile. Mar. Ecol. Prog. Ser. 270, 103–116.

Häder, D.-P., Lebert, M., Walter Helbling, E., 2003. Effects of solar radiation on the patagonian rhodophyte *Corallina officinatis* (L.). Photosynth. Res. 78, 119–132.

Henley, W.J., Levavasseur, G., Franklin, L.A., Osmond, C.B., Ramus, J., 1991 Photoacclimation and photoinhibition in *Ulva rotundata* as influenced by nitrogen availability. Planta 184, 235–243.

Hoffman, J.R., Hansen, L.J., Klinger, T., 2003. Interactions between UV radiation and temperature limit inferences from single-factor experiments. J. Phycol. 39,268–272.

Huggett, J., Griffiths, C.L., 1986. Some relationships between elevation, physicochemical variables and biota of intertidal rock pools. Mar. Ecol. Prog. Ser. 29, 189–197.

Kleypas, J.A., Feely, R.A., Fabry, V.J., Langdon, C., Sabine, C.L., Robbins, L.L., 2006. Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research, Report of a workshop held, April 18–20, 2005, NSF, NOAA, and the US Geological Survey, St. Petersburg, FL, USA, p. 88.

Kooistra, W.H.C.F., Joosten, A.M.T., van den Hoek, C., 1989. Zonation patterns in intertidal pools and their possible causes: a multivariate approach. Bot. Mar. 32, 9–26.

Korbee, N., Navarro, N.P., Garcia-Sanchez, M., Celis-Pla, P.S.M., Quintano, E., Copertino, M.S., Pedersen, A., Mariath, R., Mangaiyarkarasi, N., Perez-Ruzafa, A., Figueroa, F.L., Martinez, B., 2014. A novel in situ system to evaluate the effect of high CO_2 on photosynthesis and biochemistry of seaweeds. Aquatic Biol. 22, 245–259.

Kuffner, I.B., Andersson, A.J., Jokiel, P.L., Rodgers, K.S., Mackenzie, F.T., 2008. Decreased abundance of crustose coralline algae due to ocean acidification. Nat. Geosci. 1, 114–117.

Larsson, C., Axelsson, L., Ryberg, H., Beer, S., 1997. Photosynthetic carbon utilization by *Enteromorpha intestinalis* (Chlorophyta) from a Swedish rockpool. Eur. J. Phycol. 32, 49–54.

Lewis, E., Wallace, D.W.R., 1998. Program developed for CO_2 system calculations. Carbon dioxide information analysis center, Oak Ridge National Laboratory, U.S. Department of Energy.

Martin, S., Castets, M.D., Clavier, J., 2006. Primary production, respiration and calcification of the temperate free-living coralline alga *Lithothamnion corallioides*. Aquat Bot. 85, 121–128.

Martínez, B., Arenas, F., Rubal, M., Burgués, S., Esteban, R., García-Plazaola, I., Figueroa, F.L., Pereira, R., Saldaña, L., Sousa-Pinto, I., Trilla, A., Viejo, R.M., 2012. Physical factors driving intertidal macroalgae distribution: physiological stress of a dominant fucoid at its southern limit. Oecologia 170, 341–353.

Martins, G.M., Hawkins, S.J., Thompson, R.C., Jenkins, S.R., 2007. Community structure and functioning in intertidal rock pools: effects of pool size and shore height at different successional stages. Mar. Ecol. Prog. Ser. 329, 43–55.

McConnaughey, T.A., Whelan, J.F., 1997. Calcification generates protons for nutrient and bicarbonate uptake. Earth-Sci. Rev. 42, 95–117.

McCoy, S.J., Pfister, C.A., Olack, G., Colman, A.S., 2016. Diurnal and tidal patterns of carbon uptake and calcification in geniculate inter-tidal coralline algae. Mar. Ecol. 37, 553–564.

Mehrbach, C., Culberso. Ch, Hawley, J.E., Pytkowic, R.M., 1973. Measurement of apparent dissociation-constants of carbonic-acid in seawater at atmospheric-pressure. Limnol. Oceanogr. 18, 897–907.

Metaxas, A., Hunt, H.L., Scheibling, R.E., 1994. Spatial and temporal variability of macrobenthic communities in tidepools on a rocky shore in Nova-Scotia, Canada. Mar. Ecol. Prog. Ser. 105, 89–103.

Metaxas, A., Scheibling, R.E., 1993. Community structure and organization of tidepools. Mar. Ecol. Prog. Ser. 98, 187–198.

Morris, S., Taylor, A.C., 1983. Diurnal and seasonal variation in physicochemical conditions within intertidal rock pools. Estuar. Coast. Shelf Sci. 17, 339–355.

Norton, T.A., 1977. The growth and development of *Sargassum muticum* (Yendo) Fensholt. J. Exp. Mar. Biol. Ecol. 26, 41–53.

Olabarria, C., Arenas, F., Viejo, R.M., Gestoso, I., Vaz-Pinto, F., Incera, M., Rubal, M., Cacabelos, E., Veiga, P., Sobrino, C., 2013. Response of macroalgal assemblages from rockpools to climate change: effects of persistent increase in temperature and CO_2. Oikos 122, 1065–1079.

Rautenberger, R., Fernández, P.A., Strittmatter, M., Heesch, S., Cornwall, C.E., Hurd, C.L., Roleda, M.Y., 2015. Saturating light and not increased carbon dioxide under ocean acidification drives photosynthesis and growth in *Ulva rigida* (Chlorophyta). Ecol. Evol. 5, 874–888.

Raven, J.A., 2011. Effects on marine algae of changed seawater chemistry with increasing atmospheric CO_2. Biol. Environ.-Proc. R. Ir. Acad. 111B, 1–17.

Raven, J.A., Hurd, C.L., 2012. Ecophysiology of photosynthesis in macroalgae. Photosynth. Res. 113, 105–125.

Ruangchuay, R., Dahamat, S., Chirapat, A., Notoya, M., 2012. Effects of culture conditions on the growth and reproduction of Gut Weed, *Ulva intestinalis* Linnaeus (Ulvales, Chlorophyta). Songklanakarin J. Sci. Technol. 34, 501–507.

Steller, D.L., Hernandez-Ayon, J.M., Riosmena-Rodriguez, R., Cabello-Pasini, A., 2007. Effect of temperature on photosynthesis, growth and calcification rates of the free-living coralline alga *Lithophyllum margaritae*. Cienc. Mar. 33, 441–456.

Tagliarolo, M., Clavier, J., Chauvaud, L., Grall, J., 2013. Carbon emission associated with respiration and calcification of nine gastropod species from the intertidal rocky shore of Western Europe. Mar. Biol. 160, 2891–2901.

Tait, L.W., Schiel, D.R., 2011. Dynamics of productivity in naturally structured macroalgal assemblages: importance of canopy structure on light-use efficiency. Mar. Ecol. Prog. Ser. 421, 97–107.

Thomas, E.A., Tregunna, E.B., 1968. Bicarbonate ion assimilation in photosynthesis by *Sargassum muticum*. Can. J. Bot. 46, 411–415.

Tomanek, L., Helmuth, B., 2002. Physiological ecology of rocky intertidal organisms: A synergy of concepts. Integr. Comp. Biol. 42, 771–775.

Truchot, J.P., Duhamel-Jouve, A., 1980. Oxygen and carbon-dioxide in the marine intertidal environment - Diurnal and tidal changes in rockpools. Respir. Physiol. 39, 241–254.

Underwood, A.J., Jernakoff, P., 1984. The effects of tidal height, wave-exposure, seasonality and rock-pools on grazing and the distribution of intertidal macroalgae in New-South-Wales. J. Exp. Mar. Biol. Ecol. 75, 71–96.

Widdows, J., Brinsley, M., 2002. Impact of biotic and abiotic processes on sediment dynamics and the consequences to the structure and functioning of the intertidal zone. J. Sea Res. 48, 143–156.

Zander, C.D., Nieder, J., Martin, K., 1999. Vertical Distribution Patterns, Intertidal Fishes. Academic Press, San Diego, pp. 26–53.

Zou, D., Gao, K., Xia, J., Xu, Z., Zhang, X., Liu, S., 2007. Responses of dark respiration in the light to desiccation and temperature in the intertidal macroalga, *Ulva lactuca* (Chlorophyta) during emersion. Phycologia 46, 363–370.