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Leila Chapron, Nadine Le Bris, Xavier Durrieu de Madron, Erwan Peru, Pierre E. Galand, Franck Lartaud

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Long term monitoring of cold-water coral growth shows response to episodic meteorological events in the NW Mediterranean

Chapron L.[1], Le Bris N.[1], Durrieu De Madron X.[2], Peru E.[1], Galand P.E.[1], Lartaud F.[1]

[1] Sorbonne Université, CNRS, Laboratoire d'Ecogéochimie des Environnements Benthiques, LECOB, Observatoire Océanologique, F-66650, Banyuls/Mer, France

[2] CEFREM, CNRS-Université de Perpignan Via Domitia, 52 avenue Paul Alduy, 66860, Perpignan, France.

Abstract

Lophelia pertusa and *Madrepora oculata*, two cosmopolitan coral species of the deep ocean, build reef-like structures that provide ecological niches and nurseries for many species. These cold-water corals (CWCs) are thought to grow slowly making associated communities vulnerable to disturbance. However, *in situ* growth dynamics remains poorly known. The aim of this study was thus to quantify the growth rates of *L. pertusa* and *M. oculata* and their variability in relation to environmental conditions that are expected to influence their physiological functions. Such data can be useful to ground-truth physiological rates and improve the prediction of their sensitivity to global change. As part of a long-term monitoring programme of the Lacaze-Duthiers canyon in the Northwestern Mediterranean Sea, fragments of the two species were repeatedly sampled and redeployed at 530 m depth, from November 2010 to May 2018. Budding rates and linear extensions of *L. pertusa* and *M. oculata* were hence quantified and their inter-annual variability documented. The data were analyzed in relation to *in situ* monitoring of water temperature, current speed and turbidity.

This study presents the longest *in situ* survey of the growth patterns of *L. pertusa* and *M. oculata*. The observations revealed a strong inter-annual variability in growth rates, both for *L. pertusa* and *M. oculata*, and suggest an influence of hydrological conditions on the growth dynamics. Particularly, as regard to episodic water plumes events such as NW wind-induced dense water shelf cascades and E-SE storm-induced downwellings in autumn-winter. In this study, three types of responses were observed: (i) high budding rates but low colony linear extension for strong water plume events periods (ii) low budding rates, low linear extension and high mortality due to high sedimentation rates in the absence of water plumes event, and (iii) high budding rates and high linear extension associated to organic matter supply during medium intensity water plume events. *Lophelia pertusa* appears to be more resilient to these hydrological changes. Disturbance of the regional circulation patterns, in addition to longer-term change in water mass properties such as warming, deoxygenation and acidification, are thus important parameters to consider for CWC reef stability. This is particularly important since increased storminess, and decreased cascading/downwelling intensities, are predicted to occur within the next century.

Keywords: *Lophelia pertusa*, *Madrepora oculata*, Lacaze Duthiers submarine canyon, *in situ*, skeletal growth, dense-water cascading

1. Introduction

Engineer species forming three-dimensional structures, such as scleractinian cold-water corals (CWCs), provide ecological niches for a number of associated species (Buhl-Mortensen et al., 2010). These habitat-building species that support deep-sea biodiversity, have a great ecological value and are listed in the CITES convention (Appendix II) (Foley and Armstrong, 2010). In the last thirty years, significant research efforts by the scientific community have been dedicated to characterize their physiology and ecology, including feeding, reproduction, growth and the associated microbiome (Waller and Tyler, 2005; Roberts, 2009; Lartaud et al., 2014; Lunden et al., 2014; Meistertzheim et al., 2016). However, understanding of the CWC ecology still display important knowledge gaps due to the difficulty of studying these species in their natural environment.

Calcification is one of the key physiological indicators of calcifying organism fitness. During the last decades, a number of studies have been dedicated to characterize the growth patterns of CWCs with the aim of establishing adequate conservation strategies (see details in Lartaud et al., *in press.*). Among all known CWC species, the emblematic *Lophelia pertusa* exhibits the highest growth rates, but with a high variability, ranging from 0.01 to 38.1 mm y^{-1} (Lartaud et al., 2014; 2017). This range contrasts with the growth rate of another deep-sea coral species, *Solenosmilia variabilis* that exhibits the smallest skeletal growth for scleractinian (~1 mm y^{-1}) (at 750m depth on SW Pacific seamounts observed in Fallon et al., 2014). Differences in growth patterns are also observed for *M. oculata*, another common reef-building species, with growth rates ranging from 0.01 to 18 mm y^{-1} (Lartaud et al., 2017). The growth rate variability among studies can be partly explained by the use of different measurement methods, such as budding rates analysis, sclerochronology, buoyant weight, alkalinity anomaly or radioisotopic technics. The differences could also be due to the comparison of values originating from different geographic locations, depths, and related environmental conditions (e.g. Gulf of Mexico, Mediterranean Sea, Norway) (Lartaud et al., *in press.*). Growth rates using the same measurement method for one species like *L. pertusa* can range from 34 mm y^{-1} (the North Sea) to 6 mm y^{-1} (Rockall Bank, North Atlantic) (Gass and Roberts, 2006; Wilson, 1979; Lartaud et al., *in press*). Strong regional variability is also observed like in the Gulf of Mexico where *L. pertusa* exhibits growth rates varied from 3.8 mm y^{-1} (Brooke and Young, 2009) to 32.3 mm y^{-1} (Larcom et al., 2014), but for different time period and habitat conditions. Growth rate variability for this coral species was also observed in the Western Mediterranean Sea for different time periods at the same location, with a maximum of 38.1 mm y^{-1} (Lartaud et al., 2014; 2017). This limited set of growth rate measurements at different locations using different methods prevents robust assessment of CWC growth patterns in their natural habitat, and highlights the need for longer-term monitoring efforts of growth rates with respect to the local environmental variability.

Experimental studies have led to identify a series of factors that influence the growth patterns of cold water corals. Temperature can influence primary physiological processes like respiration and calcification (Naumann et al., 2014). The seawater pH can also impact these biological parameters (Gori et al., 2016; Hennige et al., 2014). In addition, nutrients, salinity, dissolved oxygen and current speed could affect coral calcification (Cairns and Macintyre, 1992; Thiem et al., 2006; Guinotte et al., 2006 Roberts, 2009; Purser et al., 2010; Lunden et al., 2014). Lartaud et al. (2014) showed through *in situ* experiments a seasonal difference in growth rates of *M. oculata*, which was suggested to reflect differences food supplies induced by meteorological events.

Coral growth rates likely respond differently to the combination of these factors in their environment. Available data furthermore suggests that CWC growth might be directly modulated by environmental changes. Understanding the growth dynamic of these species, and assessing response to change in habitat conditions, should take into account this variability while defining monitoring strategies.

Understanding the drivers of growth dynamics of CWCs under various environmental conditions is essential to predict their fate in a changing ocean under anthropogenic perturbations (Maier et al., 2012; Hennige et al., 2014; IPCC, 2014; Levin and Le Bris, 2015). In an effort to document the impacts of climate change and other anthropogenic disturbances on a Mediterranean submarine canyon ecosystem hosting abundant colonies of *L. pertusa* and *M. oculata* (Gori et al., 2013), we have set up a long-term *in situ* monitoring programme focusing on key ecological functions. These functions include coral growth, for which data have been lacking so far on multiannual time-scale. Growth rate can furthermore be used as an assessment tool to determine the health and conservation status of deep-sea reef-building corals in marine protected areas (Davies et al., 2008; Vad et al., 2017; Boolukos et al., 2019).

The aim of this study was to investigate the growth patterns of *L. pertusa* and *M. oculata* over time, to determine their inter-annual temporal dynamics in a region of the Mediterranean where hydrodynamic conditions are seasonally contrasted, with episodic extreme events characterizing winter conditions. These events transporting water masses and particles from the shelf down to the bathyal and abyssal regions vary interannually in frequency and intensity (Béthoux et al., 2002; Canals et al., 2006; Heussner et al., 2006; Durrieu de Madron et al., 2013). The *in situ* experimental approach implemented to study coral growth was based on yearly deployment and recovery of small coral fragments in a study site located at 530 m depth in the Lacaze-

Duthiers canyon (LDC), Gulf of Lion, in an area where these two species are naturally abundant. To avoid methodological bias, the growth of *L. pertusa* and *M. oculata* was measured using the same method over eight years (as described in Lartaud et al., 2017).

2. Material and methods

2.1. Study site and sampling

The Lacaze-Duthiers submarine canyon, 23 km long, is located in the northwestern part of the Mediterranean Sea, in the Gulf of Lion. This canyon is located in the Gulf of Lion Marine Nature Park, a Marine Protected Area that harbour abundant populations of CWCs, particularly the stony corals *L. pertusa* and *M. oculata* between 300 and 600 m depth (Fig 1-A-B), which have been explored during the MEDSEACAN cruise of the Marine Protected area agency.

Previous publications have described the experimental site for coral growth experiments, called site A (42°32.43N, 03°25.26E), located at 530 m depth in the canyon and characterized by large structures of mixed *L. pertusa*, *M. oculata* and *D. Dianthus* (Lartaud et al., 2014, 2017). Coral collections for this study were obtained during eight distinct cruises lead under the LECOB programme ‘Biodiversity, extreme environment and global change’ ,using the Remotely Operated Vehicle (ROV) Super Achille on the R/V Minibex or the R/V Janus II from COMEX S.A.. Coral samples were expected to belong to the same genetic population considering that they came from the same small area (<50 m^2). Colony fragments of *L. pertusa* and *M. oculata* were collected and then transported to the surface using thermally insulated polypropylene boxes that maintain the ambient temperature of deep seawater (i.e., 13°C). On board, the collected corals were transferred into aerated 30 L seawater tanks maintained at 13°C using a chiller. The apical part of corals was cut into small nubbins (called NS and corresponding to ~5 polyps for *L. pertusa* and ~8 polyps for *M. oculata*) and/or into longer branches (called BS, with ~15 polyps for *L. pertusa* and ~20 polyps for *M. oculata*). The use of different types of transplant unit (i.e., NS or BS) was previously shown to have no impact on the growth parameters studied (Lartaud et al., 2017). Both types of fragments were glued with an aquatic epoxy resin on transplant units following the protocols described in Lartaud et al (2014) (Fig 1- C). Following years, different deployment conditions were used. First, different nubbins were placed in different orientations on a cobblestone, but no statistical differences were observed in growth rates and polyp mortality between orientations (Lartaud et al., 2014). Also, the deployments on cobblestone directly on the sediment or on a platform about 50 cm above show no impact on cold water corals growth and mortality (Kruskal-Wallis test, p-value > 0.05).

To measure coral growth rates a catch-recapture approach was used during 6 periods of 12±2 months from November 2010 to May 2018 (Table 1). Thirty-seven transplant units were used for *L. pertusa*, which corresponded to 22 nubbins (NS) and 15 branches (BS). Fifty-one transplants units were used for *M. oculata*, which corresponded to 32 nubbins and 19 branches. Also, we performed a temporal monitoring of *L. pertusa* and *M. oculata* growth rates of the same colonies between 2015 and 2018 to exclude genetic factors.

2.4. Growth measurements

Each living and dead polyps of the coral nubbins and branches were counted and photographed before and after deployment with the same orientation for comparison. The use of a scale bar on the pictures allows to measure the linear extension of the coral fragments, which corresponds to the calcification between the last polyp observed before deployment to the summit of the calix of the last polyp observed after recapture. For each year, the maximal linear extension of each BS/NS, which represents the growth capability along a maximum growth direction, were measured using the software ImageJ (Fig 2) (Strömberg et al., 2010; Lartaud et al., 2017). As the growth of *L. pertusa* and *M. oculata* colonies is driven by the successive addition of new polyps, growing on top of previous generation of polyps, following a longitudinal axis, the addition of new polyps was counted and measured using the protocol established by Lartaud et al. (2014) to determine the budding rates. The budding rate corresponds to the percentage of new polyp added per polyp initially present per year, and thus reflects the density development of polyps within the colony.

2.2. Hydrological parameters

To monitor hydrological parameters of the Lacaze Duthiers canyon, a Nortek Aquadopp single-point acoustic current meter was installed on the experiment platforms from 2015. The probe provided measurements every half hour of the current speed and direction, temperature and acoustic echo intensity in the habitat surrounding the CWCs (~530 m depth in the Lacaze Duthier canyon). Acoustic echo intensity records were converted into suspended particle concentration using an empirical linear equation between the logarithm of concentration (C) and echo intensity (EI) (Gartner, 2004). The equation found using simple regression between concomitant backscatter data and direct sampling concentration in the Gulf of Lions was $10 \times \log(C_{mg/L}) = 0.407 * EI_{dB} - 22.55$ ($r^2 = 0.94$, $N = 66$) (Durrieu de Madron et al., 2017).

In addition, significant wave height data series were also used to identify eastern storm periods that generate plateau water export and downwelling in the Lacaze-Duthiers canyon (Palanques et al., 2006; Ulses et al., 2008a). They were measured at the Leucate houlograph located about 40 km northwest to the experimental site.

From 2010, *in situ* temperature was also monitored in the water column of the Lacaze Duthiers at 500 and 1000 m depth using a Nortek Aquadopp single-point acoustic current meter.

2.5. Statistical analyses

Statistical analyses were conducted using R software and tests for normality and homoscedasticity were performed using the Shapiro-Wilk test ($p<0.05$). Considering that the distribution was not normal for either budding rates, linear extension and mortality, multiple comparison non-parametric tests were used to assess growth differences between years: a Friedman test for the monitoring on the same colony and a multiple Kruskal-Wallis test for the monitoring on different colonies.

3. Results

3.1. Coral survival

There was no significant difference between the survival of the two species (Friedman test, $n=11$, $p<0.05$, Fig. 3 and Table S1), with the exception of the period 2017-2018, where *M. oculata* exhibited higher mortality than *L. pertusa* (average of 70 ± 40 % vs 17 ± 27 % respectively).

The mortality of *L. pertusa* polyps was generally low (<25%) except for 2013-2014 (100%), which exhibited significant higher mortalities (K-W test, $n=37$, $p<0.05$, Table S1). Also, there was a high mortality observed for *L. pertusa* polyps for 2015-2016

(71 ± 46 %), which was significantly different from 2010-2011 (0%) and 2017-2018 (17 ± 27 %) (K-W test, n=37, p<0.05, Table S1).

For *M. oculata*, the percentages of dead polyps were more variables. As for *L. pertusa*, the lowest value observed was for 2010-2011 (0 %) and the highest for 2013-2014 (98 ± 11 %), which were statistically different compared to the other periods (K-W test, n=51, p<0.05, Table S1). The periods 2015-2016 (71 ± 35 %) and 2017-2018 (70 ± 40 %) were also characterized by high polyp mortality.

3.2. Budding rates

There was no statistical difference in budding rates between *L. pertusa* and *M. oculata* except for the 2016-2017 and 2017-2018 periods, with significantly higher values for *L. pertusa* (Friedman test, n=11, p<0.05, Fig. 4 and Table S2).

Lophelia pertusa exhibited high budding rates (means ranging from 41 to 69 %), excepted for 2013-2014 (1 ± 3 %) and 2015-2016 (22 ± 34 %). Specifically, budding rates for 2013-2014 were statistically lower compared to the other periods (K-W test, n=37, p<0.05, Table S2).

For *M. oculata*, the budding rates were variable with significantly higher rates observed in 2010-2011 (54 ± 22 %) and 2016-2017 (28 ± 17 %). For the other time periods, the mean budding rates were below 25%.

3.3. Linear extension

There was no statistical difference between *L. pertusa* and *M. oculata* for the linear extensions except for the 2016-2017 and 2017-2018 periods, with significantly higher growth rates for *L. pertusa* (Friedman test, n=11, p<0.05, Fig. 5 and Table S3).

The mean linear extensions of *L. pertusa* were significantly higher during 2016-2017 (24 ± 7 mm y^{-1}) and 2017-2018 (26 ± 9 mm y^{-1}) compared to the other periods (mean values ranging from 1 to 5 mm y^{-1}) (K-W test, n=88, $p<0.05$, Table S3). The highest values were recorded for coral fragments deployed during the 2016-2017 period (40.2 mm y^{-1}).

For *M. oculata*, the average linear extension was low (≤ 4 mm y^{-1}) except for 2016-2017, which displayed a significantly higher growth rate (9 ± 6 mm.y^{-1}).

3.4. Hydrological parameters from 2015 to 2018

The monitoring of temperature, current and suspended particles matter (SPM) concentration conducted at 530 m depth in the Lacaze Duthiers canyon revealed a significant seasonal and interannual variation of the bottom hydrological and current conditions in the canyon head (Fig. 6). First, these parameters were stable during most of the year except during winter (January-March), which exhibited a period characterized by intermittent temperature drops concurrent with increases in current speed and SPM concentration.

The bottom currents during these episodes are directed down-canyon. In 2016-2017 (Fig. 6-B) and 2017-2018 (Fig 6-C), these episodic signals are often concomitant with high significant wave heights (> 2-3 m) recorded at the coast. They are therefore the signature of a water export from the continental shelf to the head of the canyon linked to downwellings induced by easterly winds (as shown by Palanques et al., 2006 and Ulses et al., 2008a). The lower temperature of the shelf waters compared to the slope waters resulted from the formation of cold and dense water along the coast, which can be rapidly exported to the slope during this eastern storms (as observed in winter 2013, Fig S1) (Ulses et al., 2008b). However, some episodes such as those in March 2015 and

January 2018 (Fig. 6-A and C) also indicate that there are periods of export and dense shelf water cascading in the canyon independently of these eastern storms. This export is possible under the effect of strong northward winds that are at the origin of the formation by evaporation of cold and dense water at the coast (as observed in winter 2012, Fig S1) (Ulses et al., 2008c).

In all cases, the increase in SPM concentration could result both from the bottom transport of fine sediment from the shelf and from the local resuspension of sediment in the canyon head. The intensity of the currents during these brief events, between 20 and 70 cm/s is sufficient to erode and resuspend fine (clayey and silty) sediments.

4. Discussion

4.1. Interannual variation in the growth of *Lophelia pertusa*

The growth patterns of *L. pertusa* (linear extension and rate of new polyp addition) varied between years. Based on the monitored parameters (mortality, budding rate and linear extension), three main response type can be described for *L. pertusa*: (i) high budding rate but low linear extension (2010-2011 and 2011-2012), (ii) low budding rate, low linear extension and high mortality (2013-2014 and 2015-2016), and (iii) high budding rate and high linear extension (2016-2017 and 2017-2018). Since the corals were deployed at the same location, their growth responses are likely primarily controlled by the surrounding environmental conditions. Particularly for the periods of survey of the same colonies.

In the Mediterranean Sea, CWCs are found in submarine canyons where the environmental conditions can vary between years because of episodic dense shelf water events (Canals et al., 2006). Three different types of water plumes are described, corresponding to autumnal storm events (stratified water masses with low intensity), winter storm events (large amount of particles) and winter cascading events (non-stratified water masses with high intensity) (Canals et al., 2006). These events lead to ventilation, changes in the temperature, current speed and transport of material such as organic matter and sediments (Canals et al., 2006; Bonnin et al., 2008; Durrieu de Madron et al., 2013). The input in organic matter is essential to CWCs that are considered to feed primarily on zooplankton and phytodetritus with a preference for living food (Houlbrèque et al., 2004; Kiriakoulakis et al., 2005; Duineveld et al., 2007; Becker et al., 2009; Purser et al., 2010; Tsounis et al., 2010). The change in intensity of these events from year to year, strongly associated with the local meteorological conditions at the surface (Heussner et al., 2006), should impact the growth of *L. pertusa*.

The periods 2013-2014 and 2015-2016 (Fig. S1) showed the lowest budding rates and linear extensions combined with the highest *L. pertusa* mortality. The present and earlier *in situ* observations (Lartaud et al., 2017) revealed a high sedimentation rate during these periods, which led to the partial burial of the coral colonies deployed. Sediment exposure leads to physical abrasions of the coral tissues and to a depletion in oxygen for the polyps (Larsson and Purser, 2011). Moreover, the accumulation of sediment particles on the tissues (e.g. coenosarc) can limit food access for the polyps. Sediment cleaning by tentacle movements, tissue distension and mucus secretion also has an energy cost for the coral (Rogers, 1999). Even though moderate concentrations of suspended particles used as nutritional sources can be beneficial, a high sediment concentration leads to coral mortality (Mortensen, 2001). The corals' energy budget are altered by sediment particles that lead to a higher metabolic activity (represented by respiration rates) (Larsson et al., 2013). It has also been reported that stress induced by sediment particles limits the tissues and skeleton growth of scleractinian corals

(Anthony et al., 2002). Thus, in a highly turbid environment, the CWCs need to maintain their essential physiological functions (e.g. respiration, remove particles) by allocating their energy away from secondary functions such as biomineralization.

In contrast, the periods 2016-2017 and 2017-2018 showed the highest budding rates and linear extension with low mortalities for *L. pertusa*. *In situ* observations showed low sedimentation coupled with winter storm events with comparable moderate intensities for both periods (Fig. 6). Laboratory studies suggest that the increase in food supply, rather than temperature, may control growth rates of CWCs (Mortensen, 2001; Roberts and Anderson, 2002; Orejas et al., 2011b). A reduction in food supply caused a significant decline in the calcification of CWCs (Naumann et al., 2011). Thus, the rapid transport of fresh and labile organic matter during downwelling and cascading events observed during these periods may promote physiological processes, as biomineralization, which is directly positively linked to their ability to catch suspended prey from the water column (van Oevelen et al., 2009). Optimal growth conditions for *L. pertusa* in the Lacaze Duthiers canyon are thus suggested to be strongly influenced by the occurrence of dense shelf water cascades or storm-induced downwelling as suggested (Lartaud et al., 2014), a major driver being the prevention of excessive sedimentation on coral surfaces.

However, strong hydrological events can reduce growth patterns as observed for the 2010-2011 and 2011-2012 periods. The combination of a high addition of new polyps together with low linear extension observed for *L. pertusa* suggests that the energy budget was allocated to the production of small polyps and not to the linear growth of the colony. This process may thicken the colony that will better resist to strong water current. It could promote an increase in number of polyp mouths to catch and ingest more food resources from the water column (Musco et al., 2018). Contrary to

2016-2017 and 2017-2018, the 2010-2011 and 2011-2012 episodic water plumes were characterized by stronger intensities. The winter 2012 exhibited one of the strongest cascade event recorded in the Gulf of Lion (Durrieu de Madron et al., 2013, Fig S1), and several strong winter storms in the Lacaze Duthiers canyon occurred in 2011 (Puig et al., 2013, Fig S1). Thus, the optimal growth for *L. pertusa* in the Lacaze Duthiers canyon seems to be favored by episodic winter downwelling events of moderate intensity. It shows that cascading events can have antagonist effects on CWCs with the positive effect of food supply in one hand, and on the other hand, the negative effect of currents that are too strong to allow cold water coral polyps to catch preys (Pusceddu et al., 2013; Orejas et al., 2016). This argument should, however, be considered with caution as the importance of these events, lasting only a few weeks, in the annual nutritional budget of corals that is still poorly known.

4.2. Interannual variation in the growth of *Madrepora oculata*

Madrepora oculata also displayed high variability in the growth patterns between years. The growth responses scenarios were: (i) high budding rates but low linear extension (2010-2011), (ii) low budding rates, low linear extension and high mortality (2011-2012, 2013-2014, 2015-2016 and 2017-2018) and (iii) high budding rates and high linear extension (2016-2017).

The scenario (ii) appeared more frequently for *M. oculata* than *L. pertusa*. As for *L. pertusa*, the unfavorable growth conditions in 2013-2014 and 2015-2016 might correspond to high sediment concentrations in the coral habitat. It has been shown that sediment cover must be considered as a fundamental limiting factor for various CWC species, and could be considered to describe the health status of deep-water coral reefs (Lartaud et al., 2017). The period 2011-2012, associated to a strong cascading event during winter 2012 (Durrieu de Madron et al., 2013, Fig S1), suggests that *M. oculata* is more sensitive to strong currents than *L. pertusa*. The high current velocities associated with cascading events may not be optimal for *M. oculata* prey capture rates, or the energy budget may not be sufficient to allow biomineralization under these environmental conditions. However, in the 2017-2018 period that was characterized by an episode of dense water plumes of moderate intensity, both the linear extension and budding rates remain low. Thus, *M. oculata* appear to be more sensitive than *L. pertusa* to environmental variations.

The scenario (i) for *M. oculata* follows the same pattern as for *L. pertusa* for 2010-2011 characterized by an intense winter storm (Puig et al., 2013, Fig S1). It suggests that high intensity hydrological events may have a negative impact on *M. oculata* biomineralization, although this species, similarly to *L. pertusa,* can display an increase in polyp density rather than the colony extension as a response to such events. In opposition, the optimal growth rates observed for *M. oculata* were in 2016-2017, which was characterized by a moderate winter storm (Fig. 6). Thus, the scenario (iii) should represent median to favorable environmental conditions for this species. Moreover, the difference between 2016-2017 and 2017-2018 are characterized by hydrological events of similar intensities but not occurring at the same period of the year (Fig. 6). The export of nutrients from surface waters to deeper water layers in the canyon are likely different in both quantity and quality considering the seasonality in phytoplankton blooms in late winter to early spring (Heussner et al., 2006).

4.3. Distinct responses of *L. pertusa* and *M. oculata* to environmental conditions

It was previously shown that *L. pertusa* has a higher growth rate than *M. oculata* (Lartaud et al., 2014; 2017), particularly at the studied location in the Lacaze-Duthiers canyon where *L. pertusa* dominates the assemblages (Gori et al., 2013; Fabri et al., 2014). This study highlights the different growth dynamics between the two species in response to local environment within a shared habitat. Both species feed primarily on zooplankton and phytodetritus (Duineveld et al., 2007; Carlier et al., 2009). *Lophelia pertusa* is, however, a more opportunistic feeder (Dodds et al., 2009) and has a higher prey capture rate (Kiriakoulakis et al., 2005; Tsounis et al., 2010). As a consequence, *L. pertusa* should be less impacted by changes in food type, likely associated to the intensity and period of occurrence of water plumes. Other factors such as the reproduction strategy (Waller and Tyler, 2005) and the microbiome (Meistertzheim et al., 2016) suggest more plasticity in the behavior of *L. pertusa* and could partly explain a higher resilience to environmental changes compared to *M. oculata*. In the NE Atlantic Ocean, *L. pertusa*'s seasonal reproductive strategy involves the spawning of a high quantity of small oocytes for a maximal dispersion, contrary to *M. oculata* that spawns a smaller quantity of bigger oocytes. This suggests that *M. oculata* may produce and spawn gametes only during optimal conditions for reproduction (Waller and Tyler, 2005). In addition, *M. oculata* is more sensitive to thermal stress compared to *L. pertusa* (Naumann et al., 2014; Brooke et al., 2013) which suggests that *L. pertusa* is more plastic in term of temperature variations. At the level of the microbiome, the difference in associated bacterial community composition could also reflect different ecological strategies. *Madrepora oculata* has a very specific microbiome in contrast with the more versatile microbiome for *L. pertusa,* suggesting again that this species is more plastic to environmental variations (Meistertzheim et al., 2016).

It is thus essential to incorporate the inter species responses to forecast future changes of deep sea reefs and establish efficient conservation measures for these critical habitats, particularly considering that CWCs are at their upper thermal tolerance in the

Mediterranean region (Freiwald et al., 2004). In this region, predictive models using the IPCC A2 scenario indicate less precipitation and river runoff in the coming century, with higher temperatures suggesting that dense water shelf cascade to the deep basin in the Gulf of Lion could disappear by 2100 (Somot et al., 2006; Herrmann et al., 2008).

4.4. Are cold-water corals slow-growing species?

Scleractinian cold-water corals have long been considered as slow-growing species with growth rates below 1 cm y^{-1} (Wilson, 1979; Freiwald and Roberts, 2006), much lower than zooxanthellate scleractinian coral growth that can exceed 15 cm y^{-1} for some species (Dullo, 2005). This study highlights that *in situ* CWCs biomineralization can be much higher and comparable to some of their shallow water analogues. Some studies already showed that scleractinian cold water corals could exceed 3 cm y^{-1} in the Mediterranean Sea and the Gulf of Mexico (Lartaud et al., 2017; Larcom et al., 2014), but here we report growth rates reaching 4 cm y^{-1}. The growth of CWCs is strongly influenced by biotic and abiotic factors such as food supply, hydrography and temperature (Cairns and Macintyre, 1992; Thiem et al., 2006; Guinotte et al., 2006; Roberts, 2009; Purser et al., 2010). Temperature increase can improve physiological processes such as growth rates due to increase metabolism efficiency (Dodds et al., 2007). However, the thermal optimum and the potential for adaptation to temperature variations are still unknown for CWCs. Although in the Mediterranean Sea, CWCs are thought to reach their upper ecological thermic limit (i.e., 14°C) (Freiwald et al., 2004), the high growth rates could reflect present particular favorable conditions compared to other coral areas, likely due to the supply of food from peculiar hydrological conditions.

5. Conclusion

This first long-term *in situ* study conducted on CWCs highlights growth rate variations associated with inter-annual changes in environmental conditions driven by hydrological processes. In the Lacaze Duthiers canyon, episodic hydrologic events (e.g. downwelling, cascading, storms) transport surface waters drive organic particles from surface production inside the canyon and are likely to modulate the quality and quantity of food available for CWCs. Consistent with these irregular inputs, the growth of CWCs differs from year to year depending on the type of dense water shelf event: (i) strong water plume events cause high budding rates but low colony linear extension by limiting prey capture rates with high current speed, (ii) the absence of water plume events cause low budding rates, low linear extension and high mortality due to high sedimentation rates, and (iii) median water plume events cause high budding rates and high linear extension associated with higher organic matter supply. Furthermore, we observed an inter-specific variability in mortality, growth rates and linear extension between *L. pertusa* and *M. oculata*. *Lophelia pertusa* appears more plastic to environmental variation as compared to *M. oculata*. Finally, we demonstrated for the first time that *L. pertusa* could reach linear extension comparable to their shallow water counterparts.

In the context of the ongoing global change, an increase of the stratification is expected in the Mediterranean Sea, which will reduce the supply of fresh oxygenated water containing organic matter from the surface to the deep ocean. The resilience of cold-water corals in the future Mediterranean Sea is threated, particularly considering that CWCs are supposed at their upper thermal tolerance. It is essential to incorporate the inter species responses to establish efficient conservation strategies for these critical habitats.

Author contributions

LC, FL, NLB and PG designed the study. LC, NLB, XDDM, EP, PG and FL conducted the study, analyzed the data and wrote the paper.

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Additional information

Supplementary information accompanies this paper.

Competing Interests: The authors declare no competing interests.

Figure and table captions

Figure 1: Cold-water coral reefs with (A) *Lophelia pertusa*, and (B) *Madrepora oculata* in the Lacaze-Duthiers canyon (C) where branches and nubbins has been deployed on transplant units fixed to a deep-sea experimentation platform (© UPMC-Fondation TOTAL).

Figure 2: The pictures represent the same replicate of *L. pertusa* during four years (in purple, the first linear extension during 2015-2016, the second in green during 2016-2017 and the third in red during 2017-2018).

Figure 3: Polyp mortality of *L. pertusa* (grey) and *M. oculata* (white bars) between 2010 and 2018. All the values represented the median and quartiles.

Figure 4: Budding rates (%) of *L. pertusa* (grey) and *M. oculata* (white bars) between 2010 and 2018. All the values represented the median and quartiles.

Figure 5: Linear extension (mm.y^{-1}) of *L. pertusa* (grey) and *M. oculata* (white bars) between 2010 and 2018. All the values represented the median and quartiles.

Figure 6: Time series of significant wave height at the Leucate site, near-bottom temperature, near-bottom current speed component along the canyon axis, and near-bottom suspended particle matter concentration, at 530 m depth in the Lacaze-Duthiers canyon for the (A) 2015-2016, (B) 2016-2017 and (C) 2017-2018.

Table 1: Characteristics of the transplant units used for each time period for *L. pertusa* and *M. oculata*. The mean ± SD is shown for the polyp mortality.

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Table 1: Characteristics of the transplant units used for each time period for *L. pertusa* and *M. oculata*. The mean ± SD is shown for the polyp mortality.

Species	Time period	Transplant unit	Number of colonies	Number of replicates	Initial number of polyps	Number of new polyps	Breakage (%)	Mortality (%)
L. pertusa	Nov2010-Sep2011	NS	2	4	12	6	8	0 ± 0
	Sep2011-Jul2012	NS	2	6	20	9	5	18 ± 36
	Jul2013-Oct2014	NS	1	4	13	0	8	100 ± 0
		BS	2	2	20	1	13	100 ± 0
	Jun2015-Jun2016	NS	2	7	31	6	9	87 ± 34
		BS	1	3	61	13	24	34 ± 57
	Jun2016-Jun2017	BS	2	5	96	66	3	15 ± 12
	Jun2017-May2018	BS	2	5	130	54	1	17 ± 27
M. oculata	Nov2010-Sep2011	NS	2	5	38	16	0	0 ± 0
	Sep2011-Jul2012	NS	2	7	76	11	0	48 ± 43
	Jul2013-Oct2014	NS	3	12	118	7	5	96 ± 13
		BS	3	6	141	10	51	100 ± 0
	Jun2015-Jun2016	NS	1	8	81	2	10	67 ± 38
		BS	1	2	39	0	34	86 ± 19
	Jun2016-Jun2017	BS	1	5	229	63	6	23 ± 12
	Jun2017-May2018	BS	1	6	226	9	0	70 ± 40

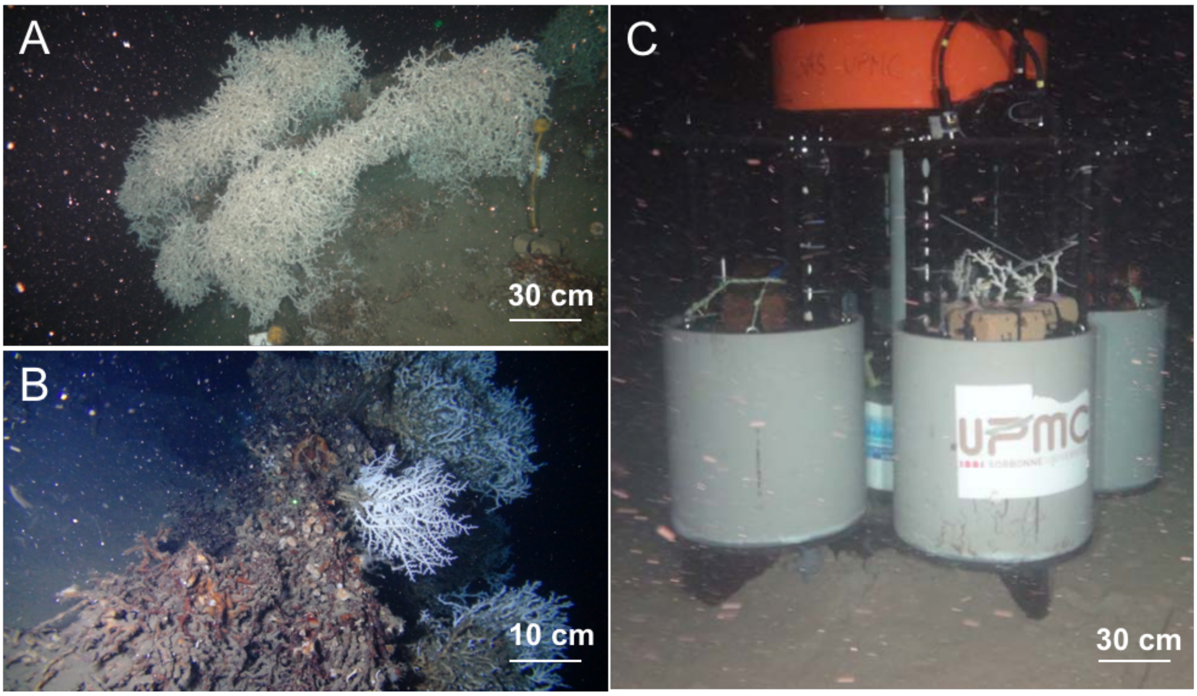


Figure 1: (A-B) Cold-water coral reefs with (A) *Lophelia pertusa* and (B) *Madrepora oculata* in the Lacaze-Duthiers canyon, (C) where branches and nubbins has been deployed on transplant units fixed to the deep-sea experimentation platform.

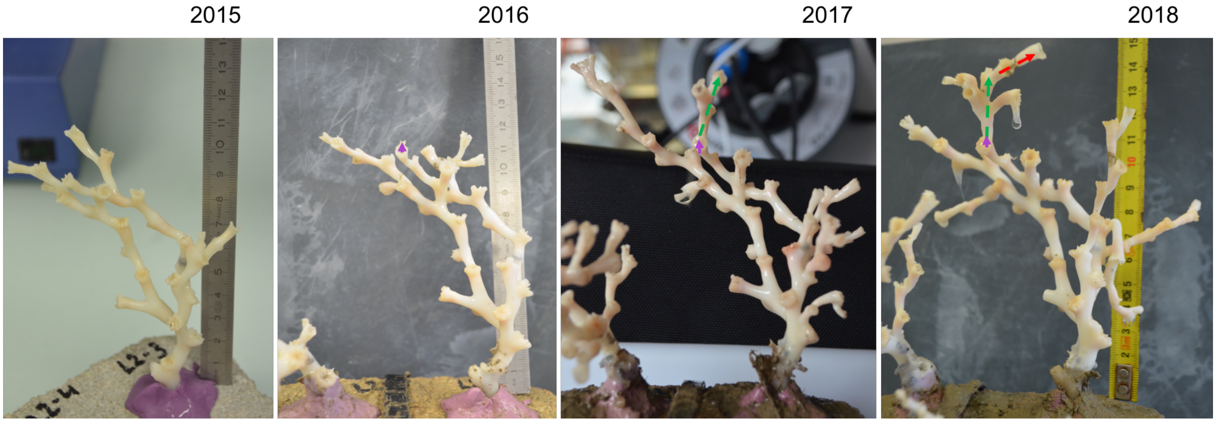


Figure 2: The pictures represent the same replicate of *L. pertusa* during four years (in purple, the first linear extension during 2015-2016, the second in green during 2016-2017 and the third in red during 2017-2018).

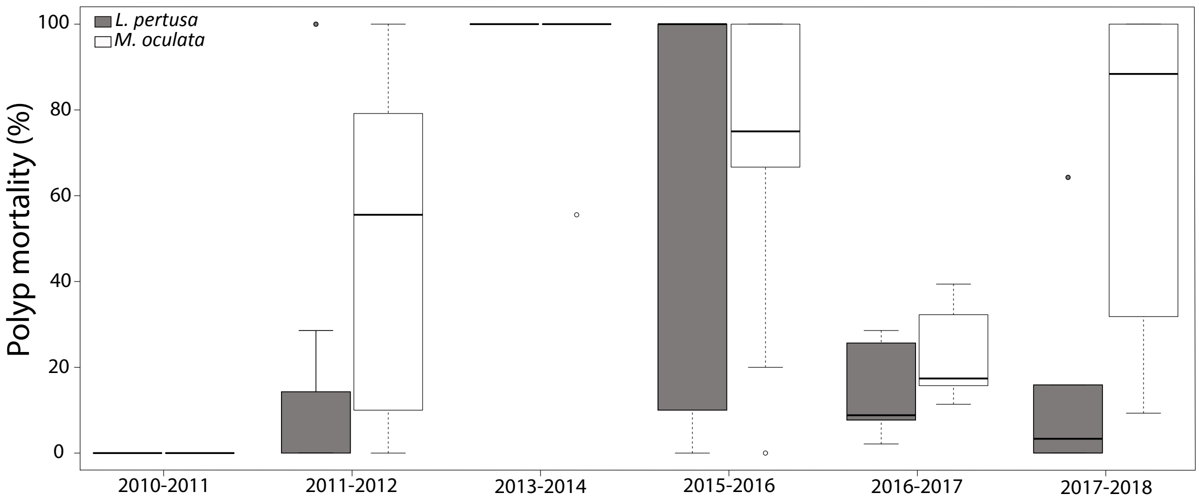


Figure 3: Polyp mortality of *L. pertusa* (grey) and *M. oculata* (white bars) between 2010 and 2018. All the values represented the median, quartiles and extrema.

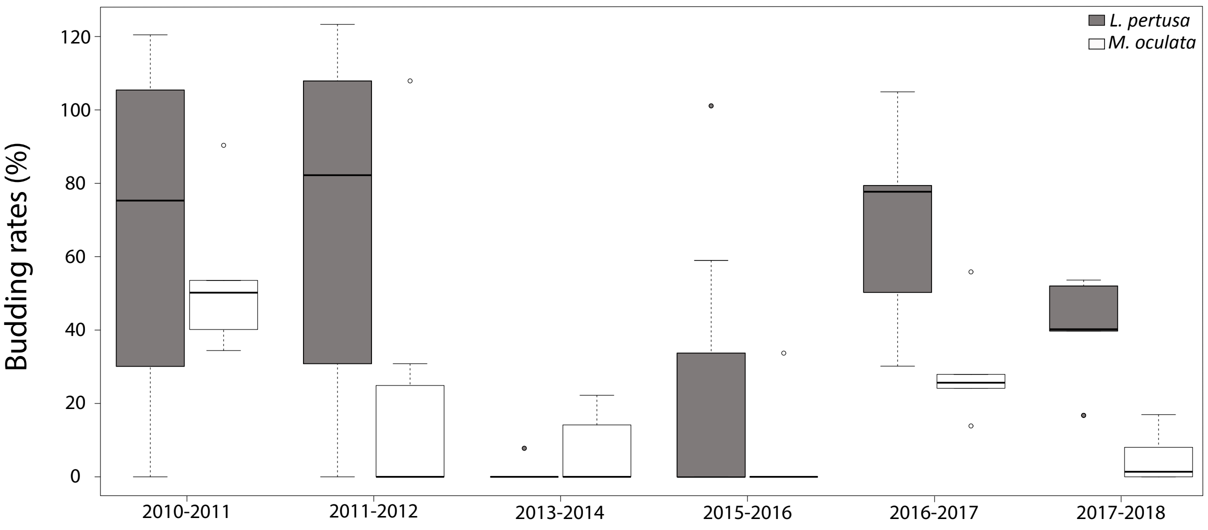


Figure 4: Budding rates (%) of *L. pertusa* (grey) and *M. oculata* (white bars) between 2010 and 2018. All the values represented the median, quartiles and extrema.

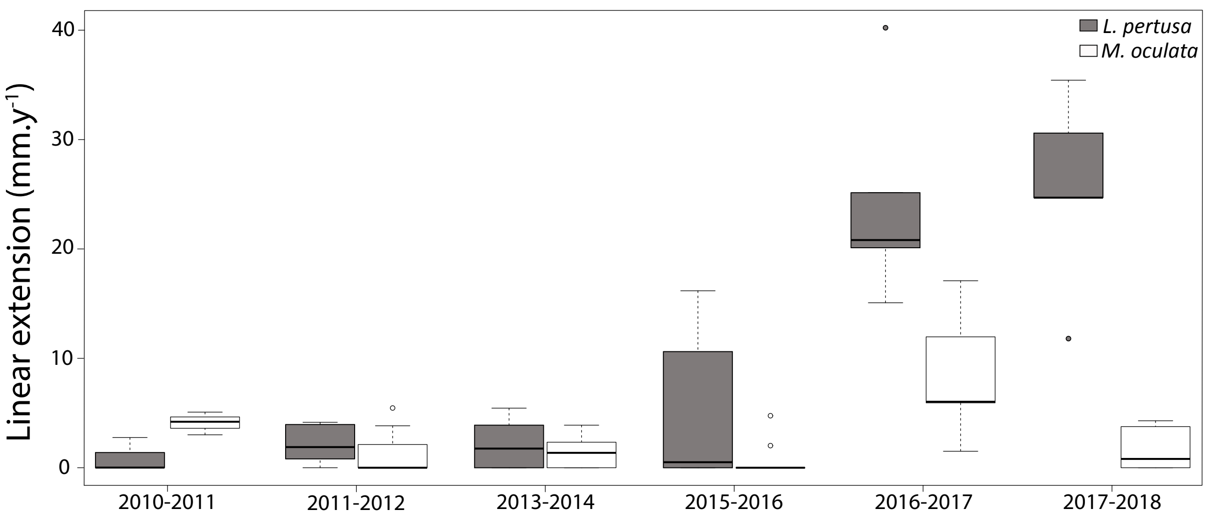
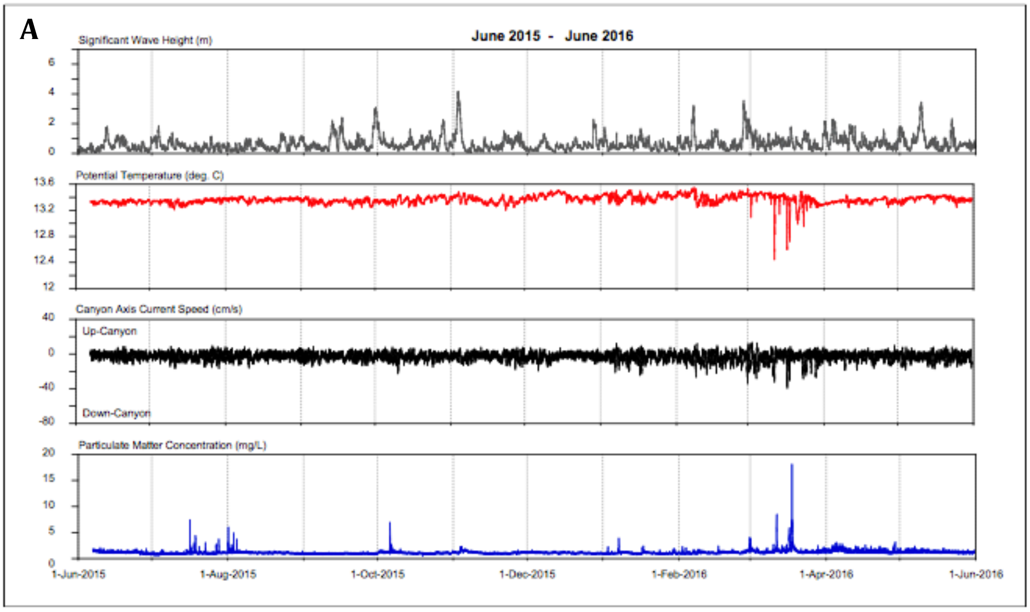
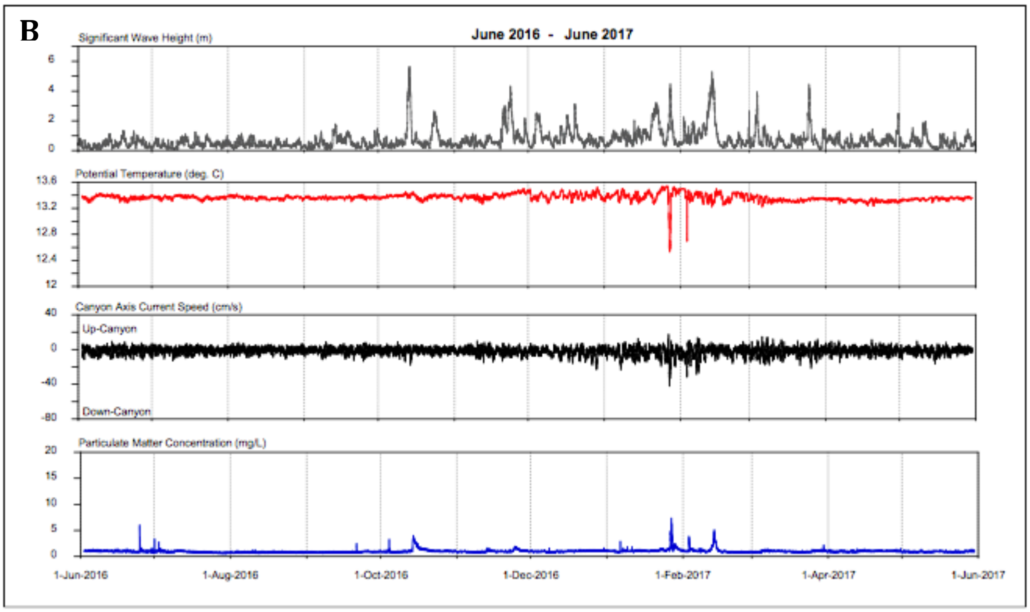


Figure 5: Linear extension (mm.y^{-1}) of *L. pertusa* (grey) and *M. oculata* (white bars) between 2010 and 2018. All the values represented the median, quartiles and extrema.


A
June 2015 - June 2016
Significant Wave Height (m)
6
4
2
0
Potential Temperature (deg. C)
13.6
13.2
12.8
12.4
12
Canyon Axis Current Speed (cm/s)
40
0
-40
-80
Up-Canyon
Down-Canyon
Particulate Matter Concentration (mg/L)
20
15
10
5
0
1-Jun-2015
1-Aug-2015
1-Oct-2015
1-Dec-2015
1-Feb-2016
1-Apr-2016
1-Jun-2016


B
June 2016 - June 2017
Significant Wave Height (m)
6
4
2
0
Potential Temperature (deg. C)
13.6
13.2
12.8
12.4
12
Canyon Axis Current Speed (cm/s)
40
0
-40
-80
Up-Canyon
Down-Canyon
Particulate Matter Concentration (mg/L)
20
15
10
5
0
1-Jun-2016
1-Aug-2016
1-Oct-2016
1-Dec-2016
1-Feb-2017
1-Apr-2017
1-Jun-2017

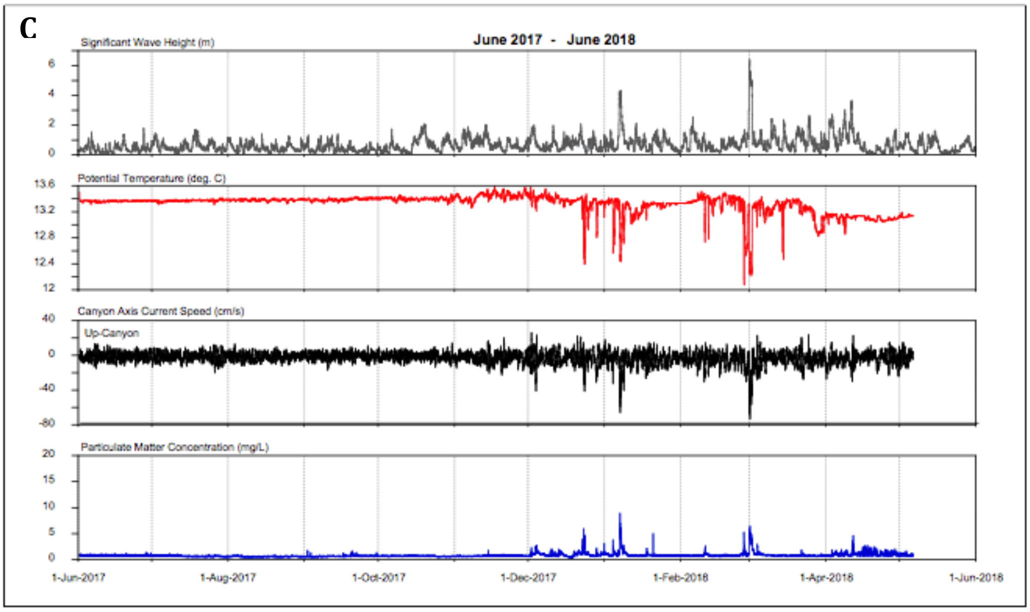

C
June 2017 - June 2018
Significant Wave Height (m)
6
4
2
0
Potential Temperature (deg. C)
13.6
13.2
12.8
12.4
12
Canyon Axis Current Speed (cm/s)
40
0
-40
-80
Up-Canyon
Particulate Matter Concentration (mg/L)
20
15
10
5
0
1-Jun-2017
1-Aug-2017
1-Oct-2017
1-Dec-2017
1-Feb-2018
1-Apr-2018
1-Jun-2018

Figure 6: Time series of significant wave height at the Leucate site, near-bottom temperature, near-bottom current speed component along the canyon axis, and near-bottom suspended particle matter concentration, at 530 m depth in the Lacaze-Duthiers canyon for the (A) 2015-2016, (B) 2016-2017 and (C) 2017-2018.