1) LIST OF RELEVANT CHANGES MADE IN THE MANUSCRIPT

1. Abstract was improved following the reviewers suggestions.
2. We modified the abstract, the caption in Fig. 6 and also included additional sentences in sections 2.2 and 4.3, in order to clarify that all coral growth rates and some of the omega values (Panamá and Galápagos) used to evaluate the relationship between carbonate chemistry and coral growth (Fig. 6) were not measured during this study, but taken from previously published data (Jiménez and Cortés, 2003; Manzello, 2010a,b).
3. Methodology used in 2009 for pH and xCO2 measurements was described in more detail (section 2.3).
4. Also in section 2.3, we included all the corresponding values of TA and DIC during periods 2012 and 2013, used as input parameters in the model. We have also included a sentence indicating that despite TA and DIC calculations derived from pH and pCO_2 measurements are prone to errors, our calculated values (including those used as input in the model) are well in range with the values previously reported by other studies.
5. The term rain-ratio was better described, as well as the procedure followed to verify the results from the model. Accordingly, redaction of last sentences in section 2.3 was improved.
6. In section 3.2 we replaced the extreme values of TA and DIC with the mean values, since the values used as input parameters in the model are in range with the mean values for each period.
7. Wording in some sections (particularly in conclusions and section 4.3) was modified, in order to reduce conjectures and improve reading. Sections 4.3 and 5 (conclusions) were highly improved by following all the comments from both reviewers. Modifications included the deletion of some sentences and inclusion of new ones. All these changes can be followed in the marked-up version of the manuscript.
8. An additional panel (b) was included in Fig. 3, in order to show the validation of pCO_2 measurements.
9. Units of pCO_2 in Figs. 4 and 5 were modified. Units of DIC and TA were included in Fig. 5.
10. All technical suggestions from both reviewers were included in the revised version.

2) POINT-BY-POINT RESPONSE TO REVIEWS

Referee #1

[RC1] First, I think it's important that the authors make it clear at the beginning of the manuscript (Abstract and Methods) that they did not measure coral growth in this study that they used previously published data to evaluate the relationships between carbonate chemistry and coral growth, because this was not obvious to me until the Discussion. I would also say what studies you derived the ecological data from in the Methods and include a brief description of the methodologies those researchers used so that readers can evaluate those data.

REPLY: We have made this point clear in the first sections of the manuscript (Abstract and Methods). The following paragraph was included at the end of section 2.2:

"All coral growth values were taken from the literature; linear extension rates from Bahía Culebra were measured by Jiménez and Cortés (2003), whilst coral growth in Panamá and Galápagos was measured by Manzello (2010a). For the correlation between coral growth and Ωa, we used the mean Ωa values from Panamá and Galápagos previously reported by Manzello (2010b)."

[RC1] The authors should also consider adding some additional text in the Methods/Discussion regarding the collection and interpretation of the carbonate-chemistry data. I've listed a number of specific comments below, but my most significant concern is with the statement that DIC is temperature-independent. Temperature impacts the solubility of CO2 and directly impacts DIC. Additionally, since the DIC data are derived from pCO2 measurements, which are dependent on T, this does not get rid of the temperature effect on pCO2. I would like to see the author address this issue more thoroughly.

REPLY: The following sentence was included in section 3.2:

"We also compared DIC and TA, in order to estimate to which extend the observedvariations of pCO_2 were caused by changes in temperature and/or DIC concentrations."

[RC1] P2, L25: But see Toth et al. 2012. Accretion rates in Panama when reefs were growing were comparable to rates observed on reefs in the Caribbean and the authors did not find a significant difference in reef accretion between upwelling and non-upwelling sites. I would suggest making the language here more conservative.

REPLY: The sentence was modified:
Original: "...resulting in poorly cemented coral reefs with low accretion rates that are subject to rapid bioerosion"

Modified: "...and have the potential to produce poorly cemented coral reefs with low accretion rates that are subject to rapid bioerosion"

[RC1] P3, L23: Please provide information on the pH scale used.

REPLY:The pH scale as included => total hydrogen ion scale

[RC1] P3, L28: How can you be sure that the carbonate chemistry at 30 cm was the same as where the instrument was (1.5 m)?

REPLY: We can't. But the samples were taken 30 cm below the surface, which is 1.2 m above the instrument and up to 7.7 m above the bottom (the distance above bottom varied with tide cycles). Since we have never seen any indication of depth related changes (e.g. in turbidity) we assume that DIC and TA changes within the water column are negligible.

[RC1] P4, L8: Did Rixen et al. 2012 use the same methodology for measuring carbonate chemistry? I think it's important to include this information so that readers can fully evaluate the results.

REPLY: The following sentence was included: "In 2009 xCO2 was measured by an underway pCO2 system (SUNDANS) equipped with an infrared gas analyzer (LI-7000), and pH was measured using an Orion ROSS electrode and an Orion Star™."

[RC1] P4, L11-12: I would suggest including the statement "All GLM assumptions were met" here instead of in the Results.

REPLY: It was included as follow : "The GLM was evaluated using graphical methods to identify violations of assumptions of homogeneity of variance and normality of residuals. All GLM assumptions were met."

[RC1] P4, L19: Please include a citation for the rain-ratio (Archer and Maier-Reimer 1994?) and describe what it is.

REPLY: The term rain-ratio seems to be confusing since it actually describes the ratio between the export of organic carbon and calcium carbonate carbon. Accordingly, it was changed as follows:

"R_{OI} describes the ratio between the production of organic carbon (POC) and precipitation of calcium carbonate carbon (PIC), and was used to link ΔPOC to ΔPIC (R_{OI}=POC/PIC) (Eq. 2, 3)."

[RC1] P4, L23: What are the ROI values of -2.6 and 0.8 based on. Please explain in the text where these numbers came from.

REPLY: These numbers were used to run the model in order to obtain the best fit between measured and calculated pH and pCO2 values. The assumption of calcium carbonate dissolution caused the negative sign.

Modified sentence read as follow: "To verify the results from the model, we used the output ΔDIC and ΔTA to calculate new pCO2 and pH values, which were further compared to the measured ones. The best fit between modeled and measured values was achieved with a respective R_{OI} of -2.6 for 2012 and 1.0 for 2013, whereas the assumption of calcium carbonate dissolution caused the negative sign."

[RC1] P5, L16-17: Temperature variability also can impact DIC. Also since these data are derived from pCO2 measurements, which are dependent on T, this does not get rid of the temperature effect

REPLY: What we meant to say was that we tried to estimate to which extends temperature and/or changes in the DIC concentrations had an effect on the observedvariations of pCO2. The following sentence was included in section 3.2:

"We also compared DIC and TA, in order to estimate to which extend the observed variations of pCO2 were caused by changes in temperature and /or DIC concentrations."

[RC1] P5, L22: include error term for the aragonite saturation state

REPLY: Standard deviation (SD) was included as follows: 3.06 ± 0.49

[RC1] P6, L5-7: It would be more informative to talk about how much DIC dropped during the "upwelling-like" event in 2012 than to talk about the overall average for the whole sampling period.

REPLY: The following sentence was included: During the seven days that lasted the cold-water intrusion event (June 10-17) the DIC concentrations dropped from 2355.39 µmol kg^{-1} down to 1715.30 µmol kg^{-1}.

[RC1] P6, L16: You can't really make conclusions about how regular these sorts of events are based on a few weeks of data from just two years. I would change the wording here to reflect this.

REPLY: Included modification:
Original: "The absence of such a cold-event during the non-upwelling season in 2013 shows that it is an irregular feature…"

Modified: "The absence of such a cold-event during the non-upwelling season in 2013 suggests that the occurrence of this kind of events might be an irregular feature…"

[RC1] P6, L26: The wording of this sentence is confusing. I would rephrase to something like: Although the pCO2 cycles in 2013 followed a similar pattern to 2012, pH was more variable (or less predicable). I would also move this sentence to the end of the previous paragraph and start the next paragraph with "To characterize..."

REPLY:
1) Modified sentence read as follows: "Although the pCO2 cycles in 2013 followed a similar pattern to 2012, pH cycles were less predictable."
2) Sentence was moved to the end of the previous paragraph and the next paragraph started with "To characterize…"

[RC1] P7, L3: I don't understand what this sentence means. Which cycles? Could not be observed in the data? In the model? I actually think that this whole paragraph needs to be fleshed out more. It's not clear to me what the authors are trying to say.

REPLY: The first sentence is certainly confusing, and after a careful reading we concluded that it has no relevance in transmitting the take-home message, which basically is: pH and pCO2 show pronounced daily cycles but the interaction of metabolic processes difficult to identify a clear pattern in the daily cycles of DIC and TA.

To improve reader understands the first sentence of the paragraph was removed. The following paragraph was rephrased and read as follows:

"However, in our case the determined TA and DIC concentrations constrain the impact of the formation of organic matter (POC = photosynthesis – respiration) and calcification (PIC = calcification – dissolution) on the carbonate system. This sets the boundaries within which the observed diurnal cycle of pH and pCO_2 has to be explained (Fig. 5c, d). In order to reconstruct the diurnal cycle of pH and pCO_2 within these boundaries we assumed a photosynthetic-enhanced calcification during the day and vice versa, dissolution and respiration at night. Thereby the best fit between pH and pCO_2 measured in 2013 and the respective calculated values could be obtained by using a R_{OI} of 1. This approach failed to explain the diurnal cycle of pH and pCO_2 as observed during the 2012 cold-water intrusion event (June 10-17). The only solution we found to explain these pronounced diurnal cycles within the given DIC and TA boundaries was to assume that photosynthesis and dissolution prevailed during the day and respiration and calcification occurred at night. The R_{OI} of -2.6 resulted in the best fit between the measured and calculated pH and pCO_2 for the 2012 event, whereas the negative sign reflects the contrasting effects of calcification and dissolution on the DIC concentration."

[RC1] P7, L10: add a reference to Fig. 5c&d at the end of the sentence ending with "respiration"

REPLY: reference to Fig. 5c and 5d was included.

[RC1] P7, L10: Clarify whether you are describing changes that just happened during the cold-water event or during the entire sampling period in 2012.

REPLY: We are describing the changes during the cold-water event (7 days), not during the full period 2012 (15 days). For a better understanding, the sentence was modified as previously described in [RC1] P7, L3.

[RC1] P7, L30-31: This sentence is misleading. I think that what you mean to say is that saturationstate in each of those locations predicts extension rate. I'm assuming that you used the saturation states/linear extension determined by Manzello 2010 for Panama and Galapagos, but this is not clear in either the text or the figure.

REPLY: The work by Manzello was cited in the text and in Fig. 6. We have also modified the sentenceto clarify that we used those values as input toestimate the correlation between omega and coral growth (Fig. 6).

Writing in text was improved in the following way:

"Aragonite saturation state (Ω_a) is known as one of the main variables influencing coral growth and therefore reef distribution around the world (Kleypas et al. 1999). By integrating the data from the present study and values previously reported by Rixen et al. (2012), we estimated that the annual mean Ω_a in Bahía Culebra is 3.06. Additionally, earlier studies in the ETP measured Ω_a values and coral extension rates from locations that are under the influence of upwelling events (Manzello 2010a), whilst extension rates from Bahía Culebra were measured by Jiménez and Cortés (2003). The correlation between our estimated Ω_a with the available data from Bahía Culebra, Panamá and Galápagos indicates that coral extension rates in each of those locations are predictable by their corresponding Ω_a values (Fig. 6)."

Figure caption was modified as follow: "Mean aragonite saturation states (Ω_a) - from present and former studies - versus previously reported mean linear extension rates of *Pocilloporadamicornis*and *Pavonaclavus*from upwelling areas in Costa Rica (CR) (Jiménez and Cortés, 2003), Panamá (PAN) and Galápagos (GAL) (Manzello, 2010a). Red broken line shows the regression equation as estimated by Rixen et al. (2012). Red mark represents our estimated Ω_a threshold for Bahía Culebra, when coral growth equals zero"

[RC1] P8, L11-12: I think it would be good to compare your observation of reef thickness with reef thickness elsewhere in Costa Rica or elsewhere in the ETP, as most reader won't be familiar with how thick a reef "should" be see:

REPLY: P8 L10-12 was modified as follows: "Despite the corals' high annual mean linear extension rates, studies carried out in 1973 showed that the thickness of the reef framework within our study area was with 0.6 to 3 m (mean 1.8 m) among the lowest in the ETP where Holocene framework accumulation in Pocillopora-dominated reefs could reach up to 9 m (Glynn et al., 1983; Toth et al., 2017). During the last decade it further decreased (Alvarado et al., 2012), and during the period of our observation the reef frameworks of Pocillopora spp in Bahía Culebra hardly exceeded a thickness of 0.5 m."

[RC1] P8, L14: It's not correct to talk about "coral" accretion because accretion is a net measure of the growth of a reef. I would re-phrase the beginning of this sentence to something like: Gaps in coral-reef accretion. I would also specify that these gaps are known from the geological record of the ETP. They are not common elsewhere.

REPLY: The sentence was modified:
Original: "Coral's accretional gaps, which are known from the geological records, document the vulnerability of these reefs. They have been..."

Modified: "Gaps in coral reef accretion at the ETP are known from the geological record (Toth et al. 2012; 2015; 2017). They have been..."

[RC1] P8, L20: It’s likely that OA will threaten places like Bahia Culebra sooner than elsewhere right? It might be interesting to include a brief discussion of when/how OA may impact reefs in the ETP vs elsewhere and what the implications of this would be.

REPLY: We have included the following sentences just before the last sentence of the current paragraph:

According to climate predictions, the global Ω_a will reach values < 2.0 by the end of this century (IPCC, 2014) and major upwelling systems such as those off California and South America will intensify (Wang et al., 2015). Combined effects of ocean acidification and impacts of stronger upwelling on Ω_a in the ETP and on Ω_a in Bahía Culebra are difficult to predict.

“Worldwide, OA is expected to reduce coral reefs’ resilience by decreasing calcification and increasing dissolution and bioerosion (Kleypas et al., 1999; Yates and Halley, 2006a; Anthony et al., 2011). Coral reefs from the ETP are affected by chronic and acute disturbances, such as thermal stress and natural acidification resulting from ENSO and upwelling events, respectively (Manzello et al., 2008; Manzello, 2010b). Historically, these reefs have shown a high resilience to both stressors by separately but their coupled interaction can cause coral reef lost within the next decades. The ETP have the lowest $\Omega_a$of the tropics, near to the threshold values for coral reef distribution,therefore the reefs from this region may be the most affected by the increasing levels of anthropogenic CO2 and also show the first negative impacts of this human induced OA (Manzello et al., 2017). This emphasizes the importance of the Paris agreement and all the global efforts to reduce the CO2 emission into the atmosphere (Figueres et al., 2017)”

[RC1] P8, L31: I would make it clear here that previous studies have shown that reef accretion is low in Bahia Culebra.

REPLY: We have modified the sentence in section 4.3 (P8, L10-11) to clarify this point; therefore we consider that this statement can be removed from the “Conclusions” section. Sentences spanning lines P8, L28 to P9, L1 were modified as follow:

Original sentence: “Rising levels of Ω_a enhance coral growth during the non-upwelling season due to which the linear extension rates of the main reef building corals in Bahía Culebra were among the highest in the ETP; however, reef accretion was low due to erosion”.

Modified sentence: “Previous studies reported that the linear extension rates measured in Bahía Culebra were among the highest in the ETP, thus is likely that coral growth in this bay is enhanced with increased Ω_a during periods with no entrainment of low-pH waters. However, coral growth must be measured during both seasons in order to confirm this assumption.Threshold values of Ω_a when coral growth likely approaches zero were derived from the...”

[RC1] Technical corrections: All technical corrections were included

Referee #2

[RC2]The calculation of TA and DIC from pH and pCO2 is unreliable and prone to large errors (see Cullison-Gray et al. 2011; Gray et al. 2011, which you cite). This is probably why you are reporting such unbelievably high values of TA (>2600) and DIC (>2300). Not only do these values never occur on coral reefs (to my knowledge), even in strong upwelling zones like the ETP, you are also reporting relatively low salinities of 32.5. This makes these high values all the more suspect because if you calculate salinity normalized for a TA = 2715, you get NTA= 2923! These types of DIC and TA values are unheard of from reef environments.As such, you need to remove all DIC and TA values that were calculated from pH and pCO2, including the model you generated from some of those values to interpret rates of metabolism driving diurnal changes. Unfortunately, this all has to be deleted from the paper.

REPLY:
We have included a sentence in section 2.3 explaining that calculation of TA and DIC from pH and pCO2 are prone to errors, which according to results from other studies could range between 16 (Millero 2007, Table 9) and 250 µmol / kg (Cullison Gray et al. 2011). For the same, reason in section 4.1 we focused on the pH and pCO2 values.

However, the model was produced to explain the observed changes in pH and pCO2 and to untangle the effects of interacting processes on the pCO2 and pH. For example, as mentioned by the reviewer (see comments below) that photosynthesis explains a drop of pCO2 and increase of pH is correct, but the model also shows that the effect on the pH is insufficient to explain the observed increase of pH in 2013. As indicated by the model, changes in pCO2 and pH can be explained only if carbonate dissolution is considered in addition to photosynthesis. The TA (2120 – 2310) and DIC (1800 – 2040) values used in the model are well within the range reported in other studies (Manzello 2010, Table 1) and far below the extremes, which raised the concern of the reviewer. To improve the understanding, we have also included in section 2.3 the TA and DIC values used as input parameters in the model and the extreme values were removed from Table 1.

In contrast to the pCO2 and the pH, TA and DIC values, which were calculated from the pCO2 and pH, do not reveal a diurnal cycle as the one in the model. However, the mean DIC and TA values of about 1800 +/- 200 µmol/kg and 2100 /- 250 µmol /kg, which were calculated from the pCO2 and pH, are well within the range of those reported from other studies (Manzello 2010, Cyronak et al. 2013) and the one used in the model. This fitting within the range implies, furthermore, that the TA and DIC values used in our model were acceptable.

[RC2] Please be clear as to what you actually measured versus what you hypothesize, or think is going on. For instance, in the abstract you discuss how calcification is enhanced during the non-upwelling season when saturation states are elevated. This may be true, but at this point it is a hypothesis as you have no data to support it. There are several other instances where hypotheses are discussed as fact.

REPLY: Writing was modified through the text, to clarify which variables were measured in the present study and which values were taken from the literature. Sentences where hypotheses were discussed as facts were removed or modified.

[RC2] What is the proximity of the instruments to an actual coral reef? You need to be clear about this because what you are measuring may actually be a result of the metabolism of the carbonate benthos directly under the dock plus the water column processes rather than anything to do with reef dynamics.

REPLY: The instruments were deployed approximately 200 m east of a small *Pocillopora* spp. patch reef. However, when compared to reefs in the western Pacific Ocean, the reefs in the ETP (e.g. in Bahía Culebra) are poorly developed. Our intention was to characterize the carbonate chemistry within the bay (Bahía Culebra) and its impact on the reefs. Our results indicate that physical oceanographic processes, such as upwelling and exchange between the bay and the open ocean waters, influence the carbonate chemistry on timescales of weeks to months, where the metabolic processes (photosynthesis and calcifications) influence the diurnal cycle. To which extend benthic and pelagic processes control the diurnal cycle, could not be studied based on our data. This was clarified in the conclusions section.

[RC2] P2, line 19: You can't say adaptation without genetics work. Reword to say "adaptation or acclimatization"

REPLY: Was changed.

[RC2] P2, last line: Thus far there is really no data out there suggesting that OA will directly lead to coral mortality. In fact, in a seminal study, Fine and Tchernov (2007, Science) exposed two coral species to undersaturation and found they stopped growing skeletons and lived in an anemone-like state. Once conditions were raised above saturation, they began producing skeletons again.

REPLY: Accordingly, we changed "coral survival" for "coral reef development within this bay".

[RC2] P3, section 2.2: You discuss taking discrete samples, but do not say how many or how often. Please mention this. The values of TA >2600 and DIC > 2300 have to be calculated from pH-pCO2. You show the result of 8 bottle samples pH relative to the SAMI pH – what about the SAMI CO2 or any other data calculated from the bottles?

REPLY: We included an additional panel in Fig. 3, showing the regression between SAMI-pCO2 and calculated pCO2 from measured TA and DIC. Due to logistics the frequency for collection of discrete water samples was irregular, but in section 2.2 was pointed out that they were collected as often as possible.

[RC2] P5: salinity is a unitless value. PSU describes the scale and is not a unit

REPLY: Accordingly, the term "psu" was removed from all the text.

[RC2] P5, line 5: Need to say what the number after the plus and minus is the first time you use it.

REPLY: The following was included after the 29.61 ± 0.93: (average ± standard deviation)

[RC2] P7, 1st line: why couldn't stimulation of photosynthesis from higher nutrients during upwelling be causing the large amplitude? You can't speak to dissolution without actual TA data and increased photosynthesis seems more likely.

REPLY: See first comment: In principle yes. But even if we would assume that photosynthesis caused the measured decrease of pCO2, the associated impact on the pH would be insufficient to explain the observed increase in pH. The assumption of carbonate dissolution is plausible and would solve this discrepancy. Therefore, we produced the model to test such hypotheses.

[RC2] P7, line 25: Say adapted and or acclimatized.

REPLY: "and/or acclimatized" was added.

[RC2] P7, last line: Reword to say saturation sate is one of the controlling factors in coral growth. Its likely of secondary or tertiary level importance behind temperature and light.
REPLY: Taking into account your observations and the comments from another reviewer, the full sentence and paragraph was modified (see reply to RC1 P7, L30-31).

[RC2] P8: delete sentence spanning lines 3 to 5 as well as last sentence of 1st paragraph

REPLY: Sentence spanning lines 3 to 5 was removed. However, we consider that the last sentence of the same paragraph is important, as point out that these coral reefs are also threatened by additional stressors resulting from human activities, therefore was not deleted from the text.

[RC2] P8, line 10: Did you measure reef thickness? Also, I'd avoid saying they are growing on the edge of their ecological tolerance. Its not clear what is meant by that.

REPLY: Reef thickness was visually estimated during numerous dives. We have been working in the study area for more than two decades.

Regarding the second comment, the sentence was modified: "These reefs are growing in an environment at the limit of reef-building corals tolerance in terms of temperature, nutrient loads and pH (Manzello et al., 2017)"

[RC2] P8, last 5 or so sentences: a lot of conjecture written as fact.

REPLY: Several modifications were included, in order to reduce conjectures and improve the text:

Original: "Challenging conditions are not restricted to the upwelling season, they occur sporadically also during non-upwelling seasons, when pH and CO2 concentrations reach values comparable to those during upwelling events. Linear extension rates of the main reef building corals in the bay are sensitive to changes in Ωa, suggesting that upwelling reduces coral growth by introducing acidic subsurface waters in the surface layers. Rising levels of Ωa enhance coral growth during the non-upwelling season due to which the linear extension rates of the main reef building corals in Bahía Culebra were among the highest in the ETP; however, reef accretions was low due to erosion. The latter indicates a sensitivity of coral reefs to the intensity of the upwelling and other processes occurring during the non-upwelling/rainy season, such as human impacts on river discharges, the occurrence of cold events (e.g. 2012), and ultimately to OA. Threshold values of Ωa when coral growth likely approaches zero were derived from the correlation of Ωa and linear extension rates and this suggests that OA will seriously threat reefs in Bahía Culebra, which are already at the verge of their ecological tolerance."

Modified: "Challenging conditions for reef development are not restricted to the upwelling season, they occur sporadically also during non-upwelling season, when pH and CO2 concentrations reach values comparable to those during upwelling events. Previous studies reported that the linear extension rates measured in Bahía Culebra were among the highest in the ETP, thus is likely that coral growth in this bay is enhanced with increased Ωa during periods with no entrainment of low-pH waters. However, coral growth must be measured during both seasons in order to confirm this supposition. Threshold values of Ωa when coral growth likely approaches zero were derived from the correlation of Ωa and previously measured annual linear extension rates. The Ωa threshold values from the present study and the fact that high-CO2 waters are occasionally hauled into the bay during non-upwelling season; suggest that coral reef development in Bahía Culebra is potentially threatened by anthropogenic OA."

[RC2] Figure 4: your units for pCO2 are incorrect

REPLY: They were also incorrect in figure 5. Both figures were corrected.

3) MARKED-UP VERSION

Natural ocean acidification at Papagayo upwelling system (North Pacific Costa Rica): implications for reef development

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Abstract. Numerous experiments have shown that ocean acidification impedes coral calcification, but knowledge about in situ reef ecosystem response to ocean acidification is still scarce. Bahía Culebra, situated at the northern Pacific coast of Costa Rica, is a location naturally exposed to acidic conditions due to the Papagayo seasonal upwelling. We measured pH and pCO_2 in situ during two non-upwelling seasons (June 2012, May-June 2013), with a high temporal resolution of every 15 and 30 min, respectively, using two Submersible Autonomous Moored Instruments (SAMI-pH, SAMI-CO2). These results were compared with published data from the 2009 upwelling season~~. 2009.~~ Findings revealed that the carbonate system in Bahía Culebra shows a high temporal variability. Incoming offshore waters drive inter- and intra-seasonal changes. Lowest pH (7.8) and highest pCO_2 (658.3 µatm) values measured during a cold-water intrusion event in the non-upwelling season were similar to those minimum values reported from upwelling season (pH = 7.8, pCO_2 = 643.5 µatm), unveiling that natural acidification also occurs sporadically ~~also~~ in the non-upwelling season. This affects the interaction of photosynthesis, respiration, calcification, and carbonate dissolution and the resulting diel cycle of pH and pCO_2 in the reefs of Bahía Culebra. During non-upwelling season~~,~~ the aragonite saturation state (Ω_a) rises to values of >3.3 and ~~enhances calcification. Aragonite saturation state values~~ during upwelling season fall~~s~~ below 2.5.~~2.5, hampering calcification and coral growth. Low reef accretion in Bahía Culebra indicates high erosion rates and that these reefs grow on the verge of their ecological tolerance.~~ The Ω_a threshold values for coral growth were~~,~~ derived from the correlation between measured Ω_a and coral linear extension rates which were obtained from the literature and~~,~~ suggest that future ocean acidification will threaten the continued growth of reefs in Bahía Culebra. These data contribute to build a better understanding of the carbonate system dynamics and coral reefs key response (e.g. coral growth) to natural low-pH conditions, in upwelling areas in the Eastern Tropical Pacific and beyond.

1 Introduction

Ocean acidification (OA) caused by human-induced increase of atmospheric CO_2 (Sabine et al., 2004; Feely et al., 2009) is considered one of the major threats to marine calcifying organisms and ecosystems (Fabry et al., 2008; Hofmann et al., 2010; Doney et al., 2012; Gattuso et al., 2015). Among all marine habitats, tropical coral reefs are recognized as the most endangered ~~ones~~ (Hoegh-Guldberg et al., 2007; Kleypas and Yates, 2009; Pörtner et al., 2014), since in addition to reduced calcification (Langdon et al., 2000; Marubini et al., 2008; Doney et al., 2009; Gattuso et al., 2014), a lower pH also weakens the reef framework by favoring bioerosion and enabling carbonate dissolution (Gattuso et al., 2014; Manzello et al., 2014; Barkley et al., 2015). According to the IPCC business-as-usual scenario, about 90% of the ocean's surface waters will become undersaturated with respect to aragonite in the next decades (Gattuso et al., 2015), emphasizing the need to study the response of natural ecosystems to OA. Nowadays, aragonite undersaturated surface waters occur naturally in some parts of the ocean, as consequence of underwater volcanic seeps (Hall-Spencer et al., 2008; Fabricius et al., 2011; Enochs et al., 2015; Fabricius et al., 2015) or upwelling that drags corrosive deep water into the surface mixed layer (Feely et al., 2008; Hauri et al., 2009; Fassbender et al., 2011; Harris et al., 2013).

~~A~~Aside from some studies at volcanic seeps (Fabricius et al., 2011; Kroeker et al., 2011; Enochs et al., 2015; Fabricius et al., 2015) or at reefs in the Eastern Tropical Pacific (ETP) (Manzello, 2008, 2010a, 2010b; Manzello et al., 2008, 2014), our understanding of OA impacts on corals derives mainly from laboratory and seawater enclosure experiments (Pörtner et al., 2014; Hall-Spencer et al., 2015). These results are used to predict ecosystem responses to future OA (Kleypas et al., 2006; Kleypas and Langdon, 2006), but their reliability is challenged by the artificial conditions under which the experiments are conducted. For example, the duration of studies is often too short to allow a full adaptation or acclimatization of the organisms/systems to the changing environmental conditions, and the missing connectivity between ecosystems in seawater enclosures restricts natural interactions between organisms (Kleypas et al., 2006; Kleypas and Langdon, 2006; Hofmann et al., 2010). In situ studies in natural low-pH conditions are able to overcome some of these problems and the ETP is well known for its CO_2-enriched and acidic subsurface waters (Takahashi et al., 2014). Upwelling events decreases the carbonate saturation state (Ω) along the Central American coast (Manzello et al., 2008; Manzello, 2010b; Rixen et al., 2012), and have the potential to produce~~resulting in~~ poorly cemented coral reefs with low accretion rates that are subject to rapid bioerosion (Manzello et al., 2008; Alvarado et al., 2012).

Corals in the northern part of the Costa Rican Pacific coast are developing under the influence of the seasonal Papagayo upwelling (Jiménez et al., 2010; Rixen et al., 2012; Stuhldreier et al., 2015a, 2015b). To contribute to the general understanding of OA impacts on coral reefs, we investigated the variability of the carbonate system in the upwelling-influenced Bahía Culebra, Costa Rica. The main objectives of this study were 1) to describe the behavior of the carbonate system on diurnal and seasonal time scales, 2) to characterize the controlling processes, and 3) to determine ecological impacts of changing carbonate systems. Furthermore, our results will allow us to draw some conclusions concerning future thresholds of coral reef development within this bay.~~survival.~~

2 Methods

2.1 Study site

Bahía Culebra, located in the Gulf of Papagayo, North Pacific coast of Costa Rica (Fig. 1), is strongly influenced by the northeasterly Papagayo winds. The strongest wind jets develop during the boreal winter (Amador et al., 2016) and are driven by large-scale variations of the trade winds (Chelton et al., 2000; Alfaro and Cortés, 2012). When Papagayo winds blow through the mountain gap between southern Nicaragua and northern Costa Rica, the resulting strong offshore winds on the Pacific side lead to upwelling of cold and nutrient-enriched subsurface waters between December and April (McCreary et al., 1989; Brenes et al., 1990; Ballestero and Coen, 2004; Kessler, 2006;). These cyclonic eddies also influence the magnitude and location of the Costa Rica Dome (CRD), which is located ca. 300 km off the Gulf of Papagayo (Fiedler, 2002). However, the CRD changes its distance to the Costa Rican coast throughout the year, as a result of differences in wind forcing (Wyrtki, 1964; Fiedler, 2002). During the dry season, particularly between February and April, offshore moving water masses strengthen upwelling at the coast and shoal the thermocline in the Gulf of Papagayo (Wyrtki, 1965, 1966; Fiedler, 2002). In May-June, during the onset of the rainy season the CRD moves offshore (Fiedler, 2002; Fiedler and Talley, 2006) and the North Equatorial Countercurrent (NECC) can carry tropical water masses into Bahía Culebra until December, when again upwelling sets in (Wyrtki, 1965, 1966).

2.2 Measurements

We measured in situ pH, pCO_2 and seawater temperature (SWT) during two non-upwelling periods (15 days in June 2012 and 7 days in May-June 2013, Fig. 2). Measurements were undertaken with two Submersible Autonomous Moored Instruments (SAMI-pH and SAMI-CO_2) (www.sunburstsensors.com), in sampling intervals of 15 (June 2012) and 30 minutes (May-June 2013). SAMI-sensors were deployed at the pier of Marina Papagayo (85°39'21.41"W; 10°32'32.89"N), on top of a carbonate sandy bottom in the inner part of Bahía Culebra (Fig. 1). The water-depth varied approximately between 5-8 m depending on the tide, but sensors, hooked to the pier, moved up and down with the tide and were always at the same depth, 1.5 m below the surface. SAMI instruments measured pH (total hydrogen ion scale) and pCO_2 spectrophotometrically by using a colorimetry reagent method (DeGrandpre et al., 1995, 1999; Seidel et al., 2008). Salinity from discrete samples was measured with a WTW probe (Cond3310) and was used for correction of pH values. Calculation of aragonite saturation state (Ω_a) from parameters measured in situ with SAMI sensors is accurate (Cullison Gray et al., 2011; Gray et al., 2012), but discrete water samples were collected as often as possible to validate the instruments (Fig. 3). 250 mL borosilicate bottles were filled with seawater at 30 cm below the surface and preserved with 200 µl of 50% saturated $HgCl_2$ solution to inhibit biological activity (Dickson et al., 2007). Samples were stored at 3-4 °C until analysis. Total alkalinity (TA) and Dissolved inorganic carbon (DIC) were measured using a VINDTA 3C (Versatile Instrument for the Determination of Total dissolved inorganic carbon and Alkalinity; Marianda, Kiel, Germany) coupled with a UIC CO_2 coulometer detector (UIC Inc., Joliet, USA). Both instruments were calibrated with Dickson Certified Reference Material

(Batch 127) (Dickson et al., 2003). DIC concentrations as well as TA and Ω_a were calculated with the CO2SYS program as a function of measured pH and pCO_2; with dissociation constants of Mehrbach et al. (1973) for carbonic acid as refit by Dickson and Millero (1987), and Dickson (1990) for boric acid.

Wind speeds were obtained from a station of the Instituto Metereológico Nacional (National Metereological Institute of Costa Rica), located at the nearby Liberia airport. The Módulo de Información Oceanográfica of the University of Costa Rica (www.miocimar.ucr.ac.cr) supplied the tidal data. All coral growth values were taken from the literature; linear extension rates from Bahía Culebra were measured by Jiménez and Cortés (2003), whilst coral growth in Panamá and Galápagos was measured by Manzello (2010a). For the correlation between coral growth and Ω_a, we used the mean Ω_a values from Panamá and Galápagos previously reported by Manzello (2010b).

2.3 Data analysis

We compared our data with values measured during upwelling season in 2009 (Rixen et al., 2012). In 2009 xCO_2 was measured by an underway pCO_2 system (SUNDANS) equipped with an infrared gas analyzer (LI-7000), and pH was measured using an Orion ROSS electrode an Orion Star™. Correlations between tidal cycles and physicochemical parameters (pH, pCO_2, T, wind) during non-upwelling periods were tested via Pearson Correlation in Python. Differences in parameters (temperature, pH, pCO_2, TA, DIC, Ω_a) between all periods (2009, 2012, 2013) were tested with a General Linear Model (GLM), in the statistical package R. The GLM was evaluated using graphical methods to identify violations of assumptions of homogeneity of variance and normality of residuals. All GLM assumptions were met. Additionally, we developed a simple model to improve our understanding of processes controlling the observed diel trends, as seen in the time series data of pH and pCO_2 (Fig. 2, 4). The model simulates combined effects of metabolic processes (photosynthesis, respiration, calcification and dissolution) on the carbonate chemistry. Input parameters for starting the model were the calculated DIC (in 2012: 2037 µmol kg^{-1} at 7:00 h and 2019 µmol kg^{-1} at 15:00 h; in 2013: 1883 µmol kg^{-1} at 5:00 h and 1805 µmol kg^{-1} at 15:00 h) and TA (in 2012: 2284 µmol kg^{-1} at 7:00 h; in 2013: 2193 µmol kg^{-1} at 5:00) values, corresponding to the highest and lowest measured pCO_2 during the day. Calculation of TA and DIC from the pair pH and pCO_2 is prone to errors (Millero, 2007; Cullison Gray et al., 2011), however the values used as input parameters in the model are in range with those reported from other studies in tropical areas (Manzello, 2010b; Cyronak et al., 2013b).~~DIC and TA values corresponding to the highest and lowest measured pCO_2 during day and night.~~ The difference between the two DIC concentrations (ΔDIC) was assumed to be caused by photosynthesis/respiration and the resulting formation and decomposition of particulate organic carbon (POC) as well as calcification/dissolution and the precipitation and dissolution of particulate inorganic carbon (PIC, Eq. 1). ~~The rain-ratio (~~R_{OI} describes the ratio between the production of organic carbon (POC) and precipitation of calcium carbonate carbon (PIC), and ~~=POC/PIC)~~ was used to link ΔPOC to ΔPIC (R_{OI}=POC/PIC) (Eq. 2, 3). The R_{OI} was further constrained by the determined change of TA (ΔTA).~~(ΔTA).~~ Therefore, it was considered that photosynthesis and ~~/~~respiration of one mole of carbon increases and reduces TA by 0.15 units, respectively

(Broecker and Peng, 1982). Calcification and /dissolution of one mole of carbon decreases and increases TA by two units (Eq. 4). To To obtain the best fit between the determined (measured) and the calculated (ΔTA a R_{OI} of -2.6 and 0.8 was used for the year 2012 and 2013, respectively. To further verify the model results from the model, we used the output the calculated ΔDIC and ΔTA were used to calculate new pCO$_2$ and pH values, which were further compared to the measured ones (Fig. 5). The best fit between modeled and measured values was achieved with a respective R_{OI} of -2.6 for 2012 and 1.0 for 2013, whereas the assumption of calcium carbonate dissolution caused the negative sign.

$$\Delta DIC = \Delta POC + \Delta PIC \quad (1)$$

$$\Delta PIC = \left(\frac{\Delta POC}{R_{OI}}\right) \quad (2)$$

$$\Delta POC = \Delta DIC \,/ \left(1 + \left(\frac{1}{R_{OI}}\right)\right) \quad (3)$$

$$\Delta TA = (\Delta POC * 0.15) - \left(\left(\frac{\Delta POC}{R_{OI}}\right) * 2\right) \quad (4)$$

This was calculated on hourly time steps, separately for 2012 and 2013, using the mean SWT (2012 = 29.61 ± 0.93 °C, 2013 = 30.08 ± 0.27 °C) and salinity (2012 = 32.5, psu, 2013 = 32.5). psu).

3 Results

3.1 Carbonate chemistry during non-upwelling season

In June 2012, average SWT was 29.61 ± 0.93 (average ± standard deviation) °C and ranged from 27.13 °C to 31.37 °C. In May-June 2013 SWT ranged from 29.3 °C to 30.7 °C (average 30.08 ± 0.27°C). During both periods, the salinity was 32.5 ± 0.8. psu. During the study periods, the wind intensified during the afternoons reaching speeds of up to 8.5 m s^{-1} and 6.0 m s^{-1} in 2012 and 2013, respectively (Fig. 2). Average pH and pCO$_2$ in June 2012 were 7.98 ± 0.04 and 456.38 ± 69.68 µatm, respectively; the corresponding averages for May-June 2013 were 8.02 ± 0.03 and 375.67 ± 24.25 µatm. Since the tidal cycle wasdid not significantly correlated with the variability of pH, pCO$_2$, T or wind ($p > 0.05$) during the periods of observations (Table 2), it was excluded from further discussions. Mean Ω_a values were 3.32 ± 0.46 in June 2012 and 3.50 ± 0.49 in May-June 2013 (Table 1).

3.2 Seasonal variation of the carbonate system

MeasuredAll GLM assumptions were met and measured parameters showed significant differences between study periods ($p < 0.05$). The SWT range differed amongbetween years (Table 1); 2013 was the warmest study period, followed by 2012 and 2009. Lowest measured pH was 7.81 in June 2012, 7.84 in April 2009 and 7.95 in May-June 2013. We alsoTo minimize the temperature effect, we compared DIC and TA, in order to estimate to which extend the observed variations instead of pCO$_2$

were caused by changes in temperature and/or DIC concentrations. Mean~~. Highest~~ DIC values were 2098.71 ± 103.81~~2360.92~~ µmol kg^{-1} in April 2009, 1924.65 ± 195.07~~2355.39~~ µmol kg^{-1} in June 2012 and 1800.92 ± 142.78~~2199.50~~ µmol kg^{-1} in May-June 2013. Similarly, mean~~highest~~ TA values were 2328.42 ± 118.45~~2714.84 µmol kg^{-1} in June 2102, 2610.47~~ µmol kg^{-1} in April 2009, 2204.54 ± 212.18 µmol kg^{-1} in June 2012 and 2102.66 ± 174.79~~ and 2599.99~~ µmol kg^{-1} in May-June 2013. According to average values, April 2009 was the period with most acidic water and greater CO_2 enrichment, followed by June 2012 and May-June 2013 (Table 1). Mean Ω_a values were 2.71 ± 0.29 during upwelling season (April 2009) and 3.41~~3.37~~ ± 0.13~~0.47~~ during non-upwelling season (June 2012, May-June 2013), resulting in an~~ an~~nual average Ω_a of 3.06 ± 0.49~~3.04~~ at Bahía Culebra. Time series of pH and pCO$_2$ in June 2012 and May-June 2013 showed a pronounced daily cycle (Fig. 4), which in addition to previously described data will be discussed in the following paragraphs.

4 Discussion

4.1 Natural OA beyond the upwelling season

The observed differences in pH and pCO$_2$ between 2012 and 2013 suggest that the non-upwelling season exhibits a strong interannual variability (Table 1). In 2012 pH was lower and pCO$_2$ higher than in 2013 (Fig. 2b, c). The June 2012 time-series data showed that SWT decreased and pCO$_2$ increased from 300 to 650 µatm in less than a week, after several days of strong afternoon winds (Fig. 2a). Similarly, this increase in pCO$_2$ was accompanied by a dropped in pH form 8.04 to 7.83 (Fig. 2a). This suggests~~This suggests,~~ that an enhanced wind-driven vertical mixing entrained cooler and CO_2-enriched waters from greater water-depth into the surface layer. The associated SWT drop from 31.4 °C to 27.1 °C was similar to that~~those~~ observed during the onset of the 2009 upwelling event (26.2 °C to 23.7 °C; Rixen et al., 2012). Nevertheless, the higher SWT during the 2012 non-upwelling season suggests that the entrained water originated from a shallower water-depth, compared with~~to~~ the water upwelled in 2009. The pCO$_2$ values with up to 650 µatm reached the same level during both events, which is partially caused by the higher SWT in 2012. However, ~~the temperature independent~~ DIC concentrations in 2012 (1924.65 ± 195.07 µmol kg^{-1}) were lower than~~fell below~~ those in 2009 (2098.71 ± 103.81 µmol kg^{-1}), but exceeded those in 2013 (1800.92 ± 142.78 µmol kg^{-1}, Table 1). During the seven days that lasted the cold-water intrusion event in 2012 (June 10-17), the DIC concentrations dropped from 2355.39 µmol kg^{-1} down to 1715.30 µmol kg^{-1}. This implies that in addition to high SWT, the entrainment of CO_2-enriched subsurface water increased the pCO$_2$ not only during the upwelling periods, but also during the 2012 non-upwelling season.

Since in 2012 the pCO$_2$ had ~~increased~~ already increased by June 7th and the SWT decreased~~ only~~ two days later (June 10th), the inflow of CO_2-enriched waters seems to have increased the pCO$_2$ already prior to the strengthening of local winds (Fig. 2b). Later, local wind-induced vertical mixing seems to have amplified the impact of the inflowing CO_2-enriched water mass on the pCO$_2$ in the surface water by increasing its input into surface layers. Accordingly, the CO_2-enriched waters were apparently supplied from a different location than they are during upwelling season.~~somewhere else.~~ Since the NECC carries offshore waters towards the Costa Rican shore during the non-upwelling season (Wyrtki, 1965, 1966; Fiedler, 2002), it is assumed that the CO_2-enriched subsurface water originated somewhere south of our study area in the open ETP. The absence of such a cold-event during the non-upwelling season in 2013 suggests~~shows~~ that the occurrence of this kind of events might be~~it is~~ an irregular feature (Fig. 2c, d), and~~whereas~~ the driving forces are still elusive. Nevertheless, these types of events have the potential to affect~~it affects~~ the metabolic processes in the bay as will be discussed in the following section, which analyzes the daily cycles during the non-upwelling seasons in 2012 and 2013.

4.2 Processes behind the variability of the carbonate system

In 2012, the pH and the pCO_2 values followed a pronounced diurnal cycle with highest pH and lowest pCO_2 values during the late afternoon and lowest pH and highest pCO_2 values around sunrise in the early morning (Fig. 4a). Such daily cycles are typical for tropical regions and are assumed to be caused by photosynthesis during the day and respiration of organic matter during the night (Shaw et al., 2012; Albright et al., 2013; Cyronak et al., 2013a). The aragonite saturation state as well as the DIC/TA ratio followed this pattern, with higher Ω_a and lower DIC/TA ratio values during the day as well as lower Ω_a and higher DIC/TA values at night (Fig. 4b). Although the pCO_2 cycles in 2013 followed a similar pattern to 2012, pH cycles were less predictable (Fig. 4).

~~In contrast to 2012, the pH in 2013 hardly followed any daily cycle, while the pCO_2 cycles were similar in both periods (Fig. 4).~~ To characterize the relative importance of the processes responsible for the observed changes in pH and pCO_2 (photosynthesis, respiration, calcification and dissolution) we used the model described earlier, which is based on the determined DIC concentrations during times when pH and pCO_2 revealed their daily minima and maxima, respectively. For example, if photosynthesis of organic matter dominates the transition from early morning maxima of pCO_2 to late afternoon minima of pCO_2 it should be associated with a decline in~~loss of~~ DIC. Whether photosynthesis was accompanied with enhanced calcification can be detected by an associated decrease of TA. Since decreasing DIC raises the pH and a decrease in TA lowers the pH, such photosynthetic enhanced calcification hardly affects the pH and could explain the weak daily cycle observed in 2013. Alternatively, if photosynthesis is accompanied by carbonate dissolution during the day, this would amplify the daily cycle of pH and pCO_2 as seen during the cold-water intrusion event in 2012. Likewise, an increased photosynthesis resulting from higher nutrient concentrations (Pennington et al., 2006) could also be causing the observed large amplitude during the event in 2012. However, in our case the determined TA and DIC concentrations constrain the impact of the formation of organic matter (POC = photosynthesis – respiration) and calcification (PIC = calcification – dissolution) on the carbonate system. This sets the boundaries within which the observed diurnal cycle of pH and pCO_2 has to be explained (Fig. 5c, d). In order to reconstruct the diurnal cycle of pH and pCO_2 within these boundaries we assumed a photosynthetic-enhanced calcification during the day and vice versa, dissolution and respiration at night. Thereby the best fit between pH and pCO_2 measured in 2013 and the respective calculated values could be obtained by using a R_{OI} of 1. This approach failed to explain the diurnal cycle of pH and pCO_2 as observed during the 2012 cold-water intrusion event (June 10-17). The only solution we found to explain these pronounced diurnal cycles within the given DIC and TA boundaries was to assume that photosynthesis and dissolution prevailed during the day and respiration and calcification occurred at night.

The R_{OI} of -2.6 resulted in the best fit between the measured and calculated pH and pCO_2 for the 2012 event, whereas the negative sign reflects the contrasting effects of calcification and dissolution on the DIC concentration.

These daily cycles in pH and pCO_2 suggest concordant cycles in DIC and TA, which unexpectedly could not be observed. The interplay of all the four metabolic processes of relevance (photosynthesis, respiration, calcification and dissolution) seems to be softening the daily cycles of DIC and TA. However, themask pronounced daily patternscycles of DIC and TA, but the pronounced daily cycle of the DIC/TA ratio raise indicate that some clues about theof these processes that are controllingcontrol the daily cycles of pH and pCO_2 (Fig. 4).

To identify the dominant processes, we developed a numerical model and recalculated the daily trends of pH and pCO_2 (Fig. 5). The calculated pCO_2 and pH agree quite well to the measured ones and support our previous interpretations that during 2013, photosynthesis and light-enhanced calcification prevailed during the day and carbonate dissolution was relegated to night hours alongside respiration (Fig. 5c, d). Based on the observed daily pH and pCO_2 cycles and in line with our model results, it seems that during. During the 2012 cold-water intrusion event (June 10-17), the diurnal cycle of the carbonate, the system was dominated by photosynthesis and calcium carbonate dissolution during light hours, with respiration and calcification occurring at night. Dissolution taking place during daytime is peculiarparticular but not completely unusual, as it has been reported on tropical sandy bottoms under ambient (Yates and Halley, 2006; Cyronak et al., 2013b) and high-CO_2 conditions (Comeau et al., 2015). Similarly, dark-calcification Dark calcification is not entirely uncommon and occurs in both, sandy bottoms and coral reefs (Yates and Halley, 2006b; Albright et al., 2013). Accordingly, the entrainment of CO_2-enriched water from the NECC seems to shift the carbonate chemistry of Bahía Culebra from a system where photosynthesis and calcification are the controlling processes during light hours to a system in which daytime is dominated by photosynthesis and dissolution. The net effect, as observed, is an enhanced pCO_2 and lower Ω_a during periods characterized by the inflow of CO_2-enriched waters (Table 1). This has strong ecological implications for local coral reef ecosystems.

4.3 Ecological implications for coral reefs

Coral reefs in Bahía Culebra were dominated by *Pocillopora* spp. and *Pavona clavus* (Jiménez, 2001; Jiménez et al., 2010), whereas *Porites lobata* is the main reef forming coral in the southern part of the Costa Rican Pacific coast (Cortés and Jiménez, 2003; Glynn et al., 2017). Although the reefs in the north are naturally exposed to periodic high-CO_2 conditions during upwelling events (Rixen et al., 2012), as well as during cold water intrusions in non-upwelling season, the linear extension rates of *Pocillopora* spp. and *P. clavus* exceeded those of the same species in other regions (Fig. 6) (Glynn, 1977; Jiménez and Cortés, 2003; Manzello, 2010a; Rixen et al., 2012). This suggests that local corals are adapted and/or acclimatized to the upwelling of cold and acidic waters.

Aragonite saturation state (Ω_a) is known as one of the main variables influencing coral growth and therefore reef distribution around the world (Kleypas et al. 1999). By integrating the data from the present study and values previously reported by Rixen et al. (2012), we estimated that the annual mean Ω_a in Bahía Culebra is 3.06. Additionally, earlier studies in the ETP measured Ω_a values and coral extension rates from locations that are under the influence of upwelling events (Manzello 2010a), whilst extension rates from Bahía Culebra were measured by Jiménez and Cortés (2003). The correlation between our estimated Ω_a with the available data from Bahía Culebra, Panamá and Galápagos indicates that coral extension rates in each of those locations are predictedable by their corresponding Ω_a values (Fig. 6).

~~Since it is generally assumed that Ω_a strongly influences coral growth, we calculated the annual mean Ω_a of 3.04 for Bahía Culebra by integrating measurements from all periods (Table 1). This average Ω_a correlates well with the extension rates of *Pocillopora damicornis* and *P. clavus* from three upwelling-influenced areas in the ETP and supports the general assumption that Ω_a controls the growth of corals (Fig. 6).~~

The dependency of coral growth on Ω_a and the mean Ω_a (2.71) during the upwelling season (Table 1) suggests that upwelling of acidic waters should reduce corals' relatively high annual mean growth rates in Bahía Culebra.~~the linear extension of these corals during upwelling season.~~ The increased Ω_a during non-upwelling season in turn must enhance linear extension and explains corals' high annual mean growth rates. ~~This furthermore implies the sensitivity of coral growth within the bay to the occurrence of cold events that lower Ω_a during the non-upwelling season, as seen in June 2012.~~ The Ω_a values from this study suggest that most favourable~~favorable~~ conditions for coral growth occur during non-upwelling season, the period that coincides with development of the rainy season. This implies that during the main growing season the eutrophication and siltation caused by human impacts on river discharges, as well as the development of harmful algal blooms, could also strongly affect the corals' annual mean growth rates (Cortés and Reyes-Bonilla, 2017).

Despite the corals' high annual mean linear extension rates, studies carried out in 1973 showed that the thickness of the reef framework within our study area was with 0.6 to 3 m (mean 1.8 m) among the lowest in the ETP, where Holocene framework accumulation in *Pocillopora*-dominated reefs could reach up to 9 m (Glynn et al., 1983; Toth et al., 2017). ~~net accretion rates of the reefs in Bahía Culebra are relatively low~~ During the last decade it further decreased (Alvarado et al., 2012), and during the period of our observation the reef frameworks of *Pocillopora* spp. in Bahía Culebra hardly exceeded a thickness of 0.5 m~~ during the period of our observation~~. This denotes that although *Pocillopora* spp. and *P. clavus* are adapted to the entrainment of acidic waters, these reefs are growing in an environment at~~on~~ the limit~~verge~~ of reef-building corals~~their ecological~~ tolerance in terms~~because~~ of temperature, nutrient loads~~bioerosion~~ and pH (Manzello et al., 2017). Gaps in coral reef accretion at the ETP~~reef erosion due to physical forces. Corals' accretional gaps, which~~ are known from the geological record (Toth et al., 2012; 2015; 2017).~~, document the vulnerability of these reefs.~~ They have been linked to increased ENSO variability (Toth et al., 2012, 2015) and stronger upwelling conditions (Glynn et al., 1983), favouring~~favoring~~ dissolution and erosion of reef frameworks while at the same time restricting coral growth.

The y-intercept of the regression equation derived from the correlation between linear extension rates and Ω_a furthermore implies that linear extension of *P. damicornis* and *P. clavus* should approach~~approaches~~ zero under a carbonate saturation state of $\Omega_a < 2.5$ (*P. damicornis*) and < 2.2 (*P. clavus*). According to climate predictions, the global Ω_a will reach values < 2.0 by the end of this century (IPCC, 2014), and major upwelling systems such as those off California and South America will intensify (Wang et al., 2015). Combined effects of ocean acidification and impacts of stronger upwelling on Ω_a in the

ETP and on Ω_a in Bahía Culebra are difficult to predict.suggesting that OA can seriously threaten the reefs in Bahía Culebra. Worldwide, OA is expected to reduce coral reefs' resilience by decreasing calcification and increasing dissolution and bioerosion (Kleypas et al., 1999; Yates and Halley, 2006a; Anthony et al., 2011). Coral reefs from the ETP are affected by chronic and acute disturbances, such as thermal stress and natural ocean acidification resulting from ENSO and upwelling events, respectively (Manzello et al., 2008; Manzello, 2010b). Historically, these reefs have shown a high resilience to both stressors by separately but their coupled interaction can cause coral reef lost within the next decades. The ETP have the lowest Ω_a of the tropics, near to the threshold values for coral reef distribution, therefore the reefs from this region may be the most affected by the increasing levels of anthropogenic CO_2 and also show the first negative impacts of this human induced OA (Manzello et al., 2017).seriously threatens the reefs in Bahía Culebra. This emphasizes the importance of the Paris agreement and all the global efforts to reduce the CO_2 emission into the atmosphere (Figueres et al., 2017).

5 Conclusions

The present study provides data from in situ measurements from a system that is naturally exposed to low-pH conditions, and seeks to characterize the carbonate chemistry within a bay (Bahía Culebra) and its potential impact on the reefs. This study builds on previous field studies in the upwelling areas of Panamá (Manzello et al., 2008; Manzello, 2010b) and Papagayo (Rixen et al., 2012). Our results indicate that physical processes, such as the coastal upwelling and the exchange of water between the bay and the open ocean, influence the carbonate chemistry on timescales of weeks to months, where metabolic processes (photosynthesis and calcification) influence the diurnal cycle. To which extend benthic and pelagic processes control the diurnal cycle, cannot be established based on our data. However, the results from the present study also 2012), contributing with data from in situ measurements carried out within a system that is naturally exposed to low-pH conditions. The results presented suggest that coral reefs from Bahía Culebra are exposed to a high intra- and interannual variability in the carbonate system. Challenging conditions for reef development are not restricted to the upwelling season, they occur sporadically also during non-upwelling season,seasons, when pH and CO_2 concentrations reach values comparable to those during upwelling events. Previous studies reported Linear extension rates of the main reef building corals in the bay are sensitive to changes in Ω_a, suggesting that upwelling reduces coral growth by introducing acidic subsurface waters in the surface layers. Rising levels of Ω_a enhance coral growth during the non-upwelling season due to which the linear extension rates measuredof the main reef building corals in Bahía Culebra were among the highest in the ETP, thus is likely that coral growth in this bay is enhanced with increased Ω_a during periods with no entrainment of ETP; however, reef accretions was low-pH waters. However, coral growth must be measured due to erosion. The latter indicates a sensitivity of coral reefs to the intensity of the upwelling and other processes occurring during both seasons in order to confirm this assumption.the non-upwelling/rainy season, such as human impacts on river discharges, the occurrence of cold events (e.g. 2012), and ultimately to OA. Threshold values of Ω_a when coral growth likely approaches zero were derived from the correlation of Ω_a and previously measured annual linear extension rates. The Ω_a threshold values from the present study and the fact that high-CO_2 waters are occasionally hauled in to the bay during non-upwelling season; suggest that coral reef development in ~~and this suggests that OA will seriously threat reefs in~~Bahía Culebra is potentially threatened by anthropogenic OA. ~~, which are already at the verge of their ecological tolerance.~~

6 Data availability

Data are available by direct request to the corresponding author.

7 Author contribution

C. Sánchez-Noguera and T. Rixen designed the study, analyzed the data, prepared figures and/or tables and wrote the paper C. Sánchez-Noguera collected and analyzed the samples~~, analyzed the data, prepared figures and/or tables and wrote the paper~~. I. Stuhldreier, J. Cortés, Á. Morales, C. Jiménez and C. Wild reviewed the paper. ~~T. Rixen designed the study and review the paper.~~

8 Competing interests

The authors declare that they have no conflict of interest.

9 Disclaimer

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Table 1: Measured and calculated (*) parameters, during upwelling (2009) and non-upwelling seasons (2012, 2013) at Bahía Culebra, Costa Rica.

	pH (Total scale)	pCO_2 (µatm)	CO_2 (µmol kg^{-1})	T (°C)	DIC* (µmol kg^{-1})	TA* (µmol kg^{-1})	Ω*
2009							
Mean ± SD	7.91 ± 0.32	578.49 ± 42.82	16.44 ± 1.35	25.09 ± 0.57	2098.71 ± 103.81	2328.42 ± 118.45	2.71 ± 0.29
2012							
Mean ± SD	7.98 ± 0.04	456.38 ± 69.68	11.77 ± 1.99	29.61 ± 0.93	1924.65 ± 195.07	2204.54 ± 212.18	3.32 ± 0.46
2013							
Mean ± SD	8.02 ± 0.03	375.67 ± 24.25	9.56 ± 0.64	30.08 ± 0.27	1800.92 ± 142.78	2102.66 ± 174.79	3.50 ± 0.49

Table 2: Correlations between tide height and four parameters during non-upwelling season (2012, 2013).

Year	pH	*p*CO_2	T	Wind
2012	-0.004	0.037	-0.005	0.033
2013	0.111	0.026	-0.093	-0.126

All p-values > 0.05

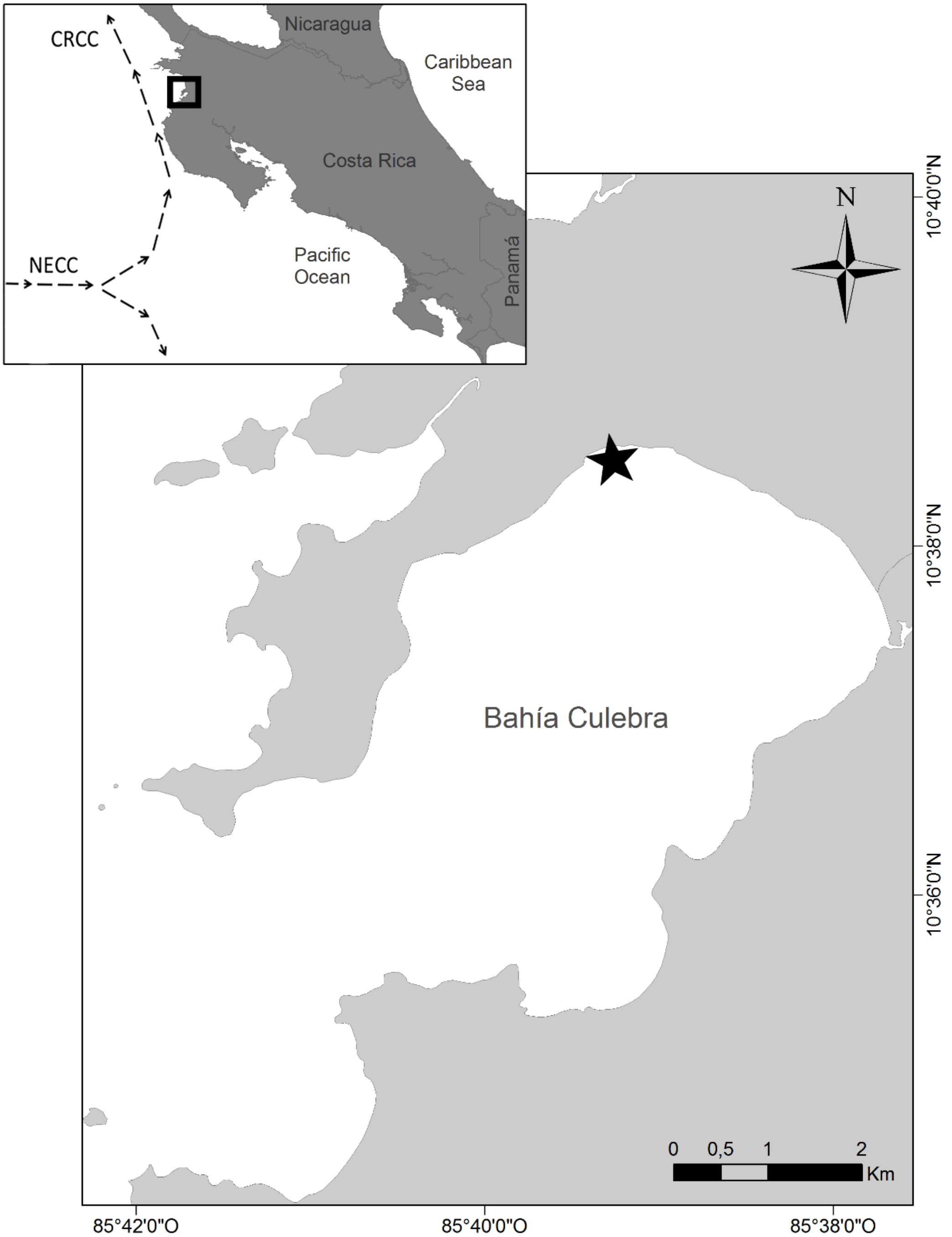

Figure 1: Location of Bahía Culebra (square) in the Gulf of Papagayo, North Pacific coast of Costa Rica (insert). Measurements were made at Marina Papagayo (star). Main ocean currents influencing the Gulf of Papagayo (dashed arrows): NECC= North Equatorial Counter Current, CRCC= Costa Rica Coastal Current.

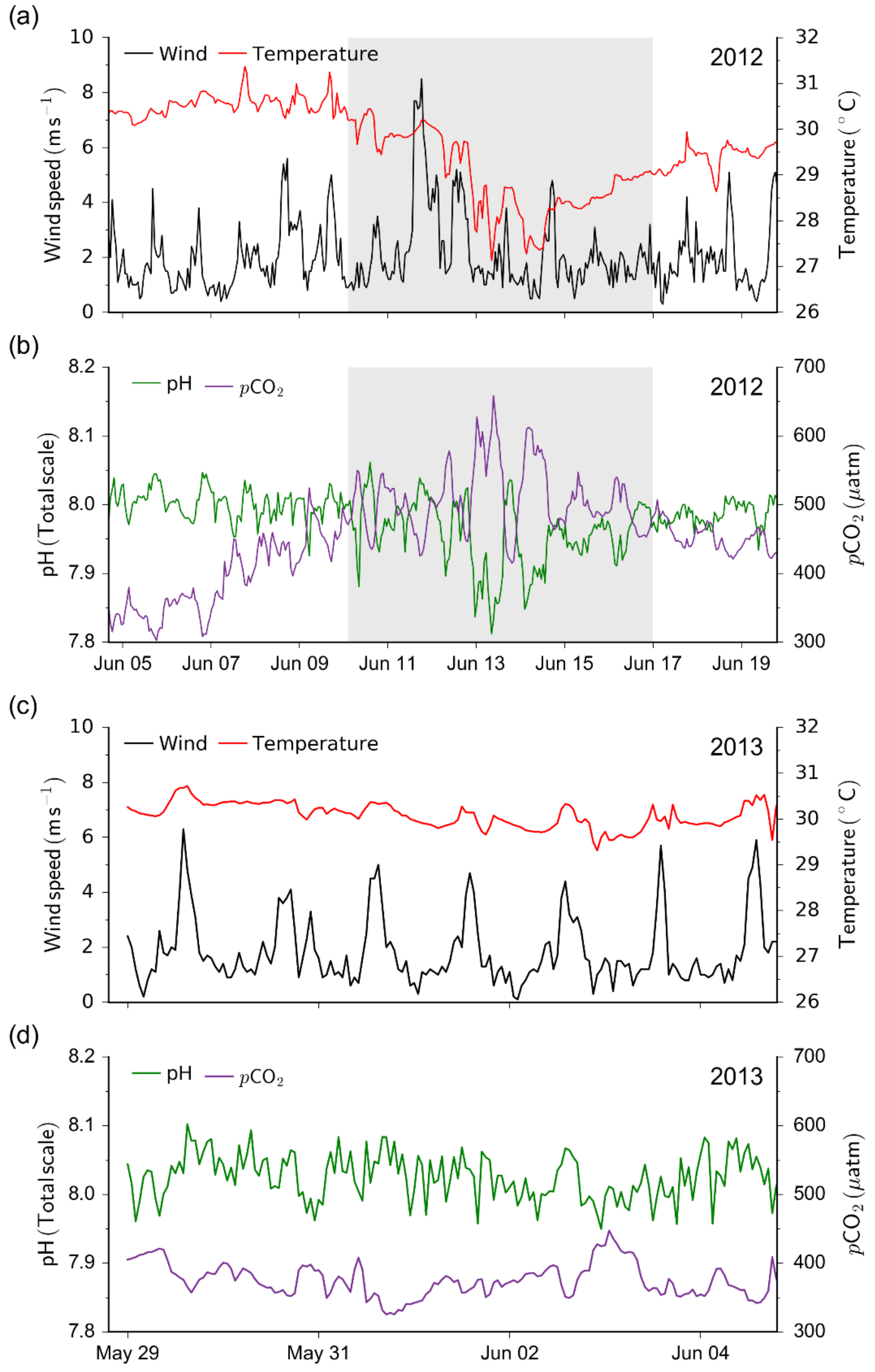

Figure 2: Measured parameters (wind speed, SWT, pH and pCO_2) during the non-upwelling seasons of June 2012 (a, b) and May-June 2013 (c, d), at Bahía Culebra. Shaded area in (a) and (b) indicates the 2012 upwelling-like event.

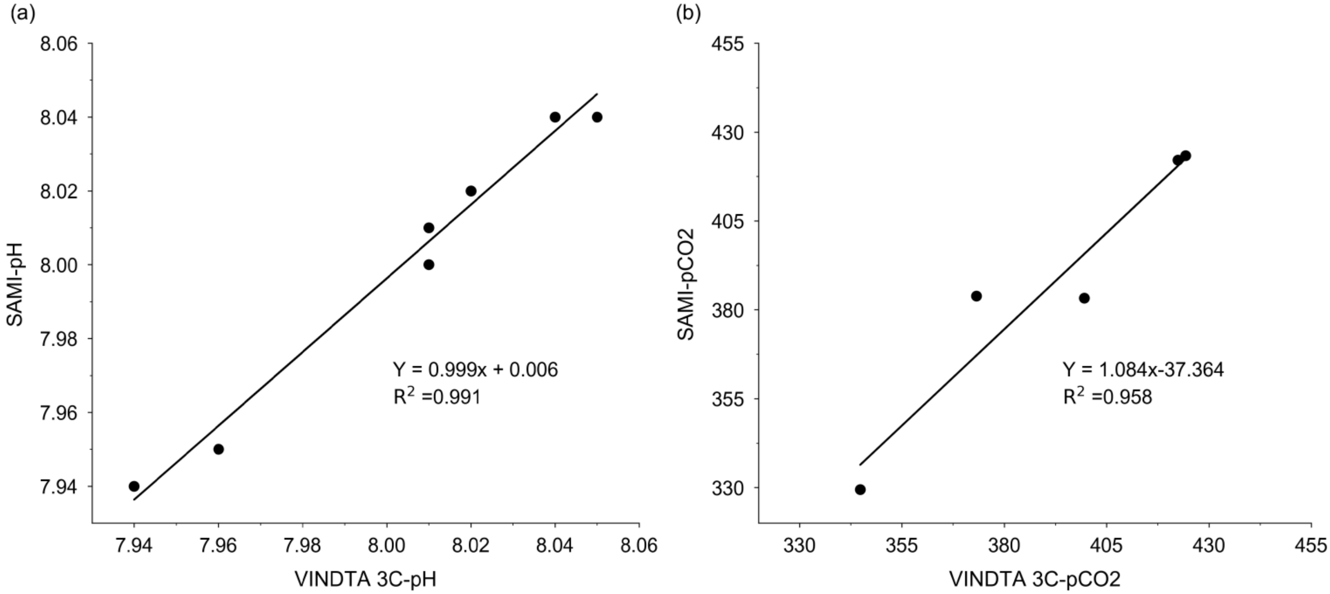

Figure 3: Validation of in situ measurements of pH (a) and *p*CO_2 (b) ~~SAMI sensors~~ using discrete water samples. SAMI sensors measured pH and *p*CO_2 directly in the water column. The pH and *p*CO_2 values used for validation were calculated with the CO2SYS program as a function of measured TA and DIC; discrete samples were measured with a VINDTA 3C system.

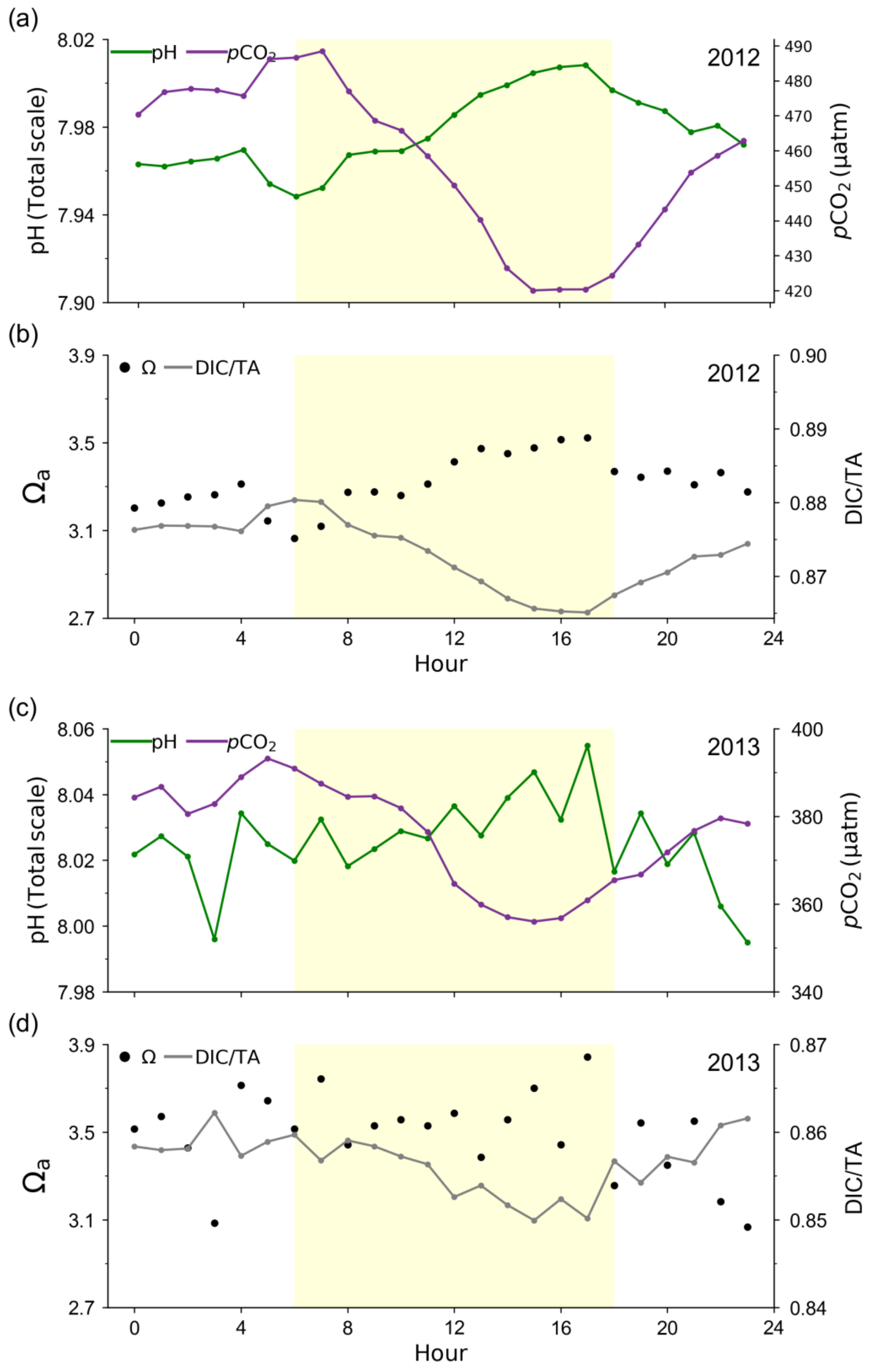

Figure 4: Diel pattern of parameters measured in Bahía Culebra. Data points are hourly averages of 15 and 7 consecutive days in 2012 (a, b) and 2013 (c, d), respectively. The shaded area represents daylight hours.

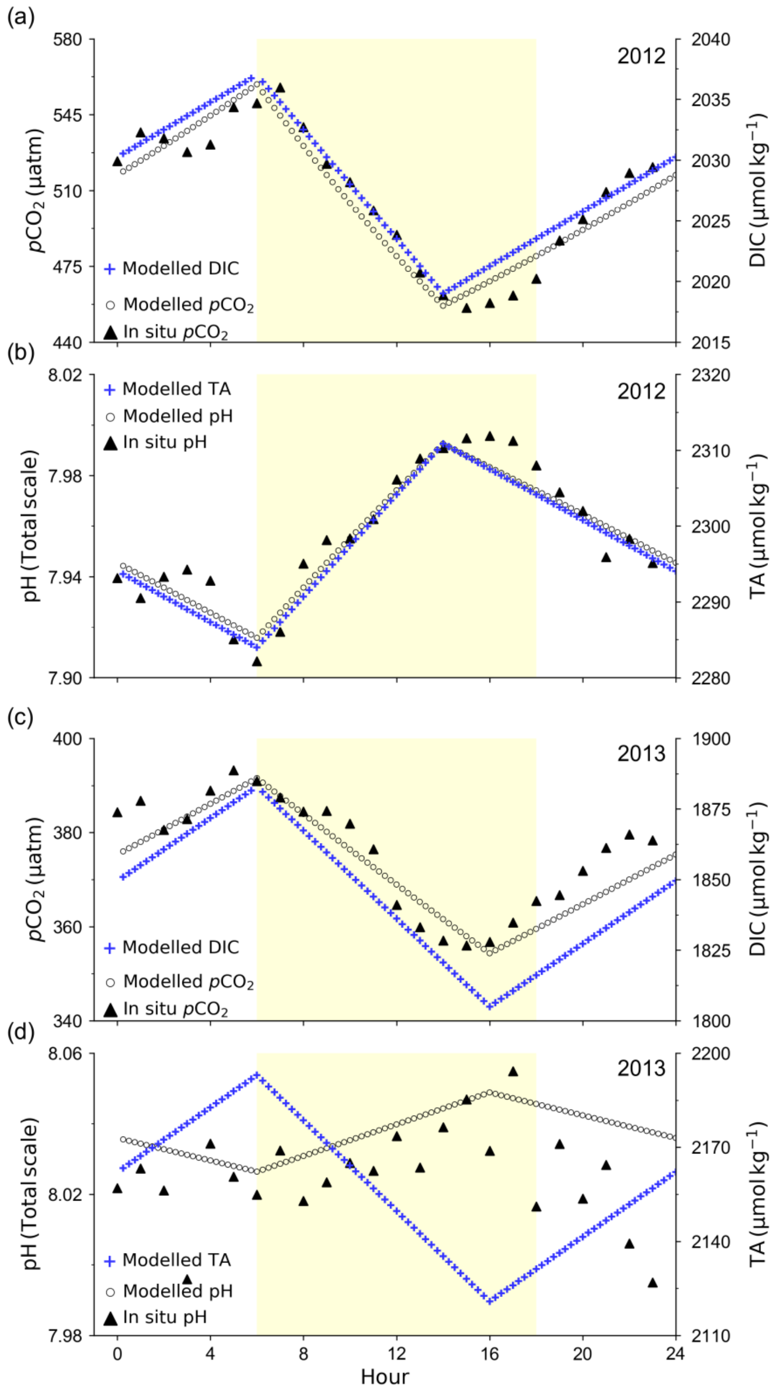

Figure 5: Expected diel behaviourbehavior of the carbonate system in 2012 (a, b) and 2013 (c, d), based on measured parameters. Modeled parameters are shown as blue crosses and empty circles;circles, the reference parameter used to adjust the model is shown in black triangles. Shaded area represents daylight hours.

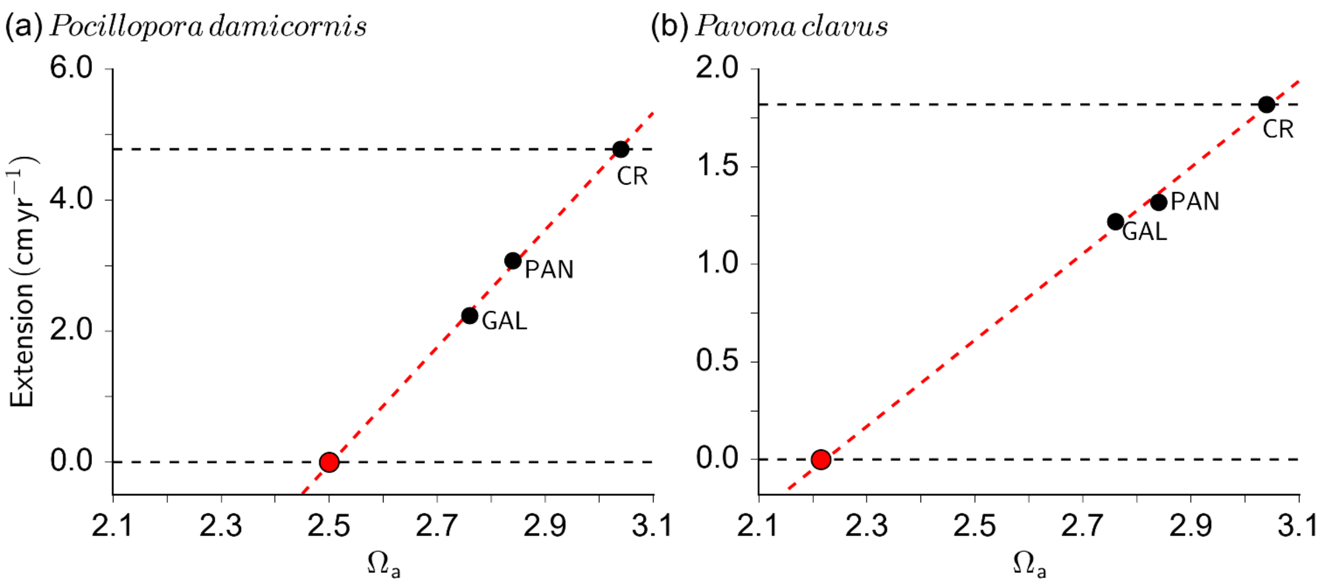

Figure 6: Mean aragonite saturation states (Ω_a) – from present and former studies - versus previously reported mean linear extension rates of (a) *Pocillopora damicornis* (a)and (b) *Pavona clavus* (b) from upwelling areas in Costa Rica (CR) (Jiménez and Cortés, 2003),, Panamá (PAN) and Galápagos (GAL) ((Jiménez and Cortés, 2003; Manzello, 2010a). Red broken line shows the regression equation as estimated by Rixen et al. (2012). Red(2012), the red mark represents our estimated Ω_a threshold for Bahía Culebra, when coral growth equals zero.