

How Does the Sexual Reproduction of Marine Life Respond to Ocean Acidification?

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Abstract: Recent research indicates that synchronicity of sexual reproduction in coral spawning events is breaking down, leading to aging populations and decreased recruitment success. In this perspective, we develop a hypothesis that this phenomenon could be caused by ongoing ocean acidification (OA). We hypothesize, that the underlying physiological machinery could be the carbon concentrating mechanism (CCM). The endosymbiotic zooxanthellae of corals could use this mechanism to sense calm water motion states in a comparable way to that known from macroalgae. In macroalgae, it is well-established that dissolved inorganic carbon (DIC) acts as the trigger for signaling low water motion. Hence, evolutionarily developed signals of low water motion, suited for gamete-release, may be misleading in the future, potentially favoring opportunistic species in a broad range of marine organisms.

Keywords: spawning; corals; macroalgae; reproduction; sexual; ocean acidification; water motion; hydrodynamics; biodiversity; ecophysiology

1. Background

In their recent paper, Shlesinger and Loya [1] describe the breakdown of Red Sea coral spawning synchrony. Despite the ongoing debate, whether or not the observed loss of spawning synchrony can be transferred to other reef systems worldwide and how the present data can be related to historical data [2], Shlesinger and Loya [1] undoubtedly showed that coral species in the Gulf of Eilat/Aqaba actually do not show a high spawning synchrony. The ecological consequences are very relevant, but the central questions are, if this also applies to other organisms and their release of gametes, particularly algae and how climate change could be responsible for the observed low spawning synchrony.

Most sessile marine organisms release their gametes into the surrounding water, where zygote formation takes place [3]. In corals, two different manners of gamete release and larvae production are known. Broadcast spawning is the most common mode. Broadcast spawners release sperm and eggs into the water column, whereas the less common brooding corals retain their eggs within the polyp and only release sperm [3]. Marine algae developed very different life-cycle strategies, but most of them also release their gametes directly in the water [4]. Still many taxa, mostly opportunistic species are able to grow in a pathogenetic manner and/or show vegetative reproduction [4].

Synchronized mass spawning in calm waters is important for the reproductive success of coastal organisms, since it prevents gamete dilution and decreases the risk for zygotes and gametes to drift towards open waters [5,6]. It also ensures that the gamete concentration in the water is high enough to ensure successful zygote formation [3,7]. The reproductive success is highly dependent on the sperm concentration in the seawater [7]. In the field, optimal sperm concentrations were only observed in a narrow time interval during calm weather conditions [7]. Hence, spawning events are the crucial

point of many marine organisms ensuring genetic connectivity and the long-time persistence of species (e.g., [7–9]), but spawning events must also be synchronized to ensure appropriate gamete concentrations [7].

Yet how is the high synchronization of spawning events reached?

The seasonality of algal reproduction is coordinated by environmental cues acting on different time scales [4]. Temperature and photoperiod are widespread environmental cues acting on an annual resolution [4]. Within weeks, the lunar cycle can synchronize reproduction [4]. The latter is reasonable, since the lunar cycle is driving the tidal cycle, which in turn is also a good predictor for the prevailing water motion and tidal flows [4]. Within the range set by the lunar cycle, the exact day or even hour of gamete release apparently depends on the agitation state of the seawater around macroalgae [5,6]. The latter is described for macroalgae [5], but likely comparable to corals, a very different taxon, releasing its gametes at preferably calm water conditions [10], whose spawning events can be delayed by strong winds [11]. The wind influence on synchronized gamete release can become problematic for marine sexual reproduction. Hu et al. [12] showed that the climate change driven intensification of surface winds is also leading to a global acceleration of ocean circulation. Hence, if strong winds delay spawning events, it is reasonable to assume that the calm water periods needed for successful mass spawning events may be delayed or hampered in future. The ecological consequences could be severe.

2. The Physiological Mechanism of Spawning

For a deeper understanding of spawning and the potential influence of climate change effects on the timing of spawning, we need to ask the question: How corals and macroalgae sense the calm water conditions physiologically? Both taxa lack equilibria organs, making it likely that they use a chemical cue to sense water motion. This chemical cue could be the seawater carbonate system. Brown algae release their gametes only if the concentration of dissolved inorganic carbon and HCO_3^- is low [6]. Furthermore, the maturation of *Ulva* is apparently stimulated by low dissolved inorganic carbon (DIC) concentrations [13,14].

In brown algae, two distinct phases of gamete release were identified: firstly, a reversible potentiation phase that is important for the triggering and the quantity of the released gametes and that is dependent on light and photosynthesis and secondly, a gamete expulsion phase [6]. The water motion may be reflected in [DIC] or $[\text{HCO}_3^-]$, because within dense stocks of algae and corals the [DIC], $[\text{CO}_2]$ and $[\text{HCO}_3^-]$ concentrations can decline due to the photosynthetic carbon uptake leading to an increase in pH and lower [DIC] (e.g., [15,16]). This effect is particularly pronounced at a low seawater agitation state [6,15]. The theory that algae sense the seawater motion state via [DIC] or $[\text{HCO}_3^-]$ is supported by the observation that brown algae release less gametes under stirred compared to unmoved conditions. In addition, gamete release was strongly impeded if inhibitors of the carbon concentration mechanism (CCM) were applied even under moved conditions [17]. Hence, Zou and Gao [17] showed that the seawater carbonate system and the CCM are involved in the sensing of water motion, at least in brown algae. Additionally, for the holocarpic green alga *Ulva lactuca*, Olischläger et al. [14] demonstrated that the maturation and propagule release were stimulated at low [DIC]. Olischläger et al. [14] also showed that maturation and consequently gamete release were strongly stimulated if the algal photosynthetic carbon uptake reduced [DIC] and $[\text{HCO}_3^-]$ and thereby increased the pH within artificial rock pools above 8.4. This is remarkable, since pH 8.4 is an important physiological threshold in the algal carbon acquisition. Below a pH of 8.4, *Ulva* facilitates the uptake of inorganic carbon by an active acidification of the diffusion boundary layer (DBL). Within the DBL the algae accelerate the conversion of HCO_3^- to CO_2 using the enzyme external carbonic anhydrase (exCA). This mechanism leads to a steeper CO_2 gradient between the DBL and the cytoplasm, facilitating the passive diffusion of CO_2 through the membrane into the cell. However, above a pH of 8.4 in the surrounding seawater the $[\text{CO}_2]$ becomes very low, and passive diffusion from the surrounding seawater into the DBL becomes too slow to maintain a positive net photosynthesis. Above pH 8.4, the carbon acquisition enzyme external carbonic anhydrase is becoming increasingly futile. Therefore, the alga is forced to shift the carbon

acquisition from the uptake facilitated by external carbonic anhydrase towards the direct uptake of HCO_3^- by anion exchangers [18]. The direct HCO_3^- uptake is energetically unfavorable, but still ensures photosynthetic activity and a positive net photosynthesis under low DIC conditions [14,18].

The above described CCM and the described pH thresholds for usage of exCA and direct HCO_3^- uptake are clearly specific for *Ulva lactuca* [18]. Other species have different types of CCMs (e.g., [19]) and may use or induce HCO_3^- import at different pH thresholds. However, different pH thresholds for the induction of HCO_3^- could explain the different precise shaped spawning intervals in Caribbean macroalgae [9]. Nevertheless, a CCM based on active transport of inorganic C across one or more cell membranes and/or external conversion of HCO_3^- to CO_2 using exCA and active H^+ efflux into the DBL occurs in a majority of marine macroalgae. Furthermore, nearly always a contribution from active influx of HCO_3^- across the plasmalemma takes place [20]. In microalgae, to which the zooxanthellae belong, the direct HCO_3^- import is of higher importance for the carbon acquisition than the conversion of HCO_3^- to CO_2 by exCA, and the role of exCA as part of the CCM is discussed [21].

Our hypothesis is based on findings with taxonomically different species, possessing different types of CCMs. The upcoming question is what could link the CCMS of algae, corals and potentially also other zooxanthellae bearing animals physiologically. We should be aware that besides providing carbon for photosynthesis another important task of the CCM is the avoidance of reactive oxygen species (ROS) formation [22–24]. If the CCM is unable to provide enough CO_2 to saturate Rubisco, ROS are increasingly produced [24]. This is a general feature occurring in all kinds of photosynthetically active organisms [24]. The studies used to develop this hypothesis examined not only different species, the observations of synchronized spawning were also made in very different marine habitats, ranging from the tropics to cold temperate zones (e.g., [1,6,9]). Within these climate zones there are pronounced differences in the sea surface temperature (SST) and the seawater carbonate system, and there are also pronounced differences in the CCM strengths [25,26]. Do these environmental and physiological differences make it unlikely that there is one global threshold in $[\text{HCO}_3^-]$ or [DIC] triggering synchronized spawning? In our opinion, it is more likely that the different organisms with their different CCMs, which are adapted to different environmental conditions, trigger spawning in response to a change in $[\text{HCO}_3^-]$ or [DIC], deviating from the usual conditions and resulting in an unusual high ROS production. Hence, it is likely that also the seawater carbonate system threshold triggering spawning is adapted to the local environmental conditions.

To strengthen the hypothesis that carbon availability influences the timing of the spawning, it should be pointed out that carbon availability and the formation of ROS are interactive [22,23]. Reactive oxygen species are important secondary messengers in numerous cellular processes in algae (e.g., [27]). Moreover, increased ROS formation is triggering crucial life cycle steps, such as the cyst formation and programmed cell death in the fresh water dinoflagellate *Peridinium gatunense* [23]. The linkage between the enzymatic carbon acquisition and ROS metabolism is explainable since under conditions of carbon limitation the drain of electrons from the photosynthetic transport chain via Ferredoxin to NADP^+ is slowed. The regeneration of NADP^+ from $\text{NADPH} + \text{H}^+$ in the Calvin cycle is hampered by carbon deficiency. Under those conditions, the production of reactive oxygen species (ROS) can increase [24]. Accordingly, if ROS is involved in the programmed cell death and cyst formation in microalgae [23], it is reasonable to assume that it also regulates important life history events such as spawning in macroalgae- and zooxanthellae-bearing animals, such as corals.

3. Would This Mechanism Be Affected by Climate Change?

The involvement of the CCM in sensing the water motion could make this physiological pathway vulnerable to ocean acidification and elevated temperatures. The reason for this vulnerability is the adjustment of the enzymatic CCM to the prevailing [DIC] and $[\text{HCO}_3^-]$ conditions (e.g., [14,18,19,25,26]). The CCM is often downregulated in response to high DIC environments, such as OA scenarios, but it is also adjusted in low DIC environments if needed [14,18].

The composition of the seawater carbonate system including [DIC] and $[\text{HCO}_3^-]$ to which the CCM has to adjust is dependent on many factors. Most important are the diffusion rate from atmospheric carbon dioxide into the seawater surface layer and the effects which photoautotrophs exert on the seawater carbonate system by its carbon uptake (e.g., [15,16]). According to Fick's law, an elevated atmospheric pCO_2 leads to steeper gradients between the air and the ocean's surface. In a high pCO_2 world, atmospheric CO_2 would diffuse faster into the sea-surface water and could counteract the effect that marine photoautotrophs exert on the seawater carbonate system in coastal environments effectively. The decreasing effect of marine photoautotrophs on the seawater carbonate system under high pCO_2 conditions was experimentally shown for the green macroalga *Ulva lactuca* already [14]. Clearly there may be species-specific factors influencing an algal effect on the seawater carbonate system. Hurd et al. [28] showed that the coralline seaweed *Sporolithon durum* rises the pH in the DBL by approximately 0.40 at low flow and 0.15–0.20 at high flow, irrespective if present (starting point pH 7.97) or predicted future pH conditions (starting point pH 7.50) were applied. However, the pH scale is logarithmic, therefore the increase in the H^+ concentrations must have been approximately 4–5 times higher in the present pH treatment compared to the OA treatment [28].

Based on the premise that algae sense the hydrodynamic state of the seawater indirectly via characteristics of the SWCS and their CCM activity [5,6], Olischläger et al. [14] concluded that the physiological explanation for the observed indices for lower maturation and gamete release in *U. lactuca* could be that the physiological threshold pH 8.4 (combined with correspondingly low $[\text{CO}_2]$, $[\text{HCO}_3^-]$ and [DIC]) was not exceeded in the OA-perturbation scenario [14]. This may be of high ecological relevance, because the changing manner of carbon acquisition is apparently involved in the signaling of suited hydrodynamic conditions for maturation and gamete release and was strongly affected by future atmospheric pCO_2 conditions [14]. We conclude that, enhanced aquatic pCO_2 would also enhance the passive diffusion of CO_2 from seawater to the DBL. It could counteract the need of enzymatic carbon acquisition and the expression of HCO_3^- importers and prevent the formation of the second messenger ROS. The lowered CCM activity and ROS formation could thus delay algal spawning.

To this point, we have presented arguments suggesting that the SWCS is used as an indirect signal for water motion. We demonstrated that the CCM and the linked ROS formation are the underlying physiological mechanisms and we explained how climate change may affect this water motion sensing system. However, most arguments were based on studies examining microalgae and macroalgae. The upcoming question is: Could this mechanism also be active in corals or other spawning invertebrates? We think that this is possible. The physiological mechanisms enabling macroalgae to sense water motion and time their spawning are also active in zooxanthellae-bearing scleractinian corals (e.g., [29,30]). Zooxanthellae acquire the inorganic carbon required for photosynthesis with the help of an own CCM adjustable to environmental conditions, being based on exCA and direct HCO_3^- uptake [31]. Many corals also facilitate the diffusion of CO_2 from the host DBL into the cell with the help of exCA, whose activity is coupled to the thickness of the DBL [31]. The exCA activity supplies approximately 50% of the inorganic carbon used in the net photosynthesis of the endosymbiont, and the remaining 50% are believed to be provided by HCO_3^- importers [31]. To our knowledge, all hermatypic corals do modify the carbonate chemistry at their surface, although the extent of this host-DBL-modification is highly species-specific [32,33]. For instance, the active pH modulation of the DBL of *Acropora yongei* and *Acropora aspera* are far lower compared to *Plesiastrea versipora* [32].

Furthermore, the zooxanthellae are already discussed to be involved in the timing of coral spawning, thereby functioning as pacemakers [34]. In other cnidaria, such as the sea-anemone *Aiptasia diaphana*, the endosymbiotic algae determined host behavior, such as the timing and the duration of the extension along with contraction of the host body [35]. This behavioral change was also reflected in a changed temporal gene expression of the host, indicating a tightly coupled interplay between the host and the photosynthetically active endosymbiont [35].

It should be considered that the fine-tuning of coral spawning is controlled by several interacting environmental factors, including regional wind field patterns, timing of the sunset, and sea surface

temperatures [36]. All these environmental factors also control the gamete release in algae [6,37]. Moreover, rapid increases in sea temperatures, but also wind fields are good predictors of coral spawning in statistical models [38]. At this point, we should ask ourselves: What are the conditions needed for a rapid temperature rise in the coastal marine environment? Firstly, a strong solar radiation is required to warm the seawater. Secondly, the water exchange between the reef and the open sea, as well as between the reef surface and the deeper water layers, must be limited. Obviously, water exchange is lower at low wind conditions. Under those conditions, the photosynthetic activity of corals and algae of the reef would strongly reduce the DIC in the surface water, resulting in low $[\text{HCO}_3^-]$, pCO_2 and a high pH. Both macroalgae and zooxanthellae in corals would be forced to acquire increasingly more carbon by using more direct HCO_3^- importers. In both taxa, ROS formation would rise. Hence, the calculated predictive effect of fast temperature rises for the timing of coral spawning also supports the idea that algal CCM activity and photosynthetic ROS formation are used as indirect signals for low water motion, signaling suited times for gamete release.

Unlike the worldwide occurring macroalgae, the distribution of hermatypic corals is limited to the tropics that provide a relatively stable environment compared to other marine regions. However, synchronized spawning also occurs under the most extreme tropical conditions, such as the southern Persian Gulf, with its high salinities and sea temperatures ranging from 12 °C to 36 °C [39]. The uprising question is: How could the CCM of corals and/or their zooxanthellae in extreme environments trigger spawning in the same manner as corals from more “moderate” regions? The answer could be the proven local adaptation of the zooxanthellae [40]. It is reasonable to assume that the CCM of different types of zooxanthellae is also adapted to local conditions. This could ensure the functioning of the proposed mechanism for synchronized spawning if ongoing global warming leads to a poleward expansion of the distribution of hermatypic corals [41]. However, ocean acidification may limit this poleward expansion by impeding the biogenic calcification [41], and potentially the discussed shift hampered synchronized spawning.

In conclusion, in a high atmospheric and aquatic pCO_2 world, the adjustment of the CCM to higher [DIC], $[\text{HCO}_3^-]$ and pCO_2 may be energetically favorable for algae and corals but hampering successful sexual reproduction if evolutionary evolved thresholds that signal calm water conditions suited for spawning are misleading or not reached at all.

4. Can We Observe Climate Change Effects in the Field Already and What Could Be the Consequences?

Since the onset of the industrial revolution the atmospheric pCO_2 increased from 280 ppm CO_2 to more than 400 ppm CO_2 at present times. The gradient between atmospheric pCO_2 and the surface aquatic pCO_2 is already more pronounced compared to preindustrial times. Accordingly, the ocean's surface pH has already dropped by at least 0.1. This results in changed SWCS conditions, meaning a lower pH but higher [DIC], $[\text{HCO}_3^-]$ and pCO_2 [42]. Based on the described scenario, we think that the ongoing ocean acidification may be one factor helping to explain the already observed irregular spawning pattern and lowered reproduction of corals [1].

If our hypothesis could be proved, we would understand marine ecosystems better, but the overall consequences of this scenario could be severe. Many tropical macroalgae, such as the Bryopsidales, and corals release their gametes in multi-species brief annual spawning events [8,9]. This event is of crucial importance for the completion of their life cycles. Many algae even reproduce in a holocarpic manner. It is reasonable to assume that their reproductive success would be lower if a higher fraction of their propagules drifts to the open sea. Shlesinger and Loya [1] even point out that the long term persistence of tropical coral reefs depends on successful external fertilization and we agree. If spawning patterns become more and more irregular in the future, we see the potential for a slowly occurring but drastic regime shift in many marine ecosystems, in our opinion most likely towards more opportunistic macroalgae species, being independent of external sexual fertilization. The expected reduced reproductive success of competitive macroalgae could also help to explain the lowered

recruitment of complex macroalgae in natural CO₂ vents [43]. We expect that opportunistic green algae able to reproduce in pathogenetic manner may profit from this ocean acidification scenario, whereas the actual ecosystem engineers, such as scleractinian corals and competitive brown or red algae that depend on the successful external fertilization for the completion of their life cycle [4,44], may get replaced in a slow, unspectacular manner. In this sense, the failure of (or reduced) successful external fertilization may help to explain the aging populations observed in the Northern Red Sea [1]. In this sense, it should be noted that *Acropora*, a coral genus with weak capacity for DBL pH-modification [31,32] and thus high OA susceptibility is also one of the coral genera for which low spawning synchronicity was observed [1]. Potentially, lowered spawning synchrony could also have contributed to the regime shift from large, broadcasting corals to smaller brooding species in Caribbean reefs in the 1980s and 1990s [3]. Compared with the broadcasting species, the brooding species show often more characteristics of opportunistic species, such as faster growth, smaller size and earlier reproduction. Furthermore, brooding species often reproduce in synchronization in a monthly interval and are able to self-fertilization [3]. The latter may be of importance if after a disturbance the density of competitive broadcasting species is low. After a disturbance, it is likely that low population density and the postulated loss in spawning synchrony interact, avoiding that the needed gamete concentrations are reached. Under those circumstances, the self-fertilization of brooding species may be advantageous. This may enable them to become dominant in a reef community, since the reproduction of competing broadcast spawners would be disproportionally hampered by low densities and lowered synchronization. Another important question concerning the future of synchronized spawning is how the proposed mechanism could impact the synchronization of split-spawning effects. Split spawning events can have a beneficial effect on disturbed reefs, by increasing the larvae supply [45]. However, if the gamete concentration on the split-spawning reefs would be suboptimal due to the proposed mechanism, it is reasonable to assume that this benefit in larvae supply is also already lowered compared to preindustrial times.

It should also not be neglected that during coral spawning events, large amounts of particulate organic matter are released into the water column, triggering chains of pelagic and benthic processes [46,47]. For instance, short but intense blooms of dinoflagellates were observed after intense mass spawning events [48]. However, the biological degradation is dependent on the chemical composition of the organic matter released by reef organisms that may highly differ [49,50]. Therefore, it is reasonable to assume that a loss of synchronicity in spawning and a slowly following regime shift in coral reefs would also affect adjacent food chains and biogeochemical cycles in an unknown manner. Thus, the role of the SWCS in the sensing of water motion, the enzymatic carbon acquisition in algae and corals should be clarified and the impact of OA on the spawning of zooxanthellae-bearing organisms and macroalgae spawning should urgently be experimentally evaluated to assess the potential of a silent threat to many marine ecosystems.

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