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Impact of CO_2-driven ocean acidification on invertebrates early life-history – What we know, what we need to know and what we can do

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Abstract

As a consequence of increasing atmospheric CO_2, the world's oceans are becoming more acidic and the rate of change is increasingly fast. This ocean acidification is expected to have significant physiological, ecological and evolutionary consequences at many organizational levels of marine biodiversity. Alarmingly little is known about the long term impact of predicted pH changes (a decrease of $-0.3/-0.4$ units for the end of this century) on marine invertebrates in general and their early developmental stages in particular, which are believed to be the more sensitive to environmental disturbances, are essential as unit of selection, recruitment and population maintenance. Ocean acidification (OA) research is in its infancy and although the field is moving forward rapidly, good data are still scarce. Available data reveal contradictory results and apparent paradoxes. In this article, we will review available information both from published sources and work in progress, drawing a general picture of what is currently known, with an emphasis on early life-history larval stages. We will also discuss what we need to know in a field with very limited time resources to obtain data and where there is a high expectation that the scientific community should rapidly be able to provide clear answers that help politicians and the public to take action. We will also provide some suggestions about what can be done to protect and rescue future ecosystems.

1 Introduction

Present knowledge and understanding of the prospective impact of CO_2-driven OA on early life-history stages is scarce. The rapidly growing literature is dominated by uncertainties with recurrent use of “may”, “potentially” and “possible”.

In her recent review, Kurihara (2008) summarized what is known of the impact of CO_2-driven OA on early developmental stages of invertebrates. At the end of 2008, she had access to less than 10 publications and most of these published studies investigated short term impacts (few days) under conditions not always relevant to predicted climate impacts on ecosystems (e.g. using unrealistic pH values and/or acid-based acidification without correcting carbonates and bicarbonates) or ecologically realistic (e.g. single species cultures) conditions. This makes any realistic prediction difficult.

For this reason, in this review, we will focus on the impact of OA on early life-history from experiments using realistic climate scenarios: (i) pH or $p\mathrm{CO}_2$ levels in the range of expected values for 2100 (a decrease of 0.3/0.4 units of pH, $p\mathrm{CO}_2$ of 750ppm; Caldeira and Wickett, 2003); (ii) experiments manipulating carbonate chemistry using CO_2 (Dickson et al., 2007). All other studies are excluded from this review. This particular aspect of OA research is moving fast and several laboratories around the world are currently collecting new data. There is an urgent need to have some clear answers and even if not published yet, these preliminary data will be included to take advantage of as much available knowledge as possible in order to help the design of future experiments and define priorities.

2 What do we know?

2.1 Impact on survival

It is widely accepted that early life-history stages may be the most sensitive to CO_2-induced OA (Royal Society, 2005; Pörtner and Farrell, 2008). For some species, a slight decrease in pH can indeed have dramatic effect. For example, a decrease of 0.2 unit of pH induces 100% mortality at only 8 days post fertilization in calcifying larvae of the brittlestar *Ophiothrix fragilis* due to larval malformations that include skeletal defects (Dupont et al., 2008). An increased mortality is also observed in many other calcifying species such as crustaceans, mollusks and echinoderms (see Table 1 for review and references). It is important to note that in these listed phyla, other species are not affected by OA or are positively affected for example with a decrease in mortality observed in some sea urchin species. Thus at low pH in the sea urchin *Strongylocen-*

trotus droebachiensis, a significantly higher proportion of larvae successfully reach metamorphosis compared to those raised in normal (current) pH level(Dupont and Thorndyke, 2008). Such decreased mortality is also observed in all tested species of the non-calcifying Tunicate larvae (see Table 1 for review and references).

Even if some of the observed differences can be interpreted as differences between regions (e.g. water chemistry), populations, or methodology, others can only be interpreted as genuine inter-specific variations. For example, opposite impacts of low pH were observed between closely related sea urchins (a negative effect on mortality in *Echinus esculentus* vs *Strongylocentrotus droebachiensis* where low pH enhanced developmental success) when the experiments were carried out under the same conditions (water chemistry, pH range, food type and concentration, density, period, etc.). These results highlight the fact that the impact of OA is species-specific, even in closely related taxa. A direct practical consequence is that it is dangerous to extrapolate from single species studies.

Such results also imply that the levels of CO_2-induced acidification predicted to occur within the next 50–100 years (pH≈−0.2 to −0.4 units, Caldeira and Wickett, 2003) would at the very least cause severe reductions in larval survivorship, and quite possibly the complete eradication of several species with little potential for acclimation and/or adaption in some of them (e.g. *O. fragilis*). On the other hand, it seems likely that there will also be winners in the future more acid ocean, such as tunicates and other taxa benefiting from OA and therefore profound changes in ecological relationships (predation, competition, etc.) is then expected.

2.2 Impact on developmental dynamics

In all tested species but tunicates (Table 1), OA is associated with a reduction in developmental rate. At low pH, it takes more time to reach the same developmental stage, increasing the time taken to reach metamorphosis. This delay in development is not correlated with mortality, at least in experimental single-species cultures. In some species such as the sea urchin *Paracentrotus lividus*, if it takes few more days to reach the post-metamorphic stage, thus the number of larvae reaching this stage is significantly higher at low pH. Again, non calcifying tunicates appear to be an exception with a faster developmental rate when exposed to OA (Table 1).

These observations were made on single-species culture experiments (for more information on the limitations of single-species culture, see Widdicombe et al., 2008). In more natural conditions, in the "real world" this delay in development will have other consequences on larval survival. During larval development, the plasticity appears suited to minimize development times, rapid development being presumably advantageous and a delayed development leading to a delayed settlement can impact local populations. Planktonic mortality is high and increasing the time a larva spends in the plankton/water column must increase the chance of loss by predation and/or by delay in the opportunity to settle. In a high quality habitat (Miner, 2005; Elkin and Marshall, 2007). Moreover, many ecological processes are synchronized. For example, barnacle larvae are released in the plankton to coincide with the spring bloom. If the development of nauplii larvae is delayed as suggested by Findlay et al. (2008), synchrony with the algal bloom will not be achieved. The timing of recruitment is also crucial and late settlers often experience the lowest survival (Kendall et al., 1985).

2.3 Impact on calcification

Because of the reduction in calcium carbonate saturation in seawater when exposed to high CO_2 concentrations, calcification and calcifying species have received a great deal of attention from the OA community. This is also true for the development community where calcifying species have been a primary target. Of the 24 species investigated so far, half are sea urchins and only 4 have non-calcifying larvae (3 Tunicates and 1 sea star, Table 1). Surprisingly, with few notable exceptions (profound skeletal malformations in the brittlestar *Ophiothrix fragilis* exposed to pH 7.9, Dupont et al., 2008; higher numbers of malformed shells in oyster and mussel larvae exposed to low pH (7.8), Kurihara, 2008), OA seems to have very little impact on larval skeletons (Dupont and Thorndyke, 2008). For example, even if some irregular mineralization and erosion was observed in several sea urchin species at low pH, their gross morphology was not affected neither their fitness, Clark et al., 2008).

Calcifying larvae should not be considered simply as small particles of calcium carbonate; the whole process of calcification is complicated. Amongst marine calcifiers, calcification mechanisms differ considerably. For example, it is frequently overlooked that echinoderms are the only invertebrates (and are thus like chordates) where their calcified support is endoskeletal, that is their skeletons are enclosed within at least one epithelial integument (Wilt, 1999; Hoffman et al., 2008). Other typical marine invertebrate calcifiers (mollusks, crustaceans, worms) produce their skeletons as epidermal secretions (exoskeletons) with direct contact with their environment. Calcification also involves different processes including ion pumps and the maintenance of a suitable microenvironment local to the site of skeletogenic calcification (Fig. 1). Analysis of the impact of OA on calcification in larvae is not an easy task and, as some data imply, may not be the most urgent question that needs to be solved.

It is perhaps time to move beyond a focus only on calcification; in particular for those early developmental stages experiencing OA for a relatively short period (few days to several weeks). Moreover, the surface ocean will remain almost entirely supersaturated with respect to calcite and aragonite with the exception of cold water (Orr et al., 2005). Under these conditions, OA may not impact calcifying larvae too strongly. For example, a significant effect is observed in mussel larvae even when only a slight undersaturation of aragonite is associated with low pH. When low pH is associated with oversaturation of aragonite, the only impact of OA is a small delay in development (Gazeau et al., 2008). Similar results were observed in sea urchins larvae when manipulating carbonate chemistry rather than CO_2 concentration (Suarez et al., 2008).

2.4 Impact on physiology

OA can affect many physiological parameters and calcification is only one of them (Fig. 2, Pörtner, 2008). Marine organisms can experience physiological stress not directly related to calcification due to an increase in CO_2 (hypercapnia) and/or a decrease in pH. For example, calcium and other ion-transport based phenomena are vital for many physiological processes (i.e. ciliary activity, muscle contraction, neural signaling and integration, etc.) and the onset of development in most species studied is triggered by one of the longest calcium transients known (Whittaker, 2006, 2008). Moreover, some calcium channels have been shown to be exquisitely sensitive to pH (Mignen and Shuttleworth, 2000). However, very little is known regarding physiological processes other than calcification on larvae.

Feeding is one of the key physiological processes that may be influenced by OA. For example, echinoderm larval feeding efficiency at low pH is significantly lower than in the control (Dupont and Thorndyke, 2008). In echinoderms, it is well known that food quantity greatly influences survival, growth and acquisition of larval competence (Boidron-Métairon, 1995).Thus, in sea urchins, high food concentration before metamorphosis can induce a delay in metamorphosis and produce juveniles with a bigger test diameter and with a higher mortality rate (Vaïtilingon et al., 2001). The influence of OA on feeding may explain observed impacts on parameters such as survival, growth rate and other energy dependent process including calcification (Fig. 2).

2.5 Adaptation potential

Very little is known about the capacity of organisms to adapt to OA. A multigeneration experiment on the copepod *Acartia tonsa* showed that only one generation is needed to cope with impacts of OA on life cycle dynamics. The main impact of low pH (7.7) on the development of this copepod is an increase in generation time. At the second generation raised at low pH, the generation time returns to a value similar to that of the control, probably a consequence of artificial selection in those animals adapted to low pH (Dupont and Thorndyke, 2008).

2.6 Synergistic effects with other stressors

In the future ocean, OA will operate in synergy with other anthropogenic stressors. Predicted scenarios indicate a threat to marine life through the specific or synergic effect of both OA and temperature (global warming). Experiments on mollusks (Parker et al., 2008) and echinoderms (Byrne and Davis, 2008; Dupont and Thorndyke, 2008; Wren et al., 2008) demonstrate that some negative impacts of OA can only be observed when combined with higher temperature (an increase of 2°C expected for the end of the century). For example, a much higher mortality was seen in sea urchin larvae (*Strongylocentrotus purpuratus*) cultured at low pH (7.7) and at 16°C compared to the control at pH 7.7 and 14°C. (Wren et al., 2008).

3 What do we need to know?

In the second International Symposium on the "Ocean in a high CO_2 world", John Baxter emphasized that however badly scientists want to investigate and understand what they think is exciting regarding the important issues of OA, it is essential that we define priorities on "what we need to know". As in any scientific community, we have limited resources but also very limited time (recent data predict dramatic impacts on the most sensitive ecosystems as soon as 2020) to understand what will be the consequences of OA on the future ocean and perhaps provide some solutions for managing predicted impacts. We need simple answers (e.g. tipping points for keystone species and ecosystems) to a simple question: what will happen in the ocean by 2100?. We must then perhaps sacrifice what are more personal goals and ambitions for the greater good by integrating our research agendas and priorities. However, *we may also not know what we are looking for* (see discussion on calcification) and we have to be careful in being too prescriptive in future experimental designs (see Widdicombe et al., 2008 for further information). In this section we will suggest some priorities for development studies based on what is known so far.

3.1 What are species/ecosystems tipping points?

If we want to predict what will happen in the future ocean, we need to be able to define a reliable way to calculate species/ecosystem tipping points.

We have shown that it is dangerous to extrapolate from single species, even within closely related taxa. Thus we suggest that *a wide range of species should be investigated* without being too prescriptive: different life-history traits, habitats (both larval and adult), physiology, morphology, adaptation potential, etc. for simple fitness related parameters (e.g. survival). We can only guess at the kind of organisms that will benefit from the mayhem of the synergistic effects of human impacts on our oceans. The impact of OA on early development is species-specific and we have already stressed the fact that it is dangerous to extrapolate from only a few model species. A good illustration comes from a posteriori interpretation of the past extinction events. For example, if a good correlation is seen between the observed impact on survival/extinction and the predicted sensitivity based on physiology (presence/absence of calcareous skeleton and physiological buffering capacities) during the dramatic environmental changes suggested to be responsible for the end-Permian mass extinction (see Knoll et al., 2007), the predictors were not 100% accurate. Some of the species predicted as sensitive survived the environmental stress. In consequence, we should again, *not be too prescriptive in our species selection*. For example, we should not only focus on calcifying species and certainly *more energy should be invested in the potential "winners" from the affects of OA and global warming*. It is as important to understand why some species might benefit from OA as it is to understand why others are negatively impacted For example, jellyfish appears as excellent candidates. There is some evidence (Attrill et al., 2007), although controversial (Haddock, 2008; Richardson and Gibbons, 2008), that OA, in concomitance with increasing temperature, may lead to increases in the abundance of jellyfish by the end of this century. However, no experimental evidence is available, in particular for the key early developmental stages.

Since it is not possible to study all species and all populations, we need to understand the origin of the observed variability and apparent paradoxes (opposite effects in closely related species). Tipping points vary among species and we need to *study the mechanisms of physiological response* to understand these differences (Pörtner, 2008).

3.2 What will happen in the real world?

Defining how best to design experiments, manipulate and measure seawater chemistry or report the data is beyond the scope of this paper and the reader should refer to "Guide to best practices for ocean CO_2 measurements" (Dickson et al., 2007) and the EPOCA's "Guide for Best Practices in Ocean Acidification Research and Data Reporting" (Riesebell et al., 2009) for further information.

Kurihara (2008), based on published data, concluded that OA will have negative impacts on larval stages in several calcifiers. This conclusion was based mainly on short term and not always climate-relevant experiments and results may have been quite different had more realistic conditions been used (e.g. analysis of the complete life cycle and several generations taken into account). For example, a short term experiment on the effect of OA on early development of sea urchin could be interpreted as having a negative impact (e.g. smaller larvae due to a delay in developmental dynamics) when a longer term observation up to and including metamorphosis can reveal a positive impact (e.g. higher survival rate, Table 1). In future experiments, it is essential to *take into account the complete developmental cycle from egg to juvenile*.

This idea should be extended to the whole life cycle. For example, many benthic organisms release pelagic larvae and therefore experience very different environmental conditions during their life. OA may have indirect impacts from one stage of the life cycle to another. For example, long term exposure of adult sea stars (*Asterias rubens*) to low pH conditions (7.7) affects future larval performance (Dupont and Thorndyke, 2008). To assess the real impact of OA on larval development as one part of the life-cycle of a species, we need to design long term experiments taking into account parameters such as generation time and, if possible, *on several generations*.

Studies on population and community level processes suggest that climate impacts (e.g. temperature) on individuals do not necessarily translate into distribution and abundance (Harley et al., 2006). Trophic structure and biodiversity are also key components of the resistance and resilience of marine ecosystems for future perturbations, but we are only now beginning to document how these parameters change in relation to OA (for an example of an ecosystem experiencing long term low pH conditions, with the limitation that the mobile species can escape from low pH conditions, see Hall-Spencer et al., 2008). As is observed for global warming, OA will change the balance between species with shifts in species distribution and abundance according to their tolerance to changes and ability to adapt. For example, extinction of some keystone species (e.g. *Ophiothrix fragilis*, Dupont et al., 2008) could create opportunities for other species with more flexible and robust regulatory systems. OA may also induce migration to regions with a more suitable habitat (e.g. higher alkalinity water). It is then essential to *include ecological relationships in future experiments*, for example through mesocosm experiments (Widdicombe et al., 2008) or manipulation of conditions "in-situ".

When studying the likely future impact of OA in the Anthropocene, we need to include other potential synergistic effects of human impacts such as warming, habitat destruction, overfishing, introduced species, toxins and/or massive runoff of nutrients. For example, oysters may be negatively impacted by OA. This will be in addition to other threats such as overfishing that nearly eliminated some species as well as hypoxia, introduced (competing) species and uncommon predators that now hamper their recovery (Jackson, 2008). OA affects will likely exacerbate those from other stresses (Pörtner and Farrell, 2008). It is then important to *include at least temperature in future experiments*.

When designing an experiment, we need to work in realistic conditions for both abiotic (e.g. *control conditions that mimic the real local environment experienced by the larvae* at the time of spawning, including natural variations of temperature, alkalinity, salinity, etc.) and biotic (e.g. density, food type and concentration). This is not always a trivial task and any experiment has to take account of their own limitations. For example, it is difficult to spawn corals in culture and pteropods do not feed in laboratory conditions. Moreover, each experiment is only an abstraction of reality and it is impossible to avoid bias such as experimental stress (see Widdicombe et al., 2008). In conclusion, we should design experiments that are as realistic as possible regarding future scenarios and natural environments.

4 Is there any chance of adaptation?

The individual is the fundamental unit in biology and the genetic differences within and between populations may have the potential to ameliorate impacts of climate change. Many responses perceived as adaptations to changing environment are environmentally-induced phenotypic plasticity rather than micro-evolutionary adaptations (Gienap et al., 2008). The study of phenotypic plasticity and reaction norms (e.g. common-garden and reciprocal transplant experiments) provides a critical understanding of species' potential to respond rapidly and effectively to challenges imposed by OA. To determine if a species will adapt to future climate changes is not an easy task and early developmental stages are key elements of this question. Intraspecific variability should be investigated to understand population resilience and adaptability on the time scale of actual climate change. We need to define simple proxies to assess adaptability.

5 What can we do?

In a speech in San Francisco, the governor of California Arnold Schwarzenegger said that "*The debate is over. We know the science. We see the threat. And we know the time for action is now.*" (cited by Petit, 2005). Today, the climate change threat has reached the public and politic conscience and has become a major concern as demonstrated by the Nobel Peace Prize 2007 to Intergovernmental Panel on Climate Change

(IPCC) and Al Gore for “for their efforts to build up and disseminate greater knowledge about man-made climate change, and to lay the foundations for the measures that are needed to counteract such change”. If potentially dramatic and more threatening for ocean life, OA is just another consequence of our increasing CO_2 emissions, the “global warming’s evil twin” (Richard Feely cited by Savitz and Harrould-Kolieb, 2008). Data available so far are clear enough to demonstrate that we need to reduce our CO_2 emissions. As scientists we still have to spread the word and provide new and convincing evidence about what will happen in the near future, but maybe it is time to *propose some solutions*.

In order to allow society and policy makers to address the big environmental questions, we need good quality information to predict what will happen at the local level and develop strategies to minimise impacts. There are few studies focusing on how responses to OA vary among individuals and populations. For example, populations already experiencing other stresses (e.g. southerly range of barnacles already stressed by temperature, Findlay et al., 2008) may be either more vulnerable to local extinction or either better adapted to face additional stressors. We need to *identify those species, populations and ecosystems that are most at risk* and suggest some key areas for conservation efforts.

We should also put some more effort into the investigation of adaptation potential, understand geographical variation in organism responses to OA and try to identify and *isolate OA resistant strains/population*s of keystone or economically important species. For example, within similar environmental conditions, genetically different individuals of the oyster *Crossostrea gigas* with different physiological potential will experience different growth rates (Pace et al., 2006) and preliminary data indicates that this may lead to differential impacts of OA (Parker et al., 2008). This approach may allow us to rescue some key ecosystems in the future ocean and help develop some sustainable aquaculture approaches.

Another approach should be to *identify refuge ecosystems* with more favourable or fluctuating conditions providing some relief from unfavourable environments (e.g.

regions where OA will be associated with permanent or seasonal oversaturation of calcium carbonates). In such approaches and ambitions, it will be essential to integrate all the environments experienced by a species during its life cycle (e.g. planktonic and benthic, meroplankton).

6 Conclusions

Predicting the future is, at best, a highly uncertain enterprise. Nevertheless, we have a sufficient basic understanding of the ecological processes involved to claim that if humans fail change their behavior and to reduce emission of CO_2 (and subsequent warming and OA), many species and ecosystems will experience profound modifications with severe socio-economic consequences. If only few data are available on impact of OA on early development, they clearly indicate that many species will be drastically affected.

We already know that OA together with other stressors such as temperature has impacts on early development. This impact of OA can be dramatic for some species while others can benefit from low pH. We can then expect significant changes in future ocean ecosystems but it appears that these changes will be difficult to predict. OA impacts many physiological processes, calcification being only one part of the problem. Few data suggest that a rapid adaptation is possible for some species and that intraspecific variability may be a source of hope, for example to select resistant strains to future OA impacts.

As scientists, we need to increase understanding of predicted future changes, in particular to determine the potential for resistance and resilience of populations to climate change in order to support local conservation. There is no need to be a catastrophist but there is an urgent need to develop strategies to provide tractable and sustainable solutions.

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Table 1. Consequences of near future CO_2-driven OA on fertilization rate, survival and developmental dynamics (temporal aspect of the developmental program) in a range of marine animals (=, no effect ; –, negative effect ; 0, no survival; +, positive effect ; na, data not available).

Species	pH tested	Survival	Developmental Dynamics	Reference
Crustaceans				
Acartia tonsa	−0.4	=	–	Dupont, Calliari, Rodriguez, Tiselius and Thorndyke, personal communication, 2009
Semibalanus balanoides	−0.4	–	–	Findlay et al., 2008
Molluscs				
Mytilus edulis	−0.3/−0.4	=	–	Renborg and Havenhand, personal communication 2009; Gazeau et al., 2008
Crassostrea gigas	−0.4	–	–	Parker et al., 2008; Schlegel and Havenhand, personal communication 2009; Kurihara, 2008
Echinoderms – Ophiuroids				
Amphiura filiformis	−0.4	–	–	Dupont and Thorndyke, personal communication 2009
Ophiocomina nigra	−0.4	–	–	Dupont and Thorndyke, personal communication 2009
Ophiothrix fragilis	−0.4	0	–	Dupont et al., 2008
Ophiura albida	−0.4	–	–	Dupont and Thorndyke, personal communication 2009.
Echinoderms – Asteroids				
Asterias rubens	−0.4	=	–	Dupont and Thorndyke, personal communication 2009

Table 1. Continued.

Species	pH tested	Survival	Developmental Dynamics	Reference
Echinoderms – Echinoids				
Brisopsis lyrifera	−0.4	–	–	Wren et al., 2008
Echinometra mathaei	−0.4	na	–	Kurihara and Shirayama, 2004a, b; Kurihara et al., 2004
Echinus esculentus	−0.4	–	–	Dupont and Thorndyke, personal communication 2009
Evechinus chloroticus	−0.4	=	–	Clark et al., 2008
Hemicentrotus pulcherrimus	−0.3	na	–	Kurihara and Shirayama, 2004a, b; Kurihara et al., 2004
Heliocidaris erythrogramma	−0.4	–	na	Byrne and Davis, 2008
Paracentrotus lividus	−0.4	+	–	Dupont and Thorndyke, personal communication 2009
Pseudechinus huttoni	−0.4	=	–	Clark et al., 2008
Sterechinus neumayeri	−0.4	=	–	Clark et al., 2008
Strongylocentrotus purpuratus	−0.4	+	–	Wren et al., 2008
Strongylocentrotus droebachiensis	−0.4	+	–	Dupont, Stumpp, Melzner and Thorndyke, personal communication, 2009.
Tripneustes gratilla	−0.4	=	–	Clark et al., 2008; Mifsud, Williamson and Havenhand, personal communication 2009.

Table 1. Continued.

Species	pH tested	Survival	Developmental Dynamics	Reference
Tunicates				
Ascidiella aspersa	−0.4	+	+	Dupont and Thorndyke, personal communication 2009.
Ciona intestinalis	−0.4	+	+	Dupont, Auger, Legendre, Joly and Thorndyke, personal communication 2009.
Oikopleura dioica	−0.4	+	+	Dupont, Bouquet, Chourrout and Thorndyke, personal communication 2009.

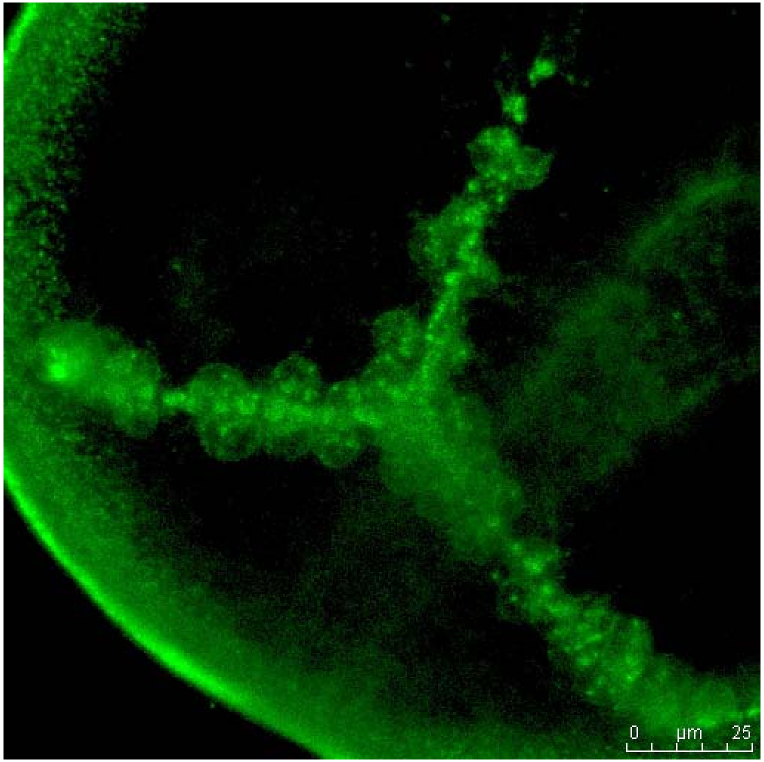

Fig. 1. Confocal image of the early development of the skeleton. Primary Mesnchyme Cells (PMC, revealed by PMC-specific cells surface marker, MSP130, Anstrom et al., 1986) surrounding the triradiate calcareous spicule typical in a 2 day late gastrula of the sea urchin *Strongylocentrotus droebachiensis*.

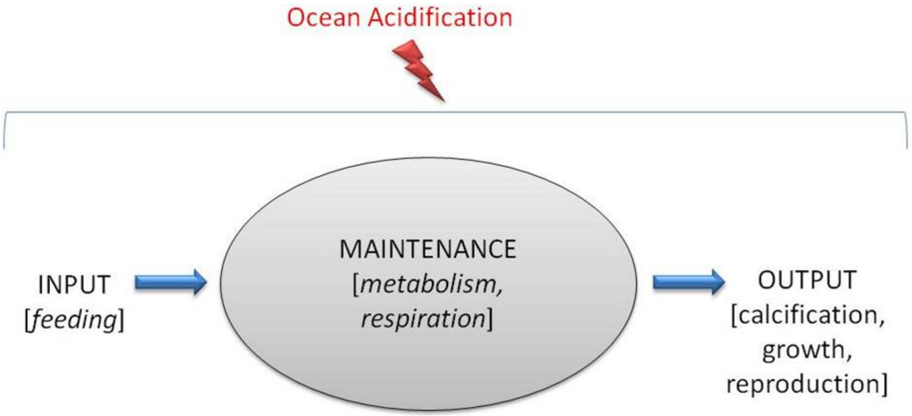

Fig. 2. OA can directly or indirectly affect many physiological processes with consequences on fitness.