The impact of ocean acidification on reproduction and early development of marine organisms

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ABSTRACT

Elevations in atmospheric carbon dioxide (CO_2) are anticipated to acidify oceans because of fundamental changes in ocean chemistry created by CO_2 absorption from the atmosphere into the oceans in a process known as ocean acidification. Over the next century, elevated CO_2 is expected to cause a reduction in the pH of the surface ocean from 8.1 to 7.7 units and a reduction in carbonate ion (CO_3^{2-}) concentration required for calcifying marine organisms. Of growing concern is the potential impact that this change in ocean chemistry will have on marine and estuarine organisms and ecosystems, particularly molluscs and echinoderms which are broadcast spawners with larvae that develop in seawater. Although fertilisation in molluscs and echinoderms appears to be robust to the effects of elevated CO_2, larval development is characterised by impacts on the rate of larval development through successive stages, larval survival and abnormality including the failure to produce shells and skeletons. Despite these trends, our current understanding of the biological consequences of an acidifying ocean over the next century is still dominated by large uncertainties. Some of the greatest gaps in our understanding is the synergistic impacts of elevated CO_2 with other environmental stressors such as increasing ocean temperature and changing salinity. Until we have a better picture from laboratory and field based experiments which investigate multiple stressors in a chronic way over multiple generations, we will be limited in predicting which mollusc or echinoderm species will be able to acclimate or adapt.

Key words: Ocean acidification, ocean warming, molluses, echinoderms, climate change

Introduction

It is essential to predict the impact of ocean acidification on marine organisms and habitats in order to anticipate the severity and consequences of future climate change and create adaptive management plans. Doing this in reality, however, is difficult (Pörtner *et al.* 2004; Przeslawski *et al.* 2008) because studies investigating the response of marine organisms to ocean acidification are comparatively in their infancy (Kleypas *et al.* 1999; Turley *et al.* 2006; Gooding *et al.* 2009) and ultimately meta-analyses attempting to draw out main effects, albeit authoritative, are restricted to small sample sizes and limited by a paucity of data (Hendriks *et al.* 2010, Dupont *et al.* 2010a, Hendriks and Duarte 2010; Hofman *et al.* 2010; Kroeker *et al.* 2010; Byrne 2011). The potential rate of acidification to marine organisms and habitats is, however, great exceeding that experienced by marine organisms at any other time on the planet (Caldeira and Wickett 2003; Turley *et al.* 2006; Guinotte and Fabry 2008). To counteract this great risk that climate change and ocean acidification specifically poses to the biodiversity of marine habitats, more recently research has turned to the impact of ocean acidification on fertilisation and early larval developmental stages of marine organisms because these life history stages may be the most sensitive and vulnerable to elevated CO_2 (Kurihara 2008; Dupont and Thorndyke 2009) and any negative impact may form a dead end in one life history stage and thus create a "bottleneck" for populations (Dupont *et al.* 2010a). In such a scenario all early life history stages of marine organisms are likely to be affected by ocean acidification, including egg and sperm development and production, fertilisation, cleavage, larval development, larval dispersal, settlement and post-settlement survival (Figure 1). Embryos and larvae in these early developmental stages have specific environmental needs (Thorson 1950) and are more likely to have acute responses to environmental stress as the first deposition of $CaCO_3$ of many marine groups is known to occur during the larval stage (Kurihara

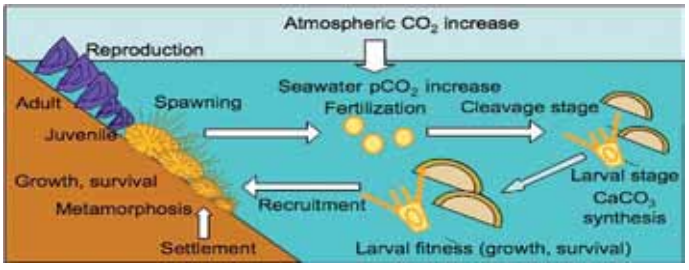

Figure 1. Different life-cycle stages of benthic calcifers, including reproduction, fertilization, planktonic lava, settlement, metamorphosis, juvenile and benthic adult stages, that are potentially affected in different manners by ocean *acidification*. With permission from Kurihara 2008

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2008). Effects from stress at fertilisation may also have profound carry-over consequences for individual larvae, larval cohorts (Green *et al.* 2004; Kurihara 2008; Parker *et al.* 2009, 2010) and larval dispersal. Collectively, the effects of elevated CO_2 on larvae may cascade, directly influencing the distribution and abundance of settlers and post settlement survival, and thus shape the structure and function of marine ecosystems and adult marine populations (Gosselin and Qian 1997; Kurihara 2008; ESF 2009). Here, we review the current literature on the effects of ocean acidification on fertilisation and larval development of molluscs and echinoderms on which the majority of work has been done and highlight the current gaps in our understanding and the areas for future research.

Historically, studies investigating the responses of early life history stages of molluscs and echinoderms to acidic conditions in a range of molluscs and echinoderms including the oysters *Crassostrea virginica* and *Saccostrea glomerata,* clams *Mercenaria mercenaria* and *Tivela stultorum* and the giant scallop *Placopecten magellanicus*; sea urchins *Paracentrrotus lividus* and; *Sphaerechinus granularis*, manipulated instead of manipulating pH by mineralisation at levels often far outside those predicted for marine environments as a response to elevated atmospheric CO_2 (Table 1; Calabrese and Davis 1966; Pagano *et al.* 1985a,b; Cipollaro *et al.* 1986; Alvarado-Alvarez *et al.* 1996; Desrosiers *et al.* 1996; Wilson and Hyne 1997). Desrosiers *et al.* (1996) found no reduction in fertilisation but did find that the speed of cleavage was slowed due to polyspermy. There were also negative impacts on fertilisation in bivalve molluscs (Alvarado-Alvarez *et al.* 1996), cleavage in echinoids (*Sphaerechinus granularis* Cipollaro *et al.* 1986; *Paracentrotus lividus* Pagano *et al.*, 1985 a and b), morphological development in bivalve molluscs (*Saccostrea glomerata* Wilson and Hyne 1997) and increased mortality, decreased growth and skeletal malformations in bivalve molluscs (*Crassostrea virginica* and *Mercenaria mercenaria* Calabrese and Davis 1966). Caution is however, required when using the results of such studies to predict potential impacts of ocean acidification on marine organisms and ecosystems given the levels of elevated CO_2 predicted by IPCC scenarios for the end of the century are considerably lower and current best practise methodologies recommend acidifying culture media seawater to most accurately reflect future carbonate chemistry by: i. directly aerating with CO_2 at required level; ii. directly adding HCO_3 and HCl in equal molar values or iii. Saturating seawater with CO_2 prior to adding to the culture media (Gattuso *et al.* 2010). Most recently, studies manipulating pH using best practise methodologies of Gattuso *et al.* (2010) and CO_2 scenarios for the end of the century (IPCC 2001; Caldeira and Wickett 2003, 2005; IPCC 2007) have found significant, non-significant and no effect of elevated CO_2 on fertilisation, larval development and growth of early developmental stages of marine organisms even when using the same or closely related species (Table 1). Nevertheless, emerging trends suggest that the impact of ocean acidification on marine organisms, particularly molluscs and echinoderms with planktotrophic larvae and feeding larval stages is more significant for larval development than for fertilisation. This is because it is during the early larval stage that shell formation occurs and amorphous calcium carbonate (ACC) crystal skeleton is deposited, known to be 30 times more soluble than stable forms of aragonite and calcite secreted later in larval and adult life (Orr *et al.* 2005; Dupont *et al.* 2010b).

Fertilisation, Cleavage and Gastrulation

The impact of ocean acidification on fertilisation has been investigated in a range of marine invertebrates, mainly echinoderms and bivalves which are broadcast spawners releasing eggs and gametes into the water column. There are fewer studies on crustaceans, corals and fish (Table 1). The life history stages of broadcast spawners potentially differ in sensitivity with early life history stages predicted to be more sensitive than later life history stages (Byrne *et al.* 2009) forming a major hypotheses in the literature being used to explain the variable responses (Kroeker *et al.* 2010) with less reference to the influence of natural variation in eggs and larvae (Przeslawski and Webb 2009) which may lead to a variability in larval response. Other hypotheses proposed to explain the variable responses of fertilisation in echinoderms and molluscs to the impact of ocean acidification include the level of elevated CO_2 used, the synergistic impact of temperature, the environment from which organisms are sourced, and debates around polyandry versus single crosses and other experimental techniques and analyses.

Echinoderms

Generally it is thought that echinoderm fertilisation is relatively robust to elevated CO_2 and decreased pH at levels predicted for the year 2100 (Byrne *et al.* 2009, 2010a, b; Dupont *et al.* 2010a), but can be negatively impacted when pH levels predicted for 2300 and lower are used (Kurihara and Shirayama 2004 and Kurihara *et al.* 2004b) or if sperm concentration is low and limiting (Byrne *et al.* 2010b, Ericson *et al.* 2010; Reuter *et al.* 2011). However, contrasting results have been reported for the same species from the same geographic region (Havenhand *et al.* 2008; Byrne *et al.* 2009).

Earliest studies by Kurihara and Shirayama (2004) and Kurihara *et al.* (2004b) exposed sea urchins, *Hemicentrotus pulcherrimus* and *Echinometra mathaei,* to pCO_2 concentrations ranging from 360 – 10365 ppm (pH 8.1-6.8). At exposures of pH 7.6 and 7.7 (-0.4-0.3 less than control levels) there was no effect on fertilisation of *Hemicentrotus pulcherrimus* and *Echinometra mathaei,* but at pH 6.8 for *Hemicentrotus pulcherrimus* and 6.8-7.1 *Echinometra mathaei* (-0.5 to - 0.2 less than that predicted for 2300), there were significant effects with reduced fertilisation success and reduced cleavage speed in both species of sea urchins (Kurihara and Shirayama 2004; Kurihara *et al.* 2004b) and a trend for decreasing fertilisation with decreasing pH between 7.3-7.4 (Table 1). These studies were criticised for using CO_2 concentrations outside that predicted even for 2300 so later studies focussed on fertilisation responses to realistic scenarios

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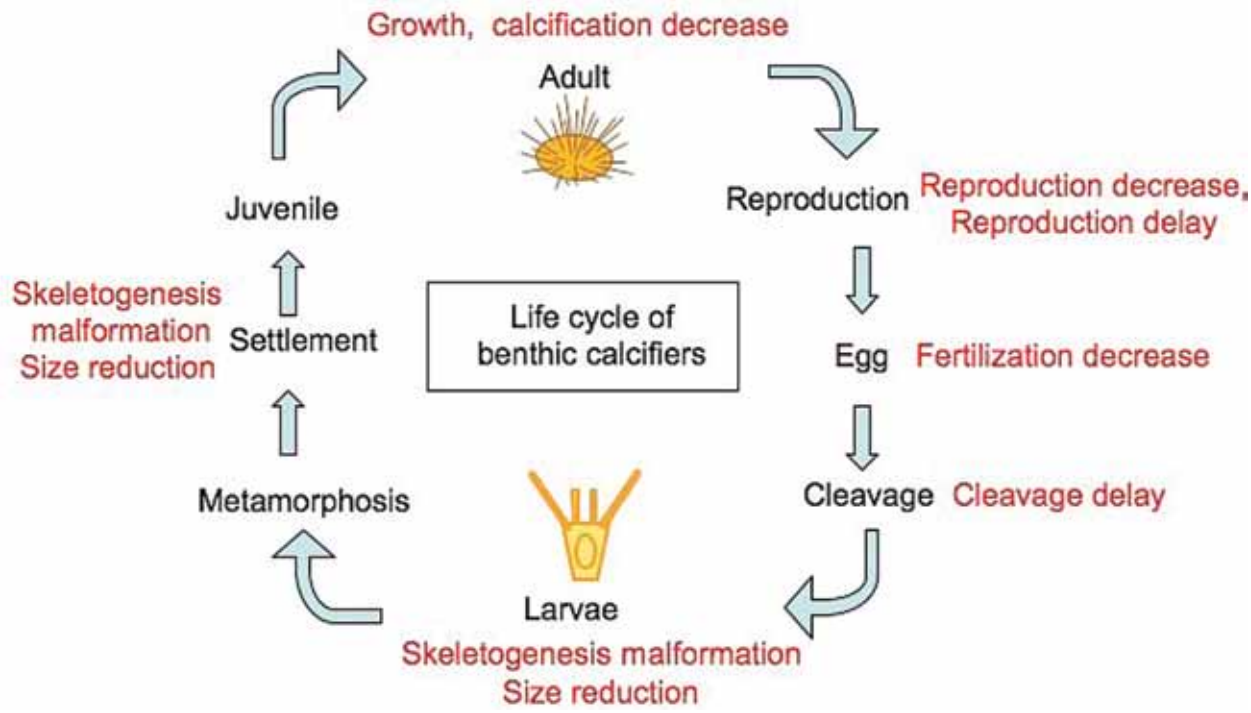

Figure 2. Summary of CO_2 effects at different life cycle stages of benthic calcifiers under CO_2 concentrations that are expected to occur in the future ocean (380~2000 µatm pCO_2 / pH 8.2~7.3). Although the magnitude of CO_2 tolerance may differ between species and life stages, effects of high CO_2 are proposed for several different life stages, including reproduction, egg, cleavage, larva, settlement and adult stages. Used with permission from Kurihara 2008.

predicted for 2100. Havenhand *et al.* (2008) found significant reductions in sperm swimming speed, motility and fertilisation success in the sea urchin *Heliocidaris erythrogramma* using a decrease of 0.4 units (pH of 7.7, 1000 ppm, -0.4 units compared to the control pH of 8.1). There was a reduction of 11.7% in swimming speed of sperm, 16.3% reduction in sperm motility, a 24.9% reduction in fertilisation success after 3-4 hours exposure. In addition the number of eggs developing into cleaving embryos after 20 hours exposure was 20% less when treated at an elevated concentration of CO_2 (Table 1). Such reductions in fertilisation were not detected in the next series of studies on the same species. Even with the additional stressor of elevated temperature, Byrne *et al.* (2009) found no significant effect of elevated CO_2 on the fertilisation success, cleavage and gastrulation in the sea urchin, *H. erythrogramma*; sourced from the same geographical region as Havenhand *et al.* (2008), with a larger pH range of 7.6-8.2 over a shorter exposure period (2-3 hours for cleavage and 19-20 hours for gastrulation). There was, however, a trend for decreased cleavage at elevated concentrations of CO_2 and pH of 7.6-7.9 compared to the control (8.2) at the higher temperature of 26 °C (4 units above ambient). Overall they detected no significant synergistic effect of elevated CO_2 and temperature on cleavage and gastrulation but rather a significant decrease in cleavage and gastrulation with increased temperature alone.

Such contrasting results, even for identical species, could be due to differences in experimental methodology arising from single male and female crosses in Havenhand *et al.* (2008) versus multiple males and females in Byrne *et al.* (2009; 2010a and 2010b) and high fertilisation success in controls (Havenhand *et al.*, 2008 62% versus Byrne *et al.*, 2010 a, b 80-90%). It remains unclear whether intra and inter specific differences are real or due to differences in experimental techniques (Byrne *et al.* 2010a; Ericson *et al.* 2010; Reuter *et al.* 2011) by the pooling of gametes from males and females (Byrne *et al.* 2009, 2010a, 2010b), creating arguments about polyandry versus single crosses and their influence on results and interpretation and or misinterpretations and measurements in fertilisation due to polyspermy. Whether polyandry or single crosses, even recent studies are based on small sample sizes of males and females (Byrne *et al.* 2009 2 males: 2 females; Byrne *et al.* 2010a 3 males: 3 females; Ericson *et al.* 2010, 1 male: 1 female) and additionally may suffer from pseudoreplication where containers are not factored as a source of variation in the analysis. This raises doubt over whether differences are representative because of low replication (Moulin *et al.* 2011). Value would be added if post-hoc tests (e.g. Byrne *et al.* 2009) were done. Indeed the experimental design of Havenhand *et al.* (2008) used 5-6 males, while Reuter *et al.* (2011) used 12 male-female pairs of replicates over eight serial sperm dilutions and emphasised that fertilisation success may be inaccurately estimated if fertilisation success is a measure of both fertilised and polyspermy embryos. Other authors agree stating that differences in experimental methodologies hamper our ability to make robust generalisations (Dupont *et al.* 2010a).

Single stressor studies also reduce our understanding of the impacts of ocean acidification. These have been replaced in recent times by synergistic studies investigating the effect of elevated CO_2 and temperature on fertilisation. Against expectation, elevated CO_2 has

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not been found to reduce fertilisation nor temperature to enhance fertilisation (Byrne *et al.* 2010a). There was also no synergistic interaction between elevated CO_2 and temperature and no trend for reduced fertilisation with increased concentration of CO_2 over a range of sperm concentrations. In a further study by Byrne *et al.* (2010b), on a range of echinoderms including once again the echinoid, *Heliocidaris erythrogramma* and the closely related species, *Heliocidaris tuberculata*, *Tripneustes gratilla*, *Centrostephanus rodgersii* and the asteroid, *Patiriella regularis,* using multiple male and female combinations, there was no significant effect of elevated CO_2 nor temperature on fertilisation. There was a trend, however, for decreased fertilisation in the subtidal sea urchin, *H. tuberculata*, prompting the comment that species characterising shallow coastal waters are perhaps more robust to fluctuations in their environment (Byrne *et al.* 2010b). Similarly, Martin *et al.* (2011) found high fertilisation rates (>97%) with no effect on fertilisation down to a low pH (7.25) for the widely distributed Mediterranean and North Atlantic sea urchin, *Paracentrotus lividus.*

Although, fertilisation remains robust when synergistic factors such as temperatures are combined with elevated CO_2 (Byrne *et al.* 2010 a, b) this may not occur when sperm is limiting (Ericson *et al.* 2010; Reuter *et al.* 2011). Similar to Byrne *et al.* (2009, 2010a, 2010b), Ericson *et al.* (2010) found no effect on fertilisation of elevated CO_2 and decreased pH at levels predicted for the year 2100 for the echinoid *Sterechinus neumayeri*, but they did find an effect of elevated CO_2 when sperm concentration was suboptimal. Sperm concentration appears to be a significant factor for organisms when other conditions are suboptimal. Reuter *et al.* (2011) found maximum fertilisation rates in the sea urchin, *Strongylocentrotus franciscanis,* were maintained only at increased sperm concentrations. A reduction in fertilisation efficiency related to sperm concentration raised at pCO_2 levels and pH 7.81 and 7.55 (800 and 1800 ppm, respectively) and the time of egg block to polyspermy was also significantly longer at pH 7.55 (Reuter *et al.* 2011).

Studies such as (Byrne *et al.* 2010a b) and more recent findings (Moulin *et al.* 2011) have led to the suggestion that robustness of fertilisation in echinoderms to ocean acidification may be because they can acclimate to the low pH conditions experienced in their environment. In addition, the natural process of fertilisation is characterised by low pH conditions, with an inhibitory effect on sperm motility (Havenhand *et al.* 2008) over ridden by jelly peptides on eggs and respiratory effects (Byrne *et al.* 2010b). Moulin *et al.* (2011) found when gametes of the temperate sea urchin, *Paracentrotus lividus,* originated from individuals sourced from a more acidic tidal pool (which recorded an overnight drop to pH 7.4) fertilisation rates were greater in the acidic pool compared to control pool. Although in general fertilisation and cleavage rates decreased in the acidic pool, below pH 7.6 (control pH 8.0). Moulin's study, however, compares an acidic with a control pool and thus any differences between the 2 pools, may be due to chance, rather than represent the responses of sea urchins in rock pools with lowered pH. Such acute studies with low replication limit our ability to make robust conclusions. Acute studies need to be replaced with chronic multigenerational studies which test hypotheses related to acclimation and pre adaptive capacity as suggested in molluscs (Parker *et al.* 2011). Thus the evidence for the potential of echinoderms to acclimate to acidification requires further investigations to be done.

Molluscs

Similar to echinoderms, the methodology of early studies investigating fertilisation in molluscs exposed eggs and sperm to elevated CO_2 used pH concentrations outside the scenarios predicted for 2300 (Caldeira and Wickett 2003; Table 1). Yet in contrast to the echinoderms there was no reduction in swimming speed of sperm, sperm motility, fertilisation or cleavage even at these low pH levels. Kurihara *et al.* (2008a) exposed the mussel, *Mytilus galloprovincialis,* to elevated concentrations of pCO_2 (2000 ppm) with resultant pH of 7.4 (a reduction of 0.7 pH units compared to controls), and found no significant differences in fertilisation between controls and elevated CO_2.

Intraspecies differences in fertilisation responses to elevated CO_2 in molluscs once again make general conclusions difficult. There was no effect of elevated CO_2 on sperm speed, sperm motility or fertilisation in the Pacific oyster, *Crassostrea gigas* (pH 7.4-7.8 Kurihara *et al.* 2007; pH 7.8 Havenhand and Schlegel 2009), located in Japan and Sweden respectively, but there was reduced fertilisation at pH 7.83 for this same species in Australia (Parker *et al.* 2010). In an unpublished follow up study using almost identical methodologies, sperm concentrations and exposure levels; there was still no difference in fertilisation responses of populations of *C. gigas* in Japan and Sweden, but significant differences for populations of *C. gigas* in Australia (Parker *et al.* unpublished data). These contrasting contradictory fertilisation responses to elevated CO_2 and lowered pH within identical species of molluscs is characteristic of acute studies done on sea urchins (Byrne *et al.* 2009, 2010b; Havenhand *et al.* 2008). Yet perhaps because the results occur even when using identical methodology, they provide support for models explaining that differences within and among populations are caused by environmental or genetic differences, rather than experimental methodology.

Intra and interspecific differences in fertilisation responses have also been found between related species of oyster; the Sydney Rock oyster, *Saccostrea glomerata* and the Pacific oyster, *Crassostrea gigas.* There were significant differences in fertilisation rates at elevated CO_2 in *S. glomerata* (pH 7.9; Parker *et al.* 2009, 2010), and when responses of *S. glomerata* and *C. gigas* were compared, there was a significantly greater reduction in fertilisation in *S. glomerata* compared to the more robust *C. gigas* (Parker *et al.* 2010). When these acute experiments combined the additional stressor of suboptimal or elevated temperature, there was a synergistic impact with elevated CO_2 and correspondingly significantly reduced fertilisation (reduction in fertilisation of up to

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26% and 51% for *C.gigas* and *S.glomerata* respectively at suboptimal temperature). In molluscs, intra and species specific differences make generalisations difficult and such variable results may mirror the fluctuations in pH in these estuarine habitats where these intertidal species are found. In the only study done on a subtidal species, where pH may fluctuate less, there was no effect on fertilisation of temperature or elevated CO_2, using concentrations of CO_2 expected for 2100 on the temperate abalone, *Haliotis coccoradiata* (Byrne *et al.* 2010b).

Recent meta-analyses of the overall effects of elevated CO_2 on fertilisation are restricted by the paucity of papers available with reductions in effect size below 2000 ppm pCO_2 for sea urchin embryos (-9%, 3 papers, 2 species; Hendriks *et al.*, 2010) and yet increased effects for bivalves (+2%, maximum 2 papers 2 species) and a cephalopod (*Sepia officinalis,* +98% Hendriks and Duarte 2010), although the ppm range was not specified. With such small databases being employed, generalisations on the overall effect on fertilisation for groups is not possible, leaving our understanding of the impacts of ocean acidification on fertilisation based on species specific studies done in sometimes different geographic regions where population and experimental similarities and differences cloud the conclusions. Despite these unanswered questions, authors are now in agreement that fertilisation in echinoderms may be relatively robust to near future ocean acidification (Dupont *et al.* 2010a, c; Hendriks *et al.* 2010; Hendriks and Duarte 2010). This cannot be supported for fertilisation of molluscs nor widely for other groups when there is still a paucity of data on the diversity of marine invertebrates (Byrne *et al.* 2010b) and where results are outside the context of the normal fluctuations of pH in their environment, which may provide some pre adaptive capacity (Clark *et al.* 2009; Moulin *et al.* 2011; Parker *et al.* 2011).

Larval development and growth

Even if it turns out that fertilisation is robust to near future predictions of ocean acidification, larval developmental stages may be more vulnerable (Dupont *et al.* 2010a). Many marine invertebrates start to calcify in their larval or juvenile stage (Kurihara 2008; Kroeker *et al.* 2010). Several studies have suggested that the early life history stages may be more sensitive to environmental perturbations (Kurihara *et al.* 2007; Kurihara 2008; Dupont *et al.* 2010a, c).

Echinoderms

Larval development has been shown to be more sensitive than fertilisation to elevated concentrations of atmospheric CO_2, particularly for echinoderm embryos and larvae, with delayed development, reduced survival and size and skeletal abnormalities mainly investigated in planktotrophic larvae (Table 1). The most dramatic impacts have been measured in the planktotrophic ecological keystone brittlestar, *Ophiothrix fragilis,* (Dupont *et al.* 2008). Larvae of *O. fragilis* grown in CO_2-acidified seawater at pH 7.7-7.9 suffered 100% mortality within 8 days, while control larvae showed 70% survival over the same time. There was also a decrease in larval size with no larvae raised at pH 7.9 reaching the normal 8 pluteus arm stage and a high proportion of these larvae were either abnormal or had altered skeletal proportions and asymmetry during skeletogenesis. Further, there was a delay in development at low pH, with larvae at elevated CO_2 treatments taking longer to reach the same developmental stage (Dupont et al, 2008); for example, 50% of the control larvae were 6 armed after 5.42 days compared to 5.73 days at pH 7.9. Similarly after 2 days while abnormalities were completely absent in the control larvae, larvae at low pH with no other abnormalities had high proportions of asymmetry (25% at pH 7.9 and 32% at 7.7, Dupont *et al.* 2008).

These more recent studies support the findings of earlier studies reporting delayed development and abnormal pluteus morphology in the planktotrophic sea urchins, *Hemicentrotus pulcherrimus* and *Echinometra mathaei*, in which used a wider range of pH levels, some being within emission scenarios for the end of the century (Kurihara and Shirayama 2004; Kurihara *et al.* 2004b). In acute exposure experiments of three days, *H. pulcherrimus* larvae grown at pH 6.8 failed to develop arms and spicules or reach pluteus stage, consequently displaying high abnormality (Kurihara and Shirayama 2004). Larvae grown at pH 7.8 and 7.6 were smaller than controls and formed normal triangular and abnormally trapezium shapes respectively (Kurihara and Shirayama 2004; Figure 3). Using a similar pH range larval development in another temperate planktotrophic sea urchin, *Paracentrotus lividus,* was only affected below pH 7.4 with an increase in abnormal pluteus larva, although rod length was shorter only below pH 7.2 (Moulin *et al.* 2011). Similar to *H. pulcherrimus* (Kurihara and Shirayama 2004), at the acute pH of 6.8 all *P. lividus* embryos failed to develop to pluteus stage, displaying an abnormal bowl-shaped morphology (Moulin *et al.* 2011).

The negative responses to elevated CO_2 in planktotrophic larvae are not necessarily reflected across all echinoderms. Elevated CO_2, had no negative impact on survival or skeletal formation on the lecithotrophic larvae of the sea star, *Crossaster papposus* over the 38 day duration of the experiment. In fact there was a positive effect, on larvae which grew 2.8 times faster and juveniles 2.2 times faster at pH 7.7 compared to controls; 50% of larvae had progressed into the juvenile stage by day 28, whilst 95% of controls had developed rudimentary, but remained in the preceding settlement stage (Dupont *et al.* 2010b). In contrast, Havenhand *et al.* (2008) found at a pH 7.7, identical to Dupont *et al.* (2008; 2010b), that the percentage of eggs which developed into swimming larvae of the lecithotrophic sea urchin, *Heliocidaris erythrogramma,* after 24 hours was 25.9% lower than the control. Dupont *et al.* (2010b) suggested the need for further investigation of the impact of ocean acidification on lecithotrophic larvae, because the lecithotrophic cephalopod, *Sepia officinalis,* developed and calcified in low pH (Gutowska and Melzner 2009). These studies show that even amongst marine organisms with lecithotrophic development there can be variability in response.

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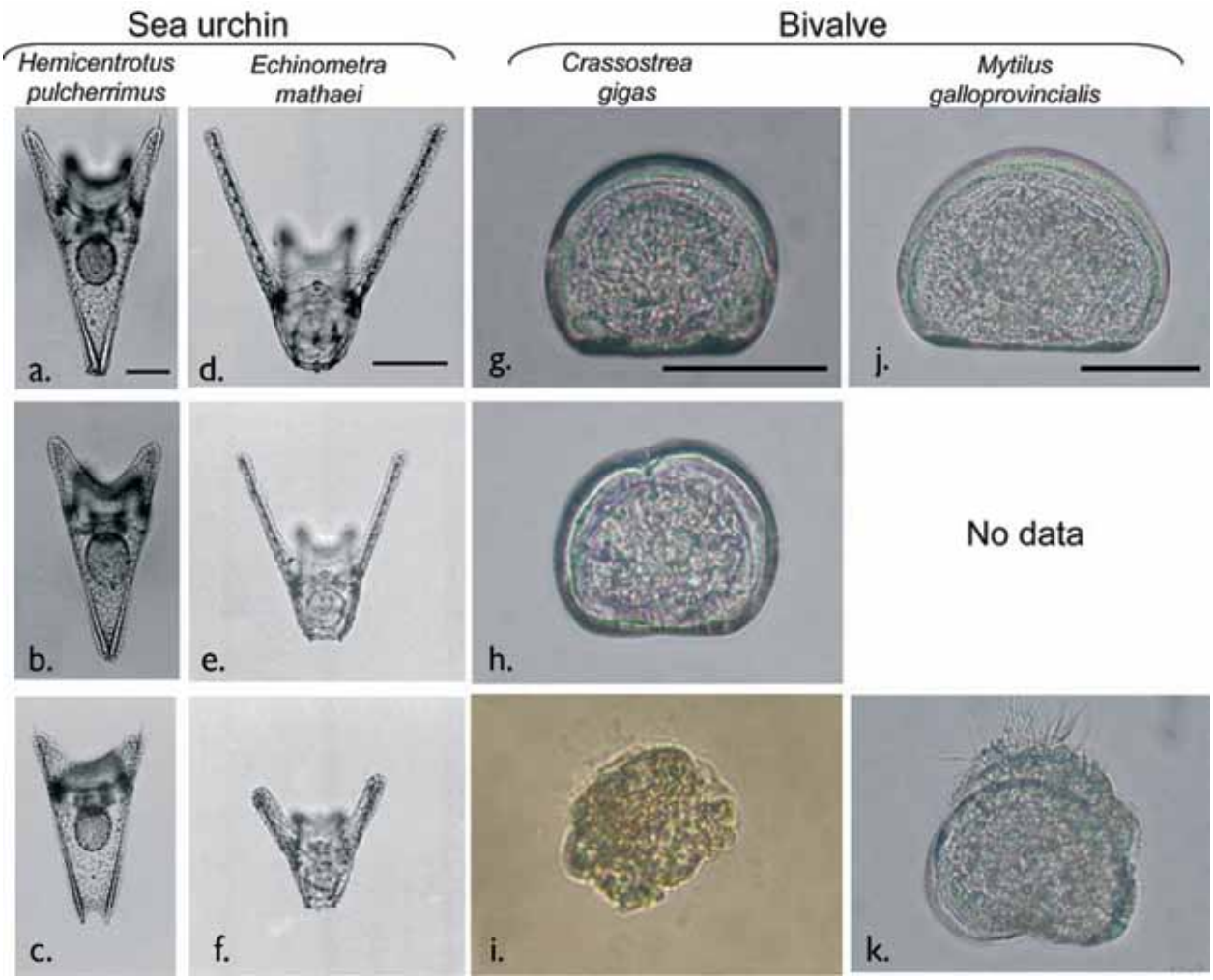

Figure 3. Larval morphology in the sea urchins *Hemicentrotus pulcherrimus* (a,b,c) *Echinometra mathaei* (d,e,f), and the bivalves *Crassostrea gigas* (g, h, i) and *Mytilus galloprovincialis* (j, k), exposed to pCO_2 concentrations of 380 ppm (control, a, d, g, j), 1000 ppm (b, e, h) and 2000 ppm (c, f, i, k). Scale bars represent 50 µm. Figure from Kurihara (2008).

There is little evidence to suggest that a geographic distribution model explains the delayed development and skeletal abnormalities in echinoderm larvae. Clark *et al.*, (2009), tested the prediction that the calcification of larvae of polar species would be more negatively impacted than temperate and tropical species because calcification is less energetically favourable at higher latitudes, and found opposite to that predicted. The Antarctic species, *Sterechinus neumayeri,* was least affected by elevated CO_2 while there were variable yet similar impacts on sea urchin larvae distributed from the tropic to Antarctic regions. Lowering of the pH to 7.0, resulted in significantly reduced survival of tropical, *Tripneustes gratilla*, but did not significantly affect survival of the temperate species, *Pseudechinus huttoni* and *Evechinus chloroticus,* or the polar species, *Sterechinus neumayeri*. The main effect, however, was a reduction in calcification of pluteus larvae which ranged from a small and non-significant decrease of 3.9% in polar, *Sterechinus neumayeri,* to significant decreases of 13.8% in tropical, *Tripneustes gratilla*, 30.6% in temperate, *Evechinus chloroticus,* and 36.9% in temperate, *Pseudechinus huttoni,* with 0.4 pH units reduction (7.51-7.87) compared to controls (7.9-8.17) and a reduction in growth for 3 out of the 4 species, but with no significant difference in *P. huttoni* (treatments pH 7.6-7.8, controls 8-8.2). Although acidified seawater did not change the morphology of larval skeletons among species. As found in other studies, there were fine scale differences in skeletal structures with an apparent loss of integrity of the surfaces of the skeletal rods for temperate, *E. cloroticus* (was pitted), *P. huttoni* (was eroded), contrasting with the smooth skeletal rods from larvae of tropical, *T. gratilla,* and polar, *S. neumayeri,* grown at ambient or reduced pH. Further, Ericson *et al.*(2010) found no difference among pH treatments (7, 7.3, 7.7 and ambient 8.0) in rate of development or visual abnormality in *Sterechinus neumayeri* larvae, the polar species used by Clark *et al.* (2009), through early development up to coeloblastula stage (day 2 post fertilisation). Significant differences among pH treatments first appeared at gastrulation (day 6) where embryos were 20% shorter, displayed no normal larval development, had rupturing of the gastrula epithelium and irregular morphology at pH 7, but no difference in abnormality levels or length among the other treatments (although at pH 7.3 some delayed development was apparent).

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Multiple stressor experiments, combining elevated CO_2 and temperature are more rare, but Sheppard Brennand *et al.* (2010), testing the hypothesis that temperature enhancement would counteract the negative effect of acidification, found elevated CO_2 reduced calcification in the tropical sea urchin, *Tripneustes gratilla*, used by Clark *et al.* (2009). Varying temperatures (24 -control, 27 and 30°C) and pH levels (7.6, 7.8 and control 8.15), significantly increased larval growth as temperature increased until the thermal limit was reached (30°C), and decreased as pH decreased, although difference in post oral arm length (larval asymmetry) was sensitive to temperature, not pH. These increased growth rates with +3°C rise in temperature effectively reduced, but did not negate, adverse effects in larvae raised at low pH (Sheppard Brennand *et al.* 2010). The effect of elevated temperature and lowered pH on growth of *T. gratilla* larvae was similar to the findings of Clark *et al.* (2009), once again highlighting the species specific nature of responses to environmental stressors. Byrne *et al.* (2011a) in a similar experiment, but on the temperate species, *Heliocidaris erythrogramma,* found that both temperature and elevated CO_2 reduced the number of spines and percentage of juveniles developing, but that increased temperature reduced the overall negative effect of elevated CO_2.

The search to determine the vital physiological mechanisms and processes affected in marine invertebrates by elevated CO_2 during larval development is revealing that gene expression can be compromised at elevated atmospheric CO_2 levels and temperature in the sea urchins, *Strongylocentrotus franciscanus* and *Lytechinus pictus* (O'Donnell *et al.* 2009, 2010). Potential impairment of physiological response to heat stress by *S. franciscanus* larvae at the four-arm echinopluteus stage was observed at pCO_2 levels of 540 and 970 ppm (pH 7.98 and 7.87 respectively), with significant up-regulation and change in expression profile of the heat stress gene *hsp70,* resulting in peak gene expression occurring 2°C higher than controls (O'Donnell *et al.* 2009). Although 540 ppm pCO_2 (pH 7.87) had no effect on *Lytechinus pictus* raised to pluteus stage, at 970 ppm (pH 7.78) larvae were significantly smaller and had more triangular skeletons and shorter arms than controls, as well as down regulation of biomineralization, skeletogenesis and energy metabolism genes, whilst some acid-base and ion regulation genes were up-regulated (O'Donnell *et al.* 2010). Similarly Martin *et al.* (2011) found up-regulation of development and biomineralisation genes by factors of up to 26 at low pH .

In the absence of adequate adaptation or acclimation, such CO_2-induced sub lethal effects on *O. fragilis* and other echinoderms species may result in the disappearance of these organisms from the surface oceans within the next 50−100 years (Dupont *et al.* 2008). As studies accumulate there is some evidence that some species may be resilient. For example, although larvae of the purple sea urchin *Strongylocentrotus purpuratus* were significantly smaller at pH of 7.7 and 7.5 after 6 days of exposure to elevated CO2, the difference was only 7-13% less than the controls suggesting potential resilience (Yu *et al.* 2011). Further, the widely distributed Mediterranean and North Atlantic sea urchin, *Paracentrotus lividus*, was extremely resistant to low pH (down to 7.25 pH) with no effect on larval survival. Also although there was a significant delay in larval development, this had no impact on relative larval morphology or calcification (Martin *et al.* 2011). Overall, however, to date studies from a range of geographical regions show that sea urchin, brittlestar and seastar larvae may develop more slowly, be smaller, have skeletal abnormalities and have impaired physiological responses to environmental stressors under elevations in CO_2 which may be either ameliorated or exacerbated by temperature increases predicted for the end of the century. Much more research is required on larval physiology to determine whether there is an increase or decrease in metabolism (Parker *et al.* 2012).

Molluscs

The vulnerability to elevated CO_2 observed in echinoderms is also reported in studies on larvae of molluscs (Table 1). Although there was no effect on fertilisation, in response to reductions of pH to 7.4, veliger larvae of the Pacific oyster *Crassostrea gigas* were reduced in size and had shell malformations (Kurihara *et al.* 2007). When embryos of *Crassostrea gigas* were reared at elevated pCO_2 of 2268 ppm for 48 hours, there was no significant difference in development relative to the controls until the D veliger stage (Kurihara *et al.* 2007) and the onset of shell mineralization (Waller 1981; Hayakaze and Tanabe 1999; Kurihara *et al.* 2007). At the completion of the experiment, however, the embryos of *C. gigas* were found to have reduced rates of development, calcification and growth and increased rates of abnormal development, with only 5% of the CO_2-stressed embryos developing normally to D-stage larvae compared to 68% in the controls (Kurihara *et al.* 2007; Table 1, Figure 3.4). In embryos of the mussel *Mytilus galloprovincialis* reared at elevated pCO_2 of 2000 ppm (pH 7.4), there was also a delay in development visible once the mussels reached the trochophore larval stage (Kurihara *et al.* 2008a). This was followed by morphological shell abnormalities such as convex hinge and mantle protrusion, as well as a 26% and 20% reduction in shell height and length, respectively (Kurihara *et al.* 2008a; Table 1, Figure 3). Similarly, a 4.5±1.3% and 12±5.4% decrease in shell length and thickness respectively was observed in mussel larvae of *Mytilus edulis* raised at pH 7.8 (Gazeau *et al.* 2010). Those raised at pH 7.6 had a reduced shell length of 6±2.3%, overall size of D-veligers was reduced 12.7±0.9% and hatching rates were suppressed by 24±4% (Gazeau *et al.* 2010). Embryos of the gastropod mollusc, *Littorina obtusata*, raised at pH 7.6 also showed shell changes with shorter lateral, but longer spiral shell length (Ellis *et al.* 2009). Mean development time was statistically significantly longer (although only 0.45 day: 27.5±0.1 day for treatments; 26.9±0.05 for controls) and hatching rate was lower at pH 7.6 than in controls (pH 8.1).

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Similarly, Parker *et al.* (2010) found reduced development, size and increased abnormality in D veliger larvae and spat for both *C. gigas* and *Saccostrea glomerata* to elevated pCO_2 (600, 750, 1000 ppm, mean pH 8.02, 7.95 and 7.83 respectively) compared to controls (375 ppm, pH 8.2) (Parker *et al.* 2009, 2010) as did Watson *et al.* (2009) for *S. glomerata*. When elevated CO_2 was combined with temperature, (18, 22, 26 and 30°C) differences increased at suboptimal temperatures (outside 26°C) and elevated CO_2. The pediveligers of *S. glomerata* were more sensitive than spat to changes to CO_2 and temperature, but this reversed in *C. gigas* with newly metamorphosed spat showing greater sensitivity than pediveligers (Parker *et al.* 2010). This result is surprising given that the $CaCO_3$ polymorph (calcite) deposited by spat is less soluble than that deposited by the preceding pediveliger larval stage. Differences in responses between closely related species have been found in other studies. For example Miller *et al.* (2009) compared the response of veliger larval development exposed to a range of elevations of CO_2 on of *Crassostrea virginica* and *C. ariakensis*. Whereas *C. virginica* experienced a 16% decrease in shell area and a 42% reduction in calcium content, there was no impact on the larval development of *C. ariakensis*. Both species demonstrated net calcification and growth even when aragonite was undersaturated.

Given that the first effects of elevated CO_2 on the bivalve species were observed during the trochophore and D-veliger stage, corresponding with the first onset of shell mineralisation, it has been suggested that calcification during larval development will be one of the major processes affected by elevated CO_2 (Kurihara *et al.* 2007; Kurihara 2008), although other authors such as Kurihara *et al.* (2007) suggest that other processes such as protein synthesis and metabolism may also be affected. Rather than earlier stages being more sensitive than later (Beiras and His 1994) there is an absence of evidence of hierarchical sensitivity and more evidence of sensitivity of larval stages being species specific. Variable sensitivity of life stages to low pH has been found in the lecithotrophic abalone, *Haliotis rufescens*. Thermal tolerance was impaired at pH 7.87 compared to control (pH 8.05) for pretorsion and late veliger life stages, but not posttorsion and premetamorphic veligers (Zippay and Hofmann 2010). Supporting the findings of Zippay and Hoffman (2010), more recent studies on abalone have found that in response to elevated CO_2 that larvae of *Haliotis coccoradiata* failed to produce skeletons when reared at -0.4-0.6 pH less than controls (Byrne *et al.* 2011a) and *Haliotis kamtschatkana* had reduced survival, increased abnormalities in shell structure at elevated CO_2, with larvae in the highest treatments of 1800 ppm CO_2 (-0.4-0.5 pH less than controls) either developed an abnormal shell or lacked a shell completely (Crim *et al.* 2011). Of those larvae that did survive to the end of the experiment, however, there was no effect on settlement whether larvae had or did not have a shell (Crim *et al.* 2011).

Shell abnormalities were observed in veliger larvae of the Mediterranean pteropod *Cavolinia inflexa* exposed to acidified seawater (Comeau *et al.* 2010). Reduced growth and flat, irregular shell shape was observed at pH 7.82, but at pH 7.61 shells were absent after 13 days due to dissolution, yet larvae displayed "normal" swimming action (Comeau *et al.* 2010). Pre-winter juveniles of the polar pteropod *Limacina helicina* also had more degraded shells when raised at or below pH 7.78 (Lischka *et al.* 2010). Shell diameter, degradation and increment were significantly affected by CO_2, but not temperature, whereas the combination of elevated temperature and CO_2 increased mortality, yet with temperature the more dominant factor (Lischka *et al.* 2010). Survival, growth, rate of metamorphosis, size, shell thickness and hinge integrity decreased significantly with increasing CO_2 of the bay scallop *Argopecten irradians* and the hard clam *Mercenaria mercenaria* at pCO_2 levels of 250, 390, 750 and 1500 ppm (pH 8.17, 8.05, 7.8 and 7.5 respectively) (Talmage and Gobler 2010). Waldbusser *et al.* (2010) also revealed a decrease in calcification rate with reducing pH and organism size, indicating size dependency of pH effects of *Mercenaria* spp. when subjected to pCO_2 of 1120 and 1950 ppm (pH 7.64 and 7.41 respectively) with calcification rate differing between source populations signifying possible genotypic variation. Parker *et al.* (2011) also found significant variation in growth of spat among populations of the endemic Sydney Rock Oyster, *Saccostrea glomerata*. There was no effect of elevated CO_2 in mass and single pair mated family lines which had been bred for resistance to overwintering and QX disease. Indicating that there may be inherent genetic diversity and feeding efficiency among populations of species or environmental pre adaptive capacity which may ameliorate the impacts of ocean acidification on oyster populations (Parker *et al.* 2011).

In contrast to the other molluscs with mainly planktotrophic larvae, the lecithotrophic juvenile European cuttlefish, *Sepia officinalis*, showed no adverse growth or developmental effects when raised at pCO_2 of 4000 and 6000 ppm (pH 7.23 and 7.1 respectively) compared to controls at 628-705 ppm (pH 7.94-8.01) (Gutowska *et al.* 2008). In fact, at 6000 ppm significantly more $CaCO_3$ (0.80 ± 0.15g) was accreted into cuttlebones than in controls (0.71 ± 0.15g) (Gutowska *et al.* 2008). A later study by Lacoue-Labarthe *et al.* (2009) found eggs of the same species increased in weight as pCO_2 decreased without affecting hatchling size (900 and 1400 ppm; pH 7.85 and 7.6 respectively). There are also potential ecotoxicological consequences associated with elevated CO_2. Lacoue-Labarthe *et al.* (2009) also found accumulation of metals varied: ^{110m}Ag increased and , ^{109}Cd decreased with decreasing pH, whereas ^{65}Zn accumulation was highest at pH 7.85, but lower at pH 7.6 than 8.1 (control). Similarly there was no effect on calcification rates, size or weight in juveniles of the grooved carpet clam *Ruditapes decussates* raised at pCO_2 of 1694 and 4245 ppm (pH 7.84 and 7.46 respectively), though mortality was reduced in acidified treatment (pH 7.46), possibly due to delayed reproductive development of clams preventing spawning in acidified treatments (Range *et al.* 2011) as an energy saving survival strategy. Decreased pH also had no effect on expression of two shell mineralisation genes *ap24* or *engrailed* at any developmental stage in the abalone *Haliotis rufescens* (Zippay and Hofmann 2010).

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Meta analyses

The overall response of larval development of both echinoderms and molluscs to elevated CO_2 and associated decrease in pH appears highly variable, yet with a general negative effect. Indeed such generalisations are difficult because such a synthesis masks the complex interaction of species specific sensitivities during progressive life stages, early feeding strategies, latitudinal distribution, previous acclimation due to habitat and robustness of gene expression processes. Meta-analyses (Hendriks *et al.* 2010; Hendriks and Duarte 2010 and Kroeker *et al.* 2010) do not support the early life history stages being the most sensitive stages to ocean acidification compared to adults. Hendriks *et al.* (2010) found reduced larval growth (-16%) in sea urchins, but found adult growth significantly more sensitive (-62%), yet data was limited with only 2 papers and 2 species contributing to the sea urchin embryo and 1 paper and 2 species contributing to the adult data. A later exercise by Hendriks and Duarte (2010) consolidated this position concluding there was no difference in effect size of different life stages by pooled groups of organisms using a dataset restricted to 16 studies species in 2 studies. Yet in contrast Dupont *et al.* (2010a) found gametes and early developmental stages of echinoderms appeared "far more impacted" than adults relative to calcification, growth and survival although the number of experimental responses was heavily weighted towards larvae with 47, 10 and 17 responses for larvae, juveniles and adults respectively. These conflicting views on sensitivity of early life stages have been further addressed by a more extensive meta-analysis by Kroeker *et al.* (2010), on the effects of ocean acidification on life stages and biological processes of marine organisms based on 73 studies with 251 experimental results finding no variation in mean effect among life stages for different biological variables concluding "this synthesis did not support all the leading hypotheses for variation in response to ocean acidification (i.e., early developmental stages and more soluble $CaCO_3$ polymorphs are more susceptible to ocean acidification). We instead found the explanatory power of these hypotheses was specific to organisms within taxonomic groups. Such meta-analyses, although authoritative are based on a paucity of studies, particularly in relation to molluscs and echinoderms and it may be premature in their attempt to use them to support hypotheses related to overall trends.

Conclusion

Despite recent research, our current understanding of the biological consequences of an acidifying ocean over the next century is relatively in its infancy and there are still large unknowns. Increasingly studies are considering the synergistic effects of other stressors (i.e. temperature, nutrients, hypoxia). In order to fully understand the consequences of ocean acidification at the population and ecosystem level the synergistic or antagonistic impacts of environmental variables must be considered. The echinoderms and molluscs discussed in this review contribute significant ecological roles to the marine environment. In the case of molluscs, forming habitats and providing ecosystem services such as water purification, as a food source for other organisms and producing large amounts of $CaCO_3$ (Comeau *et al.* 2010). Also molluscs and echinoderms have enormous economic value. In 2007 in the United States molluscs alone, accounted for 748 million USD of domestic ex-vessel revenues and in 2008, 13.1 million tonnes of shellfish were produced by aquaculture worldwide, with a market value of over 13 billion USD (Gazeau *et al.* 2010). In Japan sea urchin roe is worth over 320 million USD alone. Thus any negative impacts to fertilisation and larval development even if sub lethal may result in severe economic and ecological consequences. Over the coming decades, it is likely that a rising surface ocean CO_2 will also be accompanied by rising surface ocean temperatures, yet only a handful of studies have considered the synergistic impacts of both elevated CO_2 and temperature (Reynaud *et al.* 2003; Metzger *et al.* 2007; Anthony *et al.* 2008; Byrne *et al.* 2009; Gooding *et al.* 2009; Martin and Gattuso 2009; Munday *et al.* 2009a; Parker *et al.* 2009, 2010). Current models also remain largely based on acute experiments over single generations where the sudden drop in pH of 0.4 units does not mimic well the longer time frame over which this will occur (0.0044pH/yr Hendriks and Duarte 2010). Future experiments are needed to consider the potential for species to acclimate over long term perturbations (Parker *et al.* 2012) and not enough studies yet are investigating the variability in responses of organisms within and between populations (Parker *et al.* 2011; Waldbusser *et al.* 2010) perhaps explaining some of the variability behind contrasting findings, albeit with also contrasting methods (Byrne *et al.* 2009 with Havenhand *et al.* 2008). Those that have, are finding that differences do exist (Parker *et al.* 2011), and the potential to ameliorate climate change perhaps through environmentally induced plasticity (Bibby *et al.* 2008; Hofman *et al.* 2010). Further work is, however, required on the underlying physiological mechanisms which may allow for species adaptation or acclimation (Parker *et al.* 2012).

Negative results from short term studies on larvae make it difficult to extrapolate to long term impacts on marine environments, especially when these potentially could couple with positive effects on adults (increased production and robustness of propagules, Hendriks and Duarte 2010) and greater capacity to acclimate (Moulin *et al.* 2011; Parker *et al.* 2012). This gives further support for an entire life cycle environmental approach to measuring the impact of ocean acidification. Difficulty in extrapolation also occurs because laboratory studies and results and not necessarily repeatable in the field. Caution is required in translating between these two contexts, where in the laboratory all variables are held constant except the treatment and the opposite in the field where sources of variability are numerous and interactive (Connell 1975; Green 1979; Underwood 1997) with unforeseen consequences. In order to have a greater understanding of how organisms will respond, over the next century, to warming and acidifying oceans and the capacity for species to adapt, we must move beyond measuring acute responses and focus on identifying the underlying mechanisms involved in the sensitivity and/

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or acclimation of marine species to elevated CO_2 levels (Pörtner 2008). The physiological, molecular and gene mechanisms involved in ocean acidification responses have also been relatively unexplored (European Science Foundation 2009) and have been identified as priorities of future research (Orr *et al.* 2009; Doney *et al.* 2009; Pörtner 2008). Such research is important if we are to create the authoritative and robust meta-analyses and generalisations that we need to manage our marine environments (Hofman *et al.* 2010; Kroeker *et al.* 2010).

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Table 1. The effects of ocean acidification on the reproduction and early development of marine biota.
n/k : not known; s: seconds h: hours, d: days, w: weeks, mo: month, *: effect only when in synergy with salinity; −-:negative impact, =: no significant difference; +: positive impact

Organism or Species	Stage tested	CO_2 system parameters		Manipulation method	Exposure length	Impact			Comment	Reference
		pCO_2 (ppm)	pH	CO_2/Mineral acid		Fertilization	Larval Development	Settlement/ Recruitment		
Mollusca										
Saccostrea glomerata (Sydney rock oyster)	Egg, larva	600	7.9	Acid	48 h	−	−		Reduced fertilisation, larval development & growth; increased abnormality & mortality	Parker *et al.*, (2009)
Saccostrea glomerata (Sydney rock oyster)	Spat	1000	7.84	CO_2	4 d		=		Reduced growth varied between selectively bred (-25%) & wild caught (-64%)	Parker *et al.*, (2011)
Saccostrea glomerata (Sydney rock oyster)	Larva	508-775	7.77.6-7.8	CO_2	8 d		−		Reduced growth; larval development; increased mortality & shell abnormality	Watson *et al.*, (2009)
Saccostrea glomerata (Sydney rock oyster)	Larva	n/k	6.75	Acid H_2SO_4	48 h		−		pH ≤ 6.75 reduced development and increased abnormality of D-veliger larvae	Wilson & Hyne (1997)
Saccostrea glomerata (Sydney rock oyster)	Egg, larva	600	7.9	CO_2	48 h	−	−		Reduced fertilisation, larval development & growth; increased abnormality	Parker *et al.*, (2010)
Crassostrea gigas (Pacific oyster)	Egg, larva	600	7.9	CO_2	48 h	−	−		Reduced fertilisation, larval development & growth; increased abnormality	Parker *et al.*, (2011)
Crassostrea gigas (Pacific oyster)	Egg, larva	2268	7.4	CO_2	48 h	=	−		No effect on fertilisation; inhibition of shell synthesis; reduced larval size; increased abnormality	Kurihara *et al.*, (2007)
Crassostrea gigas (Pacific oyster)	Egg, sperm	1000 (n/k)	7.8	CO_2	1 h	=			No effect on fertilisation, sperm speed or motility	Havenhand & Schlegel (2009)
Crassostrea virginica (Eastern oyster)	Larva	n/k	6.25	Acid	12 d		−		pH < 6.25 increased mortality rate pH < 6.75 decreased growth rate	Calabrese & Davis (1966)
Crassostrea virginica (Eastern oyster)	Larva	280, 380, 560, 800	8.16 8.06 7.91 7.76	CO_2	30 d		−		<560 pCO_2 Growth significantly decreased. 800 pCO_2 calcification reduced.	Miller *et al.*, (2009)
Crassostrea ariakensis (Suminoe oyster)	Larva	280, 380, 560, 800	8.17 8.08 7.92 7.79	CO_2	32 d		=		No effect on growth or calcification	Miller *et al.*, (2009)
Mytilus galloprovincialis (Mussel)	Egg, larva	2000	7.4	CO_2	6 d	_	−		Development delayed at trochophore stage following onset of shell development; increased abnormality of larvae; 26% & 20% reduction in larval shell height and length, respectively after 6 d	Kurihara *et al.*, (2008a)

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Organism or Species	Stage tested	CO_2 system parameters		Manipulation method	Exposure length	Impact			Comment	Reference
		pCO_2 (ppm)	pH	CO_2/Mineral acid		Fertilization	Larval Development	Settlement/ Recruitment		
Mytilus edulis (Blue mussel)	Larva	1124-1929	7.8, 7.6	CO_2	15 d		–		pH 7.8 reduced shell size (4.5-6 %) & thickness (12%); pH 7.6 reduced hatching rates (24%), smaller d-veliger shells(12.7%)	Gazeau *et al.*, (2010)
Tivela stultorum (Pismo clam)	Egg	n/k	8.0	Acid???	n/k	–			pH < 8.5 Reduced fertilisation	Alvarado-Alvarez *et al.*, (1996)
Mercenaria mercenaria (Hard clam)	Larva	n/k	6.25	Acid	10 d		–		pH < 6.25 increased mortality rate pH < 6.75 decreased growth rate	Calabrese & Davis (1966)
Littorina obtusata (Intertidal gastropod)	Egg, larva	1100	7.6	CO_2	24 d		–		Reduced viability; retarded development; shorter lateral, longer spiral shell length.	Ellis *et al.*, (2009)
Cavolinia inflexa (Opistobranch gastropod/ pteropod)	Larva	857, 1713	7.82, 7.51	n/k	13 d		–		pH 7.82: malformations plus reduced shell growth ; pH 7.51 shells absent but viable with normal development	Comeau *et al.*, (2010)
Haliotis rufescens (Abalone)	Larva	570, 990	7.97, 7.87	CO_2	6 d		–		pH 7.87 thermal tolerance impaired for pretorsion and late veliger life stages, but not posttorsion and premetamorphic veligers; no effect on *ap24* or *engrailed* shell mineralisation genes	Zippay *et al.*, (2010)
Haliotis coccoradiata (Abalone)		814-1828	7.9-7.6	CO_2	2 h	=			No significant effect of elevated pCO_2, pH or temperature	Byrne *et al.*, (2010a)
Haliotis coccoradiata (Abalone)	Larva, Juvenile	700, 2000	7.8 7.6	CO_2	4 d		–		Reduced calcification and development, increased abnormality with decreasing pH and temperature, no interaction.	Byrne *et al.*, (2011a)
Haliotis kamtschatkana (Abalone)	Larva	800 1800	8.07 7.81	CO_2	8 d		–	=	Reduced survival and shell size plus increased abnormality at decreased pH. No effect on settlement by survivors.	Crim *et al.*, (2011)
Sepia officinalis (European cuttlefish)	Juvenile	4000, 6000	7.23, 7.1	CO_2	6 w		+		No effect on growth or development; at 6000ppm significantly more $CaCO_3$ (0.80+0.15g)accreted	Gutowska *et al.*, (2008)
Sepia officinalis (Common cuttlefish)	Eggs	900 1400	7.85 7.6	CO_2	65 d		+		Decreased pCO_2 increased egg weight, but not hatchling size; Accumulation of ^{110m}Ag increased, ^{109}Cd decreased with decreasing pH, ^{65}Zn highest at pH 7.85, lower at 7.6 than 8.1.	Lacoue-Labarthe *et al.*, (2009)

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Organism or Species	Stage tested	CO_2 system parameters		Manipulation method	Exposure length	Impact			Comment	Reference
		pCO_2 (ppm)	pH	CO_2/Mineral acid		Fertilization	Larval Development	Settlement/ Recruitment		
Mercenaria mercenaria (Hard clam)	Larva	250 390 750 1500	8.17 8.05 7.8 7.5	CO_2	36 d		–		Survival, growth, rate of metamorphosis, size & shell thickness all decreased significantly with increasing CO_2, hinge integrity was also impacted.	Talmage & Gobler (2010)
Argopecten irradians (Bay scallop)	Larva	250 390 750 1500	8.17 8.05 7.8 7.5	CO_2	38 d		–		Survival, growth, rate of metamorphosis, size & shell thickness all decreased significantly with increasing CO_2, hinge integrity was also impacted.	Talmage & Gobler (2010)
Ruditapes decussates (Grooved carpet clam)	Juvenile	1698 4345	7.84 7.46	CO_2	75 d		=		No effect on calcification rates, size or weight. Reduced mortality possibly due to absence of spawning.	Range *et al.*, (2011)
Mercenaria spp. (Hard clam)	Post larval	1120 1950	7.64 7.41	CO_2	n/k		–		Calcification rate decreased with pH & organism size (size dependency of pH effects). Calcification rate differed between source populations – genotypic variation.	Waldbusser *et al.*, (2010)
Limacina helicina (Polar pteropod)	Pre-winter juveniles	230 350 750 1100	8.21 8.06 7.78 7.63	CO_2	29 d		–		Increased pCO_2 (not temperature) reduced shell diameter, shell increment & increased shell degradation. pCO_2 increased mortality, though temperature overriding factor.	Lischka *et al.*, (2010)
Echinodermata										
Hemicentrotus pulcherrimus (Sea urchin)	Egg, larva	865-10365	7.8-6.8	Both HCl & CO_2	3 d	–	–		pH < 7.8 skeletal malformation, reduced larval size,fertilisation decreased with increasing pCO_2 - significant at pH 6.8 (33-50%)	Kurihara & Shirayama (2004), Kurihara *et al.*, 2004b
Echinometra mathaeii (Sea urchin)	Egg, larva	865-10365	7.8-6.8	Both HCl & CO_2	3 d	–	–		pH < 7.8 skeletal malformation, reduced larval size, Fertilisation decreased with increasing pCO_2 – significant at pH 7.1.	Kurihara & Shirayama (2004), Kurihara *et al.*, 2004b
Paracentrotus lividus (Sea urchin)	Egg, larva	n/k	7.5	Acid	48 d	–	–		pH < 7.5 skeletal malformation, pH < 7.7 morphological abnormality, Mitotic abnormality with decreasing pH	Pagano *et al.*, (1985a,b)
Paracentrotus lividus (Sea urchin)	Egg, larva	704-6632	7.9-7.0	CO_2	3 d	=	–		Development delayed to pluteus stage.<pH 7.25 morphology affected.< pH 7.5 overall length, post oral and antero-lateral arm length shorter. <pH7.9 rods shorter. Protein & biomineralisation genes upregulated at low pH.	Martin *et al.*, (2011)

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Organism or Species	Stage tested	CO_2 system parameters		Manipulation method	Exposure length	Impact			Comment	Reference
		pCO_2 (ppm)	pH	CO_2/Mineral acid		Fertilization	Larval Development	Settlement/ Recruitment		
Sphaerechinus granularis (Sea urchin)	Egg, larva	n/k	6.5	Acid HCl, H_2SO_4	5 h	–	–		pH < 6.5 total metaphase blockage	Cipollaro *et al.*, (1986)
Strongylocentrotus droebachiensis (Sea urchin)	Larva	1000	7.7	CO_2	n/k		+		Enhanced survival	Dupont & Thorndyke (2008)
Strongylocentrotus franciscanus (Sea urchin)	Sperm	800, 1800	7.81 7.55	CO_2	3 h	–			Reduction in fertilisation efficiency at raised pCO_2, maximum fertilisation rates maintained only at increased sperm concentrations; time of egg block to polyspermy longer only at 1800ppm	Reuter *et al.*, (2011)
Strongylocentrotus franciscanus (Sea urchin)	Larva	540, 970	7.98, 7.87	CO_2	94 h				*hsp70* Up-regulated at elevated temperatures, change in expression profile at raised CO_2	O'Donnell *et al.*, (2009)
Strongylocentrotus purpuratus (Sea urchin)	Larva	1000 1450	7.7 7.5	CO_2	6 d		–		Developmentally normal. Significantly (7-13%) smaller at 1450 pCO_2.	Yu *et al.*, (2011)
Lytechinus pictus (Sea urchin)	Larva	540, 970	7.87, 7.78	CO_2	140 h		–		pH 7.78 smaller, more triangular skeletons, shorter arms than controls, down regulation of biomineralization, skeletogenesis and energy metabolism genes, some acid-base and ion regulation genes up-regulated. pH 7.87 no difference in morphology or gene expression	O'Donnell *et al.*, (2010)
Heliocidaris erythrogramma (Sea urchin)	Egg, larva	690	7.6	CO_2	19-20 h	=	=		No effect of elevated pCO_2, only temperature	Byrne *et al.*, (2009)
Heliocidaris erythrogramma (Sea urchin)	Egg, larva	1124, 1892	7.8, 7.6	CO_2	2 h	=			No effect elevated pCO_2 or pH, only sperm density	Byrne *et al.*, (2010b)
Heliocidaris erythrogramma (Sea urchin)	Egg, sperm	1000	7.7	CO_2	3 h	–			Reduced sperm speed and motility, 26% reduction in fertilisation	Havenhand *et al.*, (2008)
Heliocidaris erythrogramma (Sea urchin)	Egg, larva	1051-1828	7.8-7.6	CO_2	2 h	=			No significant effect of elevated pCO_2, pH or temperature	Byrne *et al.*, (2010a)

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Organism or Species	Stage tested	CO_2 system parameters		Manipulation method	Exposure length	Impact			Comment	Reference
		pCO_2 (ppm)	pH	CO_2/Mineral acid		Fertilization	Larval Development	Settlement/ Recruitment		
Heliocidaris erythrogramma (Sea urchin)	Larva, juvenile	700 2000	7.8 7.6	CO_2	5 d		–		Both temperature and pH reduced calcification, development and spine formation with reduced impacts and a significant interaction.	Byrne *et al.*, (2011a)
Heliocidaris tuberculata (Sea urchin)	Egg, larva	814-1828	7.9-7.6	CO_2	2 h	=			No significant effect of elevated pCO_2, pH or temperature, though trend for decreased fertilisation	Byrne *et al.*, (2010a)
Tripneustes gratilla (Sea urchin)	Egg, larva	814-1828	7.9-7.6	CO_2	2 h	=			No significant effect of elevated pCO_2, pH or temperature	Byrne *et al.*, (2010a)
Centrostephanus rodgersii (Sea urchin)	Egg, larva	1051-1828	7.8-7.6	CO_2	2 h	=			No significant effect of elevated pCO_2, pH or temperature	Byrne *et al.*, (2010a)
Patiriella regularis (Sea star)	Egg, larva	1051-1828	7.8-7.6	CO_2	2 h	=			No significant effect of elevated pCO_2, pH or temperature	Byrne *et al.*, (2010a)
Crossaster papposus (Sea star)	Larva	930	7.7	CO_2	38 d		+		Larvae & Juveniles grow faster; no abnormality or affect on skeletogenesis	Dupont *et al.*, (2010b)
Ophiothrix fragilis (Brittlestar)	Larva	n/k	7.9, 7.7	CO_2	8 d		–		pH 7.9: decrease in larval size; abnormal & delayed development & skeletogenesis; 100% larval mortality within 8 d	Dupont *et al.*, (2008)
Evechinus chloroticus (Sea urchin)	Larva	1320	7.7	CO_2	13 d		–		Reduced calcification (30.6%) & size; no effect on morphology; SEM showed shell degradation; pH < 6.0 reduced survival	Clark *et al.*, (2009)
Pseudechinus huttoni (Sea urchin)	Larva	1282	7.7	CO_2	9 d		–		Reduced calcification (36.9%) & size; no effect on morphology; SEM showed shell degradation; pH < 6.5 reduced survival	Clark *et al.*, (2009)
Sterechinus neumayeri (Sea urchin)	Larva	1380	7.6	CO_2	7-17 d		–		Reduced size, no effect on calcification or morphology; pH < 6.0 reduced survival	Clark *et al.*, (2009)
Tripneustes gratilla (Sea urchin)	Larva	1119	7.8	CO_2	4 d		–		Reduced calcification (13.8%) & size; no effect on morphology; pH < 7.0 reduced survival	Clark *et al.*, (2009)
Tripneustes gratilla (Sea urchin)	Larva	n/k	7.8, 7.6	n/k	5 d		–		Larval growth significantly increased as temperature rose, and decreased as pH decreased with some counter effects, though no interaction.	Sheppard Brennand *et al.*, (2010)
Paracentrotus lividus (Intertidal temperate sea urchin)	Egg, larva	310 8335	7.8-6.8	CO_2	72 h	–	–		Fertilisation & cleavage rate decreased below pH 7.6 ; pluteus development abnormal at pH 7.4; length reduced at pH 7.2	Moulin *et al.*, (2010)

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Organism or Species	Stage tested	CO_2 system parameters		Manipulation method	Exposure length	Impact			Comment	Reference
		pCO_2 (ppm)	pH	CO_2/Mineral acid		Fertilization	Larval Development	Settlement/ Recruitment		
Sterechinus neumayeri (Sea urchin)	Egg, larva	1121, 2886, 5806	7.7, 7.3, 7.0	CO_2	2h -6 d	=	–		≤pH 7.3 reduced fertilisation only with low sperm concentrations, delayed larval development. pH 7 no normal larvae, short, asymmetric, ruptured epithelium	Ericson *et al.*, (2010)
Arthropoda										
Acartia erythraea (Copepod)	Egg, larva	2360-10360	7.31-6.82	CO_2	2 d	–	–		Increased nauplius mortality significant at pH 7 & 6.82, decreased hatching rate-significant at pH 6.82 only	Kurihara *et al.*, (2004a)
Acartia tsuensis (Copepod)	Egg, larva	2380	7.31	CO_2	9 d	=	=		No effect of elevated pCO_2	Kurihara & Ishimatsu (2008)
Calanus finmarchicus (Copepod)	Egg	8000	6.95	CO_2	72 h	–	–		Decreased hatching success	Mayor *et al.*, (2007)
Palaemon pacificus (Shrimp)	Egg Juvenile	1000, 1900	7.89, 7.64	CO_2	30 w, 15 w	–			pH 7.89 reduced survival, & egg production, increased moulting frequency after 21 weeks, second antennae shorter; pH 7.64 reduced survival & growth, decreased moulting between weeks 10 & 12	Kurihara *et al.*, (2008b)
Homarus gammarus (European lobster)	Larva	1200	8.1	CO_2	28 d		=		Significant change in carapace mass and calcium concentration, suggesting "hypercapnia interfering with normal homeostatic function", no change in carapace length, survival or zoeal progression.	Arnold *et al.*, (2009)
Echinogammarus marinus Leach (Amphipod)	Egg	1900	7.5	CO_2	Approx. 18 d	–*			Embryonic development slowed at elevated pCO_2; no effect of pCO_2 on number of hatchlings or hatchling calcium content	Egilsdottir *et al.*, (2009)
Gammarus locusta (Amphipod)	Juvenile	550, 980	7.8, 7.6	CO_2	14-28 d				No effect on growth & development. No effect on *hsp70,* but significant increase in *gapdh* gene expression	Hauton *et al.*, (2009)
Hyas araneus (Spider crab)	Larva	710 3000	n/k	CO_2	n/k		–		Increased pCO_2 delayed development, reduced growth & reduced fitness. Significant differences between source populations – evolutionary temperature adaptation.	Walther *et al.*, (2010)
Barnacles										
Amphibalanus amphitrite (Barnacle)	Larva; cyprid	n/k	7.4	CO_2	5d		=	=	No effect on larval condition, cyprid size, cyprid attachment and metamorphosis	McDonald *et al.*, (2009)

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Organism or Species	Stage tested	CO_2 system parameters		Manipulation method	Exposure length	Impact			Comment	Reference
		pCO_2 (ppm)	pH	CO_2/Mineral acid		Fertilization	Larval Development	Settlement/ Recruitment		
Semibalanus balanoides (Barnacle)	Egg	922	7.7	CO_2	104 d	=			Reduced rate of embryonic development (19 day delay), but within natural rates	Findlay *et al.*, (2009)
Semibalanus balanoides (Barnacle)	Post-larval	1000	7.7	CO_2	30 d		=		No effect on growth rate, but reduced calcium content & survival at elevated temperature & CO_2	Findlay *et al.*, (2010a)
Elminius modestus (Barnacle)	Post-larval	1000	7.7	CO_2	30 d		=		No effect on calcium content or survival; decrease in growth rate at elevated CO_2	Findlay *et al.*, (2010a)
Semibalanus balanoides (Barnacle)	Post-larval	1000 3000	7.7 7.3	CO_2	20 d		=		pH 7.7 reduced growth & development; no effect on shell mineralisation	Findlay *et al.*, (2010b)
Vertebrata										
Pagrus major (Silver seabream)	Egg, larva, juvenile	10000	6.2	CO_2	24 h	–	–		Hatching and survival decreased with increased pCO_2 & exposure; stage specific sensitivity	Kikkawa *et al.*, (2003)
Sillago japonica (Japanese sillago)	Egg, larva, juvenile	10000	6.2	CO_2	24 h	–	–		Hatching and survival decreased with increased pCO_2 & exposure; stage specific sensitivity	Kikkawa *et al.*, (2003)
Amphiprion percula Pomacentridae (Clown fish)	Egg, larva	1030	7.84	CO_2	11 d	=	=		No effect on embryonic development, egg survival and hatching size; some parental pairs increased length up to 18% & weight by 52%	Munday *et al.*, (2009b)
Amphiprion percula Pomacentridae (Clown fish)	Larva	1050, 1710	7.8, 7.6	CO_2	11 d		–		pH 7.8 disruption, pH 7.6 total Loss of larval discriminatory ability for olfactory settlement cues at elevated pCO_2	Munday *et al.*, (2009a)
Gadhus morhua (Baltic cod)	Sperm	1400	7.55	CO_2	n/k	=			No effect on sperm speed, rate of change of direction or percent motility.	Frommel *et al.*, (2010)
Corals & communities										
Pocillopora damicornis (Coral)	Larva	745	n/k c.7.6-7.9	Acid 10% HCl	10 mo		=		No effect on recruitment (effects on adults)	Jokiel *et al.*, (2008)
Montipora capitata (Coral)	Egg, sperm	745	n/k c.7.6-7.9	Acid 10% HCl	6 mo	=			No effect on gametes (effects on adults)	Jokiel *et al.*, (2008)
Acropora digitifera (Coral)	Larva, Primary polyp	905-3585	7.31-7.64	CO_2	10 d		=		pH 7.3 reduced primary polyp occupation area 14% compared to control; larvae mortality not significantly affected by pH	Suwa *et al.*, (2010)
Acropora tenuis (Coral)	Larva	905-3585	7.31-7.64	CO_2	7d		=		Mortality inconsistent- lower at pH 7.3 than in control & significantly lower at 7.3 (15.2%) than at 7.6 (38%)	Suwa *et al.*, (2010)

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		pCO_2 (ppm)	pH	CO_2/Mineral acid		Fertilization	Larval Development	Settlement/ Recruitment		
Porites panamensis	Larva Primary polyp	861-1006	7.81-7.85	CO_2	10-42 d		=	–	pH 7.85 -no effect larval survival & settlement, increased temperature (+1.2°C) or the two combined; zooxanthellae- pH no effect, temperature 60% reduction, both intermediate effect. Low pH & increased temp reduced biomass (45%), skeletal mass and dry weight (calcification) by almost one third – synergistic interaction.	Anlauf *et al.*, 2010
Cladocora caespitose (Temperate coral)	Polyp	700	7.86	CO_2	1-10 mo		=		No effect on calcification rate by pCO_2 alone or with temperature. Seasonal temperature predominant factor controlling physiology.	Rodolfo-Metalpa *et al.*, (2010)
Astrangia porculata (Temperate coral)	Polyp	780	7.78	CO_2	6 mo		–		Calcification decreased significantly with increased pCO_2; decreased ns with elevated nutrients; effect of pCO_2 may have been moderated by elevated nutrients when combined though ns interaction.	Holcomb *et al.*, (2010)
Porites sp (Long-lived temperate coral)	Polyp	1904 3970	7.49 7.19	CO_2	6-14 mo		–		Increased pCO_2 decreased skeletal growth (50-75%) & zooxanthallae density, but biomass (protein concentration 0.17%) & zooxanthellae chlorophyll was lower in controls than treatments .	Krief *et al.*, (2010)
Stylophora pistillata (Short lived temperate coral)	Polyp	1904 3970	7.49 7.19	CO_2	6-14 mo		–		Increased pCO_2 decreased skeletal growth (60%) & zooxanthallae density, but biomass (protein concentration (0.42-0.5%).) & zooxanthellae chlorophyll concentrations was lower in controls than treatments	Krief *et al.*, (2010)
Acropora digitifera (Coral)	Sperm	775-21100	7.77-6.55	CO_2	2 s	–			Reduced pH impaired motility (69% motile at control pH 8; 46% at 7.8; <20% at $\leq$7.7	Morita *et al.*, (2009)

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