



Transgenerational responses of molluscs and echinoderms to changing ocean conditions

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We are beginning to understand how the larvae of molluscs and echinoderms with complex life cycles will be affected by climate change. Early experiments using short-term exposures suggested that larvae in oceans predicted to increase in acidification and temperature will be smaller in size, take longer to develop, and have a greater incidence of abnormal development. More realistic experiments which factored in the complex life cycles of molluscs and echinoderms found impacts not as severe as predicted. This is because the performance of one life history stage led to a significant carryover effect on the subsequent life history stage. Carryover effects that arise within a generation, for example, embryonic and larval stages, can influence juvenile and adult success. Carryover effects can also arise across a generation, known as transgenerational plasticity (TGP). A transgenerational response or TGP can be defined as a phenotypic change in offspring in response to the environmental stress experienced by a parent before fertilization. In the small number of experiments which have measured the transgenerational response of molluscs and echinoderms to elevated CO₂, TGP has been observed in the larval offspring. If we are to safeguard ecological and economically significant mollusc and echinoderm species against climate change then we require more knowledge of the impacts that carryover effects have within and across generations as well as an understanding of the underlying mechanisms responsible for such adaptation.

Keywords: carryover effects, echinoderms, molluscs, ocean acidification, TPG, transgenerational effects.

Introduction

How will the larvae of molluscs and echinoderms with complex life cycles respond to climate change? The answer to this question, based on a growing body of evidence, suggests that mollusc and echinoderm larvae in acidified oceans will be smaller in size, take longer to develop, and be more abnormal. Subsequent juvenile and settler stages may also be affected. Recent reviews document a range of negative impacts from exposure to elevated CO₂ on molluscs and echinoderms larvae from intertidal and subtidal habitats (for reviews, see [Byrne, 2010, 2011](#); [Dupont *et al.*, 2010a](#); [Ross *et al.*, 2011](#); [Byrne, 2013](#); [Byrne and Przeslawski, 2013](#); [Gazeau *et al.*, 2013](#); [Parker *et al.*, 2013](#)).

Many of the studies in these reviews report on experiments where single life history stages of molluscs and echinoderms are exposed for short periods to elevated CO₂. The inferences that can be obtained from such short-term exposures are, however, potentially

limited because they may over- or underestimate the impacts of climate change on marine larvae ([Cripps *et al.*, 2014](#)) as they do not simulate the real-world scenario, one where multiple stressors will interact and pH will decline slowly ([Byrne and Przeslawski, 2013](#); [Przeslawski *et al.*, 2015](#)). Also in many experiments, the pH levels used often do not incorporate conditions in nature or natural pH variability ([Hofmann *et al.*, 2011](#)).

Further, molluscs, echinoderms, and other marine invertebrates have complex life cycles which include a series of free living larval stages as well as benthic juvenile and adult stages which go through ontogenic shifts in function and habitat. Although these stages differ dramatically in form and function and are often thought of as discrete and somewhat autonomous, they are nonetheless part of the continuum of life ([Podolsky and Moran, 2006](#); [Dupont *et al.*, 2013](#)). Anywhere along this continuum, the performance at one life history stage may lead to significant positive or negative carryover

effects on subsequent life history stages, also known as the developmental domino phenomena (Byrne, 2011). These carryover effects can arise within a generation, for example, embryonic and larval experiences can influence juvenile and adult success; as well as across a generation, with the environment experienced by one generation directly influencing the success of the subsequent generation (Byrne, 2010; Kovalchuk, 2012; Munday, 2014).

A transgenerational response or transgenerational plasticity (TGP) is an across generational carryover effect which can be defined as a phenotypic change in offspring in response to the environmental stress experienced by one or both parents (Marshall, 2008; Kovalchuk, 2012; Shama and Wegner, 2014), especially during gamete development (Hamdoun and Epel, 2007; Byrne et al., 2011). TGP occurs when the environment which is experienced by the parent influences phenotype of their offspring exposed to the same environment (Salinas et al., 2013; Munday, 2014). For example, the optimum salinity and salinity range of embryos and larvae of the oyster *Crassostrea virginica* were influenced by the salinity at which the adults were held before spawning (Davis, 1958). Similarly, the offspring of the gastropod, *Crepidula convexa*, were found to be more tolerant of copper stress when adults were collected from a copper polluted site compared with offspring from adults collected in a control unpolluted site (Untersee and Pechenik, 2007). Similarly, the thermal environmental history of adult molluscs and echinoderms can determine the temperature tolerance limits of their offspring (Andronikov, 1975; Byrne et al., 2011). More recently, a study on Antarctic marine echinoderm *Sterechinus neumayeri* found that contaminant-experienced mothers, which had higher baseline levels of antioxidants, transferred resilience against oxidative stress to their embryos (Lister et al., 2015). This resilience, however, did not lead to less abnormal development and the benefit for overall fitness and survival was unclear.

As stated above, the impacts of climate change on molluscs, echinoderms, and other marine invertebrate life histories are comprehensively covered in many reviews (e.g. Dupont et al., 2010a; Hofmann et al., 2010; Albright, 2011; Byrne, 2011, 2012; Ross et al., 2011; Byrne and Przeslawski, 2013; Parker et al., 2013; Przeslawski et al., 2015). In this review, we focus on the impacts of ocean acidification on the larvae of molluscs and echinoderms and within and across generation carryover effects to evaluate the evidence for TGP. To do this, we briefly discuss the results of studies which have measured responses of single larval life history stage of molluscs and echinoderms to short-term or acute exposures to elevated CO₂. We then concentrate on studies which have measured responses of successive life history stages (i.e. larvae to juveniles, adults to larvae), to determine within and across transgenerational impacts. We need to understand the potential for carryover effects to determine the capacity of molluscs and echinoderms to acclimate and adapt to an ocean increasing in acidification and temperature due to climate change.

Acute effects: single larval life history stages

Larvae of molluscs and echinoderms have been found to be particularly sensitive to acidification and warming. Early on it was common to investigate impacts of elevated CO₂ on shell morphology and physiology of single life history stages of mollusc and echinoderm larvae using short-term or acute exposure experiments.

Such experiments found reduced larval size of molluscs (Kurihara et al., 2007; Kurihara, 2008; Parker et al., 2009, 2010, 2011; Talmage and Gobler, 2009, 2010, 2011, 2012; Watson et al.,

2009; Comeau et al., 2010; Dupont et al., 2010a,b; Gazeau et al., 2010; Lischka et al., 2010) and echinoderms (Kurihara and Shirayama, 2004; Dupont et al., 2008; Clark et al., 2009; O'Donnell et al., 2009a, b; Sheppard Brenndand et al., 2010; Stumpp et al., 2011a, b, 2012; Byrne, 2013; Byrne et al., 2013a, b; Gonzalez-Bernat et al., 2013a, b; Uthicke et al., 2013), hinge abnormalities, erosion and pitting of the Shell (Talmage and Gobler, 2010), reduced calcification (Comeau et al., 2010; Range et al., 2011), and decreased scope for growth (Stumpp et al., 2011a, b, 2012). Overall, larvae were found to be more sensitive than adults to elevated CO₂ even in the most resilient classes of molluscs (i.e. cephalopods Gutowska et al., 2008; Gutowska and Melzner, 2009; Sigwart et al., 2015).

Larvae are thought to be particularly sensitive because of the high solubility of the amorphous calcium carbonate and aragonite that initiates skeleton development (O'Donnell et al., 2009a, b). However, as this phase of calcium carbonate is intracellular in a highly regulated environment, it is unlikely to be directly vulnerable to environmental acidification (Stumpp et al., 2012; Dubois, 2014).

Exposure to elevated CO₂ changes gene regulation (Zippay and Hofmann, 2010; Padilla-Gamino et al., 2013), including skeletogenic pathways (Evans et al., 2013; Thompson et al., 2015), spicule matrix proteins (Evans and Watson-Wynn, 2014), ion-regulation (Stumpp et al., 2012) ion transport (Evans and Watson-Wynn, 2014), and protein synthesis (Pan et al., 2015; Thompson et al., 2015).

Acute exposure to elevated CO₂ also delays development, increases abnormalities, and decreases larval survival in molluscs (Kurihara et al., 2007; Ellis et al., 2009; Kurihara et al., 2009; Parker et al., 2009, 2010, 2011; Talmage and Gobler 2009; Watson et al., 2009) and echinoderms (Kurihara et al., 2004a, b; Kurihara and Shirayama 2004; Dupont et al., 2008; Clark et al., 2009; Stumpp et al., 2011a, b, 2012; Byrne, 2013; Gonzalez-Bernat et al., 2013a, b; Uthicke et al., 2013), perhaps because of changes in lipid reserves and energetics (molluscs Talmage and Gobler, 2010, 2011), but not always (echinoplutei, Matson et al., 2012).

Studies also found physiological changes in mollusc and echinoderm larvae in response to short-term exposure to elevated CO₂ including changes in standard metabolic rate (SMR) in bivalves (Lannig et al., 2010; Parker et al., 2012, 2013) and echinoderms (Todgham and Hofmann, 2009; Beniash et al., 2010; Stumpp et al., 2012; Thomsen et al., 2013).

Larvae which are smaller in size may have less energy reserves, spending longer in the plankton to reach metamorphosis, increasing their risk of predation and mortality (Byrne et al., 2009; Ross et al., 2011). Already, mortality of larvae in the plankton is thought to exceed 90% (Thorson, 1950; Gosselin and Qian, 1997), in an ocean altered by climate change, this may increase. Even if smaller larvae survive to settle, they may have a reduced competitive ability at settlement (Hobday and Tegner, 2002; Kurihara et al., 2007; Byrne et al., 2009, 2010) and increased post-settlement mortality (molluscs Kurihara et al., 2007; Parker et al., 2009, 2010; echinoderms Talmage and Gobler, 2009; echinoderms: Dupont et al., 2008; Clark et al., 2009).

Mollusc and echinoderm larvae also experience environmental stress from factors other than elevated CO₂. Global sea surface temperatures are increasing and it is predicted that temperatures will continue to rise over this century up to 4°C by the 2100 (IPCC, 2013, 2014). Climate change will also alter salinity and turbidity regimes as a result of unpredictable rain events. Individually, each of these stressors has the potential to influence the growth and

survival of larvae. Together, how these stressors will interact to ameliorate or exacerbate conditions for larvae of molluscs and echinoderms remains unknown (Byrne, 2011; Byrne and Przeslawski, 2013; Przeslawski *et al.*, 2015).

Within-generation carryover effects: larvae to juveniles

Although studies on single life history stages using acute exposures to elevated CO₂ provide information on the vulnerabilities of embryos and larvae, they do not provide information on positive or negative carryover effects within generation from planktonic to juvenile stages. Studies have found that stressors present during early-life history stages can have carry-over effects within the generation (Hettinger *et al.*, 2012; White *et al.*, 2013). It is well known that early larval life may influence juvenile performance and adult fitness. Metamorphosis is not a new beginning, but dependent on the environmental experience of early-life history stages such as embryos and larvae (Pechenik *et al.*, 1998; Pechenik, 1999; Byrne *et al.*, 2008).

There are fewer studies which have measured the carryover effects of elevated CO₂ from larvae to juvenile stages of molluscs and echinoderms (Table 1). Those studies that have done so find negative impacts in larvae exposed to elevated CO₂ which typically continues until the juvenile stage after settlement (Byrne *et al.*, 2010; Hettinger *et al.*, 2012, 2013; Dupont *et al.*, 2013; Wangensteen *et al.*, 2013).

In echinoderms, Byrne *et al.* (2010) reported the first evidence of negative carryover effects from larvae to juveniles of the sea urchin *Heliocidaris erythrogramma* following a 5-d exposure to reduced pH (8.2_{NIST} control, 7.8_{NIST}, 7.6_{NIST}) and elevated temperature (22°C control, 24, 26°C). *Heliocidaris erythrogramma* gametes were fertilized at each pH and temperature treatments where they remained for the duration of larval development and settlement (4 d post-fertilization). Following settlement (5 d post-fertilization), the number of normal juveniles which developed and the number of spines per juvenile were significantly reduced in the low pH treatments relative to the ambient treatment. The negative effects on spine development were ameliorated at the moderately elevated temperature of +2°C, but not +4°C (Byrne *et al.*, 2010). Similar negative carryover effects from larvae to juveniles have also been observed in sea urchins following longer juvenile exposure periods (Dupont *et al.*, 2013). Larvae of the sea urchin, *Strongylocentrotus droebachiensis*, were exposed to present day (361 µatm) and elevated (941 µatm) CO₂ until settlement. Following this time, post-settled juveniles from each larval CO₂ treatment were transferred to present day (361 µatm) or elevated (941 µatm) CO₂ in a fully orthogonal design. After 3 months of juvenile exposure, pCO₂ had no direct negative impact on juvenile survival. Survival of juveniles was reduced only in treatments where both larvae and juveniles had been reared at elevated CO₂ (Dupont *et al.*, 2013). In contrast, within-generation carryover effects in the sea urchin, *Arbacia lixula*, were much less pronounced (Wangensteen *et al.*, 2013). Three-day-old juveniles of *A. lixula* reared from the beginning of larval development at elevated CO₂, pH of 7.7_T, had similar survival to juveniles reared at the control pH of 8.1_T. There was, however, a significant reduction in the diameter of juveniles (Wangensteen *et al.*, 2013).

In molluscs, exposure to elevated CO₂ during larval development has been shown to have negative carryover effects for juveniles even when the juvenile is reared at ambient CO₂ (Hettinger *et al.*, 2012, 2013). Hettinger *et al.* (2012) investigated whether the impacts of elevated CO₂ on larvae of Olympia oysters, *Ostrea lurida*, were

transferred through metamorphosis to juveniles. Larvae were reared at control (8.0 pH units) and low (7.9 and 7.8) pH for the duration of larval development. At the time of settlement, larvae reared at low pH of 7.8 had a 15% decrease in growth rate and a 7% decrease in shell area. These effects were even more pronounced following settlement, with juveniles that had been reared at pH 7.8 during larval development having a 41% decrease in growth rate. The decrease in growth rate occurred regardless of the pH level that the juvenile was reared and persisted for 1.5 months after settlement (Hettinger *et al.*, 2012). Persistent negative carryover effects have also been found for larvae of *O. lurida* exposed to elevated CO₂ and returned to natural conditions in the field (Hettinger *et al.*, 2013). Larvae of *O. lurida* were reared at ambient (500 µatm) and elevated (1000 µatm) CO₂ until settlement. Following this, the newly settled juveniles were transferred into the field where they remained for a period of 4 months. Juveniles had reduced growth rates in the field when larval development had occurred at elevated compared with control CO₂. These negative carryover effects on juvenile growth persisted for 4 months post-settlement (Hettinger *et al.*, 2013).

Other studies on molluscs have found positive carryover effects. In contrast to *O. lurida*, juveniles of the bay scallop, *Argopecten irradians*, had positive specific growth rates when larvae were exposed to elevated CO₂ (Gobler and Talmage, 2013). Gobler and Talmage (2013) reared larvae *A. irradians* at ambient (390 µatm) and elevated (750 µatm) CO₂ in the laboratory through to early days of juvenile development. Juveniles were then transferred into the field where they remained for a period of 10 months. After 13–26 weeks post-fertilization, juveniles reared at elevated CO₂ during larval development had greater specific growth rates than the juveniles reared at ambient CO₂ (control juveniles). The authors suggested that the greater specific growth rate occurred because juveniles that survive CO₂ as larvae are those with greater “fitness” (Gobler and Talmage, 2013). By 10 months, the effects of larval exposure to elevated CO₂ on juvenile growth were no longer present; both juvenile lines had similar growth. Finally, in the hard clam, *Mercenaria mercenaria*, exposure of larvae to elevated CO₂ (1500 µatm) caused a significant reduction in the survival of post-set juveniles only when the juveniles were also reared at elevated CO₂ (Gobler and Talmage, 2013). Interestingly, there was an increase in the post-settlement survival of juveniles that were reared at elevated CO₂ as larvae and ambient CO₂ as juveniles. Once again, the authors suggested that high mortality during the larval stage in the elevated CO₂ treatment led to the survival of fitter individuals (Gobler and Talmage, 2013).

Collectively, these studies emphasize the importance of investigating the potential carryover effects that larval exposure to elevated CO₂ has for juvenile and adult stages. Indeed, studies on non-marine species suggest that experiences in early life can have direct consequences for later success (Burton and Metcalfe, 2014, and references therein). From the studies done to date, it is likely that responses of echinoderm and mollusc populations to elevated CO₂ need to be measured within generation to determine the potential carryover effects.

Transgeneration carryover effects: adults to larvae

Understanding whether marine invertebrates will have the capacity to acclimate and adapt to ocean acidification by the end of the century is an area of great uncertainty (Donelson *et al.*, 2011; Sunday *et al.*, 2014). Uncertainty exists because single-generation experiments are constrained by compressing 100 years of evolution

Table 1. Within-generational carryover effects: results of studies investigating the impacts of ocean acidification (pH/pCO₂, ppm) on the life history transition from larvae to juveniles in molluscs and echinoderms.

Species	Experiment duration	Measured	Larval, juvenile CO ₂ /pH exposure	Impact compared with control	Other stressors	Additional comments	Author
Molluscs							
<i>Argopecten irradians</i> (scallop)	10 months post-settlement	Growth rate	390 μ atm, field	↑	Nil	Growth rate increased after 13–26 weeks but similar by 10 months	Gobler and Talmage (2013)
<i>Mercenaria mercenaria</i> (hard clam)	36 d post-fertilization	Survival	750 μ atm, field 390, 390 μ atm 390; 1500 μ atm 1500; 390 μ atm 1500; 1500 μ atm	= ↑ ↓	Nil		Gobler and Talmage (2013)
<i>Ostrea lurida</i> (Olympia oyster)	1.5 months post-settlement	Growth rate	8.0, 8.0 _{NIST} 8.0, 7.8 _{NIST} 7.8, 8.0 _{NIST} 7.8, 7.8 _{NIST}	↓ (41%) ↓ (41%)	Nil	41% decrease in juvenile growth rate occurred when larvae were reared at elevated CO ₂ regardless of juvenile treatment	Hettinger <i>et al.</i> (2012)
<i>Ostrea lurida</i> (Olympia oyster)	4 months post-settlement	Growth rate	500 μ atm, field 1000 μ atm, field	↓			Hettinger <i>et al.</i> (2013)
Echinoderms							
<i>Heliocidaris eurythrogramma</i> (sea urchin)	1 d post-settlement	# normal juveniles, # spines	8.2, 8.2 _{NIST} 7.8, 7.8 _{NIST} 7.6, 7.6 _{NIST}	↓, ↓ ↓, ↓	22, 24, 26°C	—ive effects on spine development were ameliorated 24°C but not +26°C	Byrne <i>et al.</i> (2010)
<i>Strongylocentrotus droebachiensis</i> (sea urchin)	3 months post-settlement	Survival	361, 361 μ atm 361, 941 μ atm 941, 361 μ atm 941, 941 μ atm	= = ↓ (95%)		Survival of juveniles was reduced when both larvae and juveniles reared at elevated CO ₂	Dupont <i>et al.</i> (2013)
<i>Arbacia lixula</i> (Sea urchin)	3 d post-settlement	Survival, juvenile diameter	8.1, 8.1 _T 7.7, 7.7 _T	=, ↓			Wangensteen <i>et al.</i> (2013)

Molluscs: three studies, three species; echinoderms: three studies, three species. Control CO₂/pH listed in italics. For all studies, experimental exposure began during fertilization or early larval development.

into a period which is experimentally feasible and fundable (Fitzer *et al.*, 2012). Such a constraint, however, will underestimate the potential for marine organisms to cope with changing ocean conditions (Donelson *et al.*, 2011; Sunday *et al.*, 2014). Whether resilience to elevated CO₂ can occur over multiple generations has been investigated in marine invertebrates (Mayor *et al.*, 2007; Kurihara and Ishimatsu, 2008; Lohbeck *et al.*, 2012; Fitzer *et al.*, 2014; De Wit *et al.*, 2015), vertebrates (fish Donelson *et al.*, 2011), and algae (Collins and Bell, 2004) with short generation times (days to months; Table 2). For organisms with long generation times (months to years), such as molluscs and echinoderms, measuring the response of species across multiple generations is much more difficult (Sunday *et al.*, 2014). Studies on these species to date have focused on the transgenerational response to elevated CO₂. Transgenerational experiments allow parents to facilitate phenotypic acclimatory processes between generations in response to the environment, not solely due to genotype (Donelson *et al.*, 2011). Overall, these studies suggest that acclimation to elevated CO₂ may be possible for marine organisms over successive generations at time-scales which may be shorter than the rate of anticipated climate change in oceans. With so few studies, however, predictive capacity remains problematic. Parker *et al.* (2012) were the first to show that the negative effects of ocean acidification on marine invertebrate larvae could be reduced following transgenerational exposure to elevated CO₂. They exposed parents of the oyster *Saccostrea glomerata* to elevated CO₂ of 856 μatm for 5 weeks during reproductive conditioning and found that parental exposure had positive carryover effects for larval offspring. Larvae from parents exposed to elevated CO₂ were larger in size, developed faster, but had similar survival at elevated CO₂ compared with larvae from control parents (Parker *et al.*, 2012). These positive carryover effects persisted into adulthood and the next generation (Parker *et al.*, 2015). When offspring from CO₂-exposed parents reached adulthood, they had a greater capacity to regulate extracellular pH (pH_e) at elevated CO₂. Furthermore, subsequent exposure of these adults to elevated CO₂ led to similar positive carryover effects in their larval and juvenile offspring during exposure to elevated CO₂ (Parker *et al.*, 2015). Interestingly, offspring from CO₂-exposed parents also performed better at present-day CO₂, leading the authors to suggest that increased maternal provisioning into eggs may have been a key mechanism involved in the observed TGP.

Fitzer *et al.* (2014) similarly investigated the impacts of transgenerational exposure to elevated CO₂ on the composition of juvenile shells of the mussel, *Mytilus edulis*. They found that parental (6 months) and offspring exposure to elevated CO₂ at 1000 μatm resulted in juveniles that no longer produced aragonite in their shells and instead produced only calcite. Fitzer *et al.* (2014) suggested this was an acclimatory mechanism, aragonite being more vulnerable to calcium carbonate under-saturation than calcite. In this study, the response of larvae to the impacts of parental exposure to elevated CO₂ was not reported.

While there have been more studies on the TGP response of echinoderms, the small number of studies makes conclusions difficult. Whether transgenerational carryover effects are positive or negative for echinoderms (i.e. sea urchins) depends on the length of time that parents are exposed to elevated CO₂ and the stage of maturity of the gonads. For example, there were negative impacts on the reproductive output and success of the larvae from adult sea urchins, *St. droebachiensis*, exposed to elevated CO₂ of 1217 μatm for a period of 4 months. Fecundity was reduced by 4.5-fold and there were five to

nine times fewer larvae reaching juvenile stages from parents exposed to elevated CO₂ (Dupont *et al.*, 2013).

Similar results were found for the larvae from adult Antarctic sea urchin, *S. neumayeri*. Larvae from parents exposed to the combined stressors of elevated CO₂ (928 and 1405 μatm) and temperature (+2°C) for either 6 or 17 months had different outcomes (Suckling *et al.*, 2015). After parents were exposed to 6 months of elevated CO₂ and temperature, egg size was smaller and hatching success was 63% lower compared with parents exposed to present-day control conditions. After parents were exposed to 17 months of elevated CO₂ and temperature, the egg size was larger and hatching success greater from parents reared at elevated CO₂ and temperature compared with ambient treatments (present-day control and elevated). Larval success (survival and development rate) was also greater from parents exposed to elevated CO₂ and temperature for 17 months. There was, however, an increase in abnormal development of larvae compared with the present-day controls (Suckling *et al.*, 2015). The authors suggested that the increase in abnormal development was because of the interactive effects of CO₂ and temperature rather than CO₂ alone.

Collectively for *St. droebachiensis* and *S. neumayeri*, it seems that parents require exposure to elevated CO₂ and/or temperature for a period more than 6 months before transgenerational carryover positive effects from parents to their larval offspring occur. This may reflect the time it takes for the adults to acclimate to the acidified conditions. For example, adult *S. neumayeri* exposed to elevated CO₂ and temperature for 6 months had an increase in SMR compared with adults exposed to present-day conditions. Following 17 months of exposure, however, SMR was restored to control levels, suggesting that adult acclimation had occurred (Suckling *et al.*, 2015). Time to acclimation may vary among sea urchin species. Suckling *et al.* (2014) exposed parents of *Psammechinus miliaris* to elevated CO₂ of 999 μatm for 28, 42, and 70 d and compared the response of larval offspring with those parents exposed to present-day CO₂ conditions. Their results showed positive carryover transgenerational effects after 42 and 70 d of parental exposure, but not after 28 d. Larvae from parents exposed to 42 and 70 d of elevated CO₂ were larger in size at the time of settlement compared with larvae from parents exposed to elevated CO₂ for 28 d or present-day conditions. Additionally, parental exposure to elevated CO₂ for 70 d ameliorated the impacts of elevated CO₂ on fertilization success.

In the only other transgenerational study on the tropical Pacific sea urchin, *Echinometra mathaei*, parents exposed to elevated CO₂ for 42 d were not long enough to facilitate positive carryover transgenerational effects in larvae (Uthicke *et al.*, 2013). There was no difference in the size of eggs from parents exposed to present-day or elevated CO₂. Irrespective of the parental exposure, the percentage and size of larvae decreased and arm asymmetry increased at elevated CO₂. Uthicke *et al.* (2013) suggested that acclimation of offspring did not occur following 42 d of adult exposure to elevated CO₂ because adults were not exposed from the onset of gonadal development. The time that the adults are introduced to ocean change stressors with respect to gametogenesis is likely to be a critical factor determining the outcomes of these experiments and identification of TGP to elevated CO₂ in echinoderm and other marine invertebrates, especially for species with seasonal reproduction and synchronous gametogenesis. The influence of maternal imprinting determined by the environment in which the eggs develop from the onset of oogenesis can have a major influence on offspring performance (Andronikov, 1975; Byrne, 2010; Byrne *et al.*, 2011).

Table 2. Transgenerational carryover effects: results of studies investigating the impacts of ocean acidification (pH/pCO₂, ppm) on the life history transition from adults to larvae in molluscs and echinoderms.

Species	Parental exposure	Measured	Adult, larval CO ₂ /pH exposure	Nature of carryover (+ive/−ive/=)	Response to transgenerational exposure	Author
Molluscs						
<i>Saccostrea glomerata</i> (oyster)	5 weeks	Survival, Shell length, % development	385, 385 μ atm 385, 856 μ atm 856, 385 μ atm 856, 856 μ atm	+ive	Larvae larger in size, developed faster but had similar survival at elevated CO ₂ compared with larvae from control parents	Parker <i>et al.</i> (2012)
<i>Mytilus edulis</i> (mussel)	6 months	Juvenile shell composition	380, 380 μ atm 550, 550 μ atm 750, 750 μ atm 1000; 1000 μ atm	+ive	Juvenile shell no longer contained aragonite at 1000 μ atm. Larval response not measured	Fitzer <i>et al.</i> (2014)
Echinoderms						
<i>Strongylocentrotus droebachiensis</i> (sea urchin)	4 and 16 months	Fecundity, # larvae to reach juvenile stage	361, 361 μ atm 1217, 1217 μ atm	−ive (4 months) +ive (16 months)	Adult exposure for 4 months had negative impacts reproductive output and larval offspring success. Fecundity reduced by 4.5-fold and 5–9 times fewer larvae reached the juvenile stage. After 16 months of adult exposure, negative effects on fecundity and larval survival no longer observed	Dupont <i>et al.</i> (2013)
<i>Sterechinus neumayeri</i> (sea urchin)	6 and 17 months	Egg size, hatching success, larval survival, development rate, % abnormal development	361, 361 μ atm; 0°C 928, 928 μ atm; 2°C 1405, 1405 μ atm; 2°C	−ive (6 months) +ive (17 months)	Adult exposure for 6 months caused reduced egg size and 63% lower hatching success compared with control adults. After 17 months of adult exposure, egg size was larger and hatching success was similar across all parental CO ₂ and temperature treatments. Larval survival and development rate also improved following 17 months of adult exposure; however, abnormal development of larvae was increased compared with the present-day controls	Suckling <i>et al.</i> (2014)
<i>Psammechinus miliaris</i> (sea urchin)	28, 48, and 70 d	Fertilization success, size	559, 559 μ atm 999, 999 μ atm	+ive (42 and 70 d)	Positive transgenerational carryover effects were observed after 42 and 70 d of parental exposure, but not after 28 d. Adult exposure for 42 and 70 d led to larger larvae at the time of settlement compared with larvae from parents exposed to elevated CO ₂ for 28 d or present-day conditions. Adult exposure for 70 d also ameliorated the impacts of elevated CO ₂ on fertilization success	Sucking <i>et al.</i> (2014b)
<i>Echinometra mathaei</i> (sea urchin)	42 d	Egg size, % normal larvae, larval size, arm asymmetry	485, 485 μ atm 1770, 1770 μ atm	=	No difference in size of eggs from parents exposed to present-day or elevated CO ₂ . Percentage of normal larvae and size of larvae reduced and arm asymmetry increase at elevated CO ₂ , irrespective of the parental environment	Uthicke <i>et al.</i> (2013)

<i>Strongylocentrotus purpuratus</i> (sea urchin)	Field study	Larval size	Gravid adults collected from two different sites along Northeast Pacific. pH of both sites varied from 7.6 to 8.3 _{NIST} , but there was a higher frequency of low pH at the northern site	+ive	Using a reciprocal breeding design the authors created 64 families with the aim of assessing the impact of maternal and paternal origin on larval offspring size when reared at elevated CO ₂ . There was a significant effect of maternal (but not paternal) origin on larval size at elevated CO ₂ . Overall, larval size was reduced in all family lines held at elevated compared with ambient CO ₂ but the extent of reduction was significantly less for larvae whose mothers were collected from the northern site	Kelly <i>et al.</i> (2013)
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Molluscs: two studies, two species; echinoderms: five studies, five species. Control CO₂/pH listed in italics.

There is also evidence of TGP in response to elevated CO₂ in an echinoderm species from field experiments (Kelly *et al.*, 2013). Kelly *et al.* (2013) collected adults of the purple sea urchin *Strongylocentrotus purpuratus* from two sites along the coast of the Northeast Pacific. The pH at both collection sites varied from 7.6 to 8.3_{NIST}, but there was a higher frequency of low pH at the northern compared with the southern site. Using a reciprocal breeding design, the authors created 64 families with the aim of assessing the impact of maternal and paternal origin on larval offspring size when reared at elevated CO₂. The results showed that there was a significant effect of maternal (but not paternal) origin on larval size at elevated CO₂. Overall, larval size was reduced in all family lines held at elevated compared with ambient CO₂, but the extent of this reduction was significantly less for larvae whose mothers were collected from the northern site with a higher frequency of low pH. Although the exact pH of the environment was not known, the authors reasonably concluded that high genetic variation within a population and the history of exposure to low pH will be critical determinants of the adaptation potential of echinoderms to elevated CO₂ over this century.

What are the mechanisms for transgenerational carryover effects/TGP?

TGP is non-genetic inheritance, whereby parents induce phenotypic changes in offspring traits without altering their DNA sequence (Salinas and Mulch, 2012). A transgenerational response or TGP can be defined as a phenotypic change in offspring in response to the environmental stress experienced by a parent(s) (Kovalchiki 2012). TGP is acclamatory and can occur over rapid time-scales because of the absence of genetic modification. In contrast to TPG, evolutionary adaptation is a slower process which relies on heritable DNA genetic modification.

The two main non-genetic pathways which have been identified as mechanisms for transgenerational exposure to elevated CO₂ leading to carryover effects from parents to offspring are: (i) increased maternal provisioning and/or (ii) epigenetic modifications in gene expression, commonly referred to as epigenetic inheritance (Murray *et al.*, 2013; Burton and Metcalfe, 2014; Munday, 2014).

Increased maternal provisioning is an adaptive strategy employed by marine and other organisms to help offspring survive in suboptimal environmental conditions (Bernardo, 1996; Untersee and Pechenik, 2007; Allen *et al.*, 2008; Marshall, 2008; Marshall *et al.*, 2008; Sanford and Kelly, 2011; Allan *et al.*, 2014). Mothers which experience suboptimal environments can increase the energy which they invest per egg, often at the expense of fecundity, thereby increasing offspring fitness and survival in those same suboptimal conditions (Allen *et al.*, 2008). Elevated CO₂ is hypothesized to increase the energy demand of marine species (Pörtner and Farrell, 2008), particularly in larvae which have limited capacity to regulate acid–base status (Parker *et al.*, 2015). As such, increased energy reserves in eggs will be beneficial for mollusc and echinoderm larvae as our oceans continue to acidify. Evidence for increased maternal provisioning in the form of increased egg size was observed in the sea urchin, *S. neumayeri* following 17 months of parental exposure to elevated CO₂ (but not 6 months of exposure; Suckling *et al.*, 2014). Further in the oyster, *Sa. glomerata*, although egg size was not measured, 24 h larvae from parents exposed to elevated CO₂ were larger in size than larvae from parents exposed to present-day CO₂ (Parker *et al.*, 2012). This led the authors to suggest that increased maternal provisioning occurred.

For *St. droebachiensis* and *P. miliaris*, there was no significant increase in the size of eggs following transgenerational exposure of parents to elevated CO₂ (Dupont *et al.*, 2013; Suckling *et al.*, 2015). In fact, the egg size of *P. miliaris* significantly decreased. Despite this, TGP was still observed in the larval offspring following parental exposure to elevated CO₂, suggesting the involvement of mechanisms other than increased maternal energy provisioning (Dupont *et al.*, 2013). It is also possible that the nature of the energy reserves was altered in the eggs (Moran and McAlister, 2009). Moran and McAlister (2009) emphasized that although egg size is simple to measure, egg size can be altered by processes that do involve increased nutritive reserves.

Epigenetic inheritance is gaining considerable ground in the literature as a key mechanism of TGP in marine organisms during exposure to environmental stress (Vandegheuchte and Janssen, 2014). Poor environmental conditions trigger beneficial modifications in the gene expression pattern of parents which are passed to their offspring, influencing the offspring phenotype. These epigenetic changes are thought to occur predominantly through DNA methylation as well as histone modification and/or non-coding RNA (Riviere, 2014; Vandegheuchte and Janssen, 2014). These changes can be transmitted through generations, especially if environmentally reinforced or can eventually disappear over two to three generations (Flores *et al.*, 2013).

Direct correlations between TGP and differential gene expression are yet to be made in marine species following exposure to elevated CO₂. It has been hypothesized, however, that changes in the expression of key genes such as those relating to acid–base regulation and mitochondrial metabolism are likely to be involved (Miller *et al.*, 2012; Murray *et al.*, 2013). Evidence of acclimation to reduced pH through epigenetic changes has been shown within a generation in fish (Deigweiher *et al.*, 2008; Horng *et al.*, 2009; Tseng *et al.*, 2013). For example, acclimation to environmental hypercapnia of 10 000 ppm of adults of the eelpout *Zoarces viviparus* involved an initial down-regulation followed by an up-regulation of a key ion transporter (Na⁺/HCO₃[−]) pivotal for acid–base regulation, as well as, a twofold increase in Na⁺–K⁺–ATPase in gill tissue (Deigweiher *et al.*, 2008).

More recently, a study of the transgenerational effects of ocean warming on offspring of the marine stickleback, *Gasterosteus aculeatus*, found that acclimation of juvenile body size following transgenerational exposure to elevated temperature was closely linked to mitochondrial respiration rates (Shama *et al.*, 2014). Mitochondrial respiration rates in offspring were significantly lower at the elevated temperature of 21°C when mothers were reared at 21°C compared with 17°C. It is believed that mothers adjusted their mitochondria respiration capacities and that this adjustment was passed to their offspring to improve their performance at elevated temperature (Shama *et al.*, 2014). Adjustment of metabolic capacities may be an epigenetic mechanism employed by echinoderms following transgenerational exposure to elevated CO₂ as improvements in larval offspring traits in sea urchins were shown to occur only when gametes used to generate offspring were from parents that had adjusted their metabolism to that seen in control conditions (Dupont *et al.*, 2013; Suckling *et al.*, 2014). In contrast, in the oyster *Sa. glomerata*, transgenerational improvements in larval offspring traits during exposure to elevated CO₂ were still seen, despite parental metabolic rates remaining elevated (Parker *et al.*, 2012).

Understanding the mechanisms involved in the TGP in molluscs and echinoderms is a key area for future research. It is likely that the

mechanisms of transfer are not mutually exclusive nor are limited to the mechanisms described above. In studies unrelated to ocean acidification, TGP has also been linked to the direct transfer of somatic factors such as protective chaperone proteins and hormones from parents to their offspring (Hamdoun and Epel, 2007). Meistertzheim *et al.* (2009) found that the concentration of heat shock proteins as well as other stress proteins in the adult gonad of the oyster *Crassostrea gigas* were threefold higher during gametogenesis compared with times of resting gonadal development. They hypothesized that high levels of stress proteins were provided to eggs via maternal transfer which is an effective strategy to overcome environmental stress (Meistertzheim *et al.*, 2009). De Wit *et al.* (2015) found that in the copepod *Pseudocalanus acuspes*, RNA transcription was down-regulated in populations with long-term exposure to elevated CO₂ even after transplantation back to control levels.

Another key question which remains unanswered is whether several mechanisms of TGP (i.e. maternal provisioning, epigenetic inheritance, somatic factors) will benefit species persistence in an ocean predicted to be increase in acidification and temperature. We do not know if one mechanism of TGP is better than another in terms of the acclimation or adaptation ability of a species? Will one mechanism benefit them more? Will one have greater negative implications for other life history stages? Will one persist longer than another? Answers to these questions remain unexplored in marine climate change research.

Are there limitations or repercussions of TGP?

From the handful of studies on mollusc and echinoderm larvae, we know that TGP may be an acclamatory mechanism that has the potential to reduce and ameliorate the impacts of elevated CO₂ over this century. Whether or not there are limitations of TGP or negative repercussions of TGP for later life history stages and future generations is unknown.

In nearly all marine species studied to date, the impacts of TGP have been considered only for larval and early juvenile development. There has been no consideration of how later stage juveniles and adult molluscs and echinoderms will respond (but see Thor and Dupont, 2015) who investigated TGP in a copepod. Each life history stage in the life cycle of marine invertebrates differs dramatically in form and function. As a result, phenotypic traits which benefit an organism during one life history stage may have negative repercussions for another (see Strauss *et al.*, 1996; Relyea, 2001, 2003 frogs; Marshall, 2008; fish Munday, 2014).

In addition, we have very limited understanding of the longevity of TGP. Are transgenerational carryover effects present only during the early-life history stages or do they persist into adulthood and possibly subsequent generations (Burton and Metcalfe, 2014; Munday, 2014; Shama and Wegner, 2014)? Early evidence in fish suggests that the persistence of transgenerational carryover effects may be trait-specific (Schade *et al.*, 2014). For example, juveniles of the three-spined stickleback *Gasterosteus aculeatus*, from parents that were exposed to elevated CO₂, had otoliths that were larger in size and area from parents at elevated CO₂ but had reduced survival and growth at ambient CO₂. The transgenerational effects on otolith size and area were still present 100 d post-hatch; however, the effects on survival and growth were transient persisting for only 40 d post-hatch. Also in the oyster, *Sa. glomerata*, transgenerational carryover effects were still present in offspring 18 months after settlement (Parker *et al.*, 2015). Parker *et al.* (2015) reared offspring from CO₂-exposed parents of *Sa. glomerata* at elevated CO₂

throughout larval development, until settlement. Newly settled juveniles were then gradually weaned off the elevated CO₂ treatment before being transferred to the field, where they remained in ambient conditions. Following 18 months in the field, the offspring, now adults, were returned to the laboratory and exposed to elevated CO₂ for 5 weeks. The authors found that these adults had a greater capacity to regulate their pH_e than those with no previous history of CO₂ exposure.

Another important consideration for mollusc and echinoderm species is whether or not TGP can improve all phenotypic traits which are affected by ocean acidification. Evidence for TGP has been shown for vast number of traits (Salinas *et al.*, 2013). Nevertheless, recent studies on fish suggest that some phenotypic traits will not respond transgenerationally (Allan *et al.*, 2014; Welch *et al.*, 2014). For example, Welch *et al.* (2014) reported reduced levels of behavioural lateralization and abnormal responses to a chemical alarm cue in juvenile damselfish following exposure to elevated CO₂. These impairments in behaviour did not improve following transgenerational exposure of their parents to elevated CO₂. In a recent review by Munday (2014), it was suggested that some cognitive functions may have limited plasticity and will therefore not be shaped by the environment in which the parent was raised. Whether there are similar functions with limited plasticity in mollusc and echinoderm species and the role that this will play in species fitness over the next century requires prompt attention.

Finally, whether or not TGP will be limited by or even possible in the presence of multiple stressors is virtually unknown. The unfortunate truth for marine organisms is that ocean acidification will not occur as a sole stressor over this century (Byrne and Przeslawski, 2013; IPCC, 2013, 2014; Przeslawski *et al.*, 2015). Increasing ocean temperatures, fluctuations in salinity, increases in the presence and severity of hypoxic zones, and reductions in food availability, are just some of the stressors that marine organisms will face in addition to elevated CO₂ (Byrne and Przeslawski, 2013). We already know that living in a high-CO₂ world will cause an increase in the energy budget for many marine invertebrate species (Lannig *et al.*, 2010; Gazeau *et al.*, 2013; Parker *et al.*, 2013). This increase in energy budget arises because in the absence of acclimation or adaptation, the cost of routine maintenance is much higher at elevated CO₂ (Pedersen *et al.*, 2014). Pedersen *et al.* (2014) exposed adult copepod *Calanus finmarchicus* to elevated CO₂ in a multigenerational exposure and found that while a transgenerational exposure did not make offspring more vulnerable to other stressors, it did show that there was a negative effect on the offspring if they were reared at both CO₂ and reduced food. Whereas previous studies on this species found no effect of elevated CO₂.

For species which use increased maternal provisioning as a mechanism of TGP during exposure to elevated CO₂, added stressors such as elevated temperature and reduced food availability will put further constraints on the energy budget. These constraints may prevent TGP from occurring or reduce its effectiveness. For example (a) parents may no longer have the capacity to increase energy provisioning to their offspring or (b) the increased energy which is provisioned may not be adequate for larvae to overcome the energetic demands of a multiple stressor environment, and further (c) acclimatory processes benefiting larvae at elevated CO₂ could make them more vulnerable to other stressors. To date, there have been no studies which have measured the transgenerational response of a mollusc species to elevated CO₂ in the presence of other stressors and only a single study on an echinoderm species.

As mentioned previously, Suckling *et al.* (2015) exposed parents of the Antarctic sea urchin, *S. neumayeri*, to the combined stressors of elevated CO₂ (928 and 1405 μ atm) and temperature (+2°C) and measured the response of their larvae at the same levels of CO₂ and temperature. After 17 months of parental exposure, adults were able to acclimate their SMRs, which were initially increased at elevated CO₂ and temperature, back to control levels. In addition to this, the adults produced eggs that were significantly larger at elevated CO₂ and temperature compared with eggs from the present-day controls. Thus, indicating that the ability of *S. neumayeri* adults to increase provisioning in their offspring was still maintained under the combined stress of elevated CO₂ and temperature. In contrast, while the survival and development of larvae was improved at elevated CO₂ and temperature following exposure of their parents, the number of abnormal larvae was significantly increased, suggesting that the energetic demands of their larvae may have been exceeded in the multiple stressor environment.

Evidence for exceeded energy budgets have also been shown in the copepod *C. finmarchicus* following multigenerational exposure to elevated CO₂ and reduced food availability (Pedersen *et al.*, 2014). Subadult copepods of the F1 generation had a reduced dry weight, body length, and were leaner in treatments with elevated CO₂ and reduced food availability compared to present-day controls. This was the first study to report negative effects of elevated CO₂ on morphometric characteristics in a *Calanus* species and highlights the importance of studying the impacts of elevated CO₂ in the presence of other stressors. Molluscs and echinoderms occupy a variety of intertidal and subtidal habitats from oceanic to estuarine locations over a large geographic range. As our oceans continue to acidify, the ability of these species to occupy such heterogeneous, multistressor habitats may be lost and species distribution may become more limited to areas where diel and seasonal fluctuations in other biotic and abiotic factors are minor. Indeed, one of the major impacts of climate change is poleward migrations of many species with predicted contractions and extinctions of species in their current range, resulting in an overall homogenization of global faunal diversity (García Molinos *et al.*, 2015).

Implications for marine larvae and future directions

Over 85% of marine invertebrates have a biphasic life history with planktonic larvae which metamorphose into benthic juveniles that grow into adults. In larval biology, it has long been recognized that dispersing larvae of all types face challenges; a time when “a huge waste takes place” (Thorson, 1950). If larval mortality increases further because of ocean acidification, there will be far reaching consequences for adult individuals, population, and community dynamics (Ross *et al.*, 2011). Larvae which are smaller with thinner, weaker shells may have less energy reserves and require a longer (Pechenik, 1999) period in the plankton to obtain sufficient energy for metamorphosis. Longer larval life may increase the risk of predation and exposure to other environmental stressors, such as an increase in temperature or hypoxia, which may decrease survival and increase mortality, particularly in the absence of properly calcified shells and skeletons (Byrne, 2011). Reduced larval size can also decrease the feeding efficiency of larvae and smaller larvae are more susceptible to starvation because they encounter comparatively less food. Reduced energy reserves may influence the transition to benthic settlement, although there is some suggestion from recent studies that a positive maternal investment may provide larvae with sufficient energy and resilience to high CO₂ (Parker *et al.*, 2012). A reduction in the survival of larvae will reduce the number of individuals reaching

settlement (Ross, 2001). Even small sublethal perturbations have the potential to cause large alterations to recruitment and adult populations (Uthicke et al., 2009).

Conclusion

Ultimately, we need a better understanding of the long-term consequences of elevated CO₂ for a wider range of marine species to improve predictive capacity. In addition, we require more knowledge on the mechanisms responsible for positive and negative carry-over transgenerational effects, the impacts that carryover effects have for subsequent life history stages and future generations, and how these carryover effects impact performance in the presence of other climate and environmental stressors. Exposure to elevated CO₂ during early life history stage will have long-term carryover effects for subsequent life history stages and generations (Burton and Metcalfe, 2014). In six of the seven studies which have measured the transgenerational response of molluscs and echinoderms to elevated CO₂ to date, TGP has been observed in the larval offspring. This phenotypic response mechanism provided by parents may buffer mollusc and echinoderm populations over multiple generations, long enough for genetic adaptation to occur (Shama and Wegner, 2014).

References

- Albright, R. 2011. Reviewing the effects of ocean acidification on sexual reproduction and early life history stages of reef-building corals. *Journal of Marine Biology*, ID 473615: 1–14.
- Allan, B. J. M., Miller, G. M., McCormick, M. I., Domenici, P., and Munday, P. L. 2014. Parental effects improve escape performance of juvenile reef fish in a high-CO₂ world. *Proceedings of the Royal Society B: Biological Sciences*, 281: 1–7.
- Allen, R. M., Buckley, Y. M., and Marshall, D. J. 2008. Offspring size plasticity in response to intraspecific competition: an adaptive maternal effect across life-history stages. *American Naturalist*, 171: 225–337.
- Andronikov, V. 1975. Heat resistance of gametes of marine invertebrates in relation to temperature conditions under which the species exist. *Marine Biology*, 30: 1–11.
- Beniash, E., Ivanina, A., Lieb, N. S., Kurochkin, I., and Sokolova, I. M. 2010. Elevated level of carbon dioxide affects metabolism and shell formation in oysters *Crassostrea virginica*. *Marine Ecology Progress Series*, 419: 95–108.
- Bernardo, J. 1996. Maternal effects in animal ecology. *American Zoologist*, 36: 83–105.
- Burton, T., and Metcalfe, N. B. 2014. Can environmental conditions experienced in early life influence future generations? *Proceedings of the Royal Society B: Biological Sciences*, 281: 20140311.
- Byrne, M. 2010. Impact of climate change stressors on marine invertebrate life histories with a focus on the Mollusca and Echinodermata. In *Climate Alert: Climate Change Monitoring and Strategy*, pp. 142–185. Ed. by J. Yu, and A. Henderson-Sellers. University of Sydney Press, Sydney.
- Byrne, M. 2011. Impact of ocean warming and ocean acidification on marine invertebrate life history stages: vulnerabilities and potential for persistence in a changing ocean. *Annual Reviews*, 49: 1–42.
- Byrne, M. 2012. Global change ecotoxicology: identification of early life history bottlenecks in marine invertebrates, variable species responses and variable experimental approaches. *Marine Environmental Research*, 76: 3–15.
- Byrne, M. 2013. Echinoderm ecotoxicology: application for assessing and monitoring vulnerabilities in a changing ocean. Echinoderms in a Changing World: 13th International Echinoderm Conference, CRC Press/Balkema, Leiden, The Netherlands.
- Byrne, M., Foo, S., Soars, N., Wolfe, K., Nguyen, H., Hardy, N., and Dworjanyn, S. 2013b. Ocean warming will mitigate the effects of acidification on calcifying sea urchin larvae (*Helicodaris tuberculata*) from the Australian global warming hot spot. *Journal of Experimental Marine Biology and Ecology*, 448: 250–257.
- Byrne, M., Ho, M., Selvakumaraswamy, P., Nguyen, H., Dworjanyn, S., and Davis, A. 2009. Temperature, but not pH, compromises sea urchin fertilization and early development under near-future climate change scenarios. *Proceedings of the Royal Society B: Biological Sciences*, 276: 1883–1888.
- Byrne, M., Ho, M., Wong, E., Soars, N. A., Selvakumaraswamy, P., Sheppard-Brennard, H., Dworjanyn, S. A., et al. 2010. Unshelled abalone and corrupted urchins: development of marine calcifiers in a changing ocean. *Proceedings of the Royal Society B: Biological Sciences*, 282: 1–8.
- Byrne, M., Lamare, M., Winter, D., Dworjanyn, S. A., and Uthicke, S. 2013a. The stunting effect of a high CO₂ ocean on calcification and development in sea urchin larvae, a synthesis from the tropics to the poles. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368: 1–13.
- Byrne, M., Prowse, T. A. A., Sewell, M. A., Dworjanyn, S., Williamson, J. E., and Våtilingon, D. 2008. Maternal provisioning for larvae and larval provisioning for juveniles in the sea urchin *Tripneustes gratilla*. *Marine Biology*, 155: 473–482.
- Byrne, M., and Przeslawski, R. 2013. Multistressor impacts of warming and acidification of the ocean on marine invertebrates' life histories. *Integrative and Comparative Biology*, 53: 582–596.
- Byrne, M., Selvakumaraswamy, P., Ho, M., Woolsey, E., and Nguyen, H. 2011. Sea urchin development in a global change hotspot, potential for southerly migration of thermotolerant propagules. *Deep Sea Research II: Topical Studies in Oceanography*, 58: 712–719.
- Clark, D., Lamare, M., and Barker, M. 2009. Response of sea urchin pluteus larvae (Echinodermata: Echinoidea) to reduced seawater pH: a comparison among a tropical, temperate, and a polar species. *Marine Biology*, 156: 1125–1137.
- Collins, S., and Bell, G. 2004. Phenotypic consequences of 1000 generations of selection at elevated CO₂ in a green alga. *Nature*, 431: 566–569.
- Comeau, S., Gorsky, G., Alliouane, S., and Gattuso, J. P. 2010. Larvae of the pteropod *Cavolinia inflexa* exposed to aragonite undersaturation are viable but shell-less. *Marine Biology*, 157: 2341–2345.
- Cripps, G., Lindeque, P., and Flynn, K. J. 2014. Have we been underestimating the effects of ocean acidification in zooplankton? *Global Change Biology*, 20: 3377–3385.
- Davis, H. C. 1958. Survival and growth of clam and oyster larvae at different salinities. *Biological Bulletin*, 114: 296–307.
- De Wit, P., Dupont, S., and Thor, P. 2015. Selection on oxidative phosphorylation and ribosomal structure as a multigenerational response to ocean acidification in the common copepod *Pseudocalanus acuspes*. *Evolutionary Applications*. doi: 10.1111/eva.12335.
- Deigweier, K., Koschnick, N., Pörtner, H.-O., and Lucassen, M. 2008. Acclimation of ion regulatory capacities in gills of marine fish under environmental hypercapnia. *The American Journal of Physiology—Regulatory, Integrative and Comparative Physiology*, 295: R1660–R1670.
- Donelson, J. M., Munday, P. L., McCormick, M. I., and Pitcher, C. R. 2011. Rapid transgenerational acclimation of a tropical reef fish to climate change. *Nature Climate Change*, 2: 30–32.
- Dubois, P. 2014. The skeleton of postmetamorphic echinoderms in a changing world. *Biological Bulletin*, 226: 223–236.
- Dupont, S., Dorey, N., Stumpp, M., Melzner, F., and Thorndyke, M. 2013. Long-term and trans-life-cycle effects of exposure to ocean acidification in the green sea urchin *Strongylocentrotus droebachiensis*. *Marine Biology*, 160: 1835–1843.
- Dupont, S., Havenhand, J., Thorndyke, W., Peck, L., and Thorndyke, M. 2008. Near-future level of CO₂-driven ocean acidification radically affects larval survival and development in the brittlestar *Ophiothrix fragilis*. *Marine Ecology Progress Series*, 373: 285–294.

- Dupont, S., Lundve, B., and Thorndyke, M. 2010b. Near future ocean acidification increases growth rate of the lecithotrophic larvae and juveniles of the sea star *Crossaster papposus*. *Journal of Experimental Zoology B: Molecular and Developmental Evolution*, 314B: 1–8.
- Dupont, S., Ortega-Martínez, O., and Thorndyke, M. 2010a. Impact of near-future ocean acidification on echinoderms. *Ecotoxicology*, 19: 449–462.
- Ellis, R. P., Bersey, J., Rundle, S. D., Hall-Spencer, J. M., and Spicer, J. I. 2009. Subtle but significant effects of CO₂ acidified seawater on embryos of the intertidal snail, *Littorina obtusata*. *Aquatic Biology*, 5: 41–48.
- Evans, T. G., Chan, F., Menge, B. A., and Hofmann, G. E. 2013. Transcriptomic responses to ocean acidification in larval sea urchins from a naturally low pH environment. *Molecular Ecology*, 22: 1609–1625.
- Evans, T. G., and Watson-Wynn, P. 2014. Effects of seawater acidification on gene expression: resolving broader-scale trends in sea urchins. *Biological Bulletin*, 226: 237–254.
- Fitzer, S. C., Caldwell, G. S., Close, A. J., Clare, A. S., Upstill-Goddard, R. C., and Bently, M. G. 2012. Ocean acidification induces multi-generational decline in copepod naupliar production with possible conflict for reproductive resource allocation. *Journal of Experimental Marine Biology and Ecology*, 418–419: 30–36.
- Fitzer, S. C., Cusack, M., Phoenix, V. R., and Kamenos, N. A. 2014. Ocean acidification reduces the crystallographic control in juvenile mussel shells. *Journal of Structural Biology*, 188: 39–45.
- Flores, K. B., Wolschin, F., and Amdam, G. V. 2013. The role of methylation of DNA in environmental adaptation. *Integrative and Comparative Biology*, 53: 359–372.
- García Molinos, J., Halpern, B. S., Schoeman, D. S., Brown, C. J., Kiessling, W., Moore, P. J., Pandolfi, J. M., *et al.* 2015. Climate velocity and the future global redistribution of marine biodiversity. *Nature Climate Change*. doi 10.1038/nclimate2769.
- Gazeau, F., Gattuso, J. P., Dawber, C., Pronker, A. E., Peene, F., Peene, J., Heip, C. H. R., *et al.* 2010. Effect of ocean acidification on the early life stages of the blue mussel (*Mytilus edulis*). *Biogeosciences Discussions*, 7: 2927.
- Gazeau, F., Parker, L. M., Comeau, S., Gattuso, J.-P., O'Connor, W. A., Martin, S., Pörtner, H.-O., *et al.* 2013. Impacts of ocean acidification on marine shelled molluscs. *Marine Biology*, 160: 2207–2245.
- Gobler, C. J., and Talmage, S. C. 2013. Short- and long-term consequences of larval stage exposure to constantly and ephemerally elevated carbon dioxide for marine bivalve populations. *Biogeosciences*, 10: 2241–2253.
- Gonzalez-Bernat, M. J., Lamare, M., and Barker, M. 2013a. Effects of reduced seawater pH on fertilisation, embryogenesis and larval development in the Antarctic seastar *Odontaster validus*. *Polar Biology*, 36: 235–247.
- Gonzalez-Bernat, M. J., Lamare, M., and Barker, M. 2013b. Fertilisation, embryogenesis and larval development in the tropical intertidal sand dollar *Arachnoides placenta* in response to reduced seawater pH. *Marine Biology*, 160: 1927–1941.
- Gosselin, L. A., and Qian, P. Y. 1997. Juvenile mortality in benthic marine invertebrates. *Marine Ecology Progress Series*, 146: 265–282.
- Gutowska, M. A., and Melzner, F. 2009. Abiotic conditions in cephalopod (*Sepia officinalis*) eggs: embryonic development at low pH and high pCO₂. *Marine Biology*, 156: 515–519.
- Gutowska, M. A., Pörtner, H. O., and Melzner, F. 2008. Growth and calcification in the cephalopod *Sepia officinalis* under elevated seawater pCO₂. *Marine Ecology Progress Series*, 373: 303–309.
- Hamdoun, A., and Epel, D. 2007. Embryo stability and vulnerability in an always changing world. *Proceedings of the National Academy of Sciences of the United States of America*, 104: 1745–1750.
- Hettinger, A., Sanford, E., Hill, T. M., Hosfelt, J. D., Russell, A. D., and Gaylord, B. 2013. The influence of food supply on the response of Olympia oyster larvae to ocean acidification. *Biogeosciences*, 10: 5781–5802.
- Hettinger, A., Sanford, E., Hill, T. M., Russell, A. D., Sato, K. N. S., Hoey, J., Forsch, M., *et al.* 2012. Persistent carry-over effects of planktonic exposure to ocean acidification in the Olympia oyster. *Ecology*, 93: 2758–2768.
- Hobday, A. J., and Tegner, M. J. 2002. The warm and the cold: influence of temperature and fishing on local populations dynamics of the red abalone. *California Cooperative Oceanic Fisheries Investigations Reports*, 43: 74–96.
- Hofmann, G. E., Barry, J. P., Edmund, P. J., Gates, R. D., Hutchins, D. A., Klinger, T., and Sewell, M. A. 2010. The effects of ocean acidification on calcifying organisms in marine ecosystems: an organism to ecosystem perspective. *Annual Review of Ecology, Evolution, and Systematics*, 41: 127–147.
- Hofmann, G. E., Smith, J. E., Johnson, K. S., Send, U., Levin, L. A., Micheli, F., Paytan, A., *et al.* 2011. High-frequency dynamics of ocean pH: a multi-ecosystem comparison. *PLoS ONE*. doi:10.1371/journal.pone.0028983.
- Hornig, J. L., Lin, L. Y., and Hwang, P. P. 2009. Functional regulation of H⁺-ATPase-rich cells in zebrafish embryos acclimated to an acidic environment. *American Journal of Physiology—Cell Physiology*, 296: C682–C692.
- IPCC. 2013. *Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge, UK and New York, NY, USA.
- IPCC. 2014. *Summary for Policymakers. In Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, pp. 1–32. Ed. by C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, *et al.* Cambridge University Press, Cambridge, UK and New York, NY, USA.
- Kelly, M. W., Padilla-Gamiño, J. L., and Hofmann, G. E. 2013. Natural variation and the capacity to adapt to ocean acidification in the key-stone sea urchin *Strongylocentrotus purpuratus*. *Global Change Biology*, 19: 2536–2546.
- Kovalchuk, I. 2012. Transgenerational epigenetic inheritance in animals. *Frontiers of Genetics*, 3: 76.
- Kurihara, H. 2008. Effects of CO₂-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology Progress Series*, 373: 275–284.
- Kurihara, H., Asai, T., Kato, S., and Ishimatsu, A. 2009. Effects of elevated pCO₂ on early development in the mussel *Mytilus galloprovincialis*. *Aquatic Biology*, 4: 225–233.
- Kurihara, H., and Ishimatsu, A. 2008. Effects of high CO₂ seawater on the copepod (*Acartia tsuensis*) through all life stages and subsequent generations. *Marine Pollution Bulletin*, 56: 1086–1090.
- Kurihara, H., Kato, S., and Ishimatsu, A. 2007. Effects of increased seawater pCO₂ on early development of the oyster *Crassostrea gigas*. *Aquatic Biology*, 1: 91–98.
- Kurihara, H., Shimode, S., and Shirayama, Y. 2004a. Effects of raised CO₂ concentration on the egg production rate and early development of two marine copepods (*Acartia steueri* and *Acartia erythraea*). *Marine Pollution Bulletin*, 49: 721–727.
- Kurihara, H., Shimode, S., and Shirayama, Y. 2004b. Sub-lethal effects of elevated concentration of CO₂ on planktonic copepods and sea urchins. *Journal of Oceanography*, 60: 743–750.
- Kurihara, H., and Shirayama, Y. 2004. Effects of increased atmospheric CO₂ on sea urchin early development. *Marine Ecology Progress Series*, 274: 161–169.
- Lannig, G., Eilers, S., Pörtner, H.-O., Sokolova, I. M., and Bock, C. 2010. Impact of ocean acidification on energy metabolism of oyster, *Crassostrea gigas*—changes in metabolic pathways and thermal response. *Marine Drugs*, 8: 2318–2339.
- Lischka, S., Büdenbender, J., Boxhammer, T., and Riebesell, U. 2010. Impact of ocean acidification and elevated temperatures on early juveniles of the polar shelled pteropod *Limacina helicina*: mortality,

- shell degradation, and shell growth. *Biogeosciences Discussions*, 7: 8177–8214.
- Lister, K. N., Lamare, M. D., and Burritt, D. J. 2015. Pollutant resilience in embryos of the Antarctic sea urchin *Sterechinus neumayeri* reflects maternal antioxidant status. *Aquatic Toxicology*, 161: 61–72.
- Lohbeck, K. T., Riebesell, U., and Reusch, T. B. H. 2012. Adaptive evolution of a key phytoplankton species to ocean acidification. *Nature Geoscience*, 5: 917–917.
- Marshall, D. J. 2008. Transgenerational plasticity in the sea: context-dependent maternal effects across the life history. *Ecology*, 89: 418–427.
- Marshall, D. J., Allen, R. M., and Crean, A. J. 2008. The ecological and evolutionary importance of maternal effects in the sea. *In* *Oceanography and Marine Biology: an Annual Review*, 46, pp. 203–250. Ed. by R. N. Gibson, R. J. A. Atkinson, and J. D. M. Gordon. CRC, Boca Raton, FL.
- Matson, P. G., Pauline, C. Y., Sewell, M. A., and Hofmann, G. E. 2012. Development under elevated $p\text{CO}_2$ conditions does not affect lipid utilization and protein content in early life-history stages of the purple sea Urchin, *Strongylocentrotus purpuratus*. *The Biological Bulletin*, 223: 312–317.
- Mayor, D. J., Matthews, C., Cook, K., Zuur, A. F., and Hay, S. 2007. CO_2 induced acidification affects hatching success in *Calanus finmarchicus*. *Marine Ecology Progress Series*, 350: 91–97.
- Meistertzheim, A. L., Lejart, M., LeGoïc, N., and Thébault, M. T. 2009. Sex, gametogenesis, and tidal height-related differences in levels of HSP70 and metallothioneins in the Pacific oyster *Crassostrea gigas*. *Comparative Biochemistry and Physiology A: Molecular Integrative Physiology*, 152: 234–239.
- Miller, G. M., Watson, S.-A., Donelson, J. M., McCormick, M., and Munday, P. L. 2012. Parental environment mediates impacts of increased carbon dioxide on a coral reef fish. *Nature Climate Change*, 2: 858–861.
- Moran, A. I., and McAlister, J. S. 2009. Egg size as a life history character of marine invertebrates: is it all it's cracked up to be? *Biological Bulletin*, 216: 226–242.
- Munday, P. L. 2014. Transgenerational acclimation of fishes to climate change and ocean acidification. *F1000 Prime Reports*, 6: 99.
- Murray, C. S., Malvezzi, A., Gobler, C. J., and Baumann, H. 2013. Offspring sensitivity to ocean acidification changes seasonally in coastal marine fish. *Marine Ecology Progress Series*, 504: 1–11.
- O'Donnell, M. J., Hammond, L. M., and Hofmann, G. E. 2009a. Predicted impact of ocean acidification on a marine invertebrate: elevated CO_2 alters response to thermal stress in sea urchin larvae. *Marine Biology*, 156: 439–446.
- O'Donnell, M. J., Todgham, A. E., Sewell, M. A., Hammond, L. M., Ruggiero, K., Fanguet, N. A., Zippay, M. L., et al. 2009b. Ocean acidification alters skeletogenesis and gene expression in larval sea urchins. *Marine Ecology Progress Series*, 398: 157–171.
- Padilla-Gamino, J. L., Kelly, M. W., Evans, T. G., and Hofmann, G. E. 2013. Temperature and CO_2 additively regulate physiology, morphology and genomic responses of larval sea urchins, *Strongylocentrotus purpuratus*. *Proceedings of the Biological Society Transactions Society B*, 280: 20130155.
- Pan, T. C. F., Applebaum, S. L., and Manahan, D. T. 2015. Experimental ocean acidification alters the allocation of metabolic energy. *Proceedings of the National Academy of Sciences of the United States of America*, 112: 4696–4701.
- Parker, L. M., O'Connor, W. A., Raftos, D. A., Pörtner, H.-O., and Ross, P. M. 2015. Persistence of positive carryover effects in oysters following transgenerational exposure to ocean. *PLoS ONE*, doi:10.1371/journal.pone.013227.
- Parker, L. M., Ross, P. M., and O'Connor, W. A. 2009. The effect of ocean acidification and temperature on the fertilization and embryonic development of the Sydney rock oyster *Saccostrea glomerata* (Gould 1850). *Global Change Biology*, 15: 2123–2136.
- Parker, L. M., Ross, P. M., and O'Connor, W. A. 2010. Comparing the effect of elevated $p\text{CO}_2$ and temperature on the fertilization and early development of two species of oysters. *Marine Biology*, 157: 2435–2452.
- Parker, L. M., Ross, P. M., and O'Connor, W. A. 2011. Populations of the Sydney rock oyster, *Saccostrea glomerata*, vary in response to ocean acidification. *Marine Biology*, 158: 689–697.
- Parker, L. M., Ross, P. M., O'Connor, W. A., Borysko, L., Raftos, D. A., and Pörtner, H.-O. 2012. Adult exposure influences offspring response to ocean acidification in oysters. *Global Change Biology*, 18: 82–92.
- Parker, L. M., Ross, P. M., O'Connor, W. A., Pörtner, H.-O., Scanes, E., and Wright, J. M. 2013. Predicting the response of molluscs to the impact of ocean acidification. *Biology*, 2: 651–692.
- Pechevnik, J. A. 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology Progress Series*, 177: 269–297.
- Pechevnik, J. A., Wendt, D., and Jarrett, J. 1998. Metamorphosis is not a new beginning: larval experience reduces rates of postlarval growth, development, and survival in marine invertebrates. *BioScience*, 48: 901–910.
- Pedersen, S. A., Ha?kedal, O. J., Salaberria, I., Tagliati, A., Gustavson, L. V., Jenssen, B. M., Olsen, A. J., et al. 2014. Multigenerational exposure to ocean acidification during food limitation reveals consequences for copepod scope for growth and vital rates. *Environmental Science and Technology*, 48: 12275–12284.
- Podolsky, R. D., and Moran, A. L. 2006. Integrating function across marine life cycles. *Integrative and Comparative Biology*, 46: 577–586.
- Pörtner, H. O., and Farrell, A. P. 2008. Physiology and climate change. *Science*, 322: 690–692.
- Przeslawski, R., Byrne, M., and Mellin, C. 2015. A review and meta-analysis of the effects of multiple abiotic stressors on marine embryos and larvae. *Global Change Biology*, 21: 2122–2140.
- Range, P., Chicharo, M. A., Ben-Hamadou, R., Piló, D., Matias, D., Joaquim, S., Oliveira, A. P., et al. 2011. Calcification, growth and mortality of juvenile clams *Ruditapes decussatus* under increased $p\text{CO}_2$ and reduced pH: variable responses to ocean acidification at local scales? *Journal of Experimental Marine Biology and Ecology*, 396: 177–184.
- Relyea, R. A. 2001. The lasting effects of adaptive plasticity: predator-induced tadpoles become long-legged frogs. *Ecology*, 82: 1947–1955.
- Relyea, R. A. 2003. Predators come and predators go: the reversibility of predator-induced traits. *Ecology*, 84: 1840–1848.
- Riviere, G. 2014. Epigenetic features in the oyster *Crassostrea gigas* suggestive of functionally relevant promoter DNA methylation in invertebrates. *Frontiers in Physiology*, 5: 1–7.
- Ross, P. M. 2001. Larval supply, settlement and survival of barnacles in a temperate mangrove forest. *Marine Ecology Progress Series*, 215: 237–249.
- Ross, P. M., Parker, L., O'Connor, W. A., and Bailey, E. A. 2011. The impact of ocean acidification on reproduction, early development and settlement of marine organisms. *Water*, 3: 1005–1030.
- Salinas, S., Brown, S. C., Mangel, M., and Munch, S. B. 2013. Non-genetic inheritance and changing environments. *Non-Genetic Inheritance*, 1: 38–50.
- Salinas, S., and Mulch, S. B. 2012. Thermal legacies: transgenerational effects of temperature on growth in a vertebrate. *Ecology Letters*, 15: 159–163.
- Sanford, E., and Kelly, M. W. 2011. Local adaptation in marine invertebrates. *Annual Review of Marine Science*, 3: 509–535.
- Schade, F. M., Clemmesen, C., and Wegner, K. M. 2014. Within- and transgenerational effects of ocean acidification on life history of marine three-spined stickleback (*Gasterosteus aculeatus*). *Marine Biology*, 161: 1667–1676.

- Shama, L. N. S., Strobel, A., Mark, F. C., and Wegner, K. M. 2014. Transgenerational plasticity in marine sticklebacks: maternal effects mediate impacts of a warming ocean. *Functional Ecology*, 15: 159–163.
- Shama, L. N. S., and Wegner, K. M. 2014. Grandparental effects in marine sticklebacks: transgenerational plasticity across multiple generations. *Journal of Evolutionary Biology*, 27: 2297–2307.
- Sheppard Brennand, H., Soars, N., Dworjanyn, S. A., Davis, A. R., and Byrne, M. 2010. Impact of ocean warming and ocean acidification on larval development and calcification in the sea urchin *Tripneustes gratilla*. *PLoS ONE*, 5: e11372.
- Sigwart, J. D., Lyons, G., Fink, A., Gutowska, A., Murray, D., Melzner, F., Houghton, J. D. R., et al. 2015. Elevated pCO₂ drives lower growth and yet increased calcification in the early life history of the cuttlefish *Sepia officinalis* (Mollusca: Cephalopoda). *ICES Journal of Marine Science*, doi:10.1093/icesjms/fsv188.
- Strauss, S. Y., Conner, J. K., and Rush, S. L. 1996. Foliar herbivory affects floral characters and pollinator attractiveness to pollinators: implications for male and female plant fitness. *American Naturalist*, 147: 1098–1107.
- Stumpp, M., Dupont, S., Thorndyke, M. C., and Melzner, F. 2011b. CO₂ induced seawater acidification impacts sea urchin larval development II: gene expression patterns in pluteus larvae. *Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology*, 160: 320–330.
- Stumpp, M., Hu, M. Y., Melzner, F., Gutowska, M. A., and Dorey, N. 2012. Acidified seawater impacts sea urchin larvae pH regulatory systems relevant for calcification. *Proceedings of the National Academy of Sciences of the United States of America*, 109: 18192–18197.
- Stumpp, M., Wren, J., Melzner, F., Thorndyke, M. C., and Dupont, S. T. 2011a. CO₂ induced seawater acidification impacts sea urchin larval development I: elevated metabolic rates decrease scope for growth and induce developmental delay. *Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology*, 160: 331–340.
- Suckling, C. C., Clark, M. S., Beveridge, C., Brunner, L., Hughes, A. D., Harper, E. M., Cook, E. J., et al. 2014. Experimental influence of pH on the early life-stages of sea urchins II: increasing parental exposure times gives rise to different responses. *Invertebrate Reproduction and Development*, 58: 161–175.
- Suckling, C. C., Clark, M. S., Richard, J., Morley, S. A., Thorne, M. A. S., Harper, E. M., and Peck, L. S. 2015. Adult acclimation to combined temperature and pH stressors significantly enhances reproductive outcomes compared to short-term exposures. *Journal of Animal Ecology*, 84: 773–784.
- Sunday, J. M., Calosi, P., Dupont, S., Munday, P. L., Stillman, J. H., and Reusch, T. B. H. 2014. Evolution in an acidifying ocean. *Trends in Ecology and Evolution*, 29: 117–125.
- Talmage, S. C., and Gobler, C. J. 2009. The effects of elevated carbon dioxide concentrations on the metamorphosis, size, and survival of larval hard clams (*Mercenaria mercenaria*), bay scallops (*Argopecten irradians*), and eastern oysters (*Crassostrea virginica*). *Limnology and Oceanography*, 54: 2072–2080.
- Talmage, S. C., and Gobler, C. J. 2010. Effects of past, present, and future ocean carbon dioxide concentrations on the growth and survival of larval shellfish. *Proceedings of the National Academy of Sciences of the United States of America*, 107: 17246–17251.
- Talmage, S. C., and Gobler, C. J. 2011. Effects of elevated temperature and carbon dioxide on the growth and survival of larvae and juveniles of three species of Northwest Atlantic bivalves. *PLoS ONE*, 6: e26941, doi:10.1371/journal.pone.0026941.
- Talmage, S. C., and Gobler, C. J. 2012. Effects of carbon dioxide and a harmful alga (*Aureococcus anophagefferens*) on the growth and survival of larval oysters (*Crassostrea virginica*) and scallops (*Argopecten irradians*). *Marine Ecology Progress Series*, 464: 121–134.
- Thomsen, J., Casties, I., Pansch, A., Kortzinger, A., and Melzner, F. 2013. Food availability outweighs ocean acidification effects in juvenile *Mytilus edulis*: laboratory and field experiments. *Global Change Biology*, 19: 1017–1027.
- Thorson, G. 1950. Reproduction and larval ecology of marine bottom invertebrates. *Biology Reviews*, 25: 1–45.
- Todgham, A. E., and Hofmann, G. E. 2009. Transcriptomic response of sea urchin larvae *Strongylocentrotus purpuratus* to CO₂-driven seawater acidification. *Journal of Experimental Biology*, 212: 2579–2594.
- Thompson, E., O'Connor, W. A., Parker, L. M., Ross, P., and Raftos, D. A. 2015. Differential proteomic responses of two Sydney rock oyster populations exposed to elevated CO₂. *Molecular Ecology Resources*, 24, doi:10.1111/mec.13111.
- Thor, P., and Dupont, S. 2015. Transgenerational effects alleviate severe fecundity loss during ocean acidification in a ubiquitous planktonic copepod. *Global Change Biology*, 21: 2261–2271.
- Tseng, Y. C., Hu, M. Y., Stumpp, M., Lin, L. Y., Melzner, F., and Hwang, P. P. 2013. CO₂-driven seawater acidification differentially affects development and molecular plasticity along life history of fish (*Oryzias latipes*). *Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology*, 165: 119–130.
- Untersee, S., and Pechenik, J. A. 2007. Local adaptation and maternal effects in two species of marine gastropod (genus *Crepidula*) that differ in dispersal potential. *Marine Ecology Progress Series*, 347: 79–85.
- Uthicke, S., Schaffelke, B., and Byrne, M. 2009. A boom-bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecological Monographs*, 79: 3–24.
- Uthicke, S., Soars, N., Foo, S., and Byrne, M. 2013. Effects of elevated pCO₂ and the effect of parent acclimation on development in the tropical Pacific sea urchin *Echinometra mathaei*. *Marine Biology*, 160: 1913–1926.
- Vandegheuchte, M. B., and Janssen, C. R. 2014. Epigenetics in an ecotoxicological context. *Mutation Research—Genetic Toxicology and Environmental Mutagenesis*, 764–765: 36–45.
- Wangensteen, O. S., Dupont, S., Castles, I., Turon, X., and Palacín, C. 2013. Some like it hot: temperature and pH modulate larval development and settlement of the sea urchin *Arbacia lixula*. *Journal of Marine Biology and Ecology*, 449: 304–311.
- Watson, S. A., Southgate, P. C., Tyler, P. A., and Peck, L. S. 2009. Early larval development of the Sydney rock oyster *Saccostrea glomerata* under near-future predictions of CO₂-driven ocean acidification. *Journal of Shellfish Research*, 28: 431–437.
- Welch, M. J., Watson, S-A., Welch, J. Q., McCormick, M. I., and Munday, P. L. 2014. Effects of elevated CO₂ on fish behaviour is undiminished by transgenerational acclimation. *Nature Climate Change*, 4: 1086–1089.
- White, M. M., McCorkle, D. C., Mullineaux, L. S., and Cohen, A. L. 2013. Early exposure of bay scallops (*Argopecten irradians*) to high CO₂ causes a decrease in larval shell growth. *PLoS ONE*, 8: e61065.
- Zippay, M. K. L., and Hofmann, G. E. 2010. Effect of pH on gene expression and thermal tolerance of early life history stages of red abalone (*Haliotis rufescens*). *Journal of Shellfish Research*, 29: 429–439.