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IMPACT OF OCEAN WARMING AND OCEAN ACIDIFICATION ON MARINE INVERTEBRATE LIFE HISTORY STAGES: VULNERABILITIES AND POTENTIAL FOR PERSISTENCE IN A CHANGING OCEAN

MARIA BYRNE
Schools of Medical and Biological Sciences, University of Sydney, Australia
E-mail: mbyrne@anatomy.usyd.edu.au

Abstract Global warming and increased atmospheric CO_2 are causing the oceans to warm, decrease in pH and become hypercapnic. These stressors have deleterious impacts on marine invertebrates. Increasing temperature has a pervasive stimulatory effect on metabolism until lethal levels are reached, whereas hypercapnia has a narcotic effect. Ocean acidification is a major threat to calcifying larvae because it decreases availability of the carbonate ions required for skeletogenesis and also exerts a direct pH effect on physiology. Marine invertebrate propagules live in a multistressor world and climate change stressors are adding to the mix. Ocean pH, pCO_2 and $CaCO_3$ covary and will change simultaneously with temperature, challenging our ability to predict future outcomes for marine biota. To address questions of future vulnerabilities, data on the thermo- and pH/pCO_2 tolerance of fertilization and development in marine invertebrates are reviewed in the context of the change in the oceans that are forecast to occur over the next 100–200 years. Gametes and fertilization in many invertebrates exhibit a broad tolerance to warming and acidification beyond stressor values projected for 2100. Available data show that all development stages are highly sensitive to warming. Larvae may be particularly sensitive to acidification/hypercapnia. Embryos that develop through the bottleneck of mortality due to warming may succumb as larvae to acidification. Early juveniles may be vulnerable to skeletal dissolution, although warming may diminish the negative impact of acidification on calcification. The effects of climate change stressors and their interaction differ among life history stages and species. Multistressor experiments show that if thermal thresholds are breached, embryos may not reach the calcifying stage. If the bottleneck for species persistence is embryonic thermotolerance, then the question of compromised calicification due to acidification may not be relevant. Our limited knowledge of the interactive effects of climate change stressors is a major knowledge gap. Although climate change is deleterious for development in a broad range of marine invertebrates, some species and regional faunas will be more resilient than others. This has implications for persistence, faunal shifts, species invasions and community function in a changing ocean.

Introduction

As the planet warms due increased atmospheric CO_2, so does the ocean. Direct uptake of CO_2 is also causing ocean acidification, physiological hypercapnia and reduced carbonate saturation (Caldiera & Wickett 2003, Feely et al. 2004, 2009, Orr et al. 2005, Intergovernmental Panel on Climate Change [IPCC] 2007). Temperature, pH, pCO_2 and calcium carbonate ($CaCO_3$) saturation are among the most important environmental factors controlling the distribution, physiological performance, morphology and behaviour of marine invertebrates (Kinne 1970, Pörtner et al. 2005, Pörtner & Knust 2007, Pörtner 2008, Widdicombe & Spicer 2008, Doney et al. 2009). Climate change is thus causing alterations to marine ecosystems with impacts that are evident from polar to tropical regions (Harley et al. 2006, Hoegh-Guldberg et al. 2007, IPCC 2007, Poloczanska et al. 2007, Przeslawski et al. 2008, Brierley & Kingsford 2009, Mueter & Litzow 2009). Ocean warming is implicated in mass mortality, increased disease, hypoxia, coral bleaching, species invasions, phenological shifts in planktonic food web dynamics, physiological limitation in oxygen delivery and increased costs of metabolism (Southward et al. 1995, Stachowicz et al. 2002, Edwards & Richardson 2004, Hoegh-Guldberg et al. 2007, Lester et al. 2007, O'Connor et al. 2007, 2009, Pörtner & Knust 2007, Richardson 2008, Smale & Barnes 2008, Coma et al. 2009, Ling et al. 2009, Montes-Hugo et al. 2009, Travers et al. 2009, Compton et al. 2010, Hofmann & Todgham 2010, Pörtner 2010). Ocean acidification is a major threat to calcifying marine invertebrates because it decreases the availability of the carbonate ions required for skeletogenesis, and it exerts a direct pH effect. Hypercapnia has a pervasive narcotic effect suppressing metabolism (Pörtner et al. 2004, Pörtner & Langenbuch 2005, Fabry et al. 2008, Pörtner 2008, Widdicome & Spicer 2008, Doney et al. 2009, Melzner et al. 2009, Christensen et al. 2011).

Ocean pH, $p\mathrm{CO}_2$ and CaCO_3 saturation covary and are changing simultaneously with ocean temperature, challenging our ability to predict future outcomes for marine invertebrates in a changing ocean. Marine propagules live in a multistressor world, and the interactive effects of climate change and other stressors are poorly understood (Harley et al. 2006, Pörtner 2008, Przeslawski et al. 2008). Early life history stages are of particular concern because sensitivity to these stressors may be the bottleneck for species persistence and ecological success in a changing ocean. For benthic organisms, compromised performance of developmental stages has negative consequent effects for adult populations and marine communities (Harley et al. 2006, Przeslawski et al. 2008, Brierley & Kingsford 2009, Uthicke et al. 2009).

Many marine invertebrates broadcast-spawn their gametes for external fertilization and have pelagic larvae that spend days to months in the water column (Figures 1, 2 and 3). Due to their sensitivity to water chemistry marine gametes and embryos have long been used as a bioassay system for monitoring of environmental pollutants (Dinnel et al. 1987, Ringwood 1992, Carr et al. 2006, Byrne et al. 2008). As the impacts of anthropogenic pressures on the marine environment became evident in the twentieth century, a plethora of ecotoxicological studies documented the response of developmental stages to pollutants including ocean warming (e.g., power plant effluent) and acidification (e.g., acid leachates, porewater) (e.g., Greenwood & Bennett 1981, Bay et al. 1993, Riveros et al. 1996, Schiel et al. 2004, Carr et al. 2006, Byrne et al. 2008). Recognition of the impact of climate change on the marine environment has generated a new focus on these stressors in order to understand how marine species will respond to ocean change. In contrast to point source pollution, the oceans are experiencing long-term pervasive perturbation due to increased warming and CO_2 uptake that has taken place since the Industrial Revolution (Caldiera & Wickett 2003, Zeebe et al. 2008).

The 'business-as-usual' scenario for global change (A1F1, IPCC 2007) provides a framework with which to assess comparative vulnerabilities of species and their life history stages. Although there is uncertainty with regard to levels of change, an increase in ocean $p\mathrm{CO}_2$ from present levels of about 380 ppm to 700–1000 ppm by 2100 and 2000 ppm by 2300 can be expected (Caldiera & Wickett 2005, IPCC 2007, Doney et al. 2009). This increase is projected to result in a drop in surface ocean pH by 0.14–0.41 units and 0.30–0.7 units, respectively, over the same timescale. Increasing temperature is the most pervasive of present-day impact of climate change on marine systems (Poloczanska et al. 2007, Halpern et al. 2008, Brierley & Kingsford 2009). The estimate for increase in mean sea-surface temperatures (SSTs) by 2100 is predicted to lie between 1.1 and 6.4°C with the best estimates ranging between 2 and 4.5°C (IPCC 2007). These are consensus projections, and the magnitude of change is differing markedly between regions (IPCC 2007, Brierley & Kingsford 2009). Regional differences in the extent of ocean warming highlight the need for a regional approach in assessment of ecosystem change and risk to species. The potential impacts

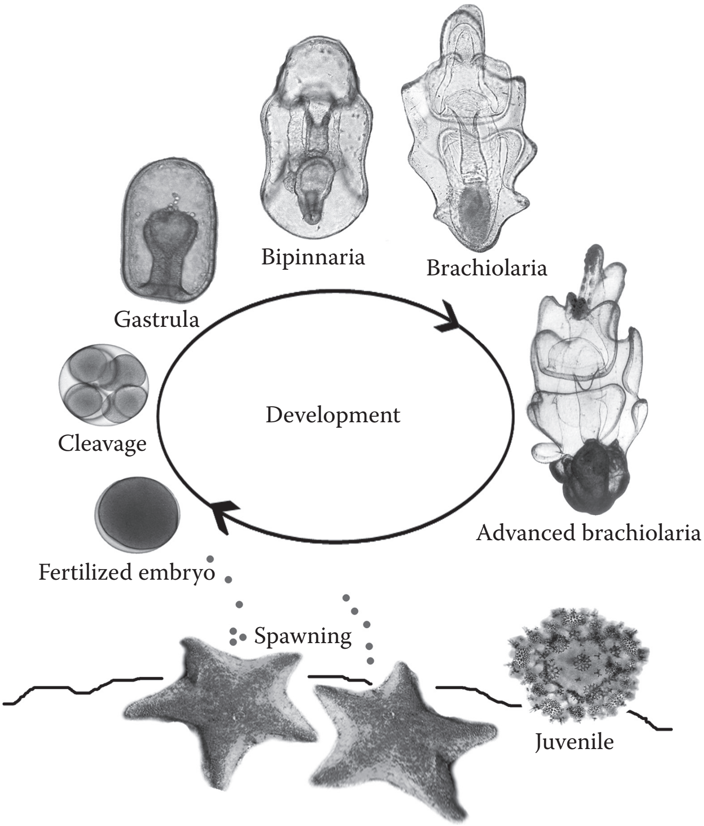

Figure 1 Life cycle of the seastar *Patiriella regularis*. For ecological success all life stages have to be completed. Different life stages will have differing sensitivities to climate change stressors. (Photographs from Byrne & Barker 1991 with permission.)

of ocean change on marine invertebrate reproduction and development need to be considered in a regional, seasonal, depth- and habitat-relevant context. For instance, cold high-latitude waters are the first to become carbonate undersaturated, so ocean acidification is a serious contemporary stressor for polar species, as seen in decalcified Arctic pteropods and poorly calcified Antarctic Foraminifera (Orr et al. 2005, Comeau et al. 2009, Fabry et al. 2009, McClintock et al. 2009, Moy et al. 2009). Ocean warming is the most serious immediate climate change stressor for some regions, including the Mediterranean, southern North Sea, Western Antarctic Peninsula and south-eastern Australia (Ridgway 2007, Barnes & Peck 2008, Coma et al. 2009, Richardson et al. 2009, Schmalenbach & Franke 2010, Schofield et al. 2010). Seasonal change is also a consideration as evidenced by disproportionate wintertime ocean warming in south-eastern Australia and the North Sea, with expected greater impacts for winter spawners and planktonic phases (Poloczanska et al. 2007, Schmalenbach & Franke 2010), and the greater wintertime decrease in $CaCO_3$ saturation in the Southern Ocean, with aragonite undersaturation projected to occur in winter by 2030 (McNeil & Matear 2008) and year round by 2050 (Orr et al. 2005).

To date most studies on the impacts of climate change on invertebrate development have focused on ocean acidification as a sole stressor (reviews: Doney et al. 2009, Byrne 2010, Dupont et al. 2010a, Hendriks et al. 2010a, Kroeker et al. 2010), with some studies on the effects of ocean warming (e.g., Negri et al. 2007, Whalan et al. 2008, Byrne et al. 2011a). A few studies have investigated the interactive effects of warming and CO_2-driven acidification on marine life histories (Findlay et al. 2008, 2010a,b, Byrne et al. 2009, 2011b, Parker et al. 2010, Sheppard Brennand et al. 2010). Development can fail at any stage, and determination of the comparative sensitivities of planktonic (e.g., gametes, fertilization, embryos, larvae) and benthic (juveniles, adults) life stages to climate change stressors is needed to identify vulnerabilities. Successful recruitment and persistence of populations require that all ontogenetic stages be completed successfully (Figure 1).

In this review, data on the thermo- and pH/$p\text{CO}_2$ tolerance of marine invertebrate gametes and developmental stages are assessed within the context of ocean change in the near future. The data are largely from single-stressor physiology, ecotoxicology and global change studies. For ocean acidification, only CO_2-driven acidification is considered. The impacts of acidification generated by use of mineral acid are reported elsewhere (Albright et al. 2008, Fabry et al. 2008, Kurihara 2008, Byrne 2010, Dupont et al. 2010a). Impacts of ocean warming and acidification on environmental control of reproduction (fecundity, maturation, spawning) and on adult physiology are documented in several reviews (Somero 2002, Przeslawski et al. 2005, 2008, Melzner et al. 2009). Identification of the marine invertebrate life history stages that are most vulnerable to climate change is needed to determine bottlenecks for species persistence in a changing ocean. Here, data on the impacts of ocean warming and acidification are used to address questions of stage-specific vulnerabilities in development and the potential resilience of marine invertebrates in a changing ocean. The focus is on the impact of warming and acidification on development from fertilization to the benthic juvenile with inclusion of key insights from studies of the adult stage.

Impacts of ocean warming and acidification on fertilization in marine invertebrates

Although the fertilization biology of marine invertebrates is highly sensitive to water chemistry and deleterious effects have been documented for a plethora of anthropogenic stressors (e.g., trace metals, acid leachates, porewater, effluents) (e.g., Riveros et al. 1996, Carr et al. 2006, Byrne et al. 2008), the weight of evidence from diverse species indicates that fertilization in many species is robust to near-future ocean warming, acidification and hypercapnia (Table 1, Figure 2). The effects of increased acidification/hypercapnia and warming on fertilization are best documented for shallow water and intertidal species, many of which have been used as model organisms for laboratory studies (Table 1).

Thermotolerance of fertilization

Single-stressor studies show that broadcast spawners (ca. 5 corals, 2 polychaetes, 4 molluscs, 16 echinoderms) achieve high rates of fertilization over a wide temperature range (Table 1, Figure 2) and at warming levels well beyond those projected for extreme ocean change. It appears that near-future upper warming scenarios of about 4–6°C would not impair fertilization in the species listed in Table 1.

Increased temperature and the associated decrease in seawater viscosity increase fertilization success due to stimulation of sperm metabolism, facilitation of the acrosome reaction and increased sperm swimming speed (Mita et al. 1984, Lewis et al. 2002, Kupriyanova & Havenhand 2005). The thermal robustness of fertilization may be due to the presence of maternal factors (e.g., heat shock proteins) that protect early embryos (prior to onset of zygotic gene expression) against environmental stressors and the temperature-independent period in early development (Yamada & Mihashi 1998, Hamdoun & Epel 2007). This protection may be enhanced in species with large eggs and lecithotrophic development for which the evolutionary (heterochronic) switch to loading of maternal transcripts into eggs facilitates rapid development (Raff & Byrne 2006). For oysters, elevated temperature over an 8°C range (18–26°C) resulted in increased fertilization at higher temperature but a decrease if the temperature increase exceeded 12°C (30°C) (Parker et al. 2010). The robust nature

Table 1 Influence of increased temperature (°C) and acidification (pH/$p\mathrm{CO}_2$, ppm) as single stressors on fertilization in marine invertebrates and levels for significant deleterious effects in the context of near-future ocean change (100–200 years)

	Temperature		Acidification (pH/$p\mathrm{CO}_2$)		
Phylum, species	Range for fertilization of 75% or more	Temperature increase above local ambient for fertilization <70–75%	pH range for fertilization of 75% or more	pH at which fertilization is reduced to <70–75%	Reference
Cnidaria					
Acropora millepora	28–31	4	ND	ND	Negri et al. 2007
Diploria strigosa	30–32	>4	ND	ND	Bassim et al. 2002
Favites abdita	26–32	>5	ND	ND	Negri et al. 2007
Favites chinensis	26–32	>5	ND	ND	Negri et al. 2007
Mycedium elephantotus	26–32	>5	ND	ND	Negri et al. 2007
Nemertea					
Parborlasia corrugatus	0–1	ND	7.0–8.0 528–5806	ND	Ericson et al. 2010
Polychaeta					
Galeolaria caespitosa	21	5	ND	ND	Kupriyanova & Havenhand 2005
Nereis virens	10–18	15	ND	ND	Lewis et al. 2002
Mollusca					
Gastropoda					
Haliotis coccoradiata	20–24	ND	7.6–8.2 327–1795	ND	Byrne et al. 2010b
Bivalvia					
Crassostrea gigas	18–30	ND	7.4–8.2 ≤2000	ND	Kurihara et al. 2007, Kurihara 2008, Havenhand & Schlegal 2009
	18–30	ND	7.9–8.2 375–750	7.8 1000	Parker et al. 2010
Mytilus galloprovincialis	13	ND	7.4–8.0 ≤2000	ND	Kurihara 2008
Saccostrea glomerata	26	>4	8.0–8.2 375–600	7.9 750	Parker et al. 2010
Spisula solidissima	8–20	>10	ND	ND	Clotteau & Dubé 1993
Echinodermata					
Asteroidea					
Acanthaster planci	28–31	6	ND	ND	Rupp 1973
Asterias amurensis	10–20	12	ND	ND	Lee et al. 2004
Culcita novaeguineae	28–34	8	ND	ND	Rupp 1973
Linckia laevigata	28–34	8	ND	ND	Rupp 1973

(continued on next page)

Table 1 (continued) Influence of increased temperature (°C) and acidification (pH/pCO_2, ppm) as single stressors on fertilization in marine invertebrates and levels for significant deleterious effects in the context of near-future ocean change (100–200 years)

	Temperature		Acidification (pH/pCO_2)		
Phylum, species	Range for fertilization of 75% or more	Temperature increase above local ambient for fertilization <70–75%	pH range for fertilization of 75% or more	pH at which fertilization is reduced to <70–75%	Reference
Patiriella regularis	20–26	ND	7.6–8.2 330–1828	ND	Byrne et al. 2010b
Meridiastra calcar	18–23	ND	7.6–8.2 330–1828	ND	Nguyen, H. pers. comm.
Echinoidea					
Anthocidaris crassispina	15–30	ND	ND	ND	Mita et al. 1984
Arbacia punctulata	ND	ND	7.0–8.6	<7.0	Carr et al. 2006
Centrostephanus rodgersii	18–24	ND	7.6–8.2 324–1695	ND	Byrne et al. 2010b
Dendraster excentricus	7–26	13	ND	ND	Bingham et al. 1997
Diadema savignyi	28–36	>8	ND	ND	Rupp 1973
Echinometra lucunter	15–36	9	ND	ND	Sewell & Young 1999
Echinometra mathaei	28–36	8	7.7–8.1 360–1360	7.3 2360	Rupp 1973, Kurihara & Shirayama 2004
Heliocidaris erythrogramma	17–26	ND	7.6–8.2 327–1729	ND	Byrne et al. 2009, 2010a,b, 2011a,b
Heliocidaris tuberculata	17–24	ND	7.6–8.2 327–1729	ND	O'Connor & Mulley 1977, Byrne et al. 2010b
Hemicentrotus pulcherrimus	0–30	15	7.4–8.0 360–2000	6.8–7.0 2000–10,000	Mita et al. 1984, Fujisawa 1995, Kurihara & Shirayama 2004
Parechinus angulosus	15–19	8	ND	ND	Greenwood & Bennett 1981
Sterechinus neumayeri	0–1	ND	7.7–8.0 527–1121	7.0–7.3[a] 2886–5806	Ericson et al. 2010
Strongylocentrotus purpuratus	ND	ND	7.3–8.2	7.2	Bay et al. 1993
Tripneustes gratilla	20–27	ND	7.6–8.2 332–1765	ND	Rahman et al. 2009, Byrne et al. 2010b

Note: The temperature data are impacts of thermal increase at ambient pH. The pH data are the response to acidification at the control/optimal temperature used for fertilization. Experimental pH was adjusted by treatment of seawater with CO_2 gas. Where temperature range was not investigated, ambient/control values were determined from the study. ND, no data

[a] At low sperm concentration.

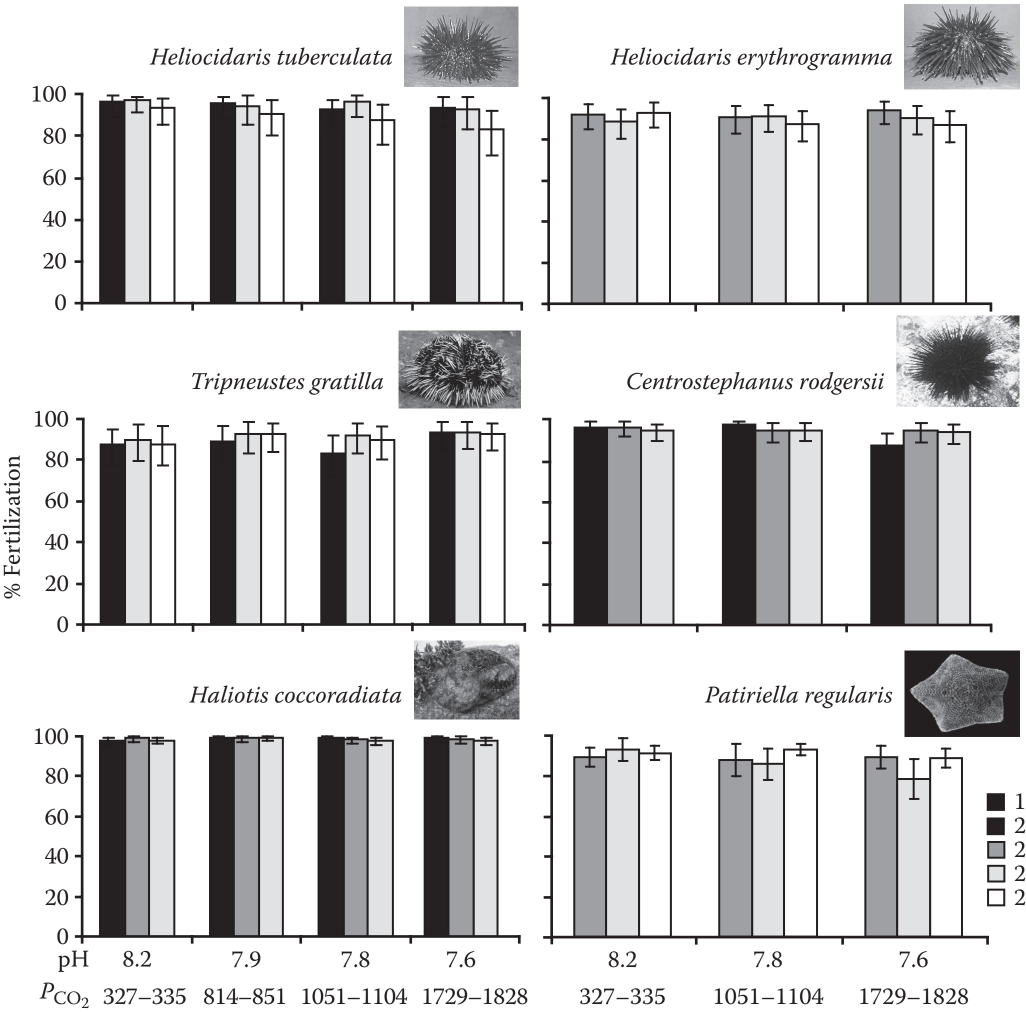

Figure 2 Percentage of fertilization in the echinoids *Heliocidaris tuberculata*, *H. erythrogramma*, *Tripneustes gratilla* and *Centrostephanus rodgersii*, the asteroid *Patiriella regularis* and the abalone *Haliotis coccoradiata* in response to ambient and projected ocean change scenarios for year 2100 (A1F1, IPCC 2007). Experiments in the left panel used four pH and three temperature levels, while those in the right panel used three pH and three temperature levels. Experimental temperatures varied due to seasonal differences in the timing of gamete maturation in the different species. $p\text{CO}_2$ levels are indicated for each pH used. Error bars are 95% confidence intervals. (From Byrne et al. 2010a, with permission.)

of marine invertebrate gametes and fertilization to warming is reflected in routine use of heat shock (ca. 10°C above ambient) to obtain fertile gametes for developmental studies and aquaculture (e.g., Selvakumaraswamy & Byrne 2000, Ramofafia et al. 2003, Parker et al. 2009).

pH/pCO$_2$ tolerance of fertilization

Hypercapnia narcotizes sperm and is used *in vivo* to maintain sperm in a quiescent state and preserve energy stores (Chia & Bickell 1983, Johnson et al. 1983, Ward et al. 1985, Brokaw 1990). The mechanisms underlying the effects of hypercapnia on sperm are well understood and involve control of intracellular pH (pHi) by CO_2. Hypercapnia reduces sperm swimming speed, so it is suggested that ocean acidification may impair fertilization (Havenhand et al. 2008, Morita et al. 2010). In nature, however, release of sperm into the water column overcomes hypercapnic effects due to the respiratory dilution effects (increased oxygen tension) of seawater (Chia & Bickell 1983). This is not the case for a sea cucumber and a coral (Morita et al. 2006, 2009). Egg-derived compounds promote sperm motility at low pH, a response reported for many species of corals, molluscs, echinoderms and ascidians and is triggered by a cGMP (cyclic guanosine monophosphate) cascade (Miller 1985, 1997, Ward et al. 1985, Bolton & Havenhand 1996, Riffell et al. 2002, Morita et al. 2006, 2009, Darszon et al. 2008). Asteroid egg jelly facilitates the acrosome reaction by increasing the pHi of sperm (Matsui et al. 1986). Where the compounds have been characterized, they are usually egg jelly peptides (Morita et al. 2006, 2009, Darszon et al. 2008). The robust nature of echinoderm eggs to acid conditions is reflected in the routine use of low pH (pH 5.0) to strip the jelly coat prior to fertilization in functional studies of fertilization and this extracellular layer (e.g., Johnson & Epel 1975).

Despite potential narcotic effects of hypercapnia on sperm swimming, many single-stressor studies (ca. 1 coral, 1 nemertean, 4 molluscs, 10 echinoderms) indicated that fertilization in diverse species is robust to pH 7.4–7.6 ($p\mathrm{CO}_2 \geq 1000$ ppm), pH levels driven by CO_2 uptake well below acidification projected for surface ocean waters by 2100 (Table 1, Figure 2). The resilience of fertilization of the species in Table 1, many of which are intertidal and shallow subtidal species, may reflect adaptation to the fluctuating pH and hypercapnic conditions in their habitat. In those studies in which far-future acidification scenarios were considered, deleterious effects on fertilization were reported at pH 7.4 and less (Table 1).

Although data are limited, there are inferences that sensitivity of fertilization to acidification may differ among species from differing habitats. In the intertidal sea urchin *Heliocidaris erythrogramma* fertilization is robust to low pH (pH 7.6) even at very low sperm concentrations (10 sperm to 1 egg, 10 sperm ml^{-1}) (Byrne et al. 2009, 2010a,b, but see Havenhand et al. 2008). By contrast, fertilization in its subtidal congener *H. tuberculata* appears to be more sensitive to near-future ocean acidification (Byrne et al. 2010a). A fertilization kinetics study of the subtidal species *Strongylocentrotus franciscanus* showed that acidification (pH 7.55, $p\mathrm{CO}_2$ 1800 ppm) shifted the fertilization curve to a lower success rate (Reuter et al. 2011). By contrast fertilization was only impaired at pH 7.4 at low sperm concentrations (50 sperm to 1 egg) in the subtidal Antarctic species *Sterechinus neumayeri* (Ericson et al. 2010). In studies of the coral *Acropora palmata* where controls were 50% of fertilization, fertilization was reduced by ca. 60% (i.e., 30% fertilization) at pH 7.7/$p\mathrm{CO}_2$ 998 (Albright et al. 2010).

Conflicting results on the effects of decreased pH on fertilization have been obtained for the same species, for example in echinoids (Havenhand et al. 2008, Byrne et al. 2009) and oysters (Kurihara et al. 2007, Havenhand & Schlegal 2009, Parker et al. 2010). In a recent study of the oyster *Crossostrea gigas* a decrease in fertilization success was recorded at pH 7.8 (Parker et al. 2010), but this was not observed in previous studies (Kurihara et al. 2007, Havenhand & Schlegal 2009) even in extreme treatments (pH 7.4, $p\mathrm{CO}_2$ 2268 ppm). For *Heliocidaris erythrogramma* a decrease in fertilization at low pH (pH 7.7) was reported (Havenhand et al. 2008), but this was not confirmed in subsequent studies (Figure 2).

Empirical data from a greater diversity of species from different habitats are needed to discern trends, with interstudy comparison facilitated by use of comparable experimental methods. Differences in experimental conditions (e.g., gamete source, gamete age, sperm-egg contact time, gamete concentration, test vessel volume, vessel type, stage scored) are well known to influence fertilization test results (Bay et al. 1993, Clotteau & Dubé 1993, Styan 1998, Palumbi 1999, Baker & Tyler 2001, Evans & Marshall 2005, Lera et al. 2006, Byrne et al. 2010a,b), highlighting problems with interstudy comparisons. For instance in various studies fertilization is arrested/reduced following treatments using a range of chemical agents (e.g., fixatives, KCl, lauryl sulphate; e.g., Styan et al. 2005, Carr et al. 2006, Reuter et al. 2010) or rinsing off excess sperm (e.g., Havenhand et al. 2008, Byrne et al. 2009), whereas other fertilization studies do not use these procedures (e.g., Evans and Marshall 2005). The source of gametes used for experiments, either pooled from multiple males and females to represent a population of spawners or in single dam-sire crosses as in fertilization kinetics and quantitative genetics studies, is also a major source of interstudy variation due to the strong genetic effect of male-by-female interactions (Evans & Marshall 2005, Levitan & Ferrell 2006, Evans et al. 2007). It is well known that variation in sperm quality and egg-sperm compatibility determine fertility in echinoids and oysters (Palumbi 1999, Boudry et al. 2002). In addition, some studies score fertilization based on the presence of a fertilization envelope, whereas others used embryonic mitosis (cleavage). These are not equivalent stages and have different sensitivities to stressors (see Byrne et al. 2009, Allen & Pechenik 2010).

Due to the plethora of factors influencing variation in fertilization tests in interlaboratory comparisons (e.g., same species, same reference toxicant) for environmental monitoring (Bay et al. 1993, Lera et al. 2006), standard test protocols have been established (e.g., Cherr et al. 1990, American Society for Testing and Materials [ASTM] 2004). It is not clear if this standardization is warranted for global change studies. It appears that fertilization may not be a suitable endpoint for assessing the impacts of climate change stressors on marine life histories. Later developmental stages provide better test endpoints with less conflict among studies (Table 2).

Impacts of ocean warming and acidification on marine embryos and larvae

With concerns about the impacts of climate change on marine biota, the impacts of ocean warming and acidification on development are being investigated in an increasing number of species. Experimental approaches to rearing embryos and larvae in ocean change conditions vary between studies. In studies investigating ocean acidification as a single stressor the most common approach has involved transfer of developmental stages from contemporary seawater conditions (e.g., hatchery-reared larvae, field recruits) to decreased pH conditions (Kurihara & Shirayama 2004, Findlay et al. 2008, 2010, Miller et al. 2009, Ries et al. 2009, Talmage & Gobler 2009, Albright et al. 2010, Beniash et al. 2010, Findlay et al. 2010a,b, Range et al. 2011). However, developmental success requires that all ontogenetic stages are completed successfully (Figure 1), so the applicability of this approach to climate change effects is not clear. The integrative and cumulative effects of stressors across ontogenetic stages are likely to influence experimental outcomes. Depending on species and stressor type, early embryos and larvae exhibit different sensitivities to stressors in many studies (Pechenik 1987, Ringwood 1992, Allen & Pechenik 2010, Ericson et al. 2010). A study comparing the effects of ocean acidification on veliger larvae derived from embryos fertilized in both control and experimental conditions found greater deleterious effects (lower survivorship, smaller larvae) in larvae from the latter treatments (Parker et al. 2010). A similar difference was seen in asteroid larvae (Foo 2010). There are insufficient data to determine if experimental outcomes differ with respect to the developmental stage at which incubations are initiated. However, it is most realistic, where possible, to assess the impact of climate change stressors from the outset of development in embryos fertilized in experimental conditions. A few studies have taken this approach (e.g., Byrne et al. 2009, 2010a, 2011b, Parker et al. 2010, Sheppard Brennand et al. 2010).

Most studies on the impacts of ocean change on development have focused on calcifying larval stages due to concerns of reduced aragonite and calcite saturation (Table 2, Figures 3, 4 and 5). In general there is only limited knowledge of effects of acidification on early stages (e.g., embryonic mitosis/cleavage, morulae, blastulae, gastrulae). More data are needed on developmental

Table 2 Influence of increased temperature (°C) and acidification (pH/$p\text{CO}_2$, ppm) as single stressors on embryonic and larval development in marine invertebrates and levels for significant deleterious effects in the context of near-future ocean change (100–200 years)

	Temperature				Acidification (pH/$p\text{CO}_2$)		
	Optimum range for development (ca. 75% normal or above)		Temperature increase negative effects (ca. less than 75% normal) on development				
Phylum, species	Embryos	Larvae	Embryos	Larvae	pH range for normal (ca. 75%) embryo and larval development	Low pH/ $p\text{CO}_2$ effects on embryos, larvae or juveniles	Reference
Porifera							
Rhopaleoeides odorabile	22–28	22–28	10	10	ND	ND	Whalan et al. 2008
Cnidaria							
Acropora digitata	27	ND	ND	NS	7.3–8.0 400–3585	7.3/3500 Smaller polyps	Suwa et al. 2010
						7.3–7.6 Reduced metamorphosis	Nakamura et al. 2011
Acropora millepora	26–30	ND	4	ND	ND	ND	Negri et al. 2007
Acropora muricata	26–32	26–32	4	ND	ND	ND	Baird et al. 2006
Acropora palmata	28–30	28–30	4	4	ND	ND	Randall & Szmant 2009a
Acropora tenuis	27	ND	ND	ND	7.3–8.0 400–3585	7.3–7.6/900–3585 Smaller polyps	Kurihara 2008, Suwa et al. 2010
Diploria strigosa	30–31	30–31	2	2	ND	ND	Bassim et al. 2002
Favites abdita	26–32	ND	>4	ND	ND	ND	Negri et al. 2007
Favia faragum	28–31	28–30	4	3	ND	ND	Randall & Szmant 2009b
Mycedium elephantotus	26–32	ND	>4	ND	ND	ND	Negri et al. 2007
Stylophora pistillata	23–25	23–25	>4	>4	ND	ND	Putnam et al. 2008
Nemertea							
Parborlasia corrugatus	0–1	ND	ND	ND	7.3–8.0 528–2886	7.0/5806	Ericson et al. 2010

Mollusca							
Gastropoda							
Haliotis coccoradiata	20–22	20	4	2–4	8.0–8.2 327–420	7.6–7.8/1080–1729 Abnormal development, decreased larval calcification	Wong et al. 2010; Byrne et al. 2011, Figure 4
Littorina obtusata	15	ND	ND	ND	ND	7.6/1093 Abnormal development, decreased metamorphosis	Ellis et al. 2009
Strombus gigas	20–32	20–32	ND	ND	ND	ND	Davis 2000
Bivalvia							
Argopecten irradians	ND	ND	ND	ND	8.1/360	7.5–7.8/690–1630	Talmage & Gobler 2009
Crassostrea ariakensis	25	ND	ND	ND	7.8–8.1 291–823	ND	Miller et al. 2009
Crassostrea gigas	18–30	18–30	ND	ND	7.8–8.2 375–1000	7.4/2268 Decreased larval calcification	Kurihara et al. 2007, Kurihara 2008
						7.8/1000 Abnormal development, decreased larval calcification	Parker et al. 2010
Crassostrea virginica	20–30	20–30	ND	ND	8.0–8.2 284–389	7.76–7.9/572–840	MacInnes & Calabrese 1979, Wright et al. 1983, Miller et al. 2009, Talmage & Gobler 2009
						7.5/3500	Beniash et al. 2010
Mercenaria mercenaria	ND	ND	ND	ND	8/360	7.5–7.8/640–1500	Talmage & Gobler 2009
Mytilus edulis	5–20	5–20	5	5	ND	ND	Brenko & Calabrese 1969
Mytilus galloprovincialis	13	ND	ND	ND	8.1/380	7.4/2000 Smaller larvae	Kurihara et al. 2008a
Pinctada margaritifera	25–30	25–30	7	7	ND	ND	Doroudi et al. 1999
Saccostrea glomerata	22–30	22–26	ND	ND	7.9–8.2 375–750	7.8–8.0/600–1000 Smaller larvae	Parker et al. 2010, Watson et al. 2009

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Table 2 (continued) Influence of increased temperature (°C) and acidification (pH/$p\text{CO}_2$, ppm) as single stressors on embryonic and larval development in marine invertebrates and levels for significant deleterious effects in the context of near-future ocean change (100–200 years)

	Temperature				Acidification (pH/$p\text{CO}_2$)		
	Optimum range for development (ca. 75% normal or above)		Temperature increase negative effects (ca. less than 75% normal) on development		pH range for normal (ca. 75%) embryo and larval development	Low pH/ $p\text{CO}_2$ effects on embryos, larvae or juveniles	
Phylum, species	Embryos	Larvae	Embryos	Larvae			Reference
Cephalopoda							
Sepia officianalis	17	ND	ND	ND	7.1–8.0 636–6148	ND	Gutowska et al. 2008, 2010a,b
Echinodermata							
Ophiuroidea							
Ophiothrix fragilis	14	ND	ND	ND	8.1	7.7–7.9 Smaller larvae	Dupont et al. 2008
Asteroidea							
Acanthaster planci	28–31	ND	6	ND	ND	ND	Rupp 1973
Asterias amurensis	10–15	10–15	>12	>12	ND	ND	Lee et al. 2004
Asterias rubens	10–20	ND	>5	ND	ND	ND	Benitez-Villalobos et al. 2006
Crossaster papposus	12	ND	ND	ND	7.7–8.1 372–930 Faster growth	ND	Dupont et al. 2010b
Culcita novaeguineae	28–31	ND	6	ND	ND	ND	Rupp 1973
Linckia laevigata	28–31	ND	6	ND	ND	ND	Rupp 1973
Marthasterias glacialis	15–20	ND	>5	ND	ND	ND	Benitez-Villalobos et al. 2006
Patiriella regularis	18–22	18–22	4	4	7.6–8.25 330–1762	ND	Byrne & Barker 1991, Foo, 2010
Meridiastra calear	18–21	ND	5	ND			Nguyen, H., pers. comm.
Echinoidea							
Anthocidaris crassispina	16–29	16–26	>4	>4	ND	ND	Fujisawa 1989
Arbacia punctulata	ND	ND	ND	ND	7.0–8.6	6.8–7.0	Carr et al. 2006

Centrostephanus rodgersii	18–22	18–22	6	ND	7.8–8.2 324–1069	7.6–78/1695–1762	Foo 2010
Dendraster excentricus	7–20	ND	9	ND	ND	ND	Fujisawa 1993, Bingham et al. 1997
Diadema savignyi	28–31	ND	6	ND	ND	ND	Rupp 1973
Echinometra lucunter	23–34	ND	8	>10	ND	ND	Sewell & Young 1999
Echinometra mathaei	28–34	ND	8	ND	7.8–8.0 360–860	7.6/1000 Smaller larvae	Rupp 1973, Kurihara 2008
Evechinus chloroticus	15	ND	ND	ND	7.7–8.1 438–1320	7.7/1320 Smaller larvae	Clark et al. 2009
Heliocidaris erythrogramma	18–24	18–24	4–6	4–6	7.6–8.2 330–1892	7.6 No effect on early development	Byrne et al. 2009, 2010a,b, 2011a
						7.6–7.8/1050–1730 Impaired juvenile calcification	Byrne et al. 2011b
						7.7/1000 Decrease in gastrula & larvae	Havenhand et al. 2008
Heliocidaris tuberculata	19–24	ND	4	ND	ND	ND	O'Connor & Mulley 1977
Hemicentrotus pulcherrimus	5–23	5–23	>6	6	7.8–8.0 360–860	7.6/1000 Smaller larvae	Fujisawa 1989, 1995, Kurihara & Shirayama 2004
Lytechinus variegatus	15–18	ND	ND	ND	ND	540–970 Smaller larvae	O'Donnell et al. 2010
Pseudechinus huttoni	10–12	ND	ND	ND	7.7–8.1 429–1282	7.7/1282 Smaller larvae	Clark et al. 2009
Pseudocentrotus depressus	9–25	9–25	>4	>4	ND	ND	Fujisawa 1989
Sterechinus neumayeri	0.2–1.7	ND	>1	ND	7.3–8.0 527–2886	7.0/5800 Abnormal blastulae	Stanwell-Smith & Peck 1998, Ericson et al. 2010
					7.6–8.0 521–1380	7.6/1380 Smaller larvae	Clark et al. 2009
Strongylocentrotus franciscanus	15–18	ND	ND	ND	ND	7.85–7.95/540–970 Reduced gene expression	O'Donnell et al. 2009
Strongylocentrotus purpuratus	5–16	ND	ND	ND	7.3–8.2	<7.2 Increased mortality	Bay et al. 1993, Fujisawa 1993

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Table 2 (continued) Influence of increased temperature (°C) and acidification (pH/$p\mathrm{CO_2}$, ppm) as single stressors on embryonic and larval development in marine invertebrates and levels for significant deleterious effects in the context of near-future ocean change (100–200 years)

	Temperature				Acidification (pH/$p\mathrm{CO_2}$)		
	Optimum range for development (ca. 75% normal or above)		Temperature increase negative effects (ca. less than 75% normal) on development		pH range for normal (ca. 75%) embryo and larval development	Low pH/ $p\mathrm{CO_2}$ effects on embryos, larvae or juveniles	
Phylum, species	Embryos	Larvae	Embryos	Larvae			Reference
Tripneustes gratilla	16–29	19–31	4	6	7.8–8.25 332–1087	7.6–7.8/1087–1795 Smaller larvae	Clark et al. 2009, Rahman et al. 2009, Sheppard Brennand et al. 2010
Arthropoda							
Acartia erythraea	27	ND	ND	ND	7.3–8.2 380–2380	6.8–7.0/5000–10,000 Increased mortality	Kurihara et al. 2004
Acartia tsuensis	25	ND	ND	ND	7.3–8.2 380–2380	ND	Kurihara & Ishimatsu 2008
Amphibalanus amphitrite	25–28	ND	ND	ND	7.4–8.2	7.4 No effect on larvae, smaller juveniles	McDonald et al. 2009
Calanus finmarchicus	8.8	ND	ND	ND	6.95–8.23 8000	ND	Mayor et al. 2007
Echinogammarus marinus	15	ND	ND	ND	7.5–8.0 380–1900	ND	Egilsdottir et al. 2009
Hommarus gammarus	19	ND	ND	ND	8.4/315	8.1/1202 No effect on early development, less-calcified terminal larvae	Arnold et al. 2009
Palaemon pacificus	25	ND	ND	ND	7.9–8.2 380–1000	7.6–7.9/1000–1900 Smaller juveniles, lower survival	Kurihara et al. 2008b

Note: The temperature data are the impacts of thermal increase at ambient pH. The pH data are the response to acidification at the control/optimal rearing temperature. Experimental pH was adjusted by treatment of seawater with $\mathrm{CO_2}$ gas. Thermal limits are represented as increase (°C) above ambient. Where temperature range was not investigated, ambient/control values were obtained from the study. ND, no data.

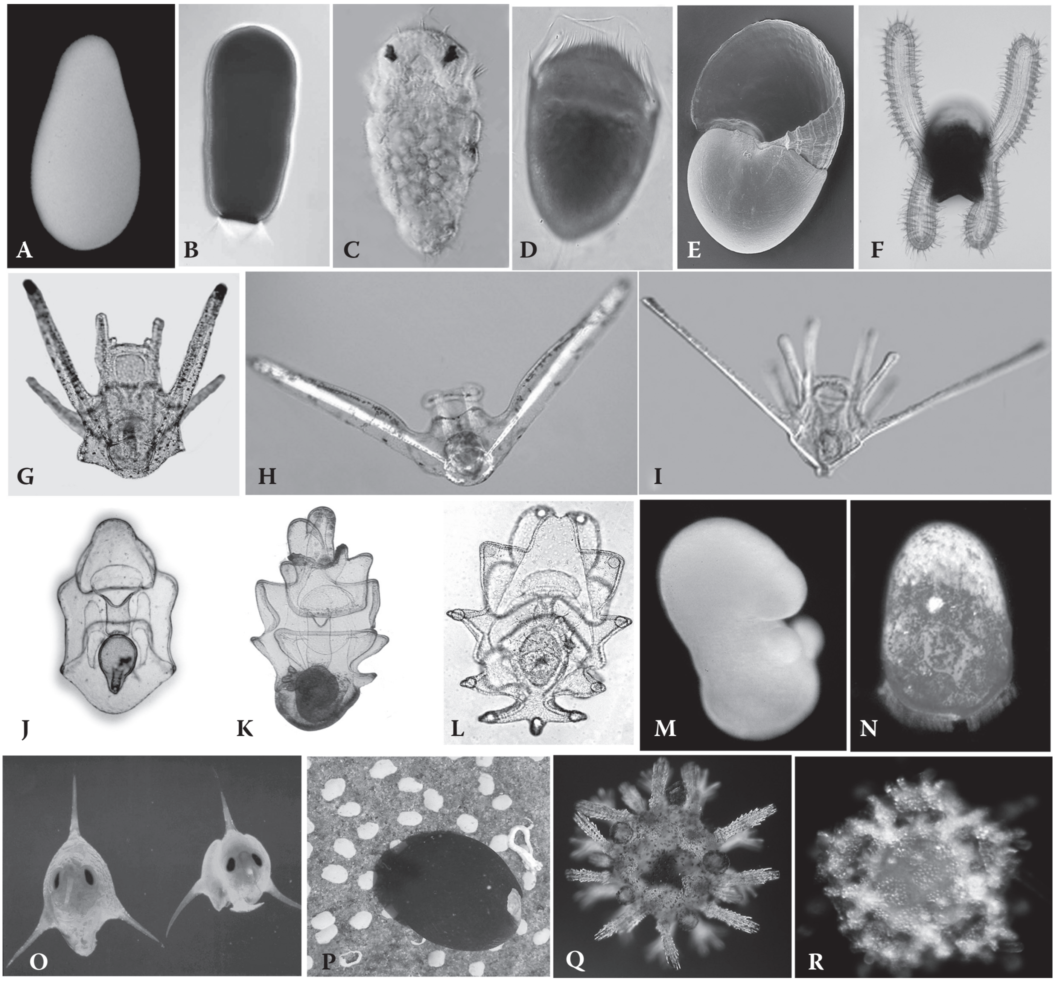

Figure 3 The life histories of benthic marine calcifiers include species with non-calcifying (A–D, J–N) and calcifying (E–I) larvae. (A) Coral planula. (B) *Reniera* sp. sponge larvae. (C) *Filograna implexa*, polychaete trochophore. (D) and (E) *Haliotis* spp. mollusc trochophore and veliger shell. (F) *Siphonaria* sp., mollusc veliger larva. (G)–(I) *Heliocidaris tuberculata*, *Centrostephanus rodgersii* and *Ophiactis resiliens*, echinoderm plutei. (J) and (K) *Patiriella regularis*, asteroid bipinnaria and brachiolaria larvae. (L) *Holothuria scabra*, holothuroid auricularia. (M) *Cryptasterina pentagona*, lecithotrophic brachiolaria. (N) *Heliocidaris erythrogramma*, reduced pluteus. (O) crab zoea larva. (P) *Nerita atramentosa* and calcareous egg capsules. (Q) *Heliocidaris erythrogramma* juvenile. (R) *Parvulastra exigua* juvenile. (Photographs courtesy of R. Babcock (A), B. Degnan (B,C), E. Wong (D), L. Page (E,F,P), I. Bennett (O). J and K from Byrne & Barker, 1991, with permission; L from Ramofafia et al. 2003. M from Byrne et al. 2003, with permission.)

thermo- and pH tolerance for diverse species from the outset of development (fertilization) and across ontogenetic stages. In particular, good comparative data for species from temperature and pH-variable (e.g., intertidal, temperate) and temperature and pH-stable (e.g., subtidal, polar) regions are needed. There is considerable variation among species in developmental sensitivity to climate change stressors (Byrne 2010, Dupont et al. 2010a, Kroeker et al. 2010), and where possible, research should involve closely related species to reduce experimental variation due to disparate phylogeny (Sokolova & Pörtner 2001, Raff & Byrne 2006).

Thermotolerance of development

There has been considerable interest in the effects of temperature on marine invertebrate development, and there is a wealth of data available (ca. 1 sponge, 4 corals, 1 nermertean, 7 molluscs, 20 echinoderms, 2 crustaceans) from developmental, physiological and global change studies across ontogenetic stages (Table 2). In general, embryos and larvae seem less thermotolerant than gametes/fertilization (Tables 1 and 2). Studies of the pace of embryogenesis, developmental constraints, swimming performance, oxygen consumption and planktonic larval duration (PLD) showed that temperature is the major environmental factor controlling invertebrate development and is a key factor controlling marine species distributions and recruitment dynamics (Thorson 1950, Kinne 1970, Pechenik 1987, Hart & Scheibling 1988, Chen & Chen 1992, Roller & Stickle 1993, Hoegh-Guldberg & Pearse 1995, Young et al. 1998, Gillooly et al. 2002, Staver & Strathmann 2002, McDonald 2004, Reitzel et al. 2004, O'Connor et al. 2007, Putnam et al. 2008, Compton et al. 2010, Hernández et al. 2010). For many species there is a tight relationship between sea temperature and spawning time, and this relationship often corresponds to the optimal temperature for larval development (Fujisawa & Shigei 1990, Johnson & Babcock 1994, Reitzel et al. 2004).

The response of developmental systems to increased temperature is typically seen as a balance between facilitation at certain levels of warming and developmental failure at upper thermal limits. This has been documented for sponge, cnidarian, mollusc and echinoderm development (Rupp 1973, Fujisawa 1989, Sewell & Young 1999, Bassim et al. 2002, Negri et al. 2007, Whalan et al. 2008, Byrne et al. 2009, 2011a,b, Byrne 2010, Parker et al. 2010, Sheppard Brennand et al. 2010). Increased temperature accelerates metabolism up to limits and results in failure when the thermal stability and function of proteins (e.g., enzymes) are compromised (Somero 2002, 2010, Hofmann & Todgham 2010, Tomanek 2010).

Moderate warming (≤4°C above ambient/thermal history) is tolerated by the life history stages of many species (Table 2) with beneficial effects of faster growth, larger size and reduced PLD. Projected near-future ocean warming has been shown to reduce the PLD of sponges, corals and echinoderms (Putnam et al. 2008, Whalan et al. 2008, Byrne et al. 2011a, Heyward & Negri 2010). Sea urchin embryos that tolerated a 4°C warming formed normal juveniles with a 25% decrease in PLD (Byrne et al. 2011a). A shortened planktonic stage may be beneficial in increasing retention of larvae within a region (Byers & Pringle 2006). Reduced PLD also shortens the vulnerable dispersive phase when mortality is high (ca. 90%) (Rumrill 1990, Lamare & Barker 1999, Schneider et al. 2003, Allen 2008). Reduced PLD, however, alters supply side ecology and genetic connectivity between populations (Shanks et al. 2003, O'Connor et al. 2007).

More extreme ocean warming (≥3–4°C above ambient) is widely deleterious to embryos (Table 2), as seen in recent studies of coral, oyster and sea urchin development (Byrne et al. 2009, 2011a, Randall & Szmant 2009a, Parker et al. 2010). In the sea urchins *Heliocidaris erythrogramma* and *Tripneustes gratilla* a 6°C warming exceeds developmental thermotolerance (Byrne et al. 2009, 2011a, Rahman et al. 2009, Sheppard Brennand et al. 2010). In response to thermal challenge the greatest mortality in coral, mollusc and sea urchin embryos occurs prior to or at gastrulation (Figure 4, Byrne et al. 2009, 2011a,b, Randall & Szmant 2009a). Elevated temperature is also a key environmental driver of recruitment dynamics and juvenile mortality (Gosselin & Qian 1997, Hunt & Scheibling 1997, Hernández et al. 2010). Development in extreme thermotolerant species may not be impaired by projected warming, as seen in the robust response of development in the tropical sponge *Rhopaloeides odorabile* and the sea urchin *Echinometra mathaei* to extreme warming (8–10°C above ambient) (Rupp 1973, Ettinger-Epstein et al. 2007, Whalan et al. 2008).

The threshold for deleterious warming (degrees above ambient) can vary among developmental stages within a species (Wright et al. 1983, Byrne et al. 2009, 2010a). For example, early development (to gastrulation) in the coral *Acropora palmata* and the sea urchin *Heliocidaris erythrogramma*, and the trochophore stage in the bivalve *Argopecten irradians*, is more vulnerable to

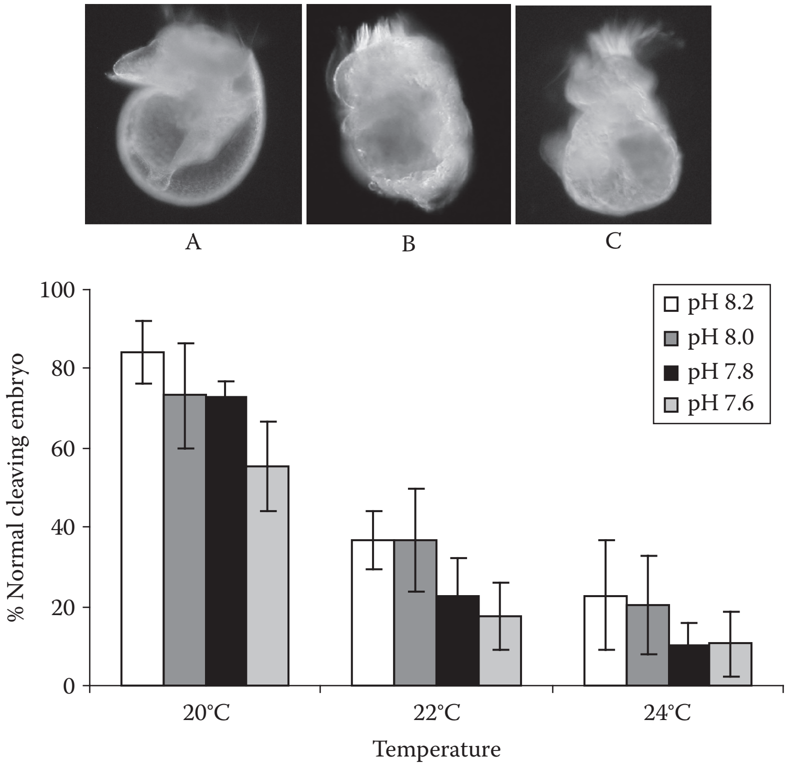

Figure 4 Percentage of normal cleavage in the abalone *Haliotis coccoradiata* in response to ocean change scenarios for year 2100 (A1F1, IPCC 2007). Both stressors significantly impaired early development (analysis of variance [ANOVA]: Temperature $F_{2,8} = 10.6$, $p < 0.001$; pH $F_{3,36} = 3.08$, $p < 0.05$) with no interaction between stressors ($n = 8$, error bars = standard error of the mean [SEM]). (A) Normal veliger larva from pH 8.0–8.2/20°C treatments. (B) and (C) Unshelled and abnormal larval phenotypes seen at an increase of 2–4°C above ambient and pH decrease by 0.4 to 0.6 units. Scale = 200 µm.

warming than later larval stages (Wright et al. 1983, Byrne et al. 2009, 2010a, Randall & Szmant 2009a). Abalone (*Haliotis coccoradiata*) development appears highly sensitive to warming, with a small increase (2°C) exerting deleterious effects (Figure 4). Limited thermotolerance seems to be a general feature of abalone development (Gilroy & Edwards 1998). Coral larvae have limited thermotolerance, a feature that may be characteristic of coral development (Table 2, Bassim et al. 2002, Randall & Szmant 2009a,b). Increased temperature exerted a major influence on response to settlement cues, and larvae changed their preference with 3°C warming (Putnam et al. 2008). In this case elevated temperature facilitated settlement to an appropriate coralline algal substratum. Growth in barnacle post-larvae was not affected by increased temperature (4°C above ambient) (Findlay et al. 2010b).

Developmental thermal thresholds can differ between species even among closely related ones from similar habitats (Table 2). Experiments with five sympatric bivalves showed that development in some species is highly tolerant to increased temperature (>10°C above ambient), while others succumbed at a comparatively lower level of increased temperature (1–5°C above ambient) (Wright et al. 1983). Development in widely distributed intertidal, shallow subtidal and tropical species and species used for aquaculture (e.g., *Crassostrea gigas*, *Tripneustes gratilla*, *Echinometra* spp., *Heliocidaris erythrogramma*) is particularly robust to thermal increase (≥4°C above ambient, Table 2). A bet-hedging type strategy is evident in corals that produce phenotypically diverse offspring that differ in their thermotolerance (Putnam et al. 2010). The broad thermotolerance of embryos and larvae of deep-water echinoids (*Stylocidaris lineata*, *Archaeopneustes histrix*) that live in relatively stable thermal regimes as adults may be associated with migration of larvae into shallow tropical water during their planktonic phase (Young et al. 1998).

In the warmer part of their range near regions of ocean thermal maxima even robust tropical species such as *Crossostrea gigas*, *Tripneustes gratilla* or *Echinometra* spp. may be living at temperatures near the lethal threshold for development (e.g., Rahman et al. 2009). Reproductive failure of populations of these and other species living at or near ocean minima and maxima (e.g., equator, poles) may occur as the ocean warms (Stanwell-Smith & Peck 1998, Tewksbury et al. 2008, Sewell & Hofmann 2011). Adults of several temperate intertidal and coral reef species live on the edge of physiological thermal tolerance windows (Sagarin et al. 1999, Tomanek & Somero 1999, Sokolova & Pörtner 2001, Hughes et al. 2003, Pörtner & Knust 2007, Tewksbury et al. 2008, Somero 2010, Tomanek 2010), but it is not known how this is reflected in the thermotolerance of their planktonic stages.

Thermal thresholds of marine propagules are influenced by adult thermal history (‘environmental imprinting’), an important consideration when designing stressor experiments. Adult thermal acclimatization, particularly during egg development, dramatically shifts the thermotolerance of embryos and larvae (O’Connor & Mulley 1977, Johnson & Babcock 1994, Fujisawa 1995, Bingham et al. 1997, Byrne et al. 2010a, Zippay & Hofmann 2010a). This developmental plasticity may be due to differences in maternal loading of protective factors (e.g., heat shock proteins) during oogenesis (Hamdoun & Epel 2007) and may be a source of non-genetic adaptation (phenotypic) to climate change (see p. 25).

With the major controlling influence that temperature exerts on reproduction in the sea, it is not surprising that phenological shifts driven by ocean warming are evident in the timing of spawning and the presence of larvae in the plankton (Edwards & Richardson 2004, Schofield et al. 2010). Warming was implicated in a shift in the timing of release of lobster larvae from brooding females, a change predicted to have a negative effect on larval success (Schmalenbach & Franke 2010). Phenological shifts driven by ocean warming are creating a trophic mismatch between larvae and their food, which is a problem for feeding larvae, ecological interactions and planktonic food web cascades (Philippart et al. 2003, Edwards & Richardson 2004, O’Connor et al. 2009, Schofield et al. 2010). These shifts are also causing major alterations in benthic-pelagic coupling and changes to benthic systems (Kirby et al. 2007).

Depending on regional patterns of ocean warming and the seasonal timing of thermal increase with regard to spawning and planktonic periods, it appears that ocean warming is likely to be broadly deleterious to core developmental mechanisms (e.g., cleavage, gastrulation, larval morphogenesis) fundamental to development across the Metazoa, with broad implications for marine ecosystems. It is essential to include regional aspects and adult thermal history when considering developmental thermotolerance of local populations to identify species at risk, species that may be resilient in the face of change, and potential for species invasion.

pH/pCO_2 tolerance of development

Investigation of the impacts of ocean acidification on development is a burgeoning field, with data currently available for about 2 coral, 1 nemertean, 11 mollusc, 14 echinoderm and 7 crustacean species (Table 2). Of major concern are the fragile skeletons produced by calcifying larvae (Figure 3E–I,O; Kurihara & Shirayama 2004, Dupont et al. 2008, Kurihara 2008, Byrne 2010, O’Donnell et al. 2010, Parker et al. 2010, Sheppard Brennand et al. 2010, Byrne et al. 2011b). Impaired ability to produce these skeletons (Figures 4 and 5) and dissolution of skeleton as the ocean decreases in pH may be the weak link for species persistence. Vulnerability to ocean acidification would lead to developmental failure of a broad suite of benthic invertebrates.

Because pH, hypercapnia and $CaCO_3$ availability or saturation covary as the ocean absorbs CO_2, it is difficult to separate main factor effects. The decrease in the size of the larval skeleton

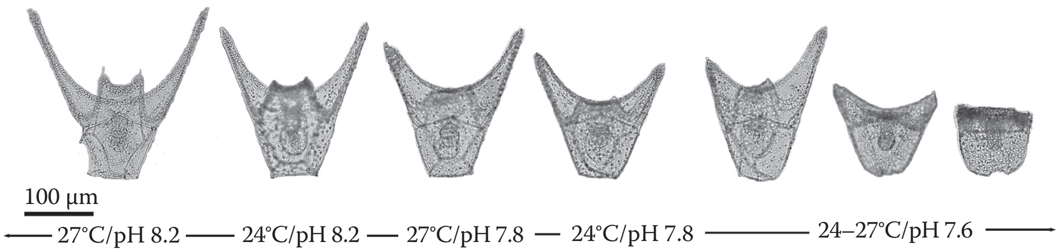

Figure 5 Echinopluteus larvae of *Tripneustes gratilla* reared for 5 days in three pH and two temperature treatments. Largest larvae were from control pH 8.15/+3°C (27°C) treatments. Acidification (to pH 7.6) and increased CO_2 stunted larval growth, causing a decrease in length of the arms and the supporting skeletal rods. There was an increase in abnormal development. (See Sheppard Brennand et al. 2010.)

observed in many calcifying larvae in response to pH/pCO$_2$ treatments (Table 2 and Figure 5) may be due to reduced $CaCO_3$ saturation or hypercapnic suppression of metabolic pathways required for calcification. Regardless of the mechanism involved, production of a smaller larva, reduced growth rate and production of weaker skeletons will have an impact on swimming and feeding efficiency and increase vulnerability of larvae to predation and physical damage (Allen 2008, Przeslawski et al. 2008, Soars et al. 2009).

Calcification in marine invertebrates is an ancient evolutionary innovation (ca. 500 million years ago [mya]), and not surprisingly, major calcifying taxa have different calcification systems (Porter 2007). The mineral composition of skeletons varies (e.g., calcite or aragonite), and this difference dictates comparative solubility as mineral saturation states decrease due to ocean acidification (Doney et al. 2009). Across marine calcifiers cell and developmental mechanisms of calcification also differ; this is likely to influence vulnerability to ocean acidification. For instance, mollusc veliger larvae develop an aragonite skeleton in ectodermal tissue with its surface in close contact with surrounding seawater (Figure 3E,F), whereas echinoderm plutei produce a high magnesian calcite skeleton in mesodermal tissue that, due to its internal location, may be more protected from seawater chemistry (Figure 3G–I). Although details of calcification of the crustacean exoskeleton still need to be determined (Luquet & Marin 2004), the high organic (chitin, protein) content of the cuticle of many species may make them more resilient to ocean acidification, as evidenced by the presence of copepods in highly acidic environments (Derry & Arnott 2007). The cuticle of marine copepods and amphipods also appear resilient to acidification (Table 2). In crustacean development, vulnerability to decreased $CaCO_3$ saturation would vary greatly between species and developmental stages with lightly (e.g., copepods, amphipods, larvae, Figure 3O) and heavily (e.g., lobsters, crabs) calcified exoskeletons (Luquet & Marin 2004, Arnold et al. 2009).

The threshold for negative impacts of ocean acidification on mollusc larval development and calcification varies among species (Table 2). For bivalves near-future decrease in pH (ca. pH 7.7–7.8; pCO$_2$ 500–800 ppm) resulted in smaller larvae, impaired calcification and delayed metamorphosis in some species (*Crassostrea gigas*, *C. virginica*, *Saccostrea glomerata*, *Argopecten irradiens*) but not in others (*Crassostrea ariakensis*, *Mytilus galloprovincialis*) (Table 2). For *M. galloprovincialis* development to the trochophore stage was normal at pH 7.4 (pCO$_2$ 2000 ppm) with deleterious effects evident in veligers (Kurihara et al. 2008a). Survival of *Crassostrea virginica* larvae diminished at pH 7.5 (pCO$_2$ 1500 ppm) (Talmage & Gobler 2009). Remarkably, cuttlefish (*Sepia officianalis*) embryos are able to produce their internal aragonite skeleton under extreme conditions (to pH 7.1), with increased calcification observed at low pH (Gutowska et al. 2008, 2010a,b).

The impacts of climate change stressors on mollusc embryos developing in benthic egg masses have been investigated for an intertidal snail, *Littorina obtusata,* with evidence of sublethal effects at pH 7.6/pCO$_2$ in chronic long-term (23-day) press experiments (Ellis et al. 2009). These included mortality, depressed heartbeat and reduced locomotion (Ellis et al. 2009). Interestingly, these embryos would experience these conditions in pulse exposures during night-time low tides (Björk et al. 2004). The calcareous capsular egg masses produced by gastropods (e.g., *Nerita* spp.) common on the shore in many regions (Figure 3P) may be vulnerable to low pH. The impacts of environmental stressors on calcareous egg capsules have not been investigated (Przeslawski 2004).

Abalone (*Haliotis coccoradiata*) veliger larvae reared from embryos fertilized in experimental conditions appear particularly sensitive to acidification (Figure 4), with deleterious effects evident at pH 7.8 and below (Table 2). This sensitivity is also reported for oyster veligers reared from the outset of development in experimental conditions (Parker et al. 2010).

The pluteus larvae of eight echinoderm species reared in near-future ocean acidification conditions (ca. pH 7.7–7.8) exhibited reduced growth and calcification (Table 2, Figure 5). Increased acidification and hypercapnia stunt larval growth and produce larvae with shorter arms. Sea urchin embryos and larvae in ocean acidification treatments also exhibit altered gene expression and changes to cellular protective biochemistry (O'Donnell et al. 2009, 2010, Todgham & Hofmann 2009).

The impacts of near-future ocean acidification on crustacean development are mixed (Table 2). In congeneric copepod species (*Acartia* spp.) neutral and negative effects are reported in larvae (Kurihara et al. 2004, Kurihara & Isimatsu 2008). In *A. erythraea* increased mortality is observed at extreme pH levels well below projected ocean acidification (pH 6.8–7.4, $p\mathrm{CO}_2$ 10,000 ppm) (Kurihara et al. 2004). In *Calanus finmarchicus* hatching success decreased at pH 6.9 ($p\mathrm{CO}_2$ 8000 ppm) (Mayor et al. 2007). It appears that ocean acidification, even at levels beyond realistic projections, does not impair development in barnacle, copepod or amphipod larvae (Kurihara et al. 2004, Kurihara & Ishimatsu 2008, Egilsdottir et al. 2009, McDonald et al. 2009). For lobster development there was no effect of reduced pH and increased hypercapnia (pH 8.1, $p\mathrm{CO}_2$ 1200 ppm) in development, survival and growth of larvae transferred to experimental conditions as zoea up until the final larval stage (Arnold et al. 2009). In final-stage lobster larvae the mineral content of the carapace was lower in experimental treatments. This effect was largely attributed to hypercapnia and indicates poor prospects for the more heavily calcified benthic adult lobster stage (Arnold et al. 2009).

Although data are limited, embryonic (prelarval) stages of species with calcifying larvae and species that do not have a calcifying stage in their development (Figures 1 and 3) may be more robust to near-future ocean acidification (ca. < pH 7.8) during their planktonic phase. Three studies of the effects of near-future acidification on non-calcifying echinoderm larvae showed either a neutral (*Patiriella regularis*, *Heliocidaris erythrogramma*) or a positive (*Crossaster papposus*) effect of acidification on larval development and growth (Table 2). This result contrasts with the miniaturizing effect of decreased pH seen for echinoplutei (Table 2, Figure 5) and suggests that the decreased pluteal calcification in conditions of ocean acidification is primarily driven by lowered CaCO_3 saturation and less by hypercapnia. Development of planula larvae of coral species (also lack a skeleton, Figure 3A) is robust to low pH (pH 7.3–7.6) (Kurihara 2008, Suwa et al. 2010), but in *Acropora palmata* larval settlement was reduced at pH 7.7–7.8/pCO_2 673–998 (Albright et al. 2010). In *Acropora digitifera* larval metamorphosis was reduced at pH 7.3–7.6 (Table 2). More data are needed on the sensitivity of non-calcifying larvae to ocean acidification to determine if future outcomes may differ for larvae that have to calcify and those that do not.

Data on the impact of near-future ocean acidification scenarios on postlarvae and early juvenile stages are scarce. Reduced larval growth in experimental conditions results in production of smaller or abnormal juveniles of some coral, barnacle, prawn and sea urchin species (Kurihara 2008, McDonald et al. 2009, Findlay et al. 2010, 2011b, Suwa et al. 2010, Byrne et al. 2011b). In contrast ocean acidification conditions resulted in an increase in the size of barnacle postlarvae but at a cost of a weaker skeleton (McDonald et al. 2009). Smaller postlarvae or weaker skeletons are likely to increase the risk of mortality in the early postlarvae and juveniles. The early benthic stages can be the major bottleneck in species population dynamics (Gosselin & Qian 1997, Hunt & Scheibling 1997). Field observations of juvenile mortality and dissolution of juvenile and shells in low pH estuarine deposits shows that a potential bottleneck in the early benthic stage is a real risk to successful recruitment and postsettlement survival (Green et al. 2004, Marshall et al. 2008).

Experiments involving transfer of juvenile or adult calcifiers from contemporary to near-future ocean acidification conditions in press-type stressor studies reported reduced growth, reduced calcification, dissolution of skeleton and compromised health in some species (e.g., echinoderms: Shirayama & Thornton 2005, Miles et al. 2007, Ries et al. 2009; bivalves: Michaelidis et al. 2005, Gazeau et al. 2007, Bibby et al. 2008; gastropods: Nienhuis et al. 2010; barnacles: Findlay et al. 2010a,b), no change in others (e.g., echinoids: Ries et al. 2009) and reports of increased calcification/growth in some species (e.g., ophiuroids: Wood et al. 2008; asteroids: Gooding et al. 2009; bivalves: Range et al. 2011; cuttlefish: Gutowska et al. 2010a; decapod crustaceans: Kurihara et al. 2008b, Ries et al. 2009). Studies of juvenile bivalves placed in more extreme distant-future ocean acidification conditions for weeks show broad deliterious effects for oysters (pH 7.5/pCO_2 3500) (Beniash et al. 2010) and enhanced growth and survival for clams (pCO_2 1698–4344) (Range et al. 2011). The latter result was attributed to buffering by high local seawater total alkalinity. In 30-week (pH 7.9, pCO_2 1000 ppm; pH 7.6, pCO_2 1900 ppm) exposure to ocean acidification a decrease in survival of adult prawns was observed. There was no change in growth of prawns in the pH 7.9 treatments, but at pH 7.6 a decline in growth was observed after about 6 weeks of incubation (Kurihara et al. 2008b).

It is difficult to assess these highly variable results in the context of future ocean change because experimental outcomes would be influenced by age, environmental history and the nutritive status of the specimens placed in the mesocosms. Some species were fed during experiments (Kurihara et al. 2008b, Ries et al. 2009, Gutowska et al. 2010a,b), but others were not (Wood et al. 2008). These studies do, however, provide valuable insights into the dissolution/calcification dynamics of established juvenile and adult skeletons in ocean change conditions. They indicate that some calcifiers are more robust than others to ocean acidification. It will be important to conduct long-term multigenerational experiments on impacts of climate change stressors for ecologically and commercially important species if deleterious effects are not evident early in their life history.

Dissolution of adult bivalve shells in the field due to influx of low pH water is reported for Antarctic pteropods, for bivalve shells placed in mesocosms and for species living in and around naturally acidic (pH 5.4–7.3) vent water (Manno et al. 2007, Hall-Spencer et al. 2008, McClintock et al. 2009, Tunnicliffe et al. 2009). A significant reduction in settlement of benthic calcifiers is observed at vent sites in the Mediterranean (Cigliano et al. 2010). Studies of deep-sea vent communities showed mussels living in highly acidic conditions (Tunnicliffe et al. 2009). Although clearly adapted to living in corrosive low pH conditions, these mussels had weaker shells and would be more vulnerable to predation than non-vent conspecifics with thicker shells (Tunnicliffe et al. 2009). It has been suggested that the survival of vent mussels in highly acidic conditions requires the presence of protective periostracum over the shell (Tunnicliffe et al. 2009).

There may be latent effects of exposure to increased acidification and hypercapnia. In experiments in which larval echinoderms, abalone, or adult crabs exposed to pH/ pCO_2 treatments were subsequently challenged with thermal stress, the history of exposure to acidification compromised thermal tolerance, aerobic ability, cellular defence mechanisms and gene expression with parameters measured varying among studies (Metzger et al. 2007, Todgham & Hofmann 2009, O'Donnell et al. 2010, Zippay & Hofmann 2010b).

Interactive effects of ocean warming and acidification on fertilization and development

Climate change impacts on invertebrate early life histories have been largely considered in terms of a single factor, but ocean change involves multiple concurrent factors. In assessing risk to marine life histories from climate change it is critical to investigate the interactive effects of stressors because this reflects the situation in the real world (Pörtner & Langenbuch 2005, Przeslawski et al. 2005, 2008, Widdicombe & Spicer 2008, Bulling et al. 2010). Environmental stressors can have simple additive effects (both significant, but no significant interaction) or have complex interactive effects where they have synergistic (increased stress) or antagonistic (decreased stress) effects on biological processes (Folt et al. 1999). Despite the well-known controlling influence of temperature on development and embryonic thermal thresholds, the interactive effects of ocean warming and CO_2-driven acidification on invertebrate life histories are only documented for a few species. Teasing out the interactive effects of climate change stressors is a challenge and requires use of factorial experimental designs.

The interactive effects of concurrent warming and acidification on marine invertebrate life history stages have been investigated in controlled multifactorial experiments with five echinoderm, three mollusc and two crustacean species (Tables 1 and 2, Byrne et al. 2009, 2010a,b, 2011b, Findlay et al. 2010a,b, Parker et al. 2010, Sheppard Brennand et al. 2010).

Fertilization

Exposure to near-future increased temperature (2 to 4°C) and decreased pH (0.4 to 0.6 pH units) conditions in all combinations did not impair fertilization in several intertidal and subtidal echinoid, asteroid and abalone species (Figure 2). There was also no significant interaction between stressors. In multifactorial experiments that incorporated sperm concentration as a third factor, increased temperature was expected to facilitate (increase) fertilization at very low sperm concentrations due to enhanced sperm motility, but hypercapnic narcosis was expected to impair fertilization at low sperm concentrations (Byrne et al. 2010b). However, neither prediction was borne out (Byrne et al. 2010b).

A study of the interactive effect of temperature (cooling and warming) and pCO_2 on fertilization in two oysters (*Saccostrea glomerata*, *Crossostrea gigas*) found that at the optimal fertilization temperature the percentage of fertilization in both species decreased at low pH (pH 7.8, pCO_2 1000 ppm) (Parker et al. 2010).

Resilience of fertilization in many of the shallow-water species listed in Table 1 to climate change stressors may be due to their adaptation to the fluctuating environmental conditions that they experience in nature. A difference may be seen in multistressor studies with species from more environmentally stable (subtidal, polar) habitats. However, as mentioned, the confounding influence of disparate methodologies used in fertilization studies makes interstudy comparisons difficult.

Development

The interactive effect of ocean warming and acidification on development in marine invertebrates is poorly understood. On one hand, decreased carbonate saturation and hypercapnia are expected to impair calcification and suppress metabolism, respectively, whereas elevated temperature would be expected to enhance developmental processes (up to thermal limits). Some researchers speculate that warming might stimulate increased calcification through enhancement of physiological processes involved and thereby buffer or ameliorate the negative effects of acidification (McNeil et al. 2004). Although this speculation is controversial (see Kleypas et al. 2005, Matear & McNeil 2006), there is evidence to suggest that low levels of warming diminish the negative effects of acidification on coral and echinoderm calcification (Kleypas & Yates 2009, Sheppard Brennand et al. 2010, Byrne 2011b).

Available data from multifactorial experiments of the interactive effects of ocean warming and acidification/hypercapnia on echinoderm development show that development is highly sensitive to stress from ocean warming. Surviving larvae and juveniles may be more sensitive to acidification/hypercapnia due to effects on calcification (Byrne et al. 2009, 2010a, Sheppard Brennand et al.

2010). Temperature is the most important stressor to early embryos (to gastrulation) of the sea urchin *Heliocidaris erythrogramma,* with no effect of pH (Byrne et al. 2009, 2011a). There was also no interactive effect of stressors. Because the echinopluteus larva is reduced in *H. erythrogramma* and maternal provisioning is enhanced, the larvae of this species do not need to construct a functional larval skeleton (cf. Figure 3G,N). As a result, development in *H. erythrogramma* may be comparatively more robust to acidification stress. For the echinopluteus larva of *Tripneustes gratilla* warming accelerated development (up to a threshold), and acidification stunted growth (Figure 5). A significant interaction between these stressors indicated that increased temperature diminished the negative effect of acidification on calcification (Sheppard Brennand et al. 2010). Total larval calcification was similar in larvae reared at pH 7.8 and 27°C and those reared in control treatments at pH 8.2 and 24°C (Figure 5). Elevated temperature and acidification both had a negative impact on skeleton development in juvenile *Heliocidaris erythrogramma* (Byrne et al. 2011b). The significant interaction between the effect of stressors indicted that warming diminished the negative effect of acidification on spine formation in the early benthic juvenile.

For molluscs, data on the interactive effects of temperature and pH/$p\mathrm{CO}_2$ on development are available for three species (Parker et al. 2010, Byrne et al. 2011b). In two oysters (*Crassostrea gigas, Saccostrea glomerata*) and an abalone (*Haliotis coccoradiata*) the percentage of normal development decreased with increasing temperature and acidification in larvae reared in experimental treatments from the onset of development (Figure 4). Development in the oysters was facilitated by an increase in temperature (ca. 4°C) but increasing acidification lowered developmental success (Parker et al. 2010). In the oyster study, complex synergistic interactions between the effects of temperature and acidification on development were evident. For abalone, near-future warming and acidification were both deleterious to development, but there were no interactive effects. A 2°C warming and 0.4 unit decrease in pH resulted in developmental failure (Figure 4).

In a study of the intertidal barnacle *Semibalanus balanoides*, warming did not affect growth of post-larvae while low pH (pH 7.7) negatively impacted growth, with no interaction between stressors (Findlay et al. 2010b).

Multistressor experiments indicated that if the thermal threshold for successful development is reached in a warm ocean, embryos may not reach the calcifying stage. Thus, depending on the magnitude of regional warming, the bottleneck for species persistence in local conditions that are changing due to climate may be embryonic thermotolerance. If embryonic development fails due to warming, then the question of comprised larval calcification due to acidification may not be relevant. The impact of climate change on adult organisms means little if development is compromised early in the life cycle.

In addition to data on the impacts of climate change stressors on morphogenesis, empirical data are also needed on the interactive impacts of climate change stressors on developmental physiology and expression of traits important to function and fitness. Alteration of individual traits and sublethal effects (e.g., immune response, respiration, predator detection, sensory ability) not evident from morphology may also be caused by climate change stressors (Thompson et al. 2002, Sultan 2007, Przeslawski et al. 2008, Munday et al. 2009, Hofmann & Todgham 2010). Physiological indices of these sublethal responses may be detected using the biomarker (e.g., heat shock and immune protein expression) or molecular (stress gene expression) approach (Tomanek & Somero 1999, O'Donnell et al. 2009, 2010, Todgham & Hofmann 2009, Nguyen et al. 2011).

There are a few laboratory studies of interactive effects of ocean warming and acidification on the adult phase and epifaunal communities on settlement plates; these have produced mixed results (e.g., corals: Anthony et al. 2008; squid: Rosa & Seibel 2008; seastars: Gooding et al. 2009; brittlestars: Wood et al. 2010, Christensen et al. 2011; communities: Hale et al. 2011). For instance metabolism was negatively affected in the squid, whereas growth was positively affected in the seastar. In the brittlestar

Ophiura ophiura metabolic upregulation was observed in low pH treatments (pH 7.3), but a significant energetic deficit was observed as elevated temperature (4–5°C) was introduced (Wood et al. 2010). For this species temperature was the most deleterious stressor. For *Ophionereis schayeri* complex interactions between warming and acidification were observed (Christensen et al. 2011).

Field studies of benthic communities living near CO_2 vents provided insights into the integrative effects of warming and acidification on benthic invertebrates in the field (Hall-Spencer et al. 2008, Cigliano et al. 2010, Rodolfo-Metalpa et al. 2010). Growth and calcification of vent fauna in the Mediterranean were negatively affected by both acidification and warming (Hall-Spencer et al. 2008, Rodolfo-Metalpa et al. 2010), and seasonal comparisons indicated that increased temperature is of greatest concern (Rodolfo-Metalpa et al. 2010). Insights into potential integrative effects of warming and acidification are also available from coral cores, where the synergistic influence of both stressors decreased the calcification and growth of corals (Cooper et al. 2008). However, these field data do not provide details on the extent and nature of stressor interactive effects.

Persistence and potential for acclimatization and adaptation in a changing ocean

Although placing embryos generated from adults living in present-day conditions into future ocean conditions is environmentally unrealistic, such experiments do provide insights into stressor tolerance levels. They also provide useful information for risk assessment with regard to invasive species and uncertain environmental futures for ecologically (e.g., keystone species) and commercially (e.g., fishery and aquaculture species) important species. Predictive ecological information is needed by managers as they work to mitigate and adapt to likely changes to key marine resources and biodiversity over the coming decades. With respect to outcomes for marine invertebrates, species will (1) tolerate change due to their existing phenotypic repertoire; (2) adapt genetically; (3) migrate or (4) undergo extinction/local extirpation (Peck 2005, Sultan 2007, Przeslawski et al. 2008, Visser 2008, Wethey & Woodin 2008). The outcome for species populations will be influenced by all of these responses.

The oceans have been changing gradually for decades, and some regions are changing more than others (IPCC 2007). Thus it seems likely that some species, populations and faunas have already experienced some phenotypic and genetic change. Gradual warming in some regions (e.g., southeastern Australian waters ca. 2.3°C since 1940; Ridgway 2007) may have promoted increased thermotolerance in species through gradual acclimatization and selection for tolerant genotypes. It is well known that progeny from the same parents can exhibit markedly different sensitivities to stressors, and those that show differential survival represent a subset of tolerant progeny (Galletly et al. 2007, Byrne et al. 2011a,b). Between-population variation in tolerance to stress is also well documented (Johnson & Babcock 1994, Bingham et al. 1997, Gaston & Spicer 1998, Kuo & Sanford 2009, Byrne et al. 2011a, Zippay & Hofmann 2010a, Sanford & Kelly 2011). Because the ocean is changing at a much faster pace than in the geological past, it is not known if adaptive genetic change can occur at a rate that will avoid local population and species extinctions.

Although the potential for evolution on ecological timescales can be significant (Levinton et al. 2003, Bridle & Vines 2006, Carroll et al. 2007), clear-cut evidence for evolutionary adaptation to current climate change stressors appears to be rare (Gienapp et al. 2008). It is not known if the variable expression in stressor tolerance within clutches of embryos from the same parents or within and between the progeny of different populations is solely due to phenotypic plasticity (diverse phenotypes within a single genotype) or if there is some genetic basis to stress tolerance. The potential contributions of phenotypic plasticity and adaptive heritable variation for species persistence in a changing ocean can be explored using the tools of quantitative genetics (Hoffmann & Merilä 1999, Lucas et al. 2006, Evans et al. 2007, Sultan 2007, Foo 2010). This approach may assist in understanding potential genetic constraints on adaptive developmental evolution (Sultan 2007).

Stressor tolerance and phenotypic plasticity

Marine invertebrate life histories may be able to tolerate change in the short term if their existing phenotypic repertoires allow. Phenotypic plasticity provides potential resilience to stressors. An in-built flexibility (polytopy, sensu Hadfield & Strathmann 1996) of life histories to environmental stress is noted for many marine invertebrates. This polytypy probably increases species persistence in geological time (Palmer 1994, Hadfield & Strathmann 1996, Davis 2000). In this situation the phenotype expressed by a given genotype depends on the environmental context in which embryos and larvae develop, that is, a developmental response system (Sultan 2007). Environmentally contingent phenotypic expression will facilitate persistence of species and populations in the short term (Sultan 2007). The scope for developmental plasticity is illustrated in the phenotypic response of sibling sea urchin echinoplutei that alter their feeding structures (larval arms) with respect to available nutrients (for review see Soars et al. 2009). In benthic-pelagic systems, ocean warming has promoted wide phenological shifts due to changes in thermal cues for gametogenesis, induction of spawning and the presence of larvae in the plankton (Hay et al. 2005, Moore et al. 2010). These changes most likely represent phenotypic adjustments as reproductive systems track environmental temperature (Giese & Pearse 1974, Olive 1995), rather than genotypic adaptation.

For species with a broad latitudinal distribution, the concept of physiological races of populations with metabolic temperature compensation to different thermal regimes suggests the presence of substantial phenotypic plasticity to cope with change (Vernberg 1962, Palmer 1994, Sokolova & Pörtner 2001, Stillman 2003, Visser 2008, Zippay & Hofmann 2010a, Sanford & Kelly 2011). Latitudinal differences in the response to heat shock by snail embryos (*Nucella ostrina*) show that embryos from cooler climes are less thermotolerant than those from the warmer parts of their range (Zippay & Hofmann 2010a), but this was not the case for *N. canaliculata* (Kuo & Sanford 2009). There was no correlation between thermal tolerance and biogeography for sea urchin development (*Strongylocentrotus purpuratus*) in gastrulae or larvae transferred from ambient to experimental treatments (Hammond & Hofmann 2010). In contrast incubation of sea urchin embryos (*Heliocidaris erythrogramma*) from the outset of development indicated that embryos derived from warm-acclimatized oocytes (from lower-latitude females) are more thermotolerant than those from cooler-acclimatized oocytes (from higher-latitude females) (Byrne et al. 2011a). The former embryos may sustain less thermal damage due maternal loading of protective factors into eggs (Hamdoun & Epel 2007) much in the same way that warm-adapted adults are phenotypically more thermotolerant due to the accumulation of heat shock proteins (Buckley et al. 2001). Broadly distributed species many also have genotypic variability to facilitate resilience in the face of environmental change (Bradshaw & Holzapfel 2001, Visser 2008, Kuo & Sanford 2009, Sanford & Kelly 2011).

The adults of some marine invertebrates appear to have considerable acid-base regulation capacity and are able to calcify in what would appear to be extreme conditions (Marshall et al. 2008, Wood et al. 2008, Tunnicliffe et al. 2009), but there are few data on acid-base regulation for larval stages (Melzner et al. 2009). Studies of larval cuttlefish showed their considerable ability to calcify in low pH conditions (Gutowska et al. 2008, 2010a,b). For larval development, data from molecular studies of development indicate that upregulation of key metabolic and stress genes occurs in response to warming (corals, Voolstra et al. 2009) and acidification (sea urchins, O'Donnell et al. 2009, 2010, Todgham & Hofmann 2009). It is not known if these changes in gene expression reflect a compensatory adaptive response of the genome or if development is succumbing to stress.

Genetic adaptation

In addition to phenotypic plasticity, variation in success of sibling embryos and larvae to ocean change stressors may be influenced by genetic differentiation. As shown for freshwater and terrestrial invertebrates where environmental stressors select for resistant populations (Bridle & Vines

2006, Derry & Arnott 2007), marine species may have the potential for an adaptive evolutionary response to climate change. A study of thermal limits in intertidal snails indicted the presence of thermally tolerant genotypes in different parts of their range (Kuo & Sanford 2009). Rapid genetic-based adaptation is evident in copepods living in lakes acidified to pH 6.0 for 6–8 years due to SO_2 emissions (Derry & Arnott 2007). Contemporary evolution of stress tolerance is also seen in the genetically based toxicant resistance of a marine oligochaete (Levinton et al. 2003). In the context of climate change, investigation of potential for evolutionary adaptation of marine life histories at range margins and in warming hot spots may be particularly informative (e.g., Bridle & Vines 2006, Somero 2010, Tomanek 2010).

Adaptive changes reflect an integrated response to multistressors (Harley et al. 2006) and will be influenced by generational turnover time. Short-lived species with fast generation times (e.g., temperate copepods, amphipods) are likely to have a greater capacity for evolutionary adaptation to climate change than slow-developing species (e.g., polar species, Smale & Barnes 2008, Fabry et al. 2009). For long-lived species with slow development and long generation times population bottlenecks may exacerbate the problem by reducing genetic variation and limit the scope for an evolutionary response.

Many marine species originated under very different conditions compared with those they experience in their present-day situation, suggesting that some species are ‘exapted’ rather than ‘adapted’ *per se* to modern conditions (Jackson & Johnson 2000). Persistence of species through past extinction events and climate change indicates adaptive capacity across the ontogenetic stages of some species through past climate change (Jackson & Johnson 2000, Uthicke et al. 2009).

Larval migration, range extensions, faunal replacements and extinction

Long-term studies of planktonic larval stages and adult distribution showed that warm-water species extend ranges during warmer periods, whereas colder-water species decline (Southward et al. 1995, Thompson et al. 2002, Wethey & Woodin 2008), although survival patterns of resident species and those that arrive in warm ocean conditions can be complex and contrary to expectations (Schiel et al. 2004). Because new corridors for larval dispersal are being created by ocean warming and changes in circulation, a number of species are exhibiting poleward range shifts as the opportunity and favourable conditions arise (Thatje et al. 2005, Jones et al. 2009, Ling et al. 2009). Range shifts in response to climate change can also be vertical, that is, shallower or deeper, or to different levels in the intertidal zone (Hellberg et al. 2001, Helmuth et al. 2006, Harley & Paine 2009). Patterns in distribution shifts are complex and are likely to be influenced by many environmental factors, with gradual and punctuated changes observed (Harley & Paine 2009).

Range shifts provide a mechanism for some species to escape degenerating conditions due to warming in their normal range. Thus some species may have the potential to keep up with a warming world through poleward migration of thermotolerant propagules and a contraction in warmer parts of their range (Visser 2008, Byrne et al. 2011a). Warm-adapted conspecifics from warming hot spots are also a potential source of thermotolerant propagules to maintain populations (Somero 2010, Tomanek 2010). Prospects appear dire for cold-water, high-latitude species that have little scope to migrate, and extinctions are predicted (Peck 2005, Barnes & Peck 2008, Fabry et al. 2009, Mueter & Litzow 2009, Sewell & Hofmann 2010, Somero 2010, Tomanek 2010). Low-latitude tropical species and species along the intertidal margin are similarly vulnerable (Przeslawski et al. 2008, Tewksbury et al. 2008, Harley & Paine 2009).

Where poleward invasions have occurred, major ecosystem changes have ensued, particularly where keystone species are involved. Examples are the invasive predatory crab (*Lithodes confundens*) to Antarctica and the ‘barrens’-forming sea urchin (*Centrostephanus rodgersii*) to Tasmania

(Thatje et al. 2005, Ling et al. 2009). These invasions are resulting in loss of biodiversity and local extinctions. The interactive effects of multiple stressors and the complexities of biological and ecological responses (Schiel et al. 2004, Przeslawski et al. 2008) however make it a challenge to predict future outcomes. For instance, larvae of the sea urchin *C. rodgersii* and other calcifying larvae in south-eastern Australia may migrate poleward, a process facilitated by increased warming and southerly flow of the East Australian Current, but may face a developmental bottleneck as acidified waters with low mineral saturation expand northward in the Southern Ocean (Richardson et al. 2009, Byrne et al. 2011a).

Thermotolerant frontier tropical, warm temperate and subpolar larvae appear to have the greatest potential to migrate and increase their range in a changing ocean, with species persisting and successfully reproducing in their new habitats (Thatje et al. 2005, Przeslawski et al. 2008, Ling et al. 2009, Figueira & Booth 2010, Parker et al. 2010). Some species introduced for aquaculture (e.g., *Crossostrea gigas*) are likely to be particularly dominant in the future and will outcompete endemic species with more sensitive developmental stages (Parker et al. 2010). Species such as the invasive crab *Carcinus maenus* (see deRivera et al. 2007, Compton et al. 2010) with large latitudinal distributions across broad thermal ranges may have an in-built adaptive capacity across ontogenetic stages (fertilization to adult) to survive and migrate in a changing ocean. Related narrow-range species by contrast are likely to be more sensitive and may go extinct as their more tolerant relatives replace them. This scenario conveys the possibility of ecological redundancy in losses and gains of species that may perform similar ecological functions. Although the copepods in acidified lakes were able to rapidly adapt to a changing environment, most of their associated species were extirpated (Derry & Arnott 2007). Significant loss of marine biodiversity due to climate change stressors seems inevitable.

Evolution of life history modes in a changing ocean

Over evolutionary time many invertebrate clades have deleted a pelagic stage from their life history or have switched from possessing a planktotrophic feeding larva (e.g., Figure 3G–L) to a lecithotrophic non-feeding larva (e.g., Figure 3M,N) (Valentine & Jablonski 1986, Pechenik 1999, Raff & Byrne 2006, Uthicke et al. 2009). Marine invertebrates may have evolved a buffered non-feeding larval life history, free of the vagaries of planktonic food supply in response to stressful conditions in the plankton, including past climate change (Valentine & Jablonski 1986, Pechenik 1999, Uthicke et al. 2009). Significant maternal provisioning in benthic or pelagic progeny provides a buffer against stress by eliminating the need to feed (Figure 3M,N). By contrast, feeding larvae are vulnerable to disruption of planktonic food webs caused by ocean warming, and those that need to calcify will face difficulties in producing their fragile skeleton (Figure 3G–I) as carbonate saturation decreases (Philippart et al. 2003, Edwards & Richardson 2004, Kurihara 2008, Clark et al. 2009, Byrne 2010, Parker et al. 2010, Sheppard Brennand et al. 2010).

For the crab *Lithodes confundens* currently undergoing poleward migration, larval lecithotrophy and cold tolerance may have enabled them to conquer polar ecosystems (Thatje et al. 2005). A meta-analysis of larval type and extinction risk over evolutionary history indicated that echinoderm species with non-feeding, non-calcifying larvae and short development times were more resilient to extinction driven by climate change than species with feeding larvae (Uthicke et al. 2009). In major echinoderm groups there has been differential extinction of species with planktotrophic development through past climate change (Valentine & Jablonski 1986, Uthicke et al. 2009). As seen in the asterinid seastars and temnopleurid echinoids, once echinoderm clades evolve lecithotrophic development this process is irreversible, and subsequent species radiation generates other lecithotrophic developers (Jeffery et al. 2003, Byrne 2006).

Different outcomes for regional faunas and habitats

As detailed in the previous discussion, there are significant differences between species and life history stages in tolerance to ocean change stressors (Tables 1 and 2). These differences are even seen among closely related sympatric species. The weight of evidence (Tables 1 and 2) indicates that life history stages of widely distributed midlatitude intertidal, estuarine and shallow subtidal species may tolerate near-future levels of ocean warming and acidification. Many of these species have a wide physiological tolerance, and some have behavioural and morphological strategies to cope with temperature, pH and other climate change stressors (e.g., salinity, ultraviolet [UV] radiation) (Thompson et al. 2002, Przeslawski 2004, Przeslawski et al. 2005, 2008, Przeslawski & Davis 2007). A review of the responses of rocky shore communities to environmental stressors attests to their remarkable resilience to perturbation (Thompson et al. 2002). Coastal and shallow water species as thermal generalists (*sensu* Pörtner & Knust 2007) may have preadaptive traits to buffer them against ocean change.

In the context of ocean warming and acidification, intertidal and shallow-water temperate species already experience marked fluctuations in environmental pH (ca. pH 6.9–10.1) and hypercapnia due to the diel interplay between respiration and photosynthesis and experience marked temperature fluctuation (ca. 12°C) due to tidal exchange (Truchot & Duhamel-Jouve 1980, Morris & Taylor 1983, Ringwood & Keppler 2002, Björk et al. 2004, Wootten et al. 2008). These changes in environmental stressors far exceed the changes anticipated for global ocean surface waters in the next 100–200 years.

The pH of body fluids of intertidal invertebrates across eight phyla (23 species) measured at low tide ranged from pH 6.8 to pH 7.8 with the coelomic fluid of echinoderms being acidic (pH 6.8–7.0) (Mangum & Shick 1972, Punzo 1977). However, physiological acidosis and warming in the intertidal are experienced as limited duration pulse stressors at low tide. If warming and acidification become permanent press-type stressors then even robust intertidal species may be less able to withstand these conditions. Newly settled juveniles with developing skeletons (Figure 3Q,R) are particularly vulnerable (Arnold et al. 2009, Cigliano et al. 2010, Byrne et al. 2011b). Although the physiological tolerance of shallow-water and coastal species may be a preadaptive feature facilitating persistence of benthic stages (juveniles, adults) faced with ocean change, this is likely to incur increased energetic cost of metabolism (Porter 2007, Pörtner 2008, Widdicomb & Spicer 2008, Hofmann & Todgham 2010).

For faunas of other habitats and regions the potential outcomes of ocean change appear more serious. The developmental stages of thermal specialists from stable low- and high-latitude environments and stenothermal habitats (e.g., poles, equator, deep water) have low scope to tolerate climate change stressors (Stanwell-Smith & Peck 1998, Pörtner & Knust 2007, Przeslawski et al. 2008, Smale & Barnes 2008, Tewksbury et al. 2008). Shallowing of $CaCO_3$ horizons is a concern for deep-water species, and fast warming is a concern for stenothermal species (Turley et al. 2007, Barnes & Peck 2008, Smale & Barnes 2008, Fabry et al. 2009, Sewell & Hofmann 2010). The fate of ecosystems based on structure and habitats generated by biogenic $CaCO_3$ such as shallow- and deep-water coral reefs seems perilous (Hoegh-Guldberg et al. 2007, Turley et al. 2007, Veron 2009). In this case, the potential for developmental adaptation may be irrelevant if their habitat and key associated species (e.g., prey) are compromised. Major habitat change caused by the demise of an ecosystem engineer is seen in the periodic disappearance of corals and associated biota from the fossil record due to ocean warming and acidification and the likely decalcification of corals (Fine & Tchernov 2007, Veron 2009, Kiessling & Simpson 2011).

Conclusion: developmental success in a multistressor world

This review focuses on two stressors: warming and acidification. Although these are the key present-day climate change stressors that affect the life histories of marine invertebrates (Pörtner et al.

2004, Pörtner & Langenbuch 2005), this generalization is an oversimplification. Marine propagules are exposed to multiple stressors from climate change (e.g., salinity, changed disease dynamics, UV radiation) and other anthropogenic influences (e.g., overfishing, pollution), and these stressors are unlikely to act independently (Przeslawski et al. 2005, 2008, Harley et al. 2006, Crain et al. 2008, Byrne 2010). For instance elevated temperature and decreased pH are both well known to exacerbate the toxicity of pollutants (e.g., metals) to life history stages and the performance of key biomolecules (e.g., enzymes) (MacInnes & Calabrese 1979, Knutzen 1981, Cotter et al. 1982, McLusky et al. 1986, Byrne et al. 1988, Millero et al. 2009). Climate change stressors are exacerbating the demise of already-stressed species and ecosystems. Ecosystem resilience will strongly influence future outcomes for species and communities (Thompson et al. 2002, Hughes et al. 2003, Harley et al. 2006, Przeslawski et al. 2008, Brierley & Kingsford 2009).

Understanding the vulnerabilities of marine life history stages is crucial as we endeavour to predict how marine populations and ecosystems will fare in the face of climate change. If development is compromised at an early stage in the life history (Figure 1), downstream consequences are likely to result in local extinction of species. There is an urgent need for multifactorial studies to assess fates for marine biodiversity under uncertain environmental futures (Bulling et al. 2010). Determination of the potential for phenotypic and genotypic adaptation in a changing ocean is crucial to identify potential ‘winners and losers’ in the climate change stakes. This is especially important for abundant and ecologically important species in marine ecosystems (Harley et al. 2006, Brierley & Kingsford 2009).

Earth has entered a new phase in its history, experiencing a pace of climate change far greater than the planet has experienced over evolutionary timescales. Predicting the outcome of the interactive effect of these stressors for marine biota remains a significant challenge.

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