The initial greater calcification seen in the larvae in the HighCO2 treatment at 24 hours post-fertilization is likely evidence of a physiological response to decreased availability of aqueous CO32-. Early *C. gigas* larval shells are made of amorphous calcium carbonate and aragonite (Weiss *et al*. 2002), two of the more soluble forms of CaCO3 at low pH. Mollusc shells are formed by biologically controlled mineralization in compartments that maintain a supersaturation of CaCO3 (Weiner and Dove 2003). Invertebrates are able to control calcification through amorphous mineral precursors and metabolites (Weiss 2011), thus decreasing the potential effects of a corrosive environment. On days 1 and 2, the time when the larvae in the HighCO2 treatment were beginning to calcify, ΩAr was below 1.0, and aragonite was undersaturated in the environment. The larvae were still able to calcify because calcification occurs in a cellular compartment that minimizes exchange with the external environment (Weiner and Dove 2003). However, even with this physiological mechanism, calcification can become energetically costly when CO32- ions become scarce in environment. Additionally, H+ can disrupt the ionic gradients of the calcifying compartment. If oyster larvae remove a fixed number of H+ from their calcifying fluid versus maintaining a fixed ratio of extracellular:intracellular H+, then their energy budget would be more taxed during environmental hypercapnia (Ries 2011). If the acidification event had been transient, as they can be in nearshore upwelling systems, the additional calcification at an early stage could have maintained the organisms until normal conditions were encountered. When the environmental stress proved to persist beyond a certain point (between 24 and 72 hours post-fertilization), the larvae could no longer maintain compensatory processes and eventually growth and calcification were negatively impacted by higher *p*CO2 levels and lower ΩAr. In general, physiological compensation to maintain or increase calcification in a high *p*CO2 environment comes at a cost to other biological processes (Findlay *et al.* 2009). It is likely that other physiological processes were affected, such as soft tissue growth (Gaylord *et al*. 2011; Beniash *et al*. 2010), scope for growth (Stumpp *et al*. 2011a), and shell integrity (Gaylord *et al.* 2011; Melzner *et al*. 2011). Since ocean acidification currently occurs as a more transient stress brought on by upwelled waters and nearshore benthic respiration, larvae that encounter the acidified water at a less vulnerable stage may not be adversely impacted.

Larvae raised at HighCO2 were smaller and less calcified by day 3 post-fertilization, though no delay in developmental progress was observed at the time points observed. The concentration of CO32- was very similar between the MidCO2 and HighCO2 treatments, but there was a big gap when compared to Ambient. The lack of negative effects on calcification in the larvae from the MidCO2 treatment suggests that a cut-off of ΩAr < 1.0 is significant in terms of the ability to biomineralize at this time in development. These results are consistent with other studies of *Crassostrea* spp. larvae in which elevated *p*CO2 resulted in decreased growth and shell mineralization (Kurihara *et al*. 2007; Miller *et al.* 2009). Kurihara *et al*. (2007) raised *C. gigas* to 48 hours post-fertilization at an elevated *p*CO2 of about 2268 µatm, much higher than *p*CO2 projected for the coming century. In contrast to our study, Kurihara *et al*. 2007 reported a negative effect on calcification as early as 24 hours post-fertilization and showed a developmental delay in reaching the D-hinge stage. Similarly, *Crassostrea virginica* larvae raised from 72 hours post-fertilization through competency at different *p*CO2 grew more slowly at elevated *p*CO2 (560 and 800 µatm) and biomineralized less CaCO3 than controls; however *Crassostrea ariakensis* showed no effect of *p*CO2 treatment (Miller *et al.* 2009). It is likely the observed differences between the studies are related to the much higher *p*CO2 level used by Kurihara *et al*. (2007) and species- and population-specific differences in tolerance to environmental hypercapnia. It is also possible that our sampling scheme missed differences between treatments that occurred around the 48 hour post-fertilization mark, which is within the time frame when the transition to D-hinge occurs.

Smaller sized larvae, as observed in the higher *p*CO2 conditions in this study, could lead to several ecological disadvantages. Smaller veliger larvae are not able to feed as efficiently as larger individuals (Strathmann and Leise 1979). Larval sand dollars, *Dendraster excentricus*, responded to increased *p*CO2 through changes in morphology that resembled a starvation response without the usual compensation of longer arms that allow for greater food capture (Chan *et al*. 2011). Exposure to ocean acidification altered the larval sand dollar ciliary beat pattern, thus decreasing the efficiency of particle capture, leading to decreased stomach size (Chan *et al*. 2011). *C. gigas* larvae also depend on ciliary movement for feeding, although the direct effects of ocean acidification on this mechanism are unknown. In this study we cannot determine if decreased ability to acquire food or less available energy for growth is the main cause for stunted larval size, but these combined impacts of ocean acidification could have additive or synergistic effects on larval growth.

Energetic resources can be reallocated under stressful conditions so that some processes can be maintained, but at a cost to others (Findlay *et al.* 2009). In the case of the early development of *C. gigas,* a certain degree of calcification was maintained in the larvae at MidCO2 and HighCO2 and one of the trade-offs in the latter treatment may have been larval size. Oyster larvae in this study likely engaged short-term compensatory mechanisms to attempt to maintain shell formation at the critical time in development as calcification was actually higher in the condition undersaturated for aragonite (HighCO2), a phenomenon observed in adults of other invertebrate species (Findlay *et al.* 2009). Numerous species experience inhibited calcification at Ω < 1.0 (Kurihara *et al*. 2007; Miller *et al.* 2009; Parker *et al*. 2011; Crim *et al*. 2011; Gazeau *et al*. 2011; Byrne *et al.* 2010), though some species are still able to form apparently normal calcified structures in undersaturated conditions (Dupont *et al*. 2010; Catarino *et al*. 2011; Yu *et al*. 2011). Studies on *C. gigas* larvae have previously demonstrated less calcification at high *p*CO2 (Kurihara *et al.* 2007; Parker *et al.* 2010; Gazeau *et al.* 2011). For example, after 72 hours of exposure to low *p*CO2 (approximately 500 µatm), pH of 7.67, and ΩAr of 1.6 (artificially enhanced by excess Ca2+), *C. gigas* larvae had more abnormalities, smaller shell size, and less Ca2+ incorporation than controls (Gazeau *et al*. 2011). Oyster larvae likely have ranges of seawater chemistry to which they can acclimatize. The success of this acclimatization may also depend on whether the broodstock experienced similarly elevated *p*CO2 (Parker *et al*. 2011).

Energetic trade-offs under hypercapnic stress have been observed across species and life stages in aquatic invertebrates. Larval *S. purpuratus* under ocean acidification conditions grew to the same size as their control counterparts and maintained normal nervous system development; however, the trade-off to achieve these developmental landmarks were a longer developmental period, a decreased scope for growth, and physiological impacts at the molecular level (Stumpp *et al.* 2011a and b). Juvenile *Crassostrea virginica* demonstrated evidence of a reduced ability to form CaCO3 shell and overall inhibited somatic growth at high *p*CO2 (Beniash *et al*. 2010). In blue mussels, *Mytilus edulis*, shell corrosion of the nacreous layer at high *p*CO2 is due to energy budget reallocations from the physiological stress (Melzner *et al*. 2011). Larval *M. californianus* showed decreased shell size and strength and decreased soft tissue mass after 5 and 8 days at elevated *p*CO2, with the latter effect being the most significant (Gaylord *et al*. 2011). This result from Gaylord *et al*. (2011) underlines the principle of energetic trade-off during environmental stress, where energy resources were shunted away from soft tissue growth in order to maximize shell integrity.

Decreased size and calcification could be direct impacts of ocean acidification on *C. gigas* larvae, or they could be a consequence of developmental delay that would have been apparent if the experiment had been longer. Larval *Strongylocentrotus purpuratus* were exposed to elevated *p*CO2 throughout their larval period and from this perspective it was apparent that ocean acidification caused a delay in development, although at discrete time points this delay could be interpreted as a slower growth rate (Stumpp *et al*. 2011). If the former is true, then these impacts would have likely persisted and/or worsened as the larval period progressed and resulted in less fit juvenile and adult oysters. If the impacts were a result of a developmental delay, such as the one observed in urchins by Stumpp *et al*. (2011a), then oysters surviving to settlement could have been equally as fit as their control counterparts. However, a delay in development opens the possibility for a host of other complications for pelagic larvae, such as greater potential to be advected to unsuitable habitat (Strathmann 1985), greater chance of being exposed to predators (Underwood and Fairweather 1989), and an overall longer time in the water column where environmental conditions are variable and risky for a free-floating larva. In a regression of shell height versus hinge length (Figure xx), the data across treatment and day did not conform to a 1:1 line indicating that growth was impacted during this time period and observations were not due to developmental delay.

Although *C. gigas* appear to be comparatively robust to moderately elevated *p*CO2, other bivalve larvae are sensitive to similar conditions. In this study, *C. gigas* tolerated the MidCO2 treatment through 3 days post-fertilization, but were sensitive to HighCO2, an emissions scenario that is expected to be reached by the end of this century. An elevated *p*CO2 of 750 ppm (ΩAr of about 1.0) had significant negative effects on hard clam (*Mercenaria mercenaria*) and bay scallop (*Argopecten irradians*) larvae after about 3 weeks of exposure as evidenced by decreased survival, development, growth and lipid synthesis (Talmage and Gobler 2011). The comparable exposure conditions in our study (MidCO2) did not have a negative impact over the time period observed. Due to the similarities of carbonate chemistry parameters with Talmage and Gobler (2011), the differential responses observed across species is likely indicative of variability in species, developmental stage tolerances, or length of exposure. Longer experiments in larvae have demonstrated that the negative effects of ocean acidification persist and sometimes worsen in mussels (Gaylord *et al*. 2011), urchins (Stumpp *et al*. 2011 a and b), abalone (Crim *et al.* 2011), and oysters (Miller *et al.* 2009). Timing of exposure can also be important in terms of larval tolerance. Barton *et al*. (2012) recently demonstrated oyster larvae produced in a hatchery exposed to seawater with ΩAr < 2.0 in the early stages of development are adversely impacted at later stages of larval development, as evidenced by lower yields and survival. Similarly, Sydney rock oyster (*Saccostrea glomerata*) and *C. gigas* larvae that were fertilized in either high *p*CO2 or ambient water and then raised at high *p*CO2 had more adverse effects at the D-hinge stage in the former fertilization scenario (Parker *et al.* 2010).