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Marine gametes in a changing ocean: Impacts of climate change stressors on fecundity and the egg

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ABSTRACT

In marine invertebrates, the environmental history of the mother can influence fecundity and egg size. Acclimation of females in climate change stressors, increased temperature and low pH, results in a decrease in egg number and size in many taxa, with the exception of cephalopods, where eggs increase in size. With respect to spawned eggs, near future levels of ocean acidification can interfere with the egg's block to polyspermy and intracellular pH. Reduction of the extracellular egg jelly coat seen in low pH conditions has implications for impaired egg function and fertilization. Some fast generation species (e.g. copepods, polychaetes) have shown restoration of female reproductive output after several generations in treatments. It will be important to determine if the changes to egg number and size induced by exposure to climate change stressors are heritable.

1. Introduction

Climate change is affecting the oceans through the alteration of currents, sea levels, sea surface temperature (SST), ocean stratification and ocean pH (Hoegh-Guldberg and Bruno, 2010; IPCC, 2014; Howes et al., 2015). These changes are influencing the abundance, distribution, phenology and physiology of marine species, especially ectotherms that have limited physiological regulative capacity (Poloczanska et al., 2013; Przeslawski et al., 2015). Most importantly, as these stressors occur concurrently, their interactive effects can have a negative influence on marine ecosystems (Przeslawski et al., 2015).

Since 1960, 90% of the excess heat in the atmosphere has been absorbed by the ocean and over the past century, SST has risen 0.4–0.8 °C, with warming observed to depths of ~2000m (Sabine et al., 2004; Roemmich et al., 2015). Under a stringent emissions scenario (Representative Concentration Pathway 2.6, RCP2.6) and a high-emissions trajectory (RCP8.5), surface ocean temperatures are projected to increase respectively by 1.2–3.2 °C by 2100 (IPCC, 2014; Gattuso et al., 2015). The oceans are a sink for atmospheric CO_2 and have absorbed around 40% of global emissions (Zeebe et al., 2008; IPCC, 2014). In seawater, dissolved CO_2 forms carbonic acid and causes a decrease in carbonate ion concentration and an increase in bicarbonate ion concentration. This results in a release of hydrogen ions to maintain equilibrium thus lowering pH, a phenomenon known as 'ocean acidification'. Since the industrial revolution, the mean pH of ocean surface water has decreased from pH_{NIST} 8.13 to 8.05, a 26% increase in hydrogen ion concentration. By 2100, ocean pH is expected to drop by 0.14–0.4 units (RCP2.6, 8.5; IPCC, 2014).

Two factors co-vary with CO_2-driven decrease in ocean pH: (1) hypercapnia which is the increase in organism partial pressure of CO_2 (pCO_2), coupled to cell acidosis which can hinder metabolism (Melzner et al., 2009) and (2) the decrease in saturation of calcium carbonate ($CaCO_3$), reducing the availability of carbonate minerals required by calcifiers to build skeletons and shells (Howes et al., 2015; Kerr, 2010). Along with fluctuations in salinity, marine invertebrates are being exposed to multiple ocean change stressors and their response and adaptive capacity to these multistressor environments remains largely unknown (Byrne and Przeslawski, 2013; Foo and Byrne, 2016).

The life cycle of many marine invertebrates involves broadcast

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spawning where eggs and sperm are released and fertilized in the water column followed by development of a planktonic larva before benthic settlement for the juvenile. Numerous studies have focused on the impacts of stressors on sperm, fertilization and development (reviews Byrne, 2011, 2012; Byrne and Przeslawski, 2013; Przeslawski et al., 2015). Meta-analyses have shown that the effects of ocean acidification and warming differ depending on the developmental stage examined (Przeslawski et al., 2015). Studies which find a reduction in fertilization in response to ocean warming or ocean acidification, often attribute this to a negative effect on sperm.

As the swimming behaviour of sperm is key to fertilization success, many studies have documented effects of ocean change stressors on the behaviour of spermatozoa (e.g. Campbell et al., 2016; Graham et al., 2015; Schlegel et al., 2015; Sung et al., 2014). For some species, ocean acidification reduces sperm motility and velocity, possibly due to significant reductions in sperm mitochondrial membrane potential. The sensitivity of the egg to ocean change stressors is poorly understood. As the main parental energetic investment for offspring, often the biggest cell produced by marine invertebrates and critical for fertilization and development, this review focuses on the effects of stressors on the reproductive output of the mother and direct effects on the egg cell. Females might be more sensitive to climate change stressors as there is a higher cost in producing eggs when compared to sperm.

Studies which acclimate mothers in experimental treatments and examine the outcomes for egg production, and egg and clutch size are reviewed. The direct effects of stressors on the egg are also discussed.

2. The impacts of ocean change stressors on female reproductive output

Fecundity and egg quality are strongly linked to maternal environmental history (Braun et al., 2013; Feiner et al., 2016). Of studies that investigate the impacts of environmental stressors on the egg, most involve exposure of females for varying lengths of time to treatment conditions during ovary development and assess the effects on egg size and fecundity (Table 1).

2.1. pH

Single stressor effects of pH on eggs have largely focused on copepods (Supplementary Table of Cripps et al., 2014 provides a review). Effects of decreased pH on copepods have been found to be species-specific with positive (Engström-Öst et al., 2014), negative (Thor and Dupont, 2015; Zhang et al., 2011; Kurihara et al., 2004) or no effects (McConville et al., 2013; Kurihara and Ishimatsu, 2008; Vehmaa et al., 2013, 2015; Zervoudaki et al., 2013; Weydmann et al., 2012) on egg production. The levels at which egg production are affected by pH are far lower than predicted for the next century (pH 7.39, Zhang et al., 2011, pH 6.84, Kurihara et al., 2004). Interestingly, when copepods were transferred back from low pH (~6.84) to control pH, egg production was restored (Kurihara et al., 2004). Thus, copepod reproduction is unlikely to be affected by near future pH levels.

Most studies on the effects of low pH on copepods involve exposing the females to the experimental treatments (Cripps et al., 2014). Different outcomes for egg production are seen depending on whether both males and females are exposed to the same environmental conditions. For *Acartia tonsa*, when males and females were exposed to pH 7.2 for 72 h, the decrease in egg production was much greater than when only females were exposed to pH 7.2. In this study, female and male copepods were simultaneously exposed to treatment conditions to see the effects of low pH on copulation. The result of a larger decrease in egg production when both sexes were exposed shows that paternal environmental history can affect female fecundity, and that this reproductive trait is not solely influenced by maternal environmental history (Cripps et al., 2014).

The impacts of low pH on female reproduction in Crustacea show mixed results, likely influenced by the developmental stage that parents were introduced into treatments (Suckling et al., 2014). For the barnacle *Amphibalanus amphitrite* reared in decreased pH levels of 7.4 from the larval stage to mature adults, there was no effect on egg production (McDonald et al., 2009). After five days acclimation of the copepod *Calanus finmarchicus* in pH 6.95, egg production was not affected (Mayor et al., 2007). On the other hand, the shrimp *Palaemon pacificus* showed a great sensitivity to near future ocean acidification levels with a decrease in egg production when mature females were exposed to pH 7.89 for 30 weeks (Kurihara et al., 2008).

Acclimation of the sea urchin *Echinometra mathaei* in low pH for seven weeks had no effect on oocyte size (Uthicke et al., 2013). For the sea urchin *Hemicentrotus pulcherrimus* acclimated for a much longer period of nine months, there was no effect of low pH on egg number (Kurihara et al., 2013). Similarly, for the oyster *Saccostrea glomerata,* exposure for eight weeks to decreased pH (8.2 vs 7.91) had no effect on egg size or total lipid content (Parker et al., 2017).

In fish studies, for the wrasse Symphodus ocellatus at CO_2 seeps in Vulcano, Italy, there was no difference in the number or size of eggs laid in nesting sites between control and low pH levels. However, dominant nesting males showed a significantly lower number of pair spawns at low pH, demonstrating a negative effect of low pH on male reproductive behaviour (Milazzo, et al. 2016). For the clownfish *Amphiprion melanopus*, low pH stimulates breeding activity, resulting in production of more clutches, more eggs per clutch and an increased egg volume, indicating a positive effect of low pH (Miller et al., 2015, 2013).

There is little information available on the effects of low pH on fecundity in corals. One study examined the long term (6 months) effects of ocean acidification on the coral *Montipora capitata*, finding no effect of low pH (7.8) on the average number of eggs per bundle or total egg production (Jokiel et al., 2008). As the costly process of producing eggs could leave little energy for female corals to sustain calcification rates in an acidifying ocean (Holcomb et al., 2010), the effect of ocean acidification on coral egg production and viability requires further investigation.

The importance of trans- and multi-generational studies to understand outcomes for female reproduction in ocean acidification conditions is highlighted in studies that show that fecundity and egg size can be restored after one or several generations. In a multigenerational experiment with the polychaete *Hydroides elegans*, the negative effects of decreased pH (pH 7.68) on egg production were diminished by the F3 generation (Rodrıguez-Romero et al., 2016).

Although the number of studies and taxonomic coverage are limited, it appears that reproductive output of the females of many species is not impacted by near future levels of acidification as a single stressor (Table 1). For species that are negatively affected, there is restoration of reproductive output after exposure to extreme low pH levels, when returned to normal pH levels (Kurihara et al., 2004) or due to trans- and multi-generational effects (Rodrıguez-Romero et al., 2016). However, an important caveat to note is that these results have not been linked to egg quality, where factors such as lipid contents (with the exception of Parker et al., 2017) and levels of protective chaperone proteins have not been investigated and associated with changes in egg size.