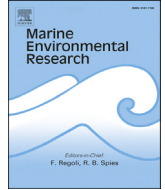




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## Acclimatory processes are likely responsible for metal tolerance in oyster embryos

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## ABSTRACT

We aimed to determine if offspring of oysters from contaminated locations were more tolerant to metals, and whether this tolerance could be attributed to acclimation. Oysters from 10 estuaries were sampled, representing a gradient in metal contamination. Tolerance to metals of the F<sub>1</sub> offspring from adults residing in these estuaries was assessed. Then, adults from these estuaries were translocated to a single estuary and their offspring tolerance reassessed. No linear relationship was found between the Cu concentrations of adults and their offspring's tolerance to Cu. A positive linear relationship was found between the Zn concentration of adults and the Zn EC<sub>50</sub>'s of their offspring. Zn tolerance was lost after translocation. Zn EC<sub>50</sub> values of offspring from transplanted adults bore no relation to the Zn EC<sub>50</sub>'s of their location of origin. Thus the initial tolerance observed could be attributed to acclimation transferred to the F<sub>1</sub> generation.

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### 1. Introduction

Tolerance to metal pollution has been described in many aquatic organisms exposed to metals at sublethal levels (Klerks and Weis, 1987). Organisms living in metal contaminated sites have to enlist physiological and biochemical processes to prevent the toxic accumulation of metals at target sites (Mason and Jenkins, 1995). The organism may respond to this challenge through physiological acclimation or adaptation (the selection of resistant genotypes) (Klerks and Weis, 1987; Johnston, 2011).

Physiological acclimation is a form of phenotypic plasticity, by which an organism can adjust its physiology and/or metabolism in an acute response in order to cope with altered environmental conditions, i.e., heavy metal stress. The tolerance resulting from physiological acclimation is not inherited by offspring or retained by individuals when maintained under non-contaminated conditions. There are three main types of acclimation mechanisms in animals (including molluscs): (1) changes in uptake/elimination rates, (2) increased ability to bind and sequester metals, and (3)

upregulation of enzymes/proteins dealing with oxidative stress induced by metal exposure (Bradley et al., 1985; Posthuma and Van Straalen, 1993; Langston et al., 1998). Conversely, genetic adaptation is an evolutionary mechanism that acts over several generations, by which genotypes with better constitutive or plastic responses toward metal stress, have a higher fitness, and hence increase their abundance in the population. Both acclimation and adaptation are genetically determined, but only the latter creates a shift in the frequency of tolerant genotypes in the population. Genetic adaptation is usually demonstrated (and distinguished from acclimation) by comparing the tolerance response of unexposed lab-reared F<sub>1</sub> generations of the putative adapted and reference populations (Klerks and Weis, 1987; Janssens et al., 2009; Johnston, 2011). If F<sub>0</sub> adults collected from the 'metal polluted' location show differential tolerance to metals in the lab, acclimation or adaptation could be responsible. If lab-reared, F<sub>1</sub> offspring show differential tolerance, adaptation could be invoked as an explanatory mechanism. Preferably, testing should be done on the first and second generations so that maternal effects which are essentially a form of physiological acclimation transferred to the first generation, derived from the mother's response to a contaminant (i.e., transmission of metals, metal responsive mRNAs or proteins, or epigenetic changes in the oocytes) may be explicitly defined (Johnston,

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2011). Further, transgenerational inheritance of contaminant-induced epigenetic effects in non-exposed subsequent generations has been previously demonstrated (Vandegheuchte and Janssen, 2011, 2014). Thus persistent inherited epigenetic modifications are indistinguishable from selection for tolerant genotypes in transgenerational phenotypic tolerance experiments.

In terms of tolerance studies where metals are the contaminant class of interest, most studies have examined differential tolerance of  $F_0$  adults between contaminated and non-contaminated sites and found that chronic exposure to metal contaminants increases tolerance to subsequent metal challenges. For example, Durou et al. (2005), examined tolerance of the worm *Nereis diversicolor* collected from a metal contaminated location and a reference location to Cd, Cu and Zn in the laboratory. Worms from the contaminated location exhibited elevated tolerance to Zn but not to Cd or Cu. Other studies in fish have gone on to examine a possible genetic basis to tolerance and have tested the response of the  $F_1$  generation, raised in clean conditions, to metals. For example, in mosquitofish, *Gambusia affinis*, the 48 and 96 h  $LC_{50}$  values for Cd were significantly higher in fish from a population exposed to elevated Cd in the field compared to a reference population. Similarly, the  $F_1$  generation of the polluted location exhibited 48 and 96  $LC_{50}$  values higher than those of the reference location (Annabi et al., 2009). In such cases, evidence for elevated tolerance could be attributed to adaptation and/or maternal effects transferred from exposed mothers to offspring.

Relatively few studies have sought to explicitly test for maternal effects and gone on to examine tolerance responses of  $F_2$  generation offspring raised in clean conditions. Klerks and Levinton (1989), found evidence for metal adaptation in the oligochaete, *Limnodrilus hoffmeisteri*. Worms from a metal polluted site were more resistant to both sediment metals and metal spiked water than conspecifics from a control site. The resistance exhibited in contaminated site worms was genetically determined, and maternal effects were discounted, as tolerance was still observed in  $F_2$  generation individuals raised in clean sediment. Conversely, other studies that have tested the tolerance of successive generations have found that tolerance can be attributed to acclimation rather than adaptation. For example, Bodar et al. (1990), assessed Cd tolerance in *Daphnia magna* by exposing successive generations ( $F_0$ – $F_2$ ) to sublethal levels of Cd. Resistance (higher Cd  $LC_{50}$ ) was acquired during a single generation, yet the tolerance was abolished in the  $F_1$  and  $F_2$  generations if Cd pretreatment was removed. Thus, there seems strong evidence that organisms can adapt in scenarios where metals act as a selection pressure, dependent on the species, the degree of contamination and genetic variability available for selection to act upon, though acclimation is also a prominent mechanism and the two are not necessarily mutually exclusive. Further, mechanisms of tolerance can vary greatly among taxa and vary dependent on the metal of interest (essential or non-essential).

In order for field-based tolerance to be studied in a species, a series of contaminated and non-contaminated locations must be established. The estuaries of NSW, Australia, range from large coastal embayments and drowned river valleys, such as Port Stephens and the Hawkesbury River, to coastal lakes, such as Lake Macquarie and Wallis Lake, and smaller intermittently open coastal lakes and lagoons. There are several land uses in the catchments of the various estuaries, from intense urban and industrial, to low-intensity rural activities, and this provides a range of potential levels of anthropogenic input in order to create a gradient of metal exposure for assessing tolerance to metals (Scanes et al., 1999). Some estuaries are relatively pristine, non-urban, and have very little history of metal exposure. Other estuaries are highly urbanised and have industrial activities such as smelters, steel works, mining, power stations, industrial chemical plants, coal export/

loading and pulp mills (Batley et al., 2013; Hart and Lake, 1987). The Sydney rock oyster, *Saccostrea glomerata* – formerly *Saccostrea commercialis* – is a native inhabitant of these estuaries, and has been widely used as biomonitor of trace metal contamination in Australia (Brown and McPherson, 1992; Scanes, 1996, 1998; Scanes and Roach, 1999). The oyster exhibits great capacity to accumulate a range of metals from the ambient environment, is a net accumulator of most metals, and appears to be a reliable indicator for metals in estuaries (Phillips, 1979). Scanes and Roach (1999) measured concentrations of trace metals in wild Sydney rock oysters from NSW estuaries. Metals such as Cu (265 mg/kg), Pb (1.1 mg/kg) and Zn (1176 mg/kg) wet weight in oysters from urban/industrialised estuaries were found to be elevated 12, 13 and 4 times, respectively, the background concentrations of oysters from rural catchments (Scanes and Roach, 1999). Native Sydney rock oysters residing in these contaminated estuaries are thus subjected to increased metal exposure stress and may exhibit elevated tolerance to metals. Thus selecting a range of urban and non-urban estuaries in NSW provides a gradient in metal exposure history for oysters to test hypotheses of tolerance of the Sydney rock oyster to metal challenges.

To define whether metal tolerance in a particular species is due to acclimation or adaptation a number of approaches could be undertaken. One approach would be a multi-generational experiment: oysters are collected from estuaries differing in metal loadings (and different gene pools). The  $F_1$  generations are made and then tested for metal tolerance. If the trend of tolerance is positively correlated to metal exposure, adaptation or acclimation could be responsible. The  $F_1$  are then taken and grown to adulthood under clean conditions. The  $F_2$  generation is produced and tested for metal tolerance. If the pattern of metal tolerance is unchanged, implying the tolerance has been transmitted from generation to generation, “adaptation” is the likely mechanism. However, if the tolerance disappears, acclimation due to maternal transfer is likely responsible (Johnston, 2011). Another, more feasible, hypothetical approach to differentiating adaptation and acclimation would be to conduct double  $F_1$  generation tests. Oysters are collected from different estuaries varying in metal loadings (and different gene pools). The  $F_1$  generations are produced and then tested for metal tolerance. If there is a positive relationship between tolerance and metal exposure of adults, adaptation or maternal acclimatory responses may be responsible. After the  $F_0$  adults have spawned, return them all to a single estuary and allow them to mature again. Then a second  $F_1$  is made and the metal tolerance test carried out. If the trend of tolerance remains, adaptation can be invoked. However, if the relationship disappears, it means that acclimation is the most likely mechanism.

When testing for potential adaptation to metal stress using such an approach, it is assumed that the oysters from different estuaries do not experience significant gene flow. However, given the close proximity of some estuaries and the potential for long-range larval dispersal, along with the historic movement of oysters between some estuaries for commercial farming, there is the possibility of significant gene flow among estuaries, meaning detecting adaptation would be difficult. Very little is known about larval dispersal and the genetic structure of populations of the Sydney rock oyster in NSW estuaries. There has, however, been some preliminary research by Banks et al. assessing dispersal and the genetic structure of populations of the Sydney rock oyster among NSW estuaries using microsatellite markers (Banks et al., 2006). They found some limited genetic differentiation between estuaries, but the pattern of genetic differentiation among populations does not fit a typical ‘isolation by distance’ model, whereby genetic differentiation increases with increasing oceanographic distance. Either this is due to the species’ dispersal or it is a consequence of the history of oyster

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