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Factors affecting the toxicity of trace metals to fertilization success in broadcast spawning marine invertebrates: A review

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A B S T R A C T

Significant amounts of trace metals have been released into both nearshore and deep sea environments in recent years, resulting in increased concentrations that can be toxic to marine organisms. Trace metals can negatively affect external fertilization processes in marine broadcast spawners and may cause a reduction in fertilization success at elevated concentrations. Due to its sensitivity and ecological importance, fertilization success has been widely used as a toxicity endpoint in ecotoxicological testing, which is an important method of evaluating the toxicity of contaminants for management planning. Ecotoxicological data regarding fertilization success are available across the major marine phyla, but there remain uncertainties that impair our ability to confidently interpret and analyse these data. At present, the cellular and biochemical events underlying trace metal toxicity in external fertilization are not known. Metal behavior and speciation play an important role in bioavailability and toxicity but are often overlooked, and disparities in experimental designs between studies limit the degree to which results can be synthesised and compared to those of other relevant species. We reviewed all available literature covering cellular toxicity mechanisms, metal toxicities and speciation, and differences in methodologies between studies. We conclude that the concept of metal toxicity should be approached in a more holistic manner that involves elucidating toxicity mechanisms, improving the understanding of metal behavior and speciation on bioavailability and toxicity, and standardizing the fertilization assay methods among different groups of organisms. We identify opportunities to improve the fertilization assay that will allow robust critical and comparative analysis between species and their sensitivities to trace metals during external fertilization, and enable data to be more readily extrapolated to field conditions.

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1. Introduction

Trace metals occur naturally in the marine environment but significant amounts have been discharged into both nearshore and deep sea environments in recent years, resulting in elevated levels that can be toxic to marine organisms (Hassan, 2006; Mason and Jenkins, 1995). Metal inputs are permanent additions to the marine environment. They do not get broken down by bacterial action and rendered inert. Metal contamination occurs primarily as a result of land-based activities, with rivers and estuaries acting as conduits for metals into the coastal and deep sea environment (van den Hove and Moreau, 2007). They are most notably associated with the mining and metal processing industry, and also enter the marine environment via industrial, sewage and stormwater discharges, anti-fouling paints and urban/agricultural run-off (Hart and Lake, 1987).

Ecotoxicological testing is an important tool used to evaluate the potential toxicity of trace metals and other environmental contaminants to inform ecosystem management (van Dam et al., 2008). Early-life stages of marine organisms are used extensively in ecotoxicological assays because it is generally agreed that they are more sensitive to chemical contaminants than their adult counterparts (reviewed by His et al., 1999). Pelagic stages are exposed in the water column, and thus multiple environmental factors can impact upon their success and development. Fertilization success is an important endpoint in ecotoxicological assays because it is sensitive, exhibiting a measurable dose-response relationship at metal concentrations similar to those found in polluted environments. It is also ecologically relevant because it has a direct bearing on the dynamics of recruitment and natural populations (Shea, 2011). Both USEPA (1995, 2002) and Environment Canada (2011) have developed standard aquatic fertilization assays using sea urchin and sand dollar gametes, which are used to evaluate the toxicity of effluents to coastal marine waters and estuaries.

Many studies have documented the negative effect of metals on external fertilization in marine invertebrates. Ecotoxicological data exist for all the major marine phyla and are used in the derivation of water quality guidelines (ANZECC/ARMCANZ, 2000; USEPA, 2002). However, there remain some uncertainties that impair our ability to confidently interpret and extrapolate these data. There is little information on precisely how metals affect fertilization (see Fitzpatrick et al., 2008) and this diminishes the extent to which we can reliably estimate the probability and extent of a toxicant's harmful effects (Shanker, 2008). The toxicity of a given trace metal is intimately linked to chemical speciation, which is governed by the physico-chemical nature of seawater and can be variable in dynamic coastal waters (Elder, 1988). However, metal speciation is not always considered during ecotoxicological testing and data analyses. Indeed, of the ecotoxicological data examined in this review (see Table 1), only one study has attempted any predictive or measured speciation study (Ward et al., 2006). There are also differences in experimental designs between studies, which may influence the variation in species' sensitivities across a range of invertebrate taxa with the same mode of fertilization (external). This limits our ability to draw direct comparisons between species.

This review aims to resolve some of the uncertainty surrounding fertilization success as a toxicity endpoint by considering the process of fertilization, metal toxicity and speciation, and the influence of experimental design, to enable us to accurately interpret data by adopting a more holistic view of metal toxicity. By exploring the fine-scale process of fertilization and the individual gametes themselves, possible mechanisms for metal toxicity will be highlighted. In considering the theoretical basis of metal behavior and speciation in marine waters, we can aid in the interpretation and prediction of bioavailability and toxicity. Finally, by scrutinizing differences in methodologies between fertilization assays, we can improve our ability to discern between genuine trends and artefacts of the experimental design.

2. Fertilization as an ecotoxicology endpoint

2.1. Biology of fertilization

Fertilization, in its simplest form, is the fusion of two specialized gametes to form a single viable cell – the zygote (Rosati, 1995). Many marine organisms have external fertilization, whereby eggs and sperm are released into the environment, and this is thought to be an ancestral reproductive strategy (Lotterhos and Levitan, 2010). Behaviors such as spawning aggregations and synchronous gamete release (Babcock and Mundy, 1992; Harrison et al., 1984) greatly increase the likelihood of gamete interaction, and species-specific sperm chemotaxis also increases gamete encounters and reduces hybridization (Riffel et al., 2004).

Once the gametes have come in contact with one another, the sperm binds to the egg and makes passage through the egg membrane. Entry of the sperm is facilitated by the acrosome reaction in several marine invertebrates (Niijima, 1963; Talbot and Chanmanon, 1980). When the acrosome of the sperm comes in contact with the extracellular matrix of the egg, the acrosome reaction (AR) is triggered. This causes the contents of the acrosome to be released and digest a passage through the egg envelope, allowing the spermatozoa to reach the egg surface (Baccetti, 1985; Levine et al., 1978). The second stage of the AR involves the extension of the acrosomal process/filament, which makes contact and fuses with the egg plasma membrane and facilitates the entry of the sperm (Franklin, 1970). However, not all marine invertebrates, including most cnidarians, have a specific acrosome (Harrison and Jamieson, 1999).

Entry of the sperm into the egg triggers a variety of metabolic changes referred to as egg activation (Gilbert, 2000). The primary response of the egg upon sperm penetration is a rapid, transient depolarization of the membrane potential that effectively prevents another sperm from entering the egg, preventing polyspermy (Jaffe, 1976; Rothschild and Swann, 1952). This brief depolarization is supplemented by a second and permanent block to polyspermy (Schatten and Chakrabarti, 2000), where the cortical granules of the egg are exocytosed and the vitelline coat becomes elevated and hardened to form the fertilization membrane (Gould and Stephano, 2003), rendering the egg impermeable to spermatozoa (Schuel et al., 1973). Cnidaria do not have a vitelline coat like higher invertebrates, but a cortical reaction occurs in some sea anemones when exposed to sperm (see Harrison and Jamieson, 1999). Once inside the egg, the sperm undergoes several changes and becomes the pronucleus; the entry of the sperm also initiates the second meiotic division of the egg, resulting in a haploid egg nucleus known as the female pronucleus (Gilbert, 2000). The male pronucleus then