



Acclimation effect and fitness cost of copper resistance in the marine copepod *Tigriopus japonicus*☆

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ABSTRACT

Copper (Cu) contamination is common and widespread in coastal marine environments. This study used the marine copepod *Tigriopus japonicus* to test whether Cu resistance can be developed through multigeneration acclimation to elevated Cu levels and whether the resistance has a fitness cost. *T. japonicus* (F0) were acclimated to three Cu concentrations (0, 10, and 100 µg l⁻¹) and offspring (F1 and F2) of each treatment were subsequently acclimated at these three concentrations, respectively. Our results evidently indicated that Cu resistance of the copepod was increased even after one generation of acclimation to 100 µg Cu l⁻¹. The acquired Cu resistance had a fitness cost, as the intrinsic population growth rate of this Cu resistant lineage was significantly lower than the control. The Cu resistance of the offspring from Cu resistant copepods, when raised under control conditions, returned to a level comparable to the control implying a plastic physiological adaptation.

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1. Introduction

Copper (Cu) is an essential micronutrient for aquatic animals but can cause toxic effects at elevated concentrations (White and Rainbow, 1985). Its contamination is common and widespread in coastal marine environments (Hall and Anderson, 1999). In uncontaminated seawater, the Cu concentration would be about 0.15 µg l⁻¹ (WHO, 1998). But in coastal areas severely affected by human activities (e.g., discharge of municipal wastewater and industrial effluents, and application of Cu-based antifouling paints), Cu concentrations can often exceed 100 µg l⁻¹ (Bowen, 1985; Nriagu and Pacyna, 1988). Ironically, Cu released from Cu-based antifouling coatings on ship hulls becomes a major source of Cu contamination in marine environments (Valkirs et al., 2003). Since the partial ban of organotins in many countries in the early 1990s, Cu-based antifouling paints have been regaining popularity and gradually replacing organotin-based antifouling paints (Voulvoulis et al., 1999; Srinivasan and Swain, 2007). The emission rate of Cu from antifouling paints on boats can vary

greatly, ranging from 0.2 to 65 µg cm⁻² day⁻¹, depending on the structure of the paint coating and environmental conditions (Valkirs et al., 2003; Schiff et al., 2004).

It has been shown that multigeneration acclimation to elevated Cu concentrations can result in an increased Cu resistance in the freshwater flea *Daphnia magna* (Bossuyt and Janssen, 2003, 2004). Such an increase in resistance has been commonly believed to have two causes: (1) organisms may acquire resistance by physiological acclimation through exposure to sublethal concentrations of the pollutant during some period of their life span, or (2) populations may evolve a genetically based resistance through natural selection (Klerks and Weis, 1987). In general, it has been shown that such increased metal resistance in aquatic organisms is often associated with a trade-off in fitness cost. For instance, Xie and Klerks (2004) demonstrated that the killifish *Heterandria formosa* with a developed resistance through multigeneration exposure to cadmium, exhibited a significantly lower fecundity and produced smaller sized offspring than the control populations.

Good understanding of the acclimation effect on Cu resistance of marine organisms at population level is crucial in assessing the long-term effects of Cu in the marine environment. To date, acclimation effect to metals has only been studied with freshwater organisms, such as daphnids (e.g., Muyssen and Janssen, 2002, 2004) and killifish (e.g., Xie and Klerks, 2003, 2004). The acclimation effect to metal in marine animal species has not yet been explored.

☆ Experimental animals were conducted in accordance with national and institutional guidelines for the protection of animal welfare, with due consideration for the alleviation of distress and discomfort.

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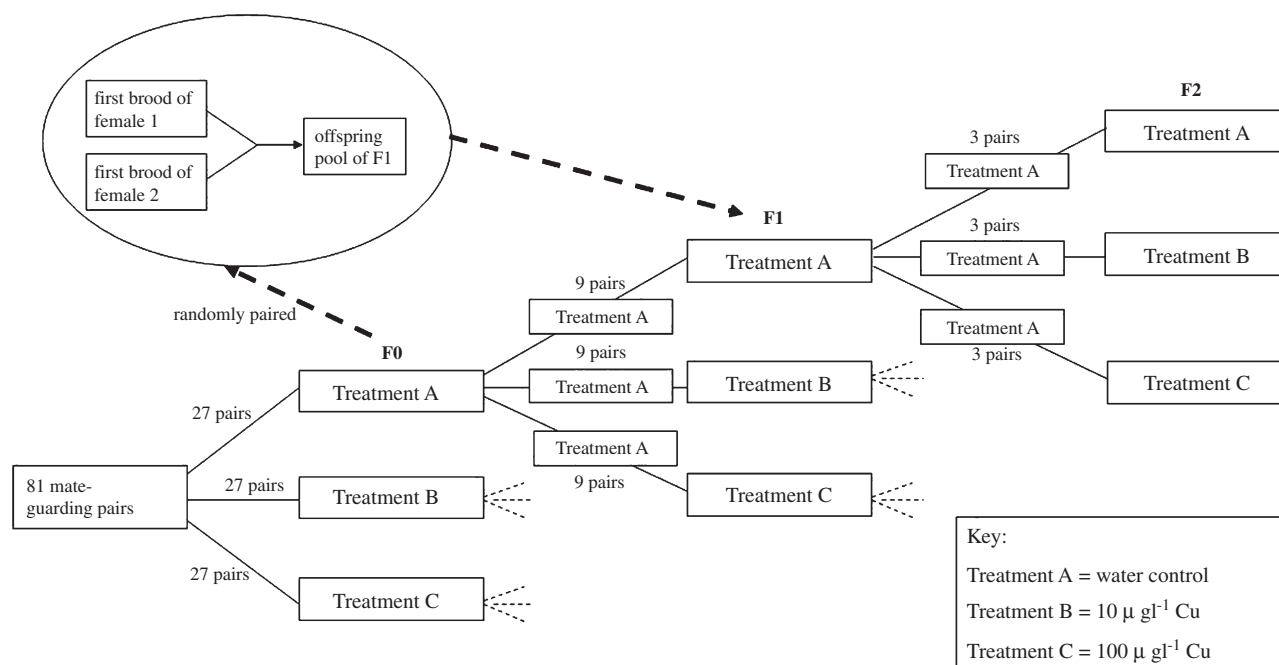


Fig. 1. Schematic illustration of the experimental design showing all the lineages from generation F0 to F2, from which each mate-guarding pair was randomly selected.

The intertidal harpacticoid copepod *Tigriopus japonicus* is commonly used in marine ecotoxicological studies (Raisuddin et al., 2007). In our previous study, we observed that *T. japonicus* in Hong Kong exhibited a high resistance to Cu with a 96 h median lethal concentration over 1 mg l⁻¹ (Kwok and Leung, 2005). As an urbanized metropolitan city and busy international shipping port, coastal waters of Hong Kong are inevitably contaminated with Cu ranging from 7 to 11 µg l⁻¹ (Wang et al., 2003). Given such high ambient Cu concentrations, it was hypothesized that Hong Kong's *T. japonicus* acquire Cu resistance through multigenerational acclimation to elevated Cu. The purpose of this study is to determine whether increased Cu resistance in *T. japonicus* can be established by multigenerational acclimation to elevated Cu concentrations and examine whether there is a fitness cost associated with any increased Cu resistance.

2. Material and methods

2.1. Test organisms

T. japonicus were obtained from established laboratory culture originated from supralittoral rock pools in the Cape D'aguilar Marine Reserve, Shek O, Hong Kong. The culture was maintained at pH 7.8–8.1; temperature 25 ± 2 °C; salinity 32 ± 2‰; 16:8 light:dark period. Commercial phytoplankton concentrate (Kent Marine PhytoPlex, USA) and ground green algae *Enteromorpha* sp. were used to feed the copepods.

2.2. Multigeneration stress resistance experiment

Eighty-one mate-guarding pairs of *T. japonicus* (henceforth referred to as generation F0) in which the females were at copepodid stage 5, were randomly chosen from the laboratory culture. Throughout the multigeneration study, laboratory conditions were well maintained with seawater pH at 8.0–8.1, water temperature at 25 ± 1 °C, salinity of 33 ± 0.5‰, and a 16:8 h light:dark photoregime. After 48 h of acclimation to test conditions, the cohort was divided into 3 groups of 27 pairs and each group was, respectively, exposed to nominal Cu concentrations of 0 (control), 10, and 100 µg Cu l⁻¹ for 25 days. The 10 µg Cu l⁻¹ concentration was considered representative of the Cu concentration in Hong Kong coastal waters while the 100 µg Cu l⁻¹ was investigated as an extreme scenario. All the 81 mate-guarding pairs were fed the commercial phytoplankton concentrate (Kent Marine PhytoPlex, USA) throughout the experiment. Each pair was kept in a separate 50 ml beaker containing 25 ml of test solution and 50 µl phytoplankton

concentrate, which was renewed once every 48–72 h. The males were removed once the female had developed the first ovisacs to prevent predation of the nauplii (Lazzaretto and Salvato, 1992). The number of broods and number of nauplii in each brood produced by the female were then recorded daily. The first brood of nauplii produced by each female was isolated and initially cultured in a beaker containing solution at the same Cu concentration as the mother. When the nauplii reached the copepodid stage 1, they were transferred to clean artificial seawater (33‰; Tropic Marine, Germany) for 8–10 days to facilitate more rapid development, until they reached copepodid stage 5. To avoid inbreeding, individuals were simultaneously mixed with the first brood of another female exposed to the same Cu concentration. Two mate-guarding pairs were then randomly selected from this sample and the same process was repeated in the next generation (henceforth referred to as F1) and subsequent generation (henceforth referred to as F2) as shown schematically in Fig. 1.

Because of limited space in environmental chambers, the experimental design was chosen to ensure that the total number of individuals kept under observation within each generation was held constant (at 81 individuals). The remaining individuals were subjected to a 96 h acute mortality test in which they were exposed to 0, 750, and 1000 µg Cu l⁻¹ (control, 96 h-LC30 and 96 h-LC50, respectively). The procedures of this acute mortality test were identical to those described in Kwok and Leung (2005). All the environmental conditions for both the acute tests were identical to those adopted in the multigeneration study. Average mortality in the acute test was used as an indicator of Cu acute resistance of different treatment groups of *T. japonicus* (Xie and Klerks, 2003). The same experimental protocol was repeated for individuals from F1 and F2.

The term 'lineage' is henceforth used to denote the ancestral exposure treatments encountered in the maternal line of a given cohort. For conciseness, we denote the treatment concentrations by A (= control), B (= 10 µg Cu l⁻¹) and C (= 100 µg Cu l⁻¹) where the letter sequence associated with a particular lineage specifies all ancestral maternal treatments, with the earliest ancestor on the left. So for example, in the F1 exposures, the lineage A represents individuals descended from parents that were raised under the control concentration in F0. In the F2 exposures, the lineage CA represents individuals descended from F1 parents raised under the control concentration (A) and F0 grandparents raised under 100 µg Cu l⁻¹ (C).

2.3. Metal analysis

To estimate the measured Cu concentrations in test solutions of the three treatment groups (i.e., the control, 10, and 100 µg Cu l⁻¹), freshly prepared testing solutions of each group were sampled in three different occasions (i.e., $n = 3$) and subject to Cu quantification. The Cu concentrations in the water samples were determined using atomic absorption spectrometry (AAS, Perkin-Elmer, Analyst 800, Wellesley, MA, USA) after appropriate dilution. Accuracy of the analysis was checked regularly using the standard reference material (oyster tissue 1566b, National Institute of Standards and Technology, Gaithersburg, MD, USA, within batches). The detection limit of Cu was 1 µg Cu l⁻¹ and the accuracy of the analysis

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