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*Short review*

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## THE EFFECT OF SALINITY ON FRESHWATER CRUSTACEANS

**ABSTRACT:** Recent advancing industrialization and urbanization have increased salt concentrations in formerly-freshwater habitats. Freshwater animals are being affected, especially those like crustaceans that are unable to emigrate to escape the problem. The effects of increased salinity, first observed at the molecular level, are found to extend to the levels of the individual, population, community and ecosystem. Crustacean morphology, behaviour and life histories may be influenced, with growth rate, and age and size at first reproduction, being disturbed, along with clutch and neonate size. Mortality rates are also elevated where the salt concentration is high, though susceptibility to salt differs both between species and between clones of the same species. The effect may be to modify the composition of crustacean assemblages in terms of the species and clones present.

**KEY WORDS:** phenotypic plasticity, salinity, life history, morphology, behaviour freshwater crustaceans

### 1. INTRODUCTION

Since saline and freshwater environments require completely different adaptations if the animals inhabiting them are to retain suitable osmotic pressure and cell homeostasis, most aquatic organisms are unambigu-

ously characteristic of either one habitat or the other (Young *et al.* 1989). Nevertheless, as salinity varies markedly in many habitats, such as estuaries or coastal lakes (Hall and Burns 2002, Schallenberg *et al.* 2003), local populations may be characterised by the presence of micro-evolutionary changes, the widening of tolerance ranges and greater phenotypic plasticity. There are many studies describing these various aspects to enhanced tolerance in types or groups of animals exposed to salinity constantly during their evolutionary history (i.e. those originating from salt and brackish waters).

Freshwater invertebrates have been submitted over a long period of time to selection to cope successfully with the low osmotic pressure of their present habitat. Their adaptations to live in low salt concentrations and low osmotic pressure, however, are presently being subject to an unexpected test in waters enriched with salts due to ongoing industrialization and urbanization, e.g. with mine waters and storm-drain runoff from streets treated with salt in winter. As the tolerance (or lack of tolerance) to high salinity in freshwater animals is poorly recognized, particularly in invertebrates which are not mobile enough

to swim away from affected habitats, the aims of this mini-review are to present the current state of knowledge of the effects of salinity on freshwater crustaceans, from the molecular level through to the ecosystem and landscape level, and to identify the areas in which further studies are needed.

## 2. THE MOLECULAR LEVEL

While the reaction of an organism to its environment is initiated by a molecular response, the nature of this kind of response in freshwater crustaceans exposed to salinity has only gained preliminary recognition, being revealed as a distinct modification of the protein pattern in copepods (Gonzalez and Bradley 1994). However, the precise role of the proteins whose concentrations change with exposure to increased salinity remains unknown. One exception concerns knowledge of heat-shock proteins and their chaperoning role. An increase in concentrations of HSP 60, 70 and 90 is to be noted in *Daphnia* after a sudden increase in salinity, and this reaction can be explained in terms of the protection of native proteins and repair of those that are damaged. Otherwise, this type of reaction (for HSP 70) has only been described once – in marine bivalves (Werner and Hinton 2000).

Weider and Hebert (1987) suggested that amino acids could also change concentration in a period of salt stress. Indeed, some clones of *Daphnia* are able to lower the osmotic gradient between the internal tissues and the external environment, precisely by adjusting internal levels of free amino acids. This ability is shown to raise tolerance to salinity changes.

There are virtually no data on freshwater crustaceans' possession (or not) of the kinds of molecular adaptations to variable salinity shown by marine crustaceans, e.g. drastic modifications of ion concentrations and ratios (e.g. Lin *et al.* 2000), changes in enzyme activity (e.g. Lucu *et al.* 2000) or changes in the concentrations of molecules participating in osmotic regulation (e.g. Vesely and Vesely 1999).

## 3. PHYSIOLOGY

Salinity is an abiotic factor delineating the environmental optimum for freshwater crustaceans. Optimal salt concentrations for freshwater crustaceans vary from a level of around zero through to roughly 2‰ (Jeppe-*sen et al.* 1994). According to Horrigan *et al.* (2005), comparisons with other freshwater animals point to the existence of salinity-tolerant crustaceans (e.g. *Cladocera* and *Palaeomonidae*) and very salinity-tolerant ones (e.g. *Copepoda*, *Ostracoda* and *Parastacidae*). Salt concentrations higher or lower than the optimal but still within the tolerance range play a role as stress factors capable of causing changes in physiology, behaviour, life history and morphology.

Salinity-dependent modifications to the life histories of freshwater crustaceans (as described below) suggest the possibility of salinity-dependent modifications to physiological processes, though the relevant data are again scarce and limited to those described by Arner and Koivisto (1993). These authors suggest that respiration and ammonium-excretion rates in *Daphnia magna* Strauss are lowest where salinity is optimal. Active regulation of internal salinity under the influence of too high or too low salt concentration entails an increased respiration rate, since osmotic regulation is associated with increased metabolic rate.

There is no information available on the possible impact of salinity on other physiological processes, and nor are there known salinity-dependent changes in the functioning of the osmotic-regulation system, e.g. in the effectiveness and selectivity of ion transport through the body surface and cell membranes, as are well described in animals living under saline conditions.

## 4. BEHAVIOUR

In contrast to large marine crustaceans like lobsters, which can increase mobility with a view to leaving local patches of high salinity (Dufort *et al.* 2001), their freshwater "cousins" are not yet known to possess any similar mechanism. We have found only two published examples of behavioural responses to salinity in freshwater crustaceans. Bail-

lieut and Blust (1999) found a reduced swimming speed in *Daphnia magna* when exposed to high salinity level. This could simply reflect an increased cost of living under toxic conditions due to damaged physiological machinery. It could also be related to the need for detoxification and thus reduced ability to invest in other requirements, or be a simple consequence of altered viscosity of the medium. Harder (1968) observed aggregation behaviour in zooplankton responding to increased salinity but did not suggest any advantages in terms of fitness. Like other organisms exposed to salinity stress, *Daphnia* can probably increase ion-uptake rate (see e.g. Aladin 1991). This would imply a markedly lower salt concentration within a dense aggregation of animals, as opposed to outside. Thus swarming behaviour could presumably reduce salinity stress to aggregating individuals, though this hypothesis would need verifying experimentally.

### 5. LIFE HISTORY

Salinity can affect such parameters of life history as lifespan, growth rate, age and size at first reproduction, offspring size and number, all of which are crucial to fitness. Lethal salt concentrations differ between the taxonomic groups of freshwater crustaceans. Thus, the LC50 lethal salt concentration for *Daphnia magna* varies from 5491 to 5736 mg NaCl L<sup>-1</sup> (Casey *et al.* 2000). Our unpublished results indicate that these values differ from one clone to another. However, the effect of salinity can be modified by other abiotic factors, albeit with the pattern of these modifications varying. A strong interaction between effects of temperature and salinity on survival in *Daphnia magna* has been demonstrated, a high temperature compounding the harmful effect of the salinity (Casey *et al.* 2000). Even where it does not reduce lifespan, salinity may limit individuals' growth rates, with freshwater animals transferred to a brackish environment found to grow more slowly: as with *Daphnia carinata* (Hall and Burns 2002) and *D. magna* (Teschner 1995, Arner and Koivisto 1993).

It is usual for a stress factor influencing growth rate to have a knock-on effect on size and age at first reproduction. As animals

grow more slowly where salt concentrations are higher, more time is needed for the optimal size for reproduction to be reached. Such delays in the onset of reproduction have been observed for salt-stressed horseshoe crabs *Limulus polyphemus* (L.) (Ehlinger and Tankersley 2004), copepods of the species *Gladiferens imparipes* Thompson (Payne and Rippongale 2001) and cladocerans *Daphnia carinata* King (Hall and Burns 2002) and *D. magna* (Arner and Koivisto 1993). Salinity can cause both delayed maturity and a smaller size at first reproduction, as Teschner (1995) showed for *Daphnia magna*. Also our unpublished data on the response to salinity by two *D. magna* clones have shown inter-clonal differences in the way the trade-off was resolved between body size and age at first reproduction in increased salinity. Whereas the *D. magna* clone

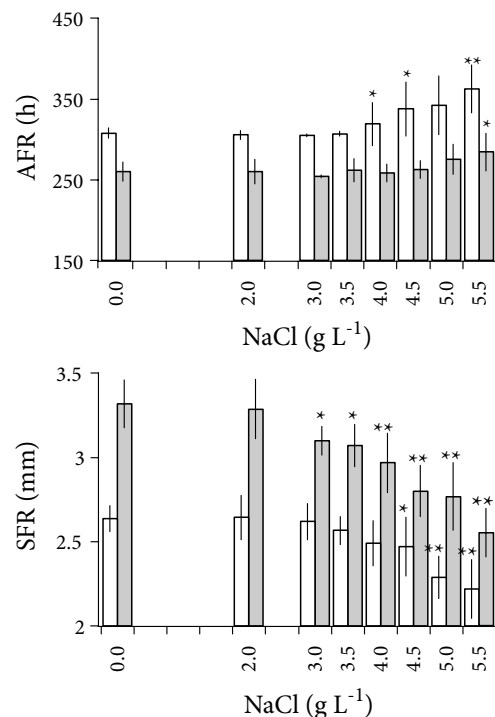


Fig 1. Age at first reproduction (AFR) and size at first reproduction (SFR) in females from two clones (Binnensee clone – open bars, and city clone – dashed bars) of *Daphnia magna* cultured from birth to first reproduction in 8 salt concentrations (temperature: 20°C, food: 1 mg C<sub>org</sub> L<sup>-1</sup>; medium changed daily); \* –  $P < 0.01$ , \*\* –  $P < 0.001$  (comparison with control group: 0 mg of additional salt, T-Tukey test).

originating from the periodically-brackish Binnensee responded to high salinity by delaying reproduction, the clone originating from a small water body in an urban environment of Warsaw started reproduction at smaller body size (Fig. 1). Unfortunately, comparisons between the two clones have not revealed any data so far to draw any general conclusion on the mechanism underpinning this inter-clonal difference.

Small female size at the time offspring are released influences both body and clutch sizes. Freshwater animals release fewer neonates in a saline than in a freshwater habitat – a regularity known from *Branchipus schaefferi* Fisher (Sarma *et al.* 2005), *Daphnia magna* (Arner and Koivisto 1993, Teschner 1995, Martinez-Jeronimo *et al.* 2005), and *Moina hutchinsoni* Brehm (Martinez-Jeronimo and Espinosa-Chávez 2005).

Most of the above life-history changes relate to the costs of living in conditions of salinity-induced stress. There is no clear evidence that freshwater crustaceans at risk of exposure to saline conditions display adaptive modifications of their life histories. This may reflect high costs of living under salinity stress that overshadow potential adaptive changes.

## 6. MORPHOLOGY

For Kikuchi (1983), the gills and digestive tracts of crustaceans are their basic osmoregulatory organs, with changes in salinity capable of modifying gill morphology in *Daphnia*, for example. These changes affect the so-called dark cells in particular, these being rich in mitochondria and possessed of an elaborate tubular system and modified cell membrane. It is probable that they play an important role in osmoregulation.

Aladin (1991) described round nuchal (neck) organs in *Daphnia magna* embryos, whose cytoplasm is seen to be very condensed and capable of intensive cellular absorption of salt on account of high permeability to ions. Adult *Daphnia* do not rely on such neck organs, relying instead on the absorption of salt with food.

An increased concentration of salt in water changes its physical characteristics, for

example increasing density and changing viscosity and flow characteristics (the Reynolds number). This ought to have consequences for optimal body shapes of animals and the structures of their filtering organs (see e.g. Rubenstein and Koehl 1977), but there appear to be no published data describing such phenomena.

## 7. POPULATION, COMMUNITY AND ECOSYSTEM

There are a number of aquatic inland ecosystems in which excessive salinity often becomes a serious limiting factor for freshwater animals. Green (1993), Jeppesen *et al.* (1994) and Schallenberg *et al.* (2003) all revealed differences between clones and species as regards salinity tolerances, which could result in sub-lethal salt concentrations drastically changing the clonal and species composition of freshwater communities. The role of the major systematic groups in an ecosystem may also change, as when *Daphnia*'s place as the main algal consumer in habitats of salinity below 2‰, is taken in more saline habitats by *Eurytemora* and *Acartia*. Furthermore, the predation pressure experienced by zooplankton is generally higher – and the algal grazing capacity lower – in brackish lakes than freshwater lakes (Green 1993, Jeppesen *et al.* 1994, Schallenberg *et al.* 2003).

## 8. LANDSCAPE

Tolerance of salinity would also seem to have been important in determining the geographical distribution of species. The logically-derived “rule” that more-tolerant species ought to be more widespread is famously exemplified by the Darwinulidae, Van Doninck *et al.* (2003) suggesting that their widest distribution reflects their broadest level of ecological tolerance. Hairston *et al.* (1999) was in turn of the opinion that tolerance to salinity may facilitate dispersion and, hence, promote invasiveness in such species as *Daphnia exilis* Herrick. As Ricciardi and MacIsaac *et al.* (2000) showed, successful dispersal, e.g. via ballast tanks, requires that otherwise-freshwater animals spend long periods in salty water. However, even the resting forms of crustaceans are not

all salt-resistant, and salt may sometimes do permanent damage to ephippial eggs, hence reducing hatching rates (Bailey *et al.* 2004).

## 9. CONCLUDING REMARKS

It can only be concluded from this short review that the effects of salinity on freshwater crustaceans are poorly recognized. Surprisingly, much more information is available on the responses to variable salt concentrations shown by saltwater or estuarine organisms, notwithstanding the fact that high salt levels are (especially more recently) posing a far greater threat to the inhabitants of fresh waters hitherto unused to them. The molecular mechanisms and adaptive responses to salinity in particular would seem to require thorough further investigation.

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