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RAPID COMMUNICATION

IS Daphnia magna AN ECOLOGICALLY REPRESENTATIVE ZOOPLANKTON SPECIES IN TOXICITY TESTS?

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Abstract

Daphnia magna is commonly used in aquatic toxicity testing because of many characters that make it easy and economical to culture in the laboratory: it is relatively small, has short life cycle, high fecundity, and parthenogenetic reproduction. On the other hand, D. magna differs from other freshwater zooplankters in size, habitat, life-history, and ability to withstand fish predation. D. magna is a relatively large zooplankton species which makes it so vulnerable to fish predation that it is excluded from fish-inhabiting lakes. It occurs mainly in ephemeral habitats like small ponds and rockpools where vertebrate predators are rare. As a result, D. magna is seldom an indigenous species in lakes which receive pollutants, although representativeness is one important criterion for the standardised toxicity test species. Small ponds are unpredictable habitats with large temporal and spatial variability in abiotic factors. Adaptation to this natural abiotic stress may increase pollution tolerance. The life-history of D. magna also differs from that of lakeinhabiting cladocerans. Large daphnids produce many small neonates, whereas the opposite is true for small cladocerans. The large neonate size allows an earlier maturation of small cladocerans compared to daphnids. In a few comparative studies D. magna tended to be less sensitive to toxic substances than other cladocerans, and this may be due in part to life-history and size differences.

Keywords: Daphnia magna, pollution, size, life history, predation.

INTRODUCTION

Toxicity tests are used for predicting the effects of chemicals on living biota, comparing sensitivity of one or more species to different chemicals, and setting rules for regulation of discharges. In order to increase reliability and replicability of tests within one laboratory as well as to facilitate the comparison of results among laboratories, standardised test methods have been developed by different organisations like EPA, ASTM and OECD. One example of a standardised toxicity

test is the acute immobilisation and reproduction test for *Daphnia* (OECD, 1984). In the acute immobilisation test, the concentration of a test compound where 50% of neonates are immobilised after 24 or 48 h is determined. The reproduction test is started with newborn daphnids which are cultured at least two weeks in sublethal concentrations of the test compound. During this time daphnids should produce three clutches. Mortality, timing of the first reproduction, and the number of offspring are observed. Laboratory bred *Daphnia* with a known history are used. Any food and water can be used provided that they will sustain good reproduction in *Daphnia*. The test conditions, such as temperature and the number of animals per test concentration are carefully described in the guideline.

Daphnia magna Straus was already used in toxicity tests during the 1940s by Anderson (1944), and in the last 20 years it has been extensively used in regulatory testing as well as in basic ecotoxicological research. D. magna has many properties making it suitable for laboratory testing, such as small size, high fecundity, short life span, parthenogenetic reproduction, ubiquitous occurrence, and ease of laboratory handling (Adema, 1978; Baudo, 1987). On the other hand, use of D. magna has been criticised partly for the same reasons. Although D. magna is widely distributed in natural aquatic ecosystems, it does not inhabit lakes of the size which are impacted by pollutants (Koivisto et al., 1992). According to Rand and Petrocelli (1985), species which are indigenous to or representative of ecosystems that receive pollutants should be used in toxicity testing. In most cases, D. magna fails to meet this criterion. The lack of D. magna in lakes is explained by strong predation pressure by visually feeding fish (Brooks & Dodson, 1965). Koivisto et al. (1992) suggested that the large size of D. magna may increase its tolerance to toxic substances compared to smaller cladocerans and other zooplankton species. D. magna also has a life-history strategy different from that of the smaller cladoceran species which live in lakes. Small cladocerans maximise reproductive effort at the cost of future survival, whereas large cladocerans increase their fecundity by

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Table 1. Lengths (mm) excluding spines of adult females of some holarctic freshwater zooplankton species (Scourfield & Harding, 1966; Blomqvist et al., 1976; Särkkä, 1984)

Cladocera		Calanoida	
Daphnia magna	5–6	Limnocalanus sp.	2.5–3
D. pulex	2.5-3.5	Eurytemora sp.	1.3-2.2
D. longispina	2.5-3	Eudiaptomus sp.	1.3–1.5
D. galeata	2.5	Heterocope sp.	2–5
D. cristata	1.5	Acartia sp.	1.1-1.5
D. cucullata	1.5-2.5	1	
Bosmina longirostris	0.7	Cyclopoida	
B. coregoni	0.5–1.5	Cyclops sp;	1.6-2.8
B. longispina	0.6–1.2	Megacyclops sp.	3–5
Chydorus sphaericus	0.5	Acanthocyclops sp.	1.5-1.9
Ceriodaphnia sp.	<1.5	Mesocyclops sp.	0.9-1.3
Sida crystallina	4	Thermocyclops sp.	1
Limnosida frontosa	1.3–2	y 1 · 1	
Diaphanosoma brachyurum	1.6	Rotifera	
Holopedium gibberum	2.5	Brachionus sp.	0.2-0.5
Bythotrephes sp.	2-3	Notholca sp.	0.1-0.4
Leptodora kindtii	10	Keratella sp.	0.52-0.4
Polyphemus sp.	12	Asplanchna sp.	1.5
		Synchaeta sp.	0.3–0.6

postponing reproductive effort to a later part of the life cycle (Lynch, 1980). Daphnids produce large clutches of small neonates, whereas the opposite is true for smaller cladocerans like *Bosmina* sp. and *Chydorus* sp. (Lynch, 1980; Koivisto et al., 1992). Large neonate size allows rapid maturation and shortens the time to first reproduction. In this paper I focus on: (i) the ecological differences between *D. magna* and other cladoceran species; and (ii) the problems in extrapolating results from *D. magna* toxicity tests to other cladoceran species, or to zooplankton in general.

THE SIZE OF Daphnia magna

Freshwater zooplankton is dominated by three taxonomic groups: Rotifera, Cladocera, and Copepoda. Most taxa have adult lengths less than 2.5 mm (Table 1). D. magna is the largest herbivorous cladoceran in the northern hemisphere, with an adult size of 5 to 6 mm. Body size is an important factor which influences the accumulation of toxicants to the animals (Boyden, 1974; Krantzberg, 1989). For example, the correlation between body weight and metal concentration ($\mu g g^{-1}$) can be positive, negative, or insignificant (Boyden, 1974; Strong & Luoma, 1981). The positive correlation between the body weight and metal concentration can be explained by age: larger individuals are older, and have accumulated the metal during a longer time than younger individuals (Groulx & Lasenby, 1992). The negative correlation between the body size and metal concentration has been found in fish, aquatic insect larvae, crustaceans, and molluscs (Boyden, 1974; Newman & Doubet, 1989; Groulx & Lasenby, 1992; Lasenby & Van Duyn, 1992). In these studies the body burden (total metal content of individual) was higher, but the metal concentration (µg g-1) was lower in larger individuals. Several mechanisms have been proposed to explain the relationship between body size and metal concentration. A common explanation is the greater surface area to volume ratio which could increase the uptake rate of toxicants to small individuals (Krantzberg, 1989). The other proposals are higher metabolic rate of small animals (Williamson, 1980), biodilution in rapidly growing animals (Groulx & Lasenby, 1992), and the different diet of small individuals (Lasenby & Van Duyn, 1992). However, the explanations are speculative, and the reasons underlying the relationship between metal concentration and body size remain to be examined thoroughly (Lasenby & Van Duyn, 1992).

Body size should be most important when chemicals are mainly adsorbed to the surface (Krantzberg, 1989). In cladocerans, the main uptake route of metals is direct from water through the body surface (Carney et al., 1986), and therefore large size should be favourable in metal-contaminated environments. When D. magna is used to estimate safe toxicant concentrations for zooplankton, the hazard may be underestimated if smaller species are more susceptible to the transfer of toxicants across the integument than are D. magna. In several interspecific comparisons large-sized Daphnia tended to be more tolerant to toxic substances than smaller zooplankton species (Winner & Farrell, 1976; Takahashi et al., 1987; Koivisto et al., 1992).

THE HABITAT OF Daphnia magna

D. magna lives in eutrophic small ponds and rockpools (Hebert, 1978) Some ponds are persistent, but others are temporary and dry up during periods of drought; other ponds freeze solid in winter. Such environments are unpredictable with wide fluctuations in pH, temperature, oxygen concentration, salinity, and other abiotic factors (Ganning, 1971). However, D. magna is well adapted to such fluctuations: it tolerates low oxygen conditions, high pH, wide ranges of salinity and temperature, and

it produces diapause eggs (ephippia), allowing survival in otherwise lethal environmental conditions (Kobayashi & Gondi, 1985; MacIsaac et al., 1985; Arnér & Koivisto, 1993).

It has been suggested that species which tolerate a high degree of natural abiotic stress may be preadapted to tolerate pollution stress as well (Fisher, 1977; LeBlanc, 1985). This would imply a lesser sensitivity of D. magna to toxicants, compared to zooplankton species living in more stable (lake) environments. Koivisto et al. (1992) compared the copper tolerance of daphnids living in ponds (D. magna, D. pulex) to lakeliving cladocerans (D. galeata, B. longirostris, C. sphaericus) and found that the latter species were more sensitive. However, it was not possible to distinguish the habitat effects from other effects, e.g. size. Therefore, further tests of this hypothesis are needed.

LIFE HISTORIES OF CLADOCERANS

Predation is probably the most important cause of cladoceran mortality in nature, and both vertebrate and invertebrate predation are regarded as major factors in the evolution of cladoceran life histories (Lynch, 1980). Larger (>2.5 mm) daphnids only thrive in fishless habitats, and are therefore mainly exposed to predation from invertebrates, such as phantom midge larvae (Chaoborus sp.) (Vanni, 1988; Swift, 1992). Such invertebrate predators are able to feed only on juvenile instars. After attaining a certain size, the daphnids are less vulnerable to invertebrate predation; this leads to increased adult survival. Small cladocerans remain exposed to invertebrate predation during their whole life cycle, but with increasing size their vulnerability to visually feeding fish increases (Lynch, 1980; Vonder Brink & Vanni, 1993). In contrast to large daphnids. small cladocerans suffer from reduced adult survival. Hence, life-history strategies of small and large cladocerans are in accordance with theoretical predictions: small cladocerans maximise reproductive effort at the cost of future survival, whereas large cladocerans increase their fecundity by postponing reproductive effort to a later part of the life cycle (Gadgil & Bossert, 1970; Reznick et al., 1990). Consequently, daphnids produce larger clutches compared to smaller cladocerans like Bosmina sp. and Chydorus sp. (Koivisto et al., 1992). Size of a small cladoceran neonate is large relative to the adult, which allows rapid maturation and shortens the time to first reproduction, whereas the size of a large daphnid neonate is small compared to that of adults.

The relationship of life-history strategy to stress tolerance has not been studied from an ecotoxicological point of view. However, it is possible that species with different life histories could react differently to stress. Collins (1980) has proposed that, under stress conditions, organisms preserve the life-history traits most important for fitness, at the cost of less critical ones. The most vital life-history traits are not necessarily the same for large and small cladocerans. Comparative

studies of stress tolerance of different cladocerans are rare (Winner & Farrell, 1976; Elnabarawy et al., 1986; Winner, 1988; Koivisto et al., 1992), and consequently little is known about the effects of toxicants on the lifehistory traits of cladocerans other than D. magna, D. pulex or Ceriodaphnia dubia (Ingersoll & Winner, 1982; Bodar et al., 1988; Belanger & Cherry, 1990). The most often studied life-history traits are survival, body length and brood size. The life-history responses of D. magna vary depending on the specific toxicant, but also depending on the population used in the experiment (Baird et al., 1990; Soares et al., 1992). It should be determined if smaller cladocerans react to specific toxicants by the same life-history traits as D. magna, and if variation in responses is larger within or between species.

Daphnia magna AND FISH PREDATION

Predation by planktivorous fish has a major impact on zooplankton species composition, abundance, age and size structure (Brooks & Dodson, 1965; Vanni, 1987a,b). The body size of zooplankton prey has been shown to be an important criterion in food selection of visually feeding fish. However, body shape, coloration and transparency also influence the vulnerability of prey (Kerfoot et al., 1980; Zaret, 1980). Compared to lake-living daphnids, D. magna is large (Table 1) and relatively strongly coloured. As a result, D. magna is unable to survive fish predation and is rarely found in environments inhabited by fish (Hebert, 1978). In experiments, D. magna is rapidly eliminated by planktivorous fish (Ranta et al., 1987; Pont et al., 1991). Daphnids that coexist with planktivorous fish are smaller and more transparent than D. magna (Hebert, 1978). Many lake-living cladocerans show cyclomorphosis (seasonal changes in body morphology), thought to confer some protection against predation (Jacobs, 1987; De Stasio et al., 1990). Behavioural responses such as vertical migration and swarming, can also decrease the risk of predation (Kerfoot et al., 1980). For example, cyclopoid and calanoid copepods avoid predation by rapid escape movements.

Until recently, the effects of xenobiotics interspecific interactions (predation, competition), or community and ecosystem properties have received far less attention than have impacts on individual species (Cairns, 1984; Clements & Kiffney, 1994). However, these kinds of effects are important to understand, when impacts of pollutants on ecosystems must be predicted. For example, the outcome of predation may vary according to which species is more sensitive to pollution; if the predator is more sensitive, it may be less efficient, and if the prey species is more sensitive, it may be more susceptible to predation. Both consequences are supported in empirical studies (Clements et al., 1989; Sandheinrich & Atchison, 1990; Gorham & Vodopich, 1992). It is not possible to study interactive effects of pollution and predation on natural zooplankton communities in Daphnia bioassays, which, of

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course, is not only the problem of test species, but also an inherent nature of the test method.

CONCLUSIONS

All of the features discussed above are inter-connected. D. magna is vulnerable to fish predation because of its large size and the lack of ability to survive fish predation excludes D. magna from lakes. D. magna represents a life-history strategy of large daphnids, evolved as an adaptation against invertebrate predators with higher abundance in the absence of fish. From the ecological point of view I suggest that D. magna is not a representative zooplankton species; hence, it is possible that the results of D. magna toxicity tests may give misleading information when they are extrapolated to natural zooplankton communities. There is no doubt that D. magna is an excellent test organism for screening tests where the relative toxicity of chemicals is studied. But this kind of testing may have little to do with predicting the effects arising from xenobiotics in natural ecosystems. To gain more information about the potential for ecological damage, we must also study the responses of species that play essential roles in these communities and develop test systems that better correspond to real nature.

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