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Short review

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## ADAPTIVE CHANGES IN MORPHOLOGY OF *DAPHNIA* FILTER APPENDAGES IN RESPONSE TO FOOD STRESS

**ABSTRACT:** Morphological adaptations of *Daphnia* filtration apparatus in response to unsuitable food conditions are examined and set against earlier published data. To maximize food gathering under limiting food conditions, *Daphnia* can respond morphologically by plastic changes in the size and structure of its filter apparatus. Under low food quantity and/or poor quality, the area of *Daphnia* filter screen increases and the mesh size decreases.

**KEY WORDS:** *Daphnia*, adaptations, filter appendages morphology, phenotypic plasticity

### 1. INTRODUCTION

Planktonic cladocerans of the genus *Daphnia* can be very effective grazers of lake phytoplankton. Food particles are retained on the filter combs attached to the third and fourth thoracic legs of *Daphnia*. Filter combs are compound, three dimensional structures consisting of three levels of organisation (Fig. 1): setae – basic elements of the filter screen, setules – structures arranged in two rows at an angle on the setae, and setular bosses – two rows of ultrafine knobs on the setules of yet unknown function (Storch 1924, Cannon 1933, Villalobos and Geller 1997).

Mechanisms of food particle collection have been studied for many decades, nonetheless this complex process still requires clarification and there is no agreement as to whether the mechanism involved in food uptake by *Daphnia* is mechanical sieving or some other mechanism, e.g. direct interception and surface attraction. However, recently Abrusán (2003, 2004) proposed a hypothesis which implies that more than one mechanism can operate simultaneously in the process of *Daphnia*'s food particle retention.

It is well known that plastic changes in morphology of feeding apparatus can enhance the amount of assembled food under conditions of low food quantity and quality (Koza and Kořínek 1985, Lampert 1994, Reinikainen and Repka 2003). Phenotypic changes in behaviour, morphology and

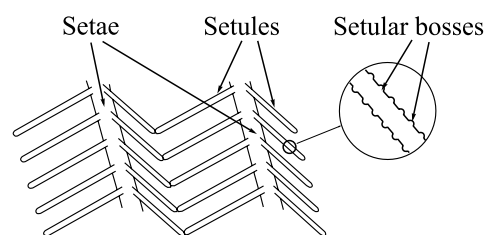


Fig. 1. Schematic diagram of the *Daphnia* filter comb structure.

life history are common in cladocerans, and guarantee the ability to cope with different, often unfavourable environmental conditions. Low food quantity and quality can be strong stress factors triggering different adaptations in *Daphnia*; it has been demonstrated that to maximize food uptake under limiting food conditions daphnids may respond in their behaviour (e.g. vertical and horizontal migrations, changes of appendage beat rate), morphology (e.g. changes of filter screen size and structure) and life history (e.g. production of large offspring).

## 2. MECHANISM OF FOOD RETENTION IN *DAPHNIA*

Planktonic cladocerans of the genus *Daphnia* are filter feeders. In the classic papers of Storch (1924) and Cannon (1933), the feeding mechanism of *Daphnia* has been defined as a process of mechanical sieving. Later, in the 1980s, discussions arose on whether it is a solely mechanical filtration. The sieving hypothesis was confirmed by a number of experimental studies and also theoretically, by means of fluid dynamic models (Gophen and Geller 1984, Brendelberger 1985, 1991, Brendelberger *et al.* 1986). These authors found evidence that animals with finer meshes (smaller intersetal distance) are able to utilize bacteria as food, while animals with coarser meshes are forced to use larger food particles, and that mesh size can be used to predict the uptake efficiency of bacteria and other small particles.

Despite the well accepted “sieving paradigm”, there have been some studies demonstrating that mechanical sieving is an insufficient explanation of the mechanism of food particle retention because cladocerans are able to feed on ultrafine particles smaller than their mesh size. Gerritsen and Porter (1982) noted that surface chemistry, i.e. ionic or hydrophobic – hydrophilic interactions, can be a crucial factor determining the effectiveness of retention of small sized particles. Moreover, Gerritsen *et al.* (1988) showed that the majority of water with suspended particles does not flow through the combs but rather tangentially to them. They proposed that the filter appendages act as paddles, not as sieves, and that the main

mechanism of food collection in *Daphnia* is direct interception. Direct interception is one of the basic mechanisms of particle retention. In streamline flow, encounter occurs if the radius of the particle is bigger than the distance between the particle and the fiber of the filter. The efficiency of particle capture depends on the size of the particle (for more details see Rubenstein and Koehl 1977, Koehl 1996, Wildish and Kristmanson 1997, Abrusán 2003).

Recently Abrusán (2003, 2004) proposed a hypothesis which allows the views on the mechanism of particle retention in *Daphnia* (mechanical sieving vs. direct interception) to be brought together. According to Abrusán, the feeding pattern depends on the Reynolds number ( $Re$ ) of the filter apparatus. The Reynolds number describes the character of the flow and is a dimensionless parameter which depends on the velocity of the flow, “characteristic length” and viscosity of the fluid. In the case of the feeding mechanism in *Daphnia*,  $Re$  can be modified e.g. by mesh size of the filter combs changing the “characteristic length” (for more details see Abrusán 2003, 2004). Following this hypothesis, under higher  $Re$  filtering appendages act more as sieves, whereas under lower  $Re$  filtering appendages act rather as paddles.

## 3. ADAPTATIONS TO LOW FOOD LEVEL

To enhance feeding effectiveness under low food level, daphnids are able to change the morphology of the filter screen on the third and fourth thoracic appendage. Both the size and structure of the filter combs can be modified in relation to the food conditions. The possibility of increasing filtering rate along with increasing the area of filter screen was first suggested by Egloff and Palmer (1971). Later, this phenomenon was confirmed experimentally for several *Daphnia* species. Koza and Kořínek (1985) showed that *Daphnia* grown in low concentrations of food develop larger filter screen areas than animals fed in high food conditions. Next, it was proved that such modifications can be developed within one population and/or within a single clonal lineage of *Daphnia* (Pop 1991, Stuchlík

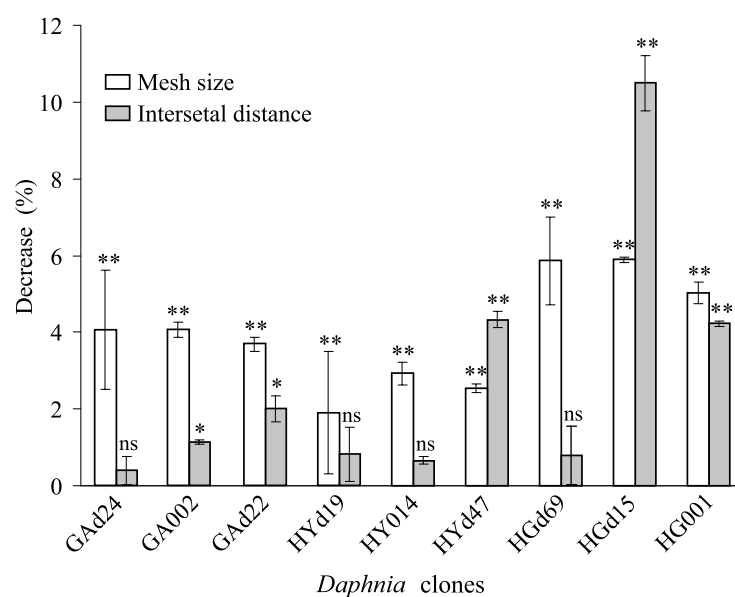


Fig. 2. Relative decrease (mean  $\pm$  SD) in mesh size and intersetal distance in nine *Daphnia* clones caused by the presence of *Cylindrospermopsis raciborskii* (Woloszynska) filaments (decrease significance at \*:  $P = 0.05$ , \*\*:  $P = 0.005$ , Tukey post-hoc comparisons). Letters in the names of clones stand for: GA - *D. galeata*, HY - *D. hyalina* and HG - *D. galeata*  $\times$  *D. hyalina* hybrids (from A. Bednarska and P. Dawidowicz - unpublished, modified).

1991, Lampert 1994). This indicates that both natural selection and phenotypic plasticity may be responsible for observed enlargements of filter screen area. It is also recognized that in response to poor food conditions, the mesh size of the filter screen decreases (Lampert and Brendelberger 1996). These changes of size and structure of filter combs have been recognized as phenotypic adaptations to low food quantity. It has been found that species differ in the degree of plasticity of filter combs, e.g. *D. pulicaria* Forbes and *D. ambigua* Scourfield have the ability to change the filter area over a far broader range than *D. magna* Strauss and *D. obtusa* Kurz (Koza and Kořínek 1985, Lampert 1994). The ability to change the morphology of filter combs in response to food stress can vary not only between taxa of *Daphnia* but also between age classes. The morphology of the filter screen can be modified with every moulting (Geller and Müller 1981, Pop 1991). The duration of juvenile instars is much shorter than adult instars, so young *Daphnia* are able to respond quicker to variable food concentrations (Voigt and Hülsmann 2001).

#### 4. ADAPTATIONS TO LOW FOOD QUALITY

In eutrophic lakes (in the presence of colonial or filamentous cyanobacteria and algae), *Daphnia* have finer meshes in their filter screens than animals from oligotrophic lakes (Geller and Müller 1981, Brendelberger and Geller 1985, Villalobos 2002). Surprisingly, unlike the detailed knowledge of the adaptations of filter combs to low food level, changes of filter screen morphology caused by low food quality have been poorly recognized. Existing studies in most cases concern the size but not the structure of the filter screen. Moreover, it has not been resolved convincingly whether smaller mesh size observed in the animals from eutrophic environments has been developed as a result of natural selection and/or by phenotypic plasticity of *Daphnia*. Presence of filamentous cyanobacteria can induce an increase in filter screen area, but only recently has it been finally proved that in response to the occurrence of cyanobacterial filaments *Daphnia* modify the filter combs structure as well (Repka *et al.* 1999, Ghadouani and Pinel-Alloul 2002, A. Bednarska and

P. Dawidowicz – unpublished). Bednarska and Dawidowicz (unpublished) showed that intersetal distance and/or mesh size decrease when the animals are cultivated in the presence of cyanobacteria. These morphological changes are not just a response to starvation (which can occur when the filaments interfere with the filtration process). Indeed, no symptoms of starvation have been recorded, since the animals kept in the presence of cyanobacteria did not differ in body length and fecundity from those in a habitat free of cyanobacteria. Moreover, it was confirmed that adaptive changes in filter screen morphology can result not only from the successions of clones (as described earlier in the literature) but also as an expression of phenotypic plasticity in *Daphnia* (A. Bednarska and P. Dawidowicz – unpublished). What is more, the degree of plastic changes of filter morphology differs between taxa (parental species and interspecific hybrids) as well as between clonal lineages of *Daphnia* (Fig. 2).

In eutrophic environments, the phytoplankton is often dominated by bacteria and picoalgae (Gliwicz 1969) and decreased mesh size allows *Daphnia* to exploit them as food sources. Furthermore, according to Abrusán (2003, 2004), in environments rich in algal and cyanobacterial filaments animals with smaller mesh size may be favoured over animals with coarser meshes. As finer mesh means lower Re on the filter apparatus, filter appendages start to act more as paddles, so the filaments cannot clog the meshes in the filter comb and the feeding process is more effective allowing a high growth rate to be maintained.

## 5. CONCLUSIONS

The morphology of filter apparatus and the mechanism of food gathering in *Daphnia* have been studied for many years. Although we now know that both mechanical sieving and direct interception can operate simultaneously in food collection of *Daphnia*, the process of so called “filter feeding” in cladocerans is still not fully understood. Also the morphology of filter combs, e.g. the function of setular bosses and their significance in food gathering, deserves further examination.

The diversity of responses to different biotic and abiotic stress can be regarded as a sign of the enormous phenotypic plasticity of *Daphnia*. Changing the size and structure of the filter screen in response to unsuitable food conditions is an adaptive trait which increases feeding efficiency and allows *Daphnia* to survive and even sustain growth and reproduction. Under poor food supply, *Daphnia* enlarges the total filter screen area and the mesh size in the filter combs is decreased. Decreasing the mesh size allows *Daphnia* to enhance filtration effectiveness for bacteria and other small food particles and makes *Daphnia* less vulnerable to filament interference in the filtration process. These observations also suggest that *Daphnia* can use the same adaptive strategy (filter mesh size reduction) in response to low food quantity as well as poor quality.

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