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Internal Water Flows and Particles Abstraction in *Daphnia*

Moshe Gophen

Migal, Scientific Research Institute, Kiryat Shmone, Israel
Email: gophen@migal.org.il

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Abstract

The operational function of the trunk limbs (thoracic appendages), of *Daphnia*, P3 and P4, is a long-term disputed definition between "solid walls", sieving filters. Sieving is unlikely process for routine particle collection, particle capture is not a simple mechanical process and not by sieving alone. Analysis promotion supported by direct observational examination of the *in-vivo* cinematographic slow-motion film and magnified solid photos of tethered *Daphnia* by high-speed camera (250 frames per second) resulted in a definite interpretation presented in this paper. The *Daphnia*'s feeding mechanism achieves particles abstraction not by sieving. The existence of two internal alternate water flow routs was indicated: Lateral and Median. These micro flow structures are suggested as vulnerability reduction.

Keywords

Daphnia, Particle Abstraction, Solid Walls, Internal Flow Rout

1. Introduction

The role of Cladoceran organisms in freshwater ecosystems is one of the oldest and most significant topics in limnological sciences. Moreover, as a result of their distribution and diversity, the impact of their feeding mechanism on the ecosystem function and consequently on water quality is a world-wide key factor in ecosystem functions. More than 95% species of eight orders (including Cladocera) Branchiopoda are known world-wide of which is above 200 in North America [1]. The class Branchiopoda includes 8 orders and 127 known genera in the world. The order Anompoda includes 65 genera which are about 50% of totally known in Branchiopoda. The highest number of genera known in Anomopoda is due to Chydoridae and Daphniidae [2]. *Daphnia* is not only globally distributed. This tiny animal was selected by limnologists as a model organism for the study of biological interaction in lakes [3]. The study of *Daphnia*'s feeding mechanism became a model for the ecological role of Caladocerans within the biological interactions in freshwater communities. The feeding mechanism of *Daphnia* is an important element in freshwater ecology, and therefore implies significant comparative evaluation of the interactions between specific parameter and general ecosystem rules and *Daphnia* is a suitable apparent organism widely common and attractive for study [4].

The Role of Cladocerans Feeding Mechanism in the Kinneret Ecosystem

Lake Kinneret was inhabited by large body *Daphnia lumholtzii* whilst intensive stocking of the lake by zooplanktivorous fishes caused a total elimination of the daphnid from the Kinneret ecosystem [5]. Very scarce daphnids are rarely sampled in the river mouth of Jordan River sourced from the catchment. Excluding the rarest *Daphnia* magna, 8 species of Cladocera are recorded routinely in lake Kinneret of which Daphniidae, Bosminidae and Sididae are dominant. The wet biomass (g (ww)/m^2) of Cladocerans in lake Knneret is commonly varied between 10 - 40 (g (ww)/m^2) or 0.9 - 1.8 (g Carbon/m^2) [6]. The seasonal changes of Cladocerans food sources (gut content) were analyzed microscopically and three types were confirmed: non-Phyrhophyte-nano-phytoplanktonic algae, bacteria and detritus. Nevertheless, discrepancy between Cladocerans metabolic demands and non-Phyrhophyte-nano-phytoplanktonic algae availability was confirmed [7]. Consequently it is suggested that feeding mechanism of the Cladocerans is appropriate for wide range of particle size such as tiny phytoplanktonic algae, bacteria and detrital particles [7].

Results given in **Figure 1** indicate the gap between annual averages of food requirements of herbivorous zooplankters and available nano-phytoplankton in lake Kinneret and given in values of Carbon contents (g C/m^2). The data was evaluated from experimental measurements of food intake under three seasonal mean Epilimnetic temperatures applied to field densities during the appropriate annual averages [6] [7] [8]. Information shown in **Figure 1** indicates algal food deficiency and consequently completed consumption of non-algal resource (probably bacteria, protozoa, detritus) during 1969-1980. Nevertheless, algal matter sufficiency and consequently reduced consumption pressure on non-algal food source during 1980-1991. The size range versatility of the ingested food particles (single algal cell and colonies, protozoa, bacteria, detritus) to be abstracted by thoracic appendages P3 and P4 is widest. Consequently, the adaptability of trunk limbs P3 and P4 to abstract ingested particles curious and the investigation how it is accomplished initiated the present study by the use of cinematographic technique. Most of vast documented studies about Cladocerans and particularly *Daphnia* feeding mechanism were focused indirectly on the mechanism and mostly on the resulted changes such as biomass reduction in the media, growth, reproduction and respiration changes of the tested organism fed by certain (biomass, quality) type of known food resource. The cinematographic

Figure 1. Temporal (1969-2001) changes of nano-phytoplankton (g_{ww}/m^2) available biomass for herbivorous zooplankters in relation to their metabolic requirement of in lake Kinneret.

technique penetrate into the organism body looking for the operational usage of the trunk limbs. The study comprised of two stages: First, close up of a careful eye scanning focused on the external surface of P3 and P4 appendages followed by solid photo prints. The second-filmed slow motion observation of documented sub-carapace internal micro currents while limbs activity, The *Daphnia*'s feeding mechanism was studied *in-vivo* by Cinematographic technique (High-Speed Camera; 250 frames per second). Results of slow-motion film projection and magnified solid pictures indicated internal water flow system comprised of two routes [9]: 1) Lateral routes start underneath P2 and directed along the carapace edge towards the distal body part of the *Daphnia* was documented as and 2) Median which start in front and flow downward between thoracic appendages P3, and P4 than turn to tangential direction between the two trunk limbs to be rejected. These two internal routes of flow are operated alternately. It was suggested that this pattern is beneficial to the *Daphnia* as predator risk reduction achieved by discriminated alternate of two separated outflows resulting in two continuous minor pulses instead of one stronger. It was suggested to be a blur of one pulsated outlet by a succession of two vortices. The results of promoted analysis that was focused on the function of the thoracic appendages P3 and P4 are given here as the epilogue of the *in-vivo* cinematographic study of *Daphnia*'s feeding mechanism. The methodological approach of Cinematographic utilization to study *Daphnia*'s feeding mechanism is not unique and was used in previous studies. Nevertheless, the present study represent innovative conclusions of two major aspects: 1) Food particle abstractions by *Daphnia* is not done by filtration, the activity of P3 and P4 trunk limbs are therefore define as "flexible solid walls"; 2) The existence of two alternate micro-sub-carapace currents through reduction of the organism vulnerability. A vast number of scientific publications about the feeding apparatus of *Daphnia* and its anatomical structure were published. Some of them considered the *Daphnia*'s thoracic appendages P3 and P4 as filter limbs which are "Not solid walls" (**Figure 2** and **Figure 3**) (NSW) [9]-[26]. In this paper, results of cinematographic film (Photo 3) and magnified solid photos renovative evaluation are presented, aimed at the response to a long-term open question: particle abstraction [27] by *Daphnia*, sieving or not only sieving? The "sieving" and "no sieving" or "not only sieving" are conclusions confirmed by fluid physical-energetical dynamic rules unequivocal confirmation is incomplete. The two approaches supported their conclusions by closely related physical rules but the unequivocal definition is incomplete. The purposes of the present study are aimed at indication of the thoracic appendages function within the entire physiological system of *Daphnia* as a model organism of Cladocerans.

2. Cinematographic Methods

A cinematographic High-speed camera (Photo-Sonics 4C) was operated (250 frames/second) through steadily fixed magnification lenses. The dorsal side of a tethered *Daphnia magna* (Straus, 1820) (3.7 mm, length), was glued (Bostic Super-glue 4-Cyanoacrilate) onto the tip of a solid plastic sieve attachment within a 50 ml glass container full of filtered (0.45 μm filter paper) lake water. The plastic

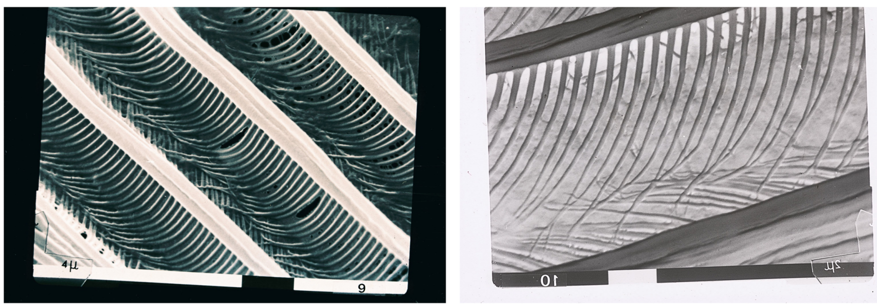

Figure 2. *Daphnia* thoracic limb P4 external view, SEM photo (Photo: W. Geller). Scale: Black rectangle (left) length-4 μm and White rectangle (right) length-2 μm

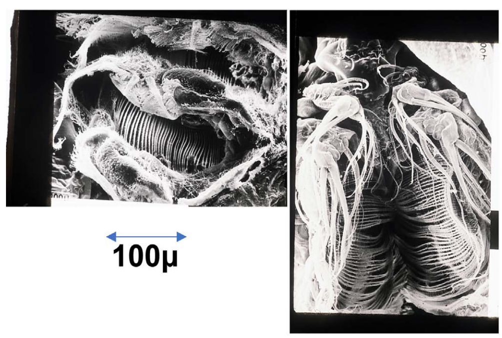

Figure 3. *Daphnia* thoracic appendeges P4: External front view of limb P4 on both sides; SEM photo (Photo: W. Geller).

sieve was held by two metal clips fixed onto a metal rod. The *Daphnia* was positioned vertically with the head upward. Three binocular magnification lenses (Wild stereomicroscope) are directed towards the *Daphnia* at three levels for focusing adjustment: left-right, forward-backward and up-down. The *Daphnia* was positioned at a distance of 0.7 - 1.1 mm from the open end of a thin glass capillary (10 μm diameter) directed towards the upper-lateral part of the body which is the space of water sucking by the animal. A rubber pipe was attached to the glass capillary equipped with a pressure stopper operated by a fine thread screw to enable sensitive control for the injection of Indian Ink lumps. The Indian Ink enabled tracing of the micro-flows within the body of the *Daphnia*. Immediately after injection of Indian Ink lumps the camera was operated for 2 - 3 seconds. The films were developed and analyzed by slow motion operation accompanied by the motion-time analyzer.

3. Results and Discussion

3.1. Flexible Solid Walls, Filters, Particle Abstractors or Chasers?

Supportive indications about the ability of biological filters to remove particles from liquid as a feeding mechanism was documented [14]. Anatomical evolution research indicates that the feeding mechanism in daphniids was derived by restricting particle abstraction to P3 and P4 thoracic appendages (**Figure 1** and **Figure 2**) whilst trunk limbs P1 and P2 are not involved in this part of the process [27]. Several studies defined the trunk limbs P3 and P4 as "Solid Paddle Filters" (SPF) but the particle abstractions are achieved not only by sieving [28] [29] [30] and the filtering function attributed to them is unlikely [31]. Moreover, the conclusion about suspended particles removal from fluid which is done not only by sieving and retention efficiency of particles smaller (0.5 μm) than the mesh-size of the animal apparatus is affected by surface chemistry [32] [33]. The classic historical research of the *Daphnia*'s feeding mechanism attributed particle abstraction to the thoracic appendages (Syn. trunk limbs, combs, filters) [2] [10] [11] [14] [15] [24] [25] [34]. Particular attention was dedicated to the role of the P3 and P4 which are not just "solid walls" but achieve particle abstraction as part of the *Daphnia*'s feeding apparatus and were widely documented [18]-[23]. Those particular studies defined *Daphnia*'s thoracic appendages as "filters" which achieve sieving. Nevertheless, the process trait of food particles abstraction is disputed between "sieving" [18]-[23], "not only sieving" [30] [32] and "the filtering function attributed to them is unlikely" [23]. Conclusions in previous studies of the mechanism of particle abstraction (feeding) by *Daphnia* discriminate between two attitudes: "No Solid Walls" (NSW) and "Solid Paddle Filters" (SPF). The NSW hypothesis suggested P3 and P4 are filters that functioned as sieves, (sifter, strainer, colander) whilst the SPF suggest they are "solid wall paddles" which maintain particle retaining. The NSW suggested that thoracic appendages structure is designated towards sieving operation and filtering is achieved as mechanical sieving [10]. Nevertheless, particles straining out of a liquid flow require flowing from one to the other side of the filter. If this is not the case and water loaded with particle suspension flow along one side only (SPF), the particles abstraction is not sieving. Water flow through the intra-setular spaces, between the seta (**Figure 3**), was not confirmed by the analysis of cinematographic slow-motion films and solid magnified photos. On the other hand, water flows within the inter-setular spaces (**Figure 2** and **Figure 3**), (between the trunk limbs and between the limbs and the carapace) were clearly indicated and two microcurrents were defined [9]. The existence of dual microcurrent inside the body of *Daphnia* and its suggested function was documented [9]. Filmed documentation of it was carried out by Cinematographic slow motion films and solid magnified photos research was reevaluated and revealed the results of the present study. The structure of P3 and P4 accompanied by physical rules analysis of fluid dynamics is the basis for both conclusions that the filters are solid wall paddles or not although water transfer through the filters was not confirmed. In both the NSW and the SPF studies, the water flow through P3 and P4 was not confirmed. Therefore, particle abstraction is not due to the straining mechanism.

Assuming, for granted, the similarity between all definitions of filtering, sieving and straining, and abstraction, the trunk limbs (combs) activity includes water flow through and strained particles adhered onto the internal face of P3 and P4. It is not clear why P3 and P4 are defined as "filters" and their function is not filtration whilst "food caught on the thoracic legs" was confirmed [26]. Two major options are relevant in enabling the mechanism of particles abstraction or capture: adhere by mucus stuff coating the inner side of P3 and P4 or chased by the inter-setae spines [35]. The present study was carried out by the examination of the external P3 and P4 views and the water flows inside the volumetric space were implicated. The limbs P3 and P4 are those which are doing particles abstraction in the feeding mechanism [27] and their external surface is masked by a membrane that moves upward and downward rhythmically exposing the external surface (like opening and closing "windows") orderly: P3 first and shortly later P4. When the membrane is in an upward position and the "window" is open, water should flow through [9] but the recent evaluation did not confirm water outflow as should happen if a filtering process occurs. A slow-motion projection of the cinematographic film as well as an examination of magnified solid photos clearly indicated no water flow through P3 and P4 when the "windows" are open. The membrane glides downward when P3 and P4 are pressing downward and water from the internal volumetric space is rejected. Consequently, if water flows through the volumetric space but not through the Inter-setular spaces, it is not filtration, it is not sieving and not straining and the comb's determination as solid-walls paddles is justified. Both NSWs and SPFs agreed upon definitions of filtering and sieving function of P3 and P4 as feeding mechanisms of *Daphnia.* Nevertheless, the usage of several synonyms is common in literature: particle abstraction, sieve, sift, strain, filter, and even colander likeness. The operation concepts of those definitions (Webster Dictionary) are: Strain, to pass through a screen, sieve, filter, to remove by filtration; Sift and Sieve, to pass through a sieve so as to separate coarse from the fine particles; Filter, separating solid particles from a liquid by passing it through a porous substance; Colander, allows liquid to drain through while retaining the solids inside. None of those linguistic definitions is appropriate as a complete match for the feeding mechanism of *Daphnia* because no evidence was found for water flow through the inter and intra-setular spaces. It is not impossible that particles are trapped by setae which is not a type of sieving. A disagreement exists between the NSW s and the SPFs about the thoracic appendages operational function: NSW, suggests food particles filtration whilst the SPWs, suggest food particles abstraction not only by sieving. Those two conclusions agreed upon "filtration" but no evidence was presented for a liquid flow through and particles retaining and the concept of the term "filtration" is therefore disputed between: A) NSW, "No reason to reject the hypothesis that *Daphnia* collects food by sieving water through its thoracic limbs" [18]; and B) SPF, "sieving through the setular mesh of limbs 3 and 4 is an unlikely process for routine particle collection by *Daphnia*" [25]. Results presented in this paper did not confirm flow through from the internal to the external facet in *Daphnia*'s thoracic appendages of P3 and P4. Consequently, supporting the SPF mechanism is confirmed. Mathematical-physical analysis of the NSW and SPF hypothesizes initiated results of the contrary. There is probably no better method other than direct observation to resolve disputed interpretations. The thoracic appendages of *Daphnia* and probably of other Cladocerans are flexible and not rigid, therefore solid or stiffy walls definition is inappropriate but filters do not match their function. Undoubtedly *Daphnia*'s thoracic appendages are part of the feeding mechanism, as well as a part of respiration and internal currents systems but not as filters.

3.2. Alternate Lateral and Median Sub-Carapace Water Motion

The existence of internal water flows in *Daphnia* that was studied by Cinematographic technique has indicates two routes: 1) <u>Lateral flow</u> which start underneath P2 and flow backward towards the distal body part along the carapace edge; and 2) <u>Median flow</u> which start from proximal body part (head) and flow downward between thoracic P3, P4 than turn to tangential direction in the space between the P3 and P4 limbs rejected outside. These two routes are operated alternately. It is suggested that this pattern is beneficial to the *Daphnia* as predator risk reduction achieved by alternate two separated outflows resulting in two continuous minor pulses instead of one stronger. It is suggested to be a blur of one pulsated outlet by a succession of two vortices.

Water suction into the internal carapace space through a narrow passage (inlet zone) located near by the mouth of the *Daphnia* was indicated. The P2 trunk limb which is located close to the doorway funnel inlet open is moving from its lowest position to the upper most water barge which is the space between P2 and

P3 (Figure 4). Then P2 is moving downward and water trapped between P2 and P3 is pressed out and flow along the internal edge of the carapace and ejected outside through the gap between the two valves of the carapace located posteriorly (Figure 2). When P2 is moving downward, P3 and P4, are simultaneously move upward and water enter from the inlet zone into the median space between the two limbs rows ("flexible solid walls") of P3n and P4 located on both sides of the middle median rout space (Figure 5 and Figure 6). Than P3 and P4 move downward and the trapped water in the median-rout is pressed tangentially towards body sides into the spaces between the combs into the carapace at the distal body zone as one lump (Figure 5 and Figure 6). When P3 and P4

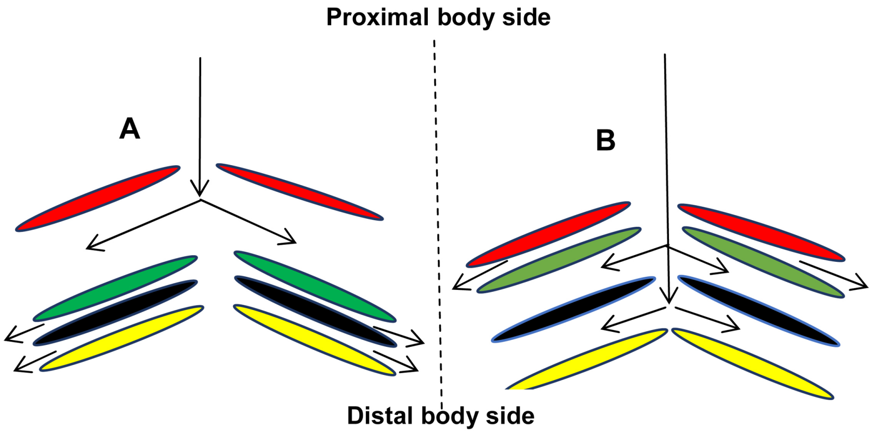

Figure 4. Schematic illustration of the alternate micro-current. Legend: Arrows define internal-water motion directions. Trunk Limbs: Red-P2; Green-P3; Black-P4; Yellow-P5. A-Lateral flow rout: P2-upward water inflow; P3- and P4 Downward water outflow. B-Median flow rout: P2 downward water outflow P3 and P4 Upward water inflow.

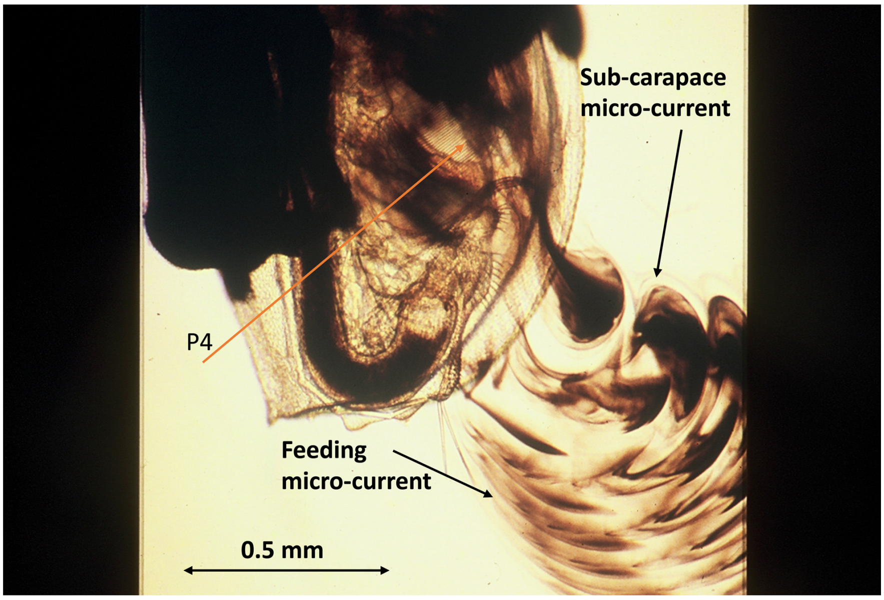

Figure 5. Solid picture (photo) taken from slow-motion film projection (Photo: W. Geller).

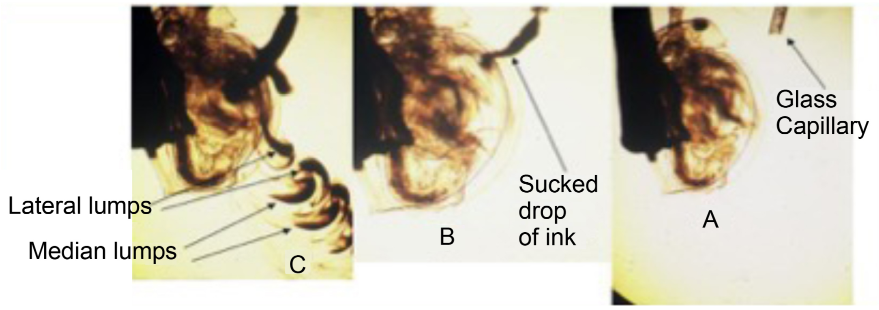

Figure 6. Three sequential still photos from filmed *Daphnia* tape are presented here: A: The empty capillary thin tip is located within the "funnel" shape inlet waters. B: A small drop of Indian Ink is injected into the water inlet zone at the very beginning of sucking it. C: The ink was sucked and moved on through the two alternate micro currents and two types of ejected lumps are seen: the upper row of lumps with downward curve shape ejected from the lateral rout and the lower row with upward curved shape were ejected from the Median route.

move downward P2 is moving upward (**Figure 1**). The upward movement of P3 and P4 is not precisely timing overlap but with a short delay (app 10 mS) of P3 after P4 and P4 start first. The time duration of one stroke, which is return movement between down most and uppermost position is 127 milli-second (ms). The ejected lumps coming from two body sides (**Figure 5** and **Figure 6**) are merged into one lump. The volume of the ejected lumps as measured by Image-Analyzer has indicated that the lateral current contribute 65% of it and the median rout-35%. In other words, 65% of the water inflow flow through the lateral route and 35% through the median flow. Stroke time duration of adults was longer (*i.e.* less strokes per second) than that of young and smaller animals. If full cycle stroke duration is 127 mS, the total volume of the ejected lumps through the median current, where suspended particles are exposed to optional setular abstraction of adult *D. magna* (3.7 mm TL) was 1.02 ml/hr which is in agreement with published data achieved by techniques of biomass or pigment elimination from experimental media. Time shorter duration in smaller daphnids (1.9 mm) was documented. The process of the double micro-currents in the internal space of *Daphnia* was previously presented [36] [37] [38] [39]. The use of different colored with probably lower density liquids was carried out enabled faster stroke frequency [39]. Moreover, continuous operation accompanied by online presented filming was documented [39]. The results of the present study are based on solid photos. The two studies represent similar pattern. The confirmation of two micro-currents routes initiated curiosities. What is the organism beneficial merit of routs partitioning? Why >50% of water income flow through the Lateral route and being exposed to just one limb, P2 and much less to setular potential particle abstraction?; and finally what might be the merit of alternately operated two currents to the animal? A comprehensive interpretation presented here as an alternate between two microcurrent was not considered before [36] [37] [38] [39]. The present study concluded an alternation between those two micro-flows. The two micro-flows, Lateral and Median are operated alternately. Although the two micro-current routes were previously documented [10] [11] [39] their integration with the complete water flow system was not considered. The function of the internal microcurrents is partly to enhance gas exchange (respiration). Nevertheless, it is suggested that it is also create the mechanism of water outflow in two separate smaller pulses instead of one bigger. Smoother double pulsated instead of one stronger (larger) ejected outflow of the water. It is probably a kind of a sound protection for the chased *Daphnia* by pulses smoothing aimed at decline of sound frequency. Two low frequencies instead of one stronger pulse creating stronger wave will reduce predation vulnerability. It is probably an evolutionary adaptation for freshwater conditions where water clarity is diminished resulted by high density of suspended particles enhancing reduction of visibility and prey detection limit. Consequently, evolvement of vibration sensuality as known in fish and predator zooplankters (cyclopoids) was developed. The advantage of lateral line system in fish for the detection and follow the vortices produced by a fleeing prey, like *Daphnia*, and the role of neuromasts was widely documented [40] [41] [42] [43] [44].

The alternation between the two micro-currents produced by chased prey as *Daphnia* possibly create blurring of vortices to improve the animal escape ability by reduction of predator fish capture probability. It is suggested that the lower stroking frequency is a kind of sound protection. Larger *Daphnia* are better visible and therefore less active resulted in sound frequency decline to reduce fish capture probability. Shock Wave is a type of propagating disturbance. Like an ordinary wave it carries energy and can propagate through the water. When a shockwave passes through the water the total energy is preserved but the energy which can be extracted as work decreases. This might create additional swimming force for the *Daphnia* with the shocks. The double alternate internal flows in *Daphnia* probably reduce the shock wave effect and make prey allocation by the predator fish less easy. It has to be considered that micro-turbulence evoked also by the swimming antennae of the *Daphnia* which might be even stronger than the currents produced by the thoracic appendages. Currents generated by the swimming antennae might reduce prey avoidance but it is also possible that the un-adjusted double pulsated outflows produce partial confounding of those strokes. The frontal swimming strokes produced by the antennae and the dorsal alternated outflows are not coordinated and therefore might be confounded. Fish are not the only predators of *Daphnia*. Invertebrate predation by *Cyclopoids*, *Chaeborus*, *Leptodora*, and others is widely known but no mechanoreceptors are known in those animals as side-line in fishes.

4. Conclusion

The history of indirect observation research of the role of *Daphnia*'s thoracic appendages P3 and P4 includes controversial conclusions: sieving not solid filters, not by sieving alone, unlikely process for routine particle collection, particle capture is not a simple mechanical process. The conclusion of direct observation study presented in this paper indicates: The *Daphnia*'s feeding mechanism achieves particles abstraction not by sieving. The filter terminology, filtration rate, filter feeding, should be replaced by chasing define, chasing rate, chase feeding. The function of water motion of alternate sub-carapace internal micro-current is supporting "tracks" blurring to the *Daphnia* aimed at reduction of vulnerability to predators. Prey avoidance mechanism by alternated two micro-flows in *Daphnia* is concluded. The role of P3, and P4, in addition to enhance gas exchange (respiration) is abstraction of food particles. Although food particle retaining mechanism was not clearly documented, the water mediated food particle that flowed smoothly through in the space between P3 and P4 without inter-setular penetration was confirmed.

Acknowledgements

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Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

References

[1] Covich, A.P. and Thorp, J.H. (2001) Introduction to the Subphylum Crustacea. In: Torph and Covich, Eds., *Ecology and Classification of North American Freshwater Invertebrates*, 2nd Edition, Academic Press, Boston, 777-800. https://doi.org/10.1016/B978-012690647-9/50020-X

[2] Dodson, S.I. and Fry, D.G. (2001) Cladocera and Other Branchiopoda. In: Torph and Covich, Eds., *Ecology and Classification of North American Freshwater Invertebrates*, 2nd Edition, Academic Press, Boston, 849-913. https://doi.org/10.1016/B978-012690647-9/50022-3

[3] Lampert, W. (2011) *Daphnia*: Development of a Model Organism in Ecology and Evolution. Volume 21, International Ecology Institute, Oldendorf/Luhe, 250 p.

[4] Peters, R.H. and De Bernardi, R. (1987) *Daphnia*. Memorie dell'Istituto Italiano di Idrobiologia, No. 45, 502 p.

[5] Gophen, M. (1979) Extinction of *Daphnia* Lumholtzi (Jars) in Lake Kinneret (Israel). *Aquaculture*, **16**, 67-71. https://doi.org/10.1016/0044-8486(79)90173-X

[6] Serruya, C., Gophen, M. and Pollingher, U. (1980) Lake Knneret: Carbon Flow Pat-

terns and Ecosystem Management. *Archiv fur Hydrobiologie*, **88**, 265-302.

[7] Gophen, M. (2015) Ecophysiology of Lake Kinneret (Israel) Zooplankton. *Open Journal of Ecology*, **5**, 187-198. https://doi.org/10.4236/oje.2015.55016

[8] Gophen, M. (1978) Zooplankton. In: Serruya, C., Ed., *Lake Kinneret Monographiae Biologicae*, Vol. 32, Dr. W. Junk bv Publishers, The Hague, 297-311. https://doi.org/10.1007/978-94-009-9954-1_11

[9] Gophen, M. (2014) Cinematographic Analysis of Internal Water Flows in *Daphnia*. *Journal of Experimental and Agricultural Sciences*, **2**, 501-507. http://www.jebas.org

[10] Storch, O. (1924) Morphologie und Physiologie des Fangapparates des Daphniden. Ergrbin. *Fortschritte Der Zoologie*, **61**, 125-234.

[11] Storch, O. (1925) Der Phyllopoden-Fangapparat. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, **12**, 369-391. https://doi.org/10.1002/iroh.19250120507

[12] Cannon, H.G. (1933) On the Feeding Mechanism of the Branchiopoda. *Phylosophical Transaction of the Royal Society of London B*, **222**, 29-226.

[13] McMahon, J.W. (1965) Some Physical Factors Influencing the Feeding Behaviour of *Daphnia* Magna Straus. *Canadian Journal of Zoology*, **43**, 603-611. https://doi.org/10.1139/z65-060

[14] Rubenstein, D.I. and Koehl, M.A. (1977) The Mechanism of Filter Feeding: Some Theoretical Considerations. *American Natural*, **111**, 981-994. https://doi.org/10.1086/283227

[15] Burns, C.W. (1968) The Relationship between Body Size of Filter-Feeding Cladocera and the Maximum Size of Particle Ingested. *Limnology and Oceanography*, **13**, 675-678. https://doi.org/10.4319/lo.1968.13.4.0675

[16] Gophen, M., Cavari, B.Z. and Berman, T. (1974) Zooplankton Feeding on Differentially Labelled Algae and Bacteria. *Nature*, **247**, 393-394. https://doi.org/10.1038/247393a0

[17] Gophen, M. (1977) Feeding of *Daphnia* on Chlamydomonas and Chlorobium. *Nature*, **265**, 271-273. https://doi.org/10.1038/265271a0

[18] Brendelbeger, H., Herbeck, M., Lang, H. and Lampert, W. (1986) *Daphnia*'s Filters Are Not Solid Walls. *Archiv fur Hydrobiologie*, **107**, 197-202.

[19] Brendelberger, H. (1985) Filter Mesh-Size and Retention Efficiency for Small Particles: Comparative Studies with Cladcera. *Archiv für Hydrobiologie*. *Beihefte*. *Ergebnisse der Limnologie*, **21**, 135-146.

[20] Brendelberger, H. (1991) Filter Mesh-Size of Cladocerans Predicts Retention Efficiency for Bacteria. *Limnology and Oceanography*, **36**, 884-894. https://doi.org/10.4319/lo.1991.36.5.0884

[21] Brendelberger, H. and Geller, W. (1985) Variability of Filter Structures in *Daphnia* Species: Mesh-Size and Filtering Areas. *Journal of Plankton Research*, **7**, 473-486. https://doi.org/10.1093/plankt/7.4.473

[22] Geller, W. and Muller, H. (1981) The Filtration Apparatus of Cladocera: Filter Mesh-Size and the Implication on Food Selectivity. *Oecologia* (*Berlin*), **49**, 316-321. https://doi.org/10.1007/BF00347591

[23] Gophen, M. and Geller, W. (1984) Filter Mesh Size and Food Particle Uptake by *Daphnia*. *Oecologia*, **64**, 408-412. https://doi.org/10.1007/BF00379140

[24] Korinek, V., Krepelova, B. and Machacek, J. (1981) Ecological Significance of Filtering Structures in Cladocera II. Species of the Genera *Daphnia* and Cerio*daphnia*.

Verhandlungen—Internationale Vereinigung fuer Theoretische und Angewandte Limnologie, **21**, 1567. https://doi.org/10.1080/03680770.1980.11897234

[25] Korinek, V. and Machacek, J. (1980) Filtering Structures of Xladocera and Their Ecological Significance I. *Daphnia* Pulicaria. *Vest es Spolec zool*, **44**, 213-218.

[26] Hessen, D.O. (1983) Filtering Structures and Particle Size Selection in Coexisting Cladocera. *Oecologia* (*Berlin*), **66**, 368-372. https://doi.org/10.1007/BF00378300

[27] Fryer, G. (1987) The Feeding Mechanisms of the Daphniidae (Crustacea: Cladocera): Recent Suggestions and Neglected Suggestions. *Journal of Plankton Research*, **9**, 419-432. https://doi.org/10.1093/plankt/9.3.419

[28] Porter, K.G. (1977) The Plant-Animal Interface in Freshwater Ecosystems. *American Scientist*, **65**, 159-170.

[29] Porter, K.G., Gerritsen, J. and Orcutt, J.D.J. (1982) The Effect of Food Concentration on Swimming Patterns, Feeding Behavior, Ingestion, Assimilation and Respiration by *Daphnia*. *Limnology and Oceanography*, **27**, 935-949. https://doi.org/10.4319/lo.1982.27.5.0935

[30] Porter, K.G., Feig, Y.S. and Vetter, E.F. (1983) Morphology, Flow Regimes, and Filtering Rates, of *Daphnia*, Cerio*daphnia*, and Bosmina, Fed Natural Bacteria. *Oecologia* (*Berlin*), **58**, 156-163. https://doi.org/10.1007/BF00399211

[31] Ganf, G.G. and Shiel, R.J. (1985) Particle Capture by *Daphnia carinata*. *Australian Journal of Marine and Freshwater Research*, **36**, 371-381. https://doi.org/10.1071/MF9850371

[32] Gerritsen, J. and Porter, K.G. (1982) The Role of Surface Chemistry in Filter Feeding by Zooplankton. *Science*, **216**, 1225-1227. https://doi.org/10.1126/science.216.4551.1225

[33] Gerritsen, J., Porter, K.G. and Strickler, J.R. (1988) Not by Sieving Alone: Observations of Suspension Feeding in *Daphnia*. *Bulletin of Marine Science*, **43**, 366-376.

[34] Smirnov, N.N. (2013) Physiology of Cladocera. Academic Press, Zoology, 352 p.

[35] Hartman, H.J. and Kunkel, D.D. (1991) Mechanisms of Food Selection in *Daphnia*. *Hydrobiologia*, **225**, 129-154. https://doi.org/10.1007/BF00028392

[36] Gophen, M., Kohlhage, K. and Geller, W. (1988) Water-Flow System of the Filtering Apparatus in *Daphnia*. *Annual Meeting of the American Society of Limnology and Oceanography*, Boulder, 12-16 June 1988, Abstract 1 p.

[37] Gophen, M., Geller, W. and Kohlhage, K. (1989) Feeding Mechanisms in *Daphnia*: Filtering and Flow Regulations. *Cladocera Symposium*, Tatranska-Lomnica, 13-20 September 1989, Abstract 1 p.

[38] Gophen, M. (1999) Internal Water Flows in *Daphnia* Reduction of Outflow Vibration Together with Particle Intake. *The* 5*th Conference on Cladocera Plon*, 14-18 September 1999, Abstract 1 p.

[39] Paul, R. (2014) Mitarbeiter Im Fachbereich Biologie. http://www.uni-muenster.de/Biologie.Zoophysiologie/tierphys/index.html

[40] Kolhage, K. (1995) Water Flows in *Daphnia*. 87*th Proceedings of the German Zoological Society*, Jena, 23-28 May 1995, 8-10.

[41] Montgomery, J.C. and Macdonald, J.A. (1987) Sensory Tuning of Lateral Line Receptors in Antarctic Fish to the Movements of Planktonic Prey. *Science*, **235**, 195-196. https://doi.org/10.1126/science.235.4785.195

[42] Montgomery, J.C. (1989) Lateral Line Detection of Planktonic Prey. In: Coombs, S., Gorner, P. and Munz, H., Eds., *The Mechanosensory Lateral Line—Neurobiology*

and Evolution, Springer Verlag, New York, 561-575. https://doi.org/10.1007/978-1-4612-3560-6_28

[43] Montgomery, J.C., Macdonald, J.A. and Housley, G.D. (1988) Lateral Line Function in an Antarctic Fish Related to the Signals Produced by Planktonic Prey. *Journal of Comparative Physiology A*, **163**, 827-833. https://doi.org/10.1007/BF00604059

[44] Montgomery, J.C., Macdonald, F., Baker, C.F. and Carton, A.G. (2002) Hydrodynamics Contributions to Multimodal Guidance of Prey Capture Behavior in Fish. *Brain Behavior and Evolution*, **59**, 190-198. https://doi.org/10.1159/000064906