Aquatic Toxicology 265 (2023) 106762

Contents lists available at ScienceDirect

Aquatic Toxicology

journal homepage: www.elsevier.com/locate/aqtox

Daphnia's phototaxis as an indicator in ecotoxicological studies: A review

Wiktoria Rajewicz [*,a], Donato Romano [b,c], Thomas Schmickl [a], Ronald Thenius [a]

[a] University of Graz, Universitätsplatz 2, Graz, 8010, Austria
[b] BioRobotics Institute, Sant'Anna School of Advanced Studies, viale Rinaldo Piaggio 34, Pontedera, 56025, Italy
[c] Department of Excellence in Robotics and AI, Sant'Anna School of Advanced Studies, Piazza Martiri della Libertá 33, Pisa, 56127, Italy

ARTICLE INFO

Keywords:
Daphnia
Phototaxis
Animal behaviour
Toxicity assessment
Biosensor

ABSTRACT

Animal-based sensors have been increasingly applied to many water monitoring systems and ecological studies. One of the staple organisms used as living sensors for such systems is *Daphnia*. This organism has been extensively studied and, with time, used in many toxicological and pharmaceutical bioassays, often used for exploring the ecology of freshwater communities. One of its behaviours used for evaluating the state of the aquatic environment is phototaxis. A disruption in the predicted behaviour is interpreted as a sign of stress and forms the basis for further investigation. However, phototaxis is a result of complex processes counteracting and interacting with each other. Predator presence, food quality, body pigmentation and other factors can greatly affect the predicted phototactic response, hampering its reliability as a bioindicator. Therefore, a holistic approach and meticulous documentation of the methods are needed for the correct interpretation of this behavioural indicator. In this review, we present the current methods used for studying phototaxis, the factors affecting it and proposed ways to optimise the reliability of the results.

1. Introduction

Biosensors are devices including biorecognition elements (e.g. enzymatic interactions, binding proteins, cells, tissues, and more) and transducers where biological selective responses are converted into measurable signals (Dincer et al., 2019; Polatoğlu et al., 2020). Leland Clark developed the first biosensors in the 1800s, which were used to monitor blood glucose (Clark et al., 1988). Since then, abundant literature has been produced, due to the interdisciplinarity and attractiveness of this field.

Recently, the paradigm of the whole-organism biosensor (e.g. biorecognition elements based on organisms) has been gaining attention due to several advantages they provide over traditional biosensors and analytical techniques (Leitch et al., 2013). The high sensitivity and selectivity of biological organisms in detecting and locating target compounds are causing their increasing application for various purposes.

Animal behaviour can go beyond the detection and identification of a compound but also to decipher its biological relevance (e.g. through their positive or negative response, they indicate the effect of compounds on natural systems). Whole-organism biosensors are highly adaptable and can process complex blends of volatile compounds and inform us about blends or concentrations based on the nature and intensity of their behavioural responses (Schiestl and Roubik, 2003; Zhou et al., 2012). These biosensors have essential advantages over traditional analytical methods: they are portable, fast, cost-effective, sustainable and non-invasive. However, they also create certain limitations, including the effect of environmental fluctuations, attention span duration, behavioural differences, etc. making the method standardisation difficult. Whole-organism biosensors also play an essential role in environmental monitoring as behavioural parameters quickly and sensitively indicate toxic substances (Bae and Park, 2014; Gerhardt et al., 2006).

1.1. *Daphnia*

The genus *Daphnia* (Fig. 1) includes small, planktonic crustaceans (Crustacea: Cladocera). They are present in almost every freshwater body and estuary and are one of the most widely used zooplanktonic organisms in ecological research. *Daphnia* have broad distribution and have shown sensitivity to various xenobiotics and other environmental changes (change in water chemistry, heavy metal presence, etc.) (Reilly et al., 2023). In freshwater environments, *Daphnia* are key organisms in the food web and the circulation of organic matter (Hansson and

---

* Corresponding author.
E-mail address: wiktoria.rajewicz@uni-graz.at (W. Rajewicz).

https://doi.org/10.1016/j.aquatox.2023.106762
Received 17 July 2023; Received in revised form 3 November 2023; Accepted 8 November 2023

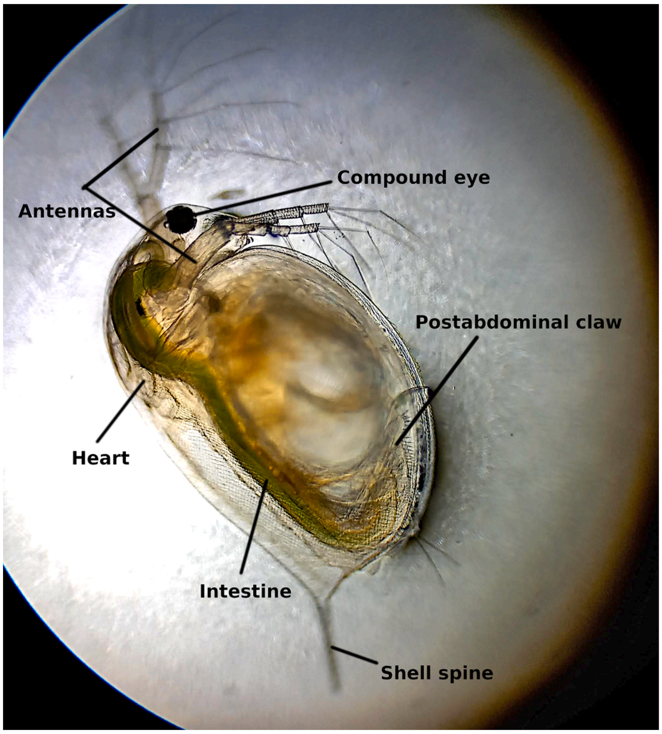

Fig. 1. A magnified (40X) photo of a *Daphnia* sp. specimen under a microscope.

Hylander, 2009). Because of this, they are a model species for freshwater toxicity tests, studying the bioaccumulation of heavy metals and microplastics, as well as adaptation to stress (Reilly et al., 2023; Zhu et al., 2010). Their use as bioindicators began in the early 1900s and has been extensively deepened and improved ever since (Viehoever and Cohen, 1938).

Similar approaches have been implemented with the use of *Daphnia*, where they have been used for toxicity tests and to study the effects of various substances on planktonic organisms and others (see Table 1). *Daphnia* as a keystone species of this group are considered a good representative for such evaluations (Awoyemi et al., 2020; Michels et al., 1999; Noss et al., 2013).

Daphnia is most commonly used in toxicological studies, especially for pharmaceutical research, when testing new compounds and their potential impact on the environment (Choi et al., 2013; Rivetti et al., 2016b). Also, thanks to their natural body transparency it is relatively simple to study their internal organs. This makes them a popular choice for studies on the effect of certain chemicals on the heart rate, for example, cardioactive drugs (Villegas-Navarro et al., 2003). Other *Daphnia* parameters are also investigated for toxicity tests, such as reproduction parameters (offspring production, number of abnormal offspring, reproductive rate, etc), acute parameters (immobilization and mortality), physiological parameters (feeding and filtration rate, hopping frequency, swimming time, etc.) (Tkaczyk et al., 2021). Their global distribution and sensitivity to water pollutants make them an important species for aquatic monitoring and they are often a subject of preliminary toxicity tests.

Table 1
Summary table of most common applications of *Daphnia* phototaxis research with examples.

Application	Example	References
Plankton Ecology	Exploring factors affecting the Diel Vertical Migrations	(Ringelberg, 1995; 1999; Van Gool and Ringelberg, 1997)
Ecotoxicology	Studying the ecotoxicity of paracetamol, antidepressants, diazepam, carbamazepine and other drugs on planktonic communities	(Rivetti et al., 2016a; Sousa and Nunes, 2021)
Environmental monitoring	Automated and continuous water quality control	(Kieu et al., 2001; Michels et al., 1999; Soldán, 2021)
Drinking water assessments	Early-warning systems with acute and chronic toxicity tests	(Soldán, 2021; Zeng et al., 2012)

1.2. History of using Daphnia as a living sensor

Experiments including bioindicators are based on studying the behavioural and physiological responses of the chosen species to various external stimuli. In the case of post-exposures to a stressor, certain documented reactions can be used to identify its presence and intensity. The use of *Daphnia* in aquatic monitoring is based on its responses to external stimuli. These responses are, amongst others, changes in swimming speed, vertical distribution, heart rate, haemoglobin accumulation and reaction to light (Magester et al., 2021; Michels et al., 1999; Nikitin, 2019; Van Gool and Ringelberg, 1997). The last one, also known as phototaxis, is a light-induced behaviour resulting in swimming upwards (positive) or downwards (negative) the gradient of light (Martins et al., 2007; Ringelberg, 1964). The phototactic behaviour of *Daphnia* has been gaining interest in recent years due to its increasing uses in aquatic monitoring.

Phototactic behaviours are most commonly notable in zooplankton species as the Diel Vertical Migrations (DVM), which are often described as the largest migration of animal biomass on the planet (Ohman and Romagnan, 2016). In the case of *Daphnia*, this is most often represented as downward swimming during the day and upward swimming at night (Rhode et al., 2001). The most widely accepted explanation for this phenomenon is a combination of predator avoidance and food-seeking mechanism (Gerhardt et al., 2006). *Daphnia* would be easily preyed upon by the hunting predators in the upper water layers and thus, they tend to migrate to deeper, darker waters during daytime. At night, *Daphnia* emerges into the shallow waters to feed on phytoplankton, until returning to the depths just before dawn (Glaholt et al., 2016). This behaviour has been observed in a variety of zooplanktonic organisms worldwide (Bandara et al., 2021).

Phototaxis has been widely used to measure the stress responses of daphnids, with the assumption that the reaction to light would be disrupted under unfavourable conditions (Kieu et al., 2001; Martins et al., 2007; Michels and De Meester, 1998; Michels et al., 1999). This, however, can lead to oversimplification of the interpretation of this complex behaviour which was shown to be affected by a large number of factors. Here, various studies are reviewed in the context of using *Daphnia*'s light responses as a stress signal and factors that can potentially affect the accuracy of the results.

As mentioned previously, other *Daphnia* behaviours have also been a subject of interest regarding their usability as biosensors. Many studies used immobilisation and mortality, number of produced offspring, feeding and respiration rate and many others as behaviours indicating the animals' reaction to a stressor (Ma et al., 2022; Nikitin, 2019; Ortells et al., 2005; Sousa and Nunes, 2021). An extensive review of behaviours, such as gravitaxis, spinning, resting time and hopping frequency, was provided by (Bownik, 2017). The effect of various specific chemicals on different *Daphnia* swimming parameters can also be found there.

In this review, we build on the aforementioned examples and focus on phototaxis, which is a special type of swimming behaviour. As phototaxis has often been used as a stand-alone stress indicator, it is worth further investigation, as it differs from the aforementioned studies investigating general swimming behaviour. In some works, it has been argued that a disruption in phototaxis can be a result of the inability to swim, rather than a direct response to the light which causes the lack of movement (Magester et al., 2021). However, in the majority of cases, phototaxis is the result of *Daphnia*'s decision-making process affected by a multitude of factors (Rhode et al., 2001; Rivetti et al., 2016a; Storz and

Paul, 1998). Here, we attempt to summarise those factors and give a comprehensive review of how they can affect the phototactic response. Additionally, we propose a guide on how to prepare the toxicological experiments using this behaviour, to ensure the optimal reliability of the behavioural results (see Table 2).

It is important to mention that the *Daphnia* genus often shows species-specific differences in response to various stimuli (Dyomin et al., 2023). This review aims at summarising the established and most recent research on the light responses of various species of *Daphnia*. This study chose not to narrow down the summary to a single species in order to be able to include all of the newest research relevant to the study on phototaxis. Certain studies investigating the *Daphnia* on a genus level (such as Rhode et al. (2001) were of great significance to this research branch. It is of merit to discuss the genus as a whole while mentioning the inter-specific differences.

Table 2

Summary of factors significantly affecting *Daphnia*'s phototactic response and proposed ways to counteract the possible distortion of the results when used in toxicity assessments.

Factor	Influence	Countermeasures	References
Predator kairomones	Enhance the negative phototaxis, with deeper migration depth	Cultivation under known conditions, for industry application preferably in a cultivation medium. For studying real-life processes, filtered pond water is preferred.	(Bellot et al., 2022; Pijanowska and Kowalczewski, 1997; Rhode et al., 2001; Ringelberg, 1964; Ringelberg and Van Gool, 1995)
Light wavelength	UV light enhances negative phototaxis causing deeper migration in unpigmented individuals. Red light can induce a positive phototactic response	Calibrate the behaviour against a known light wavelength. When investigating the wild *Daphnia* populations, it is recommended to use a sun-imitation lights	(Itoh and Hisama, 2010; Rhode et al., 2001; Storz and Paul, 1998; Tollrian and Heibl, 2004)
Pigmentation	Body pigmentation causes higher resistance to UV radiation and allows the *Daphnia* to reduce the migration depth	Account for the pigmentation of investigated individuals and when using phototaxis as a sensor, monitor the possible pigmentation change	(Rhode et al., 2001; Salonen and Lehtovaara, 1992; Tollrian and Heibl, 2004; Weider and Lampert, 1985)
Feeding regime	Starvation can induce positive phototaxis prioritizing feeding over predator avoidance. Insufficiently nutritious feeds can inhibit positive phototaxis due to unfulfilled energy requirements to perform the upward swimming	Provide enough feed, preferably green algae such as *Scenedesmus* or *Chlorella* during or prior to the lab trials. When applying the studies to wild populations, it is recommended to replicate the feeding conditions of the population of interest	(Kieu et al., 2001; Martins et al., 2007; Michels and De Meester, 1998)
Genetic differences	Clones have different phototactic responses under the same environmental conditions	For industrial purposes, select a clone of a desired phenotype and use individuals reared from its culture. For ecological studies, use a variety of clones, for a better representation of the natural ecosystem dynamics	(Martins et al., 2007; Siciliano et al., 2015)
Collective behaviour	Stronger phototactic reaction in a group rather than a single individual	For a better representation of real-life conditions use multiple individuals	(Gerhardt et al., 2006; Jensen et al., 1998; Ordemann et al., 2003)

2. Factors influencing phototaxis

2.1. Predator presence

The leading theory for *Daphnia*'s phototactic behaviour is predator avoidance (Bellot et al., 2022; Kieu et al., 2001; Ringelberg and Van Gool, 1995). This theory was supported by many studies which observed an increased intensity, whether in the speed of response or the migration depth, in *Daphnia galeata* x *hyalina* hybrid and *Daphnia magna* exposed to fish kairomones in comparison to predator-less environments (Bellot et al., 2022; Kieu et al., 2001; Ringelberg and Van Gool, 1995; Van Gool and Ringelberg, 1998)(Fig. 2). The downward migration during the daytime has a high energy cost as the temperature is lower and the food is more scarce. Moreover, egg development is slower and fewer eggs are produced which results in overall lower reproduction rates (Rhode et al., 2001). Therefore, it was speculated that in the absence of predators, *Daphnia* might be able to choose not to relocate and remain in the upper layers. Van Gool and Ringelberg (1997) performed a series of tests on *Daphnia hyalina* and *Daphnia galeata* hybrids under different predator conditions, using fish kairomones from a juvenile perch (*Perca fluviatilis*) for the tests. The strength of the phototactic response (expressed as the mean percentage of responding *Daphnia*) was measured against the increasing light intensity. With fish kairomones present in the water, a 100% negative phototaxis was achieved even with the smallest relative increase in light intensity. In the absence of kairomones, this result was not achieved until the light exposure exceeded that of the natural conditions. These results show that with the absence of the fish kairomones, *Daphnia* exhibits a significantly weaker phototactic reaction.

Moreover, *Daphnia* appears to remain sensitive to kairomones for up to 6 days after exposure, resulting in similar reactions to those in the presence of predators. This ”memory” was noted by Ringelberg and Van Gool (1995). The hybrids of *D. galeata* and *D. hyalina* sensitized to a fish kairomone, after being placed in clear water (without the predator cues) were exhibiting the negative phototaxis for several days with decreasing sensitivity.

2.2. Wavelength of the light

Storz and Paul (1998) described different light responses of *Daphnia magna* depending on the wavelength, where the addition of red light caused a positive phototaxis with the UV (blue) light having the opposite effect. The light wavelengths between 420 and 600 nm (visible light) caused positive phototaxis and the ones between 300 and 380 nm (UV light), negative phototaxis. Additionally, *Daphnia* showed a stronger reaction (faster reaction and lower average height in the water column) to 320 nm light when compared to 620 nm.

A similar reaction was observed by Itoh and Hisama (2010) who developed a motion control system based on *D. magna*'s strong positive phototaxis towards blue LED light. The wavelength of the light used was 473 nm which is just outside of the UV range (100–400 nm) (Sliney et al., 2012). Using this phototactic reaction, the group managed to control the swimming of the *Daphnia* in a desired pattern. Seeing how different light sources induce different phototactic behaviours, it is beneficial to standardize the type of light source in future experiments.

2.3. UV Avoidance

As mentioned previously, the most widely accepted theory for negative phototaxis is the predator avoidance strategy. In most

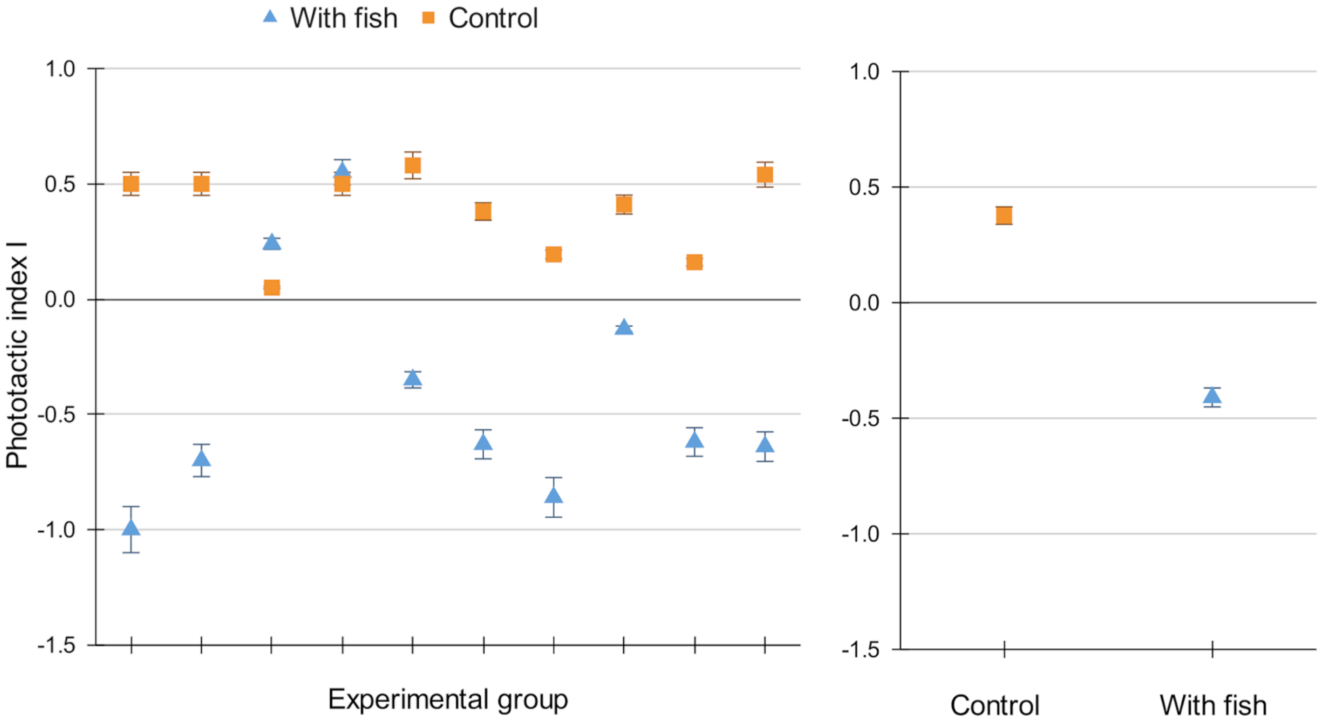

Fig. 2. Phototactic index of *Daphnia magna* clone exposed to fish kairomones. The Phototactic Index I in this and other presented studies was used as a global parameter to determine the change in phototactic reaction and is calculated as following $I = U - L/(U + M + L)$, where U, M and L are the numbers of individuals in the upper, middle and lower compartment of the water column respectively. On the right, average Phototactic Index of *Daphnia* exposed to fish kairomones vs. control group. Data compiled from De Meester and Cousyn (1997); Kieu et al. (2001); Michels et al. (1999).

environments, during the day, *Daphnia* migrates downwards to deeper water layers to minimise the predation pressure from visually-oriented predators, such as fish (Storz and Paul, 1998). Downward migration often means overcoming a temperature gradient in parallel, which can cause slower egg development, production of fewer eggs and overall slower reproduction and growth (Rhode et al., 2001). It was thought that this costly strategy might need an additional reason to compensate for these disadvantages. Moreover, it was noticed that in certain predator-less areas, such as Arctic fish-less ponds, the DVM continued regardless which was noticed in several *Daphnia* species (Rhode et al., 2001).

An additional reason for the negative phototaxis might be the increasingly damaging effects of the UV light on *Daphnia*'s transparent bodies (Rhode et al., 2001). To test this hypothesis, *Daphnia* individuals of various species and various pigmentation types were tested for light response against natural and UV light (Rhode et al., 2001). It was observed that when exposed to naturally occurring levels of UV radiation, the unpigmented *Daphnia* migrated far deeper than individuals containing melanin or carotenoids. Results indicated that pigmented *Daphnia* are significantly less responsive to light cues, which can be explained by their higher tolerance towards the harmful effects of UV radiation. Darker pigmentation would make *Daphnia* more resistant to UV radiation but also increase the risk of predation due to their higher visibility. Therefore, it was concluded that both, predator avoidance, and UV radiation avoidance are drivers for the DVM under different predator and light conditions (Rhode et al., 2001). This was later supported by the findings of Kessler et al. (2008) who called this relationship a ”transparency-gradient hypothesis” (Kessler et al., 2008). Several studies investigated the relationship between UV avoidance and predator avoidance (Ekvall et al., 2020; Rautio et al., 2003; Rose et al., 2012). Their findings confirmed an enhancement of the migration behaviour in the presence of UV light compared to the fish presence alone or lack of both cues (Fig. 3).

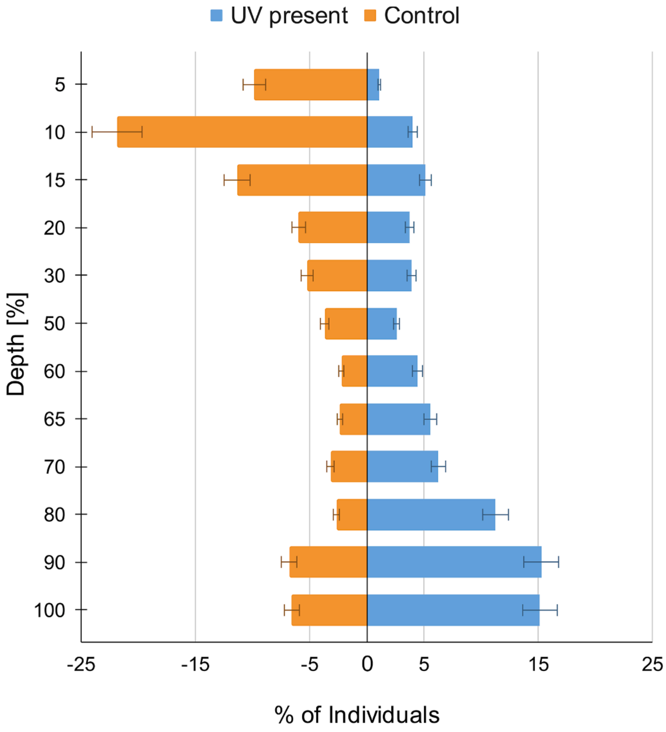

Fig. 3. Mean vertical position of *Daphnia* after exposure to UV light compared to no UV light present. Depth is expressed as a percentage of depth offered to the *Daphnia* during experiments. In the presence of the UV light, *Daphnia* chooses significantly deeper waters. Data compiled from Rhode et al. (2001); Vareschi and Wübben (2001).

2.4. Pigmentation

An increased pigmentation offers more protection against the UV rays but simultaneously increases *Daphnia*'s visibility to the predators. Tollrian and Heibl (2004) investigated which of these mutually exclusive adaptations is prioritized. Several tested species of *Daphnia* showed various phenotypic plasticity depending on their natural habitats. *D. hyalina* and *D. magna* both changed their pigmentation levels depending on the UV light and predator conditions as these two fluctuations frequently occur in their natural habitats. *Daphnia middendorffiana*, which is naturally strongly pigmented, did not change its colouration in the presence of fish kairomones. This is most likely an adaptation to the arctic waters where the UV-B is a major concern, not the predators. An opposite behaviour was presented by *Daphnia cucullata* which remained nearly transparent as an adaptation to highly eutrophic waters where the UV-B rays are not the major threat (Tollrian and Heibl, 2004). These results are in agreement with the theory of Rhode et al. (2001) stating that both UV light avoidance and predator avoidance are the drivers for vertical migrations depending on the environment. This also suggests that the pigment concentration within the carapace should be taken into account together with the predator presence and the light wavelength when using *Daphnia*'s light responses as a living sensor.

Another driver for changing pigmentation is worth mentioning in the context of the UV light effect. Under poor oxygen conditions, *Daphnia* have been observed to increase haemoglobin production. In several invertebrates, haemoglobin is produced as an additional oxygen carrier and is then a survival strategy in oxygen-depleted environments (Landon and Stasiak, 1983; Weider and Lampert, 1985). This compound is produced in such quantities that the colouration of *Daphnia*'s (e.g. *D. magna*) bodies become visibly red (Paul et al., 2004). A few studies investigated the relationship between predator avoidance and the increased visibility caused by the haemoglobin pigmentation however no direct relationship between this change in pigmentation and UV avoidance has been investigated (Salonen and Lehtovaara, 1992).

2.5. Reproduction

Daphnia reproductive strategy includes both sexual and asexual reproduction. The latter one is carried out by producing genetically identical clones through parthenogenesis (Siciliano et al., 2015). While clones show the same phototactic reaction, it is not always the case with genetically various individuals. The reproduction strategy is known to shift depending on the environment, with the asexual one dominating under favourable conditions (Siciliano et al., 2015). There are also significant differences in the phototactic response between different clones. Kieu et al. (2001) observed vastly different reactions to the presence of fish kairomones between clones of *D. magna* (Fig. 4). Studies investigating *Daphnia*'s reactions to light often use carefully selected clones that present a strong phototactic reaction and base the experiments on the population that was bred from them (Martins et al., 2007).

Martins et al. (2007) used clones that presented positive phototaxis to investigate the effects of various chemical pollutants on the light response of *D. magna*. A white light source was placed above the beakers containing the animals submerged in different media, in order to simulate the daylight and induce upward swimming (Fig. 5). They were also carefully cultured in a medium that is unlikely to modify the light responses of the individuals as overly rich mediums are likely to induce negative phototaxis (Martins et al., 2007). These experiments successfully identified lethal thresholds of many chemicals commonly found in aquatic environments, confirming that with a careful selection of the investigated individuals, *Daphnia* can be an important tool for aquatic monitoring.

A study by Magester et al. (2021) investigated the effects of microplastics on the upward swimming ability of *D. magna*, using a similar setup to Martins et al. (2007). This study, however, assumes the positive phototaxis of all the used individuals without using clones. The study also offers an explanation for the microplastic effect to be simply starvation caused by the microplastic buildup preventing the *Daphnia* from feeding normally.

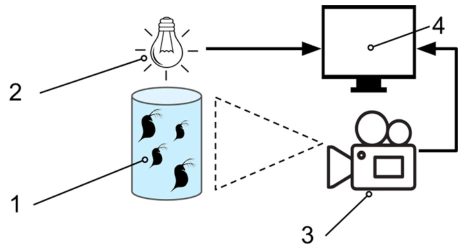

Fig. 5. The experimental setup most commonly used in studies investigating *Daphnia*'s phototactic response. The setup most often consists of the animal chamber (**1**) with a light source (**2**) suspended above it. A camera (**3**) observes animals swimming in the chamber and the videos are later analysed with image processing software (**4**). The camera observation is optional as in older studies, only manual counting was used.

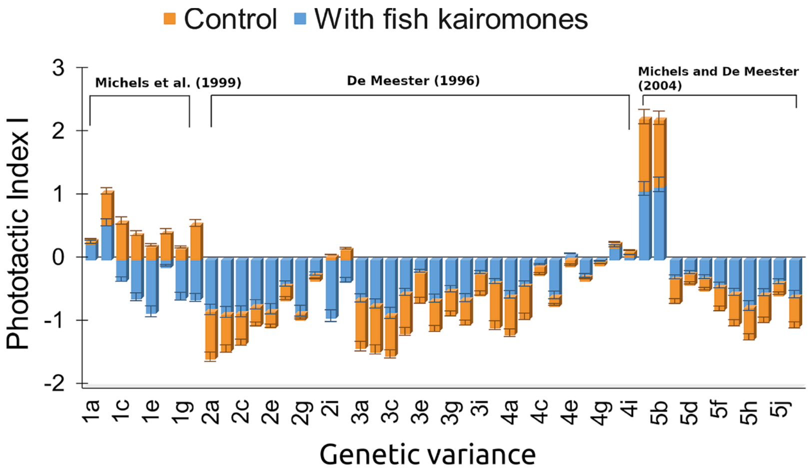

Fig. 4. Phototactic index of different clones when exposed to fish kairomones. The Phototactic Index I as explained in Fig. 2. Genetic variance corresponds to specific clones. Data compiled from De Meester and Cousyn (1997); Michels and De Meester (2004); Michels et al. (1999).

2.6. Food conditions

Another significant factor in *Daphnia*'s ability to react to light is the food quality and/or food availability (Martins et al., 2007). Since the light response is highly likely to be behaviourally conditioned by the combination of predator avoidance and food seeking, it was hypothesised that different food conditions might generate different reactions. In a study by Michels and De Meester (1998) *D. magna* was found to show different phototactic responses when fed different diets. A diet comprising for the most part of algae induced a stronger positive phototaxis than diets with partial substitution of yeast or ciliates. This can be explained by the lower nutritional value of the yeast due to their lower digestibility and low content of fatty acids essential for *Daphnia* development (Michels and De Meester, 1998). *Daphnia* fed with pure yeast showed a variety of other stress symptoms, such as pale colouration and degenerated eggs, thus it can be assumed that low food quality can be an indirect driver for a reduced positive phototaxis due to being an insufficient energy source. Similar results were obtained by Kieu et al. (2001) where the use of phototaxis for water assessment was tested under different feeding regimes. The food quality changed the detection limit, with algae allowing *Daphnia* to detect 0.4 mg/L pentachlorophenol (PCP) and 1.2 mg/L PCP with yeast as food.

One of the newest studies published by Bednarska et al. (2023) confirmed this dependence by investigating the relationship between food quality and the ability to escape predators. Predator feeding was both simulated using a pipette and induced by introducing feeding fish (*Poecilia reticulata*). In both cases, *D. magna* fed with a diet with the addition of cyanobacteria showed a less efficient predatory escape behaviour. This shows that food quality has an effect on the phototactic behaviour as it affects the general well-being of *Daphnia*.

Besides food quality, food availability plays another important role in the light response and, consequently, the migration of *Daphnia* (Johnsen and Jakobsen, 1987). Under insufficient food conditions, *Daphnia* prioritizes feeding over predation avoidance. In the field experiments performed by Johnsen and Jakobsen (1987), larger individuals of *D. longispina* showed to prioritize feeding near the surface continuously during the day and night under scarce food conditions, as opposed to migrating under normal food conditions. These results are in contrast with results obtained by De Meester and Dumont (1989) who observed *D. magna*'s decreasing positive phototaxis as food became limited De Meester and Dumont (1989). The differential factors might be the differences between laboratory and field trials and the abnormally low algae concentration tested in De Meester and Dumont (1989) which are unlikely to be noted in the field. Under this extreme food depletion, it is possible that the phototaxis was inhibited due to the lack of energy required for upward swimming.

On the contrary, in nutrient-rich waters, many other phototactic animals, for example, larvae of the crab *Rhithropanopeus harrisii* are less likely to present positive phototaxis as there is a lesser need to sacrifice the predator avoidance (Cronin and Forward Jr, 1980). With high food availability, there is less of a need to seek out food near the surface where the light intensity and the predation are the highest. A study by Van Gool and Ringelberg (1998) found that both higher food concentration and the presence of fish kairomones induce faster downward swimming when a light cue is introduced. This confirms that more food provides a sufficient energy source to enhance an already selected behaviour Van Gool and Ringelberg (1998). However, in *Daphnia*, the direct relationship between excess food and light-induced migrations have not been investigated thoroughly.

2.7. Individual and collective responses

Like many other congregating organisms, *Daphnia* has been observed to behave differently when single or in a group. *Daphnia* is thought to swarm under certain conditions as a defensive mechanism against predators (Ordemann et al., 2003). The aggregation is combined with a more uniform swimming speed, compared to predator-less samples, which together reduce the predation risk (Jensen et al., 1998). This collective behaviour has been used as a model to study the phenomenon of DVM seen in many planktonic species (Ringelberg, 1964). It was also observed that this organism shows a stronger migration pattern in a group (Gerhardt et al., 2006).

A setup constructed by Gerhardt et al. (2006) allowed for automatic *Daphnia* tracking using non-optical methods and using it to test various aspects of the phototactic behaviour. One of the results was that *D. magna* showed a clearer circadian rhythm when there were multiple individuals in the setup (Gerhardt et al., 2006). This suggests that the response to light under varying swarm conditions may differ and should be evaluated separately.

2.8. Theoretical studies

Besides the extensive empirical studies on *Daphnia*'s behaviour, various modelling analyses were also performed. As many other organisms, *Daphnia* form swarms under certain conditions. Modelling swarming can provide additional data on the environment, as this complex behaviour is often a result of various changes such as predator presence, scarce food and others (Mach and Schweitzer, 2007).

Swarming of *Daphnia* has been a subject of interest because of its importance as a link between micro and macro aquatic communities in regards to size and biological complexity (Ordemann et al., 2003). For this reason, many studies such as Øien (2004), Mach and Schweitzer (2007) and Ringelberg (1995) focused on creating a model for single individuals and groups of *Daphnia*' swimming patterns. These have successfully increased our understanding of the DVM (Ringelberg, 1995), the mechanism of creating vortex motion (Mach and Schweitzer, 2007; Ordemann et al., 2003) and general swarm dynamics (Øien, 2004). However, modelling studies on interpreting *Daphnia*'s behaviour on a large scale in the field have rarely been performed.

To be able to extrapolate from the observed behaviour the state of a larger area, empirical studies have to be combined with certain algorithms. A theoretical study by Vogrin et al. (2023) designed a sensor to optimise the interpretation of the behaviour of the *Daphnia* population subset. Two sub-sensors, one overestimating and one underestimating the state of the environment were created. The study shows that using pooled results of those two sub-optimal sensors creates a more accurate algorithm for environmental estimation (Vogrin et al., 2023). This approach can be used on behavioural data from one area of the lake and as a proxy for the more general state of the lake.

Currently, *Daphnia*'s use as a bioindicator is mostly restricted to laboratory studies from which very little extrapolation has been attempted. In order to maximise the interpretation of the results and be able to significantly move forward the use of *Daphnia* as a live sensor, more analytical and modelling studies must be performed.

3. Discussion

In this work, we presented a summary of various studies investigating the phototactic behaviour, using it as an indicator of *Daphnia*'s well-being and, as a result, an indicator of the state of the environment. This review is aimed to be a good starting point for researchers interested in the phototactic behaviour. Lifeforms react to a multitude of stimuli provided by environmental factors and those reactions can vary depending on the combination and intensity of the stressors increasing the complexity of behavioural research. The daphnids have brought sufficient results over the years to maintain their status as reliable bioindicators in aquatic monitoring. However, when using an animal's behavioural or physiological responses as an indicator, a holistic approach must be taken. The phototactic response of *Daphnia* can be affected by a great number of factors and considering all of them is essential to obtaining reliable results. The extensive research on this genus can provide a unified methodology for all further studies.

The most commonly applied and recommended approach to study *Daphnia*'s phototactic response is using clones of specific reared strains, with a known strong response to the light cues, as did Martins et al. (2007); Rhode et al. (2001); Tollrian and Heibl (2004) and many others. Providing sufficient food sources prior to or during the experiments prevents adding an additional stress factor to *Daphnia*. These and other findings of this review together with the proposed countermeasures regarding the use of *Daphnia*'s light responses in research can be found in Table 2.

During laboratory trials where all the experimental conditions can be easily controlled, proper documentation of the aforementioned parameters (Table 2) is of merit. In the field, where the conditions are much more unstable, a thorough understanding of the species' genetics and habitat is recommended, before using the phototactic behaviour as an indicator.

This organism finds its uses in many current methodologies for water assessments, both in the laboratory and in the field. An example of a field application of *Daphnia*'s swimming behaviour is the project "Robocoenosis" launched in 2020 by Thenius et al. (2021). The research team chose *Daphnia* as one of the live biosensors for continuous underwater monitoring with disrupted phototaxis being one of the potentially useful stress responses (Rajewicz et al., 2021; Thenius et al., 2021). The project constructed a "Daphnia module" hosting the organisms and analysing their swimming behaviour inside the automated setup (Fig. 6). This is an example of in-field research where the habitat, together with the behaviour it determines, will have a major impact on the results.

Daphnia have been also implemented in modern ecological laboratory-based assessments. Recently, a device called *DaphTox* produced by a German company *bbe Moldaenke* was used as a tool in many research studies (Aydin et al., 2015; Łaszczyca et al., 2023; Pilgård et al., 2010; Soldán, 2021). This piece of equipment contains a large chamber where the swimming *Daphnia* are continuously monitored with image analysis methods. Various swimming parameters (swimming depth, aggregation, sinking etc.) are taken under consideration and the number of *Daphnia* recognised as stressed is determined to sound an alarm when a threshold is exceeded (when enough individuals are presenting a stress behaviour).

Image detection is the most common method used in studying *Daphnia*'s swimming behaviour, however, new methods are being developed to overcome the limitations that come with image analysis (water turbidity, low light conditions etc.) (Noss et al., 2013). Gerhardt et al. (2006) managed to successfully track *Daphnia*'s swimming behaviour by measuring changes in impedance caused by the animals' movements in the measuring chamber. This opens the door to observation under difficult field conditions where visual analysis can not always perform well (Gerhardt et al., 2006).

It can be concluded that observing the phototactic responses and changes in certain behavioural patterns is a promising tool to monitor the state of the environment. With this in mind, it is of merit to recognise both limitations and advantages of using *Daphnia*'s light response behaviour as a sensor for water monitoring. Organisms are a wide-spectrum, low-precision sensor. This means that early detection of certain compounds is possible by adding whole-organism sensors in addition to traditional sample-taking methods. Especially in the case of compounds for which sampling surveys are required, for example, microplastics, the continuous readings of *Daphnia*'s stress levels can detect the pollution quicker than the next scheduled sampling date. However, as with many other organisms, the stress reactions can overlap for several various stressors (for example, temporal immobilisation was observed in individuals exposed to both norfloxacin and saxitoxin (Bownik, 2017)). For this reason, the use of this approach is advised when one is interested in tracking the general state of the environment. In the case of an interest in a specific contaminant, it is optimal to use a classical sensor, which will provide a precise reading on a parameter of choice. A summary of the advantages and limitations of using phototaxis as an indicator is presented in Table 3.

3.1. International regulations

Daphnia sp. fulfils most, if not all, of the criteria of a good bio-indicator: globally abundant, sensitive to a wide range of environmental stressors, easily recognisable and others (Le et al., 2016). For this reason, certain methodologies and guidelines are well-established by environmental agencies for various toxicity test procedures. The behaviour most commonly used for toxicity assessments is immobilisation (OECD, 2004) and life-cycle changes (ASTM, 1997; OECD, 1984). The guides provide protocols for determining the E_{50} value which stands for the concentration of the substance which immobilises 50% of individuals (OECD, 1984).

The most extensive guides for toxicity assessments are concluded in works such as Biesinger et al. (1987) or EPA (2002). They offer a detailed description of the conditions required for a proper investigation of *Daphnia*'s behavioural responses. The conditions include the feeding regime, the number of individuals per volume of water suitable for culturing, the experimental plan for acute and chronic tests and others. For the number of guides and protocols on *Daphnia* in toxicology, there are very few that discuss the use of phototactic behaviour as a sensor. One of the most extensive studies regarding this is Martins et al. (2007)

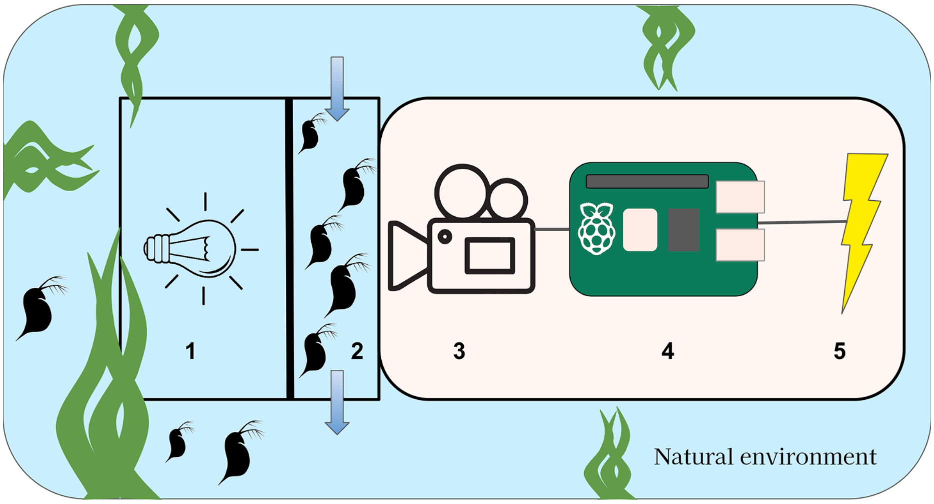

Fig. 6. A schematic representation of the "Daphnia module". The module consists of a background light (1) illuminating the flow-through *Daphnia* cage (2). The animals are recorded by a camera (3) controlled by the Raspberry Pi (4) with the energy source (5).

where the phototactic response is used to determine the severity of eleven chemicals in the aquatic environments. However, to our knowledge, no guidelines have been made by the Environmental Protection Agency (EPA) or Organisation for Economic Co-operation and Development (OECD) for the use of phototaxis as a stress indicator. Several other species were investigated in this context, such as the barnacle nauplii of *Balanus improvisus* (both laboratory-hatched and plankton-caught), zebrafish (*Danio rerio*) larvae (Brooks et al., 2008).

Table 3
Summary of advantages and limitations of using *Daphnia*'s phototactic response as a sensor for toxicological and ecological studies.

Advantage	Limitation	References
Easier detection of a broad range of toxicants	Low precision of the biosensor due to a multitude of stressors inducing similar changes in the phototactic responses	Lomba et al. (2020); Sousa and Nunes (2021)
Investigating the effects of certain chemicals on aquatic life	Organisms vary in resistance to different compounds and changes thus the effect estimation is skewed by the organism-specific reactions	(DeMott et al., 1991; Kulkarni et al., 2013; Lomba et al., 2020; Sousa and Nunes, 2021)
Early detection of certain compounds (at times, earlier than other behavioural markers)	Other stressors might lower the reaction threshold of the organism. Having to ensure that all other conditions are optimal to ensure the animal's reaction only to the substance of interest	(Dietrich et al., 2010; Kim et al., 2023; Martins et al., 2007)

The study on phototaxis reaches back to the late 1800s (Kozlowski, 1897). Since then, it has been expanded to various species of animals, plants and bacteria (Jennings, 1900; Kozlowski, 1897). From the literature search, it can be noticed that the usage of *Daphnia*'s phototaxis in toxicity assessments began only in the late 1900s (Table 4). For an overview of the timeline regarding the research on phototaxis in *Daphnia*, please see Table 4.

3.2. *Summary of recent studies*

A large part of studies published in 2023 seemed to be focused on, amongst others, *Daphnia*'s response to microplastic pollution (Savva et al., 2023; Yin et al., 2023; Zink et al., 2023) and responses to wastewater effluents (Brunelle et al., 2023; Stewart et al., 2023). Most recent research on *Daphnia* investigated several other factors that could potentially affect the phototactic response. A study by Howell et al., 2023 investigated the relationship between the light availability and the size and position of the eye and the predator-avoidance behaviour of *D. pulicaria* (which in the study was synonymous with negative phototaxis). It was observed that the low availability of light weakened the response of *Daphnia* to light cues, in other words, lessened the predator-avoidance behaviour. *Daphnia* exposed to high light intensity exhibited 18% more negative phototactic response than *Daphnia* exposed to a low light treatment. This suggests that the light conditions during the rearing phases over multiple generations can affect the results based on the phototactic index of *Daphnia*.

Table 4
Summary table of representative authors investigating the phototactic behaviour of *Daphnia* over time.

Objective	Time period	Examples
Phototaxis research	1800s	(Kozlowski, 1897)
	1900s	(Johnsen and Jakobsen, 1987; Michels and De Meester, 1998; Ringelberg, 1964; Storz and Paul, 1998; Van Gool and Ringelberg, 1997; 1998; Weider and Lampert, 1985)
	2000s	(Nikitin, 2019; Rhode et al., 2001; Ringelberg, 1964; Vareschi and Wübben, 2001)
Toxicology assessment	1900s	(di Delupis et al., 1992; Gokcen and McNaught, 1995; Michels et al., 1999; Ringelberg, 1964)
	2000s	(Kieu et al., 2001; Kolkmeier and Brooks, 2013; Lomba et al., 2020; Ma et al., 2022; Magester et al., 2021; Martins et al., 2007; Nagel et al., 2022; Reilly et al., 2023; Rivetti et al., 2016a; 2016b; Soldán, 2021; Sousa and Nunes, 2021)

Regarding the usage of the phototactic response as an environmental sensor, a study by Dyomin et al. (2023) investigated the differences in the phototropic response of *D. magna* and *D. pulex* to various light intensities. The findings showed that the daphnids have varying responses to light intensities depending on the light levels changing continuously or intermittently. The authors suggest a novel method of using phototaxis in toxicity assessments: paired photostimulation. It consists of two types of light stimuli where the first, less intense, activates the phototactic response whereas the second, more intense, is used to estimate the *Daphnia*'s physical ability to swim towards the light. These phototactic evaluations were shown to be more sensitive to changes than the established markers, like EC_{50}. This was also shown in the study by Martins et al. (2007), where the lowest concentrations of the toxicant detected were up to 43 times lower than the value EC_{50} (Dyomin et al., 2023).

3.3. *Recent studies on phototaxis as a marker for xenobiotic toxicity*

As mentioned previously, phototaxis has been used as a marker for toxicity assessments for various xenobiotics and their mixtures. A method for its implementation has been proposed, amongst others, by Goodrich and Lech (1990). The method included the analysis of *Daphnia magna* moving along the gradient of light in response to various substances. The animals showed an increase in random (instead of directional) movement to lindane, which was used a calibration substance, at concentrations as low as 50 ppb.

Other studies used this or similar methods of investigating *Daphnia magna*'s swimming behaviour to assess various mixtures of xenobiotics. For example, Schmidt et al. (2005) investigated the effect of a technical PCB mixture (polychlorinated biphenyls) and TBT (tributyltinchloride). The results showed an increased toxicity of the combination of those substances rather than their individual effects. Other mixtures investigated in the context of *Daphnia*'s swimming behaviour were copper and zinc (Vlaeminck et al., 2021), cadmium and microplastics (MP) (Zink et al., 2023), fullerenes and functionalized fullerenes (Brausch et al., 2011) and many others. In most cases, the combined effect of the xenobiotics had a greater effect on the normal behaviour than their individual effects. A study by Boyd et al. (2023) reevaluated the long-term impact of UV filters (UVf) on *Daphnia magna*. Here, a recovery was observed in physiological and behavioural traits, including the phototaxis, by the fourth generation exposed to a UVf.

An especially thoroughly investigated xenobiotic regarding *Daphnia*'s behaviour are microplastics (MP). A study by Song et al. (2021) investigated the combined effects of MP and MP particles containing benzophenone-3 (BP-3) additive. It was found that the addition of BP-3 decreased the ingestion of MP which in turn decreased the mortality levels. However, both the BP-3 and MP containing the BP-3-additive significantly lowered the phototactic index of *Daphnia* compared to the presence of just the MP fragments or the control sample. Similar results were obtained the previously mentioned research by Magester et al. (2021) where *Daphnia magna* showed a decrease in phototactic behaviour, body length and survival rates when exposed to high concetraions of MP particles.

On the other hand, De Felice et al. (2019) noticed an increased positive phototactic activity in *Daphnia magna* exposed to two sizes of MP particles. In addition, the overall swimming velocity and body length increased in the presence of MP. The study suggests that in the presence of MP, *Daphnia magna* might increase the swimming activity as an avoidance behaviour or as an attempt to excrete the MP particles. The contradictory results of these studies encourages additional research ragarding the driving factors in *Daphnia*'s response to MP. Similarly, an exposure to thallium (TI) resulted in an increated phototaxis in a study by Nagel et al. (2022). In the presence of TI at environmentally-extreme concentrations of 917 and 2099 μg/L, the daphnids showed a decreased swimming speed towards the light source, however their density in the illuminated water layer was higher compared to control. This shows that different contaminants have different effects on the phototactic response, as opposed to simply inhibiting the movement which often also results in a lower phototactic index.

While many other studies investigated the toxicity of various xenobiotics, the analysis most often included the survival rate, growth rate and other non-light-related responses. As mentioned in this study, *Daphnia* can present positive or negative phototaxis based on their natural habitats and have to prioritize UV light avoidance or predators even after they have been taken out of that habitat. It is essential to take a holistic approach when examining its phototactic behaviour. This review presents a summary of factors affecting this behavioural reaction and shows the importance of the full integration of the knowledge on *Daphnia*'s biology and ecology in ecological research. Incorporating the study of *Daphnia*'s phototactic response into the future research can provide a more comprehensive understanding of the ecological consequences of xenobiotics on *Daphnia* and the aquatic environments they inhabit.

CRediT authorship contribution statement

Wiktoria Rajewicz: Conceptualization, Methodology, Writing – original draft, Visualization, Writing – review & editing. **Donato Romano:** Conceptualization, Writing – original draft. **Thomas Schmickl:** Conceptualization, Supervision, Writing – review & editing. **Ronald Thenius:** Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgments

This work was supported by EU-H2020 Project Robocoenosis, grant agreement No 899520. Furthermore, this work was supported by The Field of Excellence COLIBRI (COmplexity of LIfe in Basic Research and Innovation) at the University of Graz. We further thank the ”Österreichische Bundesforste AG”, the ”Burgenländische Landesregierung, Abt. 4 (Natur- und Klimaschutz)” and the ”Biologische Station Illmitz” for their support.

References

ASTM, 1997. Standard guide for conducting daphnia magna life-cycle toxicity tests. Annual Book ASTM Standard. 11, 474–491.

Awoyemi, O.M., Subbiah, S., Velazquez, A., Thompson, K.N., Peace, A.L., Mayer, G.D., 2020. Nitrate-n-mediated toxicological responses of scenedesmus acutus and daphnia pulex to cadmium, arsenic and their binary mixture (cd/asmix) at environmentally relevant concentrations. J. Hazard. Mater. 400, 123189.

Aydin, M.E., Aydin, S., Tongur, S., Kara, G., Kolb, M., Bahadir, M., 2015. Application of simple and low-cost toxicity tests for ecotoxicological assessment of industrial wastewaters. Environ. Technol. 36 (22), 2825–2834.

Bae, M.-J., Park, Y.-S., 2014. Biological early warning system based on the responses of aquatic organisms to disturbances: a review. Sci. Total Environ. 466, 635–649.

Bandara, K., Varpe, Ø., Wijewardene, L., Tverberg, V., Eiane, K., 2021. Two hundred years of zooplankton vertical migration research. Biol. Rev. 96 (4), 1547–1589.

Bednarska, A., Wiśniewska, A., Dawidowicz, P., 2023. Effect of food quality on escape performance of daphnia. Ecohydrol. Hydrobiol.

Bellot, M., Gómez-Canela, C., Barata, C., 2022. Phototactic behaviour and neurotransmitter profiles in two daphnia magna clones: vertical and horizontal responses to fish kairomones and psychotropic drugs. Sci. Total Environ. 830, 154684.

Biesinger, K., Williams, L., van der Schalie, W., 1987. Users guide: Procedures for conducting daphnia magna toxicity bioassays. US Environmental Protection Agency.

Bownik, A., 2017. Daphnia swimming behaviour as a biomarker in toxicity assessment: a review. Sci. Total Environ. 601, 194–205.

Boyd, A., Choi, J., Ren, G., How, Z.T., El-Din, M.G., Tierney, K.B., Blewett, T.A., 2023. Can short-term data accurately model long-term environmental exposures? Investigating the multigenerational adaptation potential of daphnia magna to environmental concentrations of organic ultraviolet filters. J. Hazard. Mater. 445, 130598.

Brausch, K.A., Anderson, T.A., Smith, P.N., Maul, J.D., 2011. The effect of fullerenes and functionalized fullerenes on daphnia magna phototaxis and swimming behavior. Environ. Toxicol. Chem. 30 (4), 878–884.

Brooks, J., Macphail, R., Hunter, D., Padnos, B. K., Padilla, S. J., 2008. Characterization of locomotor activity of zebrafish larvae: temporal variability and photoresponse.

Brunelle, L.D., Szczygiel, B., Running, L.S., Su, L., Naas, K.M., Dai, N., Pérez-Fuentetaja, A., Aga, D.S., 2023. Effects of advanced oxidation on wastewater effluent ecotoxicity: a novel assessment through the life history and lipidomics analysis of daphnia magna. ACS ES&T Water 3 (2), 438–447.

Choi, J., Park, R., Kang, E., Oak, S., Yim, H., Chung, M., Kim, H.S., Choo, S.H., Lee, J., Suh, A., 2013. An evaluation of acute toxicity using the phototactic behavior of daphnia magna. J. Pharmacol. Toxicol. Methods 1 (68), e50–e51.

Clark Jr, L.C., Spokane, R.B., Homan, M.M., Sudan, R., Miller, M., 1988. Long-term stability of electroenzymatic glucose sensors implanted in mice. an update. ASAIO Trans. 34 (3), 259–265.

Cronin, T.W., Forward Jr, R.B., 1980. The effects of starvation on phototaxis and swimming of larvae of the crab rhithropanopeus harrisii. Biol. Bull. 158 (3), 283–294.

De Felice, B., Sabatini, V., Antenucci, S., Gattoni, G., Santo, N., Bacchetta, R., Ortenzi, M. A., Parolini, M., 2019. Polystyrene microplastics ingestion induced behavioral effects to the cladoceran daphnia magna. Chemosphere 231, 423–431.

De Meester, L., Cousyn, C., 1997. The change in phototactic behaviour of a daphnia magna clone in the presence of fish kairomones: the effect of exposure time. Hydrobiologia 360 (1), 169–175.

De Meester, L., Dumont, H.J., 1989. Phototaxis in daphnia: interaction of hunger and genotype. Limnol. Oceanogr. 34 (7), 1322–1325.

di Delupis, G.D., Macrí, A., Civitareale, C., Migliore, L., 1992. Antibiotics of zootechnical use: effects of acute high and low dose contamination on daphnia magna straus. Aquat. Toxicol. 22 (1), 53–59.

DeMott, W.R., Zhang, Q.-X., Carmichael, W.W., 1991. Effects of toxic cyanobacteria and purified toxins on the survival and feeding of a copepod and three species of daphnia. Limnol. Oceanogr. 36 (7), 1346–1357.

Dietrich, S., Ploessl, F., Bracher, F., Laforsch, C., 2010. Single and combined toxicity of pharmaceuticals at environmentally relevant concentrations in daphnia magna -a multigenerational study. Chemosphere 79 (1), 60–66.

Dincer, C., Bruch, R., Costa-Rama, E., Fernández-Abedul, M.T., Merkoçi, A., Manz, A., Urban, G.A., Güder, F., 2019. Disposable sensors in diagnostics, food, and environmental monitoring. Adv. Mater. 31 (30), 1806739.

Dyomin, V., Morgalev, Y., Morgalev, S., Morgaleva, T., Davydova, A., Polovtsev, I., Kirillov, N., Olshukov, A., Kondratova, O., 2023. Features of phototropic response of zooplankton to paired photostimulation under adverse environmental conditions. Environ. Monit. Assess. 195 (4), 503.

Ekvall, M.T., Sha, Y., Palmér, T., Bianco, G., Bäckman, J., Åström, K., Hansson, L.-A., 2020. Behavioural responses to co-occurring threats of predation and ultraviolet radiation in daphnia. Freshw. Biol. 65 (9), 1509–1517.

EPA 2002. Methods for Measuring the Acute Toxicity of Effluents and Receiving Waters to Freshwater and Marine Organisms. 1200 Pennsylvania Avenue, NW Washington, DC 20460. 5th edition.

Gerhardt, A., De Bisthoven, L.J., Schmidt, S., 2006. Automated recording of vertical negative phototactic behaviour in daphnia magna straus (crustacea). Hydrobiologia 559 (1), 433–441.

Glaholt, S.P., Kennedy, M.L., Turner, E., Colbourne, J.K., Shaw, J.R., 2016. Thermal variation and factors influencing vertical migration behavior in daphnia populations. J. Therm. Biol. 60, 70–78.

Gokcen, J.E., McNaught, D.C., 1995. A behavioral bioassay employing daphnia for detection of sublethal effects: response to polarized light. Mar. Freshwater Behav. Phy. 26 (2–4), 267–272.

Goodrich, M.S., Lech, J.J., 1990. A behavioral screening assay for daphnia magna: a method to assess the effects of xenobiotics on spacial orientation. Environ. Toxicol. Chem.: Int. J. 9 (1), 21–30.

Hansson, L.-A., Hylander, S., 2009. Size-structured risk assessments govern daphnia migration. Proc. R. Soc. B: Biol. Sci. 276 (1655), 331–336.

Howell, K., Muh, S., Parajuli, B., Walsh, M.R., 2023. Experimental test of the influence of light availability on the evolution of eye size and behaviour in daphnia. J. Evol. Biol.

Itoh, A., Hisama, H., 2010. Motion control of daphnia magna by blue LED light. J. Aero Aqua Bio-Mech. 1 (1), 93–98.

Jennings, H.S., 1900. Zoological journal club of the university of michigan. Science 12 (310), 886–887.

Jensen, K.H., Jakobsen, P.J., Kleiven, O.T., 1998. Fish kairomone regulation of internal swarm structure in daphnia pulex (cladocera: crustacea). Hydrobiologia 368 (1), 123–127.

Johnsen, G.H., Jakobsen, P.J., 1987. The effect of food limitation on vertical migration in daphnia longispina. Limnol. Oceanogr. 32 (4), 873–880.

Kessler, K., Lockwood, R.S., Williamson, C.E., Saros, J.E., 2008. Vertical distribution of zooplankton in subalpine and alpine lakes: ultraviolet radiation, fish predation, and the transparency-gradient hypothesis. Limnol. Oceanogr. 53 (6), 2374–2382.

Kieu, N.D., Michels, E., De Meester, L., 2001. Phototactic behavior of daphnia and the continuous monitoring of water quality: interference of fish kairomones and food quality. Environ. Toxicol. Chem. 20 (5), 1098–1103.

Kim, H., Kim, D., An, Y.-J., 2023. Microplastics enhance the toxicity and phototoxicity of UV filter avobenzone on daphnia magna. J. Hazard. Mater. 445, 130627.

Kolkmeier, M.A., Brooks, B.W., 2013. Sublethal silver and nacl toxicity in daphnia magna: a comparative study of standardized chronic endpoints and progeny phototaxis. Ecotoxicology 22, 693–706.

Kozlowski, W., 1897. Contribution to the theory of the movements of diatoms. Botanical Gazette 24 (1), 39–46.

Kulkarni, D., Gergs, A., Hommen, U., Ratte, H.T., Preuss, T.G., 2013. A plea for the use of copepods in freshwater ecotoxicology. Environ. Sci. Pollut. Res. 20, 75–85.

Landon, M.S., Stasiak, R.H., 1983. Daphnia hemoglobin concentration as a function of depth and oxygen availability in arco lake, minnesota. Limnol. Oceanogr. 28 (4), 731–737.

Łaszczyca, P., Nakonieczny, M., Kostecki, M., 2023. Ecotoxicological biotests as tools for continuous monitoring of water quality in dam reservoir. Archiv. Environ. Protect. 25–38.

Le, Q.-A.V., Sekhon, S.S., Lee, L., Ko, J.H., Min, J., 2016. Daphnia in water quality biomonitoring-"omic" approaches. Toxicol. Environ. Health Sci. 8, 1–6.

Leitch, O., Anderson, A., Kirkbride, K.P., Lennard, C., 2013. Biological organisms as volatile compound detectors: a review. Forensic Sci. Int. 232 (1–3), 92–103.

Lomba, L., Lapeña, D., Ros, N., Aso, E., Cannavò, M., Errazquin, D., Giner, B., 2020. Ecotoxicological study of six drugs in aliivibrio fischeri, daphnia magna and raphidocelis subcapitata. Environ. Sci. Pollut. Res. 27, 9891–9900.

Ma, Y., Xu, D., Li, C., Wei, S., Guo, R., Li, Y., Chen, J., Liu, Y., 2022. Combined toxicity and toxicity persistence of antidepressants citalopram and mirtazapine to zooplankton daphnia magna. Environ. Sci. Pollut. Res. 29 (44), 66100–66108.

Mach, R., Schweitzer, F., 2007. Modeling vortex swarming in daphnia. Bull. Math. Biol. 69, 539–562.

Magester, S., Barcelona, A., Colomer, J., Serra, T., 2021. Vertical distribution of microplastics in water bodies causes sublethal effects and changes in daphnia magna swimming behaviour. Ecotoxicol. Environ. Saf. 228, 113001. https://doi.org/10.1016/j.ecoenv.2021.113001.

Martins, J., Soares, M., Saker, M.L., Oliva-Teles, L., Vasconcelos, V., 2007. Phototactic behavior in daphnia magna straus as an indicator of toxicants in the aquatic environment. Ecotoxicol. Environ. Saf. 67 (3), 417–422.

Michels, E., De Meester, L., 1998. The influence of food quality on the phototactic behaviour of daphnia magna straus. Hydrobiologia 379 (1), 199–206.

Michels, E., De Meester, L., 2004. Inter-clonal variation in phototactic behaviour and key life-history traits in a metapopulation of the cyclical parthenogen daphnia ambigua: the effect of fish kairomones. Hydrobiologia 522, 221–233.

Michels, E., Leynen, M., Cousyn, C., De Meester, L., Ollevier, F., 1999. Phototactic behavior of daphnia as a tool in the continuous monitoring of water quality: experiments with a positively phototactic daphnia magna clone. Water Res. 33 (2), 401–408.

Nagel, A.H., Robinson, A.S., Goss, G.G., Glover, C.N., 2022. Effect of thallium on phototactic behaviour in daphnia magna. Environ. Sci. Pollut. Res. 29 (54), 81740–81748.

Nikitin, O., 2019. Effect of various temperature and light intensity regimes on Daphnia magna swimming behaviour. 19th SGEM International Multidisciplinary Scientific GeoConference EXPO. Albena, pp. 229–236. https://doi.org/10.5593/sgem2019/5.1/S20.029.

Noss, C., Dabrunz, A., Rosenfeldt, R.R., Lorke, A., Schulz, R., 2013. Three-dimensional analysis of the swimming behavior of daphnia magna exposed to nanosized titanium dioxide. PLoS ONE 8 (11), e80960.

OECD, 1984. Daphnia sp., acute immobilisation test and reproduction test. https://www.oecd.org/chemicalsafety/risk-assessment/1948249.pdf.

OECD, 2004. Test no. 202: Daphnia sp. acute immobilisation test. https://www.oecd-ilibrary.org/content/publication/9789264069947-en. 10.1787/9789264069947-en.

Ohman, M.D., Romagnan, J.-B., 2016. Nonlinear effects of body size and optical attenuation on diel vertical migration by zooplankton. Limnol. Oceanogr. 61 (2), 765–770.

Øien, A.H., 2004. Daphnicle dynamics based on kinetic theory: an analogue-modelling of swarming and behaviour of daphnia. Bull. Math. Biol. 66 (1), 1–46. https://doi.org/10.1109/ISCAS.2017.8050610.

Ordemann, A., Balazsi, G., Moss, F., 2003. Pattern formation and stochastic motion of the zooplankton daphnia in a light field. Physica A 325 (1–2), 260–266.

Ortells, R., Reusch, T.B., Lampert, W., 2005. Salinity tolerance in daphnia magna: characteristics of genotypes hatching from mixed sediments. Oecologia 143 (4), 509–516.

Paul, R.J., Zeis, B., Lamkemeyer, T., Seidl, M., Pirow, R., 2004. Control of oxygen transport in the microcrustacean daphnia: regulation of haemoglobin expression as central mechanism of adaptation to different oxygen and temperature conditions. Acta Physiol. Scand. 182 (3), 259–275.

Pijanowska, J., Kowalczewski, A., 1997. Predators can induce swarming behaviour and locomotory responses in daphnia. Freshw. Biol. 37 (3), 649–656.

Pilgård, A., De Vetter, L., Van Acker, J., Westin, M., 2010. Toxic hazard of leachates from furfurylated wood: comparison between two different aquatic organisms. Environ. Toxicol. Chem. 29 (5), 1067–1071.

Polatoğlu, İ., Aydın, L., Nevruz, B.Ç., Özer, S., 2020. A novel approach for the optimal design of a biosensor. Anal. Lett. 53 (9), 1428–1445.

Rajewicz, W., Romano, D., Varughese, J.C., Van Vuuren, G.J., Campo, A., Thenius, R., Schmickl, T., 2021. Freshwater organisms potentially useful as biosensors and power-generation mediators in biohybrid robotics. Biol. Cybern. 115 (6), 615–628.

Rautio, M., Korhola, A., Zellmer, I.D., 2003. Vertical distribution of daphnia longispina in a shallow subarctic pond: does the interaction of ultraviolet radiation and chaoborus predation explain the pattern? Polar Biol. 26 (10), 659–665.

Reilly, K., Ellis, L.-J.A., Davoudi, H.H., Supian, S., Maia, M.T., Silva, G.H., Guo, Z., Martinez, D.S.T., Lynch, I., 2023. Daphnia as a model organism to probe biological responses to nanomaterials- from individual to population effects via adverse outcome pathways. Front. Toxicol. 5, 1178482.

Rhode, S.C., Pawlowski, M., Tollrian, R., 2001. The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus daphnia. Nature 412 (6842), 69–72.

Ringelberg, J., 1964. The positively phototactic reaction of daphnia magna straus: a contribution to the understanding of diurnal vertical migration. Neth. J. Sea Res. 2 (3), 319–406.

Ringelberg, J., 1995. An account of a preliminary mechanistic model of swimming behaviour in Daphnia: its use in understanding diel vertical migration. Cladocera as Model Organisms in Biology: Proceedings of the Third International Symposium on Cladocera, held in Bergen, Norway, 9–16 August 1993. Springer, pp. 161–165.

Ringelberg, J., 1999. The photobehaviour of daphnia spp. as a model to explain diel vertical migration in zooplankton. Biol. Rev. 74, 397–423. https://doi.org/10.1017/S0006323199005381.

Ringelberg, J., Van Gool, E., 1995. Migrating daphnia have a memory for fish kairomones. Mar. Freshw. Behav. Physiol. 26 (2–4), 249–257.

Rivetti, C., Campos, B., Barata, C., 2016. Low environmental levels of neuro-active pharmaceuticals alter phototactic behaviour and reproduction in daphnia magna. Aquat. Toxicol. 170, 289–296.

Rivetti, C., Campos, B., Barata, C., 2016. Low environmental levels of neuro-active pharmaceuticals alter phototactic behaviour and reproduction in daphnia magna. Aquat. Toxicol. 170, 289–296. https://doi.org/10.1016/j.aquatox.2015.07.019.

Rose, K.C., Williamson, C.E., Fischer, J.M., Connelly, S.J., Olson, M., Tucker, A.J., Noe, D.A., 2012. The role of ultraviolet radiation and fish in regulating the vertical distribution of daphnia. Limnol. Oceanogr. 57 (6), 1867–1876.

Salonen, K., Lehtovaara, A., 1992. Migrations of haemoglobin-rich daphnia longispina in a small, steeply stratified, humic lake with an anoxic hypolimnion. Hydrobiologia 229 (1), 271–288.

Savva, K., Farré, M., Barata, C., 2023. Sublethal effects of bio-plastic microparticles and their components on the behaviour of daphnia magna. Environ. Res. 236, 116775.

Schiestl, F., Roubik, D.W., 2003. Odor compound detection in male euglossine bees. J. Chem. Ecol. 29 (1), 253–257.

Schmidt, K., Steinberg, C.E., Staaks, G.B., 2005. Influence of a xenobiotic mixture (pcb and tbt) compared to single substances on swimming behavior or reproduction of daphnia magna. Acta Hydroch. Hydrob. 33 (4), 287–300.

Siciliano, A., Gesuele, R., Pagano, G., Guida, M., 2015. How daphnia (cladocera) assays may be used as bioindicators of health effects? J. Biodiversit. Endangered Species. https://doi.org/10.4172/2332-2543.S1.005.S1:005

Sliney, D.H., Bitran, M., Murray, W., 2012. Infrared, visible, and ultraviolet radiation. In: E. Bingham, B.C., Powell, C. (Eds.), Patty's Toxicology. John Wiley & Sons, Ltd, pp. 169–208.

Soldán, P., 2021. Improvement of online monitoring of drinking water quality for the city of prague and the surrounding areas. Environ. Monit. Assess. 193 (11), 757–758.

Song, J., Na, J., An, D., Jung, J., 2021. Role of benzophenone-3 additive in chronic toxicity of polyethylene microplastic fragments to daphnia magna. Sci. Total Environ. 800, 149638.

Sousa, A.P., Nunes, B., 2021. Dangerous connections: biochemical and behavioral traits in daphnia magna and daphnia longispina exposed to ecologically relevant amounts of paracetamol. Environ. Sci. Pollut. Res. 28 (29), 38792–38808.

Stewart, C.B., Lowes, H.M., Mehler, W.T., Snihur, K.N., Flynn, S.L., Alessi, D.S., Blewett, T.A., 2023. Spatial and temporal variation in toxicity and inorganic composition of hydraulic fracturing flowback and produced water. J. Hazard. Mater. 132490.

Storz, U., Paul, R., 1998. Phototaxis in water fleas (daphnia magna) is differently influenced by visible and UV light. J. Comparat. Physiol. A 183 (6), 709–717.

Thenius, R., Rajewicz, W., Varughese, J.C., Schönwetter-Fuchs, S., Arvin, F., Casson, A.J., Wu, C., Lennox, B., Campo, A., Van Vuuren, G.J., Stefanini, C., Romano, D., Schmickl, T., 2021. Biohybrid entities for environmental monitoring. ALIFE 2021: The 2021 Conference on Artificial Life. Prague, p. 33.

Tkaczyk, A., Bownik, A., Dudka, J., Kowal, K., Ślaska, B., 2021. Daphnia magna model in the toxicity assessment of pharmaceuticals: a review. Sci. Total Environ. 763, 143038.

Tollrian, R., Heibl, C., 2004. Phenotypic plasticity in pigmentation in daphnia induced by UV radiation and fish kairomones. Funct. Ecol. 18 (4), 497–502. https://doi.org/10.1111/j.0269-8463.2004.00870.x.

Van Gool, E., Ringelberg, J., 1997. The effect of accelerations in light increase on the phototactic downward swimming of daphnia and the relevance to diel vertical migration. J. Plankton Res. 19 (12), 2041–2050.

Van Gool, E., Ringelberg, J., 1998. Light-induced migration behaviour of daphnia modified by food and predator kairomones. Anim. Behav. 56 (3), 741–747.

Vareschi, E., Wübben, D., 2001. Vertical migration of daphnia pulex in response to UV radiation. Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen 27 (6), 3349–3353.

Viehoever, A., Cohen, I., 1938. The responses of daphnia magna to vitamin e. Am. J. Pharm. Educ. 110, 297–315.

Villegas-Navarro, A., Rosas, L.E., Reyes, J.L., 2003. The heart of daphnia magna: effects of four cardioactive drugs. Compar. Biochem. Physiol. Part C: Toxicol. Pharmacol. 136 (2), 127–134. https://doi.org/10.1016/S1532-0456(03)00172-8.

Vlaeminck, K., Viaene, K.P., Van Sprang, P., De Schamphelaere, K.A., 2021. Development and validation of a mixture toxicity implementation in the dynamic energy budget–individual-based model: effects of copper and zinc on daphnia magna populations. Environ. Toxicol. Chem. 40 (2), 513–527.

Vogrin, M., Rajewicz, W., Schmickl, T., Thenius, R., 2023. Improving the accuracy of a biohybrid for environmental monitoring. Sensors 23 (5), 2722.

Weider, L.J., Lampert, W., 1985. Differential response of daphnia genotypes to oxygen stress: respiration rates, hemoglobin content and low-oxygen tolerance. Oecologia 65 (4), 487–491.

Yin, J., Long, Y., Xiao, W., Liu, D., Tian, Q., Li, Y., Liu, C., Chen, L., Pan, Y., 2023. Ecotoxicology of microplastics in daphnia: a review focusing on microplastic properties and multiscale attributes of daphnia. Ecotoxicol. Environ. Saf. 249, 114433.

Zeng, Y., Fu, X., Ren, Z., 2012. The effects of residual chlorine on the behavioural responses of daphnia magna in the early warning of drinking water accidental events. Procedia Environ. Sci. 13, 71–79.

Zhou, Z., Rains, G.C., Kulasiri, D., 2012. Development of a behavior parameter in classically conditioned parasitic wasps that detect changes in odor intensity. Biol. Eng. Trans. 5 (1), 19–31.

Zhu, X., Chang, Y., Chen, Y., 2010. Toxicity and bioaccumulation of tio2 nanoparticle aggregates in daphnia magna. Chemosphere 78 (3), 209–215.

Zink, L., Shearer, A.Y., Wiseman, S., Pyle, G.G., 2023. Effects of exposure to cadmium, microplastics, and their mixture on survival, growth, feeding, and life history of daphnia magna. Environ. Toxicol. Chem. 42 (6), 1401–1408.