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Optimal light conditions for *Daphnia* filtration

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Keywords: *Daphnia magna*, light intensity, photoperiod, *Daphnia* filtration.

Abstract

Daphnia populations are present in lakes and ponds. They are known to experience diurnal vertical migrations according to their feeding needs. During the day they migrate downwards to avoid predation in light-receiving layers and at night they migrate upwards, searching for food in the shallow productive layers. The light photoperiod and light intensity vary depending on the latitude and, therefore, the precise location of lakes and ponds will be an additional and crucial parameter in determining the development of *Daphnia*. Here we will focus on a population of *Daphnia magna* (a genus of the Cladocera order). The effect of both light intensity and photoperiod on *Daphnia* filtration was studied in laboratory experiments. An increase in the light intensity resulted in two *D. magna* responses depending on the exposure time of individuals to light. Short time exposures to a decrease in the light intensity of less than one day produced an increase in the *D. magna* filtration. However, exposures of longer than one day resulted in a decrease in the *D. magna* filtration along with a decrease in the light intensity. Photoperiod exposures of 8, 12 and 16 hours produced greater *D. magna* filtrations than photoperiods of 0, 4 and 24 hours. In this study, regulation of the light intensity and the period of exposure were used in laboratory experiments to establish *D. magna* development thresholds by latitudinal variation in the photoperiod.

Introduction

D. magna is a zooplanktonic organism found in many aquatic systems from 30°S, as is the case of certain lakes in South Africa, to artic sites situated at 66°N (Yampolsky *et al.*, 2018). The breadth of this distribution shows that *D. magna* thrive in lakes and ponds where the shortwave radiation ranges across the year from 24 to 480 W m^{-2} in artic sites and from 240 to 480 W m^{-2} in South Africa (Sellers, 1965). In addition, the hours of light throughout the year range from 2-22h in the artic lakes and from 10-14 in the lakes of South Africa (Forsythe *et al.*, 1995).

The response of *Daphnia* to environmental changes has been studied in terms of their ingestion (though filtration capacity), swimming velocity, heart beat and their survival. For example, the swimming velocity of *Daphnia* is altered by the toxicity of the water (Bownik, 2017), by turbulence (Serra *et al.*, 2019a, 2018; Seuront *et al.*, 2004), and by temperature (Simoncelli *et al.*, 2018). Low turbulence in the aquatic media enhances ingestion rates and therefore the filtration capacity of *Daphnia* (Serra et al., 2019a, 2018; Seuront *et al.*, 2004). The filtration capacity of *Daphnia* is also affected by temperature (Mourelatos and Lacroix, 1990; Ziarek *et al.*, 2011) and is maximized at around 20°C (Burns, 1969; Müller *et al.*, 2018). The presence of contaminants in the aquatic media can also decrease the capacity of filtration and the fitness of *Daphnia*, which is dependent on the compound and its concentration, and the exposure time (Barata *et al.*, 2002; Gillis *et al.*, 2005; Serra *et al.*, 2019b).

Light can also be considered crucial for the growth of *Daphnia* as daily and seasonal vertical *Daphnia* migrations through the water column have been observed as being dependend on the light climate (Simoncelli *et al.*, 2018). In experiments conducted at 20°C, the maximum size of *Daphnia* decreases when the period of daylight is increased and reproduction takes place earlier when there is a higher number of eggs (Martínez-Jerónimo, 2012). The photoperiod, which has daily and seasonal time-scale variations that are also latitude-dependent, has therefore been shown to be a key factor in determining the reproduction and growth rates of zooplankton. The main objective of the present study is to investigate the effect of the intensity of the light and the photoperiod on *Daphnia* filtration capacity at different latitudes, which has so far not been a focus of study. Laboratory conditions mimicking the latitudinal variations of light climate were carried out to determine the seasonal variation in the capacity of *Daphnia* filtration under different light climates. The results found here will be used to predict the range of latitudes where *Daphnia* filtration is expected to be optimal.

Methodology

D. magna collection and breeding.

The *D. magna* population was obtained from a laboratory culture of 40 L of volume and acclimated at 20.0±0.5°C and natural daylight for two years in our laboratory at the University of Girona (North-East of Spain). A gentle supply of air ensured constant oxygenation of the *Daphnia* container*. Daphnia* were fed twice a week with a mixture of commercial spirulina powder and baker's yeast (*Saccharomyces cerevisiae*). One third of the water from the container was renewed once a week. *D. magna* eggs were regularly collected from the container and put in darkness for one week, after which they were exposed to light for 48h and the newborn *Daphnia* were left to grow for one week.

A 1.5 mm mesh was used to collect appropriately sized *Daphnia* individuals from the beaker to perform the experiments. Individuals larger than 2 mm were discarded and returned to the container. To collect *Daphnia,* the net was placed in the beaker and gently removed with some *Daphnia* individuals, which were introduced in the experimental beakers to perform the experiment. This was repeated until the required number of *Daphnia* was collected. The mean length of the *Daphnia* in the experimental beakers, measured with Image J. software after recording a video of 25 individuals, was 1.6$\pm$0.3 mm (Moison *et al.*, 2012; Pan *et al.*, 2017; Serra *et al.*, 2018).

Experimental set-up

Laboratory experiments were designed to encompass a wide range of light conditions. Six experiments were conducted in triplicate to determine the effect of *Daphnia* filtration under six different light intensities ranging from 0% light to 100% light (0 lux, 394 lux, 985 lux, 1970 lux, 2955 lux and 3940 lux) and running with 12 hour light (L)/dark(D) photoperiods. The range of light intensities studied is wider than that used by others (Buikema, 1973). In another set of six experiments, photoperiods of 24L/0D, 0L/24D, 12L/12D, 8L/16D, 4L/20D and 16L/8D were studied at the maximum light intensity of 3940 lux. These photoperiods also widen the range of photoperiods that have previously been tested, which have been limited to 16L/8D and 12L/12D (Martínez-Jerónimo, 2012).

Five boxes containing three 2-L beakers each were used. The light intensity was regulated with a dimmer connected to a light bulb inside a wooden box. Each beaker was filled with 1900 mL of mineral water and 100 mL of spirulina suspension (Figure 1), which was prepared by diluting 1 g of spirulina powder in 1 L of mineral water and was then mixed for 30 s at 120 rpm and left for 1 h, leading to the settling of large spirulina particles. The supernatant was used as the spirulina suspension for the experiments. After introducing the suspension into the beaker, 100 *Daphnia* individuals were gently introduced into each beaker in order to obtain a final *Daphnia* concentration of 50 ind L^{-1}.

Figure 1. Scheme of the laboratory setup for experiments carried out for the six light intensities tested (0%-100%) and six different photoperiods (L, light and D, dark).

All the experiments were run for one week and performed at 20 °C, the same temperature as the *Daphnia* culture to avoid a possible effect of temperature change on filtration capacity. In order to avoid oxygen depletion in the containers, *Daphnia* were removed every day at the same hour from the spirulina-containing water daily and placed into a new beaker containing water with the same concentration of spirulina. The number of eggs produced and the number of lived *Daphnia* were counted daily for each beaker.. When *Daphnia* individuals were found to have died, they were replaced by other individuals of the same age kept in the same light conditions in another replica beaker situated near the three beakers being used in the experiment.

Previous studies (Pau *et al.* (2013); Serra *et al.* (2014)) have shown that the temporal decrease in the concentration of *spirulina* was exponential and that after four hours of filtration the *spirulina* concentration decreased by a factor of 1/e. Hence, water samples were collected at the beginning of the experiment and after four hours in order to measure the distribution of the particle size and its concentration with an in situ laser scattering and transmissometry instrument (Lisst-100X, Sequoia Scientific). For lighted experiments with different photoperiods and at light intensity of 3940 lux and for experiments with different light intensities at a photoperiod of 12L/12D, the measurement was taken during the lighted period. The Lisst-100x consists of a laser beam and an array of detector rings of progressive diameters that allow the light received at the scattering angles of the beam to be analysed. The device measures the particle volume concentrations for 32 size-classes logarithmically distributed in the size range of 2.5-500 μm using a procedure based on light diffraction theory. This procedure has successfully been applied to determine particle size distribution and concentration of both organic (Serra *et al.*, 2001) and inorganic particles (Serra *et al.*, 2002b, 2002a) in water suspensions. Cladocerans ingest particles that are in their ingestible particle size range, independently of their nature (Arruda *et al.*, 1983; Gliwicz, 1990). In the case of *D. magna,* they can feed on particles with diameters of <30 μm. Hence, in order to evaluate particle removal by *Daphnia*, the volumetric concentration of particles within the range of 2.5 to 30 μm was calculated and used as a proxy to evaluate particle removal.

Filtration capacity of Daphnia

The temporal evolution of the concentration of suspended particles (c) can be fitted to a first order kinetic equation (eq. 1):

$$\frac{dc}{dt} = -kt \qquad (1)$$

where k stands for the rate constant and t for time. The integration of this equation results in equation 2:

$$\frac{c}{c_0} = e^{-kt} \qquad (2)$$

where c_0 is the initial particle concentration. From equation (2), we can calculate k:

$$k = -\frac{1}{t} ln\left(\frac{c}{c_0}\right) \qquad (3)$$

The removal of the suspended particles can be considered as taking place through sedimentation and *Daphnia* filtration, hence, the rate constant can be represented as $k=k_s+k_{Dph}$, where k_s and k_{Dph} represent the contributions to the rate constant of both sedimentation (k_s) and *Daphnia* filtration (k_{Dph}) processes (Pau et al., 2013). k_s was determined from the experiments performed without *Daphnia* in the reactor (in which k_{Dph}=0), therefore, k_{Dph} was calculated from the results obtained in the rest of experiments with *Daphnia*. The rate of decrease of c due to *Daphnia* filtration is a function of the filtering rate of each individual *Daphnia* (F, in mL ind^{-1} h^{-1}) and the *Daphnia* concentration:

$$k_{Dph} = F \times C_{Dph} \qquad (4).$$

where C_{Dph} is the number of *Daphnia* individuals (ind mL^{-1}).

Results

Effect of the photoperiod on Daphnia filtration

Daphnia filtration presented different responses to the varying light photoperiods depending on short-scale and long-scale exposure times.. In the case of the experiments performed at short–scale time, the same initial filtration was obtained with different photoperiods but with the same light intensity (3940 lux) (Figure 2). On the other hand, the experiment conducted in complete darkness had a higher *Daphnia* filtration during the first 4 h, whereas when the exposure times to dark conditions were longer the *Daphnia* filtration decreased non-linearly, approaching to 1.2 mL ind^{-1} h^{-1} by day seven. The *Daphnia* filtration for the lighted experiments also evolved non-linearly with a peak at 3.5 ml ind^{-1} h^{-1} after an exposure time of 28 h, except for the photoperiod of 8L/16D experiments for which the maximum filtration was found after 52 h of exposure and the photoperiod of 24L/0D that decreased continuously over time. In the long-scale time experiments, *Daphnia* filtrations plateaued out by day seven in all the photoperiods tested. For continuous light (24L/0D) the *Daphnia* filtration rates were lower than those for the three photoperiods of 16L/8D, 12L/8D and 8L/16D (Figure 3). For shorter hours of light exposure (4L/20D), the filtration was the smallest of all photoperiods except for that of complete darkness (0L/24D).

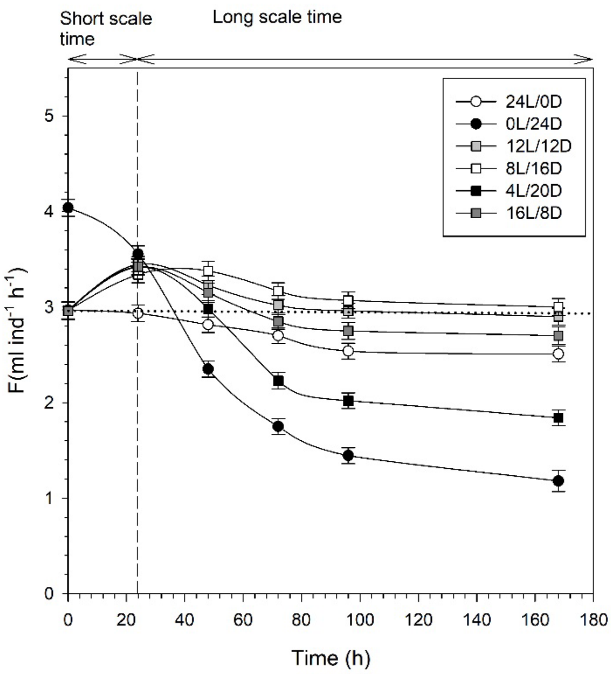

Figure 2. *D. magna* filtration versus time for a fixed light intensity of 100% of light (3940 lux) and for the six different photoperiods tested for the experiments carried out in the laboratory. The vertical dashed line separates the short-scale from the long-scale times.

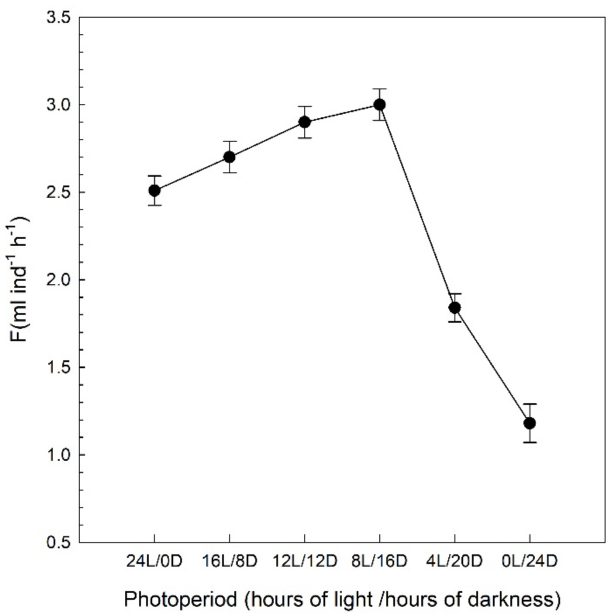

Figure 3. *D. magna* filtration versus the photoperiod after seven days of exposure.

The effect of light intensity on Daphnia filtration

The behaviour with regards to *Daphnia* filtration was different depending on the temporal exposure (short-scale of <28 h and long-scale of >28 h) to different light intensities (Figure 4). During the first four hours, *Daphnia* filtration decreased with light intensity. During the short- scale set of experiments, the *Daphnia* filtration in those experiments performed with light intensities below 50% increased with time. In contrast, *Daphnia* filtration for experiments with light intensities above 50% increased with time. After the second day of exposure to light, the filtration tended to plateau out following a trend that was the inverse to that observed in the first four hours. In other words, after seven days of exposure the filtration increased gradually with increased light intensity. With the maximum light intensity tested (100%), filtration was 2.5 times the rate of filtration in complete darkness (I=0 Wm^{-2}).

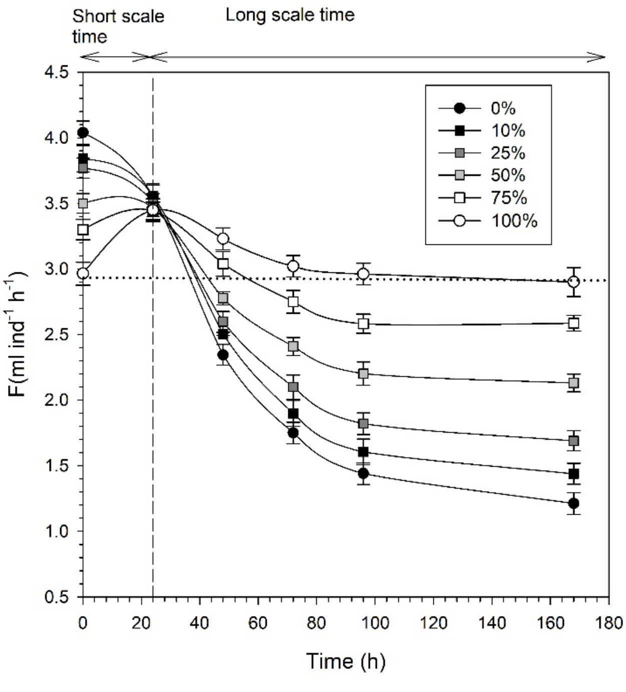

Figure 4. *D. magna* filtration versus time for the fixed photoperiod of 12L/12D and for the six different light intensities studied in the laboratory experiments. The vertical dashed line separates the short-scale from the long-scale times.

The *Daphnia* filtration obtained in the laboratory on day seven increased linearly with the light intensity (Figure 5). For the highest light intensity tested, the *D. magna* filtration was 2.42 times that obtained in darkness.

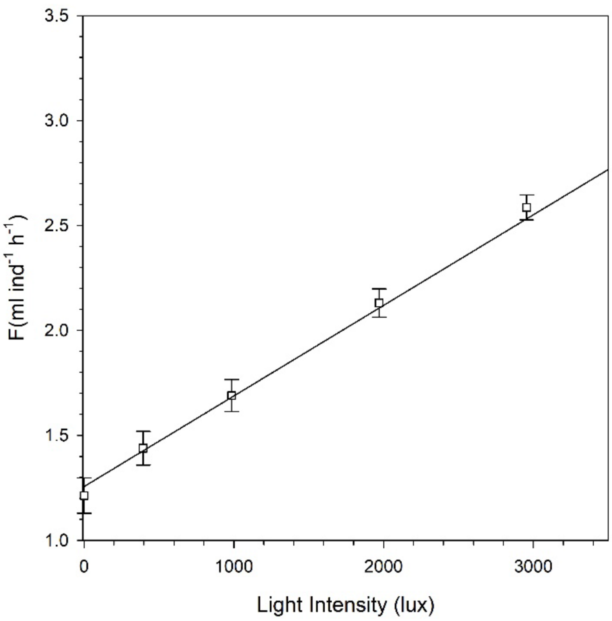

Figure 5. *D. magna* filtration versus the light intensity (I) (in lux) after seven days of exposure. The solid line corresponds to the best fitting line of the data ($F=4.32\times10^{-4}I+1.257$, $r^2=0.996$, CI: 99%).

Discussion

Irradiance is an abiotic parameter that presents latitudinal, seasonal and daily variations that have an impact on zooplanktonic populations in aquatic systems (Simoncelli et al., 2018, 2017). Both light intensity and the photoperiod have been found to modify the filtration capacity of *Daphnia* and would therefore be expected to vary in accordance with the light conditions of the day, season and latitude.

The effects of the light intensity on D. magna filtration

Laboratory analyses of the effect of light intensity at a 12L/12D photoperiod on *Daphnia* filtration revealed two light-dependent *Daphnia* responses. In the short-scale of four hours, the reduction in the light intensity produced a positive effect on the *Daphnia* filtration, i.e. *Daphnia* filtration increased with a decrease in the light intensity. During the first four hours of the experiment in complete darkness the filtration capacity of *Daphnia* was 1.33 fold greater than that at maximum light intensities. However, after a long exposure time of seven days to darkness, the filtration capacity of *Daphnia* was 0.4 times that of the maximum lighted conditions. After the first 4 hours, *Daphnia* filtration for light intensities below 50% presented an overall decrease during the first day of exposure to such light conditions. In contrast, *Daphnia* filtration for light intensities above 50% presented an increase during the first day of exposure to such light conditions. This is due to the fact that in the laboratory culture *Daphnia* was acclimated to intensities of 1000 lux, which is close to the 50% light intensity condition. In this later case, the *Daphnia* filtration remained nearly constant during the first day. Therefore, *Daphnia* moved to lower light intensities than those in the laboratory for the experiments of light intensities above 25% and to greater light intensities for experiments with light intensities above 50%. However, the behaviour changed when the exposure time was longer than 24 hours.

In the long-scale experiments of more than one day, a reduction in the light intensity produced a decrease in the *Daphnia* filtration that could be associated to the need for a longer acclimation of *Daphnia* to the change in the light intensity. The daily scale results of this study show that *Daphnia* enhance the filtration in the hours of darkness, aligning with their ecological strategy of migrating from deep to shallow waters at dawn for preying purposes and to avoid predators (Mikulski et al., 2017; Simoncelli et al., 2018). Haney (1985), who studied the filtration rate of four *Daphnia* species, found that *Daphnia* individuals filtered less during daytime hours than at night. In contrast, Chow-Fraser and Knoechel (1985) did not find differences in the filtration measured at night compared to that at dusk. The reason for this discrepancy may lie in the fact that Haney, Chow-Fraser and Knoechel (1985) studied smaller individuals (d<1.3 mm vs. 1.5 mm < d<2.1 mm). Dinh *et al*. (2018) studied the effects of light intensity on the number of *ephippia* produced by *Daphnia carinata* for what they called moderate light intensity (500 lux) and high light intensity (1000 lux). They found greater *ephippia* production with moderate light intensity than with high light intensity. McMahon (1965) observed a slight difference in the filtering rate of *Daphnia* at different light intensities in the range of 1076.4 lux to 10763.9 lux. Given the differences observed, McMahon (1965) concluded that a detailed study would be required to address the dependence between the feeding rate and the light intensity. In contrast, Nauwerk (1959) found that *Daphnia longispina* filtered more in complete darkness than in direct sunlight, a result that agrees with the results obtained here for the first 24 h. Dinh et al (2018) found that *Daphnia carinata* produced more eggs under moderate light conditions (500 lux) than in high light conditions. In the present study, the production of eggs was greatest (four eggs per litre) for the 50% of the light intensity that corresponded to 1970 lux. In contrast, when light intensity was 100% (3984 lux) egg production was half that obtained for 50%, with two eggs per litre.

Buikema (1973) studied the filtering rate of *Daphnia pulex* as a function of body size and light. The range of light intensities tested expanded from 0 ft-c to 110 ft-c, corresponding to 0 lux to 1174.03 lux. Light intensities above 301.3 lux tended to suppress the filtering rate of small animals and stimulated the filtering rate of large animals. These results are in agreement with those obtained in the present study. Moreover, the survival of *D. magna* was also unaffected by light intensity, as was also found by Buikema (1973). However, although *Daphnia* filtration increased during the hours of darkness, the present study indicates that long exposure times to both complete darkness (0L/24D) and complete light (24L/0D) resulted in low *Daphnia* filtrations, indicating that such conditions are not optimal for *Daphnia* filtration. This result is in accordance with findings for other zooplanktonic populations, such as *Mesocyclops sp.*, which presented a reduction in offspring production under continuous light or continuous darkness (Fereidouni et al., 2015).

The effects of the photoperiod on D. magna filtration

Daphnia filtration presented different responses to the varying light photoperiods depending on short-scale (<28 h) and long-scale (>28 h) exposure times. No differences in the *Daphnia* filtration were observed after short-scale time of exposure. This can be attributed to the fact that all the lighted experiments had the same conditions during the first measurement (4 h of light and the same light intensity). Only the case of complete darkness (0L/24D) had greater *Daphnia* filtration during the first four hours. This result is in agreement with the increase in the *Daphnia* filtration at darkness. In addition, an overall increase in the *Daphnia* filtration was observed during this short time scale, probably due to the fact that they have been acclimated from a light intensity of 1000 lux in the laboratory to 3940 lux in the experiment. After this shortscale time of exposure, *Daphnia* filtration presented an overall decrease for all the photoperiods tested. This can be explained by the fact that since all the experiments had the same light intensity, *Daphnia* acclimated gradually to the tested photoperiods. Therefore, the results reveal that certain photoperiods are more favourable for *Daphnia* filtration than others.

The photoperiods of 16L/8D, 12L/12D and 8L/16D presented the greatest *Daphnia* filtration capacities after seven days of acclimation. These photoperiods are characteristic of latitudes from 49°S to 49°N (non-coloured area in Figure 6). These results show that latitudes 49°S to 49°N may favour the filtration capacity of *Daphnia*. Therefore, *D. magna*- based wastewater treatments in this region are expected to perform optimally. However, *Daphnia* have been found to acclimate to temperature and light over generations (Bae *et al.*, 2016; Loudeiro *et al.*, 2015; Mikulski *et al.*, 2005). Forsythe *et al.* (1995) found *D. magna* from South Africa (37°S) to the Arctic (66°N), showing its great capacity for thermal and light adaptation. Other *Daphnia* species have been found at different latitudes and longitudes (Burns, 1969; Critescu *et al.*, 2006; DeMott, 1982; Dodson *et al.*, 1997; Filella *et al.*, 2008; Geller and Müller, 1981;

Haileselasie *et al.*, 2018; Haney, 1985; Kasprzak *et al.*, 1999; Korinek *et al.*, 2003; Laspoumaderes *et al.*, 2017; Lindlholm, 2002; Okogwu, 2010; Paes *et al.*, 2016; Rellstab and Spaak, 2007; Straile, 2000; Tessier and Goulden, 1987; Yampolsky *et al.*, 2018; Yurista and O'Brien, 2001). Therefore, it can be expected that by extending the time of exposure to light in future experiments, further adaptations will occur in individuals of later generations.

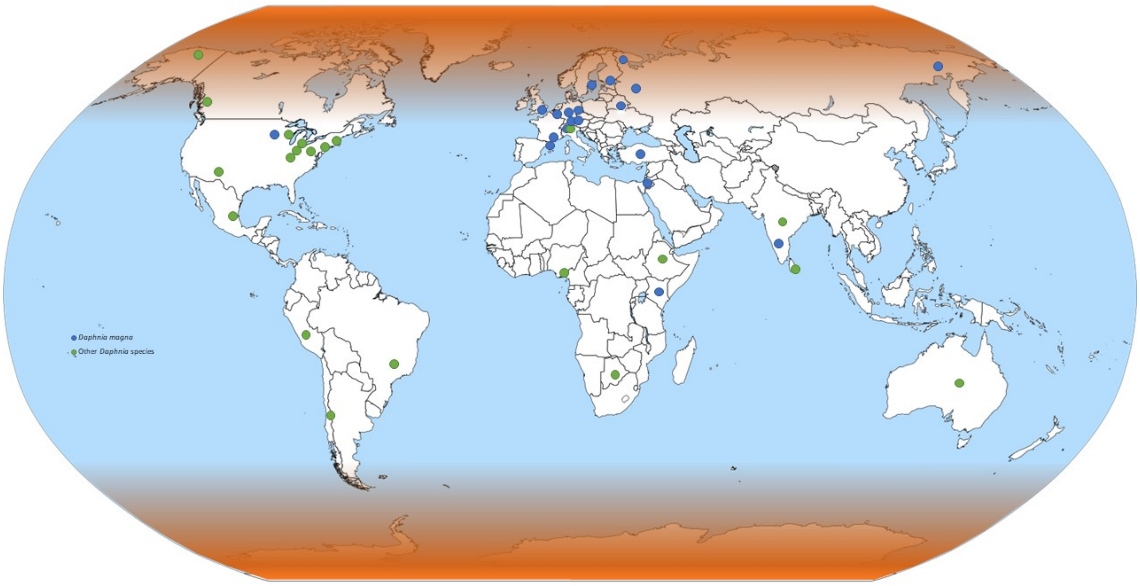

Figure 6. World map (source: https://upload.wikimedia.org/wikipedia/commons/e/e4/World_Map_Blank_-_with_blue_sea.svg) with the observations of *Daphnia* individuals. The coloured region indicates the region with photoperiods below 8 h of light. Dots represent reported sites of *Daphnia*. Blue solid dots correspond to sites where *D. magna* have been observed. Green solid dots correspond to sites where other *Daphnia* species have been observed.

Conclusions

Light intensity and light photoperiod have been found to play a crucial role in determining the fate of *Daphnia* filtration. Based on laboratory experiments, we can conclude that after a long time exposure the greater the light intensity, the greater the *Daphnia* filtration. On the other hand, with short time exposures of less than one day, *Daphnia* filtration behaves differently to longer time scales, aligning with the time-dependent differences in the migration strategies of *Daphnia* through the water column and in such cases the *Daphnia* filtration increases after a decrease in the light intensity. The results also show that there is a range in photoperiods from 8 h to 12 h of light hours that might be considered the optimal range for *Daphnia* filtration. These results indicate that regions of the Earth situated in latitudes with these photoperiods provide favourable conditions for *Daphnia* filtration. These regions of the Earth may therefore be suitable for setting up wastewater treatments based on clarification by *Daphnia* filtration. In addition, both the photoperiod and the intensity of the light will vary depending on the season and the conditions of individual days, resulting in changes in *Daphnia* filtration over a wide range of time scales. However, longer term studies on the effects of both photoperiod and light intensity should be undertaken in order to check for any potential further adaptation of future *Daphnia* generations to changing light scenarios.

Figure legends

Figure 1. Scheme of the laboratory setup for experiments carried out for the six light intensities tested (0%-100%) and six different photoperiods (L, light and D, dark).

Figure 2. *D. magna* filtration versus time for a fixed light intensity of 100% of light (=3940 lux) and for the six different photoperiods tested for the experiments carried out in the laboratory. The vertical dashed line separates the short-scale from the long-scaletimes.

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