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Abstract

Artificial light at night (ALAN) is a common anthropogenic disturbance, which alters animal behavior. However, little is known about the impact of the spectral composition of ALAN and co-occurring predation risk on the behavior of aquatic organisms. We experimentally investigated how ALAN of different spectra (cool white LED and HPS light) affects the behavior and foraging of *Gammarus jazdewskii* (Amphipoda) on chironomid prey, both as a single stressor and in combination with an olfactory predation cue. Gammarids exposed to ALAN in the absence of predation cues consumed less, compared with darkness, mainly due to their lower activity. Moreover, gammarids showed a stronger response to LED light, spending more time in the shelter and increasing prey handling time in this treatment. The addition of predation cues did not enhance the negative impact of ALAN on the foraging success. Gammarids maintained similar consumption levels as in the ALAN treatment without predation cues and in darkness with predation cues. However, gammarids in LED light altered their behavior in response to predation threat: they decreased prey handling time and consumed prey faster, which may have compensated for the higher food demand in stressful conditions. They also tended to exhibit risky behavior, leaving the shelter and moving towards the lit area, presumably to escape and avoid the combined effects of light and predation cues. Therefore, when assessing the effects of ALAN on organisms, light quality and co-occurring biotic factors should be considered, as predator pressure is common in natural environments.

Key words: foraging, invertebrates, light pollution, predator, prey.

Light is a natural cue, which regulates circadian rhythms of organisms and facilitates their orientation in space and perception of the environment (Gaston et al. 2013; Falcón et al. 2020). Hence, it influences animal behavior, including diel migration, foraging, and response to predation risk (Zapata et al. 2019; Falcón et al. 2020). Nowadays, natural light–dark cycles are being disrupted by excessive illumination produced by street lamps and other sources of artificial lighting (Longcore and Rich 2004; Davies et al. 2018). This is because urban and suburban areas, including aquatic ecosystems, are constantly exposed to unnaturally increased light levels at night, often exceeding the intensity of full moonlight (>0.3 lx) (Perkin et al. 2014a; Secondi et al. 2017).

Exposure to artificial light at night (ALAN) has been shown to alter the behavior of many organisms, which may disrupt predator–prey interactions. Positive phototaxis may locally increase prey abundance and this usually attracts predators (McMunn et al. 2019; Willmott et al. 2019; Nelson et al. 2020; Bolliger et al. 2022). Increased availability of prey benefits nocturnal predators as has been shown for some insectivorous bats (Frank et al. 2019; Bolliger et al. 2022). However, ALAN may also favor

diurnal and crepuscular predators (Bolton et al. 2017; Miller et al. 2017; Czarnecka et al. 2019; Talanda et al. 2022), which often extend their feeding into the night hours. On the other hand, predation may be suppressed by ALAN if potential prey avoids light (Hadderingh et al. 1999; Moore et al. 2000; Vowles et al. 2014). Particularly nocturnal species reduce their movements and spend more time in shelters (Perkin et al. 2014a; Fischer et al. 2020; Czarnecka et al. 2021), or delay dispersal (Perkin et al. 2014b; Riley et al. 2015), thus becoming less available to predators. It has also been found that predatory efficiency may be reduced if exposure to ALAN increases the vulnerability of predators to attack by higher-level predators (Eckhardt and Ruxton 2022).

Behavioral alterations can be induced not only by increased light intensity but also by the spectral composition of ALAN due to the species-specific sensitivity of photopigments to particular light wavelengths (Kelber and Osorio 2010; Alaasam et al. 2021; Longcore 2023). Even subtle spectral changes can alter the contrast between objects and their background and thus affect spatial orientation (Cohen et al. 2010; Kelber and Osorio 2010) and prey detection (Mc Mahon et al. 2022; Moyse et al. 2023). Sensitivity to specific wavelengths can

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also influence the distribution of organisms in the environment by their attractance to or avoidance of light, which has been most extensively studied in terrestrial insects and bats (e.g., Zeale et al. 2018; Brehm et al. 2021; Bolliger et al. 2022). Street lighting varies in spectral characteristics. For instance, illumination produced by commonly used light-emitting-diodes (LEDs) is enriched in blue wavelengths, whereas high-pressure sodium (HPS) lamps emit orange-red light (Davies and Smyth 2018). Many species are sensitive to blue light (Marshall and Arikawa 2014; Schweikert et al. 2018; Gaston and Sánchez de Miguel 2022). Some of them, such as terrestrial insects (Brehm et al. 2021; Deichmann et al. 2021), some bats (Bolliger et al. 2022) or juvenile salmonids (Hansen et al. 2019) increase their activity and are attracted by short light wavelengths. Other species may avoid blue light, as found in freshwater amphipods (Czarnecka et al. 2022) and crayfish (Fischer et al. 2020). Therefore, particularly LED light can modify prey availability and predator activity, and thus determine predation success.

Measurements in situ showed that spectral signatures of ALAN are clearly visible in fresh waters up to a depth of 0.5 m (Secondi et al. 2017), therefore various types of illumination may elicit different effects on the behavior of aquatic species. However, the effects of ALAN differing in spectral composition on predator–prey interactions in aquatic ecosystems are still poorly understood. In previous studies, these relationships were often examined either using only 1 type of lighting, e.g., LED (Underwood et al. 2017; Manríquez et al. 2019, 2021; Nelson et al. 2020), or high light intensities (Bolton et al. 2017), which rarely occur underwater. Furthermore, in natural conditions, ALAN often co-occurs with other stressors, e.g., the presence of a higher-level predator, which may change the predator response to light.

Here, we investigated how exposure to ALAN of low intensity (2 lx) and with different spectral compositions (cool white LED with a prominent peak in blue wavelength and yellow-orange HPS light) affected the foraging behavior of nocturnal macroinvertebrates. As a model species, we used *Gammarus jazdzewskii* (Amphipoda), commonly found in temperate streams (Felten et al. 2008), including suburban areas. *Gammarus jazdzewskii* is an important link in the aquatic food web as a key shredder contributing to the turnover of leaf litter (Felten et al. 2008), but it can also prey on macroinvertebrates, such as chironomid larvae, and control their abundance (Kelly et al. 2002; Syrovátka et al. 2020). Since exposure to daytime light and predation risk increases stress response in *G. jazdzewskii* (Jermacz and Kobak 2023), we tested its foraging behavior in the presence and absence of predation cues. As an indicator of predation threat, we used conspecific injury cues, which are known to induce anti-predatory behavior in gammarids, such as reduced activity and hiding (Smith and Webster 2015). We predicted that the presence of a single stressor (ALAN or predation cues) would significantly decrease prey consumption by gammarids compared with darkness. This would be a result of changed gammarid behavior, i.e., reduced activity, increased shelter use, increased food handling time, and/or delayed initiation of feeding. We expected that this effect would be enhanced (1) when both stressors occur at the same time; (2) during exposure to cool LED light with a high share of blue light, as in our previous study we found that *G. jazdzewskii* was sensitive to narrow-spectrum blue LED light of low intensity (2 lx) (Czarnecka et al. 2022).

Materials and Methods

The tested species

Gammarus jazdzewskii was collected in the Zielona Struga (52.997208 N, 18.450469 E), a forest stream located 11 km from the city of Toruń, Poland (population: 195,000). Gammarids were collected together with fine woody debris from the stream bottom by a hand net. Afterwards, the gammarids were transported to the laboratory. They were kept in an air-conditioned and darkened room in an 80 L tank filled with aerated water and fine woody debris. Since gammarids were sampled between March and May, when the water temperature in the stream was around 8–10 °C, we gradually adapted them to the temperature of 15 °C (± 0.5 °C), which was then maintained constant by an aquarium cooler (Teco R20; Teco S.l.r. Ravenna, Italy) connected to the tank. During daytime (7:00–19:00) gammarids were exposed to light of intensity of 380 lx provided by 2 full-spectrum incandescent light bulbs (46 W, 702 lm, 2,800 K, Diall), whereas nights were dark (<0.01 lx). The acclimatization to the laboratory conditions lasted for 7 days before the experiment started. During this time, gammarids were fed with living chironomid larvae purchased in a pet shop. One day before the test, we placed gammarids selected for the experiment in a separate vessel with aerated water without access to food to standardize their hunger level.

The mean total length of gammarids used in the experiment was 6.4 mm ($SD = 1.19$ mm), whereas that of chironomids was 6.6 mm ($SD = 1.00$ mm). The length of both gammarids and their prey was measured from digital photographs taken prior to the experiment using ImageJ 1.53p (Schneider et al. 2012). These measurements were used to estimate predator–prey size ratio, as prey size relative to the predator size is likely to affect the predator's behavior, and thus the values of consumption variables.

Experimental setup

We conducted the experiment in opaque white plastic circular dishes (10 cm in diameter, 9 cm in height) placed in a water bath filled with settled tap water at a constant temperature of 15 °C (± 0.5 °C) sustained by the aquarium cooler. In each dish, we placed 3 similarly sized stones (mean total surface area: 14.5 cm^2 ; $SD = 0.50 \text{ cm}^2$) serving as shelters for gammarids. Gammarid's behavior was recorded with an overhead digital video camera (SNB-6004, Samsung, South Korea). Observations in darkness were performed using infrared lamps. Gammarids were exposed to 3 light treatments: (i) darkness as a control, (ii) cool white LED light (5.5 W, 470 lm, 4,000 K, Philips) and (iii) HPS light (50 W, 4,500 lm, 2,000 K, SON-T Philips). We used black opaque screens to obtain the desired light intensity of 2 lx (measured on the water surface by a Digital Lux Meter DT-8809A, CEM Instruments, Kolkata, India), corresponding to nocturnal light levels commonly found in urban waterways (Perkin et al. 2014a). Light intensity in the dark control treatment was below 0.01 lx, which corresponds to the light emitted to the Earth's surface by the quarter moon (Gaston et al. 2014).

Experimental procedure

Consumption of prey by gammarids in the absence and presence of predation cues

We placed a single gammarid in the experimental dish. After 15 min of acclimation, we gently added 3 living chironomids

as prey to the bottom of each vessel using a pipette. Then, we started the video recording. The gammarid behavior was recorded for 2 h. After this time, the gammarid was removed and surviving chironomids were counted.

To test the feeding efficiency of gammarids in the presence of a predation cue, we followed the above-described procedure, however, we added a conspecific injury cue which is an indicator of predator threat (Smith and Webster 2015). To prepare the injury cue, we crushed a group of 8 gammarids (similar in size to those used in the tests) using a mortar and a pestle. Then we added distilled water (10 mL per each crushed individual) to the mortar and filtered the suspension through gauze to remove the gammarid carcass. Then, we added 10 mL of filtered cue water to each experimental dish immediately before the introduction of the gammarid. We repeated the procedure for each trial.

We performed 16 replicates of each light treatment (darkness, LED, and HPS light), in the absence and presence of the predation cue (a total of 96 replicates).

Behavioral analyses

The video tracking program EthoVision 10.1 (Noldus Information Technology Bv, Wageningen, The Netherlands) was used to analyze the foraging behavior, which can influence prey consumption. The following categories of gammarid activity were evaluated: time spent in movement and time spent in the shelter. We also manually assessed the time of the initiation of the first attack on prey performed by the gammarid, as well as the prey handling time (measured from the moment of the first attack on first prey to the total consumption of a chironomid).

Data analysis

Each of the 3 prey items offered to a single amphipod was counted as consumed or surviving. Consumption probability was analyzed using a Generalized Linear Mixed Model with a binomial distribution (the number of consumed prey items out of their initial number) and logit link function. The other response variables were analyzed using General Linear Mixed Models. The models included categorical fixed factors: predation cue (present or absent) and light type (darkness, HPS, or LED), as well as their interaction. Additionally, the models with consumption-related response variables (consumption probability, attack initiation time, and prey handling time) included a covariate: predator:prey size ratio (a ratio between the total amphipod length and chironomid length) to control for size effects on prey consumption. Finally, the Generalized Linear Mixed Model for consumption probability included experimental unit ID (to handle the fact that a single amphipod dealt with 3 prey items) as a random factor. Attack initiation time and prey handling time were log-transformed to reduce departures from the model assumptions (normality and homoscedasticity). As needed, significant model effects were further analyzed using sequential Bonferroni corrected post hoc tests: pairwise contrasts for the Generalized Linear Mixed Model and LSD Fisher tests for the General Linear Mixed Models. The analyses were carried out using the SPSS 28.0 statistical package (IBM Corporation).

Results

The probability of consumption of chironomid larvae by amphipods (Figure 1A) depended on a light $\times$ predation

cue interaction (Table 1A). In the absence of the predation cue, gammarids consumed significantly more prey in darkness than under both light treatments. In the presence of the predation cue and/or any light type, they reduced their consumption level compared with the animals tested in darkness without the predation cue (Table 2A). Attack initiation time (Figure 1B) was independent of light and predation cues, but was related to the predator:prey size ratio (Table 1B): amphipods tended to attack their prey later when they were larger than their prey. Prey handling time by amphipods (Figure 1C) depended on a light $\times$ predation cue interaction (Table 1C). The handling time was longer in the LED light without the predation cue than in the other light types and in the presence of the predation cue (Table 2B).

Time spent by amphipods in movement (Figure 2A) depended on a light $\times$ predation cue interaction (Table 1D): without predation cue, they moved more in darkness than in the presence of any light type, whereas in the presence of predation cue, there was no significant effect of light on amphipod activity (Table 2C). Moreover, when predation cues were present, the activity of gammarids in all light treatments and dark control was not significantly different from their activity in light treatments without predation cues. Time spent by amphipods in the shelter (Figure 2B) also depended on a light $\times$ predation cue interaction (Table 1E). In the absence of the predation cue, amphipods spent less time in the shelter in darkness than in both light treatments. Moreover, they stayed in the shelter for a longer time in the LED than in the HPS light (Table 2D). In the presence of the predation cue, there were no differences in shelter use between the light treatments, and the animals exposed to the LED light used shelters for a shorter time than in the absence of the predation cue (Table 2D).

Discussion

We found that the foraging efficiency and activity of gammarids were modified by both the presence of ALAN and predation cues. Gammarids responded to the exposure to a single stressor (light or predation threat), but their behavior also changed as a result of the interaction between the 2 factors. Moreover, in the absence of predation cues, cool LED light produced a stronger effect on prey handling time and time spent in the shelter than HPS light. However, these differences between light types were mitigated when predation cues were added.

In the absence of predation cues, *G. jazdzewskii* exposed to ALAN showed significantly decreased foraging efficiency compared with darkness, and this effect did not depend on the spectral characteristic of light. The reduced consumption was related to lower activity of gammarids, as under cool LED and HPS light *G. jazdzewskii* was less mobile than in darkness. Therefore, it was also less engaged in foraging. Reduced locomotor activity of nocturnal invertebrates exposed to ALAN has been found in several field and laboratory experiments (e.g., Luarte et al. 2016; Talanda et al. 2018; Fischer et al. 2020; Czarnecka et al. 2022). Field studies have also shown that night lighting reduces by 40–50% the dispersal of stream invertebrates, which typically drift during dark nights in search of optimal foraging conditions or to avoid predation (Henn et al. 2014; Perkin et al. 2014a). Illuminated areas can enhance the visibility of drifting invertebrates, which may suffer from increased predation, especially if visually oriented

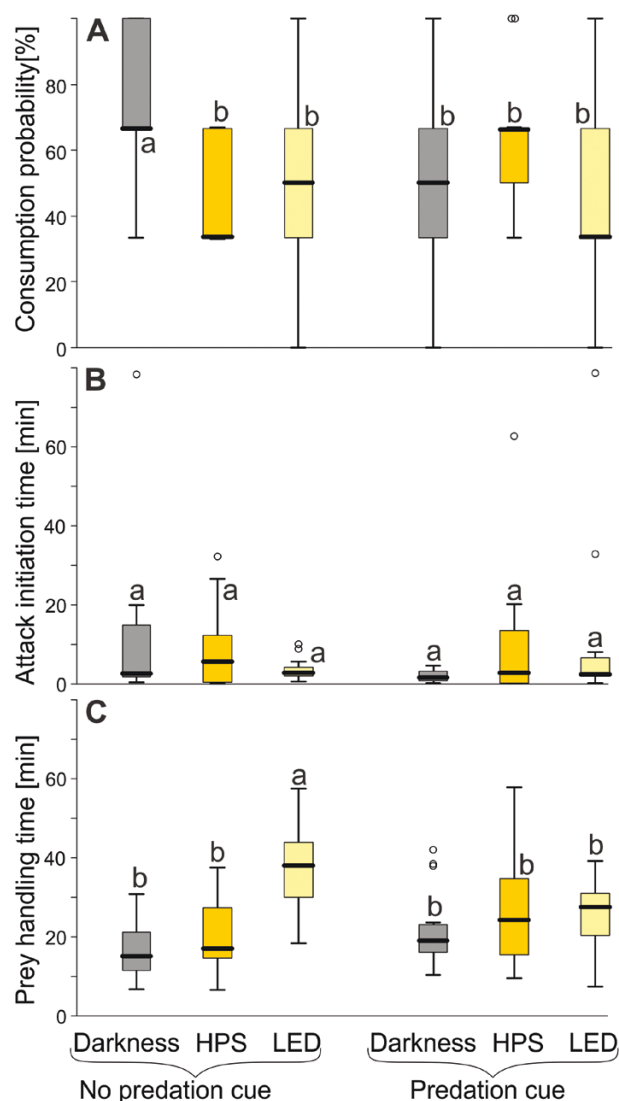


Figure 1. Food consumption probability (A), attack initiation time (B), and prey handling time (C) by amphipods exposed to various light types (darkness, HPS, and LED) in the presence or absence of the olfactory predation cue (injured conspecifics). The same letters in the boxes indicate nonsignificant differences between respective treatments (Table 2).

predators are present in their vicinity (Czarnecka et al. 2019; Nuñez et al. 2021; Talanda et al. 2022). Therefore, decreased activity under ALAN may be a beneficial strategy to avoid capture. On the other hand, it may limit the opportunity to obtain food (Manríquez et al. 2021) and exert a negative effect on growth rates (Luarte et al. 2016).

Despite similar levels of gammarid activity, we observed that individuals exposed to LED light in the absence of predation cues spent significantly more time in the refuge than in the HPS light. This suggests that gammarids may have specifically avoided cool LED light. The spectra of cool LEDs are characterized by a prominent peak emission in the blue light range (Davies and Smyth 2018). Aquatic crustaceans show peak sensitivity to short wavelengths (Marshall 2003; Cohen et al. 2010), and therefore can perceive blue-enriched LED light brighter than HPS illumination. Blue light is an important component of the twilight and moonlight spectrum (Forward et al. 1988; Kelber et al. 2017). Therefore, for

species possessing blue-sensitive pigments, this wavelength can be a cue of increased predation risk. Activity of many predators is typically enhanced during the full moon (Prugh and Golden 2014) and at dusk (Helfman 1981). Therefore, exposure to blue light can trigger avoidance behavior in vulnerable species (Fischer et al. 2020; Czarnecka et al. 2022). This may also explain the increased sheltering in *G. jazdewskii* exposed to cool LED light in our study.

We also observed that the exposure to LED light in the absence of predation cue affected the handling time in *G. jazdewskii*: complete consumption of chironomids, starting from the first attack, lasted longer in this treatment than in the other light treatments. The increased handling time often results from anti-predatory strategies employed by attacked prey to decrease its availability to predators (Boulding 1984). In our experiment, gammarids had direct access to chironomids. Despite their relatively large size, chironomids are soft-bodied, slow-moving prey, hence they could be easily attacked and consumed by gammarids. Therefore, the higher handling time was rather due to the specific foraging tactic of gammarids. We observed that *G. jazdewskii* frequently interrupted feeding under an LED light. It only partially consumed the prey and retreated to the shelter before returning to the prey again. Therefore, exposure to cool LED light, even without the presence of a predator, impeded the acquisition of food resources.

Animals in the wild are typically exposed to a variety of stressors, which may interact with each other. The risk of predation is one of the most common biotic stressors in the environment (Lima and Dill 1990). To minimize the stress associated with the presence of a predator and avoid injury or death, animals alter their behavior and employ various defense mechanisms to enhance their survival (Jermacz and Kobak 2017; Beermann et al. 2018; Dunn et al. 2008). Defensive behavior may be induced by the physical presence of a predator, but also by olfactory cues, such as predator kairomones (Jermacz et al. 2017) or alarm cues released by injured conspecifics (Smith and Webster 2015). When the presence of a higher-order predator is recognized, gammarids most often seek cover and reduce their activity, which impedes their detection and capture (David et al. 2014; Jermacz and Kobak 2017; Perrot-Minnot et al. 2017). In our study, *G. jazdewskii* exhibited a tendency to lower activity when facing alarm cues under dark night conditions compared with the treatment without predation threat. However, this effect was not significant. Moreover, we did not find any influence of predation cues on the time spent in the shelter. Nevertheless, reduced chironomid consumption in this treatment indicated that gammarids foraged less effectively.

Since anthropogenic pressures often affect biotic relationships, strengthening or suppressing them (Crain et al. 2008), we expected that ALAN would enhance the effect of predation threat on the behavior and foraging efficiency of gammarids. However, the impacts of ALAN and predation cues in our study were not additive. In the presence of predation threat, *G. jazdewskii* exposed to LED and HPS light decreased time spent in movement and consumed less compared with darkness without predation cues. Nevertheless, its activity and consumption were comparable to those observed in the single stressor treatments (ALAN only or darkness with predation cues). This suggests that for gammarids nocturnal illumination may be a similar cue informing about potentially increased predation risk as the presence of olfactory predation

Table 1. Effects of the light type (darkness, HPS, and LED) and predation cue (present/absent) on food consumption (A–C) and movement (D and E) of amphipods

	Response variable	Effect	df	MS	F	P ^a
A	Consumption probability ^b	Predation cue	1, 89		0.901	0.345
		Light type	2, 89		2.516	0.087
		Cue × light	2, 89		5.854	0.004*
		Size ratio ^c	1, 89		0.359	0.551
B	Attack initiation time ^c	Predation cue	1, 86	0.14	0.05	0.817
		Light type	2, 86	0.35	0.13	0.877
		Cue × light	2, 86	3.40	1.27	0.285
		Size ratio ^c	1, 86	11.69	4.38	0.039*
C	Handling time ^c	Predation cue	1, 86	0.01	0.06	0.801
		Light type	2, 86	1.71	9.85	<0.001*
		Cue × light	2, 86	1.16	6.66	0.002*
		Size ratio ^c	1, 86	0.01	0.03	0.858
D	Movement time ^d	Predation cue	1, 89	25.63	0.10	0.751
		Light type	2, 89	4523.66	17.95	<0.001*
		Cue × Light	2, 89	1053.14	4.18	0.018*
E	Time in shelter ^d	Predation cue	1, 89	5402.35	11.97	<0.001*
		Light type	2, 89	2989.39	6.62	0.002*
		Cue × light	2, 89	2354.32	5.21	0.007*

^aSignificant effects indicated with asterisks.

^bGeneralized linear model, binomial distribution, and logit link function.

^cGeneral linear model and data log-transformed.

^dGeneral linear model and no data transformation.

^eCovariate in the model.

Table 2. Post-hoc comparisons for significant effects of the light type (darkness, HPS, and LED) and predation cue (present/absent) on food consumption (A and B) and movement (C and D) of amphipods. The main models are shown in Table 1

Response variable	Comparison: Predation cue absent vs. present	Comparisons between light conditions				
		Predation cue				
		Absent				
A	Consumption (cue × light interaction)	Darkness	0.004*	Darkness vs. HPS	0.001*	0.140
		HPS	0.036	Darkness vs. LED	0.007*	0.746
		LED	0.546	HPS vs. LED	0.374	0.087
B	Handling time (cue × light interaction)	Darkness	0.099	Darkness vs. HPS	0.437	0.456
		HPS	0.096	Darkness vs. LED	<0.001*	0.475
		LED	0.009*	HPS vs. LED	<0.001*	0.992
C	Movement time (cue × light interaction)	Darkness	0.048	Darkness vs. HPS	<0.001*	0.019*
		HPS	0.587	Darkness vs. LED	<0.001*	0.105
		LED	0.044	HPS vs. LED	0.460	0.450
D	Time in shelter (cue × light interaction)	Darkness	0.873	Darkness vs. HPS	0.023*	0.706
		HPS	0.080	Darkness vs. LED	<0.001*	0.766
		LED	<0.001*	HPS vs. LED	0.012*	0.935

Asterisks indicate significant differences taking sequential Bonferroni corrections into account (3 comparisons for different light types and 3 comparisons between light types within each predation cue treatment).

cues. Since each of these stimuli separately (light or predation cue) elicited in *G. jazdzewskii* a strong response of the same kind, their interaction did not intensify this effect. Perhaps, a further increase in the response strength would have been maladaptive, or each stimulus triggered a response that was strong enough to handle a proper reaction to the other one.

Nevertheless, it is possible that changing conditions, e.g., increasing prey density, modifying the quality, and intensity of both stimuli (light and predation cue) or considering other behavioral responses, could show that the influence of ALAN and predation is more complex. This would definitely require further research.

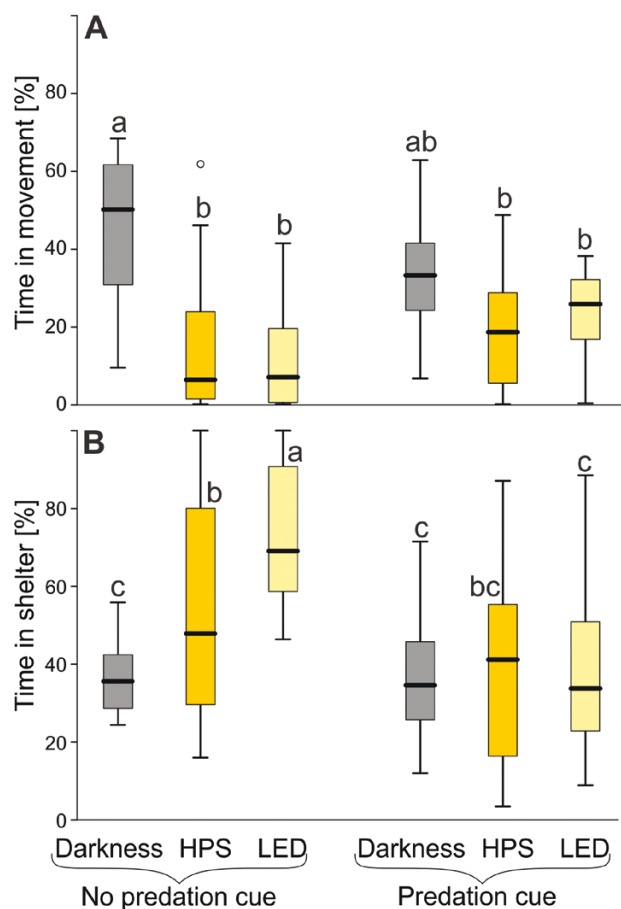


Figure 2. Time spent in movement (A) and time spent in shelter (B) by amphipods exposed to various light types (darkness, HPS, and LED) in the presence or absence of the olfactory predation cue (injured conspecifics). The same letters in the boxes indicate nonsignificant differences between respective treatments (Table 2).

When predation threat was present, we observed some modifications in the gammarid behavior under LED light. Surprisingly, in LED light, *G. jazdewskii* spent less time in a shelter in the presence of predation cues than in their absence. Furthermore, given that gammarids showed reduced locomotor activity with a lower tendency to use shelter, they must have spent more time motionless in the open area. This was rather unusual, as gammarids typically avoid open spaces or leave them as quickly as possible to find refuge or sites less exposed to light (van den Berg et al. 2023), especially under increased predation risk (David et al. 2014). Here, we can only speculate that in the presence of both stressors, LED light and predation cues, *G. jazdewskii* tried to escape from the dangerous area, i.e., leave the experimental arena. A similar response has been observed in marine snails *Concholepas concholepas*. Snails exposed only to ALAN reduced activity and used a refuge. However, when both light and olfactory cues produced by predatory sea stars were present, snails crawled off the waterline in an attempt to leave the experimental tank (Manríquez et al. 2021). The escape was impossible in our study, therefore *G. jazdewskii* remained still outside the shelter. This behavior could reduce the risk of detection by a potential higher-order predator. Previous studies demonstrated that immobilization can be one of the animal's defensive strategies, usually activated after direct

contact with a predator and used to distract its attention (Carli and Farabollini 2022). Nevertheless, leaving the shelter and moving towards a lit area is often associated with an increased risk of predation.

We also found that gammarids exposed to LED light and predation cues consumed chironomid prey faster than gammarids under LED light in the absence of predation cues. Lower prey handling time has been observed in gammarids in the presence of fish cues, and was a way to maintain relatively high food intake despite the higher risk of predation (Iacarella et al. 2018).

Summing up, although we noted the negative impacts of ALAN and predation cues on the feeding efficiency of gammarids in the single stressor treatments (only light or predation threat), we did not find any enhanced effects of the simultaneous exposure to both stressors. The consumption under ALAN and higher order predation risk was similar to that observed in ALAN in the absence of predation cues. The adverse effects of both stressors on the foraging efficiency were mitigated by optimization of gammarid behavior, which represented a compromise between safety in the face of predation risk and the need to acquire food.

In the natural environment, animals are usually subjected to multiple interacting stressors. The majority of previous studies have considered the impacts of ALAN on biota separately from other types of pressure (Gaston et al. 2021). Our results show that the interpretation of the effect of night lighting on organisms should take into account the biotic context, including predation pressure. Moreover, in the wild, some of the effects of ALAN on animals may be masked by responses to other co-occurring stressors, such as predation risk. It is also important to consider the spectral characteristics of ALAN, as some types of light may produce more diverse and/or stronger effects than others.

Authors' Contributions

Conceptualization, M.C.; conducting an experiment, W.H.; formal analysis and results visualization, J.K.; writing—original draft preparation, M.C. and W.H.; writing—review and editing, M.C. and J.K.

Conflict of Interest

The authors declare that they have no conflict of interest.

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