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Impacts of artificial light at night on interactions between four trematode parasites and their marine invertebrate hosts: species-specific effects?

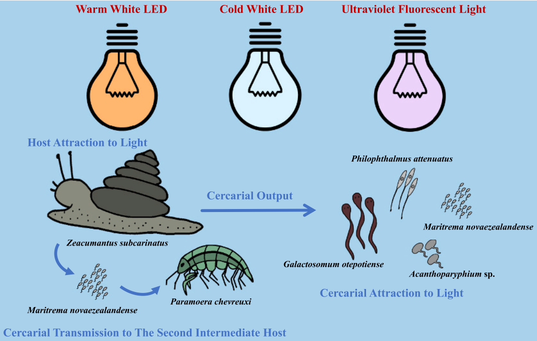
Qing-Long Li[a], Robert Poulin[a,*], Chen-Hua Li[a]

[a] Department of Zoology, University of Otago, P.O. Box 56, Dunedin 9054, New Zealand

HIGHLIGHTS

- Artificial light at night (ALAN) is a pervasive form of pollution that may influence host-parasite interactions.
- The impact of three types of night-time lighting on four species of trematode parasites was investigated.
- Our focus was on cercarial production, attraction to light in hosts and parasites, and transmission success.
- Overall, ALAN effects were species-specific and differed among the types of lighting used.
- Night-time lighting can thus influence host-parasite interactions, but its effects are context-specific.

GRAPHICAL ABSTRACT



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ABSTRACT

Parasitism is influenced by anthropogenic stressors, among which artificial light at night (ALAN) remains understudied. With the expansion of urban areas and the development of lighting technology, the range and intensity of ALAN's effects on host-parasite interactions are increasing. Trematodes, with their complex life cycles, are particularly sensitive to anthropogenic stressors, especially during the transmission of motile cercariae (infective stages) from the first to the second intermediate host while exposed to external conditions. We examined how three types of ALAN (warm white LED, cold white LED, ultraviolet fluorescent light) affect: (1) the cercarial output of four trematode species (*Acanthoparyphium* sp., *Galactosomum otepotiense*, *Maritrema novaezealandense*, and *Philophthalmus attenuatus*) from snail hosts; (2) the light attraction of snails infected by different trematode species; (3) the light attraction of cercariae of the four trematodes; and (4) the transmission of *M. novaezealandense* cercariae from snails to amphipod second intermediate hosts. We observed strong species-specific differences in cercarial output among ALAN treatments. Snails consistently avoided light containing UV radiation, while their responses to other light types varied depending on the trematode species infecting them. Cercariae of different species differed in their attraction to light. Transmission success of *M. novaezealandense* to amphipods was highest under UV light and lowest under cold white light. The interspecific differences observed can be explained by divergence among the phylogenetically-unrelated trematodes, whereas impacts on *M. novaezealandense* transmission success may reflect the amphipods' susceptibility under different ALAN

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* Corresponding author.
E-mail address: robert.poulin@otago.ac.nz (R. Poulin).

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conditions. Light pollution represents an underestimated anthropogenic stressor whose effects on host-parasite interactions demand greater recognition.

1. Introduction

Parasitism is not only the result of interactions between the internal physiological conditions of host and parasite, but also influenced by many external abiotic (e.g. temperature: Studer et al., 2010; pH: MacLeod and Poulin, 2015) and biotic factors (e.g., competition and predation: Friesen et al., 2019). Host-parasite interactions in aquatic systems have been shown to respond to a wide range of environmental stressors, which affect parasite life cycles and disease transmission dynamics (Sures et al., 2023). The effects can be positive or negative, depending on the species involved, they can be direct or indirect, and they can impact the host, the parasite, or their interaction (Sures et al., 2023). For instance, higher temperatures can enhance parasite transmission dynamics (Studer et al., 2010), whereas increased activity of filter-feeding non-host animals under warmer conditions can increase predation on environmental parasite stages, thus increasing mortality of the parasite and reducing infection risk for the target host (Gopko et al., 2020). Pollution may increase host susceptibility to infection (Rumschlag et al., 2019), while parasites that absorb nutrients passively in the host gut can sequester heavy metals and coincidentally reduce accumulation of metals in host tissues (Sures, 2003). Acidification of aquatic ecosystems, combined with metal pollution, may further increase the toxic burden on hosts and/or parasites by enhancing metal bioavailability (Campbell et al., 2014).

With the development of urbanization, several other anthropogenic stressors have emerged, many of which can influence host-parasite interactions. For example, noise stress associated with human gatherings can suppress host immune function and increase susceptibility to infection (Berkhout et al., 2023); habitat fragmentation caused by urban expansion can reduce parasite transmission efficiency (Bitters et al., 2022); and urban heat island effects from building insulation can alter abiotic conditions for survival and transmission of both hosts and parasites (Trájer, 2014).

Here, we focus on light pollution caused by urban night lighting (Poulin, 2023), specifically Artificial Light At Night (ALAN), which is known to disrupt light-mediated processes at both individual and higher levels (Marangoni et al., 2022). In diurnal animals, longer light exposure reduces melatonin production, resulting in prolonged wakefulness and increased energy expenditure (Emmer et al., 2018). To adapt, feeding activity rises, which in turn alters trophic interactions (Russ et al., 2014). At higher levels, ALAN can affect species density gradients, community composition within microhabitats, and energy flow within food webs (Jägerbrand and Spoelstra, 2023). One commonly observed effect is enhanced predation among phototactic organisms (Mcmunn et al., 2019), as well as the aggregation of positively (Quiñones-Llópiz et al., 2021) or negatively (Hale et al., 2015) phototactic species according to ALAN gradients. In marine ecosystems, particularly in intertidal zones (Quiñones-Llópiz et al., 2021) and shallow coastal regions (Navarro-Barranco and Hughes, 2015), ALAN has been shown to alter algal photosynthetic efficiency (Ayalon et al., 2021), metabolic rates of marine animals (Velasque et al., 2022), activity patterns (Luarte et al., 2016), and aggregation density (Navarro-Barranco and Hughes, 2015; Quiñones-Llópiz et al., 2021). Compared with warm white light with an amber coating, cold white ALAN with higher blue light output causes stronger impacts on wildlife (Longcore et al., 2018; Quintanilla-Ahumada et al., 2024). Blue light is considered the most harmful part of the visible spectrum, due to its shorter wavelength (≈450 nm) and stronger penetration, which results in efficient propagation in water (Davies et al., 2020; Zhao et al., 2024). Many aquatic animals have evolved photoreceptor proteins most sensitive to blue wavelengths (Murphy and Westerman, 2022), as it is usually used as an environmental cue for regulation of circadian rhythms (Stanton and Cowart, 2024).

For intertidal invertebrates such as molluscs and crustaceans, which are the focus of this study, previous research has shown that ALAN alters circadian rhythms (Lynn and Quijón, 2022), feeding rates (Luarte et al., 2016; Underwood et al., 2017) and growth rates (Luarte et al., 2016), among other processes. Many species of gastropod have been observed to show avoidance behavior toward ALAN, which demonstrates that ALAN is perceived as an environmental stressor (Trethewy et al., 2023). In the context of host-parasite interactions, although studies have investigated the effects of ALAN in terrestrial systems (e.g., Kehoe et al., 2020; Coetzee et al., 2022; Brown et al., 2023), most studies in aquatic ecosystem have focused on effects of artificial light on host and/or parasite behavior and physiology regardless of diel exposure cycles (Shaw et al., 2020; Hunt et al., 2021). Reported effects include alteration of circadian rhythms in crustacean ectoparasites, timing and size of disease outbreaks of fungal pathogens and the damage they inflict under lights of specific wavelengths, providing indirect evidence that ALAN may also influence host-parasite interactions in aquatic ecosystems (Shaw et al., 2020; Hunt et al., 2021).

The ecological influence of ALAN is increasing. Expanding urban areas increase the extent of night-time lighting, while technological progress has accelerated the shift toward new light types with greater ecological impact (Kyba et al., 2017). Traditional light sources of the 20th century, such as incandescent lamps, low-pressure sodium (LPS), and HPS lamps, generally had lower power and warmer spectra (yellow-dominated) (Davies et al., 2013). With the development of lighting technology, more efficient and whiter (blue-rich) LEDs have rapidly replaced older lamps. This shift means that under the same wattage, modern ALAN produces higher light intensity and greater proportions of blue light (Davies et al., 2013).

Ultraviolet (UV) light represents another light source that can cause biological damage with prolonged exposure (Obermüller et al., 2005; Ruelas et al., 2006, 2009; Studer et al., 2012; Wang et al., 2022). They are not usually considered part of ALAN because their use is mostly indoors, where they serve to supplement invisible radiation rather than provide illumination (Oonincx et al., 2010; James et al., 2018). UV light is further divided into UVA (315-400 nm), UVB (280-315 nm), and UVC (100-280 nm). UVA functions as a light cue for circadian regulation in many animals (Rajan et al., 2021). UVB is indispensable for diurnal animals, being required for vitamin D3 synthesis (Oonincx et al., 2010). UVC, due to its short wavelength and high energy, has strong biocidal activity by causing DNA damage and is widely applied in sterilization (Gurzadyan et al., 1995). Previous studies have shown that even UVB, despite its positive physiological role, can still cause DNA damage (Obermüller et al., 2005; Ruelas et al., 2006, 2009; Studer et al., 2012; Wang et al., 2022).

The complex life cycles of trematodes (class Digenea, phylum Platyhelminthes) makes these parasitic flatworms particularly sensitive to environmental stressors (Sures et al., 2023). A typical trematode life cycle involves three hosts, with two free-living transmission stages. Adult worms living in a vertebrate definitive host release eggs that pass out of the host in feces. Free-living larval stages hatching from those eggs infect a molluscan first intermediate host, in which they multiply asexually to produce large numbers of free-swimming cercariae, the next free-living transmission stage, which exit from the mollusk to seek the second intermediate host, such as mollusks, fish or crustaceans. In the latter, they encyst as metacercariae and await ingestion by a suitable definitive host. Trematodes often alter behavioural responses, such as phototaxis, in their invertebrate hosts, but generally in a species-specific manner (see review in Moore, 2002). Therefore, ALAN may cause the spatial aggregation of infected molluscs and create foci of cercarial emergence, depending on which trematode species they harbour. Each parasitic or free-living stage faces distinct environmental stressors (Sures et al., 2023). Small body size makes them especially vulnerable to ALAN radiation during free-living stages, particularly for transparent or lightly pigmented species (Hairston, 1976). Their lack of protection against external conditions also renders them susceptible to changes in temperature (Studer et al., 2010), salinity (Studer and Poulin, 2011), and pH (Harland et al., 2015), which can have profound effects on their physiology. In parasitic systems, UVB exposure has been shown to simultaneously damage snail hosts and their infecting trematodes (Ruelas et al., 2009). To the best of our knowledge, the only previous study on ALAN effects in aquatic host-parasite systems found that frog tadpoles were slightly more susceptible to infection by *Echinostoma* sp. trematodes, probably mediated through behavioural changes in hosts and parasites (May et al., 2019). One study has further shown that ALAN involving LED light had stronger effects than high-pressure sodium (HPS) in a snail host infected with trematodes (Hussein et al., 2022). No study has addressed ALAN effects on trematode parasitism in coastal ecosystems.

Our study system consists of four trematode species sharing the same snail first intermediate host. The mud snail (*Zeacumantus subcarinatus*) serves as the first intermediate host of multiple trematode species (Martorelli et al., 2004, 2006, 2008). In the intertidal zone of Otago Harbour, New Zealand, it hosts four trematode species: *Acanthoparyphium* sp., *Galactosomum otepotiense*, *Maritrema novaezealandense*, and *Philophthalmus attenuatus*. Larvae of these trematodes infect the gonads of the snail, castrating the host and exploiting its resources to clonally produce infective stages known as cercariae (Martorelli et al., 2004, 2006, 2008). Mature cercariae emerge in response to light and temperature stimuli to search for the next host in their life cycle. These trematodes differ in phylogenetic affinities, life cycle, and cercarial size (Table 1). These four species, especially *M. novaezealandense*, have been used as model species in studies of their sensitivity to multiple abiotic stressors, including temperature (Studer et al., 2010), salinity (Studer and Poulin, 2011), and ocean acidification (Harland et al., 2015). Regarding light, previous studies have shown that UV radiation negatively affects the survival of *M. novaezealandense* cercariae (Studer et al., 2012).

We aimed to test the effects of 3 types of light used as ALAN: LED with blue light (cold white), LED without blue light (warm white), and UV light (UVA + UVB). Focusing on host-parasite interactions in *Z. subcarinatus* and its trematodes, four experiments were designed to address the following questions: (i) How do different types of ALAN and exposure duration (weeks) affect cercarial output of different trematode species? (ii) How do different types of ALAN differ in attractiveness to snails with different infection types? (iii) How do different types of ALAN differ in attractiveness to cercariae of different species, and are there interspecific differences in phototaxis? (iv) How does *M. novaezealandense* transmission from snails to amphipods as second intermediate hosts vary among different ALAN conditions? In all cases, we predicted some impact of ALAN, however its magnitude and direction were expected to be species-specific.

2. Materials and methods

2.1. Field collections

Host snails (*Z. subcarinatus*), green algae (*Ulva lactuca*), and red algae (*Polysiphonia* sp.) were collected by hand at low tide from the intertidal zone at Lower Portobello, Otago Peninsula (45°49'54.2"S 170°40'21.0"E). Snails were obtained from early March to late June 2025. Amphipods (*Paramoera chevreuxi*), the second intermediate host of *M. novaezealandense*, were collected at Hoopers Inlet (45°51'42.2"S 170°39'36.1"E) by dragging a net (mesh size 0.5 mm) through algae (*Ulva ralfsii*), in water $<$1m deep; the algae to which they were attached were also collected to provide natural habitat and a food source in captivity. Amphipods from Hoopers Inlet are uninfected by *M. novaezealandense* or any other metazoan parasite, as confirmed in multiple prior studies using amphipods from that location (Mouritsen et al., 2018), and through dissection of a subset of individuals collected for the present study prior to the start of the experiment. All amphipods were collected on June 16 2025.

2.2. Laboratory procedures

Snails were maintained in seawater from the site of collection in separate 4-litre plastic containers at 12/12 h light-dark cycles at $\sim$10°C for 15-20 days to acclimate prior to experimentation. Lighting during the daytime period was provided by LEDs simulating the sunlight spectrum with higher brightness (10 W, 5000 K; see Table 2). Afterward, snails were individually placed in wells of 24-well tissue culture plates along with a small water volume and incubated at 25°C with light for 12-24 h to induce cercarial emergence; here, and for all incubations described below, the light in the incubator used to induce cercarial emergence was a 15 W fluorescent lamp. Infected individuals were identified by the cercariae emerging from them. Each snail was checked at least twice to confirm infection status. Cercariae of the 4 trematodes

Table 2
Radiance and other characteristics of light sources used in the experiments.

Light	Type	Power (W)	Luminance (lm)	Light color (Kelvin)	UVB + UVA productive standards (radiant output %)
Daytime light	LED	10	1000	5000	-
Warm white light	LED	8	806	4000	-
Cold white light	LED	8	680	2200	-
UV light	Fluorescent	13	-	-	5% + 30%

Table 1
Taxonomic affiliation, life cycle characteristics, and cercarial size of 4 trematode species in *Zeacumantus subcarinatus*.

Species	Family	Life stage in snail hosts	Cercarial length (μm)	Cercarial wide (μm)	Second intermediate hosts	Definitive host	References
Acanthoparyphium sp.	Himasthlidae	Rediae	400-520	105-180	Mollusks	Birds	(Martorelli et al., 2006)
*Galactosomum otepotiense**	Heterophyidae	Rediae	110-210	9-10	Fish	Birds	(Martorelli et al., 2008)
Maritrema novaezealandense	Microphallidae	Sporocysts	75-94	29-36	Crustaceans	Birds	(Martorelli et al., 2004)
Philophthalmus attenuatus	Philophthalmidae	Rediae	400-600	170-200	Hard substrates	Birds	(Martorelli et al., 2008)

* Cercariae of this species are the only ones to possess eyespots.

were identified based on their very distinctive morphology (Martorelli et al., 2004, 2006, 2008).

2.3. Environmental setting

In the field, snails and cercariae are exposed to a range of nighttime light types and intensities depending on their exact location along the coastline and the number and types of lights used nearest to them, their distance from the water surface, etc.; even snails situated just a few meters apart experience different light levels. In our experiments we used light levels corresponding to areas with the most intense nighttime illumination. For long-term experiments lasting either 2 weeks (cercarial transmission; see below) or 6 weeks (cercarial output; see below), trials were conducted in light-proof chambers (40 * 45 * 70 cm) under 4 light conditions: (i) 12 h daylight + 12 h ALAN under warm white light; (ii) 12 h daylight + 12 h ALAN under cold white light; (iii) 12 h daylight + 12 h ALAN under UV light; (iv) control conditions, 12 h daylight + 12 h dark (see Table 2). Daytime lighting conditions were provided by LEDs simulating the sunlight spectrum with higher brightness. The height of the ALAN lamps above the experimental containers was adjusted using a lightmeter with quantum sensor (detection range: 400-700 nm) to ensure that the bottom center of all containers received 5 μmol·m^{-2}·s^{-1} irradiance on average (value based on previous studies; Vega et al., 2022). As UV light emits ~35% UVA and UVB radiation outside the detection range, the standardized reading was set to 2.5 μmol·m^{-2}·s^{-1}, to match the radiation equivalence of warm and cold white lights. To guarantee uniform light exposure, all lamps were fixed at 40 cm above the bottom and positioned at the center of each chamber. Container positions were rotated twice weekly in a systematic cycle within each chamber, ensuring that average daily irradiance from both daylight and artificial sources was equal among containers throughout the experiment.

For short-term experiments (measured in minutes), the size of the light-proof chamber used was 120 * 45 * 70 cm, with one of the three types of ALAN described above as the only light source, placed at one end of the cylindrical test arenas (see 2.4.2 and 2.4.3 below). Maximum irradiance at container level was set to 5 μmol·m^{-2}·s^{-1} (warm and cold white light) and 2.5 μmol·m^{-2}·s^{-1} (UV light). (see light specifications in Table 2).

2.4. Experimental design

2.4.1. Cercarial output experiment

This experiment tested for the effect of ALAN on cercarial output using the long-term setup. Under each light condition, snails infected by different trematode species were divided into 4 groups. Each group consisted of 10 snails placed in each of two transparent 500 ml containers per light treatment (20 snails total per species per light treatment), fed with small amounts of *U. lactuca* and *Polysiphonia sp.* that did not block light. Snails were individually labelled with nail polish, allowing them to be tracked individually throughout the experiment. Over a 6-week period, incubations were performed every 2 weeks, at which times the snails were temporarily removed from their containers and incubated in 24-well plates at 25 °C and with light on for 5 hours, as described above. Immediately after incubation, snails were returned to their containers, and all cercariae in the water of each well were counted under a microscope. In total, 320 snails (20 individuals * 4 trematode species * 4 light conditions) were used, yet only 243 individuals were used in the analyses. Individuals that died before the first incubation (N = 17), those from which no cercariae emerged across 3 incubations (N = 56, spread roughly evenly across treatments), or were later identified as harboring more than one trematode species (N = 4) were excluded to avoid excessive missing values. Of the 243 snails actually used, if a snail died mid-experiment (N = 34), subsequent incubation data were entered as missing values, to distinguish them from zero cercarial counts. For detailed sample sizes per treatment, see Supplementary Table A1.

2.4.2. Host attraction to light experiment

This experiment tested the attractiveness of snails to different light types using the short-term setup. Five groups of snails were formed: one group of infected snails for each of the 4 trematode species, plus uninfected controls (15 snails per group, total N = 75). These snails were different from the ones used in the cercarial output experiment. Each snail was tested under all 3 ALAN light types, enabling control for individual movement bias unrelated to light. To avoid confounding effects of diel rhythms, trials were run only at night, with one light type per night, in random order. A 90 cm long * 10 cm diameter black semicircular PVC tube was used, with the midpoint (45 cm) serving as the light-dark boundary. The dark end (15 cm) was wrapped with blackout fabric, forming a ~7 cm fully dark zone. In each trial, 5 individually marked snails were placed in the centre position with 5 mm water depth (seawater from the site of field collection) and allowed to move for 40 minutes. Final positions were recorded, and movement was quantified as the displacement distance, either positive (toward light) or negative (toward dark) relative to the midpoint (0 cm).

2.4.3. | Cercarial attraction to light experiment

This experiment tested the attractiveness of cercariae to different light types using the short-term setup. Cercariae of the 4 trematode species were obtained from host snails, by incubation as described above, using different snails from those used in the above experiments. To ensure activity, only ‘fresh’ cercariae were used, obtained within 5 hours of emergence from their snail host; cercariae from multiple snails were pooled for this study. In glass tubes (9 cm long, 0.9 cm diameter; 4.5 cm transparent, 4.5 cm black), the dark side was covered with blackout material, whereas the rest of the tube was exposed to one of the three light types. Ten cercariae of a single species were introduced per trial (for *P. attenuatus*, only actively moving cercariae were included, excluding those irreversibly attached to the incubation wells). All cercariae were initially placed in the dark end. Counts of cercariae in the lighted zone were recorded at 5 and 10 min under a microscope. Each species was tested 15 times under each ALAN light, totaling 180 trials (15 * 4 species * 3 light types, with 10 cercariae per trial; all cercariae were only used once).

2.4.4. | Cercarial transmission to the second intermediate host experiment

This experiment tested the transmission success of *M. novaezealandense* from snails to amphipods, using the long-term setup. For each light condition, three transparent 1 L containers were set up. To simulate natural density, each contained 20 amphipods and 3 snails infected with *M. novaezealandense*. Containers were supplied with *U. ralfsii* to provide a semi-natural amphipod habitat and *Polysiphonia sp.* from the snail’s sampling location as food. In total, 240 amphipods were used (20 * 3 containers * 4 light conditions). The experiment lasted 2 weeks. After the first 7 days, 9 amphipods per container were dissected under a microscope to count the number of metacercarial cysts, with each cyst representing one successful infection by a cercaria. At day 14, all remaining amphipods were dissected. Because of unavoidable natural mortality, the sample sizes for day 14 varied between 0-9 amphipods per container (see Supplementary Table A2).

2.5. | Data analysis

All analyses were conducted in R version 4.4.1 (R Core Team, 2025). For each experiment, data were modeled using generalized linear mixed models (GLMMs) implemented in the glmmTMB package version 1.1.9 (Brooks et al., 2017) (see Supplementary Tables B1-B11 for outputs of each model). Model diagnostics were performed with DHARMa package version 0.4.7 (Hartig, 2022) to ensure homogeneous residual distribution and absence of overdispersion or zero inflation (see Supplementary Table C for results). ANOVA tables were generated using the car package version 3.1 (Fox and Weisberg, 2019) to test the significance of variables and categorical factors. Pairwise comparisons of all main effects and 2-

and 3-way interactions were assessed with emmeans package version 1.10.2 (Lenth and Piaskowski, 2024). For all experiments, plots were produced with ggplot2 package version 3.5.1 (Wickham, 2016).

2.5.1. | Models of the cercarial output experiment

Each of the 4 trematode species was modeled separately. The dependent variable was cercarial output (count), and the predictors were light condition (4 levels: control plus three ALAN light types), incubation weeks (3 levels: weeks 2, 4 and 6), and their interaction. The random effect was snail ID nested within container, to account for possible container effects and repeated measures on the same individual snails. Models used a negative binomial family based on the distribution of count values. For *Acanthoparyphium* sp. and *M. novaezealandense*, additional zero-inflation terms were included due to many missing values and zero outputs.

2.5.2. | Model of the host attraction to light experiment

The dependent variable was snail movement distance. The predictors were light condition (3 levels: each of the three ALAN light types), infection type (5 levels: infection by each of the 4 trematode species plus uninfected controls), and their interaction. The random effect was snail ID. The model used a Gaussian family with zero-inflation adjustment.

2.5.3. | Models of the cercarial attraction to light experiment

Each of the 4 trematode species was modeled separately, followed by a combined model using *M. novaezealandense* as the phototactic reference, in order to test for interspecific differences in light attraction. In species-specific models, the dependent variable was the count of cercariae observed in the lighted zone, the predictors were light condition (3 levels: each of the three ALAN light types), observation time (2 levels: 5 and 10 minutes), and their interaction, and the family was binomial. The random effect was trial replicate number, to account for variation resulting from slight variation in cercarial age. In the combined model, the dependent variable was again counts in the lighted zone, the predictors were light condition (3 levels: each of the three ALAN light types), trematode species (4 levels), and observation time (2 levels: 5 and 10 minutes), the random effect was trial replicate, and the family was beta-binomial.

2.5.4. | Model of the cercarial transmission to the second intermediate host experiment

In this final model, the dependent variable was the number of cysts per amphipod. The predictors were light condition (4 levels: control plus three ALAN light types), dissection time (2 levels: 7 and 14 days), and their interaction. The random effect was container within light treatment, to account for any possible container effect. The model used a negative binomial family.

3. Results

3.1. | Cercarial output experiment

In the cercarial output experiment, we found that the number of cercariae emerging from snails at each incubation period by all 4 trematodes (*Acanthoparyphium* sp., *G. otepotiense*, *M. novaezealandense* and *P. attenuatus*) decreased significantly as a function of time (Table 3, Figure 1; for pairwise comparisons see Supplementary Tables D1-D4). Cercarial output by *M. novaezealandense* and *P. attenuatus* responded to different light types at night, whereas in *G. otepotiense* and *M. novaezealandense* responses to light types depended on time. *Maritrema novaezealandense* showed higher cercarial production under cold white light and control (no ALAN) conditions, and lower under warm white and UV light, with the effects of each light type showing different interactions with time. In contrast, *P. attenuatus* showed higher cercarial production under UV light compared to cold white light across all 6 weeks (i.e. only in pairwise comparison when pooling data across times; not shown).

Table 3
ANOVA results for the models on cercarial output, for each trematode species, showing the effects of predictors and their interaction (significant terms shown in **bold**).

Trematode species	Factor(s)	Chisq	Df	Pr(>Chisq)
Acanthoparyphium sp.	Light	5.41574	5	0.36727
	Time	**69.86430**	**4**	**0.00001**
	Light*Time	8.57510	6	0.19892
Galactosomum otepotiense	Light	2.76882	3	0.42866
	Time	**21.11810**	**2**	**0.00003**
	Light*Time	**35.23528**	**6**	**0.00001**
Maritrema novaezealandense	**Light**	**19.62761**	**3**	**0.00020**
	Time	**161.79753**	**2**	**0.00001**
	Light*Time	**15.92692**	**6**	**0.01415**
Philophthalmus attenuatus	**Light**	**10.79680**	**3**	**0.01288**
	Time	**28.76281**	**2**	**0.00001**
	Light*Time	2.53824	6	0.86416

3.2. | Host attraction to light experiment

We found the phototaxis of host snails (*Z. subcarinatus*) was significantly affected by light types (Table 4, Figure 2; for pairwise comparisons see Supplementary Tables D5 and D6). Snails infected by *G. otepotiense* tended to avoid all light types, whereas other groups were neutral or slightly attracted to cold white light (see Supplementary Table E). Regardless of infection status or trematode species, snails preferred to move away from the UV light, but not away from warm and cold white lights.

3.3. | Cercarial attraction to light experiment

In this experiment, we found the light attraction of cercariae was significantly affected by experimental time and light type differences for *G. otepotiense* (Table 5, Figures 3 and 4; for pairwise comparisons see Supplementary Tables D7-D11), but only by light type differences for *P. attenuatus*. For *G. otepotiense*, cold white light was more attractive to cercariae compared to warm white light, and there was a clear increase in the number of cercariae that settled in the lighted zone between the checks at the 5th and 10th minute. For *P. attenuatus* cercariae, UV light was more attractive compared to the warm and cold white lights. Overall, for the 4 species, light attraction of cercariae showed significant differences among trematode species, light types used, experimental time, and interaction of species and time. The 4 species had different patterns of positive/neutral/negative phototaxis depending on the type of light; the number of cercariae settling in the lighted zone of the tube generally increased from the 5th to the 10th minute of the experiment. Compared to *M. novaezealandense*, the cercariae of the other 3 species displayed significantly positive phototaxis; *G. otepotiense* showed the strongest phototaxis, followed by *P. attenuatus* and *Acanthoparyphium* sp. in that order.

3.4. | Cercarial transmission to the second intermediate host experiment

In the cercarial transmission experiment, we found the transmission success of *M. novaezealandense* cercariae to amphipods was significantly different among light types under which they were housed (Table 6, Figure 5; for pairwise comparisons see Supplementary Table D12). Amphipods under the UV light showed the highest cyst accumulation, while those maintained with infected snails under cold white light had the lowest. There was no significant difference in cyst accumulation between amphipods dissected after the first and second weeks.

4. Discussion

Host-parasite interactions are influenced by abiotic environmental

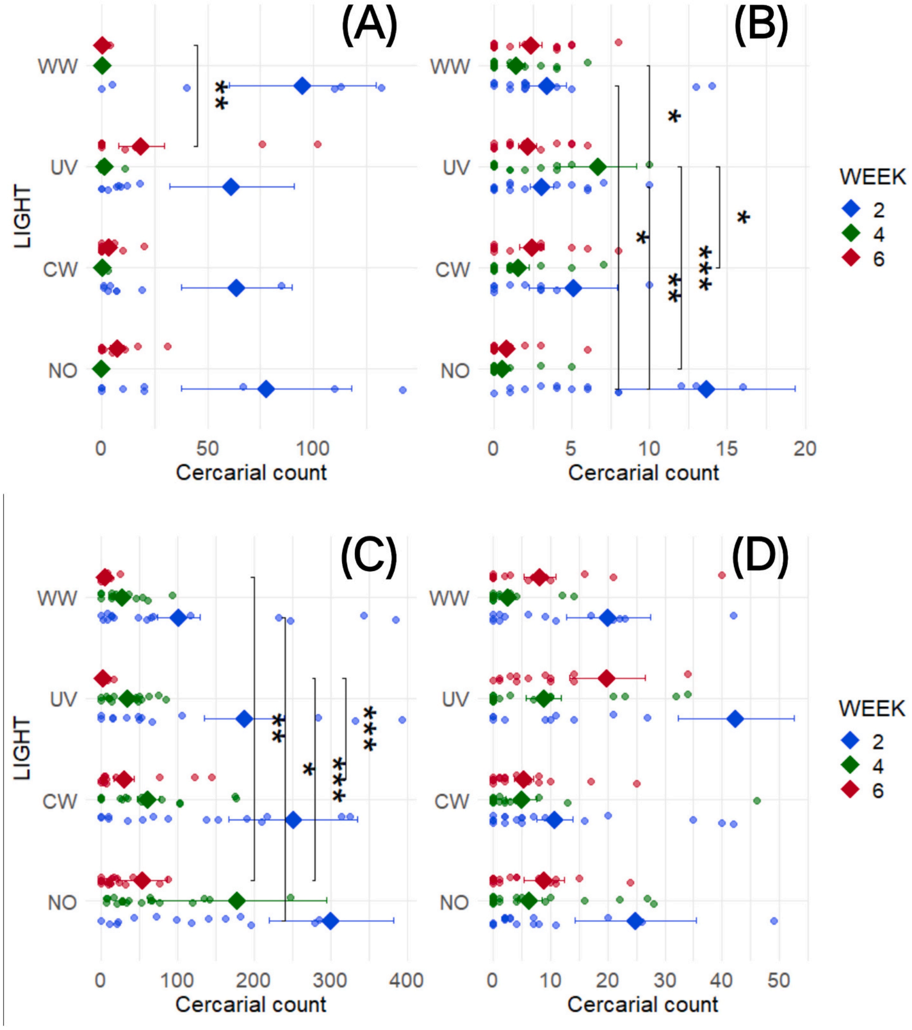

Fig. 1. Cercarial output of (A) *Acanthoparyphium* sp. (n= 39, 39, 39 for weeks 2, 4, 6), (B) *Galactosomum otepotiense* (n= 59, 58, 56), (C) *Maritrema novaezealandense* (n= 72, 66, 64) and (D) *Philophthalmus attenuatus* (n= 73, 68, 67) under 4 Artificial Light At Night (ALAN) conditions (WW: warm white light, CW: cold white light, UV: ultraviolet light, NO: no ALAN) at the end of weeks 2, 4 and 6. Diamonds represent mean values, whiskers represent standard deviations, and data points represent individual observations; extreme data points (A) > 150, (B) > 20, (C) > 500 and (D) > 50 are not shown. Links indicate the significance of pairwise differences (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$); only comparisons between ALAN conditions within the same week are shown.

Table 4
ANOVA results for the model on host attraction to light, showing the effects of predictors and their interaction (significant terms shown in **bold**). Uninfected snails are included as a category in "Trematode species infecting the snail".

Factor(s)	Chisq	Df	Pr(>Chisq)
Trematode species infecting the snail	4.29292	4	0.36781
Light	**18.21151**	**2**	**0.00011**
Trematode species infecting the snail *Light	15.39017	8	0.05199

factors, and it has been shown that many anthropogenic stressors affect parasite growth and transmission, particularly trematodes in aquatic ecosystems (Sures et al., 2023). However, the effects of ALAN on parasitic relationships in aquatic systems remain understudied (Poulin, 2023). To our knowledge, only one study has been done on the effects of ALAN on freshwater trematode transmission (May et al., 2019). The present study quantified the effects of three types of ALAN on four phylogenetically unrelated trematode species, focusing on cercarial output, light-driven attraction of both hosts and cercariae, and cercarial transmission to the second intermediate host. Overall, our results reveal light-specific and species-specific effects on these different aspects of the host-parasite interaction.

First, we assessed the production and emergence of cercariae of the four trematode species in their snail hosts over time under three ALAN conditions (warm white, cold white, and UV light) and one no ALAN control. Overall, cercarial production declined over time in all four trematode species. A straightforward explanation is that the hosts' energy availability decreased due to the chronic physiological costs of prolonged infection and maintenance under laboratory conditions (Harland et al., 2015). Another possible explanation is that, since all four trematodes are castrators relying on their hosts' gonadal resources, the experimental environment may have reduced the hosts' energy investment in reproduction. Indeed, important reproductive cues for marine gastropods (e.g., Collin et al., 2017) were not replicated in the laboratory.

For *M. novaezealandense* cercarial output, over the 6-week duration of the study, snails maintained under ALAN conditions with cold white light showed the highest total numbers of cercariae emerging during incubations, while those in the UV light group showed the lowest. This is the exact opposite of the pattern observed in terms of metacercarial cysts accumulating in the second intermediate host under these two light conditions, as seen in the experiment on cercarial transmission to amphipods. One possible explanation is that the light type affects the frequency at which *M. novaezealandense* cercariae emerge from their snail

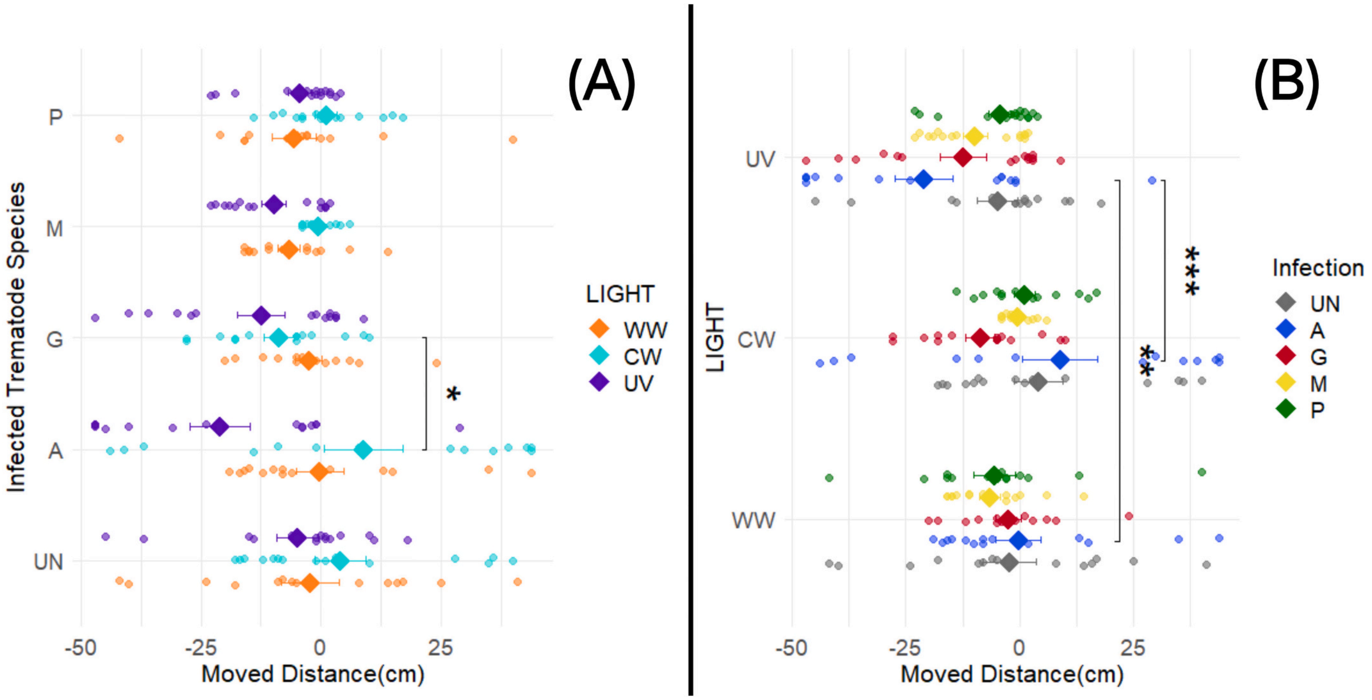

Fig. 2. Attraction of host snails (*Zeacumantus subcarinatus*) under 5 infection conditions (A: *Acanthoparyphium* sp. infected, G: *Galactosomum otepotiense* infected, M: *Maritrema novaezealandense* infected, P: *Philophthalmus attenuatus* infected, UN: uninfected) to 3 types of light (WW: warm white light, CW: cold white light, UV: ultraviolet light), comparing differences of attraction among (A) species and (B) light types. Diamonds represent mean values, whiskers represent standard deviations, and data points represent individual observations; the sample size was 15 for each infection condition, for a total of 75 snails. Links indicate the significance of pairwise differences (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$); only (A) comparisons among types of light within the same week and (B) comparisons among infection condition within the same type of light are shown.

Table 5
ANOVA results for the models on cercarial attraction to light, for each trematode species and all of them combined, showing the effects of predictors and their interaction (significant terms shown in **bold**).

Trematode species	Factor(s)	Chisq	Df	Pr (>Chisq)
Acanthoparyphium sp.	Light	0.10696	2	0.94793
	Time	2.39332	1	0.12185
	Light*Time	4.92733	2	0.08512
Galactosomum otepotiense	**Light**	**15.59663**	**2**	**0.00041**
	Time	**11.39647**	**1**	**0.00074**
	Light*Time	0.79536	2	0.67188
Maritrema novaezealandense	Light	3.87126	2	0.14433
	Time	0.54892	1	0.45876
	Light*Time	0.45390	2	0.79696
Philophthalmus attenuatus	**Light**	**22.02517**	**2**	**0.00002**
	Time	0.00462	1	0.94578
	Light*Time	0.05005	2	0.97529
All species combined	**Species**	**424.98000**	**3**	**0.00000**
	Light	**7.14488**	**2**	**0.02809**
	Time	**8.21635**	**1**	**0.00415**
	Species*Light	**26.95790**	**6**	**0.00015**
	Species*Time	3.33935	3	0.34220
	Light*Time	2.58217	2	0.27497
	Species*Light*Time	5.49706	6	0.48181

host: they may emerge from snails under UV light conditions at night more frequently or at least regularly, leading to lower numbers ready to emerge during any single experimental incubation, while those under cold white light conditions at night might show the opposite pattern, i.e., cercariae emerging at lower frequency but in greater numbers per incubation. This behavior may result from the transmission strategy of *M. novaezealandense*: since its cercariae are small and most likely energetically inexpensive to produce (Rosenkranz et al., 2018), this trematode is more likely to adopt a flexible strategy, adjusting the frequency of its cercarial emergence and quantity of cercariae emerging each time under different conditions to maximize transmission success. Cercarial emergence in trematodes is also synchronised by environmental cues other than light, such as temperature (Prokofiev et al., 2023) and desiccation stress (Zekhnini et al., 2002).

In the no ALAN treatment, the lack of light stimulation may have led to a reduction of the spontaneous frequency of cercarial emergence, leading to greater accumulation of cercariae within snails and thus more cercariae emerging during each incubation. Warm white light at night seems to increase the frequency of cercarial emergence rather than decrease their production. This explanation is based on the idea that cercarial productivity within hosts is constrained by host resource availability, which is unlikely to have decreased substantially in the early stages of the experiment (Harland et al., 2015), while cercarial emergence itself is directly regulated by environmental cues, which can shift abruptly. However, the difference in *M. novaezealandense* cercarial numbers between warm white ALAN and no ALAN groups was already evident in the first incubation after the second week, suggesting that increased frequency of emergence, rather than reduced production, was the main reason for lower numbers emerging per incubation under warm white light.

Additionally, apart from the negative effects of blue and UVB light, warm white light may have led to a less disturbing removal of total darkness. Darkness itself is an important environmental condition, regulating circadian rhythms and melatonin release (Marangoni et al., 2022). Even non- or low- blue light ALAN can still disrupt the circadian rhythms of marine organisms and have negative impacts on them (Marangoni et al., 2022). Therefore, the physiological effects of warm white light at night, which removes darkness without extra radiation hazards, are likely milder on snails compared to cold white light or UV light. Over time, this might result in less fluctuation in host energy availability.

Considering all results across the 6-week duration of the cercarial

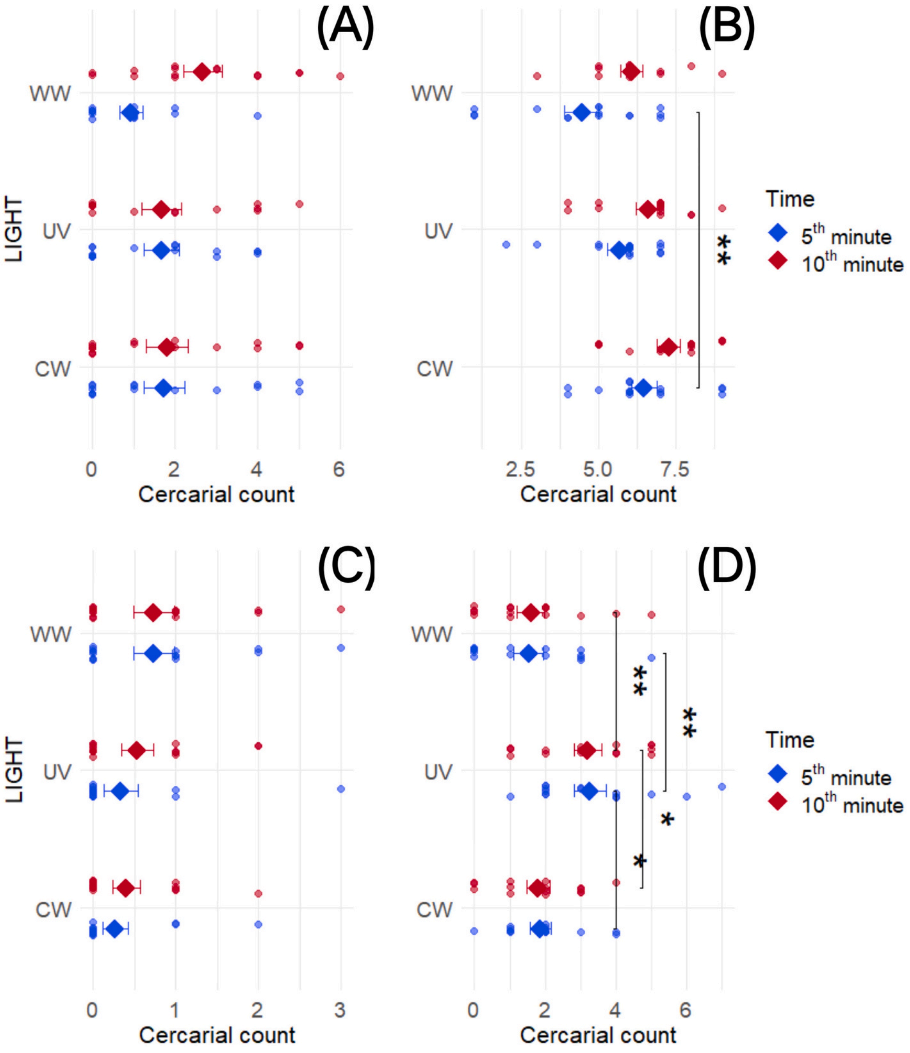

Fig. 3. Attraction of cercariae from four trematode species (A) *Acanthoparyphium* sp. (n= 150), (B) *Galactosomum otepotiense* (n= 150), (C) *Maritrema novaezealandense* (n= 150) and (D) *Philophthalmus attenuatus* (n= 150) to 3 types of light (WW: warm white light, CW: cold white light, UV: ultraviolet light). The data are numbers of cercariae that occurred on the lighted side at each of 2 observation times. Diamonds represent mean values, whiskers represent standard deviations, and data points represent individual observations. Links indicate the significance of pairwise differences (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$); only comparisons among types of light at the same observation time are shown.

output experiment, both *Acanthoparyphium* sp. and *M. novaezealandense* showed lower cercarial production under warm white light at night, whereas *Acanthoparyphium* sp. (in the third incubation) and *P. attenuatus* (across all 6 weeks) showed higher production under UV light at night. This may indicate that prolonged exposure to UV light weakens host immune systems. Previous studies have shown that UVB radiation damages the immune system of insects (Alton et al., 2023; Sabockytė et al., 2023), which in the present case could mean more energy available for the parasites to produce cercariae. Conversely, in the third incubation, *Acanthoparyphium* sp. under warm white light showed decreased cercarial output, possibly explained by a similar "accelerated emergence frequency" pattern as in *M. novaezealandense*, since *Acanthoparyphium* sp. produces small cercariae and may thus also adopt a quantity-based strategy.

Finally, the production of cercariae by *G. otepotiense*, although showing differences between light treatments and time of incubation, followed a highly stochastic pattern without consistent trends, and differences among light treatments did not intensify over time. One explanation may be that *G. otepotiense* cercariae, which may be small but have a massive tail (and are thus costly to produce), emerge only in small numbers and are unaffected by external cues, instead following their own intrinsic growth and emergence schedule. No doubt the transmission strategy and the identity of the next host in the life cycle play a role in determining how susceptible particular trematode species are to light in general.

We then tested whether and how strongly snail hosts displayed phototaxis when placed in a non-reflective black cylinder, under three light conditions (warm white, cold white, and UV light). In most cases, trematode infection did not alter light attraction patterns of snails: hosts consistently avoided UV light, while remaining neutral toward warm and cold white lights, possibly as a strategy to avoid the acute damage caused by UVB radiation (Ruelas et al., 2006). Among snails infected by *Acanthoparyphium* sp., the contrast between UV light and the other two light types was more pronounced, whereas their attraction to cold white light and warm white light remained similar. *Acanthoparyphium* sp. appears to non-directionally amplify the hosts' light sensitivity, thereby enhancing both positive and negative phototactic behaviors.

Infection by *Acanthoparyphium* sp. and infection by *G. otepotiense* resulted in significantly different changes in snail attraction toward cold white light: snails infected by *Acanthoparyphium* sp. showed the strongest attraction to cold white light, while those infected by *G. otepotiense* most strongly avoided it. In fact, based on mean values, snails infected

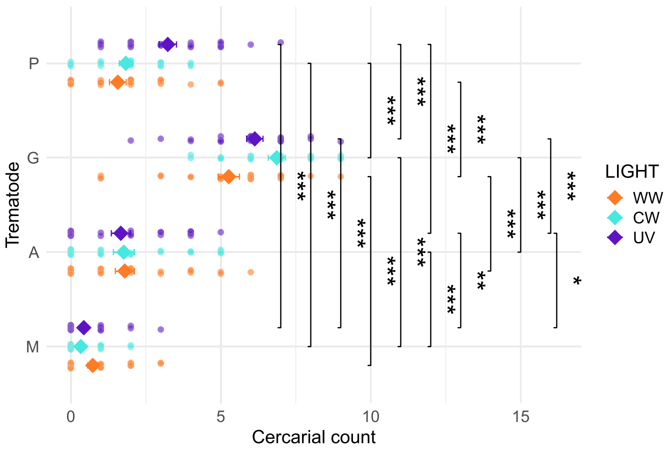

Fig. 4. Comparisons of attraction of cercariae from four trematode species (A: *Acanthoparyphium* sp.; G: *Galactosomum otepotiense*; M: *Maritrema novaezealandense*; and P: *Philophthalmus attenuatus*) to 3 types of light (WW: warm white light, CW: cold white light, UV: ultraviolet light). Comparisons are made between the numbers of cercariae of the different species that occurred on the lighted side at each of 2 observation times. Diamonds represent mean values, whiskers represent standard deviations, and data points represent individual observations. The sample size is 150 cercariae for each species, for a total of 600 cercariae. Links indicate the significance of pairwise differences (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$); only comparisons among trematode species within the same type of light are shown.

Table 6

ANOVA results for the model on *Maritrema novaezealandense* cercarial transmission to amphipod second intermediate hosts, showing the effects of predictors and their interaction (significant terms shown in **bold**).

Factor(s)	Chisq	Df	Pr(>Chisq)
Light	**161.53015**	**3**	**0.00000**
Time	2.79647	1	0.09447
Light*Time	7.24655	3	0.06444

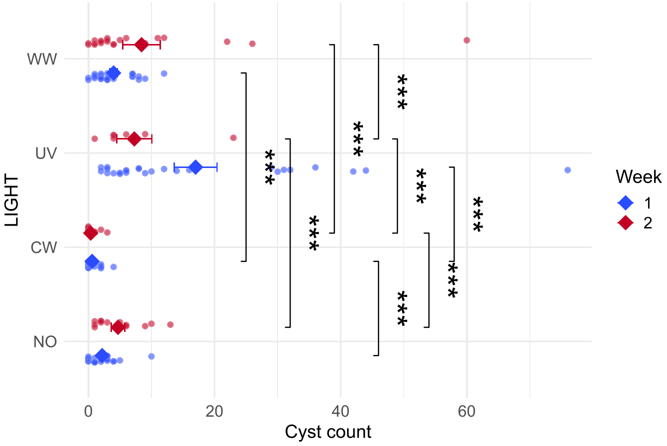

Fig. 5. Cercarial transmission success of *Maritrema novaezealandense* to amphipod second intermediate hosts (*Paramoera chevreuxi*) (n= 168) under 4 Artificial Light At Night (ALAN) conditions (WW: warm white light, CW: cold white light, UV: ultraviolet light, NO: no ALAN). The data are numbers of metacercarial cysts in amphipods at the end of weeks 1 and 2. Diamonds represent mean values, whiskers represent standard deviations, and data points represent individual observations. Links indicate the significance of pairwise differences (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$); only comparisons among ALAN conditions within the same week are shown.

by *G. otepotiense* tended to avoid all light types, whereas other groups were neutral or slightly attracted to cold white light. Although *G. otepotiense* cercariae themselves are photopositive (see next paragraph), their hosts display the opposite pattern. Overall, these findings suggest that the four different trematode species have slightly different effects (based on the nearly significant interaction term; see Table 4) on their host's attraction to light. Earlier studies have found similar patterns. For instance, these same four trematode species have different impacts on the snail's tolerance to heat and its attraction toward warmer waters (Bates et al., 2011), its pattern of shell growth post-infection (Hay et al., 2005), and its tolerance to ocean acidification (MacLeod and Poulin, 2016). Therefore, there is no universal effects of trematode infection on snails, instead the effects appear to be species-specific.

In parallel experiments on light attraction of the parasites themselves, cercariae of *G. otepotiense* were strongly attracted to cold white light, less so to warm white light, and only moderately attracted to UV light. This trend matches the order of blue light intensity emitted by these lamps. Cercariae of *G. otepotiense* seem positively phototactic toward blue light and not sensitive to the negative effects of UVB exposure, possibly because they are the only species among the four having dark pigmentation and eyespots (Martorelli et al., 2008), which may allow them to better utilize light cues and resist radiation damage compared to the other three lighter in color or transparent, eyeless species. The next hosts in the life cycle of *G. otepotiense* are fish, and thus attraction toward light should position the cercariae in the water column, where they are more likely to encounter their target hosts. In the second observation at the 10th minute, more *G. otepotiense* cercariae appeared on the lighted zone compared to the 5-minute mark, possibly because individuals need time to orient along the light gradient before initiating movement.

Cercariae of *P. attenuatus* tended to settle on the bright side under UV light. Perhaps UV radiation signals an open, unobstructed environment, and *P. attenuatus* cercariae attach to hard substrates such as mollusk shells to encyst and await ingestion by birds. Settling in open areas may increase their exposure to avian hosts. Previous studies have indeed shown that many cercariae use environmental cues to increase their chance of encountering their next host (Prinz et al., 2010; Weinersmith et al., 2018). Although cercariae of *G. otepotiense* and *P. attenuatus* may both benefit from phototaxis by achieving greater transmission success, *P. attenuatus* tends to spend time exploring surfaces before attachment, which slows its movement. Therefore, over the same observation time, fewer cercariae of *P. attenuatus* than *G. otepotiense* were expected to end up on the bright side.

The attractiveness of different light types to *Acanthoparyphium* sp. and *M. novaezealandense* cercariae did not differ significantly. Compared to the other three trematodes, *M. novaezealandense* cercariae showed weaker phototaxis. Their lack of displacement may reflect their behavior and swimming motions: although they vibrate rapidly and constantly, their horizontal displacement is minimal and occurs slowly. In addition, their transmission strategy and their search for small crustaceans as second intermediate hosts may rely more on massive production of cercariae rather than on fine-tuned responses by these cercariae.

Acanthoparyphium sp. cercariae showed great inter-individual variation in their responses to light: most were photophobic, but some photophilic individuals shifted their overall mean position, resulting in greater average phototaxis than *M. novaezealandense*. This inconsistency may result from *Acanthoparyphium* sp. likely consisting of a complex of four cryptic species (Leung et al., 2008), each responding differently to light. Cercariae of the four trematode species also differ in their responses to other environmental stressors, for example they show different tolerances to ocean acidification (MacLeod and Poulin, 2015), again emphasizing the species-specific nature of anthropogenic impacts on host-parasite interactions.

Finally, in conditions replicating natural densities of first and second intermediate hosts, we quantified the infection success of *M. novaezealandense* in amphipods, allowing spontaneous emergence of cercariae and their transmission under three ALAN conditions (warm white, cold white, and UV light) and one no-ALAN control. Amphipods in the treatment with UV light at night accumulated the most *M. novaezealandense* metacercarial cysts, while those in the cold white light group had the fewest. The results were consistent with a previous study on the effects of UV radiation on the transmission of *M. novaezealandense* to amphipod hosts, which found that amphipods became more susceptible after prolonged UV exposure (Studer et al., 2012). On the other hand, taken together with the results of the experiment on cercarial output, this likely reflects the higher frequency of cercarial emergence from infected snails: *M. novaezealandense* cercariae under UV light at night probably emerged more frequently, while those under cold white light had the lowest frequency. This could possibly result in varying transmission dynamics along the coastline, with some areas experiencing regular pulses of cercarial emergence while nearby areas do not, all depending in differences in local light sources. Another possible explanation is that UVB exposure caused both hosts of *M. novaezealandense* (snails and amphipods) to hide among algal shadows to repair light-induced damage (Obermüller et al., 2005; Studer et al., 2012), increasing small-scale host density and making it easier for cercariae to find amphipods. Some amphipod species perceive broad-spectrum cold artificial light as natural light, but do not respond to warm light in the same way (Karnaukhov et al., 2025). Thus, light-induced changes in amphipod behaviour may in part explain our results.

The no ALAN and warm white light at night treatments showed no significant difference, suggesting that in the absence of blue and UVB light, the latter with possible negative effects, warm white light may not represent a full "absence of darkness" and may not substantially affect *M. novaezealandense*'s life cycle or the physiology of its hosts, at least over 2 weeks. As for time, there was no clear difference between the first and second week with respect to cyst accumulation within amphipods, possibly due to unavoidable amphipod mortality toward the end of week 2, which created unbalanced sample sizes and limited statistical power. Other anthropogenic stressors also influence the transmission of *M. novaezealandense* to amphipods. Warmer temperatures can enhance cercarial infectivity to amphipods (Studer et al., 2010). Although increased salinity—associated with higher temperatures and evaporation—did not alter cercarial infectivity or amphipod susceptibility, it was found to increase cercarial output and survival (Studer and Poulin, 2011). Ocean acidification has also been shown to decrease cercarial survival, and also increase susceptibility of amphipod hosts (Harland et al., 2015).

In summary, cercarial output of the four trematode species declined over the course of the experiment; however, the effects of different ALAN conditions varied considerably among species. The snail hosts (*Z. subcarinatus*) tended to avoid UV light at night. Although infections with different trematode species caused variable effects on snail phototactic behavior, no clear effect was seen on this general avoidance pattern. The phototactic responses of cercariae also differed among species: *G. otepotiense* was the most strongly attracted to light, while *M. novaezealandense* showed the least movement. Transmission of *M. novaezealandense* from the first intermediate host snails to the second intermediate host amphipods was most successful under UV ALAN and lowest under cold white ALAN. Our results demonstrate that the four trematode species (*Acanthoparyphium* sp., *G. otepotiense*, *M. novaezealandense*, and *P. attenuatus*) differ in their responses to various types of light as ALAN and in how they interact with their hosts, most likely due to their distinct phylogenetic history, which has resulted in morphological and behavioral differences.

However, our transmission experiments not only involved a single amphipod species, although *M. novaezealandense* can infect a wide spectrum of crustaceans as second intermediate hosts, from amphipods and isopods to shrimp and crabs, but also did not extend to the other three trematode species. Yet the greater challenge for future studies will be to incorporate the effects of ALAN within a multi-stressor context, to quantify its interactions with other drivers of host-parasite interactions, such as temperature, salinity and ocean acidification. Nevertheless, our findings indicate that responses of trematodes to ALAN are species-specific, with each of the four trematode species investigated here showing idiosyncratic responses to different types of artificial lighting at night. As light pollution continues to intensify worldwide, it is increasingly important to recognize ALAN as a potential environmental stressor that can influence ubiquitous parasitic relationships, and indirectly impact population dynamics and community structure in aquatic ecosystems.

CRediT authorship contribution statement

Qing-Long Li: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Robert Poulin:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Conceptualization. **Chen-Hua Li:** Writing – review & editing, Supervision, Conceptualization.

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Declaration of competing interest

The authors declare having no financial or other conflict of interest.

Data availability

As stated in the manuscript: all raw data and R codes used for the analyses in the present study are available from Figshare (https://doi.org/10.6084/m9.figshare.30615104).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2026.181917.

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