CellPress
Trends in Parasitology

Opinion

Light pollution may alter host–parasite interactions in aquatic ecosystems

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With growing human populations living along freshwater shores and marine coastlines, aquatic ecosystems are experiencing rising levels of light pollution. Through its effects on hosts and parasites, anthropogenic light at night can disrupt host–parasite interactions evolved under a normal photoperiod. Yet its impact on aquatic parasites has been ignored to date. Here, I discuss the direct effects of light on the physiology and behaviour of parasite infective stages and their hosts. I argue that night-time lights can change the spatiotemporal dynamics of infection risk and drive the rapid evolution of parasites. I then highlight knowledge gaps and how impacts on parasitic diseases should be incorporated into the design of measures aimed at mitigating the impact of anthropogenic light on wildlife.

Highlights

Impacts of artificial light at night on wildlife are well documented, yet specific effects on parasitism in aquatic systems are largely unknown.

Circadian patterns in animal physiology and behaviour are light-driven, as is host-searching by many infective stages. This can be impacted by artificial light at night.

Attraction of hosts and infective stages to light sources can result in aggregations that promote direct infection by infective stages and high levels of trophic transmission.

I hypothesise that temporal fluctuations in infection risk disappear as day–night differences in lighting are reduced, that areas exposed to light at night act as hotspots of transmission, and that altered photoperiod exerts strong selective pressures.

Known effects of light on host–parasite interactions must be considered when designing measures to reduce the impact of artificial light on wildlife.

A world alight

Nearly a quarter of the world's freshwater shores and ocean coasts are illuminated by artificial lighting at night [1]. Most residential areas and industrial zones are located along lake shores, river banks, or seashores, and they generate light throughout the night. Even aquatic habitats far from the shore are impacted by **anthropogenic light** (see Glossary), such as the areas surrounding oil rigs and offshore aquaculture facilities. The **luminosity** and **spectrum** of artificial lights vary according to the type of light used, however any artificial light at night represents a change to the physical habitat experienced by living organisms. With the world's human population growing, the spatial extent of artificial lighting shining on aquatic habitats is rapidly expanding, as are its intensity and spectral characteristics [2]. The impacts of **light pollution** on the behaviour and physiology of individual aquatic animals [1,3,4], the abundance of populations ranging from zooplankton to fish and birds [5,6], and the structure of aquatic communities [5,7], are increasingly well documented. Although aquatic ecologists have been slow to recognise the threat posed by light pollution [8], its potential impact on aquatic ecosystems is now widely accepted [1].

Yet, research on the effects of light pollution on parasitism and disease is lagging well behind research on the broader impacts of anthropogenic light on wildlife (Figure 1). Recent reviews of the impact of anthropogenic light on biological systems fail to mention its potential influence on host–parasite interactions and disease [1,9,10]. However, it has been shown that artificial light at night can affect vector-borne diseases [11–13] and parasitoid attacks on insects [14,15] by extending the activity period, activity levels and/or increasing the local abundance of both vectors and parasitoids. Although such effects are not universal (see [16]), these examples pertain only to terrestrial systems. What about host–parasite interactions in aquatic ecosystems? Recent reviews of the impact of anthropogenic stressors on parasitism and disease in aquatic ecosystems completely ignore the potential effects of light pollution [17–19]. Here, I address these omissions by pulling together evidence of the known influence of light, both natural and artificial on: (i) the dispersal and activity of infective stages of all major groups of aquatic parasites, (ii) the physiology,

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 https://doi.org/10.1016/j.pt.2023.08.013

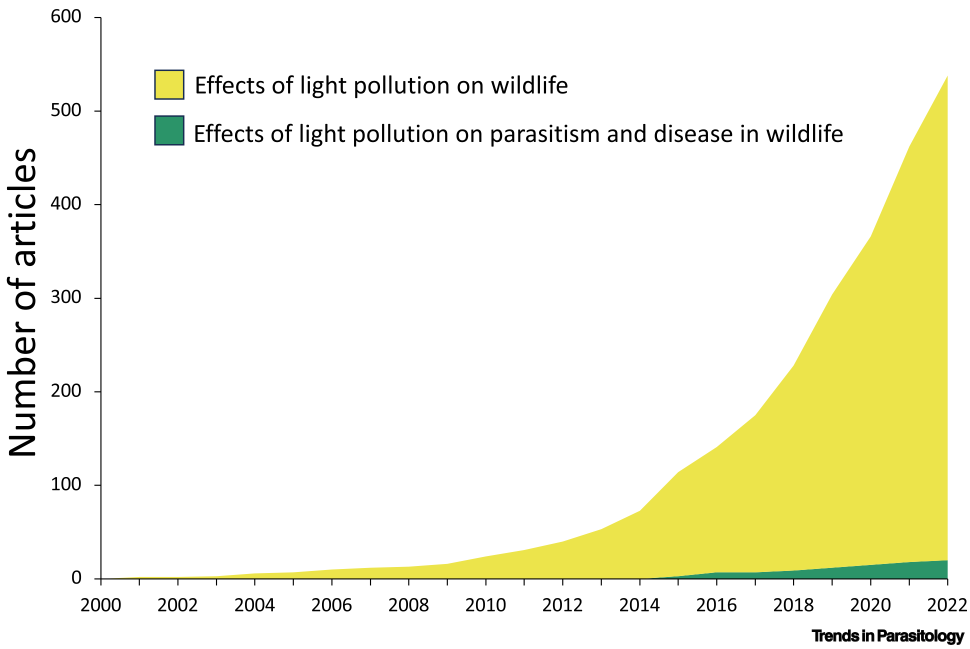

Figure 1. Historical overview of research on the effects of light pollution. Cumulative number of articles on the effects of light pollution on wildlife in general, and on parasitism and disease more specifically. Data come from a search of the Web of Science for the period 2000 to the end of 2022, using the search string ('light pollution' OR 'artificial light' OR 'anthropogenic light') AND (wildlife OR fauna* OR ecosystem*) in the first instance, and then the same string with the addition of AND (parasite* OR disease*).

behaviour, and distribution of healthy animals, and even (iii) the behaviour of infected animals. Based on the available evidence, I propose that light pollution in aquatic systems homogenises infection risk across day and night, and that stretches of freshwater shores and marine coastlines that are illuminated at night act as hotspots of transmission by many kinds of parasites for many kinds of hosts.

Parasite infective stages in the spotlight

Many aquatic parasites have evolved strategies that maximise their transmission success under natural **photoperiod** conditions. For example, temporal patterns of egg hatching in a range of fish ectoparasites, such as copepods [20] and monogeneans [21,22], are driven by the ambient photoperiod and changes in illumination at dawn and dusk. In marine ecosystems, gnathiid isopods alternate between engorging on fish blood as ectoparasites and dwelling on the bottom substrate when they moult. The timing of their emergence from the substrate in search of host fish is synchronised by the ambient photoperiod, with different species and developmental stages having their peak periods of activity at different times of the day–night cycle [23,24]. Similarly, emergence of **cercariae** from their molluscan intermediate host in many trematode species often follows a **circadian rhythm** synchronised by the day–night cycle, peaking at times of the day when encountering the next host in the life cycle is most likely [25,26]. It remains to be determined whether constant artificial lighting at night causes a temporal mismatch between the release of infective stages and the peak availability of target hosts, and whether this affects infection levels in near-shore ecosystems.

Perhaps more importantly, the free-swimming infective stages of multiple kinds of aquatic parasites show either positive or negative **phototaxis**, that is, swimming toward or away from light. This is true of helminths such as trematode cercariae [27–29] and monogenean **oncomiracidia**

Glossary

Anthropogenic light: light produced by human civilization, including building exterior and interior lighting, advertising, streetlights, industrial activities, port installations, etc.
Bioluminescence: production and emission of light by a living organism, generated through an intracellular chemical reaction.
Cercariae: free-living and short-lived trematode infective stages released from the molluscan first intermediate host.
Circadian rhythm: natural cycle of biological processes that repeats every 24 h, regulated within an organism but synchronised by the ambient photoperiod.
Density-dependent: property of any biological process that is regulated by the density of a population, such that it occurs at a rate proportional to density.
Light pollution: sum total of all adverse effects of anthropogenic light.
Luminosity: measure of radiated electromagnetic power, that is, the amount of light produced by a light-emitting object per unit time.
Oncomiracidia: ciliated and free-living larvae of monogeneans, hatched from eggs in search of a host to infect.
Photoperiod: length of the light period in the 24 h diurnal cycle.
Phototaxis: locomotory movement toward (positive phototaxis) or away from (negative phototaxis) a light source, associated with either attraction to or repulsion from light.
Spectrum: range of frequencies of electromagnetic radiation and their respective wavelength, which for light visible to the human eye ranges from about 380 nm to 750 nm, that is, between ultraviolet and infrared.
Trophic transmission: transmission of larval helminths by consumption of an intermediate host (prey) by a definitive host (predator).

[30], but also of crustaceans ectoparasitic on fish. For example, the branchiuran fish louse *Argulus foliaceus* is not only attracted to lighted areas, but also swims more actively under light than in darkness [31]. Light traps are very effective to capture the infective stages of gnathiid isopods [32] but also those of the copepod *Lepeophtheirus salmonis*, the infamous sea louse plaguing salmon aquaculture [33]. Sea lice in search of fish hosts react directionally to light, and achieve greater infection success under light conditions [34]. Since open-cage salmon farms often remain illuminated at night to increase salmon feeding efficiency, manipulate their maturation rate, and/or for reasons of maritime safety, they may inadvertently attract more sea lice than they would under natural light conditions [35].

The movement of parasite infective stages toward (or in some cases away from) artificial light at night is likely to affect their distribution and transmission dynamics. Constant illumination may decrease the lifespan of infective stages by stimulating their activity beyond the normal daytime period, however their attraction toward areas of greater availability of target hosts (see next section) can still lead to their greater transmission success. Even if these movements only occur on spatial scales of a few metres, constant illumination and cumulative displacement may lead to the aggregation of many infective stages near areas of the shore exposed to anthropogenic light (Figure 2). As I argue next, this swarm of infective stages is likely to encounter a high density of target hosts in areas illuminated at night.

Out of the darkness: effects on hosts

The day–night cycle regulates the timing of most animal activities, including periods of rest, whereas seasonal changes in daylength provide the main cue for physiological changes associated with reproduction or migration. Artificial light throughout the night across all seasons disrupts all these naturally evolved cycles [3,4,10].

In aquatic ecosystems, the biology of animals ranging from plankton and bivalves all the way to fish and birds is driven by ambient lighting and photoperiod. Artificial light at night can modify phytoplankton communities, with some wavelengths favouring diatom species associated with harmful algal blooms [36]. Diel vertical migrations of zooplankton in marine pelagic ecosystems, which are among the largest regular movements of biomass on the planet, are disrupted by artificial light, since zooplankton evolved behavioural responses to circadian light cycles [6]. Artificial light at night also impacts molluscs, modulating their feeding activity and reproduction, with several snail species showing a clear attraction to light sources [37]. This includes several freshwater genera (e.g., *Lymnaea*, *Physa*, *Helix*) known to act as first intermediate hosts for numerous trematode species. Cephalopods also show a strong attraction to artificial light, a phototactic response exploited by the commercial fishing industry [38].

Nocturnal light exposure also impacts hormonal and immune functions, reproduction, behaviour, and interspecific interactions in many vertebrates [10,39]. In fish, long-term exposure to artificial light at night can modify the blood concentration of sex steroids and gene expression associated with reproductive hormones [40], reduce activity levels [41], and decrease growth and survival [42]. These effects suggest that the general health of many fish may be compromised under constant night-time illumination. In addition to these physiological impacts of artificial light at night on fish biology, many fish species are simply attracted to light across a range of intensities and wavelengths [43,44]. The congregation of multiple fish species in areas subject to anthropogenic light can affect interspecific interactions among species, such as predation. In an experiment conducted in a South African estuary, anthropogenic night-time illumination around an artificial structure attracted more small schooling fish, and in turn more large-bodied predatory fish, than were present during nights when the lights were turned off [45]. Other studies also

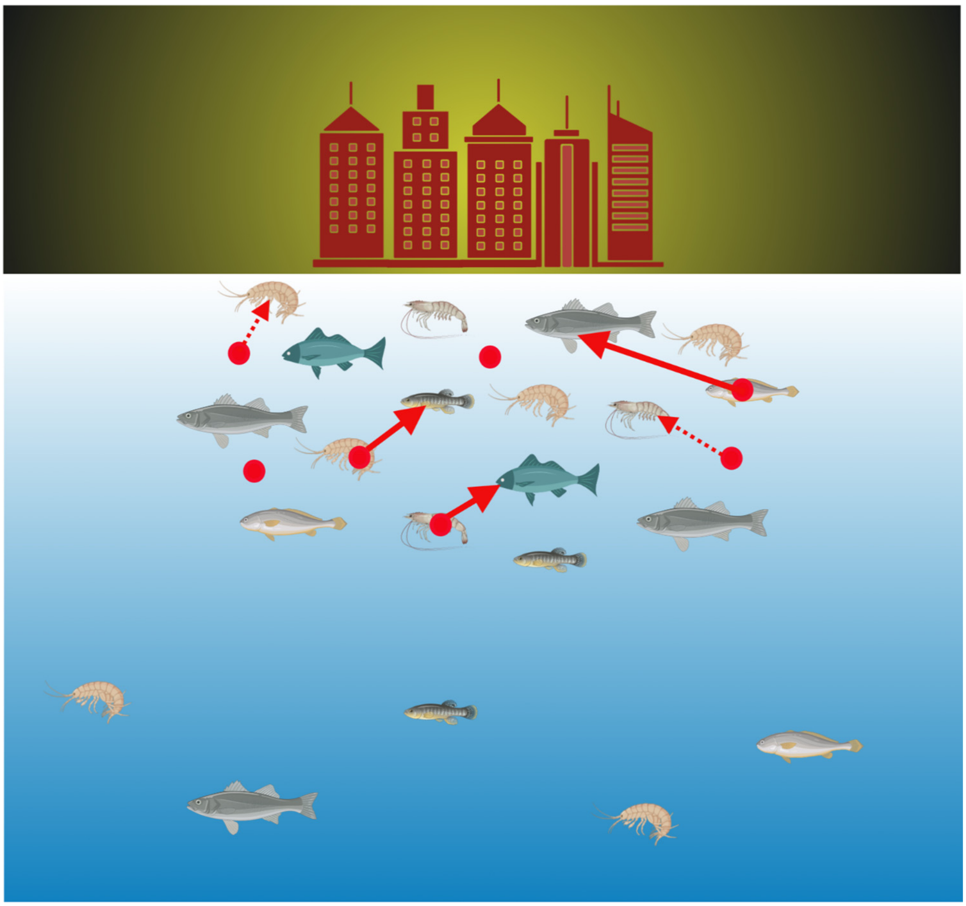

Figure 2. Artificial light at night attracts parasites and their hosts. Infective stages (red dots) of many parasite species as well as both infected (with red dot) and uninfected invertebrates and vertebrates tend to congregate near sources of anthropogenic light along the shore. This creates higher densities of hosts and parasites that maintain higher activity levels than in nonilluminated stretches of the shore. These conditions should maximize infection success by free-swimming infective stages (thin broken arrows), and also promote trophic transmission from infected intermediate hosts to definitive hosts (thick arrows). Figure created with BioRender.com.

suggest that predation on small fish increases under artificial night-time lights [46]. Anthropogenic light at night may therefore extend the foraging period of visual predators, and increase **trophic transmission** of helminths up the food chain, from intermediate hosts to definitive hosts.

In birds, the day–night cycle and seasonal changes in photoperiod control circadian patterns in activity and synchronise most behaviours from foraging to reproduction. The aspect of avian biology that has received the most attention with respect to artificial light at night is migration [47,48]. The influence of night-time illumination on bird movements and migrations depends on wavelength and varies across species, with some species being attracted to various wavelengths, others showing disorientation, yet others being unaffected [47]. From the perspective of aquatic parasites, impacts of artificial light at night on the short- or long-distance migrations of shore birds could affect dispersal of eggs and local host abundance. As with fish, night-time light shining on intertidal areas can also extend the foraging period of shore birds that depend on visual prey detection [49], and thereby increase rates of trophic transmission of helminths.

As a general rule, artificial light at night disrupts the normal physiology and behaviour of many animals. It can negatively impact hormonal and immune functions. Yet, many animals are nevertheless attracted to light and aggregate near light sources. Thus, higher densities of invertebrates and vertebrates, many of which may be immunocompromised or at least experiencing some form of light-induced physiological stress, tend to accumulate near artificial light sources (Figure 2). Host aggregation in lighted areas should increase the transmission success of free-swimming infective stages, since transmission success is generally **density-dependent**. For host and parasite taxa that are attracted to light, the upshot may therefore be that anthropogenic light at night increases the exposure and/or susceptibility of aquatic animals to infection. For those that are repelled by light, the opposite may happen; either way, light pollution may alter the infection dynamics of many parasite species.

Seeing the light: effect on infected hosts

Many helminth parasites transmitted by predation from an intermediate host to their definitive host induce behavioural changes in the former to enhance their transmission success to the latter [50]. One particularly common type of parasite-induced behavioural modification is altered phototaxis, which serves as an adaptation to bring infected intermediate hosts closer to areas where predatory definitive hosts are feeding. This has been particularly well-documented in small aquatic crustaceans infected by larval helminths including acanthocephalans [51], trematodes [52], cestodes [53], and nematodes [54]. A preference for well-lit microhabitats may also develop in fish infected with eye flukes [55]. What originally caused a vertical segregation (with solar light coming from above) between uninfected and infected individuals leading to increased parasite transmission may now also cause the horizontal displacement of infected individuals toward the illuminated sections of the shoreline (Figure 2), where the next hosts in the parasites' life cycles are also congregating.

The net effects of artificial light

For millions of years, sunlight during the day and limited moonlight and starlight at night represented the only light sources (apart from **bioluminescence**) affecting biological processes. Adaptive responses of hosts and parasites evolved through countless generations under natural light conditions are now being over-expressed under the abnormal stimulus provided by artificial light at night. This will be true in all aquatic habitats exposed to light intensities above the threshold of detection for parasites and hosts, and within the range of wavelengths to which they respond.

To encourage research in this area, I propose three testable hypotheses. First, permanent lighting at night along the shores of lakes or oceans will disrupt the temporal transmission dynamics of many parasites, and homogenise infection risk between day and night (Figure 3). In many parasite species, the emergence of infective stages from eggs or intermediate hosts, their swimming activity and orientation are all driven by light, with the changing light conditions between day and night creating periods of peak transmission separated by periods of little to no transmission. Under artificial light at night, the normal night-time period of low activity and limited infection risk may no longer exist. Anthropogenic light decreases the difference in illumination between night and day, and can even create constant daytime conditions, such that infection risk may remain similarly high all the time. The prediction could be tested using host–parasite systems maintained in replicated mesocosms exposed to different light regimes, possibly even outdoor mesocosms located in a dark sky sanctuary[i] where no other artificial light source would interfere with the experiment.

Second, the aggregation of infective stages, infected and uninfected intermediate hosts and definitive hosts near artificial light sources will create hotspots of transmission, by spatially structuring infection risk around light-driven foci of transmission (Figure 3). During the day, natural sunlight is generally diffuse and omnipresent, while the absence of significant light at

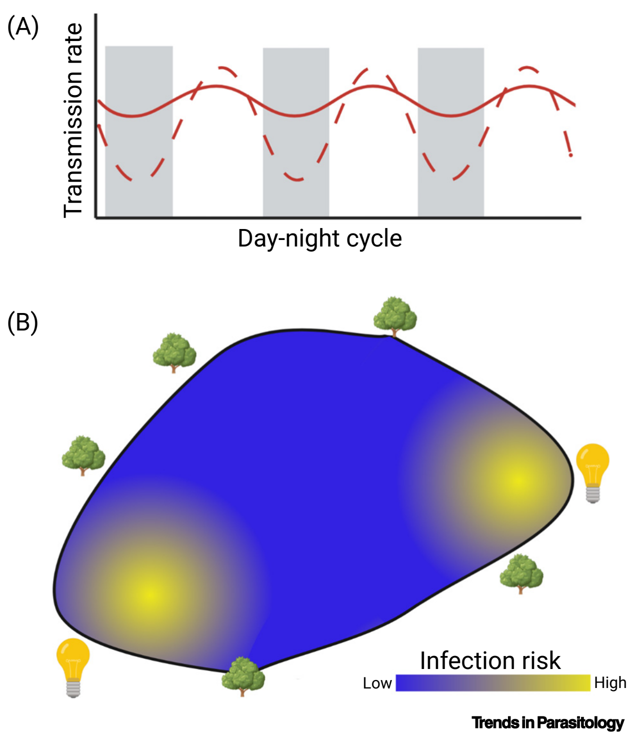

Figure 3. Predicted impact of artificial light at night on the spatiotemporal distribution of infection risk. (A) The day–night fluctuations in parasite transmission and host infections under conditions of anthropogenic light at night (unbroken line) are less pronounced than those under normal photoperiod (broken line), resulting in lower temporal variability and higher mean values. (B) The attraction of parasites and their hosts to anthropogenic light creates strong gradients in host and parasite densities along the shore, resulting in hotspots of high transmission of parasites, and thus high infection risk for hosts, in areas illuminated at night. Artificial light at night can thus drive the spatial structure of host parasite interactions in aquatic ecosystems. The hypothetical patterns in (A) and (B) pertain to positively phototactic parasites with greater hatching rates and host-seeking activities under light conditions; they would be different for other parasites. Figure created with BioRender.com.

night in areas not affected by anthropogenic activities does not cause animals to move in any particular direction. By contrast, anthropogenic light at night is more localised, creating dark versus well-illuminated areas, and thus more likely to induce directional movement. High densities of infective stages and hosts made more susceptible through light-induced immune suppression can lead to higher infection levels in aquatic animals near coastal cities, ports, or industrial areas that remain illuminated throughout the night. This prediction could be tested by sampling replicated, paired dark and illuminated coastal areas (i.e., not exposed or exposed to anthropogenic light at night) and comparing infection levels in aquatic animals of the same species. Of course, this is more difficult than it sounds, as one would also need to control for the possible effects of other environmental variables likely to differ between these areas, such as chemical pollution levels. This may be achieved by including these other factors as additional predictors in multivariate analyses, or by carefully selecting paired sites in order to limit variation in these other variables.

Third, over evolutionary time, artificial light at night will represent a strong anthropogenic selective pressure and lead to adaptive changes in the responses of hosts and parasites to light. If their environment is constantly illuminated, coastal populations of parasites may no longer be under selective pressures to synchronise egg hatching or emergence from their host with the day–night cycle, and their infective stages may no longer benefit from directional movement toward light. Helminth phenotypes can indeed respond in just a few generations to artificial conditions that exert new selective pressures on their transmission success [56]. Although more challenging to test, this hypothesis could be investigated through multigeneration selection experiments under different light regimes, with parasites being tested for phototactic responses every few generations. Cultures of parasites with simple life cycles and short generation times, such as monogeneans [57], would be ideal systems for such evolutionary studies.

Concluding remarks and future perspectives

Artificial light must be included as an important anthropogenic factor in One Health approaches to the management of aquatic parasites [58], and as a potential promoter of emerging aquatic diseases [59]. To date, the only study investigating the possible connection between artificial light at night and parasite infection in aquatic ecosystems has found that frog tadpoles exposed to night-time light were a little more susceptible to infection by cercariae of the trematode *Echinostoma* sp. than those not exposed to night-time light, possibly due to a reduction in the tadpoles' swimming activity [60]. The result suggests that anthropogenic light at night can indeed affect parasite infections, yet many unknowns remain (see Outstanding questions). Research addressing these basic unresolved issues, as well as research testing the three hypotheses presented in the previous section, is urgently needed to evaluate the consequences of light pollution for aquatic parasitism.

As with other recently recognised impacts of human activity on wildlife, such as noise pollution [61], we urgently need to determine how light pollution affects parasitism and disease. We also need to understand how this particular stressor interacts with other anthropogenic impacts on natural ecosystems, such as climate change [62] and noise pollution [63], the latter probably frequently co-occurring with light pollution. In particular, it will be important to assess whether other anthropogenic changes to aquatic habitats that dampen light penetration through water can offset the increasing use of artificial light along the land–water interface. Indeed, increasing precipitation run-off is delivering large amounts of dissolved organic matter from terrestrial sources into the littoral zones of lakes and oceanic coastal waters, causing 'lake browning' and 'coastal darkening' [64,65]. The resulting reduction in water transparency and greater attenuation of light with depth will no doubt modify the net effects of light pollution.

Importantly, we definitely need to seek ways to minimise any negative effects of light pollution on disease risk in both natural habitats and aquaculture facilities. For this reason, potential impacts on parasitism and disease must be considered in the design and implementation of mitigation measures currently proposed to limit the effects of light pollution on wildlife. To date, most research in this area has focused on designing lighting at night that will not interfere with the orientation of sea turtle hatchlings heading to the sea [66,67]. Light-emitting diode (LED) lamps (Box 1) have rapidly become widely used for a range of domestic, commercial, and industrial applications due to their energy efficiency. However, the white light they produce is rich in short-wavelength blue light, which is thought to be the most detrimental part of the light spectrum for all kinds of organisms [4,68]. Light from LEDs can penetrate coastal waters and its shortest wavelengths can reach tens of metres down to the seafloor [69]. Simple measures to mitigate the impact of light pollution would include using lower intensity lights and lamps that produce longer-wavelength 'reddish' light [70]. Indeed, shifting from short wavelengths to longer wavelengths within the visible spectrum has been demonstrated to mitigate negative physiological and behavioural impacts of artificial light on some organisms [71]. However, the widespread implementation of changes to the types of lights manufactured and commercially available would require legislative action at local and federal levels. Organisations such as DarkSky International[ii] are working with communities and manufacturers to promote and certify 'dark sky friendly' outdoor lighting, providing a great example of the way forward. Yet it remains unclear whether mitigation measures proposed to limit impacts of light pollution on free-living organisms would also limit the risk of parasitic diseases, since the responses of parasite infective stages to different wavelengths remain to be investigated. Future research aiming to answer the outstanding questions and test the hypotheses proposed here would certainly help to 'shed light' on this potential anthropogenic driver of aquatic diseases.

Outstanding questions

Does artificial light at night cause a decrease in host immune defences due to its disruption of normal physiological functions? Is this more likely in some host taxa than others?

Can constant night-time illumination lead to an overall higher rate of trophic transmission for helminth parasites, by extending the foraging period of predatory fish and avian definitive hosts?

Have parasite populations living along shores with dense human settlements, which have been exposed to night-time illumination for many generations, already evolved new adaptations, such as different phototactic responses in their search for hosts, compared with populations along shores not affected by human activities?

Are the light wavelengths that are most impactful on free-living organisms also the most influential for parasite infective stages? Are these different for different parasite taxa?

What type of light design, and what sort of spatial deployment of lights along river banks, lake shores, and marine coastlines are least likely to influence the distribution and intensity of parasitic diseases in aquatic ecosystems?

How will the impact of light pollution on aquatic disease interact with the effects of other environmental stressors of anthropogenic origin, such as eutrophication, global warming, ocean acidification, and noise pollution?

Box 1. Types of artificial light

Different electrical light sources have different characteristics and usage. Their potential impact on aquatic organisms depends on their luminosity, colour spectrum, distance from water, etc.; here, they are roughly ranked from potentially least to most impactful [72]:

Incandescent light bulb

A wire filament is heated until it glows, encased in a glass bulb in a vacuum or inert gas. Incandescent bulbs have been widely used for indoor household and commercial lighting since they were perfected by Thomas Edison.

Halogen lamp

Similar to the incandescent lamp, a tungsten filament is sealed in a mixture of an inert gas and a small amount of a halogen, such as bromine or iodine. This allows the filament to operate at a higher temperature and achieve high luminosity. Halogen lamps are often used for flood lighting, but are being phased out around the world due to their poor energy efficiency.

Fluorescent tube

An electric current passing through the tube excites the mercury vapour it contains, producing ultraviolet light that causes the phosphor lining inside the tube to glow. Fluorescent tubes are energy efficient and achieve much greater luminosity than incandescent lamps. They are widely used for indoor household and commercial lighting.

Mercury vapour lamp

This gas-discharge lamp uses an electric arc passing through vapourised mercury to produce light, within a small tube mounted within a larger glass bulb, the latter being either clear or coated with phosphor. Mercury vapour lamps have a long lifespan, are very energy efficient, and produce high-intensity clear white light. They are widely used for streetlights and for overhead lighting in factories, warehouses and sports grounds.

Metal halide lamp

This type of lamp produces light by an electrical arc through a gaseous mixture of vapourised mercury and metal halides (e.g., sodium iodide) inside a quartz tube. The intense white light produced makes this type of light ideal for large indoor or outdoor spaces, such as factories, parking lots, and sports grounds.

Light emitting diode (LED) lamp

An electrical current passing through a microchip illuminates the tiny LEDs to produce visible light in a specific direction, with the associated heat absorbed in a heat sink. LED lights are much more energy efficient that traditional incandescent and fluorescent lamps, and they last much longer. They can produce light of various colours as well as white light. They are now used for everything from indoor lighting to outdoor flood lighting and streetlights. If unfiltered, blue-rich LED lamps can be quite disruptive to the circadian rhythms of many organisms.

Acknowledgments

I thank Kate Hutson, Chris Selbach, and three anonymous reviewers for constructive comments on an earlier version of the manuscript. This work is supported through the Cawthron Institute's Emerging Aquatic Diseases programme, funded by an Endeavour grant from the New Zealand Ministry of Business, Innovation and Employment, award number CAWX2207.

Declaration of interests

The author has no conflict of interest to declare.

Resources

[i]www.darkskytasmania.org/dark-sky-sanctuary

[ii]https://darksky.org/

References

1. Davies, T.W. *et al.* (2014) The nature, extent, and ecological implications of marine light pollution. *Front. Ecol. Environ.* 12, 347–355
2. Kyba, C.C. *et al.* (2017) Artificially lit surface of Earth at night increasing in radiance and extent. *Sci. Adv.* 3, e1701528
3. Russart, K.L.G. and Nelson, R.J. (2018) Artificial light at night alters behavior in laboratory and wild animals. *J. Exp. Zool.* 329, 401–408
4. Falcón, J. *et al.* (2020) Exposure to artificial light at night and the consequences for flora, fauna, and ecosystems. *Front. Neurosci.* 14, 602796
5. Zapata, M.J. *et al.* (2019) Artificial lighting at night in estuaries: implications from individuals to ecosystems. *Estuar. Coast.* 42, 309–330
6. Marangoni, L.F.B. *et al.* (2022) Impacts of artificial light at night in marine ecosystems: a review. *Glob. Change Biol.* 28, 5346–5367

7. Perkin, E.K. *et al.* (2011) The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. *Ecosphere* 2, 122
8. Rudd, M.A. and Lawton, R.N. (2013) Scientists' prioritization of global coastal research questions. *Mar. Pol.* 39, 101–111
9. Hölker, F. *et al.* (2021) Eleven pressing research questions on how light pollution affects biodiversity. *Front. Ecol. Evol.* 9, 767177
10. Jägerbrand, A.K. and Spoelstra, K. (2023) Effects of anthropogenic light on species and ecosystems. *Science* 380, 1125–1130
11. Fyie, L.R. *et al.* (2021) Artificial light at night alters the seasonal responses of biting mosquitoes. *J. Insect Physiol.* 129, 104194
12. Kernbach, M.E. *et al.* (2021) Light pollution affects West Nile virus exposure risk across Florida. *Proc. R. Soc. B* 288, 20210253
13. Coetzee, B.W.T. *et al.* (2022) Artificial light as a modulator of mosquito-borne disease risk. *Front. Ecol. Evol.* 9, 768090
14. Kehoe, R. *et al.* (2020) Longer photoperiods through range shifts and artificial light lead to a destabilizing increase in host-parasitoid interaction strength. *J. Anim. Ecol.* 89, 2508–2516
15. Brown, J.A. *et al.* (2023) Introduction of artificial light at night increases the abundance of predators, scavengers, and parasites in arthropod communities. *iScience* 26, 106203
16. Sanders, D. *et al.* (2015) Artificial nighttime light changes aphid-parasitoid population dynamics. *Sci. Rep.* 5, 15232
17. Sures, B. *et al.* (2017) Parasite responses to pollution: what we know and where we go in 'Environmental Parasitology'. *Parasit. Vectors* 10, 65
18. Sures, B. *et al.* (2023) Environmental parasitology: stressor effects on aquatic parasites. *Trends Parasitol.* 39, 461–474
19. Marcogliese, D.J. (2023) Major drivers of biodiversity loss and their impacts on helminth parasite populations and communities. *J. Helminthol.* 97, e34
20. McGladdery, S.E. and Johnston, C.E. (1988) Egg development and control of the gill parasite, *Salmincola salmoneus*, on Atlantic salmon kelts (*Salmo salar*) exposed to four different regimes of temperature and photoperiod. *Aquaculture* 68, 193–202
21. Whittington, I.D. and Kearn, G.C. (2011) Hatching strategies in monogenean (Platyhelminth) parasites that facilitate host infection. *Integr. Comp. Biol.* 51, 91–99
22. Villar-Torres, M. *et al.* (2018) Come rain or come shine: environmental effects on the infective stages of *Sparicotyle chrysophrii*, a key pathogen in Mediterranean aquaculture. *Parasit. Vectors* 11, 558
23. Sikkel, P.C. *et al.* (2009) Diel ontogenetic shift in parasitic activity in a gnathiid isopod on Caribbean coral reefs. *Coral Reefs* 28, 489–495
24. Welicky, R.L. *et al.* (2017) Diurnal activity patterns of the temporary fish ectoparasite, *Gnathia africana* Barnard, 1914 (Isopoda, Gnathiidae), from the southern coast of South Africa. *J. Mar. Biol. Assoc. UK* 98, 1715–1723
25. Wang, S.-R. *et al.* (2015) Effect of photoperiod change on chronobiology of cercarial emergence of *Schistosoma japonicum* derived from hilly and marshy regions of China. *Exp. Parasitol.* 159, 227–232
26. Soldanova, M. *et al.* (2022) Cercariae of a bird schistosome follow a similar emergence pattern under different subarctic conditions: first experimental study. *Pathogens* 11, 647
27. Smith, N.F. and Cohen, J.H. (2012) Comparative photobehavior of marine cercariae with differing secondary host preferences. *Biol. Bull.* 222, 74–83
28. O'Leary, P.A. and Pung, O.J. (2017) Behavioral analysis of *Microphallus turgidus* cercariae in relation to microhabitat of two host grass shrimp species (*Palaemonetes* spp.). *Dis. Aquat. Org.* 122, 237–245
29. Weinersmith, K.L. *et al.* (2018) *Euhaplorchis californiensis* cercariae exhibit positive phototaxis and negative geotaxis. *J. Parasitol.* 104, 329–333
30. Shirakashi, S. *et al.* (2021) Phototactic responses in four monogenean oncomiracidia. *Parasitol. Res.* 120, 3173–3180
31. Hunt, R. *et al.* (2021) Shining a light on parasite behaviour: daily patterns of *Argulus* fish lice. *Parasitology* 148, 850–856
32. Artim, J.M. and Sikkel, P.C. (2016) Comparison of sampling methodologies and estimation of population parameters for a temporary fish ectoparasite. *Int. J. Parasitol. Parasit. Wildl.* 5, 145–157
33. Flamarique, I.N. *et al.* (2009) Monitoring and potential control of sea lice using an LED-based light trap. *Can. J. Fish. Aquat. Sci.* 66, 1371–1382
34. Mordue, A.J. and Birkett, M.A. (2009) A review of host finding behaviour in the parasitic sea louse, *Lepeophtheirus salmonis* (Caligidae: Copepoda). *J. Fish Dis.* 32, 3–13
35. Nordtug, T. *et al.* (2021) Responses and preferences of salmon louse (*Lepeophtheirus salmonis* Krøyer 1836) copepodids to underwater artificial light sources. *Aquaculture* 532, 736036
36. Diamantopoulou, C. *et al.* (2021) Wavelength-dependent effects of artificial light at night on phytoplankton growth and community structure. *Proc. R. Soc. B* 288, 20210525
37. Hussein, A.A.A. *et al.* (2021) Slowly seeing the light: an integrative review on ecological light pollution as a potential threat for mollusks. *Environ. Sci. Pollut. Res.* 28, 5036–5048
38. Clarke, M.R. and Pascoe, P.L. (1998) The influence of an electric light on the capture of oceanic cephalopods by a midwater trawl. *J. Mar. Biol. Assoc. UK* 78, 561–575
39. Chepesiuk, R. (2009) Missing the dark: health effects of light pollution. *Environ. Health Perspect.* 117, A20–A27
40. Brüning, A. *et al.* (2018) Influence of artificially induced light pollution on the hormone system of two common fish species, perch and roach, in a rural habitat. *Conserv. Physiol.* 6, coy016
41. Miner, K.A. *et al.* (2021) Artificial light at night alters the physiology and behavior of Western mosquitofish (*Gambusia affinis*). *Front. Ecol. Evol.* 9, 617063
42. Schligler, J. *et al.* (2021) Long-term exposure to artificial light at night in the wild decreases survival and growth of a coral reef fish. *Proc. R. Soc. B* 288, 20210454
43. Marchesan, M. *et al.* (2005) Behavioural effects of artificial light on fish species of commercial interest. *Fish. Res.* 73, 171–185
44. McConnell, A. *et al.* (2010) Effect of artificial light on marine invertebrate and fish abundance in an area of salmon farming. *Mar. Ecol. Prog. Ser.* 419, 147–156
45. Becker, A. *et al.* (2013) Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. *J. Appl. Ecol.* 50, 43–50
46. Nelson, T.R. *et al.* (2021) Effects of artificial lighting at night on predator density and salmonid predation. *Trans. Am. Fish. Soc.* 150, 147–159
47. Adams, C.A. *et al.* (2021) Effects of artificial light on bird movement and distribution: a systematic map. *Environ. Evid.* 10, 37
48. Burt, C.S. *et al.* (2023) The effects of light pollution on migratory animal behavior. *Trends Ecol. Evol.* 38, 355–368
49. Dwyer, R.G. *et al.* (2013) Shedding light on light: benefits of anthropogenic illumination to a nocturnally foraging shorebird. *J. Anim. Ecol.* 82, 478–485
50. Poulin, R. (2010) Parasite manipulation of host behavior: an update and frequently asked questions. *Adv. Study Behav.* 41, 151–186
51. Franceschi, N. *et al.* (2008) The effects of parasite age and intensity on variability in acanthocephalan-induced behavioural manipulation. *Int. J. Parasitol.* 38, 1161–1170
52. Guler, Y. *et al.* (2015) Impacts of a newly identified behaviour-altering trematode on its host amphipod: from the level of gene expression to population. *Parasitology* 142, 1469–1480
53. Franceschi, N. *et al.* (2007) Behavioural and physiological effects of the trophically transmitted cestode parasite, *Cyathocephalus truncatus*, on its intermediate host, *Gammarus pulex*. *Parasitology* 134, 1839–1847
54. Casalins, L.M. *et al.* (2015) The behavior response of amphipods infected by *Hedruris suttonae* (Nematoda) and *Pseudocorynosoma* sp. (Acanthocephala). *J. Parasitol.* 101, 647–650
55. Gopko, M. *et al.* (2017) Deterioration of basic components of the anti-predator behavior in fish harboring eye fluke larvae. *Behav. Ecol. Sociobiol.* 71, 68
56. Hafer-Hahmann, N. (2019) Experimental evolution of parasitic host manipulation. *Proc. R. Soc. B* 286, 20182413
57. Hutson, K.S. *et al.* (2018) Monogenean parasite cultures: current techniques and recent advances. *Adv. Parasitol.* 99, 61–91
58. Selbach, C. *et al.* (2022) Bridging the gap: aquatic parasites in the One Health concept. *Trends Parasitol.* 38, 109–111
59. Hutson, K.S. *et al.* (2023) Assigning cause for emerging diseases of aquatic organisms. *Trends Microbiol.* 31, 681–691
60. May, D. *et al.* (2019) The effect of intensified illuminance and artificial light at night on fitness and susceptibility to abiotic and biotic stressors. *Environ. Pollut.* 251, 600–608

61. Berkhout, B.W. *et al.* (2023) Anthropogenic noise pollution and wildlife diseases. *Trends Parasitol.* 39, 181–190
62. Tougeron, K. and Sanders, D. (2023) Combined light pollution and night warming as a novel threat to ecosystems. *Trends Ecol. Evol.* 38, 701–704
63. McMahon, T.A. *et al.* (2017) Light and noise pollution interact to disrupt interspecific interactions. *Ecology* 98, 1290–1299
64. Mustaffa, N.I.H. *et al.* (2020) Coastal ocean darkening effects via terrigenous DOM addition on plankton: an indoor mesocosm experiment. *Front. Mar. Sci.* 7, 547829
65. Williamson, C.E. *et al.* (2020) Habitat-mediated responses of zooplankton to decreasing light in two temperate lakes undergoing long-term browning. *Front. Environ. Sci.* 8, 73
66. Robertson, K. *et al.* (2016) An assessment of 'turtle-friendly' lights on the sea-finding behaviour of loggerhead turtle hatchlings (*Caretta caretta*). *Wildl. Res.* 43, 27–37
67. Wilson, P. *et al.* (2018) Artificial light disrupts the nearshore dispersal of neonate flatback turtles *Natator depressus*. *Mar. Ecol. Prog. Ser.* 600, 179–192
68. Boyes, D.H. *et al.* (2021) Street lighting has detrimental impacts on local insect populations. *Sci. Adv.* 7, eabi8322
69. Davies, T.W. *et al.* (2020) Biologically important artificial light at night on the seafloor. *Sci. Rep.* 10, 12545
70. McDermott, A. (2023) Light pollution is fixable: can researchers and policymakers work together to dim the lights? *Proc. Natl. Acad. Sci. U. S. A.* 120, e2309539120
71. Dimovski, A.M. and Robert, K.A. (2018) Artificial light pollution: shifting spectral wavelengths to mitigate physiological and health consequences in a nocturnal marsupial mammal. *J. Exp. Zool.* 329, 497–505
72. Longcore, T. *et al.* (2018) Rapid assessment of lamp spectrum to quantify ecological effects of light at night. *J. Exp. Zool.* 329, 511–521