The effects of artificial light at night on stream ecosystems

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Contents

Summary

Artificial light has been gaining attention for its potential to disrupt ecosystems and their functioning. However, the effects of artificial light on stream systems have only just begun to be investigated. In this thesis, I reviewed the current literature on artificial light and freshwater ecosystems, with a special emphasis on streams and identified current gaps in our knowledge. Examination of the nighttime activity in gammarids showed no affect of artificial light at night, but did find a positive correlation between gammarid drift and temperature. I found evidence that large numbers of flying insects are attracted to artificial lights and that adult aquatic insects may be more attracted to stream-side lights than terrestrial insects are. However, at a light spacing of approximately 80 m, I did not find any evidence that the inland dispersal of aquatic insects is hindered. A study on small, oligotrophic streams provided evidence that aquatic invertebrate drift is reduced by the presence of stream-side lights; however, there was only a significant difference in the fish growth rates in one stream. Similarly, there was no clear evidence that the response of emerging aquatic insects, terrestrial insects falling into the streams, leaf litter decomposition, and benthic invertebrates were altered by artificial light. Taken together, there is evidence to support the hypothesis that artificial light has a negative effect on aquatic insects.

Zusammenfassung

Aufgrund des potenziellen Risikos Ökosysteme und deren Funktionen zu stören findet künstliches Licht immer mehr Aufmerksamkeit. Der Effekt von künstlichem Licht auf Bach-Ökosysteme ist jedoch bisher nur ansatzweise verstanden. In dieser Doktorarbeit, untersuche ich zunächst die Literatur zum Thema künstliches Licht und zu Süßwasser-Ökosystemen. Ich lege dabei besonderes Gewicht auf Bäche und zeige Lücken im bisherigen Verständnis auf. Eine Untersuchungen der Nachtaktivität von Gammariden zeigte zwar keinen Effekt künstlicher Beleuchtung, fand jedoch eine positive Korrelation zwischen dem Driftverhalten der Gammariden und der Wassertemperatur. Meine nächste Untersuchung beweist, dass Fluginsekten sich zu künstlicher Beleuchtung hingezogen fühlen und dass erwachsene aquatische Insekten sich mehr zu am Ufer gelegener künstliche Beleuchtung hingezogen fühlen als terrestrische Insekten. Im Gegensatz dazu habe ich keinen Hinweis darauf gefunden, dass vereinzelt aufgestellte Leuchten, hier im Abstand von ca. 80 m, die Ausbreitung aquatischer Insekten behindern. Eine Untersuchung an kleinen, oligotrophisches Bächen erbrachte den Nachweis dafür, dass entlang des Ufers aufgestellte künstliche Beleuchtung die Driftbereitschaft aquatischer wirbelloser Insekten reduzieren. Im Gegensatz dazu zeigte jedoch nur einer der untersuchten Bäche eine signifikante Veränderung beim Fischwachstum. Analog, habe ich keinen Nachweis dafür gefunden, dass künstliche Beleuchtung bestimmte andere Faktoren beeinflusst, wie zum Beispiel die Reaktion von schlüpfenden aquatischen Insekten, von in den Bach gefallenen terrestrischen Insekten, von benthischen wirbellosen Tiere, oder das Verwesen von Blättern. Zusammen genommen jedoch, unterstützen die vorgestellten Studien die Hypothese, dass künstliche Beleuchtung negative Auswirkungen auf aquatische Insekten hat.

Introduction

Artificial life at night has, without a doubt, increased the quality of human life for more than a century. Artificial light allows us to be more productive and feel safer. However, until the past decade, ecologists rarely if ever considered the possible effects of artificial light on ecosystems. Even when we ecologists work during the night in the field, bringing lights with us, we have generally failed to consider how this light might change the behavior of the very organisms we are interested in understanding. Furthermore, artificial light at night is wide-spread, particularly in developed nations (Fig. 1). This means that understanding the ways in which light changes ecosystems is of world-wide importance.

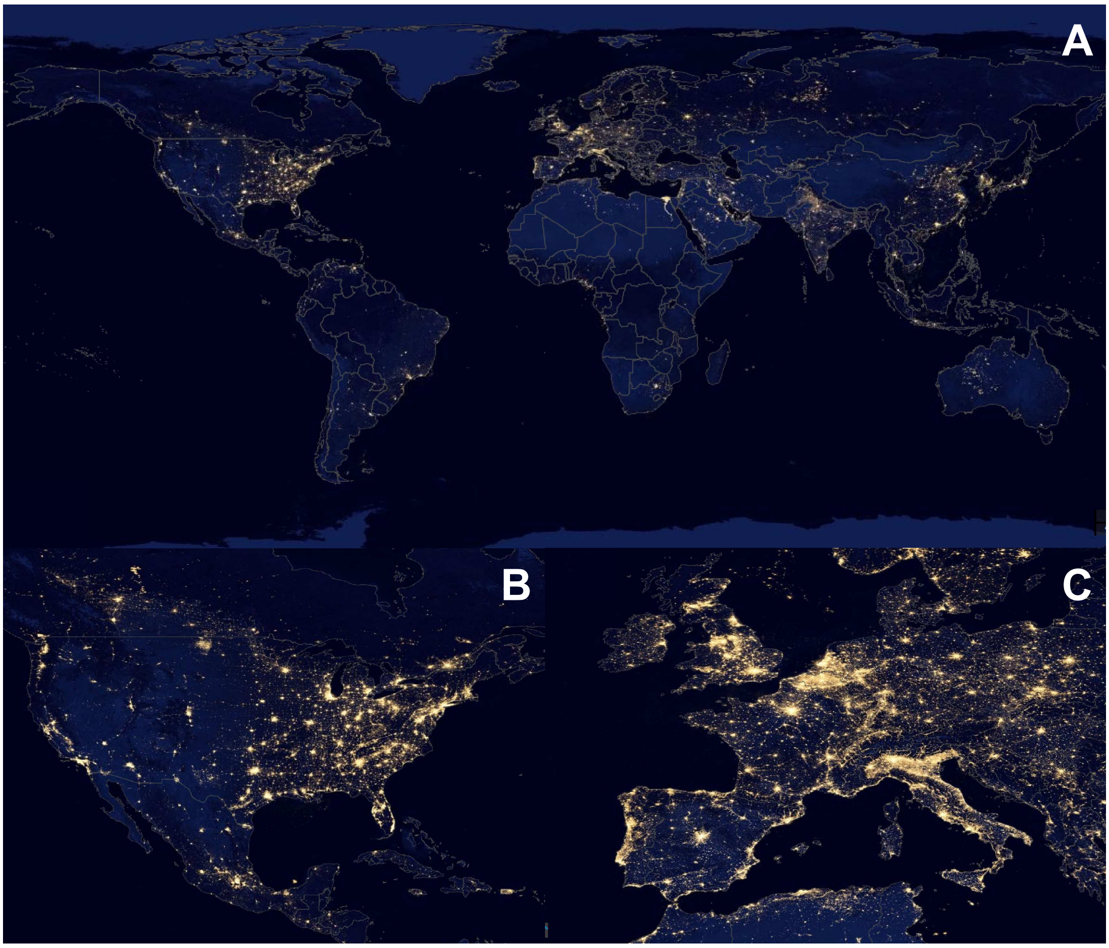

Figure 1. Artificial light at night is prevalent throughout the world (A), particularly in developed regions such as North America (B) and Europe (C). Screenshots taken from NASA's EOSDIS Worldview: http://earthdata.nasa.gov/labs/worldview/ on 28 January 2013.

Dimensions of artificial light at night

Unfortunately, most city planners and even restoration specialists do not take the potential of artificial light to act as an ecosystem disrupter when they are designing light installations or recover efforts. Examples of this include poorly planned security lighting (Fig. 2A), restoring daytime physical habitat without considering the nighttime habitat (Fig. 2B), or using unnecessary lighting to highlight architectural features within a city (Fig. 2C).

Figure 2. Artificial lights are used for security (A) and beauty (C), but both can contribute to ecological lights pollution (B). Photo credits: (A) and (B): E. K. Perkin, (C): C. C. M. Kyba.

As part of an effort to restore an endangered steelhead (*Oncorhynchus mykiss*) run to the Johnson Creek Watershed in Portland, OR, Reed College has spent 2.5 M USD between 1999-2009 building a fish ladder, restoring native riparian vegetation, and investing in other measures to improve the in-stream habitat in Reed Canyon, located in the center of the college campus (Zachariah Perry, *personal communication*). However, the potential of artificial light to disrupt steelhead re-colonization has been overlooked, as there are many lights within 20 m of the on-campus lake and stream (Fig. 2B). Undoubtedly, there are other concerns that take precedence over ecological restoration in this case. For instance, student safety is necessarily a major concern, and even if students are not actually safer with more lights, they probably feel safer (van Osch 2010). There is conceivably a similar mechanism at work behind poorly planned security lighting. Despite a lack of evidence that areas with bright lights have lower crime rates (Ramsey and Newton 1991), businesses feel much safer having them. There is probably a deep-rooted evolutionary basis for our taking comfort in brightly lit areas at night, as lights likely deterred large predators, or at least have been found to do so today (Beier 2006). This feeling of safety in lit areas may also have led to our taking enjoyment in artistically lit architectural sites (Fig. 2C). Obviously, there are many factors driving why and where we use artificial lights at night, and it will be necessary to better understand these before we can devise plans that can satisfactorily compromise human desires with ecological requirements (Hölker et al. 2010*a*).

But ecological functioning is not the only thing that might be altered by the presence of artificial light at night. Human health might also be at risk. Increased exposure to artificial light at night can disrupt sleep patterns and melatonin production, potentially leading to an increase in cancer (Kerenyi et al. 1990). Numerous studies have found a correlation between exposure to artificial light and increased rates of some kinds of cancer (reviewed in Navara and Nelson 2007); however, the connection between artificial light and increased cancer rates is still under debate. The cultural value of observing the night sky is also degraded with increasing artificial light (Font 2000). Therefore understanding the ecological effects of artificial light at night is just one important facet to determining the net negative effects of artificial light at night.

Definition of artificial light and light pollution

First it is important to distinguish between *artificial light at night* and *light pollution*. All forms of light pollution emerge from artificial, that is, human-built lights, but that does not mean that all artificial light qualifies as light pollution. Longcore and Rich defined ecological light pollution as light which “alters the natural patterns of light and dark in ecosystems” (2004, p.191). Throughout my thesis, I will refer to “artificial light,” as I was testing the “light pollution” potential of the light, but did not assume that it qualified as “light pollution” *a priori*. Well-designed artificial lighting avoids or minimizes light pollution. However, there are some instances when some light pollution is unavoidable. The obvious question in this case is, “How do we design light development so the needs of people are met while reducing the harmful ecological effects of artificial light?” First, we must better understand the ways in which artificial light affects organisms and ecosystems.

Effects of artificial light on animal behavior and ecosystem function

The potential for artificial light to alter the behavior of animals and the functioning of ecosystems is high. All the organisms around us have evolved with a distinct diel signal that is indicated by the presence or absence of light, with the highest levels of light at night coming from the full moon (Hölker et al. 2010*b*). Of course, this diel signal is very different in different habitats. For instance, arctic species have evolved with almost constant darkness in winter months and almost constant light in summer. In contrast, tropical species are adapted to a very constant twelve hours of darkness each night. As a result, we can expect that the effects of artificial light at night would be very different in these two different environments, with seasonal cues being missed in arctic habitats and daily cues being altered in tropical ones. In both cases, artificial light serves to homogenize the night environment.

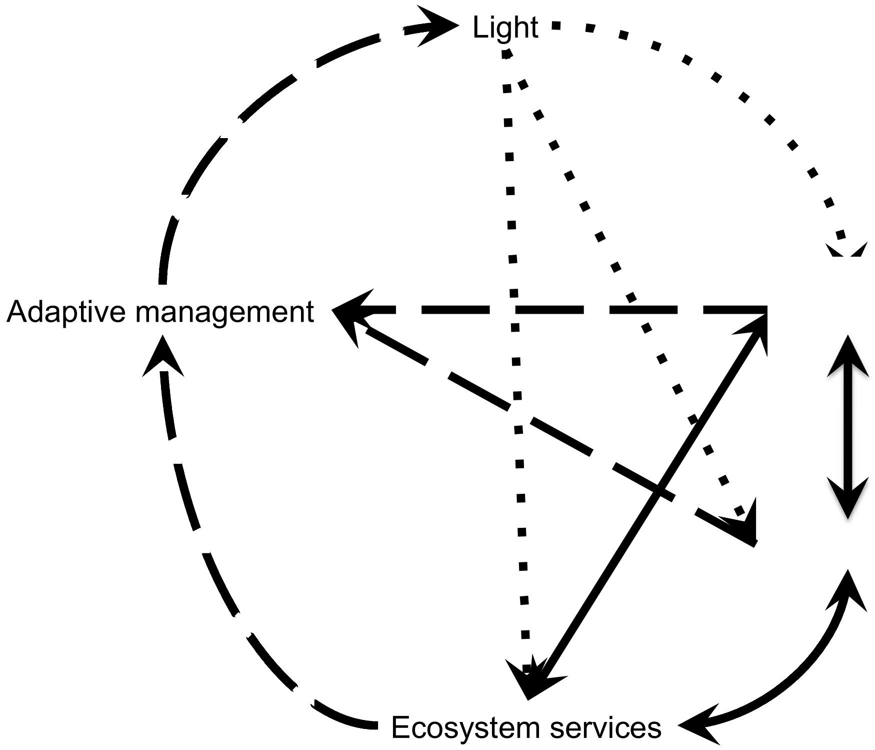

Figure 3. Artificial light at night affects (dotted lines) evolution, biodiversity, and ecosystem services, which all interact with one another (solid lines). Adaptive management will be influenced by the evolution, biodiversity, and ecosystem services (dashed line) and will in turn act on them through altering how artificial light is used.

Organisms living within large cities such as Berlin likely never experience light levels *below* that of a full moon, thanks to *sky glow* (Kyba et al. 2011). Sky glow is one of three major categories of light pollution; the other categories are glare (light striking the eye of an organism directly from light) and light trespass (light extending beyond targeted object). Every form of light pollution is in some way detrimental to organisms. The diel vertical migration of *Daphnia* is reduced when they are exposed to increased light levels from sky glow (Moore et al. 2000). Light trespass attracts sea turtle hatchlings towards human development and away from the ocean (Salmon et al. 1995). Direct glare has attracted the most attention, and has been shown to have negative effects on insects (Eisenbeis 2001, Scheibe 2003), amphibians (Buchanan 1993, Wise and Buchanan 2006), and mammals (Beier 2006). While all of these studies have brought insight to how organisms might respond to artificial light at night, they have focused only on one organismal level and have not delved into what artificial light might mean for ecological communities (though see Davies et al. 2012). Based on the current literature, it seems safe to assume that artificial light can affect the evolution of some organisms, the biodiversity of ecological communities, and the services these ecosystems provide (Fig. 3). Given how little we know about artificial lighting, it would be prudent to use adaptive management techniques to try to reduce any negative impacts of artificial light.

Thesis goal and outline

This thesis represents the first time that a research agenda has been developed to address the effects of artificial light on stream and riparian communities and ecosystems. The goals of this thesis are to develop a framework for future research in the area of artificial light and stream and riparian ecosystems, and to then work within that framework to develop our understanding of how artificial light at night influences stream and riparian systems. Research on how artificial light at night affects stream and riparian systems is not well-developed; however, through reading previous work on circadian rhythms, aquatic insect dispersal, and others, I was able to develop testable hypotheses. The overarching hypothesis that I defend in this body of work is that exposure to artificial light at night fundamentally changes the functioning of stream systems, and should therefore be as carefully managed as chemical pollutants such as phosphorus and DDT.

Because so little research has been done on artificial light and stream and riparian ecology, I had the benefit of a wide-open field of inquiry to explore. However, this sprawling intellectual landscape also made it difficult to sufficiently narrow my subject. In order to provide myself with guidelines, I reviewed the current and related literature in the topic, as well as presenting a framework for my own, and future research. This review and framework is presented in **Chapter 1** and further explored in **Chapter 2**.

Chapter 3 examines how exposure to different levels of artificial light over the course of a month alters the night-time activity in *Gammarus* spp. I was able to use indoor experimental flumes at the German environmental protection agency in order to test the hypothesis that while invertebrate drift will initially decrease, it will gradually increase over prolonged exposure to artificial light at night.

In the **fourth chapter**, I considered how the inland flight of adult aquatic insects is prevented by artificial lights. For this study, I installed high pressure sodium street lights around the edge of an island (~100 x 200 m) in the Spree River, approximately 35 km southeast of Berlin. I put insect flight intercept traps directly next to the lights, a few meters back from the lights, on the edge of the island between lights, and in the center of the island. I hypothesized that there would be fewer adult aquatic insects in the center of the field on nights when the lights were on than on dark nights.

Finally, the experiment in the **fifth chapter** brings these studies together by seeing how entire stream ecosystems are changed by artificial lights at night. At a research forest in western Canada, I added three high pressure sodium streetlights to the banks of four small streams to create experimental reaches about 40 m in length. These were paired with 40 m reaches on the same stream that were kept dark. I hypothesized that under artificial light, the number of drifting insects would decrease, and the number of terrestrial insects falling into the stream and the aquatic insect emergence from the stream would increase. I further hypothesized that these changes would result in decreased fish growth rates, leaf litter decomposition rates, and densities of benthic invertebrates, while algal biomass would increase.

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Chapter 1:

The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives

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Abstract

Artificial light at night is gaining attention for its potential to alter ecosystems. Although terrestrial ecologists have observed that artificial light at night may disrupt migrations, feeding, and other important ecological functions, we know comparatively little about the role artificial light might play in disrupting freshwater and riparian ecosystems. We identify and discuss four future research domains that artificial light may influence in freshwater and associated terrestrial ecosystems, with an emphasis on running waters: (1) dispersal, (2) population genetics and evolution, (3) ecosystem functioning, and (4) potential interactions with other stressors. We suggest that future experimental and modeling studies should focus on the effects of different spectral emissions by different light sources on freshwater organisms, the spatial and temporal scale over which artificial light acts, and the magnitude of change in light at night across the landscape relative to the distribution of running and standing waters. Improved knowledge about the effects of artificial light on freshwater ecosystems will inform policy decisions about changes to artificial light spectral emissions and distributions.

Introduction

Human activities influence and have modified the majority of the Earth's ecosystems (Vitousek et al. 1997). Freshwater ecosystems are especially affected, both because they accumulate and integrate the effects of activities within their catchments, and because they have always been preferred sites for human activities (Ricciardi and Rasmussen 1998, Dudgeon et al. 2006, Balian et al. 2008).

The effects of chemical pollution (Likens et al. 1996), alteration to natural flows (Poff et al. 1997) and nutrient cycles (Turner and Rabalais 1991), invasive species (Ricciardi and Rasmussen 1998), increasing urbanization (Morely and Karr 2004), and loss of riparian margins (Sweeney et al. 2004) on freshwater ecosystems have influenced policy decisions for the past 40–50 years (e.g., the USA Environmental Protection Agency's Clean Water Act of 1972). In contrast, the influence of artificial lighting as a human-induced impact affecting freshwater systems has only been recognized in the past 10 years or so (Moore et al. 2000, Longcore and Rich 2004, Moore et al. 2006, Nightingale et al. 2006), and there are still many gaps in empirical knowledge. This is despite the fact that the use of artificial lighting is now widespread and has increased over the past century (Holden 1992). While Cinzano et al. (2001) reported that approximately 67% of Americans and 20% of people world-wide now live in locations where Milky Way is no longer visible due to interference from artificial light sources, the wider effects of artificial light on other organisms and on ecosystems are poorly quantified. While many studies have focused on the control of natural light on biorhythms (Bishop 1969, Grau et al. 1981), few have looked at the potential of artificial light as a disrupter of these rhythms (Moore et al. 2000). This is surprising as approximately 30% of vertebrates and 60% of invertebrates are nocturnal (Hölker et al. 2010a) and could, therefore, be highly influenced by the presence of artificial light.

Longcore and Rich (2004) and Navara and Nelson (2007) presented broad reviews of artificial light and summarized a range of evidence, yet over two thirds of their examples relate to terrestrial organisms. Both Moore et al. (2006) and Nightingale et al. (2006) identified some effects of artificial light on lakes and fish, but in general, freshwater ecosystems are poorly represented in the current literature. An initial search of Web of Science (13 October 2011) of peer-reviewed literature using various terms relating to human alterations and ecosystems revealed a noticeable lack of research on artificial light and freshwater systems, especially when compared to other common pressures to which these systems are subjected (Table 1). This is despite freshwaters having high biodiversity and being disproportionally affected by species loss. Globally, freshwaters are inhabited by more than 125,000 known species, and even though freshwaters cover only about 0.8% of the Earth's surface, they are home to about 9.5% of all animal species, and one-third of all vertebrates (Balian et al. 2008). Nevertheless, there have been some seminal contributions to our understanding, for example in the use of artificial lights to: (1) increase fish growth rates in hatcheries (Boeuf and Le Bail 1999), (2) understand how it influences zooplankton movements (Moore et al. 2000), and (3) guide fish around dangerous in-stream structures (Johnson et al. 2005).

Here, we attempt to redress the balance in available literature to date by focusing on freshwaters, and in particular streams with their associated riparian margins, defined as areas that are ‘‘transitional semiterrestrial areas regularly influenced by fresh water, usually extending from the edges of water bodies to the edges of upland communities’’ (Naiman et al. 2005:2). We give special attention to adult aquatic insects, as they represent a key in the exchange of nutrients between stream and riparian systems (Richardson et al. 2010).

Our goal is to illustrate how artificial light influences species interactions and processes in stream and riparian ecosystems, and to stimulate research in an area that we consider of major importance for their future conservation and management. Ecologists have only recently started to acknowledge the alteration of the nightscape as a major concern in conservation policy and freshwaters are no exception (Rich and Longcore 2006, Hölker et al. 2010a).

Research Domains

We begin by presenting four major research domains relating to the ways artificial light can act on stream and riparian ecosystems, through altering: dispersal, population genetics and evolution, ecosystem functioning, and interactions with other common stressors; and then outline a range of key research questions which need addressing.

Table 1. Number of references returned on a Web of Science search (13 October 2011) for various human impacts and ecosystem type terms.

Human Impact Term	Ecosystem Terms			
	River	Lake	Wetland	Riparian
“Artificial Light”	7	8	0	1
“Light Pollution”	4	4	0	0
“Environmental flows”	90	14	9	24
“Climate Change”	241	213	64	41

Notes: Terms were searched for in the category of ‘‘Topic,’’ with lemmatization option off. ‘‘Ecology’’ was added as term to all searches to limit results to ecologically relevant papers.

Dispersal

There is evidence that artificial lights located near streams change the behavior of adult aquatic insects as they disperse through the terrestrial environment. Eisenbeis (2006) proposes three different ways for artificial lights to trap flying insects (Fig. 1). The first is through fixation or captivity effects (Fig. 1A). Here insects located near lights fly directly to them and are killed immediately, or they circle close to the light and are unable to leave eventually dying from exhaustion, predation, or heat. The lights may also induce settling behavior that incapacitates the insects, rendering them easy targets for predators. The second mechanism is the crash barrier effect (Fig. 1B), where insect dispersal and migration are impeded by running into a ‘‘barrier’’ of lights, such as a row of street lights. The final mechanism is termed the vacuum cleaner effect, whereby insects from a large area are attracted to a nearby light source. However, these are only hypotheses and carefully designed experiments are needed to determine how much of an effect these mechanisms actually play in disrupting aquatic insect dispersal.

Studies comparing different trapping techniques provide evidence for the vacuum cleaner effect. These studies illustrate that light traps differentially capture certain insects (e.g., Trichoptera) more readily than other kinds of traps (e.g., Collier and Smith 1998). While the height of streetlights is designed to maximize safety for car drivers, lights that are used along walking and bike paths, as well as those used for decorative purposes could be adjusted to attract fewer insects, if we can predict which heights have the highest concentrations of insects based on landscape features and insect species. Svensson (1974) found that light traps at 11 and 50 m height captured fewer trichopterans than those a 1 m due to the propensity of several species to fly low to the ground, suggesting that higher lights might trap fewer insects than lower lights, but this has yet to be generalized across taxa and habitats.

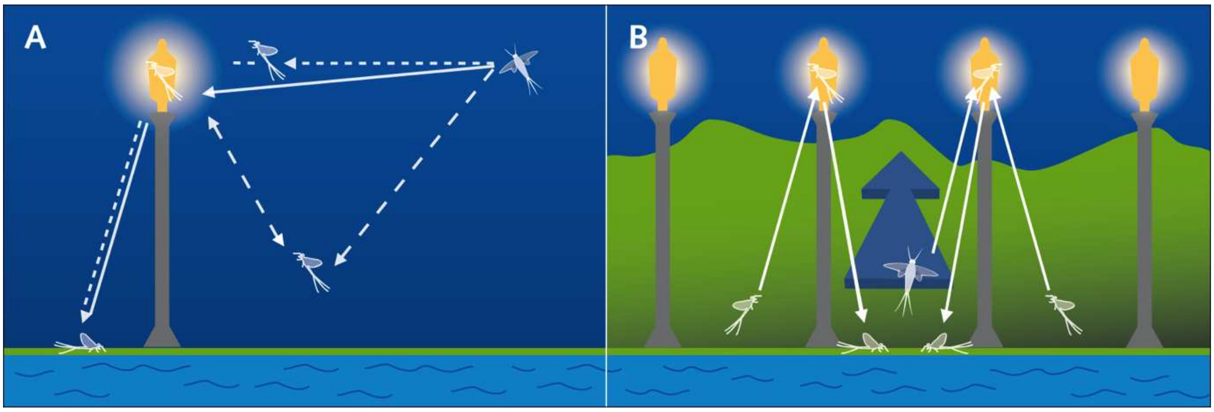

Figure 1. Eisenbeis (2006:281–304) proposes three different ways for artificial lights to trap flying insects. Two are shown here: fixation (dashed line), captivity (dotted line), and directly lethal (solid line) effects (A) and the crash barrier effect (B). Fixated insects do not suffer mortality directly from artificial light, but are stunned by it and are easy targets for predators or fail to engage in basic behaviors, such as reproduction. Captive insects fly to the light and circle around it endlessly until they die of exhaustion or are consumed by predators. The crash barrier effect is the result of a row of lights (like those lining a street) preventing the dispersal of insects through their attractive properties.

Overall, research on insect dispersal, especially adult aquatic insect dispersal, is extremely limited. Part of this lack is that it is very difficult to rigorously study insect dispersal. Stable isotope and elemental markers are potentially valuable tools, as is the increasing use of genetic analysis (Smock 2007); however, capturing insects in substantial numbers generally requires the use of light or pheromone traps. While these methods are adequate for most studies of aquatic insect dispersal, light traps cannot be used in studies of artificial light as they obviously create a confounding factor. In addition, while population genetic analyses hold promise for longer-term studies and determining if populations adapt to artificial light, they are not really useful as a tool for short-term dispersal studies.

It is also unclear how much the dispersal of adult aquatic insects matters for the population dynamics of these organisms. Masters et al. (2007) found that the recovery of the benthos from acidification is not limited by adult dispersal. Furthermore, Bunn and Hughes

(1997) calculated that it is likely that populations of *Tasiagma* spp. (Trichoptera) in a reach are maintained through the reproduction of only 3–12 females per generation. It is not obvious how much of an effect land use changes have on adult aquatic insect dispersal (Petersen et al. 2004); however, studying the effects of artificial light on insect dispersal will likely further this field.

Clearly, we need to come up with new and innovative ways to study aquatic insect dispersal. One possibility is to use Malaise traps to capture individuals marked with fluorescent dyes or stable isotope tracers (Macneale et al. 2005). Conducting more basic studies of aquatic insect dispersal will help those studying the effects of artificial light to develop hypotheses (e.g., the effect of light height, light distances from streams) more effectively.

Aquatic insects are not the only stream organisms that may have their dispersal interrupted by the addition of artificial lights. It is well-established that the migration of Pacific salmon species (*Oncorhynchus* spp.) can be slowed or stopped by the presence of artificial lights (Nightingale et al. 2006). Furthermore, exposure to constant light can decrease smoltification and increase the deterioration in body SGR associated with smoltification in chinook salmon (O. tshawytscha) (Hoffnagle and Fivizzani 1998). This might be due to the synchronization of downstream migration with the new moon; however, it is possible that the lunar timing of downstream migration is stock-dependent (Hoffnagle and Fivizzani 1998). It is likely that any species that uses lunar cycles to cue migration or dispersal will be disrupted by the addition of artificial lights (see: *Key Research Questions*; Fig. 2).

Population genetics and evolution

To our knowledge, no one has yet experimentally investigated the possibility that artificial light can act as an evolutionary force in freshwater or riparian species. However, its potential to influence evolution has received attention from Moore et al. (2006) and Nightingale et al. (2006).

Artificial light at night could reduce effective population sizes through the direct loss of individuals, reproductive failure, or changes to sex ratios. The direct mortality of individuals is probably most likely in the case of aquatic insects; either through the attraction of the adults to lights (Scheibe 2003, Eisenbeis 2006), or increased predation through improved predator vision. However, mid-trophic fish species could also suffer higher rates of predation under artificial light (see: *Ecosystem functioning: Food webs*). Reproductive failure could be due to the inability to locate suitable mates, as in the case of several amphibian species (Longcore and Rich 2004). Aquatic insects are again likely to suffer from changes to sex ratios, as there are often biases in light trap catches, depending on the species (Waringer 1989).

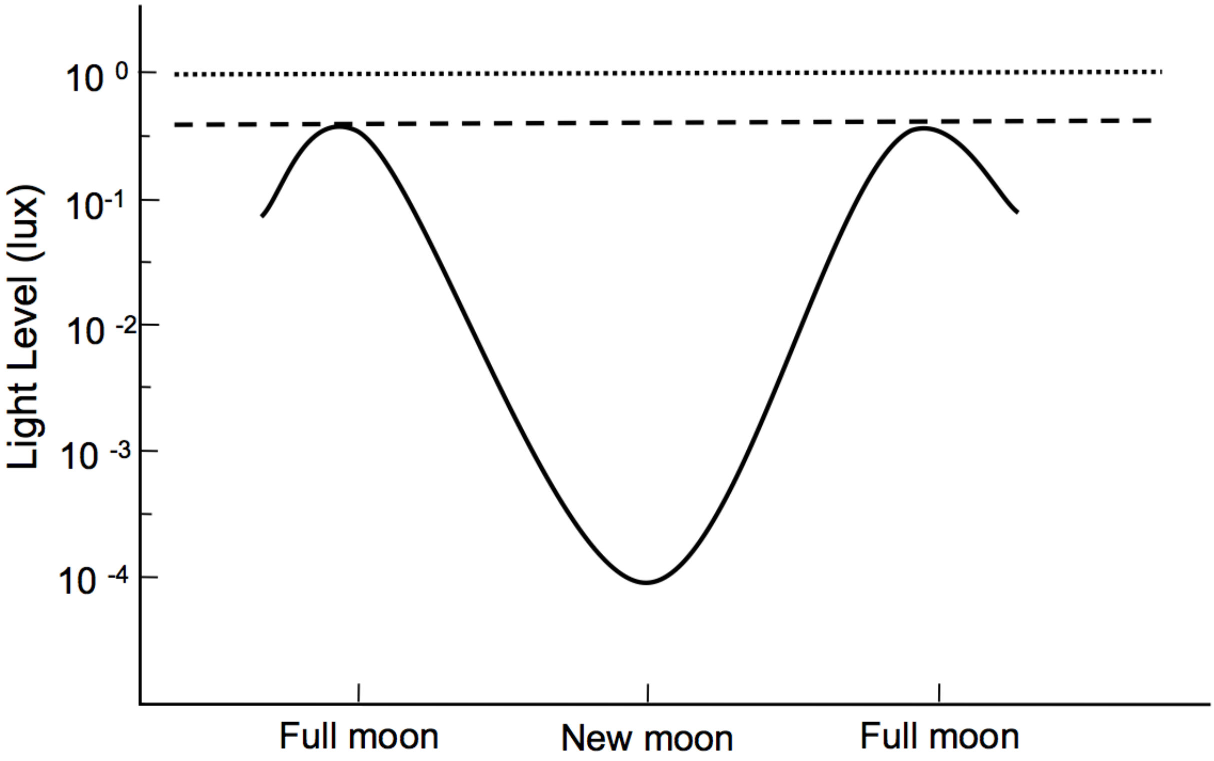

Figure 2. Sky glow eliminates monthly variation in light levels. The solid line shows the natural light provided by a full moon in a temperate region. The dashed line is the light level measured in the center of Berlin on a clear night and is roughly equivalent to a full moon, while the dotted line is the light level in the center of Berlin on a cloudy night and is roughly four times greater (Kyba et al. 2011). The y-axis is logarithmic.

Reduction in effective population sizes will lead to less genetic diversity and possibly genetic drift; leaving a population with insufficient variation to adapt to future stressors, and therefore is a major concern for species conservation (Lande and Barrowclough 1987). If some populations are eliminated, it could result in reduced gene flow across the range of some species, with the potential to lead to the diversification of populations and potentially even speciation. There is already some evidence that other environmental stressors alter genotype frequencies in a population. Populations of a common aquatic insect (*Chironomus riparius*) that were exposed to a chemical stressor (tributyltin) in a laboratory study had increased rates of larval mortality and reduced genetic variation (Nowak et al. 2009). This result was especially significant because the changes were seen in neutral markers, not in response genes, and therefore represent a true reduction in effective population size. Conversely, mosquitoes living on an arid slope showed increasing diversity (due to higher rates of recombination and mutation) as a result of exposure to greater environmental stress, such as increased temperatures and solar radiation, than those living on a humid slope of the same valley (Nevo 2001). Furthermore, females from the arid slope showed an increased tendency to mate with males that were also from the arid slope, potentially leading to sympatric speciation between the two groups (Nevo 2001). While it might be difficult to forecast which species will have increased or decreased genetic diversity, artificial light could also change the frequency of heritable behaviors that could influence the evolution of organisms.

Mating and reproductive behaviors in freshwater species are likely to be influenced by artificial light (Moore et al. 2006, Nightingale et al. 2006). Sexual selection for traits that are visually stimulating could increase or decrease with exposure to artificial light, depending on the spectral qualities of the light and species' visual sensitivities. For instance, cichlid fishes undergo strong sexual selection that favors brightly-colored individuals and has driven speciation events in populations in clear water that allows plenty of light (Seehausen et al. 1997). The effects of artificial light on sexual selection could be especially interesting and unpredictable, given the common use of high pressure sodium lamps, which have a very limited emission spectra and could prevent females from recognizing male color patterns (Fig. 3). This has taken place in Lake Victoria, where turbidity from eutrophication reduces the spectral range of light entering the water to wavelengths that are similar to the emission spectra of high pressure sodium lamps, and reduces female selectivity based on color (Seehausen et al. 1997). Similarly, guppy habitat specialization has been driven by a combination of diverse ambient light conditions, predation, and sexual selection (Endler 1992). The introduction of artificial light to these streams could lead to the visual homogenization of these environments, which could lead to reduced speciation as well as increasing susceptibility to predation.

Other behaviors that could be influenced by artificial light that are potentially important to evolution are feeding behaviors. Some spiders are more likely to build their webs in close proximity to artificial light to take advantage of the increased densities of insects found at lights (Heiling 1999). If there is a genetic basis for this behavior, then the presence of artificial light could very well contribute to the evolution of this species. Ultimately, any behavior that could be altered by artificial light and is under genetic control could allow artificial light to change the evolution of a species exhibiting such a behavior.

It is also important to consider the effect of artificial light in combination with species interactions in driving rapid evolutionary change, which could lead to altered ecological dynamics, e.g., different guppy phenotypes result in altered ecosystem structure and function (Schoener 2011). To test if artificial light causes rapid evolution of exposed organisms, researchers could hatch diapausing copepod eggs that were laid before artificial light became widespread. The feeding and diel vertical migration (DVM) behavior of pre-lighting and modern copepods could then be compared (Hairston et al. 1995). To determine what percentage of the behavioral change is really due to evolution, and not some other ecological factor, genetic techniques should be used to identify genes that are likely responsible for the observed behavior and then tested to ensure that they are responsive to altered light conditions and change organism behavior (Hairston et al. 2005, Fussmann et al. 2007). Furthermore, it will be beneficial to establish if any of these rapid evolutionary changes results in genetic isolation, and eventually, speciation (Hendry et al. 2007).

Ecosystem functioning

As previously addressed by Moore et al. (2000), Longcore and Rich (2004), and Moore et al. (2006), we expect that modified lighting regimes will lead to a range of whole freshwater ecosystem changes and also influence the linkages between freshwater and riparian ecosystems. Of particular interest is how artificial light could alter the exchange of organic matter between stream and riparian systems. Artificial light could influence ecosystems in ways that might be unexpected from single species studies, e.g., by changing species interactions, especially predator-prey interactions, and therefore have important conservation implications (Wooten et al. 1996).

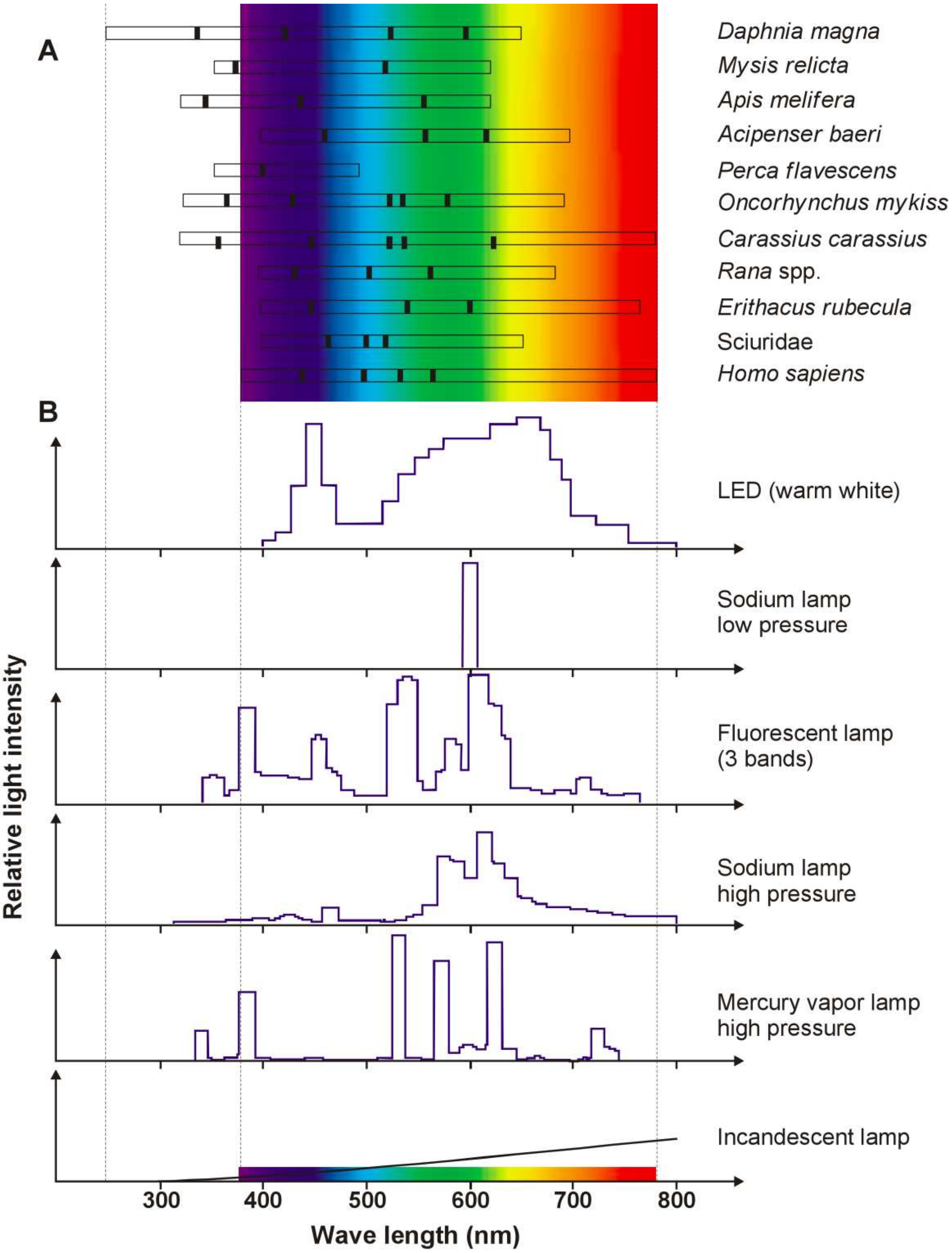

Figure 3. The light sensitivities of various animals are displayed against a background of wavelengths that humans perceive as visible light (A). The black ovals represent the peak sensitivities for each organism; note that some organisms have sensitivities in the UV range. The dashed vertical lines designate the limits of the UV (10–400 nm) and human-visible light (390–750 nm) (Menzel and Blakers 1976, Smith and Macagno 1980, Lythgoe1984, Loew and Wahl 1991, Fratzer et al. 1994, Hawryshyn and Hárosi 1994, Vorobyev and Osorio 1998, Gal et al.1999, Wiltschko and Wiltschko 1999, Sillmann and Dahlin 2004). The wavelengths of light emitted from various artificial light sources (B) are highly variable, with some emitting light over a broad spectrum and others having only a few narrow peaks.

Primary production—Primary production is a key ecosystem process controlled by light. To our knowledge, only one study has found evidence that riparian vegetation could be influenced by the presence of artificial light at night (Cathey and Campbell 1975). Their work illustrated that trees and shrubs exposed to streetlamps, particularly incandescent or high pressure sodium luminaires, may have longer growing periods, earlier leaf-out and later leaf fall times than those in darker environments (Cathey and Campbell 1975). This may have a range of bottom-up effects. For example, earlier leaf-out could cause earlier inputs of terrestrial insects (that use riparian vegetation as habitat) to freshwater systems, but only if terrestrial insects are able to use this new habitat resource. Later leaf fall could result in a mismatch of resources and consumers, as detritivorous aquatic invertebrate taxa might have evolved to match the timing of the allochthonous inputs of leaves with critical life stages (Hershey and Lamberti 1998:169–199). However, substantial changes in leaf-out/fall and growth are unlikely unless artificial lights are present with warmer temperatures that allow for a longer growing season (Cathey and Campbell 1975). While this situation is currently unlikely in temperate climates, global temperatures are projected to increase by 0.6–6.48C in the next 90 years, with greater warming in northern temperate regions (IPCC 2007), which would increase the chances that artificial light might influence riparian vegetation. The effects of increased temperatures and light could be studied in urban areas that not only have increased levels of artificial light, but also artificially high temperatures due to the heat island effect (Oke 1973).

Food webs—Light is an important cue for both predator avoidance and feeding in freshwater systems. Aquatic invertebrates in lotic systems drift at light levels below 10_3 lux (at 400–535 nm) to avoid predation by fish (Bishop 1969). However, Atlantic salmon have been shown to change foraging strategies below light levels of 10^{-1} lux, moving to areas of slow-moving water that, while not as rich in prey, allow more time for identification of prey items and night-time foraging (Metcalfe et al. 1997). Light adaptations are also evident in lentic environments, where zooplankton engage in DVM in the water column to feed on phytoplankton during the night when they are less visible to predators (Young and Watt 1996). Moore et al. (2000) were able to detect a decrease in the amplitude of DVM in *Daphnia retrocurva* as a result of artificial light from a nearby city, by monitoring the vertical migration inside darkened versus clear enclosures. Light intensity also had a significant influence on the ability of vendace (*Coregonus albula*) to feed on *Daphnia magna*, with declining efficiency down to a threshold of 0.05 lux (Ohlberger et al. 2008). On the other hand, a decrease in feeding movements to avoid artificial light has been observed in vendace (Schmidt et al. 2009). These studies suggest that artificial light can result in altered food webs in lentic systems, leading to increased algal biomass as zooplankton spend less time in the upper euphotic water column feeding on algae (Moore et al. 2000, Moore et al. 2006). Lotic systems could see higher relative abundances of armored grazers, such as glossosomatid caddisflies or snails, as invertebrates with less physical protection, such as mayflies, are eliminated through heavy predation (McNeely et al. 2007). In this case, there would eventually be a reduced number of invertebrates available to fish predators, but if there are adequate numbers of protected invertebrate grazers, they would likely control lotic algal standing biomass.

We expect that artificial light at night not only influences freshwater food webs (Fig. 4), but also the exchange of materials between stream and riparian environments (Richardson et al. 2010; Fig. 5), which can be mediated by predators (Baxter et al. 2004). Accordingly, one key question here is how artificial light changes predator-prey relationships. Some species might be able to exploit artificial light to extend foraging opportunities, at least in the short-term (Moore et al. 2006, Nightingale et al. 2006). One example of this is the spiders who build their webs near light sources (Heiling 1999). However, foraging benefits, if they exist, may be short-lived due to resulting reductions in prey populations (Beier 2006). This will probably depend on the trophic structure of specific food webs, as apex predators will benefit more than mid-trophic species that have to avoid predation themselves.

Patterns of invertebrate drift and fish feeding are both likely to change under the influence of artificial light (Moore et al. 2006, Nightingale et al. 2006). If fish are able to feed much more efficiently on drifting insects, it could result in a decrease of emerging aquatic insects. However, light is known to depress drift rates (Bishop 1969); if fish are more active under artificial lights but prey is less available, fish could suffer from increased energetic demands. Conversely, the number of terrestrial invertebrates entering the stream and available for fish to prey on could also change. Under natural conditions, terrestrial insects are an important allochthonous resource for fish (Fig. 4A). Kawaguchi and Nakano (2001) found that terrestrial insects contribute about 50% of the total annual prey consumption of salmonids in some Japanese streams, while about 84% of the consumption in a cyprinid (*Alburnus alburnus*) in a German lake comes from terrestrial sources (Mehner et al. 2005). In the presence of artificial light near a waterbody, terrestrial insects could become an even more important food source for fish. On the other hand, juvenile and other vulnerable fish might retreat to overhangs and reduce foraging efforts in order to avoid predation (Nightingale et al. 2006; Fig. 4B).

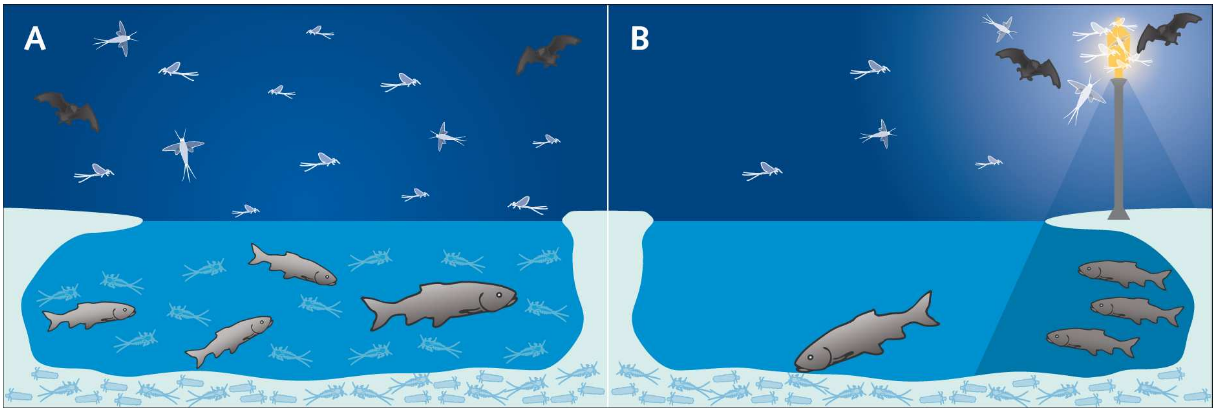

Figure 4. A schematic of a stream ecosystem under natural nighttime conditions (A), and the same system under the influence of artificial light (B). Note the predicted shifts as light is introduced from A to B in the positions of small fishes seeking cover, suppression of streaminvertebrate drift, adult insects attracted to lights, and bats shifting their foraging efforts near the lights. Refer to *Ecosystem functioning: Food webs* in the text for details.

While adult aquatic insect flight in a dark riparian forest might normally be restricted to areas immediately adjacent to streams (Petersen et al. 1999), insects may cluster around artificial lights located in floodplains (Figs. 1, 5). Many aquatic insects emerge at night (Tobias 1967, Jackson 1988, Pinder et al. 1993), and are therefore vulnerable to attraction to artificial lighting while in their adult phase. We hypothesize that as the distance of an artificial light source from a water body increases, the proportion of freshwater carbon transferred to the terrestrial ecosystem increases relative to a riparian system that does not have lights, as aquatic insects are attracted further into the terrestrial system (Fig. 5A). Preliminary support for this hypothesis comes from Kovats et al. (1996) who found adult caddisflies 5 km inland when using light traps. Conversely, we predict the amount of terrestrial carbon contributed to a freshwater system through terrestrial invertebrates will decrease as the distance of an artificial light source to a water body increases. For instance, a light situated on a dock will draw terrestrial insects to the water body, while lights from a road running parallel and several hundred meters away from a water body will draw terrestrial insects away from the water (Fig. 5B). This will create areas that are highly dense in resources for insectivorous organisms, while creating other areas that are depauperate. Outcomes of this process may be an increase in competitive interactions between insectivores (Rydell 2006) and also an increased transfer of freshwater resources to terrestrial consumers.

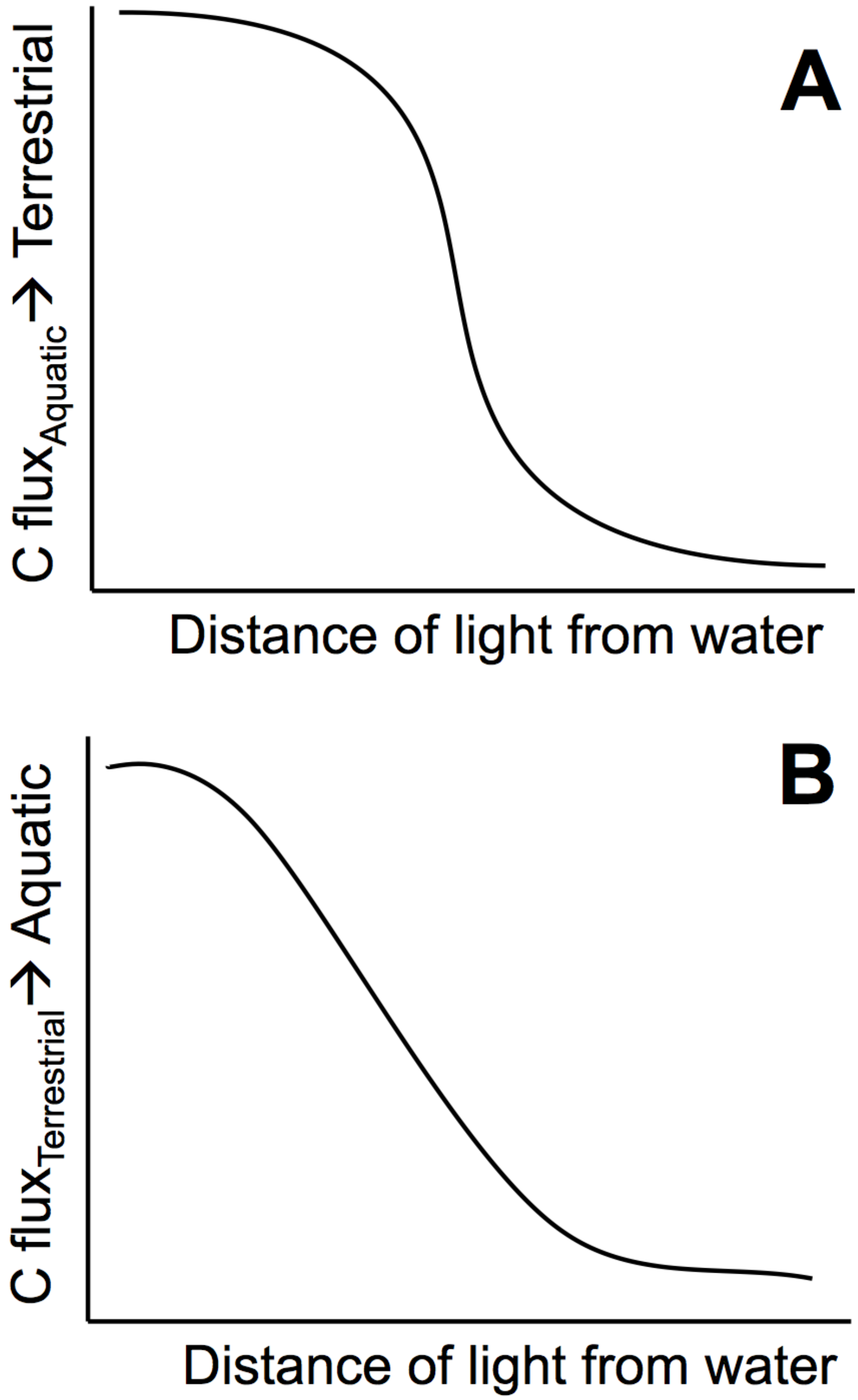

Figure 5. Theoretical changes in carbon flux from freshwater to terrestrial systems, in the form of insects. Aquatic insects will be attracted to lights very near aquatic bodies in high densities, while lights that are farther away will increase the inland dispersal of aquatic insects, up to some threshold (A). Similarly, there will be higher inputs of terrestrial insects to the aquatic system when lights are close to the aquatic environment but these inputs will decrease quickly as the light location moves inland (B).

Interaction with other stressors

There is a growing concern about how environmental stressors might interact with each other, and in fact, an entire issue of the journal Freshwater Biology (see Ormerod et al. 2010) was dedicated to this topic. However, the specific ways that artificial light might interact with other common urban stressors have not yet been described in the peer-reviewed literature. As artificial light most frequently occurs in urbanized areas, its effects may be confounded with other urban stressors, making it impossible to determine how much a role artificial light has played in declines in biodiversity and ecosystem functioning. Artificial light may already play a major role in changing organism behavior and ecosystem functioning. However, to fully understand its importance, we must elucidate how it interacts with other stressors in freshwater and riparian ecosystems. Does light pollution act synergistically with other stressors to increase the stress experienced by organisms, or does it potentially lessen the effect of some stressors? How artificial light interacts with other stressors will help prioritize what areas are most important to protect. Dudgeon et al. (2006) enumerated the five major threat categories to freshwater ecosystems as overexploitation, water pollution, habitat degradation, species invasion, and flow modification. Of course, another major threat to freshwater ecosystems is climate change. Artificial light has the potential to interact with all of these threats. By conducting carefully designed studies to understand the interaction between artificial lighting and the threats mentioned in Dudgeon et al. (2006), we will be able to develop a model for when artificial light is likely to do the most harm and be carefully controlled, or conversely, when it could be used as a mitigating factor for some other stressor.

In this section, we explain the ways artificial light could combine with changes to temperature regimes, increased chemical pollution and urban development, altered flow regimes, and increased nutrient concentrations. We also describe how the effects of artificial light might be masked by the presence of other stressors and may not become apparent until the other stressors are removed.

One potential concern is for light to interact with other common urban stressors, such as temperature and pollution, to interfere with migration and dispersal. For example, some fish have been shown to become disoriented when swimming near lights (Tabor et al. 2004, Nightingale et al. 2006), which they are more likely to encounter when traversing urban areas that also contain other stressors. In the absence of light, migratory fish, such as salmonids, travel quickly through large rivers (Økland et al. 2001) that are more likely to have sub-optimal temperatures or increased pollutants, but the disorientation caused by urban lights could increase the time these fish spend in polluted environments and, as a result, increase their risk of mortality (McCormick et al. 1998).

The interaction of artificial light and other urban stressors could also alter patterns of the dispersal of riparian obligates, such as adult aquatic insects. For instance, the presence of culverts has been shown to reduce the upstream flight of adult caddisflies (Blakely et al. 2006). These culverts are usually installed to allow roads to pass over small streams, leading to a high probability of street lighting being associated with culverts. The street lighting would most likely run perpendicular to the stream (Fig. 6), leading the insects farther away from the stream. We hypothesize that this will lead to decreased dispersal and gene flow, and potentially the elimination of up-stream populations; however, it is possible that these lights could draw the insects over to a neighboring small watershed and, as a result, enhance genetic exchange. Similarly, Málnás et al. (2011) found that a bridge reduced the upstream flight of the mayfly *Palingenia longicauda* on a river in Hungary. At least part of the disruption was caused by polarized light reflecting off the surface of the bridge, which enticed gravid females to oviposit there (Horváth et al. 2009, Málnás et al. 2011).

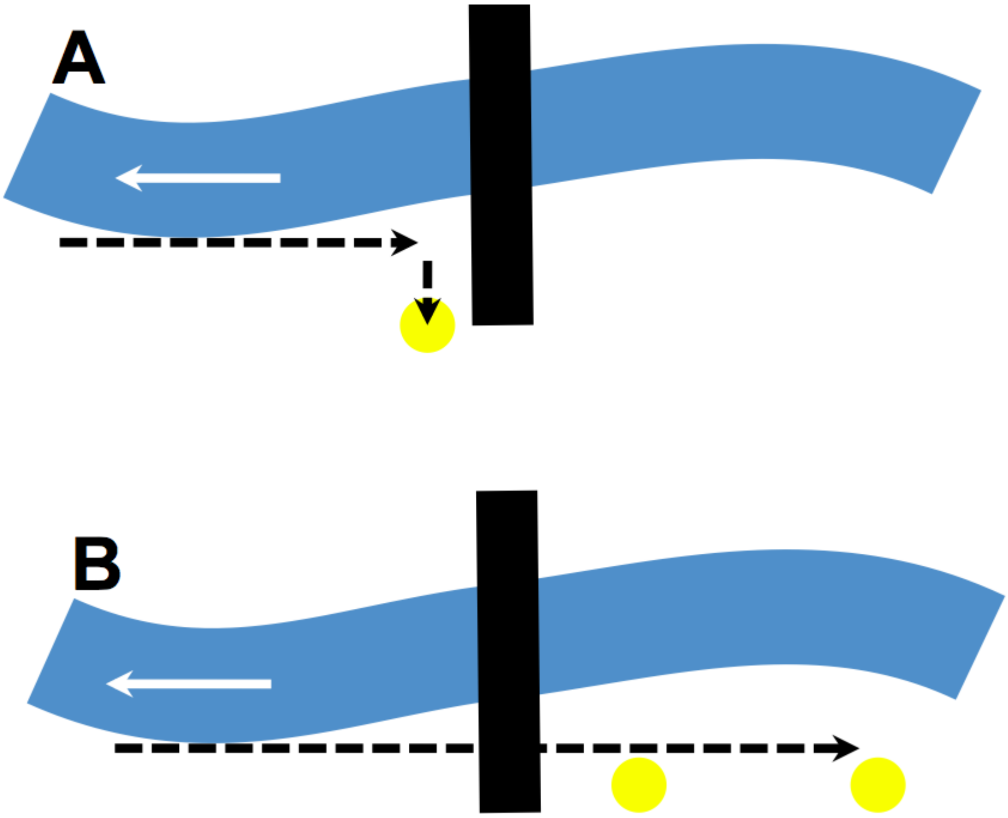

Figure 6. Artificial lights located near culverts intersecting streams may strengthen their disruption of aquatic insect upstream flight (A) or mediate it (B), depending on their location. The white arrow represents the direction of streamflow, the dashed line is the flight path of the aquatic insects, the yellow circles are lights and the black line is a culvert.

The construction of dams has led to altered flow regimes, often with a dampening of predam high flows. These high flows can serve as a signal to cue migration or spawning events (McCormick et al. 1998, Bunn and Arthington 2002). Normally, light is also a strong Zeitgeber for these behaviors (Grau et al. 1981, Greenstreet 1992), but where artificial lighting and flow alterations occur, there could be a complete loss of external cues for these behaviors. This could lead to asynchronous migration and spawning events, and ultimately result in lower population sizes.

While flow modifications are largely a concern of stream environments, increasing loads of nitrogen and phosphorus pollution is a common problem across all freshwater systems (Carpenter et al. 1998). Areas with increased nutrient loading that are also exposed to artificial light at night could be at an increased risk for algal blooms, largely as a result of night-time light altering the behavior of grazing macroinvertebrates (Moore et al. 2000, Moore et al. 2006). Other common pollutants in freshwater ecosystems could also interact with artificial light, most resulting in further reductions of biodiversity. However, bright artificial light could mitigate effects of pollutants that degrade under light exposure.

In restoration efforts, common urban stressors might act in concert to hide the negative effects of artificial light. For instance, water quality was the limiting factor in fish survival and reproduction in a central European river system. However, after decades of efforts to improve water quality, hydromorphological degradation then emerged as the main obstacle to further ecological improvement and freshwater diversity (Borchardt et al. 2005, European Commission 2007). Improving degraded habitats became important once pollutants and oxygen stress had been eliminated; similarly, after degraded habitats have been improved artificial lights could prevent a restoration site from achieving full functionality. This is important to consider as freshwater and riparian ecosystems that have undergone successful restoration often become attractive places for recreation (Woolsey et al. 2007). As recreational uses of these areas increase, user groups might call for the installation of artificial lights, particularly along biking and running paths in temperate zones with long periods of dark during winter months.

Key Research Questions

We have identified three main general questions facing researchers in artificial light that deserve more attention. These include understanding how different spectral qualities of

Table 2. Key research questions in each research domain.

Key Research Questions	Research Domains			
	Dispersal	Evolution	Ecosystem functioning	Interactions with other stressors
Spectral Qualities	How do different spectra change an organism's attraction to light? How do different spectra change hormone production?	Are there changes in sexual selection as a result of specific spectra entering the environment?	Is primary production changed? Does the spectrum of artificial light fall within visual predators or prey or both?	Is the light spectra reaching aquatic organisms altered by pollution?
Spatial & Temporal Scales	Patterns of light across the landscape: does it create traps or barriers? What time of day do species move; does the presence of artificial lights change this?	How quickly does adaptation to/selection from artificial light happen? Are entire populations affected or only fractions of some populations?	Are there refuges available? Is daytime behavior altered? Are there energetic costs?	Is light present year-round or seasonally? What effects might this have on spawning? What is the distribution across watersheds? Specifically, how does artificial light overlap with other stressors?
Magnitude of Change in Brightness	Is sky glow or direct glare a bigger problem?	Is sky glow or direct glare a bigger problem?	Is sky glow or direct glare a bigger problem? Are there thresholds of effective light levels?	Is sky glow or direct glare a bigger problem? Are there thresholds of effective light levels? Is there an increase in light brightness due to reductions in riparian vegetation (as a result of anthropogenic activities)? Are the light levels high enough to photodegrade chemicals?

various sources of artificial light, spatial and temporal scales over which artificial light acts, and the magnitude of changes in light influence organisms and ecosystems (Table 2).

Diverse organisms have sensitivities in different parts of the light spectrum, and various artificial lighting sources emit very distinctive wavelengths of light (Fig. 3). Therefore, different light sources (e.g., high pressure sodium, metal halide) with distinct color spectra are expected to elicit unique responses from different organisms (Fig. 3; Moore et al. 2006). Recently, the European Eco-Design Directive has enacted a step-by-step plan to phase out particularly energy-intensive lighting products (e.g., high-pressure mercury lamps, the European Parliament and the Council of the European Union 2009). Thus, many countries and the EU have launched a number of programs to adopt efficient lighting systems with a focus on LEDs as a promising energy efficient lighting technique. There is some evidence that LEDs will attract fewer insects than previous bulb types (Eisenbeis and Eick 2011), but this needs to be more rigorously tested, as the light levels and luminaire construction in this study varied in addition to bulb type. Further, it is completely unknown how other freshwater organisms might respond to different wavelengths, although some fish (e.g., *Acipenser baeri* and *Oncorhynchus mykiss*) have peak sensitivities that correspond to peak emissions from LEDs (Hawryshyn and Hárosi 1994, Sillmann and Dahlin 2004; Fig. 3).

The spatial and temporal scalar influence of artificial light is also an area that requires elucidation. Scheibe (2003) showed that one street light located near a stream can attract caddisflies hatching from several hundred meters of stream, but it is unclear how applicable his results are for different habitat and ecosystem types, or what the impact of multiple light sources might be. At larger spatial scales, it is clear that the sky glow created by the cumulative lights of a large city can influence natural areas 10s and even 100s of kilometers away (Albers and Duriscoe 2001, Kyba et al. 2011). For example, Moore et al. (2000) found that artificial light from 16 km away was strong enough to alter the DVM of *Daphnia*. We need to know if wide-spread use of artificial lights near freshwater and riparian habitats will contribute to the decline or disappearance of sensitive species, lead to localized decreases close to bright light sources, or even be beneficial for other species. Even if sky glow does not cause extinctions, it could very likely alter food web structure either by changing predators' ability to detect prey or prey behavior (Moore et al. 2006). Another question that needs to be answered is if light sensitive species are able to re-colonize areas when lights are removed. Mapping the occurrence of artificial light across landscapes will allow us to make better predictions about the likelihood of specific habitats being recolonized.

While the results of Scheibe (2003) and Moore et al. (2000) suggest that artificial light can influence organisms over a relatively large spatial area, we do not know the temporal scale of this influence. Does exposure to artificial light during the night alter the behavior of organisms during the day? Perhaps some organisms have life stages that are particularly vulnerable to exposure to artificial light, but are not sensitive during the rest of their lives. These species might be able to take advantage of dark refuges for sensitive life stages and then live in artificially lit areas at other times. If populations are negatively affected by artificial light, are they able to recover quickly once artificial light is removed from their habitat? This largely depends on whether artificial light alters the genetic structure of populations. Furthermore, spatial analysis is needed to determine the overlap of artificial lights and freshwater bodies. As noted in the introduction, freshwater environments are preferred sites for human activities, which will often lead to an increase of artificial lights. We expect to find the greatest amount of lighting in already damaged urban areas, but we also need to determine if vacation homes and highways introduce a meaningful amount of light to more natural areas.

The magnitude of changes in light also needs to be better understood. While direct glare is the most conspicuous form of light pollution, sky glow is a much more wide-spread phenomenon that is likely to influence animal behavior (Longcore and Rich 2004, Moore et al. 2006, Nightingale et al. 2006). Sky glow can increase ambient light levels hundreds of kilometers away from the cities from which it emanates. This is the case in several ecologically important U.S. National Parks (Everglades, Channel Islands, and Joshua Tree), which have night skies that are substantially brighter than natural due to sky glow from nearby cities (Albers and Duriscoe 2001). One potential problem of increased light from sky glow is that it reduces or eliminates the natural monthly variation in night-time light that arises from the lunar cycle (Longcore and Rich 2004, Kyba et al. 2011; Fig. 2). If the general increase in ambient light caused by sky glow can alter behavior and harm ecosystems, then managing artificial light becomes a much more pressing conservation concern. However, it will be very difficult to study the effects of sky glow on ecosystems, as there are very few places left in North America and Europe that do not have elevated levels of sky glow to use as control sites (Cinzano et al. 2001). Furthermore, once researchers have located a promising location, how do they mimic an increase in sky glow that would normally be produced by a city of 500,000+ inhabitants that is 50 km away? While researchers may be able to introduce direct glare by introducing a few lights to an ecosystem, those interested in understanding the influence of sky glow may have to introduce artificial darkness to an already lit area, as

Moore et al. (2000) did.

Conclusion

How artificial light at night might influence stream and riparian ecosystems is a relatively unexplored topic, with many possibilities for relevant research. Even though the experimental knowledge of the ecological impacts of artificial light at night is still developing, governments are creating legislation to regulate it, mostly to reduce energy costs and decrease greenhouse gas emissions (Hölker et al. 2010b). Reducing energy consumption is a desirable goal, but if it is achieved solely through changing lighting fixtures and not necessarily reducing lighting, and without knowing how different aspects of artificial light (e.g., intensity and spectral qualities) influence ecosystems, this legislation could have unintended and even negative impacts on ecosystems. We also expect that governments will not be able to regulate artificial light everywhere, but by understanding its potential consequences, we can better prepare for or mitigate them.

Carefully designed experiments are needed to determine the exact effects of artificial light on ecosystems and over what spatial and temporal scales they act. From a management perspective, it is highly important to consider and incorporate the mitigation of potential ecological impacts and losses of biodiversity and ecosystem services into new lighting concepts (Rich and Longcore 2006, Hölker et al. 2010a, b). While there are many challenges to overcome in pursuing this research, the potential for new breakthroughs in understanding ecosystems and their functioning is high and should motivate researchers to innovate new techniques.

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Chapter 2:

Light pollution as a biodiversity threat

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In a recent TREE article, Sutherland and colleagues (2010) used horizon scanning to identify fifteen emerging issues in biodiversity conservation. They discussed both threats and opportunities for a broad range of issues, including invasive species, synthetic meat, nanosilver and microplastic pollution. We recognize that the article was not intended to be comprehensive, but feel they overlooked an emerging problem of great importance and urgency, namely that of light pollution. Although the widespread use of artificial light at night has enhanced the quality of human life and is positively associated with security, wealth and modernity, the rapid global increase of artificial light has fundamentally transformed nightscapes over the past six decades, both in quantity (6% increase per year, range: 0–20%) and quality (i.e. color spectra) (Smith 2009, Hölker et al. 2010). Despite these significant increases, the impacts of artificial lighting on the biosphere, many of which are expected to be negative, are seldom considered.

Most organisms, including humans, have evolved molecular circadian clocks controlled by natural day–night cycles. These clocks play key roles in metabolism, growth and behavior (Dunlap 1999). A substantial proportion of global biodiversity is nocturnal (30% of all vertebrates and > 60% of all invertebrates, Table A1), and for these organisms their temporally differentiated niche has been promoted by highly developed senses, often including specially adapted eyesight. Circadian photoreceptors have been present in the vertebrate retina for 500 million years, and a nocturnal phase is thought to mark the early evolution of the mammals ago. It was only after the extinction of the dinosaurs that mammals radiated into the now relatively safe day niche (Menaker et al. 1997, Bowmaker 2008). Although unraveling 500 million years of circadian habituation is a difficult task, it seems that, with the exception of amphibians, the proportion of nocturnal species appears greater in recent radiations than in more ancient radiations (Figure 1). Nocturnality might therefore have been an important step in the evolution of vertebrates, and is currently threatened by the unforeseen implications of the now widespread use of artificial light.

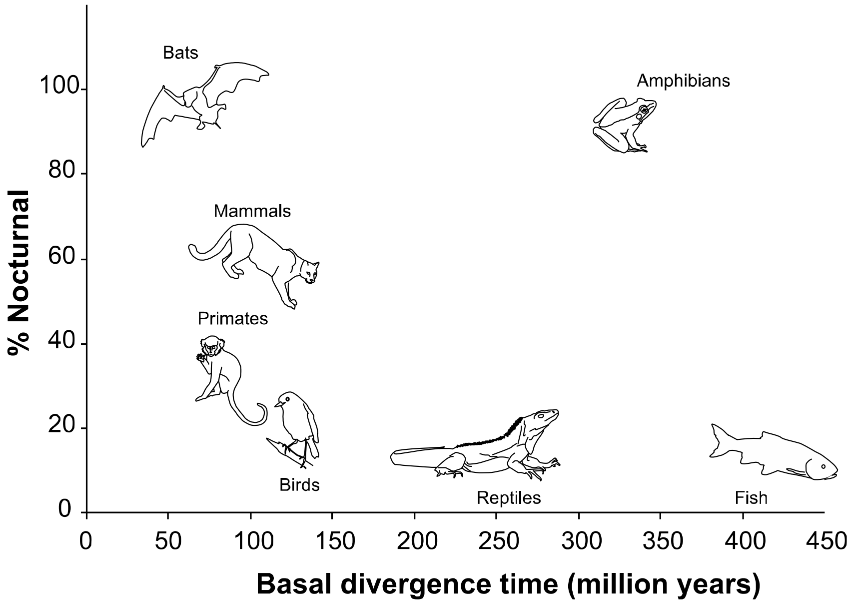

Figure 1. Percentage of extant nocturnal species within different vertebrate classes and orders. With the exception of amphibians, recent radiations have a higher proportion of nocturnal species than more ancient radiations (Bininda-Emonds et al. 2007, Alfaro et al. 2009). This fact underlines the hypothesis that nocturnality is an important step in vertebrate evolution. Because the highly permeable skin of amphibians makes them susceptible to typical daytime stressors such as heat and light, the thresholds to radiate into the day niche are probably higher for amphibians than for other vertebrates. This reduced flexibility, in turn, could result in a higher vulnerability to adverse effects from light pollution at night, and could contribute to the recent amphibian declines.

Light pollution threatens biodiversity through changed night habits (such as reproduction and migration) of insects, amphibians, fish, birds, bats and other animals and it can disrupt plants by distorting their natural day–night cycle (Rich and Longcore 2006). For example, many insects actively congregate around light sources until they die of exhaustion. Light pollution can therefore harm insects by reducing total biomass and population size, and by changing the relative composition of populations, all of which can have effects further up the food chain. Migratory fish and birds can become confused by artificial lighting, resulting in excessive energy loss and spatial impediments to migration, which in turn can result in phenological changes and reduced migratory success. Daytime feeders might extend their activity under illumination, thus increasing predation pressure on nocturnal species. For plants, artificial light at night can cause early leaf out, late leaf loss and extended growing periods, which could impact the composition of the floral community. Finally, it can be assumed that a population's genetic composition will be disturbed by light-induced selection for non-light sensitive individuals.

Furthermore, light pollution is considered an important driver behind the erosion of provisioning (for example, the loss of light-sensitive species and genotypes), regulating (for example, the decline of nocturnal pollinators such as moths and bats) and cultural ecosystem services (for example, the loss of aesthetic values such as the visibility of the Milky Way) (Carpenter et al. 2009, Smith 2009, Hölker et al. 2010, Potts et al. 2010). As the world grows ever-more illuminated, many light-sensitive species will be lost, especially in or near highly illuminated urban areas. However, some species, in particular those with short generation times, may be able to adapt to the new stressor through rapid evolution, as is described for other human disturbances (Hendry et al. 2010).

In summary, the loss of darkness has a potentially important, albeit almost completely neglected, impact on biodiversity and coupled natural–social systems. Thus, we see an urgent need to prioritize research, and to inform policy development and strategic planning.

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We are grateful to Michael Monaghan and Gernot Glöckner for helpful comments and to Peter Kappeler and Christian Voigt for information on primates and bats. This work was supported by the project 'Verlust der Nacht' (funded by the Federal Ministry of Education and Research), Milieu (FU Berlin) and the Senatsverwaltung für Bildung, Wissenschaft und Forschung, Berlin.

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Appendix A. Supplementary data

Percentage of nocturnal vertebrates and invertebrates world-wide

Table A1. Numbers of species ([a] from IUCN 2008, Frost 2010, Insektoid.info 2010, Uetz 2010) and proportion of nocturnal species (feeding, spawning or migration) by major groups of organisms, [b] = often day and night; 25% in tidal marine taxa, [c] = sexual reproduction typically at night.

	Estimated number of described species [a]	**Nocturnal species (%)**	**References**
Vertebrates			
Mammals	5 488	63.8	Campbell 1997
Primates (incl. *H. sapiens*)	432	31.0	All the World's Primates Website 2010
Bats	1100	100.0	Speakman1991, Simmons 2005
Birds	9 990	19.6	Weick 2006, World of animals 2010, Riede 2001
Reptiles	8 969	16.6	Uetz 2010
Amphibians	6 433	93.3	Frost 2010
Fishes	30 700	14.1	Helfman 1993
Subtotal	**61 580**	**28.0**	
Invertebrates			
Insects	950 000	49.4	
Lepidopterans	180 000	77.8	Insektoid.info 2010
Coleopterans	500 000	60.0	BioNetworX 2010
Crustaceans	40 000	50.0	Crustacea.net 2010
Arachnids	98 000	5.0	Insektoid.info 2010, Platnick 2010
Molluscs	81 000	[b]	Little 1989
Corals	2 175	[c]	Fadlallah 1983, Szmant 1986
Others	61 209	?	
Subtotal	**1 232 384**	**64.4**	

The number of described plant, lichen, mushroom, and brown algae species totals 348,546 (IUCN 2008). A substantial number of these taxa show major activities at night, like fragrance, flowering, growing, assimilating, spore dispersal, or germinating, which may be subjected to diurnal cycling, and thus be affected by light pollution. Fragrance and flowering at night is especially common in the tropics. Nocturnal pollinators, for example, are responsible for most gene flow between white campion (*Silene alba*) populations (Barthelmess 2006).

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Chapter 3:

Artificial light and night-time activity in gammarids

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Abstract

Artificial light is gaining attention as a potential stressor to aquatic ecosystems. Artificial lights located near streams increase light levels experienced by stream invertebrates and we hypothesized light would depress night drift rates, but that the effect of light on drift rates would decrease over time as the invertebrates acclimated to the new light level. These hypotheses were tested by placing *Gammarus* spp. in eight, 75 m x 1 m artificial flumes. One flume was exposed to strong (416 lx) artificial light at night. This strong light created a gradient between 4.19 and 0.04 lx over the neighboring six artificial flumes, while a control flume was completely covered with black plastic at night. Night-time light measurements taken in the Berlin area confirm that half the flumes were at light levels experienced by urban aquatic invertebrates. Surprisingly, there was no effect of any light treatment on gammarid drift rates. On the other hand, physical activity measurements of individually *in situ* caged gammarids showed increased short-term activity levels in *G. roeseli* in completely dark and decreased activity levels in brightly lit flumes. Night-time drift in flumes decreased relative to day-time drift and was correlated with a decrease in temperature.

Keywords: acclimation, artificial light, drift, *Gammarus*, light pollution, Multispecies Freshwater Biomonitor

Introduction

Light pollution is becoming an increasing problem across the globe (Hölker et al. 2010). Based on satellite data from 1996-1997, 71% of the population of the United States, and 51% of the population of the European Union can no longer see the Milky Way, even under the best conditions (Cinzano et al. 2001) due to an increase in ambient light from artificial sources. Although artificial lights are widespread, their potential effects on biotic communities have received relatively little attention to date (Longcore and Rich 2004, Perkin et al. 2011). Additionally, increases in "sky glow," or the general increase in light emitted from large urban areas, can influence peri-urban and even rural areas. Aquatic bodies located near (within 10-20 km) urban areas could be exposed to light levels close to, or equal to that of a full moon (Moore et al. 2000, Kyba et al. 2011). Clear, small streams are most likely to be affected by artificial lights at night, as they are most likely to transmit light through from the surface to the benthos (Moore et al. 2006). This change in the light environment experienced by aquatic organisms at night could have unintended consequences for their behavior, particularly behaviors that are triggered by changes in light availability.

The majority of stream invertebrates drift during the dark hours of the night, most likely to avoid predation by visual predators such as drift-feeding fish (Flecker 1992). While drift-feeding fish may still catch prey during the night, their efficiency will be reduced as a result of diminished visual acuity (Fraser and Metcalfe 1997). However, artificial light at night may allow visually foraging fish to capture more prey, provided that drifting invertebrate prey is still available.

It is generally understood that the changes in drift behavior are exogenously controlled by changes in ambient light levels, and do not result from endogenous circadian rhythms (Bishop 1969). Bishop (1969) showed that even brief exposure to light in the middle of the night greatly decreased drift; similarly, exposure to darkness in the middle of the day resulted in an increase in drift. However, it is unclear if invertebrates will continue to not drift if constantly exposed to low light levels, or if they eventually resume drifting despite the light, due to increased competitive interactions. For instance, invertebrates may have higher drift rates when population density is high (Walton et al. 1977), or when food availability is low (Hughes 1970, Hershey et al. 1993).

We conducted this study during the late fall/early winter of 2009 when the night is roughly twice as long as the day. *Gammarus* spp. was selected as our invertebrate of interest as they have a high propensity to enter the drift, and therefore be available to predaceous fish (Rader 1997), and they are the most abundant shredders in the sand-bottom lowland streams common in Northeastern Germany. With this study, we wanted to determine if artificial light would alter downstream drift in Gammarids resulting in changed availability as fish prey and distribution patterns. We hypothesized that the long duration of the night would lead to artificial light having an even more pronounced effect on the drift rates of aquatic invertebrates. Our study objectives were to determine 1) if nighttime invertebrate drift decreases decreases under artificial light, and 2) if the decrease in drift remains constant over time, or lessens with acclimation to the new light environment. Experimental light levels were compared to those measured in the field in the Berlin area to allow us to put the results of the drift experiment into a real-world context. We also ran a small experiment looking at the individual behavioral response of *Gammarus roeseli*, *G. pulex* and *Dikerogammarus villosus* to different levels of artificial light in order to provide a better understanding of how invertebrates might respond to artificial light at night.

Materials and Methods

The experiment was run using the indoor stream mesocosms of the artificial pond and stream system (FSA) at the test area of the German Federal Environment Agency (Umweltbundesamt, UBA) in Marienfelde (Berlin). This part of the system is housed in a hall and contains eight indoor flumes that are each 75 m long and are constructed from green fiberglass reinforced polyester (Berghahn et al. 1999). Flume width is generally 1 m, except in four pool locations of 3 m length in each channel that are 1.2 m wide (Mohr et al. 2005). The pool sections were planted with the macrophyte species *Sparganium erectum* (L.) in order to provide features similar to those encountered in the field, such as water turbulence and hiding places for aquatic animals. The substrate in all flumes was washed, uncontaminated 0/2 sand from a gravel pit that had been covered with a thin layer of uncontaminated fine sediment from a lake (Schmachter See, Mecklenburg Western Pommerania, Germany). The water depth in all flumes was 0.2 m. The flumes were operated in a circular flow mode by integrated screw pumps at a flow rate of 0.10 m s^{-1}. Flow rate, turbidity, dissolved oxygen concentration, pH, conductivity, and water temperature in each flume were taken automatically every hour throughout the duration of the experiment. For details about the measurement equipment see Mohr et al. (2005).

Invertebrate collection

Organisms for use in the experiment were collected in fall 2009 from the River Spree near the small town of Mönchwinkel, the Demnitzer Mühlenfließ, and the Löcknitz near the small town of Kienbaum, approximately 38 km, 50 km, and 23 km southeast from the city center of Berlin, Germany, respectively. Sampling, transport, and stocking followed the method described by Mohr et al. (2012). Accordingly, eighty-five mesh sacks (mesh opening 6 x 6 mm, stretched mesh), each filled with 100 g of organic triticale straw were left in the Spree from 30 September-7 October. After collection, bags were immediately taken to the flumes. Nine bags were placed in each of the 8 flumes and opened so that the straw and animals were distributed over the bottom of the flume. Prior to stocking, several "ripples" were artificially created in the sand substrate in order to capture the straw from the bags. The ripples were at a right angle to the flow direction and were ~8 cm wide and 1 cm deep. Thus, three habitats (walls, sand areas, straw areas) were available in each flume. Of the bags collected in the field, five were set aside to determine the number and species of invertebrates collected. From these five bags it was determined that not enough invertebrates were present to conduct the experiment, so two further collections were made; one at the Demnitzer Mühlenfließ (15-26 October) and at the Löcknitz (6-13 November).

Because we were limited to eight flumes, and we were interested in testing the effects of multiple light levels on invertebrate drift, we decided to have a gradient of light over the flumes rather than a replicated design with only one light level. Illuminating one stream at the far end of the experimental hall created a decreasing gradient of light over the other streams in the facility (Fig. 1). To create complete darkness, the stream most distant from the fully illuminated one was covered with black light-tight foil every night from 1600-0800. Artificial light was provided by 23, Osram Biolux T8 L 58W/965 G13. Light levels were measured twice during the experiment, once at roughly the mid-point (30 November) on the night before a full moon, and the other at the end of the experiment (14 December) on the night before a new moon. Both measurements were made with an ILT1700 light meter (International Light Technologies, Peabody, MA), and were taken between 1730 and 1800 by placing the light meter on the surface of the stream substrate. The artificial light spectrum was measured with an OceanOptics Spectrasuite® (Dunedin, FL).

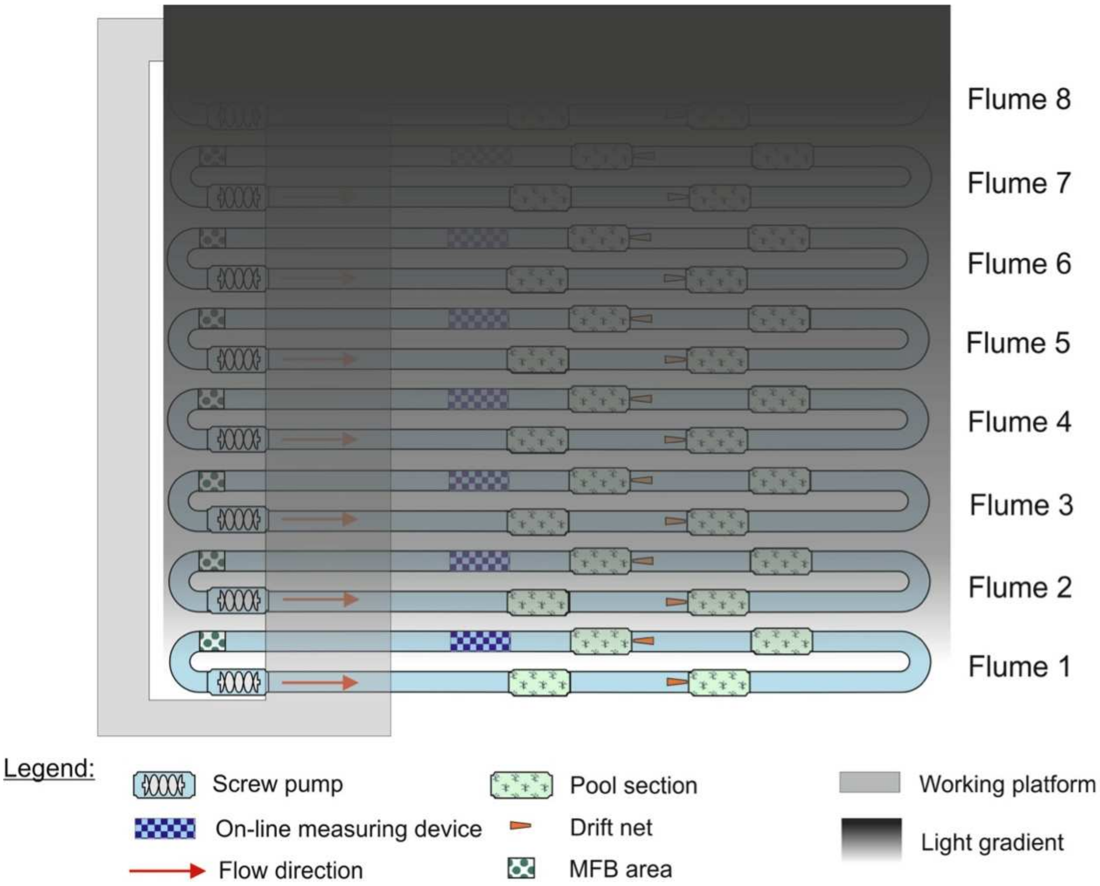

Figure 1. Configuration of the eight indoor flumes and the light gradient.

Drift experiment

Animals were allowed to acclimate to the system for at least one week before artificial night lighting of the system began on 20 November 2009 and ended on 15 December 2009. Invertebrate drift was sampled with 2 drift nets (dimensions: mouth opening = 15 x 7.5 cm, length = 140 cm, mesh = 283 µm), which were placed downstream of riffles two and four in the middle of each stream just above the sediment surface (Fig. 1). Drift samples were collected both during the day (0800-1600, on the 19 November) and during the night (1600-0800, on the 20 November), prior to the initiation of artificial night light and were used to determine the drift in the flumes under relatively natural conditions.

Two drift samples from each stream were taken during the day (from 0800-1600) on the 23 and 30 November, and the 7 and 14 December. Another two drift samples were taken from each stream during the night (from 1600-0800) on the 24 November, and the 1, 8, and 15 December. Due to the low diversity of invertebrates in the system, we were able to immediately identify and count the organisms collected in the drift samples and then return them to their respective streams within one hour, where they were observed to behave normally upon their release.

Post-experiment benthic and periphyton sampling

In order to estimate the total number of invertebrates per flume, benthic sub-samples were collected at the end of the experiment. Because each flume had three distinct habitats created by the presence or absence of straw and the walls, we took five sub-samples each from both straw and bare sediment areas in each flume by means of tube corers (inner diameter 18.7 cm, suction sampling) and from the walls with a kick-sampler modified to scrape the walls (opening 30 cm) employing stratified random sampling techniques. The five samples of each stratum were pooled for each flume and fixed in 80% ethanol for counting. Details on the sub-sampling protocol can be found in Mohr et al. (2012).

Periphyton growth during the experiment was measured with 6 sterile fiberglass reinforced polyester plates (gel-coated, 10 x 20 cm) that were placed upright in 3 flumes (at 416, 0.59 and 0.0 lx) at the beginning of the experiment. At the end of the experiment, all periphyton was scraped from the plates, diluted in 1L water and filtered onto pre-weighed and dried Whatman GF/C 1.2 µm fiberglass filter. Periphyton on the filter paper was then dried overnight at 105°C and weighed.

Multispecies freshwater biomonitor (MFB) experiment

Physical activity and drift behavior of apparently healthy caged adult *Dikerogammarus villosus*, *G. roeseli*, and *G. pulex* was measured flumes one (416 lx), four (0.59 lx), and eight (0 lx) with a Multispecies Freshwater Biomonitor® (MFB, Gerhardt et al. 1994) during the time period of the drift experiment. The MFB uses a quadropole impedance conversion technique to detect the movements of the invertebrates. As the invertebrate in the chamber moves, it alters the conductivity and the electrical field in an alternating current created by electrodes on opposite walls of the test chamber. These changes are detected by another non-current carrying pair of electrodes and can be directly linked to different kinds of behavior (from http://www.limco-int.com/multispecies-freshwater-biomonitor.html, last accessed 15 November 2012).

Animals used in the MFB experiment were acclimated in large tubs for at least 24 h to the light regime of the flume and then 6 specimens were individually transferred into 6 transparent plexiglass tubes (length 50 cm, inner diameter 1.8 cm), which were positioned directly underneath the water surface parallel to the direction of the flow. At either end of the tubes were two MFB chambers (length 6 cm) that were open at one side to the plexiglass tube. Mesh (opening 1 mm) covered the other end of the chambers, which prevented the gammarid individuals from leaving the system, but allowed for flow-through of flume water. By using the Plexiglas tubes with the MFB chambers, it was possible to monitor both the activity rate in mV and presence or absence of the invertebrates. Flow rate in the tubes was measured at about 0.05 m s^{-1}. At this flow rate, both *G. roeseli* and *G. pulex* are known to react to the current (Vobis 1973). Organisms were always transferred into the tubes at approx. 14:00, were given the chance to acclimate for 1 hour, and then monitored for 48 hours while their activity was recorded continuously at 10 minute intervals. In some cases 5-minute intervals were used for greater resolution when activity levels were high. The animals were not fed during the MFB trials and could freely move from one end of the tube to the other, including the 2 measuring chambers. When animals were active in the upstream chamber for the majority of the 48-hour period, we assumed this was indicative of positive rheotaxis. If animals were active in the downstream chamber for the majority of the 48 hour period, we assumed this was indicative of downstream drift. In addition, organisms could be in the transparent tube between the two measuring chambers. Because the measuring chambers are only able to detect the presence of an organism when it is active, we were unable to distinguish between an organism in the connecting tube and one resting (i.e. not moving) in one of the measuring chambers. Because there were only 12 chambers available, the measurements of organisms in different light levels had to take place at different times. The behavior of all 3 species was recorded under conditions of permanent bright light (416 lx) during the first week of the experiment, but measurements of behavior in completely dark nights (0.0 lx) was only possible for *G. roeseli* and *G. pulex* during the last week of the experiment. The only species which was tested in the MFB at all 3 light levels, including dimmed light at night (0.59 lx, full moon), was *G. roeseli.*

Light measurements in Berlin

In order to put the light levels used in the experiment into a real-world context, we took light measurements at several locations in waterways throughout Berlin. Light measurements were taken in lx with an ILT1700 light meter on 6 March; 25, 27, 28 May, and 24 June 2011. All measurements were taken at least 15 minutes after evening civil twilight, 15 minutes before morning civil twilight, and 15 minutes after the setting or before the rising of a new or three-quarter moon, when background illumination was lowest. Measurement locations were selected from a light map created from low-elevation flights over Berlin and observations on the ground (Kuechly et al. 2012), and were chosen to select a variety of light environments, from very dark to very bright. Most measurements were taken at an underwater depth of approximately 50 cm, though one reading was taken at a depth of 40 cm.

Analysis

Benthos sampling revealed that there were different numbers of animals in each flume, so the drift catches were standardized relative to the number of invertebrates in each flume. Furthermore, to account for any differences there might have been in the flumes other than light, the relative night drift was divided in half prior to comparing day and night drift as it sampled the drift for 16 hours while the day drift only sampled 8 hours of drift

$$Day{:}Night\ Drift\ Rate = (d_i * 100) / N_i$$

where d_i = the ratio of night to day drift in flume i, and N_i = the total number of invertebrates in flume i.

The catches of the two synchronously exposed driftnets from the same flume were checked for normal distribution and equality of variance and then compared with a paired t-test. To test if invertebrate drift increased over the course of the experiment, a regression analysis of the drift rate of each flume over light level, week of experiment, and temperature was done. Alpha for these tests was lowered to 0.017 after a Bonferroni correction for the number of tests (three). Comparisons between the time gammarids spent in the upstream vs. downstream chambers of the MFB were made with Mood's median test and Wilcoxon sign-rank test. Alpha for these tests was 0.05. Analyses were conducted using Stateasy software 2007 (Dr. J. Lozán, Hamburg), Microsoft Excel, and R (R Development Core Team 2011).

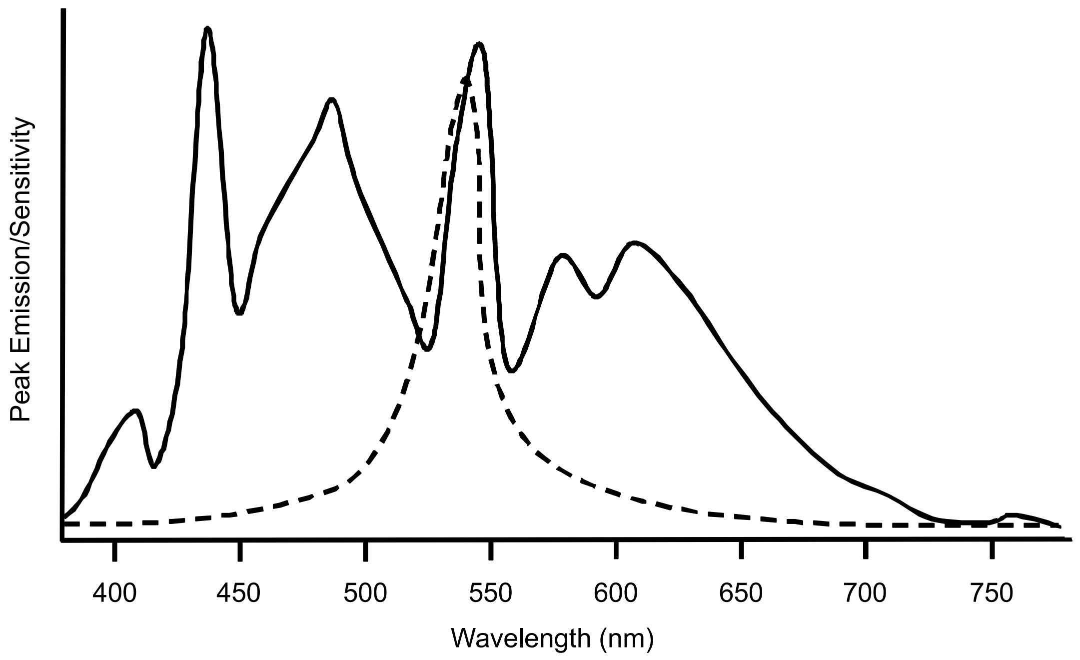

Figure 2. Spectral emission of the lights used in this study (Osram Biolx T8 L 58W/965 G13, solid line), and peak light sensitivities of 4 mysid crustaceans (dashed line) according to Porter et al. 2007 (see also Donner et al. 1994).

Results

Spectral measurements (Fig. 2) of the artificial lights used in the experiment indicated that there was a high degree of overlap between the artificial light spectrum and the peak light sensitivities of crustaceans (Donner et al. 1994, Porter et al. 2007). The water temperature in all flumes exhibited slight diurnal changes and decreased over the course of the experiment from ~12.3 to 7.4 °C (Fig. 3). Mean water temperature was the same in all flumes (9.9 to 10.0 °C, SD = 2.42 °C). According to the water temperature on-line measurements in the flumes there was no spatial gradient with regard to their position in the hall. All on-line measurements of the other parameters were also almost identical between flumes. Water conductivity ranged from 490 to 530 µS cm^{-1}, pH was between 8.1 and 8.3, and dissolved oxygen was 10.9 to 11.3 mg L^{--1}. The water was very clear and the density of particles was ≤ 1 ppm in all flumes.

Drift experiment

The numbers of invertebrates caught in the two synchronously exposed drift nets in each flume were almost identical ($t = 0.073$, $p > 0.05$). For that reason, the mean of the two synchronous catches for each flume was used for further analysis.

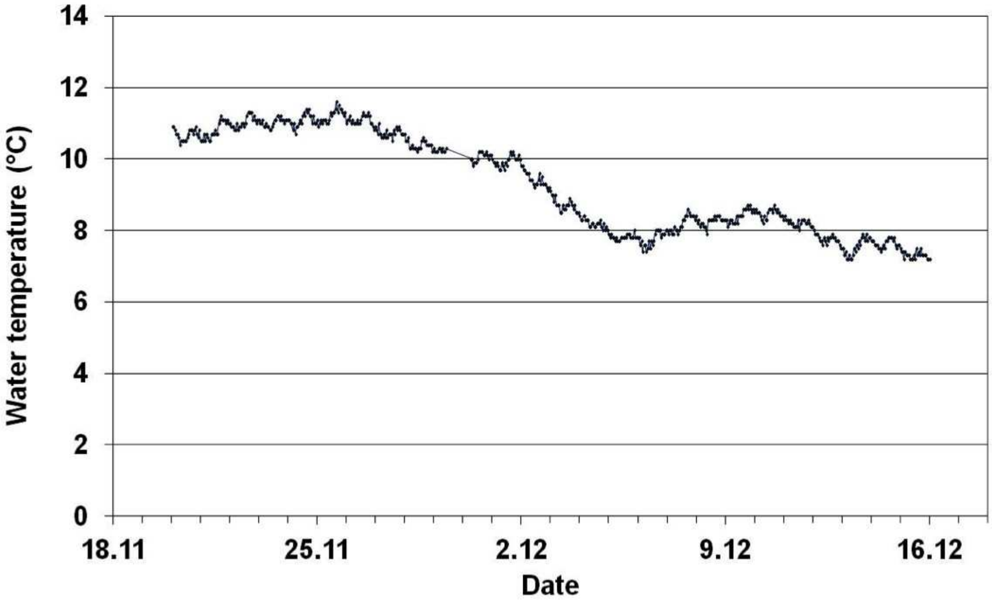

Figure 3. Water temperature in the flumes over the course of the experiment.

There was no significant relationship between light level and the drift ($R^2 = 0.007$, $F_{1,38} = 0.27$, $p = 0.61$). However, there was a significant relationship between drift and temperature ($R^2 = 0.15$, $F_{1,38} =$, $p = 0.015$) (Fig. 4), though this relationship only explained 15% of the variance in night compared to day drift.

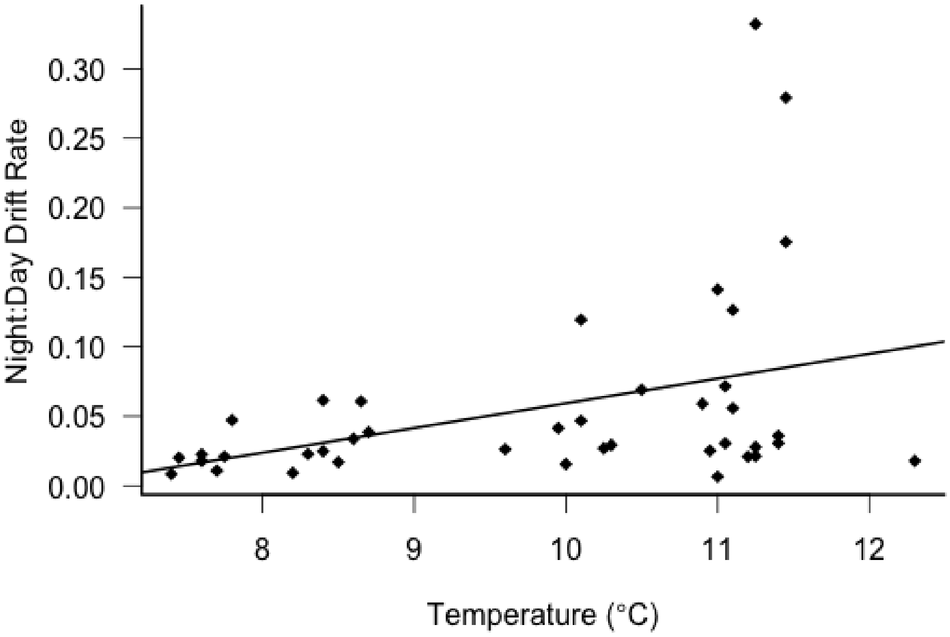

Figure 4. The night relative to day drift rate decreased as the temperature decreased.

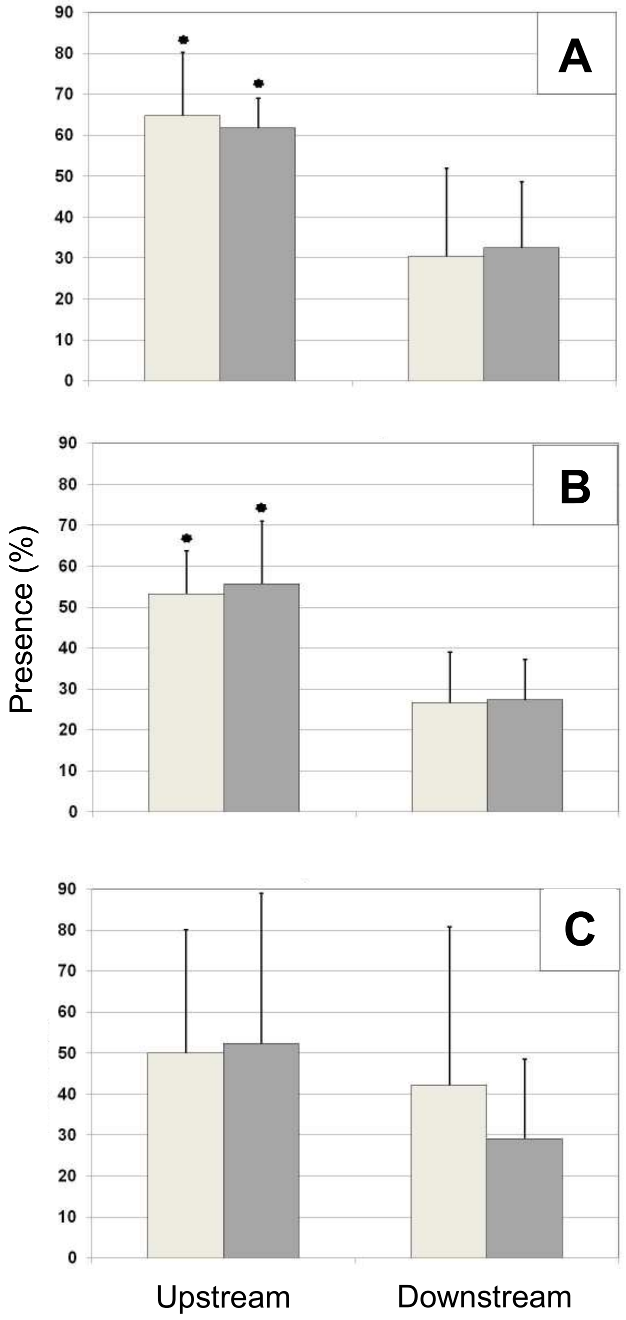

Figure 5. Comparison between the mean (± SD) presence of *G. roeseli* (A), *G. pulex* (B), and *D. villosus* (C) in the upstream and downstream chambers under permanently bright light (416 lx) during the day (beige) and night (grey). Stars indicate significance between up- and downstream chambers (Wilcoxon sign-rank test, level 5%).

Benthic and periphyton biomass results

Benthic samples revealed that the densities of invertebrates between the flumes was variable (mean = 3950 gammarids, SD = 2092.0), which is why we weighted the drift results with the corresponding population size. The highest number of invertebrates (8413 total, or

200 m^{-2}) was in flume 5 (0.28 lx), while the lowest number (1882 total, or 45 m^{-2}) was in flume 8 (0 lx).

Periphyton biomass was not correlated with artificial light, as it was highest (172.2 mg m^{-2}) in the brightest flume, but the lowest quantity grew under a medium light level in flume 4 (49.5 mg m^{-2}) and an intermediate algal growth was in the dark flume 8 (82.9 mg m^{-2}).

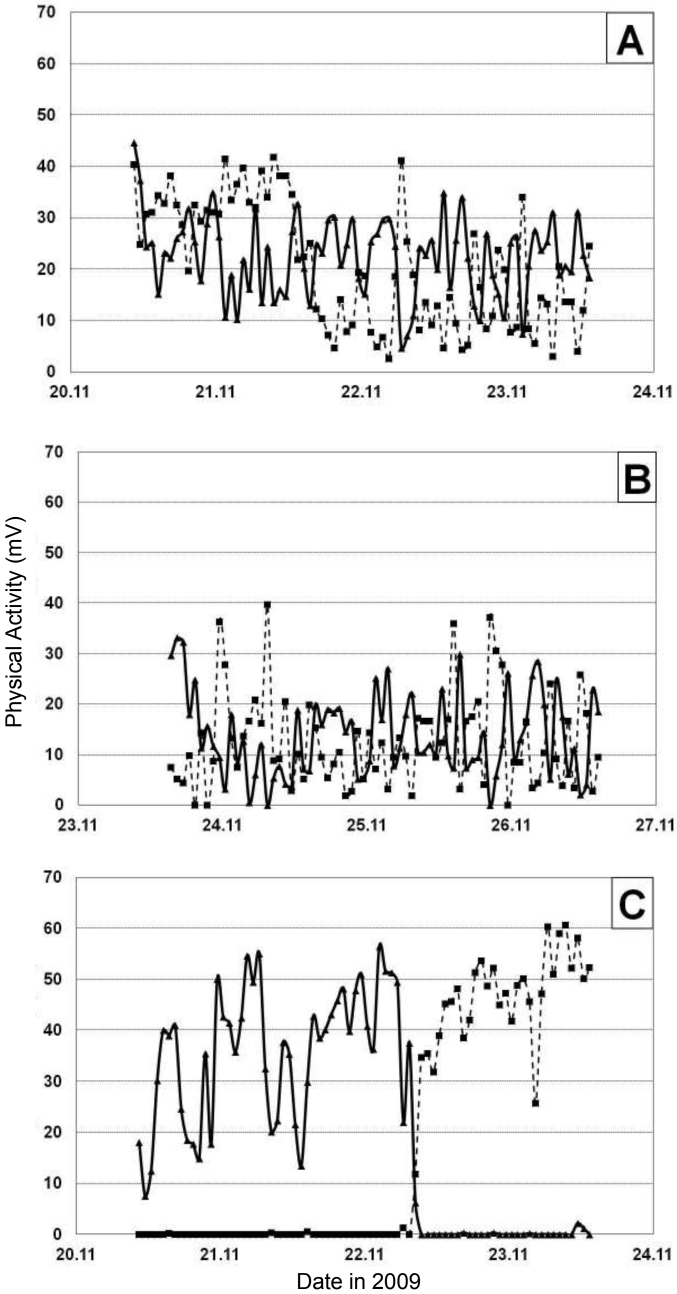

Figure 6. Species specific differences in activity patterns recorded for single specimens of A = *G. roeseli*, B = *G. pulex*, and C = *D. villosus*.

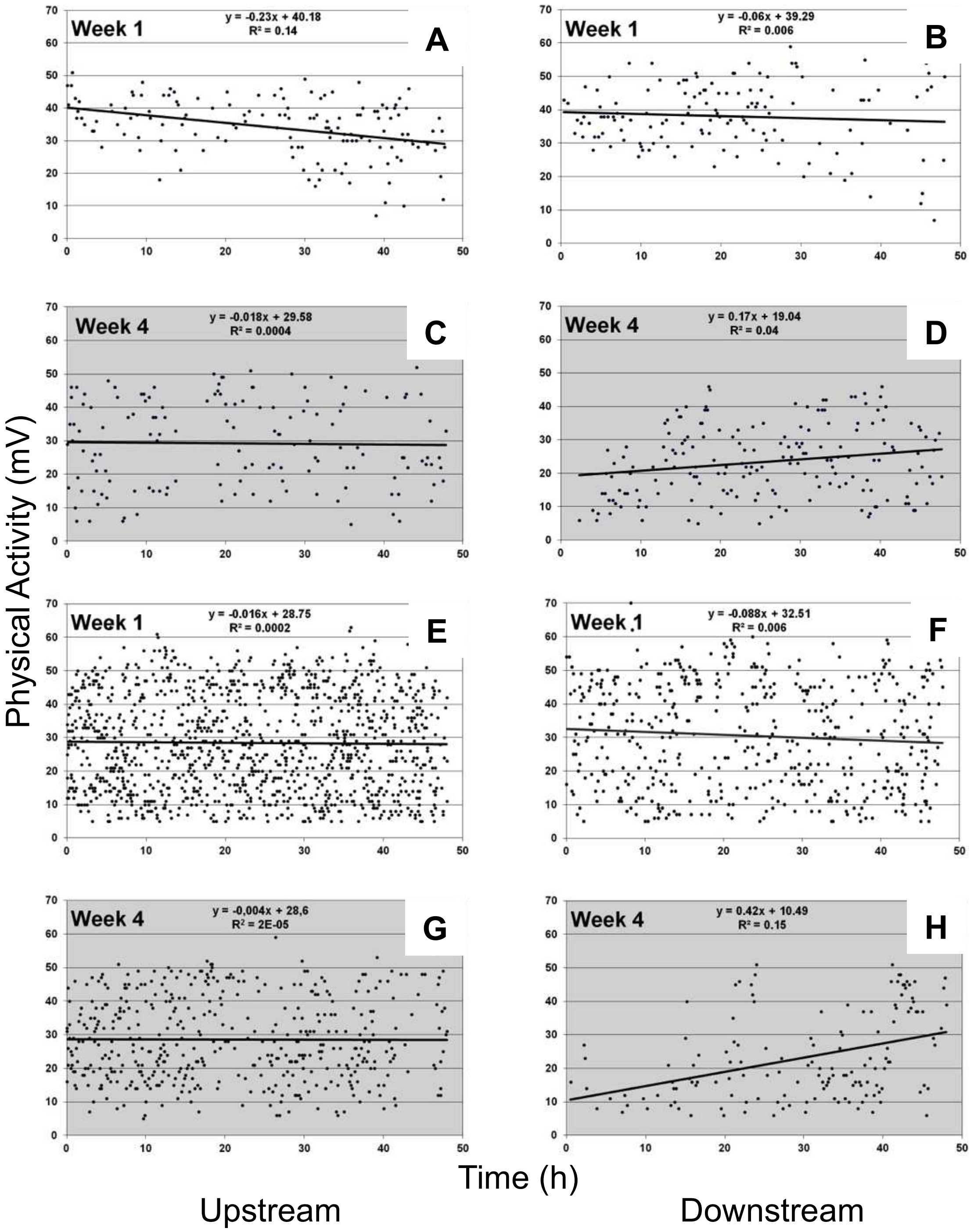

Figure 7. Physical activity of *G. roeseli* (A-D) and *G. pulex* (E-H) as measured by changes in the electric field (mV) in the flow-through chambers of the Multispecies Freshwater Biomonitor (MFB). Each data point represents the mean of all synchronously tested specimens (see materials and methods). A, B, E, and F = light nights (416 lx), C, D, G, and H = dark nights (0 lx).

MFB Experiment

All specimens used in the MFB behaved normally at the start and end of the experiment. The general activity pattern of all 3 species under bright light (416 lx) during both day and night was very similar (Fig. 5) with the upstream chambers being visited more often than the downstream chamber. This finding was insignificant for *D. villosus*, as only 3 individuals from that species could be tested. However, there were pronounced species-specific differences when individuals (i.e. each test tube) were analyzed separately. Both *G. roeseli* and *G. pulex* frequently migrated from the upstream to the downstream test chamber and back again in the course of a day (Fig. 6) and were observed in the transparent connecting tube. In contrast, *D. villosus* moved between chambers only on rare occasions (i.e. after 1 or 2 days) and were present in the transparent connection tube only during quick migrations from one chamber to the other. Unlike the two *Gammarus* species, *D. villosus* seemed to be able to detect the presence of researchers. On the rare occasions when *D. villosus* was present in the connecting tube, *D. villosus* immediately sought shelter in one of the measuring chambers whenever the experimental setup was approached by someone. In order to exclude potential bias as a result of species-specific reactions, the experimental trials with *D. villosus* under bright light at night were not repeated and *D. villosus* was not used in further trials.

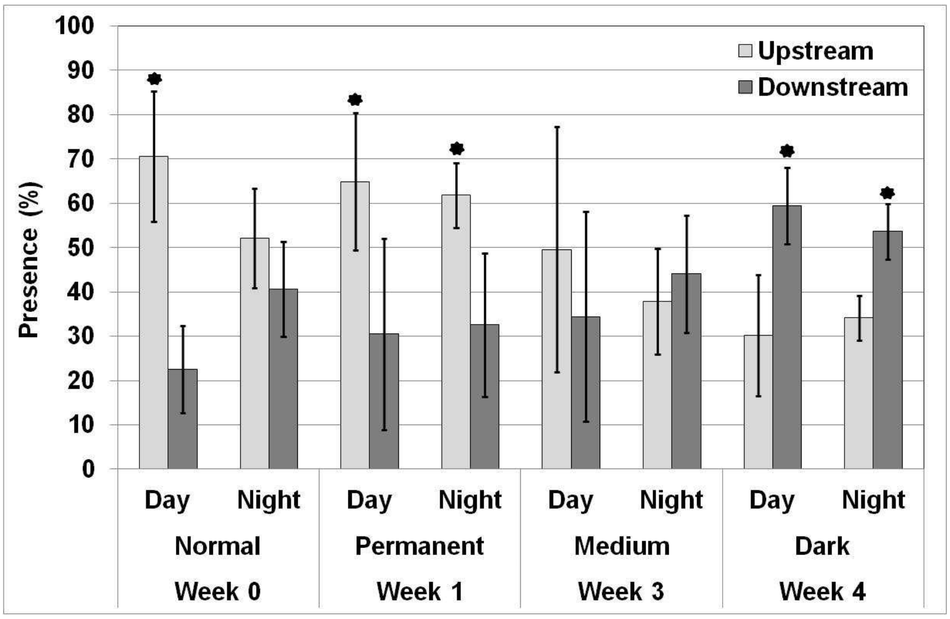

Figure 8. Mean (± SD) presence of *G. roeseli* in the upstream (light grey) and downstream (dark grey) chambers over the course of the experiment. Light at night = 416.0 lx, dimmed = 0.7 lx, dark night = 0.0 lx. Solid stars indicate significance between upstream and downstream measuring chamber (Wilcoxon sign-rank test).

Spontaneous activity was high and highly variable in all gammarid species (Fig. 7, data for *D. villosus* not shown) and there were no pronounced diurnal activity changes. In the completely dark night treatment, activity increased in the downstream chamber in both *G. roeseli* ($R^2 = 0.04$, $F_{3,9} = 20.66$, $p = 0.05$, increase by 42%) and *G. pulex* ($R^2 = 0.15$, $F_{3,9} = 8.20$, $p = 0.05$, increase by 282%) over the course of the 48 h exposure. Under light at night conditions, however, there was a significant decrease of 13% and 27% in physical activity in both the upstream and downstream chamber for *G. roeseli* and *G. pulex*, respectively ($p < 0.05$). *G. roeseli* spent significantly more time in the downstream than upstream chamber when exposed to a normal regime of light day/dark night, in contrast to spending significantly more time in the upstream chamber when exposed to constant light (Fig. 8)

Light measurements in Berlin

The brightest light levels were recorded near a large billboard display on the river (Table 1), and resulted in light readings of approximately 2.5 lx at 20 cm and 1.4 lx at 40 cm under water. The highest light level at 50 cm was 0.4288 lx and was recorded where Friedrichstraße crosses the Spree River in the city center. The lowest light level recorded in the Berlin area was 0.0004 at the end of Ullsteinstr, where the street meets a canal of the Spree River in southern Berlin. This is in a locally green area with little development and where the only buildings are mostly garden homes that are primarily used in the summer. The measurements are all approximate as the turbidity of the water was extremely variable even from second to second. All measurements were taken with the light sensor pointing straight upward; light levels were noted to increase greatly if the sensor was angled toward the nearest light source.

Discussion

There was a hypothesized increase in drift over time; however, the day drift showed an increasing trend as well, indicating that the increase might not have been due to acclimation to the light, but rather as a response to some other variable. Additionally, we found that while there was no relationship between drift rates and light levels, there were lower night-time drift rates in all flumes as temperatures decreased. These results contradict the results from the MFB experiment, which showed increased activity rates in the downstream chamber of the dark at night flume and increased activity rates in the upstream chamber of the light at night flume.

Table 1. Light levels measured[a] at various water bodies in the Berlin area at 50 cm depth, and in the flumes at 20 cm depth, with moonlight light levels for comparison.

Location/Flume/Moon	**Light level (lx)**
Flume 8	*0.0000*
Ullsteinstraße	0.0004
Alt-Gatow	0.0395
Stralauer Allee	0.0403
Flume 7	*0.0420*
Borsigturm	0.0434
Seestraße	0.0434
Großer Spreering	0.0537
Schäfersee	0.0614
Flume 6	*0.1040*
Hauptbahnhof	0.1123
Flume 5	*0.2800*
Müggelseedamm[b]	0.3183
Friedrichstraße	0.4288
Flume 4	*0.5860*
Full moon, clear sky, temperate latitude	0.7
Flume 3	*1.3100*
Kupfergraben	1.4000[c]
Flume 2	*4.1850*
Flume 1	*416.000*

[a] All readings were taken with an ILT1700 light meter with the light sensor held vertical.

[b] This measurement was taken directly below a light on a bridge.

[c] This measurement was taken at a water depth of 40 cm; a measurement at 20 cm in this same location was 2.500 lx.

It is possible that we counted some gammarids drifting in twilight as part of the day drift, given that sunset in Berlin was at 16:07 on 20 November and dusk started at 15:27. By the end of our experiment, dusk was as early as 15:10. However, we kept the bright lights of the hall on from 08:00-16:00 every day and we expect that the brightness from these lights overwhelmed any external signal of dusk from the windows of the hall.

Highly variable activity as observed in the MFB experiments is a common and normal feature in gammarid behavior (Engelhardt 2008) and is in accordance with the MFB results of Berghahn et al. (2012). However, the general pattern was the same in both species. The physical activity levels of each test animal during the dark at night treatment indicated valid measurements as a result of the light regime rather than food deprivation or temperature change. While gammarids of 6-9 mg in weight do feed even at water temperatures lower than 5°C, the periphyton biomass results gave no indication of food deprivation, which could be a reason for increased drift (Hildebrand 1974, Hinterleitner-Anderson et al. 1992). Furthermore, a decrease in water temperature in the course of the experiment should have caused a decrease in activity (Williams 1990). In any case, individuals in the light at night trials would have experienced the same food availability and temperature changes. In the light at night treatment, there was a slight but insignificant decrease in physical activity in both *G. roeseli* and *pulex*, which may be attributed to exhaustion driven by light stress.

Given previous studies have found a close relationship between exposure to light and decreased numbers of drifting macroinvertebrates (Anderson 1966, Bishop 1969, Brewin and Ormerod 1994), we were surprised to find increased drift rates in all flumes with the onset of the light gradient. However, the majority of previous studies have looked at invertebrate drift in the summer months (Anderson 1966, Bishop 1969, Flecker 1992, Brewin and Ormerod 1994). The few studies that have analyzed invertebrate drift patterns in the winter have found patterns that are very different than those found in the spring and summer (Williams 1990, Bogatov and Astakhov 2011).

There are a few possible explanations why we did not see any effect of light treatment on the gammarid drift rates. They include: unnatural invertebrate densities, changes in chemical parameters in the flumes, parasitism, food availability, a lack of drift-feeding predators, and seasonal patterns in drift rates. We will address these possible additional affects and argue that seasonal changes in drift rates are the most likely explanation for our anomalous results.

To begin with, the gammarid densities in this experiment were comparable to the lower end of the range previously found in field abundance during the winter (Welton 1979, Mortensen 1982, Crane 1994, Ladewig 2004, Duran 2007) and therefore representative. The majority of physical-chemical parameters that could have had an effect on physical activity (e.g. oxygen) remained almost constant over time; only temperature changed during the experiment. Host-parasite relationships may also increase and modify the behavior and drift rates in *G. pulex and G. roeseli* (Lagrue et al 2007). However, there were no obvious indications for parasitism in the specimens tested and if so they can be assumed to have been evenly distributed between the populations since the flumes were stocked from the same sources. As previously mentioned, there was no relationship between periphyton biomass and light levels and the periphyton levels we found were not indicative of a lack of food. There was no threat of predation in the experimental streams, and a lack of visual predators has been shown to result in aperiodic drift (Brewin and Ormerod 1994). However, Flecker (1992) found that once invertebrates have been exposed to drift-feeding fish, they retain their preference for night drifting even after the predator has been removed, and all the invertebrates used in this experiment came from streams that contained fish predators.

Finally, there is also the possibility that the patterns we saw in the day and night drift were driven by seasonal changes. Bogatov and Astakhov (2011) saw increases in day relative to night drift during the winter in a far-northern Russian river. However, the increase in day drift they saw coincided with the icing over of the river, leading to lower light levels in the water. Obviously, the water in our study did not freeze over. A previous study (Williams 1990) also found a decrease in nighttime drift when temperatures dropped, while there was no relationship between daytime drift and temperature. The change in drift pattern during the winter may be in response to altered fish feeding behavior. For example, juvenile rainbow trout (*Oncorhynchus mykiss*) have been shown to switch to a mostly night-active foraging schedule during the winter (Contor and Griffith 1995). This supports our results and suggests that diel drift patterns may be subdued during the winter.

Future work

Research is needed to clarify whether gammarids and other invertebrates exhibit seasonal changes in diel drift patterns. Experiments to explicitly test the role of temperature changes and daylight levels in altering patterns of day and night drift will be especially helpful. Furthermore, we recommend taking hourly drift samples throughout the experiment to further clarify when peaks in the drift occur.

Acknowledgments

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Chapter 4:

The effects of artificial night lighting on adult aquatic and terrestrial insects

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Abstract

There is a growing concern that artificial light might affect local insect populations, and disrupt their dispersal across the landscape. In this paper, we experimentally investigated the impact of artificial light on adult aquatic and terrestrial insects in the field, with an emphasis on the effects on aquatic insects. We wanted to know whether the lights prevented the insects' ability to disperse across the landscape; as such dispersal is crucial in repopulating previously degraded ecosystems. We set up 6 high-pressure sodium streetlights along a permanently connected oxbow in the Spree River, approximately 35 km from the city center of Berlin, Germany. We collected insects using 12 flight-intercept traps with trays at 3 different heights (0.5, 1.5, and 2.5 m) that we placed at distances 0, 3, 40, and 75 m from the lights and 5, 8, and 80 m from water. We sampled the traps 22 times between June and September 2010; the lights were on for 11 of these nights and off for the other 11. We hypothesized that the lights would attract aquatic insects and prevent them from moving inland, resulting in more aquatic insects caught at the traps 0 m from the light and fewer insects caught at the traps 75 m from the light on lit compared to dark nights. In total, we caught almost 27 times as many insects at traps 0 m from the lights when the lights were on compared to when they were off, and more insects were captured at tray heights closest to the lights at these traps when the lights were on. Furthermore, the proportion of aquatic insects caught at traps 0, 3, and 40 m from the lights when the lights were on was significantly higher than when the lights were off. Our results suggest that adult aquatic insects are more affected by artificial lights than terrestrial insects, and that city planners should take this into account when designing lighting systems around freshwater bodies.

Keywords: High Pressure Sodium Lamp, connectivity, dispersal, light pollution, river

Introduction

Artificial light at night occurs virtually everywhere there are permanent human settlements. Because people tend to live around freshwater sources (Kummu et al. 2011), artificial light is especially likely to adversely affect freshwater systems. Streams may be particularly threatened as a result of their geometry—being narrow bands of habitat. Indeed, a recent study found that linear and flowing water bodies were about 6 times brighter than standing water bodies (Kuechly et al. 2012). However, it has only been in the last 10-20 years that ecologists have turned their attention to the possible influences of artificial light on organisms and ecosystems (Longcore and Rich 2004), and freshwater ecosystems have received less attention than terrestrial and marine systems (Perkin et al. 2011). This is despite the fact that artificial light at night has the potential to negatively impact biodiversity (Hölker et al. 2010).

In addition to light trapping being used as a common method of attracting both aquatic and terrestrial adult insects in order to study dispersal, studies have found that artificial lighting used by humans, specifically streetlights, can attract large numbers of insects (Scheibe 2003, Eisenbeis 2006). The results of these studies are rather intuitive, as most people have had experience with insects being attracted to light, but lead to further questions: do artificial lights reduce the dispersal of aquatic insects across terrestrial environments? And, do artificial lights change the behavior of flying aquatic insects? Furthermore, these previous studies have weaknesses that include a limited sampling duration and spatial scope (Scheibe 2003) and comparing catches from pre-existing lights that are in very different habitat types, such as in riparian areas and along suburban streets (Eisenbeis 2006).

The dispersal of adults across the terrestrial landscape is an important component of the aquatic insect life-cycle. Adult dispersal can lead to the colonization of new habitats as well as re-colonizing streams that may have suffered losses of aquatic insects through flood events or human disturbance (Blakely et al. 2006). Dispersal also maintains gene flow between populations (Bohonak 1999). There have been few studies to understand the factors that affect adult insect dispersal, especially in urban environments (Smith et al. 2009), although Eisenbeis (2006) hypothesized that artificial lights can act as a both a barrier to insect dispersal and a vacuum cleaner which attracts insects from the surrounding area, no one has yet tried to test this hypothesis. Previous studies have shown that the inland dispersal of adult aquatic insects is limited (Petersen et al. 1999, reviewed in Bilton et al. 2001, Petersen

2004), but others have found evidence that a few adult aquatic insects travel up to 5 km inland (Kovats et al. 1996) or far enough to pass over watershed boundaries (Macneale et al. 2005). It is likely that meteorological conditions (i.e., wind speed, air temperature, humidity) influence the flight of adult aquatic insects, with fewer insects flying in instances with high wind speeds and during precipitation events, or low temperatures (Waringer 1991, Briers et al. 2003).

Both dispersing and returning adult aquatic insects play an important role in terrestrial and aquatic food webs and have been the focus of studies of terrestrial–aquatic linkages. It has been estimated that up to 97% of adult aquatic insect biomass is lost to the terrestrial system, providing an important food source for spiders, bats, and birds, among other organisms (Jackson and Fisher 1986, Nakano and Murakami 2001). Adult aquatic and terrestrial insects are also a major food source for fish (reviewed in Baxter et al. 2005). Given the importance of adult aquatic insects to both terrestrial and aquatic food webs, it is essential to determine how artificial light might affect their abundance and dispersal across the landscape.

This is the first study that has added streetlights to a non-urban environment to test how lights impact the dispersal of adult aquatic insects. This allowed us to separate the effect of light pollution from other stressors common in an urban setting. The purpose of this research was to test whether a common type of streetlight (high pressure sodium, HPS) would: 1) prevent adult aquatic insects from dispersing inland as suggested by Eisenbeis' barrier theory. Support for this hypothesis would be fewer aquatic insects being captured at inland traps on lit nights than on dark nights. 2) That artificial light at night would shift the flight height of dispersing insects upward towards the height of the lights as suggested by Eisenbeis' vacuum cleaner theory. 3) Finally, that artificial light would have a greater negative effect on aquatic than terrestrial insects. Support for this hypothesis would be trapping more aquatic than terrestrial insects in traps near lights when the lights are on.

Materials and Methods

Experimental Area

Sampling was conducted from June to September 2010 on an island in the lowland Spree River, approximately 35 km southeast of Berlin, Germany (52°22' N, 13°48' E). During the course of our experiment (9 June-9 September 2010), the Spree had a mean discharge of 17.4 m^3s^{-1} (maximum: 30.9 m^3s^{-1}, minimum: 7.7 m^3s^{-1}; J. Köhler, unpublished data). Average yearly (1971-2000) air temperature for the area was 9.6 °C (average high: 23.7 °C; average low: -1.9 °C). The area receives about 570 mm of precipitation a year, mostly falling during intense summer storms or as snow (World Meteorological Organization, http://worldweather.wmo.int/016/c00059.htm#climate, accessed 4 January 2013). Common aquatic insect groups in this area of the Spree include Chironomidae (38 spp.) and other Dipterans (20 spp.), Odonata (23 spp.), Trichoptera (38 spp.), and Ephemeroptera (20 spp.) (Köhler et al. 2002). The island and the area around it is agricultural land—the island itself is used as a cattle pasture, and cattle had access to the island during the June, July, and first two August sampling periods.

Insect Collection and Identification

Samples were taken six nights each month during June, July, and September, and 4 nights during August 2010. These nights were "paired" as two or three sets of two nights, the first of which the lights were kept off and the second of which the lights were illuminated. Generally, this created a data set where the environmental conditions were similar between the two nights (Appendix 1).

Figure 1. Flight intercept trap (location: 0 m from artificial light) with an emergence trap floating on the Spree River in front of it. Light level (lx) at each tray height written in white. Photo credit: E. K. Perkin

Trap design and placement — Insects were captured with flight intercept traps, which consisted of 100 x 50 cm Plexiglas panels and 100 cm x 17.5 cm x 14.5 cm brown plastic planters used as collection trays (Fig. 1). A total of twelve flight-intercept traps were used for insect collection; three located 5 m from the edge of the Spree with lights ("0 m"), three located 3 m inland from those with lights ("3 m"), three located 5 m from the edge of the Spree without lights ("40 m"), and three in the center of the island without lights ("75 m" Fig. 2). The plexiglas ("flight-intercept") panels were placed at heights of 50-100 cm, 150-200 cm, and 250-300 cm. Trays were fitted below and on either side of the panels, so that the local flying direction and heights of insects could be determined.

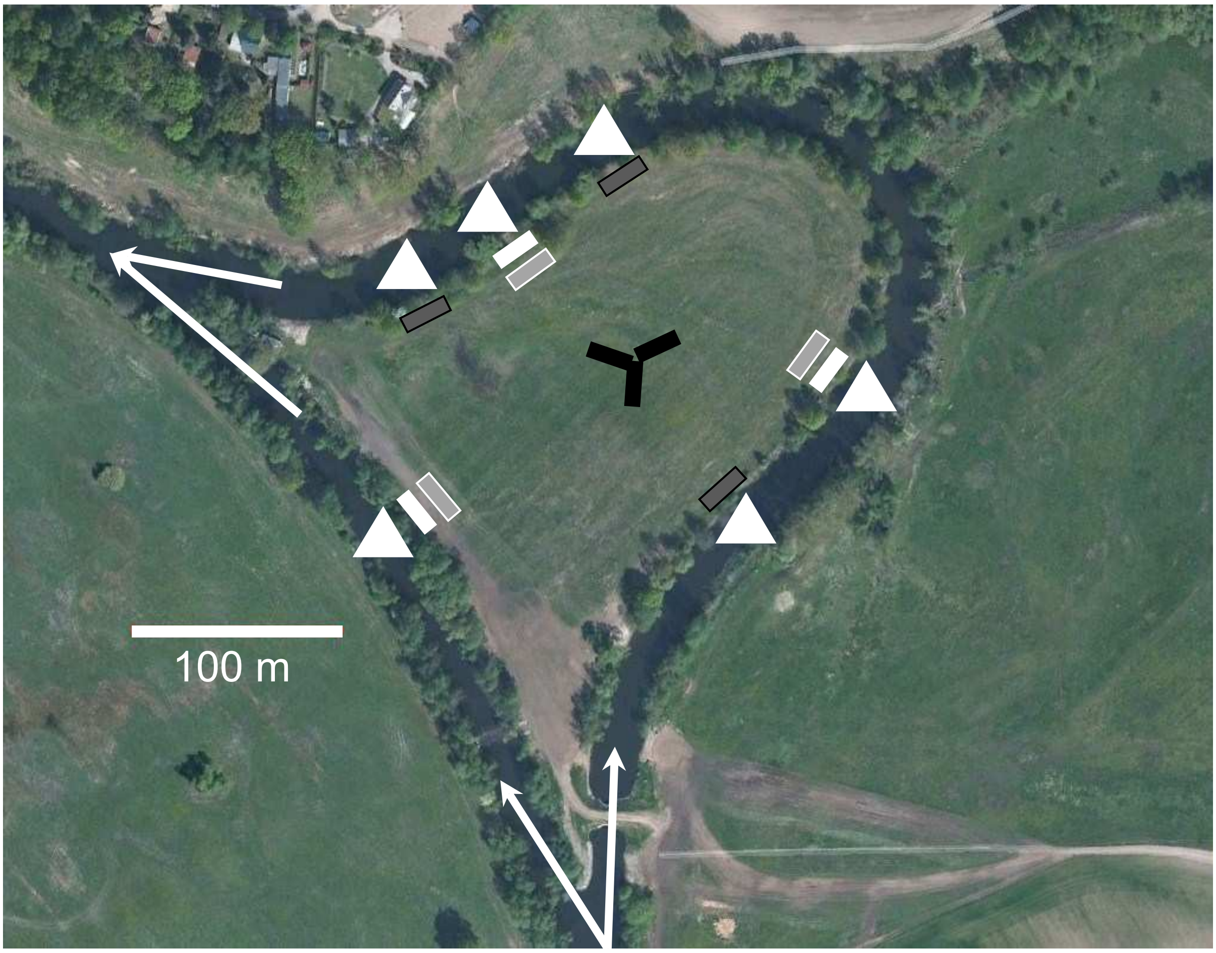

Figure 2. An aerial photo of the field site from Google Earth. The thick white lines indicate the locations of traps 0 m from lights, grey with white outline = 3 m from lights, dark grey with black outline = 40 m from lights, and black = 75 m from lights. The white triangles indicate the locations of the emergence traps. Arrows show the direction of flow of the Spree River. The long white bar = 100 m.

Sampling — In order to set-up the traps for sampling, the water in the trays was twice filtered through a 300 μm sieve. Repeated visual inspection of the trays demonstrated that this was sufficient to rid the trays of any previous foreign material. A few drops of detergent were added to water in the trays as a surfactant. Traps were set-up (water filtered) at sunset (approximately 21:45 for June, 21:35 for July, 20:35 for August, and 19:50 for September). Samples were taken at sunrise (approximately 4:45 for June, 5:00 for July, 5:40 for August, and 6:20 for September) by twice filtering the tray contents through a 300 μm sieve and then emptying the sieve contents into a bottle filled with 70% ethanol, except for the month of September, when 100% ethanol was used. The exact time of set-up and sampling was recorded for each trap so that the number of insects caught in each trap could be recorded as number of insects hr^{-1} m^{-2}.

Emergence traps — Six floating, pyramidal emergence traps were placed in the Spree River directly in front of the flight-intercept traps located on the Spree (Fig. 1). The base of the pyramid was 60 cm by 60 cm. The sides of the traps consisted of <300 μm mesh and led to a plastic top, with a funnel to allow the entrance of emerging aquatic insects but prevent their escape. This top was filled with 70% ethanol and was sampled every evening during trap set-up, in the morning during flight-intercept sampling, as well as the weeks between sampling periods. Contents of the tops were filtered through a 300 μm sieve and stored in bottles filled with 70% ethanol. Damage to some of the emergence traps prevented us from sampling every trap every night of the experiment, no emergence samples were taken in September due to the 100% ethanol breaking the adhesive holding the tops together.

Insect identification — Insects were identified using Müller (1986) to the level of order and counted under a 40 x dissecting microscope. Dipterans were classified as either “aquatic” or “terrestrial.” Chironomids were the most commonly caught dipterans and made up the bulk of the aquatic diptera. Tipulids and culicomorpha (in addition to chironomids) were also included in the “aquatic” classification. The “terrestrial” group was mostly made up of muscomorpha. While we are confident that the dipteran classified as aquatic are indeed from aquatic larvae, it is possible that some dipterans classified in the “terrestrial” group are aquatic as well, though this is a very small portion of that group. Samples containing more than approximately 1000 insects were sub-sampled. Sub-samples were taken from a randomly selected quadrant of a 15.1 cm by 8 cm plastic container. Sub-samples were then counted and identified in the same manner as the other samples. The portion of the sample remaining after sub-sampling was checked for rare taxa that were separately counted and identified.

Light Measurements

Light measurements were taken with an ILT1700 lux meter (International Light Technologies, Peabody, MA, USA) at the start and end of each night of set-up, and before the morning sampling started. This light meter was chosen as it is very accurate even at low light levels. Generally, light measurements were all taken in the same spot in an exposed area of the island; however, in July and August, light measurements taken after the evening set-up was over were also taken at three different traps located across the island: one dark trap on the edge of the island, one dark trap in the center of the island, and one light trap at the edge of the island (Fig. 2, Appendix 2A & B). Additionally, detailed spectral measurements of the lights were taken with an AvaSpec-2048 spectrometer (Avantes, Apeldoorn, The Netherlands) on the evening of 8 September (Appendix 3).

Weather Variables

Air temperature (Fig. 3), precipitation amounts, humidity, wind speed and direction were all measured every 15 min during the entire experiment with a WS 444 PC weather station (Conrad Electronic GmbH, Hirschau, Germany). Unfortunately, this weather station experienced outages at times during the experiment. In these cases, hourly weather data from another nearby (~15 km away) weather station on the Spree was used. The quarter-hourly or hourly weather data for each sampling night was averaged for the entire night, from the time of set-up to the time of sampling in the morning.

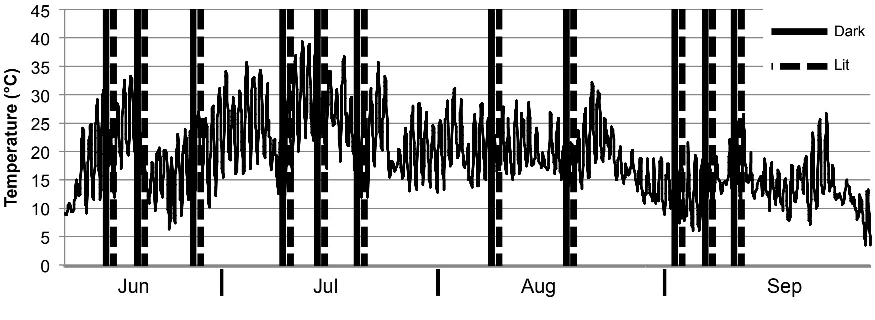

Figure 3. Air temperature during the sampling period. Sampling dates are indicated by solid (dark nights) and dashed (lit nights) bands.

Data Analysis

Wilcoxon signed-rank tests were used to test whether the dark and lit night catches for the four categories of traps (0, 3, 40, and 75 m from lights) and tray height (lower, middle, upper) and direction (facing the river or facing inland) were different from one another. To determine whether the proportion of insects caught on lit versus dark nights was different at the different traps, we used a factorial (Lights on or off, trap location, and interaction between the two) ANOVA. When results were significant, we used a Tukey's HSD *post hoc* test to determine which locations differed from one another. An ANOVA was used to test if more insects were caught at higher trays than at lower trays and in trays facing the river versus inland-facing trays, followed by a Tukey's HSD. Step-wise regression analysis was used to determine if there was a relationship between aquatic insect catches and temperature, humidity, and wind speed. For both the step-wise regression and ANOVA tests, insect catches were transformed as $\ln(y + 1)$ to better meet the condition of normality. Precipitation was excluded from this analysis, as no measurable amount of precipitation fell on sampling nights (Appendix 1). Differences in temperature, humidity, and wind speed between dark and lit nights were tested with paired t-tests. All analyses were done in R (R Development Core Team 2011). Alpha for all tests was set at 0.05, but after Bonferroni correction was applied, the alpha for all Wilcoxon signed-rank tests was set at 0.0013.

Results

Spatial distribution of insects

All trays from the traps located directly at the lights (0 m) caught significantly more aquatic insects on nights that were lit as opposed to dark (Table 1, Fig. 4), regardless of tray height and direction. However, only the catches from the middle and upper trays caught significantly more terrestrial insects on lit than dark nights. The traps that were three meters back from the lights captured significantly more aquatic insects on lit nights than dark nights (Tables 1 and 2, Fig. 4A) regardless of tray height or direction. There was no difference in the number of terrestrial insects caught at these trays whether the lights were on or off (Table 1, Fig. 4B). Traps 40 m and 75 m from the lights did not catch significantly more aquatic or terrestrial insects when the lights were on or off (Table 1, Fig. 4C & D). These patterns generally held true for the most common insect orders (Fig. 5, Appendix 4). However, the Thysanoptera were a notable exception, with more of them having been caught at all traps on dark nights than on lit nights. These results suggest that we reject the hypothesis that artificial light would prevent adult aquatic insects from dispersing inland when lights are ~80m apart.

Table 1. Summary of the Wilcoxon test statistics for trap location, height, and dispersal direction on lit vs. dark nights. *** $p \leq 1.0e^{-10}$, ** $p \leq 1.0e^{-5}$, * $p \leq 0.001$

Trap location	Tray Height/Direction	Aquatic or Terrestrial Insects	$W_{0.0013,\ 197}$†	p
0 m	Low	Aquatic	625	$1.585e^{-12}$***
	Middle		546.5	$1.145e^{-13}$***
	Upper		576	$3.129e^{-13}$***
	Inland		1403.5	$< 2.2e^{-16}$***
	River		1295	$< 2.2e^{-16}$***
	Low	Terrestrial	1752	0.05
	Middle		1375.5	0.0003*
	Upper		1304.5	$7.036e^{-5}$*
	Inland		3482	0.0004^{*}
	River		3101.5	$8.109e^{-6}$**
3 m	Low	Aquatic	1241.5	$2.041e^{-5}$*
	Middle		1309	$7.722e^{-5}$*
	Upper		1381.5	0.0003^{*}
	Inland		2613	$1.4e^{-8}$**
	River		3329	$9.742e^{-5}$*
	Low	Terrestrial	2217.5	0.86
	Middle		2431.5	0.25
	Upper		2031.5	0.51
	Inland		4966.5	0.87
	River		5054	0.70
40 m	Low	Aquatic	1880.5	0.18
	Middle		1681	0.02
	Upper		2161.5	0.94
	Inland		4198.5	0.08
	River		4394	0.21
	Low	Terrestrial	2226.5	0.83
	Middle		2407.5	0.30
	Upper		2554	0.09
	Inland		5514	0.13
	River		5238	0.40
75 m	Low	Aquatic	1917.5	0.36
	Middle		2103.5	0.97
	Upper		2287.5	0.62
	Inland		4853.5	0.91
	River		4635	0.86
	Low	Terrestrial	2098.5	0.95
	Middle		2613	0.02
	Upper		2340.5	0.46
	Inland		5285.5	0.34
	River		5307	0.12

There was an interaction between the height at which aquatic insects were captured and whether or not the lights were off ($F_{2,1531}$, $p = 0.03$), indicating that adding light altered the height at which these insects flew. This provided support for our second hypothesis that the flight height of dispersing insects would shift upward towards the height of the lights.

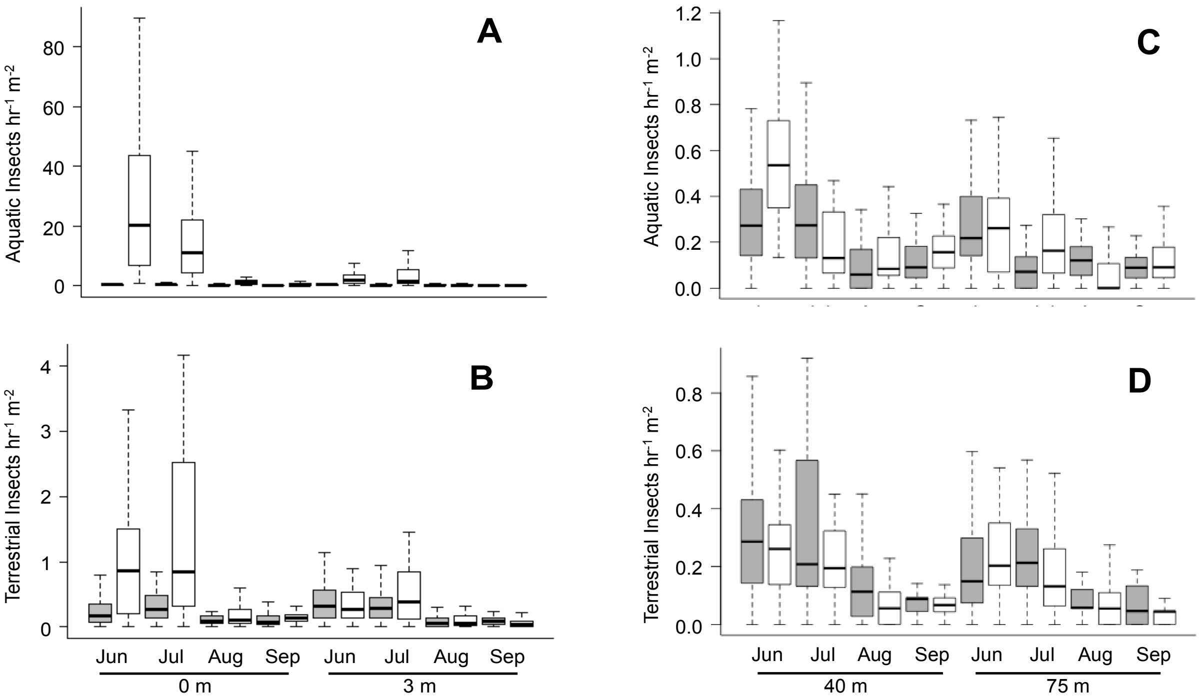

Figure 4. Aquatic (A & C) and terrestrial (B & D) insect densities caught at 0 and 3 m (A & B) and 40 and 75 m (C & D) from lights during lit (white) and dark (grey) nights for each of the months of the experiment. The center line of each box represents the mean, while the bottom and top of the boxes represent the first and third quartiles, respectively. Whiskers extending beyond the boxes range from the minimum to 1.5 x the interquantile range. Note that the scales of the y-axes are different for all four plots. N = 1579

Table 2. Mean number of insects captured ($hr^{-1}m^{-2}$) at each trap location in the different months of the study.

Month	Location	Sample Size	Mean ± SD			
			Aquatic Lit	Aquatic Dark	Terrestrial Lit	Terrestrial Dark
June	0	54	34.55 ± 40.12	0.44 ± 0.31	1.19 ± 1.28	0.25 ± 0.24
	3	54	3.05 ± 3.01	0.47 ± 0.31	0.37 ± 0.36	0.40 ± 0.35
	40	54	0.58 ± 0.34	0.32 ± 0.26	0.26 ± 0.18	0.34 ± 0.30
	75	54	0.26 ± 0.20	0.27 ± 0.17	0.28 ± 0.29	0.21 ± 0.16
July	0	54	17.71 ± 20.34	0.61 ± 0.83	1.62 ± 1.86	0.35 ± 0.28
	3	54	4.26 ± 7.40	0.43 ± 0.45	0.92 ± 1.50	0.38 ± 0.49
	40	54	0.62 ± 1.39	0.38 ± 0.49	0.33 ± 0.44	0.38 ± 0.45
	75	54	0.21 ± 0.21	0.09 ± 0.09	0.20 ± 0.22	0.23 ± 0.27
August	0	36	2.52 ± 4.48	0.23 ± 0.24	0.27 ± 0.42	0.11 ± 0.10
	3	36	0.65 ± 1.25	0.24 ± 0.28	0.13 ± 0.16	0.12 ± 0.14
	40	36	0.17 ± 0.26	0.11 ± 0.12	0.10 ± 0.13	0.13 ± 0.13
	75	36	0.05 ± 0.07	0.13 ± 0.11	0.08 ± 0.09	0.08 ± 0.07
September	0	54	0.69 ± 1.05	0.16 ± 0.14	0.14 ± 0.11	0.10 ± 0.10
	3	54	0.16 ± 0.15	0.15 ± 0.13	0.06 ± 0.07	0.09 ± 0.09
	40	54	0.12 ± 0.12	0.16 ± 0.13	0.08 ± 0.07	0.08 ± 0.06
	75	54	0.10 ± 0.09	0.12 ± 0.09	0.04 ± 0.04	0.06 ± 0.06

When the numbers of Ephemeroptera and Trichoptera caught were analyzed separately, they had some slight differences with the aquatic insect catches as a whole. There was no effect of the tray direction on the numbers caught ($F_{1,1531}$, $p = 0.97$), but there was a significant effect of tray height ($F_{2,1531}$, $p = 0.02$). The lower trays caught significantly fewer insects than the upper trays ($p = 0.013$), but there was no difference in the number of Ephemeroptera and Trichoptera caught in the lower and middle ($p = 0.12$) or the middle and upper ($p = 0.67$) trays. However, there was no interaction between height and whether the lights were on and off in the number of Ephemeroptera and Trichoptera caught ($F_{2,1531}$, $p =$ 0.11), indicating that the lights did not change the height at which these insects flew.

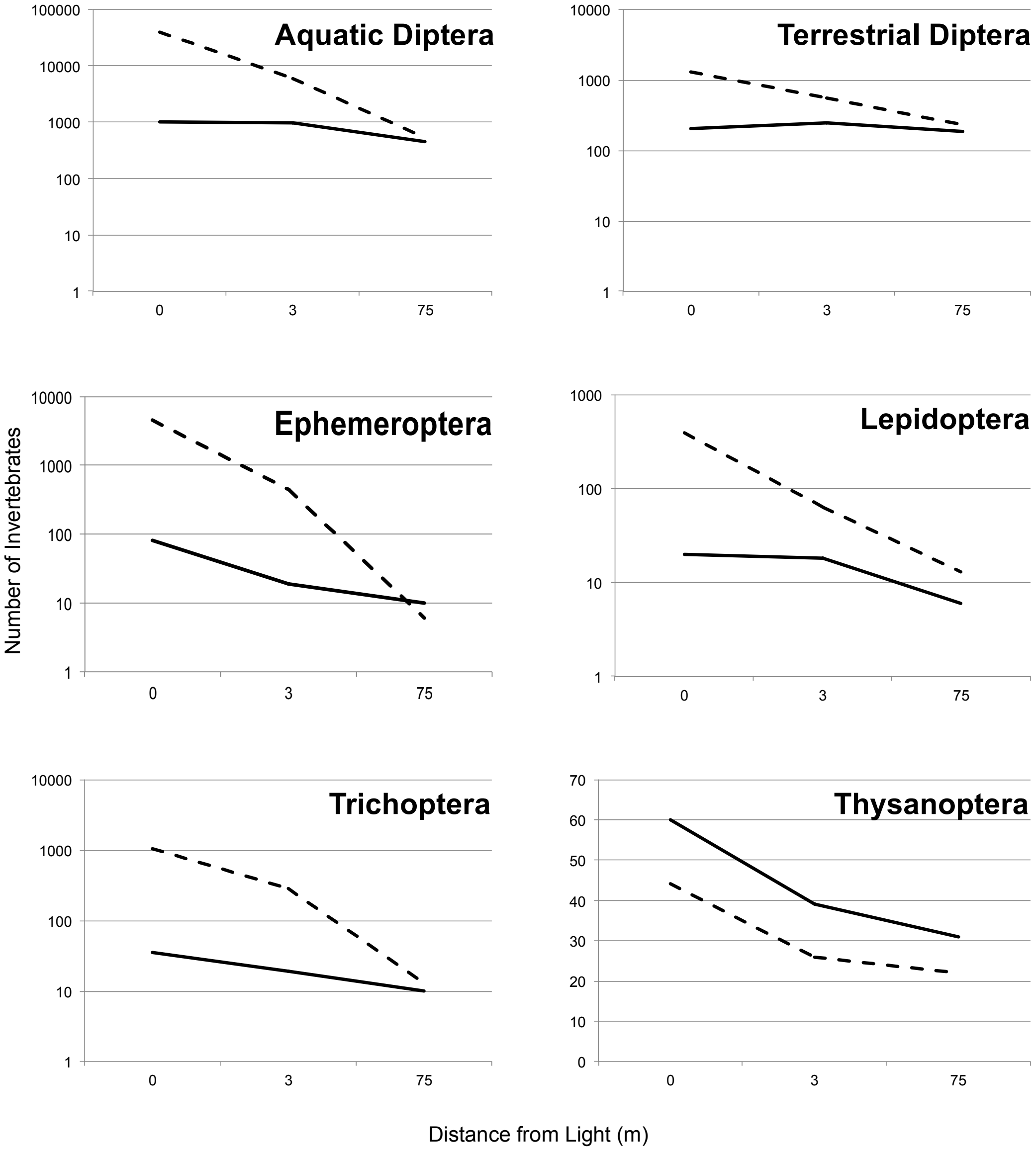

Figure 5. The total number of aquatic diptera, ephemeroptera, trichoptera, terrestrial diptera, lepidoptera, and thysanoptera caught at 0, 3, and 75 m from the lights on lit (dashed) and dark (solid) nights for the entire sampling period. The y-axes of all but the Thysanoptera plot are in log-scale.

Proportion of aquatic insects

There was a significant difference in the proportion of aquatic insects caught on lit versus dark nights ($F_{1,1571} = 122.8$, $p < 0.0001$) and at the different trap locations (Table 3, Fig. 6). There was a significant interaction between the two factors ($F_{3,1571} = 12.51$, $p < 0.0001$), indicating that the lights only had an effect at certain locations. The traps 0, 3, and 40 m from the lights all captured a significantly higher proportion of aquatic insects on lit nights as opposed to dark nights (Appendix 5). However, the proportion of insects caught at traps 75 m from the lights was about 50%, regardless of whether the lights were on or off. These results provided support for our third hypothesis, that artificial light would have a greater effect on aquatic than terrestrial insects.

Table 3. ANOVA summary table for the proportion of insects caught that were aquatic.

	DF	*SS*	*MS*	*F*	*p*
Lit-Dark	1	9.74	9.736	122.80	< 0.0001
Location	3	14.78	4.928	62.15	< 0.0001
Lit-Dark:Location	3	2.97	0.992	12.51	< 0.0001
Residuals	1571	124.57	0.079		

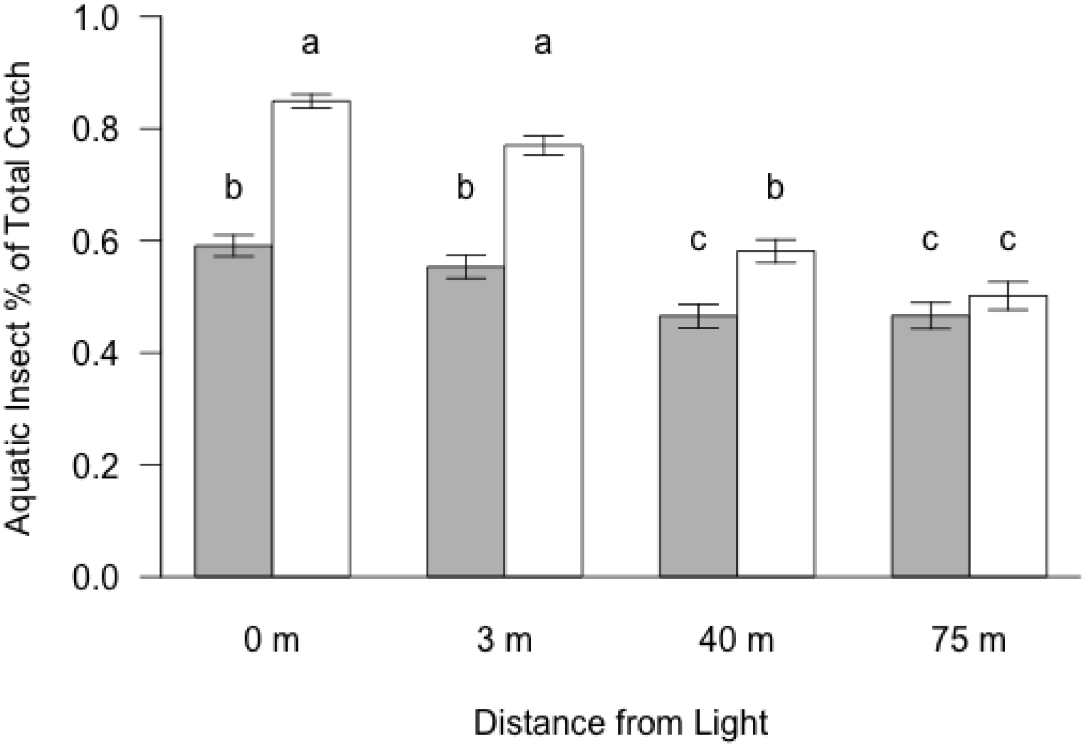

Figure 6. The mean (± SE) proportion of the insects caught at each trap location on lit (white) and dark (grey) nights that were aquatic. Letters represent statistically equivalent groups. N = 1579.

Insect catches and meteorological conditions

We found evidence for a statistically significant positive relationship between the number of aquatic insects captured during the night and temperature ($p < 0.001$), and a negative relationship between insect catches and wind speed ($p < 0.001$, $R^2 = 0.07$, $F_{2,1576} = 56$). The linear relationship between aquatic insect catches, temperature, and wind speed is described by the equation: Y ~ 0.034(Temperature) – 0.046(Wind speed) – 0.019. Humidity was not found to have any statistically significant effect on aquatic insect catches in this study.

We found no evidence that there were different temperatures ($t = -1.4$, df = 10, $p > 0.05$), levels of humidity ($t = 1.6$, df = 10, $p > 0.05$), or wind speeds ($t = 1.1$, df = 10, $p > 0.05$) on dark and lit nights from paired t-tests (Appendix 1).

Emergence Traps

There was no evidence of differing emergence numbers in dark and lit nights in either emergence traps located directly in front of lights (N = 14, $W = 173$, $p = 0.74$, mean ± S.E. dark = 11.62 ± 2.86, lit = 27.66 ± 8.31) or at traps located between lights (N = 18, $W = 77.5$, $p = 0.36$, mean ± S.E. dark = 11.28 ± 2.69, lit = 13.04 ± 3.33) (Table 4). Using the mean number of aquatic insects caught at the emergence and flight intercept traps hr^{-1} m^{-2} for each month, this means that the flight intercept traps 0 m from the lights caught, on average, approximately 109%, 49%, and 24% of emerging aquatic insects in June, July, and August, respectively. In contrast, on dark nights, approximately 3%, 4%, and 6% of emerging aquatic insects were captured at intercept traps 0 m from lights in June, July, and August, respectively.

Table 4. Mean number of aquatic insects captured ($hr^{-1}m^{-2}$) at the emergence traps in June, July, and August.

Month	Location	Sample Size	Mean ± SE	
			Aquatic Lit	Aquatic Dark
June	Between	6	4.88 ± 2.07	4.12 ± 0.82
	Light	5	31.83 ± 14.65	14.85 ± 3.78
July	Between	6	20.79 ± 7.53	16.57 ± 6.63
	Light	6	36.40 ± 16.31	14.49 ± 5.74
August	Between	6	13.44 ± 5.20	13.16 ± 3.54
	Light	5	10.37 ± 4.86	4.08 ± 0.85

Discussion

This was the first study to experimentally introduce actual streetlights to a dark area and determine how this would alter adult aquatic (and terrestrial) insect flight. Previous studies have either used existing streetlights (Eisenbeis 2006) or have not explicitly investigated the effects of artificial light on dispersal (Scheibe 2003). As such, this study provides important initial information about how the flight of adult aquatic insects is altered by artificial lights, but it is only a starting point and further work will need to be done to fully understand the underlying mechanisms and the effects of artificial light on adult aquatic insect flight.

Spatial distribution of insects

If artificial light really disrupted the inland dispersal of aquatic insects, we would have seen an increase in the number of insects caught at the traps closest to the lights on lit nights, as we did. However, this should have been coupled with a decrease in the number of aquatic insects captured 75 m from lights on lit nights. While previous studies (Collier and Smith 1998, Petersen et al. 1999, Delettre and Morvan 2000, though note exceptions have been found by Svensson 1974, and Winterbourn et al. 2007) have found that the number of aquatic insects caught at traps decreased exponentially with an increasing distance to water, we had hypothesized that there would be more aquatic insects found at the traps 75 m from the lights on dark nights than on lit nights. It is likely that these traps were simply too far from the shore to catch enough aquatic insects to see a light effect. It was originally planned to have traps located every 10 m back from the lights; however, the restrictions of the field site prevented us from doing so. A recent study suggests that rivers with high sinuosity will see a greater exchange of aquatic resources—in the form of adult aquatic insects—than rivers with straighter channels (Sabo and Hagen 2012). If that is indeed the case, then we were more likely to have seen an effect on the number of aquatic insects making it to the center of the field at our field site in a connected oxbow than had we picked a straighter river reach for the study and had just created transects of flight intercept traps perpendicular to the river.

On the other hand, this makes the results from the traps 40 m from the lights even more interesting. While these traps were 40 m from the lights, they were still only 5 m from the water. Like the traps 75 m from the lights and in the center of the island, those 40 m from the lights caught no more aquatic insects on lit nights than on dark nights. However, the proportion of insects caught at traps 40 m from lights on lit nights was significantly greater than on dark nights, suggesting that there is still some effect of the light even at a distance of 40 m.

It is possible that the lights in our study were too far apart (~ 80 m) to cause a disruption in dispersal. The spacing between lights in an urban or suburban environment is closer to 30 m (Ylinen 2011). Given the flight intercept traps in the month of June caught more aquatic insects hr^{-1} m^{-2} than were emerging (Tables 2 and 4), it is very likely that once a threshold of lighting has been reached, no more aquatic insects are able to disperse inland.

We found evidence for increased flying height to match the height of the lights, but saw no effect of the side of the traps on which insects were caught (i.e., direction of flight). That insects increased the height at which they flew when the lights were on further supports the hypothesis that artificial lights create concentrated areas of aquatic insects. In a general study of adult aquatic insect dispersal, Jackson and Resh (1989) found no difference in the number of aquatic insects they captured at heights of 2, 5, or 8 m. Most streetlights are mounted at heights between 3 and 12 m, so it is likely that we could see a shift in insect abundance from being rather widely distributed through the airspace to being concentrated in narrow bands at roughly the height of nearby artificial lights. We expected to see higher numbers of aquatic insects captured in the river-facing trays and terrestrial insects in the trays facing inland. That the direction the trays faced had no effect on the number of insects captured suggests that insects are dazed by the lights (as suggested in Eisenbeis 2006) and their flight becomes circular rather than directional.

We thought that there might be more aquatic insects emerging from the water on lit than on dark nights, as we hypothesized that the lights might prolong the dusk period in which many insects emerge (Tobias 1967, Jackson 1988, Pinder et al. 1993), but that was not the case. The same result was found in a similar study on artificial light outside Vancouver, Canada (Perkin et al. *submitted*). That is not to say that longer-term exposure to artificial light might not change emergence patterns. For example, Malicky (1981) found that the seasonality of some caddisfly emergence was reduced when artificial lights were used to maintain a constant day length.

Aquatic vs. terrestrial insects

Perhaps one of our most interesting findings was that the majority of insects caught at traps next to lights on lit nights were aquatic insects compared to nights when the lights were off; this suggests that aquatic insects might be more vulnerable to artificial lighting than terrestrial insects. Even traps 40 m from the nearest light saw a significant increase in the proportion of aquatic insects captured when the lights were on. This was particularly interesting, as these traps were also located only 5 m from the river, so we expected them to capture a fairly high proportion of aquatic insects that would then remain constant whether the lights were on or off. That the lights were able to influence the proportion of aquatic insects caught at this distance surprised us and implies that the effects of artificial lights on aquatic insects might be extensive. Further research is needed to clarify the exact extent of this effect, and which species are most impacted. We recommend installing lights further inland—perhaps at 20 m—to determine if the proportion of aquatic insects caught further inland is similarly altered when lights are present. It should also be noted that while most of the island was cattle pasture, the edge (~0-5 m from the water) was fenced off as riparian habitat, and so might have provided critical habitat for terrestrial as well as aquatic insects.

It is clear that different insect orders responded differently to the presence of artificial light. All of the aquatic orders showed the same general pattern of greatly decreasing numbers at greater distances from the lights on lit nights, with a similar but not as drastic pattern on dark nights. On the other hand, some terrestrial orders, most notably the Thysanoptera do not show any clear pattern in the numbers caught at different distances from the lights on lit and dark nights. Indeed, more Thysanoptera were actually caught on dark than on lit nights at all traps. This underlines the need for proper controls in these types of studies, as it had been previously suggested that Thysanoptera could be vulnerable to artificial light (Höttinger and Graf 2003); however, that suggestion came from a review of studies that only captured insects at lights when they were on, and never on dark nights.

Davies et al. (2012) found that the community composition of ground-dwelling invertebrates was significantly altered by the presence of light at night, with an increase in predators and scavengers compared to darker areas. Furthermore, these changes persisted even in daytime conditions. These results, combined with our own, suggest that artificial light at night may have potentially wide-reaching effects that could result in altered invertebrate food webs.

Trade-offs in experimental design

Due to the large-scale of this experiment, we had to make a trade-off between the length of exposure to light sources and having a suitable control condition. In this instance, we chose to illuminate our experimental area only on a total of 11 selected nights over the course of four months in order to be able to compare the number of insects caught on lit and dark nights in the same location. Having a proper control condition came at the expense of not lighting an experimental area for a longer period of time (i.e., every night of the four month experiment). Therefore, our results must be interpreted with the full knowledge that our experiment was not able to mimic actual permanent light exposure, and different results are expected with permanent exposure to artificial light. For instance, we always caught more aquatic insects at the traps 0 m from the light on lit than dark nights. However, it is possible that if the lights were left on for a month and then turned off for a night that the number of insects caught on that one dark night might be similar to the number of insects caught on lit nights, as longer exposure to light can change insect distribution patterns at longer time scales (Davies et al. 2012). Then again, constant exposure to artificial light could eventually lead to an overall reduction in insect abundance as more and more insects die at the lights. This study is important in that it shows that artificial light can have a strong effect on the distribution and composition of insects at locations near artificial lights, but future studies will need to analyze the impacts of long-term exposure to artificial lights on insects. This will be challenging, given the large areas needed to conduct these field experiments. Finding suitable control areas and replication will be particularly difficult.

Terrestrial and aquatic food web consequences

Based on the results of our study, we can say that there are a large number of aquatic insects around sources of light when those lights are on. Creating areas where aquatic insects are highly concentrated could have major implications for the riparian predators that feed on aquatic insects. These predators include bats and spiders, two groups that due to their nocturnal foraging habits are likely to be affected to a larger degree by any changes in aquatic insect distribution. For instance, it has already been shown that fast-flying species of bats take advantage of streetlights as high-quality feeding sites (Rydell 1992). However, this same study also noted that slower-flying species are unable to utilize this resource and might be put at a competitive disadvantage in urban and suburban areas with many streetlights. On the other hand, the bats that are able to take advantage of this resource likely benefit greatly from it, and may even specifically use it during times of the year when high-quality food sources are necessary, such as during lactation (Rydell 1991).

Spiders may also change their behavior to take advantage of artificial lights. Heiling (1999) found that *Larinioides sclopetarius*, a species of spider that often feeds on aquatic insects, intentionally builds its webs near artificial lights, likely to take advantage of the attractive properties of the lights. On the other hand, spiders choosing to build their webs near lights might be limited to making less "sticky" webs, as webs with greater amounts of viscid material are easier for insects to detect when lights are nearby (Craig 1988). Furthermore, if the height at which insects fly is shifted upward by light, as our results suggest, then ground-dwelling spiders might be at a disadvantage under artificial lights.

Conservation planning

Artificial lights spaced ~ 80 m apart might not be detrimental to aquatic insect dispersal; however, there is still evidence that it can have negative impacts on adult aquatic insects. Furthermore, the construction of artificial lights near streams should be avoided whenever possible, especially at spacing of < 40 m, as is often the case in urban areas. Future research is needed to determine how artificial lights could affect the mating success of aquatic insects. It is possible that artificial lights could end up either increasing mating success through the concentration of potential mating partners in a small area or it could decrease success by drawing insects to the light and keeping them there until they are exhausted and unable to reproduce or have reduced fitness through decreased energy stores.

Furthermore, aquatic insects could be particularly vulnerable to the effects of multiple stressors, given their complex life history (Tockner et al. 2010). Larvae can suffer increased mortality rates due to changes in stream hydrology, addition of chemical pollutants, and thermal regime. Adults are susceptible to increased mortality from altered riparian habitats and increased predation. Because artificial lights are highly correlated with human development, they are likely to co-occur with these other stressors. Future research will need to establish how artificial light interacts with these other stressors in order to develop a full picture of the impacts of artificial light on aquatic insects in urban and suburban areas (Perkin et al. 2011).

A previous study found significantly more female than male caddisflies of several species caught at light traps (Kovats et al. 1996). The opposite pattern has been found in moths (Altermatt et al. 2009). We did not identify our insects as female or male, but if there is a bias in light attraction, it could have profound effects on aquatic insect populations. Particularly if more females than males are attracted to light, we expect to see a reduced effective population size. This is another avenue for future research and conservation biology that will be of great importance.

Conclusion

As predicted, artificial light does have an effect on the flight patterns of aquatic insects and our results suggest that aquatic insects may be more vulnerable to artificial lights than terrestrial insects. This work represents the first study to carefully add realistic artificial lights to a non-urbanized area in order to determine the effects of the lights on insect dispersal. However, the results of this study raise key questions that will require further experimental research to answer. For instance, do the effects of artificial lights last into the day, as the results of Davies et al. (2012) suggest? Do the results that we saw hold up in areas with more diverse aquatic insect assemblages? There were no stoneflies in our study area, and a rather low abundance of mayflies and caddisflies. Perhaps some species are more attracted to light than others? It would also be beneficial to run a similar study but with traps maybe every 10 m inland from the lights, so proper regression models can be fitted to inland flying distance. Further research will also be needed to determine how species preying on aquatic insects are changed by the presence of artificial light.

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Appendix 1. Meteorological conditions during the experiment.

Date	Temperature (°C)	Wind (km h^{-1})	Humidity (%rH)
9 Jun†	19.5	0.3	76
10 Jun†	21	0	84
15 Jun†	13.2	0	87
16 Jun	9.2	0.1	82
23 Jun	11.5	0	88
24 Jun†	14.4	0	87
8 Jul†	14.9	0	83
9 Jul†	19.7	0.2	66
14 Jul†	20.1	0	83
15 Jul†	25.7	0.8	57
19 Jul†	14.3	0	89
20 Jul†	15.7	0	73
7 Aug	20.8	3.92	60
8 Aug	21.4	0	70
17 Aug	17.7	0.3	72
18 Aug	18.9	1	68
2 Sep	11	0	93
3 Sep	13.5	0	83
5 Sep	12.5	0	82
6 Sep	7.7	0	91
8 Sep	11.6	10.5	79
9 Sep	14.9	6.9	73
Average Dark‡	15.2 ± 3.7	1.4 ± 3.2	81 ± 9
Average Light‡	16.6 ± 5.4	0.8 ± 2.0	76 ± 10

†Data come from weather station at Institute of Freshwater Ecology and Inland Fisheries, approximately 15 km away.

‡ Average ± S.D.

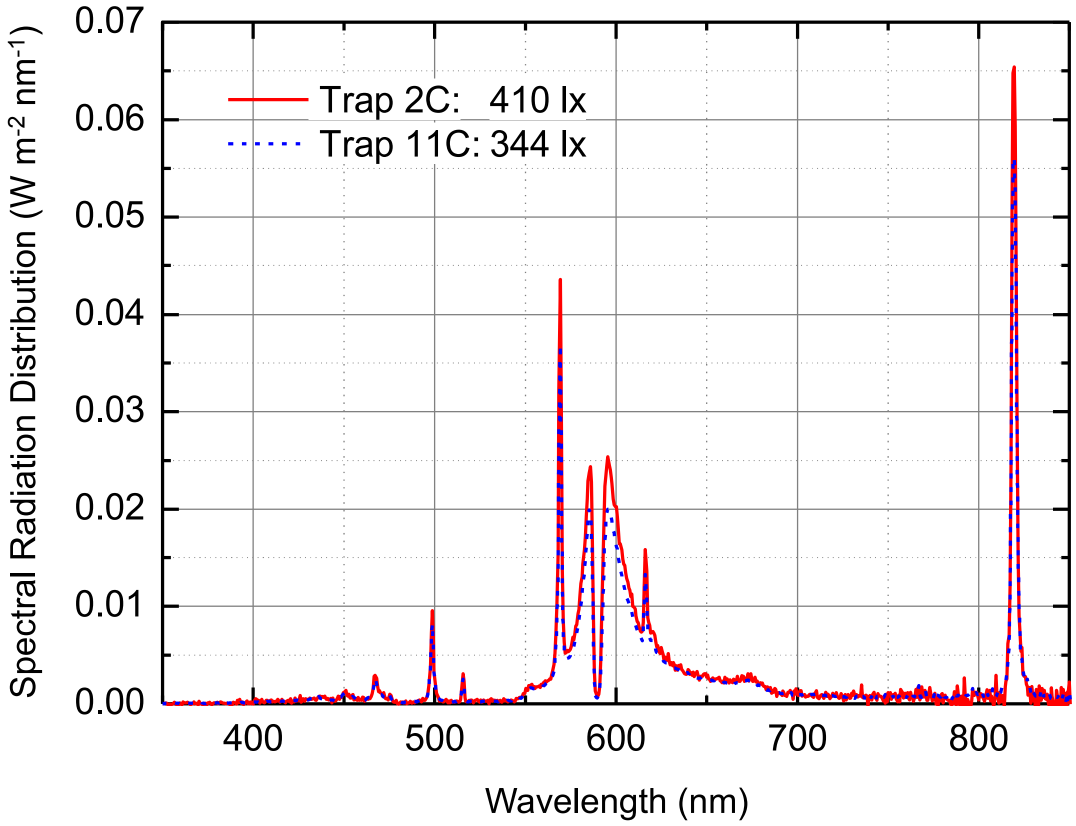
Appendix 2A. Light levels (lx) measured at traps 0, 3, and 75 m from lights. Measurements were taken with the light sensor pointing up towards the light (horizontal) or towards the water (vertical).

	0 m		3 m		75 m	
Tray Height (m)	Horizontal	Vertical	Horizontal	Vertical	Horizontal	Vertical
0.5	180	22	10	11	0.006	0.012
1.5	370	70	8	28	0.005	0.012
2.5	620	340	3	28	NA	NA

Appendix 2B. Average light levels (lx) measured at traps 0, 3, and 75 m from lights from July and August. In all cases, the light sensor was pointed up toward the light.

Tray Height (m)	0 m	40 m	75 m
1.5	338	0.04	0.02

Appendix 3. The spectral radiation distribution of the experimental lights measured at two traps 0 m from the lights at a height of 1.5 m. The spectral radiance was measured with an Avantes AvaSpec-2048 (300-900 nm) compact spectrometer between 21:00 and 23:00 on 8 September 2010.



Appendix 4. The total number of invertebrates caught in each trap location throughout the entire study (N = 66 for each location).

Location†	Aquatic Diptera		Ephemeroptera		Trichoptera		Aquatic Coleoptera		Miscellaneous Aquatic	
	Dark	Lit	Dark	Lit	Dark	Lit	Dark	Lit	Dark	Lit
0	1002	39588	82	4443	35	1059	0	23	2	19
3	963	5920	19	447	19	289	1	6	0	3
40	685	1140	19	26	48	128	0	1	1	0
75	449	532	10	6	10	13	2	2	0	1
Total	**3099**	**47180**	**130**	**4922**	**112**	**1489**	**3**	**32**	**3**	**23**

Location†	Terrestrial Diptera		Hemiptera		Terrestrial Coleoptera		Lepidoptera		Hymenoptera	
	Dark	Lit	Dark	Lit	Dark	Lit	Dark	Lit	Dark	Lit
0	203	1305	103	296	132	294	20	390	70	227
3	243	559	169	244	127	167	18	64	94	89
40	259	247	110	88	99	88	13	18	102	65
75	185	227	53	55	72	81	6	13	86	58
Total	**890**	**2338**	**435**	**683**	**430**	**630**	**57**	**485**	**352**	**439**

Location†	Thysanoptera		Orthoptera		Psocoptera		Miscellaneous Terrestrial		Arachnida	
	Dark	Lit	Dark	Lit	Dark	Lit	Dark	Lit	Dark	Lit
0	60	44	8	33	6	9	6	19	52	65
3	39	26	4	4	12	14	10	14	84	45
40	55	38	13	8	9	21	17	10	66	81
75	31	22	5	2	4	2	7	0	25	26
Total	**185**	**130**	**30**	**47**	**31**	**46**	**40**	**43**	**227**	**217**

† Location of trap in meters from the nearest light

Appendix 5. Tukey HSD summary tables for the proportion of insects caught that were aquatic. *** $p \leq 0.0001$, ** $p \leq 0.001$, * $p \leq 0.05$

Comparisons	Difference	Lower	Upper	*p* adjusted
Night				
Lit-Dark	0.157	0.129	0.185	< 0.0001***
Location (m from light)				
3-0 m	-0.058	-0.110	-0.007	0.02*
40-0 m	-0.196	-0.248	-0.145	< 0.0001***
75-0 m	-0.236	-0.288	-0.184	< 0.0001***
40-3 m	-0.138	-0.190	-0.087	< 0.0001***
75-3 m	-0.178	-0.229	-0.126	< 0.0001***
75-40 m	-0.040	-0.091	0.012	0.2
Night:Location				
D:3-D:0 m	-0.038	-0.124	-0.048	0.89
D:40-D:0 m	-0.125	-0.211	-0.039	0.0003**
D:75-D:0 m	-0.125	-0.211	-0.039	0.0003**
L:0-D:0 m	0.258	0.172	0.344	< 0.0001***
L:3-L:0 m	-0.079	-0.165	0.007	0.1
L:40-L:0 m	-0.268	-0.353	-0.182	< 0.0001***
L:75-L:0 m	-0.347	-0.434	-0.261	< 0.0001***
D:40-D:3 m	-0.088	-0.174	-0.002	0.04*
D:75-D:3 m	-0.087	-0.173	-0.001	0.04*
L:3-D:3 m	0.217	0.131	0.303	< 0.0001***
L:40-L:3 m	-0.189	-0.275	-0.103	< 0.0001***
L:75-L:3 m	-0.269	-0.355	-0.182	< 0.0001***
D:75-D:40 m	0.000	-0.086	0.086	1.0
L:40-D:40 m	0.116	0.030	0.202	0.001**
L:75-L:40 m	-0.080	-0.166	0.006	0.09
L:75-D:75 m	0.036	-0.051	0.122	0.9

Chapter 5:

The short-term effects of artificial light on different trophic levels in small streams

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Abstract

Artificial light at night is prevalent in human-dominated landscapes, and streams are heavily influenced by humans. We hypothesized that artificial light at night would reduce the activity of aquatic insects, resulting in reduced drift densities, lower fish growth rates and leaf litter decomposition rates. We tested these hypotheses by installing streetlights to reaches in four headwater streams of coastal British Columbia. Cutthroat trout (*Oncorhynchus clarkii*) are the top predators in these streams and feed mostly on terrestrial, and drifting aquatic invertebrates the latter if which in turn feed on algae and leaf litter. We found that the night-time drift of aquatic invertebrates in lit reaches was, on average, half of the drift in dark reaches. However, the density and Shannon's diversity of benthic invertebrates, the density of emerging aquatic insects, the density of insects falling into the reaches, leaf litter decomposition, and the number of trout caught were not significantly different between the dark and experimentally lit reaches. The trout caught in one lit reach did have significantly higher specific growth rate than in any other reach, possibly due to a positive interaction between the reach complexity and treatment. For now, we conclude that while short-term exposure to artificial light during the summer does appear to change invertebrate behavior, it does not significantly alter other trophic levels in small oligotrophic streams.

Key words: Cutthroat trout, light pollution, food web, ecosystem functioning, invertebrates, drift, emergence

Introduction

Already prevalent, levels of night-time artificial light are increasing at an estimated rate of 6% a year worldwide (Hölker et al. 2010*a*). Concurrently, artificial light has been implicated as a potential threat to biodiversity (Longcore and Rich 2004, Rich and Longcore 2006, Hölker et al. 2010*b*, Perkin et al. 2011), with artificial lighting being a good indicator of developed human societies (Cinzano et al. 2001). Because light is where humans are, and humans are where freshwater is (Kummu et al. 2011), it is reasonable to expect artificial light to be prevalent along streams, lakes, and ponds. Despite the ubiquity of artificial lights, their effects on ecosystems, especially freshwaters, have not yet been extensively studied (Moore 2006, but see Perkin et al. *submitted*).

Benthic insects play a critical role in stream ecosystems (Wallace and Webster 1996). They control algal growth and detrital decomposition through grazing and shredding activities. A meta-analysis by Feminella and Hawkins (1995) found that invertebrate grazers reduced periphyton biomass in 70% of the 89 studies they analyzed. Aquatic insects are also a critical source of food for predaceous fish. Nakano et al. (1999) found that decreasing invertebrate drift rates over summer months caused an increase in aggression between drift-feeding fish and caused other fish to change to a benthic foraging strategy. Further, when aquatic insects emerge from the stream, they contribute to the terrestrial system, as a food source for bats, birds, and spiders, among others (reviewed in Baxter et al. 2005, Richardson et al. 2010). Due to the central role aquatic insects play in stream and riparian ecosystems, altering their behavior or abundance has the potential to cause drastic changes in the functioning of a stream system. For instance, reducing aquatic insect abundance by ~90% led to significantly reduced rates of leaf litter breakdown and suspended particulate organic matter in comparison with a control stream (Wallace et al. 1982)

Previous studies have shown that the activity of aquatic insects is at least partially controlled by light levels. The number of aquatic invertebrates entering the drift is greatly reduced with light levels higher than 10^{-3} lux (Bishop 1969), meaning that exposure to the full light from even a quarter moon could be enough to disrupt drift. Likewise, large larval *Baetis tricaudatus* adopt a nighttime grazing strategy to reduce predation risk when fish are present (Culp and Scrimgeour 1993). Moreover, many aquatic insects emerge at dusk (Tobias 1967, Jackson 1988, Pinder 1993); because artificial lights raise illumintation levels to those similar to dusk, lights could lead to altered patterns of emergence. The addition of artificial lights to riparian areas is also expected to attract many terrestrial and adult aquatic insects (Scheibe 2003, Eisenbeis 2006, Perkin *submitted*). It has been suggested that when these lights are located very close to freshwaters, they could increase the amount of prey available to fish by increasing the density of insects falling into the water (Perkin et al. 2011).

Many studies have demonstrated a decrease in benthic biodiversity in areas with increasing urbanization (Taylor and Roff 1986, Gresens et al. 2007, Walsh et al. 2007). Generally, these studies have focused on the effects of common urban stressors, such as increased impervious surface and chemical pollution (Gresens et al. 2007, Walsh et al. 2007). However, artificial light also has the potential to decrease benthic invertebrate biodiversity and abundance. As mentioned above, it could lead to altered and perhaps increased rates of emergence of aquatic insects. These insects could find themselves drawn to the light sources rather than finding a mate and reproducing (Perkin et al. 2011). Over time, the species most attracted to lights would eventually be absent from lit reaches.

However, alterations by increased in-stream light levels are not limited to insects and other invertebrates. Contor and Griffith (1995) found that juvenile rainbow trout (*Oncoryhynchus mykiss*) were less active at night in the winter when there was a full moon, as well as in a stream reach exposed to the light from a bright billboard.

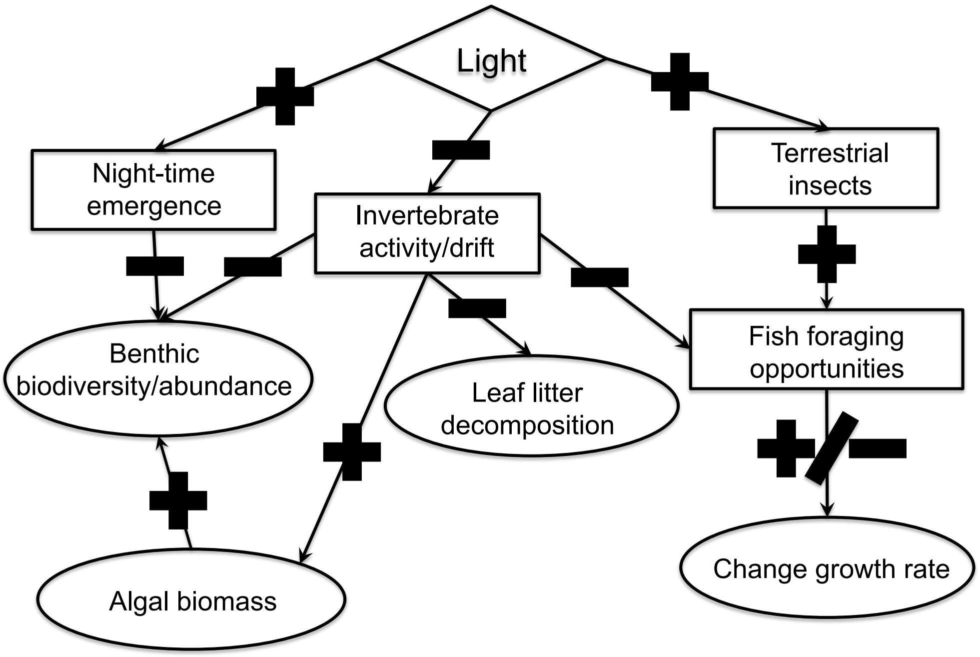

Figure 1. A conceptual model of how we hypothesize artificial light will alter in-stream trophic relationships. Whether or not fish growth will increase or decrease with exposure to artificial light depends on whether the dominant effect of light is to increase the density of terrestrial insects falling into the stream or decrease the drift of stream invertebrates.

Conceptual Model of Natural and Artificially Lit Stream and Hypotheses

Because artificial light has the potential to alter the behavior of many stream organisms, it is difficult to predict what the overall effects of artificial light on a stream ecosystem might be. To help us generate hypotheses, we constructed a conceptual model of how the various ecosystem properties and processes in a small stream might be affected by artificial light (Fig. 1). The hypotheses we developed and tested in this study were: artificial light at night will 1) decrease the number of drifting invertebrates, 2) increase the amount of terrestrial insects falling into the stream (Perkin et al. 2011), 3) increase the density of emerging aquatic insects (Tobias 1967, Jackson 1988, Pinder 1993), 4) have a net negative effect on trout growth through increased foraging activities with decreased food availability if a decrease in drifting invertebrates dominates, or a positive effect if an increase in the density of terrestrial insects falling into the stream dominates, 5) result in decreased leaf litter decomposition rates due to decreased activity by shredding invertebrates (Culp and Scrimgeour 1993), and 6) alter the taxon richness of the benthic community (Hölker et al. 2010*b*, Perkin et al. 2011). In order to test these hypotheses, we experimentally added streetlights along four natural streams for four weeks.

Materials and Methods

A manipulative experiment was conducted on four streams in the Malcolm Knapp Research Forest (49°16’N, 122°34’W) located in the Coastal Western Hemlock (*Tsuga heterophylla*) biogeoclimatic zone of British Columbia, Canada. The four experimental streams, Blaney, East, G, and Spring Creek all contain only one species of fish, i.e., resident coastal cutthroat trout (*Oncorhynchus clarkii clarkii*). The maximum distance between streams was less than 4 km. Spring Creek is a tributary of East Creek; the experimental reaches in these two streams were separated by 500 m. Both East and Spring Creeks were logged for the second time in the mid-1970s and replanted with Douglas-fir (*Pseudotsuga menziesii*). The riparian forest is currently dominated by western hemlock with sub-dominant red alder (*Alnus rubra*), salmonberry (*Rubus spectabilis*), and western redcedar (*Thuja plicata*). Blaney and G have largely intact riparian forests, with recent logging on G 10 m from the stream as part of a different study (Kiffney et al. 2003). The riparian forest of these streams is dominated by western redcedar, with sub-dominant Douglas-fir, red alder, and salmonberry.

Table 1. Artificial light levels in the lit stream reaches at the surface of, 1 cm below, and 5 cm below the water. These are the mean of three light measurements taken directly in front of each light, as well as one measurement taken between two lights. For comparison to urban light levels, measurements from 1 m above the surface, and 0.5 m below the surface of the Spree River in center of Berlin, Germany are given.

Reach	Light Level (lx)	Light Level (W cm^{-2})
Blaney DS		
Surface	1.08	0.54
1 cm	0.65	0.62
5 cm	0.54	0.52
East DS		
Surface	1.19	0.62
1 cm	1.00	0.54
5 cm	0.99	0.44
G DS		
Surface	0.59	0.43
1 cm	0.55	0.37
5 cm	0.50	0.32
Spring US		
Surface	0.37	0.34
1 cm	0.36	0.28
5 cm	0.35	0.27
Borsigturm		
1 m above	0.28	NA
0.5 m below	0.05	NA
Friedrichstraße		
1 m above	0.56	NA
0.5 m below	0.43	NA
Bellevue		
1 m above	1.29	NA
0.5 m below	1.31	NA
Control Sites	0.008†	NA

†Estimate of surface light level based on measurements made at the UBC Liquid Mirror Telescope within MKRF, and data from http://stjarnhimlen.se/comp/radfaq.html#10 (accessed 11 January 2013).

Two approximately 50 m reaches (control and experimental) consisting of three pool-riffle sequences were established on each stream. These reaches ranged from 50-290 m apart. The lit reach was generally the downstream reach. The lit reach on Spring was upstream, but the distance between these reaches was approximately 250 m and we do not expect the lit reach had any effect on the downstream control reach. Beginning the night of 31 May/ 1 June 2011, we turned on three high pressure sodium lamps (70W Lumark, Cooper Lighting, Peachtree City, GA) that had been installed along one of the reaches on each stream, approximately 10 m apart from one another. These lights increased the ambient night-time light level in the lit reaches to light levels comparable to those in an urban area (Table 1), as measured by an ILT1700 light meter (International Light Technologies, Peabody, MA) at the water surface, 1 cm below the surface, and 5 cm below the surface. These measurements were taken approximately 1 m from the base of each light as well as between lights. Variability in light levels within and between streams is due to variations in riparian vegetation and in-stream structures, such as large wood (LW) and boulders. The lights were turned off for the last time on the morning of 1 July 2011, for a total of four entire weeks of light at night. Temperature data loggers were added to each reach at midday on 4 June and were retrieved on either 7 or 8 July 2011 (Fig. 2). Air temperatures during the experiment ranged from 8-22.1 °C (mean high temperature: 18.7 ± 1.8°C (mean ± SD), mean low temperature: 11.6 ± 1.7°C), and winds were generally calm (peak gusts < 31 km h^{-1}). There was an average precipitation of 1.4 ± 3.5 mm d^{-1}, with a maximum of 15.4 mm d^{-1} and 22 days of the 31-day experiment either had no rainfall or only a trace. Weather data are from the Vancouver Airport and were retrieved from http://www.climate.weatheroffice.gc.ca/climateData/dailydata_e.html?StationID=889 (last accessed 16 January 2013).

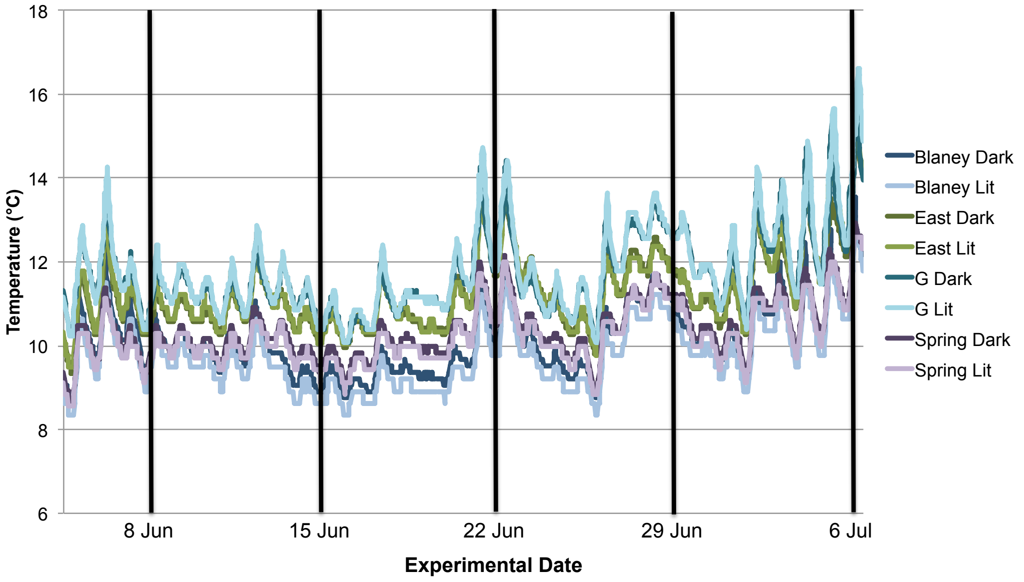

Figure 2. The stream temperature in the eight different experimental reaches over the course of the experiment. The dark vertical lines mark drift, emergence, and terrestrial input sampling dates.

Benthic Sampling

Twelve benthic samples were taken from each reach both before (3-18 May) and after (30 June-8 July) the experiment in order to characterize the aquatic invertebrate community. Samples were taken with Surber samplers (0.09 m^2, 250 µm mesh size) at two randomly selected spots at each of the three pools and riffles in each reach. Shannon's biodiversity index was calculated for each benthic sample. The average count and taxon richness of all the samples in each habitat type (pool or riffle) was calculated and the changes (post-experiment – pre-experiment) in these values were used for analyses.

Terrestrial Input, Drift, and Emerging Aquatic Insects

Inputs of terrestrial, drifting aquatic, and emerging aquatic insects were sampled weekly during the course of the experiment. In addition, drift samples were also taken before (overnight 17-18 and 18-19 May) and after (5-6 and 6-7 July) the experiment. Drifting aquatic insects were collected with a net (16 x 16 cm opening, 250 μm mesh size) secured just above the stream substrate to avoid collecting insects active on the surface of the benthos (Elliott 1970). Stream flow was measured at the mouth of the drift nets with a Model 2100 Current Velocity Meter (Swoffer Instruments Inc, Seattle, WA) in the evening and in the morning at sampling. The number of drifting insects was calculated as:

$$\text{drift density (indiv. 100 m}^{-3}\text{)} = (N * 100)/[t * W * H * V * (3600 \text{ s h}^{-1})],$$

where N = number of invertebrates in the sample; t = time that the net was in the stream (h); W = width of the net (m); H = mean height of water column in net mouth (m); and V = mean water velocity at net mouth (m s^{-1}) (Smock 2006).

Terrestrial inputs were collected with 3 trays at each reach (91 x 52.5 cm at G, 69 x 42.6 cm at Blaney, East, and Spring) filled with stream water and a small amount of dish soap to break the surface tension (total 24 trays).

Emerging insects were trapped in emergence traps that were 183 x 183 x 183 cm and had a mesh size of 965 μm. In most streams, these traps were large enough to span the entire wetted width of the stream, with the control reach of Blaney (~4 m wetted width) being the one exception. All insect sampling devices were employed within the hour before sunset and were retrieved within the hour after sunrise. Times of set-up in the evening and sampling in the morning were all noted. The sampling was done over two nights each week and was designed so that an even number of control and experimental reaches were sampled each night. The counts of insects for the drift, emergence, and terrestrial inputs were all averaged by week for analysis.

Invertebrate Identification

All collected invertebrates (benthic, terrestrial inputs, drifting, and emerging) were identified under 40× magnification to the lowest possible taxonomic classification using

Merritt et al. (2008). For larval aquatic invertebrates, this was generally to genus, with the exception of chironomids, which were left at the family level. All terrestrial and adult aquatic insects were identified to order. When necessary, invertebrates were assigned to functional feeding groups using the designations in Merritt et al. (2008).

Basal resources

Leaf litter decomposition was determined by placing 10 g (dried mass) of red alder leaves into a litterbag (1 cm x 1 cm mesh). Five litterbags were placed in each reach, with one additional litterbag placed in both reaches of G and East creeks. Litterbags were placed at the bottom of the stream and secured with a line to nearby riparian vegetation. The litterbags were added to the reaches on 4 June and were retrieved on either 7 or 8 of July and placed in a dark cooler for transport back to the lab. At the lab, samples were washed with water to remove any attached invertebrates. Removed invertebrates were preserved in 70% ethanol for later identification. Leaves were oven-dried for 24 hours at 100°C and weighed, then combusted for 1.5 hours at 550°C, reweighed and their ash-free dry mass (AFDM) calculated. The average leaf AFDM for each reach was used in the analysis.

Algal biomass was estimated by randomly collecting six rocks in each reach, three in each habitat type, i.e., pool and riffle. Rocks were then scrubbed of all periphyton with a stiff toothbrush and rinsed with distilled water to create a slurry. The slurry was stirred until homogenous, then divided evenly over two pre-weighed and dried Whatman GF/F 0.7 μm fiberglass filter. One filter paper from each sample was then dried for 24 hours at 100 °C and weighed, then combusted at 550 °C for two hours and re-weighed. The other filter was placed in a centrifuge tube with 90% buffered acetone and extracted overnight. The chlorophyll *a* content was determined with a fluorometer according to the procedures in Steinman et al. (2007). Areas of the sample rocks were determined using a 1 cm^2 sponge to paint the surface of the rock.

Unfortunately, most of the rocks were misplaced before they could be analyzed, so we excluded the algal biomass results from the results and discussion. However, we have included the data we have in Appendix 1.

Trout

Cutthroat trout were collected in standard Gee minnow traps baited with salmon roe between 11-19 May and then again between 1-8 July. Traps were checked and re-set every 24 hours. Trout were anesthetized with tricaine methanesulfonate (MS-222), tagged with PIT tags (if > 7 cm fork length), weighed, and fork length measured. If the trout were < 7 cm fork length, colored elastomer dye was injected at the base of the pectoral or caudal fins in order to create a unique marking for each fish. Fish were released to the same pool in which they had been captured after recovering from the anesthetic. Specific growth rate (SGR) was defined as:

$$\text{SGR (\% day}^{-1}\text{)} = 100\ ((\ln M_1 - \ln M_0) / (t_1 - t_0)),$$

where M_1 = mass at the end of the experiment (g); M_0 = mass at the beginning of the experiment and $t_1 - t_0$ = the number of days elapsed from the time the fish was first caught before the experiment to its recapture at the end of the experiment. SGR was averaged for each reach for analysis.

Catch per unit effort (CPUE) for the trout was determined as from 3 separate efforts on 3 days in each reach both before and after the experiment (total of 6 efforts for each reach):

$$\text{CPUE} = (N / M) / T$$

where N = number of captured trout, M = number of minnow traps in the reach, and T = time (hr) minnow traps were in water. The percent CPUE was calculated by dividing the average post-experiment CPUE by the average pre-experiment CPUE.

Analysis

When necessary, data were log-transformed to better meet the requirements for normality and homoscedasticity. The changes in density and Shannon's biodiversity index of benthic insects, leaf litter decomposition, and percent CPUE of fish before and after the experiment, in control and lit streams were compared with paired t-tests. Fish SGR in lit and dark reaches was compared with an ANOVA with stream included as a factor. Differences in terrestrial inputs, drift during the experiment, and emerging aquatic insects were determined with a linear mixed-effects model with the nlme R package. A summary of all candidate models is included in Appendix 2. The pre- and post-experimental drift in lit and dark reaches were compared with a paired t-test. In order to better understand the controls on leaf litter decomposition, we used a regression analysis between remaining leaf AFDM and the density of shredders found in the pool benthic samples. Alpha for all tests was set to 0.05. All statistical analyses were conducted in R (R Development Core Team 2011). All means are reported ± S. E.

Results

Benthic Invertebrates

There was no significant change in the density of benthic insects present in either the dark (mean = -8.54 ± 7.26) or lit (mean = -2.06 ± 8.72) reaches (t = 0.92, df = 7, p = 0.39, Fig. 3A). Similarly, there was no difference in the change in Shannon's biodiversity index between dark (mean = -1.40 ± 1.19) and lit (mean = -1.15 ± 0.63) reaches (t = 0.18, df = 7, p = 0.86, Fig. 3B). In the taxon richness analysis, all lit reaches showed a greater decrease or lesser increase in taxon richness than the paired dark reach from the same stream, except for Spring Creek, in which the benthic taxon richness in the lit reach did not change much over time but decreased greatly in the dark reach.

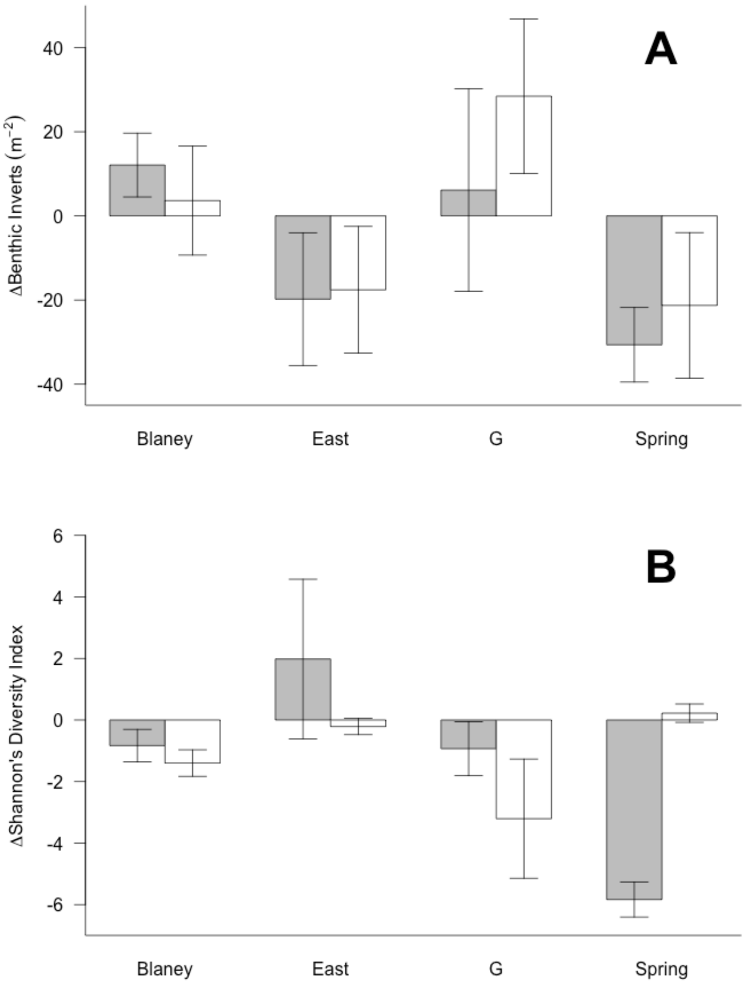

Figure 3. The mean ± S.E. change in density of benthic invertebrates m^{-2} (A) and Shannon's Diversity Index (B) from before to after the experiment in lit (white) and dark (grey) reaches.

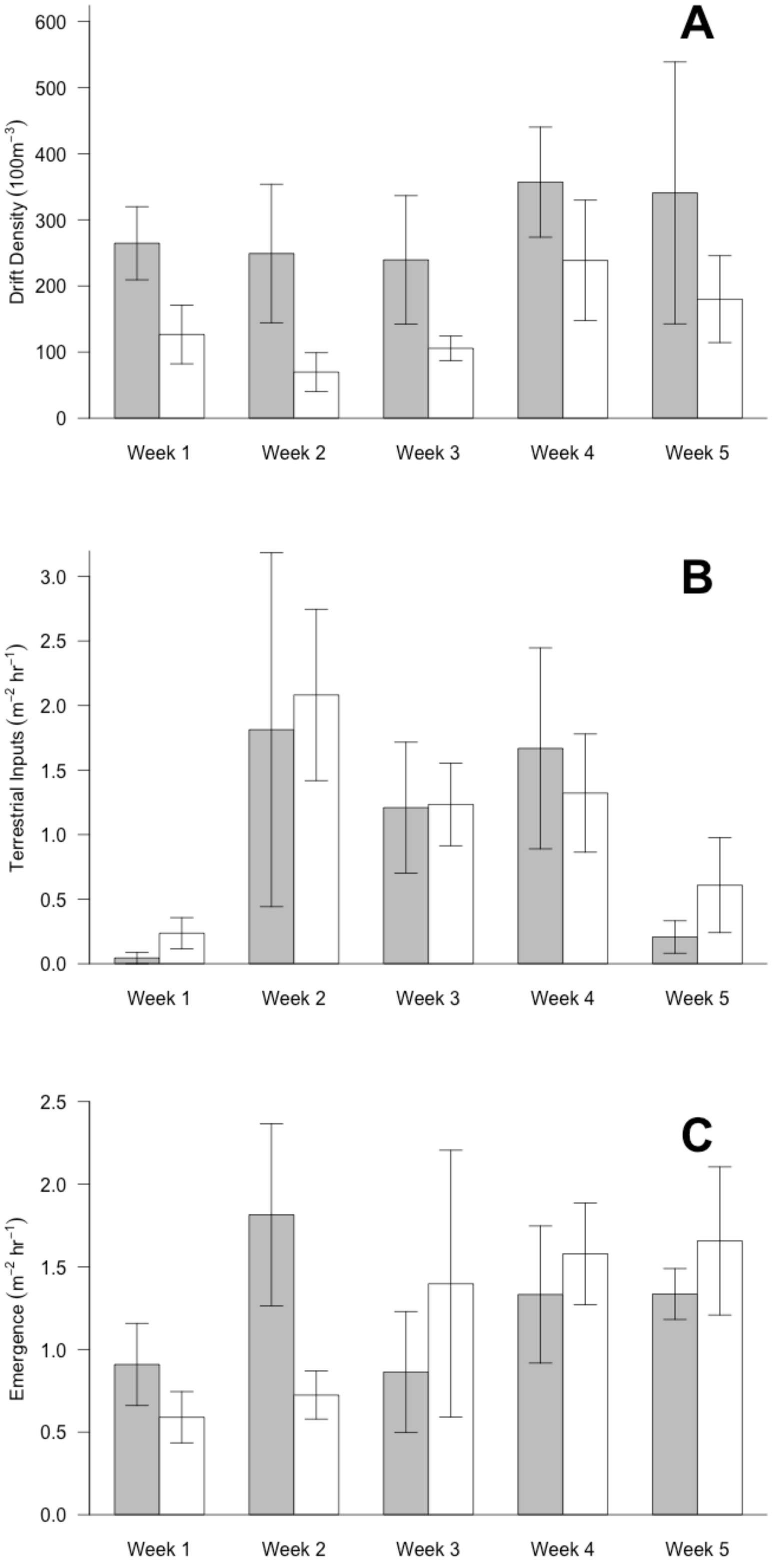

Figure 4 The mean ± SE drift density (n = 4) (A), terrestrial inputs of individual insects (B), and emergence (C) of all lit (white) and dark (grey) reaches during the different weeks of the experiment.

Drifting insects, terrestrial inputs, emerging insects

The model that best predicted invertebrate drift (AIC = 94.1) showed that there were significantly fewer drifting invertebrates in the lit (mean = 144.10 ± 26.11) than dark (mean = 290.13 ± 48.19) reaches (*t* = -4.27, df = 19, *p* < 0.001) (Fig. 4A). The number of scrapers drifting in the lit reaches was 72.6% of that drifting in the dark reaches. On the other hand, the number of detritivores drifting in the lit reaches was actually greater than the number in dark reaches (totals: 161 and 153 respectively). The number of shredders drifting in lit reaches was 90.8% of that drifting in the dark reaches. All other functional feeding groups had roughly 80% of the dark drift drifting in the lit reaches. Models including stream temperature and interactions between stream temperature and light were not successful at predicting invertebrate drift. A paired t-test showed that there were no significant differences in drift densities between lit and dark reaches either before (dark mean = 417.22 ± 119.67, lit mean = 290.37 ± 70.98) (*t* = 0.59, df = 5.9, *p* = 0.58) or after (dark mean = 383.06 ± 117.61, lit mean = 1195.65 ± 1021.79) (*t* = -0.20, df = 3.5, *p* = 0.85) the experiment.

There was no significant difference between the density of terrestrial insects falling into the dark (mean = 0.99 ± 0.34) and lit (mean = 1.10 ± 0.22) reaches (*t* = 0.42, df = 19, *p* = 0.68) (Fig. 4B). However, when both reaches from Blaney were excluded, there were significantly more terrestrial insects falling into the lit (mean = 0.95 ± 0.23) than the dark (mean = 0.45 ± 0.14) reaches (*t* = 2.29, df = 14, *p* = 0.04) (Appendix 2).

There was no significant difference in the density of insects emerging from lit (mean = 1.22 ± 0.21) or dark (mean = 1.25 ± 0.17) reaches (*t* = -0.10, df = 18, *p* = 0.92) (Fig. 4C).

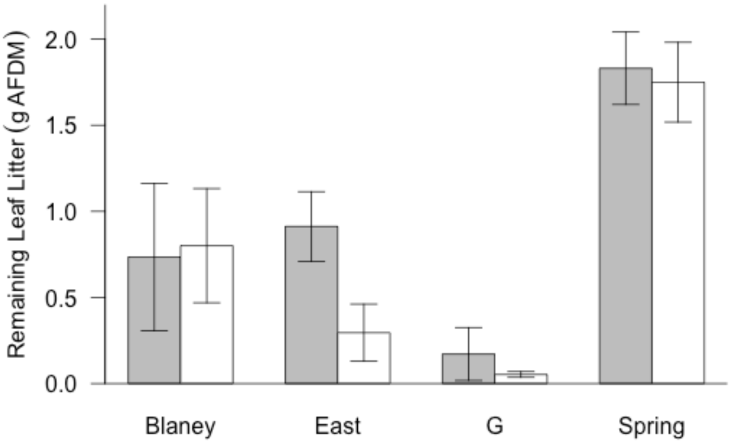

Figure 5. The mean ± SE remaining leaf litter mass of all lit (white) and dark (grey) reaches during the different weeks of the experiment. The original mass of the leaf packs was 10 g.

Leaf Litter Decomposition

There was no significant difference in leaf litter decomposition between dark (mean = 0.83 ± 0.17) and lit (mean = 0.67 ± 0.17) reaches ($t = 1.5$, df = 3, $p = 0.23$) (Fig. 5). However, there was a significant inverse relationship between leaf litter decomposition and the density of shredders collected in the benthic samples ($R^2 = 0.47$, $F_{1,6} = 5.37$, $p = 0.06$) (Fig. 6). We only used the density of shredders in the pool samples for this analysis, as the leaf packs were placed in the pools and not the riffles.

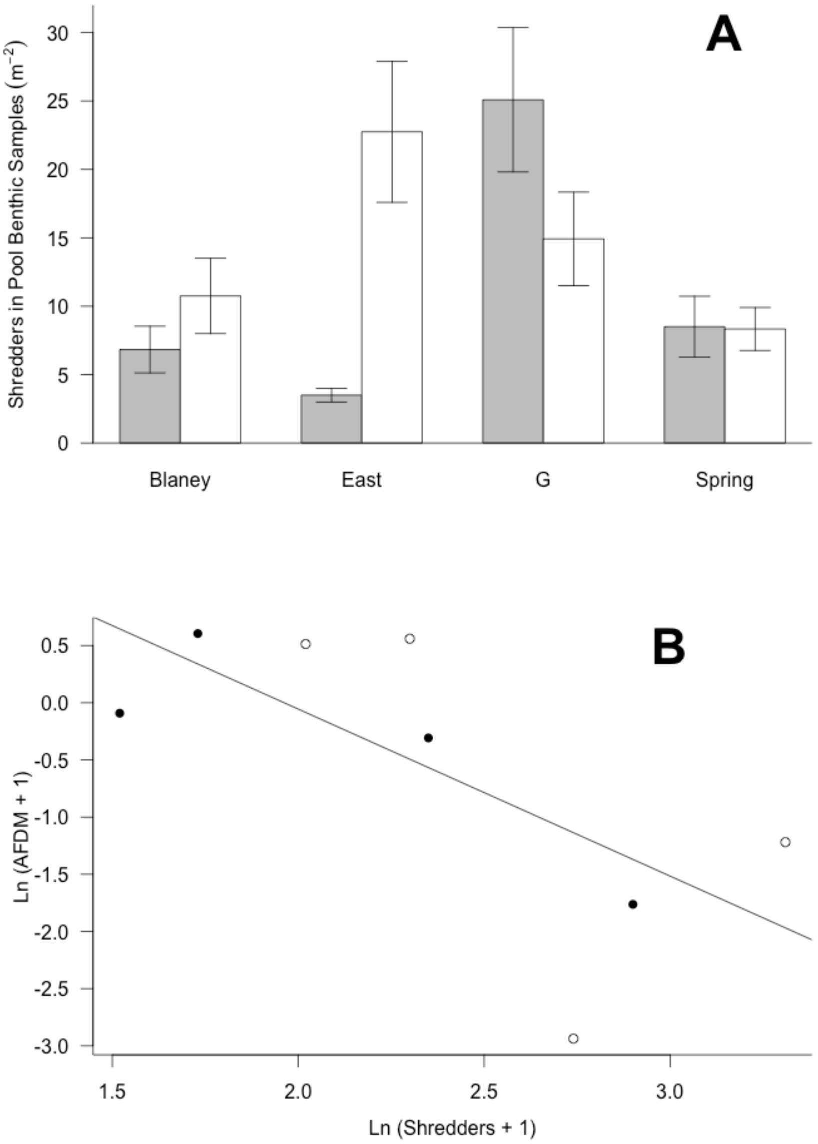

Figure 6. The mean ± SE density of shredders in the pool benthic samples of all lit (white) and dark (grey) reaches (A). The amount of remaining ash-free dry mass of leaf litter at the end of the experiment versus the density of shredders found in the pool benthic samples from dark (filled circles) and lit (open circles) reaches (B).

Fish

There was no difference in the SGR of fish captured in the dark (mean = 0.20 ± 0.04) and lit (mean = 0.24 ± 0.06) reaches ($F_{1,76} = 0.36$, $p = 0.55$). However, there was a significant effect of stream ($F_{3,76} = 4.61$, $p = 0.005$) and interaction between light and stream ($F_{3,76} = 5.84$, $p = 0.001$). The recaptured fish in the lit reach of Blaney had a significantly higher SGR compared to the fish in any other reach except for the dark reach of G (Fig. 7, Appendix 3, 4). In all other lit reaches, the mean SGR was less than that in the corresponding dark reach; however, this difference was minimal and non-significant. . Further exploratory analyses revealed that there was no relationship between trout SGR and either terrestrial inputs or drift density. There was no significant difference in the change of CPUE of fish that were caught in the dark and lit reaches ($t = 0.72$, df = 6, $p = 0.50$), however, there was a trend towards more fish being caught in lit reaches and fewer fish caught in dark reaches (Table 2).

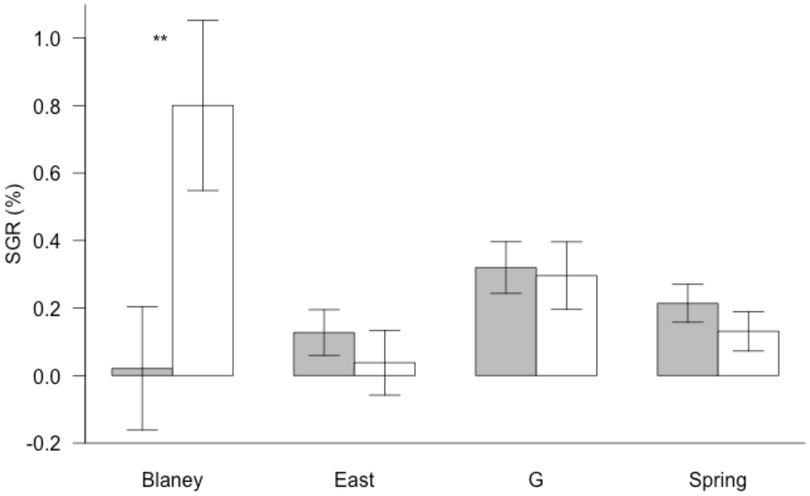

Figure 7. The mean ± SE specific growth rate (SGR) of cutthroat trout during the experiment in all lit (white) and dark (grey) reaches. ** = indicates difference significant at $p \leq 0.01$.

Discussion

This marks the first time that artificial lights have been experimentally added to a natural stream area that is completely light-naïve in order to study the stream ecosystem. Previous research into the effects of artificial light on organisms has taken place either in areas that have already been lit (Moore et al. 2000, Eisenbeis 2006, Davies et al. 2012, Rodríguez et al. 2012) or in laboratories (Buchanan 1993, Tuxbury and Salmon 2005, Brüning et al. 2011). Furthermore, previous studies have generally focused only on one organismal group, such as zooplankton (Moore et al. 2000), invertebrates (Davies et al. 2012), spiders (Heiling 1999), bats (Rydell 1992), or birds (Rodríguez et al. 2012). By including a variety of organisms and trophic levels in our study, we are able to better predict how artificial light might alter entire ecosystems, rather than just one group that is perhaps more strongly affected by light at night.

Table 2. The change in the absolute number and CPUE for cutthroat trout caught in lit and dark reaches before and after the addition of light. Negative values indicate more fish were caught before than after the experiment.

Reach	Δ Fish Dark†	Δ Fish Lit	Δ CPUE Dark‡	Δ CPUE Lit
Blaney	12	-5	0.0036	-0.0055
East	-4	4	0.0002	0.0009
G	0	-7	0.0002	-0.003
Spring	-25	33	-0.0133	0.0158
Avg ± SD	-4.3 ± 15.4	6.3 ± 18.5	-0.0023 ± 0.007	0.002 ± 0.009

† Difference in total number of unique fish captured prior to and after the experiment in each reach

‡ Catch per unit effort: see text for details; difference between average CPUE before and after the experiment in each reach

In general, our results did not support our conceptual model, though due to our small sample size our statistical power was low. The presence of artificial light did decrease invertebrate drift, as we hypothesized, but it did not have any significant effect on any other variable we measured. While not statistically different, there does seem to be a trend for an increasing density of terrestrial insects entering from the lit reaches. Similarly, the number of trout caught in the lit and dark reaches was not statistically different, but there might be a trend for an increasing number of fish in lit reaches.

Invertebrates

We did not see the hypothesized decrease in either density or taxon richness of benthic invertebrates in the lit reaches. It is likely that the duration of our study was not long enough to see any change. The mechanism we proposed would cause a decrease in abundance and taxon richness—adult aquatic insects being attracted to lights and failing to reproduce—might require several years of exposure to lights before any difference could be detected.

That artificial light disrupted invertebrate drift suggests that it does have the potential to alter other stream organisms and processes. While the post-experimental drift was not significantly different in the lit and dark reaches, the fact that the mean drift in the lit reaches was so high and highly variable suggests that there may have been some compensatory drift taking place, even several days after the lights had been shut off. Much of the decrease in the drift during the experiment was due to the response of *Baetis* spp. mayflies to light. The total number of *Baetis* spp. drifting in the dark reaches during the entire experiment was 1480, while it was only 1042 in the lit reaches. *Baetis* spp. made up over 37% of the drift in the dark reaches, while it was just under 29% of the drift in lit reaches. If we assume that a reduction in drift is symptomatic of decreased invertebrate activity (Waters 1972), then we would expect to see increased algal biomass and decreased rates of leaf litter breakdown. Unfortunately, our algal biomass data was compromised and could not be analyzed. Given the impotant role *Baetis* spp. as grazers and the degree they are influenced by light (Culp and Scrimgeour 1993, this study), examining algal biomass should play an important role in future studies of artificial light and stream systems. Given that most of the shredders in the study area are caddisflies that are armored against fish and do not generally exhibit a propensity for nocturnal drifting (Waters 1968, Gallepp 1974), it is very likely that shredder activity levels are not affected by artificial light at night. Indeed, the greatest decrease in drift was in the scraper functional feeding group, particularly *Baetis* spp. and *Epeorus* spp. There was only a slight reduction in the drift of shredders under lit conditions. It is also possible, although unlikely, that microbial activity increased due to the light at night, although we were unable to find any evidence of microbial leaf litter decay processes being altered by light.

The largest differences between drift in the lit and dark reaches was in the first three weeks of the experiment. This suggests that there could be some acclimation to the exposure to light at night. On the other hand, invertebrates may be forced to drift due to decreased food availability (Hughes 1970, Hershey et al. 1993) or increasing population densities (Walton et al. 1977, Anholt 1995). The fact that there was no change in benthic densities makes it unlikely that increasing population densities could be responsible for an eventual increase in drift; however, some of our benthic samples were taken several days after the experiment ended and benthic densities could have already normalized in this time after reaching a zenith or nadir during the experiment. Future research should monitor drift levels for at least three months to determine if there really is any acclimation, or if this was just variation.

We were surprised to see no significant difference in terrestrial inputs of insects between the lit and dark reaches. In fact, the stream reach with the highest inputs of terrestrial insects was actually the dark reach of Blaney. This is especially remarkable given that the dark reach of Blaney was the most open and widest reach. On the other hand, this reach did have a lot of low, overhanging vegetation near the banks where our pan traps were located, which provides an important transfer point of terrestrial invertebrates to streams (Baxter et al. 2005). Had our pan traps been floating in the center of the reach, perhaps the terrestrial inputs in this reach would have been much less. Interestingly, the reach with the second highest inputs of terrestrial insects was the lit reach of Blaney. When both reaches of Blaney were excluded from the analysis, there were significantly more terrestrial insects falling into the lit reaches than the dark reaches of the remaining streams (data not shown). Because the streetlights were located so closely to the streams, we expected that more flying insects would be attracted to, and fall into, the lit reaches. Numerous other studies have shown the increased insect catches near streetlights (Eisenbeis 2006, Scheibe 2003, Perkin et al. *submitted*). It is possible that any additional insects attracted to the lights at our study sites stayed very close to the lights themselves, so even when the stream was < 1 m from the lights, the insects did not fall into the stream. We hypothesize that flight intercept traps placed directly at lights will capture more insects than those at dark reaches and these data could be informative for better understanding how insects attracted to lights might subsidize stream systems. It is also possible that precipitation or wind could have affected the density of terrestrial insects falling into the stream. However, there was no relationship between precipitation levels recorded at a weather station in Vancouver and the density of insects falling into the stream (data not shown). This result is similar to that of Waringer (1991), which found that only air temperature had a significant effect on Trichopteran catches at light traps. Furthermore, wind levels were generally low during the experiment and all streams were sheltered by a dense riparian forest.

The lack of a difference in densities of emerging insects between lit and dark reaches was similar to a result in a study of streetlights on adult aquatic insect flight and emergence carried out on the Spree River outside Berlin, Germany (Perkin et al. *submitted*). However, the Spree River is dominated by chironomids and has very low taxonomic diversity in the benthic community. We expected that if there was an invertebrate group that was more likely to have its emergence affected by artificial light at night, that we would see that group in the streams in British Columbia, that have several representatives of all the major aquatic insect orders. That we also saw no difference between lit and dark reaches in this study suggests that emergence, at least in the short-term, is likely not altered by artificial light at night.

Given that shredders are relatively well-protected from predaceous fish—particularly cutthroat trout, that primarily feed on drifting terrestrial and aquatic invertebrates (Wipfli 1997)—it is perhaps not surprising that artificial light did not have an effect on leaf litter decomposition. At first glance, leaf litter decomposition appeared to be highly variable with no discernable pattern. However, leaf litter decomposition does appear to be higher when there are more benthic shredders found in the pools of the experimental reaches, regardless of whether they were lit or not. This is similar to the results found by Wallace et al. (1982) in which streams with fewer shredding insects had lower rates of leaf litter decomposition. That there was no effect of artificial light on the density of shredders in the pools indicates that artificial light is less likely to have an effect on stream organisms that are day-active. However, since pools tend to be deeper than riffles and could therefore reduce the amount of light reaching the benthic substrate, it would be informative to measure the depth of each pool where benthic samples are taken to find out if benthic organisms in shallow pools are influenced by the addition of light.

Fish

This being the first study of its kind, it was not sufficiently detailed for us to disentangle what happened to the fish in the experimental reaches. Further field research is needed to determine if fish activity is increased or decreased by the presence of artificial light. Because our reaches were not enclosed in any way, future studies might either enclose fish in lit stream reaches or use radiotelemetry to find out if they use the lit reaches for foraging and then leave them to rest. As mentioned in the introduction, the winter night-time activity of juvenile rainbow trout decreased when artificial light was present (Contor and Griffith 1995), but artificial light at night can be used to increase fish growth rates by inducing feeding (Boeuf and Le Bail 1999, Taylor et al. 2006). Furthermore, a study looking at marine fish found increased numbers and foraging behavior of both piscivorous and planktivorous fish around a pier when an artificial light was on (Becker et al. 2013).

Future studies need to observe the fish, either directly or with cameras to determine their activity rates when exposed to artificial light in the wild. We also need to take gut content samples during the experiment to see how feeding strategies might vary under artificial light. It is possible that the fish present in the lit reaches preyed more on terrestrial insects in the drift, or foraged in the benthos, as these represent important food sources for salmonids (Wipfli 1997). However, we did not find evidence to support our hypothesis that there would be an increase in the density of terrestrial insects into streams under artificial lights. In fact, the reach with the highest inputs of terrestrial invertebrates, the dark reach of Blaney, was also the reach with the lowest trout SGR. If night-time fish activity levels were reduced by the light, rather than increased, as we assumed, then fish should not have been influenced by the light at all. It is also possible that changing seasonal patterns of behavior mean that fish might be more affected by artificial light at night at some times of the year than others. For instance, the long summer days might allow them plenty of foraging opportunities and so no change in growth can be seen. All of these possibilities will need to be explicitly investigated in future studies.

One interesting result in our study was the significantly higher SGR of the trout in the lit reach of Blaney compared to the other reaches. The lit reach of Blaney was more structurally diverse than the dark reach of Blaney, with deep pools, a mix of substrate size classes, and in-stream LW. Both reaches of G were also quite structurally complex and those reaches also saw higher, though not significant, trout SGR. However, we did not actually measure habitat complexity as part of this study, and these observations are merely qualitative. Future studies on natural streams will need to take stream complexity into account, as more structurally complex streams may provide refuge from artificial light. This has important conservation implications, as streams in urban areas that are more likely to be affected by artificial light at night are also more likely to have simplified channels (Bernhardt and Palmer 2007).

Artificial lighting may not only interact with stream channelization; as increasing levels of artificial light are associated with higher levels of urbanization, we also expect other common stressors, such as increased chemical contamination and temperature regimes to also co-occur with artificial light (Perkin et al. 2011). It is unknown how common urban stressors might interact with artificial light, but it is clear that future research on artificial light will also need to take these into account.

Conclusion

Our study supports that aquatic invertebrate drift is decreased by a level of artificial lighting commonly encountered in urban streams. However, that we did not see any difference in any other of our variables of interest suggests that short-term exposure to artificial light at night may only have minimal effects on small, oligotrophic stream ecosystems. Artificial light might be an example of a "press" driver—a disturbance that acts over a longer time-period—that elicits a "ramp" or delayed and slowly increasing response, from many organisms (Lake 2000). Future studies will need to be longer term to determine if there are seasons in which certain organisms are more affected by artificial lights, or if effects are only noticeable after long-term exposure to artificial lights. Because past studies of artificial light at night have focused on only one species or group of organisms, we suggest more ecosystem-level studies be carried out to determine the larger impacts of artificial light at night. It is possible that past researchers on artificial light at night have focused on organisms that are more likely to be negatively affected by artificial light. By conducting larger-scale, multi-trophic level studies for longer time periods (i.e., > 3 months), we will be better able to discern how large of a threat artificial light is to whole ecosystems.

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Appendix 1. Algal biomass and periphyton data.

Pre/Post-Experiment	Stream	Reach	Habitat	AFDM ($\mu g\ cm^{-2}$)	Chl-a ($\mu g\ L^{-1}$)	Phaeophyton ($\mu g\ L^{-1}$)
Post	Blaney	Dark	Pool	0.22	30.46	51.78
Pre	Blaney	Dark	Riffle	0.27	36.74	62.46
Post	Blaney	Lit	Pool	0.10	12.47	21.20
Post	East	Dark	Pool	0.05	11.26	19.15
Pre	East	Dark	Pool	0.10	13.73	23.34
Pre	East	Dark	Riffle	0.09	16.46	27.98
Post	East	Lit	Pool	0.02	25.16	42.78
Pre	East	Lit	Pool	0.10	16.30	27.71
Pre	East	Lit	Riffle	0.06	11.27	19.16
Post	G	Dark	Pool	0.11	25.45	43.26
Post	G	Dark	Pool	0.04	14.03	23.85
Post	G	Lit	Pool	0.10	11.58	19.68
Pre	G	Lit	Pool	0.11	11.54	19.62
Pre	Spring	Dark	Pool	0.13	26.34	44.78
Pre	Spring	Dark	Riffle	0.06	8.79	14.94
Pre	Spring	Lit	Pool	0.08	14.75	25.08
Pre	Spring	Lit	Riffle	0.13	32.93	55.98

Appendix 2. Candidate models and fixed effects table for selected model (bold).

Drifting Invertebrates

Model nr.	Factors	Random	AIC	BIC	LL
1	+LD† +Temp +LD:Temp	stream, week	101.82	112.90	-43.91
2	+LD +Temp	stream, week	98.45	108.11	-43.22
3	**+LD**	**stream, week**	**94.14**	**102.33**	**-42.07**

† LD = Lit or Dark night

	Value	SE	DF	*t*	*p*
Intercept	5.40	0.282	19	19.14	< 0.0001
LDLit	-0.702	0.164	19	-4.274	0.0004

Terrestrial Inputs

Model nr.	Factors	Random	AIC	BIC	LL
1	**+LD**	**stream, week**	**132.53**	**140.72**	**-61.27**

	Value	SE	DF	*t*	*p*
Intercept	0.988	0.404	19	2.44	0.02
LDLit	0.108	0.256	19	0.423	0.68

without Blaney:

Model nr.	Factors	Random	AIC	BIC	LL
2	**+LD**	**stream, week**	**74.15**	**80.82**	**-32.08**

	Value	SE	DF	*t*	*p*
Intercept	0.450	0.273	14	1.645	0.12
LDLit	0.504	0.220	14	2.291	0.04

Emergence

Model nr.	Factors	Random	AIC	BIC	LL
1	+LD +Temp +LD:Temp	stream, week	105.48	116.37	-45.74
2	+LD +Temp	stream, week	102.43	111.93	-45.22
3	**+LD**	**stream, week**	**99.94**	**107.99**	**-44.97**

	Value	SE	DF	*t*	*p*
Intercept	1.269	0.311	18	4.08	0.0007
LDLit	-0.02	0.233	18	-0.10	0.92

Appendix 3. ANOVA table for fish SGR.

	DF	*SS*	*MS*	*F*	*p*
Lit/Dark	1	0.032	0.0316	0.357	0.55204
Stream	3	1.222	0.4075	4.609	0.00513
Lit/Dark:Stream	3	1.549	0.5164	5.841	0.00121
Residuals	76	6.719	0.0884		

Appendix 4. Tukey's HSD table for fish SGR.

	Difference	Lower	Upper	*p*-adjusted
Lit-Dark	0.038	-0.090	0.168	0.552
East-Blaney	-0.402	-0.717	-0.087	0.007*
G-Blaney	-0.176	-0.491	0.138	0.459
Spring-Blaney	-0.312	-0.587	-0.037	0.020*
G-East	0.225	-0.051	0.501	0.149
Spring-East	0.090	-0.140	0.319	0.733
Spring-G	0.135	-0.365	0.094	0.414
Lit:Blaney-Dark:Blaney	0.779	0.181	1.377	0.003*
Dark:East-Dark:Blaney	0.107	-0.461	0.674	0.999
Lit:East-Dark:Blaney	0.017	-0.551	0.585	1.000
Dark:G-Dark:Blaney	0.299	-0.269	0.867	0.723
Lit:G-Dark:Blaney	0.275	-0.292	0.843	0.799
Dark:Spring-Dark:Blaney	0.193	-0.312	0.699	0.932
Lit:Spring-Dark:Blaney	0.110	-0.395	0.616	0.997
Dark:East-Lit:Blaney	-0.673	-1.173	-0.172	0.002*
Lit:East-Lit:Blaney	-0.762	-1.263	-0.262	0.0002*
Dark:G-Lit:Blaney	-0.480	-0.981	0.020	0.070
Lit:G-Lit:Blaney	-0.504	-1.005	-0.003	0.047*
Dark:Spring-Lit:Blaney	-0.586	-1.015	-0.157	0.001*
Lit:Spring-Lit:Blaney	-0.669	-1.100	-0.240	0.0002*
Lit:East-Dark:East	-0.090	-0.553	0.374	0.999
Dark:G-Dark:East	0.192	-0.271	0.656	0.898
Lit:G-Dark:East	0.169	-0.295	0.632	0.947
Dark:Spring-Dark:East	0.087	-0.298	0.472	0.997
Lit:Spring-Dark:East	0.004	-0.381	0.389	1.000
Dark:G-Lit:East	0.282	-0.181	0.745	0.557
Lit:G-Lit:East	0.258	-0.205	0.721	0.664
Dark:Spring-Lit:East	0.176	-0.209	0.561	0.842
Lit:Spring-Lit:East	0.093	-0.292	0.478	0.995
Lit:G-Dark:G	-0.024	-0.487	0.439	1.000
Dark:Spring-Dark:G	-0.106	-0.491	0.279	0.989
Lit:Spring-Dark:G	-0.189	-0.574	0.196	0.790
Dark:Spring-Lit:G	-0.082	-0.467	0.303	0.998
Lit:Spring-Lit:G	-0.165	-0.550	0.220	0.883
Lit:Spring-Dark:Spring	-0.083	-0.369	0.203	0.985

Conclusion

The light shines in the darkness, and the darkness has not overcome it.

—John 1:5, New International Version of the Bible

Throughout human history, light has been seen as representing all that is good. Most major religions use light as a metaphor for good, and darkness for evil. Without a doubt, the positive attributes of light comes from using fire to keep predators at bay, and allowing us to use our sight throughout the night. But in the last 100 years or so since the invention of modern industrial lighting, light has changed from being a rare treat to be cherished to being an ever-present and potentially negative force.

Despite the pervasive presence of artificial light in our lives, ecologists have been slow to study the potential effects of artificial light on ecosystems. A thorough review of the literature on artificial light and stream ecosystems revealed many gaps in our knowledge (Chapter 1), and my colleagues and I briefly described how artificial light at night could be a major threat to biodiversity (Chapters 1 & 2). The main objective of this thesis was to use empirical studies to determine what effects artificial light has on stream ecosystems.

I hypothesized that artificial light at night would have major impacts on stream ecosystems because light is one of the primary *zeitgebers* for many organisms, both aquatic and terrestrial. By altering the light patterns that organisms have evolved with for millennia, there is the potential to not only disrupt circadian rhythms but also patterns and timing of dispersal, reproduction, and interactions with other organisms. In this thesis, I focused on patterns of dispersal and interactions with other organisms, but the other areas deserve attention as well and I will go over them in more detail in the sub-section on *Areas for Future Research*.

Major Findings

I found evidence that artificial light has the potential to negatively affect various stream organisms in my thesis research, but the group that seems to be most affected by artificial light at night is aquatic insects, at both adult and larval life stages. In my first empirical study (Chapter 3), I saw no effect of artificial light on the drifting response of gammarids. This was unexpected, as gammarids have previously been seen to respond to light levels corresponding to that of a full moon (Holt and Waters 1967, Lagrue et al. 2011), and several of the flumes in my experiment had light levels well over that of a full moon. However, these previous studies took place during the spring and summer, with water temperatures for one study (Lagrue et al. 2011) reported as around 18 °C. My study took place in the winter and the average water temperature across flumes for the duration of my experiment was 9.9 °C. This suggests that there might be some seasonal effect on diel drift behavior that deserves further investigation.

My second study (Chapter 4), in which I experimentally introduced lights to a small island in the Spree River, I found that the flight patterns of adult aquatic insects were significantly altered by the addition of the artificial lights. I expected to find a decrease in the number of aquatic insects caught in the middle of my experimental field when the lights were on relative to the nights the lights were off; however, I did not see any difference in the number of insects caught at these middle traps on dark and lit nights. This suggests that lights might not completely prevent the inland dispersal of adult aquatic insects, although the number of aquatic insects caught in these traps was very low so that my confidence in the results from these middle traps is not high. However, I caught significantly more aquatic insects at traps right next to lights than any other traps on nights when the lights were on. Furthermore, the proportion of the total number of insects caught which were aquatic was much greater at these traps. The lights actually significantly increased the proportion of insects caught at traps up to 40 m away from the lights. These results imply that the flight behavior of aquatic insects is altered by the presence of artificial light. It also has important implications for the nutrient subsidy aquatic insects provide to terrestrial predators. The high numbers of aquatic insects around streetlights may make it much easier for some predators to consume these insects, and increase the nutrient subsidy from stream to terrestrial ecosystems, but it will likely increase competition between predators and prevent some species that are not well-adapted to hunting near lights from living in illuminated areas (Rydell 1992).

In my third study (Chapter 5), I found that, in contrast to Chapter 3, the drift of stream invertebrates was significantly reduced by the addition of artificial lights; however, this study was done during the summer and the drifting community was almost entirely composed of aquatic insects, primarily mayflies, in contrast to the gammarids in my study in Chapter 3.

This was my second large-scale experimental field study and the first of its kind to introduce artificial lights to a near-natural area and study community responses.

Because aquatic invertebrates play such an important role in stream ecosystems and the invertebrates were affected by the addition of light, as the drift results show, it was surprising that the fish and leaf litter decomposition were not significantly affected by the light. On the other hand, while there were no statistically significant differences between the lit and dark reaches in regards to responses by trout and leaf litter decomposition, there were still some interesting patterns present when the results are looked at in more detail. For one thing, the trout recaptured in the lit reach of Blaney exhibited a huge increase specific growth rate (Chapter 5, Fig. 6). It is interesting to think about the interaction of artificial light and habitat complexity when looking at these results, because the different stream reaches used in the study did have varying degrees of complexity. The lit reach of Blaney probably had the greatest level of habitat complexity, as judged by the presence of very distinct pools and riffles, in-channel LW and boulders. The lit reaches of Spring and both reaches of G also had high levels of habitat complexity. The lowest levels of habitat complexity were all of East, though particularly the lit reach, and the dark reaches of both Spring and Blaney. Because I did not take any actual habitat measurements on these reaches, I cannot fully evaluate the degree to which habitat complexity might play a role in the numbers of fish caught and their body condition in the various reaches. However, I can suggest that this is an area that will need further investigation and will need to be controlled for in future studies. Comparing the change in body condition between the trout recaptured in the lit reach of Blaney (relatively complex structure) and the lit reach of East (relatively simple structure) suggests that there could be very different responses to artificial light based on habitat complexity (Chapter 5, Fig. 7). Most streams flowing through lit areas have also been modified so they have a relatively low level of habitat complexity, and fish in these streams might react more like those in the lit reach of East than those in the lit reach of Blaney.

On the other hand, leaf litter decomposition does not appear to be related to stream complexity (Chapter 5, Fig. 6) and seems to be related to the number of shredders present, with higher levels of leaf litter decomposition in reaches with more shredders in the pools. Ideally, I would have used more leaf litter bags in each reach to help reduce some of the variability and maybe even had another stream in the experiment. However, using more leaf litter bags in the streams I had was the only real possibility to reduce variability, as adding another stream to the experiment was not feasible.

That emergence was not affected by the light was not too surprising, given the complete lack of an effect on emergence in Freienbrink (Chapter 4). However, it was unexpected that there was no difference in the inputs of terrestrial invertebrates to lit as compared to dark reaches. Interestingly, the dark reach of Blaney had a very high number of terrestrial insects falling into the reach. This is surprising because 1) this reach was very wide, and 2) it had the lowest trout specific growth rates. However, even though it was very wide, it also had a lot of overhanging deciduous vegetation near the pan traps that could have inflated the amount of insects falling into the reach. The lit reach of Blaney also had very high inputs of terrestrial insects. When both reaches of Blaney were removed from the analysis, there were significantly more insects falling into the lit reaches. But there was no concordant increase in trout specific growth rates. This might mean that the increased terrestrial inputs are just balancing out the decrease in drifting benthic insects, but finding evidence to support this theory will require further research that examines trout gut contents in dark and lit reaches.

Overall, I found evidence that stream organisms, particularly aquatic insects, can be negatively affected by artificial light at night. However, it is unclear how much damage artificial lights do to populations of aquatic insects on their own. For instance, one could assume that reduced drift densities would lead to stream reaches that are completely denuded of algae by an increase in grazers and therefore increase larval mortality rates. However, drifting is likely a demographic process, where the benthic insects in the drift are there because the carrying capacity of the reach has been exceeded (Anholt 1995). If the number of grazing invertebrates who die as a result of reduced algal abundance is the same as the number who would normally drift, then there should be a relatively small impact on the stream reach. However, it seems likely that one of several other responses could take place: 1) many more benthic grazers would die from starvation than just the "surplus" individuals, 2) benthic invertebrates would be more available for fish consumption and could drive an increase in benthic foraging as opposed to drift feeding, or 3) the abundance of benthic invertebrate predators could increase to the point where the predators then consume many more grazers than the "surplus" and the number of grazers would be greatly reduced (Fig. 1). It would probably take at least several months of exposure to artificial light for any of these theories to play out, but they are worthy of investigation, especially with their potential to affect other stream organisms and processes. For instance, in the case of scenario 3, a rapid decrease in standing algal biomass would be followed by an increase, potentially altering other species interactions (Power 1990). The greatest challenge for future investigators will be to determine what any effects on the larval aquatic insect community will mean for adult aquatic insects and their predators. It is possible that in some scenarios, reduced densities of benthic invertebrates would lead to reduced numbers of emerging adult aquatic insects, which could in turn lead to reduced riparian predators and further reduced benthic densities.

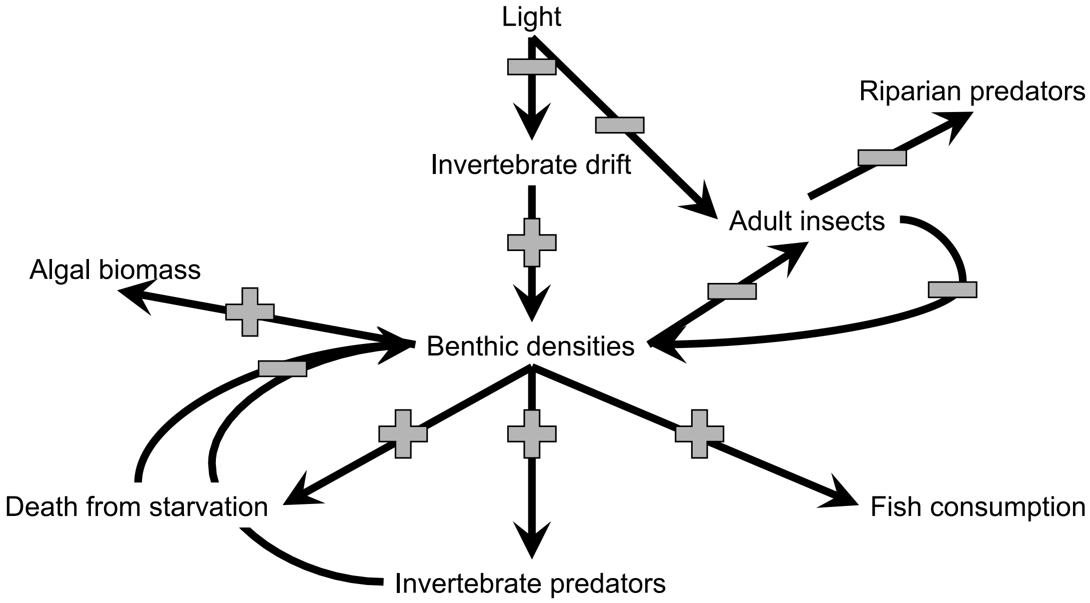

Figure 1. Possible ways in which artificial light could alter invertebrate stream and riparian relationships.

Adult Ephemeropterans might have been more affected by artificial light than any other taxonomic order in my study from Chapter 4, with almost 38 times as many Ephemeropterans captured on lit nights than dark nights compared to roughly 15 times as many aquatic Dipterans caught on lit than dark nights (Chapter 4, Appendix 4). The vast majority of the Ephemeropterans caught in the Chapter 4 study were Baetidae, which is also the family that made up most of the drift in Chapter 5. If the decreased larval drift densities and increased adult flight-to-light rates interact synergistically, this could lead to a massive decrease in the number of Baetid mayflies in lit streams.

Effectiveness of Large-Scale Field Studies

Overall, I was pleased with how the large-scale experimental field studies went. Given the lack of general research in the topic of artificial light at night, it was difficult to make predictions about what might happen by adding light, and what would be the most important thing to study. By conducting these large-scale field experiments, I was able to make observations that will help guide future lab and field studies. Even though my results were not always significant, they still revealed some patterns that need further investigation.

Implications

The results from this study should certainly encourage city planners to be cautious about installing lights near streams. Managers and scientists should work together in order to educate citizens about the potential negative impacts of artificial lights on stream ecosystems. A good example of this is the *Verlust der Nacht* project (http://www.verlustdernacht.de, accessed 27 January 2013). Not only does the project involve scientists from a wide range of fields, it has also done a commendable job reaching out to engage citizens in the research and educate them about artificial light at night. There might also be possibilities for creating incentives to encourage people living near streams to eliminate lighting near stream margins, perhaps at certain critical time periods, if they can be established.

Areas for Future Research

Clearly, much more work needs to be done in the field of artificial light ecology before we are really able to understand how organisms and ecosystems respond to this stressor. While I was able to make some interesting discoveries during my thesis, I find myself with more questions about the effects of artificial light on stream ecosystems than ever. This is an exciting place to be, and I look forward to answering some of these questions as I continue my career.

One of the main areas of future research in artificial light ecology is to look at how other stressors interact with light to affect stream and riparian organisms. This emerged as a theme repeatedly in my experiments. First, in Chapter 3’s drift experiment, it seems as though temperature could interact with artificial light in a way that actually reduces the effect of artificial light. There have been massive alterations to the riparian environment used in Chapter 4’s adult insect dispersal study, as the riparian forest is now only a very thin remnant maybe 1-3 trees deep at the edge of a cattle pasture. It is unclear how much this might have influenced the inland flight of the aquatic insects, but previous research has shown that the inland flight of some aquatic insect species is influenced by the presence of riparian vegetation (Delettre and Morvan 2000, Petersen et al. 2004). Then, in Chapter 5, there seemed to be a possible relationship between stream complexity and the response of resident trout to artificial light. Additionally, streams that are exposed to artificial light are also likely to be exposed to other anthropogenic stressors, such as invasive species, increased sedimentation, and toxic chemicals, to name just a few (Walsh et al. 2005). Future research will need to carefully examine how these various disturbances interact with artificial light in order to develop a more complete picture of how artificial light affects stream ecosystems.

Another topic that will need more consideration is finding when organisms of special concern are particularly susceptible to the effects of artificial light. For instance, it seems that gammarids may not be especially sensitive to artificial light at night during the winter, though this will require further evidence. On the other hand, species such as juvenile rainbow trout may actually be more disturbed by artificial light in the winter (Contor and Griffith 1995). It will also be important to determine if certain life stages are more likely to be affected by artificial light. Understanding more about the timing of various organisms' susceptibility to artificial light will help city planners develop better strategies for avoiding lighting areas during these times.

Related to this is how different species' circadian rhythms might be altered by artificial light at night. Clearly humans have changed patterns of melatonin production when exposed to artificial light at night, but it will be important to establish if this is the case for stream organisms, and what this might mean for their survival.

As I suggest in Chapter 4, reproduction is likely to be altered when organisms are exposed to artificial light. Future research will need to examine any differences in the reaction to artificial light between the sexes of vulnerable species. We will also need to determine if mating is disrupted by artificial light (Rand et al. 1997). If artificial lights cause individuals of normally widely dispersed species to congregate, light could be beneficial by providing increasing mating opportunities or negative by increasing competitive interactions.

In addition to studying stream invertebrates, fish, and algae, future research will also need to take other taxa into consideration. For instance, as mentioned in Chapter 1, we need to know if riparian trees will change when they begin to grow and drop their leaves, as this could influence the input of terrestrial invertebrates and leaves to streams. Furthermore, amphibians are often important stream predators, and previous research has shown that they are affected by artificial light at night (Buchanan 1993 Rand et al. 1997). It will be necessary to understand these effects on amphibians mean to stream ecosystems. Lastly, while we looked at the number of benthic shredders in Chapter 5, we did not take any samples of the microbial and fungal organisms. It will be interesting to see if these organisms are also responsive to artificial light, or if it has no effect on them.

In addition to studying the actual ecological effects of artificial light at night, the spatial and temporal patterns of artificial lights also need further study. Previous research into this topic has found that the distribution of lights across Berlin is patchy, with some environment types much more likely to be exposed to high levels of artificial light than others (Fig. 2, Kuechly et al. 2012). It will be interesting to see if these same patterns hold up in other cities as well. Knowing what habitat types are most likely to be exposed to artificial light will allow us to focus our ecological research on those areas.

Figure 2. The city of Berlin at night, showing the patchy distribution of light across the city. Photo credit: C. C. M. Kyba.

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List of Publications

Perkin, E. K., F. Hölker, J. S. Richardson, J. P. Sadler, C. Wolter, and K. Tockner. 2011. The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. Ecosphere 2: art122.

Conceived the content of and wrote the paper, with the help of the co-authors.

Hölker, F., Wolter, C., **Perkin, E. K.**, and Tockner, K. 2010. Light pollution as a biodiversity threat. *Trends in Ecology and Evolution* 25: 681-682.
Provided criticism and content suggestions to the lead author.

Curriculum Vitae

EDUCATION

4.09- 4.13	*Ph.D. Candidate, Freie Universität Berlin* Dissertation title: “The effects of artificial lighting on aquatic ecosystems” Advisors: Prof. Dr. Klement Tockner and Dr. Franz Hölker
6.06- 3.09	*M. S. School of Aquatic and Fishery Sciences, University of Washington* Thesis title, “The relationship of soil nitrogen availability and water holding capacity to riparian tree growth on the Queets River, Washington” Advisor: Dr. Robert J. Naiman
5.04	*B. A. in Biology, Reed College, Portland, OR* Thesis, “The effects of additional coho salmon carcasses on macroinvertebrate drift in western Oregon streams” Advisors: Dr. David Dalton, Reed College and Burke Strobel, United States Forest Service
8.99- 5.00	*Biology, Gonzaga University, Spokane, WA* Transferred to Reed College after first year

PUBLICATIONS (PEER REVIEWED)

Perkin, E. K., Hölker, F., Richardson, J. S., Sadler, J. P., Wolter, C., and Tockner, K. 2011. The influence of artificial light on freshwater and riparian ecosystems: questions, challenges, and perspectives. *Ecosphere* 2: 122.

Hölker, F., Wolter, C., **Perkin, E. K.**, and Tockner, K. 2010. Light pollution as a biodiversity threat. *Trends in Ecology and Evolution* 25: 681-682.

IN PREP

Perkin, E. K., Hölker, F., Tockner, K., and Richardson, J. S. The short-term effects of artificial light on different trophic levels in small streams.

Perkin, E. K., Hölker, F., and Tockner, K. The effects of artificial night lighting on adult aquatic and terrestrial insects.

Perkin, E. K., Hölker, F., Heller, S., and Tockner, K., and Berghahn, R. Artificial light and night-time activity in gammarids.

Perkin, E. K., Bechtold, J. S., and Naiman, R. J. Soil moisture and riparian tree growth on the Queets River, Washington.

OTHER PUBLICATIONS

Hölker, F., **Perkin, E. K.**, Wolter, C., Kloas, W., Staaks, G., and Tockner, K. 2009. Der Verlust der Nacht. Leibniz-Institut für Gewässerökologie und Binnenfischerei Jahresforschungsbericht 2008: 12-13.

Hölker, F., Voigt, C., Wolter, C., **Perkin, E. K.**, and Tockner, K. 2009. Der Verlust der Nacht ist auch ein ökologisches Problem. Leibniz Gemeinschaft Zwischenruf 2: 18-21.

TEACHING

.12 *Teaching Assistant, Aquatic Ecology, Freie Universität Berlin*
Professor: Dr. Michael Monaghan

.09-.11 *Teaching Assistant, Zoology, Freie Universität Berlin*
Professor: Dr. Klement Tockner and Dr. Michael Monaghan

.08 *Teaching Assistant, Watershed Ecology and Management, University of Washington*
Professor: Dr. Robert J. Naiman

.07 & .08 *Teaching Assistant, River Ecology, University of Washington*
Professor: Dr. Robert J. Naiman

.07 & .08 *Facilitator, School of Aquatic and Fishery Sciences, Teaching Assistant Training, University of Washington*

.07 *Teaching Assistant, Attaining a Sustainable Society, University of Washington*
Professor: Dr. James Karr

.01-.03 *Biology Outreach, Portland Public Schools through Reed College*

.00 *Salmon Camp Counselor, Oregon Museum of Science and Industry*

INVITED TALKS

15.02.08 Leibniz-Institute for Freshwater Ecology and Inland Fisheries, Berlin. Colloquia of the Institute. Relationship between soil N availability and riparian tree growth on the Queets River, WA.

05.03.12 Science Slam. Competitive talk to the public of Berlin. Artificial light and the Dispersal of adult aquatic insects…oder Wie Batman der Herren der Fliegen wurde. Voted best talk by the audience of 500+

FUNDING & AWARDS

.12 Ecological Society of America Student Section Travel Award. Based on research abstract and recommendation letter. $500 USD

.11 University of British Columbia Graduate Student International Research Mobility Award. Based on a short abstract of research proposal with UBC faculty. $1500 CAD

.10 North American Benthological Society President's Fund Award. Based on extended abstract of PhD research. $900 USD

.09 Galen and Helen Maxfield Fisheries Scholarship. Funded last quarter of Master's work. $7673 USD

.07 H. Mason Keeler Lake Washington Fund in Fisheries. Funded field assistant for Master's research. $2489 USD

.03 Milton L. Fischer Field Memorial Fellowship. Funded 10 weeks of independently-designed field research. $3000 USD

.02 Independent Summer Research Project Award. Funded 10 weeks of independently-designed field research. $3000 USD

CONFERENCE PRESENTATIONS/PARTICIPATION

07.08.12 Ecological Society of America Annual Meeting. Portland, OR. Does artificial light at night disrupt temperate stream ecosystem function? Oral Presentation.

26.05.11 North American Benthological Society Annual Meeting. Providence, RI. Artificial light interferes with the dispersal of adult aquatic insects across the terrestrial landscape. Oral Presentation.

8.06.10 North American Benthological Society Annual Meeting. Santa Fe, NM. Effects of artificial light at night on aquatic and riparian ecosystems. Poster.

6.08.08 Annual Meeting of the Ecological Society of America. Milwaukee, WI. Soil N availability, water holding capacity and riparian tree growth. Poster.

5.05.08 Annual Meeting of the Western Division American Fisheries Society. Portland, OR. Soil N availability and riparian tree growth. Oral Presentation.

25-29 .02.08 DIVERSITAS freshwaterBIODIVERSITY Cross Cutting Network Scientific Committee Meeting. Seattle, WA. Participant.

PROFESSIONAL SERVICE

.12 Jointly organized oral session, Ecological Effects of Artificial Light at Night. Ecological Society of America Annual Meeting, Portland, OR.

.12 Local host for the Student Section. Ecological Society of America Annual Meeting. Portland, OR.

.12 Served as reviewer for undergraduate travel award committee, Society for Freshwater Science.

.11 Jointly organized special session, Conservation Challenges for Organisms with Complex Life-Cycles. North American Benthological Society Annual Meeting. Providence, RI.

Reviewer for the following publications
Aquatic Sciences, Aquatic Ecology, and Biology Letters

MEMBERSHIP IN PROFESSIONAL SOCIETIES

Society for Freshwater Science (Formerly the North American Benthological Society, since 2009)
Ecological Society of America (since 2009)