

Consequences of Different Types of Littoral Zone Light Pollution on the Parental Care Behaviour of a Freshwater Teleost Fish

Jordann G. Foster • Dirk A. Algera • Jacob W. Brownscombe • Aaron J. Zolderdo • Steven J. Cooke

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Abstract Ecological light pollution occurs when artificial lights disrupt the natural regimes of individual organisms or their ecosystems. Increasing development of shoreline habitats leads to increased light pollution (e.g., from cottages, docks, automobile traffic), which could impact the ecology of littoral zones of lakes and rivers. Smallmouth bass (Micropterus dolomieu) engage in sole paternal care, guarding their nest continually, day and night, to protect their developing offspring. Any alterations to their behaviour—either directly because of the response to light or indirectly due to changes in nest predator activity and associated response of the bass-could lead to increased energetic demands for fish that have a fixed energy budget and ultimately reduce reproductive success. To examine this issue, triaxial accelerometer biologgers were externally attached to nesting smallmouth bass during the egg stage to determine whether light pollution (i.e., dock lights with low levels of continuous light and spotlights with high intensity irregular light simulating automobile traffic) altered behaviour of nesting males relative to control fish. Our study revealed that both types of light pollution increased overall bass activity level compared with the control group. The intermittent light treatment group had the highest activity and exhibited large fluctuations

between night and day activity levels. Fish in the continual light treatment group displayed statistically higher activity than the control fish but showed limited fluctuations between day and night activity levels. Our results suggest that continuous or intermittent light sources, common in shoreline habitats that have been developed, have the potential to alter the behaviour and thus energy use of nest-guarding fish. This study contributes to the growing body of literature on the ecological consequences of light pollution in aquatic ecosystems.

Keywords Behavioural alteration · Smallmouth bass · Light pollution

1 Highlights

Constant and intermittent light pollution altered the behaviour of smallmouth bass nesting along the shoreline of temperate lakes as revealed by use of accelerometer loggers affixed to the fish.

Remarkably, the behavioural alterations observed here persisted beyond the night when the light treatments were applied to influence parental care during the diurnal periods.

2 Introduction

Ecological light pollution occurs when artificial lights disrupt the natural regimes of individual organisms or their ecosystems yielding changes in organismal

e-mail: Steven_Cooke@carleton.ca



J. G. Foster · D. A. Algera · J. W. Brownscombe ·

A. J. Zolderdo · S. J. Cooke (☒)
Fish Ecology and Conservation Physiology Laboratory,
Department of Biology, and Institute of Environmental Science,
Carleton University, 1125 Colonel By Dr., Ottawa, ON K1S 5B6,
Canada

behaviour, physiology, feeding or habitat use (Longcore and Rich 2004). Lighted buildings, streetlights, boats, security lights and automobile lights are common contributors to ecological light pollution (Longcore and Rich 2004). Some of the more well-known adverse impacts of light pollution on organisms include migrating birds flying into lighted tall buildings (Erickson et al. 2005), moth species swarming outdoor lights (van Langevelde et al. 2011) and sea turtle hatchlings traveling away from the ocean towards lighted beachfronts (Witherington and Martin 2000). However, there have been few studies addressing the impacts of light pollution on wild fish (but see Jennings et al. 1999; Nightingale et al. 2006; Perkin et al. 2011; Becker et al., 2013; Georgiadis et al. 2014).

The influence of light pollution as a factor impacting freshwater systems has gained some recognition in the past several decades (Jennings et al. 1999). Light has been found to be an important cue for feeding behaviours and predator avoidance in freshwater systems (Jennings et al. 1999; Becker et al. 2013). Many species of teleost fish feed in schools during the day and disband from the school at night (Nightingale et al. 2006); this is due to photoreceptors recognizing decreases in light and prompting the fish to stop feeding. Artificial light could allow these fish to continue feeding in a school later into the night (Nightingale et al. 2006). Conversely, Contor and Griffith (1995) found that juvenile rainbow trout (Oncorhynchus mykiss) ceased foraging and sought cover when there was bright moon or artificial night lighting. This is likely a predator avoidance strategy; daytime hiding behaviour of juvenile salmonids has been well documented in stream habitats (Contor and Griffith 1995). In another example, Atlantic salmon (Salmo salar) fry were observed to disperse later in the day in the presence of artificial light (Riley et al. 2015). With increasing development along shorelines (Nightingale et al. 2006), other behavioral alterations due to artificial light are possible.

Smallmouth bass (*Micropterus dolomieu*) is a species of temperate, freshwater fish from the Centrarchidae family. Centrarchidae are noted for their nest building behavior; males make depressions in the substrate and then females choose a male's nest to deposit their eggs (Ridgway 1988). After egg deposition, the female departs the nest site, and the male remains behind to provide sole paternal care to the developing brood for up to 6 weeks (Cooke et al. 2006). Nest-building and spawning times are highly dependent on photoperiod

and water temperature. Earlier or later spawning can occur if the photoperiod of day length is manipulated (Brown et al. 2009). Parental care behaviours include fanning the eggs to increase oxygen flow and protecting the brood from predators (Coleman et al. 1985). Many other fish species prey on smallmouth bass eggs and hatchlings; so, guarding their young is essential for offspring survival (Ridgway 1988). Male bass display aggressive behaviours such as charging and biting that deter predators from preying on their offspring (Colgan and Brown 1988). During the parental care period, bass guard nests continually (day and night; Hinch and Collins 1991; Cooke et al. 2002) and have limited feeing activity to supplement energy expenditure (Hinch and Collins 1991). Any alterations to their behaviour—either directly because of the response to light or indirectly due to changes in nest predator activity and associated response of the bass—could lead to increased energy expenditure for these fish that are operating largely on a fixed energy budget (Cooke et al. 2002). This could have negative fitness consequences. Bass build their nests in the littoral zones of lakes and rivers; these are the same areas that are often subject to light pollution from shoreline development (cottages, houses, docks, etc., e.g., Wagner et al. 2006) and adjacent automobile traffic. As such, bass are an ideal model to experimentally evaluate the effects of light pollution.

Our objective was to determine if ecological light pollution impacts smallmouth bass nesting activity levels. We predicted that artificial light would increase overall locomotor activity level associated with greater attention by nest predators. To address our objective, we externally attached tri-axial accelerometer loggers (Brown et al. 2013) onto nest-guarding smallmouth bass to generate estimates of their activity levels. We compared control fish to two light treatments. To assess the effects of low intensity continuous light that would be consistent with dock and shoreline lighting, we placed solar light emitting diode (LED) lights 3 m from the nests. To assess the effects of short, irregular, high intensity lighting that would be consistent with automobile traffic on roads adjacent to water bodies, we used a high powered LED spotlight to "streak" the nest sites several times during darkness. This work will help to address a major knowledge gap in our understanding of the effects of light pollution on fish and will inform the development of guidelines related to shoreline development and associated lighting regimes.



3 Methods

3.1 Study Site

The study took place from 7 May through 18 May 2015 on Lake Opinicon (44°33'32" N, 76°19'40" W), Sand Lake (44°34'13" N, 76°15'12" W) and Indian Lake (44°35'33" N, 76°19'36" W), all part of the Rideau River watershed in southeastern Ontario. The moon was waning for the duration of the study, beginning the day after the full moon (May 6) and terminating of the 18th prior to the new moon that would have been observed on that evening. These interconnected lakes have been used in previous research on the reproductive biology, including parental care, of smallmouth bass and other Centrarchid species (Philipp et al. 1997; Cooke et al. 2002). Surface water temperature, measured using a hand-held thermometer, ranged between 13 and 16 °C over the course of the study. The fish communities are similar between lakes (Gravel and Cooke 2009), and previous physiological studies indicate that the costs of parental care are virtually identical across these lakes (Gravel et al. 2010). All research was conducted in accordance with the Canadian Council on Animal Care guidelines for use of fish in research (Carleton Animal Care #315774-166) and with a Scientific Collection Permit issued by the Ontario Ministry of Natural Resources and Forestry.

3.2 Fish Selection

Nest-guarding male smallmouth bass were located through snorkel surveys. Fish size, brood size and offspring developmental stage were visually assessed by a diver. Brood size was qualitatively scored using a scale of 1 to 5 (1 = low to 5 = high as outlined by Philipp et al. (1997)) with suitable scores considered as 3 and above. Nest-tending behaviours vary among egg development stages; so, only fish guarding eggs were used (Cooke et al. 2002). All fish sampled were between 380 and 510 mm in total length. Fish below 380 mm were deemed too small for accelerometer attachment, as the accelerometer tag would exceed 2 % of the fish's total body weight if we used smaller fish, which could impede swimming behaviour (Brown et al., 1999). Though mass was not directly measured, fish in this size range are expected to exceed 1000 g, as calculated from known length-weight relationship of smallmouth bass in Lake Opinicon (Dey et al. 2010). The equation was log_{10} mass = $-7.1004 \times 3.884(log_{10} TL)$ with mass reported in grams and total length reported in millimetres.

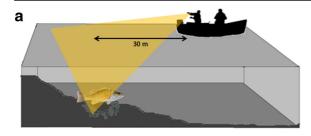
3.3 Accelerometer Attachment

Once a suitable nest-guarding male was located (spaced at least 50 m from nearest nest that was part of experiment or in an area that was out of the direct influence of a treatment such as on the opposite side of a treed island), the nest was marked with a numbered PVC tile. All nests used in the experiment were in ~0.5 m of water. The guarding male was angled off its nest using a variety of lures and bait. Fight time was minimized to less than 20 s to reduce stress associated with anaerobic exercise and capture (Cooke et al. 2003). While the fish was away from its nest, a snorkeler remained in the water and protected the nest from brood predators using a blunt pole. Following capture, each fish was measured (total length) and held in place in a foam lined trough filled with fresh lake water. Accelerometers were secured using tape to plastic and foam frontal and backing plates with 22.7 kg strength braided line threaded through the musculature on the back of the fish near the anterior aspect of the soft dorsal fins (Brownscombe et al. 2014). Accelerometers had an average weight of 28 g in air (~18 g in water) including the backing plates, tape and braided line. Prior to release, the fish was rotated along its horizontal and vertical axes, and the time was noted to calibrate the device at the start of accelerometer logging (as per Brownscombe et al. 2014). The snorkeler left the nest area after the bass returned and resumed parental care duties (generally in <2 min).

3.4 Treatments

The experimental design consisted of three treatments which were applied in a manner such that we alternated the three treatments for each tagged fish as we moved along the shoreline with our snorkel surveys. A control group had accelerometers attached but received no artificial light pollution. A second group of fish was exposed to an intermittent light treatment, intended to mimic random automobile traffic passing by at night, where an 825-lumen Browning High Noon LED Spotlight (~6000°K cool white light, Browning Arms Company, Morgan, UT) shone above the nest in 5-s sweeps for twelve repetitions from approximately 30 m away (Fig. 1a) which registered between 10.2 and 58.2 lux





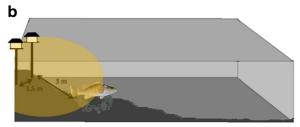
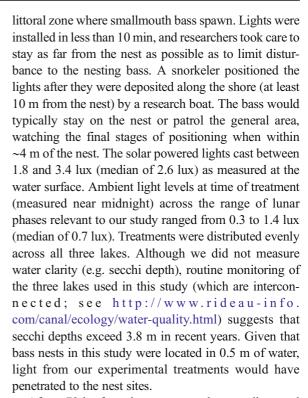


Fig. 1 Schematic representation of a tagged bass on nest undergoing **a** the intermittent light treatment, consisting of 12 five-second sweeps of the nest each minute from approximately 30 m away, and **b** the constant light treatment, consisting of low, continuous, solar powered light levels from approximately 3 m away, both treatments occurred at night

(median of 40.4 lux) at the water surface at that distance (using a Dr. Meter Digital Light Meter, Lux Tester, sample rate of 2.5 hz, range of 0.1 to 200,000 lux, light measured using the lowest range of 0.1 to 200.0 lux). The research boat was turned off 100 m away when approaching the nest to eliminate noise pollution with final positioning by paddle. This lighting treatment was conducted at midnight on the second and third night after the accelerometer was attached. This was approximately 36 and 60 h post-accelerometer attachment. Based on preliminary trials, the beam cast by the spotlight was sufficiently focused that no detectable light illuminated adjacent nests that were positioned more than ~30 m away (and we went with a minimum spacing of 50 m). The last treatment included the installation of two NOMA LED solar powered lights (~6000°K cool white light, Electrical Components International, St. Louis, MO) mounted on individual wooden posts and placed at each of the nest sites to mimic a typical cottage or shoreline dock light (Fig. 1b). The lights were positioned 0.5 m above the water surface. The solar dock lights were set up in the morning of the second day following accelerometer attachment. This was approximately 20–24 h post-accelerometer attachment. Two lights were placed at each nest site, spaced 1.5 m apart and 3 m from the nests. The lights were anchored with rocks and concrete to emulate the natural habitat in the



After ~72 h of accelerometer attachment, all control and experimental fish were recaptured, following the procedure described above. The accelerometer was removed by cutting the braided line, and the fish was released back on its nest. In total, 22 fish (8 control, 6 intermittent light, 8 constant light) were tagged across the three lakes. Egg scores were again assessed at the conclusion of the study when fish were recaptured for accelerometer removal.

3.5 Accelerometer Data Processing

Tri-axial accelerometers (model X16mini, 17 g in air, 25 Hz recording frequency, ± 16 g range, 2048 count/g sensitivity; model X8M-3, 15 g in air, 25 Hz recording frequency, ± 8 g range, 1024 count/g sensitivity; Gulf Coast Data Concepts, Waveland, MS) were programmed to continuously record total acceleration in the x- (heave), y- (surge), and z- (sway) axes (as per Brownscombe et al. 2014). Static (gravity) and dynamic (fish movement) acceleration were separated by a weighted smoother over each axis at a 2-s interval (following Brownscombe et al. 2013). Overall dynamic body acceleration (ODBA), the sum of dynamic acceleration from the three axes (Gleiss et al. 2011), was calculated per hour for each fish to estimate smallmouth



bass activity levels. Experimental calibrations have found relationships between ODBA and metabolic rate in a range of taxa including fish (Halsey et al. 2009, 2011; Gleiss et al. 2011; Wright et al. 2014). All analyses were conducted using Igor Pro 6.0 software (WaveMetrics Inc., Lake Oswego, OR), with the Ethographer package (see Sakamoto et al. 2009).

To align the data for all fish, hour zero of logging began at sunset on the second day of accelerometer attachment. This marked the start of the treatment period when the lights in the constant light treatment group turned on. The intermittent light treatment group received their first treatment around midnight. To compare fish activity levels between treatments prior to the treatment period, ODBA was compared between treatments during the 2 h prior to the treatment period with a linear mixed effect model (LME) with fish ID as a random effect. To examine activity levels during the treatment period, an LME was developed with ODBA as the response variable, treatment, diel period, and their interaction as fixed effects and fish ID as a random effect. For both models, ODBA was log10-transformed to improve model fit. Models were validated following the procedure outlined in Zuur et al. (2009). All statistical analyses were conducted using RStudio (v. 3.2.3 R Foundation for Statistical Computing, Vienna, Austria).

4 Results

During the 2 h prior to the treatment period, there was no significant difference in ODBA (i.e. activity level) between treatment groups (Table 1), indicating that bass from all treatment groups began the study with similar activity levels (Fig. 2). During the study period, there was a significant interaction between treatment and diel period (Table 1). With exception of the first 10 h, fish in both light treatments had higher activity levels than control fish, more so during the day than at night (Figs. 2 and 3). Control fish to which the other treatments were compared exhibited a pattern of decreasing locomotor activity during the monitoring period with activity levels consistently lower than fish in the two light treatments (Fig. 2). Intermittent light treatment fish activity was the highest throughout the 2 days with activity fluctuating more dramatically between night and day, peaking as high as 2.5 times greater than the control group on the second day before recapture (Fig. 2). It was our desire to be able to compare the egg score at time of capture

Table 1 Linear mixed effect model outputs comparing ODBA between treatment groups before treatments were applied and comparing ODBA between treatment groups and diel period after treatments were applied

	numDF	denDF	F-value	p value
Pre-treatment perio	d			
(Intercept)	1	22	178.178	< 0.001
Treatment	2	19	0.511	0.608
During treatment p	eriod			
(Intercept)	1	782	39.875	< 0.001
Treatment	2	19	0.722	0.498
Diel	1	782	44.553	< 0.001
Treatment:diel	2	782	8.400	< 0.001

through to recapture post-treatment. However, egg score is much more difficult to quantify reliably several days after spawning and as the eggs approach hatching so our second scoring was unreliable aside from revealing that all fish we recaptured were still actively engaged in parental care of the nest site even if eggs or offspring (i.e. egg sac fry) were cryptic.

5 Discussion

This study explored the effects of ecological light pollution on nesting bass activity levels. As predicted, fish receiving light treatments exhibited significantly higher

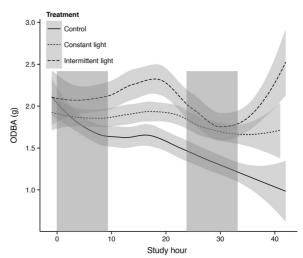


Fig 2 Bass activity across the three treatment groups fit with a loess smoother with 95 % confidence intervals surrounding lines starting at 0 as the start of the treatment period with 2 h prior to treatment starting at -2. *Gray vertical bars* represent periods at night



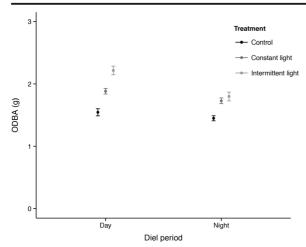


Fig 3 Overall dynamic body acceleration (mean+SD) for the three treatment groups during the study period separated into day and night values

activity level following the first artificially lit night than the control group fish that did not receive night lighting (Fig. 2). Increased levels of light throughout the night illuminate the nests and may provide more opportunity for brood predators to locate the nest. Light levels have been shown in past studies to have a large influence on feeding and foraging behaviour of teleost fish (Harden Jones 1956; Thorpe et al. 1988; Jennings et al. 1999). Brood predators, such as pumpkinseed (Lepomis gibbosus) and bluegill (Lepomis machrochirus), may have benefitted from the light treatments illuminating the nests. Becker et al. (2013) revealed that predation of estuarine fish by piscivorous fish increased when the area was illuminated at night to simulate light pollution suggesting that a similar mechanism could exist with nest depredation. Increased predation pressure would require the nest-guarding bass to more actively and continuously defend the nest from such predators, expending more energy in the process. Our attempts to evaluate changes in nest score between time of tagging and recapture failed to provide the resolution needed to determine if nest scores differed among treatments. In hindsight, use of video cameras to study predator behaviour would have been a useful complement to the accelerometer data.

The control group fish exhibited some fluctuation in activity levels between day and night throughout the study period (Fig. 2), but certainly continued to engage in care even during the night. Although some researchers have suggested that night is generally a time when nest-guarding bass can reduce their vigilance

because predation attempts by other fish are reduced (Emery 1973), Cooke et al. (2002) found that smallmouth bass activity levels during the early stages of parental care (e.g. egg stage) were similar for nocturnal and diurnal periods. Our study focused on bass guarding eggs such that the constant vigilance (albeit somewhat variable) between day and night observed here is consistent with recent literature. A significant interaction term revealed that bass receiving low and constant levels of artificial night light tended to have significantly higher activity levels than the control group fish as the study progressed, with such differences less apparent in the early phases of the study. Fish in the two lighting treatments exhibited little fluctuation between diurnal and nocturnal activity (Fig. 2), but without an apparent decrease in activity during the last night and day of accelerometer attachment, unlike the control fish. An artificial light study conducted on European perch (Perca fluviatilis) reported that there was no difference in concentrations of the stress hormone cortisol between fish subjected to varying nocturnal light intensities and control group fish (Brüning et al. 2015). A general higher activity level of the constant light treatment fish regardless of night and day could be due to the low and constant levels of light at night suppressing the production of melatonin and altering their circadian rhythm. The solar powered lights produced slightly more light (median of 2.6 lux), more than the 0.01–0.05 lux that would be cast by a full moon (Nightingale et al. 2006). The slightly increased, constant illumination may allow adaptation to the lighting level and behavioural response to the new conditions at night (Nightingale et al. 2006).

Overall activity for the intermittent light treatment group bass was highest of the three treatments and significantly higher than the control group (Fig. 2). Duration of lighting can influence fish responses, which may induce a startle response in fish. Unlike the study conducted by Brüning et al. (2015), with constant levels of low light, this light treatment used sporadic light, potentially causing fish to experience a stress response. Quick flashes of bright light, as used in the intermittent light treatment, produce large contrasts in light intensity over duration of times too short for retinal adaptation to occur (Nightingale et al. 2006). Ali (1959) found that coho (O. kisutch) and sockeye salmon (O. nerka) smolts took 20 min for both the retinal pigment light and cones to adapt to a bright light and they took >25 min for the cones to fully contract when adjusting back to the dark. Unlike a natural flickering of light caused by a wave or



clouds passing over, quick flashes of light caused by automobile traffic passing by can disturb fishes (Nightingale et al. 2006). Furthermore, fish in the intermittent light treatment group had the largest fluctuations between night and day activity levels throughout the study period. Normal behaviour for nest-guarding bass during the egg brood stage would show almost no fluctuation in activity level between night and day (Cooke et al. 2002). The bass in the intermittent light treatment were notably the most affected by the artificial light (Fig. 3).

The results from this experiment suggest that continuous low levels of light and intermittent bright light result in a higher overall activity of nest-guarding smallmouth bass compared with control fish (Fig. 2). Although we did not estimate energy use, ODBA is strongly correlated with metabolic rate in fish (see Gleiss et al. 2011; Wright et al. 2014); so, these increases in activity level presumably translate to higher levels of energy expenditure. We were unable to calibrate loggers put on nesting fish given that this would have required a lengthy nest absence (e.g. taking fish to a lab and exposing them to step-wise velocity increments in a swim tunnel and measuring oxygen consumption and relating to ODBA) during which time the nests would be fully depredated. During the parental care period, nest-guarding bass constantly tend to their brood and have limited feeding activity to supplement energy expenditure (Hinch and Collins 1991). Smallmouth bass are capital breeders, relying on a fixed energy budget for up to several weeks of nest-guarding. Any alterations to their energy expenditure, either directly due to response to artificial light or indirectly due to increased brood predator activity, could have negative fitness consequences. The additional loss of lipids and body weight associated with increased activity could lead to a higher nest abandonment rate or decreased future reproductive ability (Hinch and Collins 1991; Cooke et al. 2002), both resulting in adverse consequences for offspring production.

Parental investment (including locomotor activity) varies predictably over the parental care period of smallmouth bass reflecting the tradeoff between current and future reproduction (Cooke et al. 2002). Previous work using electromyogram transmitters evaluated parental care activity of smallmouth bass across stages of care (i.e. grouped all data collected under egg stage as "egg"; Cooke et al. 2002) but failed to provide the fine temporal resolution (i.e. hourly) measured using

accelerometer loggers here. The decline in overall activity observed in control fish during the egg stage therefore differs somewhat from the overall pattern reported by Cooke et al. (2002) but is presumably just a reflection of the differences in resolution between the two studies. Indeed, the pattern of declining locomotor activity reported here was observed among all the fish in the study (data not plotted here). Another potential contributing factor to the pattern of declining activity observed for the control fish could be related to fish becoming accustomed to the external logger. The previous electromyogram telemetry study (i.e. Cooke et al. 2002) anesthetized fish and conducted intracoelomic implantation to affix the devices to the fish. Here, we restrained the fish and affixed the loggers externally to the fish. Although such external attachment procedures have been shown to have negligible effects on the behavior of nesting confamilial rock bass (Ambloplites rupestris; Cooke 2003), that assessment was conducted using videography and lacked the resolution possible with accelerometers. It is conceivable that externally tagged fish exhibit some level of hyperactivity until they become accustomed to the presence of the device or otherwise compensate for the added burden (see Jepsen et al. 2015). Fish in all treatments were tagged in the same way and were of similar size so if there was indeed a transient alteration in behavior associated with tagging or presence of the device, we would expect that such effects would be equal across all treatments. As such, the relative differences between the treatment groups, which represent our "main effect", remain meaningful.

Parental care occurs in 60 % of freshwater fish families (Gross and Sargent 1985). The results from this study suggest that ecological light pollution could have negative consequences on fish engaged in parental care which is concerning given the many ecosystem services provided by freshwater fish (Lynch et al. In Press). Many nest-building species, such as black bass, build their nests in the littoral zones of lakes and rivers. These areas are the most susceptible to light pollution due to shoreline development (Wagner et al. 2006). The proliferation of human development has led to ever-increased sources of anthropogenic light pollution in natural ecosystems. The findings in this paper can serve to inform management of shoreline development, highlighting the potential impacts that common lighting devices such as solar dock lights, security lights or car high beams can have on aquatic ecosystems.



We encourage additional research on this topic including longer-term studies that explore how light pollution and the alterations in behaviour observed in this study translate into population-level processes. It is also worth noting that this study represents one of a growing number of studies that rely on biologging or biotelemetry devices to study how wild animals (especially fish; see Cooke et al. In Press) respond to human disturbance and environmental change (see Wilson et al. 2015). The ability to quantify behavioural and physiological states in wild animals in the field provides a level of realism that is difficult to obtain in the laboratory, notwithstanding the potential consequences of the tracking devices or attachment procedures on the animal. We submit that biologging and biotelemetry represent powerful tools for understanding how wild animals respond to light pollution.

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