

Habitat and nutrients, but not artificial lighting at night, drive fish assemblage composition in urban streams

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Abstract

Artificial light at night (ALAN) is pervasive in urban environments, yet its potential effects on biotic communities of urban streams are not fully understood. We investigated the effects of ALAN on fish assemblages in 20 lit-unlit paired stream reaches across 10 sites in Columbus, Ohio, USA across two years. Our results show that light trespass into urban streams is approximately doubled during leaf-off in winter months ($1.97 \text{ lux} \pm 0.28$) compared to leaf-on in summer months ($1.00 \text{ lux} \pm 0.19$), highlighting the important interceptive effect of canopy coverage in headwater systems. There were no differences in fish assemblages (i.e., abundance, relative abundance, biomass, diversity, guild composition) between lit and unlit reaches (> 100 m apart). Species richness and α -diversity (Hill numbers) scaled positively with mean stream depth. Nutrient concentrations were negatively related to mean fish mass and fish assemblage diversity. Species richness scaled negatively with total phosphorus and α -diversity scaled negatively with orthophosphate. Our results imply that the relatively low-levels of ALAN observed in canopied streams may exert only subtle effects on small stream fish assemblages, which are difficult to detect amongst the multiple, confounded stressors impacting these relatively species-poor, urban systems. Experimental approaches or large-scale manipulative studies may be necessary to isolate the effects of ALAN on streams and fish in urban contexts.

Introduction

Urban streams are simultaneously exposed to multiple anthropogenic stressors (Walsh et al. 2005). Of these stressors, artificial light at night (ALAN) is a pervasive ecological issue (Gaston et al. 2017) that is expanding with increased human development and urbanization (Kyba et al. 2017). Nearly a quarter (23%) of land surfaces between 75°N and 60°S (i.e. most continental land besides Antarctica) are exposed to some form of ALAN (Falchi et al. 2016). Ecological light pollution fundamentally alters one of the most consistent environmental patterns that has existed on earth for billions of years – the diurnal light cycle – making it a significant perturbation to the Earth system and a threat to biodiversity at a global scale (Hölker et al. 2010).

Nearly all organisms have evolved complex physiological and behavioral circadian rhythms that are entrained to the diurnal light cycle (Murphy and Campbell 1996). However, many studies have documented disruptive effects of ALAN on these highly conserved physiological and behavioral traits. For example, ALAN is widely recognized as suppressive of nocturnal melatonin production (Sanders et al. 2021), which proximately controls circadian rhythms and activity patterns of animals (Grubisic et al. 2019). Songbirds affected by ALAN have been documented singing later into the evening (Da Silva et al. 2015), whereas others sleep less, with later sleep onset and earlier waking (Raap et al. 2016). Navigating sea turtles, especially emerging hatchlings, confuse shore lights with celestial bodies causing navigational issues and mortality (Kamrowski et al. 2013, Thums et al. 2016, Truscott et al. 2017). The impact of ALAN on bats, which are disproportionately represented in ALAN literature, has been variable due to trait-, spectral-, and species-specific effects (Sanders et al. 2021). For example, Blake et al. (1994) found that agile *Pipistrellus pipistrellus* were three times more abundant near broad-spectrum lighting

compared to narrow-spectrum sodium lights or unlit areas, likely due to greater insect abundances observed around broad-spectrum lighting. Spoelstra et al. (2017) also found increased abundance of *Pipistrellus* sp. around white (and green) light. Slow-flying *Myotis* and *Plecotus* sp. were less abundant near white and green light compared to red light and darkness, where they were equally abundant, elucidating the complex nature of the issue.

Since ALAN is widely recognized as having significant effects on individual organisms, it might be expected that these effects can scale through higher levels of biological organization (Zapata et al. 2019). As a result, there has been increased interest in the effects of ALAN at the community and ecosystem levels of biological organization (Hölker et al. 2021). For example, grassland vegetation assemblage composition and biomass of dominant species changed in response to ALAN after multiple years of exposure (Bennie et al. 2018). For a terrestrial grassland invertebrate assemblage, ALAN was determined to increase the proportion of predatory and scavenger trophic groups (Davies et al. 2012). Effects on ecosystem function are also beginning to emerge; for example, ALAN disrupts plant-pollinator interactions by decreasing visits of nocturnal pollinators, which, in turn, decreased successful pollination and fruit development (Knop et al. 2017). Predation, however, emerged from a meta-analysis of 126 studies, as the process most consistently influenced by ALAN (Sanders et al. 2021), which can exert intensified top-down effects on food webs (Sanders and Gaston 2018).

Human settlement patterns are typically associated with water (Kummu et al. 2011), which results in aquatic environments receiving a disproportionately high amount of ALAN trespass. Though many ALAN studies have examined effects on marine organisms (Kamrowski et al. 2013, Fobert et al. 2019, Berge et al. 2020), fewer ALAN studies have been conducted in freshwater systems and have mainly focused on behavioral and physiological responses. For example, under ALAN, male Smallmouth Bass (*Micropterus dolomieu*) increase locomotor activity when nest guarding (Foster et al. 2016), while macroinvertebrates decrease their drift rates (Henn et al. 2014, Perkin et al. 2014b) and emergence (Manfrin et al. 2017). Long-term exposure to ALAN resulted in decreased activity and lower brain glucose levels in Western Mosquitofish (*Gambusia affinis*) (Miner et al. 2021), earlier onset of diurnal activity patterns in the Trinidadian Guppy (*Poecilia reticulata*) (Kurvers et al. 2018), and decreased blood concentrations of sex steroids in Eurasian Perch (*Perca fluviatilis*) and Common Roach (*Rutilus rutilus*) (Brüning et al. 2018). Even fewer studies in freshwater systems have focused on processes beyond behavior and physiology, but there is evidence that ALAN decreases periphyton biomass (Grubisic et al. 2018), riparian spider density, aquatic emergent insect richness (Meyer and Sullivan 2013), and food-chain length (Sullivan et al. 2019a). Additionally, it is now known that artificial night lighting increases predation rates (Sanders et al. 2021), and this effect has been observed in freshwater systems for example Eurasian Perch predating on invertebrate prey (*Gammarus fossarum*) (Czarnecka et al. 2019).

To our knowledge, no study has been conducted examining the effects of ALAN on stream fish assemblages, but their study is important given the critical role of fishes in freshwater ecosystems (Northcote 1988). To study the effects of ALAN on urban stream fish assemblages, we conducted electroshocking surveys in 20 paired stream reaches (ALAN-lit vs unlit) across 10 sites over two years.

Due to known effects of ALAN that facilitate predation (Czarnecka et al. 2019, Sanders et al. 2021), we hypothesized that artificial light at night would increase relative abundances of predatory fish relative to control (unlit) reaches, but only have limited effects on α -diversity as we did not expect species turnover between sites (Koleff et al. 2003). We expected ALAN to have greatest effects during leaf-off (winter months), when light trespass should be greatest, and reduced impacts during leaf-on (summer months) due to an interceptive effect of foliage.

Methods

Study area

We surveyed fish assemblages, measured ALAN characteristics (illuminance and spectral composition), and sampled nutrient concentrations and habitat characteristics at 10 urban sites in the Columbus Metropolitan Area (CMA), Ohio, USA. Site locations ranged from urban to peri-urban. Each of the 10 sites consisted of a 30 m ALAN-lit reach and a 30 m unlit reach located ~ 100m upstream from the ALAN-lit reach in the same stream (i.e., 20 paired stream reaches). Our paired design minimized environmental differences between the reaches including substrate, channel morphology, and size. All streams were first- and second-order pool-riffle tributaries of the Scioto River, a 6th -order tributary of the Ohio River (drainage area: 16882 km²), and its subcatchments including the Olentangy River (drainage area: 1410 km²), Big Walnut Creek (drainage area: 1440 km²), and Big Darby Creek (drainage area: 1442 km²).

Experimental Design

The ALAN-lit stream reaches at our study sites had a minimum reach mean illuminance of at least 0.28 lx and unlit reaches had a maximum reach mean of at most 0.11 lx (Fig. 1A; Table 1). Unlit reaches were located upstream to avoid any potentially confounding upstream-downstream effects of ALAN. There were no significant structures or tributaries between paired reaches. Light data were collected in concert with fish surveys (see below) using an ILT 1700 Radiometer with a waterproof illuminance (lx) sensor (SUD033/Y/W; International Light Technologies, Peabody, Massachusetts). Illuminance was measured at three transects (0m, 15m, 30m), two positions (left-middle, right-middle), and three heights (1cm below water surface, 1cm above surface, 1m above surface) for each reach. Spectral composition of primary light sources was recorded using an Ocean Optics® Flame UV-VIS Spectrometer (Ocean Insight, Orlando, Florida). Light sources at each site were categorized as either high-pressure sodium (HPS) or light-emitting diode (LED) based on spectral distribution (Fig. S1).

Table 1
Summary of nutrient and habitat characteristics across all 10 study sites.

Variable	Mean ($\pm$ SE)	Range (min – max)
Illuminance (lx) in ALAN-lit reaches	1.48 $\pm$ 0.18	5.22 (0.05–5.27)
Summer	1.00 $\pm$ 0.19	3.14 (0.05–3.19)
Winter	1.97 $\pm$ 0.28	4.93 (0.33–5.27)
Illuminance (lx) in unlit reaches	0.06 $\pm$ 0.02	0.55 (0.00–0.55)
Summer	0.03 $\pm$ 0.01	0.14 (0.00–0.14)
Winter	0.10 $\pm$ 0.03	0.55 (0.00–0.55)
Total N (mg N/L)	2.28 $\pm$ 0.23	11.89 (0.50–12.40)
Nitrate (mg NO ₃ -N/L)	0.88 $\pm$ 0.12	5.04 (0.15–5.19)
Ammonia (mg NH ₃ -N/L)	0.22 $\pm$ 0.08	4.84 (0.01–4.85)
Total P (mg P/L)	0.26 $\pm$ 0.02	0.72 (0–0.72)
Orthophosphate (mg PO ₄ -P/L)	0.03 $\pm$ 0.004	0.17 (0.01–0.18)
Bankfull width (m)	6.11 $\pm$ 0.22	6.05 (3.16–9.21)
Mean water depth (cm)	16.77 $\pm$ 0.85	34.67 (0–34.67)
Canopy gap fraction (%)	48.74 $\pm$ 4.10	88.79 (5.25–94.03)
D ₅₀	37.06 $\pm$ 2.97	121.4 (11.27–132.67)

Each reach was sampled four times over a two-year period for a total of 80 stream surveys. To capture maximum variation in ALAN, two surveys occurred during leaf-on (summer) and two surveys occurred during leaf-off (winter). We used two-pass depletion electroshocking surveys to assess fish assemblages in each reach, which adequately captures fish community diversity in small streams of the region (Kautza and Sullivan 2012). All surveys were conducted at night > 2 hours post sunset. Total length and mass were collected for the first 20 fish of each species and batch-weighted thereafter.

Several habitat variables were sampled at each transect (0m, 15 m, 30 m) within each reach to serve as covariates in our study. During each survey, water depth (cm) was a mean of six values measured each season at two points per transect positioned left and right of the thalweg. Three 250-mL water samples were collected seasonally (winter and summer of each year), one from each transect (0m, 15 m, 30 m) of each reach. Samples were measured for total nitrogen (TN; mg N/L), total phosphorus (TP; mg P/L), nitrate (mg NO₃-N/L), ammonia (mg NH₃-N/L), and orthophosphate (mg PO₄-P/L) at the Ohio Agricultural Research and Development Center Service Testing and Research Lab (STAR Lab, Wooster, Ohio). Canopy photos were taken seasonally using a fish eye lens attached to a Nokia Coolpix 950 to measure canopy

gap fraction (Beckschäfer 2015). After the last survey, 75 sediment clasts, from which median bed particle size (D_{50}) was derived, were sampled per transect for a total of 225 per reach (Wolman 1954).

Statistical analyses

Fish assemblage α -diversity was characterized using Hill numbers (i.e., effective number of species), which were calculated by exponentiating Shannon's entropy (Hill $q = 1$) (Jost 2006). Linear mixed effects models (LMMs) were used as our primary analytical method. Predictors included reach (lit, unlit), light technology (HPS, LED), season (summer, winter), mean stream depth, total nitrogen, total phosphorus, orthophosphate, and D_{50} . Response variables included illuminance, canopy cover, species richness, diversity (Hill numbers), abundance, relative abundance, and $\log_{10}$ -transformed mean fish mass. Nitrate and ammonia were significantly positively correlated with TN ($r = 0.87$ and $r = 0.81$, respectively), thus only TN was used in analyses to prevent multicollinearity. Total phosphorus and orthophosphate were not correlated ($r = -0.11$). A reach $\cdot$ season interaction was included in the model when analyzing illuminance and canopy cover, but not for other response variables. Mean stream depth was modeled as a 2nd -order polynomial within all LMMs, while orthophosphate was modeled as a 2nd -order polynomial in the fish mass analysis. Site was included as random effect in all models and species was included as a random effect in relative abundance and mean fish mass models. Significance for linear mixed effects models was tested with Approximate F -Tests (Type III Satterthwaite). To evaluate how predictor variables affected fish assemblage composition, we performed permutational analysis of variance (PERMANOVA) on square-root transformed species abundances using *adonis2* in **vegan** 2.5-7 (Oksanen et al. 2018). PERMANOVA models contained the same predictor variables as linear models. Permutations were constrained by site, which is used as a blocking effect in *adonis2*. Permutational analysis of multivariate dispersion (PERMDISP) was used to check for homogeneity of group variances.

We set $\alpha = 0.05$ for all analyses. We used **R** 4.0.2 (R Core Team 2017), **lme4** 1.1–26 (Bates et al. 2015) for mixed effects models, **lmerTest** 3.1-3 (Kuznetsova et al. 2015) for approximate F tests, **MuMIn** 1.43.17 for conditional and marginal R^2 values (Barton 2020), **tidyverse** 3.3.3 (Wickham et al. 2019) for graphics and data manipulation, and **vegan** 2.5-7 (Oksanen et al. 2018) for PERMANOVA, PERMDISP, and NMDS scores. We used **ggsci** 2.9 (Xiao 2018) for plot color schemes, **cowplot** 1.1.1 (Wilke 2020) for plot themes, **ggConvexHull** 0.1.0 (Martin 2017) for NMDS convex hulls, **kableExtra** 1.3.1 (Zhu 2020) for output formatting, **psych** 2.0.12 (Revelle 2020) for data summaries, and **car** 3.0–10 (Fox and Weisberg 2019) for model diagnostics.

Results

Mean illuminance was greater in lit reaches ($1.48 \text{ lx} \pm 0.18$; mean $\pm$ SE) compared to unlit reaches ($0.06 \text{ lx} \pm 0.02$) ($F_{1,67} = 87.40$, $p < 0.001$) (Fig. 1a); illuminance was greater in reaches affected by HPS luminaires ($2.30 \text{ lx} \pm 0.65$) compared to LED luminaires (0.93 ± 0.27) (Fig. 1b). Seasonal differences in canopy cover ($F_{1,63.7} = 3944.57$, $p < 0.001$) (Fig. 1c) drove a significant interaction between reach and season on mean illuminance ($F_{1,67} = 8.70$, $p = 0.004$). This interaction was the result of a positive relationship between

illuminance and canopy gap fraction in the summer months that diminished in the winter months. However, mean illuminance was ~ 1 lx greater in lit reaches during the winter months due to leaf-off ($1.00 \text{ lx} \pm 0.19$ vs. $1.97 \text{ lx} \pm 0.28$) (Fig. 1c). Nutrient and habitat characteristics were typical for urban headwater streams in the CMA, with the greatest orthophosphate concentrations at three sites ($> 0.10 \text{ mg PO}_4\text{-P/L}$) and with all 10 sites exhibiting elevated TP ($> 0.20 \text{ mg P/L}$), TN ($> 0.54 \text{ mg N/L}$), and nitrate ($> 0.30 \text{ mg NO}_3\text{-N/L}$) (Table 1; USEPA 2000).

A total of 6364 fish were collected during the study. Assemblages were numerically dominated by Creek Chub (*Semotilus atromaculatus*), Western Blacknose Dace (*Rhinichthys obtusus*), Central Stoneroller (*Campostoma anomalum*), Mottled Sculpin (*Cottus bairdii*), Bluegill Sunfish (*Lepomis macrochirus*), Green Sunfish (*Lepomis cyanellus*), and Striped Shiner (*Luxilus chrysocephalus*) (Table 2). Fish abundance and species relative abundances did not differ between reaches, light technology, or year, nor did they vary with TN, TP, orthophosphate, D_{50} , or stream depth. Abundances were greater during summer surveys, but relative abundances remained unchanged (Table 3). There were no effects of reach, season, year, light technology, D_{50} , TN, or TP (Table 3) on mean fish mass. Mean fish mass scaled positively with stream depth (Fig. 2a) and negatively with orthophosphate concentration (Fig. 2b). However, the effect of orthophosphate on mean fish mass was relatively weak ($R^2_{\text{Marginal}} = 0.05$) compared to the variance explained by site differences ($R^2_{\text{Conditional}} = 0.65$).

Table 2
Abundance of each fish species captured across all sites.

Common name	Species	Abundance
Creek Chub	<i>Semotilus atromaculatus</i>	2783
Western Blacknose Dace	<i>Rhinichthys obtusus</i>	856
Central Stoneroller	<i>Campostoma anomalum</i>	644
Mottled Sculpin	<i>Cottus bairdii</i>	609
Bluegill Sunfish	<i>Lepomis macrochirus</i>	365
Green Sunfish	<i>Lepomis cyanellus</i>	295
Striped Shiner	<i>Luxilus chrysocephalus</i>	173
Spotfin Shiner	<i>Cyprinella spiloptera</i>	91
Rainbow Darter	<i>Etheostoma caeruleum</i>	82
White Sucker	<i>Catostomus commersonii</i>	80
Yellow Bullhead	<i>Ameiurus natalis</i>	71
Johnny Darter	<i>Etheostoma nigrum</i>	59
Largemouth Bass	<i>Micropterus salmoides</i>	57
Western Mosquitofish	<i>Gambusia affinis</i>	40
Fantail Darter	<i>Etheostoma flabellare</i>	39
Bluntnose Minnow	<i>Pimephales notatus</i>	28
Bluegill x Green Sunfish	<i>Lepomis macrochirus x cyanellus</i>	20
Northern Hogsucker	<i>Hypentelium nigricans</i>	14
Smallmouth Bass	<i>Micropterus dolomieu</i>	14
Fathead Minnow	<i>Pimephales promelas</i>	9
Orangethroat Darter	<i>Etheostoma spectabile</i>	9
Rosyface Shiner	<i>Notropis rubellus</i>	8
Silver Shiner	<i>Notropis photogenis</i>	7
Greenside Darter	<i>Etheostoma blennioides</i>	2
Mimic Shiner	<i>Notropis volucellus</i>	2
Pumpkinseed Sunfish	<i>Lepomis gibbosus</i>	2
Rock Bass	<i>Ambloplites rupestris</i>	2

Common name	Species	Abundance
Golden Shiner	<i>Notemigonus crysoleucas</i>	1
Goldfish	<i>Carassius auratus</i>	1
Sand Shiner	<i>Notropis stramineus</i>	1
Total		6364

Table 3

Analysis of variance (ANOVA) results for abundance, species richness (S), species diversity (Hill numbers), and mean fish mass. D_{50} = median sediment size. Bold indicates significant results ($p < 0.05$).

(A) ANOVA	SS	DF	DDF	<i>F</i>	<i>p</i>
Abundance					
Reach (lit/unlit)	5444	1	60.65	1.58	0.214
Season	32914	1	64.11	9.555	0.003
Year	18422	2	62.56	2.674	0.077
Light technology	8440	1	8.81	2.45	0.153
Total nitrogen	619	1	56.95	0.18	0.673
Total phosphorus	11918	1	61.53	3.46	0.068
Orthophosphate	309	1	67.96	0.09	0.766
D_{50}	411	1	62.83	0.119	0.731
Depth (2nd order polynomial)	2628	2	66.48	0.381	0.684
Relative abundance					
Reach (lit/unlit)	4.37×10^{-4}	1	381.293	0.018	0.893
Season	2.32×10^{-2}	1	383.769	0.96	0.328
Year	4.20×10^{-2}	2	386.106	0.866	0.421
Light technology	8.93×10^{-2}	1	7.778	3.687	0.092
Total nitrogen	2.15×10^{-3}	1	300.726	0.089	0.766
Total phosphorus	5.93×10^{-3}	1	386.348	0.244	0.621
Orthophosphate	2.82×10^{-3}	1	384.883	0.116	0.733
D_{50}	7.88×10^{-2}	1	361.692	3.25	0.072
Depth (2nd order polynomial)	5.73×10^{-3}	2	386.356	0.118	0.889
Species richness (S)					
Reach (lit/unlit)	6.82	1	60.28	2.06	0.156
Season	15.68	1	61.28	4.74	0.033
Year	56.37	2	61.05	8.52	0.001

(A) ANOVA	SS	DF	DDF	<i>F</i>	<i>p</i>
Light technology	9.97	1	8.62	3.01	0.118
Total nitrogen	0.27	1	67.36	0.08	0.777
Total phosphorus	25.19	1	60.49	7.62	0.008
Orthophosphate	8.98	1	63.51	2.71	0.104
D ₅₀	0.84	1	66.60	0.26	0.615
Depth (2nd order polynomial)	26.16	2	62.09	3.96	0.024
Mean Fish Mass (g)					
Reach (lit/unlit)	0.024	1	373.959	0.271	0.603
Season	0.001	1	375.522	0.015	0.902
Year	0.248	2	380.113	1.379	0.253
Light technology	0.084	1	7.832	0.933	0.363
Total nitrogen	0.174	1	154.25	1.934	0.166
Total phosphorus	0.174	1	380.567	1.935	0.165
Orthophosphate (2nd order polynomial)	0.351	1	378.298	3.911	0.049
D ₅₀	0.157	1	266.492	1.749	0.187
Depth (2nd order polynomial)	1.589	2	376.064	8.844	< 0.001
α-Diversity (Hill numbers)					
Reach (lit/unlit)	0.58	1	60.31	0.60	0.440
Season	0.12	1	61.31	0.12	0.727
Year	4.61	2	61.08	2.40	0.099
Light technology	2.43	1	8.66	2.53	0.147
Total nitrogen	0.49	1	67.36	0.51	0.478
Total phosphorus	1.25	1	60.52	1.31	0.258
Orthophosphate	4.71	1	63.54	4.91	0.030
D ₅₀	0.15	1	66.61	0.15	0.697
Depth (2nd order polynomial)	8.37	2	62.12	4.37	0.017

PERMANOVA results revealed no effects of reach (Fig. 3a), season, year, TN, TP, orthophosphate, or D_{50} on fish species assemblage structure, but there was a significant effect of depth (Fig. 3b) and season (Table 4). PERMANOVA results of feeding guild composition did reveal significant effects of season (Table 4) due to greater relative abundances of Central Stoneroller, Striped Shiner, and Largemouth Bass in winter and Western Mosquitofish in summer. However, there was no effect of reach (Fig. 3c), year, TN, TP, orthophosphate, D_{50} , or stream depth on feeding guild composition (Table 4). PERMDISP confirmed no significant difference in reach, year, or season spatial median variances for species assemblage or guild composition ($p > 0.05$), but light technology (HPS vs. LED) did violate this assumption and was removed from both PERMANOVA analyses (pseudo- $F_{1,68} = 7.70$, $p = 0.007$ and pseudo- $F_{1,68} = 18.39$, $p < 0.001$, respectively).

Table 4
Permutational multivariate analysis of variance (PERMANOVA)
results for species and feeding guild compositions. D_{50} = median
sediment size. Bold indicates significant results ($p < 0.05$).

(A) PERMANOVA	SS	DF	DDF	Pseudo- <i>F</i>	<i>p</i>
Species Composition					
Reach (lit/unlit)	0.42	1	67	0.84	0.154
Season	0.69	1	67	1.38	0.002
Year	0.90	2	67	0.90	0.312
Total nitrogen	0.98	1	67	1.96	0.131
Total phosphorus	0.61	1	67	1.21	0.119
Orthophosphate	0.87	1	67	1.74	0.146
D_{50}	0.86	1	67	1.71	0.236
Depth	0.78	1	67	1.56	0.028
Guild Composition					
Reach (lit/unlit)	0.45	1	67	0.93	0.206
Season	0.62	1	67	1.26	0.012
Year	0.94	2	67	0.96	0.443
Total nitrogen	1.01	1	67	2.07	0.217
Total phosphorus	0.54	1	67	1.11	0.438
Orthophosphate	0.41	1	67	0.84	0.929
D_{50}	0.65	1	67	1.34	0.271
Depth	0.53	1	67	1.08	0.165

Species richness and α -diversity (Hill numbers) increased with stream depth, but species richness decreased with TP and α -diversity decreased with orthophosphate (Fig. 5). There was no effect of reach, light technology, total N, or D_{50} on species richness or α -diversity. Species richness was marginally greater in samples from winter 2021, driving significant year and season effects. However, these effects were not present in species diversity analyses (Table 3). Site as a random effect in our models accounted for a majority component of the variation in all response variables, ranging from 0.28 for abundance to 0.61 for mean fish mass (calculated as $R^2_{\text{Conditional}} - R^2_{\text{Marginal}}$).

Discussion

Our goal was to test the potential of ALAN to shift fish assemblage composition in urban headwater streams. We found that the range of lux trespassing from ALAN into our sites had no observable effects on urban headwater stream fish assemblages. However, it is widely recognized that a suite of collinear anthropogenic impacts including hydrologic variability (“flashiness”), fluvial geomorphic adjustment, and nutrient and contaminant pollution are common stressors for small urban streams. These combined effects typically result in reduced species richness and are symptomatic of the “urban stream syndrome” (Walsh et al. 2005). Owing to the positive scaling between urban development and artificial lighting at night, ALAN is also collinear with the multiple stressors of urban streams (Hölker et al. 2021), thereby confounding potential effects of ALAN. Influences of ALAN on biotic communities are particularly difficult to isolate in urban streams because the regional species pool becomes restricted to highly tolerant, cosmopolitan fish species that can cope with combinations of multiple stressors (Sulliván et al. 2021).

Indeed, the effects of ALAN may be subtle compared to those of more classically identified stressors identified in the urban stream syndrome (Walsh et al. 2005, Sullivan et al. 2019b). Many studies, especially those with experimental approaches, provide evidence of the influence of ALAN at multiple levels of biological organization ranging from gene expression to ecosystem functions (Meyer and Sullivan 2013, Brüning et al. 2016, Amichai and Kronfeld-Schor 2019, Sullivan et al. 2019a). Here, we provide evidence that habitat structure (depth) had the largest explanatory effects for urban stream fish assemblages and may have overwhelmed potential influences of ALAN. Stream geomorphic features are well recognized as an important factor in structuring stream fish assemblages (Sullivan et al. 2006). In fact, also working in urban streams of the CMA, Rieck and Sullivan (2020) documented temporal and spatial linkages between multiple stream hydrogeomorphic characteristics (e.g., sediment size, channel incision) and fish assemblages. Not surprisingly, fish α -diversity increased with stream depth in our study, presumably because deeper stream sites provide more habitat volume, complexity, and critical refugia (i.e., from summer dry-downs and temperature extremes) compared to our shallower stream sites. These results re-iterate the need to not only manage chemical water quality, but also fluvial geomorphic forms and processes by conserving natural hydrology and riparian zones (Sweeney and Newbold 2014).

The effects of phosphorus concentrations were generally negative in our study as both species richness and α -diversity scaled negatively with at least one phosphorus variable and mean fish mass scaled negatively with orthophosphate. For our dataset, TP and orthophosphate were not correlated ($df = 78$, $r = -0.12$, $p = 0.290$; Table 1). The negative relationship between phosphorus and diversity and fish biomass may be indicative of nutrients functioning as system stressors at elevated concentrations (King and Richardson 2007, Ouyang et al. 2018). In urban settings, nutrient enrichment is typically collinear with other stressors, thus, we cannot conclude that these effects on species richness and α -diversity were directly due to nutrient effects or whether differences in nutrient concentrations indicate differential degrees of urban impacts. However, the relationship between orthophosphate and mean fish mass was relatively weak overall, with most of the variation explained by site-level differences.

Some species (Bluegill Sunfish, Mottled Sculpin, and Central Stoneroller; Fig. 4B) showed potential patterns in raw values of relative abundance across reach types and may warrant further investigation,

but high variation in responses and relationships with covariates precluded any significant effects. ALAN might be expected to advantage Bluegill Sunfish by extending the dawn and dusk foraging windows (Zapata et al. 2019), when they are most active (Werner 1969). Conversely, for benthic invertivores such as Mottled Sculpin and Central Stonerollers, even small increases in illumination of the benthos may disrupt camouflage and make them both more vulnerable to predation and less effective in ambushing their prey (e.g., Keyler et al. 2019). Predation risk associated with ALAN, in particular, has been documented for both freshwater (i.e., Nelson et al. 2021) and marine (e.g., Bolton et al. 2017) fishes. Meyer and Sullivan (2013) hypothesized that ALAN can prompt reductions in mean body size and higher abundances of armored grazers (e.g., glossosomatid caddisflies), which could reduce the accessibility of macroinvertebrate prey for benthic insectivorous fishes. Of note, Mottled Sculpin are a species of conservation concern in Ohio, highlighting the potential for ALAN to impact rare and endangered species (e.g., Shier et al. 2020).

Small headwater streams are often characterized by dense canopy cover during warm seasons when aquatic organisms are most active. Canopy cover can mitigate or block ALAN trespass, an effect that has been seen in terrestrial studies with bats (Straka et al. 2019). The capacity for canopy cover to mitigate ALAN should vary by ecosystem type and size, with dense canopies of terrestrial ecosystems in temperate and humid climates having the largest capacity. Small headwater streams embedded in forests or surrounded by intact riparian buffers should support sufficiently dense canopy to largely mitigate ALAN effects. As streams widen, the ratio of closed-canopied water from shoreline riparian vegetation to open-canopy water decreases, potentially allowing more ALAN trespass (e.g., unobstructed ALAN from streetlights on bridges over large water bodies). This is, of course, true for the well-documented effects of ALAN in coastal regions that lack canopy between coastal developments and water (Kamrowski et al. 2013), but large rivers, lakes, and reservoirs might also have increased vulnerability due to a lower closed- to open-canopy water ratio. However, the benefits provided by canopy can be incorporated into physical infrastructure with increased usage of dark-sky friendly luminaire designs that limit light trespass with directional shielding and targeted hours of operation (Kardel 2012, Zapata et al. 2019).

Our mean illuminance values were in line with values reported in other ALAN studies focusing on small stream with intact riparian zones (Meyer and Sullivan 2013, Perkin et al. 2014a). However, these mean illuminance values (Table 1) – even during the winter leaf-off period – are lower than illuminance values reported by other ALAN studies conducted in more open habitats, where effects of ALAN have been observed. For example, Davies et al. (2012) report 19.29 lx directly under street lights and 3.02 lx between street lights in their study of terrestrial invertebrate communities in Cornwall, United Kingdom. Riley et al. (2012) measured lx above the water's surface in a river in Hampshire, UK and report 14 lx directly near street lighting and 2 lx farther away. Meyer and Sullivan (2013) state that in highly urbanized areas of the CMA, lux levels ranged from 8–12 (range 7.5–12.2, mean $\pm$ SD = 1.5 ± 1.5 lx) in mostly unbuffered streams, although they used streams with intact riparian zones (0.1–4.0 lx) in their study. Illuminance from light sources rapidly and non-linearly decreases with distance due to the inverse-square law. Street lighting at the sites used in this study was typically positioned on roads and not directly over the water

surface. Given this spatial effect and the presence of heavily canopied riparian zones at our sites, it is not surprising that we, and others (Meyer and Sullivan 2013, Perkin et al. 2014a), observed low levels of ALAN in headwater streams that may not have been strong enough to elicit fish-assemblage responses.

Site as a random factor explained a large component of variation for each response variable. Such large site effects might be expected to be largely explained by high β -diversity between subcatchments. The high β -diversity may be due to multiple underlying, unmeasured variables including, for example, differences in hydrological regimes, local-scale geological features, riparian vegetation characteristics, or upstream-downstream connectivity that would enable recolonization post-extirpation (e.g. artificial channels, culverts, and low-head dams limiting regional dispersal in CMA; e.g., Davis et al. 2017). The large site-level effect reinforces the notion that, in addition to the potential effects of ALAN, multiple stressors are at play in urban streams.

In general, the effects of ALAN are complex because biological responses have been observed at a wide range of illuminances (e.g., < 1 to > 100 lx) and spectral composition, often with species-specific effects. Effects on behavior, physiology (e.g., melatonin), and predator-prey interactions are particularly evident, but effects on biodiversity and community responses have been less consistent overall (see meta-analysis: Sanders et al. 2021), despite prominent examples in the literature (e.g., Davies et al. 2012, Grubisic et al. 2017, Bennie et al. 2018). In urban streams, the collinear impacts of urban land use strongly reduce species richness to a subset of tolerant fish species from the overall regional species pool (Booth et al. 2016, Vietz et al. 2016). While this conundrum makes teasing out the effects of collinear stressors on fish communities in natural systems, large-scale manipulative studies that are costly and logistically prohibitive are still needed (Hölker et al. 2021). However, we provide evidence that the effects of observed ALAN illuminance (Table 1) on small stream species diversity do not appear to be as extreme as other factors commonly associated with urbanization (e.g., hydrologic variability, fluvial geomorphic adjustment, contamination). This is not to say that ALAN does not exert community-to-ecosystem level effects, as other studies have clearly shown (Bennie et al. 2015, Manfrin 2017, Manfrin et al. 2017, Sullivan et al. 2019a), but simply that detection of such effects in heavily canopied streams, where ALAN illuminance tends to be relatively low (Meyer and Sullivan 2013, Perkin et al. 2014a), may be more difficult.

Declarations

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Conflicts of interest/Competing interests

There are no conflicts of interest to report.

Availability of data and material

Data and scripts will be made available on figshare.

Code availability

Data and scripts will be made available on figshare.

Author Contributions

Jason R. Bohenek conducted data collection and formal analysis; Jason R. Bohenek and S. Mažeika Patricio Sulliván were responsible for methodology; Jason R. Bohenek, S. Mažeika Patricio Sulliván, and Suzanne M. Gray were responsible for writing original drafts, review, and editing.

Ethics approval

Study conformed to The Ohio State University IACUC protocol 2008A0161-R4.

Consent to participate

N/A

Consent for publication

N/A

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Figures

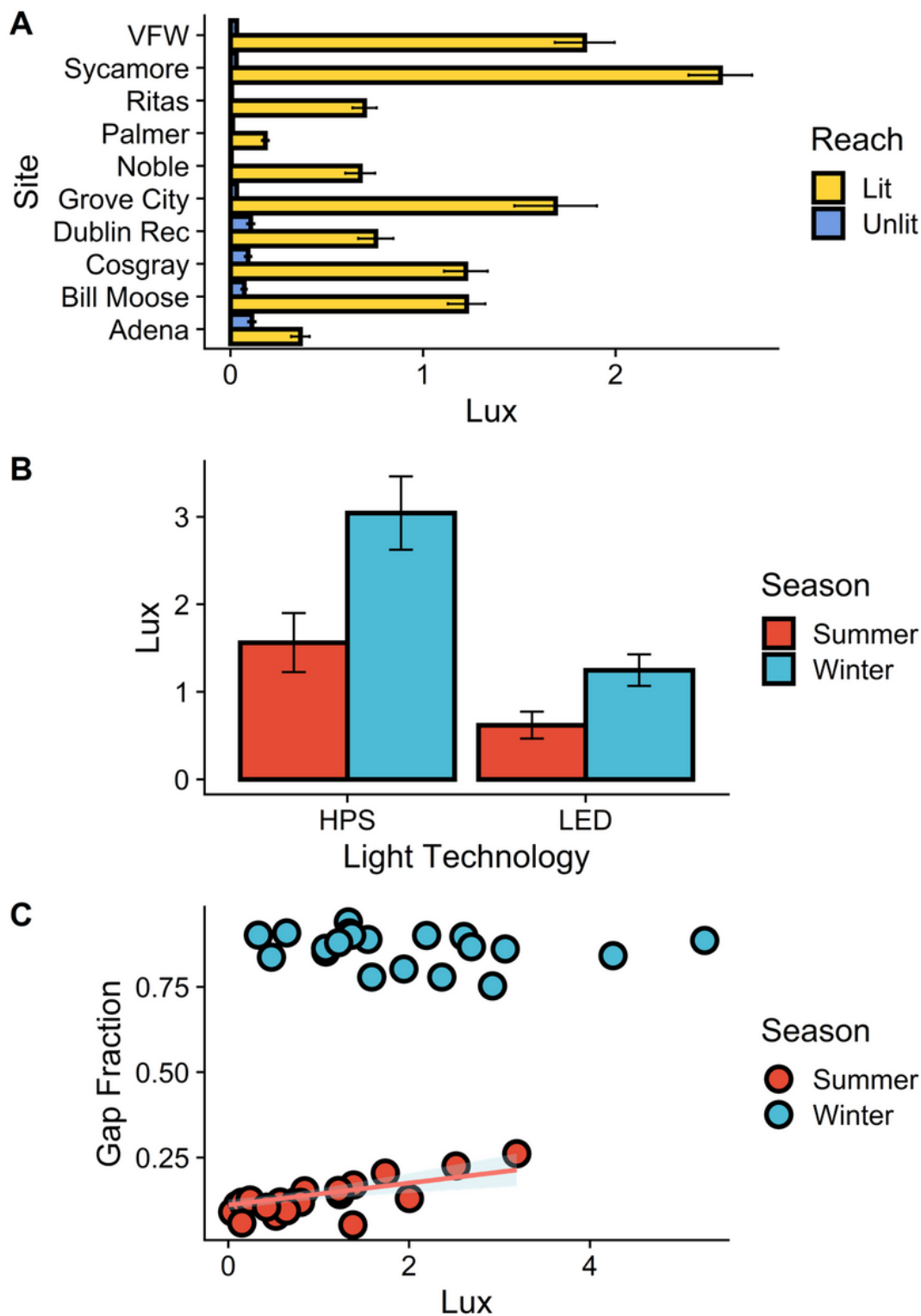


Figure 1

(A) Mean lux ($\pm$ SE) at lit (yellow) and unlit (blue) reaches at each of our 10 study sites. (B) Mean lux ($\pm$ SE) of high-pressure sodium and light-emitting diode light technologies in lit reaches across summer (red) and winter (cyan) season. (C) Relationship between mean lux and canopy gap fraction at lit reaches in summer (red) and winter (cyan) samples. There was a significant positive relationship between mean site lux and gap fraction during summer, but not winter, months ($F_{1,67} = 8.70$, $p = 0.004$). The greater gap

fraction during leaf-off of winter ($F_{1,67} = 4379, p < 0.001$) increased overall mean lux trespass to the study sites.

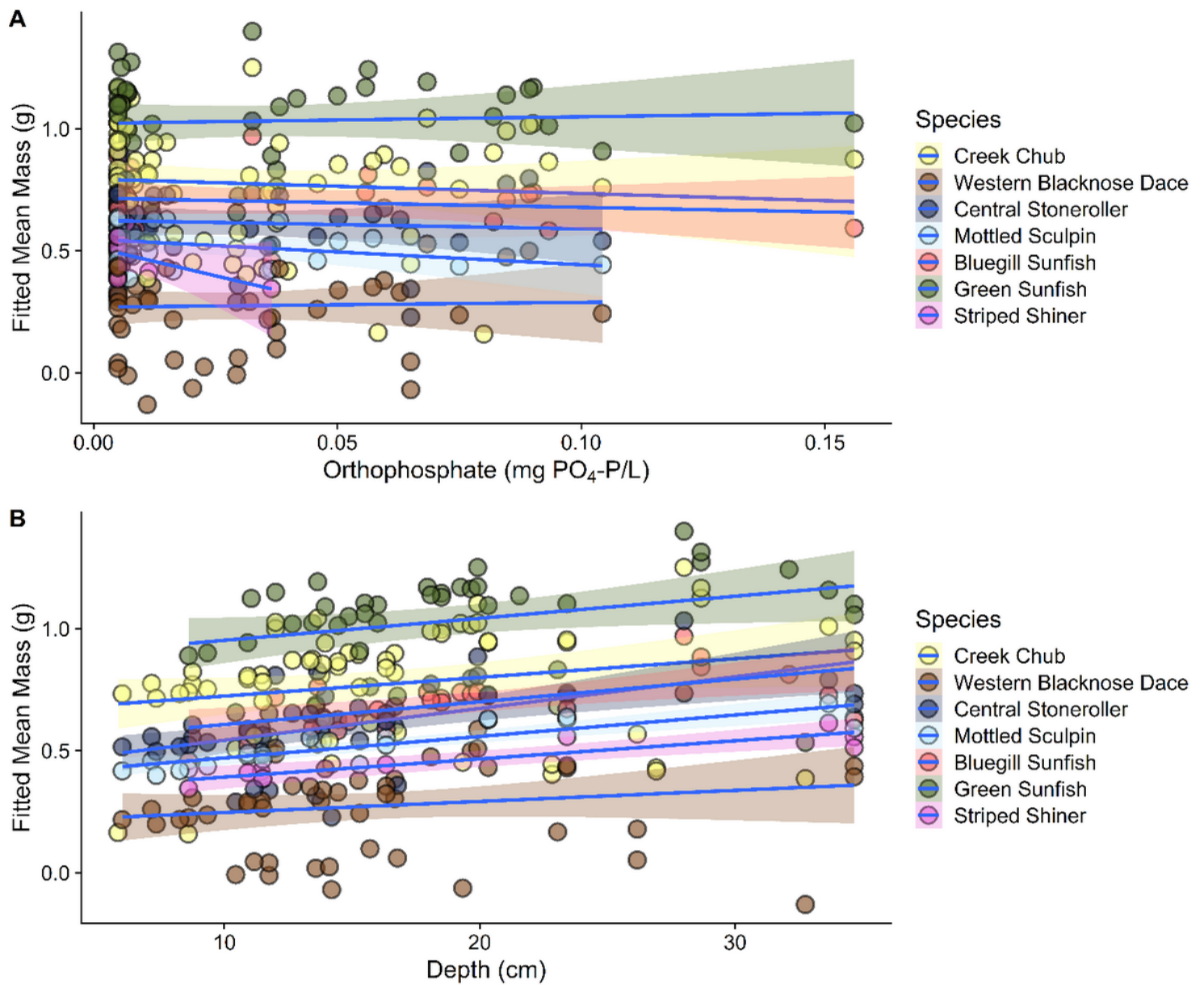


Figure 2

(A) Significant positive relationship between mean stream depth and fitted mean fish mass. The seven most common fish species are shown. (B) The significant negative relationship between mean orthophosphate concentrations (mg PO₄-P/L) and fitted mean fish mass. The seven most common fish species are shown.

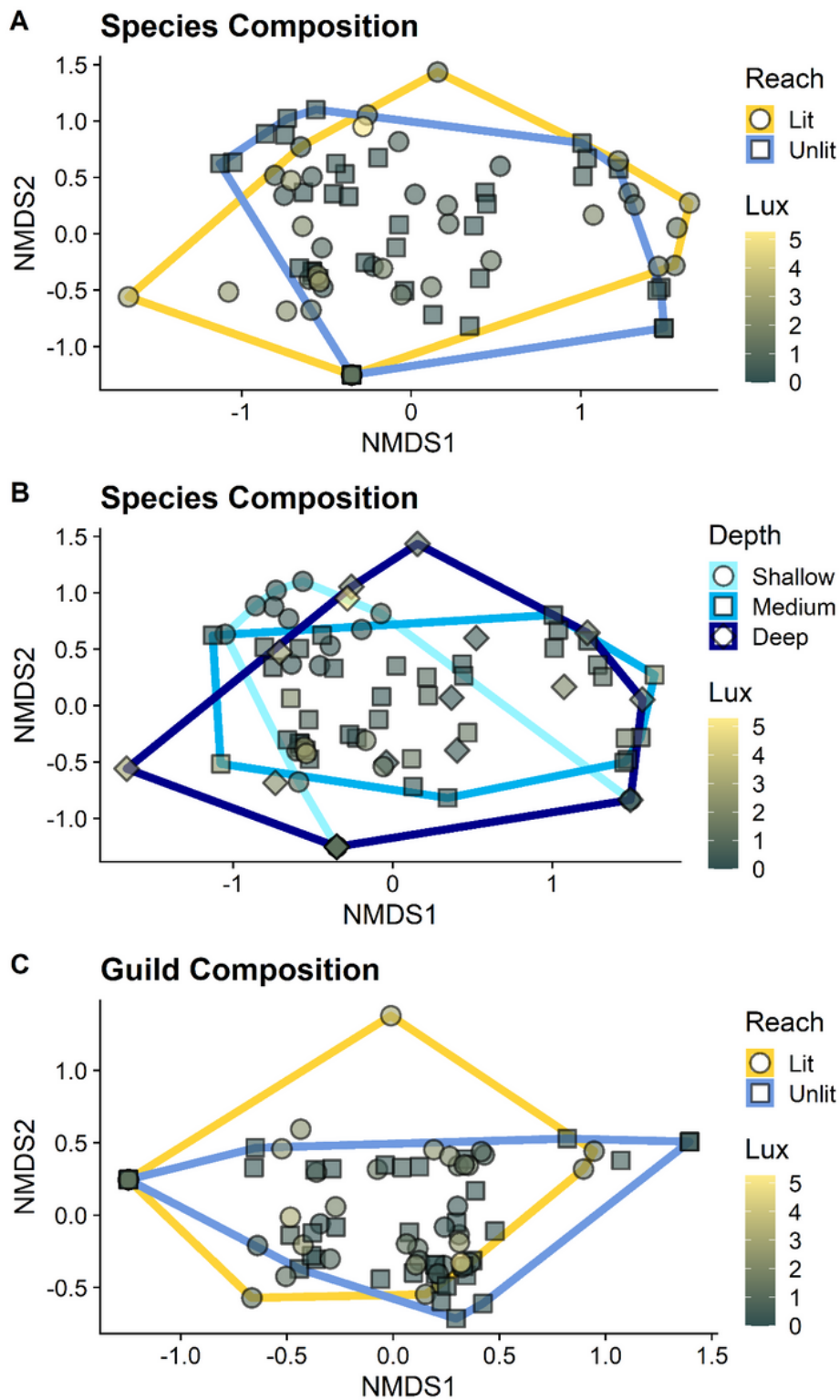


Figure 3

Non-metric multidimensional scaling plots for fish assemblages showing species composition (stress = 0.144) across (A) reaches ($p = 0.154$) and (B) depths ($p = 0.0278$). (C) Feeding guild composition (stress = 0.080) across reaches.

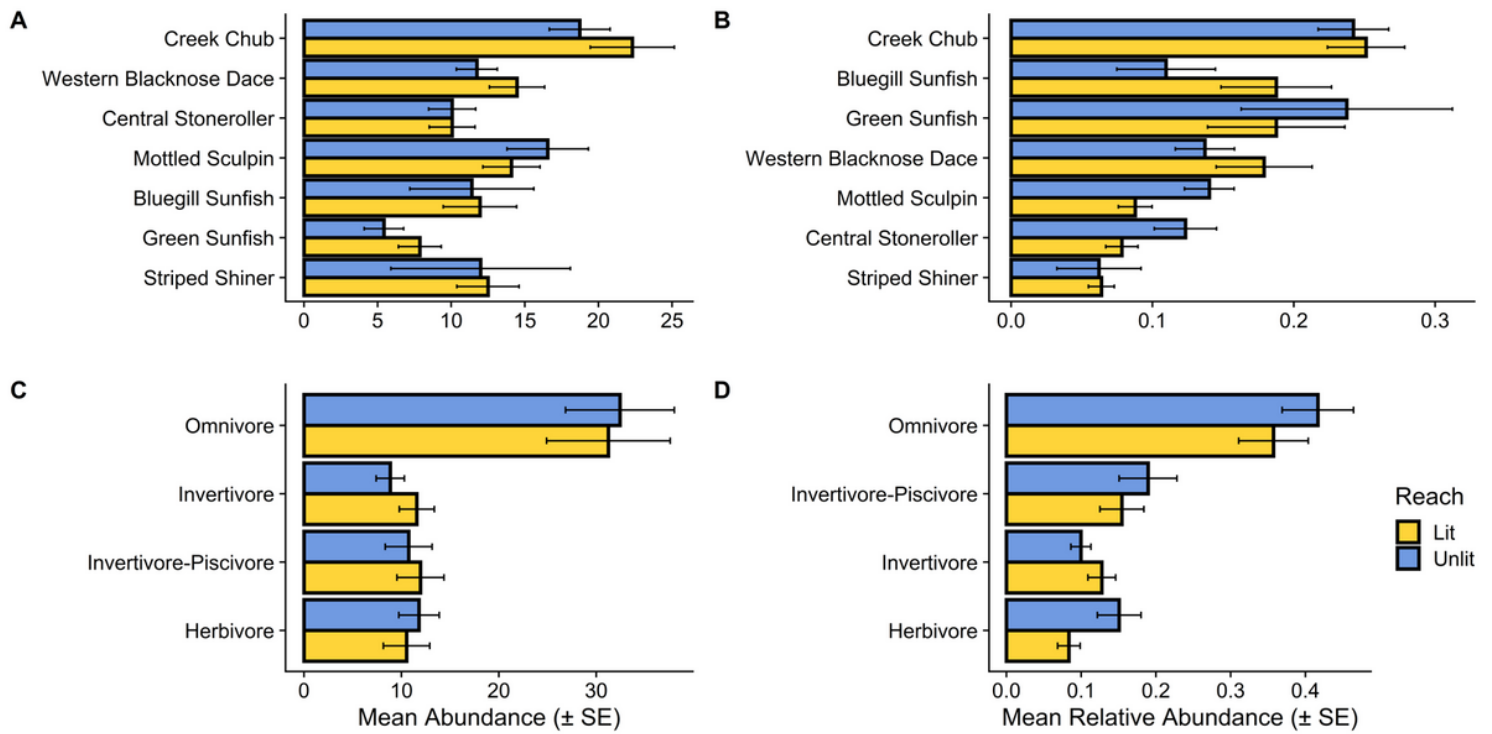


Figure 4

(A) Mean abundance ($\pm$ SE) of the seven most common fish species. (B) Mean relative abundance ($\pm$ SE) of the seven most common fish species. (C) Mean abundance ($\pm$ SE) of each fish guild. (D) Mean relative abundance ($\pm$ SE) of each fish guild. Lit reaches are represented in yellow, while unlit reaches are in blue.

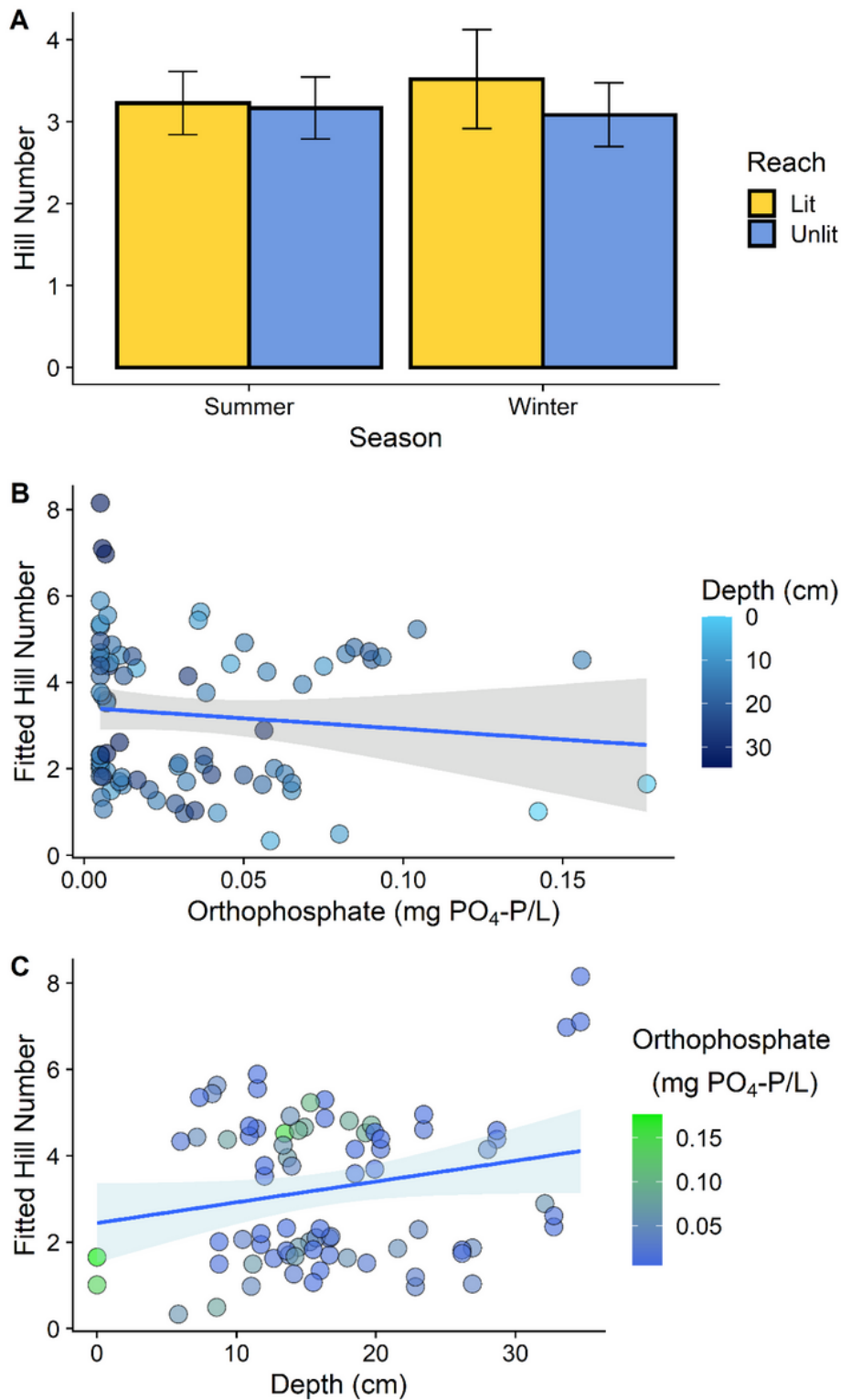


Figure 5

(A) Mean α-diversity ($\pm$ SE) measured in Hill numbers (effective numbers) across seasons and reach types (lit/unlit). (B) Significant negative relationship between orthophosphate (mg PO₄-P/L) and α-diversity measured as Hill numbers. (C) Significant positive relationship between mean stream depth and α-diversity measured as Hill numbers.

Supplementary Files

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- [S1.png](#)