

Urban light pollution alters the diel vertical migration of *Daphnia*

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Introduction

Light is the fundamental factor controlling the diel vertical migration (DVM) of zooplankton (RINGELBERG 1987, HANEY 1993). It not only serves as the proximate cue triggering the ascent of zooplankton, but it also reduces the amplitude of migration if light levels are sufficiently high at night. For example, the light of a full moon reduces the amplitude of *Daphnia* (GLIWICZ 1986, DODSON 1990) and chaoborid (SMITH et al. 1992) migrations. Night-time light intensities, however, are influenced not only by moonlight but also by artificial outdoor lighting, particularly in urban areas. Light pollution, or the sky glow produced by inefficient outdoor lighting, is prevalent in metropolitan areas (LOCKWOOD et al. 1990), and these areas often border freshwater lakes, coastal ecosystems, or both. Urban water quality may be influenced indirectly by light pollution, because zooplankton grazing influences water quality and the depth distribution of many zooplankters is affected by light.

We tested the hypothesis that light pollution associated with urban areas reduces the amplitude and magnitude of zooplankton vertical migration. A field experiment manipulating underwater light intensity at night was performed in a suburban lake bordering a large metropolitan area.

Methods

An enclosure experiment was performed on 7–8 July, 1997, 3 nights after the new moon, in Lake Waban (area 0.4 km², mean depth 4.8 m), a dimictic kettle lake, located 16 km southwest of Boston in Norfolk County, MA. Lake Waban's watershed (~36 km²) circumscribes dense residential and commercial areas as well as major highways (MOORE et al. 1998). According to Carlson's Trophic State Index, this suburban lake falls between the boundary of mesotrophy and eutrophy (see MOORE et al. 1998 for limnological details). Resident fish include bluegill (*Lepomis macrochirus*), pumpkinseed sunfish (*Lepomis gibbosus*), golden shiners (*Notemigonus crysoleucas*), yellow perch (*Perca flavescens*), black crappie

(*Pomoxis nigromaculatus*), white perch (*Morone americana*), largemouth bass (*Micropterus salmoides*), chain pickerel (*Esox niger*), brown bullhead (*Ictalurus nebulosus*), and common carp (*Cyprinus carpio*). Low densities (0.3 ± 0.1 ind./L) of the planktonic predator, *Chaoborus punctipennis*, also occur in the lake (FISCHER & MOORE 1993).

Field enclosures (diameter, 56.6 cm; length, 4.5 m), constructed from collapsible, coiled metal frames, were covered with either thick black (6 mm) or clear (4 mm) sheet plastic to shield or expose portions of the water column, respectively, to night-time downwelling irradiance. All enclosures were open at the bottom, but closed at the surface with lids made from circular plastic hoops (diameter, 80 cm) and covered with the appropriate plastic sheet. A slit, cut in the middle of the plastic of each lid, allowed passage of sampling equipment. Black enclosures blocked up to 96% of daytime downwelling irradiance according to a comparison of light measurements made with a Li-Cor quantum sensor in these enclosures and the lake.

At midday, prior to the evening experiment, the Secchi disk depth and underwater light measurements were obtained with a Li-Cor quantum sensor. The latter measurements were made per meter from the surface to the bottom of the lake. Daytime depth distributions of crustacean zooplankton were also determined at depths of 2, 4, 6, 8, and 9 m by filtering water samples collected with a Kemmerer bottle (4.2 L) through a plankton net (10 µm mesh). All zooplankton samples were preserved immediately with 5% buffered, sucrose-Formalin.

Three experimental enclosures (black plastic) and three control enclosures (clear plastic) were deployed at the deepest point (11.5 m) of the lake 30 min before sunset. In addition, three adjacent locations in the lake served as controls for "enclosure effects". A total of nine sites for the enclosures and the lake sampling were arranged in a grid pattern of three rows with three sites per row. Treatments (black, clear, and open lake) were blocked across rows, and treatments were randomly assigned a site within each row. Blocking of treatments across rows prevented isolated light sources near shore from differentially

affecting some treatments but not others.

Immediately prior to sampling the enclosures, temperature and dissolved oxygen were measured each meter from the lake surface to the substrate with a YSI model 58 oxygen meter. Night-time light intensities were below the detection limit ($0.01 \mu\text{Einst}/\text{m}^2/\text{s}$) of a Li-Cor quantum sensor so subsequent measurements were made with an Optec SPS-3 photomultiplier on 9 October, 1997. On the night of the experiment, between 23:45 and 03:45 h, three replicate water samples were collected with a Kemmerer bottle (4.2 or 3.2 L) at each of three depths (2, 4, and 6 m) inside or directly below each enclosure and in the open lake locations. Samples were filtered and preserved as described previously. Crustacean zooplankton were later identified to species and counted using a stereo microscope ($30\times$). Nauplii were sub-sampled with a 5-mL Hensen-Stempel pipette when their densities ≥ 50 ind./mL. The coefficient of variation for sub-sampling was <0.02 .

Proportions of zooplankton per taxon collected at night were compared among depths and treatments using two-way ANOVA. In the lake, zooplankton proportions per taxon were also compared among times (day vs. night) and depth to determine if taxa exhibited DVM. All zooplankton proportions were normalized using an arcsin transformation (SOKAL & ROHLF 1981).

Results and discussion

The depth distribution of a single species, *Daphnia retrocurva*, differed significantly among treatments (Table 1; $F_{4,68} = 4.11$, $P < 0.01$). The movement of *Daphnia* was significantly greater in both amplitude (2 m higher) and magnitude (10–20% more individuals) in the black enclosures than in control enclosures or the lake (Fig. 1). An ‘enclosure effect’ did not bias the results, because the depth distribution of *Daphnia* was similar in the clear enclosures and the lake. Also, because all enclosures were open at the bottom, kairomones from predators and the abundance and distribution of algal food should have been similar among enclosures. Interestingly, *Daphnia* did not exhibit DVM in the lake. Its vertical distribution was similar during the day and night in Lake Waban ($F_{2,30} = 12.26$, $P > 0.05$).

None of the other cladoceran (*Bosmina* and *Diaphanosoma*) or copepod species in Lake Waban were affected by light pollution in the

Table 1. Two-way ANOVA comparing proportional abundance of *Daphnia retrocurva* among treatments (black enclosures, clear enclosures and open lake) and depths (2, 4, and 6 m) in Lake Waban, Massachusetts on 8 July, 1997. Proportional abundance is the proportion of total density over all depths sampled.

Source	df	Sum of squares	F	P
Treatment	2	0.002	0.94	>0.05
Depth	2	0.179	99.96	<0.01
Treatment \times depth	4	0.015	4.11	<0.01
Error	68	0.061		

enclosure experiment. Copepod nauplii and *D. retrocurva* dominated numerically the crustacean zooplankton community with mean densities of 41.4 and 37.3 ind./L, respectively, across all sampling depths. Of the four copepod species present, *Diaptomus minutus* was most abundant (mean density, 5.7 ind./L across all sampling depths).

Night-time light intensity resulting from light pollution at the surface of Lake Waban was less than that of full moonlight (i.e. $0.01 \mu\text{Einst}/\text{m}^2/\text{s}$; MOORE RODENHOUSE 1986) and ten times less than that measured at the surface of an urban lake near the center of Boston, MA. Problems with the photomultiplier prevented

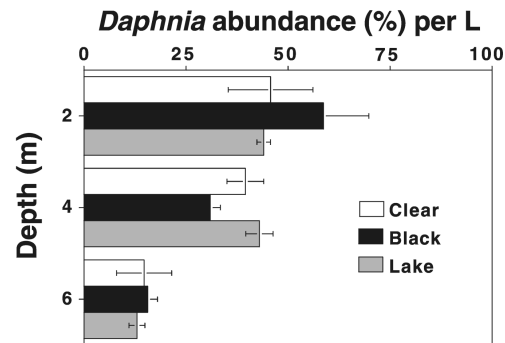


Fig. 1. Mean ($n = 3$) percent abundance ($\% \pm 1$ SD) of *Daphnia retrocurva* (per L) across all sampling depths (2, 4, and 6 m) and treatments (Clear: clear enclosure; Black: black enclosure; Lake: lake sampling site) in Lake Waban, Massachusetts on 8 July 1997.

us from obtaining absolute measurements of light intensity at night. At midday, 7 July 1997, the Secchi disc depth of Lake Waban was 1.7 m, and the light extinction coefficient (k) equaled 0.82/m. On the night of the experiment, the metalimnion occurred between 4 and 10 m, and hypoxic or anoxic conditions occurred at depths ≥ 5 m (Fig. 2).

Using the Secchi depth recorded for Lake Waban and a regression model developed by DODSON (1990), a migration amplitude of 2.1 m is predicted empirically for *Daphnia* under normal conditions (i.e. no light pollution) in Lake Waban. *Daphnia*'s upward movement of 2 m in the black enclosures, coupled with its absence of DVM in the lake, suggests that light pollution either eliminated *Daphnia* DVM or reduced its amplitude to a distance too small for detection with the experimental methods used. Interestingly, the model of DODSON (1990) also predicts that full moonlight reduces the amplitude of *Daphnia* DVM by 2 m in north temperate lakes. This prediction, in conjunction with the results of this current study, suggests that the ecological effects of light pollution in this lake are comparable to those of

full moonlight.

Suppression of zooplankton DVM by light pollution is probably most likely to occur in lakes with fish and relatively clear water. In lakes with fish, *Daphnia* genotypes most sensitive to light (i.e. negative phototaxis) occur, and these genotypes respond more strongly to the induction of DVM by fish kairomones than clones from fishless habitats (DE MEESTER 1993). Finally, the penetration of light pollution and its effects should be greater in clear lakes with low concentrations of DOC and algae.

The suppression of DVM by light pollution may have consequences for both algae and zooplankton. Algal mortality in the epilimnion may be reduced due to lower rates of zooplankton grazing. Alternatively, the lack of nutrient regeneration by zooplankton in the upper surface waters at night could actually slow algal growth in lakes experiencing severe nutrient limitation (STERNER & HESSEN 1994). If light pollution confines zooplankton to metalimnetic depths, individual growth and reproduction may decline markedly due to colder water temperatures (LOOSE & DAWIDOWICZ 1994).

Conclusions

Diel vertical migration of *Daphnia* was significantly reduced in both amplitude (2 m lower) and magnitude (10–20% fewer individuals) by urban light pollution in a suburban lake. Reduced algal grazing by zooplankton at night in epilimnetic waters could potentially contribute to enhanced algal biomass in lakes and coastal waters near urban areas, thereby lowering water quality.

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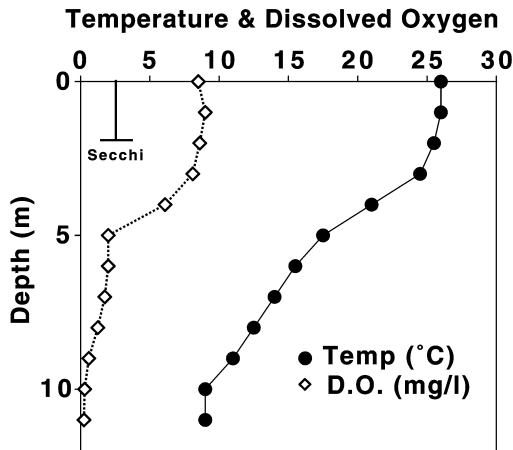


Fig. 2. Temperature ($^{\circ}\text{C}$) and dissolved oxygen (mg/L) profiles for Lake Waban, Massachusetts on 7 July 1997 at 21:00 h.

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