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NOTE AND COMMENT

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A seasonal change in the distribution of a stream-dwelling stonefly nymph reflects oxygen supply and water flow

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Abstract We examined the effects of oxygen availability, which has been viewed as a minor factor in streams, on the seasonal and spatial microhabitat distribution of a stonefly. Surveys were conducted in winter and summer in a mountain stream by collecting stones from the streambed and determining the presence or absence of the insect. At each stone sampling, we also measured physical conditions. The probability of the stonefly presence increased significantly with current velocity in summer, but not in winter. Because current influences oxygen renewal rates, our results suggest that the distribution of the insect could be restricted by oxygen.

Keywords Oxygen · Stonefly · Stream · Temperature · Water flow

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Introduction

The partial pressure of O_2 (and CO_2) is relatively invariant in terrestrial systems, but in aquatic systems variations in O_2 are large (Wiley and Kohler 1984), especially in polluted waters. In streams, oxygen availability has generally been considered of minor importance to the biota, because continuous mixing maintains oxygen concentrations near saturation (Allan 1995).

Oxygen availability in streams is related to both water temperature and current. Increased water temperature decreases the solubility of oxygen in water and current influences water renewal rates. Influences of water temperature and current on oxygen availability for aquatic insects are often apparent through their distinctive respiratory behavior. For example, ephemeropteran nymphs beat their abdominal gills (Eastham 1937), plecopteran nymphs do "push-ups" by moving their body rhythmically up and down (Knight and Gaufin 1963), and trichopteran larvae undulate their abdomens (Philipson and Moorhouse 1974). These behaviors help replace oxygen-depleted water near the gills with oxygen-rich water and their frequency increases with decreasing dissolved oxygen (DO) concentration and decreasing water flow (Knight and Gaufin 1963; Kamler 1969, 1971; Murakami 1980). Low DO and slow current can result in the death of animals (e.g., Knight and Gaufin 1963). Nevertheless, oxygen availability is rarely considered in studies of stream insect–habitat relationships.

The frequency of the "push-up" behavior performed by the stonefly nymph *Oyamia lugubris* McLachlan (Perlidae) in a mountain stream depended on the oxygen supply defined as DO × current velocity (Genkai-Kato et al. 2000). Further, there was only a small difference in the critical oxygen supply, below which the stonefly initiated the push-up behavior due to insufficient oxygen availability, between summer (low DO) and winter (high DO). Thus habitats with slow currents, such as pool or nearshore habitats, could vary in their suitability for aquatic insects between seasons. Respiratory behavior can be costly for some taxa because it cannot be carried out simultaneously with other activities such as feeding (see Philipson and Moorhouse 1974). At a microhabitat scale, mayfly nymphs (Wiley and Kohler 1980) and caddis fly larvae (Kovalak 1976) move to current-exposed positions on stones when they experience oxygen stress.

In streams with relatively stable flow regimes, DO generally varies in a particular habitat more seasonally than spatially, while current varies more spatially than temporally. Thus, oxygen availability can determine, in part, the spatial and temporal distributions of aquatic animals. Researchers have emphasized substrate (Minshall 1984), current (Hart and Finelli 1999), and temperature (Ward and Stanford 1982) as important physical habitat factors, yet oxygen availability has received relatively little attention. Our goal was to examine the effects of oxygen availability on the distribution of a stream insect. We tested the hypothesis that the distribution of the stonefly nymph *O. lugubris* varies with season owing to oxygen availability in different microhabitats.

Methods

We conducted surveys in winter (11–13 January 1999) and summer (9–11 August 1999) during the daytime (09:00–17:00 hours). Nymphs of *O. lugubris* were collected from the same stream area (35°53′N, 137°40′E) sampled by Genkai-Kato et al. (2000), Kuro-kawa River in Kiso Fukushima, Nagano Prefecture, Japan. This third-order river (14 km long) is a tributary of the Kiso River, which flows into the Pacific Ocean. The studied area included two survey riffle reaches (30 m long × 6 m wide, 9.5 km downstream from the headwater, altitude: 840 m, gradient: 3%, substrate: cobble, discharge: 3 $m^3 s^{-1}$). Sampling was conducted with a quadrat net (20×20 cm, 1-mm mesh) by collecting a stone (loose cobble) from the streambed at random and recording the presence or absence of *O. lugubris*. Reaches were sampled in a downstream to upstream manner so released nymphs would not be resampled. At each stone, we measured current velocity, depth, and its surface area. The current velocity was measured at 60% of the water column depth to estimate mean column velocity (Hynes 1970), using a portable current meter (Model CR-7WP, Cosmo-Riken Inc., Kashihara, Japan). The surface area of the stone was approximated as an elliptic shape: $\pi/4 \times$ major axis × minor axis of the stone. The surveys were in principle conducted in the same survey reaches in both seasons, but in summer we randomly collected additional nymphs and measured the physical conditions in other reaches (10 m downstream of the study area) because *O. lugubris* was not abundant. We sampled 177 and 268 stones in winter and summer, respectively. On the basis of the result from our previous experiment that the push-up frequency did not differ according to body size of stonefly (Genkai-Kato et al. 2000), measurements of stonefly size were not conducted in the field surveys. The body sizes of stonefly in the present study are comparable to our previous experimental study.

During the surveys, we monitored water temperature with a thermometer and DO by the Winkler method at a deep point (1 m deep) and a shallow point (10 cm deep) inside the survey reaches. Both parameters were measured at two depths at the deep point (10 cm from the surface and 10 cm above the bottom) and at one depth at the shallow point (5 cm from the surface).

The effects of current velocity, depth, and stone area on the presence (1) or absence (0) of *O. lugubris* nymphs in winter and summer were examined with logistic regression analysis. Significance of the regression coefficients was determined by Wald's chi-squared test (α level = 0.05). The physical conditions of the microhabitat at sampled stones were compared between seasons with *t*-tests.

Results

Water temperatures in the survey reaches were 3.5–3.8°C in winter and 17–18°C in summer. Dissolved oxygen concentrations were 12 mg O_2 l^{-1} in winter and 8.2 mg O_2 l^{-1} in summer. They did not differ between deep and shallow sampling points or near-surface and bottom depths in winter or summer.

The body size of the collected stonefly nymphs varied from 0.5–3 cm in winter and 1.2–3 cm in summer. In winter, 84 individuals were collected from 177 sampling sites and 81 individuals from 268 sites in summer. No more than one individual was found at one stone sampling. In winter, the probability of a stonefly being present increased significantly with stone area, but was independent of current velocity and depth (Table 1, Fig. 1). In summer, the probability of stonefly presence increased with current velocity and stone area, and was inversely related to depth (Table 1, Fig. 1). In contrast, none of these physical conditions at sampled stones differed significantly between seasons (Table 2).

To compare reach-wide changes in oxygen availability with those associated with stonefly-inhabited sites, we first calculated the mean oxygen supply for each season in all sites (177 sampling sites in winter and 268 in summer), and then only at sites where stonefly nymphs

Table 1 Results of logistic regression analysis testing effects of current velocity, depth, and stone area on the presence of *O. lugubris* nymphs. *Numbers in parentheses* are number of measurements

	Winter (177)		Summer (268)	
	χ^2	P	χ^2	P
Current velocity	3.59	0.06	12.04	< 0.01
Depth	1.15	0.28	6.73	< 0.01
Stone area	11.47	< 0.01	13.01	< 0.01

Table 2 Comparisons of physical conditions at sampled stones between winter and summer with *t*-tests. Values are mean ± SE. *Numbers in parentheses* are number of measurements

	Winter (177)	Summer (268)	*P*
Current velocity (cm s^{-1})	28.7 ± 1.7	32.8 ± 1.4	0.07
Depth (cm)	27.2 ± 1.3	25.3 ± 1.2	0.30
Stone area (cm^2)	309.3 ± 9.9	286.2 ± 10.9	0.14

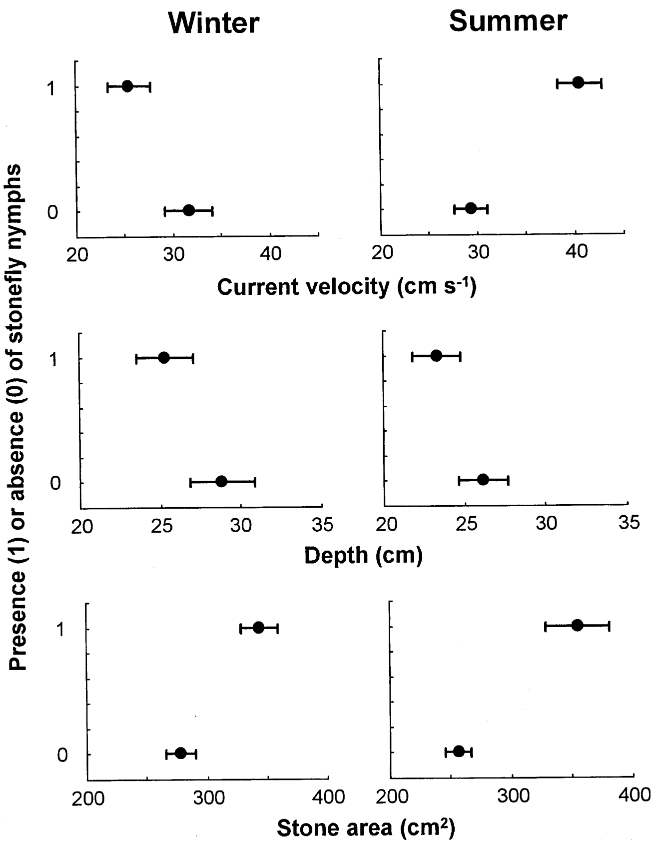

Fig. 1 Presence (*1*) or absence (*0*) of a stonefly nymph in winter (*left column*) and summer (*right column*), depending on current velocity (*top panels*), depth (*middle panels*), and stone area (*bottom panels*). *O. lugubris* was present at 84 samplings out of 177 total stone samplings in winter, and 81 out of 268 in summer. Values are expressed by mean ± SE

were present (84 sites in winter and 81 in summer). This calculation was motivated by the previous study (Genkai-Kato et al. 2000) with an experimental chamber system where we looked at the relationships between DO, current velocity, and the respiratory behavior (push-ups) by manipulating current velocity in winter (high DO) and summer (low DO). We found that the critical oxygen supply (DO × current velocity) at which a stonefly nymph ceased doing respiratory behavior differed little between the seasons. Note that the exact meaning of the critical oxygen supply in the previous study differs to that of the mean oxygen supply calculated here, but their units are the same. The mean oxygen supply, S (mg O_2 cm^{-2} s^{-1}), is defined as $S_i = \rho_i \times \bar{v}_i$ (i = winter or summer), where ρ (mg O_2 l^{-1}) is the DO concentration and $\bar{v}$ is the current velocity (cm s^{-1}) averaged over the sites considered. At all sites, S ± SE was 0.35 ± 0.02 in winter and 0.27 ± 0.01 in summer. At stonefly-inhabited sites, the values were 0.31 ± 0.03 (winter) and 0.33 ± 0.02 (summer). For all sites, the mean oxygen supply value in winter is significantly greater (1.3 times) than that in summer ($P < 0.01$ by *t*-test). In contrast, for stonefly-inhabited sites, the mean oxygen supply value in winter is not significantly different from that in summer ($P = 0.41$ by *t*-test).

Discussion

In summer, the distribution of *O. lugubris* is related to depth and current velocity as well as stone area, whereas the physical conditions under which the samplings were conducted did not differ from those in winter. A higher probability of stonefly presence in faster currents implies that oxygen is at stressful levels for stonefly nymphs under low current velocities in summer, as implied by respiratory behaviors of aquatic insects under low oxygen conditions (e.g., Murakami 1980). These mobile insects apparently cope with seasonal shortages in DO by spatially localizing in habitats with faster velocities, thus maintaining suitable oxygen supplies. This interpretation conforms to the view that oxygen availability for animals in streams is dependent on water flow as well as DO concentration (Genkai-Kato et al. 2000). Interestingly, the oxygen supply at the sites where the nymphs were present in this study and the critical oxygen supply regarding the respiratory behavior in the previous experiment (Genkai-Kato et al. 2000) differ little between seasons. These findings suggest robustness of the measurement, oxygen supply represented by DO × current velocity, as an indicator of oxygen availability for animals in streams. The probability of stonefly presence was also related to depth in summer, while DO did not differ between near-surface and bottom depths. These results imply that this depth effect could be associated with microcurrents near the streambed.

We did not measure near-bed current velocity experienced by stonefly nymphs, which is often inaccessible under stones, but current velocity at 60% depth is a good approximation for the average value in the water column (Hynes 1970). Faster average water column velocities would logically generate faster microcurrents flowing between and under stones. Therefore, while direct and accurate measurements of current in interstitial stonefly habitats remain difficult to obtain, indirect water column measurements may be sufficiently precise (see Jaag and Ambühl 1964; Petr 1970).

In spite of uncertainty in near-bed current velocity experienced by nymphs, the present study shows that the distribution of stonefly nymphs within the stream reaches is influenced by the mean column current velocity under conditions of low DO in summer. Using mean column velocity has an advantage over streambed velocity for managers assessing stream environments, because mean column current velocity is easier to measure quickly and reliably.

Although current has been long considered an important factor determining stream insect distributions, particularly suspension feeders (Edington 1968), its influence on oxygen supply may represent a neglected mechanism that further shapes distributions. Unfortunately, because current interacts with seasonally variable DO to influence oxygen supply, this mechanism would be easily overlooked in single season studies. We suspect that more multi-season studies of benthic insect distributions would find similar patterns to those in the present study, where oxygen-dependent distributions were seasonally constrained to a portion of the velocity gradient.

Our findings have implications for management in terms of stream improvements. The small difference in the oxygen supply in stonefly-inhabited sites between the seasons indicates that the requirement for oxygen by the stonefly nymphs is constant over time. On the other hand, oxygen availability in streams varies spatiotemporally. Stream modifications such as dam and levee constructions are likely to result in uniform flow throughout stream reaches and depletion of rapids. Consequently, such improvements may extirpate some species by removing their respiratory refuges for summer. Further, dams and levees may cause reductions in water quality and DO as well, threatening persistence of species vulnerable to oxygen stress. Managers should consider the direct and indirect effects of such human impacts to prevent loss of biodiversity in streams.

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References

Allan JD (1995) Stream ecology. Chapman and Hall, London

Eastham LES (1937) The gill movements of nymphal *Ecdyonurus venosus* (Ephemeroptera) and the currents produced by them in water. J Exp Biol 14:219–228

Edington JM (1968) Habitat preferences in net-spinning caddis larvae with special reference to the influence of water velocity. J Anim Ecol 37:675–692

Genkai-Kato M, Nozaki K, Mitsuhashi H, Kohmatsu Y, Miyasaka H, Nakanishi M (2000) Push-up response of stonefly larvae in low-oxygen conditions. Ecol Res 15:175–179

Hart DD, Finelli CM (1999) Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. Annu Rev Ecol Syst 30:363–395

Hynes HBN (1970) The ecology of running waters. Liverpool University Press, Liverpool

Jaag O, Ambühl H (1964) The effect of the current on the composition of biocoenoses in flowing water streams. In: Proceedings of International Conference on water pollution research, pp 31–49

Kamler E (1969) A comparison of the closed-bottle and flowing-water methods for measurement of respiration in aquatic invertebrates. Pol Arch Hydrobiol 16:31–49

Kamler E (1971) Reactions of two species of aquatic insects to the changes of temperature and oxygen concentration. Pol Arch Hydrobiol 18:303–323

Knight AW, Gaufin AR (1963) The effect of water flow, temperature, and oxygen concentration on the Plecoptera nymph, *Acroneuria pacifica* banks. Proc Utah Acad Sci Arts Lett 40:175–184

Kovalak WP (1976) Seasonal and diel changes in the positioning of *Glossosoma nigrior* banks (Trichoptera: Glossosomatidae) on artificial substrates. Can J Zool 54:1585–1594

Minshall GW (1984) Aquatic insect–substratum relationships. In: Resh VH, Rosenberg DM (eds) The ecology of aquatic insects. Praeger, New York, pp 358–400

Murakami N (1980) Observation of the respiratory movement of *Oyamia gibba* Klapálek larva (in Japanese with English summary). Biol Inland Waters 1:31–38

Petr T (1970) The bottom fauna of the rapids of the Black Volta River in Ghana. Hydrobiologia 36:399–418

Philipson GN, Moorhouse BHS (1974) Observations on ventilatory and net-spinning activities of larvae of the genus *Hydropsyche* Pictet (Trichoptera, Hydropsychidae) under experimental conditions. Freshwater Biol 4:525–533

Ward JV, Stanford JA (1982) Thermal responses in the evolutionary ecology of aquatic insects. Annu Rev Entomol 27:97–117

Wiley MJ, Kohler SL (1980) Positioning changes of mayfly nymphs due to behavioral regulation of oxygen consumption. Can J Zool 58:618–622

Wiley M, Kohler SL (1984) Behavioral adaptations of aquatic insects. In: Resh VH, Rosenberg DM (eds) The ecology of aquatic insects. Praeger, New York, pp 101–133