Positioning changes of mayfly nymphs due to behavioral regulation of oxygen consumption

MICHAEL J. WILEY AND STEVEN L. KOHLER
School of Natural Resources, The University of Michigan, Ann Arbor, MI, U.S.A. 48109

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Experimental investigations in a small artificial stream showed that the positioning of mayfly nymphs (Ephemeroptera) on stones varied with dissolved oxygen concentration (DO). At low DO levels nymphs moved to current-exposed positions, presumably to increase the renewal rate of oxygen at respiratory exchange surfaces. The expected magnitude of positioning changes under field conditions was determined and suggests that behavioral regulation of oxygen consumption may commonly influence both habitat distribution and diel behavioral patterns. The implications of these results to drift studies are also discussed.

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Des expériences sur des larves d'ephéméroptères dans un petit ruisseau expérimental ont démontré que la position des larves sur les pierres varie selon la concentration d'oxygène dissous (DO). A une faible concentration d'oxygène dissous, les larves s'installent en des points exposés au courant, probablement dans le but d'augmenter le taux de renouvellement de l'oxygène aux surfaces d'échanges respiratoires. La probabilité de l'amplitude des changements de position en nature a été évaluée et semble indiquer que le comportement qui contrôle la consommation d'oxygène exerce peut-être aussi une influence sur la distribution dans l'habitat et les patterns quotidiens du comportement. La discussion porte sur l'importance de ces résultats dans les études sur la dérive.

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Introduction

Mayfly nymphs may be classified according to their ability to regulate oxygen consumption rates. Species capable of respiratory regulation can maintain a constant oxygen consumption rate with respect to either dissolved oxygen concentration or current velocity. Species capable of regulating oxygen consumption over a range of dissolved oxygen concentrations are primarily associated with lentic habitats (Fox et al. 1937; Hynes 1970). With the exception of the burrowing Ephemeridae, lotic species do not regulate over concentration gradients but are often able to regulate only over a limited range of current velocities (Ambühl 1959; Eriksen 1963). In either case, abdominal gills beat rhythmically to replace oxygen-depleted water in the vicinity of the respiratory exchange surfaces (Eastham 1937; Eriksen 1966). Mayflies with immovable gills are not capable of respiratory regulation in this sense and are usually confined to environments with higher current velocities (Hynes 1970).

Eriksen (1966) suggested that lotic mayflies may also behaviorally regulate oxygen consumption rates by utilizing microhabitats with sufficient current velocity to ventilate exchange surfaces with minimal physiological work or by temporarily moving to areas of greater current velocity when ambient oxygen concentrations decline. Kovalak (1976) reported diel and seasonal movements of the caddisfly *Glossosoma nigrior* on bricks and proposed that such positioning changes were correlated with the insect's respiratory needs. More recently, Kovalak (1979) has suggested that diel positioning changes associated with behavioral regulation of oxygen consumption may influence the drift periodicity of stream macroinvertebrates.

In this paper we describe the results of a laboratory examination of the effects of oxygen concentration and current velocity on the positioning of four lotic mayfly species. We hypothesize that behavioral regulation of oxygen consumption will be manifested in positioning changes by mayfly nymphs on stones. When under respiratory stress, we anticipate that they will move to more current-exposed surfaces in order to increase the renewal rate of oxygen at respiratory exchange surfaces. By determining the conditions under which behavioral regulation becomes important in the laboratory and comparing these with expected field conditions, we

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attempt a preliminary evaluation of the importance of behavioral regulation of oxygen consumption to mayfly ecology.

Methods

The positioning behavior on stones of four mayfly species, *Stenacron interpunctatum* (Say), *Stenonema pulchellum* (Walsh), *Ephemerella lata* Morgan, and *Pseudocloeon* sp., was observed in a small flowing-water chamber (Fig. 1) under several combinations of dissolved oxygen concentration and current velocity. The chamber was constructed of Plexiglas and had a water volume of about 0.2 L. The substrate consisted of eight pebbles (15–30 mm in diameter) evenly spaced so as to minimize the formation of oxygen concentration gradients in the water column. Dissolved oxygen was controlled by bubbling through nitrogen gas and concentrations were continuously monitored using a Weather Measure Corporation Model DO-1A dissolved oxygen meter. Water current was generated by two jets passing an air stream over the water surface. Current velocity was continuously monitored using a calibrated, lever-type current meter. Surface current velocities of 7, 10, and 15 cm s^{-1} were used in the experiments.

Experimental animals were usually collected 1 day prior to experimentation and experiments were conducted near field temperatures. *Stenacron interpunctatum*, *Stenonema pulchellum*, and *Pseudocloeon* sp. were collected from the Huron River, Washtenaw Co., Michigan. *Ephemerella lata* was collected from the Pigeon River, Otsego Co., Michigan. Mature nymphs were used in all experiments, although nymphs with black wing pads were not used. Ten individuals of a given species were placed in the chamber and allowed to acclimate overnight before beginning an experiment the following morning. Experiments were initiated with the dissolved oxygen concentration (DO) at saturation. We then reduced the DO, usually in 2 ppm decrements. The organisms were exposed to all three current velocities at each DO. Each DO – current velocity combination was maintained for 15 min. At the end of a 15-min period, the number of individuals on current-exposed surfaces was recorded. In general, we considered the front face, top, and upper side surfaces on stones to be current exposed. Two experiments were run for each species. Experiments were conducted in July and October, 1978.

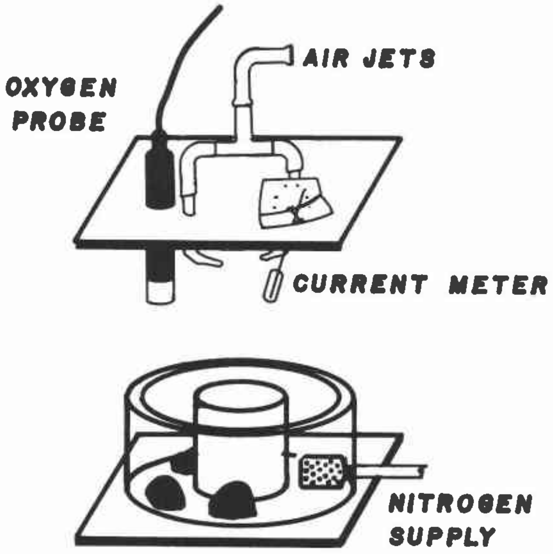

FIG. 1. Plexiglas chamber (10.2 cm outside diameter) used in experiments.

Results

All species showed significant changes in positioning in response to DO, although the degree of response varied among species (Figs. 2–5).

Stenacron interpunctatum was the species most tolerant of low DO levels (Fig. 2). Individuals remained on the bottom of stones except at very low DO levels. At the two lowest DO's current velocity also appeared to affect positioning. At 4 ppm, some individuals were observed to move their abdomen from side to side with their cerci pointing up into the water column while they remained on unexposed surfaces. At 1 ppm the nymphs were very active and some swimming and drifting occurred. The tolerance of this species to low DO is not unexpected as Flowers and Hilsenhoff (1978) indicated it is abundant in small eutrophic streams where it may be the only heptageniid present. In our collecting, this species was always found on the bottom of stones.

Another heptageniid, *Stenonema pulchellum*, responded more strongly to DO than did *Stenacron interpunctatum* (Fig. 3). In this case, the response to current velocity was ambiguous. Individuals became fairly active at a DO of 4 ppm and at 3 ppm

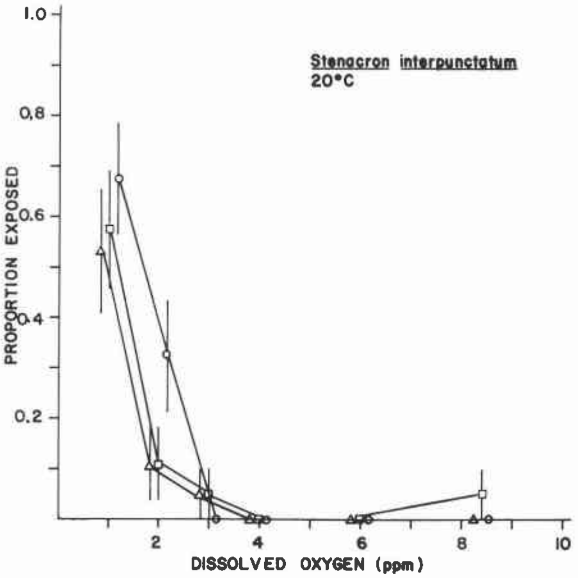

FIG. 2. Proportion (± standard deviation) of *Stenacron interpunctatum* on current-exposed surfaces at varying dissolved oxygen concentrations. ○, 7 cm s^{-1}; □, 10 cm s^{-1}; △, 15 cm s^{-1}.

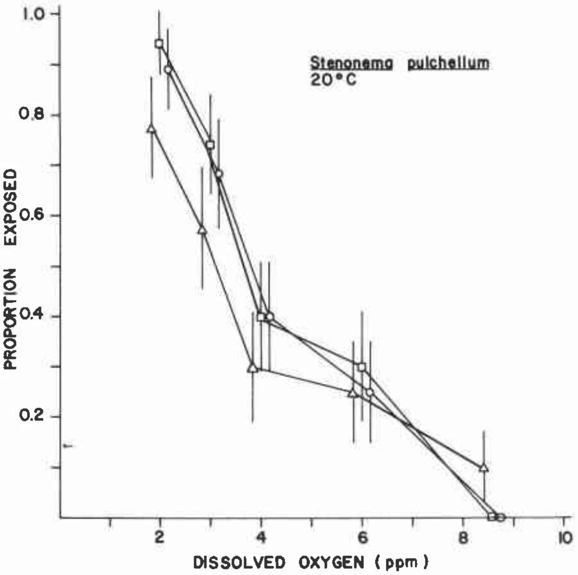

FIG. 3. Proportion (± standard deviation) of *Stenonema pulchellum* on current-exposed surfaces at varying dissolved oxygen concentrations. Symbols as in Fig. 2.

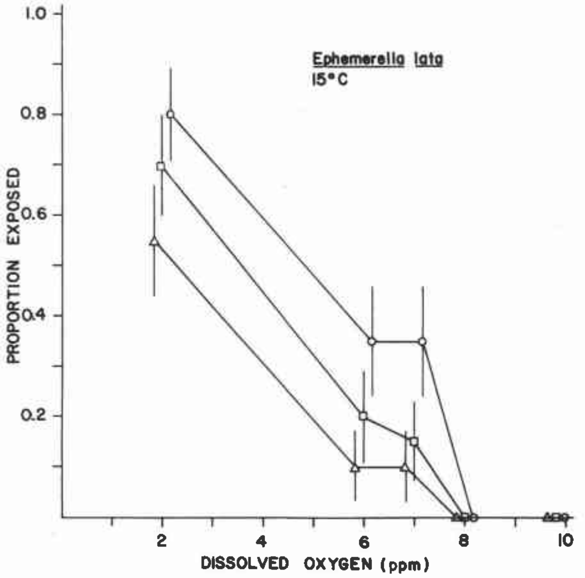

FIG. 4. Proportion (± standard deviation) of *Ephemerella lata* on current-exposed surfaces at varying dissolved oxygen concentrations. Symbols as in Fig. 2.

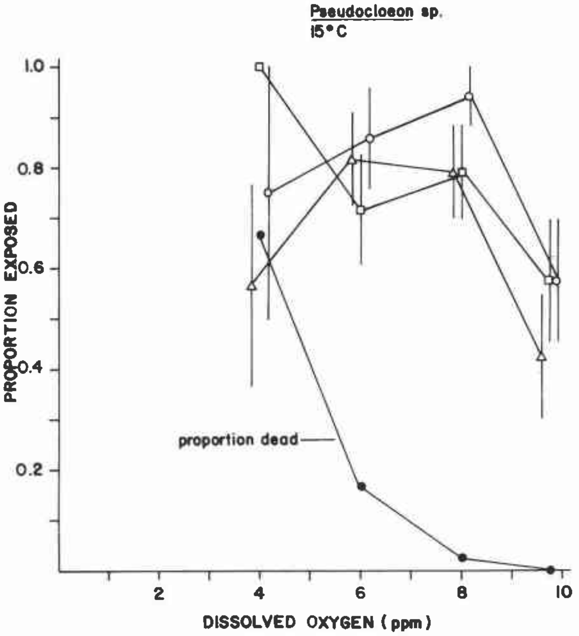

FIG. 5. Proportion (± standard deviation) of *Pseudocloeon* sp. on current-exposed surfaces and mean proportion dead at varying dissolved oxygen concentrations. Symbols as in Fig. 2.

some swimming and drifting occurred. At 3 ppm, most individuals on current-exposed surfaces held their bodies slightly off the stone surfaces and some individuals pointed their abdomen up into the water column. Positioning of this species in the field was similar to that of *Stenacron interpunctatum*.

Ephemerella lata, a common trout stream mayfly, also exhibited a significant response to DO (Fig. 4). In addition, the proportion of individuals on current-exposed surfaces was inversely proportional to current velocity. A large increase in swimming activity occurred at a DO of 2 ppm. This species was collected from both the top and bottom surfaces of stones in the field.

The baetid nymph *Pseudocloeon* sp. was the species most strongly affected by DO (Fig. 5). A large proportion of individuals occurred on current-exposed surfaces with the water saturated with oxygen. In the field, this species was collected predominantly from the top surface of large, flat rocks in a rapid riffle. *Pseudocloeon* sp. occurred almost exclusively on the top surface of artificial substrates during the day and night in the summer in a Pennsylvania stream (W. P. Kovalak, personal communication). A substantial increase in the proportion of individuals on current-exposed surfaces was observed at relatively high DO levels (Fig. 5). In addition, significant mortality occurred during the experiments as the proportion of dead individuals increased exponentially with decreasing DO. At low DO levels a large number of individuals died and the proportions on current-exposed surfaces were based on the surviving organisms. This biases the exposure values at low DO levels. At 6 ppm, most individuals held their abdomen completely off the substrate and some actively entered the drift.

Using these behavioral data and data on the field DO conditions to which these species are exposed,

TABLE 1. Expected increase in exposure and maximum exposure at minimum daily field DO levels corresponding to experimental water temperatures

Species	River	Daily DO range, ppm	Expected increase in exposure, %		Maximum exposure, %
			7 cm s^{-1}	15 cm s^{-1}	
Stenacron interpunctatum	Huron	6.0–9.0	0	0	0
Stenonema pulchellum	Huron	6.0–9.0	25	25	25
Ephemeralla lata	Pigeon	7.5–10.0	20	6	20
Pseudocloeon sp.	Huron	6.5–10.0	32	39	94

we can estimate the extent to which behavioral regulation of oxygen consumption via positioning changes may occur in the field. The expected increase in exposure for each species at the minimum daily DO corresponding to the experimental water temperatures used is given in Table 1. At experimental current velocities, significant increases in exposure would be expected for all species except *Stenacron interpunctatum*. Expected increase in exposure values may be slightly elevated for *Pseudocloeon* sp. Experimental results indicate that about 10% of the population would die of anoxia if exposed to the expected minimum daily DO of 6.5 ppm (Fig. 5). It seems likely, therefore, that *Pseudocloeon* sp. utilizes microhabitats with fast current velocities to insure adequate renewal of oxygen to respiratory exchange surfaces.

Discussion

The positioning behavior and changes in the positioning of lotic mayflies on stones have generally been related to phototactic responses (Wodsedalek 1911; Scherer 1962; Chapman and Demory 1963; Hughes 1966; Elliott 1968).[Most Ephemeroptera are considered to be photonegative, occurring on the bottom surfaces of stones during the day and moving to upper, current-exposed surfaces at night in the absence of light (Elliott 1967*a*, 1968).]We have shown that positioning changes may also occur in response to respiratory requirements. Taxa capable of gill ventilation, *Stenacron interpunctatum*, *Stenonema pulchellum*, and *Ephemerella lata*, and a taxon not capable of gill movements, *Pseudocloeon* sp., moved to current-exposed surfaces of stones when under respiratory stress. Positioning changes occur when physiological means of regulating oxygen consumption (gill ventilation) are insufficient to meet respiratory needs. In our experiments, active entry into the drift (emigration) occurred when both physiological regulation and behavioral regulation of oxygen consumption via positioning changes were insufficient to meet respiratory needs.

The degree to which positioning changes are actually used as a respiratory strategy in the field depends on how the animal in question balances the energetic costs and sufficiency of physiological regulation of oxygen consumption (gill ventilation) with the risks involved in positioning changes. The risks associated with occupying exposed surfaces primarily are increased susceptibility to predation and drift (Allan 1978). Optimally an organism should select an ideal habitat where the need for both physiological regulation and behavioral regulation of oxygen consumption via positioning changes are minimal. However, diel and seasonal variations in DO, flow, and temperature virtually ensure that such habitats are in short supply in many lotic systems. Therefore, mayfly nymphs must restrict themselves to a narrow range of habitats where behavioral regulation of oxygen consumption is never required, or they may utilize less than ideal habitats, changing positions when necessary during periods of lower oxygen availability. Our observations suggest that two of the four species we have examined, *Stenonema pulchellum* and *Ephemerella lata*, do indeed occupy habitats in the field in which we would expect some behavioral regulation. Thus, for these species, the risks of moving to exposed surfaces apparently do not outweigh the advantages of being able to utilize more marginal (with respect to respiration) habitats. It is unclear whether or not positioning changes would be expected of *Pseudocloeon*. However, expected significant mortality at field oxygen concentrations indicates that it must either occupy surfaces with high current velocities or engage in diel movements to high velocity areas.

In circumstances when positioning changes are necessary for a mayfly to meet respiratory needs, such behavior should have a significant impact on its susceptibility to drift. Stream drift has been described by Kovalak (1979) in a simple, general model:

$$P(\text{drift}) = P(\text{exposure})P(\text{erosion})$$

where P(drift) is the instantaneous probability of an organism entering the drift, P(exposure) is the instantaneous probability of an organism occurring on a current-exposed surface, and P(erosion) is the instantaneous probability of an organism being eroded from a current-exposed surface. Instantaneous drift probabilities are usually quite low and range from 0.0001 to 0.04 (Elliott 1967*b*; Bishop and Hynes 1969; Waters 1972). Information is not available on erosion probabilities. However, if a nominal range is assumed (0.0001 to 0.005), our data (P(exposure) ranges from 0.0 to 0.94) suggests instantaneous drift probabilities in the range of 0.000 to 0.0047, which compare favorably with literature values. We have shown increases in instantaneous exposure probabilities resulting from positioning changes in response to respiratory needs. It is evident that an increase in exposure probabilities in this range is sufficient to account for a significant increase in drift probabilities. Our increase in exposure probabilities are based on daily minimum DO values. Therefore, we would most likely see an effect of behavioral regulation of oxygen consumption via positioning changes on drift late at night when DO typically reaches a daily minimum. Drift rates commonly show a nocturnal maximum with peaks early and late at night (Waters 1972). Behavioral regulation of oxygen consumption, therefore, is a mechanism that could help to explain late night drift rate peaks for some species.

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