

Effect of low dissolved oxygen on survival, emergence, and drift of tropical stream macroinvertebrates

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Abstract. The effect of different dissolved oxygen (DO) concentrations on the macroinvertebrate assemblages from 2 Australian tropical streams (1 upland, 1 lowland) was measured using artificial stream mesocosms. Responses to 5-d exposures were tested. Both the upland and lowland assemblages showed a similar response. Most taxa tolerated all but very low DO levels (<10% saturation), although a reduction in emergence of insect taxa at intermediate levels (25–35% and 10–20% saturation) was observed. Mayflies showed the highest sensitivity to low oxygen conditions, and lethal effects were observed at DO levels <20% saturation for several upland and lowland species. For other taxa, including several Chironomidae, mortality was observed when oxygen concentrations were below 8% saturation. A drift response was observed only when oxygen concentrations reached near lethal levels (\leq 10% saturation). The lack of a drift response at DO concentrations of 25 to 35% and 10 to 20% saturation indicates that, in moderately poor oxygen conditions, macroinvertebrates will remain at a location and, hence, experience sublethal effects such as suppressed emergence. It is clear that these animals can persist in hypoxic conditions in the short term. However, because of sublethal effects, understanding how low DO concentrations affect natural assemblages of aquatic macroinvertebrates may require studies of populations over several generations.

Key words: dissolved oxygen concentration, hypoxia, lethal effects, mesocosm, sublethal effects, tropics.

Oxygen availability is a widely recognized factor influencing the composition of freshwater communities because it critically affects the distribution of many species (Hynes 1960, Giller and Malmqvist 1998, Dodds 2002). Dissolved oxygen (DO) concentrations can vary spatially and temporally because of respiration by organisms, photosynthesis by plants, atmospheric losses and gains, changes in pressure and temperature, and groundwater inflow (Hynes 1970, Allan 1995, Dodds 2002). Anthropogenic impacts have increased the frequency, duration, and intensity of hypoxia in many aquatic systems, resulting in changes in community composition and often a loss of diversity (Hynes

1960, Pearson and Penridge 1987). Changes in the composition of aquatic assemblages have long been used to indicate environmental conditions (e.g., Hynes 1960, Hellawell 1986, Rosenberg and Resh 1993) because different species have different water-quality requirements and tolerances, such as minima in DO concentrations. Surprisingly, there are few studies on the hypoxia tolerance of freshwater macroinvertebrates given that 1) DO concentration is a key water-quality indicator, 2) macroinvertebrates are used in bioassessment, and 3) the occurrence of anthropogenically induced hypoxia is widespread.

Aquatic macroinvertebrates possess a diverse array of structural and behavioral respiratory adaptations (Eriksen et al. 1984), suggesting that different taxa differ in their oxygen require-

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ments and tolerance to hypoxia. Some aquatic insects (and early instars of others) respire by diffusion through the cuticle, whereas some taxa (and later instars of others) with a lower surface to volume ratio require tracheal or spiracular gills for respiration. Other groups, such as adult elmids beetles, use a plastron, an air bubble that functions as a physical gill that allows diffusion of oxygen into a tracheal system. Further, some aquatic insects have respiratory pigments (e.g., haemoglobin in some Chironomidae and Notosectidae). These differences are reflected in specific physiological responses to changes in DO concentration: some species are oxygen conformers (their internal oxygen concentrations reflect the external environment, e.g., the mayflies *Baetis* sp. and *Ephemera vulgata*, Fox et al. 1937, and the chironomid *Tanytarsus brunnipes*, Walshe 1948), whereas others are oxygen regulators (their internal oxygen concentrations are largely independent of the external environment, e.g., the mayflies *Cloeon dipterum* and *Leptophlebia marginata*, Fox et al. 1937, and the chironomid *Chironomus longistylus*, Walshe 1948). Therefore, we expected that these physiological factors would interact with biophysical variables to determine the response and, ultimately, the distribution of species (Prosser and Brown 1962, Merritt and Cummins 1984).

To predict how DO concentrations influence lotic macroinvertebrate distributions requires knowledge of the specific environmental requirements of macroinvertebrates from a variety of streams across geographic regions. A review of the literature (Table 1) showed that tests of DO tolerance have been conducted for few taxa (mainly Ephemeroptera) and only in temperate regions. These studies were based primarily on acute, short-term experiments. They were usually conducted with late-instar larvae and suggested a wide range of tolerance to hypoxia. It was evident that some macroinvertebrates could tolerate exposure to short periods of very low DO concentrations, perhaps to cope with extreme diel fluctuations in oxygen and other natural processes in particular habitats (e.g., Erikson 1963, Dean and Richardson 1999).

We investigated the response of macroinvertebrates from an upland and lowland stream in the Wet Tropics World Heritage Area in northern Australia to low DO concentrations. We used upland and lowland assemblages because we expected that they would respond different-

ly to hypoxia because macroinvertebrates in warm, lowland streams typically are exposed to extreme diurnal cycles in DO and, late in the dry season, to deteriorating, eutrophic conditions exacerbated by the input of agricultural contaminants. Consequently, we believed that macroinvertebrates from lowland streams would be more tolerant to hypoxia than those from upland streams in this tropical region.

We tested respective assemblages under simulated stream conditions using artificial stream mesocosms, aiming to identify tolerant and sensitive taxa (if differences existed) and determine general assemblage responses. We chose riffle assemblages for testing because we expected riffles to be well aerated and to contain more hypoxia-intolerant species than poorly aerated habitats, as has been shown for mayflies (Fox et al. 1937) and chironomids (Walshe 1948). We examined 5-d exposure to establish acute tolerances and identify nonlethal effects. We measured survival and drift. Drift is a key behavioral response of lotic macroinvertebrates used as an avoidance mechanism to poor environmental conditions (Brittain and Eikeland 1988). We also collected emergent insects to measure the effect of different degrees of hypoxia on developmental success.

Methods

Site descriptions

The upland experiments were conducted at the James Cook University Field Station at Paluma village (lat 19°00'S, long 146°11'E; altitude 910 m asl). The climate at Paluma is seasonal, typically with dry winters (approximately May to November) and warm, wet summers (December to April). Macroinvertebrates used in the upland experiments (Experiments 1 and 2) were collected from a riffle in Camp Creek ~5 km from Paluma. It is a 2nd-order stream at ~820 m asl and is surrounded by tropical rainforest (Simple Notophyll Vine Forest, Tracey 1982). The stream consists of alternating riffles and pools, mostly with granitic substrata of cobbles, larger rocks, and sand. Flow is permanent but can be low in the dry season, whereas monsoon and cyclonic rains cause flooding in the wet season. Rosser and Pearson (1995) give a more detailed description of streams at Paluma.

The lowland experiments were conducted at

TABLE 1. Summary of literature on dissolved oxygen (DO) tolerance of lotic macroinvertebrates. Major taxa abbreviated in parentheses: T = Trichoptera, E = Ephemeroptera, P = Plecoptera, Ch = Chironomidae, Cr = Crustacea. All DO concentrations converted to % saturation, assuming 0.5 µS/cm specific conductance. LC50 = lethal concentration to kill 50% of the population.

Taxon	Temp (°C)	Duration (d)	Lethal DO (mg/L)	Estimated lethal DO (% saturation)	Author and region
<i>Anabolia nercosa</i> (T)	16	Until ceased moving	0.0	0.0	Phillipson 1954, UK
<i>Stenophylax stellatus</i> (T)	16		0.7	7.1	Phillipson 1954, UK
<i>Rhyacophila dorsalis</i> (T)	16		2.0 (0.7 stirred)	20.3 (7.1 stirred)	Phillipson 1954, UK
<i>Hydropsyche instabilis</i> (T)	16		3.3 (0.9 stirred)	33.6 (9.2 stirred)	Phillipson 1954, UK
<i>Wormaldia subnigra</i> (T)	16		4.0 (0.4 stirred)	40.7 (4.1 stirred)	Phillipson 1954, UK
<i>Polycentropus flavocinctus</i> (T)	16		0.0	0.0	Phillipson 1954, UK
<i>Ephemera simulans</i> (E)	13	2	0.44	4.2	Eriksen 1963, USA
<i>Hexagenia limbata</i> (E)	13	2	0.27	2.6	Eriksen 1963, USA
<i>Asellus intermedius</i> (Cr)	10	>7	<0.5	<4.4	Sprague 1963, Canada
	20	>7	<0.5	<5.5	Sprague 1963, Canada
	30	6	0.5 (LC50)	6.6	Sprague 1963, Canada
<i>Hyalella azteca</i> (Cr)	10	7	<0.5 (LC50)	4.4	Sprague 1963, Canada
	20	7	<1.0 (LC50)	11.1	Sprague 1963, Canada
	30	7	<1.7 (LC50)	22.6	Sprague 1963, Canada
<i>Gammarus fasciatus</i> (Cr)	20	0.125	0.06 (LC50)	0.7	Sprague 1963, Canada
<i>Gammarus pseudolimnaeus</i> (Cr)	10	0.125	0.06-0.09 (LC50)	0.5-0.8	Sprague 1963, Canada
	20	1 h	0.06-0.09 (LC50)	0.7-1.0	Sprague 1963, Canada
	30	<15 min	0.06-0.09 (LC50)	0.8-1.2	Sprague 1963, Canada
<i>Ephemerella rotunda</i> (E)	8	0.33	<2.1	<17.8	Hall 1969, USA
	20	0.33	<4.4	<48.6	Hall 1969, USA
<i>Pteronarcys dorsata</i> (P)	18.5	4	2.2 (LC50)	23.6	Nebeker 1972, USA
		30	4.8 (LC50)	63.7	Nebeker 1972, USA
<i>Acronuria lycorius</i> (P)	14	4	3.6 (LC50)	35.0	Nebeker 1972, USA
<i>Hexagenia limbata</i> (E)	18.5	4	1.4 (LC50)	15.0	Nebeker 1972, USA
<i>Baetisca laurentina</i> (E)	18.5	4	3.5 (LC50)	37.5	Nebeker 1972, USA
		30	5.0 (LC50)	53.6	Nebeker 1972, USA
<i>Leptophlebia nebulosa</i> (E)	18.5	4	2.2 (LC50)	23.6	Nebeker 1972, USA
<i>Ephemerella subvaria</i> (E)	18.5	4	3.9 (LC50)	41.8	Nebeker 1972, USA
<i>Ephemera simulans</i> (E)	18.5	30	4.5 (LC50)	48.2	Nebeker 1972, USA
<i>Tanytarsus dissimilis</i> (Ch)	18.5	4	<0.6 (LC50)	<6.4	Nebeker 1972, USA
		30	<0.6 (LC50)	<6.4	Nebeker 1972, USA
<i>Hydropsyche betteni</i> (T)	21	4	2.9 (LC50)	32.7	Nebeker 1972, USA
	18.5	4	2.6 (LC50)	27.9	Nebeker 1972, USA
	17	4	2.3 (LC50)	23.9	Nebeker 1972, USA
	10	4	1.0 (LC50)	8.9	Nebeker 1972, USA
<i>Hexagenia limbata</i> (E)	4-20	21	2.0 (80% mortality)	15.3-22.1	Winter et al. 1996, Canada
<i>Paratya curvirostris</i> (Cr)	15	2	1.0 (27% mortality)	9.9	Dean and Richardson 1999, New Zealand
<i>Baetis tricaudatus</i> (E)	4.5	14	5.0 (60-90% mortality)	38.7	Lowell and Culp 1999, Canada

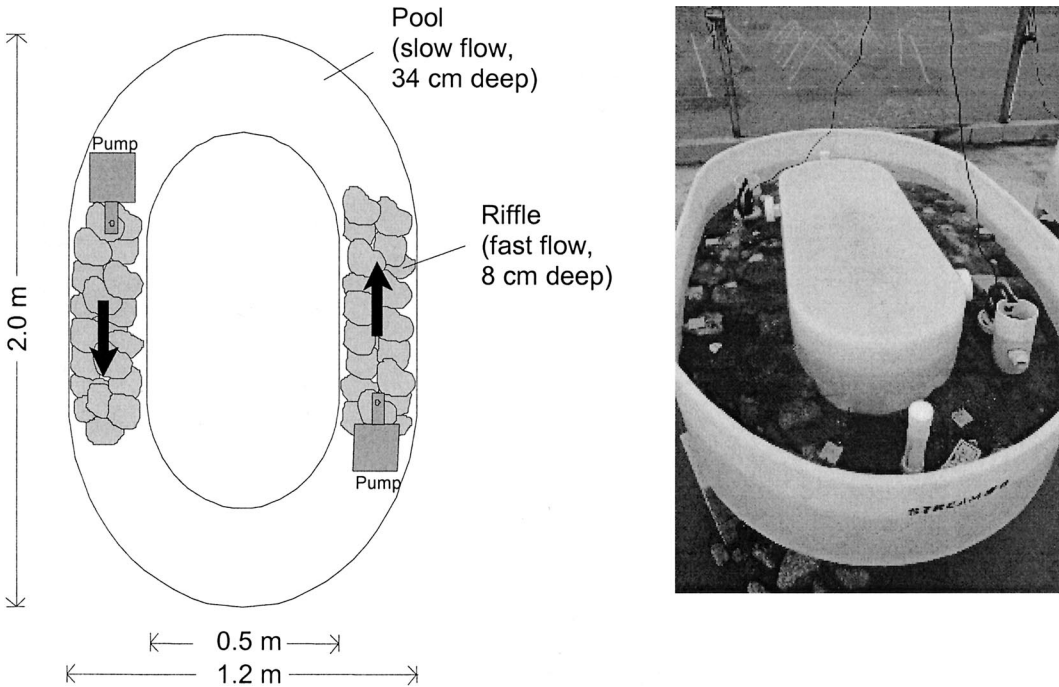


FIG. 1. Recirculating mesocosm used in the experiments (without the polyethylene seal).

James Cook University, Townsville (lat 19°20'S, long 146°45'E, altitude 25 m asl). Townsville has a tropical climate with warm, dry winters and hot, moist summers. Macroinvertebrates used in the lowland experiments (Experiments 3 and 4) were collected from a riffle in Hawkins Creek (lat 18°35'S, long 146°04'E, altitude 60 m asl) ~120 km from Townsville. Hawkins Creek is a 3rd-order stream with a catchment and riparian zone dominated by Mesophyll Rainforest (Tracey 1982). It is similar to Camp Creek in terms of instream substrata, gradient (~1%), and canopy cover (~75%).

Stream mesocosms

Experiments were conducted in recirculating artificial stream mesocosms made of polyethylene oval channels, 350 mm wide and 400 mm deep (Fig. 1). Sand and cobbles from each respective stream were washed vigorously in tap water before being used to construct the base of 2 riffle and 2 pool habitats within each mesocosm (Fig. 1). Ten cobbles (10–12 cm diameter) freshly collected from a riffle from each respective stream were transported in aerated water and placed evenly over the top of each riffle area

within each mesocosm. These cobbles were not cleaned and provided habitat for macroinvertebrates. Water completely covered the cobbles at a depth of 80 mm above the riffle sand base. Two Aquaclear™ Powerhead 802 submersible aquarium pumps controlled water flow. One was positioned at the head of each riffle, maintaining a water velocity of 0.05 to 0.10 m/s over the riffles. A venturi pipe (a narrow opening in the water outlet that draws gas into the outlet by producing a partial vacuum) sucked in air as water passed through the pumps and aerated the water to ~100% saturation. Mesocosms were shaded using 75% shade cloth.

Macroinvertebrates were collected from each study stream to seed the mesocosms using a randomized procedure. Cobbles, haphazardly selected throughout a stream riffle, were lifted from the streambed and gently washed into a container using a squirt bottle. Collecting was carried out for 20 min per container, resulting in a large number of animals with no apparent damage or mortality. The containers were aerated and transported to the mesocosms. One container was randomly selected to seed each mesocosm. This procedure was repeated daily over 4 d prior to each experiment, resulting in

each mesocosm being seeded with 4 randomly allocated containers of invertebrates. It was assumed that this resulted in similar numbers of invertebrates in each mesocosm. No attempt was made to measure numbers prior to each experiment to minimize further handling stress. The seeding of the mesocosms was randomized to avoid systematic differences between treatments. Controls were used for comparisons and as a measure of variation between mesocosms. Two liters of stream leaf litter then were added to each mesocosm to provide a source of organic material (for food, fine particulate organic matter, etc.). This leaf material accumulated at the head of each riffle section and on several rocks within each riffle in the mesocosms.

Two days after the addition of macroinvertebrates (day 6), each mesocosm was tightly covered with clear plastic film. At the start of each experiment, the DO concentration was adjusted over a 2-h period to the selected treatment level. Each experiment ran for 5 d. DO concentrations were manipulated by supplying air or N gas through the pump venturi, enabling rapid deoxygenation by N stripping or rapid reaeration, if required, to maintain treatment oxygen levels. Oxygen stripping using N gas is an established method to reduce DO concentrations without any confounding toxic effects on biota (e.g., Gaufin and Gaufin 1961, Barnhart 1995, Richardson et al. 2001). CO₂ was bubbled through the venturi when necessary to minimize pH fluctuations caused by expulsion of dissolved CO₂ by N stripping. N and CO₂ gases were supplied to mesocosms through high-pressure regulators connected to a polypropylene manifold, from which 4-mm plastic hoses were connected to each pump. Valves on each hose were used to control the amount of N, CO₂, or air entering each pump, maintaining selected DO concentrations in each mesocosm. DO, temperature, and pH levels were monitored throughout each experiment using a Hydrolab[®] Datasonde 3 multiprobe and a WTW[®] Multiline Meter. Treatment and control mesocosms used in each experiment were selected randomly.

At the end of each experiment, the plastic film was removed and the macroinvertebrates from each riffle were collected by washing the 10 cobbles from each riffle through a 63- μ m mesh sieve, and the collected macroinvertebrates were fixed in 70% ethanol. Thus, the sampling unit was 20 cobbles for each mesocosm. The macro-

invertebrate samples from all experiments were sorted, identified, and counted in the laboratory.

Upland stream experiments

Experiments 1 and 2 examined survival response of the upland macroinvertebrate assemblage exposed to hypoxia. In Experiment 2, the number of successfully emerged insects was also measured to assess the effect on development. The upland experiments were run during May 1998 (Experiment 1) and March 1999 (Experiment 2). For each experiment, 6 mesocosms were established as described above. Water temperature and pH were consistent between mesocosms but differed between experiments because of different ambient conditions. In Experiment 1, water temperature ranged from 14.9 to 18.3°C, and pH between 6.4 and 7.0. In Experiment 2, water temperature ranged from 20.2 to 22.3°C, and pH between 6.2 and 7.1. These values are within the range found normally in Camp Creek (RGP and NMC, unpublished data).

Experiments 1 (100% vs 25–35%) and 2 (100% vs 10–20%): survival and emergence.—In Experiments 1 and 2, 3 control mesocosms were maintained at 100% DO saturation (Experiment 1: 9.4–10.1 mg/L; Experiment 2: 8.6–9.0 mg/L). In the other 3 mesocosms, DO concentrations were reduced to a band between 25 and 35% saturation (2.5–3.3 mg/L) in Experiment 1, and between 10 and 20% (1.0–2.0 mg/L) in Experiment 2. The treatment levels were chosen following a review of the literature (see Table 1) and based on previous experiments (Pearson and Penridge 1992). Nebeker (1972), for example, recorded lethal effects for several ephemeropteran species between 15% and 48.2% DO saturation in experiments of similar duration to ours (Table 1). Emerged insects were collected from the underside of the plastic film and from internal tank surfaces at the end of Experiment 2 and fixed in 70% ethanol. Emerged insects were not collected during Experiment 1.

Lowland stream experiments

Experiment 3 examined survival response and emergence in the lowland stream macroinvertebrate assemblage. Experiment 4 examined behavioral responses (i.e., drift rate) in the lowland stream assemblage. The lowland ex-

periments were run during May 1999 (Experiment 3) and August 1999 (Experiment 4). The larger facilities at James Cook University enabled us to run 12 mesocosms simultaneously for each experiment. The distance from the mesocosm facility to Hawkins Creek precluded the use of Hawkins Creek water in these experiments. Instead, either dechlorinated municipal town water (Experiment 3) or water collected from a tributary in an undisturbed catchment upstream of the facility (Experiment 4) was used. Water temperatures and pH were consistent between mesocosms during each experiment (Experiment 3: 17.6–29.0°C, pH 6.4–7.4; Experiment 4: 21.1–27.5°C, pH 6.7–7.6), similar to natural conditions in Hawkins Creek (RGP and MRC, unpublished data).

Experiment 3 (100% vs 25–35%, 10–20%, and 2–8%): survival and emergence.—In Experiment 3, 12 mesocosms were established as described above and were distributed among the controls (3 replicates), with DO maintained at ~100% saturation, and 3 low DO treatments (3 replicates each). These treatments were: 25 to 35% (1.54–2.91 mg/L), 10 to 20% (0.78–1.60 mg/L), and 2 to 8% (0.19–0.74 mg/L). Treatment levels for Experiment 3 were chosen to match those used in the upland experiments (Experiments 1 and 2), with the addition of a lower saturation treatment (2–8% saturation) because of the lack of significant mortality observed in Experiments 1 and 2. Emerged insects were collected from the underside of the plastic film and from internal tank surfaces and fixed in 70% ethanol.

Experiment 4 (100% vs 50–60%, 25–35%, and ≤10%): drift response.—In Experiment 4, 12 mesocosms were established as in Experiment 3. The 12 mesocosms were distributed among the controls (3 replicates) with DO maintained at ~100% saturation, and 3 low DO treatments (3 replicates each). The treatments were: 50 to 60% (3.99–5.15 mg/L), 25 to 35% (2.02–2.84 mg/L), and ≤10% (≤0.87 mg/L). These treatment levels were just above the treatment levels used in Experiment 3 to determine whether a drift response would be detectable before effects on benthic densities were apparent. During this experiment, drifting macroinvertebrates were collected at 6-h intervals on day 1 and day 3 and 12-h intervals on days 2, 4, and 5 with a drift net (12.5 cm x 10.5 cm x 10.5 cm opening, 63- μ m mesh) placed at the downstream end of each riffle. Drift nets were removed and re-

placed through a small sealable opening in the plastic film. This procedure was done quickly and did not affect DO concentrations in the mesocosm water. Macroinvertebrates were examined for movement to ensure that they were alive when collected and then fixed in 70% ethanol.

Statistical analysis

Counts of macroinvertebrates were transformed by $\log(x + 1)$ prior to analysis to normalize data distributions (Zar 1999). When transformed data met assumptions of normality and homogeneity of variances, analyses were done using *t*-tests or analysis of variance (ANOVA) as appropriate. When transformed data failed to meet these assumptions, the nonparametric Kruskal–Wallis ANOVA was used on raw data. Significance was set at $p \leq 0.05$. Bonferroni corrections were not used in these analyses because a separate hypothesis was tested for each taxon, and the same mean was not used more than once (unlike multiple pairwise comparisons where a Bonferroni correction would be required). Post-hoc tests were unnecessary to identify significant treatment effects because of obvious differences among treatments. It was expected that treatment differences would not be detectable for rare taxa but these taxa were included to indicate overall trends and to describe the macroinvertebrate assemblage being tested.

Results

Upland vs lowland assemblages

A diverse macroinvertebrate fauna was present in the mesocosms in both the upland and lowland experiments, comprising several abundant taxa and many less numerous taxa (Tables 2, 3). The 2 assemblages were similar to each other and to those found in rainforest streams at Paluma (Rosser 1999, Rosser and Pearson 1995, Pearson and Connolly 2000) and in Hawkins Creek (RGP and MRC, unpublished data). The 2 assemblages had 38 taxa in common out of a combined 62. Twelve taxa occurred only in the upland assemblage and 12 taxa occurred only in the lowland assemblage. At the family level, the trichopterans were the most different with the upland containing 8 unique families.

At the genus and species levels, the mayfly assemblages were identical except for the occurrence of *Neboissophlebia* sp. 'NQ1' in the lowlands (it was previously collected in the uplands but occurred in low abundance; F. Christidis, James Cook University, personal communication), the Genus WT sp. 1 in the uplands (only known from Paluma; F. Christidis, personal communication), and the Genus WT sp. 2 in the lowlands (not present in the Paluma area; F. Christidis, personal communication). The chironomids were more diverse in the lowland assemblage but still had many species in common with the upland assemblage. The upland assemblage was dominated by Hydracarina, Baetidae, the chironomids *Echinocladius martini* and *Nilotanyppus* sp., and larval elmids. The lowland assemblage was dominated by Simuliidae, the chironomids *Thienemaniella* 'alpha', *T.* 'delta', and *Rheotanytarsus* 'alpha', with the Hydracarina and *Austrophlebioides* sp. common. Atyids occurred in the lowland but not the upland assemblages.

The response to comparable DO treatments was similar in the upland and lowland assemblages, with some taxa increasing in benthic densities because of suppressed emergence in the 25 to 35% and 10 to 20% saturations. For example, densities of the mayfly *Nousia* sp. 'NQ2' increased in the 25 to 35% saturation treatments and then declined sharply in the 10 to 20% saturation treatments in both the upland and lowland experiments (Tables 2, 3). Similarly, when densities of chironomids were pooled they increased in the 25 to 35% and 10 to 20% saturation treatments in the upland and lowland experiments.

Upland stream experiments

Experiment 1 (100% saturation vs 25–35% saturation): survival.—A total of 37 taxa was collected from control and treatment mesocosms in Experiment 1. Control mesocosms had an average of ~22 taxa each compared to treatment mesocosms with an average of 24 taxa each (Table 2). Most taxa showed similar mean numbers between the control and treatment mesocosms in Experiment 1 (Table 2), indicating that an oxygen saturation of 25 to 35% had little effect on survival. However, 4 taxa (Hydracarina, *Nousia* sp. 'NQ2', *Thienemaniella* 'alpha', and Elmidae adults) showed significantly higher densities in the low DO treatment. The higher densities of

these taxa contributed to a higher mean total density in the 25 to 35% saturation DO treatment (Table 2, Fig. 2); however, this difference was not statistically significant.

Experiment 2 (100% vs 10–20%): survival and emergence.—A total of 42 taxa was collected from control and treatment mesocosms in Experiment 2. Both control and treatment mesocosms had an average of ~26 taxa (Table 2). The low DO treatment (10–20% saturation) in Experiment 2 affected several taxa. Five dipterans (indeterminate small instars of Chironomidae were regarded as a taxon) showed significant increases in density, whereas 2 ephemeropteran taxa showed significant declines in the low DO treatment. Most other taxa were more numerous in treatment than control samples. The mean total density of individuals was also higher in the treatment than control samples (although the difference was not statistically significant) (Table 2, Fig. 2). However, counts of emerged insects showed an ~30-fold decrease in abundance in treatment mesocosms relative to controls (Fig. 2).

Lowland stream experiments

Experiment 3 (100% vs 25–35%, 10–20% and 2–8%): survival and emergence.—A macroinvertebrate fauna similar to that in Hawkins Creek (RGP and MRC, unpublished data) was established in the mesocosms in the lowland experiments. Approximately 30 taxa were collected from each of the 95 to 100%, 25 to 35% and 10 to 20% saturation mesocosms, compared to only 15 taxa being collected from the 2 to 8% saturation mesocosms (Table 3). The responses of several taxa were statistically significant (Table 3, Fig. 3). Effects were of 4 main types: 1) a gradual decline with decreasing DO (e.g., Psephenidae, Fig. 3A); 2) no change until the 2 to 8% treatment (e.g., Atyidae and Platyhelminthes, Fig. 3B) or the 10 to 20% treatment (e.g., WT sp. 2, Fig. 3C); 3) an increase in the 25 to 35% treatment, followed by a decline in the 10 to 20% treatment (e.g., the ephemeropterans, *Austrophlebioides* sp., *Nousia* sp. 'NQ2', and Caenidae, Fig. 3C) or the 2 to 8% treatment (e.g., the chironomids, *Thienemaniella* 'alpha', *T.* 'delta', and *Rheocricotopus* 'alpha', Fig. 3D); and 4) no significant change in numbers with changes in oxygen saturation (Table 3). No significant change in numbers with changes in oxygen sat-

TABLE 2. Density of macroinvertebrates (no./20 cobbles \pm SE) surviving in upland mesocosms after 5 d in different dissolved oxygen (DO) treatments (indicated by % saturation). 100% saturation was the control. – = no individuals were present in the sample. *p*-values <0.05 are highlighted in bold. Taxonomic name codes refer to the Australian National Insect Collection (Chironomidae—P. Cranston, University of California, Davis, California, personal communication) and the Museum of Victoria Collection (Leptophlebiidae—J. Dean, Environment Protection Agency, Victoria, Australia, personal communication).

Taxon	DO saturation					
	Experiment 1			Experiment 2		
	100%	25–35%	<i>p</i>	100%	10–20%	<i>p</i>
Turbellaria	–	–	–	–	0.6 \pm 0.6	0.374
Oligochaeta	11.0 \pm 10.5	8.6 \pm 2.9	0.841	10.0 \pm 3.6	20.0 \pm 2.6	0.089
Copepoda						
Cyclopoda	–	–	–	–	0.3 \pm 0.3	0.374
Hydracarina	12.6 \pm 3.1	43.6 \pm 16.7	0.038	83.6 \pm 46.8	100.6 \pm 57.7	0.830
Plecoptera						
Gripopterygidae	14.6 \pm 7.1	9.6 \pm 2.0	0.539	17.0 \pm 8.6	19.3 \pm 7.2	0.846
Eustheniidae	–	–	–	7.0 \pm 6.5	0.3 \pm 0.3	0.364
Ephemeroptera						
Baetidae	52.6 \pm 6.8	78.3 \pm 8.6	0.081	154.6 \pm 34.0	14.0 \pm 7.3	0.016
Caenidae	–	1.3 \pm 0.8	0.205	11.0 \pm 6.1	12.3 \pm 2.6	0.851
Leptophlebiidae						
<i>Atalomicia sexfasciata</i>	–	–	–	1.0 \pm 0.5	–	0.158
<i>Austrophlebioides</i> sp.	0.3 \pm 0.3	–	0.374	–	–	–
Genus K sp. 'AV2'	–	–	–	1.3 \pm 0.8	–	0.205
<i>Nousia</i> sp. 'NQ1'	–	–	–	0.3 \pm 0.3	–	0.374
<i>Nousia</i> sp. 'NQ2'	5.0 \pm 0.0	12.6 \pm 2.7	0.048	22.3 \pm 0.6	3.0 \pm 1.1	0.000
'WT sp. 1'	–	0.3 \pm 0.3	0.374	0.3 \pm 0.3	0.3 \pm 0.3	1.000
Odonata						
Aeshnidae	1.3 \pm 0.8	1.0 \pm 0.5	0.768	–	–	–
Amphipterygidae	0.3 \pm 0.3	1.3 \pm 0.8	0.349	0.3 \pm 0.3	0.3 \pm 0.3	1.000
Libellulidae/Cordulidae	–	–	–	0.6 \pm 0.3	0.3 \pm 0.3	0.519
Megaloptera						
Corydalidae	–	–	–	–	0.3 \pm 0.3	0.946
Lepidoptera						
Pyrilidae	1.0 \pm 1.0	–	0.374	–	–	–
Trichoptera						
Antipodoeciidae	11.0 \pm 4.9	9.6 \pm 1.7	0.812	5.6 \pm 3.7	15.6 \pm 7.0	0.278
Calamoceratidae	0.6 \pm 0.3	0.6 \pm 0.6	1.000	–	–	–
Calocidae/Helicocidae	59.6 \pm 16.6	57.6 \pm 3.5	0.912	1.0 \pm 0.5	–	0.158
Conoesucidae	0.6 \pm 0.3	–	0.116	–	–	–
Ecnomidae	–	–	–	–	0.6 \pm 0.6	0.374
Glossosomatidae	2.0 \pm 1.5	2.0 \pm 0.5	1.000	–	–	–
Helicopsychidae	–	–	–	48.6 \pm 12.4	82.0 \pm 19.8	0.228
Hydrobiosidae	1.3 \pm 1.3	0.6 \pm 0.6	0.678	0.3 \pm 0.3	–	0.374
Hydropsychidae	0.3 \pm 0.3	0.3 \pm 0.3	1.000	–	–	–
Hydroptilidae	1.3 \pm 1.3	3.0 \pm 1.7	0.488	8.0 \pm 2.6	10.6 \pm 0.8	0.393
Leptoceridae	–	–	–	0.3 \pm 0.3	1.6 \pm 1.2	0.345
Odontoceridae	–	–	–	0.3 \pm 0.3	–	0.374
Philorheithridae	0.3 \pm 0.3	1.3 \pm 0.3	0.101	1.3 \pm 0.8	2.3 \pm 1.2	0.539
Polycentropodidae	4.6 \pm 3.2	4.3 \pm 3.8	0.951	4.3 \pm 0.6	3.6 \pm 1.4	0.698
Diptera						
Chironomidae						
<i>Corynoneura</i> sp.	3.4 \pm 1.9	3.7 \pm 1.3	0.899	–	–	–
<i>Cricotopus</i> sp.	23.3 \pm 8.9	15.2 \pm 10.7	0.592	7.3 \pm 2.2	27.2 \pm 4.5	0.018
<i>Dicrotendipes</i> 'alpha'	4.5 \pm 4.5	2.2 \pm 1.1	0.642	12.6 \pm 1.3	8.8 \pm 4.3	0.440
<i>Echinocladius martini</i>	25.3 \pm 10.1	24.6 \pm 5.2	0.956	78.1 \pm 16.1	171.1 \pm 33.2	0.066

TABLE 2. Continued.

Taxon	DO saturation					
	Experiment 1			Experiment 2		
	100%	25–35%	<i>p</i>	100%	10–20%	<i>p</i>
<i>Nilotanypus</i> sp.	37.3 ± 12.6	43.8 ± 11.6	0.725	42.9 ± 4.7	84.4 ± 10.3	0.022
Orthoclad ‘beta’	1.5 ± 1.5	2.3 ± 1.2	0.688	6.5 ± 3.1	31.5 ± 0.4	0.002
<i>Rheotanytarsus</i> sp.	14.4 ± 3.3	7.8 ± 1.5	0.144	13.9 ± 4.6	25.7 ± 7.3	0.247
<i>Riethia</i> sp.	–	0.4 ± 0.4	0.374	–	–	–
<i>Tanytarsus</i> sp.	0.3 ± 0.3	0.7 ± 0.3	0.545	5.8 ± 1.2	9.7 ± 2.5	0.241
<i>Thienemanniella</i> ‘alpha’	6.2 ± 1.3	15.5 ± 2.5	0.033	16.2 ± 16.2	–	0.374
Indeterminate small instars	36.3 ± 14.5	19.0 ± 2.6	0.305	7.0 ± 1.5	57.0 ± 8.6	0.005
Empididae	0.3 ± 0.3	–	0.374	–	–	–
Simuliidae	15.0 ± 4.1	27.3 ± 5.1	0.137	6.0 ± 3.0	16.6 ± 4.9	0.137
Tipulidae	–	–	–	0.3 ± 0.3	2.0 ± 0.0	0.007
Coleoptera						
Elmidae (larvae)	29.0 ± 10.4	33.6 ± 2.3	0.685	69.0 ± 5.2	75.3 ± 14.8	0.709
Elmidae (adults)	11.0 ± 3.0	21.6 ± 1.8	0.041	33.6 ± 3.3	48.0 ± 18.5	0.490
Hydrophilidae	–	–	–	–	0.3 ± 0.3	0.374
Psephenidae	–	0.3 ± 0.3	0.374	–	1.0 ± 0.5	0.158
Scirtidae	–	–	–	0.3 ± 0.3	0.6 ± 0.3	0.519
Mean number of taxa	21.7 ± 1.4	24.0 ± 0.6	0.210	26.3 ± 1.9	26.3 ± 0.3	1.000
Mean total density of individuals	400.0 ± 82.3	465.7 ± 53.8	0.541	706.7 ± 50.0	874.0 ± 106.8	0.229

uration was detected for many of the less-numerous taxa, but it is unclear what this response represents. However, many of these uncommon taxa were absent in the 2 to 8% treatment. None of the more numerous taxa showed a type 4 response.

The response in mean total density followed the 2nd part of the type 3 pattern described above because the high numbers of *Thienemanniella* ‘alpha’ and *T.* ‘delta’ dominated total benthic densities (Table 3, Fig. 4). Although benthic densities were higher in the 25 to 35% and 10 to 20% treatments compared to the control, the number of emerged insects was much lower in these treatments (Fig. 4). Benthic densities were lower in the control mesocosms partly because of a higher emergence rate in the control mesocosms compared to treatment mesocosms. Consequently, more animals had remained in the 25 to 35% and 10 to 20% treatment mesocosms, resulting in higher benthic densities. A substantial decline in benthic densities in the 2 to 8% treatment indicated that mortality occurred, resulting in few individuals emerging.

Experiment 4 (100% vs 50–60%, 25–35%, and ≤10%): drift response.—There was no significant

difference in total drift over the duration of the experiment between control mesocosms and the 50 to 60% or 25 to 35% oxygen saturation treatments. However, ANOVA indicated that drift was enhanced in the ≤10% saturation treatment ($F_{3,8} = 15.91, p = 0.001$; Fig. 5). Four taxa showed increases in drift rate in the ≤10% treatment (Acarina: $F_{3,8} = 12.69, p = 0.002$; Caenidae: $F_{3,8} = 67.59, p < 0.001$; Chironomidae: $F_{3,8} = 23.84, p < 0.001$; and Leptophlebiidae: $F_{3,8} = 12.56, p = 0.002$; Fig. 6). Chironomidae and Leptophlebiidae had high drift on the first day (Fig. 6A, B), whereas drift accumulation was more gradual for the Caenidae (Fig. 6C) and, to a lesser extent, the Acarina (Fig. 6D). Drift remained very low in the control and intermediate oxygen treatments throughout Experiment 4 (Fig. 5).

Discussion

Survival

There were strong similarities between the upland and lowland macroinvertebrate assemblages, with some differences in presence/absence of taxa, or of relative abundances of

TABLE 3. Density of macroinvertebrates (no./20 cobbles \pm SE) surviving in lowland mesocosms after 5 d in different dissolved oxygen (DO) treatments (indicated by % saturation). 100% saturation was the control. – = no individuals were present in the sample. *p* values <0.05 are highlighted in bold. Taxonomic name codes refer to the Australian National Insect Collection (Chironomidae—P. Cranston, University of California, Davis, California, personal communication) and the Museum of Victoria Collection (Leptophlebiidae—J. Dean, Environment Protection Agency, Victoria, Australia, personal communication).

Taxon	Experiment 3				<i>p</i>
	95–100%	25–35%	10–20%	2–8%	
Turbellaria	3.7 \pm 0.3	3.0 \pm 0.6	3.7 \pm 1.8	–	0.003
Oligochaeta	0.3 \pm 0.3	–	1.3 \pm 1.3	3.0 \pm 1.2	0.113
Crustacea					
Atyidae					
<i>Caridina</i> sp.	28.0 \pm 1.2	26.0 \pm 2.0	25.7 \pm 1.9	–	< 0.001
Hydracarina	29.3 \pm 6.9	22.3 \pm 2.6	18.7 \pm 0.3	2.7 \pm 0.7	< 0.001
Plecoptera					
Gripopterygidae	1.7 \pm 0.9	1.3 \pm 0.3	–	–	0.064
Ephemeroptera					
Baetidae	8.3 \pm 0.9	6.3 \pm 0.9	4.3 \pm 3.0	1.3 \pm 0.7	0.102
Caenidae	–	5.7 \pm 0.9	3.3 \pm 2.3	0.7 \pm 0.3	0.040
Leptophlebiidae					
<i>Atalomicria sexfasciata</i>	3.0 \pm 1.5	2.0 \pm 1.2	1.7 \pm 0.7	–	0.111
<i>Austrophlebioides</i> sp.	20.7 \pm 3.2	22.7 \pm 3.8	2.3 \pm 1.5	–	< 0.001
Genus K sp. 'AV2'	–	–	–	0.3 \pm 0.3	0.392
<i>Neboissophlebia</i> sp. 'NQ1'	–	0.7 \pm 0.7	–	–	0.392
<i>Nousia</i> sp. 'NQ1'	1.3 \pm 1.3	–	–	–	0.392
<i>Nousia</i> sp. 'NQ2'	6.3 \pm 2.3	11.0 \pm 5.0	3.0 \pm 0.6	0.7 \pm 0.3	0.015
'WT sp. 2'	14.7 \pm 4.2	13.3 \pm 0.9	8.0 \pm 4.0	–	0.029
Odonata					
Aeshnidae	0.7 \pm 0.7	0.3 \pm 0.3	0.3 \pm 0.3	–	0.737
Diphlebiidae	1.0 \pm 1.0	0.7 \pm 0.3	1.0 \pm 0.6	–	0.441
Libellulidae/Cordulidae	0.7 \pm 0.3	0.3 \pm 0.3	–	–	0.214
Megaloptera					
Corydalidae	1.3 \pm 1.3	–	1.0 \pm 0.6	–	0.269
Lepidoptera					
Pyrilidae	1.0 \pm 1.0	0.7 \pm 0.7	1.7 \pm 0.3	–	0.236
Trichoptera					
Helicopsychidae	0.7 \pm 0.3	0.7 \pm 0.3	–	–	0.139
Hydropsychidae	14.3 \pm 6.3	14.3 \pm 7.5	15.3 \pm 5.9	0.7 \pm 0.7	0.112
Hydroptilidae	1.0 \pm 0.0	1.3 \pm 0.9	2.3 \pm 0.9	–	0.058
Leptoceridae	0.3 \pm 0.3	0.7 \pm 0.3	2.3 \pm 1.3	0.3 \pm 0.3	0.181
Odontoceridae	1.0 \pm 0.6	5.3 \pm 4.4	2.3 \pm 1.5	0.3 \pm 0.3	0.541
Philopotamidae	–	3.3 \pm 1.8	1.7 \pm 1.7	–	0.224
Polycentropodidae	–	0.7 \pm 0.3	–	–	0.086
Indeterminate small instars	–	4.7 \pm 4.2	1.0 \pm 0.6	–	0.153
Diptera					
Chironomidae					
? <i>Apsectrotanypus</i> 'alpha'	–	–	–	0.3 \pm 0.3	0.392
<i>Corynoneura</i> 'alpha'	10.0 \pm 2.5	13.7 \pm 6.7	32.7 \pm 5.4	2.3 \pm 0.3	0.001
<i>Cricotopus</i> ? <i>brevicornis</i>	3.7 \pm 1.8	3.7 \pm 2.7	9.7 \pm 0.9	2.0 \pm 0.6	0.164
<i>Dicrotendipes</i> 'alpha'	1.3 \pm 0.9	3.7 \pm 2.3	5.7 \pm 2.0	0.3 \pm 0.3	0.147
<i>Echinocladius martini</i>	0.3 \pm 0.3	0.3 \pm 0.3	–	–	0.532
<i>Eukiefferiella</i> 'alpha'	0.7 \pm 0.3	–	0.7 \pm 0.3	0.3 \pm 0.3	0.326
<i>Nanocladius</i> 'alpha'	1.3 \pm 0.9	3.7 \pm 1.5	16.0 \pm 3.0	–	0.001
<i>Nilotanypus</i> 'alpha'	5.7 \pm 2.0	6.7 \pm 3.7	3.7 \pm 0.9	0.3 \pm 0.3	0.031
Orthoclad 'beta'	–	–	0.3 \pm 0.3	0.3 \pm 0.3	0.532
? <i>Paratanytarsus</i> 'alpha'	–	0.3 \pm 0.3	–	–	0.392

TABLE 3. Continued.

Taxon	Experiment 3				p
	95–100%	25–35%	10–20%	2–8%	
<i>Polydora</i> ? <i>oresitrophus</i>	1.7 ± 0.3	0.3 ± 0.3	4.3 ± 1.9	1.3 ± 0.9	0.064
<i>Procladius</i> 'alpha'	–	0.3 ± 0.3	–	–	0.392
<i>Rheocricotopus</i> 'alpha'	14.7 ± 2.2	39.7 ± 9.2	78.0 ± 1.5	3.3 ± 1.8	0.016
<i>Rheotanytarsus</i> 'alpha'	82.0 ± 9.2	97.7 ± 10.5	108.7 ± 7.1	9.7 ± 3.5	<0.001
<i>Riethia</i> 'beta'	–	–	1.3 ± 1.3	–	0.392
<i>Tanytarsus</i> 'epsilon'	0.3 ± 0.3	–	0.3 ± 0.3	–	0.532
<i>Thienemanniella</i> 'alpha'	69.7 ± 33.2	232.3 ± 16.2	284.7 ± 20.2	8.3 ± 2.9	<0.001
<i>Thienemanniella</i> 'delta'	97.3 ± 33.2	220.7 ± 79.0	230.3 ± 21.3	8.0 ± 3.2	<0.001
Simuliidae	220.0 ± 78.5	395.3 ± 133.4	356.7 ± 122.1	14.7 ± 8.7	0.003
Tipulidae	8.0 ± 3.6	4.7 ± 1.8	12.7 ± 8.8	0.7 ± 0.7	0.134
Coleoptera					
Elmidae (larvae)	5.7 ± 0.7	1.7 ± 1.2	7.3 ± 3.5	–	0.045
Elmidae (adults)	0.7 ± 0.3	0.3 ± 0.3	2.7 ± 2.2	–	0.306
Hydrophilidae	–	–	0.3 ± 0.3	–	0.392
Psephenidae	7.7 ± 1.5	5.0 ± 1.2	1.7 ± 1.2	–	0.002
Scirtidae	3.7 ± 1.2	2.7 ± 2.7	6.7 ± 4.3	–	0.133
Mean number of taxa					
Mean total density of individuals	30.7 ± 1.7	30.0 ± 1.2	32.0 ± 2.5	14.7 ± 2.1	0.000
	704.0 ± 127.8	1254.3 ± 206.0	1353.3 ± 206.8	69.0 ± 13.7	0.002

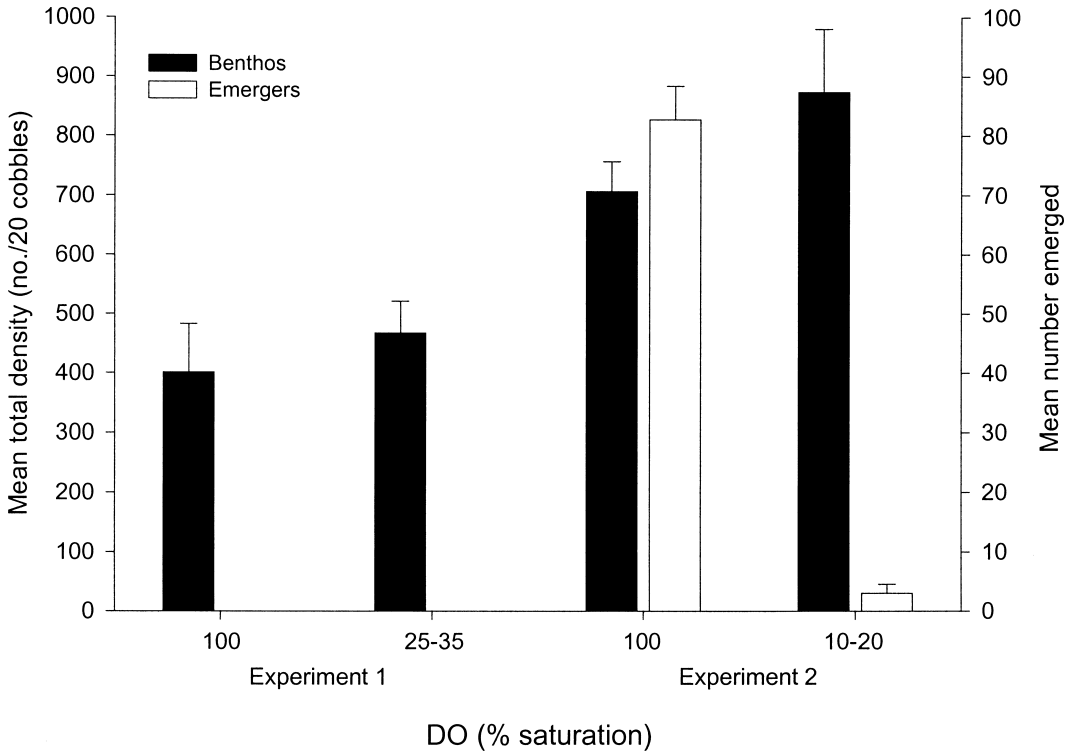


FIG. 2. Mean (+ SE) total density of benthic macroinvertebrates remaining in, and mean (+ SE) number of insects emerging from, upland mesocosms (Experiments 1 and 2) after 5 d in different dissolved oxygen (DO) treatments (indicated by % saturation). 100% saturation was the control. Emergent insects were not measured in Experiment 1.

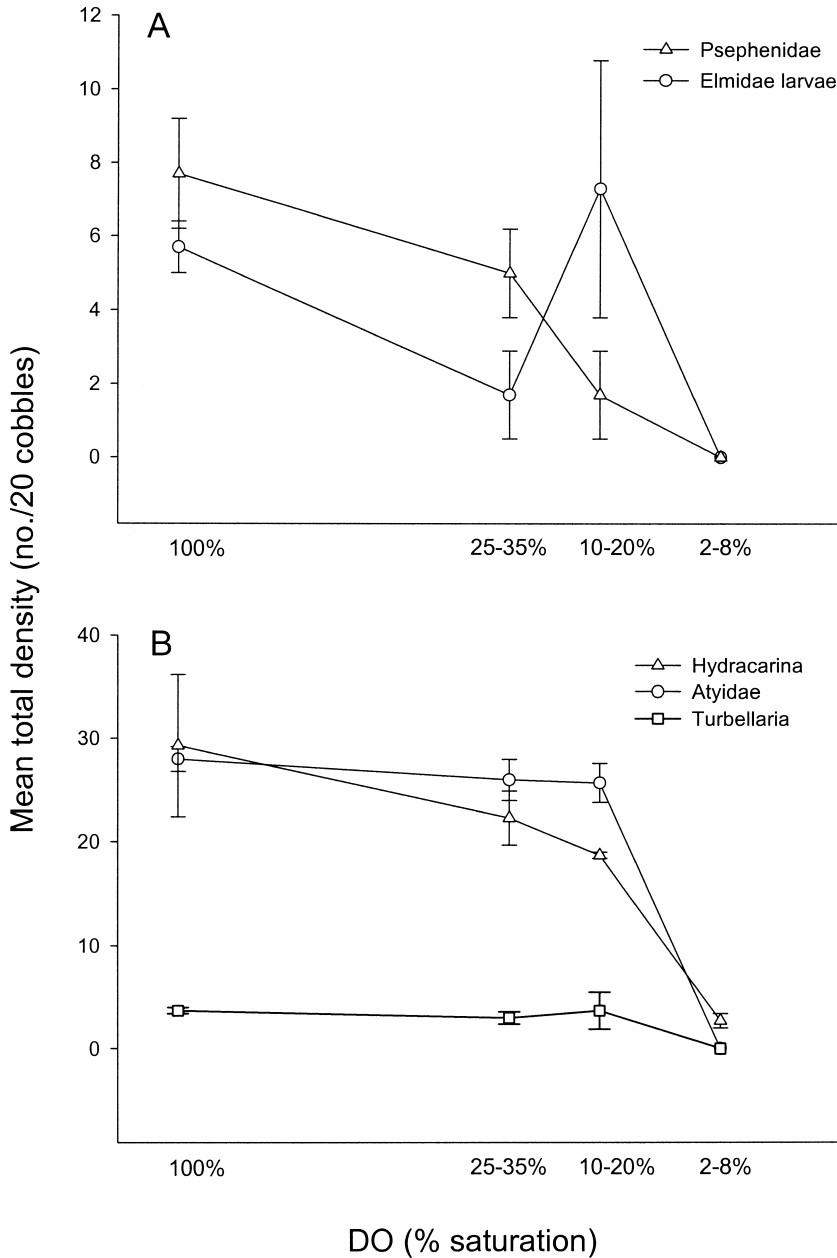


FIG. 3. Mean (\pm SE) total density of macroinvertebrates for different taxonomic groups in different dissolved oxygen (DO) treatments in lowland Experiment 3 (only taxa that had a statistically significant response are plotted). 100% saturation was the control. A.—Coleoptera taxa. B.—Hydracarina, Atyidae, and Turbellaria. C.—Ephemeroptera taxa. D.—Chironomidae taxa.

shared taxa. The similarities in the assemblages probably reflects the similarity between sites in morphology and shade, the relatively small difference in elevation between upland and low-

land sites, and the close proximity of the lowland site to the base of the range. The macroinvertebrate assemblages in our study showed high tolerance to moderate hypoxia, at least over

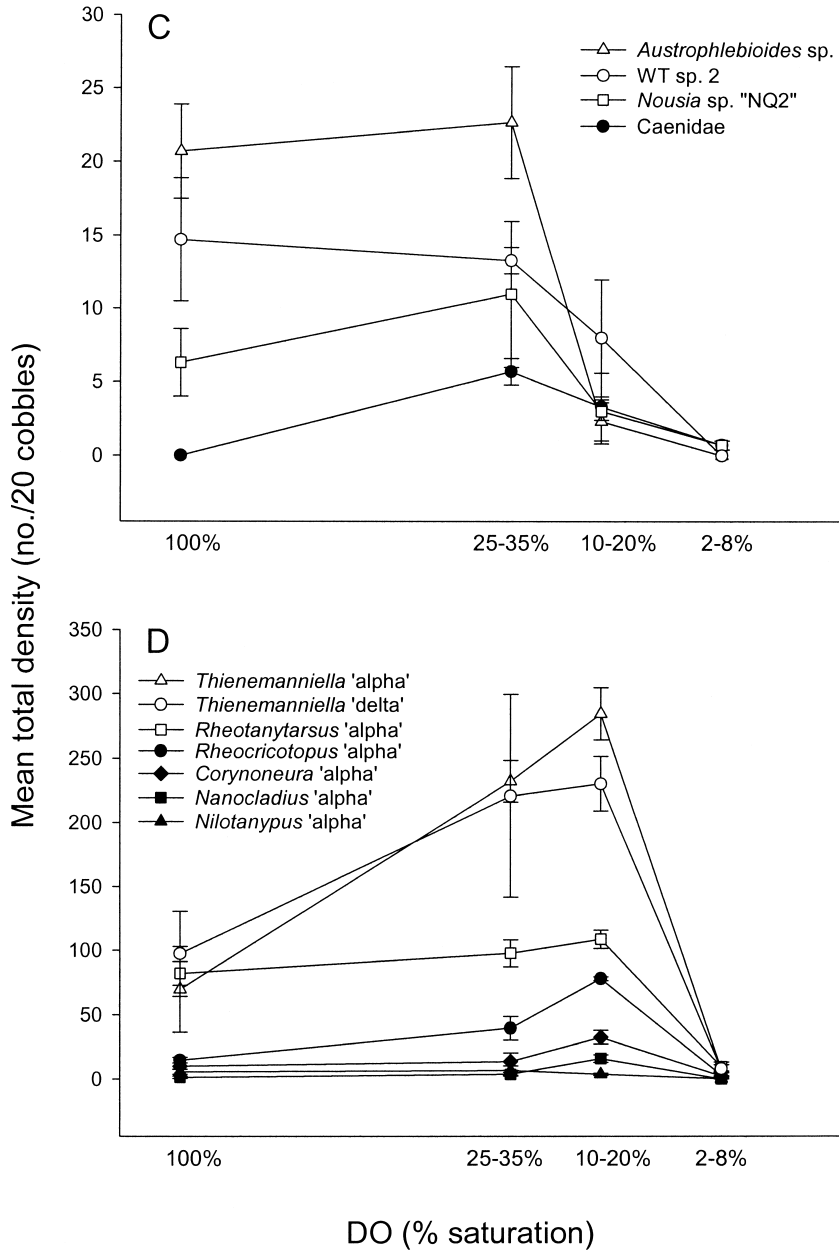


FIG. 3. Continued.

the 5-d duration of our experiments. However, all taxa were intolerant to DO saturation $\leq 10\%$, indicating there was a clear threshold of tolerance for most taxa. The common taxa made comparisons between upland and lowland assemblages possible at the species level, and it was found that the treatment response was

largely consistent between the 2 assemblages. Mayflies showed the highest sensitivity to low oxygen concentrations; for example, lethal effects occurred at DO levels $< 20\%$ saturation for the leptophlebiid *Nousia* 'NQ2' and baetids in the upland experiments, and for the leptophlebiids *Austrophlebioides* sp., *Nousia* 'NQ2', and

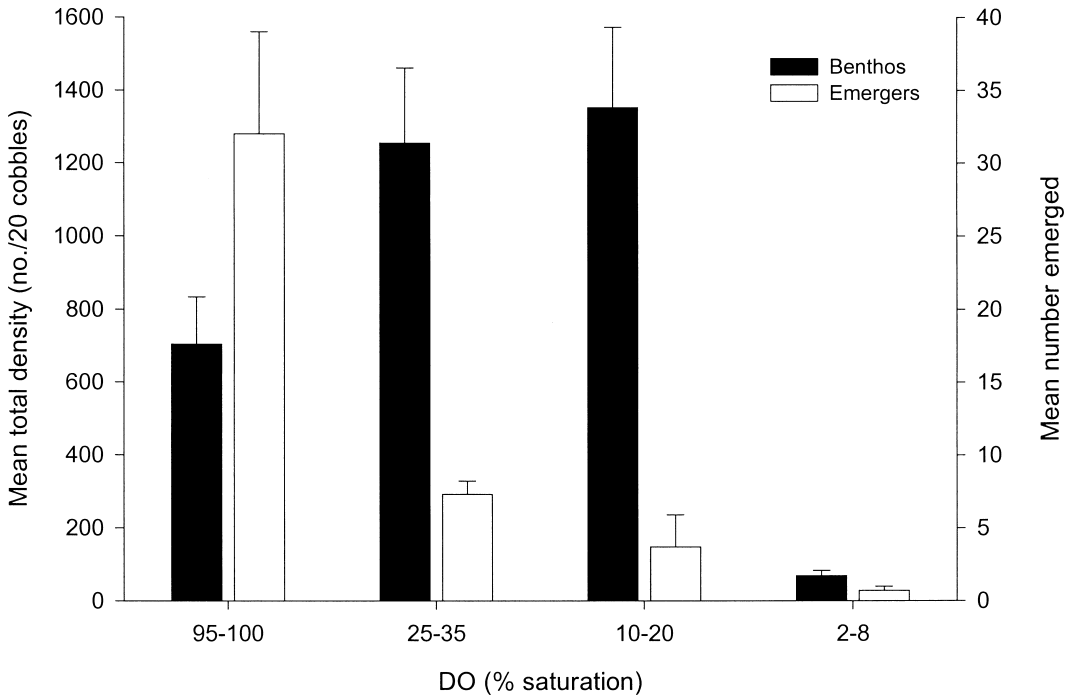


FIG. 4. Mean (+ SE) total density of benthic macroinvertebrates remaining in, and mean (+ SE) number of insects emerging from, lowland mesocosms (Experiment 3) after 5 d in different dissolved oxygen (DO) treatments (indicated by % saturation). 95 to 100% saturation was the control.

possibly WT sp. 2 in the lowland experiments. For most other taxa, including the Chironomidae, distinct reductions in numbers were not observed in the 25 to 35% or 10 to 20% DO treatments in the upland or lowland experiments but were evident in the 2 to 8% DO treatment in the lowland experiment.

Emergence suppression

Suppressed emergence was observed for many taxa at 25 to 35% saturation (lowland) and 10 to 20% saturation (lowland and upland). An initial unexpected response was higher densities in benthic samples for several taxa in the 25 to 35% and 10 to 20% oxygen treatments in both upland and lowland experiments. The most striking example of this response was observed for the chironomids *Thienemanniella* 'alpha' and *T.* 'delta', and for several Ephemeroptera in the lowland experiment. This response corresponded to reduced numbers of emergent animals in these treatments, indicating that the intermediate oxygen treatments imposed a sublethal stress on these animals by suppressing their de-

velopment. The increases in benthic abundance indicate that this effect was largely caused by a delay in pupation rather than mortality of individuals. The suppression of emergence increased with further reductions in DO, and a high number of animals perished in the 2 to 8% treatment.

Several studies have documented partial mortality or sublethal effects for macroinvertebrates exposed to low DO concentrations (Eriksen 1963, Nebeker 1972, Nebeker et al. 1992, 1996, Winter et al. 1996, Dean and Richardson 1999). Nebeker (1972) found that emergence of mayflies was inhibited at DO concentrations considerably greater than 96-h LC50 (lethal concentrations required to kill 50% of the population) values; concentrations of ~80% saturation resulted in a significant reduction in emergence. In contrast, Chironomidae larvae emerged and reproduced successfully when exposed to oxygen concentrations of <7% saturation. In the long term, a delay in pupation and emergence probably influences reproductive success, productivity and, ultimately, persistence at a location. For example, sublethal effects such as reductions in

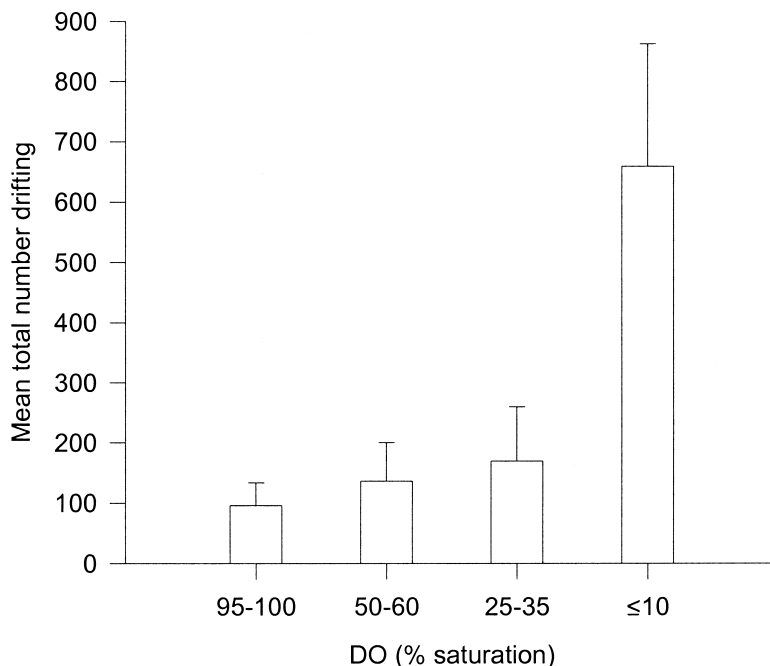


FIG. 5. Mean (+ SE) total number of macroinvertebrates drifting ($n = 3$) over 5 d in mesocosms subjected to different dissolved oxygen (DO) treatments (Experiment 4). 95 to 100% saturation was the control.

rates of feeding and growth in response to lowered DO have been documented for temperate biota (Winter et al. 1996, Lowell and Culp 1999). The overall impact clearly will depend on the duration of exposure to the oxygen stress.

The number of emergent insects indicated sublethal effects in semiaquatic taxa but it was not obvious whether fully aquatic taxa also experienced these effects. The Atyidae and the Hydracarina, persisted until the 2 to 8% oxygen saturation treatment and then declined dramatically (Experiment 3), suggesting a lethal threshold at this level. However, the Hydracarina and Elmidae adults had significantly higher numbers in the low oxygen treatments in the upland experiments (Experiments 1 and 2). It is possible that these animals had moved from other parts of the mesocosms and aggregated in the faster current of the riffles to compensate for the detrimental effects of the low oxygen conditions. Such movement also may have contributed to the high numbers of insects sampled in the 25 to 35% and 10 to 20% saturation treatments in both upland and lowland experiments. For example, Wiley and Koler (1980) found that mayfly larvae responded to low oxygen condi-

tions by moving to more current-exposed positions, and Lowell and Culp (1999) found that exposing the mayfly *Baetis tricaudatus* to 5 mg O_2/L for 14 d at 4.5°C (<40% saturation) resulted in 2 to 3x more larvae moving into regions of high current velocity compared with larvae exposed to 11 mg O_2/L (~100% saturation).

Drift response

An increased drift rate was observed for all taxa only at the lowest DO treatment ($\leq 10\%$ saturation). Many macroinvertebrates respond to deteriorating water quality (e.g., acidification, sedimentation, and pollutants) by increasing their drift rate (Brittain and Eikeland 1988). The lack of a significant drift response to intermediate DO concentrations, despite evidence of sublethal effects, suggests that animals wait, perhaps at a reduced metabolic rate (Eriksen 1963, Kapoor and Griffiths 1975), for conditions to improve. However, the delay in drift response may further disadvantage these animals in that they will remain at a location in moderately poor conditions, hence increasing their exposure

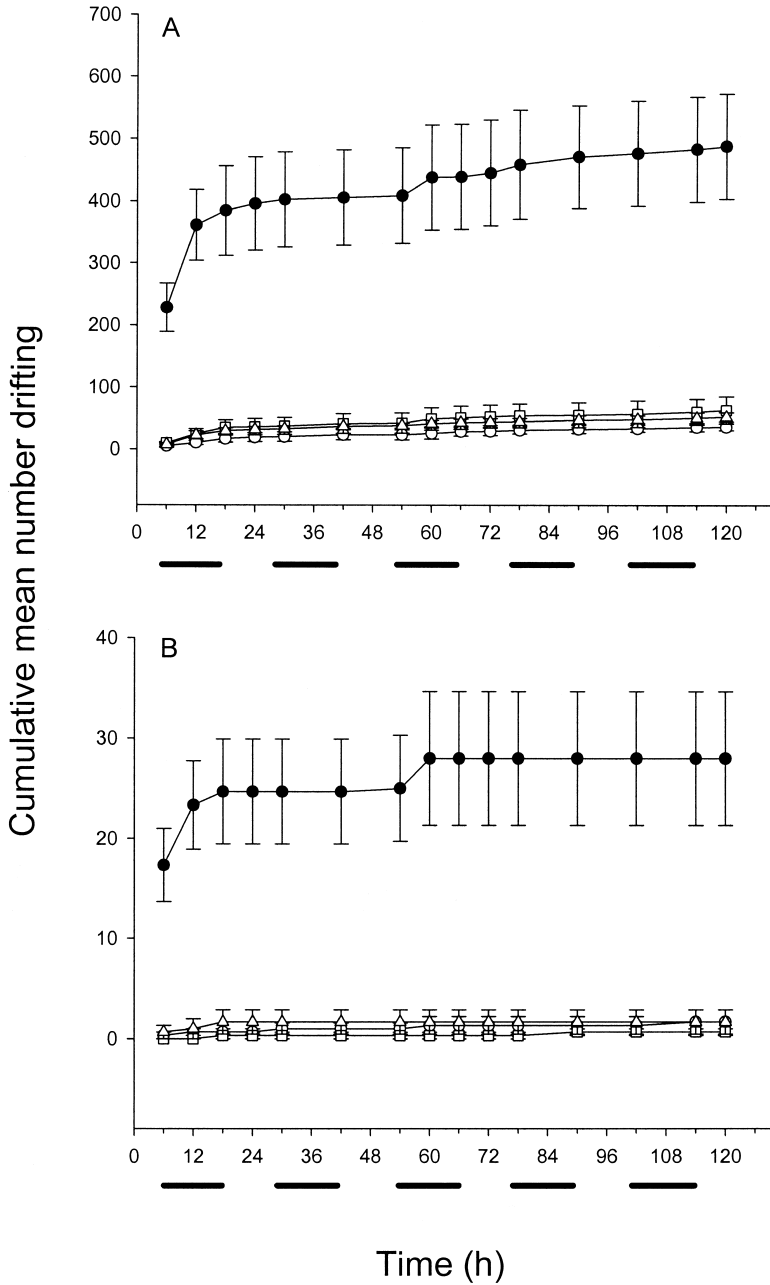


FIG. 6. Cumulative mean (\pm SE) number of individuals of 4 taxa drifting in mesocosms from Experiment 4 during 5-d exposures to oxygen saturation and various degrees of hypoxia. A.—Chironomidae. B.—Leptophlebiidae. C.—Hydracarina. D.—Caenidae. 95 to 100% saturation was the control. Dark bars represent night time. 95–100%: \circ — \circ ; 50–60%: \square — \square ; 25–35%: Δ — Δ ; and \leq 10% saturation: \bullet — \bullet .

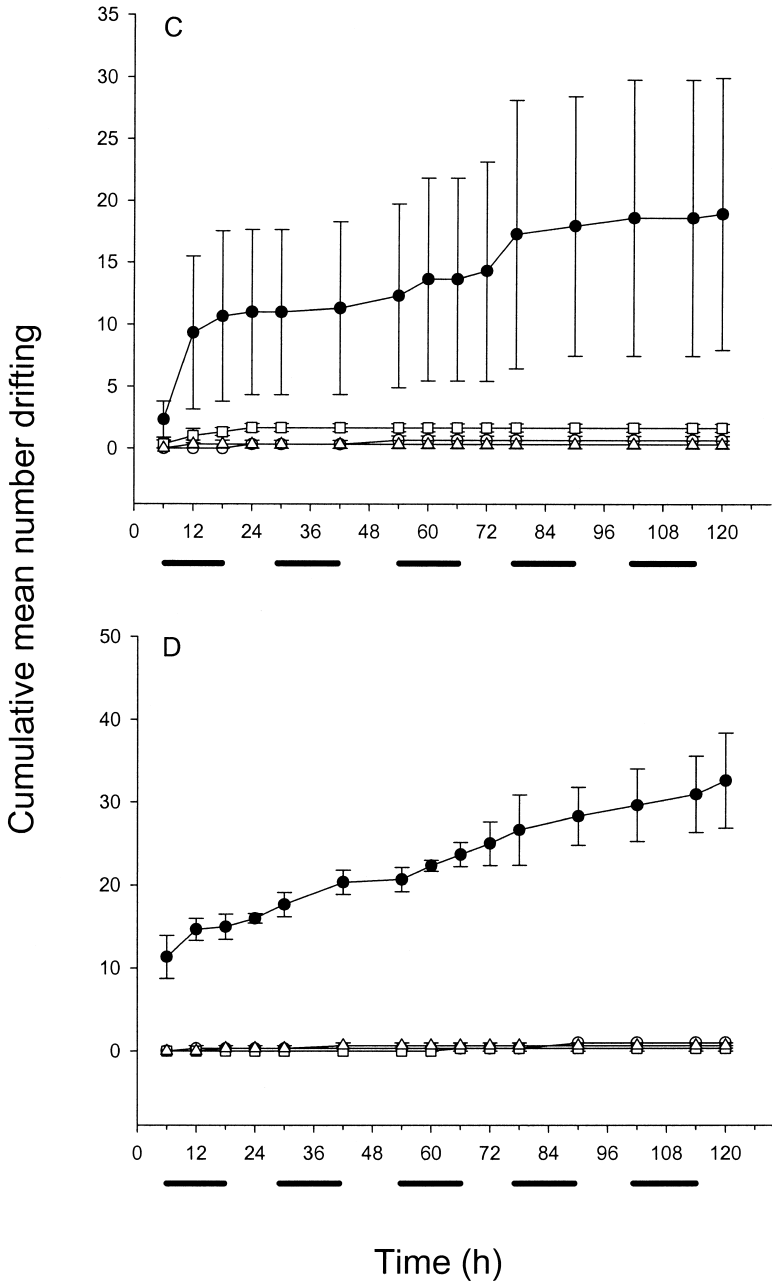


FIG. 6. Continued.

and suffering nonlethal effects if conditions do not improve. Few data are available regarding the drift response of macroinvertebrates to low levels of DO. Wiley and Kohler (1980) found that mayfly larvae exposed to 15-min episodes of

low DO showed considerable interspecific variation in response. The most sensitive species actively entered the drift at ~60% saturation, whereas the most tolerant species did not respond until ~10% saturation.

Temperate and tropical comparisons

It might be postulated that tropical stream invertebrates would be more susceptible to hypoxia than those from cooler climates because of potentially higher water temperatures and rates of metabolism. For example, Hall (1969) and Nebeker (1972) showed that a much higher DO saturation is required to maintain survival at high temperatures than would be explained by oxygen solubility alone for the ephemeropteran *Ephemerella rotunda* and the trichopteran *Hydropsyche betteni* (Table 1). However, this suggestion is not supported by our results because the tropical assemblages in our experiments were resistant to hypoxic stress. This finding was consistent from uplands to lowlands even in a single species; for example, the response of *Nousia* sp. 'NQ2' was similar in upland and lowland experiments carried out at different temperatures (14.9–18.3°C and 20.2–22.3°C in upland Experiments 1 and 2, respectively; 17.6–29.0°C in lowland Experiment 3). Acclimatization to a particular temperature before the experiment may have a strong effect on tolerance (Nagell and Fagerstrom 1978), perhaps explaining some of the response differences observed by Hall (1969) and Nebeker (1972) and the similarity in response of *Nousia* sp. 'NQ2' in upland and lowland experiments. This hypothesis may be supported by Walshe's (1948) findings that chironomid larvae become more independent of environmental oxygen after some hours of adaptation to low DO in glass tubes.

In conclusion, studies from a variety of locations and on a variety of taxa all show that severe reductions in DO saturation are required to cause mortality in the short term (Table 1). However, comparisons are hampered by the different conditions of each study (e.g., temperature, current velocity, and duration). For example, it is difficult to determine whether the amphipods tested by Sprague (1963) are more tolerant of hypoxia than the aquatic insects tested by Nebeker (1972) because Nebeker's (1972) experimental system provided some flow in test chambers, whereas Sprague's (1963) did not. Only Phillipson (1954) repeated tests with and without current, finding several trichopterans able to tolerate much lower DO saturation when water current was provided.

If we compare our results to experiments listed in Table 1 that provided flow (Phillipson

1954, Hall 1969, Nebeker 1972, Winter et al. 1996, Dean and Richardson 1999, and Lowell and Culp 1999), the response of the assemblages in our experiments are consistent. For example, the levels observed by Nebeker (1972) to induce mortality in several mayflies species (15–48% saturation) and the chironomid *Tanytarsus dissimilis*, (<6.43% saturation) are consistent with our results for both the upland and lowland stream assemblages. The hypothesis that the macroinvertebrates from the lowland stream would be more tolerant of hypoxia was not supported by our results because both assemblages showed a similar response. We detected sublethal effects for mayflies in the 25 to 35% saturation treatments. Mortality occurred in the 10 to 20% saturation treatments for the mayflies but mortality did not occur in the chironomids until the 2 to 8% saturation treatment. The suppression of emergence by insect taxa suggested that development was impeded at reduced DO concentrations well before lethal concentrations were reached. Further, the lack of drift response at DO concentrations of 25 to 35% and 10 to 20% saturation indicates that in moderately poor oxygen conditions these animals will probably remain at a location and hence experience sublethal effects that are likely to be detrimental over the longer term. Therefore, although it is clear that these animals can persist in hypoxic conditions in the short term, to understand the effects of low DO concentrations on natural assemblages of aquatic macroinvertebrates may require studies of populations over several generations.

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