Respiration rate of stream insects measured *in situ* along a large altitude range

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Abstract

Field studies of respiration in stream insects are few in comparison with laboratory studies. To evaluate the influence of temperature and oxygen along altitudinal gradients we measured the respiration rate of fully acclimatized larval Trichoptera, Plecoptera and Ephemeroptera under similar field conditions in streams from 400 to 3800 m above sea level in tropical Ecuador. Mean active respiration rates of the animals at 3800 m were approximately half of those at 400 m. Trichoptera showed a slightly larger difference in respiration with altitude than Ephemeroptera. Comparative respiration measurements at 100 and 50% oxygen saturation indicated that highland animals reduced their oxygen uptake more than their counterparts in the lowland when oxygen availability decreased. The temperature response of respiration calculated between the insect assemblages at different altitudes showed a mean assemblage Q_{10}−value of 1.50. Trichopteran larvae had a slightly stronger temperature response (Q_{10} of 1.68) than ephemeropterans (Q_{10} of 1.30). These community Q_{10}-values are considerably lower than the mean value of 2.36 found in single species in the laboratory. The weak community-wide response of respiration to temperature in tropical streams is probably due to full acclimatization of the component species to stable and narrow temperature ranges. Adaptations to the low oxygen availability at high altitude probably consist of a suite of genetic physiological and behavioural features.

Introduction

Cold and turbulent mountain streams are usually considered to be an oxygen-rich habitat for the unrestricted respiratory metabolism of the macroinvertebrates inhabiting them. This notion is mainly based on the high solubility of oxygen in cold water, the low oxygen demand from microbial respiration at low temperature and the highly turbulent flow providing good aeration and oxygen concentrations close to saturation. However, measurements in fast flowing streams from sea level to 4000 m a.s.l. in the Ecuadorian Andes showed that oxygen concentration was independent of altitude (Jacobsen, 2000). This constant oxygen concentration is attributable by the fact

that the enhanced oxygen solubility in cold water is counteracted by a reduction in oxygen partial pressure with altitude.

Uptake of oxygen in aquatic invertebrates takes place as passive diffusion driven by a difference between external (water) and internal (animal) oxygen partial pressure, and not by concentration difference *per se* (Spicer & Gaston, 1999; Jacobsen, 2000). The supply of oxygen to stream macroinvertebrates is primarily restricted by two temperature-dependent physical factors, namely the diffusion coefficient of oxygen and the kinematic viscosity of water. The latter has a strong influence on the thickness of the viscous sublayer surrounding solid surfaces, through which diffusion occurs. From these factors an oxygen supply index in relation to

temperature has been calculated, suggesting that only one-fifth of the oxygen that is available at sea level will be available at 4000 m (recalculated from Jacobsen, 2000).

As a consequence, macroinvertebrates that lack blood pigments and live in streams at high altitudes may experience a greater oxygen deficiency than their counterparts at sea level. However, potential oxygen stress should be determined by the difference between oxygen availability and oxygen demand. In poikilothermic animals the oxygen demand from respiration declines with decreasing temperature. Hence, to determine whether invertebrates in highland streams are closer to oxygen limitation than those in the lowlands, it is necessary to know how respiration rate changes along the altitudinal temperature gradient. This pattern can then be compared to the theoretical availability of oxygen in relation to altitude.

Metabolic rates of benthic macroinvertebrates are considered to be important for their occurrence and distribution in streams (Hynes, 1970; Hildrew & Edington, 1979; Bales & Badcock, 1986; Roux et al., 1992). Several factors, including temperature and external oxygen supply, but also level of activity, supply and quality of food, and physical and chemical stress, may influence the metabolism and thus the oxygen uptake. Many laboratory studies on the oxygen uptake of stream macroinvertebrates from the northern temperate region suggest they are adapted to a broad seasonal range of temperatures in their natural habitat (Collardeau, 1961; Feldmeth, 1970; Philipson & Moorhouse, 1976; Hildrew & Edington, 1979; Roux, 1979; Howell & Voshell, 1982; Bales & Badcock, 1986). Prior to respiration measurements the invertebrates were often acclimatized for some days or weeks to the experimental temperatures. The range in acclimatization temperatures often exceeded the normal temperature range met in the animal's natural habitat during the season. Thus, the temperature effect on metabolism may have been overestimated.

Studying the temperature dependence of respiration by exposing single species to different temperatures can be referred to as an 'intraspecific' approach. However, results from studies on 'intraspecific' temperature responses may not necessarily reflect patterns in respiration of whole assemblages living at different temperatures in nature (Hynes, 1970). The purpose of this study, therefore, was to obtain data on respiration rates of common stream macroinvertebrates living along a large altitudinal gradient. In other words, does the respiration rate of animals living in highland streams differ from those living in lowland streams, and how much? This study thus represents an 'interspecific' approach to the problem, and the measured response to temperature of insect larvae from different altitudes does not represent the response of single species.

The study was conducted by *in situ* measurements of the active respiration rate of Ephemeroptera and Plecoptera nymphs and caseless Trichoptera larvae in physically comparable stream reaches along a 3400 m range of altitude (400–3800 m) on the eastern slopes in the Ecuadorian Andes. These streams had a variation in monthly mean temperature of 1 °C (D. Jacobsen, unpub.), and also small daily temperature variations, and were therefore ideal for the study. Since only minor differences in mean flow velocity were measured in the studied streams, the thickness of the viscous sublayer was primarily affected by the kinematic viscosity of the water, which was controlled by temperature (Vogel, 1994; Jacobsen, 2000). Specific invertebrates inhabiting these streams are presumably metabolically adapted to narrow local temperature regimes differing along the altitudinal range.

Three main questions were addressed: (1) Does the active respiration rate of stream macroinvertebrates change similar to the change in available oxygen along a large altitudinal gradient? (2) Is the respiration response to reduced oxygen availability different in lowland and highland regions? (3) Does the 'interspecific' approach, with *in situ* measurements of the temperature response of respiration in assemblages of Ephemeroptera, Plecoptera and Trichoptera taxa, yield results similar to the common single species 'intraspecific' laboratory approach?

Methods

Study area and design

The streams used for the study were of first or second order and situated in the Cordillera Real,

in the Cordillera de Guacamayos, and on the south side of Rio Napo on the eastern side of the Andes Mountains in northern Ecuador. Many streams in this area are permanent, unaffected by humans and have no major primary production (Jacobsen, 2003). Since the aim was to perform measurements in streams with as small differences in physicochemical properties along the altitudinal gradient as possible, these streams were ideal for studying the effects of temperature and oxygen in relation to altitude. The 20 streams formed five groups according to mean height above sea level: group 1 (n = 5), 400 m (390–410 m): group 2 (n = 2), 1200 m (1135–1260 m): group 3 (n = 4), 2100 m (2000–2210 m): group 4 (n = 4), 3000 m (2900–3100 m): group 5 (n = 5), 3800 m (3770–3820 m). The streams in groups 1–3 were mainly surrounded by original, undisturbed, primary forest, with dense canopy cover or disturbed, secondary forest with less canopy cover but more dense scrub vegetation at the forest floor. Stream groups 4–5 were mainly surrounded by lightly cultivated grassland and high altitude grassland vegetation (páramo vegetation). None of the streams had major signs of erosion.

Physicochemical measurements

Physicochemical measurements were made under conditions close to base flow in the 15 streams in which most respiration measurements took place. In the five streams where no physicochemical measurements were made, only six series of a total of 74 series of respiration measurements were performed. Depth, substratum composition and current velocity were recorded at 10–20 cm intervals along five to seven transects in 8–30 m stream reaches, in order to gain a total of 50–100 measurements per stream. Current velocity was measured 1 cm above the substratum with a Höntzsch HFA flowmeter. The type of substratum was classified according to the Wentworth Scale (Allan, 1995). Measurements of the oxygen concentration and temperature of the stream water were made at 2–3 h intervals from 0630 to 1730 using an YSI 58 oxygen meter equipped with an YSI 5730 BOD probe. The oxygen meter was calibrated to the actual atmospheric oxygen level and stream temperature several times a day in oxygen and water vapour saturated atmospheric air.

Faunal sampling

Macroinvertebrates were sampled semi-quantitatively with the purpose of attaining a general overview of the faunal composition along the 3400 m gradient of altitude. All sampling was done from mid-June to mid-August 1999 in 14 of the 20 streams in which macroinvertebrate respiration was measured. The six streams where no fauna was sampled included the five streams where no physicochemical measurements were made and one stream where only one respiration measurement was performed. The six excluded streams were situated in different stream groups but close to the included streams, they were parts of the same water systems and comparable in concern of the surrounding landscape, as well as the physical properties of the streambed. The excluded streams were probably similar to the included streams concerning physicochemical factors and species diversity, but were in general low in macroinvertebrate abundance and thus less suitable for the respiration measurements.

The fauna was sampled using a hand net (mesh size 0.2 mm) at five randomly chosen sites with fine substratum (silt–pebble) and at five sites with coarser substratum (cobble–boulder) along the studied stream reaches. Fine substratum was sampled by kicking the streambed twice while holding the net in a vertical position in contact with the streambed in the flow direction. Coarse substratum was sampled by placing the hand net in the flowdirection from the site and then rolling one stone over. Attached invertebrates were brushed off and added to the suspended material caught by the net. A complete sampling in one stream reach took approximately 15 min. The material was sorted in the field and preserved in 70% ethanol. In the laboratory the invertebrates were identified to order, family or genus according to Flint (1963, 1982), Wiggins (1976), Dominguez et al. (1992), Roldán (1992), and Merrit & Cummins (1996).

Respiration measurements

Respiration measurements were performed from mid-April to late-August 1999 in 20 streams using

a closed chamber respiration method. Measuring the respiration rate under 'semi-natural' conditions at the actual site, and as close to *in situ* conditions as possible, presumably reduces some of the problems normally affecting laboratory studies such as transporting, keeping, acclimatizing and eventually starving the animals.

The respiration measurements were carried out in six identical 35 ml acrylic respiration chambers placed in a common rack (Fig. 1). A netscreened propeller inside every chamber created unidirectional water velocities ranging from 0.005 to 0.4 cm s^{-1} (measured with a micro-flow sensor: Unisense FS-20) depending on the location in the chambers. This velocity was strong enough to ensure full mixing of the water, but much less than the velocities measured in the free flowing parts of the streams. The chambers were tested for oxygen impermeability by adding anoxic tap water. After 24 h oxygen was still undetectable in the water. Before every measurement of initial oxygen concentration the oxygen meter was calibrated to the atmospheric air pressure according to the altitude. The calibration was not corrected for differences in atmospheric pressure caused by weather, since such variations can be neglected at the equatorial region of Ecuador (maximum difference in weather caused atmospheric pressure equals a change in altitude of less than 100 m. Data from a meteorological station in Guayaquil; Pers. Comm.). The chambers were sterilized with ethanol every day, and before every measurement equilibrated with the actual stream temperature.

At each altitude the most abundant invertebrate genera and primarily those belonging to families also found at other altitudes were chosen for respiration measurements. Larvae and nymphs of the taxa investigated were collected by kick-sampling or directly picked from stones and debris and placed in small cups with stream water. The chambers were filled with stream water, and 1–10 individuals were gently placed on the net inside. Total respiring biomass per chamber was thus not less than 0.1 mg dw. Individuals placed in the same chamber were of the same genus, and only in very few cases of different genera but then of the same family. The chambers were sealed with silicone stoppers perforated with a fine injection needle to release overpressure. The amount of oxygen that diffuses through the needle was insignificant. One of the six respiration chambers was always left without invertebrates and thus served as a control during the test. To keep temperature inside the chambers equal to stream water temperature, the rack with the chambers was submerged in the stream. After a period of 1–3 h the stoppers were quickly removed and the oxygen concentrations inside the chambers were measured with the YSI BOD probe. The final relative oxygen saturation was between 70 and 85%. After each experiment the invertebrates were preserved in 70% ethanol, identified to genus, dried at 80 °C for 18–24 h and weighed on a Sartorius electronic balance (precision 0.1 mg).

Additional measurements at reduced oxygen concentrations were performed in four streams from group 1 and in three streams from group 5. The aim was to compare the effect of moderate
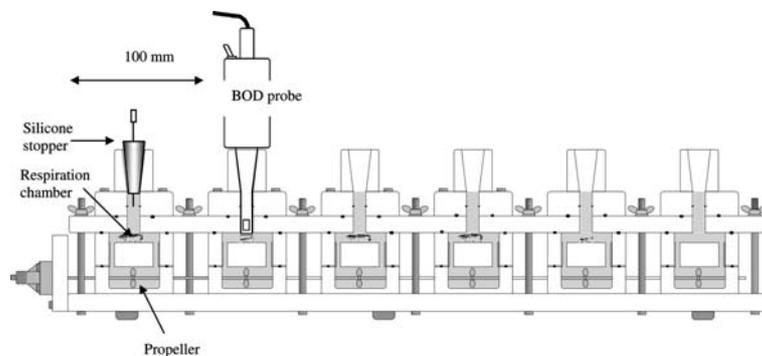

Figure 1. Sectional view of respiration chambers with invertebrates in place for measurement. Upper conical parts of chambers were sealed with silicone stoppers during the respiration period. BOD probe inserted in one chamber.

hypoxia in lowland and highland streams. The measurements were carried out in the same way as those at ambient oxygen concentration, with the exception that the initial oxygen concentration was reduced by approximately 50%, by adding Na_2SO_3. When Na_2SO_3 was dissolved in water the SO_3 ions were able to bind dissolved oxygen (DO) by forming SO_4 ions (P. Dall, pers. comm.). The reagent was mixed with stream water in a tub, and the reaction was allowed to finish (duration approximately 10 min). The desired DO concentration was gained by mixing fresh stream water in the tub, thereafter the respiration chambers were filled. We have found no evidence in the literature that indicate an effect on the oxygen uptake in macroinvertebrates caused by Na_2SO_3, but observed slightly higher pH of the treated water.

Treatment of respiration measurements

The weight specific respiration rate (WSRR, mg O_2 g^{-1} dw h^{-1}) was calculated as

$$WSRR = \frac{V(O_c - O_e)}{dw_{ind} * n * t}$$

where V is the chamber volume (ml), O_c and O_e are the control and experimental chamber oxygen concentrations (mg ml^{-1}) after time t (h), dw is the mean individual dry weight (mg) and n is number of individual per chamber.

Measurements were analysed in the nine following taxonomic groups: (1) all taxonomic groups combined, (2) Trichoptera including the gill-bearing family, (3) Hydropsychidae, represented mainly by the genera, (4) *Leptonema* and (5) *Smicridea*. (6) Ephemeroptera including the two families (7) Baetidae and (8) Leptophlebiidae. Additionally, results from measurements of the gill-bearing plecopteran family (9) Perlidae (genus *Anacroneuria*) were analysed.

Slopes between $ln(dw_{(ind)})$ and $ln(WSRR)$ for each taxonomic group in each stream group (single stream group plot), were obtained by performing a reduced major axis regression analysis (RMA). Hereafter, a common mean slope between $ln(dw_{(ind)})$ and $ln(WSRR)$ for each taxonomic group (common plot) was obtained by pooling data from all stream groups, thereafter another

RMA regression analysis was performed. If regression plots for single stream groups showed no significant negative correlation ($p > 0.05$; F-test, ANOVA) data were only included in the common plot if they did not change the slope significantly [$p > 0.05$; test for difference between slopes of two RMA regression lines (Clarke, 1980)]. Only common plots with a significant negative slope ($p < 0.05$; F-test, ANOVA), and coefficients of determination higher than 0.1 were regarded as reliable and only those were used for further analysis. The common RMA regression slope was then fitted to each stream group dataset (only datasets with $n \geq 4$) and the back-transformed (e^x) intercepts with the y-axis were used as an easily comparable standard weight specific respiration rate, denominated (*SWSRR*). The *SWSRR* corresponds to the respiration rate for an animal of 1 mg dry weight. An example of a plot is given in Figure 2.

Since the premises for using model I linear regression (simple linear regression) were not met by the sampling technique it was necessary to use model II regression. Reduced major axis regression (RMA), also called geometric mean regression (Sokal & Rohlf, 1995), was suitable for the comparison. The choice of a model II regression complicates the statistical analysis, since there are no suitable methods for testing differences between y-axis intercepts in model II regressions. Analysis of co-variance (ANCOVA) can be used for testing differences between intercepts in model I regressions and was also used in this study, as no clear recommendation was given by Sokal & Rohlf (1995).

The calculation of ratios between respiration rates under hypoxia and normoxia (Table 3) was not based on a simple ratio between the rates in the normoxia table (Table 1) and the hypoxia table (Table 2), because the *SWSRR*s of the two treatments were not based on equal slopes between respiration rate and animal dry weight. Rather the calculations were standardized in the same way as respiration rates. Measurements from high and low altitude and from both treatments were pooled, and a common slope between respiration rate and animal dry weight was calculated. This common slope was then fitted to each of the four datasets representing all combined taxa, Trichoptera, Hydropsychidae and
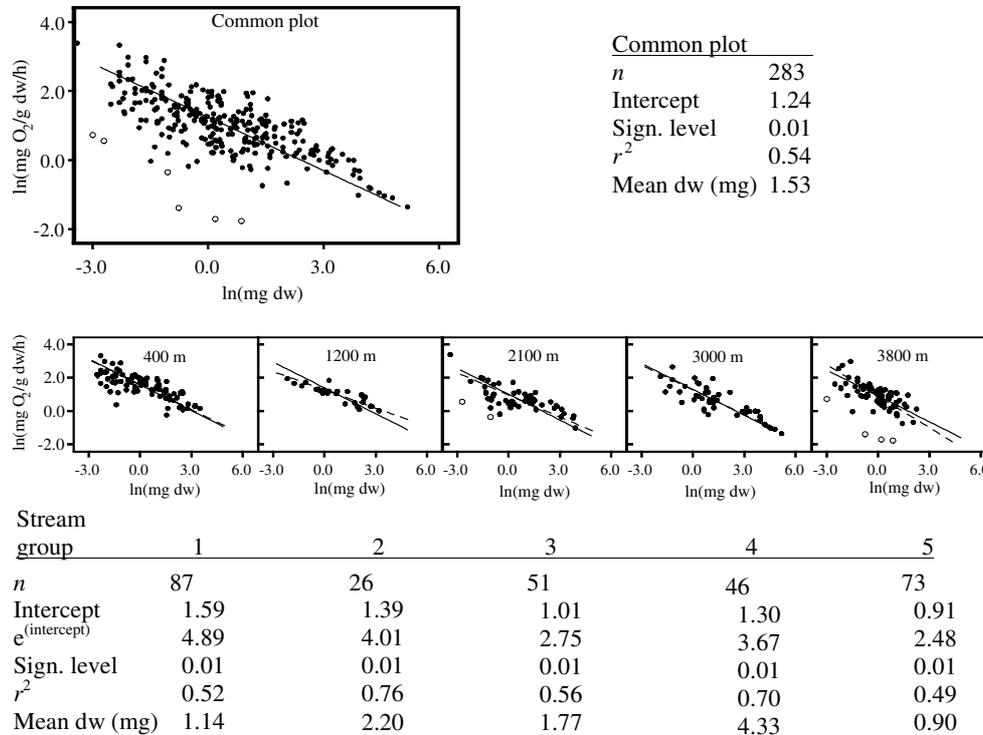
Figure 2. Weight-specific respiration rates (WSRR) vs. animal dry weight for all taxonomic groups. Common plot shows the pooled data from the five altitude datasets (400 m to 3800 m). Significant measurements shown as solid data points, excluded values (outliers) shown as open data points. The solid line in the common plot represents the common reduced major axis (RMA) regression line, i.e. the mean regression line from the five stream group (altitude) datasets. The solid lines in single stream group (altitude) plots are the slope from the common plot fitted to each stream group dataset. The y-axis intercept was subsequently backtransformed ($e^{intercept}$), and the value denominated *SWSRR*. Broken lines (only visible in some plots) are RMA regression lines based solely upon the dataset from the concerned altitude.

Ephemeroptera, and a ratio between the resulting respiration rates was calculated.

A natural metabolic temperature response Q_{10}, i.e., the proportional increase in metabolic activity when temperature is elevated by 10 °C, can be calculated by comparing *SWSRR* values of the same taxonomic group at different altitudes. This 'assemblage' Q_{10}-value was calculated between stream groups with significantly different *SWSRR* values ($p < 0.05$ ANCOVA). The Q_{10}-value was calculated as

$$Q_{10} = (SWSRR\, T_1 / SWSRR\, T_2)^{10/(T_1 - T_2)}$$

where *SWSRR* T_1 is the standardized weight specific respiration rate at temperature T_1 (mean stream temperature at the low altitude in consideration) and *SWSRR* T_2 is the same at temperature

T_2 (mean stream temperature at the high altitude in consideration).

Results

Physicochemical site characteristics

Apart from water temperature physical properties varied only slightly among the five stream groups (Fig. 3). All streams had oxygen concentrations close to atmospheric equilibrium, between 80 and 97% of saturation in stream group 1 and between 91 and 103% in stream groups 2–5. Oxygen concentration did not vary with altitude ($p > 0.05$, *t*-test) and mean oxygen concentration in the groups ranged from 7.39 to 7.92 mg l^{-1} (Fig. 3a).

Table 1. Respiration rates in measurements of normoxia

Taxon	Common group plot			Stream group plots (n, SWSRR)					ANCOVA
	Slope	*n*	SWSRR	1 (23.5 °C)	2 (18.1 °C)	3 (15.0 °C)	4 (11.4 °C)	5 (9.6 °C)	*p*<
All taxa	−0.52	283	3.46	(87, 4.89)	(26, 4.01)	(51, 2.75)	(46, 3.67)	(73, 2.48)	0.001
Trichoptera	−0.51	166	3.82	(45, 5.88)	(18, 4.53)	(28, 2.86)	(41, 3.86)	(34, 2.53)	0.001
Hydropsychidae	−0.50	131	3.71	(45, 5.88)	(18, 4.44)	(26, 2.77)	(29, 3.35)	(13, 1.40)	0.001
Leptonema	−0.55	96	5.26	(45, 6.16)	(17, 4.90)	(19, 4.00)	(15, 5.22)		0.001
Smicridea	−0.59	35	1.86		(0, –)	(7, 1.27)	(14, 2.80)	(13, 1.42)	0.001
Hydrobiosidae	−0.53	35	4.06			(0, −)	(12, 4.90)	(21, 3.63)	0.001
Atopsyche	−0.60	19	4.62			(0, −)	(6, 8.40)	(12, 3.50)	0.005
Cailloma	−0.45	13	3.74			(0, −)	(4, 3.44)	(8, 3.82)	0.75
Ephemeroptera	−0.63	114	2.72	(41, 3.28)	(8, 2.80)	(23, 2.53)	(5, 2.27)	(37, 2.33)	0.001
Baetidae	−0.63	54	2.46	(9, 2.56)	(0, –)	(11, 2.72)	(5, 2.27)	(27, 2.29)	0.05
Leptophlebiidae	−0.77	49	3.22	(27, 3.86)	(6, 2.32)	(6, 2.77)		(10, 2.61)	0.001

Common group plots: Slope of the RMA regression line from the common plot. *n* is the number of measurement on which the common regressions are based, but with outliers excluded. *SWSRR* (mg O_2 g^{-1} dw h^{-1}) is the back-transformed intercept ($e^{intercept}$) of the common RMA regression line and the *y*-axis. Stream group plots: average temperature in each stream group in Parenthesis. *n* is the number of observations at the specific altitude, with the exclusion of outliers; n is 0 in cases with 1–4 observations. SWSRR (mg O_2 g^{-1} dw h^{-1}) is the black-transformed intercepts ($e^{intercept}$) of the RMA regression line with the slope fitted to the data on the actual stream group and the *y*-axis. ANCOVA: levels of significance of the analysis of covariance of the stream groups.

Mean water depth was relatively constant between 12 and 17 cm, and difference in depth along the altitudinal gradient was not significant ($p > 0.05$, *t*-test)(Fig. 3b). The streams were significantly broader in the lowlands ($p < 0.05$, *t*-test), with mean width being greatest in stream group 2, and least in stream group 5 (Fig. 3c). Mean current velocity varied significantly with altitude ($p < 0.05$, *t*-test) and was highest in stream group 4 (33 cm s^{-1}) and lowest in stream group 1 (16 cm s^{-1}) (Fig. 3d).

Daytime water temperature decreased linearly with increasing altitude, from a mean of 23.5 °C in the lowland streams to 9.6 °C in the highlands (Fig. 3e). The lowest temperature measured was 6.0 °C one morning in a highland stream, and the highest was 25.8 °C measured on a sunny afternoon in an Amazon rainforest stream. Stream temperature fluctuated more at high- than at low altitude. This pattern was due to large diel variations in air temperature (as much as 20–25 °C) and a strong solar radiation around noon at high altitudes. The largest daily difference in temperature (4.3 °C) was measured in a stream in group 5.

Stream bed conditions varied little over the altitudinal gradient (Fig. 3f). The substratum consisted of 10–40% boulders, 30–45% cobble and 15–30% pebble. Gravel, sand and silt covered the remaining 10–25% of the stream bed.

Stream fauna composition

Thirty-three families in nine orders were found, and faunal composition varied along the altitudinal

Table 2. Respiration rates in measurements at hypoxia. Table text as in Table 1

Taxon	Common group plot			Stream group plots (*n*, SWSRR)		ANCOVA
	Slope	*n*	SWSRR	1 (23.6 °C)	(5, 8.7 °C)	*p*<
All taxa	−0.95	96	2.56	(47, 3.61)	(49, 1.87)	0.001
Trichoptera	−0.83	50	2.86	(24, 4.91)	(26, 1.74)	0.001
Hydropsychidae	−0.85	35	3.46	(23, 5.17)	(12, 1.60)	0.001
Ephemeroptera	−1.18	32	2.20	(9, 2.42)	(23, 2.12)	0.005
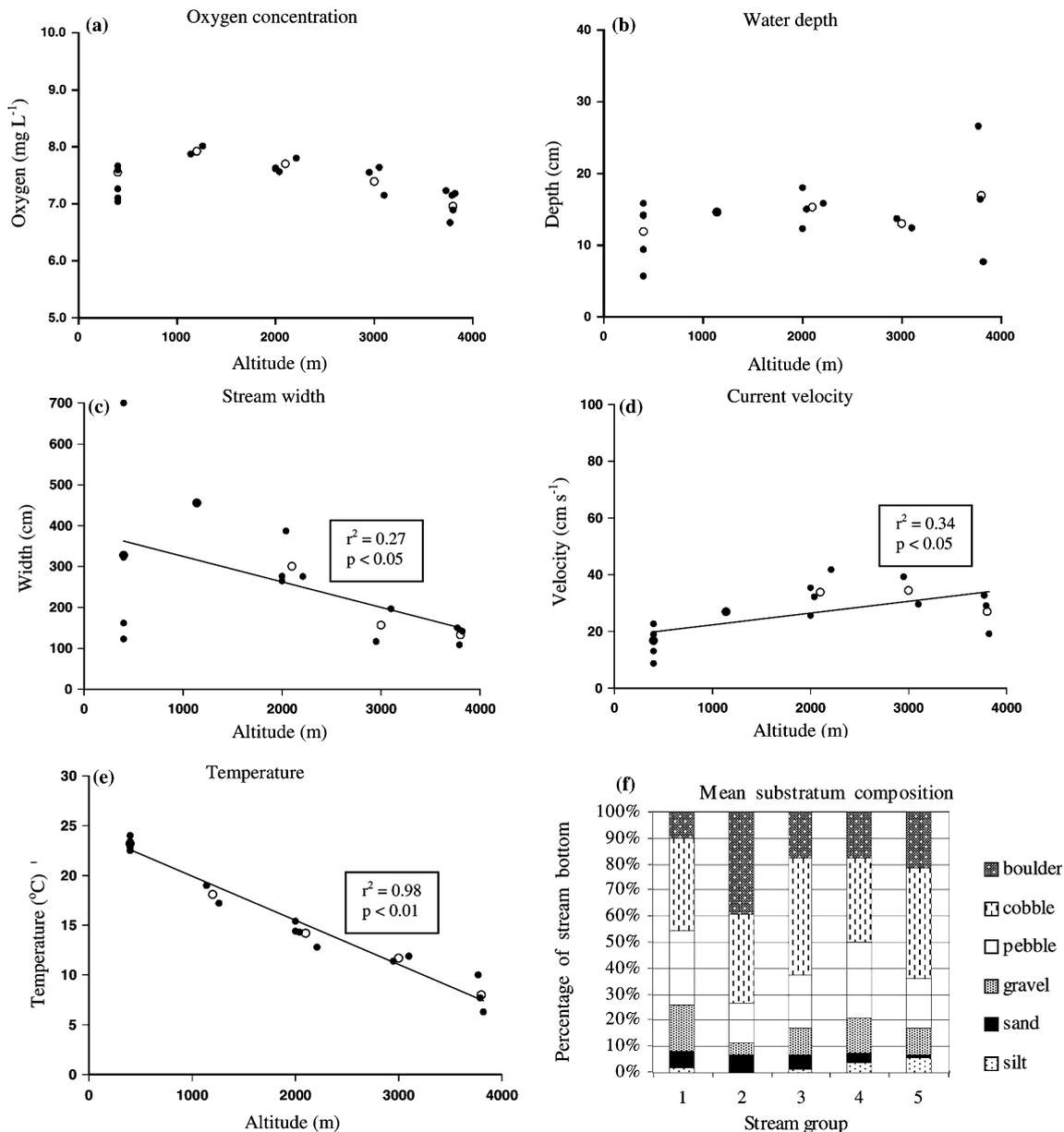
Figure 3. Physico-chemical factors in relation to altitude. Solid datapoints represent mean values from each stream, open datapoints represent mean values in each stream group. (a) Oxygen concentration, (b) water depth, (c) stream width, (d) current velocity, (e) stream temperature, (f) mean substratum composition in each stream group.

gradient (Appendix A). Three orders were found only in lowland streams: Hemiptera, Megaloptera and Lepidoptera. Odonata was most abundant in stream group 1, but was also represented in groups 2 and 3. Plecoptera was not found in group 4, whereas Ephemeroptera, Coleoptera, Trichoptera and Diptera were found at all altitudes.

Some taxa were found in all stream groups, covering a temperature range of almost 20 °C. The ephemeropteran genus *Baetis* (Baetidae) was found at all altitudes, but was most abundant in group 5 (3800 m). The trichopteran genus *Smicridea* was common at all altitudes, and the coleopteran family Elmidae and the dipteran subfamily

Orthocladiinae were found in streams along the entire range.

A large fraction of the numerically important EPT taxa was used for the respiration measurements. In stream group 2 and 3, 78 and 80% respectively of the fauna consisted of taxa belonging to the groups included in respiration measurements. Overall for the five altitudes 55% of the specimens were represented in the measurements (Appendix A). This high number indicates that the results reported should reflect the overall respirational response of the fauna to changes in altitude.

Respiration rate in relation to altitude: overall pattern

A total of 348 measurements of active respiration rates were performed under normoxia, of which 65 measurements were not included in the final analyses. Of these, 59 measurements were made on the Plecopteran genus *Anacroneuria* (Perlidae). All Perlidae measurements were excluded because none of the underlying regression analyses on stream groups datasets showed a significant relationship between respiration rate and dry weight of individuals ($p > 0.05$, F-test ANOVA). The missing relationship was probably due to large differences in activity levels during the measurements, which caused the datapoints from *Anacroneuria* scatter to much. Six measurements were excluded as outliers because they were distinctly lower than the rest, suggesting a low activity and a poor condition of the larvae.

The plot of biomass-specific respiration rate vs. animal dry weight thus included 283 measurements from about 700 individuals at five altitudes (Fig. 2 and Table 1). All regression lines were significant at the 0.01 level (F-test ANOVA) with a common slope of -0.52 and *SWSRR* (back-transformed intercepts) between 2.48 (stream group 5) and 4.90 (stream group 1). The respiration rates differed significantly among the five altitudes ($p < 0.001$ ANCOVA).

The *SWSRR* values from the plots are regarded as average biomass standardized respiration rates for the specific taxonomic group at the altitude concerned and at the mean stream temperature for the streams in the group. This data treatment implies a loss of information concerning the exact temperature at which the measurements took place. This approach was necessary to correlate and standardize respiration rates to animal dry weight. To ensure that this loss of information would not change the conclusions, some data sets were selected and the residuals of the biomass specific respiration vs. animal dry weight were plotted against the exact temperature (mean of initial and final temperature in each respiration chamber) during each measurement (data not shown). These plots showed no correlation ($p \gg 0.1$, t-test), so it was concluded that the minor variations between stream temperatures of the same stream group did not affect the respiration rates in any detectable way.

Respiration rate in relation to altitude: specific patterns

SWSRR values were highest in stream group 1 (except for Baetidae), and did in general decline with altitude, but patterns in the relationship between *SWSRR* and altitude were ambiguous since also values in stream group 4 were high compared to stream group 3 and 5. The overall (all taxa) tendency to a general decrease in *SWSRR* with increasing altitude was heavily influenced by Trichoptera, whose relationship was largely due to the contrast between lowland *Leptonema* and highland *Smicridea* (Table 1). The common slope for trichopterans was lower (-0.51) than the slope for ephemeropterans (-0.63), whereas the common *SWSRR* was higher for trichopterans (3.82) than for ephemeropterans (2.72).

The gill-bearing family Hydropsychidae constituted a major part of the trichopterans and thus the results for these groups did not differ much. The measurements included in Hydropsychidae consisted of *Leptonema* and *Smicridea*, with *Leptonema* being the single genus used for measurements at the two lowest altitudes (stream groups 1–2) and *Smicridea* being the single genus used at the highest altitude (stream group 5). The two genera had similar common slopes, but different common *SWSRR*s of 5.26 and 1.86 respectively (Table 1). Since respiration rates in *Smicridea* were very low in stream group 5 the Hydropsychidae *SWSRR* was also low. *Leptonema* larvae from stream group 4 were much larger (mean dry weight 46.9 mg) than those from the lower altitudes (mean dry weights 3.46–6.55 mg).

Among ephemeropterans it was only possible to obtain *SWSRR* values at the family level, since too few measurements were performed with single genera. The *SWSRR*s varied less than among trich- opterans, but were nevertheless significantly different ($p < 0.001$, ANCOVA) (Table 1). The family Baetidae was found in streams along the entire altitudinal gradient, but too few measurements were performed in stream group 2 to permit statistical analysis. The genus *Camelobaetis* dominated the measurements from streams in the lowland and *Baetodes* was most abundant in measurements performed in stream group 3. The genus *Baetis* was used for measurements in all stream groups and was the only Baetid genus used in stream group 5. The *SWSRR*s differed ($p < 0.05$ ANCOVA) but did not decline systematically towards higher altitudes. Measurements on the ephemeropteran family Leptophlebiidae were performed with the genus *Thraulodes* at the three lowest stream groups, and with the genus *Farrodes* at the highest stream groups. Additionally, *Haugenulopsis* and *Needhamella* were used for 5 measurements. Nymphs at the highest altitude were in general larger (mean dry weight 1.66 mg) than those in the lowland (mean dry weight 0.53 mg). The common slope was the steepest one observed, and the *SWSRR*s were scattered and did not decline systematically with altitude.

Effect of reduced oxygen concentration

Measurements at reduced oxygen concentration (hypoxia) were carried out at altitudes of 400 m (stream group 1) and 3800 m (stream group 5). The relative oxygen saturation was lowered to 26–50% (mean of 39%) in stream group 1, and to 32–58% (mean 45%) in stream group 5, corresponding to concentrations between 2.6 and 4.9 mg O_2 l^{-1} and 2.3–4.5 mg O_2 l^{-1} respectively.

Ninety-six hypoxic measurements were carried out, and there were no outliers. All groups showed significant negative correlations between respiration rates and animal dry weight, with steep slopes of the regression lines between -0.83 and -1.18 ($p < 0.01$ *F*-test ANOVA) (Table 2). The *SWSRR* for the trichopteran group in stream group 1 was approximately 3 times higher than

Table 3. Ratios of respiration rates under hypoxia relative to normoxia in lowland and highland

Taxon	Stream group	
	1	5
All taxa	0.72	0.56
Trichoptera	0.75	0.49
Hydropsychidae	0.76	0.99
Ephemeroptera	1.05	0.71

those in stream group 5, and analysis of covariance detected highly significant differences among them ($p < 0.001$ ANCOVA). The difference between *SWSRR*s at high and low altitudes was distinctly smaller for ephemeropterans.

Most of the trichopteran measurements were, as for the measurements at normal oxygen conditions, performed with Hydropsychidae larvae, mostly *Leptonema* at the low altitude and only *Smicridea* at the high altitude. The ephemeropteran group consisted mainly of *Thraulodes* (Leptophlebiidae) in stream group 1 and of approximately equal numbers of *Baetis* (Baetidae) and *Farrodes* (Leptophlebiidae) in stream group 5.

Respiration rates under normal and reduced oxygen concentrations were significantly different at both altitudes and in all four groups ($p < 0.005$, ANCOVA). Respiration rates under hypoxia relative to normoxia were 0.72 in stream group 1 and 0.56 in stream group 5 (Table 3).

The trichopterans as a whole tended to show a larger reduction in respiration rate at high altitudes, whereas the family Hydropsychidae did not reduce oxygen uptake during hypoxia in stream group 5. The ephemeropterans in stream group 1 were likewise unaffected by the hypoxic condition.

Q_{10}-values

The metabolic change to external temperature variation is often expressed as a Q_{10}-value. Based upon the *SWSRR*s and the mean water temperature in each of the five stream groups, we have calculated Q_{10}-values for the invertebrate assemblages. In Table 4 the values for the different intervals for the normoxic measurements are listed together with means of all and selected taxa. Most Q_{10}-values under normal oxygen conditions were between 1.10 and 2.00 (Table 4).

Table 4. Q_{10} values at normal oxygen conditions (normoxia) obtained from temperature intervals between mean stream temperatures in the stream groups 1–5

Taxon	Temperature interval (°C)					Q_{10}	
All taxa	9.6		15.0			1.20	
		11.4		18.1		1.14	
			15.0		23.5	1.97	
	9.6			18.1		1.76	
		11.4			23.5	1.27	
	9.6				23.5	1.63	**1.50**
Trichoptera	9.6		15.0			1.25	
		11.4		18.1		1.27	
			15.0		23.5	2.33	
	9.6			18.1		1.98	
		11.4			23.5	1.41	
	9.6				23.5	1.83	**1.68**
Hydropsychidae	9.6		15.0			3.59	
		11.4		18.1		1.52	
			15.0		23.5	2.36	
	9.6			18.1		3.91	
		11.4			23.5	1.56	
	9.6				23.5	2.78	**2.62**
Leptonema		11.4		18.1		0.91	
			15.0		23.5	1.66	
		11.4			23.5	1.15	**1.24**
Smicridea	9.6		15.0			0.82	
Ephemeroptera	9.6		15.0			1.16	
		11.4		18.1		1.37	
			15.0		23.5	1.36	
	9.6			18.1		1.24	
		11.4			23.5	1.36	
	9.6				23.5	1.28	**1.30**
Baetidae	9.6		15.0			1.37	
			15.0		23.5	0.93	
		11.4			23.5	1.10	
	9.6				23.5	1.08	**1.12**
Leptophlebiidae	9.6		15.0			1.12	
			15.0		23.5	1.47	
	9.6			18.1		0.87	
	9.6				23.5	1.32	**1.20**
Mean of groups (except: All taxa)							**1.58**
Mean of Trichoptera + Ephemeroptera							**1.49**

Mean Q_{10} values in bold. Mean of all groups, and mean of Trichoptera and Ephemeroptera. Note that only intervals which span more than 2 stream groups (altitudes) are included.

Table 5. Q_{10} values obtained from measurements under hypoxia

Taxon	Temperature interval (°C)	Q_{10}
All taxa	8.7–23.6	1.56
Trichoptera	8.7–23.6	2.01
Hydropsychidae	8.7–23.6	2.15
Ephemeroptera	8.7–23.6	1.09
Mean of Trichoptera + Ephemeroptera		1.55

The mean Q_{10}-value of all groups was 1.58, with Hydropsychidae showing the highest value (2.62) and Baetidae showing the lowest (1.12). Q_{10}-values were in general lower for ephemeropterans than for trichopterans.

The Q_{10}-values for the hypoxic conditions were in general higher than for the normoxic conditions, with a mean of 1.55 for Trichoptera and Ephemeroptera (Table 5). As was the case for the normoxic measurements, the Hydropsychidae values were high while the ephemeropteran values were low.

Discussion

Respiration rate along the altitude gradient

A theoretical index of aquatic oxygen availability in relation to altitude, proposed by Jacobsen (2000), predicted a reduction of approximately 80% from sea level to 4000 m (in Jacobsen, 2000 coefficients of diffusion were different from those used here). The *SWSRR*s obtained at high altitude in this study were approximately 50% of those in the lowland, and thus the change in respiration rate along the altitude gradient was much smaller than expected from the change in theoretical available oxygen. The small change in respiration rate indicates that the invertebrates used for the measurements at high altitudes, were able to compensate for the restrictions in oxygen availability, and thus maintain a relative higher metabolism, growth rate, etc. in comparison to their counterparts at lower altitudes. Except for temperature, none of the measured

physicochemical variables altered at such scale along the gradient, that it could cause the observed change in respiration rate. Since flow velocity of the studied streams were of comparable levels, the thickness of the viscous sublayer was primarily affected by the temperature controlled kinematic viscosity of the water (Vogel, 1994; Jacobsen, 2000).

Temperature response: Q_{10}-values

The Q_{10}-values were obtained from the *SWSRR*s, and were calculated on the basis of respiration rates for three stream groups. The all taxa Q_{10}-value of 1.50 can be considered as a mean metabolic temperature dependency for assemblages of ephemeropteran nymphs and caseless trichopteran larvae along the 3400 m gradient in altitude and the 13.9 °C gradient in temperature. Except for three values from the Hydropsychidae, all calculated Q_{10}-values are lower than those reported in the literature for single species ranging from 1.20 to 3.96 and averaging 2.36. The low Q_{10}-values are mainly caused by the relatively high respiration rates found at low temperatures at high altitudes. A ratio between the mean respiration rate observed in former laboratory studies and rates from the present study showed that a greater discrepancy was seen at low temperatures (ratio 0.41), than at high temperatures (ratio 0.63).

Similar to the previous mentioned theoretical oxygen supply index a theoretical Q_{10}-value based solely on changes in the physical conditions along the altitude gradient can be calculated. Since the average drop in temperature along 4000 m in altitude is close to 20 °C, the theoretical Q_{10}-value in this range is 2.24. This value is higher than the observed values for both the trichopterans (1.68) and the ephemeropterans (1.30). Several aspects might cause the discrepancy between the theoretically based physical predictions, the 'intraspecific' values found in experimental studies and the 'interspecific' values observed *in situ* in this study. Possible reasons for this discrepancy are discussed below.

Acclimatization to narrow temperature ranges

The first and probably the main reason for the difference between Q_{10}-values observed in this

study and values from the literature, is that the invertebrates used in this study were fully acclimatized to narrow temperature ranges. Since there is practically no seasonal variation in temperature in the Ecuadorian Andes region, the animals are able to optimize their metabolism within a narrow temperature range, where the upper limit is set by the maximum temperature during daytime and the lower limit is set by night-time temperature. These narrow temperature regimes, which are closely related to the altitude, have probably persisted since the end of the last major glaciation in the area (Seltzer, 1990; Lewis Jr. et al., 1995).

Values from the literature have typically been obtained by measurements performed on species from temperate regions, where the annual temperature range at the sampling points is much larger than in the tropics. This situation presumably leads to a broader 'normal' temperature range, but probably also to a more modest exploitation of the available oxygen, since the metabolic processes have to be optimized to a broad temperature range. Moreover, prior to measurements the studied animals were typically acclimatized to the experimental temperature for some time during which the animals were either fed with "artificial" food or starved. This acclimatization can only be accomplished by an increase in the number of active enzymes as well as a shift to other isoenzymes (Eckert et al., 1988). Such a change is metabolically expensive, and can only take place at the expense of the growth rate. If the animals have been starved during acclimatization, they are probably stressed by the lack of food (Beamish, 1964) and have no energy available to spend on changes in enzymatic systems. As a consequence the costs of increasing the metabolic ability by investing in more proteins during cold periods might not gain a proportionate benefit in terms of increased growth.

Influx of oxygen to the consuming tissues

The second possible reason for the difference between literature values and those observed in the present study concerns the amount of oxygen available to the cells. As pointed out by Herreid (1980) (see also Spicer & Gaston, 1999), the influx of oxygen from the external water to the mitochondria depends directly on the difference in partial oxygen pressure, and the influx is inversely related to the total resistance offered by the system. The oxygen flux to the consuming tissues will be directly affected by the physical resistance given by the diffusion coefficients of oxygen and the distances in the viscous sublayer, in the cuticula, in the tracheal system, in the cell membrane and in the cytoplasm. Diffusion coefficients and thicknesses of viscous sublayers clearly are temperature dependent. If special adaptations to low temperatures have developed, these adaptations are likely to reduce the resistance to transport of oxygen.

Such adaptations could involve increased respiratory movements of the animal and its gills or a change in the preferred microhabitat towards sites with higher currents (Resh & Rosenberg, 1984; Genkai-Kato et al., 2000). Both responses should reduce the thickness of the viscous sublayer. Also an increased area of respiratory surfaces, an enhanced permeability of the cuticula or enhanced transport efficiency in the trachea could counteract the presumed lower oxygen supply at high altitudes (Illies, 1964; Wigglesworth, 1965; Wichard & Komnick, 1974; Ward & Stanford, 1982; Williams & Feltmate, 1992). However, major changes in mean gill size and body volume to total surface area with altitude were not found by Jacobsen (2000) for trichopteran larvae, and no obvious differences between respiration rates in gill-bearing Hydropsychidae and gill-less Hydrobiosidae were seen in this study. Many terrestrial insects are able to create some kind of convection or circulation of gases in their trachea, instead of depending solely on slow diffusion (Sláma, 1988; Lighton, 1996), but similar kinds of adaptations in the aquatic insects have not yet been demonstrated.

Reduced oxygen availability

Respiration rates measured under hypoxia indicated that oxygen uptake was partly regulated. When oxygen saturation was lowered to about 50%, oxygen uptake ranged between 49 and 105% of the rates under normal oxygen conditions (Table 3). The largest reduction of oxygen uptake

during hypoxia was observed in animals from the high altitudes, indicating a reduced ability to compensate for low oxygen levels. This tendency is also seen in the hypoxia Q_{10}-values, where the all taxa value is 1.56 compared to 1.50 for the normoxic value, and the Trichoptera + Ephemeroptera value is 1.55 compared to 1.49 for the normoxic value (Tables 4 and 5).

Attempts to explain these findings are speculative. Basically, two mechanisms can explain the reduced ability to regulate oxygen uptake under hypoxia in invertebrates at high altitudes. Which mechanism is the most likely depends on whether the differences in oxygen partial pressure across the tissues and layers involved are constant along the entire altitudinal range, without regard to the drop in external partial pressure, or whether the internal mitochondrial oxygen partial pressure is constant. Assuming that the difference in partial pressure remains constant, the mitochondria might turn almost anaerobic in highland species, and even a slight reduction of external partial pressure could change their metabolism to anaerobic energy production. In contrast, if the internal oxygen partial pressure of the mitochondria is constant despite the drop in external partial pressure towards higher altitudes, the pressure difference that drives the oxygen influx is smaller in the highland streams, and similar reductions in oxygen saturation along the altitudinal gradient will have a proportionally greater impact on highland species.

Aquatic insect populations of high altitudes seem to use more of the available oxygen than lowland populations do, resulting in a smaller margin between the potential oxygen supply and actual oxygen use. This conclusion is supported by the ratios calculated from the respiration measurements performed at normal oxygen levels

Table 6. Respiration rates in relation to temperature

Taxon	Dry weight (mg)	Temperature interval (°C)					Q_{10}	Study
		3–7	8–12	13–17	18–22	23–27		
Plecoptera	10–40	1.0	1.6	1.5	2.4	2.5	1.65	Knight & Gaufin (1966)
–	100–200		0.7	0.7	0.8	0.9	1.20	–
–	150–250		0.4	0.6	0.7		1.79	–
–	300–400		0.3		0.7	0.8	1.85	–
–			0.9					Nagell & Larshammar (1981)
–	60–85[5]	0.3						Golubkov et al. (1992)
Ephemeroptera	0.3		3.7					Fox and Simmonds (1933) (in Fox et al. 1935)
–	1		1.4					Fox et al. (1935)
–	6.5		0.9					–
–	8–42[5]		0.4–0.7					Golubkov & Tiunova 1989)
–	83–136[5]	0.3–0.6						–
–[1]	0.1–1.0[6]	0.4[7]	1.2	1.9	2.9		2.78	Hamburger & Dall (1990)
–	12[5]	0.3						Golubkov et al. (1992)
Trichoptera	2	0.5	0.7	1.1	1.3	2.4	2.10	Collardeau (1961)
–	9	0.4	0.7	0.9	1.5	2.2	2.50	–
–	150	0.4	0.6	0.9	1.1	1.5	1.92	–
–		0.5	0.8	1.0	2.1	2.7	2.40	Roux (1969) (in Roux, 1979)
–[2]			0.2–0.5					Feldmeth (1970)
–			0.9–1.7					–

Table 6. (Continued)

Taxon	Dry weight (mg)	Temperature interval (°C)					Q_{10}	Study
		3–7	8–12	13–17	18–22	23–27		
_[2]	3–8	0.2	0.2	0.4	0.5	0.6	1.91	Philipson & Moorhouse (1976)
–		0.4	0.5	1.1	1.6	2.4	2.75	Hildrew & Edington (1979)
–		0.3	0.7	0.8	1.6	2.0	2.54	–
–		0.3	0.4	0.5	0.9	1.5	2.30	–
_[1]	35	0.6	0.5	1.1	1.2	1.2	1.64	Roux (1979)
–	3–12	0.4	0.9	1.0	3.6	4.7	3.96	Howell & Voshell (1982)
_[3]	2		1.6	3.6	5.0		3.09	Bales & Badcock (1986)
_[3]	10		0.4	0.8	1.3		3.26	–
_[4]	2	0.6	1.3	1.6	2.7		2.75	–
_[4]	10	0.2	0.4	0.5	0.6		2.18	–
_[1]	0.1–4.9[6]	0.9	1.4	2.1	4.5		3.06	Hamburger & Dall (1990)
–	66[5]	0.3						Golubkov et al. (1992)
–	6–13	0.5	0.5–0.9	0.6–1.3	1.1–1.7	1.4–2.6	2.00	Roux et al. (1992)
–	10			1.8–2.7				Jacobsen & Sand-Jensen (1994)
–	40			1.0–1.6				–
Mean							2.36	
All taxa	1	2.48[8]	3.67	2.75	4.01	4.90	1.50	This study (normoxia)
–	2	1.74[8]	2.56	1.92	2.80	3.43	–	–
–	10	0.75[8]	1.11	0.83	1.22	1.49	–	–
Ephemeroptera	1	2.34[8]	2.27	2.53	2.80	3.29	1.30	–
–	2	1.51[8]	1.47	1.64	1.81	2.12	–	–
–	10	0.55[8]	0.53	0.59	0.65	0.77	–	–
Trichoptera	1	2.53[8]	3.86	2.86	4.53	5.87	1.68	–
–	2	1.78[8]	2.70	2.00	3.17	4.11	–	–
–	10	0.78[8]	1.18	0.88	1.39	1.80	–	–
Mean (normoxia)							1.50	
All taxa	2		0.96		1.86		1.56	This study (hypoxia)
Ephemeroptera	2		0.93		1.07		1.09	–
Trichoptera	2		0.98		2.77		2.01	–
Hydropsychidae	2		0.91		2.88		2.15	–
Mean (hypoxia)							1.70	

Date obtained from previous studies. Rates in mg O_2 g^{-1} dw h^{-1} except where noted.

Notes: 1. Lentic species, 2. Anaesthetized larvae, 3. *Sericostoma personatum*, mean of 6 °C and 18 °C acclimatized larvae, 4. *Hydropsyche angustipenni*, mean of 6 °C acclimatized larvae, 5. wet weight, 6. ash free dry weight, 7. temperature 2 °C, 8. mean temperature 9.6 °C (stream group 5).

and the measurements at reduced oxygen levels. The findings indicate that even a minor oxygen deficiency caused by natural or human disturbances of the high altitude streams, may alter the faunal composition towards less sensitive groups.

Oxygen consumption under natural conditions

The respiration rates found in this study were higher than some of those observed in previous studies of stream insects, especially at low temperature. For example, Collardeau (1961) found

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rates of 0.7–2.4 mg O_2 g^{-1} dw h^{-1} at temperatures between 10 and 25 °C for trichopterans with mean dry weights of 2 mg (Table 6), whereas the present study obtained rates of 2.0–4.1 mg O_2 g^{-1} dw h^{-1} for trichopterans at standardized weights of 2 mg at temperatures between 10 and 24 °C. Kamler (1969) concluded that the closed bottle measurement technique tends to give higher rates and more scattered values than flow respirometric methods, especially when the experiments have a short duration. In addition, stirred water (Feldmeth, 1970; Roux, 1979; Golubkov et al., 1992) and the presence of an artificial substratum (Roux, 1979) tend to increase oxygen consumption, whereas the presence of a natural substratum tends to decrease consumption remarkably (Wilhelm et al., 1997).

The technique used in the present study may, in part, explain the relatively high respiration rates reported here. On the other hand, respiration rates found in many laboratory studies might be erroneously low due to the effect on natural behaviour of handling, transporting and holding under artificial conditions (Beamish, 1964). The present study should therefore more closely represent oxygen consumption during activity under natural conditions, since handling was minimal and time from collection to start of measurements was short. However, the main objective of this study was not to determine the exact levels of oxygen consumption, but to compare respiration rates in relation to altitude and temperature. Since measurements were carried out in exactly the same way at all altitudes, the differences in respiration rates along the altitudinal gradient are most likely reliable. The effect of body mass on metabolic rate has been standardized in numerous studies. Hemmingsen (1960) found a mean slope of 0.75 for metabolic rates vs. body mass in animals ranging in size from protozoans to mammals. When data from the present study are rearranged to yield absolute oxygen consumption rates (mg O_2 ind^{-1} h^{-1}) vs. animal weight (mg dw ind^{-1}), slopes were from 0.58 (Ephemeroptera) to 0.63 (Trichoptera). These values are in the lower range of the values found in the majority of earlier studies, in which slopes from 0.67 to 1.00 are common (Hemmingsen, 1960; Hamburger & Dall, 1990), though slopes as low as 0.55

have been found for larvae of *Sericostoma personatum* (Trichoptera) (Bales & Badcock, 1986). One possible explanation for the relatively lower respiration rate in relatively large animals in the present study could be that they were more restricted in their ability to move around in the respiration chamber, and therefore had a lower level of activity than the smaller animals. The high respiration rates in small animals may conversely be overestimated because of behavioural interactions between individuals in the same respiration chamber.

Fully acclimatized insect larvae inhabiting stable temperature regimes probably exploit a larger fraction of the available oxygen than is the case for their counterparts living under less stable temperature conditions. The '*in situ*' data obtained in this study imply that the results drawn from numerous laboratory studies of macroinvertebrate respiration rates can not be applied directly to evaluate respiration rates under natural conditions, and cannot explain the spatial distribution of insect taxa along temperature and partial pressure gradients.

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Appendix A. Observed orders, families and genera from the study streams

Taxon	Genus	Stream group 1 (4 streams) Aver.	Range	nr.	2 (1 streams) Aver.	Range	nr.	3 (4 streams) Aver.	Range	nr.	4 (2 streams) Aver.	Range	nr.	5 (3 streams) Aver.	Range	nr.	Total (14 streams) % of fauna	Nr.
Ephemeroptera																		
Baetidae	*Baetis*	4.25	0–7	3	6	–	1	1.75	0–6	2+	10.50	3–18	2	42.33	+82	2+	10.4	10
	Baetode				12	–	1	18.75	0–50	3	28.50	3–54	2				8.5	6
	Camelobaetis	1.50	0–6	1+				0.50	0–2	1							0.5	2
Oligoneuriidae	*Lachlania*				1	–	1	2	0–5	2							0.5	3
Leptophlebiidae	*Farrodes*							0.75	0–3	1				5.33	2–9	3	1.1	4
	Haugenulopsis			+														
	Needhamella			+														
	Terpides	1	0–4	1													0.2	1
	Thraulodes	13	7–23	4	3	–	1	15.75	2–44	4							6.9	9
Tricorythidae	*Leptohyphes*	1.75	0–4	2	20	–	1	24.50	9–41	4	15.50	3–28	2				9.2	9
	Tricorythodes							0.75	0–2	2							0.2	2
Euthyplociidae		7	0–21	3													1.6	3
Odonata		6.50	1–18	4	1	–	1	0.50	0–2	1							1.7	6
Plecoptera																		
Gripopterygidae																+		
Perlidae	*Anacroneuria*	8	1–13	4	10	–	1	9	3–20	4			+				4.6	9
Hemiptera																		
Naucoridae		1.75	0–4	2													0.4	2
Megaloptera																		
Corydalidae				+														
Coleoptera																		
Gyrinidae								0.25	0–1	1	0.50	0–1	1				0.1	1
Elmidae		8.25	4–18	4	3	–	1	2.50	0–5	3				13.67	2–35	3	5.2	12
Psephenidae	*Psephenops*	1	0–4	1	2	–	1										0.2	1
Ptilodactylidae		5	0–12	3				0.75	0–2	2	1	0–2	1				1.6	7
Scirtidae											0.50	0–1	1	2.33	0–6	2	0.5	3
Trichoptera																		
Calamoceratidae	*Phylloicus*	0.75	0–3	1	2	–	1	0.75	0–2	2							0.5	4
Glossosomatidae								1.25	0–3	3				7	0–21	1	1.5	4

Appendix A. (Continued)

Taxon	Genus	Stream group															Total	
		1 (4 streams)			2 (1 streams)			3 (4 streams)			4 (2 streams)			5 (3 streams)			(14 streams)	
		Aver.	Range	nr.	Aver.	Range	nr.	Aver.	Range	nr.	Aver.	Range	nr.	Aver.	Range	nr.	% of fauna	Nr.
Helicopsychidae	*Helicopsyche*	0.75	0–2	2				0.25	0–1	1				0.33	0–1	1	0.3	4
Hydropsychidae	*Leptonema*	9.50	3–23	4	7	–	1	10	1–33	4	4	2–6	2				5.5	11
	Macronema	2.25	0–5	3													0.5	3
	Smicridea	3.75	0–9	3	2	–	1	11.25	2–37	4	13	1–25	2	11.67	0–34	2	7.2	12
Leptoceridae								5.50	0–17	3	2.50	0–5	1	3	1–5	3	2.1	7
Limnephilidae	*Anomalocosmoecus*													1.33	0–4	1	0.2	1
Hydrobiosidae	*Atopsyche*									+	2	1–3	2	0.67	0–1	2	0.4	4
	Cailloma									+			+			+		
Odontoceridae		2	0–7	2				0.75	0–2	2							0.6	4
Philopotamidae	*Wormaldia*	0.25	0–1	1				1.50	0–5	2							0.4	3
Anomalopsychidae	*Contulma*													0.67	0–2	1	0.1	1
Lepidoptera		0.25	0–1	1													0.1	1
Diptera																		
Tipulidae		0.25	0–1	1							0.50	0–1	1				0.1	2
Limoniidae		3	0–9	3	1	–	1	1.75	0–4	3				2.33	0–7	1	1.6	8
Blepharoceridae								0.50	0–2	1	0.50	0–1	1				0.2	2
Dixidae	*Dixella*																0.1	1
Ceratopogonidae	*Stilobezzia*	0.25	0–1	1										1.33	0–4	1	0.3	2
Chironomidae	*Chironomini*	4.75	0–18	2				1.50	0–6	1							1.5	3
	Tanypodinae	7.50	0–29	2													1.8	2
	Orthocladiinae	20.75	0–74	3	3	–	1	3.50	0–6	3	73.50	34–113	2	10	4–14	3	16.3	12
	Tanytarsini	2.25	0–9	1													0.5	1
Simuliidae	*Simulium*	5.50	0–18	3	4	–	1	2.50	0–6	2				14.33	1–36	3	4.6	9
Athericidae								0.75	0–3	1							0.2	1
Empididae											1	0–2	1	0.33	0–1	1	0.2	2
Total																		
Orders		9			6			6			4			5			9	
Families		20			13			21			12			17			32	

Taxa in bold were used in the measurements. Stream group: Aver.: average number of individuals per stream. Range: range of numbers of individuals per stream. Nr.: number of streams in which the group was observed, + indicates that the taxon was used for respiration measurements in the stream group, but was not found in the fauna samples. Total: % of fauna: percentage of the total fauna.
Nr.: total number of streams in which the group was found. The last two rows show total number of orders and families.