Ecology of two large, net-spinning caddisfly species in a mountain stream: distribution, abundance, and metabolic response to a thermal gradient

Winsor H. Lowe and F. Richard Hauer

Abstract: We quantified the distribution and abundance of larvae of two species of caddisfly, *Parapsyche elsis* and *Arctopsyche grandis* (Trichoptera: Hydropsychidae), at 8 sites along a 560-m elevational gradient and a 36-km longitudinal gradient in a pristine mountain stream. Both species are widely distributed throughout the northern Rocky Mountains and have similar 2-year life-spans, similar catch-nets, and similar microhabitat requirements. However, the reach-scale distribution patterns were distinctly dissimilar. *Parapsyche elsis* larvae were most abundant in the upper reaches of the study stream, while *A. grandis* larvae were found only in lower stream segments. We examined the correlation between the stream gradient and the environmental variables that likely influence the distributions of these insects: temperature, food quantity and quality, current velocity, and substratum cobble size. Only those variables relating to temperature (i.e., annual degree-days, summer maximum) correlated with stream elevational and longitudinal gradients. Laboratory examination revealed a relationship between zones of temperature independence in the metabolism–temperature response of both species, maximum summer temperatures in the stream, and distribution of the two species. We propose that the physiological response of these species to stream temperature, with resulting bioenergetics, is the probable mechanism structuring the stream distribution and abundance patterns of these species.

Résumé : Nous avons procédé à une étude quantitative de la répartition et de l'abondance des larves de deux espèces de trichoptères, *Parapsyche elsis* et d'*Arctopsyche grandis* (Trichoptera : Hydropsychidae), dans les eaux non polluées d'un ruisseau de montagne, à 8 sites le long d'un gradient longitudinal de 36 km et d'un gradient de 560 m en altitude. Les deux espèces sont bien répandues dans tout le nord des Rocheuses, ont un cycle semblable de 2 ans, tissent des filets semblables et ont des besoins écologiques similaires. Cependant, leurs patterns de répartition à l'échelle de la section de ruisseau sont très dissemblables. Les larves de *Parapsyche elsis* sont abondantes surtout dans les zones supérieures du ruisseau, alors que celles d'*Arctopsyche grandis* se trouvent surtout dans les parties inférieures. Nous avons examiné la corrélation entre le gradient du ruisseau et les variables environnementales qui sont susceptibles d'influencer la répartition des larves : température, quantité et qualité de la nourriture, vitesse du courant et taille des composantes du substrat. Seules les variables reliées à la température (i.e., degrés-jours annuels, maximum de l'été) sont en corrélation avec l'altitude et avec les gradients longitudinaux. L'examen en laboratoire a mis en évidence une relation entre les zones d'indépendance thermique du métabolisme–réaction thermique des deux espèces, les températures maximales de l'eau du ruisseau en été et la répartition des deux espèces. Il est probable que la réaction physiologique de ces espèces à la température du ruisseau et les processus bioénergétiques qui en découlent constituent le mécanisme de structuration spatiale de la population de larves dans le ruisseau et des patterns d'abondance de ces espèces.

[Traduit par la Rédaction]

Introduction

Growing concern over the biological effects of global climate change has led to increased research on the role of temperature in structuring species distribution and abundance (Firth and Fisher 1992; Hauer et al. 1997). Because it has long been recognized that temperature plays a significant role in the ecology of stream macroinvertebrates (Ward and Stanford 1982), lotic organisms may be particularly useful as biological indicators of modified temperature regimes or for modeling and monitoring temperature change (Sweeney et al. 1992; Hogg and Williams 1996).

Among lotic organisms that appear to be particularly responsive to instream environmental gradients, the net-spinning caddisflies (Trichoptera: Hydropsychidae) have received considerable attention. They commonly occur in replacement series along the elevational gradient of river systems (Hildrew and Edington 1979; Hauer and Stanford 1982*a*; Ross and Wallace 1982; Alstad 1986; Bales and Badcock 1987; Tachet et al. 1992; Guinand et al. 1994). Owing to the high degree of trophic and functional similarity

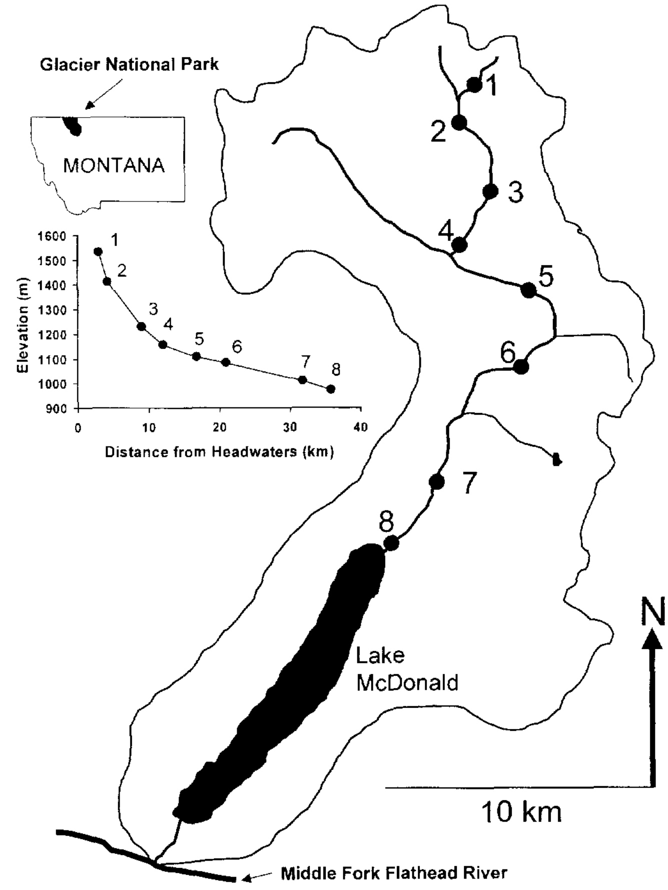
Received March 25, 1999. Accepted July 12, 1999.

W.H. Lowe[1] and F.R. Hauer.[2] Flathead Lake Biological Station, The University of Montana, 311 Bio Station Lane, Polson, MT 59860-9659, U.S.A.

[1] Present address: Department of Biology, Dartmouth College, Hanover, NH 03755, U.S.A.

[2] Author to whom all correspondence should be addressed (e-mail: rhauer@selway.umt.edu).

Fig. 1. Map of the McDonald drainage in Glacier National Park, Montana, showing the location of the study sites (1–8). The graph illustrates the elevation and distance of each study site from the stream origin.



among hydropsychid caddisflies, several mechanisms, including seston and catch-net mesh size (Wallace et al. 1977; Georgian and Wallace 1981; Thorp 1983; Thorp et al. 1986), seston concentration and the rate of catch-net filtration (Alstad 1982, 1986, 1987), and temperature (Edington and Hildrew 1973; Hildrew and Edington 1979; Hauer and Stanford 1982*b*; Stanford et al. 1988; Roux et al. 1992; Tachet et al. 1992; Guinand et al. 1994) have been suggested as possible causes of interspecific differences in longitudinal distributions. However, evaluations of these environmental gradients affecting species distribution have generally been univariate.

Here we present a study of the distribution and abundance of two species of hydropsychid caddisfly, *Parapsyche elsis* Milne and *Arctopsyche grandis* (Banks), inhabiting a pristine mountain stream in Glacier National Park in northwestern Montana, U.S.A. We examined variation across several important environmental gradients, including temperature, seston quantity, seston quality, current velocity, and substratum cobble size. We also examined the metabolic response of both species to temperature. We used the results of the laboratory experiments on the metabolism–temperature response of these species to evaluate their potential as indicators of temperature control of distribution.

Net-spinning caddisflies are common in cobble-substratum streams in the Rocky Mountains. *Parapsyche elsis* and *A. grandis* are found throughout the western Cordillera of North America. Their range extends from the Yukon and Mackenzie mountains in the Northwest Territories of Canada south to California, Utah, and Colorado (Givens and Smith 1980; Nimmo 1987; Williams 1991; Ward and Kondratieff 1992). *Parapsyche elsis* does not occur in the coastal mountain ranges of the Pacific Northwest, although *A. grandis* does (Givens and Smith 1980). *Parapsyche elsis* larvae are abundant in first- through fourth-order streams, and *A. grandis* larvae are likewise very abundant in fourth- to sixth-order streams and rivers (Hauer and Stanford 1981; Hauer and Stanford 1982*a*; Stanford et al. 1988; Hauer et al.1999). *Parapsyche elsis* and *A. grandis* are both in the subfamily Arctopsychinae, which contains the most primitive and largest bodied larvae among the hydropsychid caddisflies (Wiggins 1996). Both species are semivoltine in the northern Rocky Mountains, with adults emerging during the summer after the second year of larval growth. The nets of *P. elsis* and *A. grandis* are very large, yet similar, those of fifth-instar larvae having mesh openings of 600–800 μm. Sestonic diatoms and algae sloughed from the periphyton constitute a significant portion of the diet of Arctopsychinae in northern Rocky Mountain streams (Hauer and Stanford 1981), unlike the Arctopsychinae of Appalachian Mountain streams (Benke and Wallace 1980), which appear to be more dependent on animal material for growth.

We derived our first hypothesis from general models of species distribution along environmental gradients (Gause 1930; Whittaker et al. 1973; Gauch 1982; Hall et al. 1992), predicting that the abundance of each species would exhibit a Gaussian distribution within the spatial range of that species and along the thermal gradient of the stream. To address this hypothesis we conducted quantitative field-sampling of species density along the elevational gradient of study streams during the 1996 and 1997 field seasons.

Hildrew and Edington (1979) demonstrated a correlation between zones of temperature independence in the metabolism–temperature responses of larvae of three hydropsychid species and the thermal conditions in their longitudinal ranges in the River Usk, south Wales, U.K. Additional support for the importance of temperature-independent metabolic responses can be found in the general insect physiology literature (Newell and Northcroft 1967; Somero and Hochachka 1971; Prosser 1973; Weiser 1973; Hazel and Prosser 1974; Somero 1978, 1995; Huey and Bennett 1990). Our second working hypothesis was that the metabolic responses of *P. elsis* and *A. grandis* would be temperature-independent across experimental thermal regimes that corresponded to the thermal conditions expressed along the elevational–longitudinal gradient of the study stream. To address this hypothesis we conducted laboratory respirometry experiments across a range of temperatures (5–25°C) on fifth-instar larvae of both species.

Study site

We established 8 sampling sites along the length of McDonald Creek in Glacier National Park, northwestern Montana (Fig. 1). The McDonald drainage is a pristine fourth-order watershed (1 : 24 000, U.S. Geological Survey) tributary to the Middle Fork of the Flathead River. Its headwaters originate along the west slope

Table 1. Values for an array of location, microhabitat, seston, and temperature-related variables (mean ± 1 SD where appropriate) at 8 sampling sites in the McDonald drainage in Glacier National Park.

	Location		Microhabitat		Seston			Summer temp. (°C)		
Site No.	Distance from headwaters (km)	Elevation (m)	Current velocity (cm/s)	Substratum cobble size (cm)	Organic carbon concn. (mg/L)	Organic nitrogen concn. (mg/L)	C:N ratio	Mean	Max.	Annual degree-days
1	3.0	1532	0.34±0.07	9.1±0.80	0.54±0.10	0.028±0.02	22	4.5	9.6	853
2	4.3	1411	0.90±0.30	7.8±1.10	0.58±0.34	0.024±0.02	34	6.0	10.2	936
3	9.1	1228	0.25±0.03	8.2±0.90	0.85±0.23	0.037±0.02	31	7.9	12.9	1114
4	12.1	1155	0.21±0.04	9.5±0.70	0.54±0.37	0.032±0.03	28	8.8	13.0	1387
5	16.9	1107	0.45±0.11	8.8±0.30	0.60±0.53	0.017±0.01	34	8.3	14.8	1414
6	21.0	1082	0.28±0.03	8.5±0.20	0.31±0.14	0.012±0.004	32	8.4	14.8	1550
7	31.9	1009	0.24±0.05	8.7±0.60	0.51±0.26	0.025±0.02	30	9.2	14.1	1710
8	35.9	973	0.28±0.06	9.0±0.30	0.51±0.32	0.025±0.02	28	9.7	16.2	1812

of the Continental Divide at elevations ≈2100 m. All sampling sites were located upstream of Lake McDonald, which is at an elevation of 975 m. McDonald Creek possesses a typical northern Rocky Mountain spring-snowmelt-dominated hydrograph (see Poff and Ward 1989), a large-cobble substratum (Table 1), and waters that are generally very low in dissolved ions, nutrients, and suspended particulates (Hauer et al. 1997). The upper McDonald drainage, at the origin of the alpine first-order streams, is above the treeline. Second-order stream segments nearer the valley floor are well canopied by a coniferous overstory. The larger third- and fourth-order segments are broad enough to have a relatively open canopy.

Materials and methods

Field-sampling

We collected quantitative benthic samples at the study sites in July, August, September, and October of 1996 and March of 1997. Between November and February, sampling was prohibited by winter conditions: deep snow and ice cover over the stream. Between April and June, sampling was prevented by the extended high flows associated with spring snowmelt.

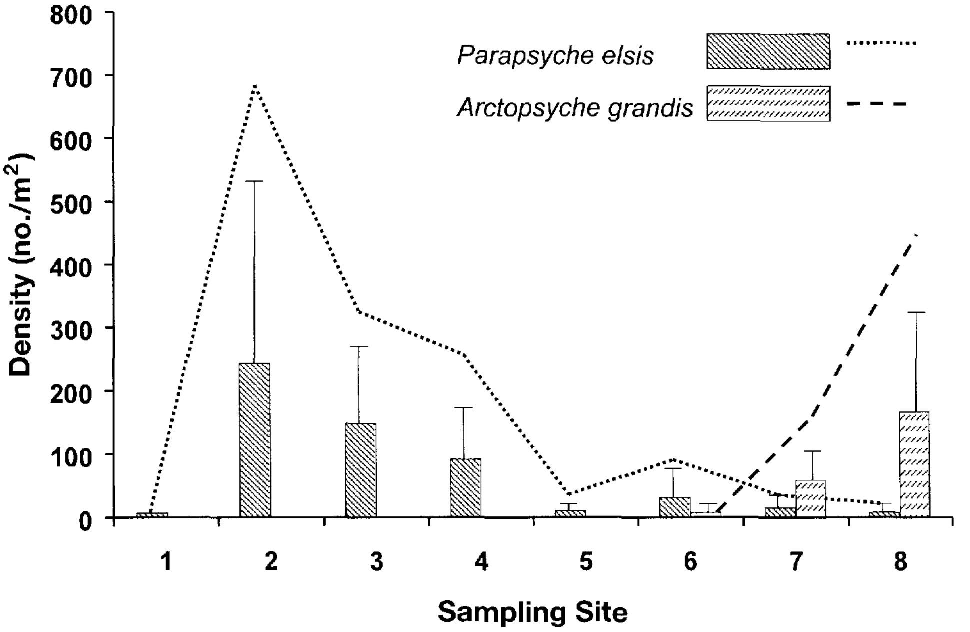
We employed a stratified random sampling design that restricted our sampling to riffle habitats known from our previous experience to be the appropriate habitat for these species. We collected three replicate samples at each site and on each sampling date. Benthic samples were taken within a 0.25-m^2 quadrat of the stream bottom using a modified kick-net procedure (Hauer and Resh 1996). All collected hydropsychid larvae were keyed to species. Interocular distance was measured on all specimens to confirm species phenology.

We quantified mean cobble size within nine 0.25-m^2 quadrats at each sampling site by employing the grid method modified for large-cobble-substratum systems (Sheldon 1980). Like Hauer and Stanford (1981), we found larvae of *P. elsis* and *A. grandis* in microhabitats in interstitial spaces under and around the surface cobble, which made measuring current velocity in microhabitats impractical. To indicate current velocities flowing over the substrata, we measured mean water velocities 5 cm above the primary cobble. Nine replicate measurements at each sampling site were made using a digital Scientific Instruments® Mini flowmeter. We quantified particulate organic carbon and nitrogen in the seston at each site and on each date. Five 1-L water samples were collected at each site and filtered onto glass-fibre filters. Carbon and nitrogen were analyzed on a Carlo Erba/Fisons® NA1500 CHN analyzer. Onset® Hobo temperature loggers recorded mean hourly water temperature at each sampling site for 1 year.

Laboratory analysis of the metabolism–temperature response

To permit a comparative analysis of the role of physiological response to temperature, we measured the metabolism–temperature response of fifth-instar *P. elsis* and *A. grandis* larvae collected in September and October 1996 (wet mass was 0.111 ± 0.036 and 0.098 ± 0.027 g (mean ± SD) for *P. elsis* and *A. grandis*, respectively). Respirometry experiments were conducted at 5, 10, 15, 20, and 25°C, thus spanning the range of stream temperatures in the region, including warm-water large river and lake outlet sites, which are dominated by the smaller bodied *Hydropsyche* spp. and *Cheumatopsyche* spp. (Stanford et al. 1988). A different larva was used for each experimental run. Each individual was placed in a flow-through acclimation chamber maintained at the experimental temperature for 36 h prior to the collection of respirometry data. The acclimation chamber contained a removable mesh frame on which the larva built a retreat and catch-net. At the time of the experiment, the mesh frame, larva, and silk retreat were removed from the acclimation chamber and placed in a 13-mL sealed vessel

Fig. 2. Yearly mean densities (mean ± 1 SE) of *Parapsyche elsis* and *Arctopsyche grandis* larvae at 8 sampling sites arrayed along the longitudinal gradient of McDonald Creek, Glacier National Park. Broken lines represent the maximum densities observed at each site throughout the study.



constructed of high-density polyethylene. The vessel was filled with oxygen-saturated water at the experimental temperature. The larva and mesh frame sat on a shelf above a magnetic stirrer that maintained the circulation of water within the respirometry vessel. Experimental temperatures were maintained by submersing the vessel in a controlled-temperature water bath.

The oxygen concentration in the respirometry vessel was sampled every 3 s for 1 h with a high-sensitivity oxygen meter (Strathkelvin Instruments® Model No. 78). The oxygen probe was embedded in the ceiling of the respirometry vessel. Linear decreases in oxygen concentration during experimentation suggest that consumption was not limited by low oxygen concentrations. A thermocouple, also embedded in the ceiling of the vessel, allowed continuous monitoring of water temperature over the course of each experimental run. This permitted the elimination of a temperature-stabilization period at the onset of each experiment. It also eliminated other experimental anomalies from calculations of oxygen-consumption rates, thereby greatly increasing accuracy relative to traditional closed-bottle methods of aquatic respirometry (Kamler 1969; Dries et al. 1979; Gnaiger and Forstner 1982).

Q_{10}, the proportional change in metabolic rate with a 10°C increase in temperature, was calculated using

$$[1] \qquad Q_{10} = \left(\frac{k_1}{k_2}\right)^{\frac{10}{t_1 - t_2}}$$

where k_1 and k_2 are the oxygen consumption rate at t_1 and t_2, respectively, and t is temperature. We also calculated metabolic amplitude (Roux 1978), the difference between the extreme oxygen-consumption values over the entire experimental temperature range.

Results

Larval distribution and abundance

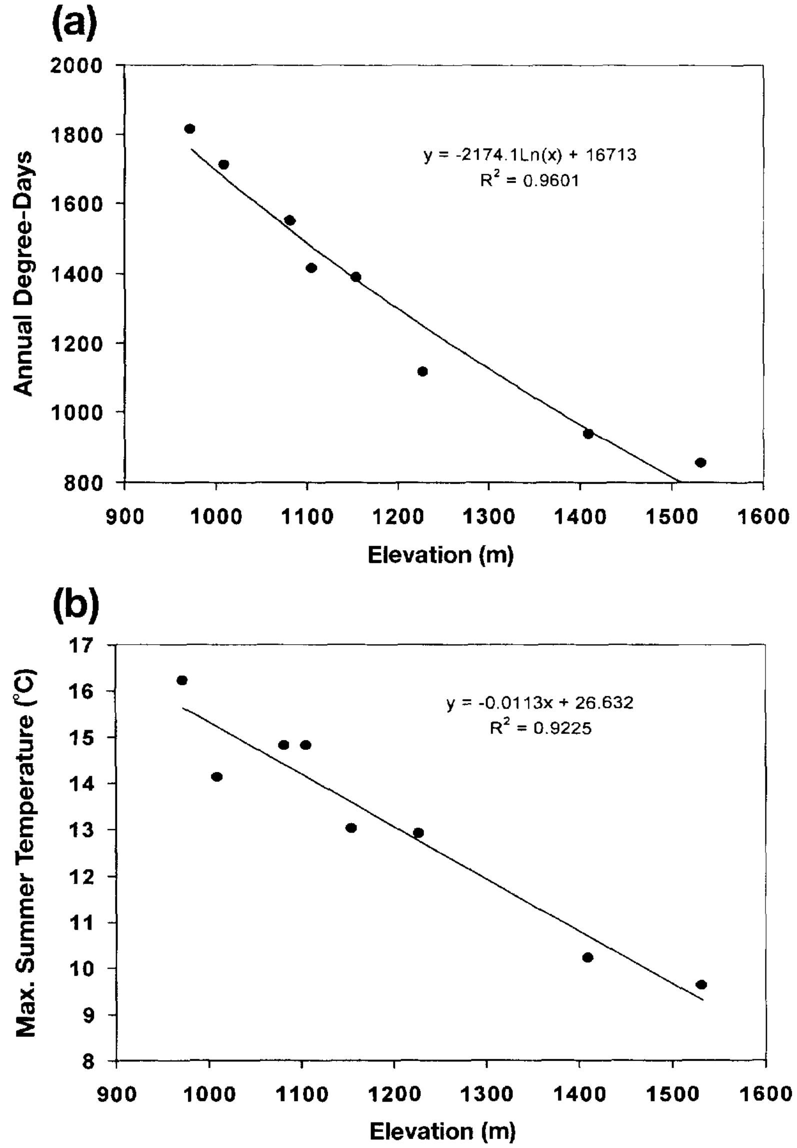
Parapsyche elsis was the dominant net-spinning caddisfly species in the upper reaches of McDonald Creek, although it was rare at the uppermost site. Abundance of *P. elsis* larvae decreased dramatically in the lower stream segments, while that of *A. grandis* larvae increased significantly in the lower reaches of the creek (Fig. 2). Qualitative sampling above sampling site 1 confirmed that the upper sampling site was near the upstream boundary of the elevation – stream gradient range of *P. elsis*. *Parapsyche elsis* larvae were most abundant at site 2 (annual mean abundance was >240/m^2 and maximum density for a sampling date was >680/m^2), located 1.3 km and at 120 m elevation downstream of site 1. The abundance of *P. elsis* larvae steadily declined downstream from site 2, to <10/m^2 at site 8. Many samples from site 8 contained no *P. elsis* larvae.

Arctopsyche grandis larvae occurred only as far upstream as site 6, where annual mean abundance was <3/m^2, and the maximum abundance on any sampling date was 20/m^2. Abundance of *A. grandis* larvae increased downstream at sites 7 and 8 to an annual mean of >160/m^2 and a maximum on any sampling date of >450/m^2 (Fig. 2). Although we know, based on extensive survey data, that *A. grandis* larvae do not occur in McDonald Creek below Lake McDonald, other studies (Hauer and Stanford 1982*a*; Stanford et al. 1988) have documented comparatively high densities in the Middle Fork of the Flathead River, both upstream and downstream of the McDonald Creek confluence with the river (see Fig. 1). We attribute the absence of both *P. elsis* and *A. grandis* larvae in the lake outlet creek to both warm epilimnetic water and a different trophic regime.

Environmental gradients

We conducted ANOVA and gradient analyses across each environmental variable: temperature, seston quality, seston quantity, current velocity, and substratum cobble size. These analyses revealed no significant differences ($p > 0.05$) or trends along the elevational or stream longitudinal gradient in current velocity, substratum cobble size, seston carbon

Fig. 3. Regression of annual degree-days (*a*) and maximum summer temperature (*b*) against elevation at 8 sampling sites arrayed along the longitudinal gradient of McDonald Creek, Glacier National Park.



concentration, seston nitrogen concentration, and carbon: nitrogen ratio (Table 1). However, we did observe a significant relationship ($p < 0.01$) of several temperature metrics regressed against both distance of the sampling site from the headwaters (i.e., the stream longitudinal gradient) and elevation of the sampling site (Fig. 3).

Metabolism–temperature response

The metabolic rate of *P. elsis* displayed a zone of relative temperature independence between 5 and 10°C (Q_{10} = 0.90; Table 2). In contrast, the metabolic rate of *A. grandis* displayed a zone of relative temperature independence between 5 and 15°C (Q_{10} = 1.14). The temperature-independent zones in the metabolism–temperature responses of *P. elsis* and *A. gra*ndis merge with zones of relative temperature dependence at higher temperatures (Q_{10} = 2.62 and 3.39, respectively). The metabolism–temperature curves for *P. elsis* and *A. grandis* had similarly modest metabolic amplitudes (0.148 and 0.122 mg $O_2 \cdot g^{-1}$ wet mass$\cdot h^{-1}$, respectively) and maximum Q_{10} values (2.39 and 2.02, respectively). Variation in the metabolic rates of larvae of both species resulting from variation in mass was insignificant relative to variation due to temperature (ANCOVA).

Discussion

This study was specifically designed to allow us to examine patterns in the distribution and abundance of *P. elsis* and *A. grandis* along the longitudinal and elevational gradients of a mountain stream. Within riffle habitats, *P. elsis* was the dominant net-spinning caddisfly in upstream reaches of McDonald Creek, while *A. grandis* replaced *P. elsis* in downstream reaches. It does not appear as though this replacement is specifically a function of competition between these species, since the frequency of *P. elsis* larvae was in significant decline by site 5, upstream of the appearance of *A. grandis* (Fig. 2). Nor does it appear that the

Table 2. Oxygen consumption rates (mean ± SD) of larvae of two species of hydropsychid caddisfly over a range of experimental temperatures.

	Parapsyche elsis			*Arctopsyche grandis*		
Temp. (°C)	n	Oxygen consumption (mg·g^{-1} wet mass·h^{-1})	Q_{10}	n	Oxygen consumption (mg·g^{-1} wet mass·h^{-1})	Q_{10}
5	4	0.058±0.010		4	0.088±0.013	
10	3	0.055±0.004	0.90 (5–10)	4	0.065±0.041	0.55 (5–10)
15	4	0.089±0.038	2.62 (10–15)	4	0.100±0.022	2.37 (10–15)
20	4	0.136±0.017	2.34 (15–20)	4	0.184±0.027	3.39 (15–20)
25	4	0.203±0.081	2.22 (20–25)	3	0.187±0.022	1.03 (20–25)

Note: Q_{10} is calculated using eq. 1; values in parentheses show the range of temperatures (°C); n is the number of larvae.

change in frequency of either species along the stream gradient was a function of change in seston quantity or quality, current velocity, or substratum cobble size, since none of these variables was correlated with either stream elevation or longitudinal gradient.

In addition to these physical and trophic variables, based on other studies it does not appear that a predator gradient can explain the observed longitudinal density pattern of *P. elsis* and *A. grandis*. Although there are species-specific changes, the total abundance of predatory stonefly (Plecoptera: Perlidae, Perlodidae, Chloroperlidae) and caddisfly (Trichoptera: Rhyacophilidae) species did not differ significantly between sampling sites (Hauer et al. 1999). Likewise, evaluations of fish abundance have shown that densities are uniformly low throughout McDonald Creek (Marnell 1988).

Physiological response to the stream temperature gradient seems the most probable explanation for the distribution and abundance patterns of these two species. This conclusion is supported by the correlation between the zone of temperature independence in the metabolism–temperature response (Table 2) of each species and the thermal conditions of occupied sites (Table 1, Fig. 3), which confirms our second hypothesis. The relatively low maximum Q_{10} values and metabolic amplitudes for both *P. elsis* and *A. grandis* may also be functions of the stream's thermal gradient. These patterns point to energetically conservative metabolic strategies.

Hall et al. (1992) provided an ideal theoretical framework for interpreting the results of this study. They hypothesized that species with distinctly different rates of energy loss or gain across an environmental gradient will respond with different energy efficiencies. In the central region of a species' distribution, energy efficiencies across gradients are maximized, while at the extremes of the distribution, energy inefficiencies are limiting. In this study, temperature, via metabolic controls, appears to be the primary environmental gradient structuring the spatial distribution and abundance patterns of *P. elsis* and *A. grandis*. The fundamental role of this bioenergetic response is underscored in this study by the extreme ecological similarity of the two species.

In assessing the broader applicability of our temperature-based model of longitudinal distribution of hydropsychid species, we must acknowledge those characteristics of the Flathead Basin that may render it particularly suitable for the application of this model. Of primary significance is the dramatic elevation gradient of first- through fourth-order streams in this system and the snowmelt-dominated hydrograph, both products of the mountainous topography. These characteristics result in a geographically condensed temperature gradient. Whereas other environmental variables, such as substratum cobble size, water velocity, seston concentration, and seston quality, may be important controlling mechanisms in other stream systems, they do not appear to vary sufficiently across the stream gradient of McDonald Creek to account for the dramatic differentiation in distributions of species of Arctopsychinae.

Our data support the hypothesis that stream temperature structures the downstream evolutionary radiation of hydropsychid species. Ross (1967) hypothesized a general model of downstream radiation among the trichopterans, where early diversification occurred in small, cool woodland streams. We propose that among the hydropsychids, speciation may have been a response to the thermal isolation of downstream subpopulations rather than a catch-net response to alteration in food size, quality, or concentration (Alstad 1982; Thorp 1983). Isolation was more likely a result of the evolution of physiological mechanisms that permitted survival under the thermal regimes of downstream habitats and the associated life-history modifications, with concurrent change in mesh-net structure and function. Because of its fundamental importance, the effect of thermal conditions on ectotherm physiology and bioenergetics (Wigglesworth 1953; Bullock 1954; Prosser 1973; Hoffman 1984), particularly in the ecology and evolution of aquatic macroinvertebrates (Vannote and Sweeney 1980; Ward and Stanford 1982; Ward 1992), provides a strong foundation for this model of the evolutionary radiation of these species.

In conclusion, we believe that we have presented a strong case for the primacy of the stream temperature gradient in structuring the distribution of *P. elsis* and *A. grandis* in montane streams of the northern Rockies. We suggest that these results further support a clear relationship between the thermal gradient and basin-scale distribution patterns in stream macroinvertebrates, particularly in mountain stream systems. The results also suggest a probable change in macroinvertebrate distributions in lotic systems in response to expected changes in temperature regimes due to anticipated global climate change. In turn, macroinvertebrate distribution and abundance may be useful indicators of climatic and concomitant environmental change.

Acknowledgements

We thank J. Biby and J. Giersch for assistance in the field. We thank Drs. Jack Stanford and Chris Frissell for their helpful insight. We particularly recognize Dr. Dan Fagre of the U.S. Geological Survey Biological Resources Division (USGS–BRD) for his assistance. The senior author is grateful for the support of the staff and fellow graduate students at Flathead Lake Biological Station. This work was funded by a grant from the USGS–BRD Global Climate Change Program.

References

Alstad, D.N. 1982. Current speed and filtration rate link caddisfly phylogeny and distributional patterns on a stream gradient. Science (Washington, D.C.), **216**: 533–534.

Alstad, D.N. 1986. Dietary overlap and net-spinning caddisfly distributions. Oikos, **47**: 251–252.

Alstad, D.N. 1987. Particle size, resource concentration, and the distribution of net-spinning caddisflies. Oecologia, **71**: 525–531.

Bales, M.T., and Badcock, R.M. 1987. Respiration rates and distribution of caddis larvae in relation to acclimation to temperature. *In* Proceedings of the Fifth International Symposium on Trichoptera, Lyon, France, 21–26 July 1986. *Edited by* M. Bournaud and H. Tachet. Dr. W. Junk, Dordrecht, the Netherlands. pp. 179–183.

Benke, A.C., and Wallace, J.B. 1980. Trophic basis of production among netspinning caddisflies in a southern Appalachian stream. Ecology, **61**: 108–118.

Bullock, T.H. 1954. Compensation for temperature in the metabolism and activity of poikilotherms. Biol. Rev. Camb. Philos. Soc. **30**: 311–342.

Dries, R.R., Eschweiler, L., and Theede, H. 1979. An improved equipment for continuous measurement of respiration of marine invertebrates. Kiel. Meeresforsch. **4**: 310–316.

Edington, J., and Hildrew, A. 1973. Experimental observations relating to the distribution of net-spinning Trichoptera in streams. Verh. Int. Ver. Theor. Angew. Limnol. **18**: 1549–1558.

Firth, P., and Fisher, S.G. 1992. Global climate change and freshwater ecosystems. Springer-Verlag, New York.

Gauch, H.G. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge.

Gause, G.F. 1930. Studies on the ecology of the Orthoptera. Ecology, **11**: 307–325.

Georgian, T.J., Jr., and Wallace, J.B. 1981. A model of seston capture by net-spinning caddisflies. Oikos, **36**: 147–157.

Givens, D.R., and Smith, S.D. 1980. A synopsis of the western Arctopsychinae. Biology Department, Central Washington University, Ellensburg.

Gnaiger, E., and Forstner, H. 1982. Handbook on polarographic oxygen sensors: aquatic and physiological applications. Springer-Verlag, New York.

Guinand, B., Tachet, H., and Roux, C. 1994. Longitudinal distribution and ecophysiological characteristics of *Hydropsyche exocellata* (Trichoptera: Hydropsychidae) in large rivers. Ecography, **17**: 189–197.

Hall, C.A.S., Stanford, J.A., and Hauer, F.R. 1992. The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients. Oikos, **65**: 377–390.

Hauer, F.R., and Resh, V.H. 1996. Benthic macroinvertebrates. *In* Methods in stream ecology. *Edited by* F.R. Hauer and G.A. Lamberti. Academic Press, San Diego. pp. 339–370.

Hauer, F.R., and Stanford, J.A. 1981. Larval specialization and phenotypic variation in *Arctopsyche grandis* (Trichoptera: Hydropsychidae). Ecology, **62**: 645–653.

Hauer, F.R., and Stanford, J.A. 1982*a*. Ecology and life histories of three net-spinning caddisfly species (Hydropsychidae: Hydropsyche) in the Flathead River, Montana. Freshwater Invertebr. Biol. **1**: 18–29.

Hauer, F.R., and Stanford, J.A. 1982*b*. Ecological responses of hydropsychid caddisflies to stream regulation. Can. J. Fish. Aquat. Sci. **39**: 1235–1242.

Hauer, F.R., Stanford, J.A., Giersch, J.J., and Lowe, W.H. 1999. Distribution and abundance patterns of macroinvertebrates in a mountain stream: an analysis along multiple environmental gradients. Verh. Int. Ver. Theor. Angew. Limnol. In press.

Hauer, F.R., Baron, J.S., Campbell, D.H., Fausch, K.D., Hostetler, S.W., Leavesley, G.H., Leavitt, P.R., McKnight, D.M., and Stanford, J.A. 1997. Assessment of climate change and freshwater ecosystems of the Rocky Mountains, U.S., and Canada. Hydrol. Processes, **11**: 903–924.

Hazel, J., and Prosser, C.L. 1974. Molecular mechanisms of temperature compensation in poikilotherms. Physiol. Rev. **54**: 620–677.

Hildrew, A.G., and Edington, J.M. 1979. Factors facilitating the coexistence of hydropsychid caddis larvae (Trichoptera) in the same river system. J. Anim. Ecol. **48**: 557–576.

Hoffman, K.H. 1984. Metabolic and enzyme adaptation to temperature. *In* Environmental physiology and biochemistry of insects. *Edited by* K.H. Hoffman. Springer-Verlag, New York. pp. 1–32.

Hogg, I.D., and Williams, D.D. 1996. Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. Ecology, **77**: 395–407.

Huey, R.B., and Bennett, A.F. 1990. Physiological adjustments to fluctuating thermal environments: an ecological and evolutionary perspective. *In* Stress proteins in biology and medicine. *Edited by* R.I. Morimoto, A. Tissieres, and C. Georgopoulos. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, N.Y. pp. 37–59.

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

Marnell, L.F. 1988. Status of the Westslope cutthroat trout in Glacier National Park, Montana. Am. Fish. Soc. Symp. **4**: 61–70.

Newell, R.C., and Northcroft, H.R. 1967. A re-interpretation of the effect of temperature on the metabolism of certain marine invertebrates. J. Zool. (1965–1984), **151**: 277–298.

Nimmo, A.P. 1987. The adult Arctopsychidae and Hydropsychidae (Trichoptera) of Canada and adjacent United States. Quaest. Entomol. **23**: 1–189.

Poff, N.L., and Ward, J.V. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Can. J. Fish. Aquat. Sci. **46**: 1805–1818.

Prosser, C.L. 1973. Comparative animal physiology. W.B. Saunders, Philadelphia.

Ross, D.H., and Wallace, J.B. 1982. Factors influencing the longitudinal distribution of larval Hydropsychidae (Trichoptera) in a southern Appalachian stream system. Hydrobiologia, **96**: 185–199.

Ross, H.H. 1967. The evolution and past dispersal of the Trichoptera. Annu. Rev. Entomol. **12**: 169–206.

Roux, C. 1978. Courbes métabolisme/temperature et écologie de quelques espèces d'invertebres dulcaquicoles. Verh. Int. Ver. Theor. Angew. Limnol. **20**: 2584–2593.

Roux, C., Tachet, H., Bournaud, M., and Cellot, B. 1992. Stream continuum and metabolic rate in the larvae of five species of Hydropsyche (Trichoptera). Ecography, **15**: 70–76.

Sheldon, A.L. 1980. Resource division by perlid stoneflies (Plecoptera) in a lake outlet ecosystem. Hydrobiologia, **71**: 155–161.

Somero, G.N. 1978. Temperature adaptation of enzymes: biological optimization through structure–function compromise. Annu. Rev. Ecol. Syst. **9**: 1–29.

Somero, G.N. 1995. Proteins and temperature. Annu. Rev. Physiol. **57**: 43–68.

Somero, G.N., and Hochachka, P.W. 1971. Biochemical adaptation to the environment. Am. Zool. **11**: 159–167.

Stanford, J.A., Hauer, F.R., and Ward, J.V. 1988. Serial discontinuity in a large river system. Verh. Int. Ver. Theor. Angew. Limnol. **23**: 1114–1118.

Sweeney, B.W., Jackson, J.K., Newbold, J.D., and Funk, D.H. 1992. Climate change and the life histories and biogeography of aquatic insects in eastern North America. *In* Global climate change and freshwater ecosystems. *Edited by* P. Firth and S.G. Fisher. Springer-Verlag, New York. pp. 143–176.

Tachet, H., Pierrot, J.P., Roux, C., and Bournaud, M. 1992. Net-building behavior of six *Hydropsyche* species (Trichoptera) in relation to current velocity and distribution along the Rhône River. J. N. Am. Benthol. Soc. **11**: 350–365.

Thorp, J.H. 1983. An evaluation of hypotheses on the evolutionary differentiation of catchnets in net-spinning caddisflies (Hydropsychidae). Oikos, **40**: 308–312.

Thorp, J.H., Wallace, J.B., and Georgian, T.J., Jr. 1986. Untangling the web of caddisfly evolution and distribution. Oikos, **47**: 253–256.

Vannote, R.L., and Sweeney, B.W. 1980. Geographical analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. Am. Nat. **115**: 667–695.

Wallace, J.B., Webster, J.R., and Woodall, W.R. 1977. The role of filter feeders in flowing waters. Arch. Hydrobiol. **79**: 506–532.

Ward, J.V. 1992. Aquatic insect ecology. John Wiley & Sons Inc., New York.

Ward, J.V., and Kondratieff, B.C. 1992. An illustrated guide to the mountain stream insects of Colorado. University Press of Colorado, Niwot.

Ward, J.V., and Stanford, J.A. 1982. Thermal responses in the evolutionary ecology of aquatic insects. Annu. Rev. Entomol. **27**: 97–117.

Weiser, W. 1973. Effects of temperature on ectothermic organisms. Springer-Verlag, New York.

Whittaker, R., Levin, S., and Root, R. 1973. Niche, habitat and ecotope. Am. Nat. **107**: 321–338.

Wiggins, G.B. 1996. Larvae of the North American caddisfly genera. University of Toronto Press, London.

Wigglesworth, V.B. 1953. The principles of insect physiology. E.P. Dutton and Co. Inc., New York.

Williams, N.E. 1991. Geographical and environmental patterns in caddisfly (Trichoptera) assemblages from coldwater springs in Canada. Mem. Entomol. Soc. Can. No. 155. pp. 107–124.