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Winsor H. Lowe
The University of Montana

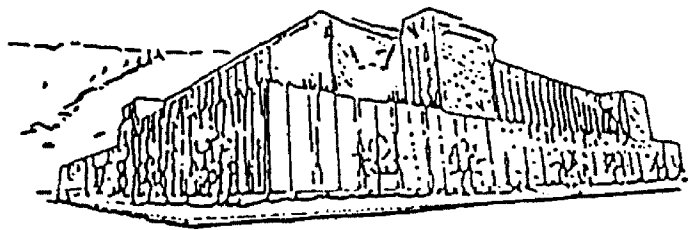
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**An evaluation of in-stream longitudinal distribution among hydropsychids
(Trichoptera: Hydropsychidae) of the Flathead Basin, northwestern
Montana: evidence for a bioenergetic response to the thermal gradient.**

by

Winsor H. Lowe

B.A., Middlebury College 1994

Presented in partial fulfillment of the requirements

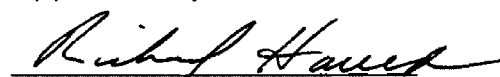
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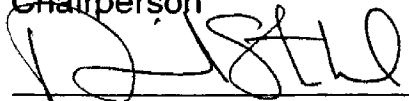
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An evaluation of in-stream longitudinal distribution among hydropsychids (Trichoptera: Hydropsychidae) of the Flathead Basin, northwestern Montana: evidence for a bioenergetic response to the thermal gradient.

Director: F. Richard Hauer



Abstract

In Chapter 1 I provide a description of the ecological context of this project. The research comprising this thesis serves as a foundation for evaluation of a bioenergetic model of species distribution and abundance along multiple environmental gradients (Hall et al. 1992). The hydropsychid caddisflies inhabiting streams of the Flathead Basin, northwestern Montana represent an ideal system for this evaluation for 3 reasons. First, these species inhabit lotic habitats, characterized by a high level of environmental continuity, and within which quantifiable physical gradients are believed to be of primary importance in structuring the distribution of organisms. Second, the hydropsychids display distinct patterns of in-stream longitudinal distribution which, considering their ecological similarity, are likely supported by interspecific differences in response to the physical gradients of the stream. Third, these species are ectotherms, increasing the probability of the thermal gradient of the stream playing a significant role in structuring both interspecific differences in longitudinal distribution and species-specific longitudinal abundance patterns.

In Chapter 2 I evaluate evidence for a bioenergetic response to stream temperature in the in-stream longitudinal abundance pattern of one hydropsychid species inhabiting low order streams (1st-3rd) of the Flathead Basin, northwestern Montana. I quantified in-stream longitudinal density of *Parapsyche elsis* (Trichoptera: Hydropsychidae) and accompanying gradients in substrate particle size, seston concentration, water velocity and water temperature in the McDonald drainage, Glacier National Park. My results indicate that the density pattern of *P. elsis* approximates a normal distribution along the longitudinal gradient of the stream, thereby corresponding to theoretical models of species distribution along multiple environmental gradients (Gause 1930, Hall et al. 1992). Of the environmental conditions examined, only stream temperature exhibited a significant gradient ($p < 0.05$) within the longitudinal range of *P. elsis*. Based upon these data, the stream-temperature gradient is shown to be the primary determinant of the longitudinal distribution of this species and a likely basis of the evolutionary radiation and current distribution of hydropsychid caddisflies. We believe that the longitudinal context offers an extremely important, yet untapped perspective on lotic macroinvertebrate distribution, potentially useful to both applied and theoretical research in these systems.

In Chapter 3 I examine evidence for metabolic adaptation to the thermal regimes of occupied reaches among 3 hydropsychid species inhabiting Flathead Basin streams. *Parapsyche elsis*, *Arctopsyche grandis* and *Hydropsyche cockerelli* occur in a longitudinal replacement series in 1st through 5th order streams of the Flathead Basin, northwestern Montana. During periods of metabolic activity, the thermal ranges of reaches occupied by *P. elsis* (5-10°C) and *A. grandis* (5-15°C) fall within biologically important zones of temperature independence in the metabolism/temperature (M/T) curves of these species ($Q_{10}=0.91$ and 1.14, respectively). These zones define species-specific ranges of thermal tolerance which place each species within the thermal gradient of the stream continuum, and are evolutionarily linked to their energetically conservative life history strategies. The M/T curve of *H. cockerelli* displays temperature dependence ($Q_{10}=7.65$) throughout the thermal range (5-20°C) of occupied reaches during periods of metabolic activity. The thermally responsive metabolism of this species, and energetic investment in metabolic mechanisms permitting this responsiveness compliment its rapid growth pattern and thermal habitat. Differences in the metabolic response to temperature and phenology among these species support a temperature-based model of the downstream radiation of hydropsychid species.

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Contents

Abstract.....	ii
Acknowledgements.....	iii
Contents.....	iv
List of Tables.....	vi
List of Figures.....	vii
Chapter 1: Introduction: The hydropsychids (Trichoptera: Hydropsychidae) of the Flathead Basin, Montana: an ideal system for evaluating the gradient-based approach to species distribution and abundance.....	1
<i>The ecological context</i>	1
<i>The physical continuity of the lotic environment</i>	3
<i>The physical environment and hydropsychid distribution</i>	5
<i>The thermal gradient and hydropsychid distribution</i>	8
<i>The project</i>	9
Literature cited.....	11
Chapter 2: An evaluation of in-stream longitudinal density of <i>Parapsyche elsis</i> (Trichoptera: Hydropsychidae) along multiple environmental gradients.....	22
Abstract.....	22
Introduction.....	23
Methods.....	24
<i>Study site</i>	24
<i>Study species</i>	25
<i>Collection of larvae</i>	25
<i>Measurement of environmental gradients</i>	26
<i>Analysis</i>	27
Results.....	27
<i>Larval density</i>	27
<i>Environmental gradients</i>	28
Discussion.....	28

Contents (contd.)

<i>Larval density patterns and response to environmental gradients</i>	28
<i>Biotic factors</i>	29
<i>The longitudinal context in stream biomonitoring</i>	30
<i>Conclusion</i>	31
Literature cited	32
Chapter 3: The metabolism-temperature response in three larval hydropsychids (Trichoptera: Hydropsychidae): evidence for the thermal basis of in-stream longitudinal distribution.	
Abstract	47
Introduction	48
Materials and methods	49
<i>Study site</i>	49
<i>Larval distribution along the thermal gradient</i>	49
<i>Respirometry</i>	51
Results	52
Discussion	53
Literature cited	56
Appendix 1	69
Appendix 2	70
Appendix 3	71

List of Tables

(Chapter 2)

Table 1. Prior publications supporting the roles of substrate, water velocity, seston and water temperature conditions in determining patterns of hydropsychid distribution.....	38
--	----

List of Tables

(Chapter 3)

Table 1. Oxygen consumption of 3 hydropsychid caddisfly larvae. °C=Temperature, n=number of larvae, x=mean O ₂ consumption in mg O ₂ /g wet weight/hour, S.E.=standard error, Q ₁₀ determination by the equation:	
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$$Q_{10} = \left(\frac{k_1}{k_2} \right)^{\frac{10}{t_1 - t_2}}$$

k ₁ and k ₂ = oxygen consumption at t ₁ and t ₂	61
---	----

Table 2. Metabolic amplitude (mg O ₂ /g wet weight/hour) of 3 hydropsychid caddisfly larvae.....	62
---	----

List of Figures

(Chapter 1)

- Fig. 1. Theoretical relative abundance curve of a species along an environmental gradient (Gause 1930) with the peak value, mode and dispersion labeled. 18
- Fig. 2. Growth of a poikilotherm in response to an environmental gradient (from Hall et al. 1992). The commonly observed bell-shaped growth curve is hypothesized to be the net difference between metabolic energy expenditures (respiration) and gains (assimilation), realized as individual growth (energy profit). 19
- Fig. 3. Typical hydropsychid net and retreat (from Wiggins 1992). 20
- Fig. 4. Distributions of 3 hydropsychid caddisfly larvae (*P. elsis*, *A. grandis* and *H. cockerelli*) relative to stream order and approximate maximum summer temperature (°C) of occupied reaches in the Flathead Basin, Montana. 21

List of Figures

(Chapter 2)

- Fig. 1. Theoretical relative abundance curve of a species along an environmental gradient (Gause 1930) with the peak value, mode and dispersion labeled. 39
- Fig. 2. Map of the Flathead Basin, northwestern Montana, with the location of the McDonald drainage. 40
- Fig. 3. Distribution of sampling sites in the McDonald drainage relative to elevation (m) and distance from headwaters (river-km). 41

Fig. 4. Yearly mean density (ind./m²) of 1st year (Instars 1, 2 and 3) and 2nd year (Instars 4 and 5) *Parapsyche elsis* larvae at 8 sampling sites arrayed along the longitudinal gradient of the McDonald drainage, Glacier National Park, Montana..... 42

Fig. 5. Linear regression of water velocity (meters per second), substrate size (cm), seston C:N ratio, and water temperature (°C) against elevation of sampling sites. P-values for the slopes of the regression lines correspond to a 95% confidence interval. Horizontal bars represent standard error..... 43

Fig. 6. Linear regression of water velocity (meters per second), substrate size (cm), seston C:N ratio, and water temperature (°C) against distance from headwaters of sampling sites. P-values for the slopes of the regression lines correspond to a 95% confidence interval. Horizontal bars represent standard error..... 44

Fig. 7. Monthly mean density (ind./m²) of 1st and 2nd instar *Parapsyche elsis* larvae at sampling sites 6, 7 and 8..... 45

Fig. 8. Yearly mean density (ind./m²) of 1st year (Instars 1, 2 and 3) and 2nd year (Instars 4 and 5) *Arctopsyche grandis* larvae at 8 sampling sites arrayed along the longitudinal gradient of the McDonald drainage, Glacier National Park, Montana..... 46

List of Figures

(Chapter 3)

Fig. 1. Map of the Flathead River Basin, Montana, indicating the location of the McDonald drainage, Glacier National Park.	63
Fig. 2. Distributions of 3 hydropsychid caddisfly larvae (<i>P. elsis</i> , <i>A. grandis</i> and <i>H. cockerelli</i>) relative to stream order and approximate maximum summer temperature (°C) of occupied reaches in the Flathead Basin, Montana.	64
Fig. 3. Phenologies of <i>Parapsyche elsis</i> , <i>Arctopsyche grandis</i> and <i>Hydropsyche cockerelli</i> in the Flathead Basin, Montana, indicating monthly distribution of larval instars (1-5) and timing of emergence (E). Modes have been joined to illustrate growth patterns. Vertical bars show range of instars present in stream.	65
Fig. 4. Mean wet weights (\pm S.D.) of 5th instar larvae of 3 hydropsychid caddisfly species selected for our respirometry experiments.	66
Fig. 5. Metabolism/Temperature (\pm S.E.) curves of 3 hydropsychid caddisfly larvae occurring in a longitudinal replacement series in streams of the Flathead Basin, Montana. Grey bar represents yearly thermal range of occupied reaches during the growth period of each species.	67
Fig. 6. Growth of a poikilotherm in response to an environmental gradient (from Hall et al. 1992). The commonly observed bell-shaped growth curve is hypothesized to be the net difference between metabolic energy expenditures (respiration) and gains (assimilation), realized as individual growth (energy profit).	68

Chapter 1

The hydropsychids (Trichoptera: Hydropsychidae) of the Flathead Basin, Montana: an ideal system for evaluating the gradient-based approach to species distribution and abundance.

The ecological context

A primary responsibility of the ecologist is to explain patterns of species distribution and abundance (sensu Andwartha and Birch 1952), a complex task which allows great latitude in both approach and focus. There do, however, exist basic principles which unify diverse efforts within the discipline of ecology. In designing and interpreting the results of this project, I have tried to address one such unifying principle. This principle states that the distribution and abundance of a particular species is a function of the degree of optimality of the environmental conditions it is exposed to. Cumulatively, these conditions, both biotic and abiotic, produce a complex environmental gradient, ranging from intolerable conditions, where species relative abundance equals 0, to ideal conditions, where relative abundance is 100%. This concept was first described by Gause (1930), who used a normal curve to illustrate the general pattern of species abundance along an environmental gradient (Fig. 1). While relatively simple in appearance, this model continues to be a powerful tool in understanding both community organization and the distribution of individual species on a complex landscape.

The Gaussian model of species distribution was placed in a bioenergetic context by Hall et al. (1992), allowing for its application at the level of the individual organism, the fundamental unit of the Gaussian curve. According to this model, an individual maintains a positive energy balance within a particular environment only when the energetic gains made in that environment outweigh the energetic costs. These authors suggest that this energetic balance plays out at the level of the metabolic processes of the individual, where energetic costs, gains and net profit are

expressed as energy used for respiration, energy gained through the assimilation of food, and energy available for growth and reproduction, respectively (Fig. 2). This model predicts that the degree of optimality of a particular environment will initially be expressed at the level of the individual by rates of growth and reproduction. These individual-level measures of environmental optimality will subsequently be reflected at the level of the population in patterns of relative abundance.

In both models the responsibility of characterizing and quantifying the environmental gradient underlying patterns of species distribution and abundance is left to the observer, a job which becomes the limiting factor in evaluating the field-applicability of these models. The multivariate-statistical arsenal developed by ecologists to accomplish this job is a perfect illustration of its complexity (Gauch 1982). To determine the field-applicability of these models requires an ecological system possessing a moderate degree of complexity. Specifically, such a system should be structured upon quantifiable environmental gradients, and a strong body of knowledge should exist which links the ecology of the focal organism to these gradients.

I believe that the net-spinning caddisflies (Trichoptera: Hydropsychidae) inhabiting the streams of the Flathead Basin represent an ideal system for evaluating the utility of these gradient-based models, and base this belief on 3 observations I have made relating to both the Flathead system and general characteristics of lotic ecosystems and the macroinvertebrates that inhabit them. First, the fundamental physical continuity of the lotic environment, second, the strong probability of physical gradients structuring the in-stream longitudinal distribution patterns of the hydropsychids, and third, theoretical support for the primacy of the thermal gradient, in particular, in structuring this pattern of distribution. In the following section I discuss these 3 points in detail, drawing upon relevant literature in the course of this discussion. In the final section of this chapter I present an overview of the original research comprising this thesis, tying this work back to the theoretical models presented above.

The physical continuity of the lotic environment

Stream systems possess a level of environmental continuity over broad geographic scales that differentiates them from many other natural systems. The environmental continuity of lotic systems is a result, fundamentally, of the unidirectional flow of water through these systems, and the longitudinal structure that this flow provides. This basic structure is best described in the River Continuum Concept (Vannote et al. 1980), a conceptual framework which describes the continuous gradient in physical conditions that occurs from the headwaters to the mouth of river systems, and suggests that this physical gradient plays the primary role in structuring the distribution of organisms in these systems. The River Continuum Concept is, however, a theoretical model of how stream and river systems might work. When this model is compared with field data on the longitudinal structure of lotic systems across different regions (Minshall et al. 1983), it becomes clear that this framework “must be visualized as a sliding scale which is shifted upstream or downstream depending on macroenvironmental forces or reset following the application of more localized “micro”-environmental influences.” In light of this conclusion, I believe that it is important to provide a general description of the longitudinal structure of the Flathead system which highlights those macro- and micro-environmental factors which influence the application of the continuum concept to this system, as well as the application of the results of this research to other systems.

The Flathead River Basin is a >24,000 km² system where high elevation streams (> 3000m) originate from glacier and snow melt. Glacier National Park, the Bob Marshall, Great Bear and Mission Mountain Wildernesses and other largely undisturbed forest lands occupy most of the upper river basins. Tributary streams and the major river segments of the Flathead are typically very low in nutrient concentration, algal biomass and secondary production. Low order streams flowing through forested areas typically receive allochthonous inputs of coniferous origin. The canopy of typical 3rd and 4th order streams is relatively open; therefore, autochthony is often a major contributor to the organic base of production. Over 70% of the annual discharge of this

system occurs during April, May and June, associated with the annual snowmelt. During this time, streams and rivers may increase 10 to 100 times mean low flow, scouring substrata and resetting annual autochthonous production.

Stream and river substrata in the Flathead system is typically composed of large cobble (10 to 30cm diameter). A complex geologic history in the area has resulted in a wide variety of parent material of this substrata, and in differential exposure to ion bearing rock and associated heterogeneity of nutrient concentrations among drainages. Riffles occupy between 5 and 20% of the mainstem rivers, and higher percentages in the tributary streams. Although current velocities within a riffle are highly variable, typical stream reaches from 1st through 7th order contain an abundance of habitats with current velocities from very fast (>1 mps) to very slow (<0.1 mps). In addition to these surficial aspects of the flow and substratum characteristics in the Flathead system, a geomorphic pattern of confined and unconfined stream reaches in the basin combines with the large-cobble and bedrock substrata to result in complex hyporheic flow pathways (Stanford and Ward 1993). These pathways may influence micro-environmental nutrient concentrations and thermal conditions in streams throughout the basin.

The temperature regime along the free-flowing, unregulated reaches of the Flathead system changes in a very predictable way. Temperature data for 15 sites along the longitudinal gradient, from 1st order, high elevation streams to the 7th order mainstem river, reveals a very close relationship between the temperature regime (expressed as annual degree days) and the longitudinal/elevational gradient of the system (Stanford et al. 1988). Algal and microbial populations colonizing detrital aggregates may be directly affected by temperature. Therefore, growth rates of important food items may be a function of their location within this thermal gradient. However, examinations of organic matter concentrations (Hauer and Stanford 1982) and food ingested by lotic fauna from streams having differing food resources suggest that there is a broad spectrum of source materials to support similar benthic communities in these streams (Hauer and Stanford 1981).

The physical environment and hydropsychid distribution

The hydropsychid, or net-spinning caddisflies are ecologically similar in their use of silken nets to filter food particles from the flowing water (Fig. 3). This common characteristic places these species in the collector/filterer functional group in streams where they occur (Wiggins and MacKay 1978). In streams of the Flathead Basin 6 hydropsychid species occur in a replacement series along the longitudinal/elevational gradient (Hauer and Stanford 1982, Stanford et al 1988), although my work focuses on only 3 of these species. This distributional pattern points to accompanying physical gradients as a likely basis. This pattern is not unique to the Flathead system, and has engendered a significant body of research examining the mechanisms underlying this distributional pattern in other areas where it has been documented. A review of previous efforts is critical in understanding the structure of the 2 projects comprising this thesis, and in establishing the suitability of the Flathead-hydropsychid system to an evaluation of the gradient-based approach to species distribution and abundance.

Four environmental variables have received the most attention in previous studies addressing hydropsychid distribution and abundance: substrate, seston, water velocity and water temperature. The majority of these studies have focused on the downstream succession of species, and interspecific differences in microhabitat use as a function of a single environmental variable (Edington 1965, Hildrew and Edington 1979, Cudney and Wallace 1980, Wallace and Merritt 1980, Ross and Wallace 1982, Hauer and Stanford 1982, Thorp 1983, Alstad 1987, Roux et al. 1994). While informative with regard to the specific questions addressed, the broader ecological implications of the findings of these studies are undermined by the narrow range of environmental variables examined, and a consistent failure to capitalize on naturally occurring gradients in focal variables to document species response.

In the work of Hildrew and Edington (1979), Hauer and Stanford (1981), and Ross and Wallace (1982) preference for substratum characteristics is proposed as a basis for coexistence among 2 hydropsychid species, or, in one case, 2 larval morphotypes of the species *Arctopsyche*

grandis. As asserted by Ward (1992), close associations of a particular species, life history stage or larval morph with a substratum type can be the result of shelter, respiratory or food requirements rather than an affinity for a particular bottom type. Therefore, the mechanism behind these preferences remains unclear, and the results of these studies inconclusive considering possible interrelationships between substrate preference and other environmental conditions. These studies also lack a longitudinal context to the sampling structure, thus the role of substrate condition in structuring basin-scale species distributions remains unknown. Likewise, previous examinations of the specific role of water velocity in hydropsychid distribution have, using a variety of approaches, successfully demonstrated interspecific differences in flow-condition preference (Philipson 1954, Edington 1965, Feldmeth 1970a,b, Ross and Wallace 1982, Tachet et al. 1992). However, the impact of a gradient in water velocity within the longitudinal range of a single species has not been examined, again limiting the applicability of results to reach-scale patterns of distribution.

The role of seston, or food resources, in structuring hydropsychid distribution has received considerable attention, both in the form of original research and debate over conflicting models of seston capture and preference. In the context of the longitudinal replacement series among the hydropsychids, such as occurs in the Flathead system, the seston “quality versus quantity” debate is particularly important. Engendered by the observation that there is a downstream trend in decreasing net-mesh size among the hydropsychid species comprising such replacement series, authors have proposed 2 conflicting, seston-based models of species distribution (Alstad 1982, Thorp 1983, Alstad 1986, Thorp et al. 1986, Alstad 1987).

Observing the striking pattern of hydropsychid distribution and catchnet morphology in 2 Utah streams and a broad dietary similarity among hydropsychid larvae, Alstad (1982, 1986, 1987) concluded that food (seston) concentration and filtration rate of large versus small meshed nets are the basis of hydropsychid community organization along the longitudinal gradient. According to this model, smaller-meshed nets are suited to the conditions of downstream, seston-

rich reaches, where relatively little water must be filtered to obtain adequate food resources. In contrast, the large-meshed nets of upstream species are adapted to the low concentrations of seston in these reaches, where a relatively large amount of water must be filtered to obtain sufficient food resources.

The opposing model in this debate suggests that mesh size differences reflect selectivity for large, high-quality food particles, mainly in the form of animal tissue, in high velocity microhabitats, such as those found more commonly in the upstream reaches of river systems (Thorp 1983, Thorp et al. 1986). Thorp et al. (1986) concluded..."that fine mesh nets may have evolved as adaptations for survival in low current velocity microhabitats where dependence on small seston particles was mandated by the relative scarcity of animal prey" and "that food quality rather than food quantity (total seston concentration) governs the distribution of net-spinning caddisflies."

In the context of both the longitudinal distribution of the hydropsychids and their role in lake outlet systems, underlying gradients in seston concentration, nutritional quality and the selectivity of hydropsychid nets of various mesh-sizes have been called into question (Oswood 1979, Fuller et al. 1983, Thorp et al. 1986, Alstad 1987, Richardson and MacKay 1991). This debate has resulted in a high level of uncertainty regarding the role of seston in structuring hydropsychid distribution. In addition, a general narrowness of focus and lack of quantitative field data on species response to seston gradients supporting the proposed models plagues the majority of the seston-oriented hydropsychid work. If nothing else then, the role of seston in hydropsychid distribution demands to be evaluated from a broader perspective than these previous efforts have taken. Seston must first be evaluated as one of several potential environmental gradients underlying hydropsychid distribution before it is subject to the intense scrutiny and debate that characterize this body of work.

The thermal gradient and hydropsychid distribution

Temperature profiles of lotic systems take many forms depending upon the temporal and spatial scale at which they are examined. The input of solar radiation (Gregory et al. 1994), hydrologic profile of the stream (Feminella and Resh 1990) and watershed-level climatic conditions combine in varying forms along the stream continuum to result in both a high degree of thermal heterogeneity in temperate stream basins, and distinct gradients in some thermal conditions along the longitudinal profile of stream systems. Especially important to an analysis of species response to thermal conditions in the stream is the assertion by Vannote and Sweeney (1980) that, while stream insect species have evolved to survive in thermally fluctuating systems and within temperature ranges of varying breadth, they display no ability to acclimate to new thermal regimes. This assertion suggests that there exist optimal thermal conditions for these insect species, and that suboptimal conditions should have demonstrable impacts on insect populations. The longitudinal dimension of stream systems is well suited to an examination of such impacts, as the thermal gradient within the longitudinal range of a particular species is likely to cover a range of optimality.

Difference in species density along the longitudinal gradient is certainly the most direct and inclusive measurement of the degree of optimality of the thermal environment; however, mechanisms behind this density response can take myriad forms. Thermal conditions have been linked to stream insect assimilation rates (Heiman and Knight 1975), larval development (Minshall 1978, Ward and Stanford 1982, Sweeney and Vannote 1986), timing of life history stages (Schaller 1968, Oberdorfer and Stewart 1977, Sweeney 1984, Rutherford and MacKay 1986, McElvay and Resh 1987) and recovery from disturbance (Sedell et al. 1990), all of which can influence reach-scale density patterns.

Considering the complexity of the thermal response among lotic macroinvertebrates, the basic bioenergetic approach presented in the Hall et al. (1992) model has the potential to be more useful than the fragmented analyses of these previous efforts. In focusing analysis on the

metabolism/temperature response of the focal organism, the most basic temperature-related response expressed at the level of the whole organism, this approach sets the foundation for all other temperature-related aspects of the biology of the insect. This response has been examined in previous studies as a potential basis for the distribution patterns of the hydropsychids (Hildrew and Edington 1979, Howell and Voshell 1982, Bales and Badcock 1987, Stanford et al. 1988, Roux et al. 1992, Guinand et al. 1994). Again, however, while authors are able to demonstrate differences in the metabolism/temperature responses of various hydropsychid species, these physiological data have been only loosely correlated to both larval-density and thermal patterns in the field.

The project

I designed this project to provide the foundation of research necessary to a larger evaluation of gradient-based distribution models in the Flathead-hydropsychid system. This design had 2 primary emphases: an examination of the in-stream longitudinal abundance pattern of 1 hydropsychid species relative to key environmental gradients within the longitudinal range of that species, and an examination of interspecific differences in the metabolic response to temperature of 3 hydropsychid species. Although complete explanations of the significance of the results of these 2 sub-projects are provided in the following chapters, it is important that their roles within the larger evaluation be made clear.

The project presented in Chapter 1 was designed to answer the question of whether or not our general hypothesis on the suitability of the Flathead-hydropsychid system to the evaluation of a gradient-based distribution model is correct. The validity of this hypothesis is upheld by a density response of the focal species, *Parapsyche elsis*, along the longitudinal gradient of the stream resembling the Gaussian response curve. Such a response sets the foundation for analysis of key environmental gradients within the longitudinal range of the focal species. In the context of this gradient analysis, the use of the Flathead-hydropsychid system is

further validated by an indication that the specific environmental gradients producing the longitudinal abundance response are both identifiable and quantifiable.

The metabolism/temperature curves for *Parapsyche elsis*, *Arctopsyche grandis* and *Hydropsyche cockerelli*, presented in Chapter 2, represent the first step in validating Hall et al.'s (1992) gradient-based bioenergetic model of species distribution. These curves represent a direct quantification of the energy costs placed on the individual by its thermal environment (Fig. 2). In conjunction with experimentally derived assimilation/temperature curves, the M/T curves can be used to determine the temperature-related net energy-profit curve of each species. This use of the M/T curves is, therefore, an expansion upon their significance as indicators of species-specific metabolic adaptation to temperature.

The results of the 2 projects composing this thesis are encouraging in the context of evaluating both population and individual-based models of species distribution along multiple environmental gradients. The abundance pattern of *Parapsyche elsis* does approximate a normal, or Gaussian distribution along the longitudinal gradient of the stream, and our analysis of associated environmental gradients points to the thermal gradient as playing a significant role in structuring this pattern. These results set the stage for the examination of interspecific differences in metabolism/temperature response presented in Chapter 2, the probable, whole-organism scale mechanism underlying the longitudinal density pattern of *P. elsis*. A next step in this research is to conduct paired analyses of species-specific longitudinal density patterns and associated environmental gradients for *A. grandis* and *H. cockerelli*. Metabolism/temperature curves should also be generated for the remaining hydropsychid species in this longitudinal replacement series, and a protocol for the assimilation/temperature experiments should be developed. Given continued effort, and the success of this project, it is likely that the results of this work will produce an evaluation of gradient-based models of species distribution and abundance which is both empirically and theoretically powerful.

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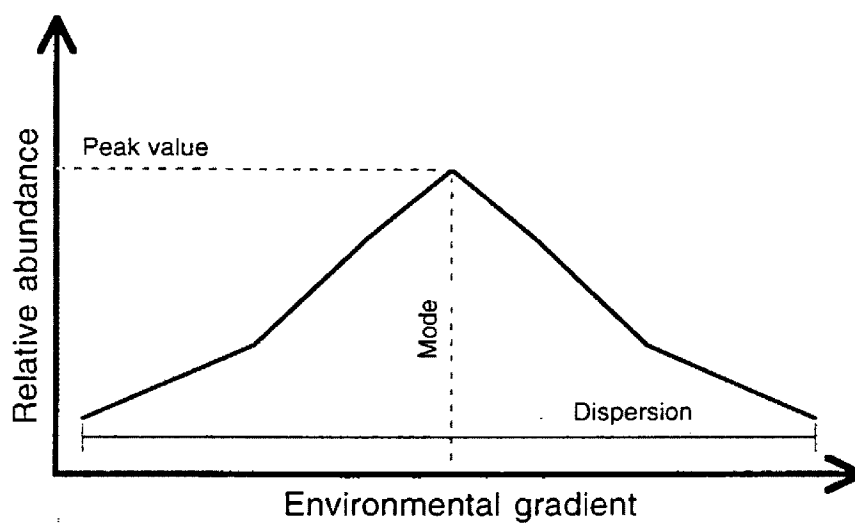


Fig. 1. Theoretical relative abundance curve of a species along an environmental gradient (Gause 1930) with the peak value, mode and dispersion labeled.

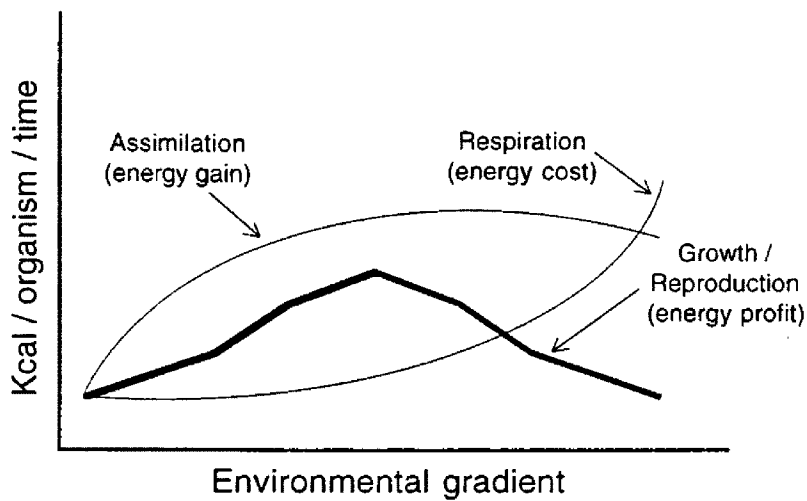


Fig. 2. Growth of a poikilotherm in response to an environmental gradient (from Hall et al. 1992). The commonly observed bell-shaped growth curve is hypothesized to be the net difference between metabolic energy expenditures (respiration) and gains (assimilation), realized as individual growth and reproduction (energy profit).

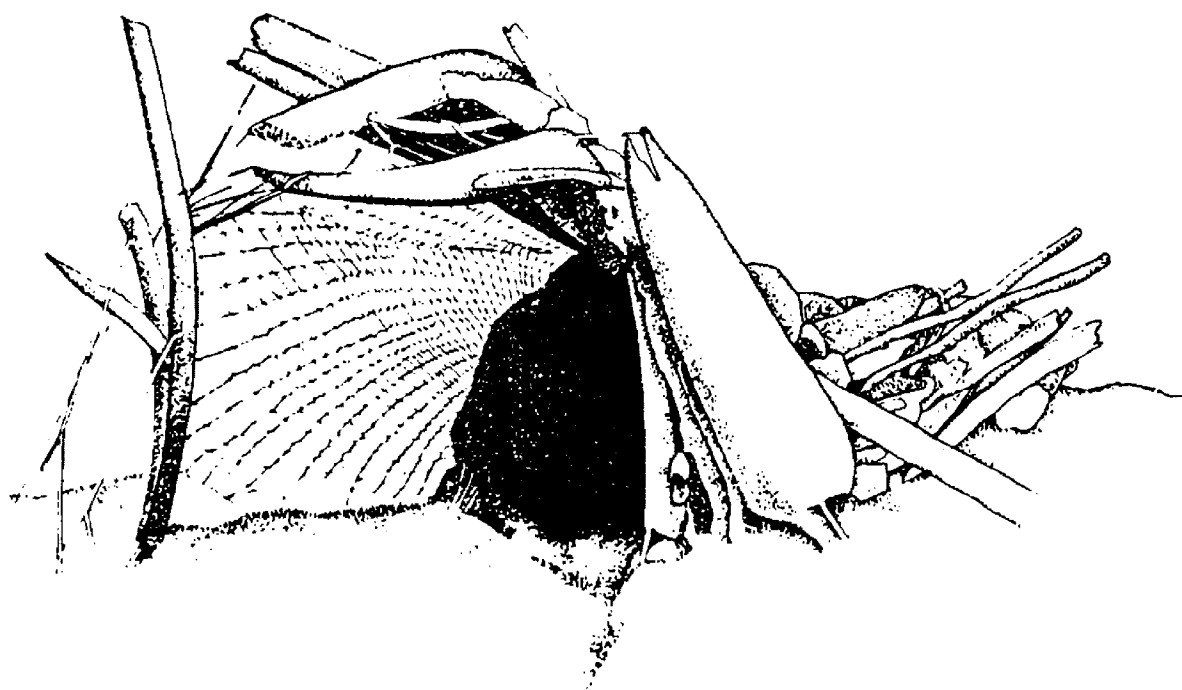


Fig. 3. Typical hydropsychid retreat and capture net (from Wiggins 1996).

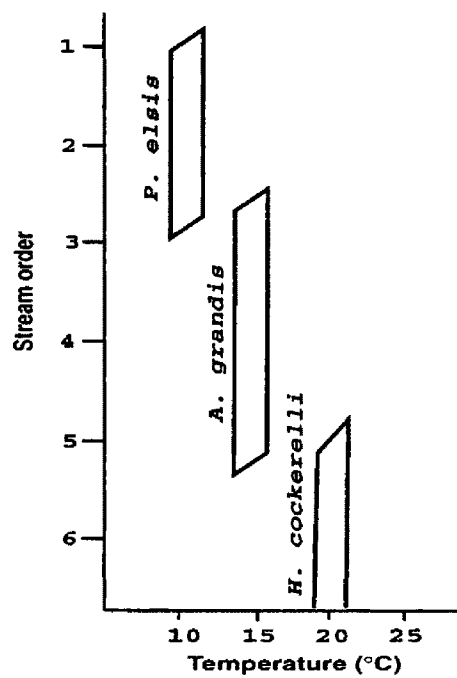


Fig. 4. Distributions of 3 hydropsychid caddisfly larvae (*P. elsis*, *A. grandis*, and *H. cockerelli*) relative to stream order and approximate maximum summer temperature (°C) of occupied reaches in the Flathead Basin, Montana.

Chapter 2

An evaluation of in-stream longitudinal density of *Parapsyche elsis* (Trichoptera: Hydropsychidae) along multiple environmental gradients.

Abstract

We quantified in-stream longitudinal density of *Parapsyche elsis* (Trichoptera: Hydropsychidae) and accompanying gradients in substrate particle size, seston concentration, water velocity and water temperature in the McDonald drainage, Glacier National Park. Our results indicate that the density pattern of *P. elsis* approximates a normal distribution along the longitudinal gradient of the stream, thereby corresponding to theoretical models of species distribution along multiple environmental gradients (Gause 1930, Hall et al. 1992). Of the environmental conditions examined, only stream temperature exhibited a significant gradient ($p < 0.05$) within the longitudinal range of *P. elsis*. Based upon these data, the stream-temperature gradient is shown to be the primary determinant of the longitudinal distribution of this species and a likely basis of the evolutionary radiation and current distribution of hydropsychid caddisflies. We believe that the longitudinal context offers an extremely important, yet untapped perspective on lotic macroinvertebrate distribution, potentially useful to both applied and theoretical research in these systems.

Introduction

Net-spinning caddisflies (Trichoptera: Hydropsychidae) commonly occur in replacement series corresponding to the longitudinal gradient of stream and river systems (Hildrew and Edington 1979, Ross and Wallace 1982, Alstad 1986, Bales and Badcock 1987, Tachet et al. 1992, Guinand et al. 1994). This is the case in the Flathead Basin, northwestern Montana, where six hydropsychid species are commonly distributed along the stream continuum (Hauer and Stanford 1982a, 1982b, Stanford et al. 1988). Due to the high degree of ecological similarity among the species composing these series, a significant effort has been made to identify factors determining interspecific differences in longitudinal distribution (Table 1). Results of these efforts have been used to support the importance of particular environmental conditions in structuring both current patterns of hydropsychid distribution and the evolutionary radiation of these species.

While informative with regard to the specific questions addressed, the broader ecological implications of previous studies are undermined by the narrow range of environmental variables considered, and a lack of quantitative data on species specific longitudinal distribution and density patterns which directly support models of resource partitioning and utilization. In an attempt to both synthesize and evaluate the results of these previous studies, we have developed an approach to the question of Hydropsychid distribution combining thorough longitudinal density data on one hydropsychid species, *Parapsyche elsis* Milne, with data for an array of potentially important environmental conditions within the longitudinal range of that species. Analysis of these data reveals the relative importance of the selected environmental conditions in determining species distribution and density. This analysis also improves understanding of interspecific differences in longitudinal distribution among the hydropsychids by revealing those environmental conditions most critical in driving niche separation and subsequent speciation.

We hypothesized that, at the sub-basin scale, the density pattern of *Parapsyche elsis* would approximate a normal distribution along the longitudinal gradient of the stream. According to general models of species distribution along environmental gradients (Gause 1930, Gauch 1982, Hall et al. 1992)(Fig. 1), this density pattern should exhibit a peak somewhere within the longitudinal range of the species, with density tapering off both upstream and downstream of that

peak. The ecological implications of this pattern are significant, as it implies a bioenergetic and/or behavioral response to resource gradients in the stream, with peak density occurring within the optimal range of these conditions.

Based upon both personal experience in the Flathead Basin and prior publications exploring similar questions (see Table 1), we identified 4 environmental variables as probably most important in structuring hydropsychid distribution: substrate particle size, seston concentration, water velocity, and water temperature. We predicted that stream temperature would be the only environmental condition exhibiting a significant gradient within the longitudinal range of *P. elsis*, thereby establishing its primacy in structuring longitudinal distribution in this hydropsychid species.

Methods

Study Site

The McDonald drainage is part of the Flathead River Basin, northwestern Montana, and is located entirely within the boundaries of Glacier National Park (Fig. 2). The headwaters of this tributary of the Middle Fork of the Flathead River descend from the western flank of the Continental Divide at an elevation of approximately 2100 meters. For this work we limited all sampling to the portion of drainage upstream of Lake McDonald, at an elevation of 975 meters. McDonald Creek above the lake is a 4th order stream with a spring-snowmelt dominated hydrograph. Peak discharge in the McDonald basin occurs in late May or early June.

Like the majority of the headwater systems in the Flathead Basin, the McDonald drainage displays a significant elevational gradient. This gradient facilitates work such as ours by geographically condensing the stream continuum and associated environmental gradients. Following the determination of the longitudinal range of *P. elsis* in this drainage through qualitative sampling efforts, the locations of 8 sampling sites were selected to cover this range. Our sampling sites were arrayed in a continuous series, covering an elevational range of 540 meters and a river distance of 34 kilometers (Fig. 3). Over this distance the creek is canopied by a predominantly coniferous overstory.

Study species

Parapsyche elsis is a large bodied hydropsychid (Family Hydropsychidae, Subfamily Arctopsychinae). Studies have described a semivoltine life cycle for this species (Smith 1968, Givens and Smith 1980), with pupation occurring between May and early August and emergence lasting from late June through early September. Observations made over the course of this study support these findings. A thorough description of the phenology of this species has not been previously been published (see Appendix 2 for larval instar discrimination by interocular distance).

P. elsis is believed to be restricted to the western Cordillera of North America, with a range extending from the Yukon and Mackenzie Mountains of the Northwest Territories of Canada south to California, Utah and Colorado (Givens and Smith 1980, Nimmo 1987, Ward and Kondratieff 1992). This species does not appear to occur in the coastal mountain ranges of the west (Givens and Smith 1980). The broad scale restriction of this species to western North America is a pattern characteristic of many stenothermic species. Indeed, where *P. elsis* has been documented it is associated with low-order, cold streams (Smith 1968, Wiggins 1977, Hauer and Stanford 1982a, Williams 1991, Ward and Kondratieff 1992). Within the Flathead Basin, *P. elsis* has been identified as the dominant member of the net-spinning collector functional group in 1st and 2nd order streams, and is typically replaced by *Arctopsyche grandis* (Banks) in 3rd and 4th order streams (Hauer and Stanford 1982a, Stanford et al. 1988).

Collection of larvae

To determine mean yearly density of *P. elsis* at the 8 sampling sites we conducted quantitative benthos sampling at the study sites in July, August, September and October of 1996, and March of 1997. Sampling in winter was prevented by deep snow and ice cover, and in late spring by heavy runoff conditions. We were unable to collect benthos samples from site 1 during the October and March efforts due to the heavy snow conditions in the basin on these dates.

We employed a stratified random sampling method in this effort. On each sampling date 3 replicate samples were taken at each site. Each sample consisted of a collection of all insects within a 0.25 m² quadrat of the stream bottom. Substrate particles within this quadrat were

vigorously disturbed to release attached larvae. We used a modified kick-net to collect the insects (Hauer and Resh 1996). These samples were processed in the lab using standard picking procedures. All hydropsychid larvae collected were keyed to species and measured for interocular distance to determine seasonal instar density at each site.

Measurement of environmental gradients

A stratified random sampling structure was used to quantify conditions of substrate particle size and water velocity at each of the sampling sites. We determined mean substrate particle length from 3 replicate samples taken at each site using a grid method modified for large-substrate systems (Sheldon 1980). Mean water velocity at a distance of 5 centimeters above the primary substrate was calculated from 9 replicate samples at each site. All water velocity measurements were taken during a two-day period in August of 1996.

One-liter water samples were collected from the thalweg of each sampling site in conjunction with the August, September, October and March benthos sampling efforts. These water samples were filtered onto pre-weighed glass fiber filters (Wattman® GN-6) which were then desiccated and weighed to determine gross seston concentrations as dry mass at each site over the sampling period. These filters were then analyzed for Carbon and Nitrogen concentrations in a Fisons® 1500 CHN analyzer.

Results of this analysis were used to calculate mean C:N at each site over the sampling period. In lotic systems, the C:N ratio of food resources has been shown to be inversely related to nutritional value and assimilation efficiency (McMahon 1975, Pandian and Marian 1986). By focusing analysis on the gross concentration and elemental composition of the seston, we believe that ours represents both an objective and efficient method for detecting changes in the fundamental nature of this food resource along the longitudinal gradient of the stream.

We placed temperature loggers at each sampling site for a 27-day period in late summer of 1996. These loggers were programmed to record water temperature every hour. Data collected by these loggers were used to calculate mean temperature at each site over the period of record.

Analysis

Benthic data were used to calculate mean 1st year (Instars 1,2 and 3) and 2nd year (Instars 4 and 5) *P. elsis* density at each site over the sampling period. We focused our analysis on 2nd year larvae because they provide a superior indication of the long-term environmental suitability of a site than 1st year larvae. However, data on the longitudinal density pattern of 1st year larvae are presented in our results, as they provide insight on potential drift and female egg-laying behavior in this species, as well as information on the the high mortality rate of these early instar larvae.

We evaluated the longitudinal density pattern of 2nd year *P. elsis* for evidence of a site of maximal density flanked by sites exhibiting regularly decreasing density in both the upstream and downstream directions. We quantified gradients in each of the selected environmental conditions within the longitudinal range of this species by conducting linear regression analyses on each of these data sets. Condition values were regressed against both the distance from headwaters and elevation of the sampling sites. P-values, corresponding to a 95% confidence interval, were calculated for the slopes of these regression lines to describe the significance of each gradient within the longitudinal range of *P. elsis*. Those environmental conditions displaying no significant gradient were eliminated as potential bases for the longitudinal density pattern.

Results

Larval density

Mean yearly density of 2nd year *P. elsis* larvae in the McDonald drainage did approximate a normal distribution along the longitudinal gradient of the stream (Fig. 4). Peak density occurred at site 3, at an elevation of 1350 meters and a distance of 5.67 kilometers from the headwaters. Density declined both upstream and downstream of this site. The decrease in *P. elsis* density was significantly more attenuated in the downstream direction, leading to an upstream skew to the peak of this density curve.

The longitudinal density pattern of 1st year *P. elsis* at our sampling sites (Fig. 4) displays a peak at site 2, located at an elevation of 1411 meters and a distance of 4.28 kilometers from the

headwaters of the drainage. Density of 1st year *P. elsis* larvae decreased dramatically upstream of this site, while downstream of site 2 mean density fell steadily, reaching a basal level at sites 6 through 8.

Environmental gradients

The results of our gradient analysis are presented in Figures 5 and 6. Regression analysis of these environmental data revealed no significant gradient ($p > 0.05$) in substrate particle size, water velocity, or seston C:N ratio in relation to elevation or river distance. However, the water temperature gradient within the longitudinal range of *P. elsis* was highly significant relative to both elevation ($p < 0.001$) and river-distance ($p = 0.011$).

Discussion

Larval density patterns and response to environmental gradients

Our results strongly support the primacy of the stream temperature gradient in structuring the longitudinal density pattern of *Parapsyche elsis*. These results also illustrate the importance of the scale of observation in the expression of environmental gradients along the stream continuum. There most certainly exist gradients in water velocity, seston concentration and substrate size in streams of the Flathead system. However, these gradients are simply not expressed within the longitudinal range of *P. elsis*, and, therefore, can play no significant role in structuring the longitudinal distribution of this hydropsychid species.

Additional information on the downstream limit of the longitudinal range of *P. elsis* is provided by examining patterns of 1st and 2nd instar density at sites 6, 7 and 8 (Fig. 7). At these three sites we observed a complete die-off of 1st instar larvae over the course of the summer and fall. This was followed by an absence of 2nd instar larvae at sites 7 and 8 and an extremely low density of these larvae at site 6. This pattern differs from that of sites 2, 3 and 4, where we observed the unbroken progression of instar recruitment over the course of the sampling period. These results indicate that sites 6, 7 and 8 may represent significant population sinks within the

drainage, where 2nd year instar representation is maintained only by erratic downstream drift of larvae from upstream sites.

The abrupt upstream limit of the distribution of 1st year *P. elsis* larvae in the McDonald drainage suggests either an upstream limit to adult flight, or significant and rapid downstream drift among larvae hatching from eggs deposited at site 1. We believe that the second explanation is the most likely of the two, as we have collected *P. elsis* adults throughout the drainage.

Biotic factors

While this work had a definite abiotic emphasis, the roles of several biotic factors in structuring the longitudinal density pattern of *P. elsis* can also be addressed. Regarding the potential for interactions with *Arctopsyche grandis* influencing the longitudinal density pattern of *P. elsis*, it is crucial to acknowledge that the Gaussian distribution pattern of *P. elsis* is well established upstream of the appearance of *A. grandis* in the stream (Figs. 4 and 8). Second-year *A. grandis* larvae were found in very low density only at sites 6, 7 and 8 (Fig. 8), supporting a characterization of these sites as marginal habitat for both *A. grandis* and *P. elsis*. This pattern suggests that while biotic interactions between these two hydropsychids may play a role in determining the limit of downstream distribution in *P. elsis*, they play no role in the location of zones of maximal density within the longitudinal range of this species. Therefore, these interactions are, at best, secondarily important in structuring the hydropsychid longitudinal replacement series.

Regarding the potential for a predator gradient structuring the longitudinal density pattern of *P. elsis* in the McDonald drainage, neither our benthos data, nor available information on fish distribution in the drainage support this hypothesis. Density patterns of predatory stonefly (Plecoptera: Perlidae, Perlodidae, Chloroperlidae) and caddisfly (Trichoptera: Rhyacophilidae) species show that these groups were evenly distributed among our sampling sites. Likewise, fish distribution is believed to be both sparse and even throughout the McDonald drainage (Marnell 1988).

The longitudinal context in stream biomonitoring

The implications of the results of this project to the monitoring and conservation of stream biota are significant, particularly in the context of assessing the impact of basin-scale environmental alteration on these systems, such as that associated with climate change. The longitudinal perspective provided by our sampling design represents an ecologically robust context for the evaluation of monitoring results. Traditional lotic biomonitoring regimes are designed to evaluate community integrity and environmental impact at a stream-reach scale (Rosenberg and Resh 1993). Results of such efforts are valuable in assessing point impacts, and can be extrapolated to reaches of similar longitudinal location in the system. However, without a deliberate longitudinal emphasis in sampling structure the basin-wide significance of these results cannot be determined and potentially critical information, such as the impact of localized species declines or community disruption on basin-wide population viability, is lost.

The longitudinal density pattern of *P. elsis* offers three monitoring variables unique to such a longitudinally-oriented sampling structure; the mode, the peak value and the dispersion (Fig. 1). The mode of the longitudinal response curve of *P. elsis* represents the location of optimal thermal conditions, and can be monitored to track the species response to modifications of the thermal regime of the stream. The peak value and its difference from density values at adjacent sites indicate the degree of environmental specificity, in this case the thermal specificity, of the focus organism. The disparity between the peak density value of *P. elsis* and values from the adjacent upstream and downstream sites suggests that this species has a relatively narrow optimal range within the thermal gradient of the stream.

In terms of the dispersion or longitudinal range of *P. elsis*, we have already noted that the peak density of *P. elsis* is skewed toward the upstream limit of this range. The dramatic decline in 1st and 2nd year *P. elsis* density upstream of sites 2 and 3 (Fig. 4), respectively, belies an abrupt upstream limit to the distribution of this species. The distinct character of extreme-headwater streams in this system resulting from a preponderance of bedrock substrate, decreased allochthonous input, heavy winter snow cover and little or no overstory shading, suggests that this limit is based on a more complex gradient response than the thermal response

controlling longitudinal density. Therefore, modifications of the thermal regime of this system resulting in a shift of optimal temperatures to a position upstream of site 1 would likely result in the extirpation of *P. elsis* at the sub-basin scale. This scenario clearly establishes the importance of determining the position of peak longitudinal density within the longitudinal dispersion of this and other species in evaluating population sensitivity to basin-scale changes in climate or other factors potentially affecting thermal regimes.

Conclusion

To conclude, we believe it is important to consider zoogeographic distribution and density data such as these from an evolutionary perspective. The established significance of the thermal gradient in structuring longitudinal density in *Parapsyche elsis* lends support to the role of stream temperature in structuring the downstream evolutionary radiation of the hydropsychids. Employing Ross' (1967) model of downstream species radiation among the hydropsychids as a theoretical foundation, we propose that speciation events occurred in response to the thermal isolation of downstream subpopulations. This isolation was likely a result of the evolution of advanced physiological mechanisms permitting survival under the ever-broader thermal ranges of downstream habitats. We believe that previous work documenting the fundamental importance of ambient thermal conditions in ectotherm physiology and bioenergetics (Wigglesworth 1953, Bullock 1954, Hoffman 1984, Prosser 1973) and in the ecology and evolution of lotic 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.

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Environmental condition	Supporting publications
Substrate	Hildrew and Edington 1979, Hauer and Stanford 1981, Ross and Wallace 1982, Rutherford and MacKay 1985.
Water velocity	Philipson 1954, Haddock 1977, Ross and Wallace 1982, Tachet et al. 1992.
Seston	Williams and Hynes 1973, Wallace 1975a, 1975b, Fuller and MacKay 1980, Georgian and Wallace 1981, Alstad 1982, 1986, 1987, Ross and Wallace 1983, Thorp 1983, 1984, Thorp et al. 1986.
Water temperature	Hildrew and Edington 1979, Hauer and Stanford 1982a, Howell and Voshell 1982, Bales and Badcock 1987, Stanford et al. 1988, Roux et al. 1992, Guinand et al. 1994.

Table 1. Prior publications supporting the roles of substrate, water velocity, seston and water temperature conditions in determining patterns of hydropsychid distribution.

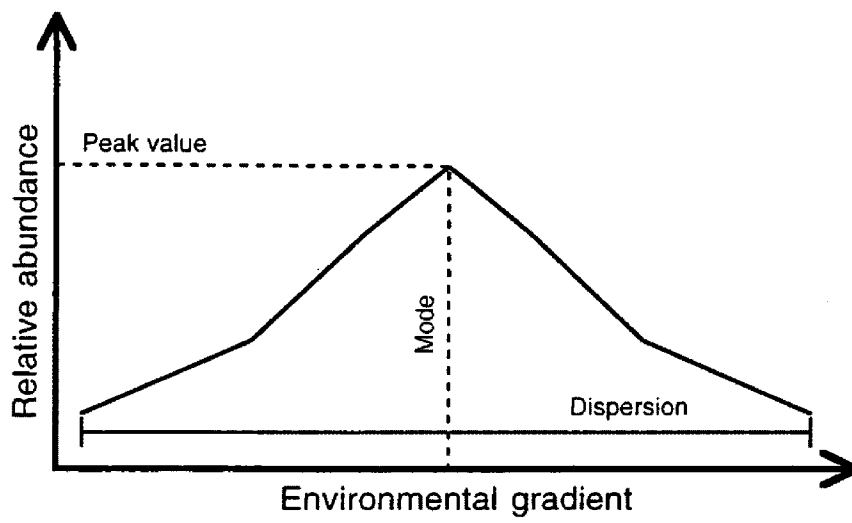


Fig. 1. Theoretical relative abundance curve of a species along an environmental gradient (Gause 1930) with the peak value, mode and dispersion labeled.

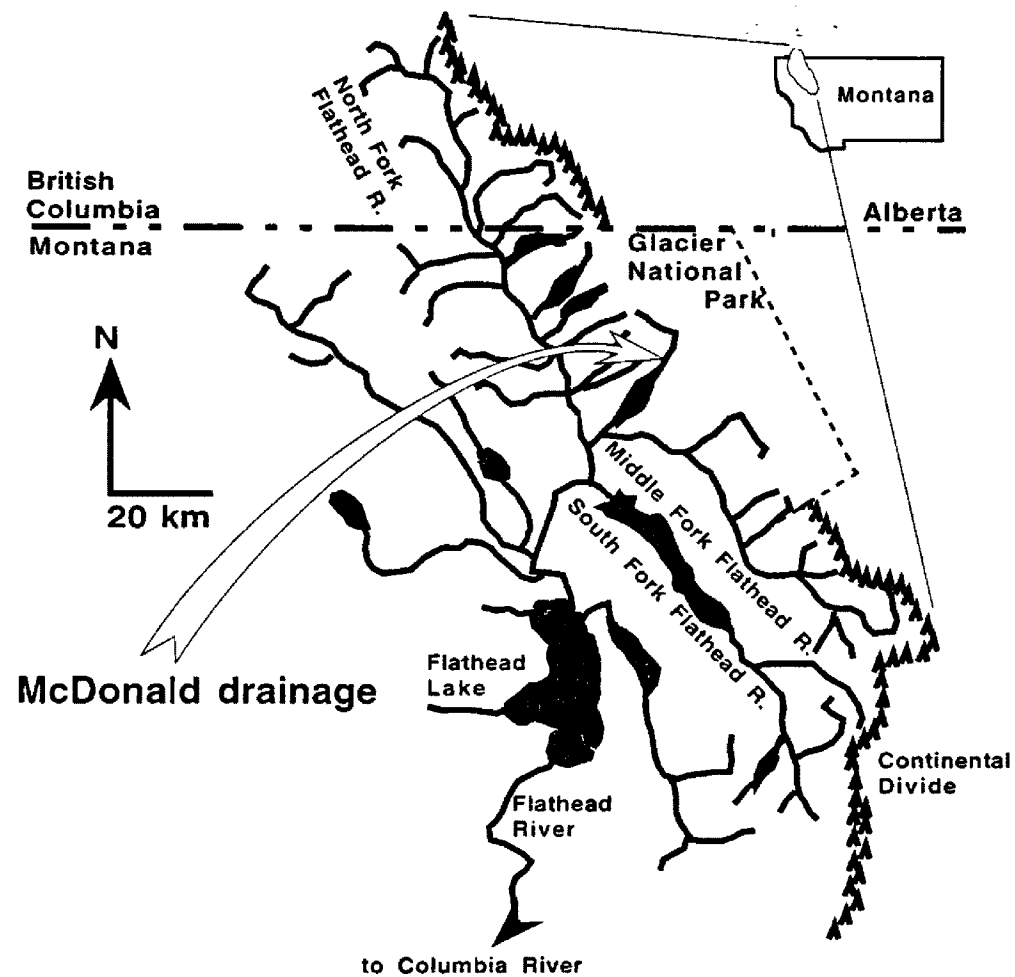


Fig. 2. Map of the Flathead Basin, northwestern Montana, with the location of the McDonald drainage.

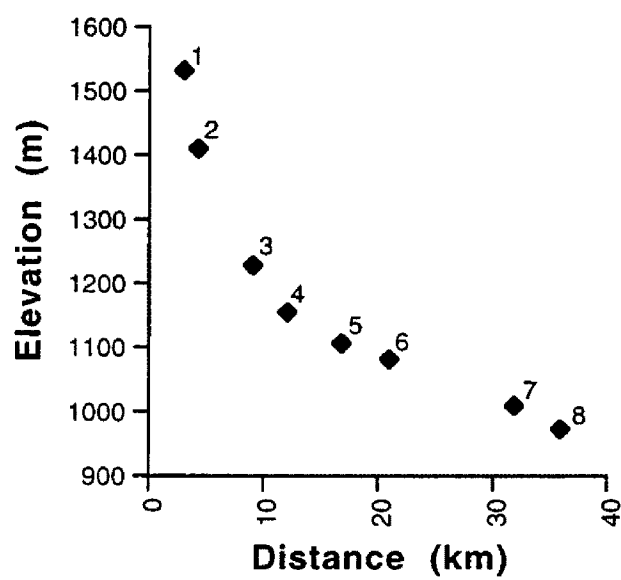


Fig. 3. Distribution of sampling sites in the McDonald drainage relative to elevation (m) and distance from headwaters (river-km).

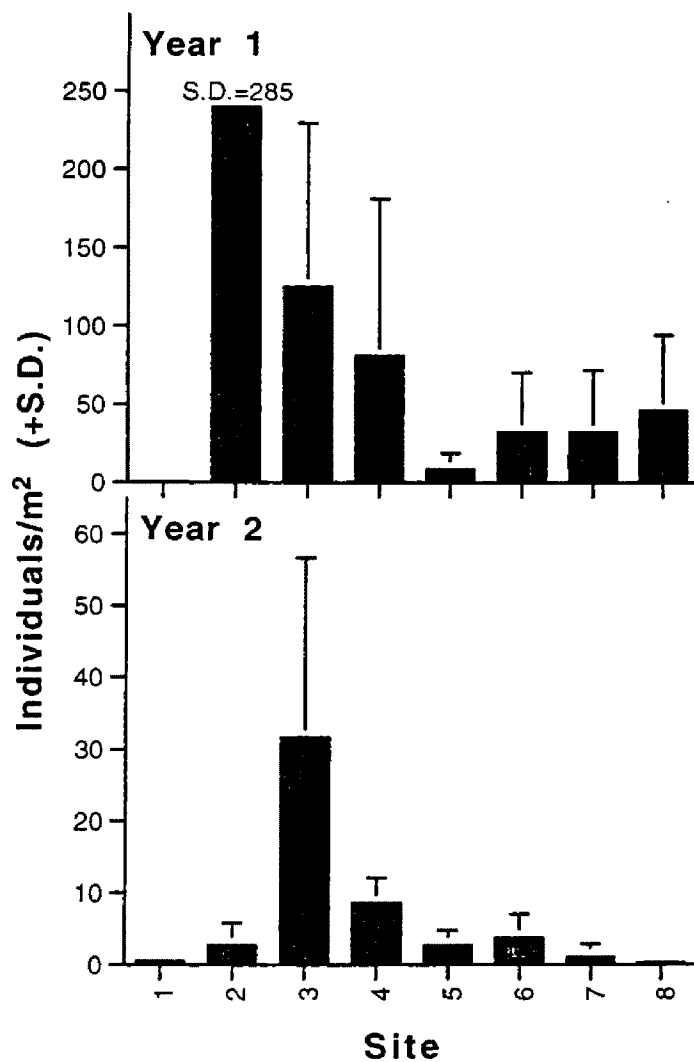


Fig. 4. Yearly mean density (ind./m²) of 1st year (Instars 1, 2 and 3) and 2nd year (Instars 4 and 5) *Parapsyche elsis* larvae at 8 sampling sites arrayed along the longitudinal gradient of the McDonald drainage, Glacier National Park, Montana.

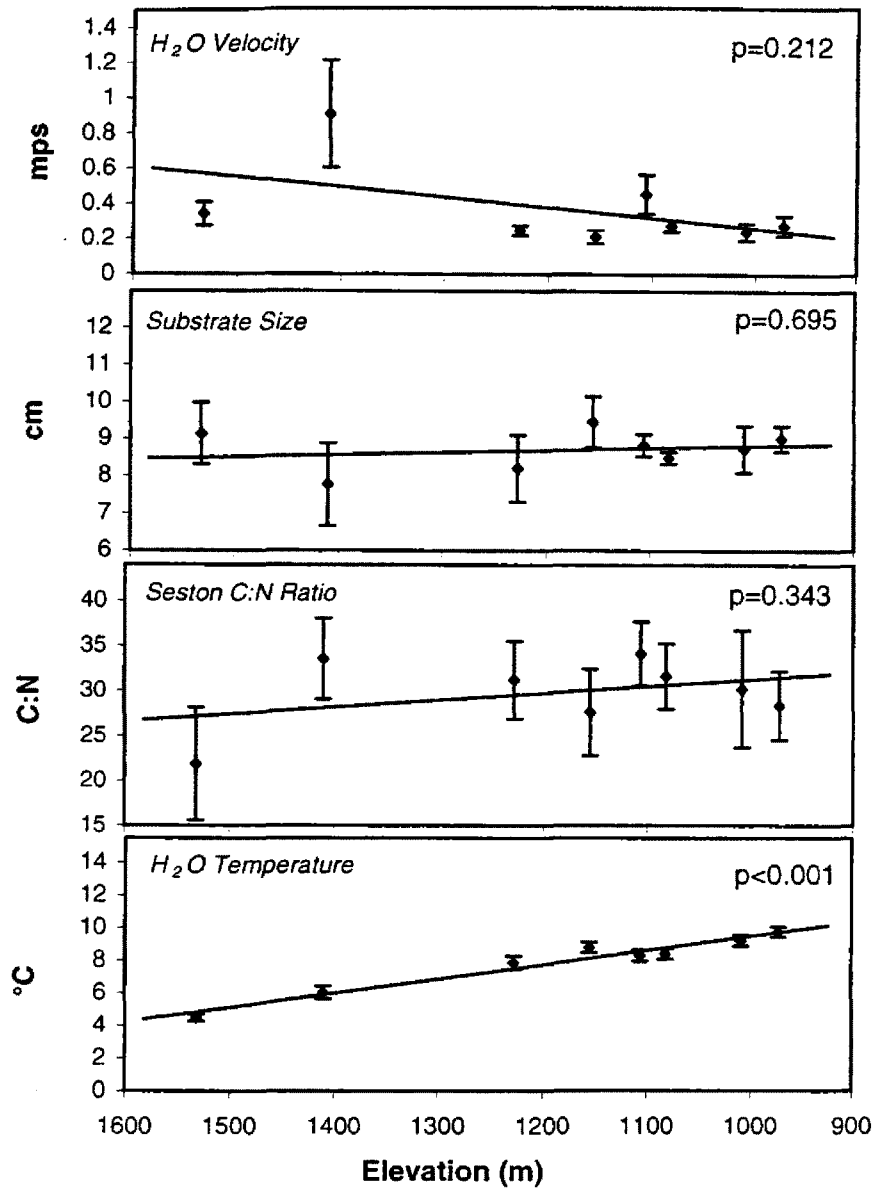


Fig. 5. Linear regression of water velocity (meters per second), substrate size (cm), seston C:N ratio, and water temperature (°C) against elevation of sampling sites. P-values for the slopes of the regression lines correspond to a 95% confidence interval. Horizontal bars represent standard error.

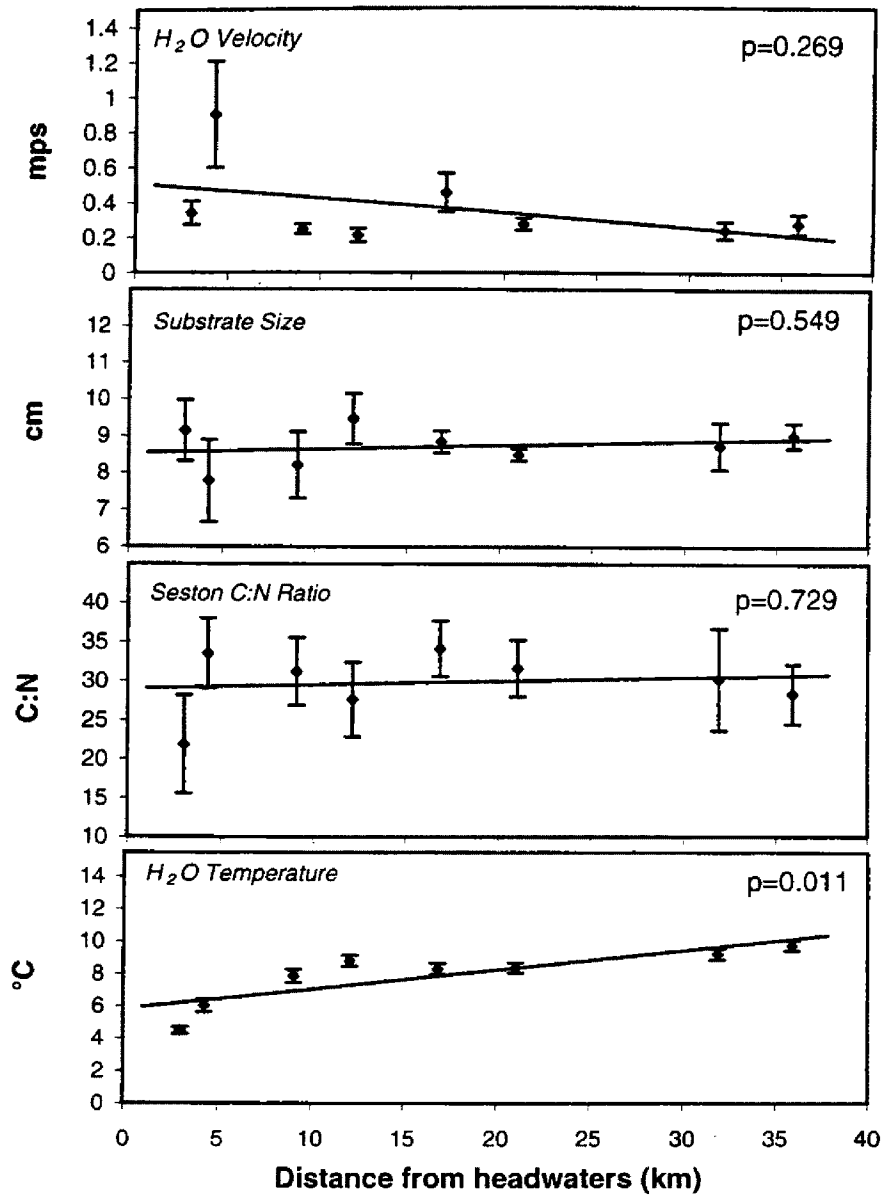


Fig. 6. Linear regression of water velocity (meters per second), substrate size (cm), seston C:N ratio, and water temperature ($^{\circ}C$) against distance from headwaters of sampling sites. P-values for the slopes of the regression lines correspond to a 95% confidence interval. Horizontal bars represent standard error.

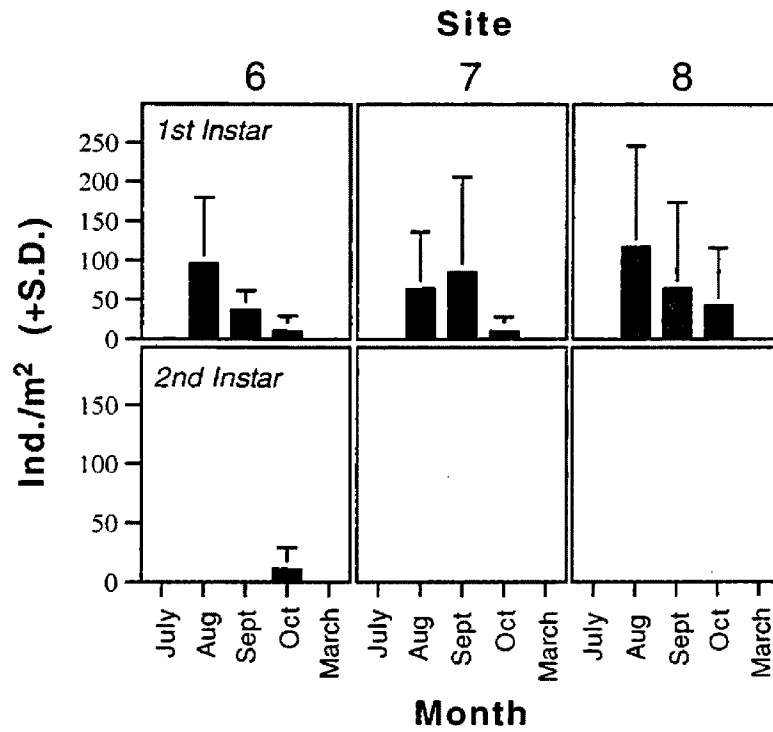


Fig. 7. Monthly mean density (ind./m²) of 1st and 2nd instar *Parapsyche elsis* larvae at sampling sites 6, 7 and 8.

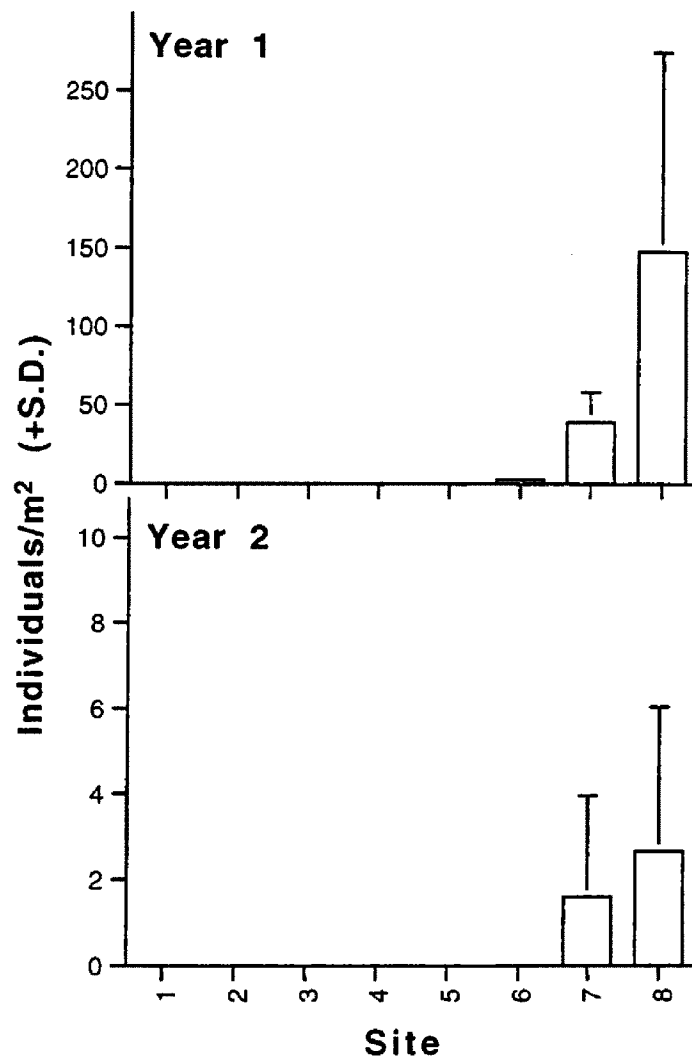


Fig. 8. Yearly mean density (ind./m²) of 1st year (Instars 1, 2 and 3) and 2nd year (Instars 4 and 5) *Arctopsyche grandis* larvae at 8 sampling sites arrayed along the longitudinal gradient of the McDonald drainage, Glacier National Park, Montana.

Chapter 3

The metabolism-temperature response in three larval hydropsychids (Trichoptera: Hydropsychidae): evidence for the thermal basis of in-stream longitudinal distribution.

Abstract

Parapsyche elsis, *Arctopsyche grandis* and *Hydropsyche cockerelli* occur in a longitudinal replacement series in 1st through 5th order streams of the Flathead Basin, northwestern Montana. During periods of metabolic activity, the thermal ranges of reaches occupied by *P. elsis* (5-10°C) and *A. grandis* (5-15°C) fall within biologically important (Weiser 1973, Roux et al. 1992) zones of temperature independence in the metabolism/temperature (M/T) curves of these species (Q_{10} =0.91 and 1.14, respectively). These zones define species-specific ranges of thermal tolerance which place each species within the thermal gradient of the stream continuum, and are evolutionarily linked to their energetically conservative life history strategies. The M/T curve of *H. cockerelli* displays temperature dependence (Q_{10} =7.65) throughout the thermal range (5-20°C) of occupied reaches during periods of metabolic activity. The thermally responsive metabolism of this species, and energetic investment in metabolic mechanisms permitting this responsiveness complement its rapid growth pattern and thermal habitat. Differences in the metabolic response to temperature and phenology among these species support a temperature-based model of the downstream radiation of hydropsychid species.

Introduction

Net-spinning caddisflies (Trichoptera: Hydropsychidae), occur in a longitudinal replacement series in the streams of the Flathead Basin, northwestern Montana (Hauer and Stanford 1982a, 1982b, Stanford et al. 1988). Similar replacement series have been documented among the hydropsychids of other North American and European river systems (Hildrew and Edington 1979, Ross and Wallace 1982, Alstad 1986, Bales and Badcock 1987, Tachet et al. 1992, Guinand et al. 1994) and significant effort has been devoted to determining possible mechanisms of resource partitioning underlying these distribution patterns (Wallace 1975, Malas and Wallace 1977, Ross and Wallace 1983, Thorp 1983, 1984, 1986, Alstad 1986, 1987, Tachet et al. 1992, Guinand et al. 1994). The species-specific characteristics of catchnet size and placement, food resource preference and metabolic response to stream temperature have been identified as potentially critical components of these mechanisms. Given evidence for a downstream trajectory in the evolutionary radiation of species in this group (Ross 1967), these characteristics are also important as potential causes of hydropsychid speciation and current diversity.

We propose that an ecophysiological model relating species-specific physiological adaptations to stream temperature is the most theoretically robust explanation of the observed longitudinal distribution patterns and hypothesized evolutionary radiation of the hydropsychids. While other authors have taken a similar approach in addressing questions of hydropsychid longitudinal distribution (Roux et al. 1992, Guinand et al. 1994), we believe that these efforts have been incomplete at the level of interpretation. Specifically, these authors claim to identify metabolism/temperature curve-types characteristic of species inhabiting each of the longitudinal zones (crenon, rithron and potomon) proposed by Illies and Botosaneanu (1963). This approach ignores the high level of geographic variability in the thermal characteristics of these zones, thereby decoupling the physiological data from actual stream temperature data for the sake of broad geographical generalization. In fact, as shown by Stanford et al. (1988), specific hydropsychid distributions follow thermal criteria regardless of the location of these conditions within the stream continuum.

Our approach places the ecophysiological data generated for the focal species within a bioenergetic context (see Hall et al. 1992) by including data on relative growth rates and the thermal conditions experienced by these species during the primary growth periods of their life cycles. We hope that by complimenting species-specific physiological data with equally specific ecological and phenological information we may reduce much of the ambiguity associated with the interpretation of M/T curves and increase the ecological pertinence of our conclusions (Bullock 1954, Prosser 1973, Hoffman 1984, Hill and Wyse 1989).

Materials and methods

Study Site

The Flathead River Basin (Fig. 1) is located along the west slope of the Continental Divide in heavily glaciated areas of northwestern Montana and the southeastern corner of British Columbia. There are 3 major tributaries of the Flathead River: the unregulated North and Middle Forks, and the South Fork, which is regulated by the Hungry Horse Dam. The mean annual flows of these tributaries are 85, 84, and 101 m³/s, respectively. Each is a 5th order river with cobble and small-boulder substrata. A dominant geomorphic pattern among streams of the Flathead Basin is the alternation of confined and unconfined reaches which, combined with the large-cobble and bedrock substrata of the basin, results in complex hyporheic flow pathways (Stanford and Ward 1993). Headwater streams originate at elevations of as much as 3000 meters. The entire system has a spring-snowmelt dominated hydrograph, with peak discharge occurring in late May or early June. Prior work in this system has documented a high degree of similarity among physiochemical parameters such as temperature, alkalinity, pH and flow in the non-regulated sub-basins of this system (Hauer and Stanford 1981).

Larval distribution along the thermal gradient

Data on the longitudinal distribution of the focal species in the Flathead Basin were obtained from 2 sources: prior quantitative, time-series sampling of sites throughout the basin (Hauer and Stanford 1981, 1982a, 1982b, Stanford et al. 1988), and sampling along the

continuum in the pristine McDonald drainage, Glacier National Park (Fig. 1). Our sources for data on the thermal gradient of streams in the Flathead Basin were similar, with initial data coming from Hauer and Stanford's (1981, 1982a, 1982b) earlier work in the system, and recent data provided by temperature loggers placed in the McDonald drainage.

Parapsyche elsis Milne, in the subfamily Arctopsychinae, is the dominant member of the net-spinning collector functional group in 1st and 2nd order streams of the Flathead Basin (Fig. 2), where maximum summer temperatures rarely exceed 12°C and annual degree day accumulation is between 800 and 1600. The broad-scale restriction of this species to western North America is a pattern characteristic of many stenothermic stream macroinvertebrate species (Williams 1991). The phenology of *P. elsis* in the Flathead system (Fig. 3) is characterized by a semivoltine life cycle with gradual growth occurring between March and October.

Arctopsyche grandis (Banks), also in the subfamily Arctopsychinae, replaces *P. elsis* in 3rd and 4th order streams of the Flathead Basin and remains the dominant hydropsychid into the 5th order rivers (Fig. 2). Within the longitudinal range of this species summer stream temperatures extend to between 15 and 18°C, and annual degree day accumulation is between 1600 and 2200. The phenology of this species is very similar to that of *P. elsis*, characterized by a semivoltine life cycle and gradual growth occurring between March and October (Fig. 3).

Hydropsyche cockerelli Banks, in the subfamily Hydropsychinae, appears in the 5th order rivers of the Flathead Basin (Fig. 2). The distribution of this species extends downstream into the 6th order mainstem Flathead River, where maximum summer stream temperatures reach between 20 and 23°C, and annual degree day accumulation is between 2300 and 2500. This species is univoltine in the Flathead Basin. Data on *H. cockerelli* phenology illustrate an extremely rapid growth rate relative to that of the upstream species (Fig. 3). Especially rapid growth in this species occurs between the months of July and October, a period closely corresponding to the peak in the yearly thermograph. In winter, stream temperatures drop below 5°C throughout the Flathead Basin; however, our data suggest that this is a period of relative metabolic inactivity in these 3 species, during which little or no growth occurs.

Respirometry

P. elsis and *A. grandis* individuals used in these experiments were collected at sites in the McDonald drainage (Fig. 1) where the two species coexist. *H. cockerelli* was collected at the confluence of McDonald Creek and the Middle Fork of the Flathead River, where it coexists with *A. grandis*. All individuals were collected as 5th instar larvae in September and October of 1996. There was no difference in the mean wet weights of *P. elsis* and *A. grandis* larvae used in these experiments. The *H. cockerelli* larvae are significantly smaller than the two Arctopsychine species (Fig. 4).

Respirometry experiments were conducted at 5, 10, 15, 20 and 25°C. Each individual was placed in a flow-through acclimation chamber maintained at the experimental temperature for 36 hours prior to the collection of respirometry data. In all cases, a removable mesh frame in each chamber was used by the larva for net attachment. At the time of the experiment the mesh frame and larva were removed from the acclimation chamber and placed in a 13 mL sealed vessel constructed of high-density polyethylene (see Appendix 1 for vessel design). 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 temperature was maintained by submersing the vessel in a controlled water bath.

Oxygen concentration in the respirometry vessel was sampled every 3 seconds over a 1-hour period with the use of a high-sensitivity oxygen meter (Strathkelvin Instruments®, model #78). The oxygen probe was embedded in the ceiling of the respirometry vessel. A thermocouple, also embedded in the ceiling of the vessel, allowed for the continuous monitoring of water temperature over the course of the experiment. This experimental methodology permitted the elimination of the temperature stabilization period occurring at the onset of each experiment and other experimental anomalies from subsequent calculations of oxygen consumption rates. We believe that the precision of this method is superior to that of the traditional closed-bottle method for aquatic respirometry in which oxygen consumption rates are determined from only initial and final oxygen concentration values, resulting in the possible

overestimation of oxygen consumption rates (Kamler 1969, Dries et al. 1979, Gnaiger and Forstner 1982).

Results

Results of our respirometry experiments are presented in Fig. 5 and Table 1. The metabolism/temperature curve of *P. elsis* displayed a distinct zone of temperature independence between 5 and 10°C ($Q_{10}=0.91$). Between 10 and 25°C this curve exhibited temperature dependence ($Q_{10}=2.34$). The position of the temperature-independent portion of this curve corresponds closely to the thermal range of reaches occupied by this species in the Flathead Basin during periods of metabolic activity.

The M/T curve of *A. grandis* is remarkably similar to that of *P. elsis*. However, in this species the zone of temperature independence extended between 5 and 15°C ($Q_{10}=1.14$), corresponding to the increased range of temperatures experienced by this species within its longitudinal range. The temperature dependent portion of this curve, between 15 and 25°C, displayed a Q_{10} response of 1.88. *P. elsis* and *A. grandis* have similar total metabolic amplitudes (Table 2).

Between 5 and 20°C, the M/T curve of *H. cockerelli* exhibited a high degree of temperature dependence ($Q_{10}=7.65$). The level section of this curve, between 20 and 25°C ($Q_{10}=0.99$), likely represents the upper limit of the metabolic range of this species, as opposed to an adaptive metabolic response. The extremely low oxygen consumption rate of this species at 5°C (0.015 mgO₂/g wet weight/hr), and subsequent high Q_{10} response between 5 and 10°C (67.85) suggest a lower metabolic limit between 5 and 10°C. The occurrence of this lower metabolic limit and its negative behavioral consequences are supported by Fuller and MacKay's (1980) observation that *Hydropsyche* species cease to maintain nets at temperatures below 5°C. The total metabolic amplitude of this species is more than twice that of both *P. elsis* and *A. grandis* (Table 2).

Discussion

The remarkably close correlation between zones of temperature independence in the M/T curves of *P. elsis* and *A. grandis* and the thermal conditions of their longitudinal ranges strongly supports the argument of a relationship between thermal regime and distribution among these species. In both species, the limit of downstream distribution occurs where stream temperatures exceed those defining the upper limit of these zones, at approximately 10°C for *P. elsis* and at 15°C for *A. grandis*.

Ample support for the significance of zones of temperature independence in ectotherm physiology can be found in the literature (Weiser 1973, Roux et al. 1992). This significance is based upon the thermal specificity of enzymes involved in fundamental metabolic processes of these organisms, with the zone of temperature independence illustrating this specificity at the whole-organism level (Somero and Hochachka 1971, Prosser 1973, Hazel and Prosser 1974, Somero 1978, 1995, Huey and Bennett 1990). Temperature dependent portions of the M/T curves of these organisms likely correspond with sub-optimal thermal conditions under which enzymes do not function correctly and survival is impossible.

The metabolism/temperature curve of *H. cockerelli* implies a metabolic constitution fundamentally different from that of *P. elsis* and *A. grandis*. This species is able to maintain a relatively rapid growth rate under thermally mediated fluctuating metabolic conditions, and under a broader range of temperatures than that experienced by either of the Arctopsychinae. To accomplish this, *H. cockerelli* must possess metabolic mechanisms that are functionally stable under a wide array of both temperatures and rates. Although the precise pathway by which this functional stability is achieved is not revealed at this whole-organism scale of experimentation, enzyme polymorphism is a strong possibility (Hoffman 1984). In this species, the limit of downstream distribution is defined by the leveling of the M/T curve at 20°C, the upper limit of its metabolic range.

The interpretation of the M/T curves of *P. elsis* and *A. grandis* and *H. cockerelli* is not complete without also considering the phenology of these species. Growth in *P. elsis* and *A. grandis* occurs at an energetically conservative rate (Fig. 3), a direct function of the M/T response

and, more basically, the energetically conservative metabolic mechanisms of these species and their associated maintenance costs. From an evolutionary perspective, we interpret the energetic conservatism of these species as a result of their cold-water, size-beneficial habitats, where a high portion of an individual's energy budget must be invested in maintenance, at the cost of both physiological complexity and reproductive output (Begon 1985, Begon et al. 1990).

The phenology and M/T response of *H. cockerelli* represent a contrasting life history strategy in which a relatively warmer thermal environment permits investment in more complex metabolic mechanisms, allowing for rapid growth and higher potential reproductive output. The significantly closer taxonomic relationship between *P. elsis* and *A. grandis*, both belonging to the subfamily Arctopsychinae, than between these species and *H. cockerelli*, subfamily Hydropsychinae, supports an evolutionary basis to the divergent life history and ecophysiological strategies of these 3 species.

Set in a bioenergetic context, the relationship between the M/T curves presented here and the patterns of distribution and abundance which form the hydropsychid longitudinal replacement series in the Flathead Basin becomes clear. As suggested by Hall et al. (1992), the metabolic-rate response curve of a species, such as the M/T curves presented here, represents an energetic cost curve for that species along the resource gradient constituting its environment (Fig. 6). The assimilation-rate response curve represents the energetic gain curve of that species over the same environmental gradient. The difference between these two curves forms a bell-shaped energetic profit curve for the species which is manifest, at the level of the individual, as rates of growth and reproduction, and, at the level of the population, as relative abundance. We believe that the thermal gradient of the stream is the primary environmental gradient structuring this energetic balance among the hydropsychids, and that by pursuing a joint analysis of physiological response to temperature and longitudinal distribution patterns among the hydropsychids, this line of research will serve as a direct evaluation of the bioenergetic approach to species distribution proposed by Hall et al. (1992).

In conclusion, these data establish a clear relationship between the distribution of *P. elsis*, *A. grandis* and *H. cockerelli* within the thermal gradient of the Flathead Basin and their

metabolic response to temperature. These results provide strong support for the utility of such ecophysiological data in answering basic questions of lotic macroinvertebrate distribution, and serve as a valuable foundation for a bioenergetic analysis of species distribution and abundance. It must be acknowledged that the ecological significance of the physiological data presented in this paper is only revealed by including precise thermo-ecological and phenological information in their interpretation. We strongly agree with Roux et al. (1992) in their assertion that such research would benefit from a shift in the level of investigation to the lower levels of organization than that of the whole organism, where the precise physiological mechanisms conferring thermal adaptation might be identified.

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	<i>P. elsis</i>				<i>A. grandis</i>				<i>H. cockerelli</i>			
°C	n	x	SE	Q ₁₀	n	x	SE	Q ₁₀	n	x	SE	Q ₁₀
5	4	0.0581	0.0050	0.9059	4	0.0875	0.0067	0.5586	3	0.0152	0.0183	67.8456
10	3	0.0553	0.0021	2.5960	4	0.0654	0.0204	2.3147	4	0.1252	0.0599	2.2548
15	4	0.0891	0.0192	2.3435	4	0.0995	0.0108	3.4086	4	0.1880	0.0157	2.9208
20	4	0.1364	0.0084	2.1029	4	0.1837	0.0135	1.0329	4	0.3213	0.0198	0.9907
25	3	0.1978	0.0567		3	0.1867	0.0128		4	0.3198	0.0545	

Table 1. Oxygen consumption of 3 hydropsychid caddisfly larvae. °C=Temperature, n=number of larvae, x=mean O₂ consumption in mg O₂/g wet weight/hour, S.E.=standard error, Q₁₀ determination by the equation:

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

k₁ and k₂ = oxygen consumption at t₁ and t₂

Species	Metabolic Amplitude
<i>P. elsis</i>	0.1425
<i>A. grandis</i>	0.1213
<i>H. cockerelli</i>	0.3061

Table 2. Metabolic amplitude (mg O₂/g wet weight/hour) of 3
hydropsychid caddisfly larvae.

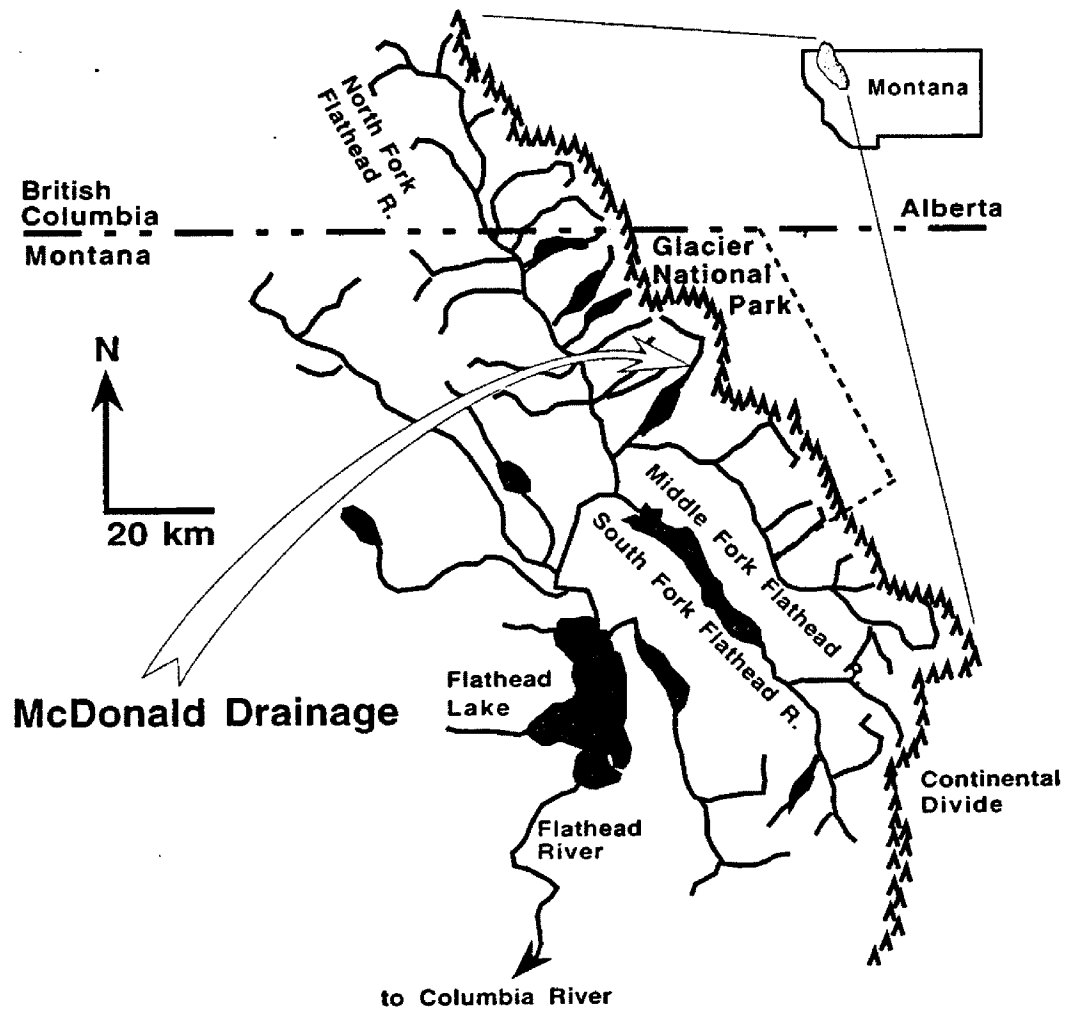


Fig. 1. Map of the Flathead River Basin, Montana, indicating the location of the McDonald drainage, Glacier National Park.

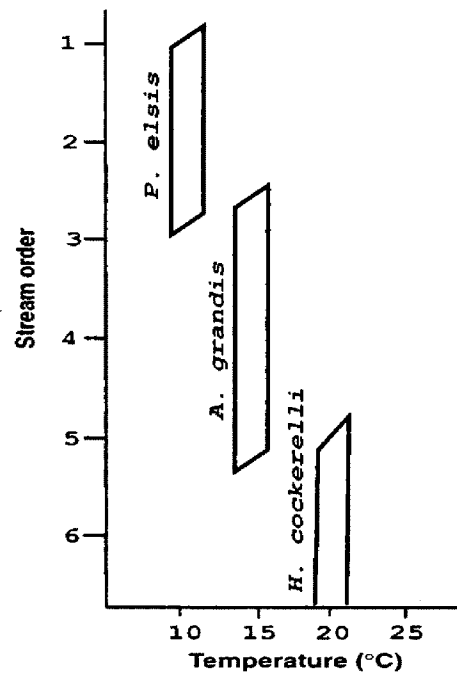


Fig. 2. Distributions of 3 hydropsychid caddisfly larvae (*P. elsis*, *A. grandis*, and *H. cockerelli*) relative to stream order and approximate maximum summer temperature (°C) of occupied reaches in the Flathead Basin, Montana.

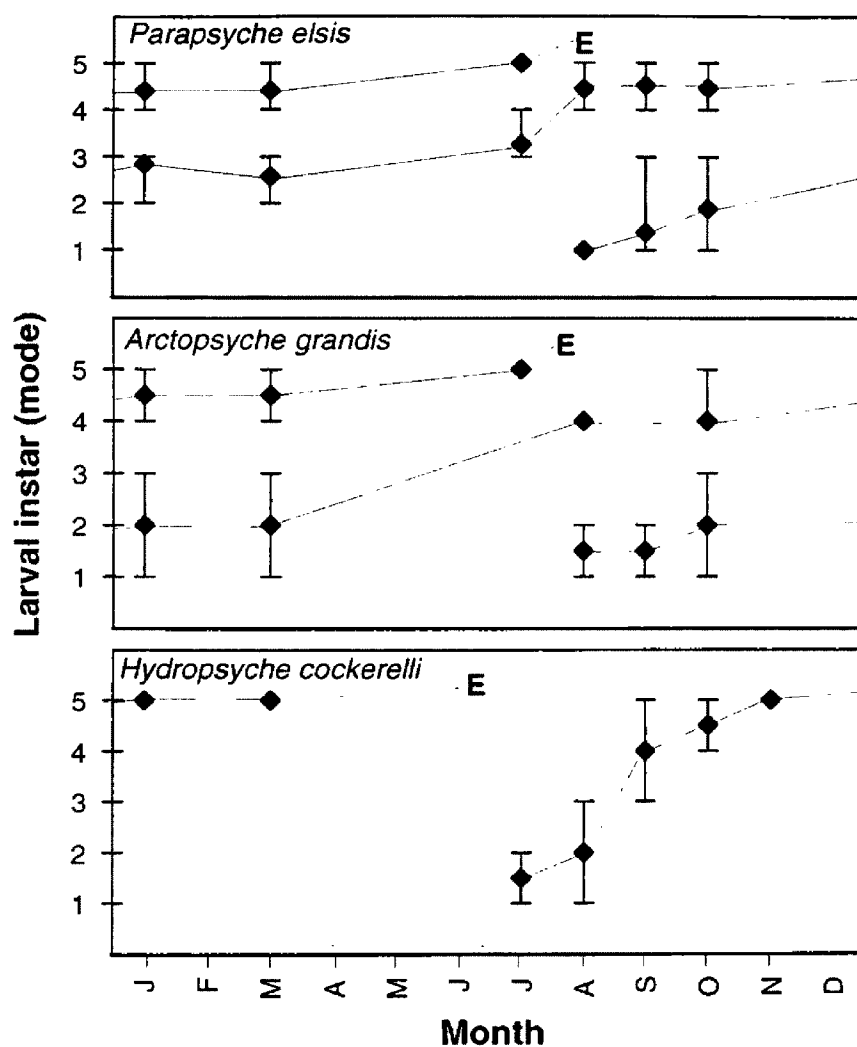


Fig. 3. Phenologies of *Parapsyche elsis* , *Arctopsyche grandis* *Hydropsyche cockerelli* in the Flathead Basin, Montana, indicating monthly distribution of larval instars (1-5) and timing of emergence (E). Modes have been joined to illustrate growth patterns. Vertical bars show range of instars present in stream.

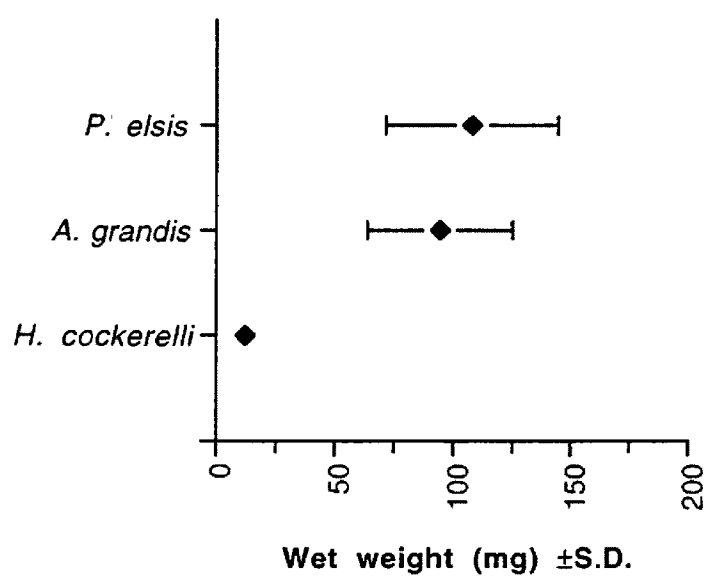


Fig. 4. Mean wet weights (\pm S.D.) of 5th instar larvae of 3 hydroptychid caddisfly species selected for our respirometry experiments.

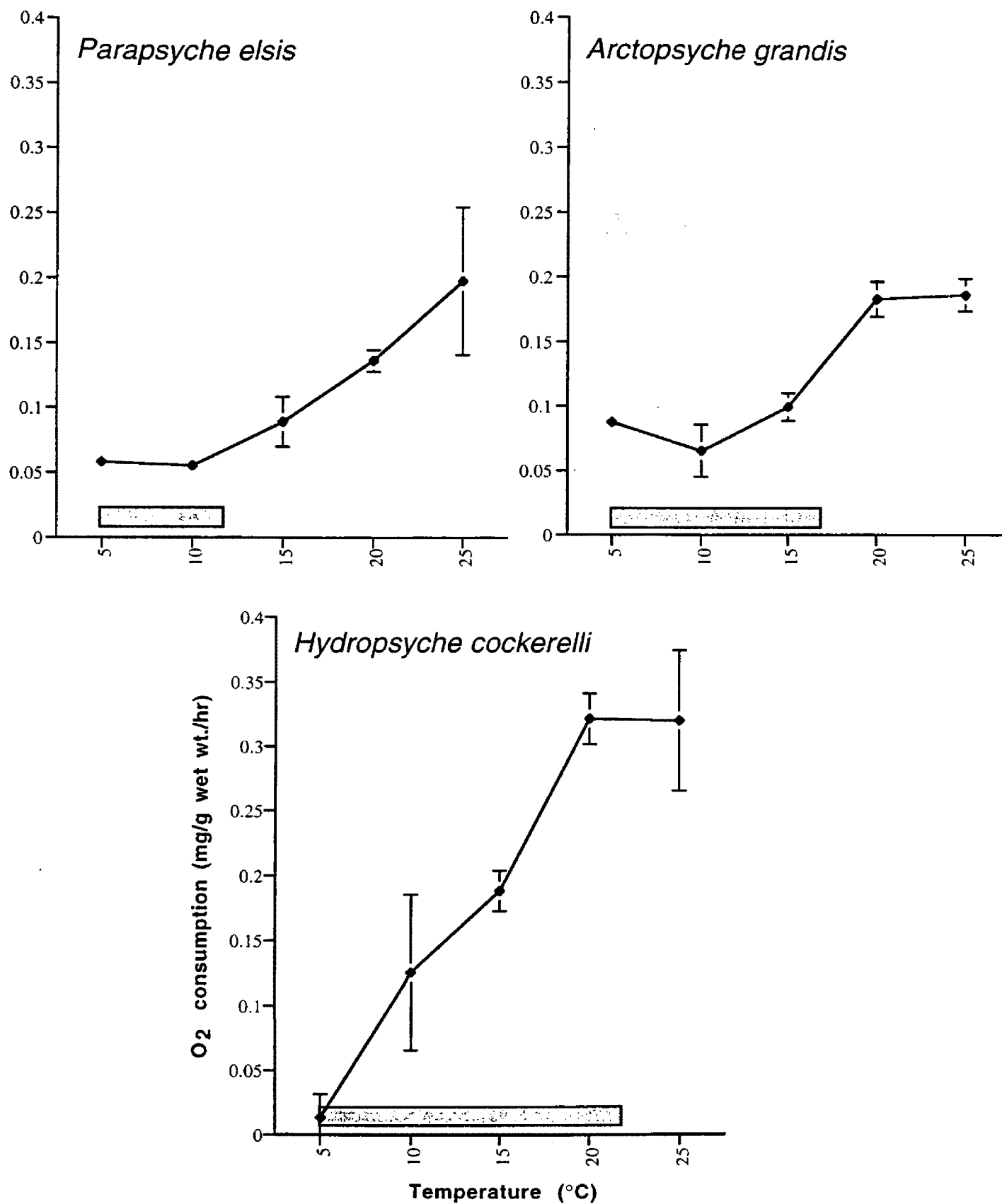


Fig. 5. Metabolism/Temperature curves (\pm S.E.) of 3 hydropsychid caddisfly larvae occurring in a longitudinal replacement series in streams of the Flathead Basin, Montana. Grey bar represents yearly thermal range of occupied reaches during the growth period of each species.

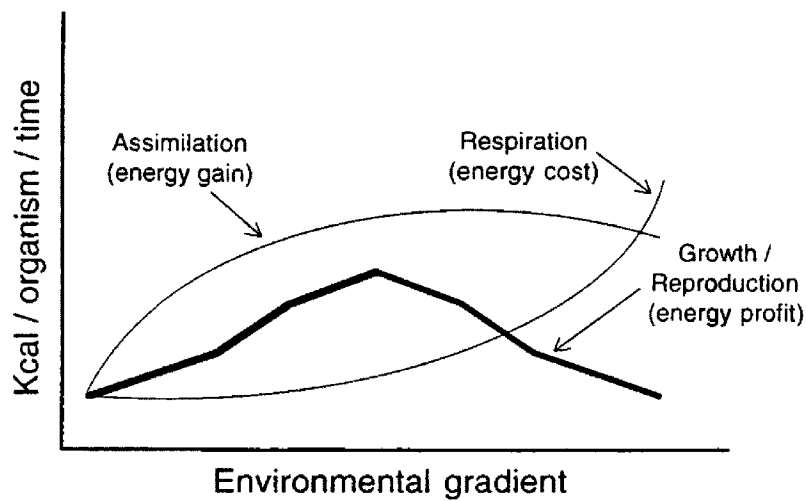
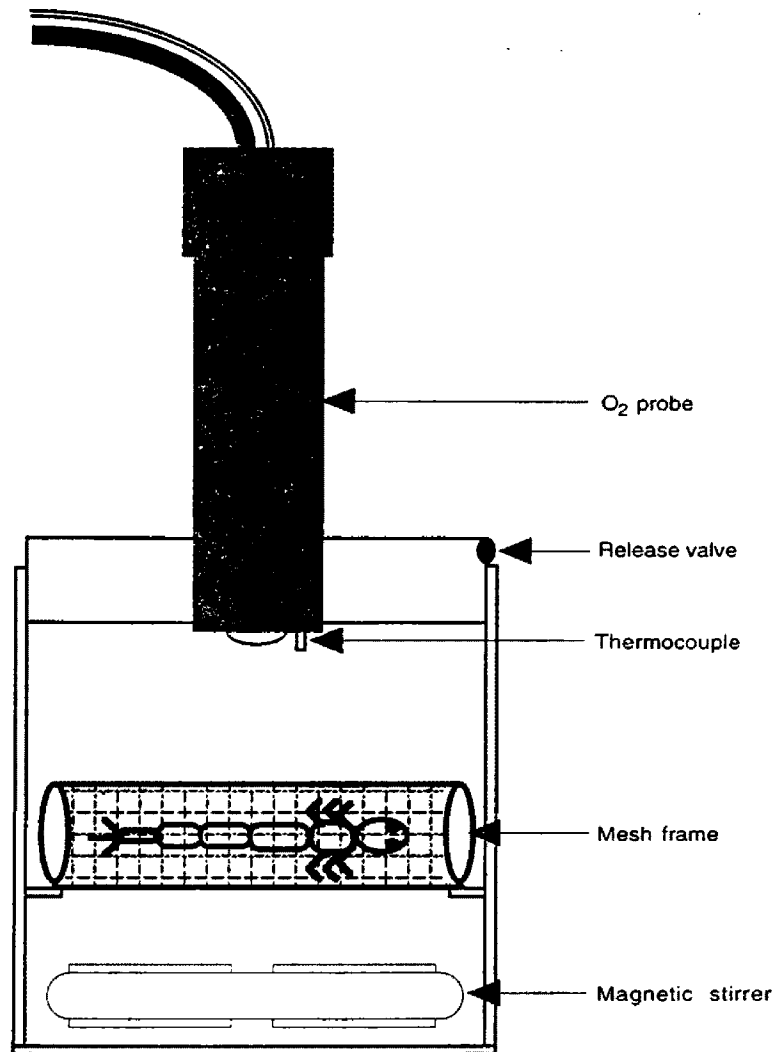
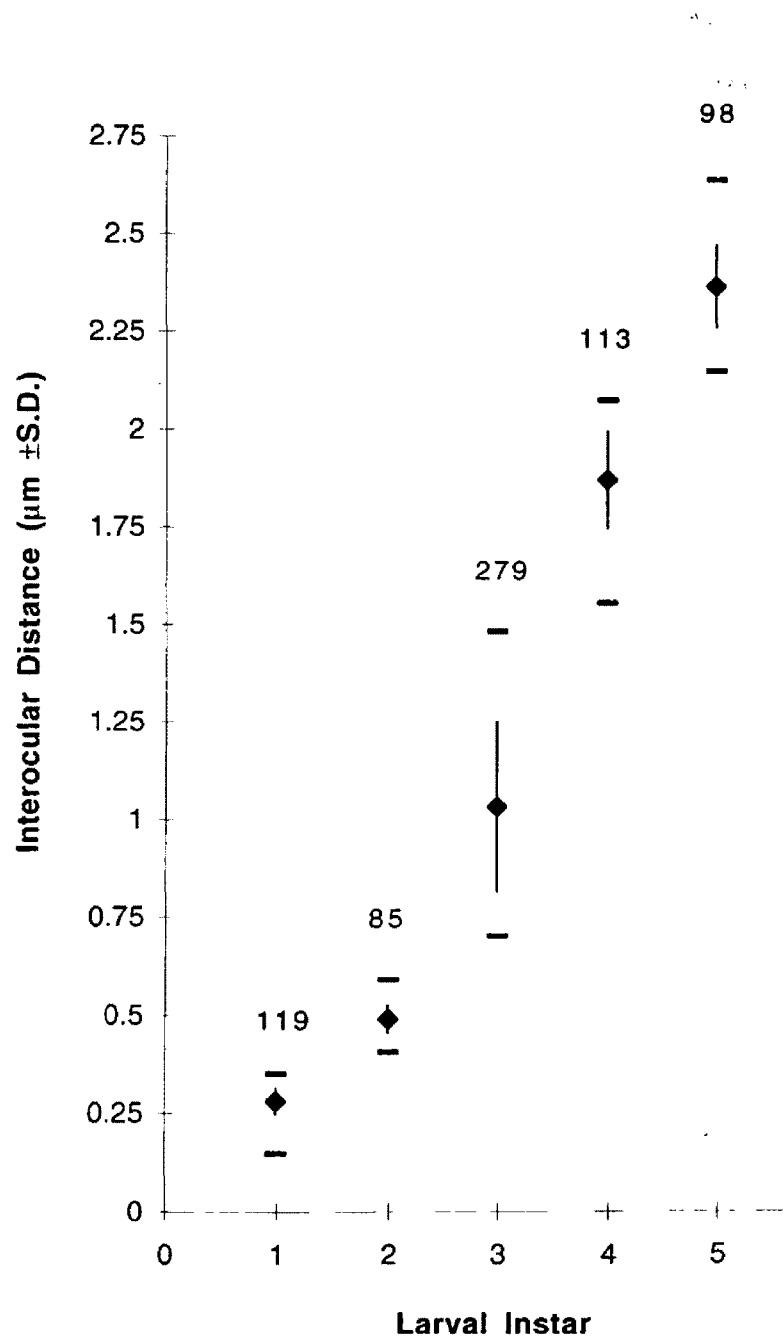


Fig. 6. Growth of a poikilotherm in response to an environmental gradient (from Hall et al. 1992). The commonly observed bell-shaped growth curve is hypothesized to be the net difference between metabolic energy expenditures (respiration) and gains (assimilation), realized as individual growth and reproduction (energy profit).



High-density polyethylene chamber used in our respirometry experiments. Volume: 13mls.



Parapsyche elsis larval instar discrimination by interocular distance. Vertical bar length equals 1 S.D., horizontal dashes represent range. Sample size is denoted by number over upper dash.

Appendix 3

Respirometry Data

Ind.#	Sp.	°C	Date	Wet Wt. (g)	Resp. Slope (m)	Baseline (c)	(m-c/g)*13.27mls
6	A.g.	5	960916	0.0754	-0.57054	-0.01048	-0.09857
7	A.g.	5	960916	0.0899	-0.59283	-0.01048	-0.08596
8	A.g.	5	960916	0.0882	-0.65103	-0.01048	-0.09637
9	A.g.	5	960916	0.074	-0.39611	-0.01048	-0.06915
10	A.g.	10	960918	0.0706	-0.60235	-0.139167	-0.08706
11	A.g.	10	960918	0.107	-0.32234	-0.139167	-0.02272
12	A.g.	10	960918	0.0724	-0.74451	-0.139167	-0.11095
13	A.g.	10	960918	0.1459	-0.58723	-0.139167	-0.04075
14	A.g.	15	960920	0.0699	-0.58017	-0.131754	-0.08513
15	A.g.	15	960920	0.1036	-1.10603	-0.131754	-0.12479
16	A.g.	15	960920	0.1091	-0.77641	-0.131754	-0.07841
17	A.g.	15	960920	0.0702	-0.71265	-0.131754	-0.10981
18	A.g.	20	960922	0.0747	-1.23876	-0.011921	-0.21794
19	A.g.	20	960922	0.1385	-1.69832	-0.011921	-0.16158
20	A.g.	20	960922	0.12	-1.48126	-0.011921	-0.16248
21	A.g.	20	960922	0.0871	-1.27605	-0.011921	-0.1926
22	P.e.	25	960924	0.0883	dead	-0.192822	#VALUE!
23	P.e.	25	960924	0.0935	-0.9636	-0.192822	-0.10939
24	P.e.	25	960924	0.127	-1.91808	-0.192822	-0.18027
25	P.e.	25	960924	0.0598	-1.5611	-0.192822	-0.30363
26	P.e.	25	960924	0.0774	-1.47554	-0.192822	-0.21992
27	P.e.	20	960926	0.0669	-0.68924	-0.011921	-0.13435
28	P.e.	20	960926	0.1702	-1.94355	-0.011921	-0.1506
29	P.e.	20	960926	0.1536	-1.32535	-0.011921	-0.11347
30	P.e.	20	960926	0.1487	-1.66087	-0.011921	-0.14715
31	P.e.	15	960928	0.0581	-0.49097	-0.131754	-0.08205
32	P.e.	15	960928	0.1513	-0.72847	-0.131754	-0.05234
33	P.e.	15	960928	0.0737	-0.92585	-0.131754	-0.14298
34	P.e.	15	960928	0.1464	-1.00138	-0.131754	-0.07883
35	P.e.	10	960930	0.0774	-0.47494	-0.139167	-0.05757
36	P.e.	10	960930	0.0603	-0.75647	-0.139167	-0.13585
37	P.e.	10	960930	0.0686	-0.43506	-0.139167	-0.05724
38	P.e.	10	960930	0.1369	-0.66632	-0.139167	-0.0511
39	P.e.	5	961002	0.1119	-0.47697	-0.01048	-0.05532
40	P.e.	5	961002	0.1316	-0.67712	-0.01048	-0.06722
41	P.e.	5	961002	0.1422	-0.70285	-0.01048	-0.06461
42	P.e.	5	961002	0.1223	-0.42748	-0.01048	-0.04525
43	A.g.	25	961004	0.1114	-1.60991	-0.192822	-0.1688
44	A.g.	25	961004	0.1628	-2.39796	-0.192822	-0.17974
45	A.g.	25	961004	0.0849	-1.54571	-0.192822	-0.21146
46	A.g.	25	961004	0.0338	dead	-0.192822	#VALUE!
47	H.c.	5	961029	0.0151	-0.26918	-0.01048	-0.22735

Ind.#	Sp.	°C	Date	Wet Wt. (g)	Resp. Slope (m)	Baseline (c)	(m-c/g)*13.27mls
48	H.c.	5	961029	0.0101	0.0257	-0.01048	0.04753
49	H.c.	5	961029	0.0138	-0.02626	-0.01048	-0.01518
50	H.c.	5	961029	0.0127	-0.00264	-0.01048	0.00819
51	H.c.	10	961030	0.0152	-0.48171	-0.139167	-0.29905
52	H.c.	10	961030	0.0103	-0.21654	-0.139167	-0.09968
53	H.c.	10	961030	0.011	-0.20125	-0.139167	-0.0749
54	H.c.	10	961030	0.0138	-0.16734	-0.139167	-0.02709
55	H.c.	15	961031	0.012	-0.321	-0.131754	-0.20928
56	H.c.	15	961031	0.0105	-0.3061	-0.131754	-0.22034
57	H.c.	15	961031	0.0086	-0.2368	-0.131754	-0.16209
58	H.c.	15	961031	0.0136	-0.29597	-0.131754	-0.16023
59	H.c.	20	961101	0.011	-0.27386	-0.011921	-0.31599
60	H.c.	20	961101	0.0129	-0.33348	-0.011921	-0.33078
61	H.c.	20	961101	0.0134	-0.38257	-0.011921	-0.36705
62	H.c.	20	961101	0.0191	-0.40244	-0.011921	-0.27132
63	H.c.	25	961102	0.0094	-0.31591	-0.192822	-0.17377
64	H.c.	25	961102	0.0101	-0.47597	-0.192822	-0.37201
65	H.c.	25	961102	0.011	-0.44729	-0.192822	-0.30698
66	H.c.	25	961102	0.012	-0.57843	-0.192822	-0.42642

Bold= rejected by Q-test
13.27mls= chamber volume

Substrate data

Site	Rep.	Particle Length (cm)
1	A	8.333
1	B	9.375
1	C	9.375
2	A	7.895
2	B	10
2	C	8.333
3	A	8.824
3	B	8.333
3	C	8.333
4	A	8.333
4	B	8.824
4	C	9.375
5	A	8.333
5	B	10.714
5	C	9.375
6	A	10
6	B	7.5
6	C	7.143
7	A	6.522
7	B	6.818
7	C	10
8	A	8.824
8	B	10.714
8	C	7.895

Seston data

Sample #	Site	Date	mls. filtered	Weight (mg)	N Area	C Area	N Conc. (g/l)	C Conc. (g/l)	C/N (g/l)
1	1	960827	959	44.395	8012	124988.8	2.6721366	41.6858646	15.6001997
2	2	960827	950	45.278	4839.55	102303.9	1.61407123	34.1200694	21.1391348
3	3	960827	945	45.874	5272.25	99479.7	1.75838395	33.1781512	18.8685476
4	4	960827	935	45.721	5712.4	82612.7	1.90518137	27.5527233	14.461995
5	5	960828	970	44.56	4924.55	181905.2	1.64242016	60.6684402	36.9384411
6	6	960828	917	43.406	5988.45	142385.8	1.99724868	47.4880564	23.7767369
7	7	960828	950	45.265	4734.15	87523.9	1.57891856	29.1906911	18.487775
8	8	960828	950	45.049	5767.95	102853.2	1.92370823	34.3032701	17.8318467
9	1	960927	980	45.137	2265.85	63825.8	0.75569904	21.2869766	28.1685902
10	2	960927	967	44.387	2010.65	71776.3	0.67058555	23.9386019	35.6980578
11	3	960927	970	45.595	2228.9	76793.4	0.7433756	25.611889	34.4534972
12	4	960925	962	44.975	1259.1	39871	0.419931	13.2976483	31.6662696
13	5	960925	955	44.614	1522.58	40293.2	0.50780434	13.4384591	26.4638524
14	6	960925	955	45.797	1478.33	41341.6	0.49304622	13.7881181	27.9651633
15	7	960925	952	45.364	1566.75	39517.7	0.52253745	13.1798168	25.2227222
16	8	960925	952	44.548	1719.05	51790	0.57333206	17.2728351	30.1271051
17	2	970408	842	44.685	516.8	17982.4	0.17236148	5.9974325	34.7956656
18	3	970325	900	45.507	553.7	17960.6	0.18466825	5.99016184	32.437421
19	4	970325	160	49.823	428.125	11783.7	0.14278688	3.93006192	27.5239708
20	5	970325	265	49.025	631.875	26915	0.21074093	8.97660467	42.59545
21	6	970324	890	45.576	776.5	31362.7	0.2589758	10.4599873	40.3898261
22	7	970318	935	45.374	733.425	35764.4	0.24460956	11.9280282	48.7635409
23	8	970318	942	45.259	1181.63	34802.1	0.39409179	11.607085	29.4527452
24	2	961022	945	44.635	1308.08	55758.1	0.43626499	18.5962631	42.6260727
25	3	961022	945	44.312	767.425	29968.2	0.25594913	9.99489817	39.0503307
26	4	961023	945	45.216	1180.85	43550.3	0.39383331	14.5247567	36.8804675
27	5	961024	950	45.986	1285.5	39298.9	0.42873585	13.1068434	30.5709063
28	6	961024	957	44.62	1331.18	45724.8	0.44396923	15.249989	34.3492028
29	7	961024	952	45.565	1394.2	39757.2	0.46498912	13.2596941	28.5161383
30	8	961024	950	46.884	1679.4	60607.35	0.56010811	20.2135694	36.0886924
31	4	970124	820	45.949	938	24871.6	0.31283876	8.29509644	26.515565
32	8	970213	978	45.842	626.875	19006.7	0.20907334	6.33905376	30.3197607
33	1	961022	No Sample						
34	1	970408	No Sample						

Water velocity data.

Site	A	B	C	D	E	F	G	H	I
1	0.647	0.244	0.181	0.265	0.336	0.712	0.311	0.217	0.156
2	0.402	0.316	0.44	0.807	0.637	0.748	3.19	1.27	0.33
3	0.193	0.231	0.3	0.139	0.185	0.238	0.196	0.394	0.346
4	0.254	0.322	0.095	0.078	0.151	0.328	0.119	0.169	0.396
5	0.271	0.224	0.688	0.453	0.164	0.317	0.665	1.15	0.152
6	0.113	0.474	0.297	0.276	0.306	0.304	0.172	0.31	0.229
7	0.098	0.089	0.381	0.277	0.314	0.094	0.117	0.464	0.348
8	0.174	0.428	0.291	0.094	0.634	0.343	0.194	0.179	0.155

Bold= rejected by Q-test