Distribution of benthic algae and macroinvertebrates along a thermal stream gradient

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Keywords: algae, benthic, geothermal, macroinvertebrates, stream, thermal

Abstract

The distribution and abundance of benthic algae and macroinvertebrates were examined along a natural thermal gradient formed by hot springs in Little Geysers Creek, Sonoma Co., California, USA. Maximum water temperatures ranged from 52 °C at the uppermost station to 23 °C at a station 400 m downstream. Benthic chlorophyll *a* decreased exponentially from 2.5 g m^{-2} at 52 °C to less than 0.1 g m^{-2} at 23 °C, a pattern of decline also exhibited by algal phaeophytin. Blue-green algae dominated at higher temperatures but were replaced by filamentous green algae and diatoms at lower temperatures.

Macroinvertebrates were absent at temperatures $\geqslant$45 °C; the highest density ($>$150 000 m^{-2}, mainly Chironomidae) occurred at 34 °C, whereas biomass was highest (4.6 g m^{-2}, as dry weight) at 23 °C and species richness (15 species) was highest at 27 °C. The two predominant macroinvertebrate populations (the midge *Tanytarsus* sp. and the caddisfly *Helicopsyche borealis*) occurred at sites that were several degrees below their lethal thermal threshold, suggesting that a temperature 'buffer' is maintained.

Introduction

Thermal gradients in aquatic habitats can be formed either by natural processes, such as geothermal activity, or by human activities, such as the release of waste heat from electric power generating plants (Brock, 1978). Because thermal effluents can alter the structure of biological communities, numerous investigators have examined the thermal tolerances of aquatic organisms, including algae (e.g. Castenholz, 1969; Moore, 1978; Hein & Koppen, 1979; Wilde & Tilly, 1981), macroinvertebrates (e.g. deKozlowski & Bunting, 1981; Nichols, 1981; Rasmussen, 1982), and fishes (e.g. Matthews & Maness, 1979; Paladino *et al.*, 1980; Feldmeth, 1981).

The outflows of hot springs are particularly useful systems in which to examine the responses of aquatic organisms to temperature gradients. Such 'thermal streams' typically exhibit substantial change in temperature within a relatively short distance (as heated discharges cool to ambient temperatures); these gradients are often thermally stable on a seasonal basis (Brock, 1970). Most previous studies on temperature gradients of geothermal origin have emphasized either the distribution of algae in hot-spring effluents, such as those in North America (Brock, 1967; Stockner, 1967; Wiegert & Fraleigh, 1972), New Zealand (Winterbourn, 1969), and Iceland (Castenholz, 1969), or the insect fauna of similar habitats (Brues, 1924, 1928; Robinson & Turner, 1975; Collins *et al.*, 1976; Resh & Barnby, 1984; see also review by Mitchell, 1974).

We examined the distribution of both benthic algae and macroinvertebrates along a natural temperature gradient, which was of geothermal origin, in a northern California, USA, stream. Our specific objectives were: (1) to determine the biomass of algae and the abundance and species richness of macroinvertebrates along the thermal gra-

Hydrobiologia 128, 13-21 (1985).

dient, (2) to relate qualitative and quantitative changes in the biota to gradient temperature and to other important physical features, and (3) to compare the distribution limits of selected macroinvertebrate populations with their maximum thermal tolerances.

Study area

The study area is located within The Geysers Known Geothermal Resource Area (The Geysers KGRA) in the coastal mountains of northeastern Sonoma Co., California (38° 47′ N, 122° 47′ W; elev. = 670 m), USA. In the temperate climate of this area, nearly all precipitation falls as rain ($\bar{x}$ = 137 cm a^{-1}) during the period November to April, and most streams recede to their base flow by midsummer.

The thermal gradient examined in this study encompassed contiguous segments of Little Geysers Creek and Big Sulphur Creek (Fig. 1). Little Geysers Creek is a cold, permanent stream at its source, but is heated by several hot springs that issue from the banks and streambed about 200–300 m above its confluence with Big Sulphur Creek. Big Sulphur Creek is a cold, intermittant stream at its source; it is heated by its main tributary, Little Geysers Creek.

Every summer, discharge declines in Big Sulphur Creek upstream of the confluence with Little Geysers Creek and the stream recedes to isolated pools. As a result, Little Geysers Creek essentially becomes the headwaters of Big Sulphur Creek (Fig. 1); these two streams form an uninterrupted thermal gradient that originates in Little Geysers Creek and extends into Big Sulphur Creek. This gradient spans about 400 m before temperatures return to those of downstream reaches in Big Sulphur Creek; the gradient normally persists from July until the onset of winter rains (usually in November). This stream segment (which actually contains the heated sections of both Little Geysers Creek and Big Sulphur Creek) will hereafter be referred to as Little Geysers Creek.

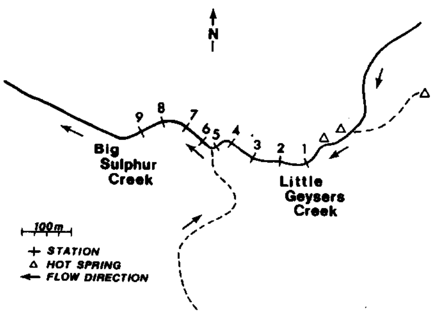

Fig. 1. Study area showing location of thermal gradient stations 1–9. Broken lines indicate intermittant stream segments.

Nine sampling stations were established along the thermal gradient, with intervals of about 50 m between adjacent stations (Fig. 1). The first station was in Little Geysers Creek, just below the hot spring inputs. Further details of the study area are given by Lamberti & Resh (1983a).

Materials and methods

Maximum and minimum water temperatures were measured with a thermometer at each gradient station during a 24 h period on 15–16 October 1982; in addition, midday measurements of water temperature were taken at each station on 30 August 1982 and again on 23 September 1982. Light was measured using a quantum meter, with hourly readings taken at each station from dawn to dusk (6:00–18:00) on 5 November 1982. These values were then plotted and the area under the light curve was calculated by digitation; this quantity was used as a relative measurement of total light for each station.

Algae and macroinvertebrates were sampled quantitatively using introduced substrates, which were unglazed, red clay tiles that were cut into 7.6×7.6 cm squares (0.006 m^2). On 30 August 1982, five sterile tiles were placed on the stream bottom at each gradient station in shallow (5–15 cm in depth) riffles that had moderate current velocity (10–20 cm s^{-1}). These tiles were retrieved 46 d later, on 15 October 1982. Previous studies in Big Sulphur Creek have shown that a 4- to 5-wk colonization period is adequate for these tiles to represent accurately the flora and fauna of natural substrates (Lamberti & Resh, 1985).

Each tile was lifted off the substrate and placed into a downstream net (125 μm mesh) to entrap fleeing macroinvertebrates. Amounts of chlorophyll *a* and phaeophytin, which were used as indices of algal biomass, were determined for each tile by removing a 4 cm^2 area of material from the upper tile surface. A cork borer was used to remove loosely attached algae (Brock, 1967); a scalpel was used to scrape tightly adherent algae (Barton & Lock, 1979). Each sample was filtered through a glass fiber filter and the pigments were stabilized with $MgCO_3$; the filter was then frozen in the field. In the laboratory, the filters were ground in a small volume homogenizer and the photosynthetic pigments were extracted in 90% acetone for 24 h at -10 °C. Pigment concentrations were measured with a spectrophotometer, according to the technique of Moss (1967a, 1967b).

Macroinvertebrates on the tiles were collected and preserved in 5% formalin. All macroinvertebrates (> 125 μm in size) from each tile were classified at the species level (either by name or by using an OTU designation such as sp. A) and enumerated. Ash-free dry weights (AFDW) of macroinvertebrates were obtained by drying the samples for 24 h at 105 °C in a vacuum oven followed by ashing for 1 h at 500 °C in a muffle furnace.

Abundances of algal pigments and macroinvertebrates were compared among the stations using one-way analysis of variance (ANOVA). *A posteriori* multiple contrasts were done using the Student-Newman-Keuls (SNK) procedure. All comparisons were made at a significance level of $P = 0.05$.

Results

Abiotic features

Along the thermal gradient in Little Geysers Creek, maximum water temperatures on 15–16 October ranged from 52 °C at station 1 to 23 °C at station 9 (Fig. 2A). These autumn temperatures were several degrees lower than temperatures taken at the same sites during the summer (e.g. temperatures ranged from 58 °C to 26 °C on 30 August and from 55 °C to 25 °C on 23 September). Diel fluctuations in water temperature were typically 3–4 °C at all stations (Fig. 2A). For standardization, we will refer to the stations by the maximum water temperatures reached on 15–16 October.

Light measurements were used to produce a curve for each gradient station; the integrated area of each curve was then compared to those of the other stations (Fig. 2B). This index of total light indicated that station 4 had the highest light level; levels for other stations ranged from 5–60% of that amount. Stations 1–4 had higher light levels than the other stations because there was little riparian vegetation near these high-temperature zones. Stations 5–9 had well developed riparian vegetation and this, coupled with a narrowing of the stream canyon, resulted in reduced light levels.

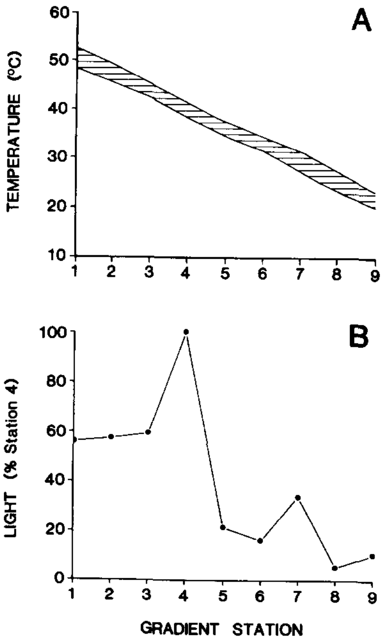

Fig. 2. Abiotic features of the thermal gradient: (A) maximum-minimum temperature ranges at each gradient station on 15–16 October 1982; (B) light at each gradient station as percentage of light at station 4.

Water chemistry parameters have been measured in Little Geysers Creek near station 1 and in Big Sulphur Creek near station 6 (Enriquez, 1978; Gilbert, 1981 summarized in Lamberti & Resh, 1983a). In general, chemical concentrations did not show the longitudinal variation that temperature or light displayed, although some differences were present. For example, nitrate-N increased from 0.1 mg l^{-1} at station 1 to 0.6 mg l^{-1} at station 6, whereas ammonia declined from 2.2 mg l^{-1} at station 1 to 0.8 mg l^{-1} at station 6.

Algal pigments

Benthic chlorophyll *a* declined sharply as temperature decreased along the thermal gradient

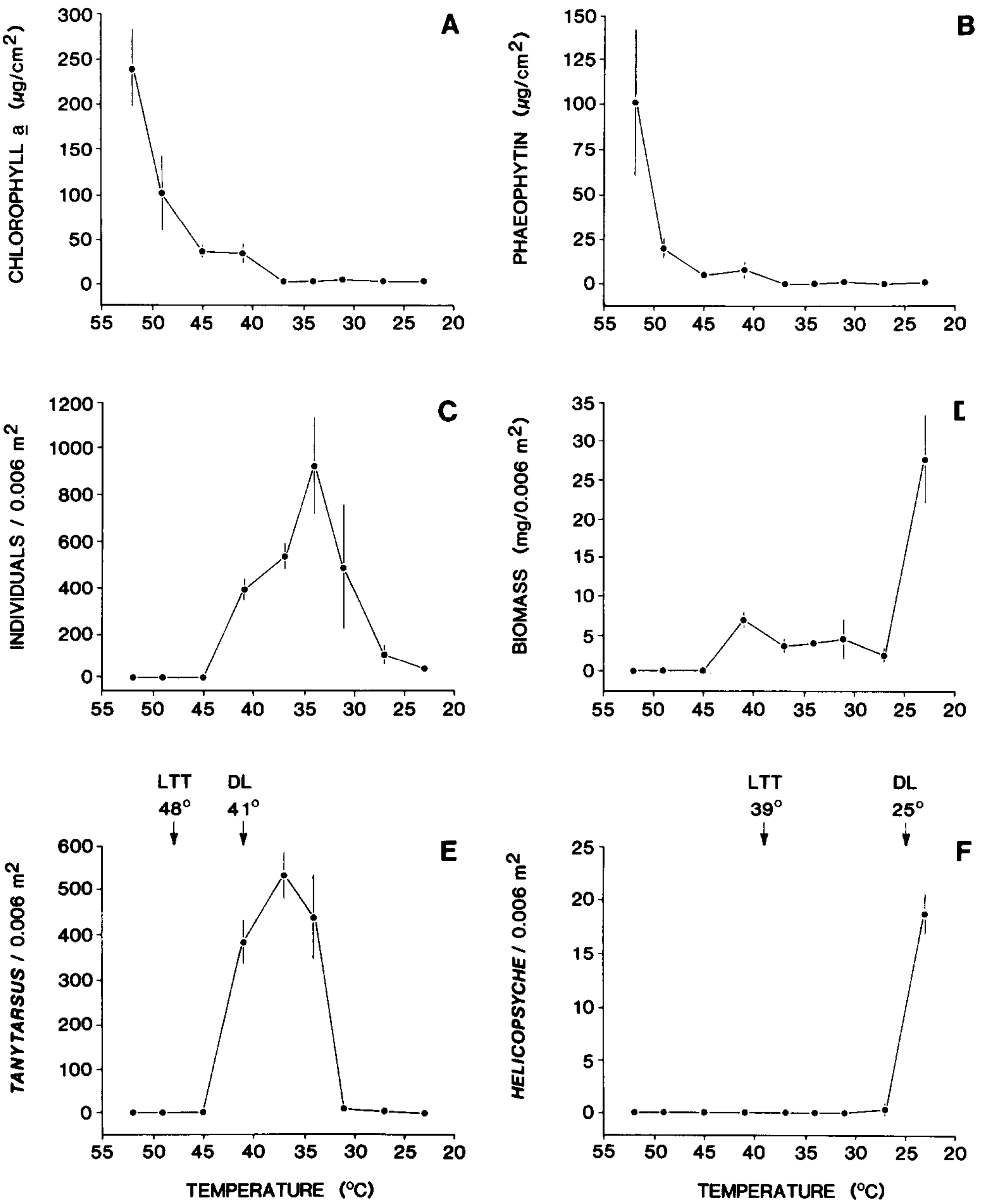

Fig. 3. Biological features of the thermal gradient ($\bar{x} \pm$ SD; n = 5): (A) chlorophyll *a*; (B) phaeophytin; (C) macroinvertebrate density; (D) macroinvertebrate biomass, as AFDW; (E) *Tanytarsus* density; (F) *Helicopsyche borealis* density. LTT = lethal thermal threshold, DL = upper distribution limit.

(Fig. 3A). Although the amount of chlorophyll *a* peaked at approximately 250 µg cm^{-2} at 52 °C and exceeded 100 µg cm^{-2} at 45 °C, it was less than 3 µg cm^{-2} below 40 °C. SNK tests of chlorophyll *a* indicated that the 52 °C and 49 °C stations were distinct from the remainder of the stations, but there were no significant differences among the 45–23 °C stations (Fig. 4). Phaeophytin, the degradation product of chlorophyll, also displayed a sharp decline in abundance as temperature decreased (Fig. 3B). Phaeophytin ranged from a high of 100 µg cm^{-2} at 52 °C to less than 1 µg cm^{-2} below 40 °C. SNK tests of phaeophytin indicated that the 52 °C station was significantly different from the

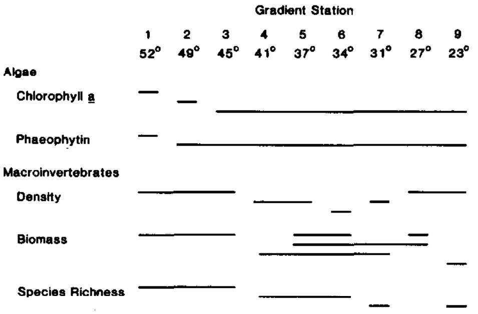

Fig. 4. Homogeneous subsets of stations along the thermal gradient, based on algal and macroinvertebrate measurements. Breaks in horizontal lines indicate significantly ($P<0.05$) different subsets as determined by the SNK procedure.

other gradient stations (Fig. 4).

Qualitative observations indicated that there were changes in algal community composition along the gradient. For example, at the highest temperatures (52–41 °C), blue-green algae (Cyanophyta) were predominant, especially *Oscillatoria* (cf. *terebriformis*), a filamentous form, and *Aphanocapsa* (cf. *thermalis*), a colonial form. At intermediate temperatures (37–31 °C), blue-green algae were replaced in large part by green algae (Chlorophyta), especially *Spirogyra*. At the lowest temperatures (27–23 °C), the algal community consisted primarily of diatoms (Chrysophyta).

Macroinvertebrates

Macroinvertebrates were absent at temperatures of 45 °C and higher (Fig. 3C). They were present in moderate densities at 41 °C [388/0.006 m^2 (64 667 m^{-2})] but highest densities [926/0.006 m^2 (154 333 m^{-2})] occurred at 34 °C. At 23 °C, densities were only 40/0.006 m^2 (6 667 m^{-2}). The macroinvertebrate community in the high density zone (41–31 °C) was composed largely of three species of chironomid (Diptera) midge larvae, *Tanytarsus* sp. A, *Rheotanytarsus* sp. A, and *Corynoneura* sp. A. SNK tests indicated that there were three subsets among the gradient stations (Fig. 4): (1) 34 °C, the highest-density station, was significantly different from all other stations; (2) 41 °C, 37 °C, and 31 °C stations formed a second subset that was distinct from the other stations; (3) the remaining stations formed a third subset.

Macroinvertebrate biomass showed a distinctly different pattern than did density (Fig. 3D compared to Fig. 3C). Biomass, as AFDW, was low at most stations [<7 mg/0.006 m^2 (<1.2 g m^{-2})], but increased sharply at 23 °C [28 mg/0.006 m^2 (4.7 g m^{-2})]. This increase was due largely to larvae of the caddisfly *Helicopsyche borealis* (Hagen) at that station, which were rare or absent at the higher-temperature stations. Although small in comparison with many other species of Trichoptera in Big Sulphur Creek, *Helicopsyche* larvae are much larger than the midges that dominated at the higher temperatures. SNK tests of biomass indicated that there were several overlapping subsets of stations between 41–27 °C, but that the 23 °C station was dinstinct from the remaining stations (Fig. 4).

The number of macroinvertebrate species generally increased as temperature declined (Fig. 5), and was highest at 27 °C (i.e. station 8) where 15 species occurred on the tile substrates. In contrast to macroinvertebrate biomass, SNK tests of macroinvertebrate species richness indicated that several distinct subsets of stations were present (Fig. 4).

Tanytarsus was the most abundant macroinvertebrate along the gradient, reaching densities >80 000 m^{-2}; however, over 99% of those larvae occurred between 41–34 °C (Fig. 3E). *Helicopsyche* was the dominant macroinvertebrate by weight, but almost all larvae were collected at 23 °C (Fig. 3F). Other dominant macroinvertebrate populations also showed restricted distributions along the gradient. For example, *Rheotanytarsus* was confined (>99%) to the 34 °C and 31 °C stations, and more than 97% of *Corynoneura* were found at the 31 °C and 27 °C stations.

The degree of similarity between the macroinvertebrate communities at adjacent gradient stations was measured with the coefficient of similarity *S* (Cox, 1980), which considers both species com-

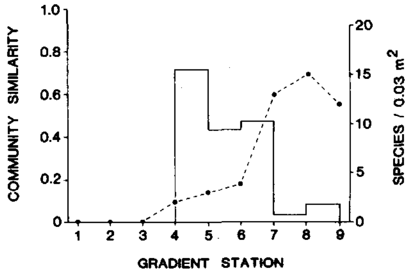

Fig. 5. Species richness (broken line; 0.03 m^2 = five samples pooled) compared with similary *S* (histogram) of communities at adjacent gradient stations.

position and relative abundance. S can vary from 0 to 1, where '1' indicates identical communities and '0' indicates no shared species. Since no macroinvertebrates were present at stations 1–3, the first comparison was between stations 4 and 5. Although these two stations were similar ($S = 0.71$), other adjacent stations were less so (Fig. 5), and few species were shared by either stations 7–8 or 8–9 ($S<0.1$).

Discussion

Several investigators have observed a high degree of temporal stability in the thermal gradients of hot-spring effluents. For example, Winterbourn (1969) reported only a 2 °C annual fluctuation in water temperature along any point in the outflow channel of a New Zealand hot spring, and Stockner (1967) reported that several North American hot springs also were thermally stable. In contrast, the hot-spring effluents in The Geysers KGRA are subject to a high degree of seasonal variation in temperature because of dilution caused by precipitation and runoff. For example, during winter months when discharge of Little Geysers Creek increases as a result of precipitation runoff, maximum in-stream temperatures are only a few degrees above ambient, and a thermal gradient is virtually absent. This gradient is typically reestablished after winter rains cease, and both maximum temperatures for each site and maximum longitudinal differences in temperature among sites occur during mid-summer.

Thus, only during summer and autumn does a biota that is typical of hot springs (e.g. Brock, 1978; Castenholz, 1978) exist in Little Geysers Creek. During that time, however, dramatic differences in algal abundances occur along the thermal gradient. For example, the amount of benthic chlorophyll *a* varied by almost 200X along this gradient. The maximum value of approximately 250 μg cm^{-2} (2.5 g m^{-2}) at 52 °C is higher than any reported values of benthic chlorophyll *a* that we have seen for hot-spring habitats. In fact, although Fraleigh & Wiegert (1975) found chlorophyll *a* abundances of up to 1.7 g m^{-2} in artifical hot-spring channels, most previous studies of algae in natural hot springs have reported maximum values of less than 1 g m^{-2} (e.g. Brock, 1967; Winterbourn, 1969).

The upper temperature limit for algal growth is between 70–75 °C (Brock, 1967, 1978); however, the maximum standing crop of benthic algae usually occurs between 50–60 °C (Brock, 1967; Winterbourn, 1969). In our study, highest standing crop was found at 52 °C, the highest temperature examined. At 52 °C the samples from the periphyton (taken as cores) indicated that the blue-green algae grew as a thick mat that probably included significant bacterial biomass as well (Lamberti & Resh, 1983a).

Multiple regression analysis of the influences of temperature, light, macroinvertebrate density, and macroinvertebrate biomass (the latter two parameters measure potential grazing pressure) on chlorophyll *a* along the Little Geysers Creek gradient indicated that variation in temperature alone accounted for 60% of the differences in chlorophyll *a* along the entire gradient. The other variables together explained only an additional 13% of the variation in chlorophyll *a*. Thus, changes in algal abundance were most highly associated with differences in temperature.

In hot springs, temperature is frequently the most important abiotic feature affecting the abundance and distribution of algal populations (Stockner, 1967; Brock, 1970). However, variation in light levels and chemical concentrations can have significant effects on algal growth and species composition (Stockner, 1967). For example, in some hot springs, blue-green algae are probably light-saturated during most of the summer, but production may become light-limited during the winter due to reductions in photoperiod and light intensity (Fraleigh & Wiegert, 1975). In other instances, high light intensity can inhibit the productivity of cyanophyte mats (Castenholz, 1972). In other hot springs, water chemistry (especially pH and concentration of soluble sulfide), may determine the species composition of thermophilic algae (Castenholz, 1976).

Grazing pressure probably becomes increasingly important in the regulation of algal standing crop at lower temperatures (Wickstrom & Wiegert, 1980; Lamberti & Moore, 1984). Brock (1967) and Stockner (1967) also have noted that grazing by macroinvertebrates at lower temperatures can disrupt the cohesiveness of algal mats in hot springs and substantially reduce algal standing crop. At lower temperatures (<25 °C) in Big Sulphur Creek, grazing by *Helicopsyche* larvae regulates the standing crop and productivity of algal communities (Lamberti & Resh, 1983b).

Many macroinvertebrate species had restricted longitudinal distributions along the thermal gradient, as demonstrated by the chironomids *Tanytarsus, Rheotanytarsus*, and *Corynoneura*. This pattern, coupled with the addition of species as temperature declined, resulted in a fauna that was dissimilar at adjacent stations. Apparently, small (3–4 °C) changes in maximum temperature can result in substantial changes in macroinvertebrate communities.

McElravy & Wood (unpub. data) examined the thermal tolerances of *Tanytarsus* and *Helicopsyche* in Little Geysers Creek by determining the lethal thermal threshold (LTT) for each species, which they defined as the temperature at which 50% of the animals died after a 1 h exposure. The 1 h LTT was 48 °C for *Tanytarsus*, and 39 °C for *Helicopsyche*. Along the thermal gradient, *Tanytarsus* was not found above the 41 °C station; thus, there was a 7 °C difference between *Tanytarsus*' highest temperature occurrence and its LTT (Fig. 3E). Since only a single *Helicopsyche* larva was found at 27 °C, the upper distribution limit for *Helicopsyche* was probably closer to 25 °C. Thus, there was a large difference, at least 12 °C, between *Helicopsyche*'s highest temperature occurrence and its LTT (Fig. 3F).

In previous studies, *Helicopsyche* larvae have been found in thermal habitats up to 34 °C (Wiggins, 1977; Williams *et al.*, 1983), which is 5 °C less than its 39 °C LTT and in the range of *Tanytarsus*' 7 °C difference. A possible explanation for the greater difference between the upper distribution limit of *Helicopsyche* in Little Geysers Creek and its LTT, when compared to the results observed in other studies, is that water temperatures in Little Geysers Creek were higher along the gradient in the summer months prior to our autumn study period. For example, when temperatures exceeded 34 °C (the thermal limit found in other studies), *Helicopsyche* larvae were probably eliminated from mid-gradient stations. Since *Helicopsyche* is univoltine and adult females do not emerge to oviposit until the following spring (Resh *et al.*, 1984), recolonization of those stations via oviposition cannot occur until then, even if temperatures decline into favorable ranges. In addition, upstream movement by *Helicopsyche* larvae is probably prevented by a high-gradient cascade between stations 8 and 9. *Tanytarsus*, however, has multiple generations each year; thus, females are present nearly year-round to oviposit as favorable thermal regimes become available.

Summary

(1) Hot-spring inputs into Little Geysers Creek, and subsequently Big Sulphur Creek, California, USA, form a thermal gradient in which temperatures declines (on October 15–16, 1982) from 52 °C to 23 °C in 400 m. Benthic algae and macroinvertebrates display temperature-dependent distribution patterns along the gradient.

(2) Chlorophyll *a* ranged from 2.5 g m^{-2} at 52 °C to less than 0.1 g m^{-2} at 23 °C. High-temperature zones were dominated by blue-green algae, (especially *Oscillatoria*), which were replaced by filamentous green algae (especially *Spirogyra*) and diatoms at lower temperatures.

(3) Macroinvertebrates were absent at temperatures above 45 °C. Densities peaked at about 150 000 m^{-2} at 34 °C, most of which were chironomid midge larvae. Species richness was highest at 27 °C whereas macroinvertebrate biomass peaked at 23 °C.

(4) The chironomid midge *Tanytarsus* leaves a moderate temperature 'buffer' between its upper distribution limit (41 °C) and its lethal temperature threshold (48 °C). The caddisfly *Helicopsyche* displays a wider margin (25–27 °C vs. 39 °C), but this is probably due to its phenology.

Acknowledgments

We thank E. McElravy and J. Wood for permission to cite unpublished data and K. Gallagher and J. Feminella for technical assistance. The research leading to this report was supported by the Office of Water Research and Technology, USDI, under the Annual Cooperative Program of Public Law 95–467, and by the University of California Water Resources Center, as part of Office of Water Research and Technology Project No. A–084–CAL and Waters Resources Center Project UCAL–WRC–W–612.

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Received 2 May 1984; in revised form 20 March 1985; accepted 23 April 1985.