

HUMMOCKING BY LOTIC *CHARA*: OBSERVATIONS ON ALTERATIONS OF HYPORHEIC TEMPERATURE PATTERNS

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(Accepted for publication 18 January 1988)

ABSTRACT

Hendricks, S.P. and White, D.S., 1988. Hummocking by lotic *Chara*: observations on alterations of hyporheic temperature patterns. *Aquat. Bot.*, 31: 13-22

Stream-bed temperature profiles were used to examine hyporheic water patterns beneath *Chara* hummocks in a northern Michigan (U.S.A.) stream. Hummocks were found to alter expected hyporheic temperature patterns significantly, causing apparent upwellings of deeper, colder waters into the hummock. The magnitude of temperature pattern alterations was proportional to the size of the hummock, and hummocks were often situated in areas of the stream where cooler hyporheic water was closest to the stream-bed surface. Upwelling and downwelling patterns caused by hummocks conformed to the literature on hyporheic flow alterations imposed by inanimate objects on the stream-bed surface. Hyporheic water upwellings may be of benefit to *Chara* by exposing the anchorage system to higher nutrient or ion levels existing in interstitial water.

INTRODUCTION

Chara hummocks are often a conspicuous feature of cooler temperate streams (Prescott, 1962; Haslam, 1978), creating a substratum for periphyton, a habitat for a variety of aquatic insects, and a sink for sand and fine particulate organics. Hummocks similar to those produced by *Chara* are characteristic of species in a variety of aquatic plant genera growing in slow to fast stream currents including *Nitella*, *Berula*, *Callitriche*, *Ranunculus*, *Elodea*, *Myriophyllum*, *Fissidens*, *Zannichellia* and *Rorippa* (Gessner, 1955; Tindall, 1962; Minckley, 1963; Casey and Westlake, 1974; Haslam, 1978).

The dynamics of hummock formation for several taxa have been described in detail by Tindall (1962) and Haslam (1978) and illustrated by Minckley (1963; also see Hynes, 1970). Once a shoot becomes established in early sum-

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mer, sand deposition occurs on the downstream side. Hummocks develop as plant growth and sand and silt deposition occur. Final hummock shapes are products of stream current velocity and direction (Gessner, 1955), and larger hummocks further modify local surface-water flow patterns (Gessner, 1955; Kopecky, 1965; Hynes, 1970).

Hummock distribution in rivers has been followed over several seasons for a variety of macrophytes (Gessner, 1955). However, only weak correlations have been demonstrated between hummock distribution and stream flow, stream depth, substrate type, light, or position across the stream (Gessner, 1950; Haslam, 1978). Other than providing a seemingly favorable habitat for expansion of the plant colony (Gessner, 1950; Haslam, 1978), little is known of hummock function as it relates to the ecology of the plant or to biophysical stream processes.

A variety of *Chara* species is associated with spring-fed lakes, rivers, natural and man-made ponds, and gravel pits, suggesting that mineral nutrition from groundwater is important in distribution (Daily, 1953, 1958; Krause, 1983; Castilla and Amoros, 1984). Many aquatic vascular plants (Huebert and Gorham, 1983; Smith and Adams, 1986) and at least one species of *Chara* (Littlefield and Forsberg, 1965) are known to obtain a significant portion of their nutrient supply through root and rhizoidal anchorage systems, respectively. Groundwater and hyporheic (substratum) interstitial water often contain greater amounts of nutrients and ions than surface waters (Wallis et al., 1981; Bencala, 1984; Grimm and Fisher, 1984). Assuming that hummock-forming *Chara* also obtain nutrients through the rhizoids, it is of interest to determine if hummocks function in some fashion which promotes delivery of groundwater or hyporheic nutrients.

Investigations of hyporheic temperature patterns (e.g. White et al., 1987) have shown that unconsolidated sediments beneath streams contain regular and predictable gradients of surface water-hyporheic water mixtures. Hyporheic water, ranges from primarily stream water just below the stream-bed-stream water interface to primarily groundwater within the deeper sediment layers. Changes in stream-bed relief produce alterations in hyporheic flow patterns (Vaux, 1962, 1968; Cooper, 1965; Thibodeaux and Boyle, 1987). Where stream-bed relief is convex, such as at the heads of riffles, stream water downwells (i.e. downwardly deflected) into the substratum. Where stream-bed relief is concave, such as at the ends of riffles, hyporheic water upwells (i.e. upwardly deflected) toward the bed surface. Stream-bed surface objects such as large rocks or logs increase bed surface roughness, further augmenting hyporheic flow patterns, and producing localized changes in stream-bed relief and surface flow (Cooper, 1965).

Based on what is known about alterations of hyporheic flow patterns caused by stream-bed surface objects, the primary objective of this study was to de-

scribe hyporheic patterns beneath hummocks and to determine if hummocks also altered the observed patterns.

STUDY SITE

The study site was located on the east branch of the Maple River in Emmet County, MI (U.S.A.) on the University of Michigan Biological Station tract 3 km directly east of Pellston. The river is characteristic of a third to fourth-order stream (Vannote et al., 1980) with shallow riffles <0.5-m deep alternating with pools up to 2.5-m deep. The stream-bed ranges from sand to gravel (particles typically <1-cm diameter) in the riffles and fast-flowing reaches to fine sand with some silt accumulations in the pools. The site used was approximately 7 km below the Douglas Lake outfall. Stream discharge at the time of this study was $<0.5 \text{ m}^3 \text{ s}^{-1}$, depth was from 0.2 to 1.0 m, and width was from 4 to 10 m. The river at this site flows primarily through second growth aspen (*Populus grandidentata* Michx. and *P. tremuloides* Michx.), mixed hardwoods and conifers.

August mid-day water temperatures of 27°C were not uncommon as much of the discharge was from Douglas Lake surface water. The mean annual air temperature (U.S. Weather Bureau records) was approximately 11.5°C which was the mid-summer temperature of most flowing springs in the area. The distinct temperature differences between stream water and deep hyporheic water provided the basis for determining hyporheic patterns (White et al., 1987).

MATERIAL AND METHODS

Two types of temperature measurements were taken. The first was a detailed examination of the hyporheic interstitial water temperatures beneath two large, well-established *Chara* hummocks. Hummock A was 3-m long and slightly less than 1-m wide. Hummock B was 55-cm long and a little more than 25-cm wide. Hyporheic temperature patterns were determined from temperature profiles in regularly-spaced grids covering the hummocks and distances upstream, downstream and to the sides of the hummocks. Grid corners were marked with small flags attached to wires pushed down securely into the bed. A 0.5×0.5 -m grid was laid out for Hummock A (Fig. 1), and a 0.25×0.5 -m grid was laid out for Hummock B (see Fig. 5). Grids were begun 2 m upstream from Hummock A and 1 m upstream from Hummock B. Temperatures were recorded in the center of each grid section to the nearest 0.5°C in the stream water, at Depth 0 (bed surface), and at 5, 10, 15, 20, 25 and 30-cm deep into the bed using a 90-cm long YSI Series-400 stainless-steel probe and thermistor. Within the hummocks, Depth 0 (the stream-bed surface) was easily found by pushing the temperature probe through the deposited sand to the original surface gravel layer.

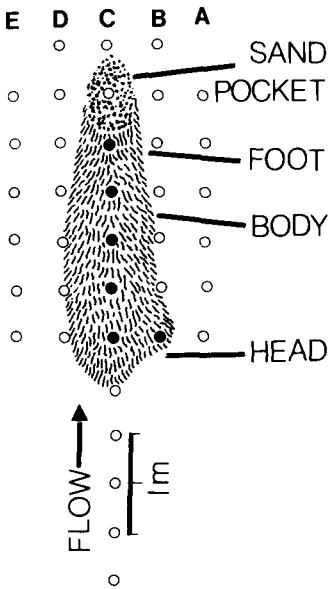


Fig. 1. Outline of Hummock A showing hummock features, location of temperature sampling points (○) on the 0.5 m×0.5 m grid, location of downstream transects A-E, and direction of streamwater flow.

After hyporheic temperatures were recorded, Hummock A and all accumulated sand were carefully removed down to the original stream-bed surface leaving the grid markers in place. Approximately 2 weeks later, hyporheic temperatures were remeasured.

In a second series of measurements, the temperatures beneath 35 hummocks of varying sizes were measured approximately 5 cm below the original stream bed in the head, body, foot and sand pocket of each (see Fig. 1). Other data were recorded on hummock length and approximate across-stream/downstream positioning. To determine if alterations of temperature patterns were significant and if the patterns were related to hummock size (as measured by length), data from the 35 hummocks underwent 2-way analysis of variance using the Statistical Analysis System (S.A.S.) with location of measurements within the hummock and hummock length as main effects. For the ANOVA, three length groupings were used, < 50 cm (small, $n=14$), 50–99 cm (medium, $n=13$), and > 100 cm (large, $n=8$). Scheffé's (S) statistic was used for multiple comparison of means. Significance levels were set at $\alpha=0.05$ throughout the analyses. Assumptions of normality and homogeneity were met by examination of skewness and kurtosis coefficients, normal probability plots, and plots of residuals against predicted values.

RESULTS AND DISCUSSION

The *Chara* found in the east branch of the Maple River was identified as *Chara vulgaris* L. (Charales: Characeae), a species quite common in non-eutrophic, temperate, lotic and lentic habitats in North America (Prescott, 1962; Haslam, 1978).

The east branch of the Maple River is not highly subject to spates or flooding until spring snow-melt, and from our observations over the past 8 years, *Chara* hummocks and vascular macrophyte beds often persist until late winter before breaking down. In May and June, shoots reappear throughout the riffles and pools. Hummocks are well-established by mid-June and appear in roughly the same areas of stream from year to year, although exact positions vary. Maximum development of the hummocks occurs in August to early September when the stream reaches lowest discharge. These observations are similar to annual hummock cycles described by Tindall (1962) and Haslam (1978).

Hyporheic temperature patterns around and beneath *Chara* Hummocks A and B were similar (Figs. 2a, 3, 5). Temperature patterns upstream and to the sides of both hummocks were relatively uniform with respect to depth, while much cooler water was detected directly beneath each body and foot. Temperatures beneath the sand pockets were slightly lower than, but more similar to, patterns at the sides and upstream. Two weeks after complete removal, the original pattern beneath Hummock A was no longer evident (Figs. 2b, 4). The generally lower hyporheic temperatures following removal reflected a seasonal

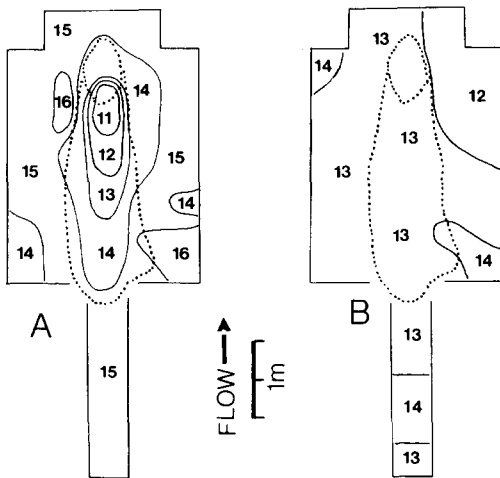


Fig. 2. (A) Areal plot of hyporheic temperatures 15-cm deep in the bed beneath Hummock A. Location of hummock on surface shown by dotted line. (B) Areal plot of hyporheic temperatures 15-cm deep in the substratum 2 weeks after removal of Hummock A. Location of original hummock on surface shown by dotted line.

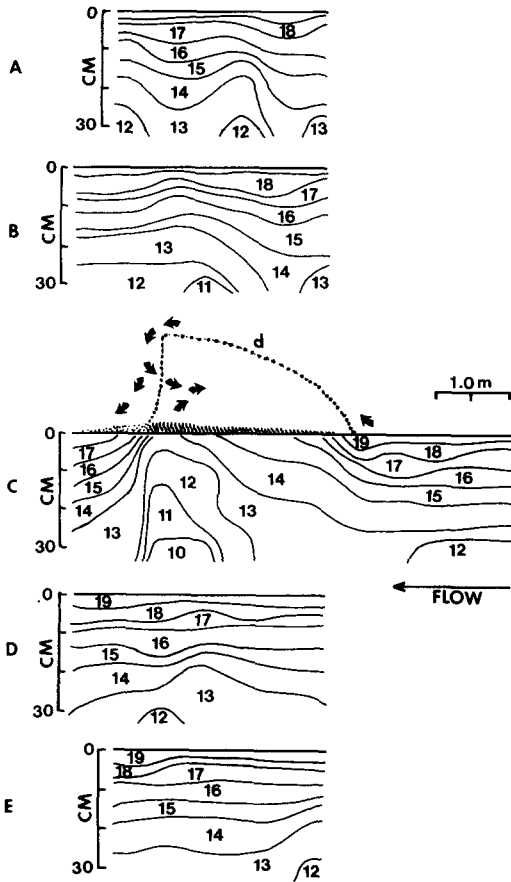


Fig. 3. Plots of vertical hyporheic temperature profiles along transects A-E (see Fig. 1) of Hummock A. Note that vertical scale is exaggerated. Position of hummock along Transect C is shown in relation to horizontal axis and to exaggerated vertical axis (d). Arrows indicate water movement over and into hummock.

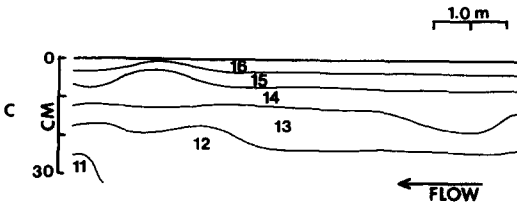


Fig. 4. Plot of vertical hyporheic temperature profile along Transect C (see Figs. 1, 3) 2 weeks after removal of Hummock A.

stream water temperature decrease from 19 to 16°C in the time period between the two Hummock A profiles.

Temperature measurements taken beneath the head, body, foot and sand pocket of the additional 35 *Chara* hummocks showed overall patterns consistent with Hummocks A and B. Hyporheic temperatures were significantly lower ($P=0.0001$) at the body and foot locations compared with the head or sand pocket (Table I). Also, a significant interaction occurred between hummock length and temperature ($P=0.0006$) demonstrating that hyporheic temperatures were proportionately lower beneath the body and foot of larger hummocks (Table I).

Hyporheic temperature pattern data were consistent with theoretical and experimental modifications of hyporheic upwellings by stream-bed surface objects (Cooper, 1965). Conforming to the general pattern given by Vaux (1962, 1968) and Thibodeaux and Boyle (1987), the head of the hummock created a convex change in the stream-bed promoting an upwelling of hyporheic water; concave changes occurred between the foot and sand pocket promoting the downwelling of stream water into the stream-bed (Figs. 3, 5). Also consistent with the literature, the magnitude of upwelling-downwelling was dependent upon the size of the surface object, i.e. hummock.

Position along the riffle-pool sequence also appeared to be important. White et al. (1987) demonstrated that the sharpest temperature gradients between stream water and near-surface hyporheic water occur in the middle of the stream toward the downstream ends of riffles and the beginnings of pools. Qualitative observations showed that *Chara* hummocks were also more abundant toward the middle of the river in the transitional areas from riffles to pools.

The hyporheic temperature patterns beneath *Chara* hummocks infer the alteration of hyporheic water flow into the hummock sand deposits, particularly at the foot. Within and just above the sand deposits, water movement has been shown to be in an upstream direction towards the hummock head (Tindall, 1962; Minckley, 1963; D.S. White, unpublished data, 1987) (Figs. 3, 5). This

TABLE I

Results of Scheffé's all-pairwise comparisons of temperature means between and within *Chara* hummocks of three size classes in the east branch of the Maple River. All means listed are significantly different ($\alpha=0.05$) from one another. Temperatures are from 5 cm beneath hummocks

Hummock length (cm)	no.	Temperature (C°)			
		Head	Center	Foot	Sand Pocket
< 50	14	16.07	13.96	13.17	15.25
50-100	13	16.11	13.04	12.00	15.35
> 100	8	16.25	11.88	10.94	15.44

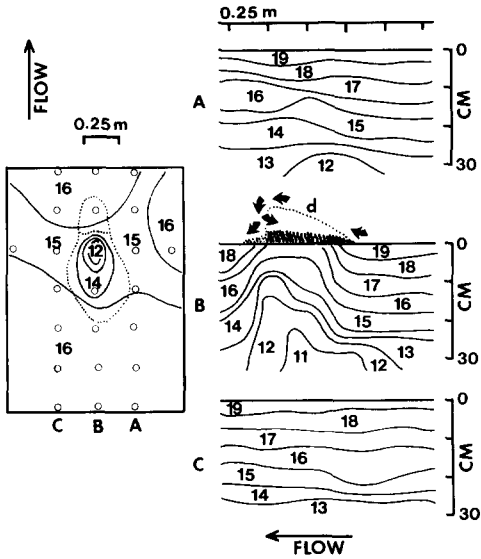


Fig. 5. Hummock B. Left: areal plot of hyporheic temperatures 15-cm deep beneath hummock showing location of temperature sampling points (\circ) on the $0.25\text{ m} \times 0.50\text{ m}$ grid, location of downstream Transects A-C, and direction of streamwater flow. Location of hummock on surface shown by dotted line. Right: plots of vertical hyporheic temperature profiles along Transects A-C. Note that vertical scale is exaggerated. Position of hummock along Transect B is shown in relation to horizontal axis and to exaggerated vertical axis (d). Arrows indicate water movement over and into hummock.

upwelling pattern would serve to distribute hyporheic water and associated nutrients and ions throughout the hummock.

Daily (1953, 1958), Krause (1983), Bilby (1984) and Castilla and Amoros (1984) have suggested that relationships exist between nutrient sources originating in the substratum (from groundwater) and macroalgae distribution, particularly *Chara*. Their studies did not differentiate between groundwater and hyporheic sources. Littlefield and Forsberg (1965) determined that all plant parts, including the rhizoids, of *Chara globularis* Thuill. have equal ability to take up phosphorus (P-32) and translocate it to other plant parts. Although the mechanism for translocation in *Chara* is not well understood, endoplasmic movement of absorbed nutrients from the rhizoids to other plant parts has been suggested (Littlefield and Forsberg, 1965). Nutrient uptake through the root system, particularly nitrogen and phosphorus, also has been demonstrated for a variety of lentic aquatic vascular macrophytes (Best and Mantai, 1978; Carignan and Kalff, 1980; Barko and Smart, 1980, 1981; Huebert and Gorham, 1983; Smith and Adams, 1986) and is suspected for lotic taxa (Fortner and White, 1988).

Surface and hyporheic water in the east branch of the Maple River differ

with respect to dissolved phosphorus and nitrate–nitrogen concentrations. The P:N ratio in surface water during the August study period was 1:12.5, whereas, the P:N ratio in the hyporheic water (10–20 cm deep into the bed) was 1:3.4 (S.P. Hendricks, unpublished data, 1987). Thus, the hyporheic zone may act as a reservoir for ions and nutrients as has been shown in other studies (Grimm et al., 1981; Wallis et al., 1981; Godbout and Hynes, 1982; Bencala, 1984; Grimm and Fisher, 1984). In this case, although purely conjectural, it can be speculated that during times of nutrient depletion in the Maple River, hyporheic upwellings beneath *Chara* hummocks expose rhizoids to potentially higher levels of nutrients and ions than would be expected to occur in stream water alone.

These data demonstrate that hummocks produced by *Chara* alter hyporheic temperature patterns in a manner similar to other types of bed surface objects. Inferred hyporheic underflow resulting from the alterations suggests that hummocking may be of some advantage to the plant colony. Although we can only speculate on thermal and nutrient advantages of the hyporheic interstitial water to *Chara* at this time, in situ manipulations and further nutrient uptake studies might link hyporheic nutrient concentrations with the distribution and function of *Chara* hummocks in lotic systems.

ACKNOWLEDGEMENTS

We wish to thank Dr. A. Reznicek for translation of the paper by Krause. Drs. E.F. Stoermer and A. Reznicek critically reviewed the manuscript and their suggestions are greatly appreciated. The University of Michigan Biological Station provided us with needed laboratory space, field equipment and general support of this research. Contribution No. 479 from the Great Lakes Research Division, University of Michigan.

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