Epipelic diatoms from an extreme acid environment: Beowulf Spring, Yellowstone National Park, U.S.A.

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With 3 figures and 2 tables

Abstract: A floristic study is presented of the diatom community from Beowulf Spring, Yellowstone National Park (YNP), U.S.A., a strongly acidic (pH<3) and thermophilous (temperature >50 °C) environment with potentially toxic concentrations of dissolved metals. A sampling transect between regions of active hydrous ferric oxide (HFO) precipitation and mats of periphytic red algae (Cyanidiaceae) revealed that diatoms are present mainly in the regions of the spring characterized by the highest temperatures and brown arsenic-rich HFO mats. The diatom flora is dominated by a deme within the Nitzschia thermalis complex, in association with N. ovalis, Pinnularia acoricola, and Eunotia exigua. Abiotic silica precipitates were observed on the surfaces of most diatom cells in uncleaned material. Cells of Cyanidiaceae also participate in active silica deposition. These observations not only highlight the tolerance of hot-spring diatoms to extreme environments with respect to temperature, pH, and arsenic (As) concentration, but also illustrate the clear zonation between epipelic algal communities within a hot spring.

Introduction

Although diatoms have been shown to respond to temperature in culture (Patrick 1977, Suzuki & Takahashi 1995), it remains uncertain whether they are directly thermophilous in an ecophysiological sense, or indirectly influenced by environmental conditions that covary with climate (Anderson 2001, Wolfe 2002). The bulk of previous studies on diatoms from hot spring environments has focused solely on temperature (Hustedt 1937–1938, Stockner 1967, Brock & Brock 1966), with some attention to the influences of low ambient pH and elevated concentrations of potentially toxic elements, such as arsenic (As) and copper (Cu) (Hargreaves et al. 1975, Whitton & Diaz 1981).

In this paper, we present an account of the diatom flora from the Beowulf Spring in the Norris Geyser Basin, Yellowstone National Park (YNP). This epipelic community inhabits As-rich hydrous ferric oxide (HFO) mats that coat the sandy substratum of the spring proximal to the vent (Fig. 1). Peripheral to the HFO zone, a green algal mat composed of cyanidiaceous Rhodophyta contains few, if any, diatoms. Light & scanning electron microscopic (SEM) investigations of these
communities are presented from both uncleaned and oxidized materials. Water chemistry implies that the diatoms are exploiting an ecological niche that may be toxic to other algae. Contrary to Villeneuve & Pienitz's (1998) suggestion that there is no single diatom assemblage typical of thermal springs, our study suggests a strong floristic similarity among highly acidic hot springs globally (Hustedt 1937–1938, Carter 1972, Hargreaves et al. 1975, Whitton & Diaz 1981, Cassie & Cooper 1989, Watanabe & Asai 1995, DeNicola 2000, Jordan 2001), implying that indeed there exists a distinct but biogeographically-disjunct flora in these extreme environments.

Methods

Beowulf Hot Spring (44°43'53" N, 110°42'41" W) lies within the Norris Geyser Basin, Yellowstone National Park, Wyoming, U.S.A. (YNP Thermal Inventory #NHSP35)) (Fig. 1A). Surface sediment collections were obtained from both the central portion of the spring, which is coated by HFO, and peripheral green algal mats (Fig. 1B). Samples were either cleaned using 30 % H2O2, or mounted uncleaned following dilution of the slurry in deionized water. Valves were mounted in Naphrax and observed at 100x under oil immersion with differential interference contrast optics (Leica DMLB). For scanning electron microscopy (SEM), slurry was evaporated onto stubs at room temperature in a desiccator, prior to sputter-coating with Au, and examination in a JEOL-6301F field-emission SEM. Archives of these samples are kept at 4 °C at the University of Alberta. Our results confirm that it is clearly advantageous to examine both cleaned and uncleaned material (Stockner 1967).

Beowulf is considered an acid-sulfate-chloride spring, where the spring discharges extremely acidic (pH<3) and hot (>50 °C) water, with mM concentrations of Na+, K+, Cl−, SO42− and Si (Fig. 1, Table 1, Inskeep et al. 2004). Water samples were obtained by syringe and filtered through 0.45 μm in-line nylon syringe filters. Samples were further acidified with TraceMetal-grade HNO3 and kept refrigerated until analysis by ion chromatography. Temperature and pH were measured in the field using a digital thermometer and an Orion Ross (8165BN) pH meter calibrated between 2 and 4, respectively.

Results and Discussion

Water chemistry

The Beowulf Spring has an ionic strength of 0.02 M, which is comparable to a marine–brackish estuarine salinity classification (Juggins 1992). Aqueous chemistry from Beowulf Spring has been characterized on multiple occasions and exhibits very little range in concentrations (±10 % or less for most constituents, Inskeep et al. 2004). The water chemistry reveals the presence of

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Fig. 1. A: Beowulf Spring, Norris Geyser Basin. Brown areas are hydrous ferric oxides (HFO) and green areas represent cover by rhodophytes including Cyanidium. B: Close-up of the transition between the HFO mat and Cyanidiaceae, with penry for scale. C: SEM photograph of silica casts produced by coccolid Cyanidiaceae cells. D: Close-up of cells in (C) showing remnants of soft-bodied cells within the silica cast (cc). E-H: SEM micrographs of diatoms from the HFO mat. (E) Nitzschia cf. thermalis var. minor with clean areolae devoid of precipitate. (F) Nitzschia ovalis (No) and Pinnularia aciculata (Pa), also with clean areolae; the cast of a Cyanidiaceae cell is also visible below N. ovalis. (G) A cell of N. ovalis encrusted in a diagenetic silica precipitate that completely sheathes the cell and blocks areolae. (H) A Pinnularia aciculata cell with diagenetic silica papillae on the apical cell surface; areolae are visible beneath. Scale bars are 10 μm, except (H) where it is 1 μm.
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Table 1. Water chemistry of Beowulf Hot Spring, Yellowstone National Park. All concentrations are reported in µM, except where indicated.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Concentration</th>
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<tbody>
<tr>
<td>Na</td>
<td>11136</td>
</tr>
<tr>
<td>*Si</td>
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<td>K</td>
<td>1225</td>
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<tr>
<td>As</td>
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<td>Mg</td>
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<td>Fe</td>
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<tr>
<td>*P</td>
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<tr>
<td>Zn</td>
<td>0.9</td>
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<tr>
<td>Mn</td>
<td>0.6</td>
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<tr>
<td>Cu</td>
<td>0.1</td>
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<tr>
<td>anions</td>
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</tr>
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</tr>
<tr>
<td>*F</td>
<td>147</td>
</tr>
<tr>
<td>*NO₃⁻</td>
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<tr>
<td>Temp (°C)</td>
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<tr>
<td>Ionic strength (M)</td>
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</table>

* data from Inskeep et al. (2004)

potentially toxic metals to algal growth, namely Cu and As (Table 1). In particular, As concentrations reach 20 µM, much higher than minimum concentrations required to inhibit growth of diatoms in culture (Saunders & Riedel 1998). Similarly, Beowulf Cu concentrations are two to three orders of magnitude greater than those used by Saunders & Riedel (1998). Thus, natural concentrations of As and Cu in the Beowulf Spring approach or exceed those from the most highly impacted acid-mine drainages (Whitton & Diaz 1981, Verb & Vis 2000).

While it is not our intention to speculate as to whether there is active uptake of As by diatoms in Beowulf Spring, As uptake is likely occurring among other microorganisms in YNP hot springs, namely bacteria (Langner et al. 2001, Inskeep et al. 2004). Metabolism of As by marine algae is hypothesized to occur because of the molecular similarity between phosphorous and As (Edmonds & Francesconi 1998). General pathways of metals metabolism by algae include sequestration, complexation with exuded dissolved organic carbon, and redox transformations during uptake (Saunders & Riedel 1998). Thus, a range of biogeochemical processes exist to allow not only the survival, but indeed the success, of algae inhabiting these extreme environments.

The pH of Beowulf Spring at the time of sampling was 2.26, and the temperature was 67 °C. A number of diatom communities have been documented at pH of <3, although species rich-

**Green mats**

Samples of the green Cyanidiaceae mat lack diatoms (Fig. 1A–B), with the exception of occasional frustules that presumably originate from transport. However, significant amorphous silica precipitation occurs in association with Cyanidiaceae cells (Fig. 1C–D). Silica biominalization under highly acidic conditions is not well-documented, with the exception of Asada & Tazaki’s (2001) study of *Cyanidium caldarium* in a Japanese spring at pH<2. They proposed passive models including nucleation of silica on cell walls, polymerization of silicic acid, and adhesion of colloidal silica gel. These models, however, contradict general observations that spontaneous silica polymerization and sinter formation typically occur at circumneutral pH (Konhauser et al. 2004), and that excess H+ inhibits silica polymerization (Fournier 1985). Nonetheless, the end product, smooth cyst-like features that frequently coalesce between adjacent cyanidiacean cells (Asada & Tazaki 2001), is identical to our observations from the Beowulf material (Fig. 1C–D).

**Brown mats**

The HFO mat contained abundant diatoms that occur as solitary epipellic forms. All observed specimens are biraphid taxa, hence capable of motile displacement within the mat. Several specimens preserved intact chloroplasts when viewed in LM. SEM revealed diatom surfaces both completely free of secondary silica precipitates and with clean areolae (Fig. 1E & F), as well as thoroughly Si-encrusted specimens (Fig. 1G & H). In the latter instances, inorganic Si precipitation has formed a continuous botryoidal coating, comprised of coalescent individual papillae of approximately 100 nm diameter. We hypothesize that living diatoms have cleaner valve surfaces than dead ones, and perhaps that inorganic silica precipitation may at times overwhelm living cells. Inskipp et al. (2004) have provided a complete characterization of the brown mat, revealing a variety of SiO2 crystalline polymorphs and microbial communities encrusted with As-rich HFO. It is unclear to us at this time what aspect of the HFO mat contributes to the success of the diatoms living there, in sharp contrast to their absence in the green mat. Given that Cyanidiaceae are virtually absent in the HFO mats, it is also possible that resource competition plays a role in delimiting these algae.

**Floristic description**

The epipelagic diatom community in Beowulf Spring consisted of five species (Table 1). The dominant diatom taxon was *Nitzschia cf. thermalis* var. minor Hilsé (56 %), followed in decreasing order of relative abundance by *Pinnularia acoricola* Hust. (21 %), *Eunotia exigua* (de Brébisson ex Kützing) Rabenhorst (15 %), *Nitzschia ovalis* Arnott (7 %) and *Enyonema minutum* (Hilsé ex Rabenhorst) D.G. Mann (<1 %). We discuss the four dominant diatoms further below, and provide LM and SEM micrographs of each. We do not consider *E. minutum* further because its abundance is insufficient to ascertain with confidence that it was truly living in the spring.
**Nitzschia cf. thermalis var. minor** (Figs. 1E, 2F–H & 3A–E, Table 2)
Length: 15–28 μm
Width: 2–4 μm
Striae / 10 μm: 23–27
Fibulae / 10 μm: 8–11
We have identified specimens from the Beowulf Spring that appear to conform with *N. thermalis var. minor* Hilse according to sketches by Grunow in Van Heurck (1880–1885; Plate 59, Fig. 22) of the isotype material collected by Rabenhorst (no. 1266). Lange-Bertalot (1978) considered *Nitzschia thermalis var. minor sensu* Hustedt (Simonsen 1987, Plate 346, Fig. 9–11) to actually represent a small specimen of *N. umbonata* (Ehrenberg) Lange-Bertalot. He then proposed a new taxon, *N. homburgiensis* Lange-Bertalot, for the *N. thermalis* complex, based on fibula morphology and the central constriction of the cell margin. *N. umbonata* was combined from Ehrenberg's basionym *Navicula umbonata* and is a synonym for *Nitzschia thermalis sensu* Grunow (Lange-Bertalot 1978). Of the two species *N. umbonata* and *N. homburgiensis*, the Beowulf specimens more closely conform to the latter (Table 2). Both our specimens and *N. homburgiensis* are linear with apiculate ends, transapical striae composed of fine areolae, and a constricted central

![Image of diatoms](image)

**Fig. 2.** Light micrographs of Beowulf Spring diatoms from cleaned samples (1000x magnification). A-E: *Eunotia exigua*. (A-D) Valve views showing variable morphology. (E) Girdle view showing terminal raphe nodule at the apices (arrows). F-H: *Nitzschia cf. thermalis var. minor*. (F-G) Valve view; central constriction of valve margin and interruption of raphe and fibulae; fine striae (H) girdle view. I-J: *Nitzschia ovalis* valve view; dense fibulae and striae not resolvable under LM. K-M: *Pinnularia acoricola* (K-L) valve view. (M) girdle view. Scale bar is 10 μm.

<table>
<thead>
<tr>
<th></th>
<th><em>N. hombergiensis</em></th>
<th><em>N. umbonata</em></th>
<th><em>N. steynii</em></th>
<th><em>N. rimos</em> <em>a</em></th>
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<tbody>
<tr>
<td>Length (µm)</td>
<td>15–28</td>
<td>32–52</td>
<td>22–125</td>
<td>27–54.5</td>
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<tr>
<td>Width (µm)</td>
<td>2–4</td>
<td>5–6</td>
<td>6–9</td>
<td>4–5</td>
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<td>23–27</td>
<td>34–40</td>
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<td>Fibulae / 10µm</td>
<td>8–10</td>
<td>9–15</td>
<td>7–10</td>
<td>10–12</td>
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<tr>
<td>Fibulae notes</td>
<td>Irregular &amp; widely spaced; can extend to centre of valve</td>
<td>Short, narrow, regularly spaced; convergence of 2–3 striae</td>
<td>Prominent &amp; evenly spaced</td>
<td>Robust</td>
</tr>
<tr>
<td>Central area constricted</td>
<td>yes</td>
<td>yes</td>
<td>slight</td>
<td>variable</td>
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<tr>
<td>Habitat</td>
<td>Thermal springs</td>
<td>Circumneutral; unpolluted waters</td>
<td>Thermal springs; eutrophic waters; acid mine drainage</td>
<td>Thermal springs</td>
</tr>
</tbody>
</table>

a. Description of specimens from Beowulf Spring, Yellowstone Nat. Park, U.S.A (this paper).
b. Lange-Bertalot (1978) and Krammer & Lange-Bertalot (1988)
d. Bourelly & Manguin (1952)

margin (Figs. 3A–E). REM of *N. hombergiensis* and the isotype material of *N. thermalis* var. *minor* Hulse reveal that the fibulae are irregular, widely spaced, and can extend to the center of the transapical axis (Plate 39 of Lange-Bertalot 1978). Comparatively, the fibulae from Beowulf specimens range in thickness from 0.5 to 1.0 µm along the apical axis (Fig. 2C) and are confined to the margin of the valve. In addition the raphe of our specimens is more eccentric than that of *N. hombergiensis* (Fig. 3B). Cassie (1989) illustrated *N. umbonata* from a shallow thermal pool (Tokanui, New Zealand) with similar fibulae and raphe structures to Beowulf specimens, but associated with significantly larger valves (36–45 µm). Morphometric comparisons of *N. cf. thermalis* var. *minor*, *N. hombergiensis*, *N. umbonata*, *N. steynii* Cholnoky emend. (Schoeman & Archibald 1988), and *N. rimos* Manguin (Bourelly & Manguin 1952) indicate that each of these taxa has a distinctive morphology (Table 2).

Further questions arise in considering the ecologies of these diatoms. Lange-Bertalot (1978) associates *N. hombergiensis* with circumneutral, unpolluted freshwaters, including the Arctic, whereas *N. umbonata* inhabits both polluted localities and, moreover, hot springs. From a strictly ecological standpoint, specimens from Beowulf have far closer affinity to Lange-Bertalot's (1978) *N. umbonata*. Because the combination *thermalis* var. *minor* predates all of the potentially equivalent taxa (and/or closely-allied forms), we have identified the Beowulf specimens as *Nitzschia* cf. *thermalis* var. *minor* Hilse. At this point, and pending further analysis, we feel that proposing a new name would only further confuse nomenclatural issues within the '*N. thermalis*' complex. There appear to be no similar specimens held in the collections of either the Canadian Museum of Nature or the Philadelphia Academy of Natural Sciences (P.B. Hamilton & M.B. Edlund, pers. comm.).

Nonetheless, it is clear that diatoms of the *N. umbonata-thermalis* cluster occur in a number of locations in Europe and N. America that have extreme water chemistries. For example, Whitto & Diaz (1981) recorded *N. thermalis* at acid mine drainage sites with pH between 3 and 4 in the U.K. and Belgium. Stockner (1967) noted the presence of *N. thermalis* in alkaline hot springs...
(>35°C) situated in Mount Rainier, Washington, USA, but not in similar springs from the Upper Geyser Basin, YNP, suggesting that this species is not necessarily acidobiontic. It should be noted that *N. thermals* is larger and has no central interruption of the fibulae, in contrast to our specimens and *N. thermals var. minor sensu* Hilse (Van Heurck 1880–1885), though both nominate and varietal forms seem to occur in similar environments. Weed (1889) found specimens of *Denticula thermals* Kütz. in hot springs of the Pelican Creek area in YNP, which he may have confused with any number of *Nitzschia*. From our extensive literature survey, it appears that *Nitzschia cf. thermals var. minor* is not widespread in hot springs (Copeland 1936, Stockner 1967, Whitton & Diaz 1981, Villeneuve & Pienitz 1998, DeNicoia 2000). This may suggest that *N. cf. thermals var. minor* may be restricted to only the hottest springs of high ionic strength and greatest acidity.

**Pinnularia acoricola** Hustedt (Figs. 2K–M & 3G–I)

Length: 11–17.5 μm
Width: 2.5–3.5 μm
Striae / 10 μm: 13–17

*P. acoricola* has a lanceolate to slightly oval valve morphology, with broadly rounded apices. The striae are strongly convergent at the poles and radial in the central area. The central area is either rounded or interrupts striae extending to the valve margin. The external distal ends of the raphe are hooked in the opposite direction to the proximal ends. DeNicola (2000) discusses the misidentification of *P. acoricola as P. obscura*, and similarities to *P. chamaezius*. However, neither of these species can be considered synonyms to *P. acoricola*. Our specimens, examples of which are shown both in LM (Figs. 2K–M) and SEM (Figs. 3G–I), are consistent with detailed descriptions and light micrographs offered by Carter (1972), Krammer & Lange-Bertalot (1986) and Watanabe & Asai (1995).

*P. acoricola* has been observed in a number of acidic waters globally (Hustedt 1937–1938, Carter 1972, Hargreaves et al. 1975, Whitton & Diaz 1981, Cassie & Cooper 1989, Watanabe & Asai 1995, DeNicola 2000, Jordan 2001). From the literature, it seems clear that this species is endemic to highly acidic environments, namely hot springs and acid mine drainage. The pH of waters in which it has been observed ranges from <1 to 4, and temperatures up to 50°C. Whitton & Diaz (1981) present one of the few studies which considers the direct influence of dissolved heavy metals on the success of diatoms in acidic waters. The authors use 59 records of *P. acoricola* in an attempt to elucidate any relationships between pH and Cu and Zn, they present upper limits for this diatom of 10 mg Cu l⁻¹ (0.16 mM) and 100 mg Zn l⁻¹ (1.53 mM). Comparatively, aqueous concentrations of Cu and Zn in Beowulf Spring are four orders of magnitude lower (Table 1). It is also noted that *P. acoricola* has been documented in close association with *Cyanidium caldararium* elsewhere, in both hot springs (Whitton & Diaz 1981) and endolithic habitats (Hernández-Chavarria & Sittenfeld 2006).

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**Fig. 3.** SEM photographs of diatoms from cleaned samples of Beowulf Spring. A-E: *Nitzschia cf. thermals v. minor*. (B) Shows the external view of the central nodule (cn) with the eccentric raphe. (C) An internal view showing the fibulae on the valve margin with the interior of central nodule (cn) visible. (D) Apiculate end with eccentric raphe F: *Nitzschia ovalis* cell. G-I: Pinnularia acoricola. (G) Hypovalve view showing the strongly convergent striae at the poles and radial pattern in the central area. (H) Girdle view (I) distal raphe end deflected; striae appear as groups of individual puncta in costa-like areas. J-L: *Eunotia exigua*. (J) Valve view with the curved raphe terminus on the valve face. (K) Raphe structure on the valve mantle with helicoglossa evident. (L) Close-up of the internal raphe terminus showing the helicoglossa (h) and rimoportulae (r). White scale bars are 1 μm, except A, G, H, J, & K where it is 10 μm.
Epipelic diatoms from an extreme acid environment: Beowulf Spring
**Eunotia exigua** (de Brébisson ex. Kützing) Rabenhorst 1864 (Figs. 2A–E & 3J–L)

Length: 8–31 μm
Width: 3–5 μm

Valves are crescent-shaped and isopolar, with ends capitulate to rostrate, the ventral margin is slightly concave. Striae are punctate and transapical. Raphe is short, located on the ventral margin of the mantle, and occasionally migrate to the valve face distally with a curved terminal fissure (Fig. 3J), where it terminates internally in a helictoglossa (Fig. 3L). A single rimoportula occurs at one pole of each valve. There is considerable variability in the morphology of *Eunotia exigua*, which has led to the reference of the species as a complex or ‘*E. exigua sensu lato*’ (Krammer & Lange-Bertalot 1991, DeNicola 2000).

*Eunotia exigua* is truly a cosmopolitan species, present in lakes, ponds, bogs and hot springs from tropical to arctic regions (Scherer 1981, Whitten & Díaz 1981, Round 1991, DeNicola 2000, Joynt & Wolfe 2001). *E. exigua* is an acidobiontic taxa occurring almost exclusively in acidic environments, and having a pH optimum ≤ 5 (Charles 1985). Whitten & Díaz (1981) observed a pH range of 2–4 in 44 samples from hot springs and acid mine drainage. Furthermore, concentrations of Cu and Zn >100 mg l⁻¹ did not impede the diatom’s viability.

**Nitzschia ovalis** Arnott (Figs 2I–J & 3F)

Length: 12–20.5 μm
Width: 3.5–5 μm

Valves are elliptical with rounded apices. Striae are fine and generally unresolvable in light microscopy (Figs. 2I–J) and require SEM to reveal their morphology (Fig. 3F). There is no central area or nodule, and fibulae are regularly spaced on the valve margin with no central interruption. The raphe structure is peripheral and not visible in LM. There is potential for misidentification of *N. ovalis* as *N. communis* Rabenhorst, and *vice versa* (DeNicola 2000). The morphology of *N. communis* is slightly narrower, and striae are more evident under LM. *Nitzschia ovalis* also shares features with *N. pusilla* Grunow emend. Lange-Bertalot and *N. aurariæ* Cholnoky, both of which are narrower and, in the case of *N. pusilla*, exhibits slightly rostrate apices (Krammer & Lange-Bertalot 1988, DeNicola 2000). The Beowulf specimens of *N. ovalis* are consistent with both type material in Van Heurck (1880–1885) and European specimens described and illustrated by Krammer & Lange-Bertalot (1988).

Very few records of *N. ovalis* exist for freshwater environments despite its original description as a continental species. However, there are a number of marine accounts for this diatom, and it has been referred to as an estuarine benthic taxon (Saks 1982). Laboratory work showed that optimal growth occurred in waters of high ionic strength (i.e., 0.03 M) and the cultures tolerated temperatures up to 36°C (Saks 1982). Its presence in Beowulf Spring most likely relates to the high ionic strength of the water, coupled to broad tolerances with respect to pH. Other reported occurrences of *N. ovalis* in freshwaters seem to be restricted to acid mine drainage in the U.K. (Hargreaves et al. 1975).

**Conclusions**

The extreme conditions of Beowulf Spring reduce algal diversity to taxa with tolerance of low pH, high ionic strength, and elevated concentrations of aqueous metals that are inhibitory or toxic to other groups. Clear zonation between cyanidiacean (green) and diatom (brown) mats within the Beowulf Spring show that the habitat is further subdivided spatially (Fig. 1). The possibility of competitive exclusion between the habitats occupied by either group cannot be dismissed, all the more as both groups appear to metabolize silica actively. Epipelic diatoms from
the brown mats in Beowulf Spring, and their close affinities with other hot-spring assemblages, raise several interesting questions concerning the ecophysiology and biogeography of diatoms. It appears that the algae in the Beowulf system are not merely surviving extreme environmental conditions beyond the tolerances of other forms, but potentially deriving benefits from certain aspects of this habitat. Low diatom diversity and hence reduced inter-specific competition, coupled to the absence of predators, are obvious factors that may contribute to the success of this community. The potential metabolism of toxic metals by these diatoms must also be considered, and this merits further investigation. The apparent active silica metabolism of Cyanidiaceae may provide considerable phylogenetic insight, given the relationship between diatoms and red algae (Keeling et al. 2004). In terms of biogeography, two of the diatoms, *Pinnularia acorica* and *Nitzschia* cf. *thermalis* var. *minor*, appear almost exclusively associated with hot-springs, whereas another, *N. ovalis*, is halophilous, and a fourth, *Eunotia exigua*, is an acidobiont that inhabits acid-mine drainages and naturally-acidic environments with equal facility. It remains a mystery how such disjunct associations have emerged. Together, our observations provide strong incentives to more thoroughly catalog the diatom floras of YNP springs.

**Acknowledgments**

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**References**


