

***Fragilaria* and *Staurosira* (Bacillariophyceae) from sediment surfaces of 40 lakes in the Austrian Alps in relation to environmental variables, and their potential for palaeoclimatology**

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ABSTRACT

The percentage distributions of *Fragilaria* and *Staurosira* taxa in surface sediment samples from 40 oligo- to ultra-oligotrophic, pH neutral to alkaline, mountain lakes of the central Austrian Alps (Niedere Tauern) were studied in relation to environmental variables using multivariate statistics. Selected taxa that were of uncertain taxonomy or that might be difficult to distinguish were illustrated in LM or SEM. The same statistics as they were applied to the total diatom data set were run on a *Fragilariaceae* subset with *Fragilaria* and *Staurosira*. These analyses emphasized on the high sensitivity of these genera to climate-driven environmental variables in mountain lakes. Canonical Correspondence Analyses (CCA) indicated that the pH, mean July water temperature (T_{July}), length of ice cover, and dissolved organic carbon (DOC) made significant contributions to explain the variation in the diatom assemblages. In addition, water depth affected the distribution of benthic and planktonic taxa. Differences or similarities in ecological preferences of taxa provided suggestions for taxonomy. Correlations between the mean valve length and summer water temperatures increase the overall high potential of *Fragilaria* and *Staurosira* for palaeoclimatological reconstructions in mountain lakes.

Key words: Diatoms, *Fragilariaceae*, Alpine lakes, Canonical Correspondence Analyses, pH, water temperature relations, ice cover, DOC

1. INTRODUCTION

Diatom species within the genera of *Fragilaria* and *Staurosira* are frequent in Alpine (e.g. Hustedt 1943; Lotter *et al.* 1999; Lotter & Bigler 2000; Schmidt *et al.* 2001), arctic and subarctic lakes (e.g. Foged 1974; Smol 1988; Pienitz *et al.* 1995; Douglas & Smol 1995; Weckström *et al.* 1997a, b; Laing *et al.* 1999), and under comparable environmental conditions in the past (e.g. Haworth 1975, 1976; Marciniak 1986, 1988). Alpine lakes are characterized by prolonged ice over, short growing seasons, low or moderate water temperatures, rapid changes in the chemical-physical properties during the melt period, low nutrients, clear-water phases with high light penetration, and intense UV radiation (Wögrath & Psenner 1995; Sommaruga-Wögrath *et al.* 1999; Catalan *et al.* 2002).

The overall goal of this study was to evaluate the potential of *Fragilariaceae* for palaeoclimate reconstructions in Alpine lakes. *Fragilariaceae* are characterized by a high variability in shape, size, and microstructure (e.g. Williams & Round 1987; Krammer & Lange-Bertalot 1991). The following steps were performed: (1) We have split taxa with morphological variability into morphotypes. (2) Selected taxa that might be difficult to distinguish or of uncertain taxonomy were illustrated in the light microscope (LM) or were studied in the electron microscope (SEM). (3) We analyzed the chemical and physical variables in 40 lakes of the cen-

tral Austrian Alps. (4) This environmental data set was used to explain changes in the total diatom assemblages and within a *Fragilariaceae* subset. (5) We also examined the effect of water temperature on valve length of selected taxa.

2. STUDY SITES

The 40 oligo- to ultra-oligotrophic lakes are located in the Niedere (Schladminger) Tauern, Eastern Central Alps (47°13'15"N-47°21'31"N, 13°36'06"E-14°04'12"E), along an altitude gradient ranging from 1502 m a.s.l. to 2309 m a.s.l. The spatial extension of the study area (580 km²) and the catchment areas of the individual lakes (<9 km²) are small (Fig. 1). Crystalline bedrock predominates, associated by schists and diagenetic or metamorphic carbonates. The lakes are not acidified (the lowest pH is 6.9). Glaciers are not present in the study area.

3. MATERIAL AND METHODS

3.1. Diatom analysis

Surface sediment samples (0.5 cm) were collected during the summer of 1999 from the deepest parts of the lakes with the use of a gravity corer. Samples (0.5 g wet sediment) for diatom analyses were treated through standard procedures (Battarbee 1986: HCl and H₂O₂, and repeated washing in distilled water; slides were prepared using Naphrax high resolution mountant). At least

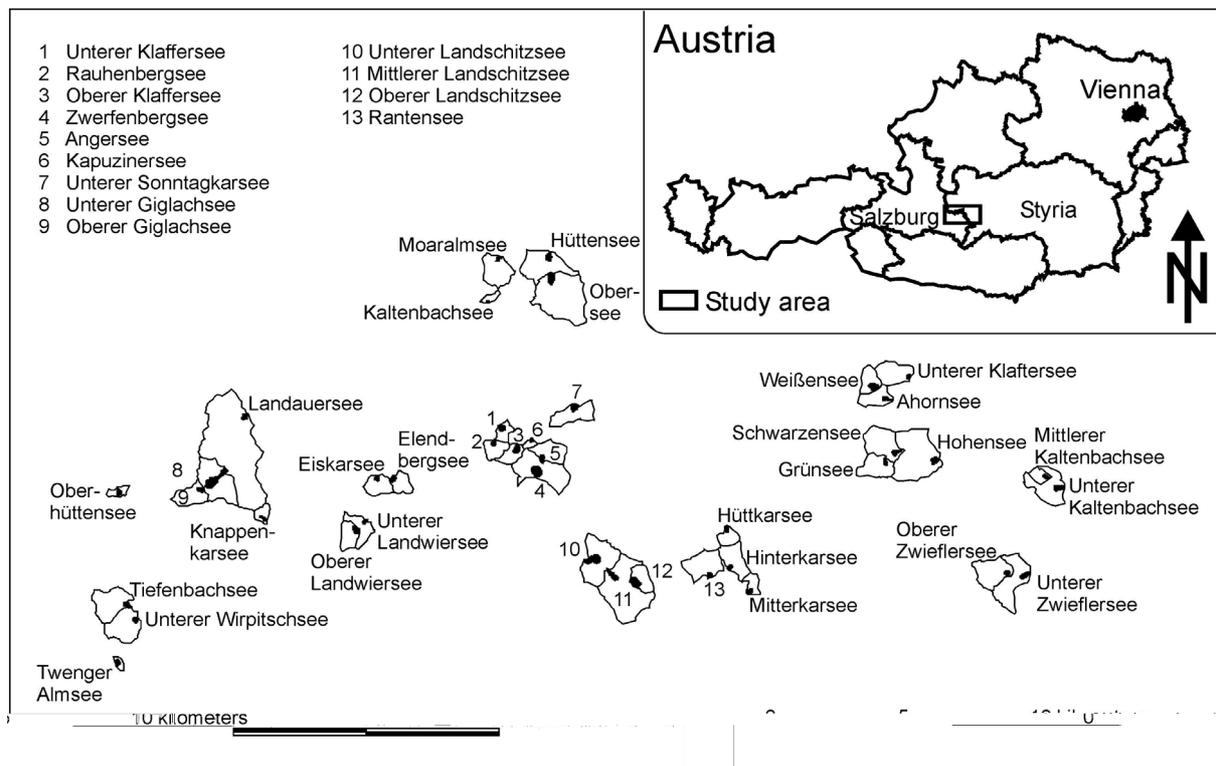


Fig. 1. Study area, geographic position, and catchments of the individual lakes located in the central Austrian Alps (Niedere Tauern).

500 diatom valves were counted using a Leitz microscope with 100× oil immersion and phase contrast objectives (PL APO 1.32). In addition to this total diatom set a subset of at least 500 valves of only *Fragilaria* and *Staurosira* (in the text called Fragilariaceae subset) was counted for an analysis of changes within these genera. Taxa that could not be differentiated in the LM, or with high numbers of broken valves, were grouped together. Valves in the girdle view that could not be assigned to a specific taxon were assigned among the taxa using the same % relative abundance as the taxa identified by valve surfaces. For valve size measurements, the maximum length of the apical axis was measured. SEM studies were performed on a Hitachi S3000N.

3.2. Environmental variables

Maximum water depth (Z_{\max}) was determined by echo sounding (FURUNO FE-4200). Relative water depth (Z_{rel}) is a ratio of lake surface area to maximum water depth. Lake surface area was measured using digitized aerial photographs (resolution of 2 m), using ArcView Spatial Analyst 3.1 (ESRI). Water temperature was measured in two hour intervals from July/August 1998 – September 1999 using 8 bit MINILOG – TR thermistors (VEMCO ltd.). Two thermistors per lake were placed between 1.4 and 3.3 m water depth. The depth of thermistor exposure could not be set more precisely, because of sediment-specific, technical, and logistic restrictions. Therefore, after the exposure, water temperature measurements were corrected for a standard

depth of 2.3 m (i.e. the median water depth of exposure) by linear interpolation of the two thermistor readings. Water temperatures were not standardized for 6 lakes because only one logger could be retrieved. Seasonal and among lake variability, however, exceeded the temperature differences caused by varying exposure depths. These lakes were therefore retained in the study. During ice cover water temperatures were set to 0 °C. This coding was necessary, because the measured water temperatures varied considerably within a lake at that time. The variation depended on whether the thermistors were frozen in the ice or not. If not, the distance between the thermistor and the ice cover had a major influence on the water temperature measurements. The corrected bi-hourly water temperature measurements were averaged for the months June - October ($T_{\text{Jun}} - T_{\text{Oct}}$). Ice freezing (freeze) and break up dates (break) were estimated using temperature readings (Fig. 2). The reference dates 'date of spring mixing' (S_{mix}) and 'date of autumn mixing' (A_{mix}) were defined as the first day after thawing or summer stratification when the mean daily water temperature was 4 °C.

Water chemistry samples were taken with a Patalas-Schindler sampler from a water depth of 2.5 m on the 18th and 19th of October 1999, which were sampled by means of a helicopter hovering over the lake. Conductivity and pH were measured in the field (Mettler Toledo M125 and M126). Alkalinity was measured by Gran titration. Main anions (sulfate, nitrate and chloride) and cations (calcium, magnesium, sodium and po-

tassium) were analyzed with ion chromatography (Dionex DX-120). Samples were filtered at the same day of collection using Whatman GF/C glass fiber filters with a pore width of $<0.45 \mu\text{m}$. Ammonium, total dissolved reactive silica (DRSi), total dissolved (P_{dis}) and total (P_{tot}) phosphorus (after digestion with sulfuric acid and hydrogen peroxide) were analyzed spectrophotometrically (Hitachi U-2000). Particulate phosphorus (P_{part}) was calculated from the total phosphorus minus total dissolved phosphorus. Total dissolved nitrogen (DN) was measured after digestion with sodium peroxodisulfate at 120°C and the reduction of nitrate to nitrite by passage through a cadmium-copper column. Ammonium and nitrate were summarized as total inorganic nitrogen (TIN) for all statistical analyses to take into account their transformation by oxidation and reduction. Dissolved organic carbon (DOC) was measured with a high temperature combustion method on platinum wire (Shimadzu TOC 5000).

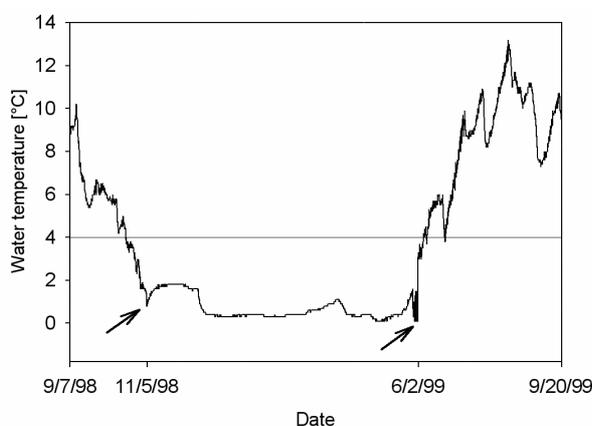


Fig. 2. Example of a lake water temperature record. Temperature curve from Hinterkarsee, situated 2,074 m a.s.l. and exposed to the south. Dates of the beginning and end of temperature readings (thermistors), freeze and break up (arrowed), and autumn and spring mixing (lined) are shown.

3.3. Multivariate statistics

All parameters, except pH, were \log_{10} transformed to avoid skewed distributions. Ice freeze and break up dates, as well as the dates S_{mix} and A_{mix} were expressed as Julian days. Diatom relative abundances were square root transformed to stabilize their variances (ter Braak & Šmilauer 2002). Taxa with a maximum abundance of $<1\%$ and occurrences in only one lake were disregarded.

Principal Components Analysis (PCA) was used to display the main gradients in the environmental parameters. A preliminary detrended correspondence analysis (DCA with detrending by segments) on the diatom assemblages (DA) resulted in a gradient length of 2.6 standard deviation units, suggesting the appropriateness of unimodal versus linear ordination methods (ter Braak 1987; Birks 1995). The DA were screened for outliers using correspondence analysis (CA). Within the

Fragilariaceae subset three lakes were dominated by one species (Mittlerer Kaltenbachsee, Tiefenbachsee, Twenger Almsee; abundance of $>90\%$). They were made passive in all of the analyses (i.e. they were retained, but had no influence on the result). Ordinations were performed using the program CANOCO 4.5 (ter Braak & Šmilauer 2002). A series of Canonical Correspondence Analyses (CCA), constrained to a single environmental variable at a time in order to examine the influence of each variable on the DA (marginal effects), as well as partial CCAs were used to analyze species environment relationships (ter Braak 1987; Borcard *et al.* 1992). The significance of PCA and CA axes was tested using the broken stick model (Jackson 1993). The significance of environmental variables on the DA was evaluated using Monte Carlo permutations (9,999 unrestricted permutation cycles, reduced model; ter Braak & Šmilauer 2002). Probability values were adjusted for multiple testing (P_{adj}) using a Bonferroni-type test procedure (Hochberg 1988). The response of individual taxa to selected environmental variables was tested by Huisman-Olff-Fresco-models (Huisman *et al.* 1993) with maximum likelihood, using the program HOF (J. Oksanen, unpublished program). Bootstrapped species optima were calculated by the program C2 (Juggins 2003).

4. TAXONOMY

The taxonomy of the polymorphic family of Fragilariaceae is controversial (see e. g. Lange-Bertalot 1980; Williams & Round 1986, 1987; Krammer & Lange-Bertalot 1991, 2000). We followed the concepts presented by Krammer & Lange-Bertalot (2000) that were modified by Lange-Bertalot & Compère (2001). The taxa of the two genera *Fragilaria* Lyngbye and *Staurosira* Ehrenberg are listed in table 1. Basionyms and synonyms are added to appoint taxonomic names that are still in common usage. Additionally, the following remarks together with illustrations should help to appoint taxa that might be difficult to distinguish or that their taxonomy is uncertain:

FRAGILARIA Lyngbye

Fragilaria delicatissima Lange-Bertalot

Fragilaria delicatissima (Figs 3a-c) differed in the LM from *F. nanoides* Lange-Bertalot (Fig. 3d; Lange-Bertalot & Metzeltin, 1996, Tab. 109, Figs 2 – 6) by more distinct capitate poles, less dense striae ($<18/10 \mu\text{m}$), marginal spines that reach the poles, a more illuminated light refraction in the phase contrast (probably due to a heavier silicification), and the occurrence of cell pairs (cells that have not separated following vegetative division). According to Krammer & Lange-Bertalot (1991) *F. delicatissima* differs by the more spindle-like form and the less dense ($14\text{--}16/10\mu\text{m}$), finer, striae from *F. tenera* (W. Smith) Lange-Bertalot.

Tab. 1. Species list (following the concepts of Krammer & Lange-Bertalot 2000, and Lange-Bertalot & Compère 2001) with abbreviations, basionyms and synonyms. * Rare species not included in the multivariate statistics.

Taxa	Abbreviations	Basionyms	Synonyms
* <i>Fragilaria alpestris</i> Krasske			
<i>F. amphicephala</i> (Kütz.) Lange-Bertalot	Famp	<i>Synedra amphicephala</i> Kützing	<i>Fragilaria capucina</i> ssp. <i>amphicephala</i> (Kütz.) Lange-Bertalot
<i>F. arcus</i> (Ehrenb.) Cleve	Farc	<i>Navicula arcus</i> Ehrenberg	<i>Ceratoneis arcus</i> (Ehrenb.) Kützing, <i>Hannaea arcus</i> (Ehrenb.) Patrick
* <i>F. austriaca</i> (Grun.) Lange-Bertalot		<i>Synedra amphicephala</i> var. <i>austriaca</i> Grunow	<i>Fragilaria capucina</i> var. <i>austriaca</i> (Grunow) Lange-Bertalot
<i>F. capucina</i> Desmazieres	Fcap		
<i>F. danica</i> (Kütz.) Lange-Bertalot	Fdan	<i>Synedra danica</i> Kützing	<i>Synedra ulna</i> var. <i>danica</i> (Kütz.) Van Heurck
<i>F. delicatissima</i> (W. Smith) Lange-Bertalot	Fdel	<i>Synedra delicatissima</i> W. Smith	
<i>F. cf. exiguiformis</i> Lange-Bertalot	Fexi FragFrumpGrun	<i>Fragilaria virescens</i> var. <i>exigua</i> Grunow	<i>Fragilaria exigua</i> (Grun.) Krammer & Lange-Bertalot, <i>Stauroforma exiguiformis</i> Flower <i>et al.</i>
<i>F. gracilis</i> Oestrup	Fgrac/nano (Group)		<i>Fragilaria capucina</i> var. <i>gracilis</i> (Oestrup) Hustedt
<i>F. nanana</i> Lange-Bertalot	Fnan	<i>Synedra nana</i> Meister	
<i>F. nanoides</i> Lange-Bertalot	Fgrac/nano (Group)		
* <i>F. opacolineata</i> Lange-Bertalot			
<i>F. parasitica</i> (W. Smith) Grunow	Fpar	<i>Odontidium parasiticum</i> W. Smith	<i>Synedra parasitica</i> (W. Smith) Hustedt, <i>Synedrella parasitica</i> Round & Maidana
* <i>F. polonica</i> Witak & Lange-Bertalot			
<i>F. rumpens</i> (u)-8.42 Tw5it0.56.4(e-Ber)10.3(t)48.9(282 0 T((m)(38 1 T0:4.9t)8(i)(3Tc0a)8(n)-0.6(a)TJ/zua)-0.6m021 Tpa)-0.6yump5e747D -0.0042 Tc 14.9935 Tw [(Fr)-8.2(ag)-8.5			

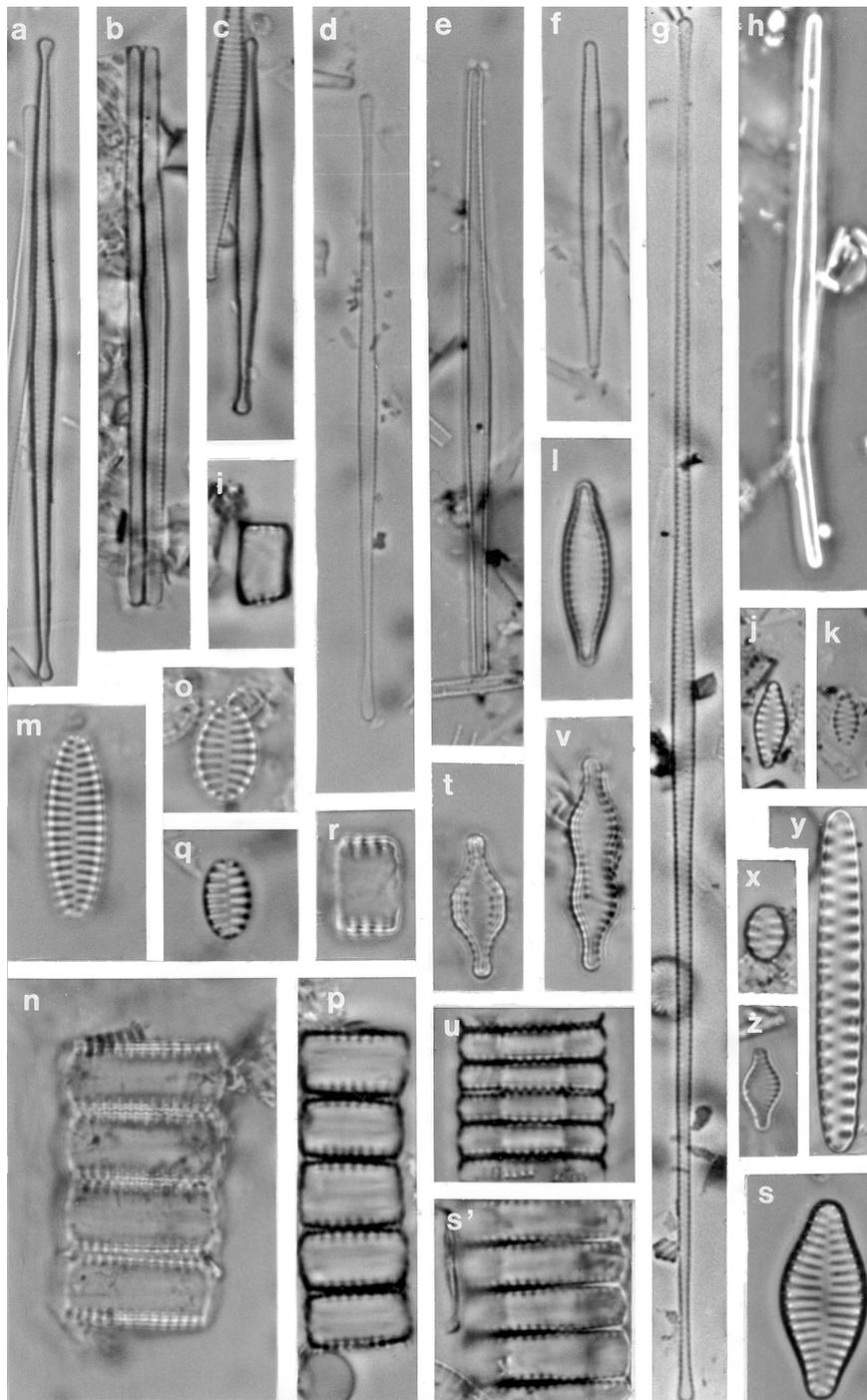


Fig. 3. LM photographs of selected diatom taxa (magnification 1,200 \times). **3a-c.** *Fragilaria delicatissima*. Valve face (Fig. **3a**); cell pair in girdle view (Fig. **3b**); smaller-sized valve in valve face (Fig. **3c**). **3d.** *Fragilaria nanoides* in valve face. **3e-f.** *Fragilaria gracilis*. Elongated (Fig. **3e**) and smaller-sized (Fig. **3f**) valves in valve faces. **3g.** *Fragilaria* spec. 1 in valve face. **3h.** *Fragilaria nanana* in valve face (phase contrast). **3i.** Species 2 in girdle view. **3j-l.** *Staurosira microstriata* (Fig. **3j**), small-sized morphotype (a) (Fig. **3k**), and (b) *Staurosira* cf. *microstriata* in valve face (Fig. **3l**). **3m-r.** *Staurosira* aff. *venter*. Elongated morphotype (1a) in valve face (Fig. **3m**) and girdle view (Fig. **3n**); Broadly-elliptical morphotype (1b) in valve face (Fig. **3o**) and girdle view (Fig. **3p**); small-sized morphotype (1c) in valve face (Fig. **3q**) and girdle view (Fig. **3r**). Note the rows of discernable mantle areoli in girdle views in contrast to Species 2 (Fig. **3i**). See correspondent to figure **3r** the SEM figure 5d. Morphotype with protruded poles (Fig. **3s**). **3s'**. "Girdles parallel" (*S.* aff. *venter*, see figure **3s**, or *S. pseudoconstruens*). **3t-v.** *Staurosira robusta*. Morphotypes with parallel contours (a) in valve face (Fig. **3t**) and girdle view (Fig. **3u**), and distinctly concave (b) (Fig. **3v**) central contours in valve face. **3x, y.** *Staurosira pinnata* s.l. *Staurosira pinnata* var. *subrotundata* (Fig. **3x**) and *S. pinnata* var. *intercedens* (Fig. **3y**) in valve faces. **3z.** *Staurosira parasitoides* in valve face.

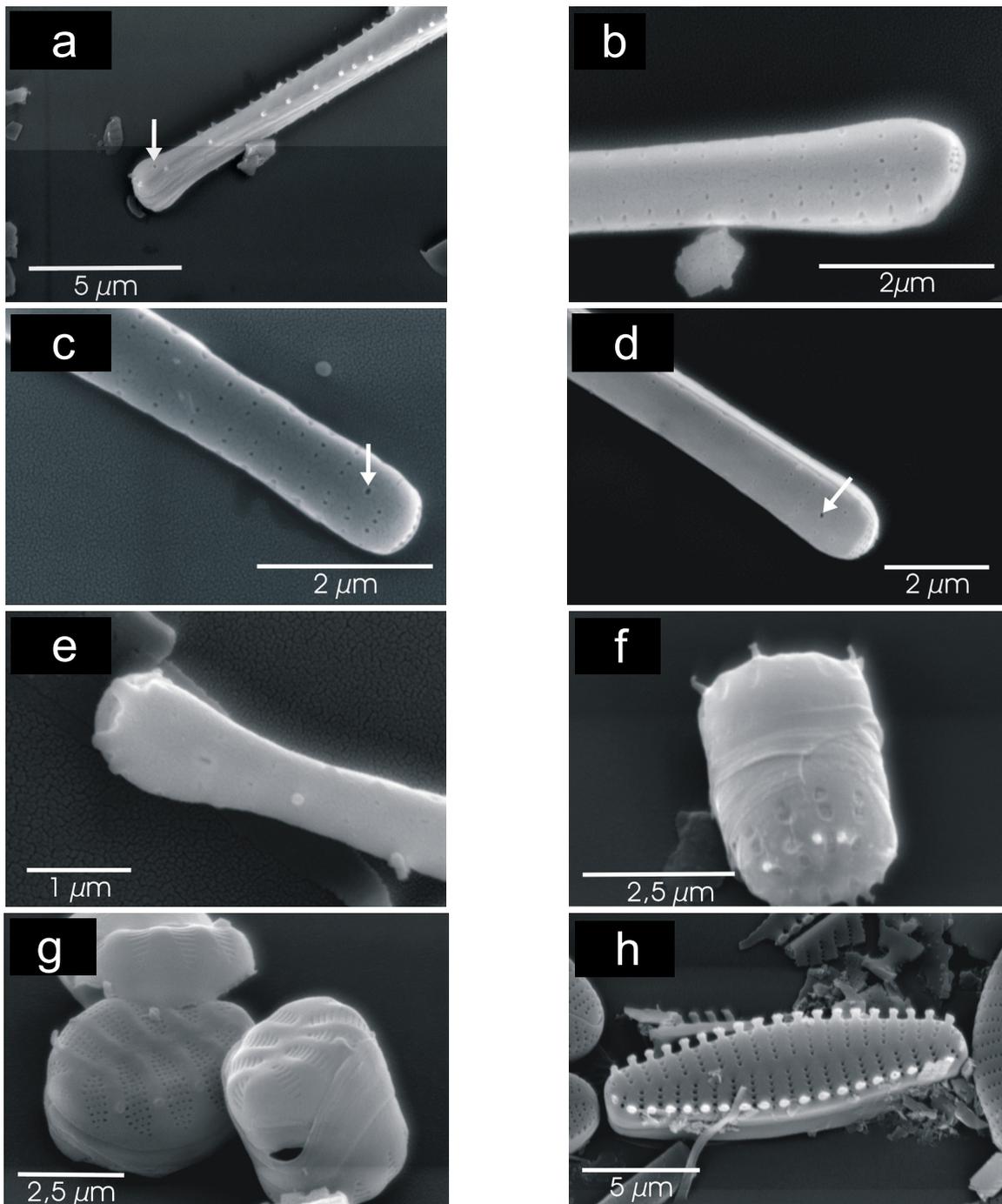


Fig. 4. SEM micrographs of selected diatom taxa. **4a.** Polar part of *Fragilaria delicatissima* showing the spine-formation and the external opening of the rimoportula (arrowed). **4b.** Polar part of *Fragilaria nanoides* with apical pore-field. **4c.** Polar part of *Fragilaria gracilis* with the external opening of the rimoportula (arrowed), and the presence of an apical pore-field. **4d.** Polar part of *Fragilaria nanana* showing the external opening of the rimoportula (arrowed). **4e.** Polar part of *Fragilaria* spec. 1 showing the external opening of the rimoportula and the apical horn-like appendices. **4f.** Species 2? Side view and part of the valve surface. **4g.** *Staurosira pinnata* var. *subrotundata* (right) and *Punctastriata ovalis* (left). Note transitions between punctate and "pinnate" structure of alveoli in the taxon at right from one and the same sample. **4h.** *Staurosira* aff. *venter* (2) in side view.

In the SEM the marginal spines of *F. delicatissima* are saw-tooth-like (Fig. 4a). A rimoportula is present near the end of at least one pole (Fig. 4a). Both lack in *F. nanoides* (Fig. 4b).

Fragilaria gracilis Oestrup and *Fragilaria nanoides* Lange-Bertalot

In the LM, elongated valves of *F. gracilis* (Fig. 3e) mainly differ from *F. nanoides*, at least by the less distinct capitate valves, median parallel (towards the poles the striae are also offset on either sides of the valve as in the entire valve of *F. nanoides*), and the coarser (18 – 20/10 µm) striae. The smaller-sized valves of *F. gracilis* greatly differ from *F. rumpens* by the median parallel striae, which are also offset in the latter.

In the SEM, both taxa showed no marginal spines towards the poles (Figs 4b, c). The polar pore field of *F. gracilis* consists of one row of porelli (Fig. 4c) whereas *F. nanoides* has two rows (Fig. 4b). *F. gracilis*, in contrast to *F. nanoides*, showed a rimoportula (Figs 4b, c).

Because of fragmentation of larger-sized valves, we combined the taxa *F. gracilis* and *F. nanoides* into one group (*F. grac/nano*).

Fragilaria nanana Lange-Bertalot

Fragilaria nanana differs in LM from *F. gracilis* and *F. nanoides* by the more narrow (median 1.5 – 2 µm), needle-like valves that appear to be more silicified (Fig. 3h), and the very tiny striae that are difficult to resolve.

According to SEM (Fig. 4d) towards the top of the valve no striae occur or if so they are restricted to tiny marginal areolae.

Fragilaria spec. 1

The strongly elongated (>100 µm), needle-like (Fig. 3g), slightly capitate valves with central indistinct striae are similar to those commonly referred in the literature as *Synedra acus* var. *angustissima* Grunow. The number of striae ranged from 15 to 18 in 10 µm.

In the SEM (Fig. 4e) the slightly enlarged poles show horn-like appendices and the opening of a rimoportula. Only single, elliptically elongated areolae (10 in 10 µm) occur at the valve margins towards the end of the valves. These characters clearly distinguish *Fragilaria spec 1* from *F. nanoides* (see Fig. 4b).

Fragilaria (Stauroforma) cf. exiguiformis

In the SEM (Figs 5g and h) the valve morphology corresponds with illustrations from Flower *et al.* (1996) for the spinose (the spines are also visible in LM, Figs 5e, f) form of *Fragilaria exiguiformis* (Grun.) Lange-Bertalot. The valves in our material are, however, distinctly larger (23.7 – 44.8 µm) than mentioned in Flower *et al.* (1996) for European populations of *Stauroforma exiguiformis* (13.4 – 16.4 µm).

STAUROSIRA Ehrenberg

Staurosira aff. *venter*

1) Elliptical valves with distinctly raised costae which bear marginal spines; in the LM the striae (12 to 15 in 10 µm) are punctate; in the SEM the areolae are elliptically-elongated and increase in size from the valve center towards the valve margin and mantle. Size ranged from 5.4 µm to 17.4 µm. Three different morphotypes were distinguished and counted separately:

- a) elongated valves >12 µm in length (Figs 3 m and n; 5a, b);
- b) broadly-elliptical valves 7.5 to 12 µm in length (Figs 3o and p; 5c);
- c) small valves <7.5 µm (Figs 3q and r; 5d).

The small valves differ from the former by the window-like areolae on the broadly enlarged mantle (Fig. 5d; also visible in LM, Fig. 3r), sometimes showing a grill-like microstructure in the SEM. More than two apical rows of areolae occur on the enlarged mantle that is also visible in LM (Fig. 3r).

At the present stage it is unclear as to whether all of the three morphotypes (1a – c) belong to one and the same species. Morphotypes which possess coarser areolae resemble *Fragilaria elliptica* in the sense of some authors, but the type of *Fragilaria elliptica* Schumann is unknown and seem to be lost (Krammer & Lange-Bertalot 1991). *Fragilaria (Staurosira)*, see Krammer & Lange-Bertalot 2000 *neoelliptica* was described by Witkowski (1994) from a brackish environment, and hence differs distinctly in the autecology from the Alpine populations. In the SEM (Fig. 5c) the broadly elliptical morphotype (1b) is similar to *Staurosira aventralis* that was described by Lange-Bertalot and Rumrich in Rumrich *et al.* (2000) from the Andes (3300 m a.s.l.). Similar taxa might be identified under the name of *Fragilaria construens* var. *venter* Ehrenberg (for its combination with *Staurosira* see Hamilton *et al.* 1992).

- 2) Elliptical elongated valves as in morphotype 1a. From the latter they differ, however, by the less raised costae, the smaller, rounded areolae of more or less the same size (SEM) that are not discernible in LM, in addition by only one row of mantle areolae (Fig. 4h).
- 3) Valves with distinctly protruded poles (Fig. 3s). It is unclear if the single valve surfaces which were found belong to girdle views showing valves with a parallel or convex median part and distinctly narrowed polar parts (Fig. 3s') or to *Staurosira pseudoconstruens*. Hence, they were counted separately ("girdles parallel").

Staurosira? Species 2

This taxon has small valves (<7 µm) with distinctly elongated, barrel-like, girdle views (Fig. 3i). Valve sur-

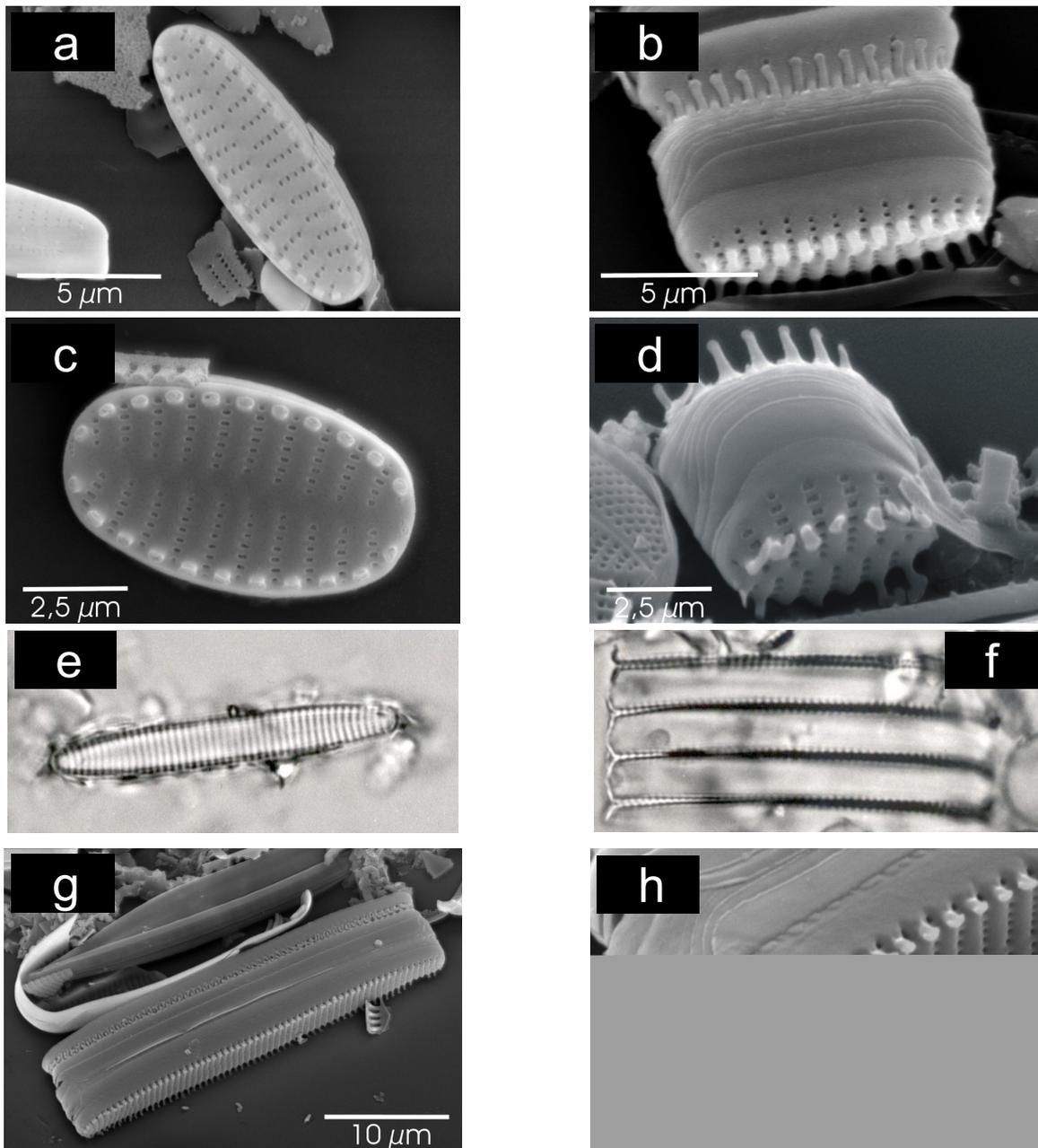


Fig. 5. SEM micrographs of selected diatom taxa (continued). **5a-d.** *Staurosira* aff. *venter* (1). Elongated morphotype (a) in valve (Fig. 5a) and girdle view (Fig. 5b); Broadly-elliptical morphotype (b) in valve view (Fig. 5c); Small-sized morphotype (c) in girdle view (Fig. 5d). Note the 3-4 rows of rectangular-elongated areolae on the enlarged valve mantle. **5e-h.** *F. cf. exiguiiformis*. Valve face (Fig. 5e) and girdle view (Fig. 5f) in LM; Side overview (Fig. 5g) and polar part (Fig. 5h) in SEM.

faces might be confused with the small morphotype (a) of *F. microstriata* illustrated in figure 3k. The marginal spines and striae of Species 2 are, however, offset, whereas in *F. microstriata* (a), as characteristic for the *F. brevistriata* complex, mantle areolae (lacking in Species 2), marginal spines, and ghost striae are arranged in one row (see Schmidt *et al.* 2004).

It is unknown if the barrel-like valve illustrated in the SEM (Fig. 4f) that was found together with Species 2 belongs to the same species. The valve surface under the SEM showed partly punctate alveoli. Marginal

spines may be branched or anchor-like. The valve mantle is ornamented by low depressions.

Staurosira microstriata (Marciniak) Lange-Bertalot and *Staurosira parasitoides* Lange-Bertalot *et al.*

Both taxa were studied and illustrated in detail by Schmidt *et al.* (2004). They are characterized by the presence of the so-called "ghost striae" (Lange-Bertalot & Metzeltin 1996), which means that the marginal areolae characterizing the *S. brevistriata* complex con-

tinue channel-like towards the valve center. In this feature and probably also in ecological preferences (see discussion) both taxa differ from other taxa of the *Fragilaria brevistriata* complex. *S. microstriata* was differentiated into two morphotypes which were counted separately: Small (<7.5 µm) boat-shaped valves (a) (Fig. 3k; see Schmidt *et al.* 2004, Fig. 10), and larger valves (b) (>15 µm) showing the same microstructure as *S. microstriata* noted as *F. cf. microstriata* by Marciniak (1988) (Fig. 3l).

S. parasitoides (Fig. 3z) differs from *S. microstriata* by its broadly fusiform bulbous shape, small conical, densely crowded marginal spines, and additional areolae in the enlarged part of the valve surface.

Staurosira pinnata s. l.

Three groups were distinguished and enumerated separately.

- a) Small (<7.5 µm), broadly elliptical valves which probably correspond with *F. pinnata* var. *subrotundata* A. Mayer (Fig. 3x). According to SEM studies (Fig. 4g) small valves co-occurred with the former which conform to *Punctastriata ovalis* as described by Williams & Round (1987). Since the areolate alveoli of the latter could not be differentiated in LM from the transapically elongated alveoli structure of the small *F. pinnata* specimens, and in the SEM both structures could be observed in one and the same sample (Fig. 4g), both forms were combined in this group.
- b) Mid-sized valves, 7.5 – 13 µm, occurred in two morphotypes, elliptical and slightly heteropolar valves.
- c) Large (> 13 µm) cigar-like, elongated valves. Within a single sample, valves were found that differed in width of the axial area from 1 to 2.5 µm. Valves with enlarged axial area correspond with *F. pinnata* var. *intercedens* (Grunow) Hustedt (Fig. 3y).

Staurosira robusta (Fusey) Lange-Bertalot

Two morphotypes were differentiated; (a) valves with more or less parallel sides (Figs 3t, u), and (b) those formerly described as *F. pseudoconstruens* fo. *bigibba* Marciniak which are characterized by distinctly concave valves (Fig. 3v).

5. RESULTS

5.1. Environmental variables

Geographical, morphological, and limnological features of the 40 study lakes are summarized in table 2A/B. These variables could be assigned to 4 major environmental gradients, (1) climate (PCA axis 1), (2) nutrients (PCA axis 2), (3) catchment characteristics (bedrock mineralogy and vegetation cover; PCA axis 3), and (4) water depth (PCA axis 4, Tab. 3). The four signifi-

cant PCA axes explained 75.2% of the variation in the abiotic variables.

The physical variables (water temperature, ice cover, date of mixing) explained most of the variation in the environmental data-set (PCA axis 1: 34.7%). Nutrients were largely independent from PCA axis 1. Within the chemical variables that characterize nutrients (the phosphorus and nitrogen fractions, DOC, DRSi), dissolved phosphorus had a higher correlation with the PCA axis 1 than with PCA axis 2. DOC correlates with PCA axis 2 and 3, and shows some correlation with PCA axis 1. Chemical variables characterizing bedrock mineralogy (pH, alkalinity, conductivity, Ca²⁺, Mg²⁺ and SO₄²⁻) were also correlated with PCA axis 1. Relative and, to a minor extent, absolute water depth were correlated with PCA axis 1 and 2.

5.2. Diatom analysis

A Correspondence Analysis (CA) on the total diatom assemblages resulted in three significant axes, explaining 33.7% of the variation. The Fragilariaceae were evenly spaced among the other diatoms (Fig. 6). Table 3 summarizes the amount of variation each environmental variable explained singly in a series of CCAs (marginal effects). Alkalinity and related variables (pH, conductivity, Ca²⁺, Mg²⁺) explained most of the variation in the total diatom dataset and the Fragilariaceae subset. DOC had a significant ($P_{adj} < 0.05$) influence on the total diatom assemblage, but not on the Fragilariaceae subset. Among the weather related variables were that of the July water temperature, which had a significant influence on total diatom dataset, whereas the length of the ice cover significantly affected the Fragilariaceae subset. Both variables, however, were highly correlated. Among the variables that had significant marginal effects on the entire diatoms, pH and T_{Jul} explained a significant unique (i.e., effects of other environmental variables removed) amount of variation (5.9% and 5.3%, respectively). The same analysis on the Fragilariaceae subset revealed, that only the length of the ice cover uniquely explained a significant amount of variation (7.3%) within this subset. Conductivity was deleted prior to both analyses because of a high colinearity (VIF >20) with the other significant variables.

Variables characterizing the catchment (mineralogy and vegetation cover) were highly correlated with CA axis 1 (Fig. 6). Weather driven variables (water temperature, variables related to ice cover and mixing) were correlated with CA axis 2 (Fig. 6). DOC was correlated with both CA axes 1 and 2. Water depth was correlated with CA axis 3. Figure 6 and 7 summarize species environmental variables relationships. The variables were included as passive environmental data in the CAs in which were selected according to their significance ($P < 0.05$) for the entire diatom dataset and the Fragilariaceae subset (Tab. 3B).

Tab. 2A. Altitude, morphometric, and physical characteristics of the 40 lakes of the study area (T = mean monthly temperature).

	Altitude m a.s.l.	Z _{max} m	Z _{el} m	Lake area ha	Autumn Mixing 98 Julian day	Freeze up 98 Julian day	Break up 99 Julian day	Spring Mixing 99 Julian day	Length of ice cover Julian day	T June 99	T July 99	T Aug 99	T Sep 98	T Oct 98
										°C	°C	°C	°C	°C
Alhornsee	2069	6.9	3.8	2.64	286	303	495	524	192	4.7	9.4	11.1	7.3	4.3
Angerse	2096	6.3	3.1	3.27	285	303	547	549	244	0.0	5.2	8.8	6.0	3.4
Eiskarse	1940	14.2	8.4	2.26	294	302	509	540	207	3.6	9.1	12.3	9.3	4.9
Eiendbergsee	2215	21.0	11.0	2.84	284	303	540	547	237	0.5	6.8	9.8	7.0	3.5
Grünsee	1984	6.7	3.7	2.54	285	303	510	516	207	5.8	8.0	8.7	6.4	3.6
Hinterkarse	2074	11.3	7.2	1.92	291	308	517	521	209	4.7	9.2	11.3	7.7	4.5
Hohense	1541	7.3	3.0	4.62	299	306	488	498	182	9.1	11.4	12.2	8.5	5.6
Hüttnensee	1502	7.7	3.2	4.62	300	305	500	501	195	7.9	10.2	11.0	8.4	5.9
Hürtkarse	2137	7.8	6.9	1.00	276	286	514	532	228	3.4	8.0	9.0	5.4	1.6
Kaltenbachsee	2214	9.9	11.3	0.60	262	286	563	571	277	0.0	1.7	7.8	6.3	2.3
Kapuzinersee	2147	20.0	16.0	1.23	277	286	538	563	252	0.3	4.1	9.0	5.5	1.6
Knappenkarse	2257	8.0	6.1	1.36	285	299	546	549	247	0.0	4.4	9.5	6.5	3.6
Landauersee	1653	16.6	7.7	3.64	297	326	489	510	163	7.1	10.6	11.3	7.7	5.2
Mitterkarse	2150	11.5	6.1	2.77	286	308	507	523	199	5.0	10.3	12.0	7.7	3.9
Mittlerer Kaltenbachsee	1912	8.8	5.3	2.17	297	308	512	521	204	5.8	11.5	12.9	9.1	5.4
Mittlerer Landschitzsee	1940	20.3	7.0	6.63	298	308	513	517	205	5.6	9.0	10.7	7.9	5.0
Moaralmsee	1825	5.9	3.6	2.13	286	304	507	509	203	5.4	6.6	6.1	5.9	4.2
Oberer Giglachsee	1930	10.5	5.0	3.53	297	304	519	523	215	5.7	12.4	13.7	9.5	5.3
Oberer Klaffsee	2309	32.5	12.7	5.12	284	303	547	563	244	0.0	3.7	9.9	6.7	3.3
Oberer Landschitzsee	2067	13.6	4.0	8.88	297	308	517	521	209	5.7	10.7	12.6	8.6	5.1
Oberer Landwiersee	2047	13.4	5.8	4.26	286	304	511	550	207	1.3	6.0	10.6	7.1	3.8
Oberer Zwieflersee	1925	18.6	9.2	3.22	299	309	508	515	199	6.1	8.8	10.1	7.9	5.3
Oberhüttnensee	1863	10.7	5.0	3.66	293	308	510	515	202	8.2	11.9	12.9	8.5	5.1
Obersee	1672	23.4	7.7	7.24	303	310	503	509	193	6.5	8.3	9.4	7.9	5.9
Rantensee	1880	7.6	4.4	2.32	291	305	507	513	202	6.8	10.0	11.0	7.1	4.6
Rauhenbergsee	2263	26.3	13.9	2.82	282	305	548	558	243	0.0	5.0	9.9	6.4	3.1
Schwarzensee	1916	13.3	6.0	3.91	294	305	507	514	202	7.7	10.7	11.5	8.2	4.8
Tiefenbachsee	1844	8.0	3.9	3.22	298	305	510	510	205	7.7	10.0	10.9	8.4	5.6
Twenger Almsee	2118	33.6	16.9	3.11	301	309	538	541	229	1.0	9.2	11.7	8.2	5.4
Unterer Giglachsee	1922	18.0	3.9	16.83	299	309	513	521	204	6.8	12.3	13.3	9.2	5.7
Unterer Kaltenbachsee	1749	32.0	12.0	5.57	302	317	507	513	190	7.8	11.9	12.9	8.4	5.3
Unterer Klaffsee	2103	39.6	17.9	3.86	294	305	538	541	233	1.0	7.8	10.5	7.6	4.4
Unterer Klaffsee	1883	11.4	7.9	1.64	292	302	508	517	206	6.8	10.6	11.9	7.6	4.9
Unterer Landschitzsee	1782	15.8	4.0	11.99	302	310	491	509	181	7.8	11.0	12.7	9.5	6.2
Unterer Landwiersee	1978	5.7	3.8	1.76	284	302	519	540	217	3.3	8.1	10.6	6.1	3.2
Unterer Sonntagkarse	1962	25.9	10.3	4.94	297	314	513	530	199	3.8	9.0	10.7	7.6	4.9
Unterer Wirpitschsee	1700	8.0	4.3	2.72	298	305	489	508	184	7.4	9.8	10.4	7.8	5.4
Unterer Zwieflersee	1808	19.4	8.0	4.64	301	315	493	509	178	8.3	10.6	11.6	8.6	5.7
Weißensee	2226	43.6	15.1	6.53	297	306	511	544	205	2.6	7.2	10.1	7.3	4.8
Zwerfenbergsee	2025	35.7	9.5	10.98	298	315	511	549	196	1.7	6.5	9.9	7.4	4.9

Tab. 2B. Chemical characteristics of the 40 lakes of the study area.

	Cond.	pH	Alk.	TIN	SO ₄ ²⁻	Cl ⁻	Na ⁺	K ⁺	Mg ²⁺	Ca ²⁺	P _{tot}	P _{dis}	P _{part}	DOC	DN	DRSi
	µS cm ⁻¹		µeq l ⁻¹	µeq l ⁻¹	µeq l ⁻¹	µeq l ⁻¹	µeq l ⁻¹	µeq l ⁻¹	µeq l ⁻¹	µeq l ⁻¹	µg l ⁻¹	µg l ⁻¹	µg l ⁻¹	mg l ⁻¹	µg l ⁻¹	µg l ⁻¹
Ahomsee	17.6	7.1	94	8.9	44.6	2.8	13.2	9.6	17.6	135.3	2.2	0.8	1.4	0.59	201	711
Angersee	21.7	7.1	110	9.8	64.2	2.8	20.2	9.5	15.1	171.5	2.1	1.3	0.8	0.46	230	1075
Eiskarsee	38.8	7.6	297	12.9	51.7	1.9	11.4	5.0	45.2	325.5	1.9	1.4	0.5	0.49	310	601
Elendbergsee	20.6	7.1	89	14.5	67.9	2.6	13.3	7.2	12.9	170.0	4.3	1.1	3.2	0.56	282	501
Grünsee	27.6	7.1	87	13.8	119.2	3.1	23.3	11.1	25.4	191.4	1.4	0.9	0.5	0.40	297	1558
Hinterkarsee	38.7	7.4	277	7.6	72.0	2.6	16.3	5.5	28.5	338.3	2.6	1.2	1.4	0.58	216	672
Hohensee	23.4	7.0	90	9.9	85.7	4.1	23.3	9.7	28.8	156.6	2.9	1.6	1.3	1.07	271	1611
Hüttensee	23.2	7.1	123	18.1	57.3	3.7	21.2	11.2	18.4	177.9	2.8	1.7	1.1	0.65	377	966
Hüttkarsee	64.6	7.2	224	14.6	295.8	3.7	32.4	10.9	59.5	468.0	1.3	0.7	0.6	0.44	309	1470
Kaltenbachsee	12.4	7.1	66	10.9	28.7	2.4	14.8	6.0	11.1	99.8	4.7	1.4	3.3	0.56	255	884
Kapuzinersee	21.1	7.2	96	8.4	71.3	2.7	15.2	8.0	16.4	165.6	2.9	0.7	2.2	0.81	212	656
Knappenkarsee	31.6	7.4	172	11.4	95.4	1.7	13.2	3.4	22.3	266.0	1.7	1.5	0.2	0.43	305	504
Landauersee	54.6	7.5	401	8.1	102.5	3.7	18.2	4.3	122.5	380.1	3.0	2.6	0.4	0.93	236	759
Mitterkarsee	11.9	7.1	22	0.1	41.8	2.3	14.0	5.1	13.2	70.1	7.8	1.4	6.4	1.55	105	516
Mittlerer Kaltenbachsee	14.8	6.9	47	5.5	60.0	4.8	22.0	7.7	28.6	89.9	3.5	1.7	1.8	1.14	189	847
Mittlerer Landschitzsee	29.0	7.0	104	10.3	119.3	2.4	19.7	8.3	18.2	223.6	1.1	1.0	0.1	0.48	228	1106
Moaralmsee	32.5	7.3	197	16.0	73.7	2.6	25.1	7.6	22.0	264.7	2.9	1.3	1.6	0.60	337	1327
Oberer Giglachsee	38.8	7.6	352	0.2	33.3	2.8	9.7	3.4	143.5	228.8	5.8	3.0	2.8	1.22	106	279
Oberer Klaffersee	15.0	7.1	42	6.1	69.2	2.2	12.9	6.8	16.7	105.9	4.0	0.2	3.8	0.99	226	571
Oberer Landschitzsee	13.8	7.0	61	4.7	46.5	2.3	14.0	6.9	10.5	106.8	2.2	1.4	0.8	1.01	172	705
Oberer Landwiersee	24.2	7.4	168	4.8	46.8	2.0	12.5	8.6	14.1	211.7	4.0	1.5	2.5	0.75	170	431
Oberer Zwieflersee	32.1	7.3	205	6.7	75.6	3.1	19.7	9.0	45.7	235.3	3.6	1.3	2.3	0.77	185	853
Oberhüttensee	137.3	8.2	1364	4.1	61.5	4.7	15.1	3.8	303.8	1058.8	4.7	1.5	3.2	0.89	223	535
Obersee	25.1	7.0	134	17.3	60.2	2.8	21.2	14.3	20.4	185.1	6.9	1.7	5.2	0.60	397	1106
Rantensee	26.6	7.1	144	9.2	74.0	3.3	24.1	6.5	26.8	200.2	1.7	0.6	1.1	0.51	395	1293
Rauhenbergsee	18.7	7.0	73	8.9	71.1	2.1	14.4	9.1	19.7	136.3	4.0	0.8	3.2	0.46	263	315
Schwarzensee	22.2	7.0	67	9.1	100.2	4.3	24.7	10.3	26.3	142.3	1.7	0.7	1.0	0.61	272	1685
Tiefenbachsee	82.4	8.1	703	6.1	98.9	2.9	25.2	7.2	71.7	718.8	4.7	2.7	2.0	0.59	156	1148
Twenger Almsee	74.9	7.9	558	0.1	175.0	2.9	20.8	4.6	206.7	476.3	3.2	2.1	1.1	0.67	121	419
Unterer Giglachsee	73.5	7.8	579	3.3	115.9	4.5	20.9	3.9	147.9	535.4	5.6	3.3	2.3	0.80	158	644
Unterer Kaltenbachsee	80.1	7.5	681	16.7	62.5	3.6	17.6	20.5	112.9	625.4	5.0	1.7	3.3	0.99	362	817
Unterer Klaffersee	23.8	7.2	133	7.7	63.9	1.9	12.7	10.9	15.3	193.1	4.3	2.3	2.0	0.44	263	324
Unterer Klaffersee	14.7	6.9	85	3.1	32.0	3.6	11.4	7.9	16.2	120.1	4.0	1.7	2.3	2.06	156	498
Unterer Landschitzsee	29.0	7.1	130	10.4	102.4	2.8	23.2	11.6	19.2	222.4	3.1	1.1	2.0	0.69	301	1159
Unterer Landwiersee	36.6	7.4	225	7.8	88.1	2.3	15.9	10.9	21.1	304.0	2.1	1.9	0.2	0.55	197	741
Unterer Sonntagkarsee	17.5	6.9	63	9.0	65.3	2.7	15.4	9.1	13.7	130.1	3.2	1.1	2.1	0.73	228	714
Unterer Wirpitschsee	86.0	7.7	738	10.5	101.7	3.7	27.1	5.8	111.3	707.0	3.2	1.8	1.4	0.49	231	1072
Unterer Zwieflersee	30.5	7.2	194	7.4	70.9	4.2	24.1	9.8	44.5	220.8	3.0	2.3	0.7	1.16	208	990
Weifensee	18.6	7.0	84	14.6	54.5	2.8	14.6	12.0	19.6	135.5	1.0	0.8	0.2	0.40	304	841
Zwerfenbergsee	24.7	7.2	114	11.4	86.8	2.7	17.5	10.5	16.2	197.1	1.6	1.1	0.5	0.53	253	863

Tab. 3. (A). PCA axes 1 – 4 scores (correlation coefficients with axes 1- 4) for the environmental variables listed in table 2. The axes represent 4 significant gradients related to climate (axis 1), nutrients (axis 2), bedrock mineralogy and vegetation cover (axis 3) and water depth (axis 4). (B): Amount of variation explained singly (marginal effects) by each of the variables from table 2 on the total diatom assemblage, and the Fragilariaceae subset. Asterisks indicate a significant influence ($P < 0.05$). Superscript B indicate significant P values ($P_{\text{adj}} < 0.05$) corrected for multiple testing.

	(A) PCA				(B) CCA: marginal effects (%)	
	axis 1	axis 2	axis 3	axis 4	all diatoms	Fragilariaceae
Altitude	0.80	0.31	0.17	0.09	4.52*	5.66*
Temperature						
T June 99	-0.89	-0.23	-0.22	-0.18	5.75*	7.07*
T July 99	-0.90	0.11	-0.20	-0.05	5.75 ^B	7.07*
T Aug 99	-0.64	0.47	-0.24	0.08	4.93*	6.36*
T Sep 98	-0.74	0.34	-0.30	0.18	4.93*	5.66*
T Oct 98	-0.83	0.09	-0.28	0.28	5.34*	7.07*
Ice Cover and Mixing						
Autumn mixing 98	-0.79	0.04	-0.22	0.46	5.34*	6.36*
Freeze up 98	-0.63	0.10	-0.27	0.48	4.52*	7.07*
Break up 99	0.79	0.33	0.26	0.02	4.93*	7.07*
Spring mixing 99	0.87	0.30	0.21	0.16	5.34*	7.07*
Length of ice cover	0.83	0.24	0.29	-0.14	5.34*	8.49 ^B
Chemistry						
Conductivity	-0.60	0.06	0.78	0.07	9.86 ^B	11.32 ^B
pH	-0.45	0.41	0.73	-0.06	9.86 ^B	11.32 ^B
Alkalinity	-0.59	0.17	0.73	0.07	11.50 ^B	12.02 ^B
TIN	0.14	-0.75	0.01	0.18	4.52	1.41
SO ₄ ²⁻	-0.19	-0.43	0.58	0.20	2.87	2.12
Cl ⁻	-0.67	-0.22	-0.03	-0.21	3.70	4.24
Na ⁺	-0.41	-0.67	0.23	-0.12	2.46	2.12
K ⁺	0.08	-0.58	-0.34	0.32	3.29	4.24
Mg ²⁺	-0.67	0.29	0.59	0.02	7.80 ^B	8.49 ^B
Ca ²⁺	-0.54	0.03	0.80	0.09	10.68 ^B	11.32 ^B
P _{tot}	-0.18	0.66	-0.17	-0.21	2.87	2.83
P _{dis}	-0.56	0.36	0.13	-0.10	4.93*	4.95
P _{part}	-0.01	0.47	-0.25	-0.25	2.46	2.83
DOC	-0.35	0.50	-0.51	-0.28	6.16 ^B	6.36*
DN	0.11	-0.73	0.06	0.29	3.29	1.41
DRSi	-0.26	-0.87	-0.02	-0.18	2.87	2.83
Water depth						
Z _{max}	0.13	0.31	-0.12	0.86	4.93*	5.66*
Z _{rel}	0.45	0.34	0.05	0.64	4.11*	5.66*

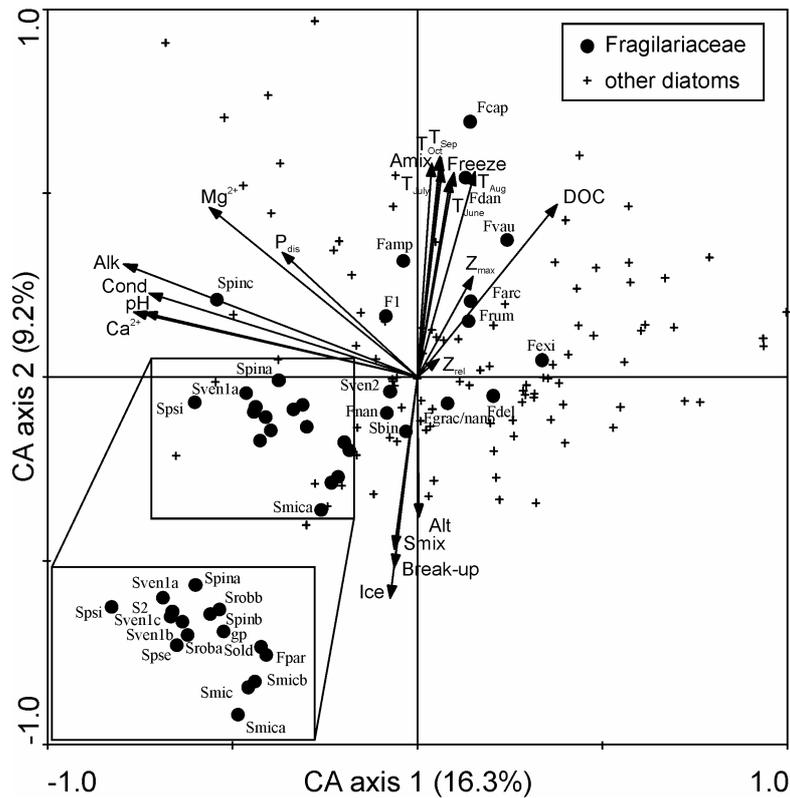


Fig. 6. Correspondence Analysis (CA) ordination biplot of the Niedere Tauern diatom training set with species scores of *Fragilaria* and *Staurosira* (for abbreviations see Tab. 1) and significant (marginal effects, $P < 0.05$) passive environmental variables (Alk = alkalinity, Alt = altitude, A_{mix} = date of autumn mixing, Break-up = ice break up date, Cond = conductivity, DOC = dissolved organic carbon, Freeze = date of freezing, ice = duration of ice cover, ions, pH, S_{mix} = date of spring mixing, T_{month} = mean monthly temperature, Z_{max} = maximum water depth, Z_{rel} = ratio of lake surface area/max. water depth). Percentages accounting for species variation at the first and second axis are added.

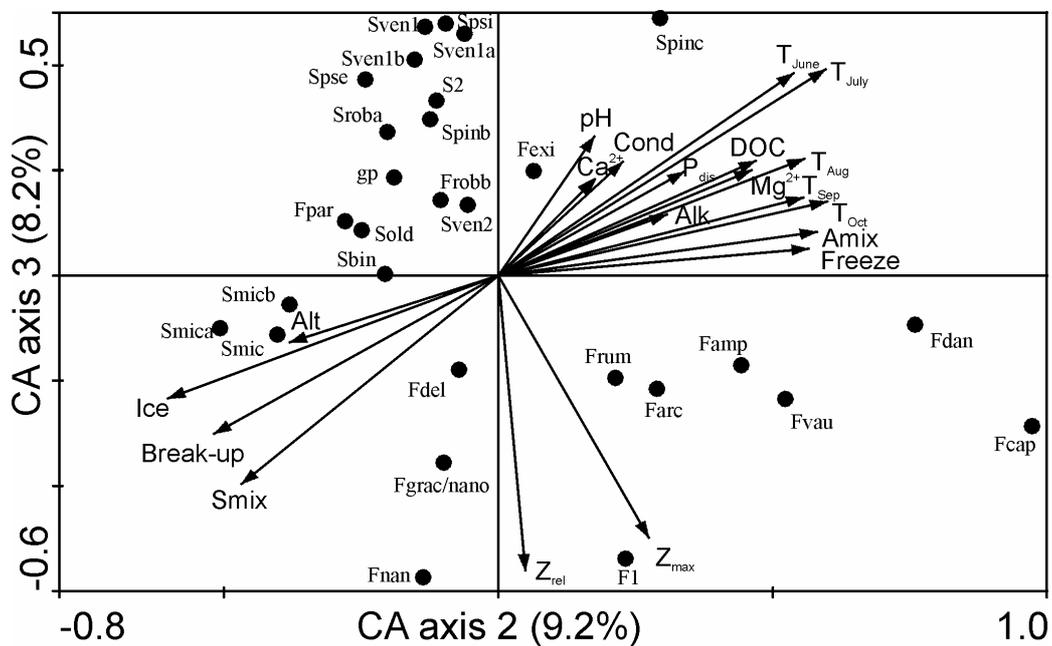


Fig. 7. Correspondence Analysis (CA) ordination biplot of the Niedere Tauern diatom training set with species scores of *Fragilaria* and *Staurosira* (for abbreviations see Tab. 1) and significant (marginal effects, $P < 0.05$) passive environmental variables (for abbreviations see Fig. 6). Percentages accounting for species variation at the second and third axis are added.

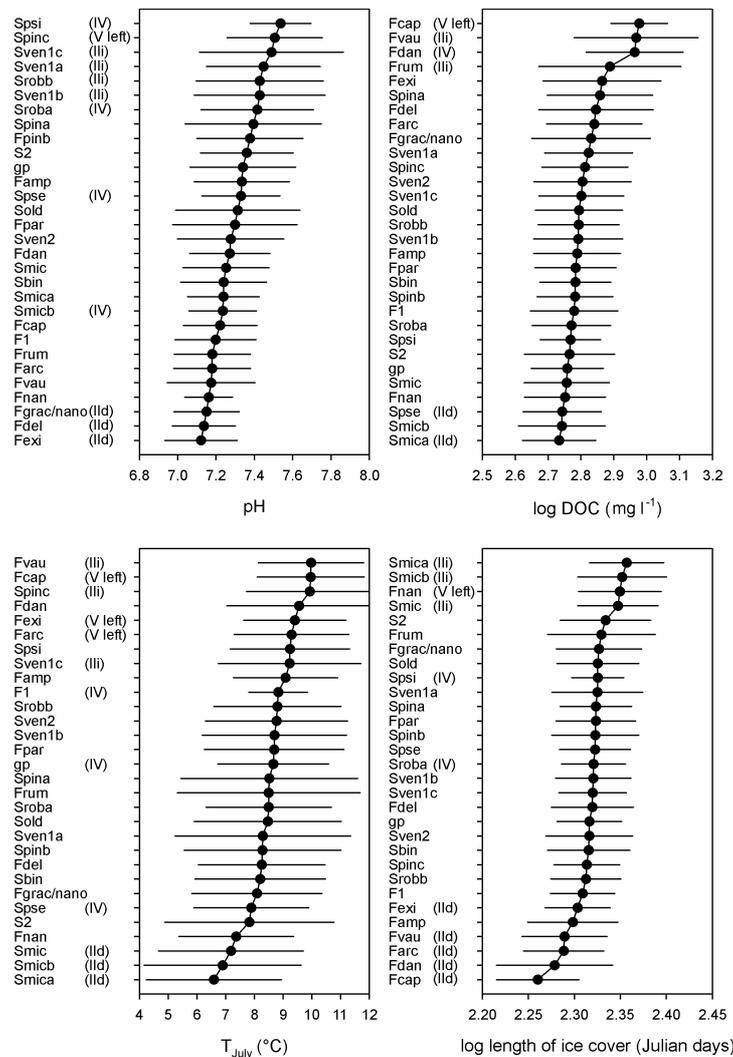


Fig. 8. Bootstrapped optima and tolerances of the main environmental variables for selected *Fragilaria* and *Staurosira* (for abbreviations see Tab. 1). Significant species response models are given in brackets (V: skewed unimodal response; IV: symmetric Gaussian unimodal; II i: monotonically increasing sigmoidal response model; II d: monotonically increasing sigmoidal response model).

5.3. Ecology of diatom taxa

In figure 8 the taxa were arranged according to their bootstrapped optima within the range of the 4 main environmental variables (see Fig. 6). The taxa significantly ($P < 0.05$) responding to the selected environmental variables were:

A) Taxa responding to pH (range 6.9 to 8.2; in increasing order) were:

F. cf. exiguiformis, *F. delicatissima*, *F. gracilis/nanoides*, *S. cf. microstriata* (b), *S. pseudoconstruens*, *S. robusta* (a), *S. aff. venter* (1b), *S. robusta* (b), *S. aff. venter* (1a and 1c), *S. pinnata* var. *intercedens* (c), *S. parasitoides*.

B) Taxa responding to mean July water temperature (T_{July}) (range 1.7 – 12.4 °C; in increasing order) were:

S. microstriata (a), *S. cf. microstriata* (b), *S. microstriata*, *S. pseudoconstruens*, "girdles parallel", *F. spec. 1*, *S. aff. venter* (1c), *F. arcus*, *F. cf. exiguiformis*, *S. pinnata* var. *intercedens* (c), *F. capucina*, *F. vaucheriae*.

C) Taxa responding to the length of ice cover (range 163 – 277 days; in increasing order) were:

F. capucina, *F. danica*, *F. arcus*, *F. vaucheriae*, *F. cf. exiguiformis*, *S. robusta* (a), *S. parasitoides*, *S. microstriata*, *F. nanana*, *S. cf. microstriata* (b), *S. microstriata* (a).

D) Taxa responding to DOC (log. range from 0.4 – 2.1 mg l⁻¹; in increasing order) were: *S. microstriata* (a), *S. pseudoconstruens*, *F. rumpens*, *F. danica*, *F. vaucheriae*, *F. capucina*.

In addition to the four main environmental variables, *F. gracilis/nanoides* and *F. delicatissima* responded to

increasing relative water depth (Z_{rel}). Along the environmental gradient of maximum water depth (Z_{max}), *Fragilaria* spec. 1 occurred in the deepest lakes, followed by taxa of the *F. capucina* complex, *F. danica*, and *F. arcus* at decreasing water depths. Most of the *Staurosira* taxa (benthic) occurred in shallow waters, with the exception of *S. microstriata* that was present when water depth increase (Figs 6 and 7).

5.4. Relationship valve length/water temperature

The distribution of the mean valve lengths of three selected taxa versus mean summer water temperatures (July, August) is illustrated in figure 9. Despite the errors associated with estimating the mean valve lengths, all three species show a minimum valve length within the temperature range of the lakes where the species occur. *Fragilaria delicatissima* and *F. nanoides* showed a minimum in valve length between 10 and 11 °C mean August water temperature (Fig. 9A). In *F. cf. exiguiformis* the size minimum corresponds with the mean July water temperature optimum of this taxon at 9.4°C as estimated from the transfer function (see arrow in Fig. 9B).

6. DISCUSSION

The PCA indicates correlations between the main environmental variables pH, T_{July} , length of ice cover, DOC and water depth. The length of ice cover and T_{July} show, however, unique effects on the diatom assemblages. The main difference between the total diatom data set and the Fragilariaceae subset is the minor importance of DOC and nutrients for the latter.

6.1. pH/alkalinity response

The CCA results (Tab. 3B) and the high number of significant responses (Fig. 8) support the strong impact of pH/alkalinity on diatom distribution in Alpine lakes (Marchetto & Schmidt 1993; Koinig *et al.* 1998; Cameron *et al.* 1999). Bedrock mineralogy strongly determines the chemistry (e.g. by Ca^{2+} availability) of the Niedere Tauern lakes (Kamenik *et al.* 2001). *Staurosira pinnata* s. l. prevailed in shallow waters with an increased pH that occurred in lakes on carbonate-bearing bedrock. This result conforms to observations from Lotter & Bigler (2000) who observed high abundances of *Fragilaria pinnata* in the littoral and sublittoral of a Swiss Alpine lake on carbonate bedrock.

In the lakes of the Niedere Tauern *S. aff. venter* (1) was associated with *S. pinnata* s. l. Similar ecological preferences suggest that the three morphotypes of *S. aff. venter* (1a-c) belong to one and the same taxon. The bootstrapped pH optimum of the morphotype (2) of *F. aff. venter* indicate, however, a lower pH optimum than for type (1) supporting the differentiation from type (1). This finding supports the meaning that *F. construens* var. *venter* auct. resembles taxa with different ecological preferences (see Rumrich *et al.* 2000).

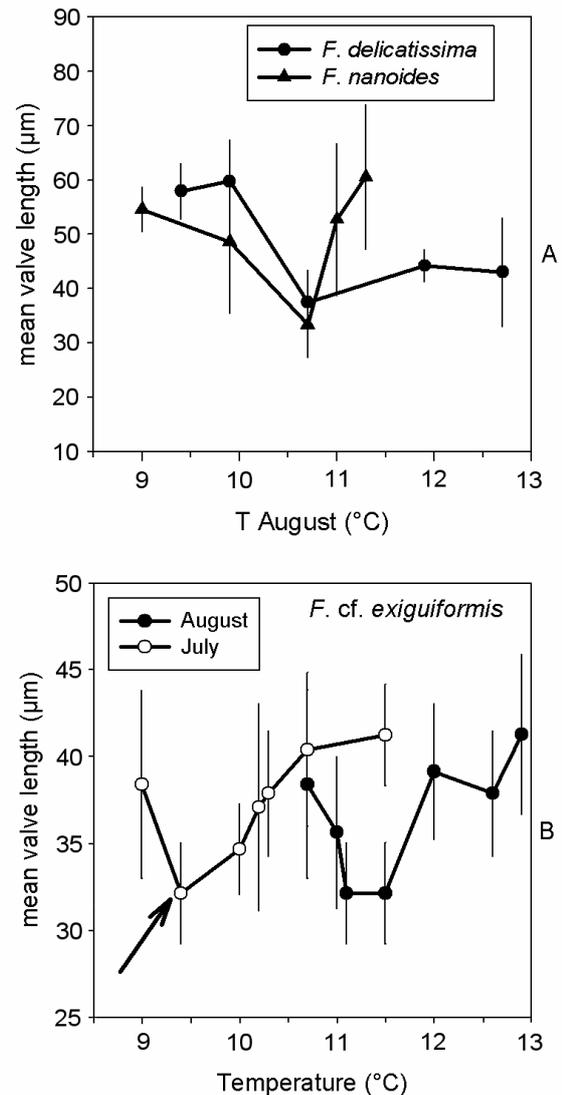


Fig. 9. Mean valve length ($n = 50$, standard deviation is indicated) of (A) two selected planktonic taxa versus mean August water temperature, and (B) *F. cf. exiguiformis* versus mean July and August water temperatures. The bootstrapped mean July water temperature of this species in the Niedere Tauern training set (see Fig. 8) is arrowed. Note the correspondent minimum mean valve length.

Similar to *S. pinnata* s. l., *S. robusta* belongs to this group that is primarily ordinated by pH. The morphotype (b) has, however, a higher pH optimum than morphotype (a).

With the lowering of the pH, *S. microstriata* and *S. cf. microstriata*, which belong to the *Fragilaria brevisstriata* complex, became abundant. From the benthic taxa *F. cf. exiguiformis* had the lowest pH optimum (Fig. 8). The larger-sized taxon *F. cf. exiguiformis* of the Niedere Tauern occurred, however, at the upper limit of the pH range which was mentioned by Flower *et al.* (1996) for European populations of *F. exiguiformis*. The sigmoidal species response to pH (see HOF report in Fig. 8) indi-

cating a truncated curve, as was illustrated by Flower *et al.* (1996) for Antarctic populations of *F. exiguiformis*. The truncated curve may also explain the larger valve size of the Niedere Tauern population when we hypothesize that minimum valve length corresponds with the species pH optimum (see chapter 4).

6.2. Duration of ice cover, mean July water temperature, and lake water depths

Staurosira pinnata var. *intercedens* at higher pH, and *F. cf. exiguiformis* at a lower pH characterize littoral benthic diatom assemblages in warmer waters. Both differ by their higher T_{July} optimum from *S. microstriata* that characterize deeper cold waters with prolonged ice cover. This finding corresponds with the temperature inference of "*F. exigua*" and "*F. brevistriata*" in Swedish lakes by Bigler *et al.* (2000). As a result of the taxonomic uncertainty in the *F. brevistriata* complex, comparisons with other areas are limited at the present stage. *S. microstriata* was common in the sediments of the Alpine lake Hobschensee, Swiss Alps, as well as in late-glacial sediments of the Tatra Mountains (Marciniak 1986, 1988). Taxa comparable with *S. microstriata* and *S. cf. microstriata* were illustrated by Lange-Bertalot & Metzeltin (1996) for Julma Ölkky, an oligotrophic lake in Finland. These findings suggest that both might be widespread in alpine and arctic/subarctic environments. The similar ecological preferences in the Niedere Tauern data set suggest that both belong to the same species. The ecological preferences of *S. parasitoides*, which also belongs to the *F. brevistriata* complex, for shallow habitats that become warmer during the summer in lakes with an increased pH supports the splitting from the closely related *S. microstriata* (Schmidt *et al.* 2004). Geographical distribution and ecology separate this group of taxa from others of the *F. brevistriata* complex that occur in alkaline, high conductivity, lakes e.g. in coastal lakes (Wunsam *et al.* 1999).

Fragilaria capucina, *F. amphicephala*, *F. arcus*, and *F. vaucheriae* occurred in the lakes of the Niedere Tauern with a longer growing season and increased summer water temperatures. They might belong, however, to different habitats at increasing water depths (see Fig. 7); probably more elaborate benthic, or even tychoplanktonic taxa (switching between benthic and planktonic life forms) accompany attached ones (e.g. *F. vaucheriae*). Their occurrences at an increased summer temperature conform to their distribution in lakes below the subarctic treeline (Stevenson *et al.* 1996; Laing & Smol 2000). The early formation of an ice-free "moat" (Smol 1988; Smol & Cumming 2000), which provides marginal open waters in a still ice covered lake, might favor this diatom group. It is possible that minor scaling exists. In lakes with a lower pH, *F. rumpens* at the expense of the former group might increase in abundance when the length of ice cover increases (*vice versa* T_{July} decrease).

The duration of ice cover (*vice versa* the length of the growing season) affects the abundance of planktonic taxa in Alpine (Lotter & Bigler 2000) and subarctic to high Arctic lakes (Douglas *et al.* 1994; Pienitz *et al.* 1995; Adrian *et al.* 1999; Laing & Smol 2000). Our data set indicated that the duration of ice cover and July summer water temperatures are closely related with each other, and affect species distribution. *F. danica* and *F. spec. 1* occurred in warmer lakes with an increased growing season when compared with the planktonic groups as mentioned above. Within these planktonic taxa, *F. nanana* tolerates a longer ice cover. In lakes with open waters less than 2 month, no planktonic *Fragilaria* taxa were present. Hence, most of the lakes without planktonic *Fragilaria* occur above the alpine treeline. These findings compare with observations from planktonic taxa in circum-subarctic treeline lakes (Pienitz *et al.* 1995; Weckström *et al.* 1997a, b; Rosén *et al.*, 2000; Bigler *et al.* 2000; Laing & Smol 2000).

The significance of lake size and water depth which explains the planktonic diatom variation in the Niedere Tauern data set conforms to the hypotheses which relate occurrences of planktonic taxa to increasing water depth and water volume (see Wolin & Duthie 1999). The commonly high light penetration extends the euphotic zone in alpine lakes, favoring planktonic diatoms. The planktonic needle-like elongated taxa *F. delicatissima*, *F. nanoides*, *F. spec 1*, and *F. nanana* characterize these larger and deeper lakes. At least the elongated valves of *F. gracilis* might also belong to this group. Only the planktonic *F. danica* occurred in smaller, shallower lakes.

6.3. DOC and nutrient response

Taxa of the *Fragilaria capucina* complex (*F. capucina*, *F. vaucheriae*, *F. rumpens*) and *F. danica* that occurred at highest DOC increase in abundance in lakes below the alpine treeline. This diatom distribution follows the general trend of DOC increase from high alpine lakes towards lakes located at the forested belts (Sommaruga-Wögrath *et al.* 1999). In contrast to the former group, *S. microstriata* and *S. pseudoconstruens* characterize highly oligotrophic cold water lakes with low DOC. The lower altitude lakes are commonly more affected by human impact than the remote lakes at higher altitudes. DOC is associated with dissolved phosphorus. Probably due to the low concentrations, dissolved phosphorus and nitrogen showed, however, no significant ($P_{adj} < 0.05$) impact on the distribution of the *Fragilaria* and *Staurosira* taxa in the Niedere Tauern lakes. The occurrences of *Fragilaria* Spec. 1 in the mountain lakes question the conspecificity of this taxon with "*F. acus* var. *angustissima*" (see the chapter taxonomy) which commonly is mentioned from meso- to eutrophic low altitude lakes, or there exists a mountain strain which is adapted to oligo- to ultra-oligotrophic conditions.

6.4. Valve size variation

According to Atkinson (1994, 1996), variations in size between organisms can be produced by genetic adaptation to temperature and by environmentally induction among individuals of a given genotype. Small-sized taxa of Fragilariaceae frequently occur in high altitude and latitude lakes. Prolonged ice cover (Smol 1988) and low temperatures (Pienitz *et al.* 1995; Weckström *et al.* 1997a, b; Bigler *et al.* 2000; Laing & Smol 2000; Rosén *et al.* 2000) have been cited as a possible factor explaining high abundances of small Fragilariaceae in these areas. In our data set also taxa on intra-specific level follow this trend. The larger-sized *S. pinnata* var. *intercedens* occurred at higher T_{July} than the small *S. pinnata* var. *subrotundata*. The same is true for the larger *S. robusta* (b) (forma "*bigibba*") that showed a higher temperature optimum than morphotype (a). In both cases, the larger-sized taxa also have a higher pH optimum. The finding of the pH/temperature coupling fits to diatom-inferred pH and correspondent temperature curves which were recognized in Alpine lake sediment cores (Psenner & Schmidt 1992; Koinig *et al.* 1998).

Montagnes & Franklin (2001) postulated, based on temperature/size experiments on cultured diatom clones, and on the literature, that the size of diatoms decrease with increasing temperature, and thus diatoms follow the rule of Atkinson (1994) of temperature-dependent organism size. In the Niedere Tauern data set the minimum mean valve length in *F. cf. exiguiformis* approximates the bootstrapped temperature optimum of this taxon. This finding was explained that the temperature optimum (i) stimulates enhanced cell division, or (ii) cells did not reproduce sexually. Cell division was observed to accelerate with increasing temperature (Lloyd *et al.* 1982). Probably, July water temperature is accompanied by other environmental variables all together stimulating growth and cell division of algae in mountain lakes during summer season; e.g. higher light intensities and duration stimulating photosynthesis, or enhanced nutrient availability after snow and ice-melt (Sommaruga-Wögrath *et al.* 1999).

7. CONCLUSIONS

- The pH/alkalinity, mean July water temperature (T_{July}), duration of ice cover, and DOC were the main environmental variables significantly ($P_{\text{adj}} < 0.05$) explaining *Fragilaria* and *Staurosira* distribution in the 40 mountain lakes of the Niedere Tauern (Austria). At the third CA axis, water depths made an additional significant contribution to explain their distribution.
- The pH and the related variable alkalinity depend on catchment geology (crystalline vs carbonate-bearing schists and metamorphic carbonates), and both are related to T_{July} .

- The comparison between the total diatom training set and the Fragilariaceae subset stressed the high sensitivity of *Fragilaria* and *Staurosira* to the climate-driven variables "duration of ice cover" and "mean July water temperature". DOC showed a lower impact in the Fragilariaceae subset than in the total diatom data set.
- The *Staurosira pinnata*, *S. aff. venter* (1), and *S. robusta* complexes are frequent benthic taxa in the littoral and sublittoral of lakes with higher pH, whereas at a lower pH *F. cf. exiguiformis* predominates. This taxon differs by a higher summer temperature optimum from the *F. brevistriata* complex (*S. microstriata*) that characterizes deeper cold water lakes with prolonged ice cover.
- The planktonic and possible tycho planktonic *Fragilaria* taxa occurred at higher T_{July} (and *vice versa* shorter duration of ice cover) and DOC (*F. danica*, *F. spec. 1*, and *F. capucina* complex), and increasing lake water depth and size (needle-like planktonic taxa).
- Differences or similarities along environmental gradients suggested the splitting (e.g. *S. parasitoides* from *S. microstriata*, *S. aff. venter* (1) from (2)), or lumping of taxa (e.g. *S. aff. venter* morphotypes (1a-c)).
- Valve length appeared to be affected by temperature in two different ways; (i) Generally, smaller-sized taxa on species and intra-specific levels (e.g. *S. brevistriata* and *S. pinnata* s. l.) indicate (genetic) adaptation to cold waters (low temperature optimum); (ii) Stimulation of enhanced cell division and suppression of sexual reproduction at the species temperature optimum are thought to be responsible for the minimum mean valve length within populations.
- The high importance of the climate-driven environmental variables for species distribution and reproduction affecting valve size underline the high potential of *Fragilaria* and *Staurosira* for palaeoclimatic reconstructions in mountain lakes.

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