

Reconstructing the salinity and environment of the Limfjord and Vejlerne Nature Reserve, Denmark, using a diatom model for brackish lakes and fjords

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Abstract: Diatoms in surface sediments from a data set of 27 brackish lakes and nine fjords in Jutland, Denmark (range 0.2 – 31 g·L⁻¹ total dissolved solids (TDS)), were analysed using multivariate methods to determine response to measured parameters (depth, total phosphorus (TP), total nitrogen (TN), TN/TP, salinity, water body type). Water body type, salinity, depth and TP together explained 25.3% of the variation in the diatom data and were all independently significant predictors. A diatom–salinity model ($r^2_{\text{jack}} = 0.887$, root mean square error of prediction = 0.246 log salinity, g·L⁻¹) was developed from the 36 sample training set and applied to fossil diatom assemblages in three sediment cores from the east Vejlerne wetland, Denmark, a nature reserve created after the damming of an embayment of the polyhaline Limfjord (~26 g·L⁻¹ TDS) in the late 19th century. The diatom-inferred salinity reconstructions reflect the known salinity history of the Limfjord and the freshwater–subsaline Vejlerne lakes, and appear sensitive to documented North Sea storms in the 16th and 17th centuries, which had major impacts on the brackish Limfjord herring fishery. Diatom–salinity models may be useful tools in long-term studies of coastal and estuarine areas to test hypotheses concerning aquatic resources and ecological, hydrographic, and cultural change.

Résumé : Des méthodes multidimensionnelles nous ont permis d'analyser les données sur les diatomées dans les sédiments de surface dans une série de 27 lacs saumâtres et neuf fjords du Jutland, Danemark, (étendue de 0,2–31 g·L⁻¹ des solides totaux dissous (TDS)) afin de déterminer la réaction de diatomées à des paramètres choisis (profondeur, phosphore total (TP), azote total (TN), TN/TP, salinité, type de milieu aquatique). Le type de milieu, la salinité, la profondeur et TP expliquent ensemble 25,3 % de la variation des données sur les diatomées; ce sont tous individuellement des facteurs prédictifs significatifs. Nous avons mis au point un modèle des diatomées en fonction de la salinité ($r^2_{\text{jack}} = 0.887$, erreur quadratique moyenne de la prédiction = 0,246 log salinité, g·L⁻¹) à partir de ces 36 échantillons expérimentaux et l'avons appliqué aux regroupements de diatomées fossiles dans trois carottes de sédiments prélevées dans la section est des terres humides de Vejlerne, Danemark, une réserve naturelle créée après le barrage d'une baie du Limfjord polyhalin (~26 g·L⁻¹ TDS) à la fin du 19^e siècle. Les reconstitutions des salinités basées sur les diatomées correspondent aux salinités connues dans le passé dans le Limfjord et les lacs d'eau douce–subsaline de Vejlerne; elles semblent tenir compte des tempêtes signalées dans la mer du Nord aux 16^e et 17^e siècles, qui ont eu un impact majeur sur la pêche de harengs dans les eaux saumâtres du Limfjord. Les modèles de diatomées–salinités peuvent être des outils utiles pour les études à grande échelle temporelle des régions côtières et estuariennes, afin de vérifier des hypothèses concernant les ressources aquatiques et les changements écologiques, hydrographiques et culturels.

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Introduction

At the boundary of offshore (marine) and inland (freshwater) systems, coastal environments are sensitive to changes that affect both environments, for example, fluctuations in freshwater input, sea level, and nutrient supply. As a result, coastal sediments contain important archives of environmental change, recording signals of past changes in salinity, sea level, and nutrient concentrations in sedimentology, geochemistry, and biological remains (Cooper and Brush 1991; Dellwig et al. 1998; Bianchi et al. 2000). Diatoms have been particularly favoured as tools for palaeoenvironmental reconstruction, as many coastal taxa are globally distributed, and their silica frustules tend to preserve well in sediments and are identifiable to species level. A long European tradition of research into contemporary diatom distributions along coasts has produced species classifications according to salinity and habitat preference (e.g., van der Werff and Huls 1976; Snoeijs 1993; Snoeijs and Balashova 1998). This remains the basis for much palaeoenvironmental interpretation of coastal sediments (Cooper 1995; Dellwig et al. 1999; Andr  n et al. 2000), despite the growing application of transfer function methodologies in palaeoecology (Birks 1998). Quantitative reconstructions of such important parameters as salinity, sea level, and nutrient concentrations are essential to test ecological hypotheses put forward to explain historical and archaeological variations in aquatic resources (e.g., Holm and Bager 2002; MacKenzie et al. 2002) especially in the context of major climatic and cultural shifts (Rowley-Conwy 1984; Bailey and Milner 2005). Knowledge of long-term variability of coastal environments provides the framework for evaluating recent changes and assessing predictions about future developments.

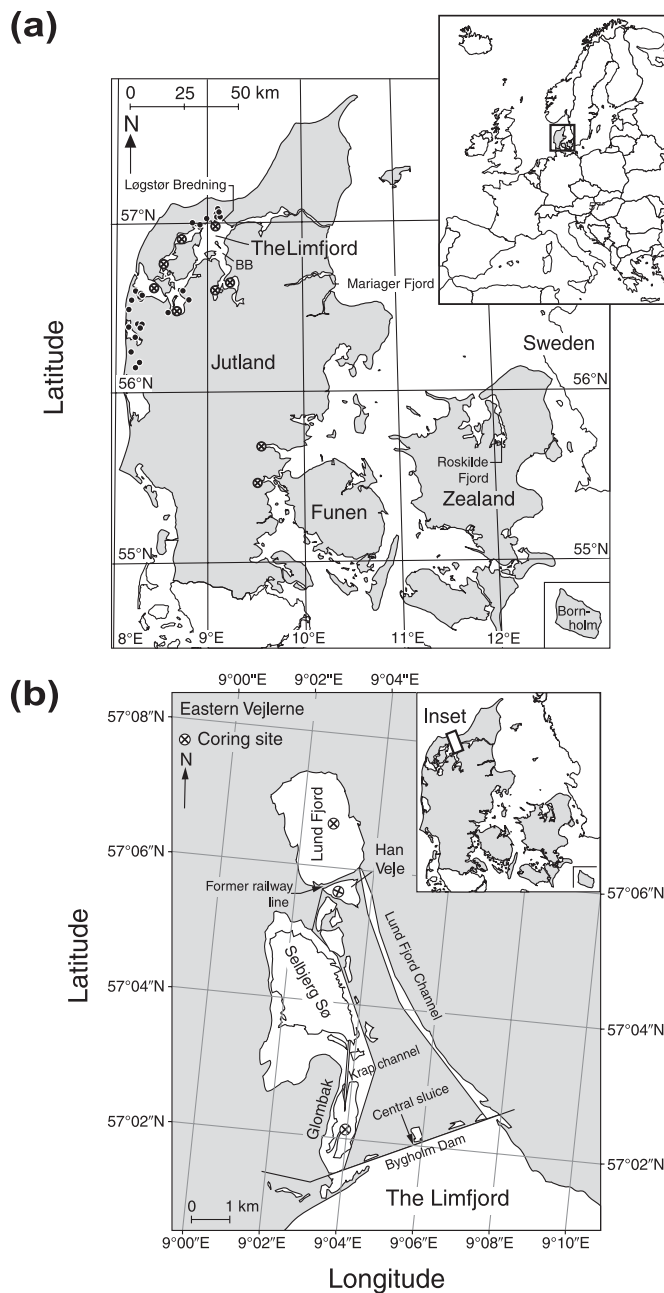
While much is known about the functioning of maritime, coastal, and freshwater habitats, relatively little research has been conducted in brackish lakes and lagoons across this gradient and how these systems might respond to environmental change (e.g., climate, salinity, eutrophication). Diatom assemblages in surface sediments were analysed as part of an ongoing project examining the ecology and palaeoecology of brackish lakes in Vejlerne, a nature reserve in North Jutland and once part of the marine-brackish Limfjord (Jeppesen et al. 2002; Amsinck et al. 2003). Additionally, diatom assemblages from higher salinity, shallow Danish fjords were added to the lake samples to extend the salinity gradient into the full marine range. As these aquatic environments cover a gradient of salinity and trophic status, we aimed to establish whether these parameters exerted a strong control on diatom communities and therefore could be used to create models for quantitative reconstruction. A resultant diatom-salinity model was then applied to subfossil diatom assemblages from three sediment cores collected from nearby shallow lakes in the east Vejlerne wetlands to reconstruct salinity in the context of major land use change in this area over the last few centuries.

Methods

Study area and fieldwork

The northern part of Jutland, Denmark, contains many small, shallow coastal lakes and lagoons, which exhibit a range of salinity (0.2–18 g·L⁻¹ total dissolved solids, TDS)

Fig. 1. Location map. (a) Training set sites in Denmark. Solid circles are lakes and lagoons (27 sites), and circles with cross are fjords (9 sites). The locations of other sites mentioned in the text are also shown. BB, Bj  rnsholm Bay. (b) East Vejlerne nature reserve with coring sites indicated for the three lakes (Glombak, Han Vejle, and Lund Fjord).



according to their degree of connection to nearby coastal waters or inland fjords (e.g., the Limfjord; Fig. 1). Although much of the region has a relatively low population density and includes areas of seminatural heath and wetland, agricultural land use predominates and has resulted in the enrichment of both N and P of many surface waters. Both salinity and trophic gradients exist among coastal lakes and lagoons today (Table 1). As the salinity gradient does not extend into full marine conditions, a further nine samples collected from nearby Danish fjords were added to the

Table 1. Summary of six parameters measured for lake and fjord groups and the combined data set of 36 sites.

	Salinity (g·L ⁻¹)	TN (µg·L ⁻¹)	TP (µg·L ⁻¹)	TN/TP	Depth (m)	F index (ratio)
All sites (n = 36)						
Average	9.0	1724	110	22.4	2.8	—
Maximum	31.1	5600	331	94.0	12.0	—
Minimum	0.2	616	25	3.7	0.5	—
Range	30.9	4984	306	90.3	11.5	—
Lakes (n = 27)						
Average	3.6	1972	127	24.3	1.6	0.76
Maximum	17.4	5600	331	94.0	4.2	0.93
Minimum	0.2	850	25	3.7	0.5	0.50
Range	17.2	4750	306	90.3	3.7	0.43
Fjords (n = 9)						
Average	25.2	980	59	16.7	6.3	—
Maximum	31.1	1440	83	18.6	12.0	—
Minimum	18.7	616	45	12.2	3.4	—
Range	12.4	824	38	6.3	8.6	—

Note: TN, total nitrogen; TP, total phosphorus. The diatom dissolution index, *F*, was only assessed for the lake samples.

brackish lakes training set, covering the range 19–31 g·L⁻¹ (Fig. 1; Table 1). These samples were selected from a larger data set of Danish fjords and estuaries included in an earlier study on diatom distribution in north European coastal waters (Clarke 2001; MOLTEN Project 2003). Combining these samples from the same geographical area allows the full salinity gradient to be covered. While estuarine and fjord habitats are hydrographically different from lake sites, including these environments in inference models provides analogues for reconstructions at coastal sites under changing sea levels in the past. This is especially appropriate for the Vejlerne cores discussed here, which include Limfjord sediments.

East Vejlerne is an artificial wetland created when a shallow embayment on the northern shore of the saline (~26 g·L⁻¹) Limfjord was separated by the Bygholm Dam, completed in 1876 (Fig. 1), in an attempt to create agricultural land to offset the loss of Danish territory elsewhere. A series of sluices and drainage canals was set up to regulate water level and salinity within Vejlerne, and in 1906 a railway was built to encourage regional development, which separated Han Vejle from Lund Fjord. Nonetheless, by the early 20th century efforts to reclaim the land for agriculture were proving unsuccessful, and by 1920 land reclamation was finally abandoned (Jakobsen and Sørensen 1998). Since this time, Vejlerne has developed as a mixed wetland of about 6000 ha, consisting of shallow lakes, meadow, and marshland of varying salinity, largely depending on distance from the Limfjord. These varied habitats seasonally attract large numbers of migrating birds, and Vejlerne's international importance for bird conservation was formally recognised by accreditation under the Ramsar Convention in 1977 and the European Union Bird Directive in 1983 (Hald-Mortensen 1998). Changes to the drainage system were made during the 20th century, notably in the 1960s, when self-regulating sluices were replaced by a central sluice on the Limfjord dam (Amsinck et al. 2003).

Surface sediments were collected from the deepest parts of 43 fresh and brackish lakes and lagoons in the northern part of Jutland from June to November 1999, using a simple Kajak-type corer. A subset of 27 lakes selected for diatom

analysis (Fig. 1) was chosen to provide approximately equal coverage across the salinity and nutrient range to minimize bias in any one part. Sediments from nine fjord and estuarine sites (Fig. 1) were collected using a HON-Kajak corer (Renberg 1991). Water samples from all sites were analysed for total phosphorus, total nitrogen, and salinity (g·L⁻¹ TDS). Lake water total phosphorus (TP) was determined as molybdate-reactive phosphorus (Murphy and Riley 1972) following persulphate digestion (Koroleff 1970). Total nitrogen (TN) was the sum of ammonia, nitrite, and nitrate after potassium persulphate digestion (Solórzano and Sharp 1980) using the phenate method (APHA 1985). Salinity was measured on site using a portable YSI 30 instrument (YSI Environmental Inc., Yellow Springs, Ohio, USA). Lake water samples were analysed at the National Environmental Research Institute, Silkeborg, and were also compared with survey data collated by the Danish counties.

Lake chemistry values are summer means (sampled May to October 1996–2000; median number of measurements per lake = 4.5) for 16 of the 27 lakes; values are based on single samples for the remaining sites collected at the same time as coring. Examining data from the 16 lakes sampled for water chemistry more than once gives some idea of the variability in the abiotic environment in these systems. The coefficient of variation (CV) for both salinity and TP were similar (salinity: mean CV = 20%, range 1%–66%; TP: mean CV = 18%, range 5%–52%; *n* = 16 for both) over the period 1996–2000. For fjords, the uppermost 10 m of the water column was analysed monthly over 5 years as part of the Danish National Monitoring and Assessment Program (Conley et al. 2002), and means for each site were calculated on the basis of 965–4180 individual measurements for salinity and between 65 and 285 measurements for TP and TN, respectively.

Short sediment cores (<1 m long, diameter 5.2 cm) were also taken from several shallow lakes in the east Vejlerne wetlands (including Han Vejle, Glombak, and Lund Fjord; Fig. 1). Cores were taken in October 1998 (Glombak) or June 1999 (Han Vejle and Lund Fjord) with a 1-m Mackereth piston corer (Glombak and Lund Fjord) or a modified Kajak

corer (Han Vejle). Only cores with an undisturbed sediment–water interface were kept, and one core was chosen from each site for dating and zooplankton and diatom analysis, while replicate cores were reserved for future analyses. Cores were sectioned in 1-cm intervals and samples stored in dark refrigeration until analysis.

Laboratory methods

All samples for diatom analysis were prepared following the method of Renberg (1990). Diatom analysis was made on surface sediment assemblages from 27 lake sites and nine fjords, and for the sediment core work, counts on 21 levels from Han Vejle, 26 from Glombak, and 18 from Lund Fjord were made. Strewn slides were mounted in Naphrax, and where preservation permitted, at least 300 valves (average 480 for surface sediments) per sample were counted in transects under oil-immersion phase-contrast light microscopy at $\times 1000$ (numerical aperture = 1.4) and identified where possible to species level. Taxa were identified according to a variety of general (e.g., Krammer and Lange-Bertalot 1986–1991; Witkowski et al. 2000) and regional floras (e.g., Snoeijs and Vilbaste 1994; Snoeijs and Potapova 1995; Snoeijs and Kasperovičienė 1996). Diatom taxonomy was harmonized between the lake and fjord samples according to agreements reached by the two analysts during a workshop. Species grouped into aggregate taxa are indicated as “agg.”.

Samples from all cores were analysed every 1 cm (Han Vejle and Lund Fjord) or 2 cm (Glombak) for the fraction of dry weight loss-on-ignition at 550 °C (LOI%) after drying overnight at 105 °C (Dean 1974). For Glombak and Lund Fjord, whole core bulk magnetic susceptibility measurements (using a Bartington MS2-C loop; Bartington Instruments Ltd., Oxford, UK) were made before extruding the cores from the Perspex core tubes. Values of magnetic susceptibility are reported in SI units (Système International d’Unités). Homogenized subsamples were analysed for the radionuclides ^{210}Pb , ^{226}Ra , and ^{137}Cs by direct gamma assay using Ortec HPGe GWL series well-type coaxial low background intrinsic germanium detectors (Ortec, Oak Ridge, Tennessee) (Appleby et al. 1986). Dates were calculated using a constant rate of supply ^{210}Pb model (Appleby and Oldfield 1978). Full details of all dating analyses referred to here are available from the authors upon request.

Numerical methods

Environmental data consist of four measured parameters (TN, TP, salinity, and depth) and one derived variable, TN/TP ratio (Table 1). Additionally, a diatom dissolution index (F) was calculated for the 27 lake samples and all core samples. This index is the proportion of all valves counted under light microscopy that are well preserved and varies between 1 (excellent preservation) and 0 (all valves visibly dissolved). It has been previously used to estimate dissolution in diatom studies and permits preservation to be compared between samples (Ryves et al. 2001, 2002). Diatom counts were expressed as relative abundance (percentages) of total counts, and taxa not identified to species level were removed. For multivariate analyses, environmental variables were log transformed to reduce the effect of extreme values. A dummy variable (0/1) was included to take into account

the contrast between aquatic system type (lake or fjord) not captured by parameters measured. Ordinations were carried out using CANOCO 4.0 (ter Braak and Šmilauer 1998). Monte Carlo permutation significance tests were carried out with 999 permutations. Downweighting was applied in all unimodal analyses, with detrending by segments (where appropriate).

For model development, detrended correspondence analysis (DCA) of diatom data was used to estimate the species gradient length, values <2 standard deviation (SD) units indicating that most species have monotonic responses to underlying ecological gradients and should thus be modelled using linear methods (ter Braak 1995). Canonical correspondence analysis (CCA) was performed to identify which variables might be suitable candidates for model development, using Bonferroni-adjusted forward selection, inspection of variance inflation factors, and t values of regression coefficients (ter Braak and Šmilauer 1998). Detrended CCA (DCCA) was run to confirm a similar gradient length to that under DCA with any chosen variable (Birks 1995). Candidate parameters should also explain a statistically significant amount of the total species variance in single-variable CCA, where the ratio of the constrained axis (axis 1) to the first unconstrained axis (axis 2) should be >0.5 (Kingston et al. 1992).

A variety of models was investigated using weighted-averaging methods (WA), partial least squares (PLS), and weighted-averaging partial least squares (WA-PLS; ter Braak and Juggins 1993). Both tolerance-downweighting and simple WA were used, with both classical and inverse deshrinking (Birks 1995). All models were internally validated using the leave-one-out jackknife method (Birks 1995) and critically compared according to the root mean square error of prediction (RMSEP). As a rule of thumb, a higher component WA-PLS model should only be accepted if there is $>5\%$ improvement in RMSEP over the simpler (lower component) alternative (Birks 1998). Bias (value-dependent error) should be as low as possible. Model building, validation, and reconstruction was carried out using the programs CALIBRATE 0.81 (Juggins and ter Braak 1997) and WAPLS 1.2 (S. Juggins, School of Geography, Politics and Sociology, Newcastle University, UK, and C.J.F. ter Braak, Biometris, P.O. Box 100, 6700 AC Wageningen, The Netherlands, unpublished data), with sample-specific errors calculated using 9999 permutations. Estimates of species richness, $E(S)$, in samples of different count size were made using RAREPOLL (Birks and Line 1992) using $N = 300$ valves.

Results

Environmental and diatom data sets

Environmental data for all sites are summarized in Table 1. While the addition of the fjord sites has extended the salinity range appreciably from 17.4 to 31.1 $\text{g}\cdot\text{L}^{-1}$ TDS, lakes and fjords also differ in average TN, TP, and depth. Both the range and mean values of TN and TP are greater among lakes than fjords, with mean TN and TP values in lakes (1972 $\mu\text{g}\cdot\text{L}^{-1}$ and 127 $\mu\text{g}\cdot\text{L}^{-1}$, respectively) about twice those measured in fjords (980 $\mu\text{g}\cdot\text{L}^{-1}$ and 59 $\mu\text{g}\cdot\text{L}^{-1}$, respectively; Table 1). Among the 36 sites, a strong positive correlation ($p = 0.001$, $n = 36$) exists between salinity and depth

($r = +0.799$), and weaker, negative correlations ($p = 0.01$, $n = 36$) between salinity and TN ($r = -0.464$), depth and TN ($r = -0.447$), and TP and TN/TP ($r = -0.488$). Limnologically, a strong contrast appears between the shallow, nutrient-enriched and lower salinity lakes and the deeper, estuarine fjords, as expected from the varying influence that terrestrial and marine processes have on aquatic systems across a coastal gradient.

After removal of unknown types, 263 diatom taxa could be identified from the 27 lake sites and 240 from the nine fjord samples. This may reflect in part the larger number of valves counted in the fjord data set (average 569 valves) compared with the lake samples (average 424 valves), although fjord assemblages may include valves originating from a greater range of environments and a larger geographical area than the sites on land. Owing to taxonomic difficulties in positive identification of *Chaetoceros* species from the cysts, it was decided to remove these taxa from the merged data set before further analyses. *Skeletonema costatum*, only recorded from the fjord samples, was also removed from the merged data set, as it was considered unlikely to be well preserved in sediments. Removing these taxa reduced the total diatom count by ~5% (by on average 15 and 54 valves per sample for lakes and fjords, respectively).

The combined diatom data set after these deletions consists of 413 taxa, of which about 21% (87) are common to both site types. Many taxa in this diverse flora are rare. In the combined data set, about one third of taxa (137) appear only once among the 36 sites, while only 41% (171) occur at a relative abundance of 1% or above. These proportions are closely mirrored within the lake and fjord data sets individually. However, many of the most important taxa are found in both lake and fjord sites (Fig. 2), supporting the idea that lake and fjord systems are ecologically as well as geographically continuous. Moreover, salinity appears important in structuring the pattern of species' distribution among these varied sites (Fig. 2). While some species (e.g., *Ctenophora* (= *Synedra*) *pulchella* and *Stephanodiscus parvus*) are entirely confined to lakes, and others (e.g., *Eunotogramma dubium* and *Nitzschia distans*) are found only in fjord samples, the majority of important taxa are found in both types, although often with a clear abundance peak in one part of the salinity spectrum. Although diatom preservation is generally good among lake sites ($F_{\text{mean}} = 0.76$, $F_{\text{min}} = 0.5$; Table 1), there is a tendency for diatom dissolution to increase with salinity (Fig. 2).

Multivariate analyses and model development

The gradient length of the first DCA axis (3.98 SD units) of the diatom data confirmed that diatom species' responses were largely unimodal (cf. Fig. 2), with about 11.8% of variation in the species data captured by axis 1 and a further 6.1% along axis 2. Constraining the diatom data by transformed environmental variables revealed that salinity, depth, and TP were all significant in explaining fractions of the species variance, even after accounting for the lake–fjord contrast (Table 2). These four variables explain 25.3% of the diatom data (significant at $p = 0.001$, $n = 999$), and each independently explains 3.5% (TP) to 6% (salinity) of total variance when the other three factors are included as co-variables in the analysis (Table 2). There is relatively little

variance (~8%, 30% of the total explained) shared between two or more factors, despite the large number of combinations involving 2, 3, and 4 factors possible (11 permutations).

Salinity is the most important parameter, explaining 6% of variation uniquely and 10.4% when it is the only constraining variable (axis 1/axis 2 = 1.18; Table 2), with a gradient >3.2 units under DCCA and is thus the most suitable candidate for construction of a diatom model. While both WA and WA-PLS methods produced strong apparent models, the most robust under jackknifing was found to be the second component WA-PLS model (WA-PLS(2); Fig. 3). The improvement in RMSEP under the second component (4.6% smaller than component 1) was accompanied by a reduction in average bias by almost 40% and was deemed a significant improvement overall. The final diatom–salinity model for 36 sites appears robust across the salinity gradient from freshwater to near-full marine conditions ($r^2 = 0.977$, RMSE = 0.11 log salinity $\text{g}\cdot\text{L}^{-1}$), even under internal validation ($r^2_{\text{jack}} = 0.887$, RMSEP = 0.246; Fig. 3).

Application to Vejlerne cores

The diatom–salinity model was applied to sedimentary diatom assemblages from cores collected from three sites in the eastern Vejlerne (Fig. 1; Han Vejle, Glombak, and Lund Fjord). Stratigraphical plots summarizing physical and diatom analyses of these sequences are presented (Figs. 4–6). All three cores contain a striking lithological contrast between uppermost dark, organic-rich, lower density gyttja and grey, organic-poor, higher density clays below, although the relative length of these two sections varies greatly among the three sites. This lithological difference between these sediment types is paralleled by physical and biological analyses (Jeppesen et al. 2002; Amsinck et al. 2003), reflecting sedimentation under marine–brackish (lower unit) and lacustrine conditions (upper unit) following the building of the Bygholm Dam.

Glombak

The 82-cm core from Glombak can be divided into two sections according to lithological, physical, and diatom analyses, the major change occurring at about 54 cm (Fig. 4). Dating results are consistent with this transition occurring in the late 19th century, agreeing with the known age of dam construction. The uppermost 45 cm (post-1915) are characterized by high organic (30%–50% LOI) and water content, low but variable carbonate content, and low bulk magnetic susceptibility (BMS). A transition period from 45 to 54 cm shows declines in LOI, CO_3^{2-} , and water content with increases in magnetic susceptibility. The lower 28 cm of the core consists of low organic, carbonate, and water-poor material, with slight increases in these towards the bottom of the core. A peak in BMS centred on 72 cm is due to a large, rounded 2-cm diameter pebble found in the centre of the core (and so not carried down during coring). Dry mass flux and sedimentation rate show highest values towards the top of the core, where values over $0.06 \text{ g}\cdot\text{cm}^{-2}\cdot\text{year}^{-1}$ flux and $1 \text{ cm}\cdot\text{year}^{-1}$, respectively, are recorded. Values decline until a lower peak of 35–45 cm (~1915–1929).

Diatom assemblages also show a major transition across this lithological boundary; taxa with the highest salinity optima (as derived from the modern training set) are generally

[illegible]

Table 2. Unique variance explained by significant variables during a variance partitioning analysis (using canonical correspondence analysis, CCA) of the 36-site diatom data set.

Variable	Unique explanation		
	λ_{var}	Species variance (%)	p level ($n = 999$)
Salinity	0.322	6.0	0.001
Lake–Fjord	0.219	4.1	0.002
Depth	0.208	3.9	0.003
Total P	0.189	3.5	0.014
Interactions	0.42	7.8	—
Total explained	1.358	25.3	0.001
Salinity (alone)	0.56	10.4	0.001
$\lambda_{\text{salinity}}/\lambda_{\text{axis 2}}$	ratio = 1.18		

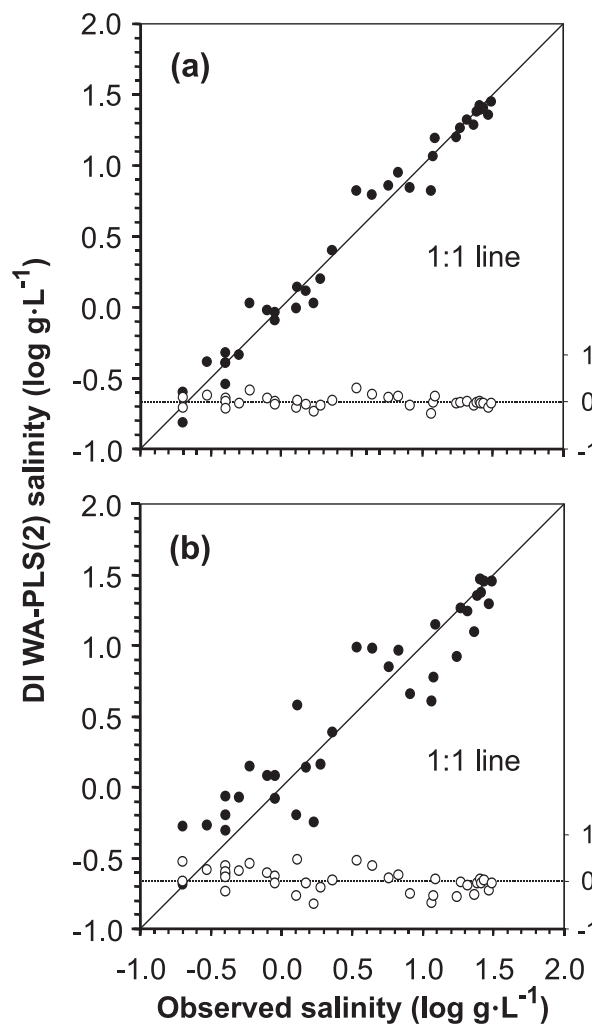
Note: For salinity, results of a single-variable CCA are also given.

replaced by those with lower optima in a stratigraphic sequence from bottom to top. In the lowermost section from 75 to 82 cm, littoral taxa with the highest salinity optima (17.5–29 g·L⁻¹) are important (e.g., *Cocconeis stauro-neiformis*, *Cymatosira belgica*, and *Delphineis* spp.). These are gradually replaced by somewhat lower salinity forms (e.g., *Cocconeis scutellum* agg., *Opephora mutabilis* (= *Opephora olsenii*) and *Grammatophora oceanica* (optima 2.5–13 g·L⁻¹)). Several other brackish–marine taxa (3–12 g·L⁻¹) are also essentially confined to the lower 30 cm of the core, but show little trend within this part (e.g., *Paralia sulcata*, *Tabularia fasciculata* agg., *Planothidium delicatulum* (= *Achnanthes delicatula*) spp., and *Navicula starmachiodes*).

The transition at 54 cm within the diatom flora is abrupt, with assemblages suddenly dominated by freshwater and subsaline *Fragilaria*, *Staurosira*, *Pseudostaurosira*, *Staurosirella*, and *Martyana* spp. (termed here *Fragilaria sensu lato*). Notably present are several taxa which in this data set have salinity optima <3 g·L⁻¹: *Pseudostaurosira brevistriata*, *Staurosirella pinnata*, *Martyana atomus*, *Fragilaria sopotensis*/*Staurosira punctiformis* agg., and *Staurosira elliptica* agg., the latter which includes *Staurosira elliptica* and *Pseudostaurosira perminuta* (= *Fragilaria neoelliptica*). Within the freshwater phase, however, there is evidence of ecological and environmental change. Low salinity littoral taxa (*Amphora pediculus* and *Rhoicosphenia curvata*) are important from 35 to 55 cm (late 19th century to 1930). From 25 cm (circa 1960), the higher salinity pelagic species *Cyclotella choctawhatcheeana* (optimum 9.7 g·L⁻¹) appears together with *Achnanthes fogedii*, both maintaining an abundance of 10% or more in all subsequent samples.

Diatom-inferred (DI) salinity accurately reconstructs contemporary conditions (1.3 g·L⁻¹), and species coverage in the model is good, between 83% and 99% (average 93%). There is relatively little change in DI salinity throughout the last century, although values tend to increase in the upper 25 cm (from the 1960s). Across the lithological transition, however, salinity rises consistently to a maximum of 28 g·L⁻¹ at 76 cm before dropping to 15 g·L⁻¹ at the bottom of the core. Diatom preservation is good in the upper 40 cm ($F_{\text{mean}} = 0.77$) but falls appreciably from 45 to 70 cm ($F_{\text{mean}} = 0.35$), reaching a minimum of $F = 0.21$ at 60 cm. Preservation im-

Fig. 3. Diatom–salinity model using weighted-average partial least squares (WA-PLS) (2nd component). Diatom-inferred (DI) salinity for apparent (a) and jackknifed (b) models is plotted against observed salinity (in log salinity, g·L⁻¹) for 36 sites. Solid circles, DI salinity; open circles, residuals. (a) Apparent model: $r^2 = 0.977$, root mean square error (RMSE) = 0.11 log salinity units; (b) jackknifed model: $r^2_{\text{jack}} = 0.887$, root mean square error of prediction (RMSEP) = 0.246 log salinity units.



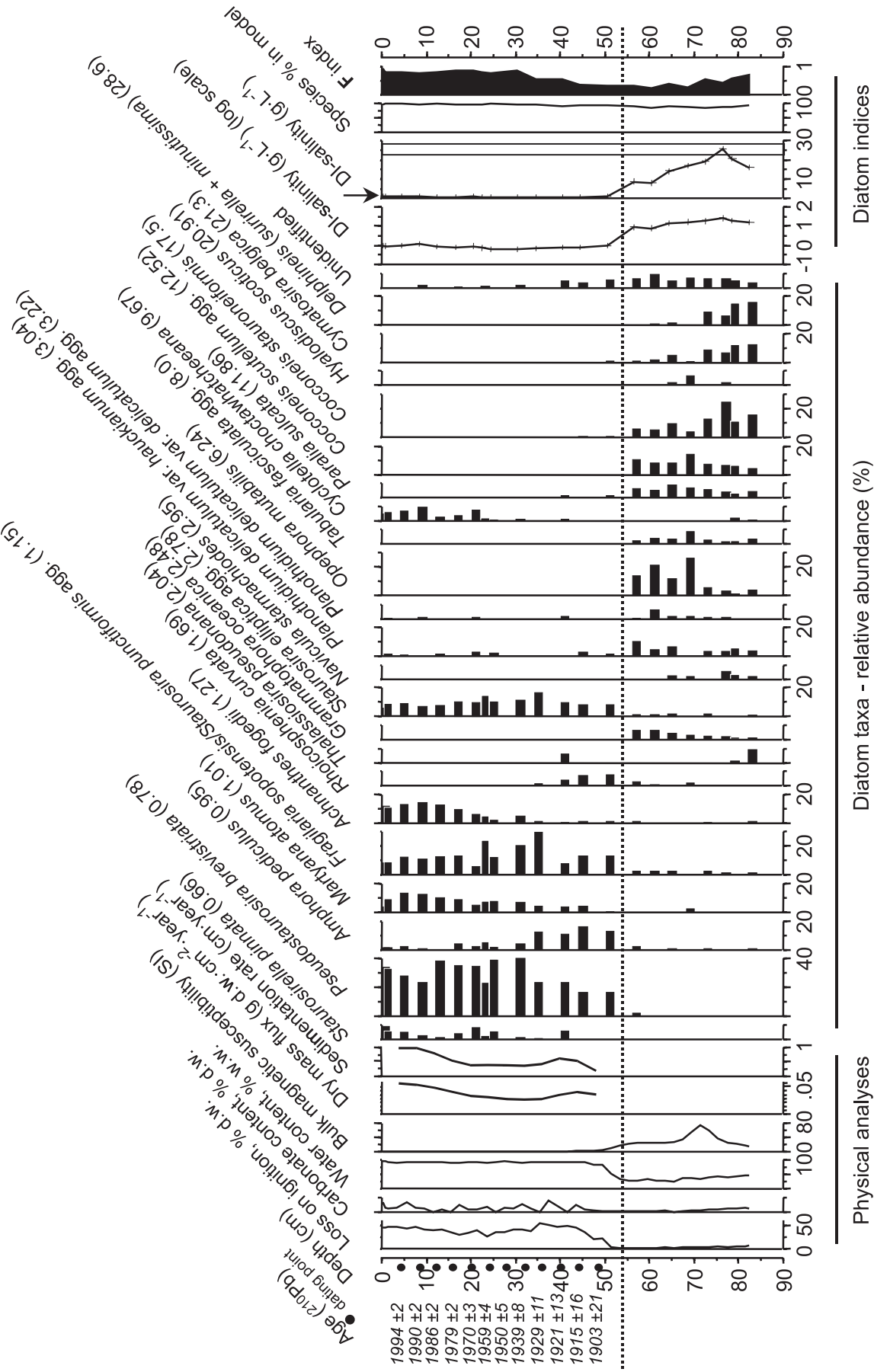
proves in the bottom 10 cm, reaching 0.69 in the lowermost sample. The proportion of unidentifiable valves closely follows the dissolution index ($r^2 = 0.77$, $n = 22$, $p < 0.001$).

Han Vejle

This 46-cm core consists almost entirely of gyttja, with the major visible lithological change at approximately 45 cm (Fig. 5). Data from ²¹⁰Pb and ¹³⁷Cs analyses suggest that there is a hiatus below 43 cm. Using a constant rate of supply model, the lowest horizon that can be securely dated is 40 cm (1941 ± 12 years), while the sediments below probably predate 1880.

Organic content (as LOI%), which varies between 10% and 40% in the upper 35 cm (~1950) and peaks from 7 to 15 cm (1993–1989) and 20–35 cm (1960–1980), falls below 10% some 3 cm before the lithological boundary, in tandem with a drop in water content. Dry mass flux varies down-

Fig. 4. Stratigraphic diatom analysis from Glombak core, GLOM I. Selected physical parameters, diatom taxa (relative abundance of all taxa >5% in any sample), and diatom indices (diatom-inferred (DI) salinity, % fossil data present in training set, and preservation index, *F*) are plotted. Dotted horizontal line indicates lithological transition from marine (lower) to freshwater (upper) sedimentary units. Age estimates from ²¹⁰Pb and ¹³⁷Cs analyses are shown on left. Arrow in DI salinity plot indicates current salinity at site; vertical lines indicate current (1990s) salinity range of Limfjord in Bjørnsholm Bay.



core, with a maximum value at 18 cm (~1983) and a secondary peak below 35 cm (in the 1940s). Sediment accumulation rates rise from a value of $0.4 \text{ cm}\cdot\text{year}^{-1}$ at 40 cm (dated 1941) to a peak of $2 \text{ cm}\cdot\text{year}^{-1}$ at 8 cm (~1992), before falling off slightly. Diatom valve concentrations and flux data are available for this core. Concentrations rise unevenly from values $<1 \times 10^6 \text{ valves}\cdot\text{g}^{-1}$ dry weight (d.w.) at the base of the core to maximum values of almost $260 \times 10^6 \text{ valves}\cdot\text{g}^{-1}$ d.w. in the surface sediment and follow the LOI% curve. Diatom flux, however, is greatest from 15 to 20 cm (in the early 1980s, with a peak of nearly $60 \times 10^6 \text{ valves}\cdot\text{cm}^{-2}\cdot\text{year}^{-1}$), and at 3 cm (1996), with enhanced values below 35 cm (1940s).

The diatom flora shows only minor changes throughout the sequence, being dominated by many of the same oligosaline *Fragilaria sensu lato* (optima $<3 \text{ g}\cdot\text{L}^{-1}$) as found in the upper sections of the Glombak core (especially *Staurisirella pinnata*, *Pseudostaurisira brevistriata*, *Fragilaria sopotensis/Staurisira punctiformis* agg., and *Staurisira elliptica* agg.). Littoral taxa (e.g., *Achnanthes* spp., *Amphora pediculus*, *Navicula* spp.) become less abundant above 15–20 cm (from the early 1980s). The lowermost two samples contain few, generally poorly preserved diatoms ($F < 0.5$), and <100 valves could be counted from these levels. *Fragilaria sensu lato* are still important, but valves of polyhaline species appear (e.g., *Paralia sulcata*, *Cymatosira belgica*), indicating a transition to, or a mixture of, marine Limfjord sediments. DI salinity in the surface sediment matches measured values well ($0.4 \text{ g}\cdot\text{L}^{-1}$ in 1998) and remains low throughout the upper 45 cm of the core ($<1 \text{ g}\cdot\text{L}^{-1}$), with almost 100% species coverage in the model. Even below 45 cm, DI salinity only rises to $1.5 \text{ g}\cdot\text{L}^{-1}$, although these values are based on few valves. Diatom preservation is good for all samples above 45 cm ($F_{\text{mean}} = 0.71$).

Lund Fjord

The 80-cm core retrieved from this shallow lake contains the longest section of Limfjord sediments, with the lithological transition at only 6–7 cm below the surface (Fig. 6). Radiometric ^{210}Pb and ^{137}Cs analyses suggest a discontinuity in sedimentation at 5–6 cm, with all sediments above this depth postdating the early 1960s and a hiatus of unknown duration beneath, but spanning at least the first half of the 20th century.

Organic content is lower in this core than that found at Glombak and Han Vejle, fluctuating between 3% and 12% LOI below 5 cm and reaching 20% only in the surface sediment. This trend is repeated by carbonate and water content, with BMS showing the reverse (although values remain below 3 SI units throughout the sequence). Given the dating results, sedimentation rates can only be calculated for the uppermost section. Dry mass flux shows a subsurface peak of $0.04 \text{ g}\cdot\text{cm}^{-2}\cdot\text{year}^{-1}$ at 3 cm (~1978) while accumulation rates are low (always $<0.2 \text{ cm}\cdot\text{year}^{-1}$) and decline sharply by 4 cm (~1968) to $0.05 \text{ cm}\cdot\text{year}^{-1}$. Diatom concentrations fall rapidly within the upper 5 cm from 800×10^6 to $12 \times 10^6 \text{ valves}\cdot\text{g}^{-1}$ d.w. and remain low throughout the lower section varying between 3×10^6 and $140 \times 10^6 \text{ valves}\cdot\text{g}^{-1}$ d.w. (average $<70 \times 10^6 \text{ valves}\cdot\text{g}^{-1}$ d.w.). Diatom fluxes, again only available for the uppermost three samples, mirror the concentrations and fall from 20×10^6 to $0.2 \times 10^6 \text{ valves}\cdot\text{cm}^{-2}$.

year^{-1} by 6 cm. Levels with few diatoms and marked by poor diatom preservation were found in the lower section at 10 cm and from 30 to 35 cm.

As might be expected, the diatom flora shifts almost completely across the lithological transition, from dominance by freshwater *Fragilaria sensu lato* assemblage, with some higher salinity elements (e.g., *Opephora* spp. and *Cocconeis neothumensis*), to assemblages dominated by taxa with a marine affinity (especially *Paralia sulcata*, *Cocconeis scutellum* agg. and *Cocconeis stauroneiformis*, *Fallacia cryptolyra*, *Cymatosira belgica*, and *Delphineis* spp.). There is little systematic stratigraphic pattern within the lower core section, with assemblages dominated by littoral (epiphytic and benthic) taxa throughout. Subtle shifts among species abundance may indicate changes in habitat availability (e.g., patterns within *Navicula perminuta*, *Paralia sulcata*, *Cocconeis stauroneiformis*, *Tryblionella punctata*, and *Tryblionella coarctata*) within a more or less high salinity period.

DI salinity reflects these lithological and ecological transitions. The model predicts present-day salinity accurately ($0.4 \text{ g}\cdot\text{L}^{-1}$) and changes little within the uppermost post-damming section. The sample below this boundary contains few and very poorly preserved diatom valves ($F = 0.08$) and reconstructs salinity higher than fully marine conditions ($45 \text{ g}\cdot\text{L}^{-1}$). Inferred values below this point vary between 13 and $24 \text{ g}\cdot\text{L}^{-1}$, at or below present-day observations in the Limfjord ($23\text{--}31 \text{ g}\cdot\text{L}^{-1}$), even for other poorly preserved assemblages with low counts. Species coverage is good for all samples throughout the core (on average 88%). Diatom dissolution shows a close correspondence with total diatom abundance (log concentration; $r^2 = 0.41$, $n = 18$, $p < 0.005$) and % unidentified taxa ($r^2 = 0.63$, $n = 18$, $p < 0.001$). While F values are high in the freshwater sediments ($F_{\text{mean}} = 0.79$), preservation falls at the transition to marine conditions and, although lower throughout this part ($F_{\text{mean}} = 0.38$), tends to improve with depth to the core base.

Discussion

Diatom distributions with respect to environmental gradients

Salinity, depth, and nutrient concentration have been shown to be important variables structuring diatom assemblages in surface sediments in Danish coastal areas (Clarke et al. 2003; this study). Covariation of environmental gradients in coastal areas and along estuaries (especially inversely between salinity and nutrients; Underwood et al. 1998) may make it difficult to determine which factors algal communities are primarily responding to, particularly if response to one variable is modulated by another (i.e., dependant effects). Although sophisticated techniques are now available to separate and test the independent effects of different parameters on biological data sets and estimate covariation between them (e.g., Muylaert et al. 2000), there is a need for experimental data to confirm these empirical models and underpin them with physiological and autecological evidence (e.g., Underwood et al. 1998; Saros and Fritz 2002). This is especially evident where biological data sets show strong spatial or temporal structure, which eludes statistical explanation by measured environmental variables (e.g., Lapointe

[illegible]

Figure 1 is a multi-panel figure showing diatom indices and physical analyses from 1948 to 1985. The top section displays diatom indices for 28 taxa, including *Cocconeis scutellum*, *Cocconeis radiosa*, and others. The bottom section shows physical analyses such as sedimentation rate, diatom abundance, and water content. A vertical dashed line at 1968 marks the age of the core.

2000), particularly when commonly 60%–80% or more variation in contemporary biological data sets remains statistically unexplained (e.g., Zong and Horton 1999; Muylaert et al. 2000; this study). Part of the problem undoubtedly relates to the quality of the measured environmental data on which the models are based and also to potential mismatches between time-smoothed sedimentary assemblages and discrete, point measurements of the environment. Single water samples (defining the water chemistry for 11 lakes in this study) will fail to integrate temporally the chemical conditions that affect diatom growth, and this has likely contributed to the large amount of unexplained variation in the present data set.

Salinity was found to explain over 10% of species variance within the lake–fjord data set, and of the variables included, salinity accounted for the greatest unique fraction (6%). Studies on estuarine planktonic (Muylaert et al. 2000) and periphytic diatom communities (Juggins 1992; Underwood et al. 1998) and from epilithic habitats in the northern Baltic (Bothnian Bay; Busse and Snoeijs 2002) have demonstrated the importance of salinity in determining diatom distributions. While this is expected given the observed salinity gradient from fresh to fully marine within a freshwater tidal estuary (e.g., within the Schelde, Belgium, where salinity accounted for 18.9% of diatom variance; Muylaert et al. 2000), salinity was important in the northern Baltic where the range was 0.4–3.3 g·L⁻¹ (Busse and Snoeijs 2002). Similarly in lakes across large salinity (conductivity) gradients, species assemblages in surface sediments are dominated by salinity (e.g., Fritz 1990; Gasse et al. 1995; Reed 1998b), but strong responses have also been demonstrated at low salinity across much smaller gradients similar to that found in the Bothnian Bay (e.g., in West Greenland, Ryves et al. 2002). Approaching marine conditions, Underwood et al. (1998) also demonstrated that algal communities responded to salinity along a saltmarsh creek within the range of 22.5–33 g·L⁻¹, although this co-varied with a nutrient gradient, whereas Jiang (1996) found that sedimentary diatom assemblages varied over a salinity range of 14–35 g·L⁻¹ in the shallow Danish coastal waters of the Skagerrak and Kattegat. The physiological stress resulting from changes in osmotic pressure appears sufficient to cause total species turnover several times across a series of thresholds, although as earlier halobian classifications recognised (e.g., van der Werff and Huls 1976), this sensitivity is nonlinear across the salinity gradient, with small differences at the freshwater–brackish part as important as larger changes at higher salinities. Diatoms exhibit similar nonlinear responses to other environmental gradients, e.g., phosphorus (Bennion et al. 1996) and pH (Birks et al. 1990).

Salinity has also been shown to be a major factor affecting zooplankton and fish communities (Jeppesen et al. 1994, 2002), which may have direct effects on diatom communities via grazing and predation on grazers. Indeed, within the same regional data set of lakes and lagoons analysed here (salinity 0.2–17.4 g·L⁻¹, 36 lakes; S.L. Amsinck, unpublished data), variation in zooplankton assemblages in surface sediments was explained by salinity, TP, and planktivorous fish density. Salinity plays an important structural role at all trophic levels, both directly (physiologically) and indirectly on habitat (affecting macrophyte coverage, which appears to

be partly independent of nutrients in brackish lakes; Jeppesen et al. 1994, 1997). Potentially, both top-down (via fish-predation effects on zooplankton) and bottom-up (independent importance of TP) effects also exert significant influence on diatom communities, at least in brackish non-fjord systems. Unfortunately, we do not currently have enough information about these aspects within this data set to permit a proper evaluation here.

Water body type (lake–fjord) is also independently important in explaining variation in the diatom data. Species richness was significantly higher in fjords ($n = 9$, $E(S) = 72$) than in lakes ($n = 27$, $E(S) = 40$; $p < 0.001$) and showed no correlation to salinity within either group ($r^2 < 0.03$), in contrast with a strong decline in zooplankton richness with salinity within the lakes group (S.L. Amsinck, unpublished data). Unsurprisingly, the difference between the lake and fjord sites is not fully captured by the few variables measured here. As salinity and its dependent factors — such as macrophyte and zooplankton communities that exhibit their greatest change below 7–8 g·L⁻¹ (i.e., within the lake group; Jeppesen et al. 1994; S.L. Amsinck, unpublished data) — have been factored out, functional differences due to hydrographic settings may be important. As the tidal range is generally small (<1 m) in the western Baltic, tidal effects (depth fluctuations and diurnal turbidity changes) are unlikely to account for this difference. Salinity varies seasonally in both estuaries and coastal lakes, but over 5 years monitoring, seasonal changes in salinity at sites within the Limfjord were muted, varying by only 0.7–2.1 g·L⁻¹, and at Vejle and Kolding by 2.5–3.7 g·L⁻¹ (MOLTEN Project 2003). In contrast, some lakes vary from almost fresh to saline from winter to summer. Stratification patterns and duration, ice cover, and other factors such as differences in silica cycling between lake and fjord sites may also be important. Differences in biological structure between these systems may also be relevant; for example, mussels (*Mytilus* spp.) are present in fjords but not in lakes.

Depth and TP also explained significant fractions of diatom species variance, independently accounting for 3.9% and 3.5%, respectively. The role of depth appears to act through the availability of periphytic and littoral habitats compared with pelagic habitats, perhaps mediated through macrophyte cover, and as although the deepest sites are fjords with the highest salinity, this covariation has been factored out. Muylaert et al. (2000) also found that the ratio of maximum to photic depth explained significant amounts of variation among algal communities along the Schelde estuary, which they related to a turbidity maximum in the freshwater tidal part. In a study of benthic diatoms in the Gulf of Riga, Vilbaste et al. (2000) found depth important, both due to deposition of planktonic valves from the overlying water column and the availability of fine-grained substrates for epipelagic taxa. Depth in this case was inversely correlated with exposure to wave action, which affects diatom communities by direct hydraulic stress and by allowing epipelagic habitats to replace coarser-grained epipsammic habitats. Substrate type may also affect the abundance and types of macrophytes that can colonize benthic areas, which may be more important than nutrient levels (see above) in brackish systems. Exposure to wave action was also found to structure epilithic diatom communities in the Bothnian Bay

within an area of similar salinity ($\sim 5 \text{ g}\cdot\text{L}^{-1}$; Busse 2002). In the present study, depth may reflect the availability of pelagic habitats, as pelagic species (e.g., *Thalassiosira*, *Cyclotella*, *Chaetoceros* spp.) develop in the deeper lake sites (e.g., Kås Sjø and Kilen, both $\sim 4 \text{ m}$ deep) across a range of salinities, as well as within the fjords.

TP is known to dominate variation within diatom assemblages in freshwater lakes in modern agricultural landscapes (Bennion et al. 1996) and to affect brackish diatom communities from impacted coasts (Cooper 1995). Despite the 10-fold variation in TP values among sites in the present study ($25\text{--}331 \mu\text{g}\cdot\text{L}^{-1}$ TP), salinity has an overriding effect on diatom distributions. Neither TN nor TN/TP was found to be important in explaining diatom distributions, which may be attributed to high water column TN/TP ratios above Redfield (N:P = 16:1 on a molar basis, 7.23:1 by weight) for all but two sites (both lakes), indicating N enrichment. Coastal waters in the western Baltic often have high N loads from terrestrial human activity (agricultural runoff, sewage, and industrial effluents), funnelled along freshwater estuaries draining large inland areas and also from other point sources along coasts (e.g., sewage treatment works). While large diatom–environmental data sets of freshwater lakes have not shown major responses to TN, brackish diatoms from large regional Baltic data sets exhibit strong responses to both N (Clarke et al. 2003) and P (MOLTEN Project 2003). Such data sets show promise as a means to infer nutrient concentrations from diatom assemblages in coastal areas.

Diatom–salinity model

Several models for inferring tidal level (e.g., Zong and Horton 1999) and salinity (Juggins 1992; Jiang et al. 1998; Parsons et al. 1999) have been developed from sedimentary diatom assemblages in coastal environments. Tidal fluctuations will often be associated with salinity variations, and within a tidal estuary the dominant response may be to salinity rather than to tidal range per se (Juggins 1992). Parsons et al. (1999) used a salinity index to infer salinity changes over the last 300 years in Louisiana coastal marshes based on an empirical relationship between observed salinity (range $2\text{--}23 \text{ g}\cdot\text{L}^{-1}$) and proportions of freshwater, estuarine, and marine diatoms in dated horizons from sediment cores. As pointed out by the authors, this technique is sensitive to dating errors and performed less well at the ends of the gradient, especially $>20 \text{ g}\cdot\text{L}^{-1}$ (Parsons et al. 1999).

Surface sediment diatom assemblages from the Skagerrak–Kattegat showed strong response to summer and winter sea-surface salinity (Jiang 1996). From this, WA models were created from a 19-sample training set (salinity range $14\text{--}35 \text{ g}\cdot\text{L}^{-1}$) and used to reconstruct sea-surface salinity over the Holocene (RMSEP = $2\text{--}5 \text{ g}\cdot\text{L}^{-1}$; Jiang et al. 1998). Similarly, Juggins (1992) used surface sediment diatom assemblages to infer mean half-tide salinity along the tidal Thames estuary (range $\sim 0.1\text{--}24 \text{ g}\cdot\text{L}^{-1}$) and found WA-PLS methods improved predictive power (ter Braak and Juggins 1993). The salinity model presented here compares well with these other studies, both in terms of model diagnostics ($r^2_{\text{jack}} = 0.887$, RMSEP = 0.246) and the salinity gradient covered. Coherence in the order of modelled salinity optima of major diatom taxa among these three data sets supports the contention that while these empirical models make great ecological

assumptions to simplify real-world complexity, the approach captures the strong underlying and ecologically meaningful response to salinity that studies on living diatom communities have shown.

Although it might be argued that inclusion of shallow fjord sites might weaken the model in terms of its application to wetland areas such as Vejlerne, especially as water body type was itself significant, validation is provided both internally (via jackknifing) and by independent comparison to known historical events (see below). Indeed, a model that includes freshwater and brackish lakes and shallow, marine fjord systems is necessary to provide the range of modern analogues for the variety of conditions that sites in the Vejlerne wetlands (and many other shallow, coastal margins) have experienced in the past. While important differences exist between lakes and fjords, the present study suggests an underlying coherence between these shallow, brackish–marine systems.

Recently, other biological groups have shown potential as quantitative salinity indicators. Morphological variations in several dinoflagellate cyst taxa have been related to changes in salinity (Ellegaard 2000), and a predictive model has been developed for the Baltic cyst *Gonyaulax baltica*, which experiments have shown grows longer cyst processes at lower salinity (Ellegaard et al. 2002). Stratigraphic variations in cyst morphology for three taxa (including *Gonyaulax baltica*) have been observed in fossil samples from a 5.5-m sedimentary sequence from the Limfjord, also taken from Bjørnsholm Bay, and two zones were dominated by cysts with aberrant (reduced) processes (Ellegaard 2000) but appeared to overestimate salinity (J.T. Christensen, M. Ellegaard, T. Cedhagen, and J. Hylleberg, unpublished data). As the diatom and historical evidence suggests (see below), salinity may not have been stable within zones, and sample-specific salinity estimates may provide more realistic estimates.

Diatom dissolution

Diatom dissolution is strongly correlated with (log) inferred salinity within the three Vejlerne cores ($r^2 = 0.33\text{--}0.74$, $p < 0.025$ in all cases) and for all core samples together ($r^2 = 0.56$, $n = 61$, $p < 0.001$), although this might be expected, as dissolution increases with salinity in the lake training set ($r^2 = 0.41$, $n = 27$, $p < 0.001$). Poor diatom preservation has been linked to periods of changing hydrography and salinity during Holocene sequences from the Baltic (e.g., during the Litorina – post-Litorina Sea stage; Andrén et al. 2000) and to increases in salinity (conductivity) in some lake records (e.g., Ryves et al. 2001). Decreasing diatom preservation with increasing salinity has also been observed in other diatom training sets (e.g., Reed 1998a; Ryves et al. 2002). Although experimental studies suggest silica dissolution rates increase with increasing NaCl concentration beyond the salinity of seawater (Barker et al. 1994), preservation differences between marine Limfjord and freshwater Vejlerne sedimentary units may owe much to differences in silica cycling between freshwater and marine systems. Silica dissolution in marine systems may be promoted by physico-chemical conditions of higher pH, greater turbulence, and water movement, and Si cycling may alter under eutrophication. Rates of bacterial degradation of organic coatings protecting diatom walls may differ, and more

effective bioturbation of upper sediments by marine macrofauna may enhance release of dissolved pore water silica back into the water column.

Dissolution does appear to be an important control on diatom concentration at both Han Vejle and Lund Fjord individually (see previous sections) and combined ($r^2 = 0.36$, $n = 39$, $p < 0.001$). Dissolution thus appears an important taphonomic process affecting the interpretation of diatom accumulation rates as a record of productivity, as has been found in estuarine systems elsewhere (DeMaster 1981, 2002). Differential dissolution of valves biases assemblages towards more robust forms (Ryves et al. 2001), and since many littoral brackish and marine forms are more heavily silicified than littoral freshwater taxa, or contain elements that are easily identifiable even when badly corroded, DI salinity may be overestimated in some assemblages. A dissolution index can thus be a guide to the reliability of qualitative and quantitative inferences made from fossil assemblages.

Recent environmental history of the Limfjord: pre-1880

Documentary and palaeoecological evidence has shown that salinity in the Limfjord has undergone major and dramatic shifts according to the opening or closing of the western end (and in Viking times, perhaps the northern margin) to the North Sea. Based on known salinity ranges of foraminifera, ostracods, molluscs, and other fauna and flora, major trends in salinity have been reconstructed from sediment cores in Bjørnsholm Bay, in the Limfjord south of Vejlerne, over the last 2000 years (Fig. 1; Kristensen et al. 1995) and before (J.T. Christensen, M. Ellegaard, T. Cedhagen, and J. Hylleberg, unpublished data). While these autecological approaches provide a basic framework of salinity and ecosystem-scale change within the Limfjord, the salinity estimates themselves are semiquantitative with wide uncertainty and may not be sensitive to short-term fluctuations. Temporal resolution is reduced by the need for large sample sizes, while the collection of several parallel cores brings with it problems of core correlation, macrofossil patchiness, and site-specific sedimentation rate. A documented low-salinity period, measured at $\sim 8 \text{ g}\cdot\text{L}^{-1}$ in 1811 by Mr. Jacobsen, a local chemist (Kristensen et al. 1995), began around 1220 and lasted until 1825, when the North Sea broke through the western end of the Limfjord during a storm, a connection that is artificially maintained today. Palaeoecological evidence suggests that the Limfjord has experienced near-marine conditions since then (Kristensen et al. 1995). Presently, salinity within the Limfjord varies from 23–26 $\text{g}\cdot\text{L}^{-1}$ in the central-east to 31 $\text{g}\cdot\text{L}^{-1}$ in the west (MOLTEN Project 2003).

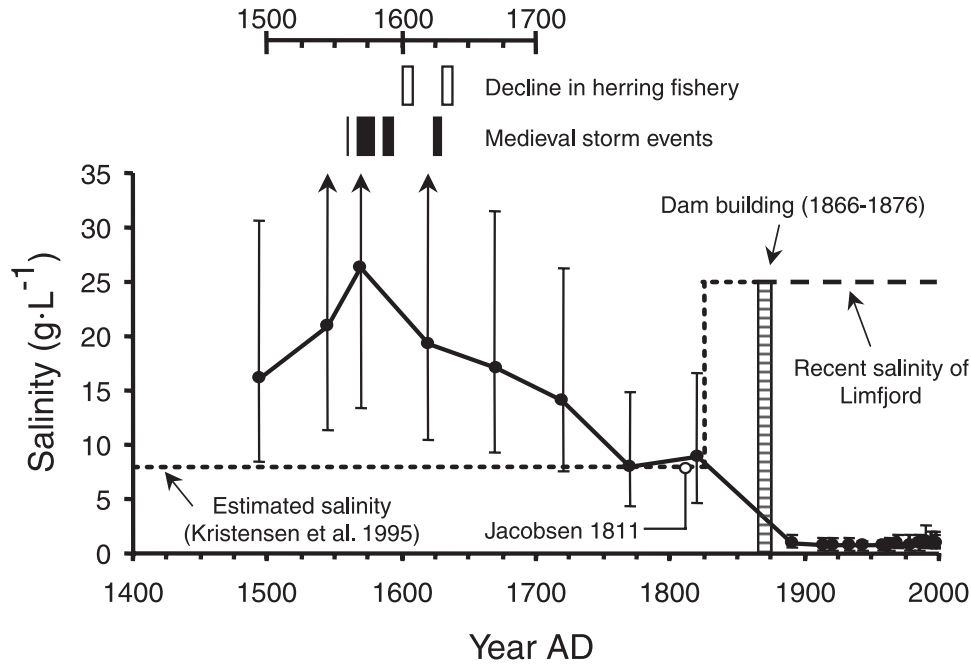
Salinity in the Limfjord is known to have varied within this brackish phase (circa 1220–1825). Severe storms caused marine breakthroughs in this period, which lasted for a decade or more, particularly in the late 16th and early 17th centuries (Kristensen et al. 1995), perhaps linked to the deterioration in climate of the Little Ice Age (Andr  n et al. 2000). While such major events have been preserved in the sedimentary macrofaunal record, shorter-term changes may leave little trace if there is insufficient time for a new faunal community to develop, especially if dependent on the availability of suitable habitat. Less complex organisms, such as algae and dinoflagellates, will generally respond rapidly,

particularly pelagic forms. Diatom stratigraphies can potentially provide sensitive palaeoenvironmental reconstructions at high temporal resolution to test such hypotheses.

Both diatom records that extend significantly into the Limfjord phase of Vejlerne (Glombak and Lund Fjord) show variations in diatom composition and inferred salinity. Diatom assemblages are dominated by littoral taxa indicative of shallow water, principally *Planorbulina mediterranensis* spp., *Amphora* spp., *Cocconeis* spp., *Cymatosira belgica*, *Delphineis* spp., *Opephora* spp., and benthic *Navicula* and *Fallacia* spp., with stratigraphic change more pronounced at Glombak leading to a distinct trend in DI salinity. *Paralia sulcata*, found in both records and common in coastal sediments across a range of salinity, is found in both plankton and benthic habitats (Zong 1997). While its ecology is poorly known, within the Vejlerne training set ($n = 20$ occurrences) it exhibited unimodal distributions with well-defined optima for depth (3.5 m), TP ($63 \mu\text{g}\cdot\text{L}^{-1}$), and salinity ($11.9 \text{ g}\cdot\text{L}^{-1}$), although both salinity and depth showed broad tolerances. While *Paralia sulcata* has been seen as an indicator of high productivity (especially when small cell sizes dominate; McQuoid and Nordberg 2003), in sediment cores from the southwestern Baltic, *Paralia sulcata* declines as *Cyclotella choctawhatcheeana* (indicating nutrient enrichment; see below) increases (Andr  n et al. 1999). Similarly, in cores from the mesohaline Chesapeake Bay along the eastern seaboard of the USA, *Paralia sulcata* is abundant prior to anthropogenic disturbance (Cooper 1995). McQuoid and Nordberg (2003) found that the relative abundance of *Paralia sulcata* among surface sediments from the Swedish west coast was positively correlated with degree of mixing of the water column and, contrary to expectation, negatively with nitrogen concentration (as both total N and NO_3). Within a similar salinity and depth regime, nutrient enrichment may favour other taxa that are better competitors at lower Si:P (or Si:N) ratios (cf. McQuoid and Nordberg 2003), while increased organic sedimentation may reduce the area of suitable sandy substrates. *Paralia sulcata* valves are generally robust and identifiable even when badly corroded, which may also favour its (over)representation in marine sediments.

Direct comparison of the stratigraphies within the marine period is hampered by a lack of dating, especially as the Lund Fjord record contains a hiatus before the 1940s of unknown duration. The lack of unsupported ^{210}Pb below the organic upper layer in these sites and from another nearby sequence from another lake within Vejlerne (Selbjerg S  ), however, implies that all these sections must predate circa 1880, approximately when Vejlerne was separated from the Limfjord. A dam was first built across the L  gst  r Bredning in 1866–1868, and pumping out of salt water from the enclosed area began soon after. Experimental grass planting began on land below what is now Lund Fjord in 1871, and by 1873, ~ 830 ha were under grass cover (Jakobsen and S  rensen 1998). In January 1874, the main dam failed during a storm, and salt water flooded the area. Vejlerne was abandoned for 2 years until a new dam was built in 1874–1876 and draining began again. Despite minor incursions of salt water later, for example in 1880, pumping allowed grass planting in the north (Lund Fjord) and eastern parts, although the results were poor. Finally soon after 1912, attempts to drain east Vejlerne were abandoned, after which

Fig. 7. Diatom-inferred salinity (solid line) for Glombak core, GLOM I, plotted against age (assuming a net sedimentation rate of $0.08 \text{ cm}\cdot\text{year}^{-1}$), with sample-specific errors based on 9999 permutations within weighted-average partial least squares (WA-PLS). Values above $35 \text{ g}\cdot\text{L}^{-1}$ are shown as up arrows. Also shown are documented periods when the western barrier to the North Sea was open in the 16th–17th centuries following storms (solid bars) and periods when the Limfjord herring fishery was in decline (open bars; from Holm and Bager 2002). Estimated salinity fluctuations of the inner Limfjord based on macrofossil evidence (Kristensen et al. 1995) are shown (dotted line), as well as the period of dam construction across the Løgstør Bredning, which created the east Vejlerne wetland. A historical salinity measurement made in 1811 in the inner Limfjord is also plotted (cited in Kristensen et al. 1995).



water levels rose throughout the area. Further disruption occurred when a railway line was built across the southern part of Lund Fjord in 1906, which permanently separated Han Vejle from Lund Fjord (Hald-Mortensen 1998). These historical events may explain why the Lund Fjord and Han Vejle sediment records are disturbed and may both contain hiatuses from before the dam building until well into the 20th century. In contrast, maps from 1883 and throughout the 20th century show that both Glombak and Selbjerg have existed as lakes since the earliest dams were built (Hald-Mortensen 1998; Jakobsen and Sørensen 1998). It is likely that sediment has accumulated more or less continuously at these sites since separation from the Limfjord in the late 19th century, as ^{210}Pb data suggest.

Independent dating controls (e.g., ^{14}C) on the marine sections in Lund Fjord and Glombak cores are not available. A ~2-m sediment sequence, collected further south within the Limfjord at Bjørnsholm Bay from a depth of 10 m, was dated by ^{14}C analyses on foraminifera and molluscs using a constant 400-year reservoir (Kristensen et al. 1995). A linear age–depth model fitted 10 of the 16 dates (within errors), with average net sedimentation rates of $\sim 0.08 \text{ cm}\cdot\text{year}^{-1}$ throughout the last 2500 years. Using this figure for the Vejlerne cores suggests that the marine section in GLOM I spans ~375 years (30 cm) and LUND I, ~925 years (74 cm). Given the likelihood of extensive stratigraphic disturbance at Lund Fjord and observed poor sample preservation at several levels, it seems unwise to attempt to match the DI salinity in LUND I with that of Kristensen et al. (1995). This comparison may be justified at Glombak, however, if it is accepted

that sedimentation has been continuous throughout the sequence (see above). We show DI salinity at Glombak over the last 500 years compared with that in the Limfjord estimated by Kristensen et al. (1995), assuming a net sedimentation rate of $0.08 \text{ cm}\cdot\text{year}^{-1}$ below 52.5 cm in GLOM I (Fig. 7, ~AD 1870 from ^{210}Pb data).

Kristensen et al. (1995) used biostratigraphical zones (based on foraminifera, ostracods, molluscs, and other aquatic macrofossils) to define high and low salinity phases in the last 2500 years, with salinity estimated semiquantitatively using autecological information from several species. Although they noted biological assemblages vary within these zones, monotonic salinity estimates were applied within zones. From 1220 until 1825, they inferred generally low salinity (brackish) conditions of around $8 \text{ g}\cdot\text{L}^{-1}$ (Kristensen et al. 1995). Several storms are known to have breached the opening to the North Sea in the west of the Limfjord during this period, however, especially during the mediaeval period, with four separate events from 1560 to 1624, lasting up to 12–14 years (Kristensen et al. 1995), coinciding with the level at which the large pebble was found (72 cm, ~1620). While macrofossil assemblages at these times imply higher salinity excursions (Kristensen et al. 1995; J.T. Christensen, M. Ellegaard, T. Cedhagen, and J. Hylleberg, unpublished data), the DI salinity profile suggests that since the storm breakthroughs of the 16th century, the Limfjord might only have been $<10 \text{ g}\cdot\text{L}^{-1}$ for short periods (Fig. 7).

Rather than being a stable, brackish period in the Limfjord, this phase may have been characterized by wide fluctuations in salinity, with aperiodic marine incursions having major

ecological impacts. The Limfjord has supported a herring fishery as early as 1200 (Holm and Bager 2002), relying on the lower salinity waters as a feeding ground before spawning in the higher salinity Kattegat. Historical records from the Limfjord brackish herring fishery from the 16th to early 19th century seem to reflect large, long-term fluctuations in herring stocks rather than changes in economic conditions (Holm and Bager 2002). The herring fishery was depressed in the early 1600s (perhaps in response to the series of breakthroughs in the late 1500s), peaked from 1610 to 1620, and was poor when records continued in 1630, when the westerly opening to the North Sea closed, but thereafter improved. Similarly, the fishery collapsed within a decade of the 1825 breach and did not recover. The DI salinity profile agrees with the known storm history of the Limfjord, the trends in the herring fishery in the late 16th to 17th century, and the measured salinity in 1811, giving confidence in the salinity model and the dating assumptions used in this section of the core (Fig. 7).

Plant and animal macrofossil analyses of a replicate but undated core to GLOM I show a similar trend in increasing salinity below the marine–freshwater transition (Jeppesen et al. 2002). The lowermost sediments contain a near-marine assemblage, including the foraminifer *Ammonia beccarii*, the mussel *Mytilus edulis*, and the marine polychaete *Nereis* sp. This is replaced by a brackish assemblage, including eelgrass (*Zostera* sp.), charophyte algae (*Tolypella* sp.), horned pondweed (*Zannichellia major*), and fennel-leaf pondweed (*Potamogeton pectinatus*), together suggesting a salinity of 12–15 g·L⁻¹ (Jeppesen et al. 2002), close to that estimated by the diatom model below the freshwater transition (Fig. 7).

In GLOM I, no samples were analysed in the period between 1825, when present-day salinity (~26 g·L⁻¹) was established, and before the dam building was completed in 1876, when Glombak developed as a freshwater–subsaline lake. It is perhaps possible that the extreme (and overestimated) salinity (45 g·L⁻¹) inferred at Lund Fjord at 10.5 cm represents this high salinity period from 1825 to 1876 (Fig. 7), but given the very poor sample preservation ($F = 0.08$) and uncertain sedimentation at this site, this remains speculative.

Development of the east Vejlerne wetland and Limfjord: post-1880

Postdamming development of the east Vejlerne area followed that of many shallow Danish freshwater lakes in the 20th century, dominated by periphytic *Fragilaria* sensu lato (e.g., *Pseudostaurosira brevistriata*, *Staurosirella pinnata*) typical of mesotrophic conditions (10–100 µg·L⁻¹ TP; Bradshaw et al. 2002). Forms found in slightly elevated salinities are more common (e.g., *Fragilaria sopotensis*/*Staurosira punctiformis* agg. and *Staurosira elliptica* agg.), and rare mesohaline (e.g., *Cocconeis neothumensis*, *Opephora* spp., or *Planothidium delicatulum* spp.) or polyhaline taxa (e.g., *Navicula cryptotenella* in Han Vejle) attest to continuing saline influences, from direct connection to the Limfjord, storms in the North Sea to the north, or salts leaching out from the marine sediments underlying Vejlerne. Throughout the preserved freshwater record, zooplankton and macrofossil evidence show that Han Vejle has been clear and macrophyte-dominated since at least the 1940s, while Glombak is comparatively macrophyte-poor and more

turbid, reflecting a higher TP and salinity (Amsinck et al. 2003). Freshwater Lund Fjord, with a much larger agricultural catchment, is a turbid system with higher levels of TP (~154 µg·L⁻¹) and TN and the lowest macrophyte coverage (Jeppesen et al. 2002). Despite these divergent functional pathways in the 20th century, diatom assemblages seem to reflect local hydrology and perhaps nutrient conditions rather than macrophyte development directly, although the greater importance of littoral–benthic taxa to planktonic taxa in Han Vejle may reflect its lower turbidity.

Changes in the influence of the Limfjord on east Vejlerne are most clearly reflected in the diatom record from Glombak, nearest the Limfjord and directly connected via a drainage canal. At around 22 cm (~1963), there is a marked increase in the mesohaline planktonic *Cyclotella choctawhatcheeana*, coincident with the oligohaline periphytic *Achnanthes fagedii*. *Cyclotella choctawhatcheeana* is common in coastal waters in the Baltic (Snoeijs 1993) and in Chesapeake Bay (as *Cyclotella* cf. *Caspia*, *Cyclotella* cf. *caspia*, Cooper 1995). It has been found to dominate sediment records in the southwestern and central Baltic since the early 20th century (Andrén et al. 1999, 2000), although in Roskilde Fjord it was important in sediments dating pre-1860 (Clarke et al. 2003) and is found sporadically in the marine sections of both Glombak and Lund Fjord cores. In Baltic records *Cyclotella choctawhatcheeana* is linked to increasing nutrient concentrations (Andrén et al. 1999, 2000), while in Chesapeake Bay sediments, it is thought to be an indicator of human disturbance (Cooper 1995). Within the present training set, *Cyclotella choctawhatcheeana* seems to be an indicator of high TP rather than TN (TP optimum 150 µg TP·L⁻¹, $n = 22$). This is in contrast to its distribution within a larger Baltic–Netherlands surface sediment data set, however, where *Cyclotella choctawhatcheeana* shows its highest abundance in Swedish and Finnish data sets, with relatively low TP and TN optima in both (MOLTEN Project 2003).

The timing of the major appearance of this taxon in the Glombak record agrees with the construction of a new central sluice controlling water outflow from east Vejlerne to the Limfjord, built from 1963 to 1965. This resulted in a 10–15 cm lowering of water level and an increased risk of intrusion of saline Limfjord water (Hald-Mortensen 1998). *Cyclotella choctawhatcheeana* is found in surface sediments from the Limfjord, Mariager Fjord, and other Danish fjords (Clarke 2001; MOLTEN Project 2003). If the dating of the Glombak Limfjord sequence is accepted (Fig. 7), the major increase must postdate 1825, as seen elsewhere in the Baltic (Andrén et al. 1999, 2000). In the Limfjord, its rise is likely to be linked to increasing anthropogenic coastal eutrophication rather than salinity changes, as it has a broad salinity tolerance from subsaline to almost marine conditions, with an optimum of 9.7 g·L⁻¹ (this study; MOLTEN Project 2003). A diatom-inferred TN record from Roskilde Fjord on Zealand, Denmark, shows that TN concentrations began to rise ~1900 and accelerated in the postwar period coincident with major increases in the use of artificial fertilizers (Clarke et al. 2003).

Diatom analysis may be a more effective tool for reconstructing salinity in rapidly changing environments, as diatoms respond quickly to changes in salinity, whereas higher organisms need time to establish populations seeded from elsewhere and may be more dependent on habitat constraints.

Oysters (*Ostrea edulis*), for example, were not recorded in the Limfjord until 1849, some 24 years after high salinity conditions returned (Bailey and Milner, in press). Furthermore, as smaller sediment samples are needed, stratigraphic profiles can be analysed at high temporal resolution, and salinity for each assemblage can be quantitatively reconstructed, with sample-specific error estimates. Diatom-salinity models may be very useful tools in studies of coastal and estuarine areas where knowledge of past salinity regimes can test hypotheses about aquatic ecosystem development (Holm and Bager 2002; MacKenzie et al. 2002) and can shed light on cultural, hydrographic, and climatic transitions affecting aquatic resources.

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