

# Multi-indicator conductivity transfer functions for Quaternary palaeoclimate reconstruction

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## Abstract

Diatoms (Bacillariophyceae; single-celled algae) and ostracods (Ostracoda; shelled microcrustacea) are known for their sensitivity to salinity. In palaeolimnology, the potential has yet to be tested for quantifying past salinity, lake level, and by inference, climate change, by application of multiple-indicator transfer functions. We used weighted averaging techniques to derive diatom ( $n = 91$ ;  $r^2 = 0.92$ ) and ostracod ( $n = 53$ ;  $r^2 = 0.83$ ) conductivity transfer functions from modern diatom, ostracod and water chemistry data collected in lakes of central, western and northern Turkey. Diatoms were better represented across the full gradient than ostracods, at intermediate levels of conductivity in particular, but both transfer functions were statistically robust. Because transfer functions are not infallible, we further tested the strength and simplicity of salinity response and the potential for identifying characteristic associations of diatom and ostracod taxa in different parts of the salinity gradient, to improve palaeoclimate reconstruction. We identified a subset of 51 samples that contained both diatoms and ostracods, collected at the same time from the same habitat. We used Two-Way Indicator Species Analysis of a combined diatom-ostracod data set, transformed to achieve numerical equivalence, to explore distributions in more detail. A clear ecological threshold was apparent at  $\sim 3 \text{ g l}^{-1}$  salinity, rather than at  $5 \text{ g l}^{-1}$ , the boundary used by some workers, equating to the oligosaline-mesosaline boundary. Other salinity boundaries were poorly defined, indicating lack of a simple, well-defined salinity response. We did, however, define characteristic associations of taxa, to facilitate the distinction to be drawn between a hydrologically open, fresh lake and an oligosaline lake, in palaeoenvironmental reconstruction. Over the rest of the salinity gradient, we highlighted the potential for the multi-proxy approach to strengthen ostracod-based reconstruction in particular, to overcome the problem of broad apparent tolerance ranges in common halophilic taxa such as *Limnocythere inopinata*, which often dominate in low-diversity fossil assemblages. The combination of multi-proxy quantitative reconstruction, complemented by qualitative understanding of ecological responses generated by the analysis, remains a powerful tool in Quaternary palaeoclimate research.

## Keywords

Transfer functions  
Diatoms  
Ostracoda  
Conductivity  
Saline lakes  
Turkey

## Introduction

Palaeolimnological proxy data for past changes in salinity and lake level have been instrumental in reconstructing Quaternary climate change from analysis of hydrologically-closed, saline lake sediment sequences (Fritz et al. 2010). Of the various biological proxies for salinity, diatoms (Bacillariophyceae; siliceous algae) and ostracods (Ostracoda; shelled microcrustacea) are sensitive and can be powerful in combination. Differential preservation may allow a focus on one or the other at different stages in a lake's history (Reed et al. 2001). Alternately, where remains of both are preserved, the multi-proxy approach can strengthen inferences of past environmental change. Nevertheless, multi-proxy diatom-ostracod reconstruction has been achieved in surprisingly few saline-lake palaeoclimate studies (Whitmore et al. 1996; Porter et al. 1999; Reed et al. 2001; Markgraf et al. 2003; Hoelzmann et al. 2010).

Palaeoecological reconstruction relies on an understanding of modern ecology for interpretation of proxy data. The weighted averaging transfer function technique is a well-regarded approach for quantifying past changes from species-rich palaeolimnological data. Diatoms have been at the forefront of research, and salinity or conductivity transfer functions have been developed for many saline-lake regions (Fritz et al. 2010). The ostracod-salinity transfer function was developed relatively recently, having been derived by Mezquita et al. (2005) for the Iberian Peninsula and Mischke et al. (2007, 2010) for Tibet and Israel. Multiple-indicator transfer functions, such as that proposed by Lotter et al. (1997) for Alpine lakes, offer the potential to strengthen multi-proxy reconstructions, but specialists still tend not to work collaboratively.

The transfer function technique is not infallible, and the reliability of reconstructions may be affected by a variety of factors such as a poor match between biota and water chemistry at the time of sampling, taxonomic uncertainty, lack of a good modern analogue or a bias in modern and/or fossil assemblages through taphonomic effects. More fundamentally, there remains a debate as to whether salinity *per se* dictates the presence or absence of biota, through physiological stress, or whether associated factors such as brine composition (Herbst 2001) or habitat restructuring with lake-level change (Verschuren et al. 2000) also play a part, particularly at intermediate levels of salinity (Williams et al. 1990). Telford and Birks (2011) highlight the potential for large statistical error in reconstructions. Estimated diatom salinity and conductivity optima show greater inter-regional coherency than do nutrient optima derived from more complex, eutrophic systems (Reed 2007), supporting the apparent importance of salinity in determining diatom distribution.

Palaeolimnological research in Turkey has provided regionally coherent diatom-based evidence for Quaternary climate change (Roberts and Reed 2009). Ostracods are also preserved in many of these sequences, but to date the only combined diatom-ostracod study is of recent human impact (Reed et al. 2008). Quantitative modern diatom studies include a diatom-salinity transfer function for 23 rivers and lakes of central Turkey (Kashima 1996) and one for 10 sites in central Turkey (Akbulut and Dügel 2008). Numerous small-scale ostracod ecological studies have been completed, such as Altınışlı and Griffiths (2001) and Külköylüoğlu (2004). Quantitative ostracod analysis is limited to northern Turkish lakes (Sarı and Külköylüoğlu 2010). Species-environment relationships have yet to be quantified at a regional scale, although a 38-site transfer function has been derived for neighbouring Israel (Mischke et al. 2010).

This study was undertaken to develop conductivity transfer functions for diatoms and ostracods from Turkish lake training sets. Related to the debate over salinity response and with the objective of strengthening palaeoclimate reconstructions, we also tested the strength and simplicity of biotic salinity response to establish whether characteristic associations of diatoms and ostracods may be defined for different parts of the salinity gradient.

## The study region

The study focused on lakes of western, central and northern Turkey (Table 1, Fig. 1). Turkish lakes are distributed widely across Mediterranean and continental climatic zones with temperate or cold winters and long, hot, dry summers. According to Unal et al. (2003), they occur in five out of seven climate zones (Fig. 1), being absent along the wetter Black Sea coastal zone and in the arid coastal strip around Adana, where lagoons are the only lakes. Within the five zones, minimum temperature varies from  $-6.6^{\circ}\text{C}$  (Eastern Anatolia) to  $4.2^{\circ}\text{C}$  (Southern Anatolia) and maximum temperature from  $24.4^{\circ}\text{C}$  (Central Anatolia) to  $27.6^{\circ}\text{C}$  (Aegean-Western Mediterranean). Mean annual precipitation varies from 417.5 mm (Eastern Anatolia) to 686.2 mm (Marmara).

Table 1

List of sampling sites referred to in Fig. 1. Site names are lakes ('Göl, Gölü') unless otherwise specified, citing latitude (Lat.) and longitude (Long.)

Site Code	Name	Lat.	Long.	Site Code	Name	Lat.	Long.
1	KUS Kuş [Manyas]	40° 13"	28° 03" 31	MEK Meke		37° 41"	33° 37"
2	ULU Uluabat [Apolyont]	40° 10"	28° 41" 32	ACM Acı Krater		37° 43"	33° 38"
3	IZN İznik	40° 29"	29° 34" 33	AGL Adabağ marsh		37° 31"	33° 46"
4	MAM Marmara	38° 36"	27° 59" 34	AKG Akgöl Düden, Ereğli		37° 31"	33° 46"
5	AZA Azap	37° 35"	27° 26" 35	NAR Nar		38° 22"	34° 27"
6	BAF Bafa	37° 29"	27° 29" 36	SUL Sultan Sazlığı marsh		38° 18"	35° 18"
7	KOY Köyceğiz	36° 57"	28° 42" 37	YAY Yay		38° 22"	35° 18"
8	PAT Patara lagoon	36° 14"	29° 22" 38	YAN Yanvanlı		38° 41"	35° 17"
9	YAZ Yazır	37° 00"	29° 44" 39	ESM Esmekaya Reserv.		38° 19"	33° 48"
10	GLH Gölhisar	37° 08"	29° 36" 40	ACI Acıgöl, Gölyazı		38° 33"	33° 12"
11	AYD Aydoğdu Reservoir	37° 28"	29° 07" 41	BOL Bolluk		38° 32"	32° 56"
12	KAR Karataş	37° 23"	29° 58" 42	KDU Küçük, Kulu		39° 07"	33° 09"
13	SAL Salda	37° 33"	29° 42" 43	DUD Düden, Kulu		39° 07"	33° 09"
14	BAY Akgöl, Yeşilova	37° 42"	29° 46" 44	CEL Çeltek		39° 18"	32° 53"
15	ACG Acıgöl, Denizli	37° 51"	29° 52" 45	GOK Üyüz		39° 19"	32° 55"
16	SOG Soğanlı marsh	37° 38"	30° 03" 46	SEY Seyfe		39° 13"	34° 25°
17	ISK Işıklı [Civril] Reservoir	38° 14"	29° 55" 47	DIP Dipsiz		40° 36"	33° 48"
18	BUR Burdur	37° 45"	30° 10" 48	BAK Bakkal		40° 35"	33° 42"
19	GLC Gölcük, Isparta	37° 44"	30° 29" 49	COL Cöl, Bolu		40° 34"	33° 44"
20	YAR Yarışlı	37° 35"	29° 59" 50	PAZ Pazar Reservoir		40° 20"	32° 47"
21	KRM Karamikbataklığı lake	38° 26"	30° 51" 51	SUK Sülüklü		38° 25"	32° 10"
22	KRD Karamikbataklığı düden	38° 26"	30° 51" 52	BGR Unnamed, Gerece		40° 46"	32° 04"
23	EGR Eğirdir	38° 00"	30° 53" 53	KEC Keçigöl		40° 50"	32° 28"
24	KOV Kovada artificial lake	37° 38"	30° 53" 54	YEN Yenicağa		40° 46"	32° 02"
25	BEY Beyşehir	37° 40"	31° 28" 55	GCK Gölcük, Bolu		40° 34"	31° 09"
26	EBE Eber	38° 38"	31° 10" 56	ABA Abant		40° 37"	31° 16"
27	AKS Akşehir	38° 32"	31° 26" 57	SIV Siviş		40° 34"	33° 45"
28	OBK Obruk	37° 31"	32° 44" 58	TDE Torundede		37° 17"	32° 23"
29	SMH Süleymanhacı	37° 30"	33° 04" 59	TZL Tuzla, Kayseri		39° 02"	35° 50"
30	PIN Pınarbaşı spring	37° 27"	33° 07"				

Fig. 1

In a region of active compressional tectonism, many basins are of tectonic origin (Warren 2006), and display diverse morphometries. The surface area of ephemeral playa lakes varies from <1 km<sup>2</sup> to large, infilled grabens such as Acıgöl, Denizli (no. 15 on Fig. 1; maximum depth <2 m, current lake area ~60 km<sup>2</sup>; Mutlu et al. 1999). Many lakes are clustered in south-central Turkey. Those in the east, on the Anatolian plateau, form shallow vestiges of large Pleistocene Lake Konya (Roberts et al. 1999). To the west, there are several deep, saline grabens such as Lake Burdur (no. 18; maximum depth ~100 m; Girgin et al. 2004) or Lake Salda (no. 13; 184 m; Warren 2006). Fault-bounded lakes also occur on the western Turkish coastline (e.g. İznik; no. 3; Franz et al. 2006), and in the North Anatolian fault region (Bolu-Cankiri district). In regions of karst and evaporite formation, such as the Akgöl (Adabağ; nos. 33–34) and Karamikbataklığı (nos. 21–22) marshes of southern-central Turkey, small perennial springs and sinkholes (düdens) are common. Lake water chemistry is often influenced by groundwater input. Lake Salda, for example, is enriched in Mg, due in part to evaporative concentration, but also to seepage through Mg-rich substrates (Warren, 2006). Volcanic lakes such as Nar Gölü (no. 35) and Gölcük, Isparta (no. 19), also occur (Roberts and Reed 2009).

## Materials and methods

### Field and laboratory techniques

The training sets were derived from samples from 59 lakes (Table 1; Fig. 1) that span a salinity gradient from fresh to hypersaline (Table 2). Samples were collected in summer (July–September, 1996, 1999, 2000), spring 1997 (April, under ice) and December 2000 (one sample). Where feasible, samples were collected both from the centre and edge(s) of lakes. To achieve equivalence between diatom and ostracod samples, and to maximise the equivalence between modern and fossil assemblages for reconstruction, sediment samples were used in preference to a hand net, a common technique for collecting ostracods (Griffiths and Holmes 2000). At the lake centre and in littoral zones with soft mud, a 5.5-cm-diameter Glew gravity corer (Glew 1991) was used to collect undisturbed surface sediment samples. The tube was pushed in manually in shallow waters. Cores were extruded in the field. The top 0.5 cm was used for diatom analysis and, where feasible, three 3-cm core-top samples were taken to provide enough material for ostracod analysis. In the sandy littoral zone, surface scrapes for diatoms and hand-collected surface sediment samples of ~3 cm depth and 400–500 ml volume for ostracods were collected. In rocky shorelines, diatom epilithon scrapes or epiphyton samples from submerged plants were collected. No ostracods were collected in this habitat. If coring at the lake centre was impossible because of wind, rooted macrophyte cover, or sand substrate, collected samples were comprised of diatom epiphyton or plankton alone.

Table 2

Summary physico-chemical characteristics of the training set samples

Code(S)	Date	TUR	Water depth	pH	COND	[Na]	[K]	[Mg]	[Ca]	[Cl]	[SO <sub>4</sub> ]	[Carb]	Anion ratio	Cat. ratio
ABA00C(E)	22/07/00	2	13.5 (4.0)	7.8	205	0.1	0.02	0.3	2.2	0.0	0.0	2.6	42.53	0.03
ACG97C	11/04/97	1	0.15	8.1	77,600	1,204.5	22.10	206.1	24.3	874.2	561.6	191.7	0.13	5.33
ACI96C	12/08/96	1	0.05	8.4	32,200	318.1	21.41	419.6	7.2	315.8	457.6	250.8	0.32	0.80
ACM96E	19/08/96	1	0.6	8.3	77,200	744.7	10.17	285.3	12.1	987.0	166.4	327.9	0.28	2.54
ACM99C	30/08/99	1	68.0	7.7	80,500	744.7	10.17	285.3	12.1	987.0	166.4	327.9	0.28	2.54
AGL97C	07/04/97	1	0.5	7.8	7,700	50.9	1.87	26.5	9.3	45.4	47.8	32.1	0.34	1.48
AKG96C	17/08/96	1	4.3	10.1	3,100	20.1	0.86	11.6	0.7	15.5	3.3	8.4	0.44	1.72
AKG97C	07/04/97	1	4.2	8.5	1,890	13.6	0.61	8.3	1.1	10.7	6.7	8.4	0.48	1.50
AKS00E	24/07/00	3	0.1	9.0	9,080	85.6	4.77	33.1	0.3	65.4	54.1	6.0	0.05	2.71
AKS96C	25/08/96	3	1.0	8.7	6,500	60.3	3.46	28.0	0.7	33.3	37.4	13.1	0.19	2.22
AKS96E	26/08/96	3	0.05	8.9	7,800	60.3	3.46	28.0	0.7	33.3	37.4	13.1	0.19	2.22
AYD99E	09/09/99	2	0.5	7.7	265									
AZA00E	14/09/00	2	0.7	8.9	1,058	4.9	0.53	5.4	2.1	6.0	0.0	6.9	1.14	0.71
BAF00C(E)	10/09/00	3	17.0 (1.0)	8.6	18,600	180.1	4.32	44.8	12.8	275.2	28.3	319.7	1.05	3.20

Code(S)	Date	TU R	Water r depth	pH	COND	[Na]	[K]	[Mg]	[Ca ]	[Cl]	[SO4 ]	[Carb ]	Anio n ratio	Cat. ratio
<b>BAK00E</b>	20/07/00	3	0.1	8.4	25,600	109.2	1.18	411. 3	27.0	59.2	509.6	50.0	0.09	0.25
BAK99C	17/09/99	3	2.5	8.4	25,600	109.2	1.18	411. 3	27.0	59.2	509.6	50.0	0.09	0.25
<b>BAY97C</b>	11/04/97	1	0.04	9.2	620	1.7	0.18	12.2	0.1	2.1	1.4	11.0	3.19	0.15
<b>BEY00E</b>	27/07/00	3	0.4	8.7	278	0.4	0.04	2.3	1.3	0.2	0.6	3.2	3.97	0.12
BEY96C	20/08/96	3	2.5	8.4	380	2.4	0.03	3.5	1.2	0.2	2.2	3.7	1.55	0.53
<b>BEY99C</b>	02/09/99	3	5.8	8.4	385	2.4	0.03	3.5	1.2	0.2	2.2	3.7	1.55	0.53
<b>BGR00C(E)</b>	23/07/00	3	5.0 (0.1)	7.9	754	2.4	0.07	1.5	4.7	3.2	0.1	5.3	1.61	0.39
BOL96C	11/08/96	1	0.3	7.3	125,000									
<b>BUR96E</b>	21/08/96	2	7.5	8.7	30,400	300.5	1.60	119. 7	2.9	186.1	239.2	65.6	0.15	2.46
BUR99E	04/09/99	2	0.2	8.9	28,000	299.4	1.92	119. 0	3.0	214.3	249.6	65.6	0.14	2.47
<b>CEL97C</b>	05/04/97	3	0.1	8.2	1,110	14.6	0.13	3.1	1.1	5.0	1.9	2.0	0.29	3.44
<b>COL00E</b>	20/07/00	3	0.3	7.7	4,550	8.0	0.19	56.2	28.5	2.8	88.4	6.0	0.07	0.10
<b>COL99C</b>	17/09/99	3	6.8	7.9	8,000	14.2	0.40	91.0	27.2	3.9	145.6	2.0	0.01	0.12
DIP00E	20/07/00	3	0.2	7.4	4,000	14.4	0.23	45.4	31.6	14.5	74.4	6.0	0.07	0.19
DUD96E	09/08/96	2	0.2	9.5	30,400									
<b>DUD97E</b>	05/04/97	2	0.3	8.7	47,200	285.4	0.46	12.3	0.3	186.1	72.8	39.6	0.15	22.6 3
EBE00E	25/07/00	2	0.7	9.6	1,700	13.4	1.42	3.8	0.9	8.6	1.7	9.2	0.90	3.19
<b>EBE97E</b>	10/04/97	1	0.4	7.3	1,160	8.0	0.49	5.4	6.4	4.2	5.5	10.0	1.03	0.71
<b>EGR96C</b>	21/08/96	1	6.2	8.3	490	0.5	0.07	3.1	1.3	0.3	0.4	3.1	4.48	0.14
<b>ESM96C</b>	12/08/96	1	0.7	9.5	1,450	8.7	0.20	8.8	1.0	9.0	4.2	5.9	0.44	0.91
GCK00E	22/07/00	2	0.3	8.5	142	0.2	0.07	0.2	1.1	0.1	0.0	1.5	10.71	0.21
GLC96E	21/08/96	1	0.5	8.0	250	0.6	0.18	0.5	1.5	0.1	0.4	2.0	4.32	0.37
<b>GLC99C</b>	03/09/99	1	23.0	8.0	253	0.6	0.32	0.2	1.6	0.2	0.5	2.0	2.81	0.50
GLC99E/E2	03/09/99	1	0.5	8.1	251	0.6	0.32	0.2	1.6	0.2	0.5	2.0	2.81	0.50
<b>GLH96C</b>	22/08/96	2	2.0	8.3	920	1.3	0.09	8.6	1.7	0.8	1.7	7.0	2.82	0.13

Code(S)	Date	TUR	Water r depth	pH	COND	[Na]	[K]	[Mg]	[Ca ]	[Cl]	[SO4 ]	[Carb ]	Anio n ratio	Cat. ratio
GLH99E	05/09/99	2	2.3 (1.0)	8.1	800	0.7	0.09	7.5	1.7	0.6	0.3	9.1	9.67	0.09
GOK96E	10/08/96	1	0.5	9.9	3,100	30.7	0.05	8.8	0.4	4.8	3.1	21.8	2.75	3.34
ISK00E	25/07/00	1	0.1	9.7	231	0.6	0.40	1.6	0.6	0.3	0.0	2.8	8.09	0.48
IZN00C(E)	08/09/00	2	8.0 (2.0)	9.0	923	5.2	0.30	6.3	0.3	4.2	0.0	7.8	1.83	0.84
KAR00E, E2	26/07/00	3	0.8	8.6	579	1.8	0.19	4.7	1.3	0.5	0.6	6.9	6.46	0.32
KAR96C	22/08/96	3	0.7	8.7	790	3.5	0.12	6.1	1.2	0.8	1.6	5.9	2.44	0.49
KDU99E	22/08/99	2	0.1	9.4	20,000									
KEC00C(E,E2)	21/07/00	1	6.0 (0.1)	8.3	480	1.1	0.10	2.6	2.2	0.6	0.7	4.7	3.63	0.26
KOV00E	27/07/00	2	0.3	9.8	248	0.5	0.04	2.2	0.6	0.1	0.1	3.1	15.69	0.18
KOY00C	16/09/00	2	4.0	8.5	6,290	48.4	1.16	15.4	3.4	83.5	7.5	2.0	0.02	2.64
KOY96E	23/08/96	2	0.5	8.6	2,900									
KOY99E	08/09/99	2	4.5	8.4	3,700									
KRD97E	10/04/97	1	0.2	8.6	1,150	11.8	0.64	5.6	3.4	4.1	4.4	6.4	0.76	1.36
KRM00E	25/07/00	2	0.1	8.5	1,500	8.9	0.64	4.8	1.7	7.7	2.2	6.2	0.63	1.48
KRM97C	10/04/97	1	0.4	7.9	1,280	7.3	0.28	5.3	2.8	5.6	3.5	5.9	0.64	0.93
KRM99E	10/09/99	1	0.5	8.6	594									
KUS00C	09/09/00	3	1.2	9.2	323	1.4	0.33	0.7	1.7	1.6	0.6	1.9	0.83	0.72
MAM00C(E)	10/09/00	2	2.5 (0.1)	8.0	490	2.4	0.22	2.9	2.1	1.5	1.3	4.8	1.76	0.52
MEK96E	19/08/96	1	1.7	8.0	66,800	928.3	14.5 3	316. 6	50.5	992.6	395.2	18.7	0.01	2.57
MEK99C(E)	30/08/99	1	20.0 (0.2)	7.8	115,600	928.3	14.5 3	316. 6	50.5	992.6	395.2	18.7	0.01	2.57
NAR97E	16/09/97	1	0.3	7.1	3,500	6.7	1.48	3.8	2.0	22.3	3.7	15.7	0.60	1.41
NAR99C	28/08/99	1	21.0	7.1	2,500	16.5	3.70	8.5	3.0	27.4	3.2	10.0	0.33	1.76
OBK96E	04/09/96	1	0.5	7.7	610	0.7	0.07	2.1	4.2	0.4	1.1	4.5	2.97	0.13
PAT96E	24/08/96	2	0.04	8.2	15,300	126.6	2.93	41.4	12.4	155.1	29.1	7.8	0.04	2.41
PAZ99C(E)	18/09/99	3	3.0 (0.1)	6.2	177	0.2	0.24	0.2	0.8	0.1	0.0	1.4	17.59	0.50

Code(S)	Date	TUR	Water depth	pH	COND	[Na]	[K]	[Mg]	[Ca]	[Cl]	[SO <sub>4</sub> ]	[Carb]	Anion ratio	Cat. ratio
PIN97C	06/04/97	1	0.3	8.1	800	1.5	0.26	4.3	4.1	1.7	4.6	5.9	0.93	0.21
SAL96E	22/08/96	1	0.5	8.8	2,900	9.0	0.68	26.4	0.2	6.6	0.0	18.7	2.81	0.36
SEY96C	13/08/96	3	0.6	8.3	43,500	1,058.4	14.64	294.6	55.58	1,161.8	374.4	61.3	0.04	3.06
SIV00E	20/07/00	3	0.5	8.4	6,860	25.4	0.61	97.8	28.1	13.0	141.4	1.0	0.01	0.21
SMH96C	19/08/96	1	0.5	8.1	53,800	353.5	50.63	250.6	1.8	406.1	374.4	146.6	0.19	1.60
SMH97E	06/04/97	1	0.2	7.7	50,100	416.2	58.91	298.1	1.7	327.1	426.4	93.8	0.12	1.59
SOG99C	04/09/99	1	0.3	8.4	3,800	21.1	0.38	10.5	0.9	13.7	8.2	10.9	0.50	1.89
SUK99C	20/09/99	3	0.6	7.0	550									
SUK99E	20/09/99	3	0.1	7.0	900									
SUL96C	15/08/96	2	2.5	7.8	1,850	10.9	0.01	7.0	3.7	4.0	3.1	5.4	0.75	1.02
TDE96C	27/08/96	1	1.8	9.3	1,370	6.5	1.58	6.7	2.0	2.5	6.4	4.9	0.55	0.92
ULU00C(E)	09/09/00	2	2.0 (1.0)	8.5	461	0.9	0.11	4.2	1.1	0.7	1.6	4.0	1.74	0.18
YAN97C	08/04/97	1	0.1	7.6	1,030	7.8	0.26	3.0	1.5	5.4	0.8	3.7	0.61	1.80
YAR97C	11/04/97	1	0.04	10.2	10,600	116.6	0.18	2.9	1.0	71.9	39.5	2.9	0.03	30.17
YAY96E	14/08/96	3	0.4	7.6	9,500	63.8	5.09	7.8	0.6	53.9	18.7	8.4	0.12	8.25
YAZ96E	22/08/96	3	0.02		670									
YEN00C(E)	24/07/00	3	3.5	8.2	394	0.6	0.10	1.3	3.2	0.6	0.0	4.5	6.71	0.16

Hypersaline Lake Tuzla, without diatoms or ostracods, is omitted. Site codes end in numerals for the year and C (centre) or E (edge); E2 = additional samples with distinct diatoms for inclusion in the transfer function. TUR = qualitative turbidity scale; 3 = high turbidity. Water depth is at the sampling site (m). COND = electrical conductivity ( $\mu\text{S cm}^{-1}$ ). Molar concentrations of major ions are meq the Anion ( $[\text{CO}_3] + \text{HCO}_3$ ]:Cl + SO<sub>4</sub>) and Cation ([Na] + [K]:[Mg] + [Ca]) ratios. Major ion chemistry data are used twice for some samples of similar conductivity, as shown. Gaps represent missing values. 51 paired diatom-ostracod samples are marked in *bold*

Electrical conductivity, water temperature and pH were measured in the field using probes, and water depth was measured with a hand-held echo sounder. Turbidity was assessed on a 3-point scale because many sites were too shallow for Secchi disc measurement. Samples for major ion analysis were passed through a 0.45  $\mu\text{m}$  filter and stored at 4°C in the UK. Brine composition may vary across large lake basins, but salinity was unlikely to vary significantly across a single basin, at least compared to the full salinity gradient of the training set. Single samples were assumed to be representative and were collected from the surface in the centre of the lake if possible. Although water ephemerality may influence distribution (Reed 1998; Roca et al. 2000), some Turkish lakes are desiccating rapidly and it was difficult to classify permanence. Lake Süleymanhacı, for example, switched from a permanent lake to an ephemeral salt pan and then dried out completely during the sampling period.

In the laboratory, chloride and sulphate concentrations were analysed using Hach DR/2000 and Palintest 5000 photometers, with dilution of hypersaline samples. Because facilities were not available for carbonate titration in the field, carbonate plus bicarbonate concentrations were estimated for 1996–1997 samples using a hardness probe attached to a Hanna HI 931300 microprocessor-logging pH meter with temperature compensation (Univ. of Lancaster Environment Centre), checked by reference to molar balances and, for hypersaline samples, by reference to laboratory estimates of total dissolved solids by evaporation of 0.25–1 water samples. Molar balances were used to estimate concentrations for the rest of the samples. Major cations were analysed on the inductively coupled plasma spectrophotometers in Geography, Kingston University (1996–1997 samples) and by R. Knight, Chemistry Department, Hull University (1999–2000 samples). Mean annual January and July temperatures were taken from the World Meteorological Organisation (2001).

Diatom samples were prepared using standard techniques (Battarbee 1986), with hot H<sub>2</sub>O<sub>2</sub> to oxidise organics and concentrated HCl to remove carbonates. Slides were mounted in Naphrax<sup>®</sup> and approximately 500 valves per slide were counted on Axioskop and Zeiss microscopes with bright field DIC and phase contrast. Diatoms were identified using Krammer and Lange-Bertalot (1986–2000), Witkowski et al. (2000) and Levkov et al. (2007), using updated nomenclature (Aboal et al. 2003). Some morphologically variable taxa such as *Fragilaria capucina* and *Nitzschia palea* were merged in line with harmonisation of diatom training sets in the European Diatom Database (Juggins 2011). After screening at 125 µm, ostracod samples were wet sieved through a 250-µm mesh, sufficient to retain adults and larger instars, but large enough so that unidentifiable juveniles were discarded (Griffiths and Holmes 2000). Next, samples were oven-dried and picked for preparation of palaeontological slides. Ostracods were counted using a Leica MZ6 low-power binocular microscope. Where <250 valves were preserved, total counts were done. Sediment samples were subsampled randomly after sieving for more abundant samples. Taxa were identified using Bronshtein (1947), Sywula (1974) and Meisch (2000). Janz (1994) and Petkovski et al. (2000) were also consulted for the genera *Ilyocypris* and *Heterocypris*, respectively.

### Data analysis

For descriptive purposes, a definition of salinity classes used by Gasse et al. (1987) is adopted, with 0.5 g l<sup>-1</sup> (~0.5 mS cm<sup>-1</sup>) as the fresh-oligosaline boundary, 5 g l<sup>-1</sup> (~6 mS cm<sup>-1</sup>) as oligosaline-mesosaline and hypersaline as >40 g l<sup>-1</sup>. Canoco version 3.14 (ter Braak 1990) was used for ordination. To explore variation in the biological data, detrended correspondence analysis (DCA) was appropriate for indirect gradient analysis of noisy data-sets with gradient length >4.0 standard deviation units (Lepš and Šmilauer 2003). To reduce bias in the data, samples were screened qualitatively after initial DCA to eliminate any highly similar edge samples from individual lakes. Samples from Lake Bafa (BAF00) were deleted. The edge sample was influenced by its proximity to a river inflow and the freshwater ostracod fauna did not match the measured lake-centre conductivity of 18.6 mS cm<sup>-1</sup>. The lake centre sample (no ostracods) was dominated by a marine diatom, *Thalassionema nitzschioides*, and was a major outlier in initial exploratory analysis. Where conductivity values were similar, water chemistry data were matched for samples lacking full data. The resultant data set of 92 samples comprised 82 samples with full chemistry data from 51 sites. An additional ten samples from eight sites (including two duplicate sites with differing conductivity values) had limited chemistry data.

For paired analysis of diatom and ostracod salinity response, 50 samples from 38 sites contained diatoms, ostracods and full water chemistry data. An additional paired sample with partial chemistry (KDU99E) was used for Two-Way Indicator Species Analysis (TWINSPAN). Canonical correspondence analysis (CCA) with forward selection was performed on these diatom (146 taxa present at >2%) and ostracod (44 taxa present at >2%) data sets using 23 environmental variables (turbidity, water temperature, January and July mean temperature, water depth, pH, conductivity, molar concentrations and proportions of major ions, and cation and anion ratios) to determine the significance of salinity (expressed as conductivity) in explaining variance in the biological data. For CCA, water depth was square-root transformed, and conductivity and major ion concentrations were log<sub>10</sub> transformed to prevent skewness.

The larger total diatom ( $n = 91$ ) and ostracod ( $n = 54$ ) data sets, including partial chemistry data, were used for derivation of conductivity transfer functions, after using further DCA to compare the quality of these larger data sets with those of the 50-sample paired data sets. After removal of outliers, transfer functions were derived by weighted averaging (WA) using the program C2 version 1.5 (Juggins 2007). Bootstrapped error predictions were selected for cross validation rather than jackknifing, to avoid low error prediction where central and edge sample biota might overlap in single sites.

The clustering technique, TWINSpan (Hill 1979), was used to explore the degree to which diatoms and ostracods demonstrated parallel patterns of distribution between sites of differing salinity. Initial TWINSpan of the paired data sets individually (not reported) showed little similarity in group sample content for diatoms versus ostracods. A combined diatom-ostracod data set was therefore constructed. Because ostracods are less diverse than diatoms, the data sets were not equivalent numerically. The ostracod data set contained 28 taxa present at >2%. The 28 most abundant diatom taxa were selected from the diatom data set. Being more diverse, diatoms contained a higher proportion of low counts, and a lower proportion of counts >90%. Using Excel, 20 percentile values were calculated for each data set. Using these values, percentage counts were transformed to class variables, with values from 0 to 20. The data sets were combined and TWINSpan was performed.

## Results

Table 2 lists 58 of the 59 sites, omitting hypersaline Tuzla (TZL96), which lacked diatoms and ostracods. The only other samples without diatoms were non-epiphyton samples from Düden (DUD96E) and Burdur (BUR, sample not used). Ostracods were absent more often, e.g. in the sandy littoral zone of Kecigöl (KEC00E) and Meke (MEK96E, 99E). At the lake centre, they were present in some deep-water samples at <20 m depth, such as Abant (ABA00C) and Burdur (BUR99C), but absent from the deepest site at 68 m in Acıgöl (ACM99C) and at ~20 m depth in Meke (MEK99C) and Nar (NAR99C).

DCA of the 91-sample diatom data set showed KUS00C (Lake Kuş) to be the lone outlier with high Axis 2 scores, dominated by the single occurrence in the training set of *Fragilaria berolinensis*, a hypereutrophic taxon common in Dutch brackish lakes (van Dam and Mertens 1993). After its removal, the importance of conductivity in explaining variance in the diatom data, and the similar quality of the two data sets, is supported by the high  $r^2$  coefficient of determination between Axis 1 scores and observed, log-transformed conductivity for the 90-sample and 50-sample data sets (0.66 and 0.72, respectively) and by their similar DCA eigenvalues and gradient lengths (Table 3). Ostracod DCA eigenvalues and gradient lengths for the 61-sample and 50-sample data sets are also similar (Table 2), but  $r^2$  values are low (0.06 and 0.21, respectively). The proportion of variability explained is not improved with removal of outliers, suggesting that factors other than salinity explain a greater proportion of the variance in the data than for diatoms, or that the less species-rich data are less robust than the diatoms in terms of the indicator value of individual taxa.

Table 3

Summary statistics for detrended (DCA) and canonical (CCA) correspondence analysis of full and paired diatom and ostracod training set data

	<b>Diatom DCA</b>	<b>Diatom DCA</b>	<b>Ostracod DCA</b>	<b>Ostracod DCA</b>
	<i>n</i> = 90	<i>n</i> = 50	<i>n</i> = 61	<i>n</i> = 50
$\lambda_1, \lambda_2$	0.79, 0.63	0.80, 0.67	0.93, 0.75	0.94, 0.78
Gradient length	5.6	5.6	5.34	5.6
Cumul. % variance in first two axes	8.8	14.1	16.4	16.8
$r^2$ value: Axis 1 and observed $\log_{10}$ cond.	0.66	0.72	0.06	0.21
			<b>Diatom CCA</b>	<b>Ostracod CCA</b>
			<i>n</i> = 49	<i>n</i> = 48
$\lambda_1, \lambda_2$			0.74, 0.46	0.70, 0.47
Cumul. % variance of the species data in first two axes			11.9	12.2
Cumul. % variance of the species—env. relation in first two axes			30.2	39.2
Total inertia			10.1	9.5
Sum of canonical eigenvalues			4.0	3.0

Eigenvalues ( $\lambda_1, \lambda_2$ ) for the first two axes are displayed. Cumul. = cumulative

CCA of 50 diatom samples and 16 significant environmental variables identified from forward selection showed DUD97E (Düden) to have an extreme influence ( $\times 84$ ), and the carbonate proportion to exhibit collinearity. Both

were deleted in the final CCA (Fig. 2). Hypersaline Lake Düden ( $47 \text{ mS cm}^{-1}$ ) contained saline taxa such as *Navicula salinicola* and *N. digitoradiata* at <10%, but the sample was dominated by *Nitzschia cf. palea* fo. *tenuirostris*. For taxonomic harmonisation, this was merged with the predominantly freshwater taxon, *N. palea*. It was separated as *N. sp.* for subsequent analyses. The apparent importance of salinity in explaining variation in the diatom data is clear. Saline samples are separated with high positive scores on Axis 1, correlating closely with conductivity and both chloride and sulphate concentration variables. Saline taxa such as *Navicula salinicola* (NA039A), *Parlibellus crucicula* (NA040A), *Navicella pusilla* (CM005A), *Nitzschia bergii* (NI041A) and *N. epithemioides* (NI043A) plot to the right of the diagram. The distribution of planktonic taxa is also marked on Fig. 2. Freshwater taxa (e.g. *Asterionella formosa* AS001A; *Aulacoseira granulata* AU001A) plot to the left of the diagram, and dominate many of the deeper lakes in the data set such as Abant (ABA) and Eğirdir (EGR). Dominance of salinity over nutrient variables is demonstrated by the scatter of hypereutrophic planktonic taxa (*A. granulata* AU001A; *Stephanodiscus hantzschii* ST002A; *Cyclostephanos dubius* CS002A) and their overlap with oligotrophic taxa such as *Cyclotella radiosa* (CY006A) and *Discostella pseudostelligera* (CY007A). Eutrophic and salt-tolerant species *Cyclotella meneghiniana* (CY004A) has higher Axis 1 scores than other plankton, suggesting its response is to salinity rather than trophic status.

Fig. 2

CCA of 50 ostracod samples showed the two samples from Lake Cöl (COL) to be major outliers driving variation along Axis 2. The lake has high abundance and the only occurrence of *Heterocypris cf. bulgarica* in the data set. This species was deleted and CCA was run with forward selection with 48 samples and 13 significant environmental variables. The collinearity of the carbonate proportion was again detected, giving 12 environmental variables (Fig. 2). The importance of salinity is demonstrated by the correlation between conductivity, chloride and sulphate concentrations along a gradient of high positive Axis 1 scores and negative Axis 2 scores, but with the most saline sites plotting in two clusters of high positive Axis 1 and Axis 2 scores (ACI, SEY, ACG) and in the centre of the diagram with negative Axis 2 scores (e.g. BAK, SMH, DUD). The former is dominated by the most halophilic ostracods, *Eucypris mareotica* (Eumar) and *Cyprideis torosa* (Cptor, smooth-shelled morphotype), and their extreme Axis 1 scores extend the gradient length. Other samples and species form more of a single cluster than the diatom data, with other salt-tolerant taxa most typical of temporary environments, such as *Heterocypris salina* (Htsal) and *H. incongruens* (Htinc), plotting on one edge of the cluster and taxa usually living in permanent freshwater lakes, including *Cypria ophthalmica* (Cyoph), *Candona candida* (Cacan), *Cypridopsis vidua* (Cdvid) and *Cyclocypris laevis* (Cylae) plotting on the other. Another species known for its tolerance of temporary water bodies with varying salinity, *Limnocythere inopinata* (Liino), plots centrally. Populations of *L. inopinata* were found to be sexual in some lakes, including AKG, BAY, BUR, SAL, YAY and parthenogenetic in others (AKS, DUD, GLH, KAR, SMH). Both groups range from slightly oligosaline to hypersaline, so there is no simple relationship with salinity. The lack of significance of water depth, in contrast to the diatom results, is unsurprising. Unlike the array of diatom taxa, none of the ostracod taxa here is truly planktonic.

In development of transfer functions, regression of the diatom data ( $n = 91$ ) showed none of the samples was a major outlier if defined with an apparent residual >25% of the gradient length (1.27; Jones and Juggins 1995). Initial regression of the ostracod data ( $n = 53$ ) produced one outlier, BAY97C (Lake Bayındır; 25% of gradient length = 1.22; residual under inverse deshrinking 1.40). The lake appeared to have desiccated and filled with snow melt. In this case, use of 3 cm of sediment for the ostracod sample may have caused a mismatch between the assemblage and water salinity, as the fauna (100% *Limnocythere inopinata*) is that of a more saline lake. Alternately, since *L. inopinata* is also common in freshwater lakes (Yin et al. 1999), it is an artefact of the data set, which otherwise lacks examples of dominance by this taxon in non-saline environments.

Summary statistics for transfer functions are given in Table 4. The gradient length for diatoms is higher than for ostracods because the diatom training set includes the samples of maximum (BOL; Bolluk) and minimum (GCK; Gölcük) conductivity, in which ostracods were absent. Both exhibit similar performance between classic and inverse deshrinking techniques, with slightly lower RMSE for WA with inverse deshrinking (WA-INV). The diatom transfer functions have more robust performance statistics (RMSE for WA-INV = 0.24 for diatoms and 0.31 for ostracods). Tolerance downweighting improves performance slightly, but with higher RMSEP. Adopting WA-INV, a plot of inferred against observed conductivity for diatoms (Fig. 3a) exhibits less scatter than for ostracods (Fig. 3b), with high residuals mainly at the upper end of the conductivity gradient. There is low scatter at the fresh end of the ostracod gradient, but high residuals in the centre of the range, between ~3.2

and 4.3 observed  $\log_{10}$  conductivity. This equates to a conductivity range of about 2–20  $\text{mS cm}^{-1}$ , spanning the important biological threshold of the oligosaline-mesosaline boundary. The greater breadth of ostracod tolerance ranges is shown in a comparative plot of optima and tolerances (Fig. 4, Appendix 1, Appendix 2). Diatom optima show good coverage of the conductivity gradient from fresh to hypersaline. Ostracods show a gap in optima between 3.31 and 3.77 (about 2–6  $\text{mS cm}^{-1}$ ), possibly reflecting the disjunct distribution identified in CCA.

Table 4

Summary statistics for diatom and ostracod transfer functions based on simple weighted averaging (WA), WA with inverse deshrinking (INV) and WA with tolerance downweighting (TOL), showing the  $r^2$  coefficient of determination, the root mean squared error of prediction (RMSEP), and the bootstrapped error estimates ( $s_1$  = standard error of prediction;  $s_2$  = actual error of prediction)

	$r^2$	RMSE	Boot $r^2$	$s_1$	$s_2$	RMSEP
Diatom $n = 91$ , gradient length 5.10						
Simple WA	0.92	0.25	0.78	0.15	0.39	0.41
WA-INV	0.92	0.24	0.78	0.14	0.38	0.41
WA-TOL	0.94	0.21	0.81	0.26	0.36	0.45
Ostracod $n = 52$ , gradient length 4.89						
Simple WA	0.83	0.34	0.70	0.26	0.41	0.49
WA-INV	0.83	0.31	0.70	0.23	0.42	0.47
WA-TOL	0.84	0.33	0.60	0.32	0.48	0.56

Fig. 3

Fig. 4

The clearest distinction in paired TWINSpan results (Fig. 5) is between samples from fresh to slightly oligosaline waters and those from high oligosaline to hypersaline waters. Group 1 (mean 0.9  $\text{mS cm}^{-1}$ ), Group 2 (0.6  $\text{mS cm}^{-1}$ ) and Group 5 sites (1.0  $\text{mS cm}^{-1}$ , excluding SIV00E) are fresh to slightly oligosaline. Group 4 sites are saline (mean excluding PIN97C, 26.6  $\text{mS cm}^{-1}$ ), but span a wide gradient from high oligosaline (Akgöl dünden, AKG96C, 3.1  $\text{mS cm}^{-1}$ ) to hypersaline, >40  $\text{mS cm}^{-1}$ . Group 3 (four sites; range 1.5–7.8  $\text{mS cm}^{-1}$ ; mean 4.3  $\text{mS cm}^{-1}$ ) is the only group to overlap the accepted oligosaline-mesosaline boundary. Species clusters defined in TWINSpan do not split samples definitively around the fresh-oligosaline boundary of 0.5  $\text{mS cm}^{-1}$ . From the conductivity ranges of Groups 1, 2, 5 and 4, ~3  $\text{mS cm}^{-1}$  is the most significant ecological threshold (approaching 3  $\text{g l}^{-1}$ ), but higher salinity boundaries are not well defined.

Fig. 5

Results of TWINSpan of paired diatom and ostracod class variable data ( $n = 51$ ). Numbers are proportional to relative abundance of taxa. TWINSpan sample groups 1–5 are displayed at the top of the diagram with conductivity range and mean ( $\text{mS cm}^{-1}$ ). Group 4 values are displayed with and without inclusion of the low-conductivity sample, PIN97C, (Pınarbaşı), shaded grey; the high-conductivity sample SIV00E (Siviş) is excluded similarly. † 1.5–7.8 (4.3); ‡ 0.6–1.3 (6.8); 1.0 (2.2)

Taxa that are well represented and restricted to the above sample groupings are likely to be the strongest indicator taxa above and below an ecological boundary of about 3  $\text{mS cm}^{-1}$ . At the fresh end these mainly comprise taxa in the first and fourth species clusters, including the eutrophic planktonic diatoms, *Stephanodiscus hantzschii* and *Aulacoseira granulata* and mesotrophic *Cyclotella distinguenda* var. *unipunctata* and *Cyclotella comensis*, together with the facultative planktonic taxon, *Staurosira construens* var. *venter*. The overlapping Group 3 was separated at the third level from Group 2; it is dominated by taxa from Group 2, but also contains diatoms that are common in Group 4, including *Navicella pusilla*, *Anomoeoneis sphaerophora* and *Mastogloia elliptica*. Ostracods are well represented at the fresh end of the gradient; those with narrow distributions include *Darwinula stevensoni*, *Physocypris kraepelini*, *Fabaeformiscandona fabaeformis*, *Cyclocypris laevis*, *Cypridopsis vidua*, *Candona candida*, *Cypria ophthalmica* and *Pseudocandona marchica*. The main taxonomic distinction in the clustering is against the abundance in Group 4 of taxa in the bottom two

species clusters of the diagram. Diatom species comprise *Chaetoceros* spp., *Anomoeoneis sphaerophora*, *Mastogloia elliptica*, *Tabularia fasciculata*, *Navicula salinarum*, *Navicella pusilla*, *Tryblionella compressa* var. *compressa* and *Navicula digitoradiata* var. *minima*, all of which are well known as salt-tolerant taxa. Ostracods of Group 4 are less clearly classified. They include *Limnocythere inopinata* and *Heterocypris salina*, species that can inhabit both fresh and saline waters and also occur in Groups 1 and 2, and *Ilyocypris monstifica*, a species of difficult taxonomy which is mainly described elsewhere from fresh, eutrophic waters (Meisch 2000) and which has a relatively low optimum here of 2.0 mS cm<sup>-1</sup>. Well-known halophilic taxa only occur sporadically, and include *Eucypris mareotica* and smooth-shelled *Cyprideis torosa*. Group 5 is also small; apart from the more saline sample from Siviş (SIV00E), it comprises four samples from shallow, oligosaline waters, which were sampled from under ice in April 1997 (CEL97C, KR97E, KRM97C and BAY97C). Group 5 is poorly defined by TWINSPAN on the basis of low abundance of *Navicella pusilla*, absence of *A. sphaerophora* and high abundance of the widely distributed diatom, *Navicula veneta*. It again has taxonomic affinity with Group 2, but with sporadic occurrence of Group 4 taxa, including *N. pusilla* and the ostracod, *H. salina*.

Although transfer function output incorporates estimates of tolerance ranges, Fig. 5 highlights more clearly those taxa with extremely broad distributions across the salinity gradient. Common taxa include the diatoms *Cocconeis placentula*, *Encyonopsis microcephala*, *Achnanthydium minutissimum*, *Navicula veneta* and *Anomoeoneis sphaerophora* and the ostracods *Potamocypris arcuata*, *Heterocypris salina* and *Limnocythere inopinata*.

## Discussion

### Performance of transfer functions and regional comparison of optima

With good coverage of the salinity gradient, although more complete for diatoms, ordination results and derivation of transfer functions for both diatoms and ostracods are robust, with slightly higher apparent  $r^2$  values reflecting the smaller size of the Turkish training sets compared to those of other regions from which conductivity transfer functions have been derived (Diatoms: Africa  $n = 282$ ;  $r^2 = 0.82$  [Gasse et al. 1995]; Turkey  $r^2 = 0.92$ . Ostracods: Spain  $n = 465$ ;  $r^2 = 0.78$  [Mezquita et al. 2005]; Turkey  $r^2 = 0.83$ ). Equally, the estimated optima offer few surprises compared to adjacent biogeographic regions. Reed (1998, 2007) noted the similarity of many Spanish and African diatom optima. Hypersaline examples include the diatom *Navicula salinicola*: optimum 71.3 mS cm<sup>-1</sup> [Turkey]; 32.8 mS cm<sup>-1</sup> [Spain]; 29.5 mS cm<sup>-1</sup> [Africa] and the ostracod *Eucypris mareotica*: optimum 36.6 mS cm<sup>-1</sup> [Turkey]; 49.0 mS cm<sup>-1</sup> [Spain]; 16.7 mS cm<sup>-1</sup> [Tibetan Plateau] (Mischke personal communication). At the fresh end, where smaller-scale variability in conductivity inferences may be important in distinguishing true open systems from hydrologically-closed, oligosaline systems, there is variability within the fresh-oligosaline range. In the diatoms, *Cyclotella ocellata* has an optimum in the fresh range in Turkey (0.5 mS cm<sup>-1</sup>), slightly oligosaline in Spain (0.8 mS cm<sup>-1</sup>) and full oligosaline in Africa (1.5 mS cm<sup>-1</sup>). The apparently high African optimum, however, is due to the inclusion of a hypersaline sample contaminated by freshwater diatoms transported by river inflow in Lake Bogoria (Gasse et al. 1997). Application of the African transfer function in reconstructing Late Quaternary palaeoclimates in Eski Acıgöl, Cappadocia (Roberts et al. 2001) undoubtedly overestimated salinity in *C. ocellata*-dominated assemblages of the deep, fresh glacial lake.

### Biogeographic variability, taxonomy and ecological representativity

Few remarkable taxa are here to suggest biogeographic variability. The cosmopolitan character of many saline-lake diatom and ostracod taxa is well known, and it is possible that their dominance increases with water quality deterioration (Külköylüoğlu 2004). One example is *Scoliopleura peisonis* (optimum 5.8 mS cm<sup>-1</sup>), a taxonomically distinct diatom that is absent in Spanish and African training sets. Although characteristic of saline, chloride-dominated waters in North America (Patrick and Reimer 1966), it is also known from ultra-oligotrophic waters (0.09 mS cm<sup>-1</sup>) in Lake Lama, Central Siberia, with a partial limestone catchment (Kienel and Kumke 2002) and presumably carbonate-dominated waters. For some taxa, the ability to distinguish biogeographic variation may be affected by taxonomic classification. Among the ostracods, dominance of *Heterocypris* cf. *bulgarica* in Lake Cöl, near the Black Sea Coast, may indicate close affinity with the Balkan region, but its taxonomic identity is uncertain. Similarly, the apparent absence in Africa of the diatom *Navicula wildii*, which is present in alkaline waters of Turkey and Spain, may be due to its relatively recent description, having been described initially as indeterminate in Krammer and Lange-Bertalot (1986). Ecological information may be lost by merging difficult taxa. *Nitzschia* cf. *palea* var. *tenuirostris* in Lake Düden was mentioned above. Although difficult to quantify without further dedicated taxonomic study, hyaline *Nitzschia* taxa are often 'non-

classic' in Turkey. In contrast, they are clearly identifiable in Spain, where unusual morphotypes are instead common in saline *Navicula* taxa, including *N. salinarum* and *N. phyllepta* (Reed, unpublished). Amongst the ostracods, identification of *Ilyocypris* taxa is notoriously difficult, such that Mischke et al. (2010) preferred an indeterminate designation.

Bimodal distributions cause inaccuracy in the estimation of optima. The problem of apparent bimodality due to taxonomic merging of difficult taxa has been highlighted in pH data sets, within the small Fragilariales (Flower et al. 1996). In the Turkish transfer functions, this was originally the case with merged *N. palea* and *N. palea* cf. *tenuirostris*. Apparent bimodality could also be created as an artefact of poor representativity in the training set, where taxa are only represented in parts of their full ecological tolerance range. *Heterocypris salina*, for example, can occur in both fresh and saline waters (Meisch 2000). Here, it is mainly in mesosaline waters, but also occurs at conductivity of  $1.5 \text{ mS cm}^{-1}$  and  $1.8 \text{ mS cm}^{-1}$  in Karamikbataklığı (KRM00E) and Sultan Sazlığı (SUL96C) marshes, respectively. *Cyprideis torosa* is known for its tolerance of saline, chloride-dominated waters, as here, but in rare cases such as in eastern Spain, may also occur in fresh, chloride-rich lakes (Mezquita et al. 2005; Poquet et al. 2008). Most notably, *Limnocythere inopinata* occurs mainly in saline waters in the Turkish training set, and is rare in oligosaline lakes. It was well represented across the salinity gradient in Tibet (Mischke et al. 2007). This may be partly a function of the smaller size of the Turkish data set ( $n = 53$  Turkey;  $n = 94$  Tibet), but species richness is greater in Turkey (45 Turkey; 36 Tibet), presumably reflecting a greater diversity of lakes. It is likely that variation in ecological preference of *L. inopinata* reflects the existence of different genetic lineages, which are difficult to separate morphologically (Yin et al. 1999). Nevertheless, where fossil assemblages are dominated by taxa such as these, with apparently broad tolerance ranges or with known broader distributions elsewhere, it is unwise to rely on the optimum.

In testing the strength and simplicity of salinity response in more detail, the results of paired TWINSPAN analysis highlighted a major ecological boundary at  $\sim 3 \text{ mS cm}^{-1}$  (approaching  $3 \text{ g l}^{-1}$ ), rather than the higher accepted value of  $5 \text{ g l}^{-1}$ . In other respects, the lack of a clearly-defined boundary indicated the complexity rather than simplicity of apparent salinity response. Although this supports the argument that other factors such as brine composition and habitat change might contribute to species shifts, seasonality may also play a part. Training sets comprising surface sediment samples contain an element of time averaging. In large, freshwater lakes with stable salinity this is not a problem. It is likely, however, to affect seasonally fluctuating, saline lakes in particular, although those that do not preserve biota, such as Burdur's lack of fossil diatoms, should still show a close relationship with measured chemistry. In this study, Akşehir is an example of a lake that was undergoing salinisation during the sampling period. The separation in TWINSPAN of the more saline 2000 sample from those of 1996 and 1999 appears to demonstrate a reliable relationship with measured water chemistry. In contrast, clustering of some samples collected in April 1997 under ice may reflect hidden bias due to seasonal variation. The Karamikbataklığı 1997 sample (Group 5) is separated from those of summer 1996 and 1999 (Group 2), but in this case the measured conductivity ( $1.3 \text{ mS cm}^{-1}$ ) is close to that of 1996 ( $1.5 \text{ mS cm}^{-1}$ ), and higher than that of 1999 ( $0.6 \text{ mS cm}^{-1}$ ). A dominant diatom species in this group is *Achnanthydium minutissimum*, which has a surprisingly broad distribution across the training sets. Known as a freshwater species common in lakes and flowing waters, it is possible that its occurrence across a broad salinity range is indicative of seasonal freshwater stream input to saline lakes, and it should be deleted from reconstructions. The degree to which time averaging and seasonality has affected the relationship to measured water chemistry cannot be evaluated more effectively without dedicated monitoring study. In Nar, for example, Woodbridge and Roberts (2010) discuss the bias in surface sediment assemblage composition from seasonal dominance of freshwater taxa that bloom following snow melt.

In the light of the foregoing, it is not surprising that multiple sets of characteristic diatom and ostracod taxa cannot be defined as indicator groups for all salinity classes. Instead, a large number of characteristic, fresh to slightly oligosaline diatom and ostracod taxa, and a group of 'saline' taxa, mainly comprising diatoms, were described above. Apart from distinguishing the oligosaline-mesosaline boundary with confidence, the results also offer the potential to strengthen reconstructions in multi-proxy analyses where assemblages are dominated by taxa with extreme broad or bimodal distributions and uncertain optima (the diatoms, *Cocconeis placentula*, *Encyonopsis microcephala*, *Achnanthydium minutissimum*, *Navicula veneta* and *Anomoeoneis sphaerophora* and the ostracods, *Potamocypris arcuata*, *Heterocypris salina* and *Limnocythere inopinata*). Most of these are already recognised as tolerant. *L. inopinata* was discussed above. Diatoms such as *A. sphaerophora* are described as halophilic, but are also common in eutrophic or generally 'polluted' fresh waters with relatively high ionic concentration. For example, by pairing diatom and ostracod analysis, a coupling of *L. inopinata* with *Cyclotella ocellata* and *Pseudostaurosira brevistriata* is indicative of fresh waters, whereas its occurrence with *Mastogloia elliptica* and other Group 4 diatoms is indicative of saline waters. Although parallel quantification would simply highlight inconsistencies in reconstructions, results indicate that qualitative understanding of

patterns of variation is indispensable. The combination of multi-proxy quantitative reconstruction, complemented by the qualitative understanding of ecological response generated by the analysis, remains a powerful tool in Quaternary palaeoclimate research.

## Conclusions

Statistically robust conductivity transfer functions were derived for diatoms and ostracods of Turkish lakes. The study confirmed the potential for diatoms and ostracods to strengthen palaeoclimate inferences by quantitative multi-proxy reconstruction. Results of paired diatom-ostracod analysis indicated that the most important ecological threshold occurs at a conductivity boundary of  $\sim 3 \text{ mS cm}^{-1}$ . Multi-proxy analysis makes it possible to reduce uncertainty in cases where fossil assemblages are dominated by taxa with apparently broad ecological preferences, whether this is an artefact of taxonomy or the fact that taxa which appear to exhibit broader distributions in other biogeographic regions are poorly represented in the Turkish training sets. The approach needs testing via parallel reconstruction of fossil diatom and ostracod sequences. There is also obvious potential to harmonise and combine data sets, and to carry out monitoring studies to explore ecological responses in greater detail.

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## Appendix 1

See Table 5.  
Table 5

List of estimated diatom optima, tolerance range (2SD) and bootstrapped error estimates, for taxa with 2 or more occurrences

Diatom species name	Code	N. occ	Max %	N2	Optimum	Tolerance	Boot_Opt	Boot_Tol	SE_Opt	SE_Tol
<i>Achnanthes</i> sp. 1 (cf. <i>submarina</i> )	AC004A	13	37.1	2.4	4.637	0.839	4.472	0.787	0.372	0.201
<i>Achnanthes</i> sp. 2 (cf. <i>rosenstockii</i> )	AC014A	4	7.1	2.3	2.399	0.002	2.399	0.067	0.001	0.144
<i>Achnantheidium exilis</i>	AC007A	6	21.8	1.4	3.484	0.521	3.361	0.521	0.269	0.331
<i>Achnantheidium minutissimum</i>	AC001A	58	75.2	18.5	2.866	0.506	2.868	0.486	0.122	0.056
<i>Adlafia minuscula</i>	NA050A	4	2.1	2.2	2.568	0.951	2.734	0.650	0.485	0.346
<i>Amphora acutiuscula</i>	AM004A	10	9.7	3.5	4.418	0.451	4.368	0.409	0.183	0.102
<i>Amphora coffeaeformis</i>	AM002A	21	14.8	9.0	4.531	0.570	4.498	0.539	0.165	0.071
<i>Amphora commutata</i>	AM005A	5	5.9	2.7	4.480	0.268	4.450	0.265	0.167	0.142
<i>Amphora copulata</i>	AM003A	32	5.0	14.8	2.923	0.442	2.933	0.406	0.072	0.114
<i>Amphora holsatica</i>	AM011A	3	12.6	2.0	3.751	0.267	3.854	0.347	0.356	0.243

<b>Diatom species name</b>	<b>Code</b>	<b>N. occ</b>	<b>Max %</b>	<b>N2</b>	<b>Optimum</b>	<b>Tolerance</b>	<b>Boot_Opt</b>	<b>Boot_Tol</b>	<b>SE_Opt</b>	<b>SE_Tol</b>
<i>Amphora micrometra</i>	AM006A	9	4.7	5.1	4.914	0.398	4.881	0.398	0.121	0.197
<i>Amphora pediculus</i>	AM001A	50	85.7	8.3	2.777	0.438	2.775	0.431	0.081	0.085
<i>Amphora</i> sp. 1 ( <i>veneta</i> / <i>subcapitata</i> )	AM008A	14	26.2	2.5	3.516	0.305	3.537	0.295	0.083	0.085
<i>Amphora tenerrima</i>	AM010A	7	6.5	4.0	4.843	0.270	4.812	0.319	0.130	0.284
<i>Amphora thumensis</i>	AM014A	4	1.4	2.7	2.523	0.340	2.565	0.310	0.160	0.144
<i>Amphora veneta</i>	AM007A	33	22.3	8.7	3.186	0.473	3.190	0.428	0.154	0.097
<i>Aneumastus tusculus</i>	NA015A	5	5.5	1.5	2.474	0.376	2.573	0.326	0.196	0.126
<i>Anomoeoneis sphaerophora</i>	AN001A	31	55.5	2.7	4.101	0.533	4.004	0.520	0.184	0.098
<i>Asterionella formosa</i>	AS001A	9	6.0	4.1	2.640	0.209	2.636	0.196	0.081	0.066
<i>Aulacoseira granulata</i>	AU001A	19	29.0	5.7	2.738	0.160	2.745	0.153	0.057	0.029
<i>Berkeleya rutilans</i>	AP001A	4	5.1	1.4	4.515	0.994	4.142	0.694	0.716	0.443
<i>Brachysira aponina</i>	BR002A	7	11.9	1.5	4.680	0.570	4.516	0.438	0.293	0.157
<i>Brachysira vitrea</i>	BR001A	4	5.3	1.5	3.147	0.385	3.119	0.321	0.220	0.177
<i>Caloneis bacillum</i>	CA001A	19	2.9	8.6	2.911	0.500	2.902	0.455	0.144	0.098
<i>Caloneis silicula</i>	CA003A	9	1.4	4.6	2.791	0.217	2.796	0.200	0.055	0.060
<i>Caloneis westii</i>	CA002A	4	6.2	1.4	4.354	0.719	3.986	0.507	0.572	0.259
<i>Campylodiscus clypeus</i>	CP001A	8	1.6	5.9	4.033	0.428	4.036	0.402	0.127	0.153
<i>Chaetoceros muelleri</i>	CH002A	3	1.2	2.4	3.824	0.868	3.754	0.631	0.543	0.315
<i>Chaetoceros</i> spp.	CH999A	14	25.9	4.7	3.536	0.312	3.576	0.316	0.116	0.083
<i>Cocconeis disculus</i>	CO002A	3	3.3	2.1	3.076	0.703	3.154	0.505	0.359	0.187
<i>Cocconeis neothumensis</i>	CO003A	8	3.9	4.5	2.606	0.176	2.604	0.152	0.075	0.042
<i>Cocconeis pediculus</i>	CO004A	14	7.3	4.8	3.899	1.234	3.737	0.991	0.582	0.372
<i>Cocconeis placentula</i>	CO001B	49	71.8	7.8	3.052	0.660	3.053	0.649	0.144	0.156
<i>Craticula cuspidata</i>	CR002A	16	65.6	1.3	2.842	0.381	2.937	0.325	0.169	0.133
<i>Craticula halophila</i>	CR001A	33	23.0	7.8	3.454	0.378	3.470	0.377	0.081	0.067
<i>Ctenophora pulchella</i>	FR009A	20	12.0	5.0	3.816	0.416	3.835	0.403	0.120	0.078
<i>Cyclostephanos dubius</i>	CS002A	7	15.4	4.0	2.685	0.129	2.689	0.125	0.055	0.059
<i>Cyclostephanos</i> sp. 1	CS003A	6	20.1	1.7	2.970	0.204	2.875	0.165	0.140	0.083
<i>Cyclotella atomus</i>	CY011A	3	9.6	1.6	2.688	0.177	2.730	0.210	0.145	0.148
<i>Cyclotella comensis</i>	CY003A	4	24.1	2.2	2.338	0.134	2.411	0.228	0.153	0.124
<i>Cyclotella distinguenda</i>	CY002A	6	3.5	3.1	2.866	0.291	2.869	0.268	0.129	0.091
<i>Cyclotella distinguenda</i> var. <i>unipunctata</i>	CY002B	6	16.0	3.7	2.363	0.051	2.369	0.054	0.023	0.066

Diatom species name	Code	N. occ	Max %	N2	Optimum	Tolerance	Boot_Opt	Boot_Tol	SE_Opt	SE_Tol
<i>Cyclotella gordonensis</i>	CY012A	3	1.7	2.2	2.317	0.027	2.326	0.179	0.026	0.173
<i>Cyclotella meneghiniana</i>	CY004A	29	9.5	10.8	3.303	0.487	3.299	0.476	0.120	0.104
<i>Cyclotella ocellata</i>	CY001A	37	70.0	8.1	2.729	0.301	2.724	0.286	0.066	0.067
<i>Cymatopleura solea</i>	CT001A	11	1.3	6.9	2.789	0.284	2.790	0.272	0.095	0.052
<i>Cymbella affinis</i>	CM001A	27	24.0	5.2	2.831	0.361	2.845	0.368	0.075	0.094
<i>Cymbella cistula</i>	CM014A	4	1.7	2.2	3.489	0.547	3.321	0.349	0.311	0.159
<i>Cymbella cymbiformis</i>	CM020A	21	57.6	1.5	2.745	0.332	2.836	0.307	0.134	0.102
<i>Cymbella leptoceros</i>	CM002A	8	3.5	5.5	2.909	0.328	2.898	0.271	0.135	0.098
<i>Diatoma moniliformis</i>	DI004A	3	35.8	1.3	2.476	0.391	2.648	0.341	0.247	0.095
<i>Diatoma tenuis</i>	DI001A	16	8.4	5.1	3.287	0.405	3.257	0.352	0.166	0.109
<i>Diploneis elliptica</i>	DP001A	3	1.4	1.9	2.297	0.159	2.326	0.227	0.115	0.121
<i>Diploneis oculata</i>	DP005A	3	3.5	2.5	2.563	0.163	2.569	0.176	0.079	0.116
<i>Diploneis ovalis</i>	DP003A	4	1.5	2.5	2.565	0.230	2.603	0.209	0.116	0.098
<i>Discostella pseudostelligera</i>	CY007A	9	7.3	2.8	2.468	0.375	2.559	0.310	0.192	0.095
<i>Discostella radiosa</i>	CY006A	12	3.9	5.3	2.616	0.352	2.633	0.306	0.146	0.067
<i>Encyonema caespitosum</i>	CM008A	9	16.1	1.8	2.817	0.202	2.868	0.156	0.081	0.083
<i>Encyonema silesiacum</i>	CM019A	8	2.3	4.6	2.568	0.346	2.597	0.284	0.162	0.094
<i>Encyonopsis cesatii</i>	CM006A	8	2.6	4.4	2.952	0.261	2.932	0.235	0.100	0.077
<i>Encyonopsis microcephala</i>	CM004A	44	39.9	11.9	2.886	0.359	2.890	0.360	0.063	0.058
<i>Epithemia adnata</i>	EP002A	27	14.2	9.1	2.802	0.412	2.813	0.395	0.105	0.087
<i>Epithemia sorex</i>	EP001A	30	58.1	5.6	2.966	0.594	2.942	0.518	0.233	0.086
<i>Epithemia turgida</i>	EP004A	14	1.1	9.7	2.589	0.342	2.621	0.326	0.108	0.061
<i>Fallacia pygmaea</i>	NA036A	13	10.7	2.9	3.021	0.563	3.132	0.515	0.246	0.130
<i>Fallacia tenera</i>	NA083A	3	6.0	2.7	3.530	0.520	3.531	0.417	0.276	0.155
<i>Fragilaria capucina</i> var. <i>mesolepta</i>	FR005H	6	8.3	1.5	2.380	0.475	2.591	0.262	0.299	0.180
<i>Fragilaria capucina</i> var. <i>perminuta</i>	FR005E	6	9.9	3.5	2.747	0.233	2.751	0.215	0.117	0.078
<i>Fragilaria capucina</i> var. <i>rumpens</i>	FR005D	5	4.1	2.6	3.175	0.376	3.208	0.323	0.187	0.164
<i>Fragilaria capucina</i> var. <i>vaucheriae</i>	FR005B	30	15.2	8.2	2.753	0.202	2.756	0.192	0.059	0.025
<i>Fragilaria capucina</i> vars.	FR014A	14	2.7	6.6	3.030	0.673	3.045	0.605	0.219	0.133
<i>Fragilaria fasciculata</i>	FR012A	19	30.6	6.0	4.000	0.850	3.998	0.741	0.336	0.211
<i>Fragilaria gracilis</i>	FR005F	10	7.7	5.0	2.556	0.381	2.606	0.330	0.169	0.081
<i>Fragilaria</i> sp. 1	FR016A	3	6.2	1.3	2.775	0.329	2.672	0.259	0.195	0.128
<i>Fragilaria</i> sp. 2	FR017A	5	3.7	3.6	3.156	0.138	3.153	0.127	0.063	0.061
<i>Geissleria decussis</i>	NA070A	3	6.1	1.3	2.439	0.229	2.485	0.282	0.125	0.110

Diatom species name	Code	N. occ	Max %	N2	Optimum	Tolerance	Boot_Opt	Boot_Tol	SE_Opt	SE_Tol
<i>Gomphonema angustatum</i>	GO006A	6	1.2	3.9	2.730	0.605	2.794	0.507	0.254	0.181
<i>Gomphonema angustum</i>	GO001A	18	5.4	6.3	2.545	0.408	2.578	0.389	0.102	0.097
<i>Gomphonema clavatum</i>	GO007A	8	32.9	1.2	3.516	0.734	3.203	0.507	0.444	0.214
<i>Gomphonema gracile</i>	GO003A	10	1.9	6.0	2.713	0.441	2.713	0.399	0.165	0.098
<i>Gomphonema minutum</i>	GO009A	5	3.5	2.4	2.552	0.172	2.536	0.183	0.096	0.096
<i>Gomphonema olivaceum</i>	GO004A	20	21.2	3.7	3.248	0.391	3.215	0.359	0.150	0.067
<i>Gomphonema olivaceum</i> var. <i>salinarum</i>	GO004B	4	1.8	3.5	3.390	0.534	3.410	0.415	0.264	0.170
<i>Gomphonema parvulum</i>	GO002A	32	9.0	9.4	2.754	0.459	2.777	0.424	0.144	0.065
<i>Gomphonema</i> sp. 1	GO008A	4	6.7	1.7	2.564	0.077	2.541	0.111	0.053	0.116
<i>Gomphonema subtile</i>	GO014A	3	1.4	2.9	2.425	0.164	2.426	0.267	0.095	0.118
<i>Gomphonema truncatum</i>	GO005A	13	1.2	9.8	2.925	0.353	2.936	0.327	0.100	0.076
<i>Gyrosigma acuminatum</i>	GY003A	7	1.8	4.2	2.657	0.243	2.692	0.189	0.104	0.066
<i>Gyrosigma peisonis</i>	GY002A	13	2.3	6.5	3.520	0.751	3.517	0.698	0.275	0.136
<i>Gyrosigma spencerii</i>	GY004A	3	2.8	2.7	2.653	0.053	2.657	0.124	0.027	0.153
<i>Hantzschia amphioxys</i>	HA001A	4	17.3	2.2	2.909	0.175	2.926	0.151	0.095	0.109
<i>Hippodonta capitata</i>	NA006A	9	1.6	4.8	3.065	0.410	3.028	0.346	0.152	0.130
<i>Hippodonta hungarica</i>	NA006B	15	1.4	9.6	3.064	0.658	3.125	0.646	0.224	0.184
<i>Karayevia clevei</i>	AC002A	11	4.3	3.2	2.597	0.191	2.589	0.170	0.067	0.044
<i>Lemnicola hungarica</i>	AC011A	3	18.3	1.7	2.271	0.306	2.480	0.490	0.553	0.349
<i>Luticola mutica</i>	NA012A	15	2.4	5.6	3.301	0.674	3.320	0.631	0.188	0.145
<i>Mastogloia elliptica</i>	MA002A	20	46.7	3.4	4.117	0.752	4.001	0.684	0.333	0.165
<i>Mastogloia smithii</i> var. <i>lacustris</i>	MA001B	21	36.0	6.0	3.839	0.672	3.817	0.626	0.260	0.113
<i>Navicella pusilla</i>	CM005A	36	100.0	11.0	4.407	0.456	4.395	0.446	0.114	0.058
<i>Navicula bacilloides</i>	NA066A	5	6.0	2.4	2.681	0.267	2.688	0.267	0.128	0.089
<i>Navicula capitoradiata</i>	NA023A	14	3.6	7.0	2.801	0.400	2.793	0.389	0.112	0.101
<i>Navicula cari</i>	NA001A	4	1.3	2.3	2.966	0.048	2.963	0.109	0.027	0.139
<i>Navicula</i> cf. <i>complanata</i>	NA041A	4	1.8	3.1	5.021	0.116	5.007	0.142	0.065	0.112
<i>Navicula cincta</i>	NA008A	31	17.1	9.5	3.786	0.607	3.782	0.597	0.138	0.101
<i>Navicula cryptocephala</i>	NA016A	15	9.4	3.4	2.605	0.670	2.714	0.569	0.296	0.137

Diatom species name	Code	N. occ	Max %	N2	Optimum	Tolerance	Boot_Opt	Boot_Tol	SE_Opt	SE_Tol
<i>Navicula cryptotenella</i>	NA007A	44	55.1	5.1	3.094	0.589	3.034	0.561	0.186	0.072
<i>Navicula digitoradiata</i>	NA020A	11	13.0	5.9	4.203	0.621	4.133	0.527	0.254	0.165
<i>Navicula digitoradiata</i> var. <i>minima</i>	NA049A	3	25.3	2.1	4.414	0.684	4.312	0.414	0.370	0.220
<i>Navicula duerrenbergiana</i>	NA037A	6	1.6	3.9	4.139	0.410	4.134	0.379	0.144	0.119
<i>Navicula erifuga</i>	NA065A	7	23.3	1.4	2.938	0.209	2.907	0.180	0.096	0.097
<i>Navicula gregaria</i>	NA057A	5	24.3	2.6	2.966	0.159	2.956	0.183	0.107	0.102
<i>Navicula menisculus</i>	NA002A	22	15.3	3.5	2.595	0.203	2.583	0.176	0.070	0.042
<i>Navicula minima</i>	NA067A	5	14.9	1.3	3.423	0.708	3.173	0.437	0.428	0.222
<i>Navicula oblonga</i>	NA010A	15	18.9	1.9	3.650	0.535	3.466	0.475	0.240	0.102
<i>Navicula perminuta</i>	NA053A	4	2.5	3.1	4.132	0.677	4.123	0.491	0.368	0.217
<i>Navicula phyllepta</i>	NA038A	8	10.1	3.9	4.054	0.952	4.030	0.739	0.484	0.285
<i>Navicula pseudanglica</i>	NA075A	3	3.9	1.4	2.390	0.198	2.399	0.241	0.102	0.116
<i>Navicula radiosa</i>	NA005A	23	6.6	6.5	2.769	0.305	2.775	0.294	0.077	0.057
<i>Navicula rhyncocephala</i>	NA030A	11	1.6	6.2	3.169	0.387	3.177	0.393	0.086	0.105
<i>Navicula salinarum</i>	NA058A	12	23.4	1.7	3.248	0.674	3.412	0.592	0.316	0.159
<i>Navicula salinicola</i>	NA039A	12	71.4	2.5	5.023	0.338	4.963	0.361	0.164	0.229
<i>Navicula</i> sp. 2 (KLB)	NA089A	3	2.3	2.6	2.540	0.120	2.563	0.195	0.072	0.135
<i>Navicula subrhyncocephala</i>	NA048A	4	17.5	1.2	3.868	0.504	3.694	0.438	0.400	0.246
<i>Navicula subrotundata</i>	NA054A	6	12.7	2.5	2.591	0.127	2.594	0.128	0.052	0.056
<i>Navicula tripunctata</i>	NA087A	6	1.4	3.7	2.763	0.250	2.750	0.202	0.122	0.067
<i>Navicula trivialis</i>	NA045A	11	12.9	3.2	2.804	0.301	2.767	0.258	0.137	0.073
<i>Navicula veneta</i>	NA004A	39	23.5	7.9	3.435	0.648	3.424	0.605	0.203	0.098
<i>Navicula wildii</i>	NA047A	11	11.5	2.8	2.598	0.288	2.658	0.227	0.145	0.069
<i>Nitzschia acicularis</i>	NI046A	3	1.5	1.7	2.939	0.357	2.875	0.284	0.192	0.126
<i>Nitzschia amphibia</i>	NI006A	39	8.4	14.8	3.790	0.989	3.703	0.886	0.306	0.146
<i>Nitzschia angusteforaminata</i>	NI007A	10	4.3	3.9	3.853	0.568	3.834	0.544	0.176	0.176
<i>Nitzschia bergii</i>	NI041A	4	12.2	1.5	4.110	0.700	4.151	0.585	0.426	0.323
<i>Nitzschia capitellata</i>	NI039A	9	18.4	2.1	2.945	0.312	2.928	0.277	0.138	0.132
<i>Nitzschia communis</i>	NI012A	5	2.9	2.1	3.335	0.399	3.370	0.343	0.190	0.123
<i>Nitzschia commutata</i>	NI009A	13	2.1	6.5	3.024	0.711	3.085	0.611	0.274	0.129
<i>Nitzschia denticula</i>	NI005A	4	1.4	2.5	3.206	0.555	3.232	0.487	0.263	0.359
<i>Nitzschia dissipata</i> and vars.	NI017A	26	2.2	14.1	2.954	0.689	2.956	0.649	0.122	0.178
<i>Nitzschia elegantula</i>	NI014A	11	2.6	5.7	3.471	0.747	3.490	0.619	0.264	0.197
<i>Nitzschia fonticola</i>	NI003A	26	6.6	9.9	3.651	0.951	3.635	0.862	0.328	0.185
<i>Nitzschia frustulum</i>	NI001A	57	27.9	16.4	3.180	0.628	3.189	0.609	0.104	0.078

<b>Diatom species name</b>	<b>Code</b>	<b>N. occ</b>	<b>Max %</b>	<b>N2</b>	<b>Optimum</b>	<b>Tolerance</b>	<b>Boot_Opt</b>	<b>Boot_Tol</b>	<b>SE_Opt</b>	<b>SE_Tol</b>
<i>Nitzschia graciliformis</i>	NI037A	6	12.0	2.0	3.046	0.232	3.015	0.228	0.142	0.160
<i>Nitzschia gracilis</i>	NI028A	21	3.6	7.6	3.276	0.473	3.264	0.421	0.174	0.124
<i>Nitzschia incognita</i>	NI008A	3	2.6	2.2	2.923	0.102	2.927	0.170	0.066	0.137
<i>Nitzschia inconspicua</i>	NI011A	10	2.9	4.2	3.984	1.011	3.852	0.793	0.462	0.236
<i>Nitzschia lacuum</i>	NI054A	15	19.9	5.3	4.411	1.133	4.302	0.998	0.469	0.307
<i>Nitzschia liebethuthii</i>	NI002A	36	89.2	3.4	3.765	0.477	3.666	0.431	0.196	0.067
<i>Nitzschia linearis</i>	NI026A	18	6.1	4.8	2.921	0.445	2.893	0.420	0.141	0.112
<i>Nitzschia microcephala</i>	NI015A	8	26.1	1.5	3.729	0.427	3.638	0.399	0.187	0.179
<i>Nitzschia obtusa</i>	NI020A	11	26.7	2.0	4.391	0.401	4.383	0.372	0.146	0.129
<i>Nitzschia palea</i>	NI004A	45	16.3	14.3	2.856	0.508	2.871	0.489	0.128	0.082
<i>Nitzschia paleacea</i>	NI034A	27	71.4	2.3	3.354	0.625	3.329	0.586	0.207	0.265
<i>Nitzschia pusilla</i>	NI013A	17	4.3	10.3	3.854	0.781	3.844	0.719	0.261	0.135
<i>Nitzschia radricula</i>	NI062A	6	2.8	3.2	2.716	0.330	2.718	0.255	0.163	0.104
<i>Nitzschia sigma</i>	NI016A	5	1.5	3.1	4.212	0.882	4.071	0.657	0.465	0.267
<i>Nitzschia solita</i>	NI018A	20	46.2	2.1	2.884	0.407	2.966	0.387	0.159	0.119
<i>Nitzschia tropica</i>	NI060A	7	0.7	6.4	2.834	0.542	2.850	0.526	0.178	0.216
<i>Nitzschia valdecostata</i>	NI019A	5	3.1	2.0	3.137	0.524	3.248	0.465	0.286	0.232
<i>Parlibellus crucicula</i>	NA040A	6	14.4	2.5	4.853	0.433	4.781	0.355	0.213	0.129
<i>Parlibellus cruciculoides</i>	NA024B	8	10.6	3.0	4.960	0.332	4.867	0.325	0.225	0.160
<i>Parlibellus cruciculoides</i>	NA026A	5	6.8	2.3	2.496	0.091	2.524	0.085	0.053	0.105
<i>Pinnularia appendiculata</i>	PI001A	7	2.1	4.8	3.167	0.392	3.142	0.306	0.160	0.120
<i>Pinnularia microstauron</i>	PI002A	20	1.4	10.8	3.100	0.617	3.102	0.562	0.202	0.102
<i>Planothidium delicatulum</i>	AC015A	12	3.8	3.5	2.791	0.528	2.818	0.473	0.198	0.138
<i>Planothidium lanceolatum</i>	AC003A	18	12.6	5.0	2.590	0.430	2.620	0.413	0.129	0.106
<i>Proschkinia bulnheimii</i>	NA042A	5	1.7	3.9	4.901	0.149	4.900	0.154	0.065	0.071
<i>Pseudostaurosira brevistriata</i>	FR001A	30	37.5	10.8	2.827	0.371	2.839	0.353	0.091	0.049
<i>Rhoicosphenia abbreviata</i>	RC001A	28	6.0	11.5	3.188	0.558	3.145	0.514	0.159	0.067
<i>Rhopalodia constricta</i>	RH003A	3	3.4	2.1	4.634	1.060	4.395	0.705	0.780	0.546
<i>Rhopalodia gibba</i>	RH001A	29	18.7	6.6	3.224	0.511	3.175	0.481	0.178	0.059
<i>Rhopalodia gibberula</i>	RH002A	3	5.4	1.2	3.562	0.345	3.475	0.281	0.182	0.135
<i>Rhopalodia operculata</i>	RH007A	6	5.2	3.3	4.326	0.353	4.268	0.325	0.182	0.115

Diatom species name	Code	N. occ	Max %	N2	Optimum	Tolerance	Boot_Opt	Boot_Tol	SE_Opt	SE_Tol
<i>Scoliopleura peisonis</i>	SC001A	8	10.0	1.9	3.764	0.631	3.608	0.507	0.321	0.176
<i>Sellaphora pupula</i>	NA009A	34	47.8	3.0	2.629	0.466	2.703	0.423	0.170	0.130
<i>Sellaphora seminulum</i>	NA013A	7	2.0	3.7	2.868	0.326	2.853	0.308	0.118	0.083
<i>Stauroneis anceps</i>	SA002A	4	1.1	3.4	2.465	0.318	2.506	0.306	0.157	0.076
<i>Staurosira construens</i> var. <i>binodis</i>	FR002C	5	2.4	2.8	2.482	0.442	2.561	0.316	0.225	0.119
<i>Staurosira construens</i> var. <i>construens</i>	FR002A	7	21.7	1.5	3.177	0.352	3.072	0.264	0.200	0.104
<i>Staurosira construens</i> var. <i>subsalina</i>	FR002D	5	14.8	1.6	3.071	0.149	3.080	0.157	0.076	0.083
<i>Staurosira construens</i> var. <i>venter</i>	FR002B	15	13.9	6.2	2.937	0.353	2.939	0.309	0.126	0.068
<i>Staurosirella lapponica</i>	FR010A	6	3.6	4.4	2.905	0.272	2.891	0.256	0.102	0.095
<i>Staurosirella leptostauron</i> var. <i>dubia</i>	FR006B	5	1.1	3.4	2.429	0.184	2.462	0.198	0.108	0.099
<i>Staurosirella pinnata</i>	FR004A	24	24.0	6.8	2.504	0.368	2.538	0.347	0.108	0.068
<i>Stephanodiscus</i> cf. <i>neoastraea</i>	ST001A	3	6.6	2.3	2.697	0.101	2.711	0.177	0.065	0.136
<i>Stephanodiscus hantzschii</i>	ST002A	6	27.4	2.4	2.969	0.156	2.923	0.158	0.094	0.073
<i>Stephanodiscus medius</i>	ST004A	7	2.0	2.8	2.754	0.306	2.774	0.274	0.127	0.127
<i>Stephanodiscus parvus</i>	ST003A	10	4.7	4.1	2.714	0.314	2.722	0.257	0.116	0.096
<i>Surirella brebissonii</i> var. <i>kuetzingii</i>	SU001B	3	2.7	1.3	3.047	0.094	3.019	0.163	0.056	0.147
<i>Surirella ovalis</i>	SU002A	3	3.4	1.9	3.052	0.184	2.980	0.258	0.210	0.159
<i>Tryblionella angustata</i>	NI010A	13	2.0	7.7	2.857	0.333	2.863	0.320	0.078	0.126
<i>Tryblionella apiculata</i>	NI022A	31	2.1	24.6	3.662	0.692	3.665	0.660	0.151	0.064
<i>Tryblionella calida</i>	NI032A	10	2.8	5.6	2.888	0.137	2.890	0.136	0.043	0.042
<i>Tryblionella compressa</i>	NI035A	3	73.5	1.2	4.541	0.636	4.290	0.423	0.390	0.189
<i>Tryblionella gracilis</i>	NI029A	10	1.3	6.1	3.139	0.458	3.143	0.429	0.146	0.089
<i>Tryblionella hungarica</i>	NI023A	32	4.7	13.6	3.683	0.704	3.676	0.677	0.172	0.063
<i>Ulnaria acus</i>	FR008A	20	10.1	6.5	3.235	0.501	3.187	0.429	0.204	0.112
<i>Ulnaria ulna</i>	FR007A	40	4.9	14.1	3.044	0.365	3.036	0.358	0.065	0.055

## Appendix 2

Table 6

List of estimated ostracod optima, tolerance range (2SD) and bootstrapped error estimates, for all taxa; tolerance range is deleted for taxa with single occurrence

Ostracod species name	Code	N. occ	Max %	N2	Optimum	Tolerance	Boot_Opt	Boot_Tol	SE_Opt	SE_Tol
<i>Bradleystrandesia reticulata</i>	Brret	1	38.5	1.0	3.045					
<i>Candona angulata</i>	Caang	12	100.0	8.0	3.126	0.529	3.144	0.510	0.161	0.108
<i>Candona candida</i>	Cacan	4	17.2	3.7	2.647	0.325	2.608	0.323	0.172	0.055
<i>Candona neglecta</i>	Caneg	16	97.2	10.6	2.899	0.400	2.918	0.378	0.113	0.058
<i>Cyclocypris laevis</i>	Cylae	3	14.7	2.3	2.596	0.439	2.659	0.338	0.231	0.104
<i>Cypria ophthalmica</i>	Cyoph	4	30.4	2.4	2.579	0.314	2.554	0.247	0.173	0.136
<i>Cyprideis torosa</i>	Cptor	4	100.0	2.0	4.319	0.765	4.229	0.472	0.388	0.266
<i>Cypridopsis vidua</i>	Cdvid	16	37.1	9.0	2.771	0.386	2.785	0.359	0.111	0.070
<i>Cypris pubera</i>	Cspub	4	24.1	2.2	3.191	0.330	3.229	0.235	0.184	0.118
<i>Darwinula stevensoni</i>	Daste	8	71.8	3.4	2.670	0.254	2.703	0.201	0.120	0.060
<i>Eucypris mareotica</i>	Eumar	3	99.6	2.0	4.565	0.183	4.374	0.300	0.414	0.218
<i>Eucypris virens</i>	Euvir	2	7.7	1.1	3.071	0.378	3.217	0.355	0.236	0.106
<i>Fabaeformiscandona fabaeformis</i>	Fafab	3	29.1	1.7	2.617	0.435	2.807	0.308	0.283	0.131
<i>Herpetocypris chevreuxi</i>	Heche	2	4.0	1.4	3.126	0.193	3.079	0.293	0.113	0.131
<i>Heterocypris cf. bulgarica</i>	Htbul	2	94.3	2.0	3.765	0.173	3.757	0.278	0.088	0.134
<i>Heterocypris incongruens</i>	Htinc	4	4.0	2.9	3.980	1.033	3.859	0.671	0.505	0.304
<i>Heterocypris salina</i>	Htsal	17	94.0	8.1	3.969	0.559	3.959	0.533	0.171	0.097
<i>Ilyocypris bradyi</i>	Ilbra	18	59.8	10.7	3.005	0.473	3.028	0.463	0.132	0.090
<i>Ilyocypris decipiens</i>	Ildec	1	3.8	1.0	2.394					
<i>Ilyocypris gibba</i>	Ilgib	15	46.0	7.8	3.193	0.520	3.199	0.488	0.108	0.122
<i>Ilyocypris monstifrica</i>	Ilmon	8	84.4	3.4	3.307	0.453	3.323	0.420	0.173	0.149
<i>Isocypris beauchampi</i>	Isbea	4	41.4	1.3	2.956	0.046	2.941	0.115	0.025	0.156
<i>Limnocythere inopinata</i>	Liino	19	99.3	11.0	4.186	0.592	4.152	0.570	0.167	0.076
<i>Lincocythere af. dubija</i>	Lcdub	1	10.3	1.0	2.965					
<i>Physocypris kraepelini</i>	Phkra	13	93.2	5.3	2.758	0.370	2.780	0.385	0.112	0.112
<i>Plesiocypridopsis newtoni</i>	Plnew	3	6.3	2.7	3.044	0.307	3.078	0.306	0.165	0.136
<i>Potamocypris arcuata</i>	Poarc	1	4.3	1.0	3.580					
<i>Potamocypris unicaudata</i>	Pouni	2	17.1	2.0	2.936	0.043	2.934	0.240	0.023	0.189
<i>Potamocypris villosa</i>	Povill	1	2.5	1.0	2.444					
<i>Potamocypris zschokkei</i>	Pozsc	2	30.8	1.1	2.412	0.209	2.484	0.266	0.125	0.131
<i>Prionocypris zenkeri</i>	Przen	1	3.3	1.0	2.763					
<i>Pseudocandona af. compressa</i>	Pscom	2	2.8	2.0	2.523	0.107	2.523	0.277	0.060	0.156
<i>Pseudocandona marchica</i>	Psmar	10	51.7	5.5	2.933	0.717	2.990	0.651	0.269	0.123

Ostracod species name	Code	N. occ	Max %	N2	Optimum	Tolerance	Boot_Opt	Boot_Tol	SE_Opt	SE_Tol
<i>Sarocypridopsis aculeata</i>	Saacu	1	1.1	1.0	3.958					
<i>Trajancypris clavata</i>	Trcla	1	1.2	1.0	3.580					
<i>Trajancypris serrata</i>	Trser	1	45.9	1.0	2.903					

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