INHOUD nr. 39 DECEMBER 2015

... van de voorzitter 3
Verslag van de NVKD bijeenkomst in Mont Rigi (België) 4-6 juni 2015.....5
Verslag van de 6de taxonomische workshop van de NVKD:
Navicula cryptocephala & co 8
Verslag ledenvergadering NVKD op vrijdag 5 juni 2015 bij Mont Rigi, België.10
Kort jaaroverzicht 2014 12
Studentenbeurzen voor NVKD studiedagen in Utrecht, Nederland
19-21 mei 2016 13

Artikelen

The Plateau of the Hautes Fagnes.....15
by Louis Leclercq
As time goes by
Veranderingen in soortconcepten in relatie tot analyseprotocollen
en ecologische beoordelingen.....19
door G.L. Verweij, J.H. Wanink & F.A.C. Kouwets
Diatoms and their environment in lime-rich springs in The Netherlands 29
by Herman van Dam, Bert Pex & Harry Boonstra
Development of Diatom-Based models for Inferring Salinity in Dutch
wetlands 31
by Alejandra Goldenberg-Vilar, Timme Donders, Gert van Ee & Friederike Wagner-Cremer
Aquatic ecosystem shifts in response to early human land-use in two low-elevation lakes in northwestern Europe.....41
by Keechy Akkerman, Timme H. Donders, Wim Z. Hoek & Aleksandra Cvetkoska
Diatom response and planktonic diversity in ancient lakes under the pressure of Quaternary climate change: lessons learned from lakes Ohrid and Prespa 57
by Aleksandra Cvetkoska, Elena Jovanovska, Zlatko Levkov & Friederike Wagner-Cremer

The diatom flora of Lake Kinneret (Israel). Palaeolimnological evidence for holocene climate change and human impact in the southeastern Mediterranean.73
Door Hannah Vossel

Rubrieken

Nieuwe literatuur 2016 85
Congressen 2016.....90

... van de voorzitter

Beste diatomisten,

Gefeliciteerd Dr. Vos met je doctorstitel! Op 10 juni jl. promoveerde Peter Vos, penningmeester en medeoprichter van de NVKD, op de ontwikkeling van het Nederlandse kustgebied in het Holoceen. Op die dag verdedigde Peter zijn proefschrift '*Origin of the Dutch coastal landscape*' in de uiterst sfeervolle senaatszaal van het Academiegebouw aan het Domplein te Utrecht. De senaatszaal barstte uit zijn voegen zodat een deel van de toehoorders de plechtigheid vanuit een andere zaal via een videoscherm moest volgen. Onder de velen familieleden, vrienden en collega's was ook een afvaardiging van de NVKD met Gert van Ee, Herman van Dam, Adrienne Mertens, Gerhard Cadée en de schrijver van deze rubriek om Peter te feliciteren.

Peter, de NVKD wenst je na het bereiken van dit mijlpaal ook in de toekomst veel enthousiasme en succes met het reconstrueren van het Nederlandse paleolandschap. Leuk dat de diatomeeën nog steeds een klein deel bij mogen dragen aan dit werk.

Impressies van Peter's promotie. Overhandiging van de promotieoorkonde in de senaatszaal (links), receptie in het Pandhof van de Dom (midden) en op een glas bier met zijn vrouw Willy (rechts).

Het hoogtepunt van ons verenigingsjaar waren uiteraard de studiedagen op het Station Scientifique des Hautes Fagnes in Mont Rigi. Louis Leclercq, de stationsleider, was een uitstekende gastheer (Dank Louis!) en heeft ons op zaterdag een leuke wandeling in de Vallei De Hoëgne voor de laarzen geschoteld. In de verschillende rubrieken van dit nummer leest u zoals gebruikelijk meer over de 6de taxonomische workshop, de lezingendag en de ledenvergadering.

Als gastspreker mochten wij Frédéric Rimet uit Thonon-les-Bains verwelkomen die een tot veel discussie leidende presentatie gaf over de toepassing van diatomeeënbarcoding in waterkwaliteits-analyses.

Ook heeft de NVKD dit jaar voor het eerst studiebeurzen voor studenten aangeboden. Eveline Pinseel (Gent), Keechy Akkerman en Karlijn Smit (beiden Utrecht) konden dankzij de beurs van 200 euro afreizen naar Mont Rigi. De NVKD hoopt op deze manier in de toekomst meer studenten naar de studiedagen te kunnen lokken.

Tenslotte wil ik Jako van der Wal (AQUON) feliciteren die tijdens de ledenvergadering in Mont Rigi gekozen werd tot bestuurslid van de NVKD. Op de volgende bestuursvergadering in November gaan we zien welke taken je op je gaat nemen in de komende jaren. Welkom Jako!

Ik wens jullie weer inspirerend leesplezier met nr. 39 van *Diatomededelingen*!

Holger Cremer
Voorzitter NVKD

Verslag van de NVKD bijeenkomst in Mont Rigi (België) 4-6 juni 2015

Gert Van Ee (secretaris NVKD)

De jaarlijkse driedaagse bijeenkomst van de NVKD vond dit jaar plaats op een bijzondere locatie. We waren te gast op het Station Scientifique des Hautes Fagnes, Rue de Botrange, Mont Rigi. Gastheer dr Louis Leclercq ontving ons hier op uitstekende wijze en zorgde voor een onvergetelijke bijeenkomst. Het biologisch station ligt op een schitterende locatie op de hoogvlakte in de Hautes Fagnes. Met 30 deelnemers uit België, Nederland en Frankrijk, waarvan 23 leden, was deze bijeenkomst zeer goed bezocht. Ook deze bijeenkomst kende de inmiddels traditionele indeling in drie verschillende dagen: donderdag 4 juni de taxonomische studiedag, vrijdag 5 juni de lezingendag en zaterdag 6 juni de excursie.

Figuur 1. Deelnemers aan de NVKD bijeenkomst 4-6 juni 2015 in Mont Rigi.

De taxonomische studiedag, de zesde inmiddels alweer, werd goed bezocht met 16 deelnemers. Onder leiding van Bart Van de Vijver werd het soortcomplex van de lastige *Navicula cryptotenella* en *N. cryptocephala* groep besproken. Met veel aandacht werden de verschillen, die vaak gering zijn, besproken. De workshop wordt door Bart altijd zeer goed voorbereid en t.z.t. komt hiervan een werkboek op de website te staan.

Op vrijdag 5 juni was de lezingendag. We werden welkom geheten door dr Louis Leclercq, waarna de lezingen begonnen. Er waren zeven lezingen met als hoofdgast Frédéric Trimet uit Frankrijk van de Université Savoie Mont Blanc, Institut National de la Recherche Agronomique (INRA), Laboratoire de biodiversité et de biologie moléculaire in Thonon-les-Bains aan het meer van Geneve (Lac Leman). Zijn voordracht was over een belangrijke nieuwe ontwikkeling over het gebruik van DNA technieken bij diatomeeën voor bepalen van de waterkwaliteit.

Figuur 2. Aandacht voor de lastige soorten uit het genus *Navicula* in Mont Rigi.

Na de lunch en de ledenvergadering (zie het verslag elders in dit nummer) was het de beurt aan Geurt Verweij (Koeman en Bijkerk, Haren, Groningen). Hij ging in op de vraag of veranderende naamgeving zorgt voor effecten op tellingen en ecologische beoordeling systemen. Hannah Vossel van de Universiteit van Bonn (Duitsland) besprak de diatomeeënflora van Lake Kinneret (Israël) waarbij de diatomeeën werden gebruikt als bewijs voor klimaatveranderingen in het holoceen en menselijke beïnvloeding van het milieu. Keechy Akkerman (Universiteit Utrecht) vertelde over vroege menselijke beïnvloeding van de waterkwaliteit in twee meren: Llangorse Lake (Wales, UK) en het Hijkermeer (Nederland).

Na de pauze was Aleksandra Cvetkoska van de Universiteit Utrecht aan de beurt met een lezing over lessen die konden worden getrokken uit klimaatverandering in het Kwartair en de reactie hierop van diatomeeën en fytoplankton in de meren Lake Ohrid en Lake Prespa. Tenslotte vertelde Herman van Dam (Water en Natuur, Amsterdam) over onderzoek naar de diatomeeënflora in kalkrijke bronnen in Limburg.

Na de lezingen was het heerlijk ontspannen op het terras van het naast gelegen restaurant Mont Rigi in de warme zon met een heerlijk biertje. Nadat iedereen was opgefrist genoten we van het diner. Later op de avond werden we verrast door een pittig onweer en vanuit het biologisch station was dit prachtig te zien. Buiten zitten in de donkere uurtjes werd verstoord door knutjes, die in groten getale opdoken; iedereen die nog nooit met deze zeer kleine bijtende insecten had kennis gemaakt weet nu ook wat dit zijn.

Zaterdag 6 juni was de excursie. Na een uitgebreide inleiding op het station over het landschap, het ontstaan, de geologie, hydrologie en de invloed van de mens (bosbouw) door dr Louis Leclercq gingen we met de auto naar de prachtige vallei van de rivier de Hoëgne. Er was een prachtige wandeling langs het riviertje waar af en toe werd stilgehouden en Louis Leclercq ons vertelde wat we hier konden zien aan bijzonderheden in de geologie, maar ook aan bijzondere plantensoorten. Een enkeling nam de gelegenheid om diatomeeën stalen te nemen. Eveline Pinseel verzamelde stalen voor haar onderzoek naar de sterk verkiezelde *Pinnularia borealis* groep. Na de

wandeling werd er heerlijk geluncht en nam iedereen weer afscheid van elkaar. Opnieuw een zeer geslaagde bijeenkomst op een dit keer heel bijzondere plaats.

Figuur 3. Links: Eveline Pinseel neemt stalen voor haar onderzoek aan het *Pinnularia borealis* complex. Rechts: een van de prachtige bronnetjes in de wand langs de rivier.

! WANTED !

BIJDRAGEN voor DIATOMEDEDELINGEN

Het bestuur van de NVKD verzoekt iedereen om stukjes te schrijven voor Diatomededelingen. Dat kan gaan over onderzoek, nieuwe of interessante vondsten, een anekdote of elk ander diatomeeën-gerelateerd onderwerp. Doel is om Diatomededelingen verder uit te bouwen tot een leuk en leesbaar tijdschrift met iets meer dan de huidige kopij. Voor vragen of inlichtingen graag even een mailtje naar Holger Cremer of Bart Van de Vijver.

Verslag van de 6de taxonomische workshop van de NVKD: *Navicula cryptocephala* & co

Frans Kouwets (lid NVKD)

Nadat in vier opeenvolgende jaren de studiedagen van de NVKD in Nederland waren gehouden waren we dit jaar weer eens te gast in België, en wel in het fraai gelegen Station Scientifique des Hautes Fagnes, bij Robertville (Mont Rigi) in de Ardennen. Vast onderdeel van de studiedagen en welhaast een voorjaarsklassieker is de taxonomische workshop. Bij de afsluiting van de 5de workshop was reeds aangekondigd dat dit keer de groep kleinere *Navicula*'s rond *N. cryptocephala* onder de loep zou worden genomen, en zo geschiedde!

Voor deze workshop, op 4 juni, hadden zich 16 mensen opgegeven. Toen de koffie op sterkte was konden we beginnen. De openingszin was dit jaar:

Once upon a time, there was a dustbin genus … and it was called …

In samenwerking met een hele trits experts uit binnen- en buitenland had Bart Van de Vijver een gedetailleerd overzicht samengesteld van zes verschillende groepen *Navicula*'s waarvan er drie dit jaar zouden worden behandeld; de overige drie zijn vast gereserveerd voor de workshop in 2016. Het bijbehorende cursusboek leek nog dikker dan de andere jaren, dus dat beloofde wat, maar het bleek dat dit jaar éénzijdig was gekopieerd, en dat scheelde gelukkig de helft …

Allereerst werd een korte uitleg gegeven over het ontstaan van de Voigt fault, een onregelmatigheid in het patroon van striae aan de zogeheten secondary side van een schaaltje, een gevolg van de typische wijze waarop een nieuw schaaltje uitgroeit. Afbuiging van de proximale raphe-einden ten opzichte van de secondary side van het schaaltje bepaalt of de desbetreffende soort in de secie *Navicula*, of in de sectie *Alinea* thuishoort.

Vervolgens werden soortgroepen rond *N. cryptocephala*, *N. cryptotenella* en *N. cincta* tegen het licht gehouden, waarbij dankbaar gebruik gemaakt kon worden van typemateriaal van een aantal soorten (waarbij bleek dat zelfs van gerenommeerde specialisten de preparaten niet steeds de schoonheidsprijs verdienden …). Als een van de belangrijke kenmerken bij het determineren werd de breedte van de schaaltjes aangegeven.

Na de – voortreffelijke! – lunch in de naastgelegen Brasserie, die de liefhebbers vergezeld lieten gaan van een "bière Gilles", was het tijd het meegebrachte materiaal te bekijken. Met name wat betreft de onderlinge verschillen bij het koppel *N. lundii* / *N. exilis* ontspon zich een levendige discussie, waarbij kon worden geconcludeerd dat ook in veelgebruikte handboeken de determinaties niet altijd kloppen!

's Middags vijf uur begon het interne geheugen van de meeste deelnemers vol te raken en werd besloten vóór het diner nog even van het fraaie weer en de fantastische omgeving te gaan genieten. Het was wederom een bijzonder leerzame workshop, waarbij in korte tijd een flink aantal meer of minder sterk op elkaar lijkende soorten kon worden bestudeerd en bediscussieerd. Ik geef me hierbij vast op voor deel II volgend jaar!

Verslag ledenvergadering NVKD op vrijdag 5 juni 2015 bij Mont Rigi, België

Gert van Ee (secretaris NVKD)

1. De voorzitter Holger Cremer opent de vergadering om 14.00 u en heet iedereen welkom. Op de agenda wordt na punt 12 (beurzen voor studenten) een extra punt ingevoegd: de toekomst van diatomeeën onderzoek.
Algemeen. Het aantal leden mag wel toenemen. Er zijn vandaag in Mont Rigi 23 leden en 7 niet leden aanwezig en er zijn weinig niet-professionals lid. In totaal zijn er 52 NVKD leden en 10 instituut leden. Punt voor de komende bestuursveragdering.

2. Het verslag van de ledenvergadering van 16 mei 2014 staat in Diatomededelingen 38: p. 9-12. Met dank aan Caroline Souffreau die bij afwezigheid van de secretaris dit heeft opgemaakt.

3. De secretaris geeft een kort jaaroverzicht over 2014; zie elders in dit nummer van Diatomededelingen 39.

4. Financieel overzicht. Bij afwezigheid van Peter Vos geeft voorzitter Holger Cremer toelichting op het jaaroverzicht en een vooruitblik op de begroting van komend jaar. Het gaat de vereniging financieel goed. Dit mede dankzij onze (meestal) gratis onderkomens voor de bijeenkomst, waardoor we relatief weinig onkosten maken. We denken na over besteding van (een deel) van het geld (o.a. beurzen voor studenten).

5. De kascommissie doet verslag over 2014, de boeken zijn in orde. Zij stelt voor de penningmeester voor zijn goede beleid te dechargeren, hetgeen door de vergadering wordt gedaan onder applaus en met dank.
Adrienne Mertens treedt na twee jaar af en Arthur van Dulmen zal haar vervangen voor 2016 en 2017; Marianne Thannhauser blijft nog in 2016 in de kascommissie.

6. Bestuursverkiezing. Het bestuur heeft besloten op haar laatste vergadering op 26 september 2014 om Jako van der Wal te vragen toe te treden tot het bestuur. De leden stemmen hiermee in onder applaus en we wensen Jako een goed tijd toe in het bestuur.

7. De website wordt te weinig bezocht. Dat is jammer; leden en anderen kunnen hier veel nuttige informatie vinden. Bert, webmaster, werkt aan modernisering van de website en wordt hierbij ondersteund door Caroline Souffreau.

8. Taxonomische workshop 4 juni. Deze wordt opnieuw verzorgd door Bart Van de Vijver. Frans Kouwets zal een verslag hiervan maken voor Diatomededelingen 39. Bart vindt het een nuttige en leuke manier om kennis over te brengen en afstemming te bewerkstelligen tussen de deelnemers over determinatieproblemen. Ook in 2016 zal hij

een workshop geven; onderwerp is dan de groep rond *Navicula veneta* en *N. tenelloides*. Daarna in 2017 en verder komen ook centrische groepen aan bod: *Melosira, Aulacosira.*

9. Ringtest. Bart verzorgt opnieuw een ringtest (opgeven bij Bart). In 2016 zal Bart hiervan verslag doen op de studiedagen.

10. Webbased taxonomie. Nog veel onduidelijkheden. Er is weinig tijd en ruimte (financiën) om dit in gang te zetten. Wordt vervolgd.

11. Diatomededelingen 39. Streven is dit nummer voor de kerst uit te brengen.

12. NVKD beurzen. Studenten (per keer maximaal vijf) kunnen een tegemoetkoming in geld aanvragen bij het bestuur voor deelname aan de studiedagen. In Mont Rigi is hiervan gebruik gemaakt door drie studenten.

12b. Toekomst van diatomeeën onderzoek. Het onderzoek komt door verschillende oorzaken onder druk. Vanwege de tijd wordt dit verder besproken bij "pot en pint".

13. Rondvraag. Ronald Bijkerk. Peter Vos zal gaan promoveren binnenkort; kan de NVKD zorgen voor een passend cadeau? Antwoord: de NVKD zal voor een passend cadeau zorgen.
Bart: in 2016 bestaat de NVKD 30 jaar. Zijn er ideeën voor een jubileum bijeenkomst? Antwoord: het bestuur zal dit in de komende bestuursvergadering verder uitwerken, maar ideeën van leden zijn zeer welkom!

De voorzitter sluit de vergadering en dankt alle aanwezigen voor zijn of haar bijdrage.

Kort jaaroverzicht 2014

Gert van Ee (secretaris NVKD)

Het jaar 2014 is goed verlopen met als hoogtepunt de bijeenkomst in Leiden in mei en het verschijnen van Diatomededelingen 38 in december.

Het aantal leden is gegroeid! Dat is goed nieuws. In 2014 zijn er 4 nieuwe leden bijgekomen: twee uit Belgie, één uit Nederland en één uit Zweden. Hierdoor komt het aantal leden op 51. Daarnaast zijn er tien instituten lid van de NVKD. Het actualiseren van het ledenbestand wordt verder doorgezet in 2015. Wanneer u wijzigingen heeft in werkplek, adres, mailadres of anders, graag doorgeven aan de secretaris.

De bijeenkomst in Leiden bij Aquon van 15 tot 17 mei was een groot succes. Het verslag is terug te vinden in Diatomededelingen 38. Ook is hierin het verslag opgenomen van de 5e taxonomische workshop door Prof. Dr. Bart Van de Vijver evenals het verslag van de ledenvergadering op 16 mei. De organisatie was in handen van Jako van der Wal.

In Diatomededelingen 38 wordt bekend gemaakt dat we studenten willen aanmoedigen om naar de bijeenkomsten van de NVKD te komen door middel van een beurs. Deze kunnen ze aanvragen bij het bestuur.

Er is in Diatomededelingen 38 ook een oproep geplaatst om artikelen te maken voor Diatomededelingen. Hierbij kunt u hulp krijgen van bestuursleden als dat nodig is. Er worden veel interessante zaken gevonden die het vermelden waard zijn en leuk zijn om te delen met collega diatomisten.

Op de website van de NVKD www.diatom.nl is van alles te vinden: studiedagen, de cursusboeken van de workshops, nieuws over diatomeeën, bijeenkomsten in binnen- en buitenland, microscopie, etc. Ook is de bibliotheek hier te vinden met honderden titels van diatomeeën literatuur. U kunt die opvragen bij Caroline Souffreau.

Op de bestuursvergadering in september 2014 zijn voorbereidingen getroffen voor de bijeenkomst in 2015 in de Hautes Fagnes van 4-6 juni 2015. We zijn hier eerder te gast geweest in het biologisch station van de universiteit van Luik in deze prachtige omgeving.

Studentenbeurzen voor NVKD studiedagen in Utrecht, Nederland 19-21 mei 2016

De Nederlands-Vlaamse Kring van Diatomisten (NVKD; www.diatom.nl) is dé netwerkvereniging voor diatomeeëndeskundigen in Nederland en België met zo'n 60 leden. Hoogtepunt van het verenigingsjaar zijn de studiedagen – telkens georganiseerd van donderdag tot zaterdag – bestaande uit drie onderdelen: een taxonomische workshop op donderdag, een lezingendag en diner op vrijdag en een excursie op zaterdagvoormiddag. Elk jaar worden de studiedagen op een schitterende locatie in Nederland of België gehouden.

De NVKD wil meer jonge diatomisten aantrekken en biedt daarom in 2016 vijf beurzen aan gemotiveerde studenten om deel te nemen aan de NVKD studiedagen op 19-21 mei 2016 in Utrecht (Nederland). Dit geeft studenten te kans om te proeven van diatomeeënonderzoek in de Lage Landen en om de NVKD collega's te leren kennen.

Beurzen

De NVKD stelt in totaal 5 beurzen, elk ter waarde van 100-200 € ter beschikking. De beurs is bedoeld om de reis-, verblijf- en accommodatiekosten van de student te bekostigen. Alle studenten, ingeschreven bij een universiteit en nog niet gepromoveerd/gedoctoreerd, komen in aanmerking.

Procedure

Geïnteresseerde studenten kunnen tot 28 februari 2016 een brief sturen naar de voorzitter van de NVKD, Holger Cremer (holger.cremer@tno.nl) met daarin een kort CV van de student, een attest van hum promotor en hun motivatie voor het bezoek van de studiedagen (max. 300 woorden). Alle aanvragers krijgen voor 31 maart 2016 bericht over de honorering van de beursaanvraag.

Informatie NVKD

Bij de voorzitter Holger Cremer (holger.cremer@tno.nl; +31 6 52803590) of via de NVKD website (www.diatom.nl). Nummers van de Diatomededelingen, het tijdschrift van de NVKD, zijn via de website verkrijgbaar.

Diatomededelingen 39, 2015

The Plateau of the Hautes Fagnes

Louis Leclercq (gebaseerd op een tekst van René Schumacker)

Station Biologique de Mont Rigi, Eupen, België

Introduction

The plateau of the Hautes-Fagnes extends from latitudes 50° 10' to 50° 25' N and from longitudes 5° 45' to 6° 25'.

lt occupies the highest elevations, much smoothed down by erosion, of the northeastern extreme of the Ardennes massif, on very hard rocks, which date back some 650 million years.

The exact geographical boundaries of the region which cornes under the term "Hautes-Fagnes" are difficult to trace. Roughly speaking, the region in question is situated at an altitude of over 450 m in the area boundered by the Vesdre valley to the N.W. and N.E., and by that of the Ruhr and the Warche in the S.E. and the south. In the west, it is marked by the middle Amblève and the Winamplanche. The topography, heavy rainfall, severe climate and poor soils with impeded drainage have determined for almost 10,000 years the development of humid to marshy woodland and the development of marshes and sphagnum bogs over considerable areas. Southwards the boundary is clearly defined by the drastic change in geological strate in contact with the Ruhr and the Warche (a transition from the hard, poor Cambrian rocks to the richer, more softer Ordovician and Lower Devonian ones). Northwards the Cambrian massif extends forth with rapidly decreasing altitude as far as the vicinity of the Vesdre valley. There, the peaty formations become discontinuous and the boundary is more difficult to trace.

The term "Hautes-Fagnes", in fact of relatively recent origin, has gradually come to embody the whole area of vast moorland and peatland opened up by extensive agriculture until the twentieth century, within the perimeter of Eupen, Verviers, Spa, Trois-Ponts, Malmedy, Fringshaus and Mützenich.

The word "Fagnes" is most often applied in a very wide sense, covering not only the marshy or peaty parts, but also the heaths and moors. In other words, the ensemble of non-forested and non-agricultural territory.

Similar landscapes, but with a much more limited expanse, existed and can still be found on the other highlands of the central Ardennes (Plateau des Tailles) and of the southern Ardennes (Croix-Scaille and Plateau des Hautes Buttes).

Until the beginning of the 20th century the Hautes-Fagnes always appeared to the visitor as a treeless open landscape, seemingly harsh and wild.

This was, and still is, for what remains, nothing other than a huge artifact stemming from the activity of man, coming to settle on the immediate periphery of the plateau some ten centuries ago.

The plateau itself, too inhospitable for habitation and particulary for the indispensable cultivation of cereals, lent itself nonetheless to exploitation as extensive grazing land and for the production of hay, wood and peat.

I dare say few walkers realise that barely a thousand years ago the fagne territory demarcated above, was wooded over more than 90% of its area: namely with white woodrush-beech forest, mixed birch-pedunculate oak forest with birch and purple moorgrass and carrs of black alder and downy birch.

Only a few zones covered by more than a metre of peat, where the water table was constantly maintained very close to the ground surface, were not wooded, namely some hundred hectares at the centre of the great peaty areas of what are today called the Fagne Wallonne, those of Clefaye, the Deux-Séries and the Misten.

Such Fagnes as those of Malchamps or those which extend to the north of the Eupen-Monschau road, were, before man's arrival on the plateau, completely overrun by deciduous forests.

The combination of the geographical location and the peculiarities of the soil and the climate, have given rise to the growth of a variety of vegetation, particularly peatbogs, which preserve elements of the faune and flore that withdrew into the boreal regions or into mountains or subalpine regions when the ice-caps of northern Europe retreated.

But, just beside and often intermixed with them, are oceanic elements, whose optimum lies along the Atlantic seaboard.

Crossroads of contradictory climatic influences, location of physical extremes, the Hautes-Fagnes constitute an islet rich in floristic, faunistic and scenic elements, quite removed from their main area of distribution in the North of Europe.

The climate

The north-western flanc of the plateau ascends rather sharply from the Vesdre valley, at about 250 to 280 m altitude, up to the ridge which stretches at great length between Malchamps and Hoscheid, from 550 to 694 m altitude. This constitutes the first obstacle encountered by the masses of damp air of oceanic origin. Forced to rise rapidly, they expand and consequently cool down, causing condensation of water vapeur. Microscopic droplets (mists), drops (of rain) or ice crystals (snow) form and fall onto the ground. Therefore the north-western flanc and the summit are more frequently, and above all more abundantly, watered than the Vesdre valley in the north or the Elsenborn plateau in the South-eastern rear.

On the ridge of the "Baraque-Michel - Botrange (670 to 694 m high) an average rainfall of 1,318 mm is recorded with extremes ranging from 670 mm to 1,890 mm. The Eifel, close at hand, and of similar altitude, only receives half as many precipitations.

As a rule, precipitation reaches a maximum in July and December and a minimum in March and October.

An outstanding feature of the Fagne climate is the significant snowfall which represents nearly a quarter of the total precipitation. The snow, with a depth rarely surpassing 60 cm, is often divided into three periods, the main phase centres around the months of January and February, and the other two – sometimes scanty – around November and December, and March and April. An average snowfall of 43 days a year is recorded, with extremes ranging from 17 to 72 days.

In addition to this directly measurable precipitation, there are other kinds, more subite, but not negligible, which make up another outstanding feature of the fagne climate: the mists which preside for over 150 days a year, the dew and finally the hoar-frosts whose white-sheets sometimes reach a thickness of 5 centimetres.

Even if the snowy blanket and the frost are normally interrupted by milder periods, the winter is nonetheless long and severe, often knocking at the door on All Saints Day, to set its foot firmly on the ground from December to April and only to make a definite retreat alter the 15th April and sometimes the 15th May.

The frost makes its presence felt for 90 to 120 days per year and frozen soil can even be recorded in summer. Extremely cold temperatures, below -20°C, are not uncommon.

Il is hardly surprising then that despite the fairly modest altitude, the plateau experiences a particularly low average temperature of 6,1°C; the January mean maximum temperature is only 1.51, that of July 18.2°C.

The relative coolness in summer must be seen in relation to the importance of the bogs, marshes and dense coniferous plantations, whose intense evapotranspiration during the vegetation period, gives rise to a notable cooling down of the atmosphere, near the ground.

In general, the climate of the plateau manifests an oceanic and a boreal character alike.The crest of the Hautes-Fagnes is also a privileged focal point for the masses of hostile air, both warm and cold, of high or low pressure. The war of the winds is not an unusual occurrence there, which, besides the breath-taking spectacles it presents, brings about rapid changes in temperature: depending on the case in question, the sky may cloud over or clear in a few seconds, the rain or snow may beat down or abruptly cease, the fog may envelop air or mysteriously fade away, the wind may get up or suddenly die down.

Thus, here the prudent walker will always be well-equipped with cloches for every eventuality.

Remnants of the fast ice-age

How often has one evoked the ice islet of the Baraque-Michel, so dear to the Professors Leon Fredericq and Kurt Stamm, on the basis of biological and geomorphological arguments.

There is no longer any substance to the serious scientific argument in favour of the belief that an ice cap covered the plateau during the last ice-age. On the contrary, various geomorphological features notably remnants of palsas and scree slopes, testify to the effects of the periglacial climate which reigned some 10,000 years ago. The climate was like that of the tundra today, less than 500 km from the edge of the ice cap.

"Viviers", traces of palsas

These can be spotted in their hundreds all along the Malchamps to Hoscheit crest where they appear in the shape of circular hollows (averaging 80 m in diameter) or elongated ones (250 m long on more), offert densely vegetated, surrounded by an outer wall raised by several metres higher up, a wall which clearly stands out in the serial photographe by reason of the darker shades of moorland vegetation which develop there.

Formerly considered as the work of prehistoric man, we now know, thanks to the research of Professer A. Pissart, that they result from the formation of huge ice wedges at a shallow depth under the ground. In semi-permanently frozen soils with fine-textured particles, the water moves within the soil towards the frozen surface and accumulates in wedges of ice. The ensuing increase of volume during the continuation of the process over several thousand years, pushes or ejects the materials outwards. With the advent of a progressively less harsh climate, the wedges of ice melted: what remains is the hollow and the outer wall, or rampart.

The scree slopes and erratic boulders

Made up of fairly abundant piles or traits of rocky boulders of quartzite or sandstone, but sometimes larger than one cubic metre in site, are sited in very numerous places on the plateau. Once considered to be remnants of moraines, they in fact result from the phenomena of solifluxion in a periglacial climate. During periods of thaw, the soil surface, saturated in melting water, is transformed into a muddy mass slowly sliding down the slopes, even gentle ones, over the frozen subsoil. The rocky materials gradually brought to the surface by means of the alternating freezes and thaws, are transported towards the gullies which they clog up as they accumulate there.

The advent of a milder, welter climate will then release them from their muddy matrix, which is rapidly transported downstream. Today, the largest accumulations are located on the soil surface, where there is a change of slope, and on the alluvial plain of most of the fagne streams. In the valleys of the largest streams, they still presently undergo an active transportation which shifts them somewhat speedily over hundreds of metres

Diatomededelingen 39, 2015

As time goes by

Veranderingen in soortconcepten in relatie tot analyseprotocollen en ecologische beoordelingen

G. L. Verweij[1], J.H. Wanink[1] & F.A.C. Kouwets[2]

[1]Koeman en Bijkerk bv, Postbus 111, 9750 AC Haren
[2]Rijkswaterstaat CIV, Zuiderwagenplein 2, 8224 AD Lelystad

Inleiding

De indruk bestaat dat er tegenwoordig meer soorten in de kiezelalgmonsters worden aangetroffen dan twintig jaar geleden. Is deze stijging een gevolg van veranderingen in de waterkwaliteit, of is het een gevolg van de veranderingen in de soortconcepten? In de jaren negentig van de vorige eeuw konden diatomeeënanalyses nog worden uitgevoerd met behulp van de vier "groene boekjes" (Krammer & Lange-Bertalot, 1986, 1988, 1991a, 1991b). Tegenwoordig zijn ongeveer vijftien determinatieboeken en aanvullende artikelen noodzakelijk om soorten juist op naam te brengen.

Als de stijging van het aantal waargenomen soorten wordt veroorzaakt door de nieuwe soortconcepten, moeten we ons dan niet de vraag stellen of de huidige analyseprotocollen nog wel voldoen? En hebben de veranderingen in soortconcepten ook hun weerslag op de uiteindelijke ecologische beoordeling? Om deze twee vragen te beantwoorden, is een experiment opgezet waarvan we hier de eerste resultaten presenteren.

Hypothese

Als bij hertelling van een kiezelalgmonster meer taxa worden waargenomen dan twintig jaar geleden, beïnvloedt dat de telling-taxoncurve. Immers, als bij een telling van 200 schaaltjes nu meer soorten worden gevonden, zal de asymptoot verschuiven. Om tot eenzelfde inschatting van de soortensamenstelling te komen (het getelde aantal als percentage van het aantal aanwezige soorten) zullen meer schaaltjes moeten worden geteld. Dit kan worden getoetst door analyses op basis van verschillende aantallen getelde schaaltjes van eenzelfde monster te vergelijken.

De oorzaak van de toename van het aantal aangetroffen soorten kan liggen in een verandering van soortconcepten, een verandering van waterkwaliteit of een combinatie van beide. De bijdrage van veranderde soortconcepten kan worden onderzocht door heranalyse van oude preparaten op basis van de huidige soortconcepten, en vergelijking van de analyseresultaten.

Als de aangepaste soortconcepten (welke veelal zijn gekenmerkt door nauwere soortgrenzen) leiden tot andere analyseresultaten, dan zal dit ook zijn weerslag hebben

op de ecologische beoordeling. Kiezelalgen worden in een grote diversiteit aan milieus gevonden en zijn zeer gevoelig voor veranderingen in hun leefomgeving. Nutriënten, pH, saliniteit en temperatuur zijn enkele factoren die de aanwezigheid van kiezelalgen sturen. De mogelijke combinaties van deze stuurfactoren zorgen voor een grote diversiteit aan niches waarin specifieke soorten zich kunnen vestigen (Julius & Theriot, 2010). De gevoeligheid van kiezelalgen voor die verschillende ecologische condities maakt ze tot zeer waardevolle indicatoren (R.J. Stevenson *et al.*, 2010). Op basis van het voorgaande, kan worden gesteld dat een nieuw beschreven (als gevolg van taxonomisch onderzoek van een andere soort afgesplitste) kiezelalg een eigen ecologische niche heeft en zodoende invloed heeft op de beoordeling van de waterkwaliteit. De impact van veranderingen in soortconcepten kan worden onderzocht door het vergelijken van ecologische beoordelingen van eenzelfde monster, op basis van de oude en de nieuwe taxonomische concepten.

Opzet experiment

Het onderzoek betreft vijf locaties in West-Brabant, die in 1996 en 1997 zijn bemonsterd en geanalyseerd. De preparaten van deze locaties zijn in 2014 opnieuw geanalyseerd met gebruikmaking van de meest recente literatuur. Voor de analyses zijn twee methoden gebruikt.

De eerste methode volgt het analyseprotocol uit 1996/1997. Er zijn 200 waarnemingen verzameld, waarbij van elke waarneming het aantal schaaltjes is genoteerd. De resultaten zijn vergeleken met de analyseresultaten van de oude telling.

Bij de tweede methode zijn in totaal 1000 schaaltjes geteld, waarbij voor elk beeldveld het aantal getelde schaaltjes is genoteerd. De resultaten zijn gebruikt om nieuwe tellingen van verschillende omvang te genereren. Hiertoe zijn telkens zoveel beeldvelden getrokken (random, zonder teruglegging) dat het minimum aantal schaaltjes van respectievelijk 200, 300, 400 en 500 schaaltjes werd bereikt. Om statistische toetsing mogelijk te maken, zijn alle trekkingen in tienvoud uitgevoerd.

De moderne naamgeving is vastgelegd in de lijst Taxa Waterbeheer Nederland (TWN); de oude naamgeving is terug te vinden in de lijst van de Interprovinciale Ambtelijke Werkgroep Milieu (IAWM). Om de oude analyseresultaten te kunnen vergelijken met de nieuwe, zijn de soortnamen uit de nieuwe tellingen ‘terug vertaald’ naar de oude naamgeving en soortconcepten. Van elke nieuw gegenereerde telling is dus steeds een oude en een nieuwe soortnaamlijst aanwezig. De gegenereerde tellingen zijn gebruikt om te toetsen a) hoeveel schaaltjes minimaal moeten worden geteld voor een betrouwbaar beeld van de soortensamenstelling, b) in welke mate het aantal getelde schaaltjes invloed heeft op de ecologische beoordeling en c) of veranderingen in soortconcepten invloed hebben op de ecologische beoordeling.

Om de invloed van de verschillen in soortconcepten op de ecologische beoordeling te testen, is gekeken naar de IPS (Indice de Polluo-Sensibilité Spécifique). Deze index is in 1984 geïntroduceerd door Coste en sindsdien meermalen geactualiseerd. De IPS wordt gebruikt voor de ecologische beoordeling in Nederland in het software-programma QBWat (Pot 2015). Voor de oude naamgeving worden de oude indices uit 1984 gebruikt. Voor de nieuwe naamgeving zijn de meest recente indices gebruikt die

zijn gepubliceerd op de Europese website “Freshwaterecology.info” (Schmidt-Kloiber *et al*, 2015).

Resultaten

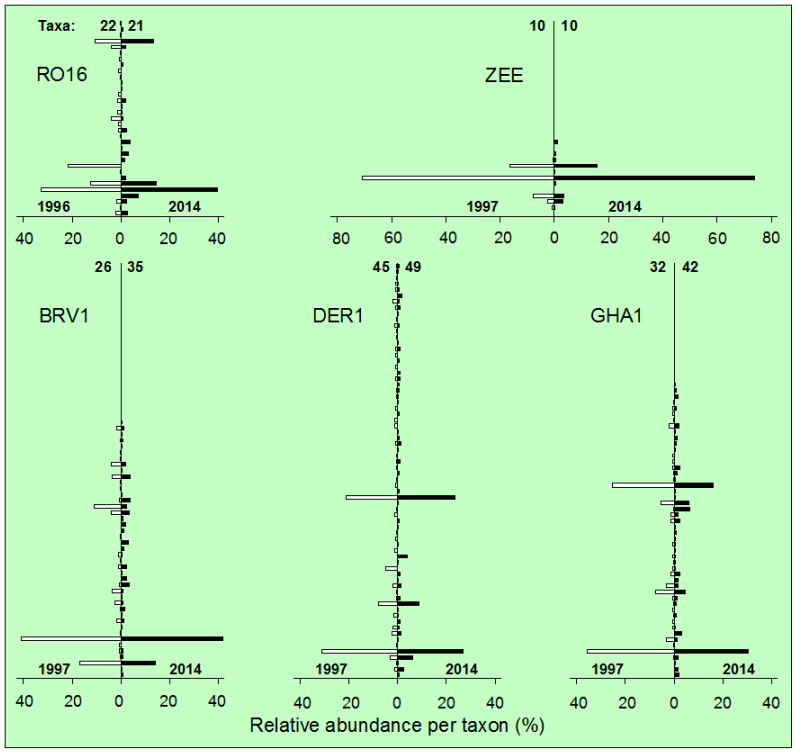
Telprotocol

Bij de hertelling van de preparaten zijn meer taxa aangetroffen dan in 1996/1997 (tabel 1).

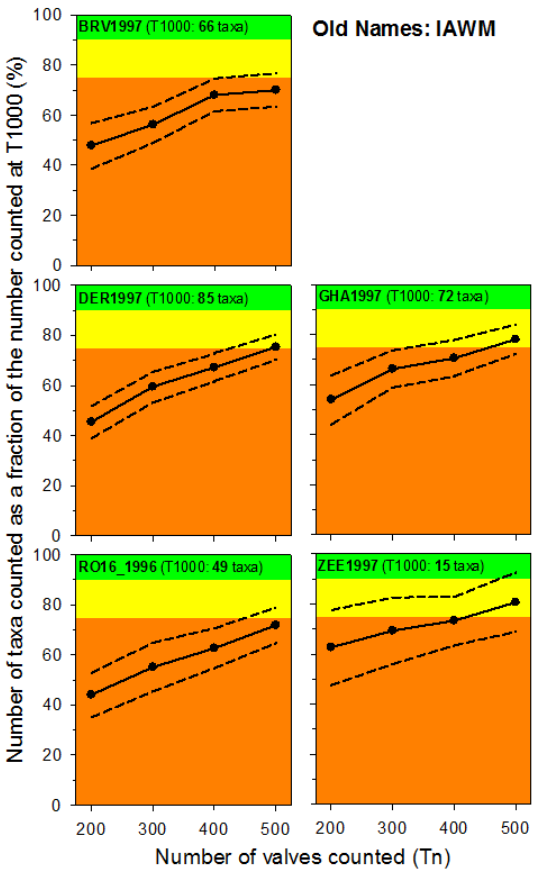
Locatie	1996/1997	2014
RO16	22 (+4)	22 (+10)
ZEE	10 (+5)	10 (+6)
BRV1	26 (+3)	39 (+10)
DER1	45 (+16)	55 (+30)
GHA1	32 (+10)	45 (+16)

TABEL 1 *Aantal aangetroffen taxa in 1996/1997 (IAWM-naamgeving = oude soortconcept) en 2014 (TWN-naamgeving = nieuwe soortconcept) . De getallen tussen haakjes zijn het aantal taxa aangetroffen buiten de telling.*

Om de betrouwbaarheid van de hertellingen te toetsen, is de moderne naamgeving omgezet naar de naamgeving gebruikt in 1996/1997. Vervolgens is de similariteit van beide tellingen getoetst (Kolmogorov-Smirnov toets, Figuur 1.) Deze toets wijst uit dat de resultaten van de hertellingen na de naamsomzetting vergelijkbaar zijn met die uit 1996/1997. De verschillen in aantallen gevonden taxa zijn derhalve volledig te verklaren uit de veranderingen in soortconcepten.

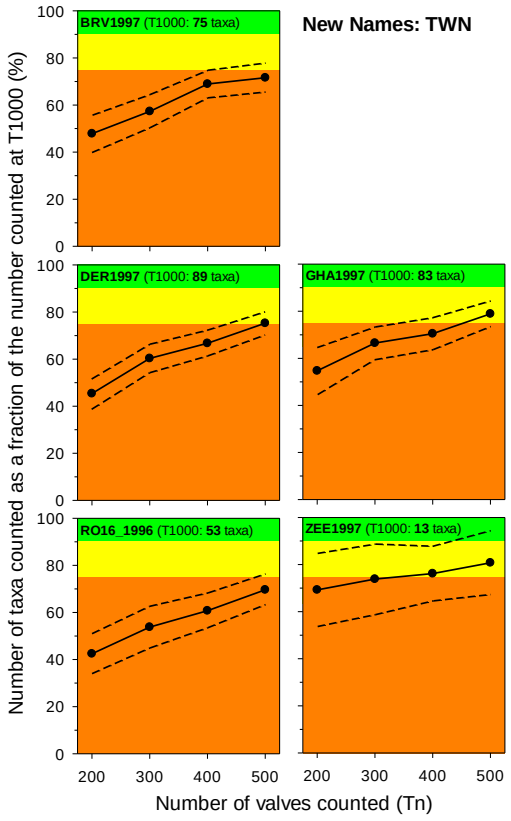


FIGUUR 1 *Resultaten van similariteitstoets na vertaling van nieuwe naamgeving (links) naar de oude naamgeving (rechts). Kolmogorov-Smirnov test: RO16, p=0.957; ZEE, p=0.993; BRV1, p=0.269; DER1, p=0.992; GHA1, p=0.155.*

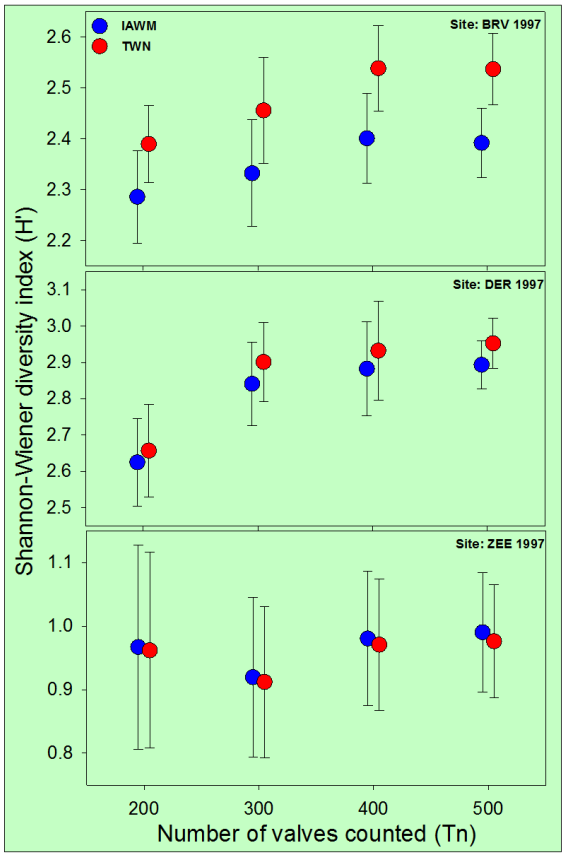


Als het aantal aangetroffen taxa wordt uitgezet tegen het aantal getelde schaaltjes, blijkt dat de asymptoot nooit bij 500 schaaltjes wordt bereikt (figuur 2a/b). Om minimaal 60% van aanwezige taxa (in een telling van 1000 schaaltjes) te vinden, moeten minimaal 400 schaaltjes worden geteld. Voor 75% is een telling van 500 schaaltjes vereist. Hierbij dient te worden opgemerkt dat de hoeveelheid te tellen schaaltjes ook is afhankelijk van soortdiversiteit van de locatie. Bij soortenarme locaties, zoals ZEE (totaal 13 taxa) is een telling van 300 schaaltje voldoende om 75% van de taxa te detecteren.

FIGUUR 2A. *Aantal getelde schaaltjes versus het aantal aangetroffen taxa op basis van de oude taxonomische namen.*



FIGUUR 2B. *Aantal getelde schaaltjes versus het aantal aangetroffen taxa op basis van de nieuwe taxonomische namen.*

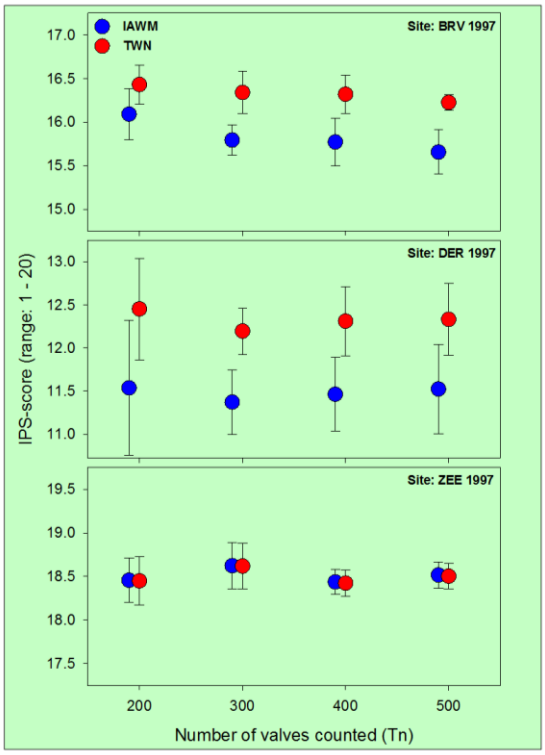


Als de soortdiversiteit wordt uitgezet tegen het aantal te tellen schaaltjes, zien we een vergelijkbaar beeld (figuur 3). De asymptoot wordt hier wel bereikt en ligt tussen de 300 en 400 getelde schaaltjes. Bij een hoger aantal getelde schaaltjes neemt de betrouwbaarheid van de uitkomst toe, ook bij de soortenarme locatie ZEE.

FIGUUR 3. *Aantal getelde schaaltjes versus soortendiversiteit.*

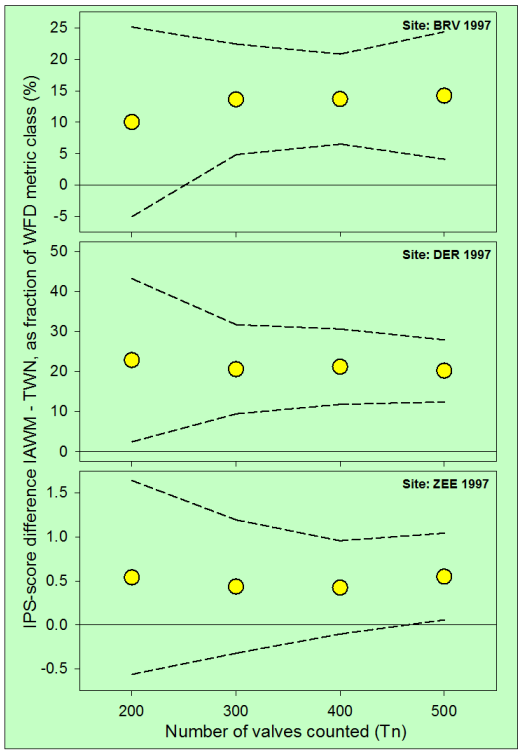
Ecologische beoordeling

Voor drie locaties (BRV, DER en ZEE) is de IPS-score berekend. Deze locaties verschillen in soortdiversiteit (DER = hoog, BRV = gemiddeld, ZEE=laag). De IPS-score (figuur 4) is bij toepassing van de nieuwe soortnamen (TWN) hoger dan bij gebruik van de oude (IAWM). De betrouwbaarheid van de uitkomsten neemt toe naarmate meer schaaltjes worden geteld.



FIGUUR 4. *Aantal getelde schaaltjes versus de waterkwaliteit berekend volgens de IPS-index.*

In figuur 5 is het verschil in IPS- score tussen tellingen met de oude en die met de nieuwe naamgeving uitgezet als fractie van de klassenbreedte op de KRW-maatlat. Bij locaties met een gemiddelde en hoge soortdiversiteit is het verschil 10 tot 20%. De standaardafwijking wordt over het algemeen kleiner naarmate meer schaaltjes worden geteld. Bij locaties met een lage soortdiversiteit zijn de verschillen nihil.



FIGUUR 5. *Aantal getelde schaaltjes versus het verschil in IPS-score berekend op basis van de oude taxonomische namen en de nieuwe namen.*

Discussie

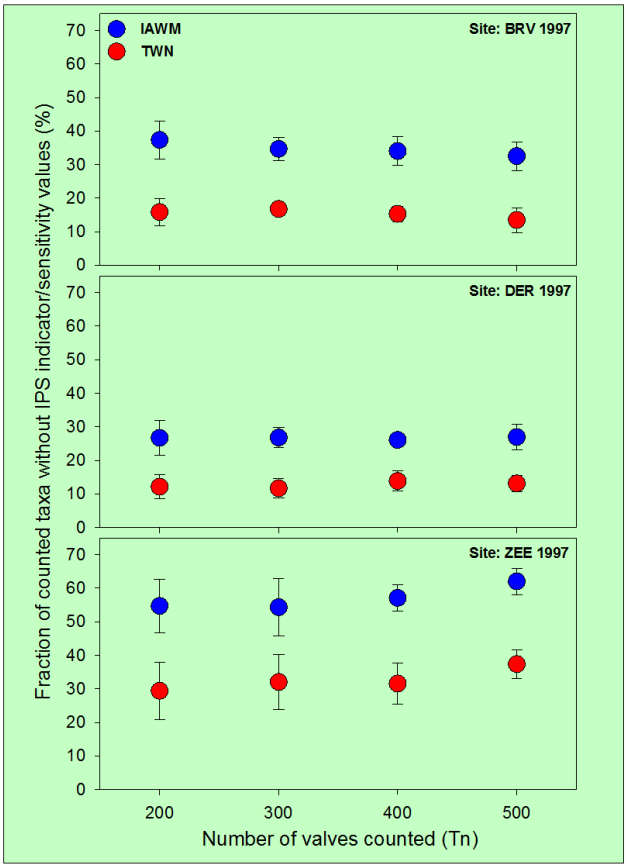
Algemeen

Bij de oorspronkelijke tellingen zijn steeds alle taxa tot op soort gedetermineerd. Dit suggereert dat alle aanwezige taxa in de gebruikte determinatieliteratuur terug waren te vinden. Bij de vertaling van de nieuwe soorten naar de oude soorten is hier steeds rekening mee gehouden. Soorten die in 1996-1997 nog niet waren beschreven, zijn benoemd als de meest waarschijnlijke soort uit de gebruikte determinatiewerken. Toch konden niet alle in de hertelling gevonden taxa aan een oude naam worden toegewezen. Deze taxa zijn samengevoegd tot de groep Bacillariophyceae.

Telprotocol

Volgens de Europese norm uit 2014 (NEN-EN 14407, 2014) is het tellen van 300 tot 500 schaaltjes de standaard, maar kan deze voor specifieke doelstellingen worden aangepast. In de meeste Europese landen wordt een telling van minimaal 400 schaaltjes aangehouden (Kahlert *et al*, 2012). Het in Nederland gebruikelijke telprotocol (STOWA 2014) waarbij 200 schaaltjes worden geteld, wijkt hiermee sterk af van de huidige Europese norm uit 2014. Vergelijkbaarheid met andere Europese protocollen is niet goed mogelijk. Hoewel de Europese norm aanpassingen aan het telprotocol toestaat, laat ons onderzoek zien dat het tellen van 200 schaaltjes onvoldoende is. Dit geldt zowel voor het verkrijgen van een goed beeld van de soortdiversiteit als voor een betrouwbare ecologische beoordeling.

Ecologische beoordeling



Voor de berekening van de IPS-scores zijn gegevens van Coste uit 1984 en de meest recente gegevens van de website "Freshwaterecology.info" gebruikt. De indices zijn niet aangepast of aangevuld. In de praktijk worden de indices van soorten met een onbekende waarde door middel van de zogenaamde 'expert-judgement' ingevuld. Omdat dit tot verschillende uitkomsten kan leiden, is dat in dit onderzoek niet gedaan. In figuur 6 is te zien dat van 15 tot 50% van de getelde schaaltjes geen index bekend is. Dit betekent dat de ecologische beoordeling is gebaseerd op slechts een deel van de getelde schaaltjes.

FIGUUR 6. Aantal getelde schaaltjes versus het aantal schaaltjes waarvoor geen IPS-waarde bekend is.

Uit dezelfde figuur valt af te lezen dat bij de nieuwe soortconcepten (TWN) een lager percentage van de soorten géén indicatorwaarde heeft, hetgeen suggereert dat er meer autecologische kennis aanwezig is. Dat is echter nauwelijks terug te vinden in de uitkomsten van de ecologische beoordelingen. Als de IPS-waarden van oude en nieuwe namen worden vergeleken, valt het op dat de veranderingen van soortconcepten niet terug komen in de indices. Als voorbeeld zijn hier de gegevens van *Cymbella affinis* Kützing uitgezet in tabel 2. Het soortbegrip rond *Cymbella affinis* Kützing heeft sinds 1986 een drastische verandering ondergaan (Krammer & Lange-Bertalot, 1986; Krammer, 2002). Hofmann (1994) geeft aan dat elk morfotype binnen de soortgroep van *Cymbella affinis* een andere ecologische voorkeur lijkt te hebben. De gebruikte indices zijn echter niet veranderd en 'gewoon' overgenomen van de oude, met het brede soortbegrip corresponderende, namen. Dit verklaart waarom er bijna geen veranderingen in de ecologische beoordeling optreden.

De gevoeligheid van kiezelalgen voor een groot aantal ecologische factoren, maakt ze tot zeer waardevolle indicatoren voor veranderingen in het milieu (Stevenson *et al.*, 2010). Kiezelalgen kunnen een rol spelen als 'early warning indicatoren' bij korte termijn veranderingen in het milieu. Echter, dit is alleen mogelijk als onderscheid kan worden gemaakt in soortspecifieke factoren en effecten. Hiervoor is gedegen kennis over de autecologie van kiezelalgsoorten noodzakelijk. Dit kan alleen worden bereikt als taxonomisch onderzoek wordt gevolgd door (aut)ecologisch onderzoek.

TABEL 2 *Indices van de taxa uit de groep rond* Cymbella affinis, Cymbella excisa *en* Cymbella parva *zoals gebruikt door verschillende auteurs/bronnen.*

Naam	IPS 1984 Coste		Freshwaterecology.info		QBWat	
	ind	W	IPS ind	IPS W	IPS ind	IPS W
Cymbella affinis Kützing	4	2	4	2	4	2
Cymbella affinis var. affinis	--	--	4	2	--	--
Cymbella affinis var. procera	--	--	4	2	--	--
Cymbella tumidula Grunow	--	--	4	2	--	--
Cymbella tumidula var. lancettula	--	--	4	2	--	--
Cymbella excisa var. excisa	--	--	4	2	4	2
Cymbella excisa var. procera	--	--	4	1	--	--
Cymbella parva (W.Sm.) Kirchner in Cohn	5	3	5	3	5	3
Cymbella affiniformis	--	--	4	2	--	--
Cymbella vulgata	--	--	--	--	--	--

Conclusie

Op basis van dit experiment kan worden gesteld dat het huidige telprotocol moet worden aangepast. Het minimum aantal te tellen schaaltjes is afhankelijk van de soortdiversiteit: bij zeer soortenarme locaties is een minimum van 300 schaaltjes toereikend om 75% van de aanwezige taxa te scoren. Bij soortenrijkere locaties ligt de ondergrens op 400 schaaltjes. Door het aanpassen van het aantal te tellen schaaltjes tot 500 wordt het Nederlandse telprotocol beter afgestemd op de telprotocollen van andere Europese landen. Bovendien wordt bij hogere aantallen ook de bijdrage van zeldzame soorten aan de beoordeling beter meegerekend.

De nieuwe taxonomische soortconcepten lijken nauwelijks invloed te hebben op de ecologische beoordeling. Dit heeft vooral te maken met een gebrek aan autecologische kennis van de nieuwe en oude soorten en soortgroepen. Vaak krijgt elk nieuw afgesplitst taxon dezelfde ecologische index mee als het taxon waar het van is afgesplitst. De uitkomsten van de ecologische beoordelingen zijn hierdoor minder betrouwbaar dan mogelijk is.

SUMMARY

Modern diatom taxonomy is a dynamic discipline, generating a flood of changes ecologists have to deal with. New species are constantly being described and at the same time, species complexes are investigated and split in two or more separate taxa. As a result, nowadays more species are found in a sample, irrespective of water quality. Effects of these taxonomical changes on the ecological assessment of surface waters can be expected. To investigate such effects, we started an experiment that should give answers to the following questions: 1) Are the currently used counting

strategies still valid? 2) Should the impact of rare species on ecological assessment be valued differently?

Five diatom samples were selected from different WFD water body types. The samples were taken and analyzed almost two decades ago, in 1996 and 1997. They were reanalyzed using current taxonomical and ecological knowledge. Two different counting protocols were used. The first one, counting 200 individuals, was also used in 1996-1997. According to the second protocol, 1000 valves were counted. From the latter countings, several subsets of 200, 300, 400 and 500 valves were drawn randomly for further statistical analysis. For this purpose the observations in each field of view were recorded in those '1000-valves countings'.

The outcome of this experiment shows that the current Dutch counting protocol should be altered. The number of valves to be counted must be at least 300 and preferably 500. The ecological assessments appear not to be affected by the changes in taxonomy. However, the autecological information on diatom species seems to be insufficient and has its effect on the reliability of ecological assessments. Therefore, after revision or description of species and species complexes, autecological research should follow.

References

Hofmann, G. (1994) Aufwuchs-Diatomeen in Seen und ihre Eignung als Indikatoren der Trophie. Bibliotheca diatomologica Band 30. J.Cramer, Berlin.

Julius M.L. & E.C. Theriot (2010) The diatoms: a primer. In Smol, J.P. & E.F. Stoermer. 2010. The diatoms: applications for the environmental and earth sciences. Second edition. Cambrigde University Press, Cambrigde] pp 8-22.

Kahlert, M. M. Kelly, R. Albert, S.F.P. Almeida, T. Besta, S. Blanco, M. Coste, L. Denys, L. Ector, M. Fránková, D. Hlúbiková, P. Ivanov, B. Kennedy, P. Marvan, A. Mertens, J. Miettinen, J. Picinska-Faltynowicz, J. Rosebery, E. Tornés, S. Vilbaste & A. Vogel (2012) Identification versus counting protocols as sources of uncertainty in Diatom-based ecological status assessments. Hydrobiologia 695:109-124.

Krammer, K. (2002) Diatoms of Europe. Volume 3; Cymbella. A.R.G.Gantner Verlag Kommanditgesellschaft, Ruggell.

Krammer, K. & H. Lange-Bertalot. (1986) Bacillariophyceae. 1. Teil: Naviculaceae. Gustav Fischer Verlag, Stuttgart.

Krammer, K. & H. Lange-Bertalot. (1988) Bacillariophyceae. 2. Teil: Bacillariaceae, Epithemaceae, Surirellaceae. Gustav Fischer Verlag, Stuttgart.

Krammer, K. & H. Lange-Bertalot. (1991a) Bacillariophyceae. 3. Teil: Centrales, Fragilariaceae, Eunotiaceae. Gustav Fischer Verlag, Stuttgart.

Krammer, K. & H. Lange-Bertalot. (1991) Bacillariophyceae. 4. Teil: Achnanthaceae, kritische Ergänzungen zu Navicula (Lineolatae) und Gomphonema. Gustav Fischer Verlag, Stuttgart.

NEN-EN 14407 (2014) Water quality - Guidance for the identification and enumeration of benthic diatom samples from rivers and lakes. [Water – Richtlijn voor determinatie, telling en interpretatie van monsters van benthische diatomeeën van rivieren en meren] Nederlands Normalisatie-instituut, Delft.

Pot, R. (2015) QBWat, programma voor KRW-beoordeling. Versie 5.33. http://www.roelfpot.nl/qbwat .

Schmidt-Kloiber, A. & D. Hering (2015): www.freshwaterecology.info - an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. Ecological Indicators 53: 271-282. doi: 10.1016/j.ecolind.2015.02.007

Stevenson, R.J., Y. Pan & H. van Dam (2010). Assessing environmental conditions in rivers and streams with diatoms. In: Smol, J.P. & E.F. Stoermer. 2010. The diatoms: applications for the environmental and earth sciences. Second edition. Cambrigde University Press, Cambrigde.

STOWA (2014) Werkvoorschrift 9B Analyse van kiezelwieren in oppervlaktewater In: Bijkerk, R. (red.) 2014. Handboek Hydrobiologie. Biologisch onderzoek voor de ecologische beoordeling van Nederlandse zoete en brakke oppervlaktewateren. Deels aangepaste versie. Rapport 2014 - 02, Stichting Toegepast Onderzoek Waterbeheer, Amersfoort.

Diatomededelingen 39, 2015

Diatoms and their environment in lime-rich springs in The Netherlands

Herman van Dam[1], Bert Pex[2] & Harry Boonstra[3]

[1] Consultancy for Water and Nature, Amsterdam, Netherlands (info@waternatuur.nl), [2]Roer and Overmaas Water Authority (WRO), Sittard, Netherlands (b.pex@overmaas.nl)
[3] Koeman en Bijkerk bv, Haren, Netherlands (h.boonstra@koemanenbijkerk.nl)

In the period 2008-2012 WRO sampled 64 permanent springs in the hilly landscape east of Maastricht, a district different from the rest of The Netherlands, but similar to adjoining areas in Belgium and Germany. The sedimentary rocks are mainly covered with fertile loess soils, which are predominantly used for agriculture, mixed with urbanized and small forested areas.

Habitat variation and hydromorphological variables were recorded along with physico-chemical variables (e.g. nutrients, major ions). The springs are rich in ions (medians: conductivity 55 mS/m, Ca 120 mg/l, HCO_3 230 mg/l) and nutrients (NO_3-N 10 mg/l, total-P 0,10 mg/l) and slow flowing (3 dm/s) and there is travertine in some springs.

Diatoms were studied in composite samples (cobbles, gravel, sand, detritus, branches, mosses and other plants). In the slides about 200 valves were counted and identified. Grazing pressure was estimated from simultaneously taken samples of macro-invertebrates.

An IPS-based EQR and ecological indicator values (including moisture) were calculated from the species composition, just like proportions of rare species in The Netherlands and threatened species from the German Red List.

As a whole the springs are rich in diatoms (in total 212 taxa, 98 rare in The Netherlands, 11 new for The Netherlands, 10 threatened Red List ones). Many of the rare species are xerotolerant, as in other European springs. The numbers of rare species are positively related to the coverage of the moss layer and habitat diversity. Despite the high nutrient load the EQR values indicate a (very) good quality.

The most frequent and abundant taxa, *e.g. Planothidium lanceolatum, Achnanthidium minutissimum, P. frequentissimum, Amphora pediculus* and *Achn. affine* are commonly found in all kinds of eutrophic waters, but also taxa with a more limited distribution were met, *e.g. Caloneis fontinalis, Diploneis krammeri* and *D. separanda*, which are also known from travertine springs elsewhere in Europe

Relations between diatoms and environmental variables (including grazing pressure) were retrieved by grouping diatom data clusters and testing the significance of differences of median values of environmental variables between clusters. Moreover an ordination of the diatoms was applied using the environmental variables as supplementary ones.

The driving environmental variable for the diatoms seems to be the current velocity and its variation. A high current velocity implies a high habitat variation, enabling diatoms from different substrates to coexist. From the chemical variables the major ions, particularly bicarbonate, are important, but they are less important than the physical ones. Surprisingly, nitrate was not found as a significant environmental variable, as it is in many other spring areas. Probably the concentrations are so high in all our springs that phosphate controls the algal growth. Indeed, median phosphate concentrations between clusters do differ significantly. Also grazing pressure may be important.

Full data are presented by Boonstra *et al.* (2015).

References

Boonstra H, van Dam H, Bijkerk R, Wanink JH (2015) Bronnen van inspiratie: verkennende analyse van vijf jaar bronnenonderzoek in Zuid-Limburg. KenB rapport 2015-014. Koeman en Bijkerk bv, Haren. Rapport 1405. Herman van Dam, Adviseur Water en Natuur, Amsterdam. 133p.

Diatomededelingen 39, 2015

Development of Diatom-Based models for Inferring Salinity in Dutch wetlands

Alejandra Goldenberg Vilar[1], Timme Donders[1], Gert van Ee[2] & Friederike Wagner-Cremer[1]

[1]Palaeoecology, Department of Physical Geography, Faculty of Geosciences, Utrecht University, Laboratory of Palaeobotany and Palynology, Utrecht, The Netherlands.
[2]Hoogheemraadschap Hollands Noorderkwartier, Heerhugowaard, The Netherlands

Introduction

The development of statistical models to predict future changes in the environment has focused attention on the role of palaeoecology on testing the accuracy of climate model predictions and in identifying past analogues for future climate change (Fritz et al., 1991). One of the most discussed issues regarding climate change is the uncertainty behind the ongoing sea level rise and the effect of such sea level rise (SLR) and human disturbance in estuaries and shallow coastal embayments. Several management activities such as dredging, sand suppletion, mineral exploitation or urbanization have replaced much of the natural environment with a built, agricultural landscape that has left an unprecedented legacy of hydrologic engineering and ecological alteration (Anderson and Vos, 1992).

Diatom assemblages are a well-established proxy to reconstruct environmental changes and assess the impact of human activities in freshwater and coastal ecosystems (Bennion, 1994; Jones and Juggins, 1995; Wachnicka et al., 2010). Although extensive literature highlights the use of diatoms as indicators of salinity (Van Dam et al., 1994) and sedimentary environments in Dutch coastal wetlands (Vos and de Wolf, 1993), diatom transfer functions to infer salinity or tidal levels have not yet been developed for The Netherlands. Long-term and spatially explicit data required to document these changes are sparse. The applications of such type of inference models in The Netherlands, however, are of great importance for assessing the impact of water management activities in coastal systems or the establishment of reference conditions for the many marine-brackish artificial ditches. In addition, these models can be used to reconstruct sea level changes complementing geological mapping and therefore potentially decreasing uncertainties in SLR predictions. In the present study, we use a regional database comprising a long salinity gradient in the province of North Holland to develop quantitative diatom species based models for inferring salinity. The performance of the model is consequently tested against an independent and regional data set taken at different locations in the same province.

Materials & Methods

Study area and datasets

The study is conducted in the province of North Holland. The samples were collected in modified wetlands that have been reclaimed for agriculture representing a system of shallow drainage ditches. Detailed explanation of the study area can be found in (Goldenberg Vilar et al., 2014).

FIGURE 1. *Sampling locations training dataset (triangles) and calibration dataset (dots) in the province North Holland.*

The dataset for the development of the diatom inference models (henceforth referred to as "training set") consists of a total of 96 samples of 32 locations sampled in March, June and September 1993 spanning a salinity gradient from 200-9000 mg/l chloride. Water samples were collected in the same months and locations as the diatom samples and the following variables were determined: surface water oxygen, pH, conductivity, chloride, sulphates, transparency (Sechii depth), total nitrogen, Kjeldahl nitrogen, total phosphorus, ortho-phosphate and chlorophyll *a*. In this dataset, 400 diatom valves were identified per sample. The dataset for testing the performance of the models (henceforth referred to as "calibration set") consists of 295 samples collected in the framework of a long-term monitoring program in North-Holland carried out by the local water authority during spring 2008-2010 (April-June). In the calibration set, 200-300 valves were identified per sample. Figure 1 shows the sampling locations for both datasets. In the calibration set, water samples (for the determination of chloride) were collected every four weeks following standardized national protocols accredited by the Dutch Standards Institute (NEN, 2001). We used chloride average values of the half-year summer months (i.e. April through September), assuming that these values reflect local conditions better than single measurements. In both datasets, diatoms were sampled from reed stems (*Phragmites australis*). This widely distributed emergent macrophyte is the recommended substratum for sampling periphyton in the Netherlands (STOWA, 2010), avoiding differences caused by substratum heterogeneity. Attached diatoms were prepared using H_2O_2 digestion and mounted on microscope slides with Permount Mounting Medium (Fischer Scientific, Pittsburgh). Taxonomic identification was based on Krammer et al. (1986) and Hofmann et al. (2011) following standard protocols (NEN-EN 14407).

Data analysis

Canonical Correspondence Analysis (CCA) were performed to evaluate the importance of chloride and other environmental variables in structuring the diatom communities in the training set before the development of the transfer function. CCA were selected as the more appropriate technique due to the unimodal relationship of species and environmental variables in the dataset. The relative abundance of the diatoms was square-root-transformed to more closely approximate a normal distribution, and environmental data with a skewness of >1 were log-transformed prior the ordination analysis. The ordinations were performed in Canoco5.

The optima of each species along the salinity gradient (chloride) were determined by averaging all values for each variable from the sites where the taxon occurred, weighted by its abundance at each site. The taxon's tolerance along each gradient was then calculated as an abundance-weighted standard deviation of the environmental variable (Fritz et al., 1991).

The WA-PLS regression (ter Braak and Juggins, 1993) with "leave one out" cross-validation was used to develop statistical prediction models. This method combines the features of weighted averaging (WA) and partial least squares (PLS) and uses the residual correlation structure in the data to improve the fit between the biological data and environmental data in the training set (Birks, 1995). The predictive abilities of

transfer functions were assessed by examining the relationship between the observed and diatom-inferred values, as well as the observed and jackknife-estimated values of the variables of interest in the training set ($r^{2apparent}$ and $r^{2jackknife}$), and evaluation of root mean square error of prediction (RMSEP) (Birks et al., 1990). We further evaluated the ability to predict each variable through an independent validation. We used the data from the training set to develop transfer functions and tested their precision using the calibration set. These analyses were performed using C2 version 1.7.6 software.

Results

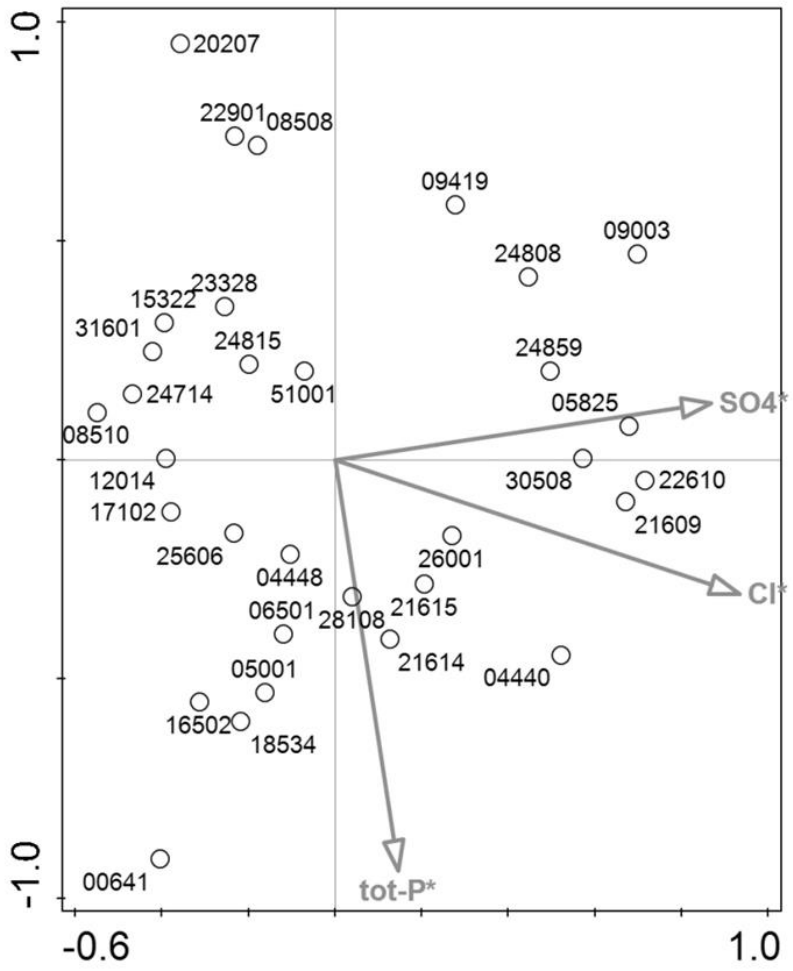
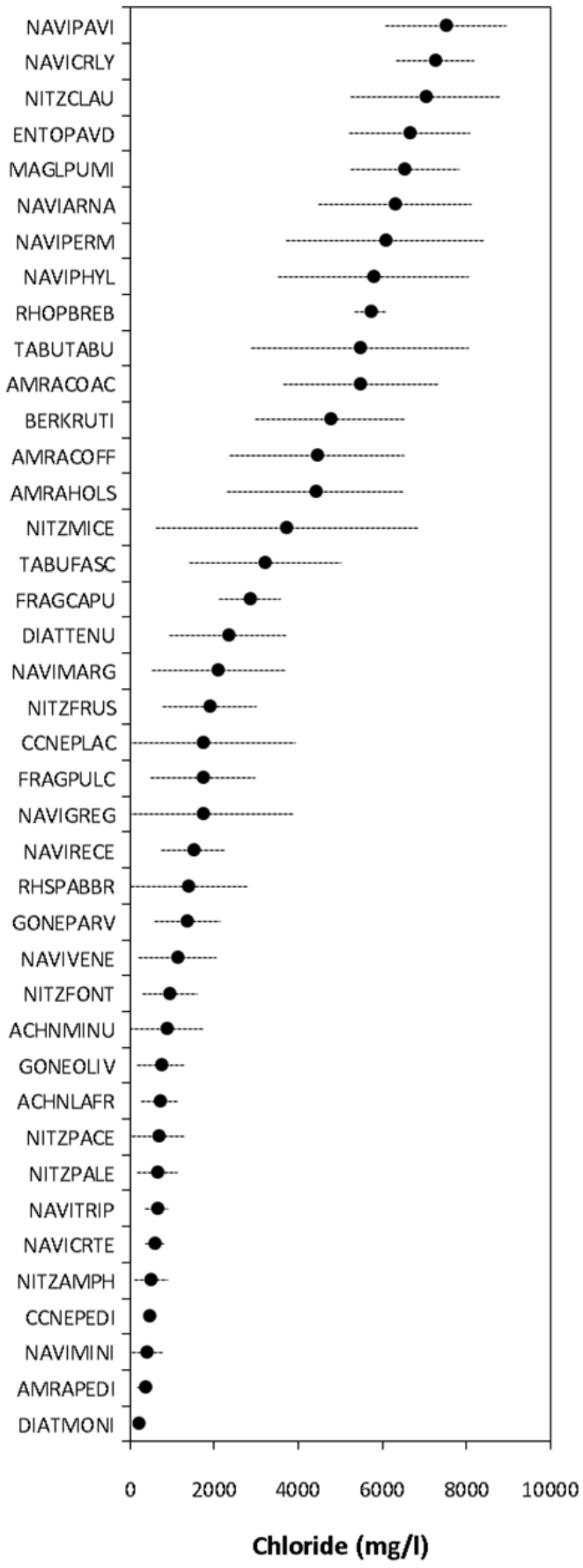


FIGURE 2. *Canonical Correspondence Analysis (CCA) showing the relationship of diatom communities and environmental variables in the training data set. Only significant environmental variables are shown. The cumulative percentage of explained variance for axis 1 and 2 is 19.35%. Asterisks denoted log transformed environmental variables.*

In total, 306 and 438 species from the training and calibration data sets were identified respectively, of which 160 and 181 species covered 98% of all observations. The remaining species were mainly singletons and were omitted in further analysis.

The CCA (Fig. 2) shows two main groups of variables driving the distribution of diatom communities in North Holland. The most prominent, reflected in axis 1, are chloride and sulphate (17.6% of the total variation explained; p= 0.002 for both variables). The second axis shows that nutrients in the form of total phosphorus is also a significant variable in explaining the distribution of diatoms in North Holland (5.8% of the total variation explained; p=0.004).



Optima and tolerances of selected diatom taxa and a comparison between inferred and measured salinity for each site of the training set is shown in Figures 3 and 4 respectively. The WA-PLS technique revealed that the most parsimonious models for inference of chloride would be a three-component model. The data indicate a very close agreement between inferred and measured salinity with no apparent outliers ($r^{2apparent}$= 0.99 and $r^{2jackknife}$=0.88; RMSEP=0.17).

FIGURE 3. *Estimated optima (dots: abundance-weighted means) and tolerances (dashed lines: abundance-weighted standard deviations) of the 40 most abundant taxa.*

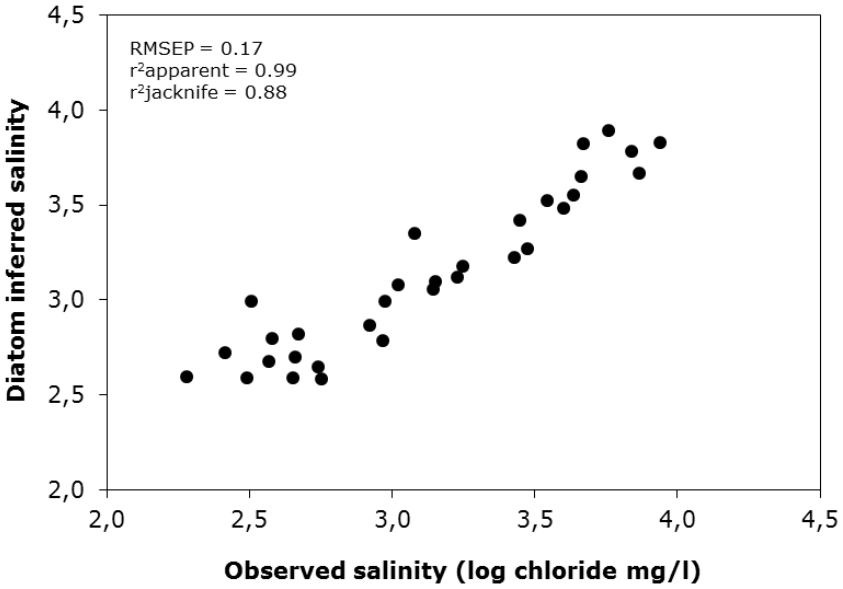


FIGURE 4. *Observed salinity against diatom inferred salinity using weighted averaging partial least squares regression with jackknife cross-validation of the training dataset.*

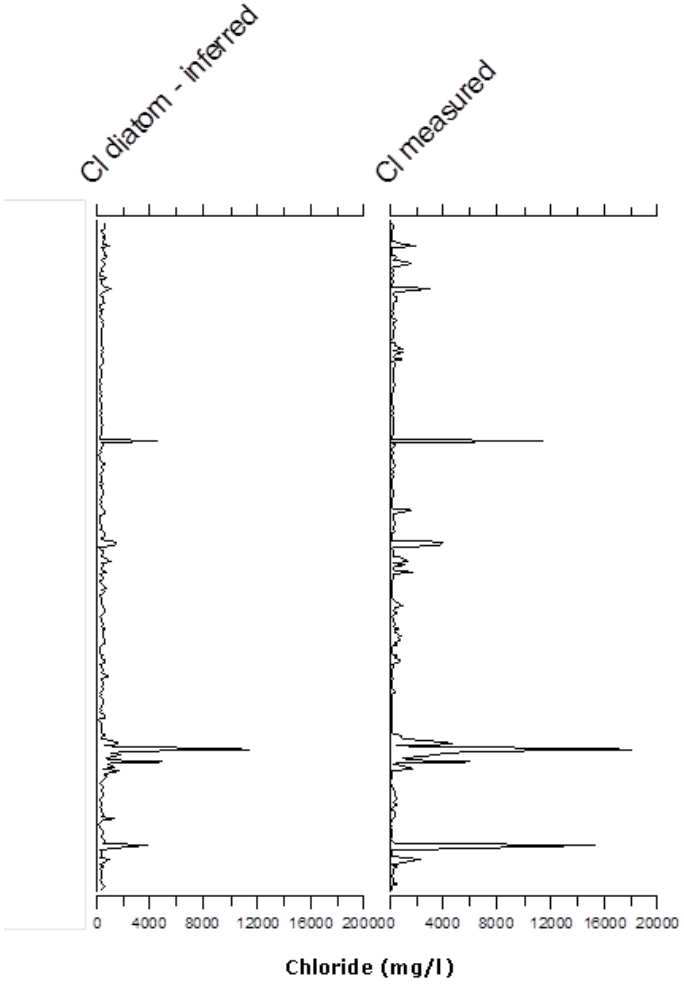


Figure 5 shows the good agreement between the observed and measured chloride concentrations in the validation with the independent dataset.

FIGURE 5. *Validation of the model with the calibration data set (295 sampling locations).*

Discussion

This study clearly demonstrates that diatom assemblages from the province North Holland are suitable to construct accurate diatom transfer functions to infer salinity conditions. The sensitivity of diatom species to salinity (Potapova and Charles, 2002) is also shown in the CCA. Salinity (measured as chloride) is the most important variable determining the distribution of diatom communities in the province of North Holland. Additional factors such as total phosphorus also exerts an important influence on diatom distribution in the province of North Holland given the well-known sensitivity of diatoms to this variable (Soininen, 2007). Since the salinity related variables such as chloride and sulphate are not correlated with nutrients, the transfer function however can be considered independent from nutrient and related variables such as secchii depth, pH, oxygen or chlorophyll *a*.

Diatom species tolerances are the narrowest at the freshwater end of the salinity gradient such as for *Amphora pediculus, Navicula minima, Navicula tripunctata*. Some brackish species such as *Navicula cryptolyra* or *Surirella brebissonii* also show narrow tolerances. In contrast, species including *Nitzschia microcephala, Tabularia fasciculata or Delphineis surirella* that occur at intermediate ranges of the gradient, have much wider tolerances. It has been reported that the extreme variability in conditions in estuaries selects for taxa with broad tolerances (Admiraal, 1984). In the artificial wetlands of North Holland, it is also expected that diatom communities suffered from abrupt changes in salinity caused by pumping in/out water from the main canals to keep fixed water levels.

The relationship between observed and diatom-predicted salinity is very strong, which illustrates the powerful performance of the WA-PLS transfer functions. The precision of the transfer function is similar to comparable salinity transfer functions based on diatom training sets (Wachnicka et al., 2010; Szkornik et al., 2006).

The model validation shows that the salinity transfer function based on the 32-site training set provided a good estimation of chloride concentration in the 295 site calibration set. However, the model slightly overestimated the values of chloride at the low end of the gradients and underestimated the values at the high end. This condition is most likely due to the "edge effect" (truncation at the gradient edges) and inverse deshrinking (inverse linear regression) that are known to introduce such a bias between measured and inferred values (ter Braak and Juggins, 1993). The salinity gradient in our dataset does not cover marine conditions (≈ 18000 mg/l chloride), a likely additional reason for the underestimation of the higher chloride concentrations measured in the calibration set. The performance of these transfer functions can be improved further by adding locations in coastal areas with higher salinity concentrations (> 8000 mg/l or 18 PSU) to cover the full range of freshwater to marine assemblages. Because diatom communities in Dutch wetlands and coastal areas significantly overlap (Vos and de Wolf, 1993; Vos and De Wolf, 1994) transfer functions developed in this study should perform well along other wetlands and coastal systems in The Netherlands. The application of a broad regional data set as presented in this study, has been shown to produce more reliable diatom based models than local datasets for reconstructions of past environmental conditions (Watcham et al., 2013).

The results presented in this study, therefore, bears the strong potential to support SLR estimates through time.

References

Admiraal W (1984) The ecology of estuarine sediment-inhabiting diatoms. Progr Phycol Res 3:269–322.

Anderson NJ, Vos P (1992) Learning from the past: diatoms as palaeoecological indicators of changes in marine environments. Neth J Aquat Ecol 26: 19–30.

Bennion H (1994) A diatom-phosphorus transfer function for shallow, eutrophic ponds in southeast England, in Anonymous Nutrient Dynamics and Biological Structure in Shallow Freshwater and Brackish Lakes. Springer, pp. 391-410.

Birks H (1995) Quantitative palaeoenvironmental reconstructions. Statistical modelling of quaternary science data.Technical guide 5:161–254.

Birks H, Line J, Juggins S, Stevenson A, Ter Braak C (1990) Diatoms and pH reconstruction. Phil Trans Roy Soc B: Biol Sci 327: 263–278.

Fritz S, Juggins S, Battarbee R, Engstrom D (1991) Reconstruction of past changes in salinity and climate using a diatom-based transfer function. Nature 352: 706–708.

Goldenberg Vilar AG, van Dam H, Vonk JA, van der Geest Harm G, Admiraal W (2014) Typology of diatom communities in the Dutch delta: Recognizing patterns of environmental drivers in nutrient rich ditches. Ecol Ind 45: 561–569.

Hofmann G, Werum M, Lange-Bertalot H, (2011) Diatomeen Im Süßwasser-Benthos Von Mitteleuropa: Bestimmungsflora Kieselalgen Für Die Ökologische Praxis; Über 700 Der Häufigsten Arten Und Ihre Ökologie. Gantner.

Jones V, Juggins S (1995) The construction of a diatom based chlorophyll a transfer function and its application at three lakes on Signy Island (maritime Antarctic) subject to differing degrees of nutrient enrichment. Freshw Biol 34: 433–445.

Krammer K, Lange-Bertalot H, Krammer K, Lange-Bertalot H, Bate N, Podzorski A, Bukowska J (1986). Bd. 2: Bacillariophyceae. Stuttgart.

NEN-EN 14407 (2004) Water quality - Guidance for the identification and enumeration of benthic diatom samples from rivers and lakes. European committee for standardization (CEN). Brussels.

Potapova MG, Charles DF (2002) Benthic diatoms in USA rivers: distributions along spatial and environmental gradients. J Biogeogr 29: 167–187.

Soininen J (2007) Environmental and spatial control of freshwater diatoms—a review. Diatom Res 22: 473–490.

Szkornik K, Gehrels WR, Kirby JR (2006) Salt-marsh diatom distributions in Ho Bugt (western Denmark) and the development of a transfer function for reconstructing Holocene sea-level changes. Mar Geol 235: 137–150.

STOWA (2010) Handboek Hydrobiologie. Biologisch Onderzoek voor de Ecologische Beoordeling van Nederlandse Zoete en Brakke Oppervlaktewateren. Report 2010 – 028. Stichting Toegepast Onderzoek Waterbeheer, Amersfoort, The Netherlands.

ter Braak CJ, Juggins S (1993) Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. Hydrobiol 269: 485–502.

Van Dam H, Mertens A, Sinkeldam J, (1994) A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. Neth J of Aquat Ecol 28: 117–133.

Vos PC, De Wolf H (1994) Palaeoenvironmental research on diatoms in early and middle Holocene deposits in central North Holland (The Netherlands). Neth J Aquat Ecol 28: 97–115.

Vos PC, de Wolf H (1993) Diatoms as a tool for reconstructing sedimentary environments in coastal wetlands; methodological aspects. Hydrobiol 269: 285–296.

Wachnicka A, Gaiser E, Collins L, Frankovich T, Boyer J (2010) Distribution of diatoms and development of diatom-based models for inferring salinity and nutrient concentrations in Florida Bay and adjacent coastal wetlands of south Florida (USA). Estuaries Coasts 33: 1080–1098.

Watcham EP, Shennan I, Barlow NL (2013) Scale considerations in using diatoms as indicators of sea level change: lessons from Alaska. J Quat Sci 28: 165–179.

Diatomededelingen 39, 2015

Aquatic ecosystem shifts in response to early human land-use in two low-elevation lakes in northwestern Europe

Keechy Akkerman[1*], Timme H. Donders[1], Wim Z. Hoek[2] & Aleksandra Cvetkoska[1]

[1]Palaeoecology, Department of Physical Geography, Faculty of Geosciences, Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands
[2]Global Change Geomorphology, Department of Physical Geography, Faculty of Geosciences, Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands

Introduction

Increasing anthropogenic pressure on aquatic systems through enhanced nutrient input (phosphorus, P, and nitrogen, N) from agriculture and sewage is causing major problems with the ecosystems water quality at local and global scale (Elser et al., 2007; Conley et al., 2009). This human induced eutrophication triggers numerous shifts in ecosystem structure (Davidson and Jeppesen, 2013), generally leading to excessive growth of bloom-forming (noxious) algae (Paerl and Huisman, 2008; Burford et al., 2012). The subsequent results are development of hypoxia, light limitation and loss of biodiversity (Davidson and Jeppesen, 2013). These changes impact the quality and availability of clean water, which threatens the recreational and food services the ecosystem supplies, leading to costly mitigation measures (Davidson and Jeppesen, 2013). Conversely, defining the natural pre-disturbed nutrient status is of great significance for adequate management, restoration and conservation of the freshwater ecosystems.

In absence of long-term monitoring data, the biotic proxy data from sedimentary archives can be used as a tool to reconstruct past environmental change (e.g. Battarbee, 1999; Cremer et al., 2009; Kirilova et al., 2010). Most ecological baseline research focuses on the period since the industrialisation i.e. the last ca. 200 years (Bennion and Appleby, 1999; Cremer et al., 2009). However, anthropogenic activity, especially in the form of deforestation, has potentially impacted aquatic systems years prior (Messerli et al., 2000; Edwards and Whittington, 2001). Forest clearance associated with early agriculture leads to erosion and less uptake of nutrients by the soil, enhancing nutrient leaching into the aquatic environments (Edwards and Whittington, 2001; Dearing et al., 2006).

Vegetation reconstructions, based on pollen preserved in lake sediments are feasible to determine the onset of agriculture and its intensification: identified through simultaneous increase in crops (e.g. *Secale spp.*), and ruderal weeds (e.g. *Centaurea cyanus*) (Behre, 1981). Archaeological evidence in the catchment of the lake can be also used to support the pollen record (Bakker, 2003).

As diatoms are known to be highly sensitive to water chemical composition, they are often used as proxies for changes in water quality (Bradshaw et al., 2005; Davidson &

Jeppesen, 2013; Smol & Stroemer, 2010). Available diatom autecological data provides both qualitative (Vos and de Wolf, 1993; Van Dam et al., 1994) and quantitative tools (Bennion et al., 1996; Nodine and Gaiser, 2014), which can be used to infer past environmental change based on core diatom assemblage data (Van Dam et al., 1994).

For example, mathematical transfer functions have been generated to quantitatively infer past total phosphorus (TP) concentrations based on training set of modern surface-sediment diatom samples and contemporary TP concentrations from a large number of lakes (Nodine and Gaiser, 2014).

Moreover, spatial (Jeppesen et al., 2000) and temporal (Das et al., 2008) studies highlight the unimodal relation between TP and diversity, where increasing TP concentrations stimulate primary production, which initially leads to higher biodiversity. In case of further TP increase, leading to highly eutrophic conditions, certain blooming species are favoured causing a subsequent decline in biodiversity (Das et al., 2015). However, linking early agriculture practice over longer timeframes to shifts in water quality and associated ecosystem disturbances has not been analysed extensively. Especially understanding ecosystem recovery in areas where human activity showed a temporary increase is of great significance for restoration purposes.

Therefore, we studied two low-elevation lakes in northwestern Europe, Llangorse Lake (Wales, UK) and Hijkermeer (The Netherlands), by use of diatom analysis. The goal was to (1) define the timing and reconstruct the water quality of pre-, maximum and post-disturbance water bodies, (2) attempt to separate the imprint of anthropogenic activity from natural variability, so that natural baselines can be identified and (3) relate the shifts in biodiversity to this increasing (and/or decreasing) human impact over a timeframe of 5000 years.

The reconstructions will be compared to the land-use history from available and new pollen data. Both lakes, currently differing in trophic state and physical parameters such as depth, size and drainage area, are located in areas where archaeological and pollen data indicate the presence of early human settlements. Since the anthropogenic pressure differs between the two lake systems of the present study and changes over time, the associated ecosystem response and the natural recovery rates after a maximum in landscape disturbance will be investigated.

Study area

Hijkermeer (52°53'23"N 6°29'31"E, 14m a.s.l.) is a pingo-remnant located near the town of Beilen on the Drenthe Plateau in The Netherlands (Fig. 1). The Drenthe Plateau is well known for the megalith tomb constructions, or 'Hunebedden', built by farmers of the Funnel Beaker Culture in the Neolithic around 5000 years BP (Bakker, 2003). The lake is small and shallow, with a 200m diameter and 1.6m maximum depth; river inlet and outlets are absent, minimizing the catchment area. A late-glacial chironomid, pollen and diatom study of Hijkermeer has already been provided by Heiri et al. (2007), indicating that the lake was oligo- to mesotrophic during this time-frame (14000 −10700 cal. yr BP).

Llangorse Lake (51°55'40.2"N 3°15'10.9"W, 150m a.s.l.) is a late-glacial basin located in the Brecon Beacons in Wales, United Kingdom (Fig. 1). The lake consists of two basins and is mainly fed by the river Afon Llynfi, entering in the south and draining in the north, giving the lake a large catchment size. The area surrounding the lake has a long history of anthropogenic activity, indicated by the presence of megalith tombs (Cummings et al., 2002), an old roman road (Chambers 1999) and a 10th century artificial island (crannog), built in the northwest of the lake (Campbell and Lane 1989). Moreover, medieval literature already suggested the presence of algal blooms occurring within the lake (Griffiths 1939). Water chemistry data for the period between 1995−1996 indicates that the lake was alkaline, 2331−2560 µeq/L, at that time, the pH ranged from 7.88 to 8.08 and the TP from 69.6 to 149.7 µg/L, indicative of nutrient-rich conditions and large seasonal differences (Duigan et al. 1999). The TP concentration is currently enhanced by anthropogenic activity, but additionally by the release of the internal phosphorus load stored in the sediment, underlining the need for conservation and management measures (Bennion and Appleby 1999).

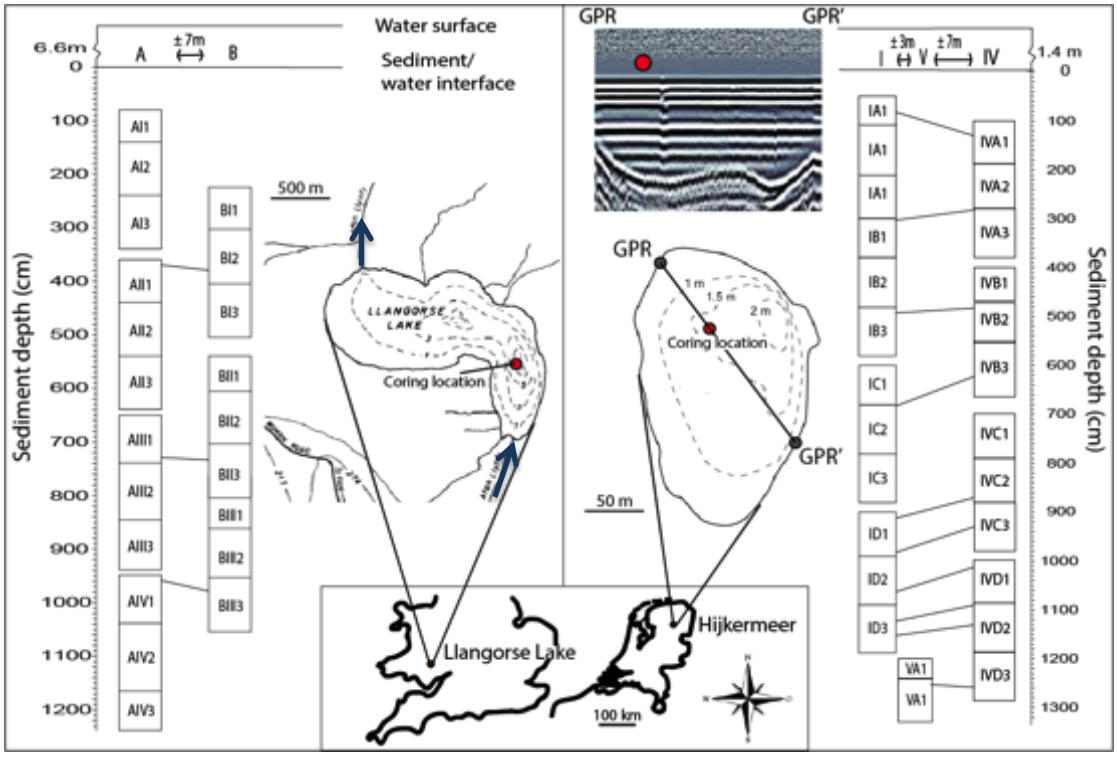


Figure 1. *Topographic setting of Llangorse Lake and Hijkermeer, including bathymetry based on Jones et al. (1985) and Heiri et al. (2007) respectively, with an overview of the retrieved cores in both lakes and the basin structure of Hijkermeer based on GPR measurements.*

Material and methods

Two parallel sediment cores were recovered from Hijkermeer at 1.4m water-depth in spring 2013. At Llangorse Lake two parallel sediment cores were collected in summer

2014 at 7m water-depth. Cores were transported horizontally and after splitting, the sediments were described and photographed... High-resolution loss-on-ignition (LOI) was performed on 99 samples representing the entire sequence from Llangorse Lake to determine the organic content, according to standard techniques defined by Heiri et al. (2001).

A radiocarbon chronology is available for both lakes (Akkerman et al, in prep) based on independent data of Hijkermeer. The chronology of the sedimentary record of Llangorse Lake is based on correlation by means of loss-on-ignition profile to a previous radiocarbon-dated core retrieved from Llangorse Lake by Jones et al. (1985).

A total of 73 samples of the Hijkermeer sequence were processed for pollen analysis following Faegri and Iversen (1989). In samples with sufficient pollen concentration a minimum of 300 palynomorphs was counted, of which at least 200 tree pollen, at 400x magnification under an Olympus CX41 microscope. Pollen zones were defined following Janssen and Törnqvist (1991).

Subsampling for diatom analysis was focused on sections in the time interval corresponding to the period between 5000 yr BP and present, with increased resolution in parts of interest for the study. A total of 17 samples for Hijkermeer and a total of 19 samples for Llangorse Lake were freeze dried and a known weight was processed using potassium permanganate ($KMnO_4$) and 30% HCl to remove the organic material and carbonates, respectively. Slides were prepared using the evaporation tray method of Battarbee (1973). Permanent slides for diatom analysis were prepared using Naphrax® as mounting medium.

In most samples, a minimum of 300 valves were counted at 1500x magnification using Olympus BX51 microscope, fitted with inference phase contrast. Identification and taxonomy was primarily based on Krammer and Lange-Bertalot (1986; 1988; 1991a; 1991b). The stratigraphically constrained sum of squares cluster analysis of the CONISS program (Grimm 1987) provided by TILIA 1.7.16 (Grimm, 2011) was used to determine diatom zonation; species with less than 2% abundances were excluded from the calculation.

Water quality was estimated using two methods. The first one (further referred to as TS-VD) was based on the ecological preference list of Van Dam et al. (1994), which includes the ecological preference of diatoms in brackish and freshwater Dutch lakes comprising 948 taxa. In the second method (further referred to as DI-TP), TP was estimated using statistical prediction models based on the Combined TP-dataset comprising data on 345 lakes, available on the EDDI website (http://craticula.ncl.ac.uk/Eddi/jsp/)(Battarbee et al., 2000). WA-PLS (Ter Braak and Juggins, 1993) regression was applied to the database, and the performance of the inferred model was assessed by use of bootstrapping (Birks et al. 2003). The similarity between the fossil and the modern training set samples was validated with the χ^2

distance coefficient of the modern analogue technique (MAT). The percentage of fossil species represented in the modern dataset was calculated separately as well. All the analyses were performed using the software C2 version 1.7.4 (Juggins, 2007). Diversity was analysed using a basic rarefaction index (Birks and Line, 1992) in order to account for sampling size.

Results

The Hijkermeer sediment cores consist of a dark brown gyttja (organic mud) with mossy intervals, a few thin (0.5−1 cm) sandy layers and intervals with rootlets/organic material (Fig. 4). The density of these rootlets/sandy layers is especially high around an inferred hiatus at a depth of ca. 1000 cm (Fig. 2 & 4). The two parallel cores show a similar pattern in the major elemental ratios, indicating that they provide a reliable overview of the lake (Fig. 6). The lower part of the sediment cores at Llangorse Lake consist of organic mud, which towards the top rapidly shifts to red-brown silty clay at a depth of ca. 390cm (Fig. 5), represented by a major drop in the LOI-curve (Fig. 7).

The Hijkermeer sequence contains a hiatus occurs at ca. 1000 cm (3040 cal. yr BP); above it the radiocarbon dates indicate similar ages of ca. 1000 cal. yr BP up to a depth of ca. 650cm. No datable material was found above this depth, but combined with the geochemical data (Akkerman et al., in prep), the upper part could be interpolated.

The summary pollen diagram of Hijkermeer (Fig. 4) indicates a general decrease in arboreal pollen and an increase in cereals and herbs. A first increase in Cereals occurred during the hiatus at a depth of ca. 1000 cm and a second at a depth of ca. 700 cm (ca. 900 cal. yr BP) coinciding with a sharp increase in aquatic plants and a decline in *Sphagnum*. In contrast to Hijkermeer, the summary pollen diagram of Llangorse lake (Fig. 5), provided by Chambers (1999), does not indicate gradual changes in the vegetation, starting with a sharp decrease in non-arboreal pollen (NAP) at a depth of ca. 600cm. Cereals temporarily increase between 425cm and 250cm depth, ca. 3000 to 1000 cal. yr BP.

The diatom assemblages of the Hijkermeer sequence are dominated by *Fragilaria spp.* Lyngbye, *Tabellaria flocculosa* (Roth) Knudson and various benthic species including *Achnanthidium minitissimum* (Kützing) Czarnecki (Fig. 2). Two major zones were defined, subdivided into seven subzones (Hijkermeer Diatom Zone; HDZ). The most prominent ecological shift in the sequence occures in HDZ 2a (910-840 cm; ca. 1020-990 cal. yr BP), when the planktonic species *Aulacoseira subarctica* (Müller) Haworth and *Asterionella formosa* Hassall peak at ca. 1000 cal. yr BP with 70% and 10% respectively. Overall, there was a generally increasing trend in TSVD (1.3 to 3.5) and DI-TP (12 to 32 µg TP/L) and the diversity appears to follow shifts in TSVD and DI-TP (Fig. 4). The second component of the model to reconstruct TP performed well, indicated by an R^2 of 0.80 with a root mean square error (RMSE) of 0.25 $\log_{10}$ TP units and a cross-validated RMSE of prediction (RMSEP) of 0.33 $\log_{10}$ TP units. In

most of the samples, at least 70% of the fossil species were represented in the training set and in some even more than 90% (Fig. 6).

Diatom assemblages of the Llangorse Lake are dominated by *Fragilaria spp.* and several planktonic species including *Stephanodiscus rotula* (Kützing) Hendey and *Aulacoseira granulata* (Ehrenberg) Simonsen (Fig. 3). Ecosystem shifts are mainly driven by the planktonic species and *Fragilaria spp*. is abundant throughout the record. Two major zones were defined, which were subdivided into six subzones (Llangorse Lake Diatom Zone; LDZ). A temporary increase can be observed in the TSVD (4.4 to 5 to 4.4) and DI-TP (54 to 168 to 66 µg TP/L) (Fig. 5). The diversity follows an inverse pattern in relation to the water quality. The model performance values are the same as for Hijkermeer. Between 50% and 94 % of the fossil species were represented in the training set.

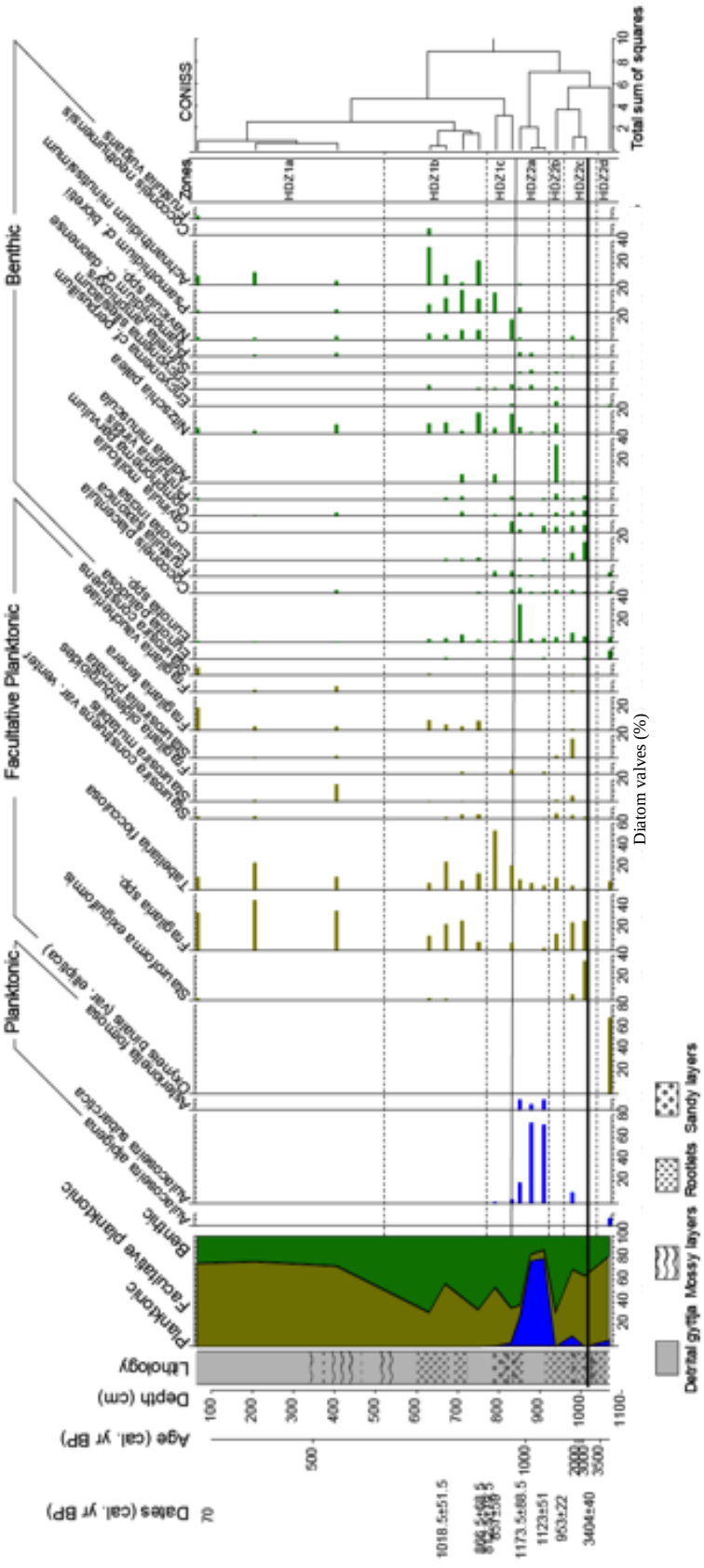


FIGURE 4. *Diatom stratigraphy of Hijkermeer, including the lithology. Values are given as percentage of total diatoms counted. Only selected species, with >2% abundance are presented and diatom zonation was based on the CONISS program.*

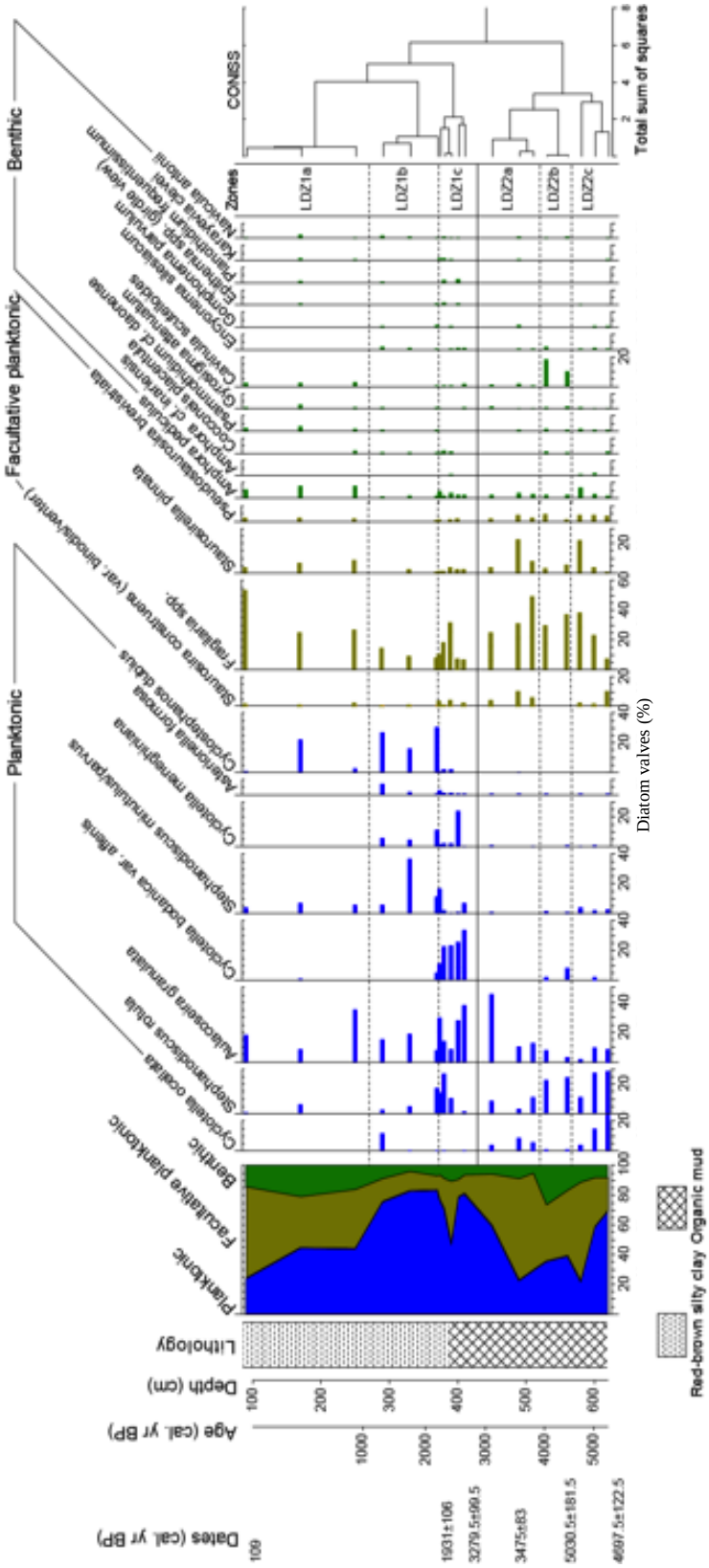


FIGURE 5. *Diatom stratigraphy of Llangorse Lake, including the lithology. Values are given as percentage of total diatoms counted. Only selected species, with >2% abundance are presented and diatom zonation was based on the CONISS program.*

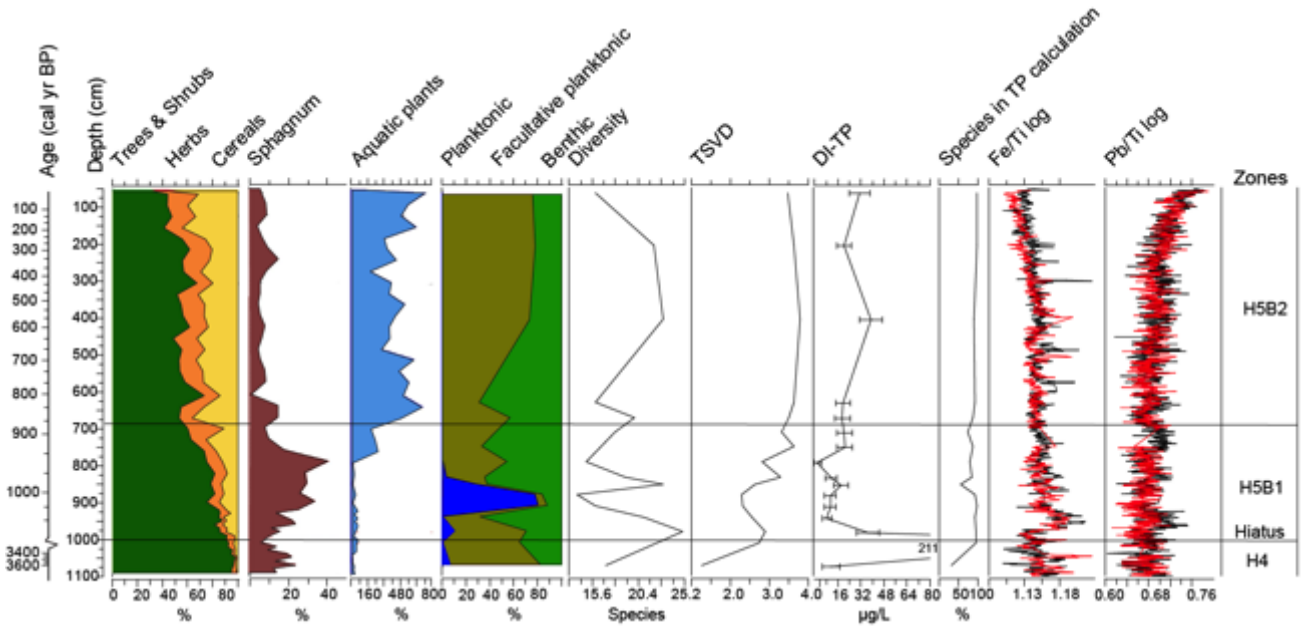


FIGURE 6. *Overview of multiple proxies used in this study for the sediment record of Hijkermeer: summary pollen stratigraphy together with Sphagnum and Aquatic plants, summary diatom stratigraphy, rarefaction diversity, TSVD, DI-TP and iron and lead reconstructions. Zones are defined as pollen zones, highlighting major Holocene climate and landscape transitions (H4= Subboreal; H5 is Subatlantic).*

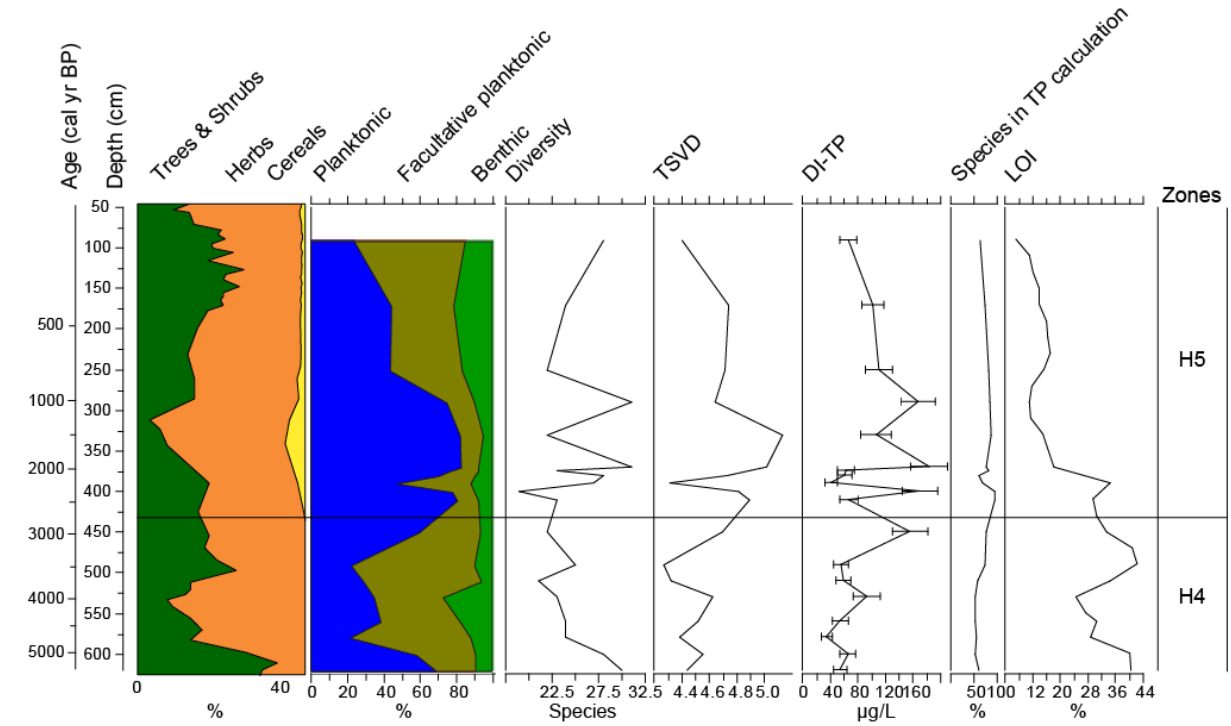


FIGURE 7. O*verview of multiple proxies used in this study for the sediment record of Llangorse Lake: summary pollen stratigraphy (Jones et al. 1985), summary diatom stratigraphy, rarefaction diversity, TSVD, DI-TP and LOI reconstructions. Zones are defined on a northwestern European Holocene climate transition at ca. 2800 cal. yr BP (H4= Subboreal; H5 is Subatlantic).*

Discussion

Early human influence on Hijkermeer

The lack of planktonic species in most of the Hijkermeer samples suggests that the lake has been shallow throughout the sequence, which is confirmed by intervals with rootlets in several parts of the core (Fig. 4). During the Subboreal (1071−1031 cm depth; 3650−3400 cal. yr BP), the diatom data reflects primarily climate forcing (Wilson et al., 2012) and little to almost no anthropogenic influence in the lake during a period that coincides with the Early/Middle Iron Age, when human habitation increased together with cattle grazing. The low diatom species diversity corresponds to the oligotrophic circumstances (Davidson and Jeppesen, 2013). The most notable feature in the record is the hiatus at a depth of ca. 1000 cm and most of the shifts in the diatom assemblages appear to be related to it. The most likely explanation would be lowering of the lake level, resulting in partial or complete drying of the lake. This hypothesis is supported by the presence of reed and rootlets in the sediment at the depth of the hiatus, suggesting that the reed belts surrounding the lake expanded towards the middle of the lake. The potential mechanism for this could be a shift in the seasonal distribution of precipitation, where a series of dry summers can cause the lake to dry out, oxidizing the top of the organic sediment (Covich and Stuiver, 1974). In depth research and comparison between more pingo lakes across the region is required to draw a final conclusion on this matter. Since the first increase in Cereals in the pollen record occurs within the time frame of the hiatus, the timing of the first imprint of agricultural activity and its effect on the water quality cannot be defined exactly, although post-hiatus cereal percentages are still low (<5%).

The initial phase after the lake reformed at ca. 1050 cal. yr BP was characterized by shallow conditions, indicated by the dominance of epiphytic diatoms at >40% followed by increased abundances of benthic and epiphytic species (Van Dam et al., 1994). The simultaneous peak in trophic state during shallow lake levels may be related to increased allochtonous input and increased nutrient availability due to sediment re-suspension. The peak of planktonic species between 1030 and 990 yr BP suggest a temporarily enhanced inflow of water at the start of the Medieval period. Following the planktonic event, the decline in *Sphagnum* together with an increase in Cereals can be interpreted as active removal of peat by humans in the littoral zone of the lake. Furthermore, it also coincides with increased TSVD and DI-TP values, which can be related to the increase in agricultural activities.

Early human influence on Llangorse Lake

Unlike for Hijkermeer, fluctuations in planktonic species, indicative of higher lake levels, represent the main shifts in Llangorse Lake diatom assemblages. A clear increasing and decreasing trend can be correlated between the relative abundance of planktonic species, Cereals and the trophic state of the lake, and most likely related to anthropogenic activity. The base of this interval corresponds to the Neolithic period and is characterised by relatively high abundances in trees and shrubs (40%). Abundant *S. rotula* and *C. ocellata* Pantocsek indicate that the lake was meso- to eutrophic (Van Dam et al., 1994) during that time. A sharp increase in relative

abundance of facultative planktonic species compared to the aforementioned planktonic species at ca. 600cm, ca. 5000 cal. yr BP implies a shallower, more turbulent water column. This event coincides with a major decline in arboreal pollen, suggesting forest clearings. A major increase of *A. granulata* corresponds to a large increase in TSVD and DI-TP (Kilham et al., 1986; Van Dam et al., 1994). The increased availability of nutrients can be related to a further increase in sedimentation, enhancing nutrient leaching and leading to more turbulent waters, which results in re-suspension of nutrients from the sediment.

During the Subatlantic (430-0 cm; 2800~ cal. yr BP), high abundances of eutrophic species *A. granulata* and *C. bodanica* (Grunow in Van Heurck) Cleve-Euler relate to the high values of the TSVD and DI-TP, indicating high nutrient availability and increased primary productivity (Kilham et al., 1986; Van Dam et al., 1994). A relative decrease in planktonic species and an increase in *Fragilaria spp.* at a depth of ca. 390 cm (ca. 2025 cal. yr BP) coincide with an abrupt change in sediment stratigraphy from organic lake mud to silty clay, ,presumably reflecting anthropogenically-forced enhanced soil input. A shift to smaller planktonic species can be related to decreased light availability, e.g. lower water transparency, as small-sized species with low sinking velocities have a competitive advantage in remaining a sufficient amount of time in the euphotic zone (Winder et al., 2009).

Following the Roman Period, Cereals decline and increased arboreal pollen suggest woodland regeneration, and critically, resulting again in lower reconstructed nutrient availability, as indicated by the relative increase in facultative planktonic and benthic species. This points to a decline in human influence on the lake, corresponding to the medieval depression. Rapidly after anthropogenic activity appears to decrease and the water quality of the lake improves, the diversity increases again as well, highlighting the resilience of the ecosystem.

(Early) human impact on water quality and diversity

Despite the high amount of poor analogues within the DI-TP transfer function, both methods applied to reconstruct the water quality, followed a similar pattern. By means of comparison between the lakes, the Llangorse Lake diatom and pollen data reveal higher intensity of human activity. Despite the hiatus, at Hijkermeer, nutrient availability increases along the gradient of increased human agricultural activities as indicated by increase in NAP. A major factor contributing to the difference between the two lakes could be the relatively minor anthropogenic activity around Hijkermeer, but it can also reflect differences in the lakes' physical parameters. As mentioned in the study area, Hijkermeer has a small drainage area, whereas Llangorse Lake has a larger catchment and the sediment core was collected close to a river inlet. Therefore, the anthropogenic impact of a far larger area can be expected to affect Llangorse Lake. Also, differences in soil properties can cause such a discrepancy: erosion related to deforestation will have a larger impact on lake systems when the soil is enriched in nutrients, but information on the subsurface characters is required in order to support this theory.

Noteworthy is the relation of diversity to water quality, clearly expressed in both lakes. In Hijkermeer the diversity increased with the shift from oligotrophic to mesotrophic conditions and in Llangorse Lake the diversity was highest in the periods of eutrophic conditions, as opposed to the period with hypereutrophic conditions. This suggests that diversity is highest in meso- to eutrophic conditions. Many spatial and temporal studies on the relation between diversity and trophic state found this unimodal distribution as well (Jeppesen et al., 2000; Rusak et al., 2004; Das et al., 2008). Few species can cope with very low nutrient availability, whereas very high nutrient availability also increases competition and production, resulting in low light availability and hypoxia due to the decomposition of organic matter (Interlandi & Kilham, 2001; Tilman, 1982). Furthermore, sedimentation not only increases nutrient availability, but it also causes turbulence, which appears to have major impact on the species diversity in Llangorse Lake. Other parameters, such as lake level and area, largely driven by climatic changes, seem to contribute largely to changes in diversity in Hijkermeer.

The most remarkable result of this study is the quick recovery of the diversity after the decrease in human impact and the corresponding eutrophication in the sediment record of Llangorse Lake. Here, the resilience of the ecosystem is clearly reflected: returning to the pre-disturbed stable state following a shift to an undesirable alternative stable state related to a maximum of human impact (Scheffer et al., 2001; Elmqvist et al., 2003). This implies that proper management of the lake suffering from eutrophication can result in recovering of the ecosystem and is crucial for on-going management and conservation activities, especially relating to the present eutrophication problems in Llangorse Lake (Bennion and Appleby, 1999). However, the species assemblages show that the ecosystem does not recover to pre-human influence conditions but rather to pre-roman conditions.

Conclusions

Early human impact on water quality can be traced back to as early as 5000 years BP with the use of diatom based qualitative and a quantitative reconstruction. It appears that the onset and increase in agriculture, as indicated by the appearance of Cereals in the pollen record, lead to an increase in nutrient availability in both lakes and a subsequent decrease in Cereals in Llangorse Lake coincided with a decrease in nutrients. Our data support the view that diversity is unimodally related to water quality with the highest diversity occurring in meso- to eutrophic conditions in the studied lakes. Llangorse Lake showcased the ecosystem resilience, as the return to the baseline trophic state led to increase in diversity. This can be used as a model for the management and conservation of the present eutrophication problems, specifically at Llangorse Lake. However, caution has to be taken with regards to the relation between diversity and DI-TP, since shifts in diatom assemblages can also relate to increased turbulence, which is not necessarily related to an increase in TP and could also affect the diversity.

Acknowledgements

We gratefully acknowledge the Quaternary Research Association (QRA) for sponsoring the field campaign in the United Kingdom and D. Maas and dr. A. McLeod for making it a success. Furthermore, we are grateful for the help dr. H. Cremer gave with the diatom analysis and interpretation as well as the NVKD (Dutch Flemish Circle of Diatomists) for letting the first author present her work at the NVKD meeting. Also, thanks goes to dr. A. Goldenberg for sharing her knowledge on diatom ecology, dr. F.P.M. Bunnik and H. Koolmees for providing guidance and contributing to the pollen analysis and M.T.I.J. Gouw-Bouman for helping with the chronology. For the interpretation of the XRF elemental ratio data we wish to thank prof. dr. G.J. Reichart and M. Bakker for providing the GPR measurements.

References

Bakker R (2003) The emergence of agriculture on the Drenthe Plateau: a paleobotanical study supported by high resolution 14C dating. PhD thesis Archäologisch Berichte

Battarbee RW (1973) A new method for the estimation of absolute microfossil numbers, with reference especially to diatoms. Limnology and Oceanography 18(4): 647-653.

Battarbee RW (1999) The importance of palaeolimnology to lake restoration. The Ecological Bases for Lake and Reservoir Management (149-159). Springer Netherlands.

Battarbee RW, Juggins S, Gasse F, Anderson NJ, Bennion H, Cameron NG (2000) European Diatom Database (EDDI). An Information System for Palaeoenvironmental Reconstruction.

Behre KE (1981) The interpretation of anthropogenic indicators in pollen diagrams. Pollen et spores 23:225–245.

Bennion H, Appleby P (1999) An assessment of recent environmental change in Llangorse Lake using palaeolimnology. Aquat Conserv Mar Freshw Ecosyst 9:361–375.

Bennion H, Juggins S, Anderson N (1996) Predicting epilimnetic phosphorus concentrations using an improved diatom-based transfer function and its application to lake eutrophication management. Environmental Science & Technology 30(6): 2004-2007.

Birks HJB, Line JM (1992) The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. The Holocene 2(1): 1-10.

Birks HJB, Mackay A, Battarbee RW, Birks J, Oldfiel F (2003) Quantitative palaeoenvironmental reconstructions from Holocene biological data. Global change in the Holocene 107-123.

Bradshaw EG, Rasmussen P, Nielsen H, Anderson NJ (2005) Mid- to late-Holocene land-use change and lake development at Dallund So, Denmark: trends in lake primary production as reflected by algal and macrophyte remains. Holocene 15:1130–1142.

Burford MA, Gobler CJ, O'Neil JM, Davis TW (2012) The rise of harmful cyanobacteria blooms: The potential roles of eutrophication and climate change. Harmful Algae 14:313–334.

Campbell E, Lane A (1989) Llangorse : a 10th-century royal crannog in Wales. Antiquity 63:675–681.

Chambers FM (1999) The Quaternary history of Llangorse Lake: Implications for conservation. Aquat Conserv Mar Freshw Ecosyst 9:343–359.

Conley DJ, Paerl HW, Howarth RW, et al (2009) Controlling eutrophication: nitrogen and phosphorus. Science 323:1014–1015.

Covich A, Stuiver M (1974) Changes in oxygen 18 as a measure of long-term fluctuations in tropical lake levels and molluscan populations. Limnol Oceanogr 19:682–691.

Cremer H, Bunnik FPM, Kirilova EP, Lammens EH, Lotter AF (2009) Diatom-inferred trophic history of IJsselmeer (The Netherlands). Hydrobiologia 631:279–287.

Cummings V, Jones A, Watson A (2002) Divided places: phenomenology and asymmetry in the monuments of the Black Mountains, Southeast Wales. Cambridge Archaeological Journal 12(01): 57-70.

Van Dam H, Mertens A, Sinkeldam J (1994) A coded checklist and ecological indicator values of freshwater diatoms from The Netherlands. Netherlands J Aquat Ecol 28:117–133.

Das B, Nordin R, Mazumder A (2008) Relationship between phytoplankton paleoproduction and diversity in contrasting trophic states. Aquat Ecosyst Health Manag 11:78–90.

Davidson TA, Jeppesen E (2013) The role of palaeolimnology in assessing eutrophication and its impact on lakes. J Paleolimnol 49:391–410.

Dearing JA, Battarbee RW, Dikau R, Larocque, I, Oldfield F (2006) Human-environment interactions: Learning from the past. Reg Environ Chang 6:1–16.

Duigan CA, Reid S, Monteith DT, Bennion H, Seda, JM, Hutchinson J (1999) The past, present and future of Llangorse Lake—a shallow nutrient-rich lake in the Brecon Beacons National Park, Wales, UK. Aquatic Conservation: Marine and Freshwater Ecosystems 9(4): 329-341.

Edwards KJ, Whittington G (2001) Lake sediments, erosion and landscape change during the Holocene in Britain and Ireland. Catena 42:143–173.

Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1(9): 488-494.

Elser JJ, Bracken MES, Cleland EE, et al (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10:1135–1142.

Faegri K, Iversen J (1989) Textbook of Pollen Analysis, revised by Faegri K, Kaland PE, Krzywinski K. J Wiley, New York.

Griffiths BM (1939) Early references to waterblooms in Britisch Lakes. Proc. Linn. Soc. (London) 151 (1): 14-19.

Grimm EC (1987) CONISS: A FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Computers and Geoscience 13: 13-35.

Grimm, E. C. (2011). Tilia version 1.7. 16 [software]. Illinois State Museum, Springfield, Illinois, USA.

Heiri O, Cremer H, Engels S, Hoek WZ, Peeters W, Lotter AF (2007) Lateglacial summer temperatures in the Northwest European lowlands: a chironomid record from Hijkermeer, the Netherlands. Quat Sci Rev 26:2420–2437.

Heiri O, Lotter AF, Lemcke G (2001) Loss on ignition as a method for estimating organic and carbonate content in sediments: Reproducibility and comparability of results. J Paleolimnol 25:101–110.

Interlandi SJ, Kilham SS (2001) Limiting resources and the regultation of diversity in phytoplankton communities. Ecology 82:1270–1282.

Janssen CR, Törnqvist TE (1991) The role of scale in the biostratigraphy and chronostratigraphy of the Holocene Series in The Netherlands. The Holocene 1(2): 112-120.

Jeppesen E, Jensen JP, Søndergaard M, Lauridsen T, Landkildehus F (2000) Trophic structure, species richness and diversity in Danish lakes: changes along a phosphorus gradient. Freshw Biol 45:201–218.

Jones R, Benson-Evans K, Chambers FM (1985) Human influence upon sedimentation in Llangorse Lake, Wales. Earth Surf Process Landforms 10:227–235.

Juggins S (2007) C2 Version 1.5: software for ecological and palaeoecological data analysis and visualisation. University of Newcastle, Newcastle upon Tyne.

Kilham P, Kilham SS, Hecky RE (1986) Hypothesized resource relationships among African planktonic diatoms. Limnol Oceanogr 31:1169–1181.

Kirilova EP, Cremer H, Heiri O, Lotter AF (2010) Eutrophication of moderately deep Dutch lakes during the past century: Flaws in the expectations of water management? Hydrobiologia 637:157–171.

Krammer K, Lange-Bertalot H (1986) Subwasserflora von Mitteleuropa. Bacillariophyceae i Tiel: Naviculaceae. Gustav Fisher Verlag, Stuttgart .

Krammer K, Lange-Bertalot H (1988) Subwasserflora von Mitteleuropa. Bacillariophyceae ii Tiel: Bacillariaceae, Epithmicaea, Surirellacaea. Gustav Fisher Verlag, Stuttgart.

Krammer K, Lange-Bertalot H (1991a) Subwasserflora von Mitteleuropa. Bacillariophyceae iii Tiel: Centrales, Fragiliariaceae, Eunotiaceae. Gustav Fisher Verlag, Stuttgart.

Krammer K, Lange-Bertalot H (1991b) Subwasserflora von Mitteleuropa. Bacillariophyceae iv Tiel: Achnanthaceae. Gustav Fisher Verlag, Stuttgart.

Messerli B, Grosjean M, Hofer T, Nunez L, Pfister C (2000) From nature-dominated to human-dominated environmental changes. 19:459–479.

Nodine ER, Gaiser EE (2014) Distribution of Diatoms Along Environmental Gradients in the Charlotte Harbor, Florida (USA), Estuary and Its Watershed: Implications for Bioassessment of Salinity and Nutrient Concentrations. Estuaries and coasts 37(4): 864-879.

Paerl HW, Huisman J (2008) Blooms like it hot. Science 320:57–58.

Rusak JA, Leavitt PR, McGowan S, Chen G, Olson O, Wunsam S, Cumming BF (2004) Millennial-scale relationships of diatom species richness and production in two prairie lakes. Limnol Oceanogr 49:1290–1299.

Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. Nature 413(6856): 591–596.

Smol JP, Stoermer EF (2010). The diatoms: applications for the environmental and earth sciences. Cambridge University Press, Cambridge.

Ter Braak CJ, Juggins S (1993) Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. Hydrobiologia 269:485–502.

Tilman D (1982) Resource Competition and Community Structure. (Mpb-17). Princeton, NJ: Princeton University Press.

Vos PC, de Wolf H (1993) Diatoms as a tool for reconstrcuting sedimentary environments in coastal wetlands; methodological aspects. In Twelfth International Diatom Symposium. Springer Netherlands.

Wilson CR, Michelutti N, Cooke CA, Briner JP, Wolfe AP, Smol JP (2012) Arctic lake ontogeny across multiple interglaciations. Quaternary Science Reviews 31: 112-126.

Winder M, Reuter JE, Schladow SG (2009) Lake warming favours small-sized planktonic diatom species. Proc. R. Soc. B Biol. Sci. 276: 427–435.

Diatomededelingen 39, 2015

Diatom response and planktonic diversity in ancient lakes under the pressure of Quaternary climate change: lessons learned from lakes Ohrid and Prespa

Aleksandra Cvetkoska[1], Elena Jovanovska[2], Zlatko Levkov[3] & Friederike Wagner-Cremer[1]

[1]Palaeoecology, Department of Physical Geography, Faculty of Geosciences, Utrecht University, Utrecht, The Netherlands, (acvetkoska@yahoo.com).
[2]Department of Animal Ecology and Systematics, Justus Liebig University, Giessen, Germany.
[3]Institute of Biology, Faculty of Natural Sciences, Skopje, R. of Macedonia.

Abstract

Ancient "sister" lakes Ohrid and Prespa represent the oldest and most diverse extant lake system in Europe. Diatom research during the last century demonstrated relatively low percentage of shared diversity and presence of different endemic species in the extant and fossil planktonic flora of both lakes. Intensive palaeoclimate and palaeoenvironmental research in the last decade acknowledged the lakes as important archives that offer unique opportunity for Quaternary climate research and evolutionary studies. This paper presents an overview of the diatom research conveyed on the sediment sequences recovered from both lakes, Ohrid and Prespa.

Key words: diatoms, *Cyclotella*, lakes Ohrid and Prespa, sediment sequence.

Introduction

The geological evolution of some of the largest, deepest and oldest lakes on Earth is driven by tectonic processes, and such lakes are often found within grabens in active rift zones. Examples include lakes Baikal (Russia); Ohrid (Macedonia, Albania); Hövsgöl (Mongolia); Biwa (Japan); Malawi, Tanganyika and Victoria (African Great Lake region); and Titicaca (Bolivia, Peru). Ancient lakes are defined as extant lakes that have continuously existed since before the Pleistocene (Martens 1997). Despite having different origins and characteristics, they share the common feature of high diversity and endemism that typically distinguish ancient, from short-lived, postglacial lakes (Albrecht & Wilke 2008). The extraordinary biodiversity and high number of neo-endemic species flocks is result of their prolonged isolation from other ecosystems (Brooks 1950; Martens 1997). Furthermore, they hold sediment archives, often of Quaternary age, and thus represent unique chronicles that contain the material evidence of events from the past (Fedotov et al., 2003).

Diatom records from ancient lakes provide powerful insight not only into the past glacial-interglacial climate and environmental change, but also offer unique opportunity to link the past eco-evolutionary events (Khursevich et al., 2001; Mackay

et al., 2010; Reed et al., 2010; Cvetkoska et al., 2012). Nonetheless, interpretation of such records is often limited by the lack of modern analogue species, therefore, reliable taxonomic approach on the extant and extinct flora is essential to understand the species-lineages, diversity and biogeographic distribution.

At the Balkan Peninsula, ancient lakes Ohrid and Prespa co-existed for 2−5 Ma (Stanković 1960; Albrecht & Wilke 2008). Representing the oldest lake system in Europe, these "sister" lakes occupy an important geographic position at the meeting point of three great world regions–Central Europe, the Eurasiatic steppe, and the Mediterranean. Both lakes are renowned for their extraordinary biodiversity and high endemism (Albrecht & Wilke 2008), which combined with their location, make the lakes extraordinary target sites for biodiversity, evolutionary and Quaternary research. A century of diatom research on lakes Ohrid and Prespa was dedicated to studying the extant diatom flora, its diversity, taxonomy and ecology. Diatom application in palaeolimnological and palaeoenvironmental research on the lakes started with the first analysis of Roelofs & Kilham (1983) carried on a core recovered from Lake Ohrid. Later on, in 1993, Lake Ohrid was included as a target area of the International Continental Scientific Drilling Program (ICDP), and an interdisciplinary research project "Scientific Collaboration on Past Speciation Conditions in Lake Ohrid (SCOPSCO)" was initiated in 2007. Several drilling campaigns on both lakes were performed within the frames of the project, prior an ICDP deep drilling campaign on Lake Ohrid in 2013. Here, we summarize the diatom-based palaeoenvironmental research on the sediment sequences recovered from lakes Ohrid and Prespa, outline our present knowledge about the diversity of the dominant diatom groups, and the species-specific and community responses to the past geologic, climate and environmental events.

The study area

Lakes Ohrid and Prespa are ancient "sister" lakes located in a tectonically active graben system within the Southern Balkan Extensional Regime (Lindhorst et al., 2015). The complex karstic geomorphology of the area enabled formation of a fractured mountain aquifer influencing the surface inflow and the groundwater outflow, and forming an underground connection between the lakes (Anovski et al., 1997, 2001; Popovska & Bonacci 2007). Isotope studies have shown that the largest feeder spring areas of Lake Ohrid (St. Naum, Biljana and Zavir in Macedonia and Tushemishte in Albania) are partially fed by underground inflow from Lake Prespa (Anovski et al., 2001).

Lake Ohrid (41°01'N, 20°43'E, Fig. 1) is probably the most diverse ecosystem in the world, taking the surface area into account, with >300 known endemic species (Albrecht & Wilke 2008; Levkov & Williams 2012; Föller et al., 2015). The most recent results based on borehole data, core logging and geochemical measurements of the 569 m long sediment sequence recovered during the SCOPSCO drilling campaign on Lake Ohrid indicate age of ca. 2 Ma (Lindhorst et al., 2015). Today, Lake Ohrid is located at 693 m a.s.l., and covers a surface area of 358 km^2 (Matzinger et al. 2006). The maximum water depth of the lake is 289 m, the mean water depth is 155 m, and

the total volume of the lake is 55.4 km^3. Including the catchment area of Lake Prespa, the total watershed of Lake Ohrid is 2610 km^2. The average monthly temperature is 26 °C during the summer and -1°C in winter and the average precipitation is 750 mm/year. Lake Ohrid is at present oligotrophic and a typical calcium-bicarbonate marl lake, in which $Ca(HCO_3)_2$ dominates.

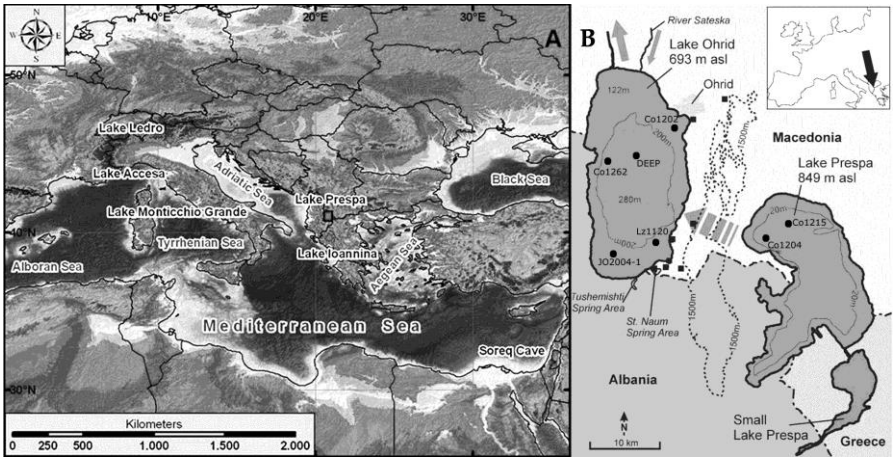


FIGURE 1. *(A) Map of the Mediterranean region and parts of Europe, Africa and Asia showing the location of lakes Prespa and Ohrid (B) Map of lakes Ohrid and Prespa showing the flow direction (grey arrows), underground flow (broken arrow) and the core locations (black dots). The map in the right hand corner shows the location of the study area within Europe (modified from Matzinger et al., 2006; Cvetkoska et al., 2014b).*

Lake Prespa (40° 46'–41° 00' N, 20° 54'–21° 07' E, or Macro Prespa, Fig. 1) occupies the central part of the N–S trending tectonic graben in the western zone of the Dinarides and consists of two lakes, Macro and Micri Prespa (Fig. 1). The exact age of Lake Prespa is not known today. Despite the lower number of endemic species than Lake Ohrid, Lake Prespa is an important biodiversity "hot spot" and a migratory corridor for many bird species. Most recently the "Ohrid–Prespa Watershed" has been nominated as a Transboundary Biosphere Reserve by the International Union for Conservation of Nature (IUCN) and the World Commission on Protected Areas (WCPA). Lake Prespa has a surface area of 254 km^2, a mean water depth of ca. 14 m, a maximum water depth of ca. 48 m and a total volume of 3.6 km^3. Mean temperatures vary from 1°C in winter to 21°C in summer, and mean annual precipitation varies between 750 and 1200 mm/yr in the lake valley and the surrounding mountain ranges, respectively (Hollis & Stevenson 1997). Recently, surveillance monitoring (April 2010–June 2011) of Lake Prespa and its watershed revealed TP concentrations of ca. 2.5 mg/l and ca. 162 t/yr TP loads from the river tributaries, which defines the lake as eutrophic according to both, EU and domestic legislation (Krstić 2012).

Diversity and distribution of the genus *Cyclotella* (Kützing) Brébisson in lakes Ohrid and Prespa

The diversity and distribution of the genus *Cyclotella* is addressed (Table 1), due its dominance and high morphological variability in the modern and fossil diatom communities in both lakes.

Previous diatom research enumerated a total of 15 *Cyclotella* taxa for lakes Ohrid and Prespa (Levkov & Williams 2012). *Cyclotella juriljii* nom.nud *sensu* Kocev et al. (2010) and *Cyclotella* sp. *sensu* Levkov et al. (2007) were found only in Lake Prespa, while *C. fottii* Hustedt and *C. ocellata* Pantocsek were reported from both lakes. However, *C. fottii* was not identified in any diatom sample from Lake Prespa (Cvetkoska et al., 2014a, 2015a). However, the recent analyses of the Lake Prespa fossil and extant diatom assemblages revealed the presence of a distinct taxon, *Cyclotella prespanensis* Cvetkoska, Hamilton, Ognjanova-Rumenova & Levkov (Cvetkoska et al., 2014a). Probably, *C. ocellata* initial cells *sensu* Levkov et al. (p. 167, figs 4–7, 2007) belong to the diminution series of *C. prespanensis*, leading to the conclusion that previously, this taxon was misidentified as *C. fottii.*

Cyclotella ocellata is present in the diatom flora of both lakes, but another distinct taxon, *C. paraocellata* Cvetkoska, Hamilton, Ognjanova-Rumenova & Levkov dominates the sediment record and the extant diatom flora in Lake Prespa. Light and scanning electron microscope analyses of *C. paraocellata* revealed an intriguing presence of populations with circular and rectangular valve shape (Cvetkoska et al., 2014a). This triggers the question whether these populations represent distinct species, or ecotypes of the same species. The similar occurrence of valves with rectangular shape in *C. ocellata* supports the second hypothesis, but detailed taxonomic and molecular analyses are preferable to better define the relation between these morphologically variable populations.

Cyclotella minuscula (Jurilj) Cvetkoska, is also present with high abundance in the extant flora and the fossil diatom record of lakes Ohrid and Prespa, previously misidentified or neglected due to its small size. Morphological comparison revealed differences in the species populations from both lakes, especially in the presence of triangular forms in Lake Prespa's fossil assemblages.

Most recent analyses revealed presence of nine potentially new *Cyclotella* species in the fossil diatom record in Lake Ohrid (Wagner et al., 2014), two of them, *Cyclotella cavitata* Tofilovska, Cvetkoska, Jovanovska, Ognanova-Rumenova & Levkov and *C. sollevata* Tofilovska, Cvetkoska, Jovanovska, Ognanova-Rumenova & Levkov are already validly described (Tofilovska et al., in press).

Although the genus *Cyclotella* is dominant in lakes Ohrid and Prespa, different species are present in the fossil and extant diatom planktonic assemblages, with the exception of *C. ocellata* and *C. minuscula.* Further investigations are necessary to explore the evolution of this genus in the lakes and reveal the possible patterns and processes of speciation.

TABLE. 1. *List of* Cyclotella *(Kützing) Brébisson taxa based on published data and their distribution in lakes Ohrid and Prespa (modified from Levkov & Williams 2012 and Cvetkoska et al., 2014a). Legend: O = Lake Ohrid; P = Lake Prespa; 1 = species with wide distribution; 2 = endemic species; * observed only in fossil samples; ^ observed only in modern samples; "observed in fossil and modern samples.*

Species	Distribution
Cyclotella bifacialis Jurilj	O
Cyclotella cavitata Tofilovska, Cvetkoska, Jovanovska, Ognanova-Rumenova & Levkov	O^{2*}
Cyclotella cyclopuncta Håkansson & Carter	O
Cyclotella distinguenda Hustedt	O
Cyclotella fottii f. II *sensu* Kozarov 1960	-
Cyclotella fottii Hustedt	$O^{2"}$
Cyclotella glabriuscula (Grunow) Håkansson	O
Cyclotella juriljii nom.nud *sensu* Kocev et al. 2010	P
Cyclotella kuetzingiana Thwaites	O
Cyclotella meneghiniana Kützing	O
Cyclotella minuscula (Jurilj) Cvetkoska stat. nov.	$O/P^{1"}$
Cyclotella ocellata Pantocsek	$O/P^{1"}$
Cyclotella paraocellata Cvetkoska, Hamilton, Ognjanova-Rumenova & Levkov sp. nov.	$P^{2"}$
Cyclotella prespanensis Cvetkoska, Hamilton, Ognjanova-Rumenova & Levkov sp. nov.	$P^{2"}$
Cyclotella sp. *sensu* Levkov et al. 2007	P
Cyclotella sp. *sensu* Pavlov 2010	O
C. sollevata Tofilovska, Cvetkoska, Jovanovska, Ognanova-Rumenova & Levkov	O^{2*}
Cyclotella striata (Kützing) Grunow	O
Cyclotella verrucosa Jerković & Čado*	O

* *C. verrucosa* is most likely a misidentification of *C. fottii*

Palaeolimnological research on lakes Ohrid and Prespa: the diatom story

a) Lake Ohrid

Palaeolimnological research on lakes Ohrid and Prespa started in the late 20th century; the first insights into Lake Ohrid's fossil diatom communities derived from analysis of an 8.85 m long core (Core 9), collected in 1973 by Roelofs & Kilham (1983). At that

time, the limited radiocarbon dating suggested an age of >30 ka for the core recovered with the aim to determine to which extent the present oligotrophy and the unique diatom endemism was typical in the past. Core 9, was mostly dominated by centric diatoms from the genus *Cyclotella*. One group was notable for being persistent throughout, including: *Cyclotella fottii*, *C. hustedtii* Jurilj and *C. hustedtii* var.1, marked as the *Cyclotella* complex group (Roelofs & Kilham 1983). Nonetheless, interpretation of the results was hampered by chronological uncertainty, probably due to sediment slumping resulting from tectonically-induced mass movement (Wagner et al., 2009).

After the inclusion of Lake Ohrid into the ICDP program and the initiation of the project SCOPSCO in 2007, a 1075 cm long core (ca. 40 ka), Lz1120 was recovered from a water depth of 105 m in the southeastern part of the lake (Wagner et al., 2009). Low-resolution diatom analysis was carried to add the diatom record to the multi-proxy dataset (geochemistry, tephrastratigraphy, pollen, ostracodes) obtained with the aim to study the potential of Lake Ohrid for long-term palaeoenvironmental research. Tracking the diatom stratigraphy, Wagner et al. (2009) identified two main diatom zones in core Lz1120, dominated mainly by the planktonic species *Discostella stelligera* (Cleve et Grunow) Houk & Klee, *Cyclotella ocellata* and *C. fottii*. In this case, it is likely that *C. minuscula* was misidentified as *D. stelligera* and/or *Discostella* sp.

Reed et al. (2010) tested the diatom response to climate change across the last interglacial-glacial cycle in a ca. 15 m long (ca. 135 ka) sediment sequence, Co1202, recovered in 2007, from the northeastern part of the lake basin, at a water depth of 145 m (Vogel et al., 2010). The study demonstrated the diatom sensitivity as palaeoclimate proxies and provided evidence for climate change through the glacial-interglacial shifts. Changes were indicated mainly by shifts in the relative abundance of the dominant planktonic taxa *Cyclotella fottii* and *C. ocellata*, along with a range of facultative planktonic and benthic taxa present at lower relative abundance.

Detailed studies of the species morphologies and diversity in core Co1202 are presented by Cvetkoska et al. (2012). The results acknowledged the diatoms as palaeo-proxies in Lake Ohrid, tracking not only the glacial-interglacial climate shifts but also some of the short-term climate events. In terms of diversity, 22 different morphotypes of *Cyclotella ocellata* were delineated in the sequence, with clear shift in types between the successive interglacials. One of the key hypotheses raised by Cvetkoska et al. (2012) is that the higher diversity of the *C. ocellata* complex during Marine Isotope Stage (MIS) 5 compared to the interstadial (MIS 3) and the Holocene, most probably represents some form of evolution at a sub-species level.

Zhang et al. (2015) analyzed the diatom assemblage shifts during the late-glacial and Holocene period in a 1008 cm-long core, Co1262 recovered in 2011 from 260 m water depth in front of the Lini Peninsula at the western margin of Lake Ohrid. The results were interpreted in terms of direct temperature dependent diatom response and indirect response to temperature-related stratification/mixing regime and epilimnetic nutrient availability (Zhang et al., 2015).

Most recently, the SCOPSCO, ICDP deep drilling campaign carried at Lake Ohrid in 2013 resulted with a total recovery of 2100 m sediments from four drill sites with water depths ranging from 125 to 260 m. A maximum drill depth of 569 m below the lake floor was reached at the main drill site "DEEP", located in the central part of the lake, at a water depth of ca. 255 m (Wagner et al., 2014). The initial borehole logging, core logging and geochemical data indicate that the sediment succession covers roughly 2 million years (Lindhorst et al., 2015). Ongoing multi-proxy analyses of the "DEEP" site core proceed towards understanding the influence of the past geological and environmental events on the biological evolution of the lake taxa. Preliminary diatom analyses of smear slides from core catcher samples indicated continuous diatom preservation in the upper most 480 m of the sequence. Approximately 122 diatom taxa were identified throughout the sequence, mostly belonging to the benthic group, ca. 60% of the total species number. Despite the higher diversity of benthic taxa, the planktonic diatom genus *Cyclotella* was clearly dominant in the assemblages with 23 taxa identified during the preliminary analysis. Clear shifts between the *Cyclotella* groups were recorded throughout the sequence (Fig. 2); the most prominent occurring at ca. 430 m, 320 m, 230 m and 80 m blf were interpreted to likely represent key stages of evolution and/or environmental change (Wagner et al., 2014).

Initial diatom analyses of the composite sediment sequence from the "DEEP" site were already undertaken to assess the changes in the multi-proxy data record and study the ecosystem regimes and resilience to past geologic, climate and environmental events. By applying the concept of panarchy, Cvetkoska et al. (2015b) compared the diatom and lake specific response differences between lakes Ohrid and Prespa over the past ca. 91 ka. The study shows that on a long time scale, trends in the regime shifts appear synchronous in both lakes, but Lake Ohrid exhibits a high buffer capacity, whereas Lake Prespa is more resilient and "recovers" in relatively short time. Moreover, potential regime shifts of Lake Ohrid due to the hydrological connectivity with Lake Prespa were not evidenced in the multi-proxy dataset (Cvetkoska et al., 2015b). In addition, Jovanovska et al. (2015) compared the responses of both lakes to the pulse disturbance of the Y5 tephra influx/deposition from the Campi Flegrei caldera eruption event, dated at ca. 39.6 ka (De Vivo et al., 2001; Leicher et al., 2015). The comparison between lakes Ohrid and Prespa demonstrated high resilience of both lakes to environmental disturbance and moreover, did not find evidence for tephra disturbance-related species extinction events.

b) Lake Prespa

Although Lake Prespa probably shares similar age of co-existence with Lake Ohrid, its different phisico-chemical properties offer contrasting potential for palaeolimnological climate reconstruction. Palaeoclimate research on Lake Prespa started in 2007, upon the retrieval of the first long sediment sequence (Co1204) at a coring location in the northwestern part of the lake. The sedimentology, geochemistry and isotope records of the 10.5 m long score, ca. 48 ka BP, are presented by Leng et al. (2010) and Wagner et al. (2010). Apart from the above-mentioned study of Jovanovska et al. (2015), the long-term changes in the diatom assemblage composition were not analyzed in core Co1204. In 2009 the lake was included as a target site of the "The Collaborative

Research Centre (CRC) 806: "Our Way to Europe - Culture-Environment Interaction and Human Mobility in the Late Quaternary" B2 project (http://www.sfb806.uni-koeln.de/index.php/project/cluster-b/b2) with the aim to reconstruct the environmental history of the Balkan region during the last glacial-interglacial cycle on a sub-millennial time scale. The longest sediment sequence recovered for the purpose of this project is core Co1215, dated to cover the last 91.0 cal ka BP (Damaschke et al., 2013).

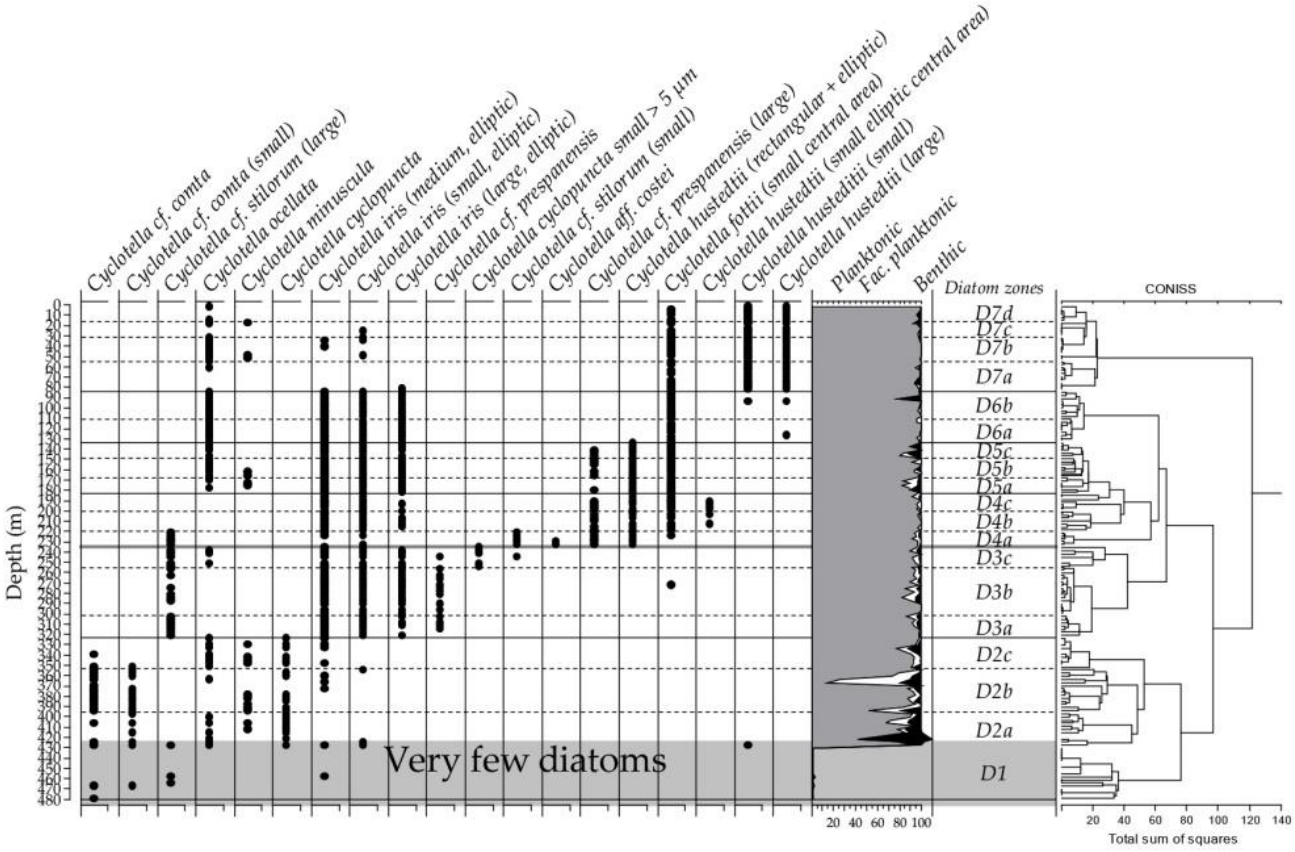
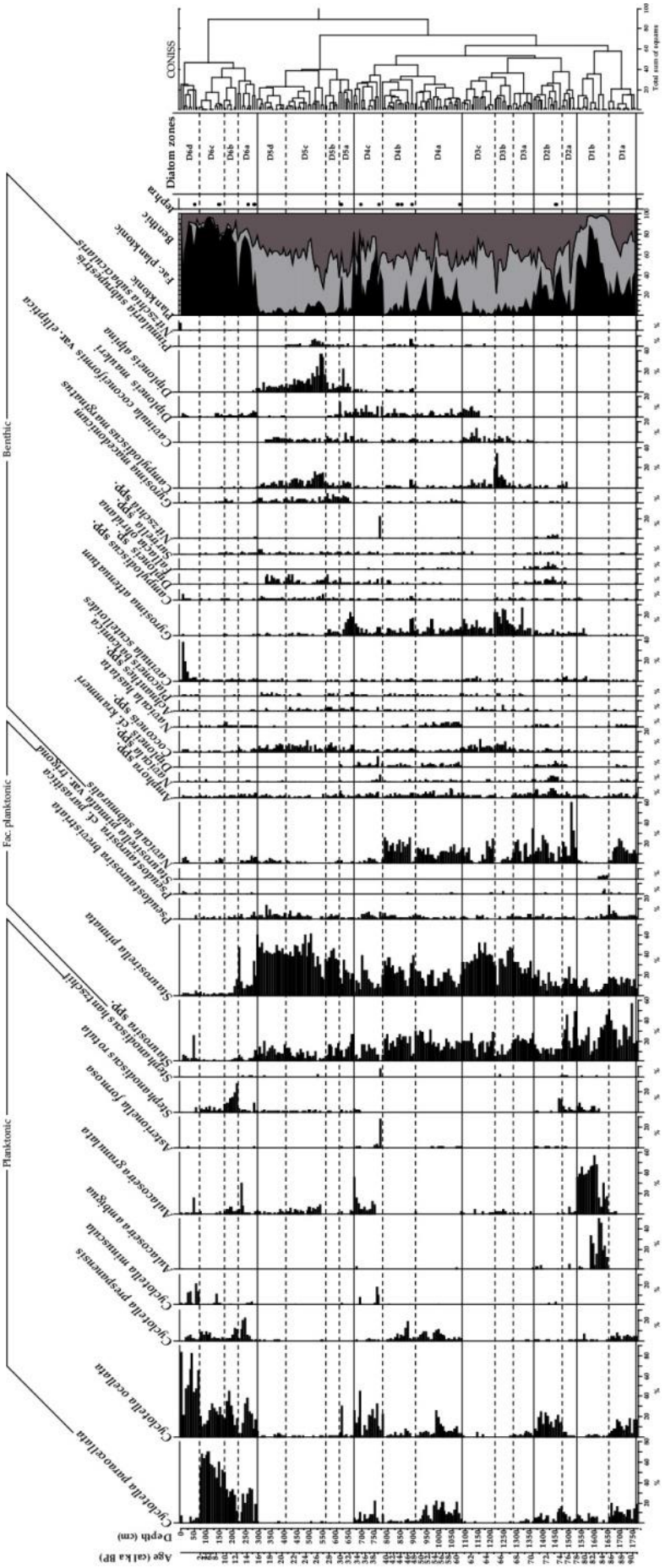


FIGURE 2. *Preliminary diatom data showing the presence of the dominant* Cyclotella *groups in the sediment sequence recovered from hole 1C at the DEEP site in Lake Ohrid. Modified from Wagner et al. (2014).*

Diatom-based palaeoclimate and palaeoenvironmental research on Lake Prespa focuses on core Co1215. By using a multi-proxy approach and comparing the diatom and the geochemical, pollen and isotope proxy data, Cvetkoska et al. (2014b) provided valuable information and a detailed insight into the lake's properties in terms of changes in lake level and trophy as response to the late glacial and Holocene climate variability. The results demonstrated that the shifts in diatom assemblage composition in Lake Prespa are primarily driven by lake-level changes, thus allowing interpretation of shifts in moisture availability over time. The diatom analysis of the last ca. 17 ka in Lake Prespa and the comparison with other regional and global records was important to show that unlike, many other lakes, Lake Prespa did not experience the mid-Holocene Mediterranean drought periods and maintained high lake levels until the late



Holocene. The results suggested close correlation of Lake Prespa to the North Atlantic climate oscillations. The diatom analyses of the complete Co1215 sediment sequence (Fig. 3) resulted with identification of a total number of 270 diatom taxa. Importantly, the study demonstrated high diatom sensitivity to the millennial-scale variability recorded in the Greenland oxygen isotope records by reflecting a clear impact of the Heinrich H6, H5 and H3–1 ice-rafting events in the diatom data (Cvetkoska et al., 2015a). Overall, the results highlighted the important role of precipitation for maintaining the hydrological balance of Lake Prespa, and indirectly, its biodiversity.

FIGURE 3. *Stratigraphic diatom diagram showing taxa present at >2 % abundance in Lake Prespa core Co1215. Modified from Cvetkoska et al. (2015a)*

Conclusions

Diatom research on Quaternary sediments from ancient lakes Ohird and Prespa provides valuable insight into the fossil species richness, and ecosystem responses to the past geologic, climate and environmental change. As from the results, it appears that the strong diatom response in Lake Ohrid is primarily driven by temperature change, while in Lake Prespa in the change of moisture availability. The taxonomic study of the dominant planktonic species already yielded information on climatically forced morphological variation within the dominant planktonic genus *Cyclotella*. Nonetheless, the hypothesis of environmentally forced morphological variation vs. evolution within the *Cyclotella ocellata* complex requires future testing. The ca. 550 m long (ca. 2 Ma) sediment sequence recovered from Lake Ohrid is of outstanding potential for testing eco-evolutionary hypotheses. Preliminary analyses already reveal distinct turnovers of the dominant planktonic species groups and high morphological variability within the identified species complexes; *Cyclotella ocellata*, *Cyclotella sollevata* and *Cyclotella cavitata*. An ongoing set of analyses will be used to determine their morphology, taxonomy and stratigraphic range in the sediment record, in order to reveal the Quaternary climate and environmental pressures in the diversification processes in lakes Ohrid and Prespa.

Acknowledgements

The authors would like to thank Dr. Bernd Wagner from the University of Cologne and Dr. Jane M. Reed from the University of Hull for helpful discussions about palaeolimnology. We thank our colleagues from the Institute of Geology and Mineralogy, the Seminar of Geography and Education at the University of Cologne, and the SCOPSCO science team members for their collaboration. The SCOPSCO Lake Ohrid drilling campaign was funded by ICDP, the German Ministry of Higher Education and Research, the German Research Foundation, the University of Cologne, the British Geological Survey, the INGV and CNR (both Italy), and the governments of the Republics of Macedonia and Albania. Logistic support was provided by the Hydrobiological Institute in Ohrid.

References

Albrecht C, Wilke T (2008) Ancient Lake Ohrid: biodiversity and evolution. Hydrobiol 615:103–140.

Anovski T, Jovanovski N, Arsov Lj (1997) Rate determination of water leakage from Prespa Lake. In: Proceeding of the International Symposium Towards Integrated Conservation and Sustainable Development of Transboundary Macro and Micro Prespa Lakes, Korca, Albania: 29–31.

Anovski T, Leontijadis I, Zoto J (2001) Progress in study of Lake Prespa using nuclear and related techniques. IAEA Regional Project, RER/8/808.

Brooks JL (1950) Speciation in ancient lakes. Q Rev Biol 25: 30–60, 131–176.

Cvetkoska A, Reed JM, Levkov Z (2012) Diatoms as indicators of environmental change in ancient Lake Ohrid during the last glacial-interglacial cycle (ca. 140 ka). In: Witkowski, A. (Ed.), ARG Gartner Verlag. Diatom Monogr 15: 220 pp.

Cvetkoska A, Hamilton PB, Ognjanova-Rumenova N, Levkov Z (2014a) Observations of the genus *Cyclotella* (Kützing) Brébisson in ancient lakes Ohrid and Prespa and a description of two new species *C. paraocellata* sp. nov. and *C. prespanensis* sp. nov. Nova Hedw 98(3-4): 313–340.

Cvetkoska A, Levkov Z, Reed JM, Wagner B (2014b) Late glacial to Holocene climate change and human impact in the Mediterranean: the last ca. 17 ka diatom record of Lake Prespa (Macedonia/Albania/Greece). Palaeogeogr Palaeoclimat Palaeoecol 406: 22–32.

Cvetkoska A, Levkov Z, Reed JM, Wagner B, Panagiotopoulos K, Leng M, Lacey J, (2015a) Quaternary climate change and Heinrich events in the southern Balkans: Lake Prespa diatom palaeolimnology from the last interglacial to present. J Paleolimnol 53: 215– 231.

Cvetkoska A, Jovanovska E, Francke A, Tofilovska S, Vogel H, Levkov Z, Donders, TH, Wagner B, Wagner-Cremer F (2015b) Ecosystem regimes and responses in a coupled ancient lake system from MIS 5b to present: the diatom record of lakes Ohrid and Prespa. Biogeosciences Discuss 12: 15051–15086.

Damaschke M, Sulpizio R, Zanchetta G, Wagner B, Böhm A, Nowaczyk N, Rethemeyer J, Hilgers A (2013) Tephrostratigraphic studies on a sediment core from Lake Prespa in the Balkans. Climate of the Past 9: 267–287.

De Vivo B, Rolandi G, Gans PB, Calvert A, Bohrson WA, Spera FJ, Belkin HE (2001) New constraints on the pyroclastic eruptive history of the Campanian volcanic Plain (Italy). Miner Petrol 73: 47–65.

Föller K, Stelbrink B, Hauffe T, Albrecht C, Wilke T (2015) Constant diversification rates of endemic gastropods in ancient Lake Ohrid: ecosystem resilience likely buffers environmental fluctuations. Biogeosciences Discuss 12: 14271–14302.

Hollis GE, Stevenson AC (1997) The physical basis of the Lake Mikri Prespa systems: geology, climate, hydrology and water quality. Hydrobiol 35: 1–19.

Jovanovska E, Cvetkoska A, Hauffe T, Levkov Z, Wagner B, Sulpizio R, Francke A, Albrecht C, Wilke T (2015) Differential resilience of ancient sister lakes Ohrid and Prespa to environmental disturbances during the Late Pleistocene. Biogeosciences Discuss 12: 16049–16079.

Khursevich GK, Karabanov EB, Prokopenko AA, Williams DF, Kuzmin MI, Fedenya SA (2001) Biostratigraphic significance of new fossil species of the diatom genera *Stephanodiscus* and *Cyclotella* from Upper Cenozoic deposits of Lake Baikal, Siberia. Micropaleontol 47: 47–71.

Kozarov G (1960) Lake Prespa phytoplankton investigations during the course of three years. – Zbornik na Rabotite Hidrobioloski Zavod. Ohrid. Prirodno-Matematicki Fakultet na Universitetot (Recueil des Travaux/ Station Hydrobiologique, Faculte de Philosophie de l' Universite de Skopje) 8: 1–57.

Krstić S (2012) Environmental Changes in Lakes Catchments as a Trigger for Rapid Eutrophication - A Prespa Lake Case Study. In: T. Piacentini (Ed.), Studies on Environmental and Applied Geomorphology, 63–118.

Leicher N, Zanchetta G, Sulpizio R, Giaccio B, Wagner B, Nomade S, Francke A, Del Carlo P (2015) First tephrostratigraphic results of the DEEP site record from Lake Ohrid, Macedonia. Biogeosciences Discuss 12: 15411–15460.

Leng MJ, Baneschi I, Zanchetta G, Jex CN, Wagner B, Vogel H (2010) Late Quaternary palaeoenvironmental reconstruction from lakes Ohrid and Prespa (Macedonia/Albania border) using stable isotopes. Biogeosciences 7: 3109–3122.

Levkov Z, Krstic S, Metzeltin D, Nakov T (2007) Diatoms of Lakes Prespa and Ohrid. About 500 taxa from ancient lake system. ARG Gartner Verlag. Iconogr Diatomol 16: 603pp.

Levkov Z, Williams D (2012) Checklist of diatoms (Bacillariophyta) from Lake Ohrid and Lake Prespa (Macedonia) and their watersheds. Phytotaxa 45: 1–76.

Lindhorst K, Krastel S, Reicherter K, Stipp M, Wagner B, Schwenk T (2015) Sedimentary and tectonic evolution of Lake Ohrid (Macedonia/Albania). Basin Res 27: 84–101.

Mackay A, Edlund BM, Khursevich G (2010) Diatoms in ancient lakes. In: The Diatoms: Applications for the Environmental and Earth Sciences. Cambridge University Press, 2nd ed., Cambridge, 209–230.

Martens K (1997) Speciation in Ancient Lakes. Trends Ecol Evol 12: 177–182.

Matzinger A, Spirkovski Z, Patceva S, Wüest A (2006) Sensitivity of ancient Lake Ohrid to local anthropogenic impacts and global warming. J Great Lakes Res 32: 158–179.

Popovska C, Bonacci O (2007) Basic data on the hydrology of Lakes Ohrid and Prespa. Hydrological Processes 21: 658–664.

Reed JM, Cvetkoska A, Levkov Z, Vogel H, Wagner B (2010) The last glacial-interglacial cycle in Lake Ohrid (Macedonia/Albania): testing diatom response to climate. Biogeosciences 7: 3083–3094.

Roelofs AK, Kilham P (1983) The diatom stratigraphy and paleoecology of lake Ohrid, Yugoslavia. Palaeogeogr Palaeoclimat Palaeoecol 42: 225–245.

Stanković S (1960) The Balkan Lake Ohrid and its living world. Monogr. Biol. IX. Uitgeverij Dr. W. Junk, Den Haag, Netherlands, 357 pp.

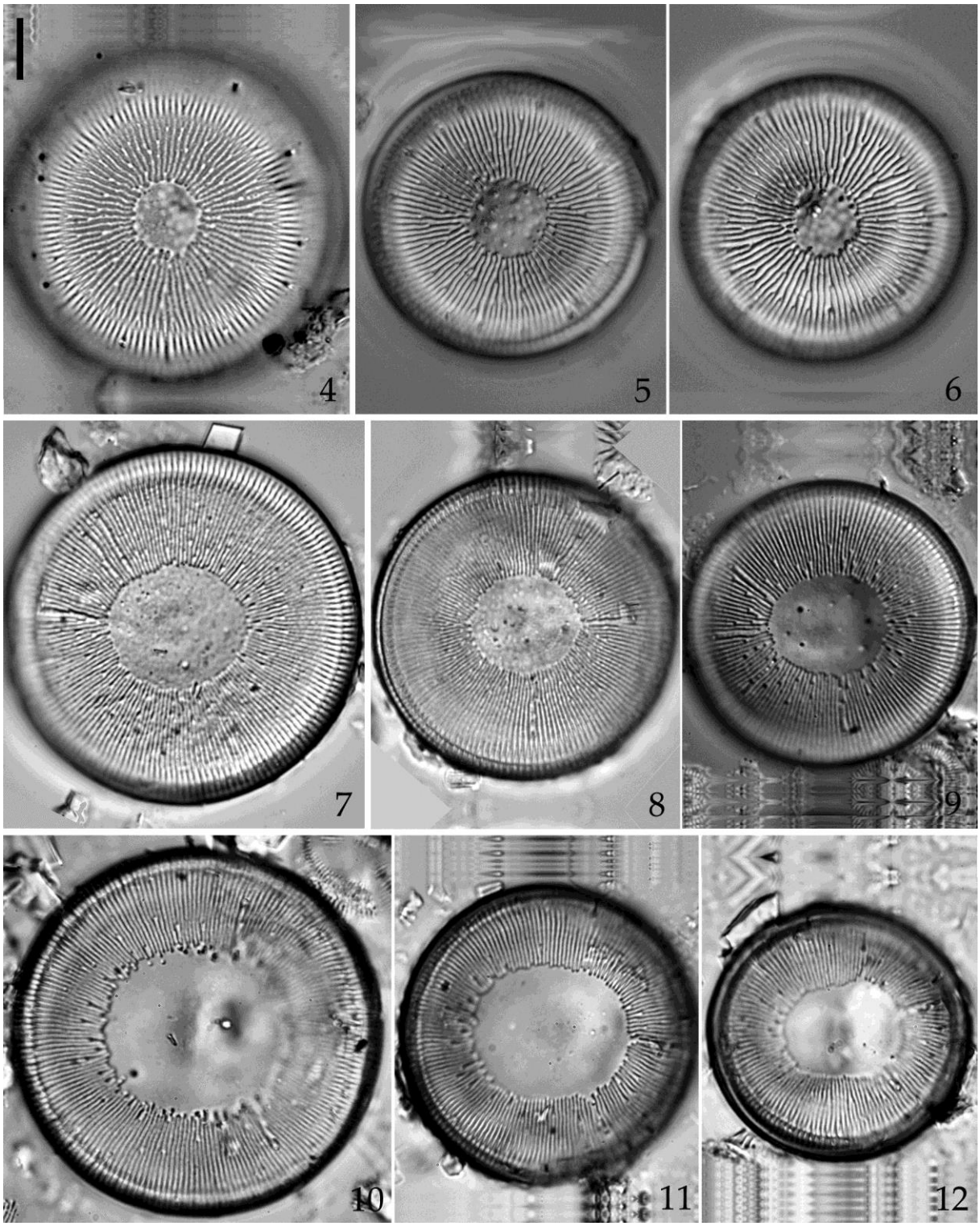
Vogel H, Wagner B, Zanchetta G, Sulpizio R, Rosén P (2010) A palaeoclimate record with tephrochronological age control for the last glacial-interglacial cycle from Lake Ohrid, Albania and Macedonia. J Paleolim 44: 295–310.

Wagner B, Lotter AF, Nowaczyk N, Reed JM, Schwalb A, Sulpizio R, Valsecchi V, Wessels M, Zanchetta G (2009) A 40.000-year record of environmental change from ancient Lake Ohrid (Albania and Macedonia). J Paleolimn 41: 407–430.

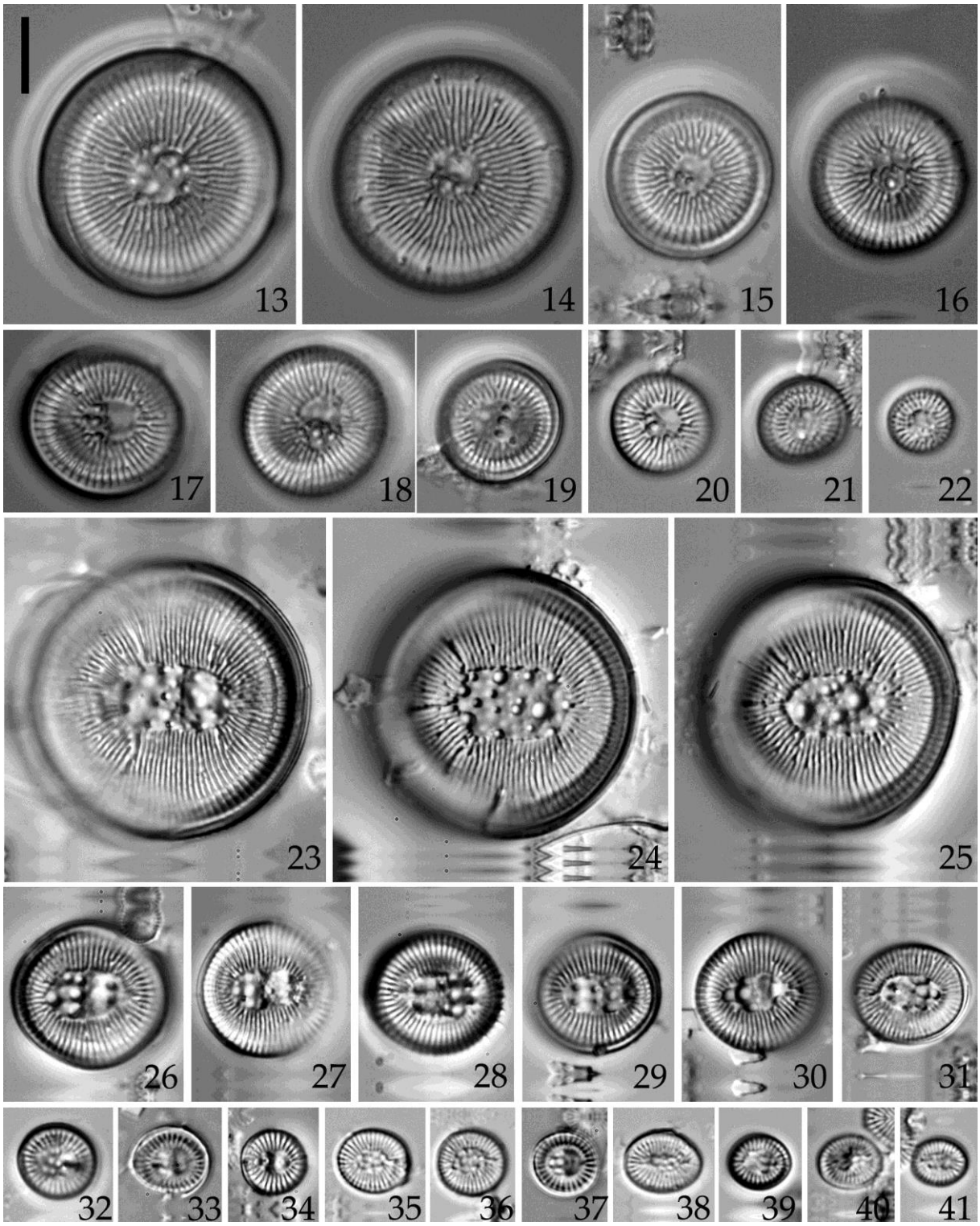
Wagner B, Vogel H, Zanchetta G, Sulpizio R (2010) Environmental changes on the Balkans recorded in the sediments from lakes Prespa and Ohrid. Biogeosciences 7: 3365–3392.

Wagner B, Wilke T, Krastel S, Zanchetta G, Sulpizio R, Reicherter K, Leng MJ, Grazhdani A, Trajanovski S, Francke A, Lindhorst K, Levkov Z, Cvetkoska A, Reed JM, Zhang X, Lacey JH, Wonik T, Baumgarten H, Vogel H (2014) The SCOPSCO drilling project recovers more than 1.2 million years history from Lake Ohrid. Scientific Drilling.

Zhang XS, Reed JM, Lacey JH, Francke A, Leng MJ, Levkov Z, Wagner B (2015) Complexity of diatom response to Lateglacial and Holocene climate and environmental change in ancient, deep, and oligotrophic Lake Ohrid (Macedonia/Albania), Biogeosciences Discuss 12: 14343–14375.



FIGURES 4−12. Cyclotella fottii, *part of the morphological variability recorded in the DEEP site sediment sequence from Lake Ohrid; Figs 4−6. Samples correspond to Marine Isotope Stage (MIS) 1 (ca. 14 ka BP to present). Figs 7−9. Morphotypes with large central area; samples correspond to MIS 5 (ca. 130−71 ka BP). Figs 10−12. Morphotypes with large rectangular or elliptic central area; samples correspond to MIS 11 (424−374 ka BP). Scale bar: 10 µm.*



FIGURES 13−41. Cyclotella *species from sediment samples of the DEEP core recovered from Lake Ohrid. Figs 13−16.* Cyclotella *cf.* hustedtii*; samples correspond to MIS 5−1. Figs 17−22.* Cyclotella *cf.* hustedtii *(small central area); samples correspond to MIS 2. Figs 23−25.* Cyclotella *cf.* hustedtii *(large elliptic central area). Figs 26−41.* Cyclotella *cf. iris (medium/small, elliptic central area); samples depth: ca. 321−83 m b.l.f. Scale bar: 10 µm.*

Diatomededelingen 39, 2015

The diatom flora of Lake Kinneret (Israel) Palaeolimnological evidence for holocene climate change and human impact in the southeastern Mediterranean

Hannah Vossel

[1]Rheinische Friedrich–Wilhelms–University of Bonn, Steinmann Institute of Geology, Mineralogy & Paleontology, Nussallee 8, 53115 Bonn, Germany (hvossel@uni–bonn.de)

Introduction

The Mediterranean basin is a region of highly complex topography and climatic variability, such that our understanding of the past environmental variability is still limited. Diatoms (single-celled siliceous algae, Bacillariophyceae) are abundant, diverse and sensitive to a wide range of environmental parameters. They are often well preserved in lake sediment records, and have well-recognised potential to generate high-quality paleolimnological data. Diatoms remain one of the least-exploited proxies in Mediterranean palaeoclimate research.

Firstly, a brief summary of a taxonomical study of a new described *Cyclotella* species belonging to the *Cyclotella-ocellata* species complex is given, which was discovered during paleolimnological analysis of subfossil sediments of Lake Kinneret (Israel).

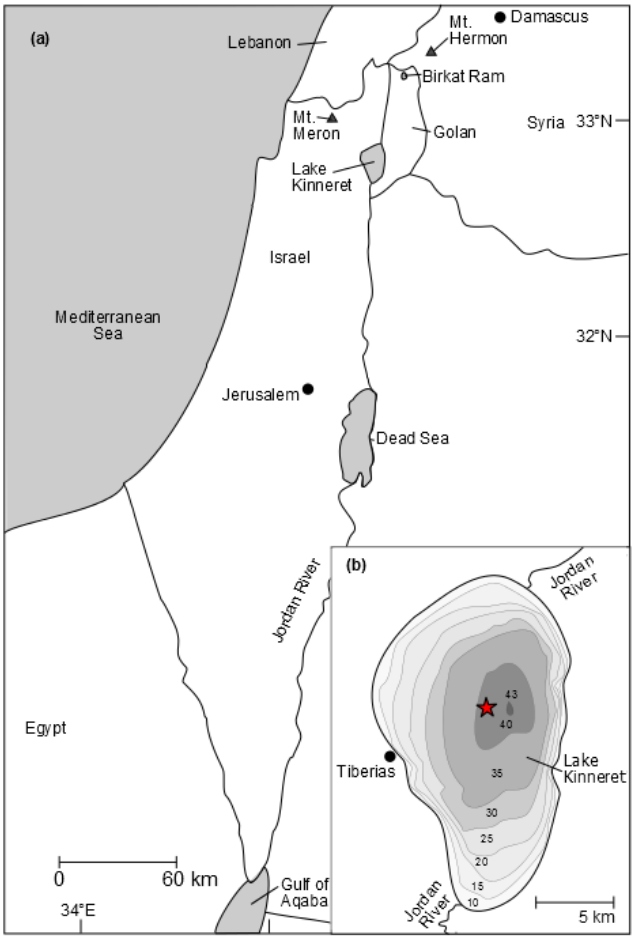
Secondly, the results of a detailed diatom analysis of an 18 m sediment core from Lake Kinneret are presented as part of a multi-proxy study of Holocene climate change and human impact in the Levant (http://www.sfb806.uni-koeln.de). Results are compared with other proxy data including pollen, and with output data from regional climate modelling, to strengthen interpretation of environmental change in the southeastern Mediterranean.

Study site

Lake Kinneret (from Hebrew word *kinnṓr* = 'harp', reflecting the shape of the lake) is also known as the Sea of Galilee or Lake Tiberias and is located in the northern part of the Jordan Rift Valley in the North of Israel (32°48'08.12'' N, 35°35'20.62'' E; Fig. 1). It is situated, together with the Dead Sea basin, on the "Dead Sea Transform Fault (DSTF)". The DSTF currently forms a more than 1000 km long transform fault, connecting the divergent plate boundary along the Red Sea with the Alpine convergent zone in Turkey (Hurwitz et al., 2002). The modern and Holocene Sea of Galilee has evolved from ancient water bodies that filled the Kinneret tectonic depression in the northern Jordan basin during the Late Pleistocene (Hazan et al., 2004). The lake basin is mainly surrounded by volcanic igneous rocks (basalts in the Golan Heights), which

were formed during the Oligocene, Miocene and Pleistocene and now form escarpments of up to 500 m in height around the lake.

The lake is 22 (N-S) km long, 12 km (W-E) wide and up to 43 m deep, and is situated 210 m below sea level. The lake surface area is almost 167 km2 and the catchment (total surface = 2730 km2) extends to parts of the Upper Galilee in NE Israel, the Golan Heights, the Hermon range (with the peak of Mt. Hermon at 2814 m a.s.l.) and the southern Anti-Lebanon mountains (Baruch, 1986). The lake is mainly fed from the north by the River Jordan, which also drains the lake southwards to the Dead Sea. The lake is warm and monomictic, being stratified with an anoxic hypolimnion from May to December and fully mixed from December to April (Gophen, 2002). An overview of the main limnological parameters (i.e. chemical components of the lake water, composition of bottom sediments & secchi depth) are given in table 1. Lake level fluctuates by up to 4 m depending on precipitation, evaporation and water abstraction by the National Water Carrier operation. The Kinneret area has a Mediterranean climate, characterized by mild, rainy winters and hot, dry summers (Baruch, 1986).



Limmnological parameters:		
water depth	42	m
secchi depth	2,6	m
water body	warm monomictic	
Chemical parameters:		
pH	8,6	
salinity (as Cl)	250	mg/l
silica (as SiO_2)	9	mg/l
soluble P (as PO_4)	2	µg/l
total phosphorus (TP)	20	µg/l
Nitrogen (as NO_3)	80	µg/l
Pelagic bottom sediments:		
clay minerals	35	%
calcium carbonate	55	%
organic matter	5	%
residual	3	%

FIGURE 1. *(a) Location of Lake Kinneret in the North of Israel; (b) Bathymetrical map of the lake (interval of isobathic curves is 5 m). The drilling location is marked by a 'red star' (modified after SCHIEBEL, 2013).*

TABLE 1. *Table of typical annual limnological parameters for the epilimnion of Lake Kinneret based on the Lake Kinneret data base supplied by NISHRI (2014).*

Material and Methods

Two parallel sediment cores (core KI_10_I and KI_10_II) were recovered from a water depth of 38.8 m at the central, deepest part of the lake basin (32°49'13.8''N, 35°35'19.7''E; Fig. 1 'red star') in March 2010, using an UWITEC Universal Sampling Platform (http://www.uwitec.at) with a piston corer system. Sediment cores were transported for storage to the University of Bonn. The 17.8 m continuous master sequence covers approximately the last 8200 cal yrs BP (Schiebel 2013).

All samples were prepared using standard techniques (Battarbee 1986): 0.2 g of wet sediment was treated with H2O2 (30 %) and heated on a hotplate for several hours to oxidize organic matter. Afterwards a few drops of concentrated HCl (35 %) were added to the hot sample residual to remove carbonates. Samples were washed with distilled water and centrifuged several times (1200 rpm for 7 min) to eliminate the acid residual and avoid dissolution during storage. The cleaned sample material is stored at 4 °C in a cooling chamber at the University of Bonn (Germany).

For taxonomical analysis, a subsample from the cleaned, organic-free material was mounted in Naphrax™ for diatom community analysis using an Olympus BX53 light microscope (LM) at x1000 magnification, equipped with Differential Interference Contrast and an Olympus UC30 digital camera. For scanning electron microscopy (SEM), parts of the oxidized suspensions were filtered through a 1-µm Isopore™ polycarbonate membrane filter (Merck Millipore). The stubs were sputter-coated with a Gold-Palladium layer of 20 nm and studied using a ZEISS Ultra SEM microscope at 3 kV (Natural History Museum London, UK). Diatom terminology follows ROSS et al. (1979), Kiss et al. (1996, 1999), Håkansson (2002) and Houk et al. (2010).

Fifty non-dissolved valves were photographed and used for morphometric analysis of the following valve features: diameter (µm), length of the marginal striae (µm), number of striae in 10 µm, number of central fultoportulae, number of orbiculi depressi, number of rimoportulae and number of costae between the marginal fultoportulae.

For paleolimnological (diatom community) analysis, subsamples from the cleaned, organic-free material were mounted in Naphrax™. Where diatoms were well preserved, 500 valves were counted using a Leica DME or an Olympus BX51 light microscope (LM) at x1000 magnification. In some samples, counts were lower due to preservation problems or the complete lack of diatoms. Diatom taxonomy and nomenclature was based on a range of published literature (Ehrlich, 1995; Krammer & Lange-Bertalot, 1986, 1988, 1991a, 1991b). Tillia version 1.7.16 was used to display diatom percentages. Zone boundaries were defined using Constrained Incremental Sum of Squares (CONNISS) cluster analysis (Grimm, 2011).

Taxonomical study: A new described species: *Cyclotella paleo-ocellata* Vossel et Van de Vijver

Large, subfossil populations of an unknown centric, planktonic diatom were observed in a lake sediment core from Lake Kinneret and was described as *Cyclotella paleo-ocellata* sp. nov. in Vossel et al. (2015). The new taxon, which belongs to the

Cyclotella ocellata species complex, is described and separated from other similar taxa (e.g., *Cyclotella ocellata*, *Cyclotella kuetzingiana*, *Cyclotella polymorpha*, *Cyclotella paraocellata*) based on a combination of the following morphological characters: valve diameter, number of orbiculi depressi (circular depressions), number of striae/10 µm, stria length, number and position of rimoportulae and the number of central and marginal fultoportulae. *Cyclotella paleo-ocellata* (Figs. 2 & 3) can be distinguished mainly by two prominent characteristics: (1) the number and the arrangement of the orbiculi depressi (4–8) which increase with the valve diameter and (2) the marginal fultoportulae, situated on each, every second or third costa.

Since *Cyclotella paleo-ocellata* is at present only known from the subfossil bottom sediments of Lake Kinneret, its ecological preferences can be inferred instead based on its association with other taxa of known ecology. *Cyclotella paleo-ocellata* is often abundant where *C. ocellata* Pantocsek is dominating the diatom flora, together accounting for almost 90 % of the assemblage. Several Aneumastus taxa such as A. stroesei Østrup, are also present but at very low abundance. These taxa are known to prefer oligotrophic lakes (Lange-Bertalot 2001). The broad ecological preference of *C. ocellata* makes ecological interpretations difficult. However, the period between 6500 and 3000 cal yrs BP is known as a humid phase (Litt et al., 2012), when the lake-level of Lake Kinneret was higher than at present (Hazan et al. 2005). *Cyclotella paleo-ocellata* has large, thick robust silica frustules, suggesting based on life habit preferences of similar taxa [e.g., cylotelloid species from Lake Malawi, Afrika (Huisman & Sommeijer, 2002; Stone et al., 2011)] that it has an adaptive advantage in staying in suspension in deep turbulent open waters. Larger varieties of the *C. ocellata* complex often seem to occur in deeper open-water lakes [e.g., deeper phases of the Ioaninna sequence in Greece (Wilson, et al. 2008)].

Both *Cyclotella paleo-ocellata* and *Stephanodiscus galileensis* Håkansson & Ehrlich, disappear at c. 2500 cal yrs BP in the sediment record (Vossel unpublished). Since this disappearance coincides with human-induced eutrophication indicated by a phase of forest clearance and the cultivation of olive trees identified in the pollen record (Schiebel 2013), it can be inferred that *C. paleo-ocellata* developed in an oligotrophic phase of lake development and has low tolerance of nutrient enrichment. Convincingly, the decrease of *Cyclotella paleo-ocellata* coincides with the rise of a range of centric taxa which are strong indicators for eutrophication, including *Cyclotella meneghiniana* Kützing, *C. polymorpha* Meyer & Håkansson, *Aulacoseira granulata* Ehrenberg and several small *Stephanodiscus* species including S. hantzschii Grunow, *S. minutulus* Kützing and *S. medius* Håkansson also indicating a clear shift from oligotrophic to more eutrophic conditions (Krammer & Lange-Bertalot, 1991).

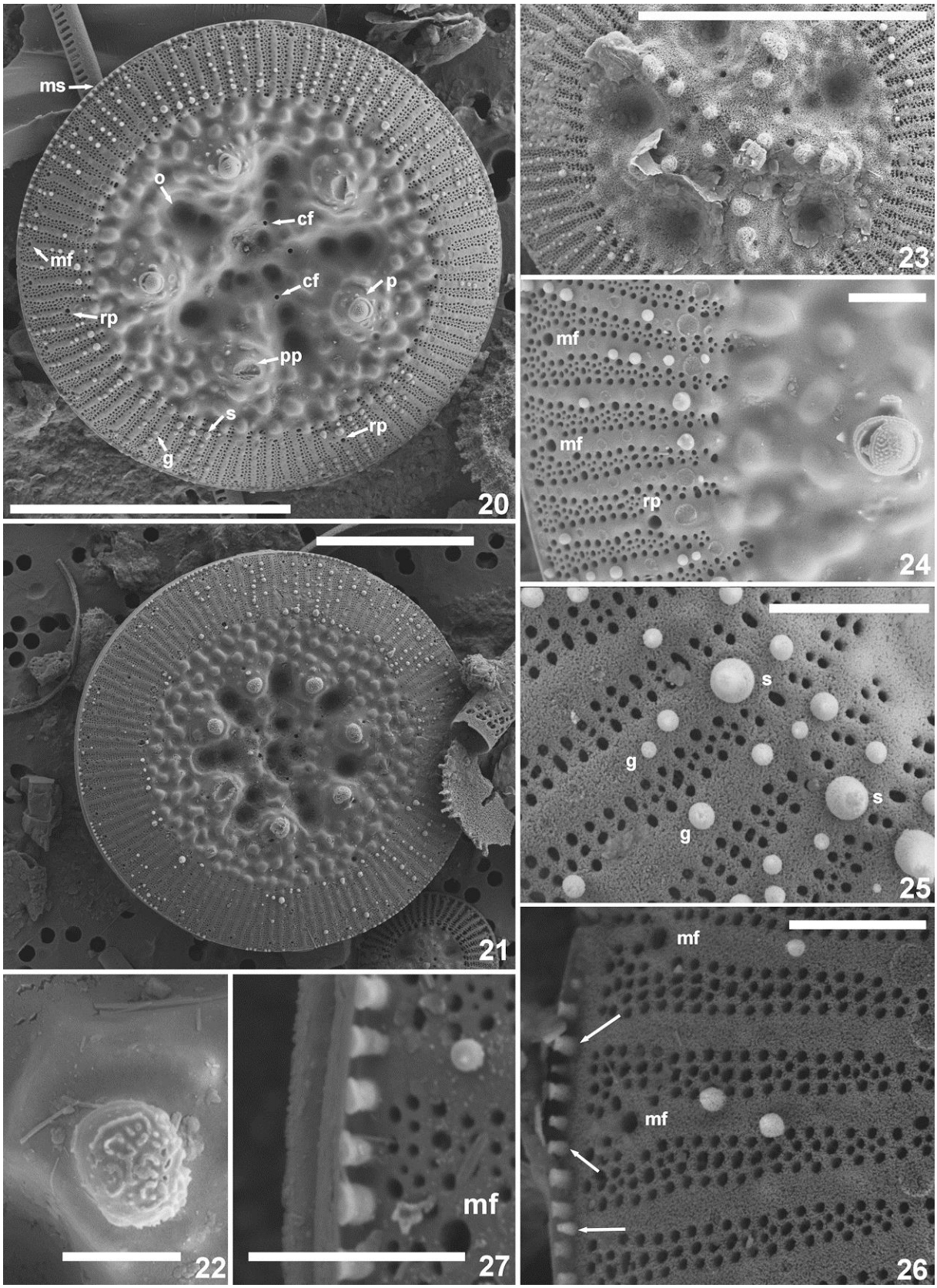


FIGURE 2. *External scanning electron microscopy view of* Cyclotella paleo-ocellata *sp. nov. (type population, Lake Kinneret, sample H44).*

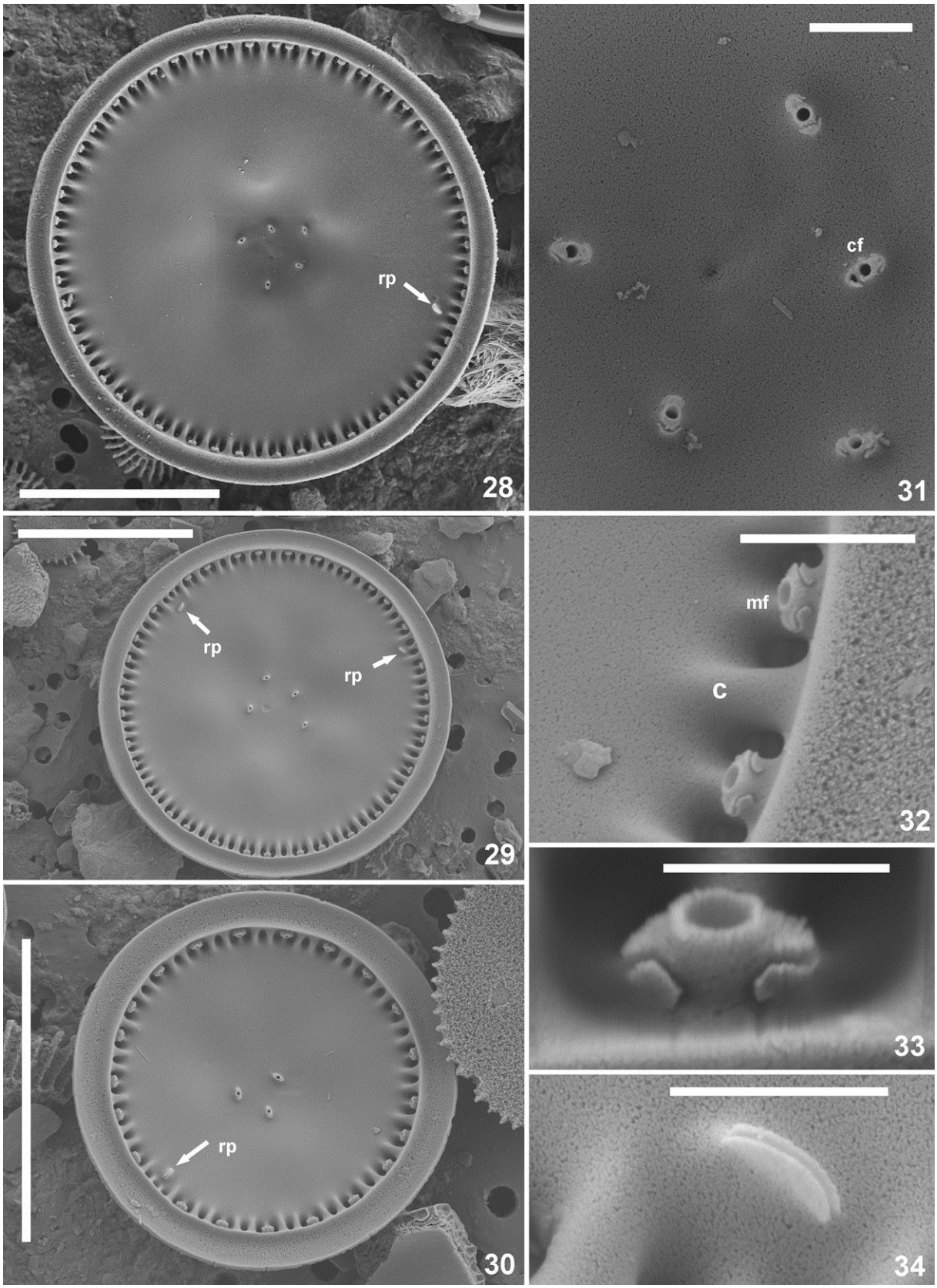


FIGURE 3. *Internal scanning electron microscopy view of* Cyclotella paleo-ocellata *sp. nov. (type population, Lake Kinneret, sample H44)*

Previous results from paleolimnological analysis

General information (Fig. 4):

142 different diatom taxa were identified during the quantitative paleolimnological analysis till present, most of whom (98 %) can be classified as oligohalobous-indifferent, requiring alkaline water for optimal growth. Diatoms are preserved in most samples, varying from rare (with signs of dissolution and if present, valves were mainly broken) to abundant (the majority was well-preserved). In three sections of the diagram diatoms were not preserved or very rare. In general the diatom flora is dominated by planktonic taxa most of the time.

5 diatom zones can be distinguished, because the diatom flora exhibits marked fluctuations in species assemblage composition (also tested by a CONISS analysis) in contrast to the quite homogenous sediment lithology.

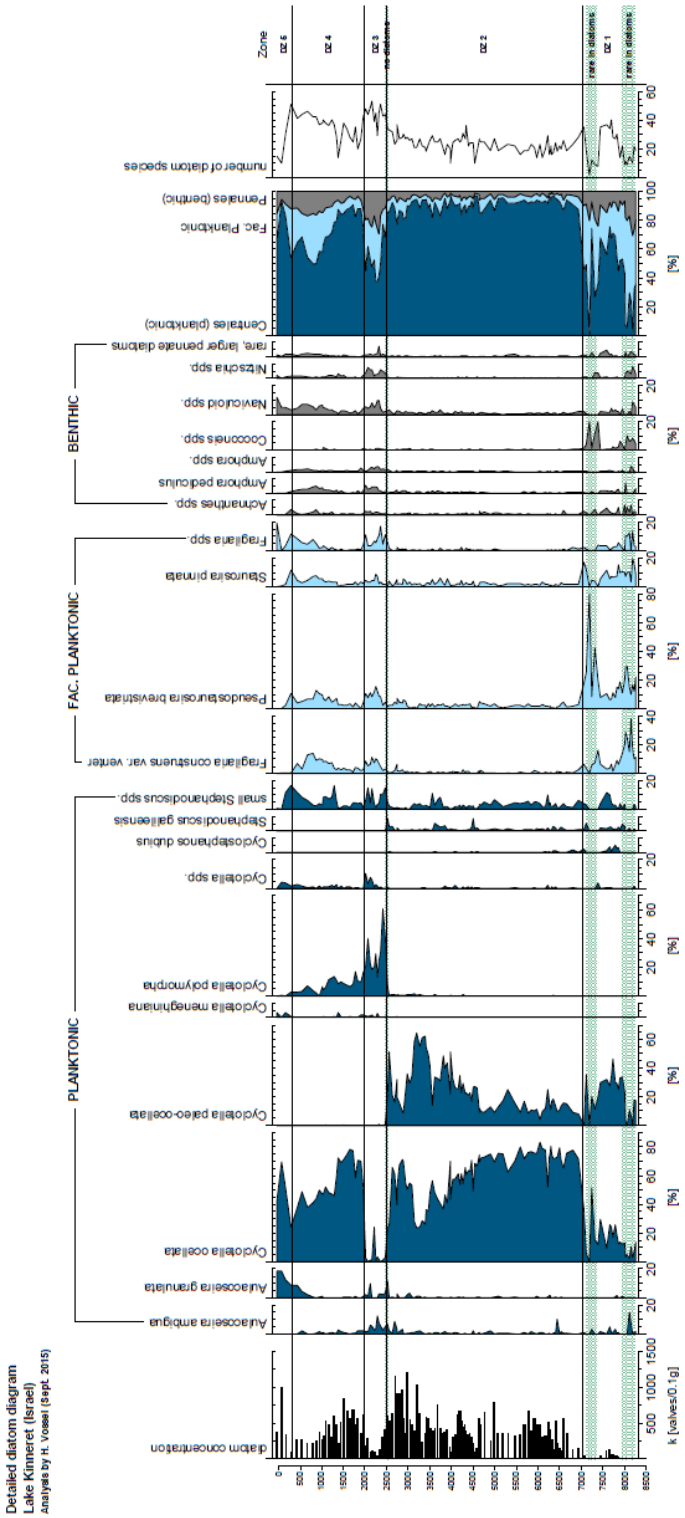


FIGURE 4. *Summarizing diatom diagram of Lake Kinneret (Israel)*

As 98 % of taxa have the same ecological requirements for the pH-value and the salinity content, changes in the diatom flora can be interpreted mainly as changes in the trophic level of the lake water and productivity shifts of the assemblages:

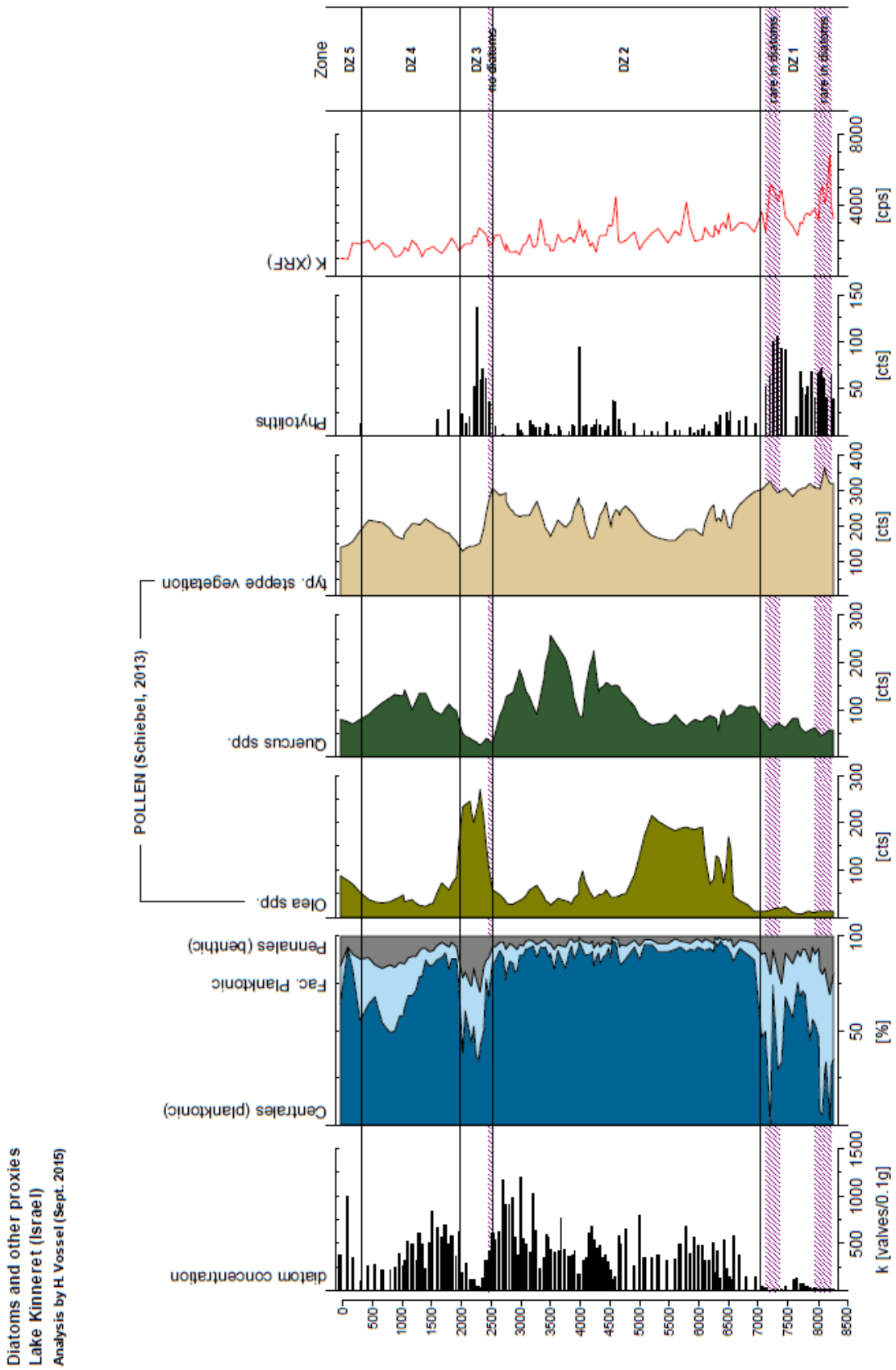


Figure 5. *Summarizing diatom diagram compared to other proxy data. Palynological data by SCHIEBEL 2013.*

Till 3.000 yrs cal BP Lake Kinneret was an oligotrophic lake system: The diatom flora was dominated by planktonic, centric taxa such as *Cyclotella ocellata*, a new discovered species-we named *C. paleo-ocellata*, bigger Stephanodiscus galilenenis and a few facultative planktonic *Fragilaria*, which prefere nutrient-poor, clear, non-polluted water, which is rich in oxygen (Krammer & Lange-Bertalot, 1991a). Human settlements around the lake were low in number; smaller rural communities were common.

Trophic level and productivity shifts (Figs.4 & 5):

A shift towards a more meso – to eutrophic level begun around 3,000 yrs cal BP, marked by a strong decrease in oligotrophic diatom taxa and a rise in taxa which prefer more nutrient-rich and oxygen-poor water conditions (Krammer & Lange-Bertalot, 1986, 1988, 1991a, 1991b).

Especially small *Stephanodiscus* taxa such as *Stepanodiscus minutiulus* and *Amphora pediculus* are good indicator for polluted, nutrient-rich water.

If we compare these shifts with other given proxies, such as pollen, XRF data and phytoliths, we can recognize a major increase in *Olea* pollen as well as the number of phytoliths; a clear decrease in the typical, natural vegetation and the potassium XRF curve is also showing a small peak. High values of phytoliths and potassium can be interpreted as a proxy, showing higher terrestrial sediment input or land erosion (Cohen, 2003).

Population density rose, bigger urban societies with continuous agriculture activities become more and more common in the Hellenistic time period. The increased human activity in the catchment area is well reflected by the diatom flora as well as by the compared proxy data. Pollen data show, that massive olive tree cultivation took place during that time in the catchment area of the lake (Schiebel, 2013). Clearance of the surrounding natural vegetation increased erosion and by this fact the input of nutrient and terrestrial contents in the lake system, which led to a shift from an oligotrophic to a more eutrophic diatom community.

A short period of recovery with low settlement activities and economic regressions as well as a decline of agriculture is visible in diatom zone 4 and is marked by the repeated occurrence of the oligotrophic *C. ocellata* in large numbers. A lot of settlements were destroyed at the end of the Roman period which might be also a reason for the short recovery of the oligotrophic diatom flora.

The modern diatom flora of Lake Kinneret is in contrast strongly influenced by the economical revival in this area: where industry has been developed and tourism is playing an important role. The diatom flora is dominated by *Aulacoseira* taxa (*A. granulata*), several eutrophic *Cyclotella* taxa (*C. meneghiniana*), large *Fragilaria* species such as *Fragilaria capucina* and *Anomoeoneis sphaerophora*, which needs hyper-eutrophic water conditions and also are able to tolerate the high pollution of the lake water (Krammer & Lange-Bertalot, 1986, 1988, 1991a, 1991b). Please note, that the diatom concentration is low nowadays, because the lake flora and its

phytoplankton is manly dominated by Pyrrhophyta-Chlorophyta assemblages, which displace the diatom flora (Pollingher et al., 1984).

Summarizing these trends, the trophic state of Lake Kinneret has changed over the last 8.000 years from an oligotrophic to an hyper-eutrophic environment, mainly caused by major human influence.

Assumption of lake-level shifts in Lake Kinneret (Figs 4 & 5):

(1) From 8.2 to 7.0 yrs cal BP lake level was shallow: The diatom concentration is very low and the flora is mainly dominated by littoral taxa. Also the XRF curve from the element potassium is showing higher values, which indicates an increased soil weathering and a higher terrestrial sediment discharge in the lake system (COHEN 2003).
This time period is known as arid phase with reduced precipitation values and high annual average temperatures. Low lake level stands are recorded for many localities in the Levant region, for example the Dead Sea (LITT et al. 2012). Further investigations with a higher resolution have to prove, if the 8.2-event is visible in this record.

(2) From 7.0 to 2.5 k yrs cal BP lake level must be very deep. Diatom concentrations show very high values and the diatom flora is strongly dominated by planktonic and facultative planktonic taxa, such as Cyclotella ocellata, which prefer a deeper water column.
In the Levant region this time period is known as humid phase, with high rain amounts (> than 650 mm/a) and low winter temperatures. Lake high stands are also reported from several localities for this time period (LITT et al., 2012).
Around 4.2 k yrs cal BP a drop in diatom concentration is visible. It can be assumed, that this might show the short, dry 4.2-event, but this has to be verified in future with a higher resolution analysis.

(3) From 2.5 to 2.0 k yrs cal BP a drop in the diatom concentration and in the occurance of the planktonic flora is visible. Littoral taxa have a higher proportion in the P/B-ratio. High amounts of phytoliths are counted. These shifts could indicate a phase of a shallower lake level, but in this case the diatom flora displays the strong human impact and the lower productivity of the planktonic diatom communities due to the extreme changes in the trophic level.

(4) From 2.0 k yrs cal BP till nowadays constantly lake level fluctuations occurred, visible by the shifts in the diatom concentration and the P/B-ratio. In modern times also the drinking water abstraction is playing a role for lake level shifts.

Summary

Changes in the diatom composition of Lake Kinneret over the last ca. 8,200 years can be interpreted mainly in terms of productivity shifts, with a clear trend from oligotrophic at the base to hypereutrophic in the modern lake. The eutrophication trend accelerates after ca. 3,000 cal. yrs. BP, indicating the influence of increased human activity in the catchment, identified previously by analysis of the vegetational history (Schiebel, 2013).

The analysis of the composition of the diatom flora also provides some evidence for lake-level fluctuations, as a proxy for shifts in moisture availability. Low lake-level stands are characterized by low diatom concentration and increased relative abundance of littoral taxa. High lake-level stands are marked by the clear dominance of planktonic species, such as *Cyclotella ocellata* and *Cyclotella paleo-ocellata* (a newly described centric diatom which may be endemic (Vossel et al., 2015), in phases of high diatom concentration. Such inferred lake-level oscillations correlate well with the output from the climatic models from the Levant region, representing changes in moisture availability (LITT et al. 2012), although the signal is obscured in the last 3,000 years by the effects of anthropogenic eutrophication.

References

Baruch U (1986) The Late Holocene Vegetational History of Lake Kinneret (Sea of Galilee), Israel. Paléorient 12: 37–48.

Battarbee RW (1986) Diatom analysis. In: Berglund, BE (ed.): Handbook of Holocene palaeoecology and palaeohydrology. Wiley, Chichester: 527–670.

Cohen AS (2003) Paleolimnology – 1. Edition. Oxford University Press, Inc. New York, 268 p.

Ehrlich A (1995) Atlas of the Inland-water diatom flora of Israel. Flora Palaestina. The Geological Survey of Isreal, 166 p.; Jerusalem.

Gophen M (2002) Water quality management in Lake Kinneret (Israel): hydrological and food web perspectives. Papers from Bolsena Conference (2002). Residence time in lakes: Science, Management, Education. J Limnol 62: 91–101.

Grimm EC (2011) Tilia Version 1.7.16., Illinois State Museum, Springfield.

Håkansson H (2002) A compilation and evaluation of species in the genera *Stephanodiscus*, *Cyclostephanos* and *Cyclotella* with a new genus in the family Stephanodiscaceae. Diatom Res 17: 1–139.

Hazan N, Stein M, Marco S (2004) Lake Kinneret levels and active faulting in the Tiberias area. Israel J Earth Sci53: 199–205.

Hazan N, Stein M, Agnon A, Marco S, Nadel D, Negendank JFW, Schwab MJ, & Neev D (2005) The late Quaternary limnological history of Lake Kinneret (Sea of Galilee), Israel. Quat Res 63: 60–77.

Houk V, Klee R, Tanaka H (2010) Atlas of freshwater centric diatoms with a brief key and descriptions. Part 3. Stephanodiscaceae A. *Cyclotella*, *Tertiarius*, *Discostella*. Fottea 10 (supplement): 1–498.

Huisman J, Sommeijer B (2002) Maximal sustainable sinking velocity of phytoplankton. Marine Ecol Progr Ser 244: 39–48.

Hurwitz S, Garfunkel Z, Ben-Gai Y, Reznikov M, Rotstein Y, Gvirtzman H (2002) The tectonic framework of a complex pull-apart basin: seismic reflection observations in the Sea of Galilee, Dead Sea transform. Tectonophysics, 359: 289–306

Kiss KT, Rojo K, Cobelas AM (1996) Morphological variability of a Cyclotella ocellata (Bacillariophyceae) population in the Lake Las Madres (Spain). Algol Stud 82: 37–55.

Kiss KT, Klee R, Hegewald E (1999) A reinvestigation of the original material of *Cyclotella ocellata* Pantocsek (Bacillariophyceae). Algol Stud 93: 39–53.

Krammer K, Lange-Bertalot L (1986): Bacillariophyceae 2/1. Teil. Naviculaceae. In: Ettl H, Gärtner G, Gerloff J, Heyning H, Mollenhauer D (eds) Süsswasserflora von Mitteleuropa. Gustav Fisher Verlag, Stuttgart, New York.

Krammer K, Lange-Bertalot L (1988): Bacillariophyceae 2/2. Teil. Bacillariaceae, Epithemiacceae, Surirellaceae. In: Ettl H, Gärtner G, Gerloff J, Heyning H, Mollenhauer D (eds) Süsswasserflora von Mitteleuropa. Gustav Fisher Verlag, Stuttgart, New York.

Krammer K, Lange-Bertalot L (1991a): Bacillariophyceae 2/3. Teil. Centrales, Fragilariaceae, Eunotiaceae. In: Ettl H, Gärtner G, Gerloff J, Heyning H, Mollenhauer D (eds) Süsswasserflora von Mitteleuropa. Gustav Fisher Verlag, Stuttgart, New York.

Krammer K, Lange-Bertalot L (1991b) Bacillariophyceae 2/4. Teil. Achnanthacae. In: Ettl H, Gärtner G, Gerloff J, Heyning H, Mollenhauer D (eds) Süsswasserflora von Mitteleuropa. Gustav Fisher Verlag, Stuttgart, New York.

Lange-Bertalot H (2001) *Navicula* sensu stricto, 10 genera separated from *Navicula* sensu lato, *Frustulia*. Diatom Europe 2: 1–526.

Litt T, Ohlwein C, Neumann FH, Hense A, Stein M (2012) Holocene climate variability in the Levant from the Dead Sea pollen record. Quat Sci Rev 49: 95–105.

Pollingher U, Ehrlich A, Serruya S (1984) The planktonic diatoms of Lake Kinneret (Israel) during the last 5000 Years – Their contribution to the algal Biomass. In: Ricard, M. (ed.) Proceedings of the International Diatom Symposium 459–470.

Ross R, Cox EJ, Karayeva NI, Mann DG, Paddock TBB, Simonsen R, & Sim, PA (1979) An amended terminology for the siliceous components of the diatom cell. Nova Hedw 64: 513–533.

Schiebel V (2013) Vegetation and climate history of the southern Levant during the last 30,000 years based on palynological investigation. Unpublished PhD thesis; Rheinische Friedrich-Wilhelms University of Bonn, 104 pp.

Stone JR, Westover KS, Cohen AS (2011): Late Pleistocene paleohydrography and diatom paleoecology of the central basin of Lake Malawi, Africa. Papers Earth Atmosph Sci Paper 279: 52–70

Vossel H, Reed JM, Houk V, Cvetkoska A Van de Vijver B (2015) *Cyclotella paleo-ocellata*, a new centric diatom (Bacillariophyta) from Lake Kinneret (Israel). Fottea, 15 (1): 63–75.

Wilson GP, Reed JM, Lawson IT, Frogley MR, Tzedakis PC, Preece RC (2008) Diatom response to the last glacial-interglacial transition in the Ioannina basin, northwest Greece: implications for Mediterranean palaeoclimate reconstruction. Quat Sci Rev 27: 428–440.

Nieuwe literatuur

samengesteld door Holger Cremer (voorzitter NVKD)

Diatom research over time and space. Morphology, taxonomy, ecology and distribution of diatoms - from fossil to recent, marine to freshwater, established species and genera to new ones. Celebrating the work and impact of Nina Strelnikova on the occasion of her 80th birthday

J.P. Kociolek, L.S. Kulikovskiy, J. Witkowski, D. Harwood
Nova Hedwigia, Beihefte 143
2014, ISBN 978-3-44351-065-7, J. Cramer, Stuttgart
Readers of this Beiheft of Nova Hedwigia will find articles on a large variety of diatoms, from fossil to recent, marine to freshwater, established species and genera to new ones. Fifty-two authors have contributed to this volume by their diversity of interests. Topics range from morphology, taxonomy, ecology and distribution of diatoms found all over the world (from Europe to Russia and Asia, from the entire American Continent and even the Antarctica) and from past to recent. The variety of the papers presented in this volume reflects the diversity of scientific interests of Nina Strelnikova, to whom this Beiheft is dedicated. This volume is of interest for every scientist working on diatoms and interested in the variety of diatom research. It should not be missing in any library

Diatoms and the continuing relevance of morphology to studies on taxonomy, systematics and biogeography. Celebrating the work and impact of Patricia A. Sims on the occasion of her 80th birthday

J. Witkowski, D. Williams, J.P. Kociolek
Nova Hedwigia, Beihefte 144
2015, ISBN 978-3-44351-066-4, J. Cramer, Stuttgart
The collection of 13 papers in this volume of Nova Hedwigia Beihefte all focus on aspects of diatom taxonomy and systematics. Amongst these contributions are papers describing new species, both fossil and recent, marine and freshwater; bibliographic matters, necessary for taxonomic priority issues as well as specimen recognition; structural-functional interpretations of the silica parts, studies that are far too infrequent these days; and the results, both illuminating and confounding, of culturing studies. The papers in this volume reflect the work of Patricia Sims peer group and new and emerging leaders in the fields of marine micropaleontology, diatom taxonomy, systematics, biogeography and evolution. The volume is richly illustrated, and new genera and species are proposed, from freshwater and marine environments, fossil and recent and, reflecting Pat Sims' own worldwide perspective. This volume is dedicated to Patricia Sims of the Natural History Museum, London, on the occasion of

her 80th birthday (in 2012) and her contributions to diatom research. It is of interest for every scientist working on diatoms and interested in the variety of diatom research.

Centric, Araphid and Eunotioid Diatoms of the Coastal Laurentian Great Lakes. Sampling, Taxonomic Descriptions and Environm. Characteristics

E.D. Reavie, A.R. Kireta
Bibliotheca Diatomologica 62
2015, ISBN 978-3-44357-053-8, J. Cramer, Stuttgart
The authors present the first detailed description of the freshwater centric, araphid and eunotioid diatoms of coastal ecosystems of the Laurentian Great Lakes. 49 plates with hundreds of light micrographs of diatom taxa, from 28 genera, recorded in 207 samples from 106 wetlands, embayments, high energy and deep, nearshore locales of the Great Lakes are presented. Descriptions and illustrations of the taxa encountered, as well as autecological information are presented to round up the content of this volume. In addition to taxonomic information, these data are intended to assist future biomonitoring and paleolimnological efforts. This volume is of interest to scientists working on diatoms, particularly those interested in diatoms from the Great Lakes area. It will help in the study of hydrological changes, eutrophication, the effects of invasive species, climate change and pollutant impacts not only in the Laurentian Great Lakes but in most freshwater habitats.

Catalogue of continental diatoms from Portugal, including the Archipelagos of Azores and Madeira: updated nomenclature, distribution and bibliography

M.H. Novais, S. Blanco, M. Morais, L. Hoffmann, L. Ector
Diatom Monographs 17 A-C
2015, ISBN 978-3-87429-453-9 [CD ROM], A.R.G. Ganter Verlag, Ruggell
This catalogue aims to compile the information available on continental (recent and fossil) diatoms in Portugal, including the Archipelagos of Madeira and Azores, since the early beginnings of the diatom studies in Portugal at the middle of the XIXth century until 2010. The diatom taxa are presented following an updated taxonomy; nevertheless, in order to provide a historical overview, the nomenclatural synonyms found in the literature from Portugal are also included. For the 1381 taxa the following information is presented: basionym, nomenclatural synonyms, citations (with the precise indication of the sampling sites), frequent taxonomical synonyms and a distribution map.

Freshwater Algae of North America. Ecology and Classification

J.D. Wehr, R.G. Sheath, J.P. Kociolek
2015, 2nd Edition, ISBN 978-01-238-5876-4, Academic Press.
Freshwater algae are among the most diverse and ubiquitous organisms on earth. They occupy an enormous range of ecological conditions from lakes and rivers to acidic peat swamps, inland saline lakes, snow and ice, damp soils, wetlands, desert soils, wastewater treatment plants, and are symbionts in and on many plants, fungi, and animals. In North America, the variety of freshwater habitats colonized by algae is very rich, and offers an enormous and fascinating range of environments for their

study. They form the base of most aquatic food webs and are critical to studies of ecosystem health. Algal ecologists and taxonomists play an important role in the understanding of aquatic ecosystems: their biodiversity, productivity, interactions with other organisms, and water quality. This book provides in one volume a practical and comprehensive guide to the genera of freshwater algae known from North America. The format combines the necessary ecological, taxonomic and methodological information for all scientists working in aquatic environments, whether their specialty is in environmental monitoring and water quality assessment, biological composition, ecology, evolution, or molecular biology. Key Features * The first complete accounting of North America's freshwater algal genera in more than 50 years * Includes a guide to the current literature on species identification in each group of algae * High-quality photographs and drawings of more than 770 genera * A clear, easy-to-use introductory key to the diagnostic chapters * Synthetic chapters on freshwater habitats, use of algae in environmental assessment, and control of nuisance algae * Contributions from 27 experts in all areas of freshwater algae * Extensive literature citations.

Freshwater Algae. Identification, enumeration and use as bioindicators

E.G. Bellinger, D.C. Sigee
2015, 2nd Edition, ISBN 978-11-189-1716-9, Wiley Blackwell.
Freshwater Algae provides a comprehensive guide to temperate freshwater algae, with additional information on key species in relation to environmental characteristics and implications for aquatic management.Existing books on freshwater algae fall into two categories: simple identification texts or highly specialised research volumes. There is currently nothing in between that practitioners and students can use on a regular basis. The authors filled this gap with the first edition which provided an accessible, visually appealing volume that is of immediate use to aquatic biologists for algal identification that includes key environmental information on major species.The book is divided into two parts: part I is a general introduction to algae and techniques for sampling, measuring and observation and then looks at the role of algae as bioindicators and the implications for aquatic management, part II provides the identification of major genera and 250 important species. The book is well illustrated in full colour with numerous original illustrations and photographs. This new revised edition will retain the same clear writing style and accessible format of the first edition with new coverage of species from North America, Asia and Australia in addition to expanded coverage of molecular and computational techniques in algal biology.

The Algae World

D. Sahoo, J. Seckbach
2015, ISBN 978-94-017-7321-8, Springer, New York
Algal World has been carefully written and edited with an interdisciplinary appeal and aims to bring all aspects of Algae together in one volume. The 22 chapters are divided into two different parts which have been authored by eminent researchers from across the world. The first part, Biology of Algae, contains 10 chapters dealing with the general characteristics, classification and description of different groups such as Blue Green Algae, Green Algae, Brown Algae, Red Algae, Diatoms, Xanthophyceae,

Dinophyceae, etc. In , it has two important chapters covering Algae in Extreme Environments and Life Histories and Growth Forms in Green Algae. The second part, Applied Phycology, contains 12 chapters dealing with the more applied aspects ranging from Algal Biotechnology, Biofuel, Phycoremediation, Bioactive Compounds, Biofertilizer, Fatty Acids, Harmful Algal Blooms, Industrial Applications of Seaweeds, Nanotechnology, Phylogenomics and Algal culture Techniques, etc.

Marine Protists. Diversity and Dynamics

D. Sahoo, J. Seckbach
2015, ISBN 978-4-431-55130-0, Springer, New York
This comprehensive book provides a unique overview of advances in the biology and ecology of marine protists. Nowadays marine protistology is a hot spot in science to disclose life phenomena using the latest techniques. Although many protistological textbooks deal with the cytology, genetics, ecology, and pathology of specific organisms, none keeps up with the quick pace of new discoveries on the diversity and dynamics of marine protists in general. The book Marine Protists: Diversity and Dynamics gives an overview of current research on the phylogeny, cytology, genomics, biology, ecology, fisheries, applied sciences, geology and pathology of marine free-living and symbiotic protists. Poorly known but ecologically important protists such as labyrinthulids and apostome ciliates are also presented in detail. Special attention is paid to complex interactions between marine protists and other organisms including human beings. An understanding of the ecological roles of marine protists is essential for conservation of nature and human welfare. This book will be of great interest not only to scientists and students but also to a larger audience, to give a better understanding of protists' diverse roles in marine ecosystems.

De natuur als uitvinder. Miljarden jaren aan innovaties gratis beschikbaar

Y. Poelman
2015, ISBN 978-9-048-82541-7, Uitgeverij Carrera
Als u aan de natuur denkt, waar denkt u dan aan? Bos? Bergen? Pluizige beestjes? Waar u waarschijnlijk niet aan denkt is techniek, maar hoe gek het ook klinkt: de natuur zit er vol mee. In bijna 4 miljard jaar zijn fantastische biologische oplossingen ontstaan die we kunnen gebruiken als inspiratie voor onze eigen menselijke toepassingen. Dat is precies wat bionica doet. Zo is een hogesnelheidstrein in Japan uitgerust met een efficiënte 'ijsvogelneus' en leveren botten inspiratie voor materiaalbesparing. De out-of-the-box toepassingen kunnen technisch zijn, maar bieden ook oplossingen voor maatschappelijke uitdagingen en sociale innovatie. De natuur heeft efficiëntie en duurzaamheid bedacht als basis voor het voortbestaan van het leven op aarde en daar kan de mens, door goed af te kijken nog veel van leren

Das große Kosmos-Buch der Mikroskopie

B.P. Kremer
2015, 3. Auflage, ISBN 978-3-440-14675-0, Kosmos Verlag
Dieses Buch hat einen bisher unerreichten Standard gesetzt: Es ist das Rezept-, Anleitungs- und Arbeitsbuch für Mikroskopiker, das umfangreiches Wissen vermittelt

und dieses sehr verständlich beschreibt. Von Viren in Zimmerpflanzen über die bizarren Einzeller aus dem Gartenteich bis zur Untersuchung von Blutzellen regt dieses Buch zu eigenen Analysen an. Dabei führt es in alle wichtigen Techniken zur Bearbeitung einfacher und anspruchsvoller Objekte ein.

FOTTEA, 2015, Volume 1

Journal of the Czech Phycological Society
Website: [http://fottea.czechphycology.cz/magno/fot/2015/mn1.php]; free download.
This issue includes seven diatom related articles on various topics.

FOTTEA, 2015, Volume 2

Journal of the Czech Phycological Society
Website: [http://fottea.czechphycology.cz/magno/fot/2015/mn2.php]; free download.
This issue includes seven diatom related articles on various topics.

Alg kan heel wat onder de leden hebben

T. van Oijen
Artikel WadWeten van de Waddenvereniging geplaatst op 29 oktober 2015
[http://www.waddenvereniging.nl/wadweten/8771-alg-kan-heel-wat-onder-de-leden-hebben.html]

Congressen 2016

Samengesteld door Bart Van de Vijver (redactie Diatomededelingen)

NVKD STUDIEDAGEN, 19-21 MEI 2016, UNIVERSITEIT UTRECHT, NEDERLAND

Voor de viering van 30 jaar NVKD, trekken we opnieuw naar Nederland. De studiedagen van de Nederlands-Vlaamse Kring van Diatomisten zullen immers doorgaan in de Universiteit Utrecht. De organisatie is in handen van Prof. F. Wagner-Cremer. De bijeenkomst zal zoals ondertussen traditiegetrouw bestaan uit drie delen: een taxonomische cursusdag op donderdag 19 mei met als onderwerp het vervolg op de kleine *Navicula* soorten, een lezingendag op vrijdag 20 mei en een excursie op zaterdag 21 mei. Het wordt een bijeenkomst die volledig in het Nederlands zal doorgaan. Sprekers zullen onder andere zijn: Ronald Bijkerk, Bart Van de Vijver en F. Wanger-Cremer en Meer informatie en het definitieve programma worden op tijd bekend gemaakt.

Informatie is te verkrijgen bij Holger Cremer (holger.cremer@tno.nl).

INTERNATIONALE CONFERENTIES

April 2016
10th Central European Diatom Meeting (CD-Diatom), Boedapest, Hongarije, 20-23.04.2016, meer informatie: http://10thcedm.okologia.mta.hu

Juni 2016
35th International Conference of the Polish Phycological Society, Łódź-Stryków, Poland, 01-04.06.2016, meer informatie: www.fyko.lodz.pl.

Augustus 2016
24th International Diatom Symposium (IDS 2016), Université Laval, Québec City, Canada, 21-26.08.2016, meer informatie: http://www.cen.ulaval.ca/ids2016

September 2016
35th Meeting of the French speaking Diatomists Association (ADLaF), Luxemburg, 13-15.09.2016, meer informatie: http://adlaf.free.fr/