Year: 2017

Abrupt stop of deep water turnover with lake warming: Drastic consequences for algal primary producers

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Abstract: After strong fertilization in the 20th century, many deep lakes in Central Europe are again nutrient poor due to long-lasting restoration (re-oligotrophication). In line with reduced phosphorus and nitrogen loadings, total organismic productivity decreased and lakes have now historically low nutrient and biomass concentrations. This caused speculations that restoration was overdone and intended fertilizations are needed to ensure ecological functionality. Here we show that recent re-oligotrophication processes indeed accelerated, however caused by lake warming. Rising air temperatures strengthen thermal stabilization of water columns which prevents thorough turnover (holomixis). Reduced mixis impedes down-welling of oxygen rich epilimnetic (surface) and up-welling of phosphorus and nitrogen rich hypolimnetic (deep) water. However, nutrient inputs are essential for algal spring blooms acting as boost for annual food web successions. We show that repeated lack (since 1977) and complete stop (since 2013) of holomixis caused drastic epilimnetic phosphorus depletions and an absence of phytoplankton spring blooms in Lake Zurich (Switzerland). By simulating holomixis in experiments, we could induce significant vernal algal blooms, confirming that there would be sufficient hypolimnetic phosphorus which presently accumulates due to reduced export. Thus, intended fertilizations are highly questionable, as hypolimnetic nutrients will become available during future natural or artificial turnovers.

DOI: https://doi.org/10.1038/s41598-017-13159-9

Originally published at:
Yankova, Yana; Neuenschwander, Stefan; Köster, Oliver; Posch, Thomas (2017). Abrupt stop of deep water turnover with lake warming: Drastic consequences for algal primary producers. Scientific Reports, 7(1):13770.
DOI: https://doi.org/10.1038/s41598-017-13159-9

Abrupt stop of deep water turnover with lake warming: Drastic consequences for algal primary producers

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Supplementary Information

Supplementary Figures & Legends S1 – S5 and Tables S1 – S4

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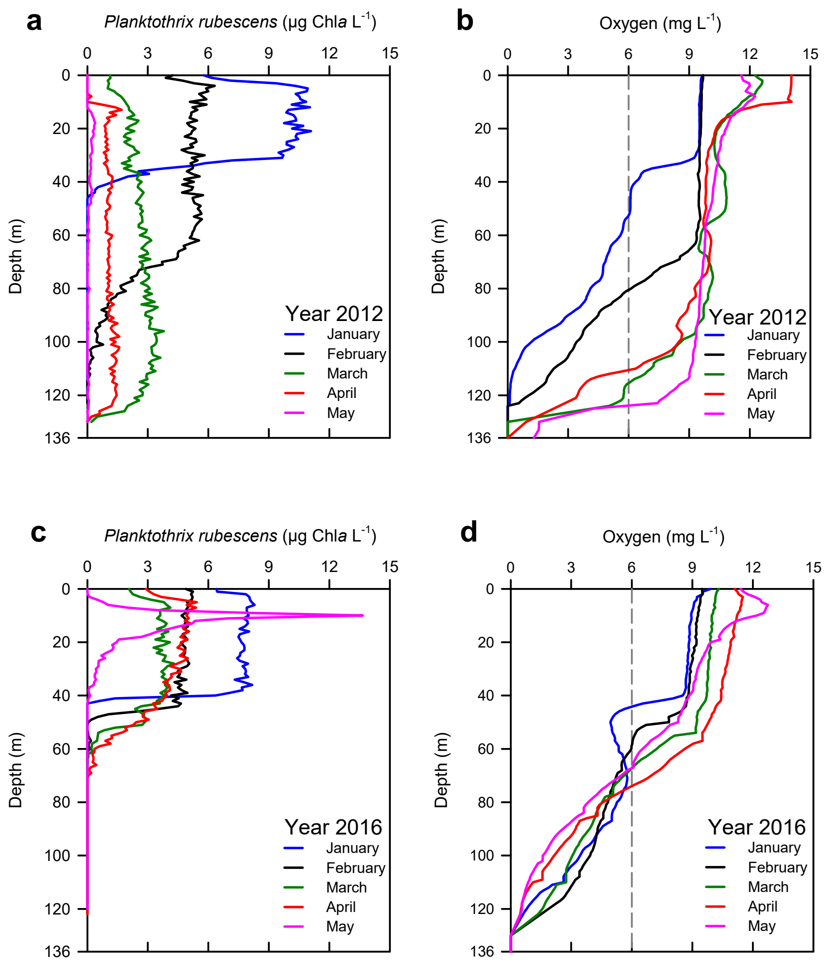
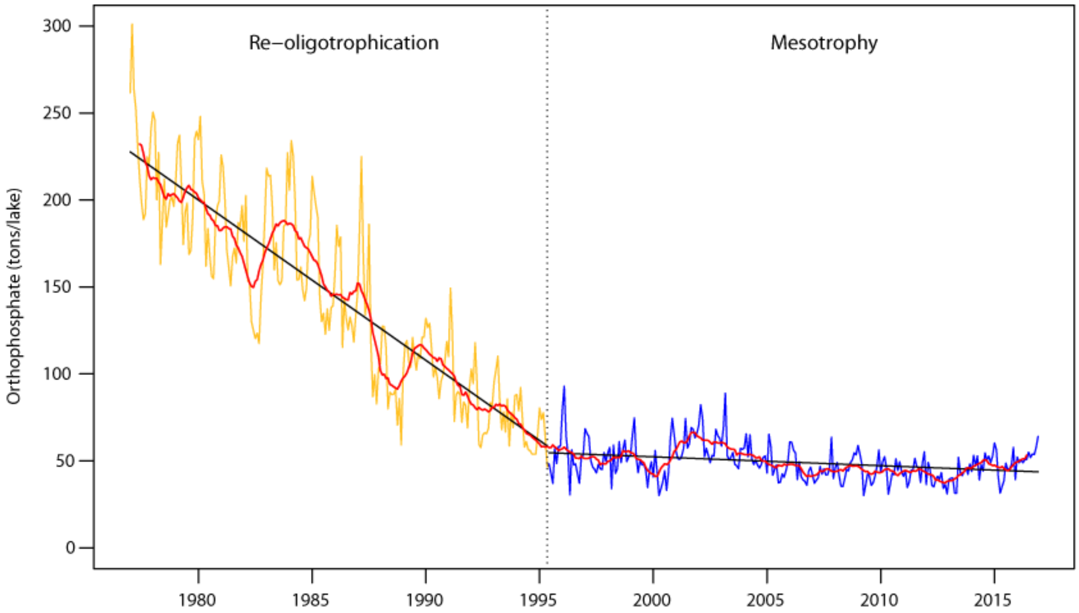
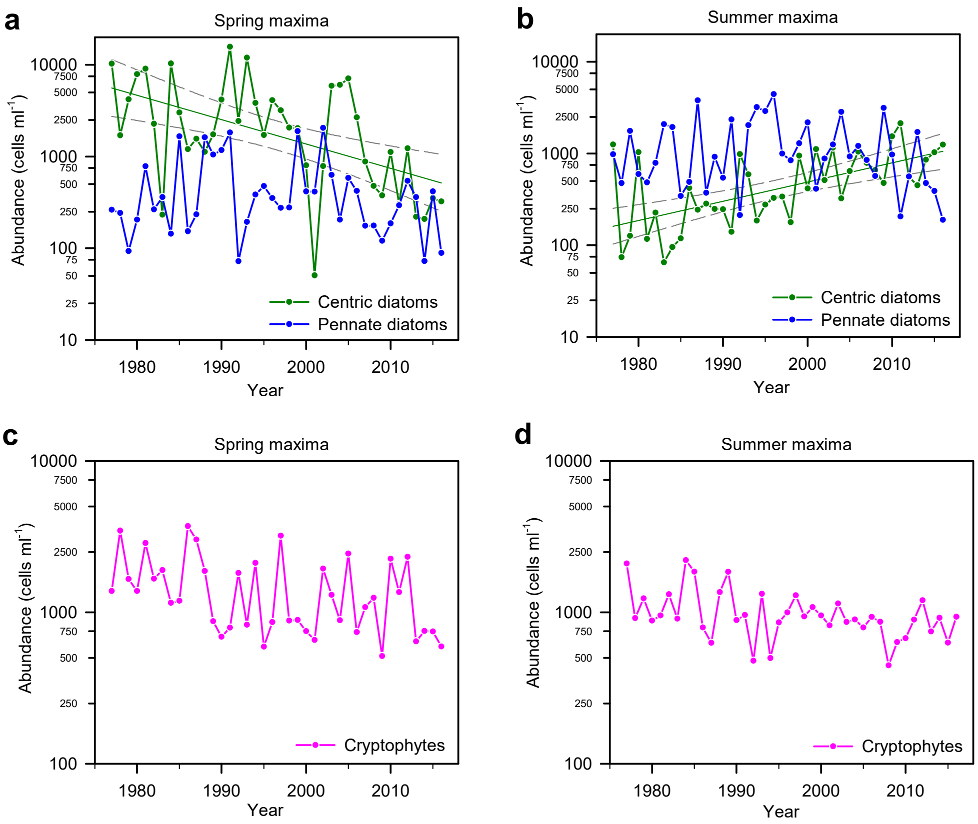


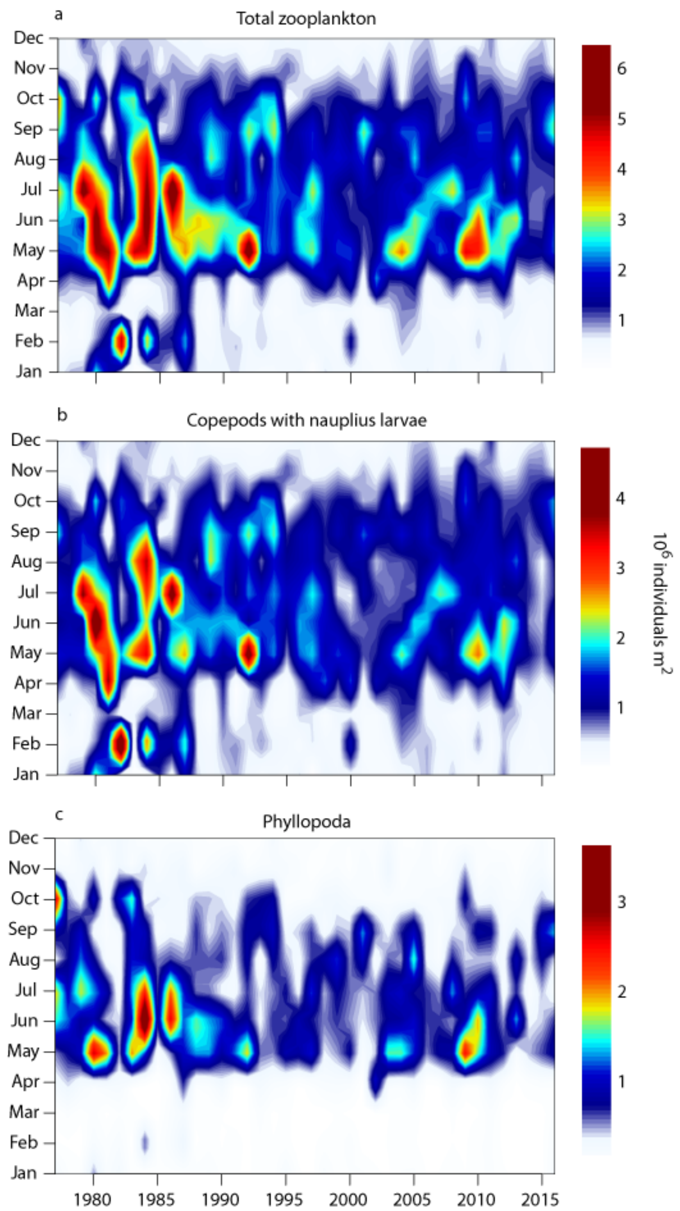
Supplementary Figure S1 | Monthly vertical profiles (January to May) of the cyanobacterium *Planktothrix rubescens* and oxygen concentrations in two years with different water turnover dynamics. In the year 2012 vernal water turnover (mixis depth) affected water strata down to a depth of ~120m, resulting in a deep entrainment of *P. rubescens* (**a**) and a strong oxygen enrichment of the hypolimnion (**b**). Note that the proxy for mixis intensity ($\geq$6 mg O_2 L^{-1}; gray stippled line in (**b**) and (**d**)) adequately reflected the depth of water turnover. Such deep mixis events led to a drastic decline of *P. rubescens* (due to the collapse of their gas vesicles), causing a minimal starting population in May. In the year 2016 vernal water turnover affected water strata only down to ~70m. This partial mixis was reflected by the vertical distribution of *P. rubescens* (**c**) and oxygen concentrations (**d**). Due to the partial mixis a large proportion of *P. rubescens* survived, which formed a densely stratified starting population already in May.



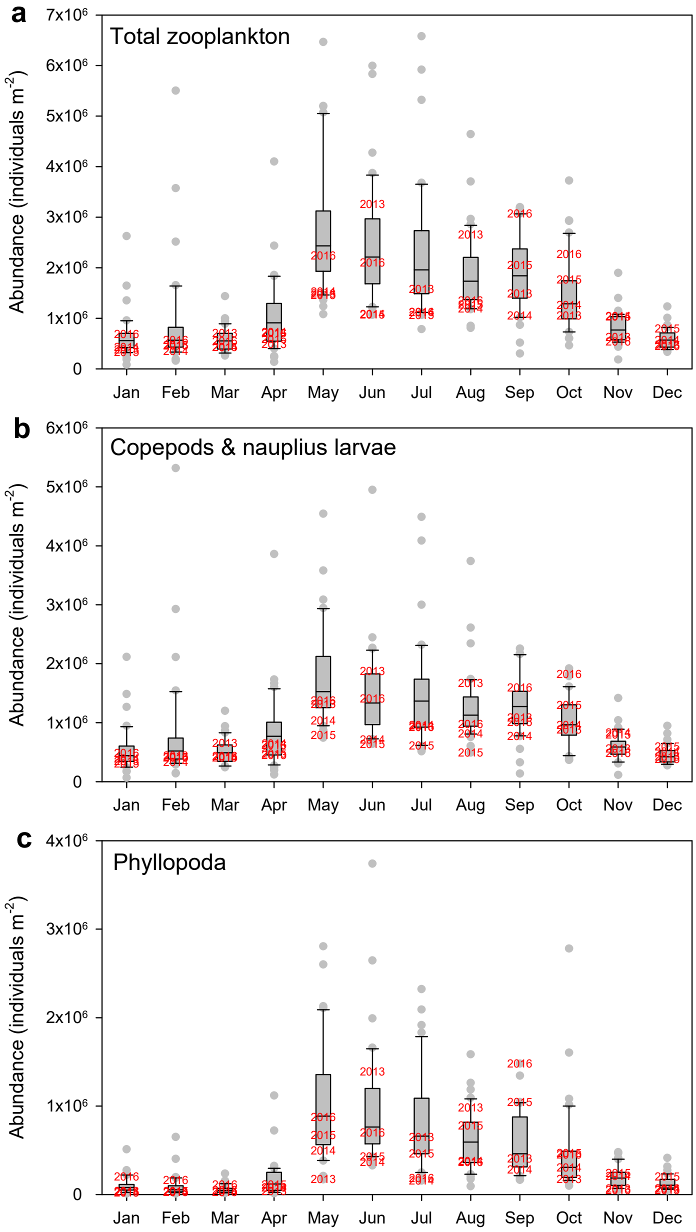
Supplementary Figure S2 | Change point in the development of total orthophosphate content. The change point (dotted line) in whole-lake orthophosphate content (*n* = 480) was determined for May 1995 by applying an iterative searching approach (details in Methods). Piece-wise regressions (black solid lines, $f = b*x + a$) signify transition from a re-oligotrophication mediated rapid orthophosphate decrease (orange line) to a stable oligo-mesotrophic status (blue line). Red line: continuous running average (*n* = 12).



Supplementary Figure S3 | Seasonal trends of centric / pennate diatoms and cryptophytes abundances between 1977 and 2016. a,**b,** Maximal abundances of centric and pennate diatoms in spring (**a**) and summer (**b**). Linear regressions (solid lines with confidence intervals; log(y) = $b*x + a$, r^2 = 0.29 for centric diatoms in spring, r^2 = 0.39 for centric diatoms in summer) were included when significant time trends on detrended data (see Supplementary Table S3) were detected. Maximal abundances of cryptophytes in spring (**c**) and summer (**d**). No significant time trends were detected for detrended data about cryptophytes (see Supplementary Table S3). Spring = March-May, summer = July-October. For all parameters: n = 40.



Supplementary Figure S4 | Zooplankton abundance in Lake Zurich for the period 1977-2016. Monthly abundance (n = 480 each) of total zooplankton (**a,** copepods + nauplius larvae + Phyllopoda), copepods with nauplius larvae (**b**) and Phyllopoda (**c**), averaged for 0-136 m.



Supplementary Figure S5 | Seasonality pattern of zooplankton abundance in Lake Zurich for the period 1977-2016. Monthly abundance of total zooplankton (**a**, copepods + nauplius larvae + Phyllopoda), copepods with nauplius larvae (**b**) and Phyllopoda (**c**), averaged for 0-136 m. The bars show the 25th, 50th and 75th percentiles, whiskers stand for the 10th and the 90th percentiles and grey points show outliers. Values for the four last years (2013-2016) are shown in red with years as labels. For the 40 years period, the highest zooplankton abundances were reached in May (clear water phase of Lake Zurich). For all parameters: n = 480.

Supplementary Table S1 | Statistical time-trends of physico-chemical long-term data (1977 until 2016) of Lake Zurich. Trends were analyzed for the whole datasets and for periods before and after 1995. This workflow was chosen as orthophosphate values showed a change point in 1995. Phosphorus concentrations in lakes are major parameters to characterize the trophic status.

Parameter	n	Seasonal Mann Kendall's tau (period = 12)	Mann Kendall's tau	Autocorrelation of detrended time series	p-value	Significant trend
Epilimnetic orthophosphate						
whole period	480	-0.520	-	-	< 0.001	negative
< 1995	216	-0.569	-	-	< 0.001	negative
≥ 1995	264	-0.212	-	-	0.018	negative
Hypolimnetic orthophosphate						
whole period	480	-0.443	-	-	< 0.001	negative
< 1995	216	-0.484	-	-	< 0.001	negative
≥ 1995	264	0.204	-	-	0.026	positive
Epilimnetic silica						
whole period	480	0.541	-	-	< 0.001	positive
< 1995	216	-0.158	-	-	0.212	no trend
≥ 1995	264	0.470	-	-	< 0.001	positive
Epilimnetic nitrate						
whole period	480	-0.264	-	-	0.004	negative
< 1995	216	0.510	-	-	< 0.001	positive
≥ 1995	264	-0.350	-	-	0.004	negative
Average mixing depth	40	-	-0.446	0.004	< 0.001	negative

Supplementary Table S2 | Spearman's correlation analysis of interactions between detrended and not detrended average mixing depth, key biological and chemical variables for the period 1977-2016 (all *n* = 40). All variables (except mixis depth) are maxima of weighted averages for 0-20 m, except zooplankton (for 0-136 m). Zooplankton = copepods with nauplius larvae + Phyllopoda. Significant correlations are bold.

	Spearman's *rho* (detrended)	*p*-value (detrended)	Spearman's *rho* (not detrended)	*p*-value (not detrended)
Mixis depth – PO_4-P jan-mar	**0.631**	**< 0.001**	**0.713**	**< 0.001**
Mixis depth – NO_3-N jan-mar	**0.443**	**0.005**	**0.510**	**0.001**
Mixis depth – SiO_2 jan-mar	**0.390**	**0.014**	**-0.411**	**0.008**
Mixis depth – centric diatoms mar-may	0.232	0.156	**0.472**	**0.002**
Mixis depth – cryptomonads mar-may	0.225	0.169	0.278	0.083
Mixis depth – zooplankton apr-jun	0.129	0.434	0.165	0.310
Mixis depth – *P. rubescens* mar-may	**-0.716**	**< 0.001**	**-0.701**	**< 0.001**
PO_4-P jan-mar – NO_3-N jan-mar	**0.518**	**0.001**	**0.467**	**0.002**
PO_4-P jan-mar – SiO_2 jan-mar	**0.399**	**0.012**	**-0.733**	**< 0.001**
PO_4-P jan-mar – centric diatoms mar-may	**0.645**	**< 0.001**	**0.616**	**< 0.001**
PO_4-P jan-mar – cryptomonads mar-may	0.188	0.252	**0.395**	**0.012**
PO_4-P jan-mar – zooplankton apr-jun	0.165	0.317	**0.379**	**0.016**
PO_4-P jan-mar – *P. rubescens* mar-may	**-0.659**	**< 0.001**	**-0.840**	**< 0.001**
NO_3-N jan-mar – SiO_2 jan-mar	0.221	0.177	**-0.622**	**< 0.001**
NO_3-N jan-mar – centric diatoms mar-may	**0.372**	**0.020**	**0.468**	**0.002**
NO_3-N jan-mar – cryptomonads mar-may	0.079	0.634	0.169	0.295
NO_3-N jan-mar – zooplankton apr-jun	0.151	0.357	0.261	0.104
NO_3-N jan-mar – *P. rubescens* mar-may	**-0.428**	**0.007**	**-0.412**	**0.008**
SiO_2 jan-mar – centric diatoms mar-may	0.259	0.112	**-0.374**	**0.017**
SiO_2 jan-mar – cryptomonads mar-may	-0.005	0.975	-0.272	0.089
SiO_2 jan-mar – zooplankton apr-jun	0.043	0.793	-0.281	0.079
SiO_2 jan-mar – *P. rubescens* mar-may	-0.295	0.069	**0.569**	**0.001**
Centric diatoms mar-may – cryptomonads mar-may	0.118	0.473	0.191	0.237
Centric diatoms mar-may – zooplankton apr-jun	0.076	0.646	0.255	0.113
Centric diatoms mar-may – *P. rubescens* mar-may	**-0.385**	**0.016**	**-0.566**	**< 0.001**
Cryptomonads mar-may – zooplankton apr-jun	0.245	0.132	**0.440**	**0.005**
Cryptomonads mar-may – *P. rubescens* mar-may	-0.226	0.167	**-0.427**	**0.006**
Zooplankton apr-jun – *P. rubescens* mar-may	-0.250	0.125	**-0.431**	**0.005**

Supplementary Table S3 | Statistical time-trends of biological long-term data (1977 until 2016) of Lake Zurich. Trends were analyzed for the whole datasets and for periods before and after 1995 (for centric and pennate diatoms, cryptophytes and *Planktothrix rubescens*). This workflow was chosen as orthophosphate values showed a change point in 1995. Phosphorus concentrations in lakes are major parameters to characterize the trophic status.

Parameter	n	Seasonal Mann Kendall's tau (period = 12)	Mann Kendall's tau	Autocorrelation of detrended time series	p-value	Significant trend
Centric diatoms						
all seasons	480	-0.026	-	-	0.594	no trend
spring	40	-	-0.357	0.047	0.001	negative
< 1995	18	-	0.176	-0.153	0.343	no trend
≥ 1995	22	-	-0.400	0.581	0.012	negative
summer	40	-	0.498	-0.051	< 0.001	positive
Pennate diatoms						
all seasons	480	-0.106	-	-	0.004	negative
spring	40	-	-0.069	0.114	0.545	no trend
< 1995	18	-	0.088	0.130	0.650	no trend
≥ 1995	22	-	-0.257	-0.150	0.110	no trend
summer	40	-	0.009	-0.121	0.942	no trend
Cryptophytes						
all seasons	480	-0.127	-	-	0.010	negative
spring	40	-	-0.217	-0.011	0.052	no trend
< 1995	18	-	-0.117	0.223	0.536	no trend
≥ 1995	22	-	-0.123	-0.203	0.450	no trend
summer	40	-	-0.217	0.004	0.053	no trend
P. rubescens						
all seasons	480	0.442	-	-	< 0.001	positive
spring	40	-	0.527	0.057	< 0.001	positive
< 1995	18	-	0.412	0.122	0.023	positive
≥ 1995	22	-	0.209	0.025	0.194	no trend
summer	40	-	0.320	0.190	0.004	positive
Zooplankton						
total	480	-0.138	-	-	0.001	negative
Copepods and nauplius larvae	480	-0.092	-	-	0.029	negative
Phyllopoda	480	-0.176	-	-	< 0.001	negative

Centric and pennate diatoms/cryptophytes/*P. rubescens* spring = maximal abundance between March and May. Centric and pennate diatoms/cryptophytes/*P. rubescens* summer = maximal abundance between July and October. Zooplankton total = copepods with nauplius larvae + Phyllopoda.

Supplementary Table S4 | Summary of multiple regression analyses for variables predicting (a) centric diatoms and (b) zooplankton for the period 1977-2016 (all *n* = 40). All biological variables and PO_4-P are maxima of weighted averages for 0-20 m, except zooplankton (for 0-136 m). Temperatures are mean values of weighted averages for 0-20 m. Zooplankton = copepods with nauplius larvae + Phyllopoda. Significant p-values are bold.

(a)

	Centric diatoms $_{mar-may}$		
Variable	β	*t*	*p*
Temperature $_{mar-may}$	0.205	1.213	0.233
PO_4-P $_{jan-mar}$	0.554	3.255	**0.002**
Zooplankton $_{apr-jun}$	0.094	0.601	0.551
R^2	0.267		
F-statistic	4.36 (df = 3;36), ***p* = 0.010**		

(b)

	Zooplankton $_{apr-jun}$		
Variable	β	*t*	*p*
Temperature $_{apr-jun}$	-0.305	-2.121	**0.041**
Cryptomonads $_{mar-may}$	0.331	2.311	**0.027**
Centric diatoms $_{mar-may}$	0.198	1.378	0.177
R^2	0.262		
F-statistic	4.26 (df = 3;36), ***p* = 0.011**		