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### Recommended Citation

Izmet's'eva, L. R., et al. (2016). Lake-wide physical and biological trends associated with warming in Lake Baikal. *Journal of Great Lakes Research* 42: 6–17. <http://dx.doi.org/10.1016/j.jglr.2015.11.006>

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## Lake-wide physical and biological trends associated with warming in Lake Baikal



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### ARTICLE INFO

#### Article history:

Received 9 June 2015

Accepted 29 October 2015

Available online 6 January 2016

Communicated by R. Michael McKay

#### Index words:

Lake warming

Eutrophication

Zooplankton

Lake Baikal

Lake monitoring

### ABSTRACT

Eutrophication and warming of lakes are occurring globally. Lake Baikal, a large ancient lake composed of three basins, has recently experienced benthic eutrophication at local sites and lake warming in the south basin. Here, we look for signals of warming and pelagic eutrophication across the entire lake using physical and biological data collected at a subset of 79 stations sampled ca. annually (1977–2003) during the period of summer stratification. Lake-wide, surface waters warmed 2.0 °C; and, consistent with this warming, the abundance of two warm-water, cosmopolitan zooplankton taxa increased between two (pelagic cladocerans) and 12-fold (*Cyclops kolensis*). *C. kolensis* increased throughout the lake, whereas cladocerans increased significantly only in the north basin. In contrast, abundance of the cold-water endemic copepod, *Epischura baikalensis*, that dominates the crustacean zooplankton community, did not change. With the exception of one coastal station in the north basin, there is no evidence of pelagic eutrophication. Although chlorophyll concentrations increased 46% lake-wide (0.82 to 1.20 µg/L), the increasing trend was significant only in the south basin. Surprisingly, mean Secchi transparency increased by 1.4 m lake-wide across the 26-year time series with significant deepening of water transparency occurring in the central and north basins. This suggests a decline in productivity in the north and middle basins, but an increase in the south basin. Taken together, these findings suggest that physical and biological changes associated with warming have occurred in Lake Baikal, but wide-spread pelagic eutrophication in the lake's three basins has not.

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### Introduction

Lakes world-wide are impacted by climate change, eutrophication, and their interactive effects (Jeppesen et al., 2010, 2014; Moss et al., 2011). Among ancient lakes – those containing water since at least the last interglacial period – evidence of recent warming, eutrophication, or both have been reported for Lake Biwa (warming and eutrophication; Hsieh et al., 2010, 2011), Lake Hovsgol (warming; Batima et al., 2004), Lake Ohrid (warming; Matzinger et al., 2006, 2007), Lake Tanganyika (warming; Verburg et al., 2003), Lake Malawi (eutrophication; Hecky et al., 2003; Otu et al., 2011), and the brackish Caspian Sea (warming and eutrophication; Huseynov, 2011; Leonov and Stygar, 2001).

Surface waters in the south basin of Lake Baikal, the world's most voluminous and ancient lake, have warmed 2.4 °C in summer over the

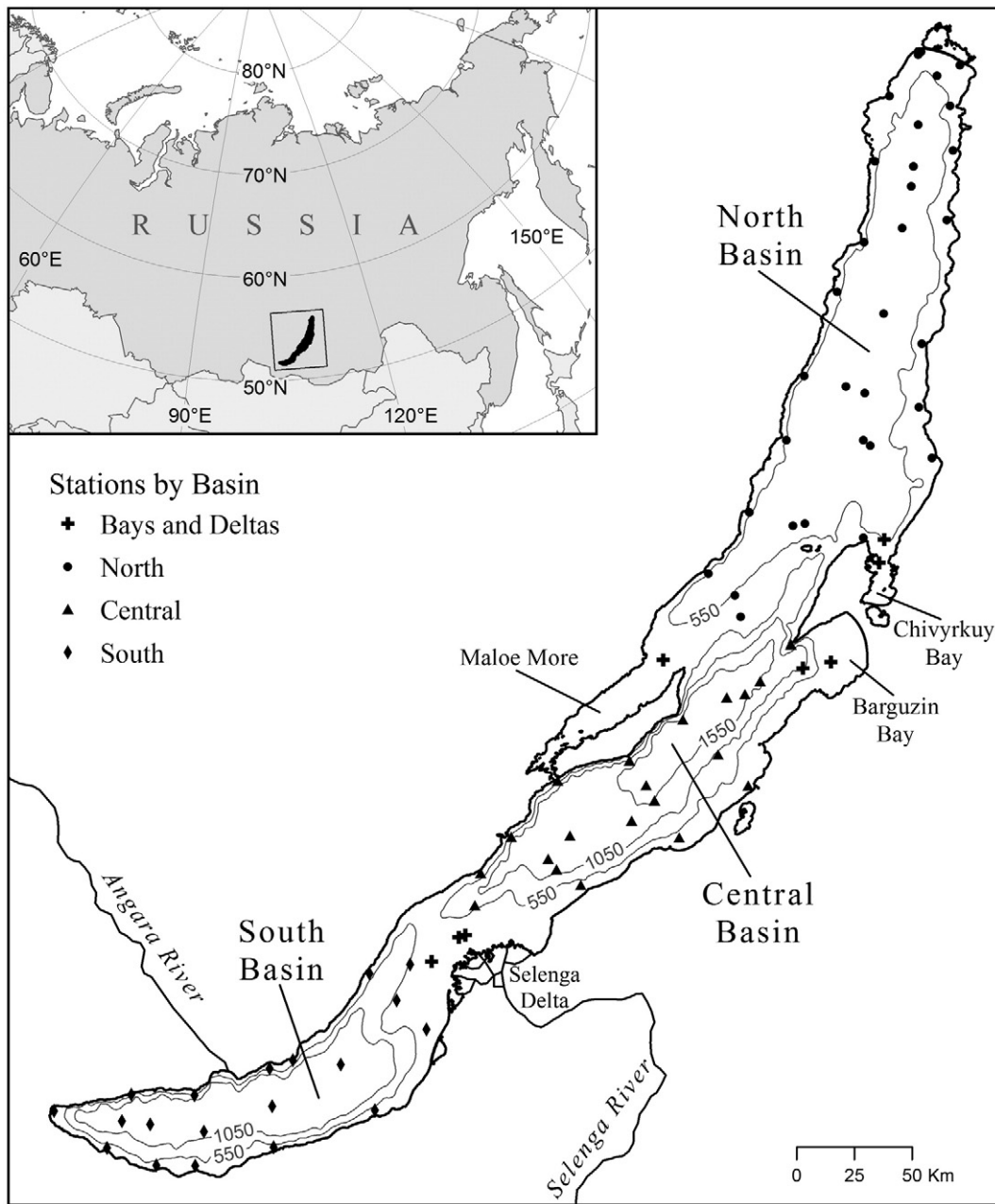
last 60 years (Hampton et al., 2008; Shimaraev and Domysheva, 2013). Likewise, recent surveys confirm that benthic cultural eutrophication is occurring at localized sites in the coastal zone of this lake (Kravtsova et al., 2012, 2014). Specifically, large increases in benthic algal abundance and shifts in zonation, coupled with high concentrations of nutrients, illustrate the perils of discharging untreated sewage into the coastal zone of oligotrophic Lake Baikal (Kravtsova et al., 2012, 2014; Timoshkin et al., 2014). Despite evidence for localized warming and coastal benthic eutrophication, it is still unknown whether warming and eutrophication of the water column are occurring lake-wide.

Detecting lake-wide warming or eutrophication of the pelagic zone at Lake Baikal is challenging due to the lake's great size and its heterogeneous geomorphology. Stretching across four degrees of latitude (52–56°N), the lake contains three distinct basins and multiple bays (Fig. 1), some of the latter are considerably more productive than offshore waters. Although plankton and various physical parameters have been monitored for more than 60 years at Lake Baikal by Russian

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**Fig. 1.** Map of Lake Baikal showing sampling stations, depth contours (meters), basins, and largest bays (Barguzin, Chivyrkuy Bay, Maloe More Strait). Stations within areas sampled are identified by diamonds (south basin), triangles (middle basin), circles (north basin), and crosses (Selenga River delta, bays, or Maloe More Strait). The lake, located near the Russian–Mongolian border, stretches from 52 to 56° north latitude (inset map).

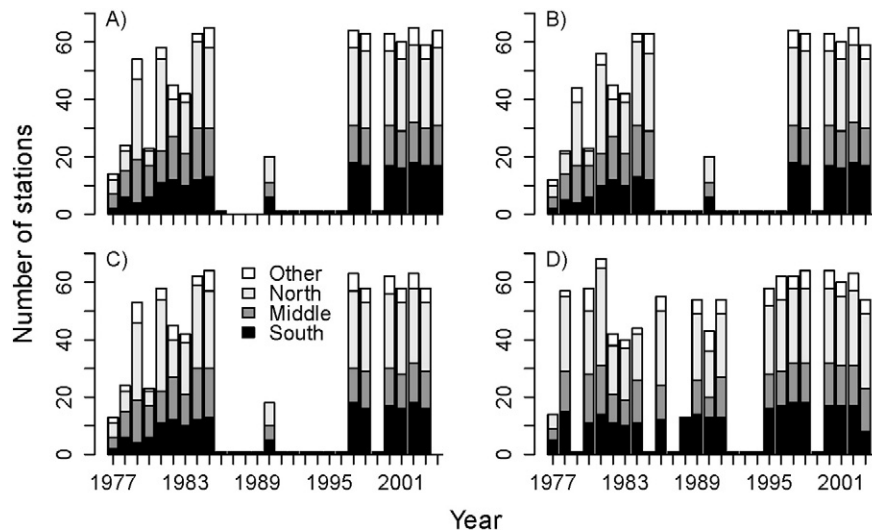
researchers (Galazyi, 1993; Kozhov, 1963; Kozhova and Izmet'eva, 1998; Popovskaya, 2000; Shimaraev et al. 2002), a spatially intensive, multi-decadal investigation that integrates the responses of multiple physical and biological variables across the entire lake has not been published previously.

Here we use lake-wide physical and biological data collected across 26 years to assess two environmental challenges facing the lake today: climate warming and pelagic eutrophication. We address three questions: 1) Is warming similar in magnitude to that reported for the south basin occurring throughout Lake Baikal? 2) Is the pelagic zone of the lake eutrophying? 3) Are zooplankton (i.e., copepods and cladocerans) community structure and abundance changing in ways that are consistent with warming, eutrophication, or both? Results from our spatial–temporal analyses suggest that physical and biological changes

associated with warming have occurred in Lake Baikal, but there is no evidence of wide-spread pelagic eutrophication.

## Methods

Samples were collected once per year at a subset of 79 stations (typically >54 stations) throughout the lake (Fig. 1). Water temperature, Secchi transparency and zooplankton species composition and abundance were sampled from 1977 to 2003; chlorophyll *a* was sampled from 1977 to 2004. All sampling occurred during the months of August and September when the lake was stratified, with a median sampling date of 29 August in the south basin, 4 September in the central basin, and 10 September in the north basin. Lake-wide sampling for water temperature, Secchi depth, and chlorophyll did not occur for



**Fig. 2.** Number of stations sampled each year from 1977 to 2004 for chlorophyll (A), temperature (B), Secchi transparency (C), and zooplankton (D). Data from years in which only one station was sampled per basin were not included in regressions, calculations of Sen's slope, or kriging.

8–11 years during the middle of the time series; however, zooplankton sampling occurred at multiple stations throughout the lake for 20 of the 26 years of the time series (Fig. 2). Despite this sampling irregularity, a sufficient number of stations were sampled to characterize lake-wide trends in temperature, chlorophyll, Secchi, and zooplankton abundance in each of the basins over the 26-year period.

Sampling stations were generally distributed along transects extending from the west to east shore across each of the lake's three basins with additional stations located within shallow, more productive bays (Chivyrkuy Bay, Barguzin Bay, and Maloe More Strait) and the Selenga River delta (Fig. 1). Stations  $\leq 8$  km from the Baikalsk Pulp and Paper Mill or its discharge pipe were not included in the data set.

Water temperature, chlorophyll, Secchi depth, and zooplankton abundances were quantified using standard procedures described elsewhere (Timoshkin, 1995; UNESCO, 1966). Although water temperature and chlorophyll *a* concentrations were determined at 0 m, as well as additional depths (e.g., 10 and 50 m) in some years, we restrict our temperature and chlorophyll analyses to surface values only. Rotifer and crustacean zooplankton were sampled with a closing plankton net (37.5-cm diameter, 100  $\mu$ m mesh) generally at depth layers of 0–50 m or each of the co-terminous depth layers of 0–25 and 25–50 m. At shallow stations ( $< 50$  m), however, sampled depth layers varied with maximum depth of the sampling station. Zooplankton samples were preserved with formalin, and three subsamples per net tow were counted in their entirety in a Bogorov chamber under 100 $\times$  magnification. Counts for each zooplankton taxa included juvenile life stages (e.g., copepodites and nauplii for copepods) as well as adults.

Among zooplankton, we focus on crustacean taxa as sensitive indicators to lake warming, eutrophication, and other types of environmental change (Jeppesen et al., 2011). Also, the pelagic zooplankton of Lake Baikal are particularly amenable to use as ecological indicators because there are few species, and they have contrasting thermal niches and expected responses to eutrophication. For example, *Epischura baikalensis*, an endemic calanoid copepod and a cold-water stenotherm, typically comprises 90% of the zooplankton biomass. The two other taxonomic groups present during summer include the cladocerans (*Daphnia* spp. and *Bosmina longirostris*) and a cyclopoid copepod (*Cyclops kolensis*). These are warm-water cosmopolitan taxa that increase in abundance in warmer water and under eutrophic conditions (Hampton et al., 2008; Hsieh et al., 2011; Straile and Geller, 1998). Although the zooplankton community of Lake Baikal also includes rotifers and an endemic pelagic amphipod, we did not include these taxa in our analyses because thermal tolerances of the rotifer taxa are

less well known than those of the crustacean zooplankton, and the pelagic amphipod, which enters surface waters (0–50 m) only at night, was not sampled.

#### Spatial–temporal analyses

Lake-wide temporal trends in surface water temperature, surface chlorophyll *a*, Secchi transparency, and the abundance of each of the three zooplankton groups were determined using linear regression applied to basin means. These means were calculated by averaging values across all stations for each of the three basins per year in which sampling occurred between 1977 and 2003. In other words, three means – one for each basin – were plotted for each variable and year in which sampling occurred across the time series. When calculating basin means, data from stations in the shallow bays (i.e., Chivyrkuy Bay, Maloe More Strait, Barguzin Bay) and the Selenga River delta were excluded, because these shallow areas can be considerably warmer and more eutrophic than the rest of the lake, and they are not representative of the lake as a whole. Separate regressions describing temporal trends for the bays (Chivyrkuy Bay, Barguzin Bay, and Maloe More), and the Selenga Delta were not possible due to too few samples across time in these locations. For lake-wide and basin-wide regressions, values for chlorophyll, Secchi depth, and zooplankton abundances were log (ln) transformed to improve normality.

#### Sen's slopes

To describe temporal trends at individual stations for the environmental variables (temperature, chlorophyll, and Secchi depth) and the abundance of each zooplankton group, we carried out Mann–Kendall trend tests. The Mann–Kendall test is a nonparametric method that uses Kendall's Tau to evaluate if significant trends exist in time-series data (Mann, 1945). To determine the rate of change for significant trends, we used Sen's slope – an estimate of the rate of change which represents the median slope of all possible pairwise slopes (Sen, 1968). These methods were chosen as they are not sensitive to outliers, can handle missing data, and are more accurate than linear regression for skewed or heteroskedastic data (Rousseeuw and Leroy, 1987). The Mann–Kendall tests and Sen's slope calculations were carried out in the R programming language using the TheilSen function found in the openair package (Carslaw and Ropkins, 2012). Stations with fewer than 10 years of environmental or zooplankton data were excluded from trend calculations.



### Kriging

Ordinary kriging was used to estimate the average spatial variability of environmental variables and abundance of zooplankton groups throughout the lake over the entire time series. Analyses of environmental variables used summer surface water temperature and chlorophyll concentrations averaged for each station across the entire time series. The chlorophyll model included only stations having at least 4 years of data, with the exception of one station sampled three times in Chivyrkuy Bay and one station sampled three times in the Selenga Delta. These two stations were included to better reflect spatial trends in these less frequently sampled areas. The temperature model included only stations having at least 6 (south basin and Selenga Delta stations) or 9 (middle and north basin stations) years of data. For each model, stations were selected to ensure optimal models and to minimize artificial 'bulls-eye' effects around individual points. The kriging models also included first order trend removal to account for a slight spatial trend in both chlorophyll and temperature. Secchi depth values were not kriged because the data showed no spatial autocorrelation (i.e., no spatial patterns). The kriged models for the zooplankton groups included stations sampled at least 10 times in the main body of the lake or 4 times in the bays and deltas to mirror the stations used in Sen's slope analysis while still capturing patterns in the less-sampled bays and deltas.

### Hotspot analysis

To identify clusters of stations in the lake where *E. baikalensis* and the pelagic cladocerans increased or decreased in abundance over time, hotspot analysis (Ord and Getis, 1995) was applied to Sen's slopes. To prevent zero Sen's slopes from being considered 'low' values in the analysis, we multiplied all Sen's slopes by  $10^9$ . We chose the distance band at which spatial autocorrelation was highest, based on calculations from incremental Moran's I. No hotspot analysis of Sen's slope values was performed for *C. kolensis* because this crustacean increased in abundance at nearly all stations throughout the entire lake, resulting in no significant spatial autocorrelation. In addition, no hotspot analyses of Sen's slopes were performed for the environmental variables due to a lack of spatial autocorrelation.

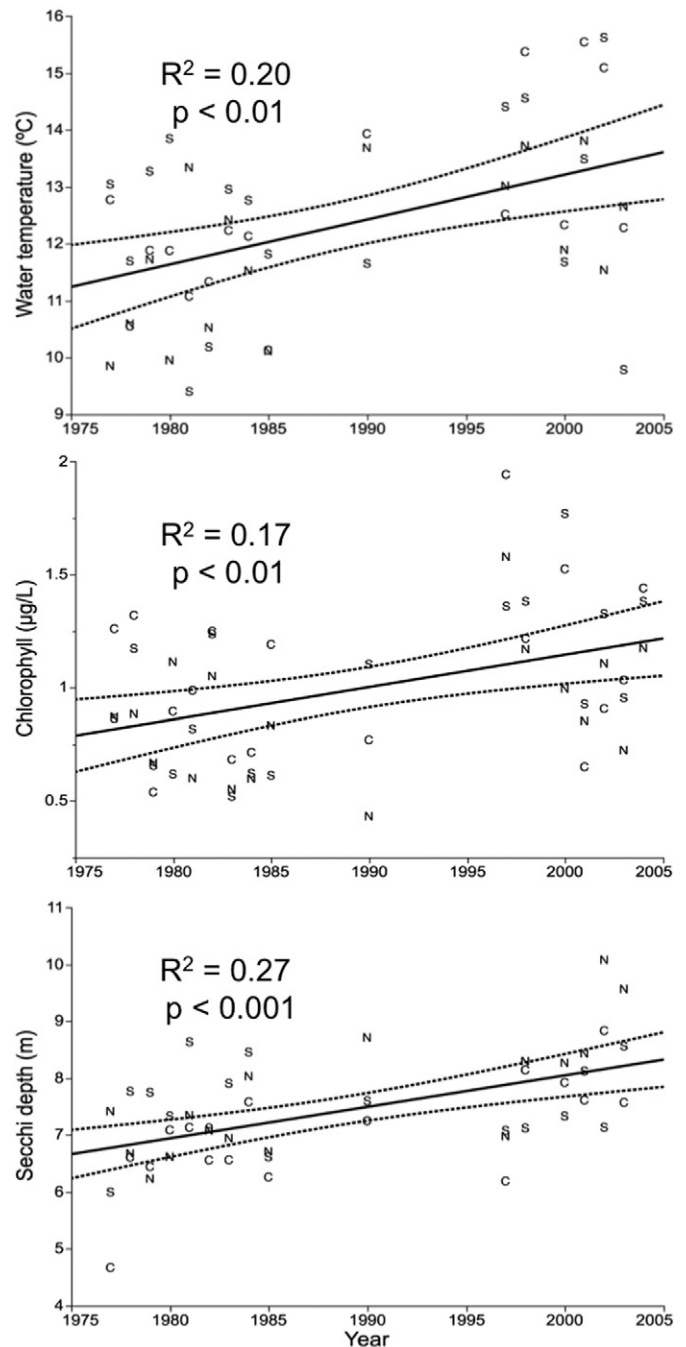
### Multiple regression

To determine if warmer waters, increased chlorophyll, or both were associated with changes in zooplankton abundance, we performed mixed effects multiple regression modeling on log transformed calanoid copepod, cyclopoid copepod, and cladoceran abundances as separate response variables. Before proceeding, we confirmed that spatial autocorrelation among neighboring stations in this data set was insufficient to violate model assumptions, based on examination of variograms, but that a north to south spatial trend did seem apparent. Accordingly, we used both basin (north, central, south) and sampling year as random effects and focused on examining temperature and chlorophyll as fixed effects. We used the Akaike information criterion (AIC) to select best-fit models (Burnham and Anderson, 2010), and for the best-fit models, we calculated "conditional" and "marginal  $R^2$ " using the formulations of Nakagawa and Shielzeth (2013). Conditional  $R^2$  is an assessment of the full model fit, and marginal  $R^2$  describes the proportion of variance explained by the fixed factors alone.

## Results

### Environmental variables

Temperature, chlorophyll, and Secchi depth all increased significantly lake-wide and across the time series (Fig. 3); however, temporal trends within individual basins sometimes differed from that observed for the lake as a whole (Table 1). For example, summer surface waters of Lake Baikal warmed significantly, increasing on average 2.0 °C across the entire lake from 1977 to 2003 (Fig. 3), but the increase was



**Fig. 3.** Lake-wide temporal trends ( $\pm 95\%$  CI) of surface water temperature, surface chlorophyll concentrations, and Secchi depth during August–September across the time series (1977–2003 for temperature and Secchi; 1977–2004 for chlorophyll). Each letter is an annual mean of values for all stations sampled in a given basin (S = south, C = central, N = north basin). Thus, three basin means are plotted per year for each variable. Statistical tests were performed on log transformed data for chlorophyll and Secchi depth only to improve normality. Regression equations: water temperature =  $0.074 \text{ * year} - 135.2$ ; chlorophyll  $a = 0.016 \text{ * year} - 30.3$ ; Secchi depth =  $0.056 \text{ * year} - 103.7$ .

significant in only two of the lake's three basins (Table 1; central basin and north basin). Chlorophyll *a* increased significantly and on average by 46% across the entire lake during the 27-year (1977–2004) time series (Fig. 3). Although chlorophyll *a* trended upward in each basin with time, a significant increase occurred only in the south basin, but not in the other two basins (Table 1). Likewise Secchi transparency increased significantly lake-wide (Fig. 3) and on average 1.4 m across the 26-year

**Table 1**

Results of lake-wide and basin-wide univariate regressions for each environmental variable (surface water temperature, °C; surface chlorophyll *a* concentrations, µg/L; Secchi depth, m) versus year across the time series (1977–2003 for temperature and Secchi, 1977–2004 for chlorophyll). Lake-wide regressions were based on annual basin means for each variable; basin-wide regressions were performed on the station values. Stations within bays (Chivyrkuy Bay, Barguzin Bay), Maloe More Strait, and the two stations closest to the Selenga Delta were not included in these regressions. Values for chlorophyll concentrations and Secchi depth were log transformed to improve normality; it was not necessary to transform the water temperature data. *m* = regression slope. Bolded values are significant at the 0.05 level.

Model	df	<i>m</i>	<i>F</i>	<i>p</i>	<i>R</i> <sup>2</sup>
Temperature					
Lake-wide	1, 46	0.080	13.15	<0.01	0.20
North basin	1, 14	0.083	7.08	0.02	0.29
Central basin	1, 14	0.110	10.42	<0.01	0.39
South basin	1, 14	0.043	0.83	0.38	0.0
Chlorophyll					
Lake-wide	1, 49	0.016	11.09	<0.01	0.17
North basin	1, 15	0.013	2.31	0.15	0.08
Central basin	1, 15	0.012	1.78	0.20	0.05
South basin	1, 15	0.023	7.64	0.01	0.29
Secchi					
Lake-wide	1, 46	0.007	18.53	<0.001	0.27
North basin	1, 14	0.011	25.22	<0.001	0.62
Central basin	1, 14	0.010	11.06	<0.01	0.40
South basin	1, 14	0.001	0.07	0.79	0.0

time series. Similarly to temperature, however, Secchi depth values increased significantly in the north and central basins but not in the south basin (Table 1).

#### Sen's slopes

Temporal trends for water temperature, chlorophyll, and Secchi depth varied spatially across stations both within and among basins according to the values of Sen's slope (Fig. 4). For example, even though surface waters warmed significantly in the north and central basins (see above), there were locations within each of these two basins where temperature decreased across the time series (Fig. 4). The largest decrease in surface temperatures occurred for stations at the southern tip of the south basin although none of these decreases were significant. Significant Sen's slope values for temperature occurred at 7 stations with all values being positive indicating a significant warming of surface

waters across the time series at these stations, most of which were located in the north and central basins. Of these 7 stations, three were near or at the mouth of two shallow bays, Chivyrkuy Bay and Barguzin Bay.

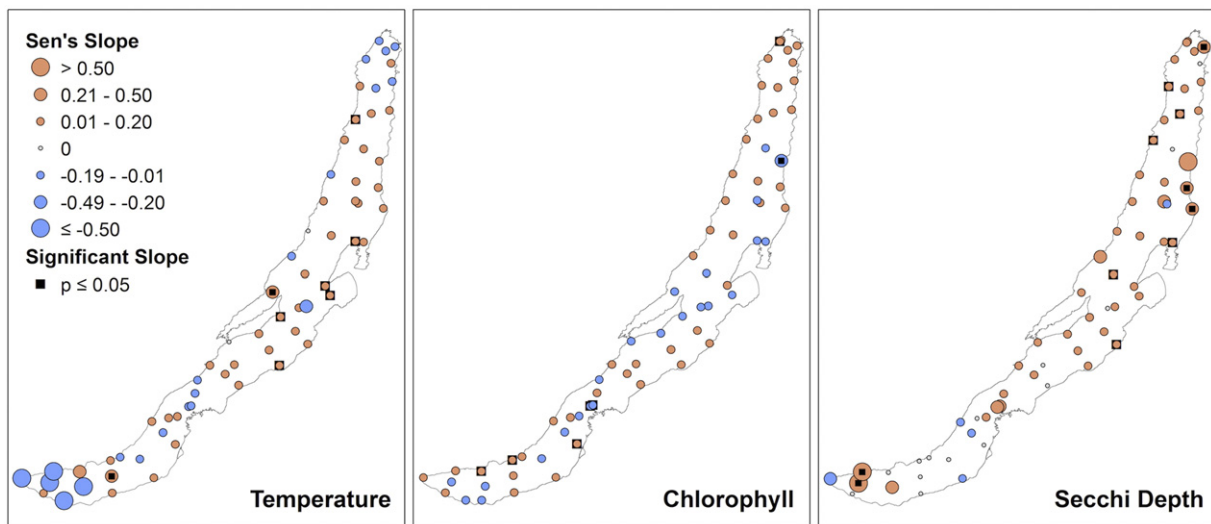
Forty four stations, or 67% of the sampling stations, exhibited a positive Sen's slope value for chlorophyll meaning that chlorophyll increased across much of the lake during the 27 year time series (Fig. 4). Similarly to temperature, however, only seven stations exhibited significant Sen's slope values for chlorophyll, with chlorophyll increasing at 4 of these stations, while it decreased at the remaining three stations. Among the four stations where chlorophyll increased significantly, three were located in the south basin while the remaining station was 1.4 km from the mouth of the Tyva River near Severobaikalsk in the North basin.

Water transparency, as measured by Secchi depth, increased across the time series for 70% (45 out of 64 stations) of the stations throughout the lake according to the values of Sen's slope (Fig. 4). Eleven stations, or only 17% of the total, exhibited significant Sen's slope values with all values being positive indicating increasing water transparency. Seven of these 11 stations were located in the north basin.

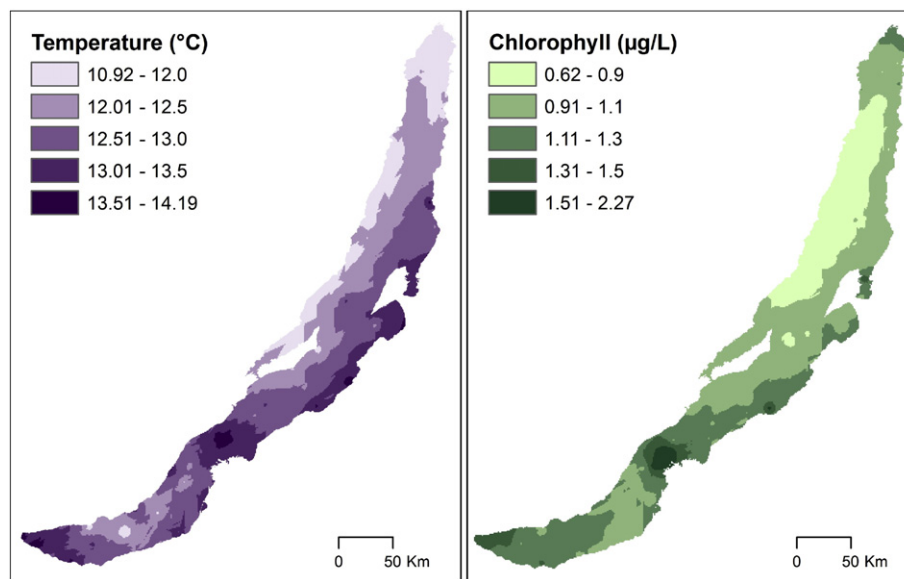
Finally, Sen's slope values sometimes lacked a one-to-one correspondence among the three environmental variables at a given location. In other words, the direction of temporal trends (increasing or decreasing) at any given station for the three environmental variables was sometimes unrelated. For example, at eight stations exhibiting a significant increase in water transparency, chlorophyll increased when the opposite would be expected if algal increases were reducing water transparency (Fig. 4).

#### Kriging

Considerable spatial variability in average surface water temperature and chlorophyll concentrations existed in the lake during summer (Fig. 5). Warmest surface waters (13–14 °C) occurred in Chivyrkuy Bay, the Selenga Delta, the eastern side of the north and central basins, and the southernmost tip of the lake. Colder waters (11–12 °C) were found at the northern tip of the north basin and in parts of Maloe More. Highest chlorophyll concentrations (1.4–2.3 µg/L) occurred in the waters of the Selenga Delta, extending nearly across the lake to the opposite shore. Other smaller areas with high chlorophyll concentrations included small bays within Chivyrkuy Bay and the waters near the settlement of Talanka on the eastern shore of



**Fig. 4.** Sen's slope values depicting the rate of change for surface water temperature (°C), surface chlorophyll concentrations (µg/L), and Secchi depth (m) across the time series at each station with 10 or more years of data. Dots represent stations sampled; the color of the dot indicates whether Sen's slope was positive or negative (orange represents an increase, blue a decrease), and the size of the dot represents the relative magnitude of the rate of change at a particular station. Black squares identify stations where Sen's slope was significant ( $p < 0.05$ ) across the time series for that station.



**Fig. 5.** Average surface water temperature (°C) and surface chlorophyll (µg/L) concentrations throughout the lake during August–September as revealed by kriging. Darker shades represent higher temperatures or chlorophyll concentrations, while lighter shades represent lower temperatures and chlorophyll concentrations. The chlorophyll kriging model included stations sampled at least three (bay stations) or four times (basin stations), whereas the temperature model included only stations sampled at least six (south basin and Selenga delta stations) or nine times (middle and north basin stations). The time series used for kriging was 1977–2003 for water temperature and 1977–2004 for chlorophyll. Secchi depth values were not kriged because these data showed no spatial patterning.

the central basin opposite Olkon Island. Lowest chlorophyll concentrations (0.6–0.9 µg/L) occurred throughout much of the north basin.

#### Zooplankton abundance

Abundance of the two cosmopolitan taxa, *C. kolensis* and pelagic cladocerans, increased significantly throughout the entire lake and across the time series, whereas densities of the endemic *E. baikalensis* did not change (Fig. 6). *C. kolensis* abundance increased 12-fold across the time series and at a rate that was approximately 2 times faster than that for pelagic cladocerans. Also, *C. kolensis* abundance increased significantly across time within each of the lake's 3 basins (Table 2). Although pelagic cladoceran abundance trended upward in each basin with time, their increase was significant only in the north basin, but not in the other two basins (Table 2). *E. baikalensis* abundance did not change within any of the three basins across the time series (Table 2).

#### Sen's slopes

More complex temporal–spatial patterns for the zooplankton were evident when examining the Sen's slope values calculated for each individual station. *E. baikalensis* and pelagic cladoceran abundances increased at most stations in the north basin across the time series, while *C. kolensis* abundance increased at 92% of the 52 total sampling stations throughout the entire lake (Fig. 7). The increasing trend in *C. kolensis* abundance was significant at 23% of the total sampling stations, with these stations distributed approximately equally between offshore and nearshore locations and among basins. This significant positive trend in *C. kolensis* abundance occurred at 6 times more sampling stations than it did for pelagic cladocerans. Also noteworthy was the decreasing trend in *E. baikalensis* abundance at most stations (78%) throughout the south and central basins, however only two of these stations exhibited a significant decline. In contrast, the abundance trend for pelagic cladocerans across stations in these same basins was more variable. For example, pelagic cladoceran abundance increased at 36% of the stations, remained stationary (28% of stations), or decreased (36% of stations) in these two basins across the time series.

#### Hotspot analysis

The northern half of the north basin contained hotspots, or significant clusters of stations, where *E. baikalensis* and pelagic cladocerans increased in abundance over time (Fig. 8). Likewise the central basin and south basin contained cold spots where significant clustering of stations with decreasing abundances of *E. baikalensis* and pelagic cladocerans, respectively, occurred. No hotspot analysis was performed for *C. kolensis* because this crustacean increased at nearly all stations throughout the lake.

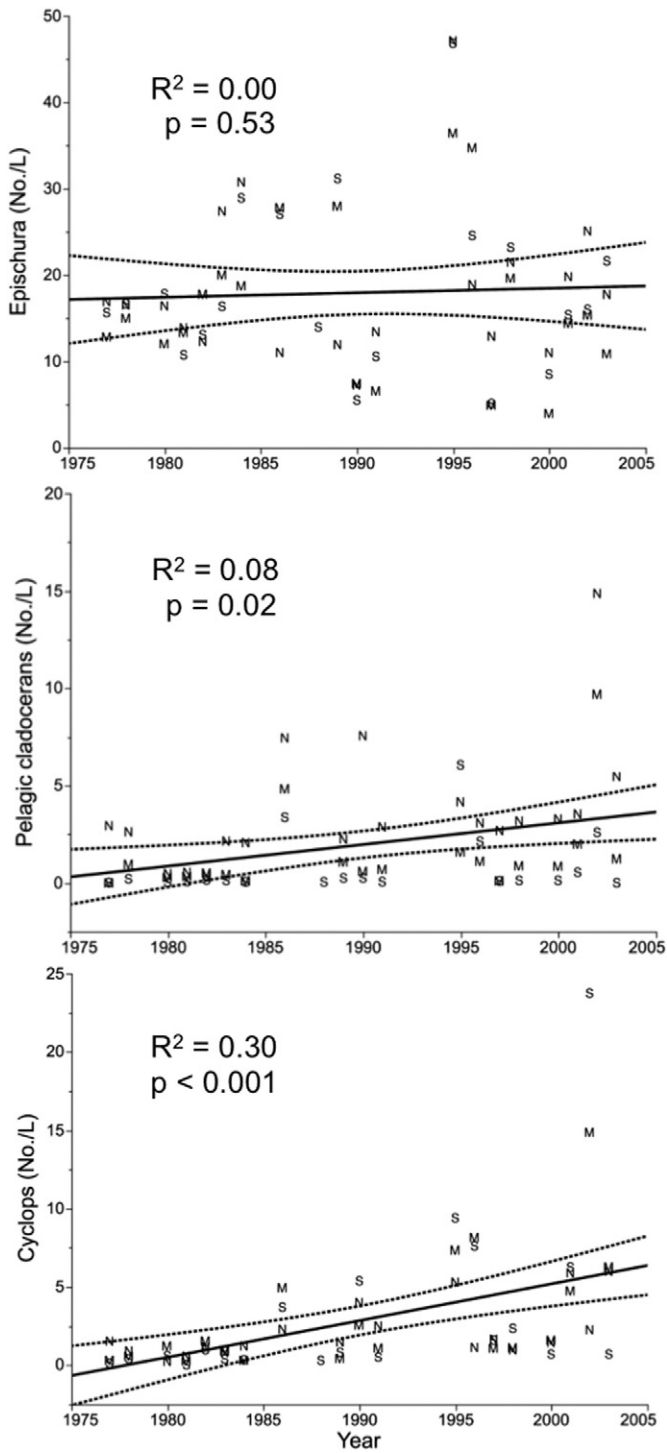
#### Kriging

The spatial distribution of average abundances of the three zooplankton groups across the time series revealed contrasting patterns (Fig. 9). Highest abundance for each of the two warm-loving cosmopolitan taxa (pelagic cladocerans, 10.0–16.9 number/L; *C. kolensis*, 9.0–11.8 number/L) occurred in Chivyrkuy Bay, the warmest part of the lake; whereas the cold-water stenotherm, *E. baikalensis*, was present at its lowest densities (9.95–12.0 number/L) here. Somewhat surprisingly, the highest densities of *E. baikalensis* (22.0–25.9 number/L) occurred in a fairly large area in the north basin where pelagic cladoceran densities were also high (5.0–10.0 number/L). In contrast, *C. kolensis* abundance was lowest (1.4–2.0 number/L) in this area. Both *C. kolensis* and *E. baikalensis*, however, coexisted at relatively high abundances at the southernmost tip of the south basin.

#### Multiple regression

Including year and basin as random effects helped to produce models with relatively good explanatory power, with conditional  $R^2$  values ranging from 0.314 to 0.563; but the fixed effects of temperature and chlorophyll had low explanatory power for zooplankton abundance patterns overall (Table 3). The best model for *E. baikalensis* included a significant interaction between temperature and chlorophyll, characterized by a negative relationship with temperature under higher chlorophyll conditions (unpublished), but the explanatory power of this model was weak (marginal  $R^2 = 0.0379$ ). The best models for cladocerans included a positive relationship with temperature, but they also had low explanatory power (marginal  $R^2 = 0.0284$ ). The top





**Fig. 6.** Lake-wide temporal trends in abundance (number/L;  $\pm 95\%$  CI) of *Epischura baikalensis*, pelagic cladocerans, and *Cyclops kolensis* in the 0–50 m water layer during August–September across the 26-year time series (1977–2003). Abundances are sums of all post-egg life stages per taxon (e.g., nauplii, copepodites and adults for copepods). See Fig. 3 caption for explanation to letters indicating annual mean abundance values per taxon for all stations sampled in a given basin. Three basin means are plotted per year for each taxon. Shallow stations (<50 m) or stations located in the bays or near the Selenga Delta were not included in these analyses. Statistical tests were performed on log transformed data to improve normality. Regression equations: *Epischura* abundance =  $0.033 \cdot \text{year} - 47.6$ ; pelagic cladoceran abundance =  $0.141 \cdot \text{year} - 278.9$ ; *Cyclops* abundance =  $0.263 \cdot \text{year} - 520.0$ .

model for *Cyclops* was a better fit (marginal  $R^2 = 0.1256$ ) with *Cyclops* abundance positively associated with both temperature and chlorophyll.

**Table 2**

Results of lake-wide and basin-wide univariate regressions of abundance (number/L) of each zooplankton group (*Epischura baikalensis*, pelagic cladocerans, and *Cyclops kolensis*) versus year across the time series (1977–2003). Lake-wide regressions were based on annual basin means for each zooplankton group; basin-wide regressions were performed on the station values. Stations within bays (Chivyrkuy Bay, Barguzin Bay), Maloe More Strait, and the two stations closest to the Selenga Delta were not included in these regressions. All zooplankton abundance values were log transformed to improve normality. *m* = regression slope. Bolded values are significant at the 0.05 level.

Model	df	<i>m</i>	<i>F</i>	<i>p</i>	$R^2$
<i>Epischura baikalensis</i>					
Lake-wide	1, 56	0.005	0.39	0.53	0.00
North basin	1, 17	0.001	0.01	0.92	0.00
Central basin	1, 17	0.013	0.74	0.40	0.00
South basin	1, 18	0.002	0.03	0.86	0.00
Pelagic cladocerans					
Lake-wide	1, 56	0.022	5.61	<b>0.02</b>	0.08
North basin	1, 17	0.028	4.26	<b>0.05</b>	0.15
Central basin	1, 17	0.021	2.57	0.13	0.08
South basin	1, 18	0.015	1.48	0.24	0.02
<i>Cyclops kolensis</i>					
Lake-wide	1, 56	0.042	25.06	<b>&lt;0.001</b>	0.30
North basin	1, 17	0.029	10.10	<b>&lt;0.01</b>	0.34
Central basin	1, 17	0.046	9.26	<b>&lt;0.01</b>	0.31
South basin	1, 18	0.050	7.53	<b>0.01</b>	0.26

## Discussion

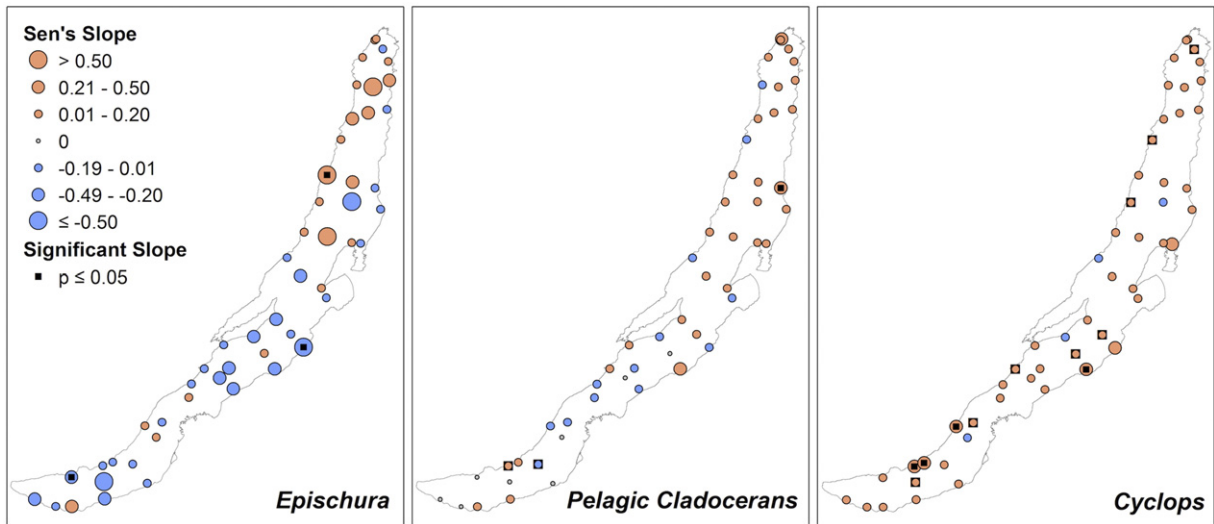
Much has been learned from the inter-annual sampling of plankton and physical parameters about the trophic status of different parts of Lake Baikal (Kozhov, 1963; Kozhova and Izmet's'eva, 1998; Popovskaya, 2000), the horizontal, vertical and seasonal distribution of its plankton (e.g., Fietz et al., 2005; Kozhova and Izmet's'eva, 1998; Timoshkin, 1995), and the response of the lake's south basin to climate warming (Hampton et al., 2008, 2014; Moore et al., 2009; Shimaraev et al., 2002; Todd and Mackay, 2003). Here we discuss our findings from the first multi-decadal analysis that integrates responses of physical and biological variables across the entire lake. Our analyses show that surface water temperature and zooplankton community structure in summer have changed in ways that are consistent with epilimnetic warming. We found no evidence in these data that lake-wide pelagic eutrophication has occurred.

### Lake warming

#### Physical response

The 2.0 °C average increase in surface water temperature in summer across the entire lake during the 26 year time series (Fig. 3) is a remarkable increase for the world's largest, deepest lake where annual surface temperatures average only 5 °C (Kozhova and Izmet's'eva, 1998). This increase is similar to the 2.4 °C warming of surface waters reported in the southern basin at a nearshore station during June–August over the last 60 years (Hampton et al., 2008). The detection of warming surface waters in late summer is perhaps all the more surprising given the large variability in surface temperatures at this time of year resulting from complex downwellings and upwellings that occur throughout Lake Baikal (Troitskaya et al., 2015).

The physical response of deep lakes to climate warming extends beyond simple warming of surface waters to include increased strength and length of summer stratification which can reduce the transport of nutrient-rich deep waters to the surface mixed layer (Verburg et al., 2003). Neither of these stratification changes, however, could be assessed here, because too few depths were sampled per station and year precluded quantifying the duration of summer stratification. It should be noted, however, that high-resolution depth sampling of temperature and plankton at a single station in the south basin in



**Fig. 7.** Sen's slope values depicting the rate of change in abundance of *E. baikalensis*, *C. kolensis*, and pelagic cladocerans at each station with 10 or more years of data. Sampling was conducted during August–September across the time series (1977–2003). See Fig. 4 caption for interpretation of Sen's slope symbols. Shallow stations (surface to substrate <50 m) or stations located in the bays or near the Selenga Delta were not included in analyses.

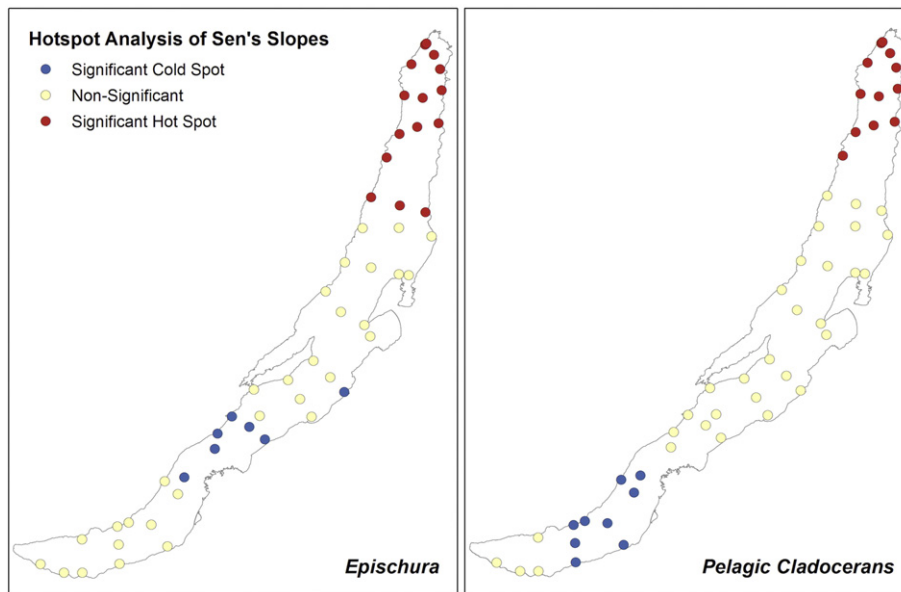
summer revealed a strengthening thermal gradient in the top 50 m of the lake over the last 45 years (Hampton et al., 2014). The reduced mixing in the upper waters may explain why diatoms, heavy cells dependent upon mixing to keep them in surface waters, have shifted steadily to deeper depths over this time period (Hampton et al., 2014).

Finally, climate warming can lead to thawing of permafrost and vegetation changes, dramatically increasing inputs of DOC to rivers and lakes in northern boreal watersheds (Frey and Smith, 2005; Larsen et al., 2011). This, in turn, can cause a decline in lake productivity if light rather than nutrients becomes limiting (Karlsson et al., 2009). Given the widespread increase in water transparency across Lake Baikal during the 26-year time series (Figs. 3 and 4), this consequence of increasing inputs of DOC from the watershed seems unlikely. However, our data suggest that DOC driven reductions in light penetration may be happening at two stations closest to the Selenga Delta where water

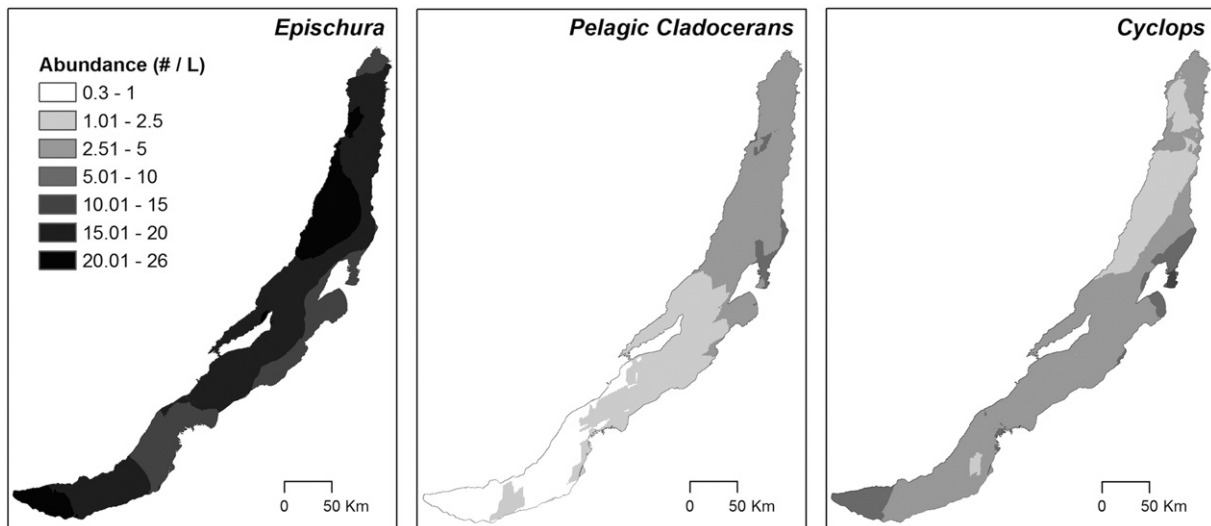
transparency decreased while algal biomass declined significantly across the time series (Fig. 4). Given that the Selenga River delivers more surface inflow from the watershed than any other river to the lake (i.e., 50% of the lake's total; Kozhov, 1963), and that permafrost melting is occurring within parts of this river's watershed (Bohannon, 2008), a climatically-induced increase in DOC input might be expected first near the delta of this river.

#### Biological responses

Among the zooplankton, the two cosmopolitan groups that are thought to perform best in warmer water – *C. kolensis* and cladocerans – were associated positively with lake temperatures (Table 3) and increased significantly in abundance across time throughout the lake (Fig. 6). Our results regarding the spatial distribution of these taxa (Fig. 9) are in agreement with previous studies (Melnik et al.,



**Fig. 8.** Hotspot analysis of Sen's slopes for *E. baikalensis* and pelagic cladocerans. Dots represent stations with the color of the dot indicating the Z score which tests for significant spatial clustering of high or low values. Red dots represent a significant ( $p < 0.05$ ) cluster of high values at a station and nearby stations, while a blue dot indicates a significant cluster of low values at the station and nearby stations. White dots represent no significant spatial clustering of values. No hotspot results are presented for *C. kolensis* because it increased across the entire lake, meaning the whole lake was identified as a hotspot for this species.



**Fig. 9.** Average abundances (number/L) of *E. baikalensis*, *C. kolensis*, and pelagic cladocerans throughout the lake during August–September across the entire time series (1977–2003) as revealed by kriging. Darker shades represent higher abundances, while lighter shades represent lower abundances. The kriged models for the zooplankton taxa included stations sampled at least 10 times in the main body of the lake or 4 times in the bays and deltas. Abundances are sums of all post-egg life stages per taxon (e.g., nauplii, copepodites and adults for copepods) in the 0–50 m water layer. At shallow stations (<50 m), sampled depth layers varied with maximum depth at the sampling station.

1998, 2006) and show that their abundances are highest in the warmest parts of the lake (e.g., Chivyrkuy Bay). Surprisingly, abundances of *E. baikalensis*, a cold loving stenotherm, did not decrease significantly through time as waters warmed and were not negatively associated with temperature. This species may be protected from

**Table 3**

Results from mixed effects multiple regression models (nlme package in R; Pinheiro et al 2014), with temperature and chlorophyll as fixed effects and sampling year and basin as random effects. Conditional  $R^2$  is an estimate of model fit that includes both the fixed and random effects, and marginal  $R^2$  describes the proportion of variance explained by the fixed effects (Nakagawa and Schielzeth, 2013). All models included the random effects. The full model (Temperature  $\times$  Chl) includes an interaction between temperature and chlorophyll as well as the main effects Temperature and Chlorophyll. We dropped the interaction in the Temperature + Chlorophyll, and then considered Temperature and Chlorophyll alone. The null model includes only the random effects. The five models for each of the three taxa are ranked by AIC scores, where the lowest AIC indicates the best fit (bold), and those models with AIC score differences of less than 2 are not considered significantly different. Estimated coefficients are shown for each model, with bold indicating coefficients that are significant with the model ( $p < 0.05$ ). The model uses Type 2 sums of squares; thus main effects should not be considered when the interaction term is significant and these are not shown. We excluded observations for which one or more of the predictor values was missing (Chlorophyll = 344 missing values, Temperature = 342 missing values) such that a total of 412 observations were included in the models.

	Model fit			Coefficient estimates		
	AIC	Marginal $R^2$	Conditional $R^2$	Temp $\times$ Chl	Temp	Chl
<i>Epischura</i>						
Temp $\times$ Chl	<b>840.45</b>	<b>0.037</b>	<b>0.314</b>	<b>−2.465</b>		
Chl	851.57					−0.238
Null	851.59					
Temp	852.60				0.198	
Temp + Chl	852.69				0.187	−0.231
<i>Cyclops</i>						
Temp $\times$ Chl	<b>873.14</b>	<b>0.125</b>	<b>0.517</b>	<b>2.035</b>		
Temp + Chl	880.57				<b>1.440</b>	<b>0.405</b>
Temp	884.18				<b>1.415</b>	
Chl	927.54					0.333
Null	929.13					
<i>Pelagic cladocerans</i>						
Temp	<b>890.74</b>	<b>0.028</b>	<b>0.563</b>		<b>0.859</b>	
Temp + Chl	<b>892.42</b>	<b>0.029</b>	<b>0.563</b>		<b>0.854</b>	−0.095
Temp $\times$ Chl	894.42			−0.040	0.879	0.008
Null	906.74					
Chl	908.16					−0.132

warming surface waters by diel vertical migration below the summer thermocline (10 to 20 m; Yoshioka et al. 2002) where it inhabits depths as deep as 250 to 500 m (Kozhova and Izmet'seva 1998). In contrast, the warm-loving cosmopolitans are largely limited to the upper surface waters (0 to 25–30 m) during summer stratification (Kozhova & Izmet'seva 1998; Hampton et al. 2014). Although it could be argued that an increase in fishing pressure across time could indirectly drive an increase in *Daphnia* spp. and *C. kolensis* by reducing fish predation on them, at least two lines of evidence argue against this. The abundance of omul (*Coregonus autumnalis*), a planktivorous fish that is the main target of commercial and private fishers in Lake Baikal, does not seem to have changed during the period of our study; however, uncertainty estimates are large for the survey methods used (Melnik et al. 2009). Second, planktivorous fish are unlikely to consume many *Cyclops* due to its effective escape response (Drenner et al., 1978).

The large, rapid, increase of *C. kolensis* throughout all three basins of the lake (Table 2, Fig. 7) was particularly striking, and we suggest that warmer water temperatures, either directly or indirectly, were responsible. Based on the results of laboratory growth and reproduction experiments performed across a range of temps (5, 10, 15, and 20 °C) typical for Lake Baikal, *C. kolensis* is expected to respond first to warming surface waters, because it occupies an intermediate thermal niche (optimal survival and reproduction at 10–15 °C) between the cold-loving *E. baikalensis* (5–10 °C) and the warm-water loving pelagic cladocerans (15–20 °C) (Ted Ozersky, University of Minnesota–Duluth, 2014, personal communication) that flourish only in summer when the lake is warmest ( $\geq 15$  °C). These laboratory results are also consistent with Kozhova's (1963) suggestion based on field observations that the optimum temperature for *C. kolensis* was 12–14 °C. He also noted that this species spreads and increases in abundance through all the open waters when water temperatures are greater than usual. Interestingly, warmer water temperatures may also favor *C. kolensis* indirectly by increasing food for *C. kolensis* nauplii, ameliorating a juvenile bottleneck reported for this species in a German lake (Santer and Lampert, 1995). *C. kolensis* nauplii require high concentrations of flagellates for survival and development, and these small flagellated cells become abundant in Baikal only when waters warm in summer and thermal stratification intensifies (Fietz et al., 2005).

The increasing trend in *C. kolensis* and pelagic cladoceran abundances could have food web consequences for Lake Baikal, because *C. kolensis*

adults, when abundant in warm years, consume *E. baikalensis* nauplii (Mazepova, 1978, 1998), and cladoceran grazers are likely competitors with the largely herbivorous *Epischura*. This suggests that *C. kolensis* and the pelagic cladocerans could potentially suppress densities of the endemic *E. baikalensis*, a purported keystone species; yet, average lake-wide densities of *E. baikalensis* did not change across the time series (Fig. 6), with its densities declining significantly at only 2 of the 52 lake-wide stations (Fig. 7). We suggest that the deep cold waters below the thermocline may offer both a biotic refuge as well as a thermal refuge for all life stages of *E. baikalensis* where it can escape predation and reduce competition with the warm-loving cosmopolitan zooplankton.

While *C. kolensis* abundance increased significantly in all lake basins and over the 26-year time series, pelagic cladoceran and *E. baikalensis* densities increased mostly in the northern end of the lake and at a significant cluster of 12 to 15 stations (Fig. 8). Intriguingly, pelagic cladocerans and *E. baikalensis* are both more herbivorous than *C. kolensis*. Their joint increase in the northern parts of the lake may be related indirectly to interannual changes in upwelling dynamics. For example, in the northern basin, cold, nutrient-rich water begins to upwell earlier in summer (late August) than in the other two basins and the upwelling rapidly intensifies through September and October, possibly stimulating phytoplankton growth, relative to the rest of the lake (Troitskaya et al., 2015). Also intriguing is the inverse abundance pattern of *C. kolensis* in the north basin relative to that of *E. baikalensis* and the pelagic cladocerans that are maximally abundant here (Fig. 8). Because *C. kolensis* nauplii, that feed only on flagellates, have a threshold food concentration that is more than 4 times higher than that for *Daphnia* (Santer and Lampert, 1995), *C. kolensis* may be competitively excluded by the filter feeding *Daphnia* and *E. baikalensis* in the north basin. The time lags that would be associated with such indirect effects of temperature and chlorophyll changes may help explain why relatively simple correlation models do not have strong explanatory power with this data set (Table 3).

#### Eutrophication

Although our analyses lack nutrient data, the trends we report here for chlorophyll and water transparency provide no evidence of pelagic eutrophication of Lake Baikal between 1977 and 2004. Chlorophyll concentrations increased 46% lake-wide; but the increase was modest, from 0.82 to 1.20  $\mu\text{g/L}$  (Fig. 3), and the increasing trend was significant only in the south basin (Table 1). Furthermore, water transparency increased 1.4 m lake-wide with significant increases in the north and central basins but not the south basin. Taken together this suggests that productivity may have increased in the south basin while decreasing in the north and central basins across the time series. Although increased nutrient input from the Selenga River into the south basin may have contributed to increasing algal biomass there, a detailed study of Lake Baikal's phytoplankton community conducted in all 3 basins in July during the years 2001–2003 concluded that elevated algal biomass in parts of the lake were not due to nutrient enrichment but instead were associated with areas of warmer water and enhanced stratification (Fietz et al., 2005). Interestingly, paleoanalysis of sedimentary diatoms also provided no evidence of eutrophication in Baikal's offshore waters (Mackay et al., 1998). Although corrections for differential diatom dissolution were not known to be necessary at the time of Mackay et al.'s (1998) research, a recent paleoanalysis incorporating the corrections suggests the same outcome (Sarah Roberts, University of Nottingham, 2015, personal communication).

The only caveat to our conclusion of no pelagic eutrophication is a significant positive trend in algal biomass at a single station in the north basin (Fig. 4). This station, located near the mouth of the Tyra River where sewage from the town of Severobaikalsk is discharged into the lake, is also where severe benthic eutrophication resulting from a malfunctioning sewage treatment plant was discovered in 2013 (Timoshkin et al., 2014). Our data raise the possibility that

nutrients from sewage may have fertilized phytoplankton growth at this site many years prior to 2013, but this site is also influenced by inputs from the Upper Angara and Kichera Rivers to the northeast (Kozhov, 1963). Interestingly, the first increase in chlorophyll *a* in this region was recorded in 1979 (Kozhova et al., 1984).

It is possible that the description of spatial and temporal patterns for chlorophyll (and other variables) will differ with the scale of analysis (entire lake, separate basins, or individual stations). We argue that basin responses are most useful for interpretation of temporal trends because of the relative isolation of the different basins, their different climates and watersheds, and their very different trends in development and human usage. At the smallest scale, substantial uncertainty is associated with trends at individual stations because: 1) stations were not randomly located throughout the lake; 2) they were not all sampled on the same date (or phenological date) in a given year; and 3) horizontal and vertical mixing can cause contrasting trends in multiple parameters (e.g., temperature, chlorophyll, Secchi depth and zooplankton community composition) at stations separated by as little as 20 km. This high degree of local uncertainty helps explain why so few temporal trends at any given station were significant for a particular variable. Station responses are presented here only to identify where within a basin a significant trend may have occurred.

Even though the spatial distribution of sampling stations in the lake was not ideal, the spatial pattern we report for chlorophyll abundance across the lake (Fig. 5) agrees well with previous reports of higher algal biomass in the south basin than in the north basin (Fietz et al., 2005; Heim et al., 2004; Popovskaya, 2000). For example, Popovskaya (2000) described a 3.5 fold higher algal biomass in the south basin relative to the north basin in June, and she attributed this to nutrients supplied by the Selenga River and a longer summer growing season in the south than in the north. Our results, from August and September, show on average, a slightly higher chlorophyll biomass in the south than in the north basin; and our average chlorophyll concentrations (south,  $1.02 \pm 0.09$ ; north,  $0.90 \pm 0.07$   $\mu\text{g/L}$ , mean  $\pm$  95% CI, respectively) compare well with those (south,  $1.27 \pm 0.23$ ; north,  $0.86 \pm 0.13$   $\mu\text{g/L}$ ) reported by Fietz et al. (2005).

Finally, early signals of eutrophication in Lake Baikal may be expected to appear first in the littoral rather than the pelagic zone of Lake Baikal, as seems to be happening around the towns of Severobaikalsk in the northern part of the lake (Timoshkin et al., 2014) and Listvianka and Bol'shie Koty in the south (Kravtsova et al., 2012; Timoshkin et al., 2015), all places where benthic eutrophication was reported recently. In contrast to Baikal's coastal areas, the enormous pelagic zone of Baikal, equivalent in volume to that of all the Laurentian Great Lakes combined, is thought to be resistant to widespread cultural eutrophication, because a very large amount of nutrients would be necessary to eutrophy such a large volume of water. However, the thin summer epilimnion (upper 10–20 m water layer) constitutes a volume that is <3% of the lake as a whole, making eutrophication of the upper mixed layer possible. Importantly, the water column in summer is unstable, experiencing sporadic, wind-driven upwelling and downwelling events (Troitskaya et al., 2015). These may protect the open waters from cultural eutrophication in summer by episodically mixing and diluting nutrients to a maximum depth of 250 m (Moore et al., 2009). If climate warming reduces the intensity or frequency of this sporadic mixing by diminishing wind strength or continued warming of surface waters (enhancing thermal stratification), the pelagic zone may become more vulnerable to nutrient additions.

#### Lake-wide versus single station monitoring

The results of this study, and their comparison with high temporal resolution monitoring of a single station in the south basin of Lake Baikal (Hampton et al., 2008), underscore the difficult trade-off between spatial and temporal resolutions in the design of monitoring programs. The immense size and physically dynamic nature of Lake Baikal



(Troitskaya et al., 2015) lead to large variations in physical, chemical and biological parameters in time and space, raising questions about the appropriate scale over which long-term trends should be monitored and interpreted. For example, results of high temporal resolution (every 10–14 days) sampling of a single station in the south-western portion of the lake (Hampton et al., 2008) agree well with the trends we show here for chlorophyll and Secchi transparency for the entire south basin, even though sampling for the present study was conducted only once per year. However, trends in the central and northern basins differ from those in the south basin, emphasizing the necessity of lake-wide monitoring.

Ideally, ecological monitoring programs for large lakes should combine high spatial and temporal resolution of data collection (Hampton, 2013). While practical constraints limit the resolution of ecological monitoring programs in all systems, monitoring in large ancient lakes is often limited in its extent. We urge increased investment in monitoring ancient lake ecosystems and greater focus on monitoring and protecting their littoral zones (Cohen, 1992; Timoshkin et al., 2005) where much of the biodiversity in these systems is concentrated (Vadeboncoeur et al., 2011). The adoption of techniques such as remote sensing of temperature and chlorophyll in surface waters and the deployment of AUVs with sensors and cameras for underwater surveys in coastal and pelagic waters would help increase the resolution of sampling and therefore provide advanced warning of change that may threaten the numerous endemic inhabitants of these venerable ecosystems.

## Acknowledgments

This paper is dedicated to Nadezhda P. Blokhina, Olga H. Pen'kova, Galina I. Pomazkova (zooplankton specialists) and other students, staff, faculty, ship captains, and crew members who collected or processed the limnological samples from the circumBaikal sampling program at Irkutsk State University's General Hydrobiology Laboratory of the Institute of Biology now supported by the Russian Ministry of Education and Science research project GR 01201461929. These Lake Baikal data are part of a data set (No. 2005620028 and No. 2014621482) registered with the government of the Russian Federation. Data analyses were supported by the Dimensions of Biodiversity program of the US National Science Foundation (DEB-1136637; DEB-1136657) in addition to the awards from the Brachman Hoffman Fund, Fiske Fund, and the Committee on Faculty Awards at Wellesley College. E. Silow was partially supported by the Russian Science Foundation Project No. 14-14-00400. A Howard Hughes grant and a Strategic Investment in Research and Teaching grant to Wellesley College supported student assistants from Irkutsk State University: Denis Axenov-Gribanov, Margarita Tsitsenko, Kirill Shchapov, and Nadia Shakhtanova. Student assistants from Wellesley College included Ashley Ortiz, Julia Shalnova, Genia Nizkorodov, Iris Lin, and Graeme Durovich. We are grateful to Jonathan Lefcheck for sharing the code to calculate the goodness of fit for mixed models and Steve Katz for many conversations about mixed models. We thank Oleg Timoshkin, Ted Ozersky, Nick Rodenhouse, and two anonymous reviewers for comments that improved the manuscript.

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