1   Title
2   Benthic community metabolism in deep and shallow arctic lakes during 13 years of whole-lake
3   fertilization
4
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9
10   Running Head: Nutrient effects on Arctic lake benthos

22   Abstract

23   Benthic primary production and oxygen consumption are important components of lake

24   biogeochemical cycling. We performed whole-lake nutrient manipulations in arctic

25   Alaska to assess the controls of lake morphometry, nutrients, and light on benthic

26   community metabolism. One deep, stratified lake (Lake E5) and one shallow, well-

27   mixed lake (Lake E6) in the Alaskan Arctic were fertilized with low levels of nitrogen

28   ($56 \text{ mg N m}^{-3} \text{ y}^{-1}$) and phosphorus ($8 \text{ mg P m}^{-3} \text{ y}^{-1}$) from 2001-2013. Benthic primary

29   production was not stimulated by fertilization in either lake. In the deep lake, decreased

30   water clarity is consistent with an increase in phytoplankton biomass during fertilization.

31   Benthic GPP decreased by 7 - 47 $\text{mg C m}^{-2} \text{ d}^{-1}$ (not statistically significant) and benthic

32   respiration increased from 87 ± 20 to 167 ± 9 (SE) $\text{mg C m}^{-2} \text{ d}^{-1}$. The areal hypolimnetic

33   oxygen deficit increased by 15 $\text{mg O}_2 \text{ m}^{-2} \text{ d}^{-1}$ each year during the 13 years of monitoring,

34   apparently driven by lower (more negative) benthic NEP. In the shallow lake,

35   phytoplankton concentration did not change with fertilization. As a result, the light

36   environment did not change and benthic GPP did not decrease. Overall the data suggest

37   that (1) benthic algae are not nutrient limited in either the deep or shallow lake, (2) lake

38   morphometry modulated the overall nutrient impact on benthic metabolism by controlling

39   the response of phytoplankton, and by extension, light and organic carbon supply to the

40   benthos, (3) year-to-year variability in light attenuation explains considerable variability

41   in benthic GPP between lakes and years, (4) correlations between both dissolved organic

42   carbon concentrations and light attenuation coefficients (k_d) between lakes suggests a

43   regional control on light attenuation, and (5) the dissolved oxygen concentrations in the

44   deep experimental lake are highly sensitive to nutrient enrichment.

45   Introduction

46   Quantifying the ecosystem level response to variations in nutrient loading has

47   been the focus of many water quality and lake ecosystem studies (Schindler 1978,

48   Howarth 1988, Morris and Lewis 1988). However, recent work on the importance of

49   primary production by benthic algae, including epipelon, epilithon, and epiphyton,

50   suggests that assessments of nutrient limitation based only on pelagic responses may not

51   accurately reflect whole-lake nutrient limitation (Vadeboncoeur et al. 2001 and 2003,

52   Karlsson et al. 2009). The reason is that there is a compensatory trade-off between

53   benthic and pelagic GPP across trophic gradients because the concentration of

54   phytoplankton affects the amount of light available to benthic habitats (Vadeboncoeur

55   and Steinman 2002). In most cases epipelic algae are light limited, rather than nutrient

56   limited, and, much of the epipelon nutrient demand is met by within-sediment

57   remineralization (Jäger and Diehl 2014). As such, nutrient addition to the water column

58   tends to benefit phytoplankton more than benthic algae. The resulting effect of decreased

59   water clarity can suppress benthic primary production. Nutrient addition impacts on

60   whole-lake primary production are therefore proportionately smaller if both benthic and

61   pelagic processes are considered than if pelagic processes are considered alone.

62   In lakes where benthic substrates are well-lit, either because of low background

63   light attenuation or because they are shallow, nutrient addition can potentially stimulate

64   benthic production while simultaneously increasing phytoplankton production and

65   biomass (Hansson 1992, Stanley 1976, Jäger and Diehl 2014). Ultraoligotrophic lakes at

66   high latitudes commonly fit this description. In these cases, model simulations show that

67   the stimulation of benthic algae and benthic nutrient uptake can act to diminish the

68   anticipated increase in phytoplankton growth (Genkai-Kato et al. 2012). Benthic algae

69   are effective at trapping nutrients when water column P concentration is less than

70   approximately 10 mg P m^{-3}, depending on background light attenuation. Below this level,

71   increasing nutrients can either increase (Jäger and Diehl 2014) or have little effect

72   (Genkai-Kato et al. 2012) on total lake production. At phosphorus concentrations on the

73   order of 10-100 mg P m^{-3} (Jäger and Diehl 2014) or P loading rates of 2-5 mg P m^{-2} d^{-1}

74   (Genkai-Kato et al. 2012), phytoplankton shading overwhelms benthic productivity,

75   benthic production decreases, and a positive feedback of sediment nutrient release further

76   fuels planktonic production (Jäger and Diehl 2014). Above these levels, models indicate

77   that benthic algae decline precipitously.

78   At the whole-lake scale, lake morphometry is an important control on the relative

79   contribution of benthic production to total lake production (Whalen et al. 2008,

80   Vadeboncoeur et al. 2008). The reason again relates to the light environment of the lake

81   – benthic GPP may be relatively more important in shallow lakes because the ratio of

82   sediments in the photic zone to the volume of the epilimnion is high. In deep lakes,

83   especially those with steep slopes (Vadeboncoeur et al. 2008), phytoplankton may

84   dominate the annual GPP on a whole-lake scale.

85   Morphometry can also influence the fate of nutrients entering a lake and the

86   dynamic biological response to changing nutrient inputs (Fee 1979, Vadeboncoeur et al.

87   2008). Fee proposed that in deep and stratified lakes, phytoplankton are more likely to

88   settle through the thermocline where the nutrients they contain are more effectively

89   trapped in the hypolimnion. In such cases, additional nutrients may not benefit benthic

90   algae especially considering the shading effects of increased phytoplankton biomass in

91   surface waters. In shallow lakes with weak or no stratification, there is a balance

92   between greater recycling of nutrients to the photic zone through physical mixing (Fee

93   1979, Nolen et al. 1985) and greater uptake of nutrients by benthic algae (Jäger and Diehl

94   2014).

95   In most arctic lakes, pelagic primary production is low because the growing

96   season is short and nutrient concentrations are low. Benthic algae therefore tend to be

97   relatively important to whole lake production – they can fix up to 18 g C m^{-2} y^{-1} (Welch

98   and Kalff 1974) or contribute upwards of 98% of a lake's total annual production

99   (Vadeboncoeur 2003, see also review by Quesada et al. 2008). Because of the extremely

100 low nutrient levels in arctic lakes, there is potential for benthic algae to be nutrient

101 limited rather than light limited (Hansson 1992, Stanley 1976). We tested this hypothesis

102 by performing two whole-lake fertilization experiments in ultraoligotrophic arctic lakes.

103 The study lakes and their un-manipulated reference lakes are located near Toolik Lake in

104 the arctic tundra of northern Alaska. Because the nutrient impact may depend on lake

105 shape, as described above, the two lakes in this experiment were chosen to represent two

106 basic morphometries – one was shallow (z_{max} = 3.2 m) and polymictic while the other

107 was deeper (z_{max} = 12.7 m) and dimictic. We hypothesized that benthic GPP would only

108 be stimulated in the shallow lake where a greater proportion of lake floor lies above the

109 1% light level (100% of lake floor in the shallow lake vs. 35% of lake floor in the deep

110 lake), and that nutrients added to the deeper lake would be recycled within the water

111 column or lost to the hypolimnion during the summer growing season resulting in no

112 effect on benthic algae.

113   We assessed changes in the benthic communities during the fertilization time

114   course in both experimental and both reference lakes by examining chlorophyll content,

115   measured and modeled photosynthesis parameters, and respiration rates. We also

116   calculated benthic GPP and NEP by combining the photosynthesis parameters with

117   measured light availability, which is influenced by changes in water transparency and

118   ambient incoming insolation.

119   While most arctic lakes are not exposed to point-source nutrient pollution because

120   of their distance from population centers, it has been suggested that global climate change

121   will increase the delivery of nutrients from land to water (Hobbie et al. 1999). Increased

122   nutrient loading may result from enhanced precipitation and runoff events (MacIntyre et

123   al. 2009) or from thermally-driven erosion and weathering of permafrost soils (Bowden

124   et al. 2008, Rowland et al. 2010, Mesquita et al. 2010). Thermokarst failures exemplify

125   one type of thermal erosion and are characterized by mass transport of soil (turbidity),

126   vegetation, and dissolved constituents (nutrients) into surface waters.

127

128   Methods

129   *Study Sites*—The four study lakes lie within 25 km of the Toolik Lake Field Station on

130   the North Slope of Alaska (68°37' N,149°36' W, Fig. 1). Mean annual air temperature for

131   the region is -7 °C and mean July temperature is 12 °C (Cherry et al. 2014). The study

132   lakes are surrounded by permafrost soils with summer active layers less than 1 m thick.

133   The lakes are ultraoligotrophic (Table 1; surface TP 3.8 - 17 mg m^{-3}; surface chlorophyll

134   a 0.4 - 9.3 mg m^{-3}) and ice free from mid-June to late-September. Dissolved organic

135   carbon (DOC) concentrations range from 200 - 895 µmol L^{-1}. The lakes represent two

136   basic morphometries: Lake Fog 2 and E5 are classified as deep ($z_{max} > 12$ m, $z_{mean} > 5$ m)

137   and thermally stratify during summer. Lakes Fog 4 and E6 are shallow ($z_{max} < 5$ m, z_{mean}

138   < 2.5 m) and the water columns are frequently mixed. Two of the lakes underwent

139   artificial N and P additions from 2001 until 2013. Fog 2 served as a reference lake for

140   the deep, fertilized Lake E5. Fog 4 was intended to serve as a reference lake for the

141   shallow, fertilized Lake E6. From 2002 to 2005, however, a small thermokarst failure

142   occurred along its northern shoreline and a plume of sediment could be seen entering the

143   lake. While we did not quantify the nutrient or sediment loading during this event, it is

144   likely to have impacted the lake ecosystem rendering it unsuitable as a reference lake.

145   Fog 4, however, did serve as an additional model system in which to examine the impact

146   of nutrient and light disturbance on benthic production. The benthic substrate of the

147   lakes is dominated by unconsolidated silt-sized clastic sediments. Unlike benthic

148   communities of many polar freshwaters (Quesada et al. 2008), the benthic algae in our

149   study lakes were not mat-forming, but instead exhibited a gradual transition from algae-

150   rich to algae-poor moving down the sediment column. With the exception of Lake Fog 2,

151   the sediment matrices are visibly greenish. Rocks are present along the lake margins to

152   the depth of ice-scour (approximately 1.5 m) and sparse macrophytes were observed only

153   in Lake Fog 2.

154

155   *Fertilization regime*—Benthic monitoring of the lakes began in 1999 in the experimental

156   E lakes and in 2000 in the Fog lakes. Nutrient manipulations began in 2001. For the

157   nutrient manipulation, N and P were added at the Redfield Ratio by slowly dripping a

158   solution of ammonium nitrate and phosphoric acid into the lakes from a raft tethered near

159   the lakes' centers. The target fertilization rates of 56 mg N m^{-3} y^{-1} and 8 mg P m^{-3} y^{-1}

160   were approximately three times larger than the background loading rates of inorganic N

161   and P to nearby Toolik Lake (Whalen and Cornwall 1985). The fertilization increased

162   the annual loading by approximately four-fold. For Lake E5, the amount of added N and

163   P was scaled to the epilimnion volume only, whereas for Lake E6 the fertilization was

164   scaled for the entire volume. On an areal basis, this equates to 280 mg N m^{-2} y^{-1} and 40

165   mg P m^{-2} y^{-1} for the 5 m deep mixed layer in Lake E5, and 112 mg N m^{-2} y^{-1} and 16 mg P

166   m^{-2} y^{-1} for the 2 m average depth of Lake E6. In comparison to other whole-lake

167   fertilization experiments, the manipulation strength is quite moderate (Table 2; Bettez et

168   al. 2002, Bjork-Ramberg and Anell 1985, Bergmann and Welch 1990, Vadeboncoeur

169   2001, O'Brien et al. 2005). The level of enrichment in this experiment represents a low-

170   intensity press disturbance to the lakes.

171

172   *Meteorological and water column data*—Hourly incident photosynthetically active

173   radiation (PAR, 400-700 nm) was obtained from the Arctic-LTER meteorological station

174   (ARC LTER database). Mean summer values of incident PAR were calculated using

175   hourly data over the time period of June 15 to August 31. Measurements of water

176   column light attenuation were made every 10 days during the summer for the fertilized

177   lakes. The same measurements were made 1-3 times each summer in Fog 2 and Fog 4.

178   Light attenuation coefficients with depth (k_d) were calculated as the absolute value of the

179   slope of the natural logarithm of PAR, measured at 1 m intervals, plotted against depth.

180   A Hydrolab multisonde unit (DS4) was used to measure depth profiles of dissolved

9

181   oxygen (DO), temperature, pH, and conductivity at the same time that light

182   measurements were made.

183

184   *Benthic metabolism*—Because most of the benthic surface area in each lake is comprised

185   of soft sediments, we focused on characterizing the epipelic algal community rather than

186   the marginal epilithic communities. We measured the oxygen flux across the sediment-

187   water interface to estimate net ecosystem production (NEP), community respiration (R),

188   and gross primary production (GPP = NEP + R) during the ice-free season from 1999-

189   2005, 2007, and 2009-2013. No measurements were made in Lake Fog 4 from 2009-

190   2012. Two O_2 flux methods were used. From 1999-2003, O_2 flux was measured in-situ

191   using plexiglass chambers placed on the lake floor using SCUBA (see Gettel et al. 2013

192   for method details). From 2001-2013 we generated photosynthesis-irradiance (PI) curves

193   by measuring O_2 flux in sediment cores incubated in laboratory facilities at the Toolik

194   Field Station. We compared results from these two methods in years where both were

195   employed. Estimates of GPP from the laboratory PI incubations were on average 40 mg

196   C m^{-2} d^{-1} higher than from in-situ chamber measurements (p = 0.072). Respiration

197   averaged 87 mg C m^{-2} d^{-1} higher with the laboratory incubations method (p = 0.005). As

198   such, the two methods are reported independently for both GPP and respiration.

199   Between late-June and mid-July of each core-sampling year, oxygen flux

200   measurements were performed on 6-8 sediment cores. Sampling sites and depths were

201   dictated in part by the substrate distribution in the lake and in part by the desire to sample

202   sediments representative of the shallow littoral zone and the deep hypolimnetic zone. In

203   the shallow lakes (E6 and Fog 4), epipelon were confined to depths between 1 m

204   (shallower depths had rocks), and 3 m (maximum depth), and we sampled at

205   approximately 1.5 and 2.5 m depth. In the deep lakes (E5 and Fog 2), rocks extend to

206   about 3 meters depth and the lake basins are steep-sided. For these lakes, half the cores

207   were taken from the epilimnetic sediments (3-4 m) and half were from the hypolimnetic

208   sediments (5-7 m). The cores were 9.5 cm in diameter and 40 cm long. For each sample,

209   we collected approximately 25 cm of sediment, leaving about 15 cm of water-filled

210   headspace in each core. Cores were returned to the laboratory within 2 hours of sampling

211   and placed in water baths at in situ lake temperatures for 8-12 hours prior to the start of

212   incubation. The overlying water of each core was replaced with filtered lake water (0.45

213   μm) in order to minimize the influence of pelagic particulates on oxygen flux. Cores

214   were sealed bubble-free and a DO probe (membrane probes 2001-2009, optical probes

215   2010-2012) was inserted into a port in each core top. Core headspaces were gently mixed

216   by magnetic stirrers activated by an external rotating magnet. DO probes were

217   programmed to record DO every 5 minutes. Cores were first incubated in the dark and

218   then under multiple light intensities in order to generate photosynthesis-irradiance

219   relationships. Community respiration (R) in the dark, and net ecosystem production

220   (NEP) in the light, were calculated from the change in oxygen over time. Oxygen fluxes

221   were converted to carbon flux assuming photosynthetic and respiratory quotients of 1.0.

222   We assumed that R_{light} was equivalent to R_{dark}, although in some cases R_{light} exceeds R_{dark}

223   because of photorespiration (Bender 1987).

224   Typically, 4-5 light levels, ranging from $<$ 50 to $>$ 350 μmol quanta (μEinstein)

225   m^{-2} s^{-1} were used to model GPP against PAR using Michelis-Menten kinetics (Equation

226   1) for each core. We assumed GPP is a function of light-saturated GPP (P_{max}), the PAR

227   half-saturation constant ($k_{1/2}$), and the incoming PAR (I). Optimized values of P_{max} and

228    $k_{1/2}$ and associated error for each sampling effort were simultaneously solved using

229   Graphpad PRISM software.

230   Eq. 1 $GPP = \frac{(P_{max} x I)}{(k_{1/2} + I)}$

231   Average rates of GPP at the depth of sampling were estimated by combining

232   parameters for the above relationship with the hourly incident PAR from June 15 to

233   August 31, and lake-specific light attenuation coefficients linearly-interpolated between

234   sampling times. Hourly PAR measurements were modified to account for reflectance off

235   the water surface. Reflectance was calculated hourly using zenith angle of the sun

236   (http://www.nrel.gov/midc/solpos/solpos.html, Vahatalo et al. 2000) and averaged 35.5%

237   over the time period of interest. The resulting value agrees well with a suite of empirical

238   values measured for lakes around the Toolik Field Station (average 30%; ARC LTER

239   database). For the deep lakes, Fog 2 and E5, GPP was estimated at 3.5 m and 6 m depth.

240   For the shallow lakes, Fog 4 and E6, GPP was estimated at 2 m depth. Error was

241   estimated by Monte Carlo simulation with error attributed to the photosynthetic

242   parameters. The average and standard deviation (SD) of 500 simulations was used to

243   characterize the GPP of each year. In addition to simulating GPP at the sampling depths,

244   we calculated GPP on a whole lake basis by applying the P-I curves to light calculated at

245   1 meter depth intervals, summing the calculated GPP, and dividing by the total surface

246   area of each lake.

247

248   *Benthic Chlorophyll a*— Acetone-extractable chlorophyll a was measured from surface

249   sediments to help characterize the benthic algal community. While benthic chlorophyll a

250   is not a direct measure of algal biomass, it can serve as a useful proxy for benthic algal

251   photosynthetic capacity. From 1999-2003, a 2.7 cm diameter core was used to collect

252   sediment samples for chlorophyll analysis in association with the GPP chamber

253   measurements (Gettel et al. 2013). After 2003, benthic algae biomass was assessed in

254   sediments from the cores used for the incubations. In all cases, the surface 2 cm from

255   each core was homogenized, and five mL of wet sediment were subsampled and frozen.

256   We later added 35 mL of 100% acetone (which, with porewater, led to a 90% acetone

257   solution) and extracted in the dark overnight with occasional shaking. All samples were

258   kept frozen in the dark until analysis. Samples were analyzed spectrophotometrically,

259   using the acidification protocol and equations of Lorenzen (1967) to correct for

260   phaeopigments.

261

262   *Statistical analysis—*For each fertilized lake we compared pre- and post-fertilization

263   values of benthic chlorophyll, GPP, and water column light extinction. Because it was

264   not possible to transform all data to have normal distributions, the non-parametric Mann-

265   Whitney rank test was used for all comparisons. For the thermokarst-impacted lake, we

266   pooled years of active thermokarst slumping (2002-2005) and non-thermokarst years

267   (1999-2001 and 2006-2013) for comparison. Standard errors are reported for light

268   extinction coefficients and benthic and pelagic chlorophyll a. Standard deviations are

269   reported for benthic GPP and respiration.

270

271   Results

272   *Light environment*—Photosynthetically active radiation (PAR) incident at the water

273   surface averaged 354 μmol quanta m^{-2} s^{-1} from June 15 to August 31 when all years and

274   hours of the day were pooled. There was no temporal trend in incoming PAR during the

275   13 years, but there was large year-to-year variability with summer averages ranging from

276   306 μmol quanta m^{-2} s^{-1} in 2006 to 473 μmol quanta m^{-2} s^{-1} in 2007 (Fig. 2a).

277   Light attenuation was lowest in the deep reference lake, Fog 2 ($k_d = 0.33 \pm 0.02$

278   m^{-1}) and did not change over time (Fig. 2b). In the deep fertilized lake, E5, k_d increased

279   significantly from 0.71 ± 0.01 m^{-1} before fertilization to 0.96 ± 0.03 m^{-1} after fertilization

280   ($p < 0.0009$). Water column chlorophyll a increased from 1.7 ± 0.06 to 2.65 ± 0.06 μg L^{-}

281   ^{1} ($p = 0.0002$, ARC LTER database). In the shallow fertilized lake, E6, k_d did not

282   increase significantly (pre-fertilization: 1.12 ± 0.08; post-fertilization: 1.27 ± 0.04; $p =$

283   0.153). Water column chlorophyll a was also unchanged with fertilization (pre-

284   fertilization: 2.1 ± 0.06 μg L^{-1}; post-fertilization: 2.2 ± 1.1 μg L^{-1}; $p = 0.23$, ARC LTER

285   database). In the shallow, thermokarst-impacted lake Fog 4, non-thermokarst years had

286   significantly lower k_d values of 1.02 ± 0.05 m^{-1} compared to 1.38 ± 0.15 m^{-1} during

287   thermokarst years ($p = 0.04$). However, water column chlorophyll a concentrations were

288   not statistically higher during thermokarst years ($p = 0.074$).

289

290   *Deep reference Lake, Fog 2*— In the deep reference lake, Fog 2, benthic chlorophyll a in

291   the epilimnetic sampling sites ranged from 29 to 368 mg m^{-2} (average 141 mg m^{-2} to 2

292   cm depth; Fig. 3). Concentrations were similar at the deeper (6 m) sampling sites. At our

293   sampling depths, benthic respiration exceeded benthic GPP in most, but not all years (Fig.

294   3). In this unmanipulated lake there was considerable interannual variability in PAR

295   striking the sediment surface, as well as benthic chlorophyll a, P_{max}, GPP, and respiration.

296   The benthic variables increased from 2002 to a peak in 2007, then declined to a local

297   minimum in 2011.

298

299   *Shallow reference lake, Fog 4*— Lake Fog 4 was intended as the shallow reference lake,

300   but experienced a shoreline failure during our monitoring program. Sediment was

301   observed slumping from a localized point along the northwest shore and mixing into the

302   water column during four consecutive summers (2002-2005). Of our study lakes, Fog 4

303   had the highest concentration of benthic chlorophyll a and there was more chlorophyll a

304   during the years of high sediment influx relative to the years with a stable shoreline -

305   concentrations averaged 573 ± 24 mg m^{-2} during the years of active thermokarst failure

306   and 361 ± 40 mg m^{-2} during the non-thermokarst years (p = 0.0001, Table 3). Years in

307   which the shoreline failure was an active sediment source were also characterized by

308   lower rates of benthic GPP (105 ± 59 mg C m^{-2} d^{-1} compared to 235 ± 106 mg C m^{-2} d^{-1}

309   for years with no thermokarst activity; p< 0.0001) (Table 3, Fig. 3 and 5). Respiration

310   was variable during the thermokarst disturbance, but on average was lower (223 ± 77 mg

311   C m^{-2} d^{-1} compared to 347 ± 88 mg C m^{-2} d^{-1} for years with no thermokarst activity; p =

312   0.0024).

313

314   *Deep fertilized lake, E5*— In the deep fertilized lake, E5, chlorophyll concentrations in

315   the epilimnetic sediments were 139 ± 7 mg m^{-2} in 1999 and 2000, and 179 ± 13 mg m^{-2}

316   after fertilization, which was not a statistically significant change (p = 0.75, Table 3).

317   There was less year-to-year variation in chlorophyll a in this lake compared to the other

318   lakes, but we note that, as in the deep reference lake, both chlorophyll a and P_{max}

319   increased from 2002 to 2007, and declined in the following 3 years (Fig. 4). Based on in-

320   situ chamber measurements, the pre-fertilization GPP in the deep manipulated lake, E5,

321   was 68 ± 13 mg C m^{-2} d^{-1}. The in-situ chamber measurements in the two years after the

322   fertilization began were unchanged (Gettel et al. 2013). After incorporating the longer

323   time series of simulated GPP, we found that GPP remained unchanged during the

324   fertilization period (p = 0.32; Table 3) although considering the change in methodology,

325   where lab incubation estimates of GPP averaged 40 mg C m^{-2} d^{-1} higher than the in-situ

326   chamber measurements for the same time periods, it is possible that fertilization induced

327   a reduction in benthic GPP. Respiration rates were 87 ± 28 mg C m^{-2} y^{-1} in 1999 and

328   2000 and 167 ± 80 mg C m^{-2} d^{-1} during the fertilization period (p = 0.11), which suggests

329   that fertilization induced a positive change in benthic respiration. Benthic net ecosystem

330   production was substantially lower during the fertilization period (Table 3).

331   Hypolimnetic (6 m depth) GPP averaged 8 mg C m^{-2} d^{-1} and respiration averaged $185 \pm$

332   94 mg C m^{-2} d^{-1} during the fertilization period. No pre-fertilization data is available from

333   the hypolimnetic site of this lake.

334

335   *Shallow fertilized lake, E6—* In the shallow fertilized lake, E6, chlorophyll a increased

336   from 126 ± 13 mg m^{-2} in pre-fertilization years to 212 ± 12 mg m^{-2} after the onset of

337   fertilization (p = 0.02, Fig. 4), although in the last three years of monitoring, chlorophyll

338   a had returned to pre-fertilization levels. In-situ chamber data revealed no difference in

339   GPP with fertilization for the shallow lake, E6 (Gettel et al. 2013). The longer-term GPP

340   measurements made from core incubations also show no statistically significant change

341 upon fertilization – GPP was 62 ± 46 mg C m^{-2} d^{-1} prior to fertilization and 131 ± 147 mg

342 C m^{-2} d^{-1} (p = 0.19) after fertilization. Taking into account the change in methodology

343 described above, GPP only increased by approximately 30 mg C m^{-2} d^{-1}. Respiration rose

344 from a pre-fertilization average of 111 ± 35 mg C m^{-2} d^{-1} to a post-fertilization average

345 of 297 ± 157 mg C m^{-2} d^{-1} (p = 0.0007). However, considering the methods change, the

346 respiration increased by approximately 107 mg C m^{-2} d^{-1} from pre- to post-fertilization

347 and there was no clear temporal trend in respiration in either the chamber or core data

348 alone.

349

350 *Benthic photosynthesis parameters*— From the photosynthesis vs. irradiance curves, the

351 average P$_{max}$ for all lakes and years was 495 mg C m^{-2} d^{-1} and the average k$_{1/2}$ was 163

352 μmol quanta m^{-2} s^{-1}. From P$_{max}$ and k$_{1/2}$ values, we calculated the quantum efficiency

353 (mol C fixed mol quanta^{-1}) for the sub-saturating part of the P-I curves. The efficiency

354 ranged from 0.0001 to 0.014 mol C per mol quanta (Fig. 4) with an average for all lakes

355 and sampling dates of 0.004 mol C mol quanta^{-1}. Quantum efficiency was significantly

356 related to benthic chlorophyll a across all lakes in the post fertilization period (Fig. 6).

357 Unfortunately, estimates of P$_{max}$ and k$_{1/2}$ are not available from the chamber

358 measurements made before fertilization started. The model parameters for each lake,

359 year, and sampling depth can be found in the supplemental tables 1-3.

360   To test the fertilization impact on benthic GPP without the confounding factor of

361 changing light, we looked for differences in quantum efficiency between lakes, expecting

362 that the fertilized lakes would have greater efficiency. A one-way ANOVA showed no

363 differences between lakes (p = 0.273). We also plotted average summer GPP vs average

364   summer ambient light levels at the sediment surface (Supp Fig. 1). There is considerable

365   scatter ($R^2 = 0.37$) but the results show no clear impact of fertilization on average

366   summer GPP, especially considering the pre-fertilization years may be somewhat

367   underestimated. Core incubation temperature was not strongly or significantly correlated

368   with either P_{max} (p = 0.43), $k_{1/2}$ (p = 0.42) or summer GPP (p = 0.982).

369

370   *Community metabolism at the whole-lake scale—*

371   Integrating benthic GPP across all lake depths and area and normalizing to lake

372   surface area reveals that benthic respiration exceeded benthic GPP (NEP was negative,

373   sediments were net heterotrophic) in all lakes (Fig. 7). At this scale, benthic GPP was

374   highest in the shallow fertilized lake, E6 (15 g C m^{-2} summer^{-1}), and lowest in the deep

375   fertilized lake, E5 (4 g C m^{-2} summer^{-1}). The reference lakes were intermediate at 11 g C

376   m^{-2} summer^{-1} for the deep Lake Fog 2 and 9 g C m^{-2} summer^{-1} in the shallow Lake Fog 4.

377   Whole lake benthic NEP ranged from -12 to -15 g C m^{-2} summer^{-1}.

378   The nutrient manipulation effect on the benthic NEP lead to increased oxygen

379   depletion in the deep stratified lake, E5. Prior to fertilization, the lowest DO

380   concentration in E5 at any water depth was 5.96 mg L^{-1}. As fertilization progressed, the

381   hypolimnion became increasingly depleted in DO at the time of late-summer

382   stratification. Using 8 m water depth as an indicator, DO declined by 0.3 mg L^{-1} y^{-1} over

383   the 13 years of measurement. The first incidences of hypoxia (DO < 3 mg L^{-1}) and

384   anoxia (DO < 0.5 mg L^{-1}) in the bottom waters at 11 m depth occurred in 2008 and 2011,

385   respectively. In contrast, there was no trend in DO concentrations over time in reference

386   lake Fog 2 (Fig. 8), suggesting that the oxygen depletion was a response to fertilization

387   rather than to factors independent of the fertilization. No change in summertime

388   dissolved oxygen levels was evident in the shallow fertilized lake (E6) because the lake

389   did not stratify during our monitoring.

390   The areal hypolimnetic oxygen deficit (AHOD) in E5 was calculated from

391   bathymetric maps and summertime oxygen profiles for periods when thermal

392   stratification was stable. The AHOD was between 203 and 664 mg O_2 m^{-2} d^{-1} and

393   increased by 15 mg O_2 m^{-2} d^{-1} per year during the 13 years of monitoring ($R^2 = 0.34$, p =

394   0.042; Fig. 9a). The AHOD of Lake E5 is positively, but not statistically, correlated with

395   the estimated NEP of the benthic community at 6 m depth ($R^2 = 0.26$, p = 0.16; Fig. 9b).

396   Water column sampling of the deep reference lake Fog 2 lacked the temporal resolution

397   necessary to calculate AHOD with confidence.

398

399   Discussion

400   We performed whole-lake nutrient enrichment experiments to test the relative

401   importance of nutrients and light as limiting factors to benthic primary production in

402   arctic lakes. Our results support several previous studies which demonstrate that water

403   clarity and lake morphometry are important regulators of benthic GPP at the whole-lake

404   scale (Liboriussen and Jeppesen 2003, Vadeboncoeur et al. 2008, Whalen et al. 2008).

405   Our results also suggest that (1) slight nutrient enrichment did not stimulate benthic algae

406   regardless of lake shape, (2) variation in PAR is an important control on benthic GPP in

407   the study lakes and the effect of fertilization on water column light attenuation was

408   greater in the deep lake than in the shallow lake, and (3) low-level nutrient enrichment

409   can drive an increase in AHOD by increasing benthic respiration and decreasing benthic

410   NEP.

411

412   *Benthic algae response to nutrient addition*— Previous experiments in arctic and sub-

413   arctic lakes have tested the response of benthic microalgae to nutrient additions. From

414   shallow ponds ($z_{max} = 0.2$ m) near Barrow, AK, Stanley (1976) observed a doubling of

415   benthic GPP from 540 to 1080 mg C m^{-2} d^{-1} with the addition of phosphorus. Likewise,

416   N and P addition stimulated benthic chlorophyll (but not GPP) in shallow Lake

417   Hymenjaure ($z_{max} = 3.4$ m) in Sweden (Bjork-Ramberg and Anell 1985). However, in

418   the majority of whole-lake enrichment experiments, especially those in lakes that we

419   would classify as deep enough to routinely stratify, there was no such response by

420   benthic algae, and in many cases, benthic GPP was suppressed due to lower light

421   conditions upon fertilization (Vadeboncoeur et al. 2001). As such, benthic microalgae

422   are generally considered light, rather than nutrient limited.

423   Light seems to be the limiting resource for benthic algae in our study lakes,

424   despite the low water column nutrient concentrations. This is exemplified at two scales

425   in our study. First, the interactions of lake depth and water quality interact to affect

426   available light, and by extension benthic GPP, at the whole-lake scale. Specifically, even

427   though the clear and deep reference lake (Fog 2) had similar benthic P_{max} and $k_{1/2}$ values

428   as did the DOC-rich lake of similar morphometry (E5), it had ~250% higher summer

429   benthic GPP on an areal basis because light penetrated to sediment deeper in the lake.

430   Likewise, the shallow lakes, E6 and Fog 4, had 370% and 220% higher productivity on

431   an areal basis than did Lake E5 at the whole-lake scale, despite similar water column

432   light attenuation properties. Secondly, nutrient addition did not stimulate benthic GPP at

433   the depth-specific scale. While the increase in benthic chlorophyll a in the first 3 years of

434   fertilization in both Lake E5 and E6 suggested a positive response of benthic algae to

435   fertilization (Gettel et al. 2013), during the 13-year fertilization period, benthic

436   chlorophyll a returned to pre-fertilization levels. This, together with the observations that

437   (1) there was no difference in quantum efficiency between the fertilized and reference

438   lakes, (2) no obvious change in the relationship between GPP and ambient PAR from

439   pre- to post-fertilization (Supp Fig. 1), and (3) GPP did not increase significantly during

440   the course of the experiment in either fertilized lake, indicates that the nutrient addition

441   did not positively impact benthic algae.

442   The prevalence of light limitation is further supported by nutrient addition

443   experiments performed on individual cores incubated under saturating light conditions by

444   Gettel et al. (2013). They added N, P, or N plus P to the overlying water of cores from

445   Lake Fog 2 and observed no response in terms of GPP or chlorophyll a over periods up to

446   9 days. A similar finding, in terms of benthic pigments, was found in Ward Hunt Lake in

447   Canada by Bonilla et al. (2005). While the turnover time of benthic algae is on the order

448   of 2 months to years in high-latitude lakes (Bjork-Ramberg and Anell 1985), longer than

449   the 9-day incubations, our time series of 13 years should be sufficiently long to capture

450   potential nutrient stimulation effects.

451   Our measured lack of benthic stimulation to nutrients may have been different in

452   the epilithon of the rocky littoral area because epilithon do not have access to sediment

453   porewater nutrients and because they receive more light (Vadeboncoeur et al. 2001). The

454   rocky littoral zone, however, comprises a relatively small proportion of each lake study

455   and thus is unlikely to impact the overall benthic GPP at the whole-lake scale.

456   The concentrations of benthic chlorophyll a we observed are quite high compared

457   to benthic mats, epilithon, and epipelon measured in other polar freshwaters (Quesada et

458   al. 2008, Bowden et al. 2014), but are not unprecedented. Whalen et al. (2008) measured

459   benthic chlorophyll a concentrations of 258-699 mg m^{-2} in the top 2 cm of sediment in

460   Alaska tundra lakes, which were two orders of magnitude greater than the areal

461   phytoplankton chlorophyll a. We also measured chlorophyll a in the surface two cm of

462   sediment. The positive correlation between benthic chlorophyll a and quantum efficiency

463   suggests that chlorophyll a over this sediment depth is a reasonable parameter for

464   estimating community photosynthetic potential, although we expect the relationship in

465   Figure 6 would have been stronger had we sampled a thinner layer of sediment because

466   only algae residing in the sediment photic zone (1-4 mm) can actively photosynthesize at

467   a given time (MacIntyre and Cullen 1995). Regardless, one would expect an increase in

468   benthic chlorophyll a concentrations during the experiment if N and P from the overlying

469   water column were limiting benthic algae growth. Because benthic chlorophyll a was not

470   higher in a sustained way in either lake, we conclude that these benthic algae were not

471   limited by N or P during the summers.

472

473   *Regulation of light* — Because light is commonly limiting for benthic algae production

474   (Vadeboncoeur et al. 2001), understanding the fertilization impact on light attenuation is

475   an important aspect of this study. High concentrations of DOC, and especially the

476   fraction of colored dissolved organic matter (CDOM), and lake morphology can interact

477   to modulate the impact of nutrient addition on light availability to benthic algae. To our

478   knowledge, our study is the first to assess the dynamic, long-term response of benthic

479   algae in high-DOC, low-chlorophyll lakes (Table 1) during low-level nutrient enrichment

480   (Table 2). This scenario may typify the trajectory of boreal lakes and some arctic lakes

481   (Tranvik et al. 2009, Rautio et al. 2011) in a warmer and more nitrogen-rich world

482   (Hobbs et al. 2010, Prowse et al. 2006, Elser et al. 2009).

483   In this study, the fertilization experiments had a higher impact on light extinction

484   coefficients in the deep lake (E5) than in the shallow lake (E6). This different response

485   suggests a morphological control on the impact of low-level enrichment. The difference

486   derives from lower stimulation of phytoplankton biomass, on a volumetric basis,

487   observed in Lake E6. In the absence of a strong benthic algal response, we hypothesize

488   that high abiotic nutrient sequestration by lake sediments contributes to the weak

489   phytoplankton response in Lake E6. This explanation is plausible considering the affinity

490   for phosphorus to complex with the iron-rich lake sediments (Cornwell and Kipphut

491   1992) and the potentially rapid transfer of phosphorus to the sediments in a shallow

492   setting. Gekai-Kato et al. (2012) proposed that at nutrient loading rates above 2-5 mg P

493     $m^{-2} d^{-1}$, lakes could alternate from a clear to a turbid stable state. We did not observe

494   such a transition in Lake E6 despite our experimental loading rates of 16 mg $m^{-2} d^{-1}$. The

495   threshold for stable-state transition may therefore be somewhat higher in these

496   experimental lakes due to the abiotic P absorption capacity of the sediments. In the

497   deeper Lake E5, we suggest that added nutrients had less contact with the sediments,

498   allowing for greater recycling within the water column, thereby having a stronger effect

499   on phytoplankton biomass than in the shallow lake.

500   The similar temporal variation of light attenuation and benthic GPP in the non-

501   thermokarst lakes suggests a regional influence on the light environment and benthic

502   processes. The amount of light absorbed in these lakes by CDOM is related strongly to

503   DOC concentrations (e.g., Cory et al. 2014; ARC LTER database), and because summer

504   average DOC concentrations were correlated between lakes (ARC LTER database), a

505   regional control on DOC inputs may explain the temporal patterns in light attenuation.

506   The export of DOC from land to surface waters is dependent on water flow, and by

507   extension, spring melting and precipitation events (Judd and Kling 2002), and thus it is

508   not surprising that light attenuation would vary synchronously across nearby lakes.

509   Factors that regulate DOC in arctic lakes on seasonal and interannual timescales no doubt

510   play an important role on the annual benthic GPP. Our experiment was meant to mimic

511   slight changes to nutrient loading that may result from warming climate. However,

512   excess nutrients that stem from increased flushing of soils are likely to be accompanied

513   by additional allochthonous DOC (Kling et al. 2014, Sobek et al. 2007, Prowse et al.

514   2006). Thus, stimulated phytoplankton biomass and greater DOC delivery can work in

515   tandem to reduce the light available to benthic algae.

516

517   *Benthic respiration and dissolved oxygen*—Benthic respiration exceeded gross primary

518   production in nearly all lakes, years, and sampling depths in our study. This is a common,

519   but not universal (Ask et al. 2009), trait of lake benthos and contributes to the net

520   heterotrophic nature of most lakes worldwide (Cole et al. 2000). In the arctic, benthic

521   communities are important for oxygen consumption in lakes (Miller and Reed 1975,

522   Lienesch et al. 2005, Jonsson et al. 2003), although the oligotrophic status of most arctic

523   lakes usually prevents development of hypoxia or anoxia.

524   Dissolved oxygen depletion is a well-established sign and symptom of nutrient

525   enrichment (Wetzel 2001 and references therein). In two enrichment experiments using

526   high nutrient levels in lakes near Toolik Lake, anoxia was induced after just three years

527   of fertilization (Lake N2; O'Brien et al. 2005) and two years of fertilization (Lake N1;

528   Lienesch et al. 2005). In the second experiment, anoxia near the sediment-water interface

529   lead to reduced survivorship of fish eggs and reduced recruitment of lake trout during the

530   fertilization period (Lienesch et al. 2005). The AHOD of Lake E5 is comparable to other

531   oligo- to mesotrophic lakes (e.g., Wetzel 2001) but less severe than the oxygen depletion

532   from other nearby arctic experimental lakes (O'Brien et al. 2005). The difference in

533   severity probably stems from the lower-level of nutrient addition employed in our study.

534   The strong oxygen depletion observed in Lake E5 was not observed in the

535   reference lake and was accompanied by a decline in benthic NEP over time due to the

536   steady increase in benthic respiration. It is extremely difficult to separate benthic

537   respiration into autotrophic and heterotrophic components. Because autotrophic

538   respiration is proportional to GPP, and GPP did not increase, we assume that

539   heterotrophic activity must be the cause of the increased respiration. It is probable that

540   this increase in respiration in the deep fertilized lake, E5, was due to greater flux of

541   phytoplankton to the sediments. In E5, pelagic NPP rates increased six-fold between the

542   pre- and post-fertilization periods (pre-fertilization NPP 18 ± 10 mg C m^{-2} d^{-1} versus

543   post-fertilization average of 108 ± 30 mg C m^{-2} d^{-1} for 2001-2009; M. Evans, G. Kling

544   unpubl. data). This equates to an extra ~90 mg C m^{-2} d^{-1}, compared to an increase in

545   benthic respiration of 80 mg C m^{-2} d^{-1}. While some fraction of the extra pelagic

546   production is respired in the water column, the similarity in these values suggests that

547   increased phytoplankton deposition can account for the majority of the increase in

548   benthic respiration in E5.

549   There is less potential for significant oxygen depletion in the bottom of Lake E6

550   compared to Lake E5 because bottom waters are more frequently equilibrated with the

551   atmosphere through wind-driven mixing of the water column. The benthic data from

552   Lake E6 hint at increases in both benthic GPP and respiration (Fig. 5), resulting in little

553   change in benthic NEP. In Lake E5 settling phytoplankton likely contributed to

554   decreasing benthic NEP during the experiment. This effect was smaller in shallow Lake

555   E6 where pelagic NPP only increased by ~41 mg C m^{-2} d^{-1} (pre-fertilization NPP 38 ± 24

556   mg C m^{-2} d^{-1} in 2000, versus post-fertilization average of 79 ± 29 mg C m^{-2} d^{-1} for 2001-

557   2009; M. Evans, G. Kling unpubl. data) and pelagic chlorophyll a was unchanged. This

558   difference may result from the different area-based fertilization rates among the

559   experimental lakes (E5 received higher N and P loading on an area-basis than E6, even

560   though volumetric loading was the same), which could have produced a higher depth-

561   integrated phytoplankton response. Because pelagic chlorophyll a did not increase on a

562   volumetric-basis in Lake E6, however, this explanation is less likely.

563

564   *Thermokarst failure*— The frequency of thermokarst failures is thought to be increasing

565   in the Arctic (Rowland 2010). When active layer detachments or retrogressive thaw

566   slumps occur adjacent to lakes, they have the potential to radically alter lake ecosystem

567   processes. The lifespan of these disturbance events is generally on the order of 1-5 years

568   of active release of nutrients and sediment into surface waters (Bowden et al. 2008), and

569   the impact can vary in severity.

570   In terms of benthic processes, it is thought that clastic sediment released from

571   thermokarst failures initially has a smothering effect on benthic algae, effectively burying

572   the benthic community and suppressing photosynthesis (C. Johnson unpubl. data).

573   Additionally, during the period of active sediment delivery from these features, water

574   clarity is likely to be reduced because of greater suspended solids. This was observed in

575   Lake Fog 4 as an increase in light attenuation coefficients from 2002-2005 that lowered

576   light available at the sediments by 53% at 2 m depth, and lowered GPP by 120 mg C m^{-2}

577   d^{-1}, or ~55%. This decrease is considerably greater than the decrease driven by our low-

578   level fertilization in Lake E5. Mesquita et al. (2010) reported that suspended clay

579   particles delivered during a thermokarst failure are effective at adsorbing and removing

580   CDOM from lakes, resulting in a clarifying effect upon settling, which would benefit the

581   benthic algae. In Lake Fog 4 light attenuation recovered to, but not below, pre-

582   thermokarst values, which we suggest is due to a combination of low initial DOC

583   concentration (less potential for a clarifying effect) and active resuspension of sediments.

584   As such, one must consider initial lake properties when predicting shoreline disturbance

585   impacts on lake light attenuation and benthic productivity response.

586   Benthic changes in the thermokarst-impacted Fog 4 differed from the

587   experimental N and P manipulation lakes. GPP and respiration both decreased, while

588   benthic chlorophyll increased to the highest values observed in any lake. The decrease in

589   respiration is consistent with the smothering effect by clastic deposition. While we did

590   not do textural analysis of the thermokarst-sourced material, we postulate that dilution of

27

591 organic matter by clay and silt, and capping of the active surface sediments, would have

592 lowered the rates of both autotrophic and heterotrophic respiration. It is difficult to

593 ascertain whether this conclusion is consistent with the large increase in chlorophyll a

594 concentration. An explanation for such high chlorophyll a concentrations could be that as

595 sediment rapidly accumulated during the summers of thermokarst activity, the surface

596 layer was constantly colonized by algae, resulting in a relatively deep layer of active

597 chlorophyll-containing sediments. This scenario would explain why Lake Fog 4

598 sediments fall below the regression line in Figure 6 – only the surface-most sediment

599 contribute to the observed P_{max} and quantum efficiency observed in the core incubations,

600 because light is typically absent below millimeters of the sediment surface (Stanley 1976,

601 MacIntyre and Cullen 1995); therefore, despite high chlorophyll a concentrations over 2

602 cm, the photosynthesis parameters were not especially high.

603

604 Conclusion

605   Our results indicate that rates of benthic GPP of our study lakes did not respond to

606 low-level nutrient addition, despite the extremely oligotrophic nature of the lakes.

607 Instead, light seems to limit benthic algae productivity, even for sediments in the shallow

608 littoral zone. Changes in light attenuation caused by variations in DOC appear correlated

609 between lakes and can possibly be linked to meteorological controls. Changes in light

610 attenuation due to fertilization were different in the two experimental lakes, with an effect

611 on water column properties only evident in the deep, stratified lake. Likewise, benthic

612 respiration was impacted by the addition of nutrients only in the deep, stratified lake.

613 Lake morphology may therefore play an important role in the fate of nutrients and

614   subsequent impact on benthic processes. If our low-level fertilization regime realistically

615   simulates future changes in nutrient loading to deep arctic lakes, then hypoxia driven by

616   benthic respiration could become a more common feature of those lakes. The importance

617   of light is also illustrated by our observations in a shallow lake that experienced a

618   shoreline thermokarst failure. In this case, elevated nutrients and sediment inputs and

619   deposition worked in tandem to increase water-column light attenuation and substantially

620   decrease benthic GPP during the period of active sediment delivery.

621

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788   Table 1: Physical and chemical properties of the study lakes. Values are from pre-

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790   values are averages from 0-3 m water depth. PP = particulate phosphorus.

	Fog 2 (reference)	Fog 4 (reference)	E5 (fertilized)	E6 (fertilized)
Surface area (ha)	5.6	1.9	11.3	2.0
Maximum depth (m)	20.3	5.4	12.7	3.2
Mean depth (m)	8.3	2.3	5.2	2.0
A_e/V_e	0.07	0.44	0.1	0.63
Secchi depth (m)	6.8	2.0	3.5	2.3
Sp. conductivity ($\mu S\ cm^{-1}$)	143	85	13	12
DOC ($mg\ L^{-1}$)	4.1	4.8	6.0	6.6
Epilimnion PP ($mg\ m^{-3}$)	5	13	7	12
Epilimnion chl. a ($mg\ m^{-3}$)	1.8	8.1	5.0	6.1
Fish	Present	Absent	Present	Absent

791

792

Table 2: Background and fertilized rates of annual P and N loading ($mg\ m^{-3}\ y^{-1}$) to the

794 lake surface mixed layer (equivalent to the whole lake for shallow systems). Values from

795 other whole-lake manipulations are either as reported or converted to a volumetric basis

796 (m^{-3}) from an areal basis (m^{-2}) by dividing by the mean depth of the lake or mixed layer

797 where appropriate and scaled to the annual addition rates.

Study	Lake	P ambient	P added	N Ambient	N added
This study	E5		8		56
	E6		8		56
Bettez et al. 2002	N1		44 - 65		250 - 368
O'Brien et al. 2005	N2		75 - 91		426 - 535
Vadeboncoeur et al. 2001	Peter	105	41-122		
	West Long	105	42-150		
	East Long	105	92-134		
Bjork-Ramberg and Anell 1985	Hymenjaure		75-258		3216
Bergmann and Welch 1990	Spring	88	0	175	0
	Far	108	25	145	0
	P&N	82	25	115	290

798

Table 3: Pre-disturbance and post-disturbance estimates of the epipelic community

800   characteristics (average (SE) for chlorophyll; average (SD) for GPP and R; NEP

801   calculated as sum of GPP and R with a combined SD). Pre-fertilization values are from

802   chamber measurements while post-fertilization values are from a combination of

803   chamber and core measurements. For lake Fog 4, TK and NTK refer to the periods with

804   an observed thermokarst-related sediment plume, and periods with no sediment plume,

805   respectively.

	Benthic chlorophyll (mg m^{-2})		Benthic GPP (mg C m^{-2} d^{-1})		Benthic R (mg C m^{-2} d^{-1})		Benthic NEP (mg C m^{-2} d^{-1})	
	Pre-fert	Post-fert	Pre-fert	Post-fert	Pre-fert	Post-fert	Pre-fert	Post-fert
Fog 2								
3.5m	100 (48)	150 (23)	110	175 (142)	-142	-220 (105)	-32	-45 (176)
6 m	351 (54)	303 (29)		197 (148)		-256 (206)		-59 (253)
E5								
3.5 m	139 (7)	179 (13)	68 (13)	61 (24)	-87 (28)	-167 (80)	-19 (35)	-106 (83)
6 m	66 (26)	121 (12)		8 (57)		-185 (94)		-177 (110)
E6								
2 m	126 (13)	210 (12)	62 (40)	128 (132)	-111 (35)	-297 (157)	-49 (21)	-169 (205)
	NTK	TK	NTK	TK	NTK	TK	NTK	TK
Fog 4								
2 m	372 (44)	573 (23)	235 (106)	105 (59)	-347 (88)	-223 (77)	-112 (138)	-118 (97)

806
807

808   **Figure 1**: Map of the study region showing locations of the fertilized lakes (E5, E6) and

809   reference lakes (Fog 2, Fog 4) and the proximity to Toolik Lake Field Station.

810   **Figure 2**: A) Average incoming PAR, measured at Toolik Field Station, from June 15 to

811   August 31 during each year of the experiment. B) Time series of light extinction

812   coefficients. Points are summer averages for each year. Standard deviation within years

813   ranged from 0.02 to 0.5. Horizontal bars denote periods of fertilization and the

814   thermokarst failure (TK) in Lake Fog 4.

815   **Figure 3:** Benthic data from the shallow reference Lake Fog 4 and the two sampling

816   sites in the deep, reference lake, Fog 2. Top panel: Average PAR from June 15-August

817   31 at the sampling depth (2 m for Fog 4, 3.5 and 6 m for Fog 2). Middle panel: Benthic

818   chlorophyll a and modeled P_{max} from core incubations. Bottom panel: Benthic

819   respiration and GPP. Vertical gray bar in Lake Fog 4 panels represents years with an

820   observed sediment plume.

821   **Figure 4:** Same as in Fig. 3, but for the fertilized E lakes. Measurements in the shallow

822   lake, E6, were taken at 2 m depth and in the deep lake, E5, at 3.5 and 6 m depth. The

823   vertical bar in 2001 represents the first year of fertilization.

824   **Figure 5:** Summary of disturbance impacts on benthic GPP and respiration. This

825   combines *in-situ* chamber measurements and core-incubation modeled GPP so does not

826   account for the change in methodology. For thermokarst-impacted Lake Fog 4,

827   disturbance years are 2002-2005, for the deep and shallow fertilized lakes (E5 and E6,

828   respectively), disturbance years refers to the fertilization period 2001-2013. Only

829   thermokarst-impacted Lake Fog 4 showed a statistically significant difference in benthic

830   GPP ($p < 0.001$).

831   **Figure 6:** Quantum efficiency determined from laboratory core incubations plotted

832   against areal benthic chlorophyll a concentration. Points represent each sampling date

833   and depth. The line is the type II least squares regression fit for all lakes combined. The

834   equation is $\log_{10}QE = 1.45 \times \log_{10}Chl - 6.04$, where QE is quantum efficiency (mol C mol

835   photons^{-1}), Chl is chlorophyll a (mg m^{-2}), and the standard deviations for the slope and y-

836   intercept are 0.12 and 0.27, respectively. Lake treatments are: Fog 2 – deep, reference;

837   Fog 4 – shallow, reference; E5 – deep, fertilized; E6 – shallow, fertilized.

838   **Figure 7:** GPP, R, and NEP (g C m^{-2} summer^{-1}) calculated at the whole-lake scale and

839   summed from June 15 to August 31. Lake treatments are: Fog 2 – deep, reference; Fog 4

840   – shallow, reference; E5 – deep, fertilized; E6 – shallow, fertilized.

841   **Figure 8**: Summer (JJA) average dissolved oxygen concentrations measured at 8 m

842   depth in the two deep stratified lakes. Horizontal bar as in previous figures.

843   **Figure 9**: A) Summertime areal hypolimnetic oxygen deficit in Lake E5, with the

844   fertilization period represented by the horizontal bar. B) Lake E5 AHOD versus benthic

845   net ecosystem production determined from our hypolimnion sampling stations.

846   **Supplementary Figure 1:** Average summer benthic GPP vs. ambient PAR incident at

847   the sediment surface from June 15 to Aug. 31. Each point represents one year of data for

848   each lake and depth. For the experimental lakes, E5 (deep lake) and E6 (shallow lake),

849   pre-fertilization points are outlined in black. Across all lakes, depths, and years, r^2=0.37.

850

A

PAR (μmol quanta m⁻² s⁻¹) — $PAR\ (\mu mol\ quanta\ m^{-2}\ s^{-1})$

B

Fog 4 TK

Fertilization period

Light Extinction, k_d (m^{-1})

—○— Fog 2   ‑‑△‑‑ Fog 4   —●— E5   ‑‑▲‑‑ E6

Shallow Reference Lake Fog 4 (2 m)

Deep Reference Lake Fog 2 (3.5 m)

Deep Reference Lake Fog 2 (6 m)

PAR (µmol quanta m^{-2} s^{-1})

Thermokarst Failure

Chl. a (mg m^{-2})

P$_{max}$ (mg C m^{-2} d^{-1})

- Chl. a
- P$_{max}$

Respiration and GPP (mg C m^{-2} d^{-1})

- Resp. (in-situ)
- Resp. (incubation)
- GPP (in-situ)
- GPP (incubation)

Year

Year

Year

Shallow Fertilized Lake E6 (2 m) — **Deep Fertilized Lake E5 (3.5 m)** — **Deep Fertilized Lake E5 (6 m)**

PAR (μmol quanta m^{-1} s^{-1})

Chl. a (mg m^{-2}) P$_{max}$ (mg C m^{-2} d^{-1})

Respiration and GPP (mg C m^{-2} d^{-1})

Year

Start Fertilization

- Chl. a
- ○ P$_{max}$

- ■ Resp. (in-situ)
- ● Resp. (incubation)
- □ GPP (in-situ)
- ○ GPP (incubation)

Benthic GPP (mg C m^{-2} d^{-1})

Respiration (mg C m^{-2} d^{-1})

☐ Non-disturbance period
■ Disturbance period

Fog 4   E5   E6

Figure axes: Quantum efficiency (mol C mol quanta^{-1}) on the y-axis (ranging from 0.0001 to 0.01) versus Chlorophyll a (mg m^{-2}) on the x-axis (ranging from 10 to 1000).

Legend:
- ● E5
- ▲ E6
- ○ Fog 2
- △ Fog 4

Fertilization period

Fog 2 (ref.)
p = 0.784

E5 (fert.)
p = 0.001

A

Fertilization Period

P=0.042

AHOD (mg O$_2$ m^{-2} d^{-1})

Year

B

AHOD (mg O$_2$ m^{-2} d^{-1})

1:1

Benthic NEP (mg O$_2$ m^{-2} d^{-1})