Habitat, not resource availability, limits consumer production in lake ecosystems

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Abstract

Food web productivity in lakes can be limited by dissolved organic carbon (DOC), which reduces fish production by limiting the abundance of their zoobenthic prey. We demonstrate that in a set of 10 small, north temperate lakes spanning a wide DOC gradient, these negative effects of high DOC concentrations on zoobenthos production are driven primarily by availability of warm, well-oxygenated habitat, rather than by light limitation of benthic primary production as previously proposed. There was no significant effect of benthic primary production on zoobenthos production after controlling for oxygen, even though stable isotope analysis indicated that zoobenthos do use this resource. Mean whole-lake zoobenthos production was lower in high-DOC lakes with reduced availability of oxygenated habitat, as was fish biomass. These insights improve understanding of lake food webs and inform management in the face of spatial variability and ongoing temporal change in lake DOC concentrations.

In lake ecosystems, consumers in benthic habitats—the zoobenthos—are a key food web link between basal resources and fishes. For instance, reliance of fishes on zoobenthic prey was 65% on average in a survey of 470 lacustrine fish populations (Vander Zanden and Vadeboncoeur 2002), and varied from 60% to 80% in an intensive study of three species in a single lake (Weidel et al. 2008). Fishes have strong ecological effects on lakes (Carpenter et al. 2001; Vanni 2002) and support economically and culturally valuable fisheries. Although zoobenthos play a central role in structuring lakes in ecologically and societally important ways, surprisingly little is known about the ecological factors that limit their productivity. The most comprehensive analyses indicate that zoobenthos productivity may be regulated by lake trophic status and availability of resources such as detritus formed from settling particulates, and benthic algae (Strayer and Likens 1986; Rasmussen 1988); as well as abiotic factors like habitat structure, lake morphometry, humic water color, and dissolved oxygen concentration (Rasmussen and Kalff 1987; Dermott 1988; Rasmussen 1988; Babler et al. 2008). However, the considerable effort required to quantify zoobenthos abundance, especially given their patchy distribu-

tions in space and time, means that robust comparative analyses are rare.

The current conceptual model of food web productivity in nutrient-poor lake ecosystems emphasizes light-mediated resource limitation of zoobenthos and ultimately fish populations (Karlsson et al. 2009; Finstad et al. 2014). Dissolved organic carbon (DOC) derived from terrestrial organic matter stains the water, such that lakes with higher DOC concentrations have darker water (Jones 1992). This reduces light penetration and thereby also benthic primary production (Ask et al. 2012; Godwin et al. 2014). Karlsson et al. (2009) proposed that reduced benthic primary production in higher-DOC lakes limits zoobenthos production, which in turn limits fish production. This proposed causal chain fits with major established patterns in lake ecology including light limitation of benthic primary production (Hansson 1992; Vadeboncoeur et al. 2008; Ask et al. 2012) and the importance of zoobenthos prey in supporting fish production (Vander Zanden and Vadeboncoeur 2002; Weidel et al. 2008). However, there is limited evidence to support the idea that benthic primary production can limit zoobenthos production. While some zoobenthos can and do rely on benthic primary production (Strayer and Likens 1986; Hecky and Hesslein 1995; Devlin et al. 2013; Lau et al. 2014), others employ a diversity of other feeding strategies (Cummins and Klug 1979) and can feed on resources such as terrestrial particulates, settling phytoplankton and other

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animals (Merritt et al. 2008). In a survey of eight oligotrophic Arctic lakes, Northington et al. (2010) found only a weak relationship between zoobenthos production and benthic primary production.

An alternative mechanism by which DOC might limit zoobenthos production could be its effects on the availability of thermally suitable and well-oxygenated habitat. Because DOC absorbs incoming heat as well as light, darker lakes develop stronger, shallower thermal stratification (Snucins and Gunn 2000; Read and Rose 2013). This means that a greater proportion of their volume and sediment surface area lies in the hypolimnion, where the water is cold and isolated from light and atmospheric exchange such that respiration may drive dissolved oxygen to extremely low levels (Arvola 1984; Wetzel 2001; Wissel et al. 2003). Most zoobenthos, like other aerobic poikilotherms, are strongly affected by both temperature and dissolved oxygen concentration (Dermott 1988; Plante and Downing 1989), although there are some taxa, such as *Chironomus* spp., which can tolerate periods of anoxia at the expense of growth (Jónasson 1984).

In this study, we tested the importance of the DOC-mediated resource-limitation and habitat-limitation mechanisms for controlling zoobenthos production. We estimated zoobenthos production and resource use in 10 low-nutrient lakes spanning a wide DOC gradient, and related rates of production to measurements of benthic primary production, dissolved oxygen, and temperature. Our results confirm a strong negative effect of DOC on zoobenthos production. However, they indicate that this effect occurs mainly via reductions in dissolved oxygen and available habitat, not via resource limitation driven by light availability and benthic primary production.

Methods

Study site and sample collection

We estimated zoobenthos production in 10 lakes at the University of Notre Dame Environmental Research Centre located on the Wisconsin–Michigan border, U.S.A. (46.228° N 89.524° W). The lakes spanned broad environmental gradients; for instance, DOC ranged from 5.3 mg/L to 23.0 mg/L and total phosphorous (TP) ranged from 11.4 μg/L to 33.9 μg/L (Table 1).

We collected zoobenthos samples from each lake on three occasions across the summer growing period, in late May, late June and early August 2012. On each sampling occasion samples were taken at 4–5 depths, depending on the maximum depth of the lake, along four replicate transects. All lakes were sampled at 0.5 m, 1 m, and 3 m; deep lakes were also sampled at 8 m and 12 m and shallower lakes (< 8 m) were sampled at the deepest depth available. We used a push corer to sample sediment at depths of 1 m or less (five cores per sample, 0.017 m^2 total) and an Ekman grab (0.023 m^2) to sample at all deeper depths. Sediment samples were seived

through 250 μm mesh bags and organisms were sorted visually from the debris on the same day as collection and stored in 70% ethanol. Spot checks on $\sim$ 10% of samples indicated that we were effective at picking macrozoobenthos from the samples, but it is likely that some small macrozoobenthos were missed. In addition, this method was not designed to collect small meiofauna. Thus our production estimates should be viewed as macroinvertebrate-specific and as minimal estimates of total zoobenthos production (Strayer and Likens 1986).

Zoobenthos production

We identified zoobenthos to genus or the lowest possible taxonomic level using a stereo microscope, following the keys of Holsinger (1972), Stern (1990), and Merritt et al. (2008). We photographed each individual using a digital microscope camera and measured head capsule width, body length, or shell width from the images using ImageJ software (National Institutes of Health, U.S.A.). Zoobenthos dry mass was calculated from these measurements following published length-mass relationships (Supporting Information Appendix 1). We calculated production for each taxon at each sample site using the Plante and Downing (1989) predictive regression model, which uses mean annual biomass, maximum individual body mass, and mean annual surface water temperature as predictors. We used data from the summer rather than the entire year to estimate these predictors, which probably biased our production estimates toward higher values. To check the magnitude of this bias, we applied this method to the data of Babler et al. (2008), who previously estimated zoobenthos production using the size-frequency method in one of the lakes that we studied here. Estimates of zoobenthos production from the Plante and Downing method with summer data were 10–42% higher than those from the size-frequency method.

We summed production across taxa and reported it in two different manners in the results. Depth-specific production is the average production from the four replicate samples taken at each depth within each lake. Whole-lake average production was calculated by dividing each lake up into depth bands centered around our sampling depths, multiplying the area of each depth band by the average depth-specific production, summing across the depth bands, and dividing by the total area.

Enviromental variables

We measured depth-specific water temperatures and dissolved oxygen concentrations on each of the three zoobenthos sampling occasions using a handheld polarigraphic sensor (YSI Pro 20, Yellow Springs Instruments, U.S.A.), and used the mean of these three measurements as an indicator of average summertime conditions at each depth. We similarly calculated average light availability at each depth based on profile measurements of photosynthetically active

Table 1. Summary of lake bathymetry and water chemistry for the 10 survey lakes during the study period. DOC is dissolved organic carbon. Average light climate is the average percentage of surface light available in each lake, calculated using weighted depth bands (see whole-lake zoobenthos production methods). Metalimnion depth was characterised as the shallowest depth at which the change in temperature exceeded $1°C\ m^{-1}$.

Lake	Area (ha)	Mean depth (m)	Max depth (m)	DOC (mg/L)	Average light climate (% surface light)	Surface temperature (°C)	Average lake temperature (°C)	Metalimnion depth (m)	Average lake dissolved oxygen (mg/L)	Total phosphorus (µg/L)	Total nitrogen (µg/L)	Average benthic primary production (mg C m^{-2} d^{-1})
Crampton	25.81	5	15.2	5.3	14.2	21.6	16.8	3.5	7.1	11.4	343.2	286.4
Bay	67.3	4.3	13.7	6.1	17.7	21.4	17.3	3.7	6.2	12.4	406.1	184.6
Raspberry	4.63	3.1	6	7.3	9.1	22.2	16.7	1.8	4.2	25.9	552.0	71.7
Brown	32.57	2.8	5.5	7.4	7.3	21.2	19.7	2.5	4.3	33.7	623.8	190.5
Long	7.87	3.9	14	7.6	10.6	21.9	15.1	1.8	5.7	21.0	441.5	103
Bergner	17.85	3.6	12	8.1	13.7	21.3	17.7	2.5	5	18.8	487.2	233.9
Inkpot	6.61	2.9	5.2	9.1	9.1	21.7	18.2	2.3	4.9	28.3	540.7	79
Morris	5.93	2.6	6.7	15.7	6.4	21.4	15.3	1.2	3.5	29.5	772.7	31.8
Hummingbird	0.76	3.7	7	19.9	0.7	20.9	9.6	0.7	1.4	32.5	880.5	9.3
Reddington	1.24	2.5	16	23.0	5.2	21.4	10.9	0.8	2.5	33.9	798.3	13.6

radiation (PAR) with an underwater quantum PAR sensor and light meter (LICOR LI-192SA and LI-250A, LICOR, U.S.A.).

We measured depth-specific benthic primary production using in situ benthic chambers and the diel oxygen method, as described in Godwin et al. (2014). Briefly, we placed optical dissolved oxygen sensors inside clear skylight domes deployed for 3–7 d on the bottom at depths corresponding to the 60%, 25%, and 5% light level in each lake, and calculated daily esimates of primary production based on the rate of change in dissolved oxygen in each dome using a modified version of the method described by Cole et al. (2000). We repeated these deployments three times over the course of the summer. For every set of deployments in a given lake, benthic primary production estimates were linearly interpolated at 0.5 m depth intervals from the rates calculated at the deployment depths. To make these interpolation calculations, we assumed that benthic primary production was zero below the 1% light level and that it was constant between the minimum deployment depth and the surface of the lake. We calculated the mean depth-specific benthic primary production by averaging across all of the available measurements for each lake-depth.

In addition to these depth-specific measures, we calculated average whole-lake temperature, dissolved oxygen, light availability, and benthic primary production by weighting depth-specific values by the area of each depth band, as described above for zoobenthos production calculations. We also measured water column DOC, chlorophyll *a*, total phosphorous, and total nitrogen concentrations in each lake based on epilimnion samples collected on the three sampling occassions across the summer, and processed as described in Kelly et al. (2014). We estimated fish biomass in six of our lakes in 2013 using catch per unit effort of zoobenthivorous fishes from overnight fyke net sets to estimate the relationship between benthic invertebrate production and fish biomass.

Resource use

We estimated the reliance of zoobenthos on benthic, pelagic, and terrestrial sources of primary production using measurements of C, N, and H stable isotope ratios and a Bayesian mixing model, following the methods in Solomon et al. (2011). For the benthic end member of the mixing model we scraped periphyton from ceramic tiles positioned at 0.5 m depth in each lake. For the pelagic end member, we estimated the stable isotope ratios of phytoplankton following the method of Cole et al. (2011). For the terrestrial end member, we used published stable isotope ratios for leaf litter collected within 5 km of our study lakes (Cole et al. 2011). Finally, for the environmental water end member in the H equation of the mixing model, we measured the δD of surface water in each lake on three occasions throughout the summer. Zoobenthos for stable isotope analysis were col-

lected simultaneously with the other zoobenthos samples from four sites on each lake at 1 m depth. We picked chironomids, odonates, and trichopterans from these samples, held them overnight to allow for gut evacuation, then pooled them by taxon and sample date, dried them at 60°C, and ground them to a fine powder. We measured stable isotope ratios on isotope ratio mass spectrometers at the University of Notre Dame ($\delta^{13}C$ and $\delta^{15}N$) and Northern Arizona University (δD). Stable isotope ratios of the three zoobenthos taxa were similar within each lake, so we fit a single mixing model for each lake using all of the available zoobenthos samples.

Identifying predictors of zoobenthos production

We fit linear regression models, including lake as a blocking factor, to describe the effects of benthic primary production, dissolved oxygen, and water temperature (singly and in all possible combinations; seven candidate models in all) on depth-specific zoobenthos production. We compared the candidate models using AICc to identify the model(s) with the best predictive ability. Our predictors (particularly benthic primary production) are themselves measured with error, which can lead to biased parameter estimates and loss of power in classical regression models (Fuller 1987). To avoid these issues we used a measurement error model (also known as an error-in-variables model). Specifically, we calculated the maximum likelihood estimates of the parameters, and the associated likelihood, following Equations 2.2.10 through 2.2.12 of Fuller (1987). We bootstrapped the residuals of our fitted models 10,000 times to determine 95% confidence intervals for the parameters (Carroll et al. 2006; Manly 2007). All predictors were $\log(x + 1)$ transformed and converted to Z-scores prior to analysis, to normalize distributions and facilitate comparisons among the coefficients. We present the coefficient of determination (R^2) for each model, but note that these should be used only as rough aids to interpretation because the R^2 calculation is not strictly valid in the presence of measurement error (e.g., Cheng et al. 2014). While we report results from these error-in-variables models here, we note that results were qualitatively similar when we used standard least-squares regression. We also used standard least-squares regression to ask whether there was a relationship between zoobenthos production at the whole-lake level and DOC concentration or other lake-level predictors.

Results

We collected a total of 529 zoobenthos samples and measured 10,950 individuals from 11 orders and 32 families. Total zoobenthos biomass per sample averaged 0.85 g dry mass m^{-2} and ranged between 0 g dry mass m^{-2} and 9.87 g dry mass m^{-2}. Chironomidae was the dominant taxon in all lakes, constituting 13.1–100% of the biomass in shallow samples (0.5–1 m) and an even greater portion of biomass
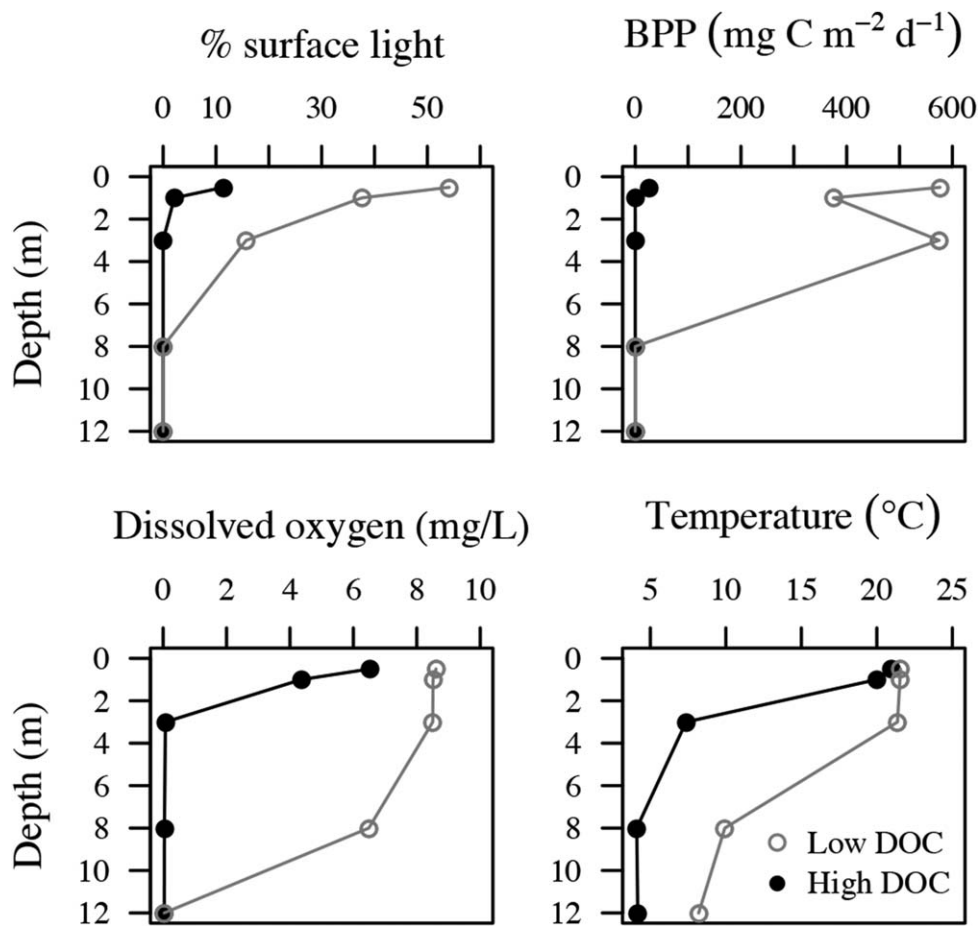
Fig. 1. Depth profiles of habitat and resource characteristics for the clearest (gray circles; Crampton Lake, DOC = 5.26 mg/L) and darkest (black circles; Reddington Lake, DOC = 23.0 mg/L) lakes in this study. BPP represents benthic primary production.

(39.7–100%) in deeper samples (3–12 m). We did not see strong evidence for a shift in the proportion of biomass associated with any particular order of invertebrates along the DOC gradient although some genera appeared to be more associated with clear or dark lakes.

Depth gradients and DOC

Differences in DOC concentration between lakes were associated with large differences in environmental depth gradients within lakes. To illustrate this, we show depth profiles for two lakes representing the clear and dark ends of our DOC gradient (Fig. 1; values for lakes with intermediate DOC concentration fall between the two extremes displayed). Depth profiles of limnological variables showed that high-DOC "dark" lakes become colder, darker and oxygen depleted at much shallower depths than do low-DOC "clear" lakes. For example, the dissolved oxygen concentration at 3 m depth was 0.1 mg/L in our darkest lake, compared to 8.5 mg/L in our clearest lake. Similar comparisons can be made for temperature (7.4°C compared to 21.4°C) and benthic primary production (0 mg C m^{-2} d^{-1} compared to

575 mg C m^{-2} d^{-1}). Pearson's correlation coefficients between dissolved oxygen, temperature, benthic primary production, and light ranged from 0.59 to 0.88. Both the thermocline depth (the depth at which the change in temperature with depth, between warm surface waters and cold hypolimnetic waters, is most rapid) and the oxycline depth (similarly defined for dissolved oxygen concentration) were shallower in lakes with higher DOC concentrations ($F_{1,8} = 20.13$, $p = <0.01$, $R^2 = 0.72$, and $F_{1,8} = 10.54$, $p = 0.01$, $R^2 = 0.57$, respectively).

Depth-specific zoobenthos production

Dissolved oxygen was the best single predictor of within- and among-lake variation in depth-specific zoobenthos production that we considered, while benthic primary production was the worst (Fig. 2; Table 2). The best model as indicated by AICc was the one that contained only dissolved oxygen and the lake term as predictors, and this model was clearly better than the next-best model (ΔAICc = 11), which contained only temperature and the lake term. Individually, benthic primary production was the least effective predictor

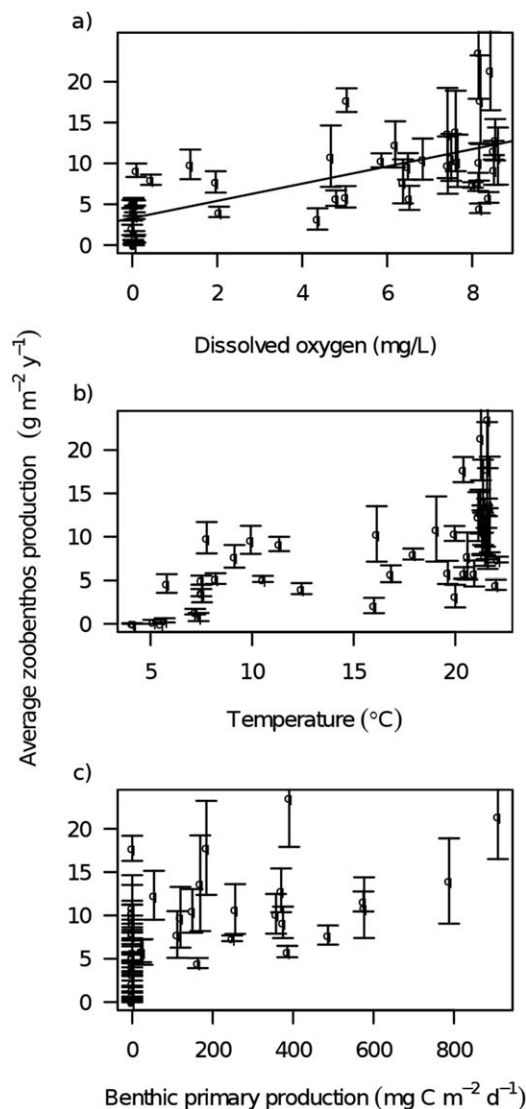**Fig. 2.** Depth-specific zoobenthos production plotted against mean depth-specific (**a**) dissolved oxygen concentration, (**b**) water temperature, and (**c**) benthic primary production. Each point represents a depth-lake combination; error bars are ± 1 SE of production estimates across four replicate sites per depth. The best model describing variation in zoobenthos production included dissolved oxygen and a lake blocking term, but not temperature or benthic primary production.

of zoobenthos production, and its estimated coefficient did not differ from zero in any model that included either dissolved oxygen or temperature as a predictor. We observed that sites with zero benthic primary production had zoobenthos production ranging between 0 g m^{-2} yr^{-1} and 17.7 g m^{-2} yr^{-1} (i.e., including the lowest and nearly the highest rates of zoobenthos production that we measured); furthermore, there was little or no trend in zoobenthos production with increasing benthic primary production above 0 (Fig. 2c).

Patterns of zoobenthos production with depth mirrored the depth response of dissolved oxygen and other environ-mental gradients observed within the lakes, which were strongly influenced by DOC. In clear (low DOC) lakes, zoobenthos production was fairly constant across depths, with high production even at the deepest sites (Fig. 3a). In stark contrast, production in the darkest (high DOC) lakes was negligible at 4–5 m and deeper (Fig. 3c). Considering that thermocline and oxycline depths are reduced in darker lakes (Fig. 1) and that zoobenthos production is related to these variables (Fig. 2), it appears that zoobenthos production is limited in dark lakes by availability of suitable habitat because oxygen is depleted at shallower depths.

Whole-lake zoobenthos production

Whole-lake average zoobenthos production was nega-tively related to DOC concentration, reflecting the loss of productivity at deeper depths in darker lakes (Fig. 4a, $F_{1,8} = 7.89$, $p = 0.02$, $R^2 = 0.50$, log-log regression). While zoobenthos production varied substantially among the lakes with low DOC concentrations, it was low in all of the lakes with high DOC concentrations (Fig. 3 & 4a). Whole-lake zoobenthos production was positively related to whole-lake average estimates of dissolved oxygen ($F_{1,8} = 9.25$, $p = 0.02$, $R^2 = 0.54$, log-log regression), temperature ($F_{1,8} = 20.73$, $p = < 0.01$, $R^2 = 0.72$, log-log regression) and benthic primary production ($F_{1,8} = 13.4$, $p = < 0.01$, $R^2 = 0.62$, log-log regres-sion), all of which were also negatively related to DOC con-centration. There was no relationship between water column nutrient concentrations (total phosphorus and total nitro-gen) and whole-lake zoobenthos production ($p > 0.13$, $R^2 < 0.26$). Fish biomass (measured as biomass catch per unit effort) was positively related to zoobenthos production for the six lakes in which data was available (Fig. 4b, $F1,4 = 18.46$, $p = 0.01$, $R^2 = 0.82$).

Resource use

Reliance of zoobenthos collected from 1 m depth on benthic primary production was moderate to high in the clearest lakes, declined over a DOC range of ~7–9 mg/L, and was generally lower in the dark lakes with DOC > 9 mg/L (Fig. 5). Zoobenthos reliance on terrestrial and pelagic pri-mary production (medians of posterior distributions; see Supporting Information Appendix 2 for additional detail) ranged from 19% to 65% and from 6% to 46%, respectively; neither was clearly related to DOC concentration.

Discussion

A revised conceptual model for the effects of DOC on food web productivity

The current conceptual model of lake food webs in nutrient-poor settings posits that the effect of DOC on light availability limits resource availability in the form of benthic primary production, thereby limiting zoobenthos and ulti-mately fish production (Karlsson et al. 2009; Finstad et al. 2014). This conceptual model assumes that benthic primary

Table 2. Summary of bias-corrected linear measurement error models relating depth-specific zoobenthos production in 10 lakes to mean depth-specific dissolved oxygen concentration (DO, mg/L), water temperature (Temp, °C), and benthic primary production (BPP, mg C m^{-2} d^{-1}). All predictor variables were log($x + 1$) transformed and converted to Z-scores. Models are sorted by ΔAICc, with the best model in the top row. Estimates of the coefficients included in the model (with bootstrapped 95% confidence intervals) are given in the first three columns; each model also included lake as a blocking term. Bold text indicates coefficients for which the 95% CI does not include zero. R^2 estimates are not valid in the presence of measurement error and are provided only as rough aids to interpretation.

DO	Temp	BPP	R^2	ΔAICc
3.4 (2.5, 4.1)	–	–	0.76	0
–	**3.0 (1.9, 4.0)**	–	0.66	11
–	–	**3.0 (1.6, 3.8)**	0.65	18
4.2 (2.3, 5.9)	−0.9 (−2.8, 1.0)	–	0.77	52
2.9 (1.6, 4.4)	–	0.7 (−1.1, 2.0)	0.77	93
–	**1.6 (0.3, 3.5)**	1.8 (−0.3, 3.0)	0.69	105
3.7 (1.8, 5.8)	−1.1 (−3.0, 0.9)	0.8 (−1.0, 2.1)	0.77	143

production is the essential resource that limits zoobenthos production, such that zoobenthos production increases when benthic primary production increases. Our results do not support that assumption. While benthic primary production by itself is significantly related to zoobenthos production, this model had much lower predictive ability than models that included water temperature or, especially, dissolved oxygen as predictors. Furthermore, confidence intervals for this effect overlapped zero whenever water temperature or dissolved oxygen also appeared in the model. Many sites with zero benthic primary production had quite high rates of zoobenthos production, up to 75% of the maximum zoobenthos production that we observed at any site. Similarly to the results of Northington et al. (2010), only a weak relationship existed between zoobenthos production and benthic primary production at sites with nonzero benthic primary production. If we consider patterns at 1 m depth across lakes of increasing DOC, we observed decreases in benthic primary production ($F_{1,8} = 14.52$, $p = <0.01$, $R^2 = 0.64$) and reliance of zoobenthos on benthic primary production (Fig. 5), yet no decrease in production of zoobenthos ($F_{1,8} = 0.44$, $p = 0.52$, $R^2 = 0.05$). Taken as a whole, our results do not support the idea that benthic primary production is the key limiting factor for zoobenthos production.

Instead, our results suggest that DOC affects zoobenthos and ultimately fish production largely by limiting the availability of warm and well-oxygenated habitat. Dissolved oxygen concentration was by far the strongest single predictor of depth-specific zoobenthos production in these lakes, followed by temperature. Zoobenthos production was generally very low at sites with hypoxic conditions (near-zero dissolved oxygen; Fig. 2). Because hypoxic conditions persisted across most of the potentially available habitat in high-DOC lakes, these lakes had much lower whole-lake zoobenthos production than did low-DOC lakes. Hypoxia has been identified as a limiting factor for zoobenthos production in previous studies, usually in cases where hypoxia results from eutrophication (e.g., Jónasson 1984; Dermott 1988). Some authors have also suggested that a similar effect might occur as a result of high DOC concentrations (Rasmussen and Kalff 1987; Estlander et al. 2010). However, our study is the first clear demonstration that DOC-driven variability in dissolved oxygen concentrations can control zoobenthos production. One simple way to conceptualize this pattern is as a DOC-induced "squeeze" of the habitat available to support appreciable zoobenthos production. A similar habitat squeeze has been suggested to drive DOC effects on zooplankton production (Kelly et al. 2014), and could also play a role in limiting fish production in high-DOC lakes (Coutant 1985; Finstad et al. 2014).

The lack of a strong connection between zoobenthos production and benthic primary production suggests that additional basal resources must also be important for supporting zoobenthos. Evidence from our study and a considerable body of literature support this idea. The zoobenthos is a diverse group consisting of specialist and generalist feeders of many guilds, including shredders, predators, collectors, and others (Cummins and Klug 1979; Merritt et al. 2008; Strayer 2009). It is likely that in light-limited sites with low benthic primary production but high zoobenthos production, the zoobenthos are feeding on other resources such as sedimented phytoplankton, bacteria, terrestrial particulate matter, or other invertebrates (Hecky and Hesslein 1995; James et al. 2000; Solomon et al. 2008; Premke et al. 2010; Lau et al. 2014). This idea is supported by our stable isotope results, which showed that zoobenthos reliance on combined terrestrial and pelagic primary production was, in the majority of cases, higher than their reliance on benthic primary production (Supporting Information Appendix 2). While benthic primary production clearly can be an important food resource for some zoobenthos in some locations (Strayer and Likens 1986; Hillebrand and Kahlert 2001;
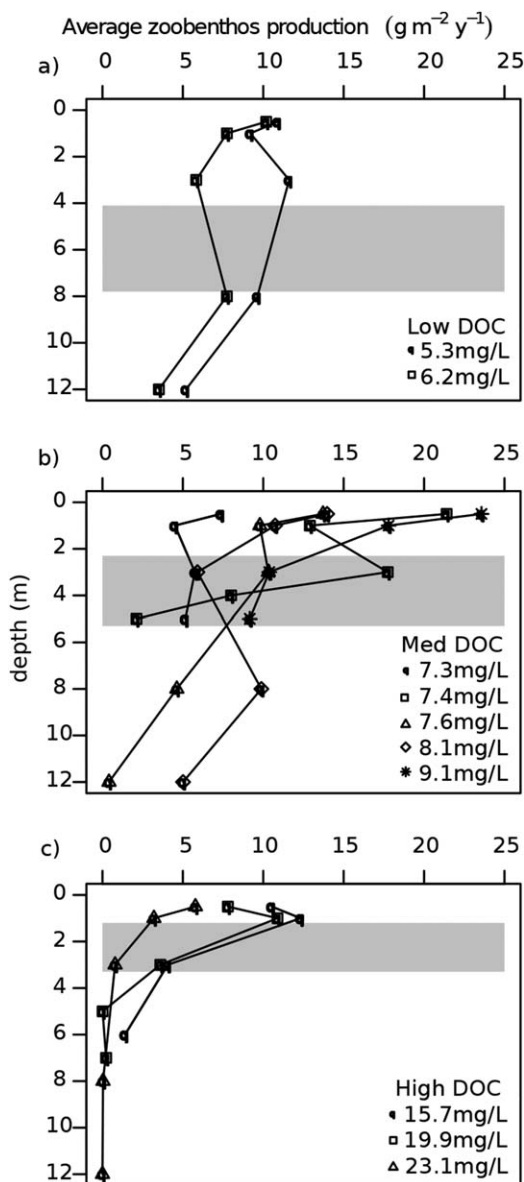
Fig. 3. Zoobenthos production across depths in lakes where DOC concentrations are (**a**) low, (**b**) intermediate, and (**c**) high. The average position of the metalimnion (the depth zone where temperature is changing at $> 1°C\ m^{-1}$) in each set of lakes is indicated by the horizontal gray bands.

Vadeboncoeur and Steinman 2002; Solomon et al. 2011; Devlin et al. 2013), our results, like those of Northington et al. (2010), demonstrate that it is not the strongest predictor of zoobenthos biomass and production.

It is important to note that our results do support the central idea of the conceptual model proposed by Karlsson et al. (2009)—that DOC concentrations can limit zoobenthos and fish production—as well as most of the mechanisms within that model. We saw that high-DOC lakes had more rapid light extinction, lower benthic primary production,

and lower zoobenthos production. Furthermore, the data that we have available on fish populations in these lakes suggests that fish biomass is positively related to zoobenthos production (Fig. 4b), although other mechanisms such as the oxygen-mediated habitat squeeze might also affect fish biomass. This result is consistent with the patterns in fish production across DOC gradients observed by Karlsson et al. (2009) and Finstad et al. (2014), and with the idea that zoobenthos are a major contributor to fish production in lakes (Vander Zanden and Vadeboncoeur 2002; Weidel et al. 2008). Our major contribution is to show that this DOC effect on food web productivity of higher consumers is primarily a function of oxygen and habitat limitation rather than light limitation.

Unexplained variability in zoobenthos production

While the environmental factors that we considered explain a great deal of the within- and among-lake variation in zoobenthos production, there is appreciable variation not explained by our statistical models. Two aspects of this unexplained variation are particularly instructive to consider. First, we observed considerable variation in zoobenthos production at shallow depths that was not related to dissolved oxygen concentration, benthic primary production, or temperature. Factors such as sediment and macrophyte structure, wave action, and predation have been shown to have important influences on zoobenthos biomass in littoral zones, and likely played a role in our study as well (Rasmussen and Kalff 1987; Moss and Timms 1989; Tolonen et al. 2001). Lake depth and stratification strength also seem to play a role; the two lakes with the highest rates of zoobenthos production at shallow sites, Brown and Inkpot, were the only two in our study that never fully stratified, due to their relatively large size and shallow depth. Because periodic mixing of the water column reduces hypoxia and regenerates nutrients, shallow systems like these may have higher zoobenthos productivity than would be predicted on the basis of DOC alone (Finstad et al. 2014). Second, zoobenthos production varied appreciably (from 0 g m^{-2} yr^{-1} to 5.2 g m^{-2} yr^{-1}) even among hypoxic sites where mean dissolved oxygen concentrations were < 0.05 mg L^{-1}. Previous work has shown that the duration of hypoxia can be an important control on zoobenthos; for instance, Jónasson (1984) found that chironomid growth and reproduction in a eutrophic lake was negatively related to the duration of summer stratification in which oxygen concentrations over sediments were depleted. Logistical constraints prevented us from obtaining oxygen profiles for our ten lakes on more than the three sampling occasions, but if we regress site-specific zoobenthos production against the number of sampling dates per site that experienced hypoxic conditions (dissolved oxygen < 0.05 mg/L), we see a significant negative trend ($F_{10,36} = 11.82$, $p = < 0.001$, $R^2 = 0.7$, including lake as a blocking factor). Future studies might be able to better resolve this effect. It is interesting to note the
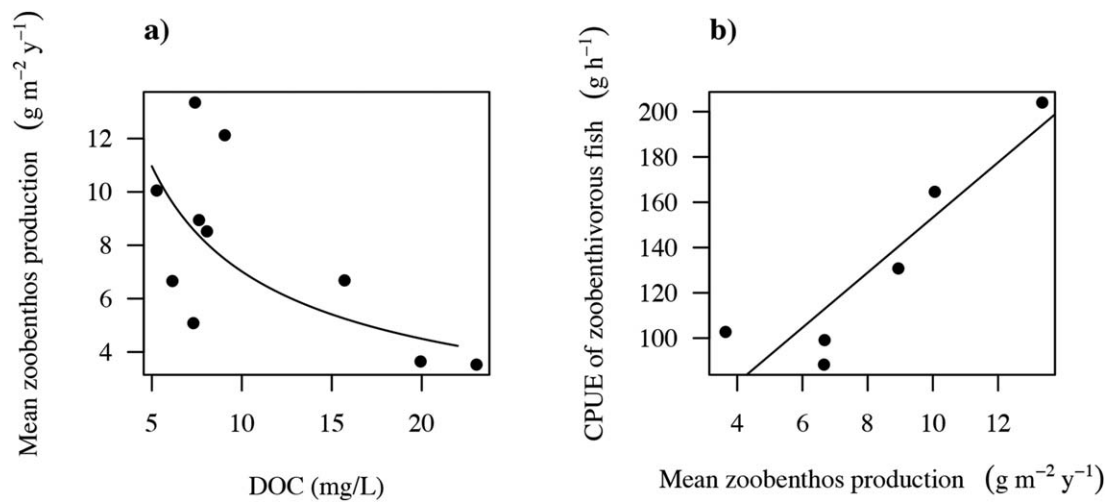
Fig. 4. Relationships between zoobenthos production and, (**a**) DOC concentration for the 10 survey lakes ($F_{1,8} = 7.89$, $p = 0.02$, $R^2 = 0.50$, log-log regression), (**b**) catch-per-unit effort of zoobenthivorous fish (CPUE, in biomass units) for the six survey lakes where fish data were available ($F_{1,4} = 18.46$, $p = 0.01$, $R^2 = 0.82$).
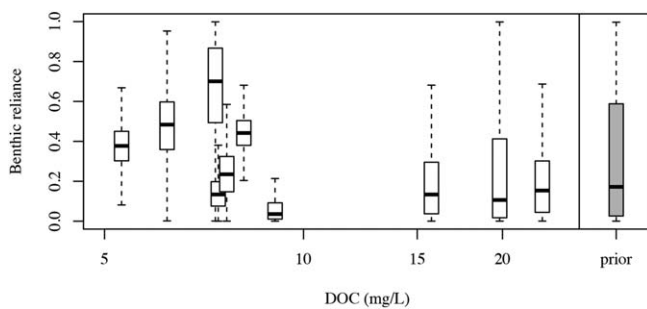

Fig. 5. Benthic reliance (proportion of biomass derived from benthic primary production) of zoobenthos in ten lakes across a gradient of DOC concentrations. Box plots show the 2.5th, 25th, 50th, 75th, and 97.5th percentiles of the posterior probability distributions for benthic reliance, based on a Bayesian stable isotope mixing model. The prior probability distribution is shown at the right edge of the figure. Zoobenthos for this analysis were collected from 1 m depth in each lake.

parallels between high nutrient and high DOC concentrations, both of which are increasing globally (Bennett et al. 2001; Monteith et al. 2007), affect water clarity, and can increase hypolimnetic hypoxia and therefore decrease zoobenthos production.

Conclusions

Ecologists have long debated the role of resources and habitat in controlling consumer populations. In lake ecosystems, nutrient limitation of primary producers is often recognized as a major control on the production of higher trophic levels. More recently it has become clear that, in the relatively nutrient-poor systems that dominate northern landscapes, DOC is a major regulator of productivity from the base of the food web to its apex (Prairie 2008; Karlsson

et al. 2009; Finstad et al. 2014; Kelly et al. 2014). It is important to note that this study focused on a restricted number of relatively small, shallow lakes, which although numerically dominant (Verpoorter et al. 2014), may react differently compared to large, deep, highly mixed ones. Nonetheless, our results confirm that DOC concentrations can limit productivity of zoobenthos and ultimately fishes, and demonstrate that this occurs mainly via oxygen-mediated habitat limitation rather than light-mediated resource limitation. In the face of considerable spatial variability and ongoing temporal change in DOC concentrations in northern lake ecosystems (Monteith et al. 2007; Sobek et al. 2007), this mechanistic insight may improve understanding and management of lake food webs.

References

Arvola, L. 1984. Vertical distribution of primary production and phytoplankton in two small lakes with different humus concentration in Southern Finland. Holarctic Ecol. **7**: 390–398. doi:10.1111/j.1600-0587.1984.tb01140x

Ask, J., J. Karlsson, and M. Jansson. 2012. Net ecosystem production in clear-water and brown-water lakes. Global Biogeochem. Cycles **26**: GB1017. doi:10.1029/2010GB003951

Babler, A. L., C. T. Solomon, and P. R. Schilke. 2008. Depth-specific patterns of benthic secondary production in an oligotrophic lake. J. N. Am. Benthol. Soc. **27**: 108–119. doi:10.1899/07-053.1

Bennett, E. M., S. R. Carpenter, and N. F. Caraco. 2001. Human impact of erodible phosphorus and eutrophication: A global perspective. Bioscience **51**: 227–234. doi:10.1641/0006-3568(2001)051[0227:HIOEPA]2.0.CO;2

Carpenter, S. R., and others. 2001. Trophic cascades, nutrients, and lake productivity: Whole-lake experiments.

Ecol. Monogr. **71**: 163–186. doi:10.1890/0012-9615(2001)071[0163:TCNALP]2.0.CO;2

Carroll, R. J., D. Ruppert, L. A. Stefanski, and C. M. Crainiceanu. 2006. Measurement error in non-linear models: A modern perspective, 2nd ed., p. 55–57. Chapman & Hall.

Cheng, C.-L., Shalabh, and G. Garg. 2014. Coefficient of determination for multiple measurement error models. J. Multivariate Anal. **126**: 137–152. doi:10.1016/j.jmva.2014.01.006

Cole, J. J., M. L. Pace, S. R. Carpenter, and J. F. Kitchell. 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulations. Limnol. Oceanogr. **45**: 1718–1730. doi:10.4319/lo.2000.45.8.1718

Cole, J. J., S. R. Carpenter, J. Kitchell, M. L. Pace, C. T. Solomon, and B. Weidel. 2011. Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. Proc. Natl. Acad. Sci. USA **108**: 1975–1980. doi:10.1073/pnas.1012807108

Coutant, C. C. 1985. Striped bass, temperature, and dissolved oxygen: A speculative hypothesis for environmental risk. Trans. Am. Fish. Soc. **114**: 31–61. doi:10.1577/1548-8659(1985)114<31:SBTADO>2.0.CO;2

Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. Annu. Rev. Ecol. Syst. **10**: 147–172. doi:10.1146/annurev.es.10.110179.001051

Dermott, R. M. 1988. Zoobenthic distribution and biomass in the Turkey Lakes. Can. J. Fish. Aquat. Sci. **45**: 107–114. doi:10.1139/f88-274

Devlin, S. P., M. J. Vander Zanden, and Y. Vadeboncoeur. 2013. Depth-specific variation in carbon isotopes demonstrates resource partitioning among the littoral zoobenthos. Freshw. Biol. **58**: 2389–2400. doi:10.1111/fwb.12218

Estlander, S., and others. 2010. Diet shifts and food selection of perch *Perca fluviatilis* and roach *Rutilus rutilus* in humic lakes of varying water colour. J. Fish Biol. **77**: 241–256. doi:10.1111/j.1095-8649.2010.02682.x

Finstad, A. G., I. P. Helland, O. Ugedal, T. Hesthagen, and D. O. Hessen. 2014. Unimodal response of fish yield to dissolved organic carbon. Ecol. Lett. **17**: 36–43. doi:10.1111/ele.12201

Fuller, W. A. 1987. Measurement error models. Wiley.

Godwin, S. C., S. E. Jones, B. C. Weidel, and C. T. Solomon. 2014. Dissolved organic carbon concentration controls benthic primary production: Results from in situ chambers in north-temperate lakes. Limnol. Oceanogr. **59**: 2112–2120. doi:10.4319/lo.2014.59.6.2112

Hansson, L.-A. 1992. Factors regulating periphytic algal biomass. Limnol. Oceanogr. **37**: 322–328. doi:10.4319/lo.1992.37.2.0322

Hecky, R. E., and R. H. Hesslein. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analysis. J. N. Am. Benthol. Soc. **14**: 631–653. doi:10.2307/1467546

Hillebrand, H., and M. Kahlert. 2001. Effect on grazing and nutrient supply on periphyton biomass and nutrient stoichiometry in habitats of different productivity. Limnol. Oceanogr. **46**: 1881–1898. doi:10.4319/lo.2001.46.8.1881

Holsinger, J. R. 1972. The freshwater amphipod crustaceans (Gammaridae) of North America. Biota of Freshwater Ecosystems, Identification Manual 5. U.S. EPA, 89 p.

James, M. R., I. Hawes, M. Weatherhead, C. Stanger, and M. Gibbs. 2000. Carbon flow in the littoral food web of an oligotrophic lake. Hydrobiologia **441**: 93–106. doi:10.1023/A:1017504820168

Jónasson, P. M. 1984. Oxygen demand and long term changes of profundal zoobenthos. Hydrobiologia **115**: 121–126. doi:10.1007/BF00027905

Jones, R. I. 1992. The influence of humic substances on lacustrine planktonic food chains. Hydrobiologia **229**: 73–91. doi:10.1007/BF00006992

Karlsson, J., P. Byström, J. Ask, P. Ask, L. Persson, and M. Jansson. 2009. Light limitation of nutrient-poor lake ecosystems. Nature **460**: 506–509. doi:10.1038/nature08179

Kelly, P. T., C. T. Solomon, B. C. Weidel, and S. E. Jones. 2014. Terrestrial carbon is a resource, but not a subsidy, for lake zooplankton. Ecology **95**: 1236–1242. doi:10.1890/13-1586.1

Lau, D. C. P., I. Sundh, T. Vrede, J. Pickova, and W. Goedkoop. 2014. Autochthonous resources are the main driver of consumer production in dystrophic boreal lakes. Ecology **95**: 1506–1519. doi:10.1890/13-1141.1

Manly, B. F. J. 2007. Randomization, bootstrap and Monte Carlo methods in biology, 3rd ed., p. 41–80. Chapman & Hall.

Merritt, R. W., K. W. Cummins, and M. B. Berg. 2008. An introduction to the aquatic insects of North America, 4th ed. Kendall Hunt.

Monteith, D. T., and others. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature **450**: 537–541. doi:10.1038/nature06316

Moss, B., and M. Timms. 1989. Predation, sediment stability and food availability as determinants of the benthic invertebrate fauna in two shallow lakes. Hydrobiologia **185**: 249–257. doi:10.1007/BF00036613

Northington, R. C., M. D. Keyse, S. R. Beaty, S. C. Whalen, E. R. Sokol, and A. E. Hershey. 2010. Benthic secondary production in eight oligotrophic arctic Alaskan lakes. J. N. Am. Benthol. Soc. **29**: 465–479. doi:10.1899/09-026.1

Plante, C., and J. A. Downing. 1989. Production of freshwater invertebrate populations in lakes. Can. J. Fish. Aquat. Sci. **46**: 1489–1498. doi:10.1139/f89-191

Prairie, Y. T. 2008. Carbocentric limnology: Looking back, looking forward. Can. J. Fish. Aquat. Sci. **65**: 543–548. doi:10.1139/f08-011

Premke, K., J. Karlsson, K. Steger, C. Gudasz, E. von Wachenfeldt, and L. J. Tranvik. 2010. Stable isotope

analysis of benthic fauna and their food sources in boreal lakes. J. N. Am. Benthol. Soc. **29**: 1339–1348. doi:10.1899/10-002.1

Rasmussen, J. B. 1988. Littoral zoobenthic biomass in lakes, and its relationship to physical, chemical, and trophic factors. Can. J. Fish. Aquat. Sci. **45**: 1436–1447. doi:10.1139/f88-168

Rasmussen, J. B., and J. Kalff. 1987. Empirical models for zoobenthic biomass in lakes. Can. J. Fish. Aquat. Sci. **44**: 990–1001. doi:10.1139/f87-117

Read, J. S., and K. C. Rose. 2013. Physical responses of small temperate lakes to variation in dissolved organic carbon concentrations. Limnol. Oceanogr. **58**: 921–931. doi:10.4319/lo.2013.58.3.0921

Snucins, E., and J. Gunn. 2000. Interannual variation in the thermal structure of clear and colored lakes. Limnol. Oceanogr. **45**: 1639–1646. doi:10.4319/lo.2000.45.7.1639

Sobek, S., L. J. Tranvik, Y. T. Prairie, P. Kortelainen, and J. J. Cole. 2007. Patterns and regulation of dissolved organic carbon: An analysis of 7,500 widely distributed lakes. Limnol. Oceanogr. **52**: 1208–1219. doi:10.4319/lo.2007.52.3.1208

Solomon, C. T., S. R. Carpenter, J. J. Cole, and M. L. Pace. 2008. Support of benthic invertebrates by detrital resources and current autochthonous primary production: Results from a whole-lake ^{13}C addition. Freshw. Biol. **53**: 42–54. doi:10.1111/j.1365-2427.2007.01866.x

Solomon, C. T., and others. 2011. Terrestrial, benthic, and pelagic resource use in lakes: Results from a three-isotope Bayesian mixing model. Ecology **92**: 1115–1125. doi:10.1890/10-1185.1

Stern, E. M. 1990. An illustrated key to the freshwater mussels (Bivalvia: Unionacea) of Wisconsin. Reports of the Museum of Natural History, University of Wisconsin-Stevens Point, Wisconsin.

Strayer, D. L. 2009. Benthic invertebrate fauna, lakes and reservoirs, p. 191–204. *In* E. Likens [ed.], Encyclopedia of inland waters, v. 2. Elsevier.

Strayer, D., and G. E. Likens. 1986. An energy budget for the zoobenthos of Mirror Lake, New Hampshire. Ecology **67**: 303–313. doi:10.2307/1938574

Tolonen, K. T., H. Hämäläinen, I. J. Holopainen, and J. Karjalainen. 2001. Influences of habitat type and environmental variables on littoral macroinvertebrate communities in a large lake system. Fundam. Appl. Limnol. **152**: 39–67.

Vadeboncoeur, Y., and A. D. Steinman. 2002. Periphyton function in lake ecosystems. ScientificWorldJournal **2**: 1449–1468. doi:10.1100/tsw.2002.294

Vadeboncoeur, Y., G. Peterson, M. J. Vander Zanden, and J. Kalff. 2008. Benthic algal production across lake size gradients: Interactions among morphometry, nutrients, and light. Ecology **89**: 2542–2552. doi:10.1890/07-1058.1

Vander Zanden, M. J., and Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology **83**: 2152–2161. doi:10.1890/0012-9658(2002)083[2152:FAIOBA]2.0.CO;2

Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. Annu. Rev. Ecol. Syst. **33**: 341–370. doi:10.1146/annurev.ecolsys.33.010802.150519

Verpoorter, C., T. Kutser, D. A. Seekell, and L. J. Tranvik. 2014. A global inventory of lakes based on high-resolution satellite imagery. Geophys. Res. Lett. **41**: 6396–6402. doi:10.1002/2014GL060641

Weidel, B., S. Carpenter, J. Cole, J. Hodgson, J. Kitchell, M. Pace, and C. Solomon. 2008. Carbon sources supporting fish growth in a north temperate lake. Aquat. Sci. **70**: 446–458. doi:10.1007/s00027-008-8113-2

Wetzel, R. G. 2001. Limnology: Lake and river ecosystems, 3rd ed. Academic.

Wissel, B., W. J. Boeing, and C. W. Ramcharan. 2003. Effects of water color on predation regimes and zooplankton assemblages in freshwater lakes. Limnol. Oceanogr. **48**: 1965–1976. doi:10.4319/lo.2003.48.5.1965