

# Terrestrial carbon is a resource, but not a subsidy, for lake zooplankton

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**Abstract.** Inputs of terrestrial organic carbon (t-OC) into lakes are often considered a resource subsidy for aquatic consumer production. Although there is evidence that terrestrial carbon can be incorporated into the tissues of aquatic consumers, its ability to enhance consumer production has been debated. Our research aims to evaluate the net effect of t-OC input on zooplankton. We used a survey of zooplankton production and resource use in ten lakes along a naturally occurring gradient of t-OC concentration to address these questions. Total and group-specific zooplankton production was negatively related to t-OC. Residual variation in zooplankton production that was not explained by t-OC was negatively related to terrestrial resource use (allochthony) by zooplankton. These results challenge the designation of terrestrial carbon as a resource subsidy; rather, the negative effect of reduced light penetration on the amount of suitable habitat and the low resource quality of t-OC appear to diminish zooplankton production. Our findings suggest that ongoing continental-scale increases in t-OC concentrations of lakes will likely have negative impacts on the productivity of aquatic food webs.

**Key words:** *allochthony; DOC; light extinction coefficient; resource subsidy; terrestrial carbon; zooplankton production.*

## INTRODUCTION

Polis et al. (1997) describe a resource subsidy as “a donor-controlled resource (prey, detritus, nutrients) from one habitat to a recipient from a second habitat that increases population productivity of the recipient.” From this definition, it is the (1) cross-ecosystem flux of material and (2) increase in recipient consumer productivity that distinguishes a resource as a subsidy. Despite an increase in attention by ecologists, resource subsidies as a whole are still not well understood, and there is surprisingly little empirical data on consumer responses to the cross boundary flow of matter or energy, especially from freshwater ecosystems (Marczak et al. 2007).

Input of terrestrial dissolved and particulate organic carbon (t-OC) to aquatic ecosystems is commonly cited as an example of a resource subsidy (Polis et al. 1997). Terrestrial organic carbon often dominates the carbon pools of lakes, and may represent a significant resource for zooplankton consumers (Karlsson et al. 2002, Cole et al. 2006, Jonsson et al. 2007). However, low nutritional quality and negative effects of dissolved t-OC on aquatic primary production cast some doubt on the designation of t-OC as a resource subsidy (Brett et

al. 2009, Jones et al. 2012). Because zooplankton represent an important link in aquatic food webs, their response to observed and projected global increases in t-OC supply (Clark et al. 2010) is likely to have broad implications for lake food webs.

Existing evidence suggests that zooplankton assimilate significant amounts of terrestrial carbon in some lakes (Carpenter et al. 2005, Cole et al. 2006, 2011). For example, mean zooplankton allochthony, or the proportion of biomass derived from terrestrial material, was estimated as 53% in a set of 15 Swedish lakes (Karlsson et al. 2003). Similarly, Solomon et al. (2011) reported zooplankton allochthony estimates as high as 80%. There are also lakes, usually with low inputs of t-OC, where zooplankton allochthony approaches zero (Pace et al. 2007, Francis et al. 2011). Studies suggesting significant support of zooplankton biomass from allochthonous carbon in unproductive systems provide evidence for its use as a resource subsidy (Carpenter et al. 2005).

Despite the growing view of t-OC as a resource subsidy for zooplankton there are reasons to believe that terrestrial carbon may actually reduce zooplankton production. Greater dissolved t-OC concentrations increase light attenuation and consequently lead to a constrained epilimnion and decreased phytoplankton abundance (Carpenter et al. 1998, Ask et al. 2009, Jones et al. 2012). This shading causes a replacement of high quality phytoplankton resources with lower-quality t-OC (Brett et al. 2009). Therefore, greater light attenu-

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ation may decrease zooplankton production as a result of reduced volume of ideal habitat via a shrinking of the mixed layer, and diminished availability of high-quality food (primary production and/or chlorophyll *a*). Terrestrial organic matter is also hypothesized to be a poor quality food for zooplankton. The high C:P and low essential fatty acid content of t-OC suggests it is insufficient to promote biomass production (Sterner 1993, Brett et al. 2009), although recent work suggests that terrestrial carbon inputs may be of higher quality than previously thought (Preston et al. 2008, Berggren et al. 2010).

Our study exploits natural, among-lake variation in t-OC concentration to determine the net effect of this putative resource subsidy on zooplankton productivity. Using a survey of 10 lakes, we identified a strong negative relationship between zooplankton biomass production and both t-OC concentration (measured as either the dissolved organic carbon concentration, DOC, or as the diffuse light attenuation coefficient,  $K_d$ ) and terrestrial resource reliance (allochthony). The results from our study challenge the idea that t-OC is a resource subsidy for zooplankton, and provide expectations for the food web implications of observed continental-scale increases in supply of terrestrial carbon to aquatic ecosystems (Monteith et al. 2007).

## METHODS

### *Sample collection*

We conducted our 10-lake survey at the University of Notre Dame Environmental Research Center (UNDERC), located in the northern Midwest of the United States. Lakes varied in trophic status from clear-water, oligo-mesotrophic systems to humic, dystrophic lakes (Wetzel 2001). The lakes also varied in food web structures, with the main planktivores being juvenile centrarchids, cyprinids, and the invertebrate *Chaoborus*.

Zooplankton samples were collected each week from late May through mid-August 2011. Duplicate vertical tows were taken with an 80- $\mu\text{m}$  mesh zooplankton net (Aquatic Research Instruments, Hope, Idaho, USA) from 2 m from the bottom to the surface at the approximate deepest location of each lake. Tows were combined and fixed using Lugol's solution. For samples to be used for stable isotope analysis, multiple tows were taken at the deepest location of each lake, and live zooplankton were separated by taxon and dried at 60°C until analysis. Particulate organic carbon (POC) was analyzed for stable isotopes by filtering approximately 200 mL of water from the upper mixed layer through 0.45- $\mu\text{m}$  GF/F filters. Both zooplankton and POC samples were run on a Finnigan Delta Plus isotope ratio mass-spectrometer (Thermo Scientific, Waltham, Massachusetts, USA) to determine  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . Zooplankton, particulate organic carbon (POC), and water for  $\delta^2\text{H}$  analysis were atmosphere equilibrated and processed by the Colorado Plateau Stable Isotope Laboratory (CPSIL, Northern Arizona University,

Flagstaff, Arizona, USA). Integrated water samples were taken from the upper mixed layer for analysis of water chemistry characteristics. Total nitrogen (following persulfate digestion) was analyzed using a spectrophotometric method (Olsen 2008), total phosphorous (following persulfate digestion) was measured using a colorimetric assay (Menzel and Corwin 1965), chlorophyll *a* was analyzed using methanol extraction and a fluorometric method (Welschmeyer 1994), and dissolved organic carbon was analyzed using a Shimadzu TOC-V total organic carbon analyzer (Shimadzu Scientific Instruments, Kyoto, Japan). Light extinction coefficients ( $K_d$ ) were determined using water column photosynthetically active radiation (PAR) measurements every 0.5 m from the surface to the depth at 1% of surface light. Mixed layer depth was calculated as the first depth at which there is a greater than 1 degree temperature change over a one meter change in depth.

### *Zooplankton production estimation*

Zooplankton samples were subsampled and counted according to the following taxonomic classifications: calanoid copepods, cyclopoid copepods, *Daphnia* spp., *Holopedium*, *Diaphanasoma*, *Bosmina*, and *Chydorus* using a Bogorov counting tray and a stereo microscope. A sample of 1000 individuals, or all individuals if less than 1000 were present, were counted from each sample. Subsamples were extrapolated to estimate whole sample abundance of each taxon. Approximately 25 individuals from each taxonomic group in each sample were photographed using Leica imaging software (Leica, Solms, Germany), and their lengths were measured using imageJ software (*available online*).<sup>5</sup> Lengths were converted to biomass estimates for each taxon using published length-mass relationships (McCauley 1984). Secondary production was preferentially used as a response variable over standing biomass due to its importance as a measure of energy flow through an ecosystem (Dolbeth et al. 2012). Zooplankton biomass production for each taxon was calculated with a previously published regression model for the production of freshwater invertebrates ( $r^2 = 0.79$ ; Plante and Downing 1989). Total zooplankton production was calculated as the sum of all individual taxon productions.

### *Data analysis*

A Bayesian mixing model, using C, N, and H stable isotope ratios, was used to estimate resource use by zooplankton (Solomon et al. 2011). End members for the model were phytoplankton, t-OC, and methane oxidizing bacteria (Jones et al. 1999). Terrestrial end members were taken from averages of the leaves from the most common trees in the watersheds (Cole et al. 2011). As phytoplankton is difficult to separate from

<sup>5</sup> <http://rsbweb.nih.gov/ij/>

TABLE 1. Summary of water chemistry and planktivore characteristics for each survey lake.

Lake	Area (ha)	Temperature (°C)	DOC (mg/L)	$K_d$ ( $m^{-1}$ )	Chlorophyll <i>a</i> ( $\mu g/L$ )	Total N ( $\mu g/L$ )	Total P ( $\mu g/L$ )	<i>Chaoborus</i> density (no./ $m^2$ )	Mixed layer depth (m)	Piscivore present/absent
Bay	67.30	22.7 (1.1)	5.9 (0.7)	0.99	4.5 (0.7)	427.8 (5.6)	14.6 (3.8)	154.4 (47.4)	2.7 (0.1)	present
Bergner	17.85	22.1 (0.9)	11.8 (2.5)	1.50	5.9 (0.8)	497.7 (13.5)	21.5 (4.7)	430.2 (113.5)	3.3 (0.3)	present
Brown	32.57	21.8 (1.0)	9.3 (0.6)	1.09	8.9 (3.7)	511.1 (27.0)	36.3 (8.6)	58.0 (29.4)	3.0 (0.0)	present
Crampton	25.81	21.9 (1.0)	5.4 (1.1)	0.77	5.6 (0.7)	430.6 (52.9)	20.1 (5.4)	156.5 (47.7)	5.0 (0.2)	present
Hummingbird	0.76	23.3 (1.3)	25.9 (1.6)	3.09	14.2 (4.0)	903.8 (88.7)	35.0 (7.9)	1113.7 (305.2)	0.8 (0.1)	present
Inkpot	6.61	22.3 (0.9)	11.4 (2.2)	1.23	3.9 (0.5)	451.1 (13.8)	25.8 (5.7)	232.4 (81.6)	2.7 (0.1)	present
Long	7.87	21.6 (1.1)	8.0 (0.4)	1.83	8.2 (1.8)	422.1 (7.91)	11.3 (1.5)	955.4 (180.2)	1.3 (0.1)	present
Morris	5.93	22.8 (1.1)	17.4 (2.1)	3.22	9.0 (3.0)	709.4 (72.6)	33.3 (7.6)	405.9 (88.7)	1.1 (0.1)	present
Raspberry	4.63	23.2 (1.0)	6.4 (0.4)	1.28	5.0 (0.8)	486.1 (29.7)	27.4 (6.2)	334.6 (133.4)	1.7 (0.1)	present
Reddington	1.24	24.2 (1.1)	22.0 (1.3)	4.64	9.4 (2.3)	693.5 (115.2)	33.8 (8.7)	178.8 (36.3)	0.9 (0.0)	absent

Notes: Values are means with SE in parentheses. DOC stands for dissolved organic carbon. The diffuse light attenuation coefficient is  $K_d$ .

POC in the water column, estimates of phytoplankton isotopic ratios were made based on methods from Cole et al. (2011). Isotope values for methane oxidizing bacteria were taken from Kankaala et al. (2006). Specific end member values for t-OC and methane oxidizing bacteria are given in Appendix A. The median of the posterior distribution for the fractional contribution of terrestrial material from the model was used as the point estimate for zooplankton terrestrial resource use. Terrestrial resource reliance by zooplankton was determined for cladoceran and copepods separately, as well as for total zooplankton. Two lakes (Reddington and Brown) were excluded from this analysis due to insufficient sample size.

We evaluated the support for different hypothesized drivers of zooplankton production, including t-OC, lake productivity, and predation by planktivores, by comparing simple regression models. Direct quantification of the concentration of terrestrial carbon in surface waters is extremely difficult, but a number of reasonable proxies exist. The majority of dissolved organic carbon (DOC) in north temperate lakes is of terrestrial origin (Wilkinson et al. 2013), but algal-derived carbon contributes to this pool. In temperate forested regions terrestrial DOC is responsible for the majority of light attenuation ( $K_d$ ), but algal density and particulates can also contribute to light attenuation, so we evaluated both DOC and  $K_d$  as proxies for t-OC concentration. Total phosphorous and chlorophyll *a* concentrations were used as estimates of lake primary production and thereby resource availability. *Chaoborus* density and food web structure (presence/absence of piscivores) were used to evaluate the effect of predation on zooplankton production.

We used an additional regression analysis to further explore the mechanisms underlying the relationship between t-OC and zooplankton production. Terrestrial resource reliance was used as an indicator of food quality; due to the previously mentioned low EFA content and high C:P of terrestrial carbon, zooplankton with high terrestrial reliance should be consuming lower quality food on average. Mixed layer depth was used as

an indicator of habitat availability. Effect sizes were calculated to compare the relative impacts of the variables on zooplankton production for the most likely model (Coe 2002).

## RESULTS

### *Limnological conditions*

The lakes were selected to span a gradient of terrestrial carbon concentrations, and also covered broad gradients in other limnological characteristics (Table 1). Light attenuation ( $K_d$ ) ranged from 0.8 to 3.1  $m^{-1}$ , and was highly correlated with DOC concentration ( $r = 0.87$ ,  $P < 0.01$ ; Table 1). DOC also correlated strongly with total phosphorous ( $r = 0.64$ ,  $P = 0.04$ ) and volumetric chlorophyll *a* concentrations ( $r = 0.86$ ,  $P < 0.01$ ). There was no relationship between  $K_d$  or DOC and *Chaoborus* densities or food web structure.

### *Zooplankton resource reliance*

Zooplankton reliance on terrestrial resources ranged from 29% (median posterior estimate of total zooplankton assemblage) at Bergner Lake to 52% at Long Lake. The 95% confidence intervals of these estimates were fairly broad (Appendix B). Terrestrial reliance varied by taxa, with cladoceran zooplankton generally containing more terrestrially derived carbon across survey lakes (median posterior terrestrial reliance 29.2% at Bergner Lake to 75% at Inkpot Lake, average 51% across lakes). Copepods were less reliant on terrestrial resources on average (36%), with a maximum of 47% in Crampton Lake (Appendix C). Zooplankton reliance on methanotrophic bacteria ranged from 3% to 21%. These estimates were small relative to reliance on phytoplankton and terrestrial sources, and were comparable to previously reported values (Bastviken et al. 2003).

### *Zooplankton production*

Total and group-specific zooplankton production were strongly negatively related to t-OC, and did not show any significant relationship with other drivers commonly thought to influence zooplankton productivity (Fig. 1, Table 2). Total zooplankton production did

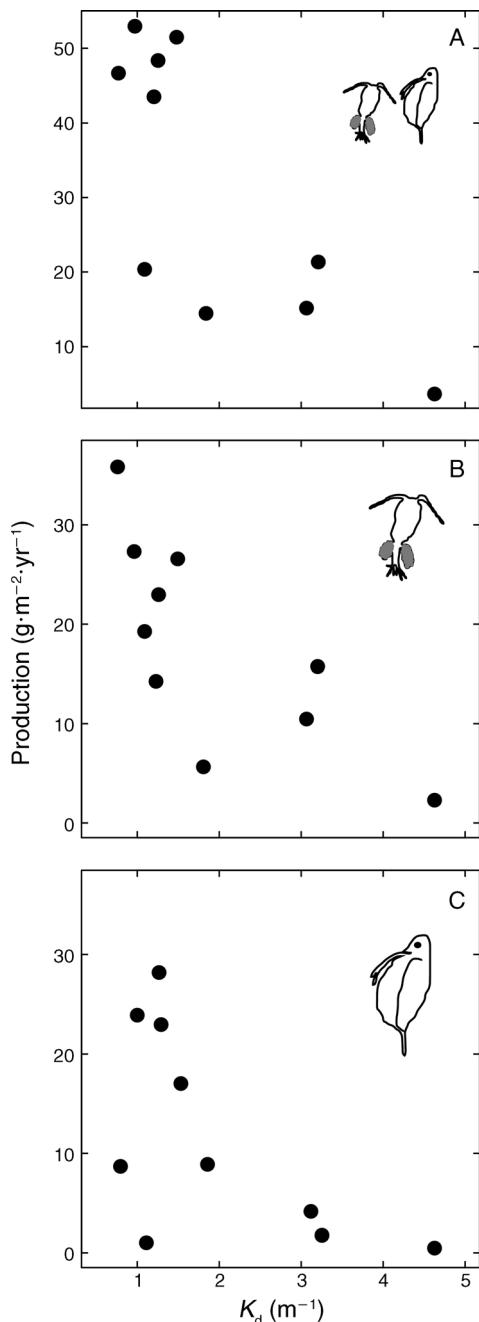


FIG. 1. Relationships between zooplankton production and terrestrial carbon concentration as inferred from the rate of light attenuation (diffuse light attenuation coefficient)  $K_d$ , for (A) total zooplankton, (B) copepod production, and (C) cladoceran production. Total zooplankton production was linearly related to  $K_d$  ( $r^2 = 0.60$ ,  $P < 0.01$ ;  $y = 54.1 - 11.3x$ ).

not show any significant relationship with total phosphorus or chlorophyll *a* as indicators of lake primary production, and there was similarly no significant relationship with *Chaoborus* density or food web structure (Table 2).

Reductions in resource quality and habitat availability at higher t-OC concentrations appear to be likely mechanisms for the negative relationship between zooplankton production and t-OC. Terrestrial resource reliance explained a large amount of residual variation in total zooplankton production after accounting for  $K_d$  ( $r^2 = 0.89$ ,  $P < 0.01$ ; Fig. 2), with both  $K_d$  and terrestrial resource reliance negatively related to zooplankton production. The effect size of  $K_d$  was twice as large as that of terrestrial reliance, and terrestrial reliance was not a significant predictor of production unless  $K_d$  was also included in the model. Total zooplankton production was also significantly positively related to mixed layer depth ( $r^2 = 0.45$ ,  $P = 0.03$ ), which was deeper in lake with low t-OC ( $r = -0.75$ ,  $P = 0.01$ ).

DISCUSSION

Using a cross-lake survey, we identified a negative influence of t-OC concentration on zooplankton production. Our results challenge the idea that allochthonous carbon is a subsidy for zooplankton. While we observe levels of terrestrial support of zooplankton similar to those reported in previous studies, we found that greater t-OC concentration and terrestrial resource reliance by zooplankton appears to diminish zooplankton production rather than increase it. These results highlight the importance of considering the diverse set of resource- and non-resource-mediated effects of t-OC on aquatic food webs.

Our results highlight the habitat-reducing potential and low quality of t-OC as likely mechanisms for the reduction in zooplankton production with greater t-OC. This is supported by the strong negative relationships between zooplankton production and both  $K_d$  (Fig. 1) and mixed layer depth, and by the fact that higher terrestrial reliance was correlated with lower production (Fig. 2). Light attenuation best explained the decrease in production probably because it better quantifies the shading effect of t-OC in the water column, which drives a decrease in habitat through a reduction in mixed layer depth.

Counterintuitively, algal biomass did not predict zooplankton production. In fact, zooplankton produc-

TABLE 2. Model comparisons for relationships between zooplankton production and dissolved organic carbon (DOC), light attenuation ( $K_d$ ), total phosphorous (TP), chlorophyll *a*, piscivore presence/absence (piscivore), and *Chaoborus* density (Chaob).

Model	Hypothesis	Slope	$r^2$	$P$
Production ~ $K_d$	t-OC	-11.31	0.60	<0.01
Production ~ DOC	t-OC	-1.76	0.46	0.03
Production ~ chlorophyll <i>a</i>	resource	-1.12	0.37	0.06
Production ~ piscivore	predation	31.23	0.28	0.11
Production ~ TP	resource	-0.99	0.23	0.16
Production ~ Chaob	predation	-0.02	0.04	0.69

Note: Models were categorized based on hypothesized drivers of zooplankton production (terrestrial organic carbon [t-OC] concentration, resource availability, or predation).

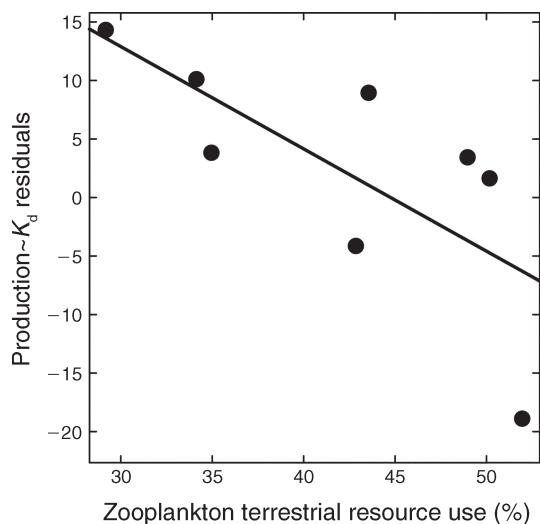


FIG. 2. Partial regression of variation in zooplankton production that was not explained by  $K_d$  (i.e., residuals; y-axis) and terrestrial resource reliance of zooplankton (x-axis;  $r^2 = 0.66$ ,  $P < 0.01$ ).

tion was negatively related to algal biomass. This is potentially due to the tight correlation between TP and DOC, likely from concurrent loading from the watershed (Lennon and Pfaff 2005). Additionally, there was no evidence for reduction of algal biomass due to t-OC-mediated shading in our lakes; in fact, the residuals of the relationship between TP and chlorophyll were positively related to DOC ( $r = 0.58$ ,  $P = 0.08$ ). It is possible that the observed negative relationship between algal biomass and zooplankton production is driven by top-down control of phytoplankton by zooplankton, which has been observed in this region previously (Carpenter et al. 1987).

There are several hypothesized benefits to zooplankton from shading by t-OC; however, the habitat reduction associated with greater t-OC appears to outweigh these potential positive mechanisms in our lakes. Terrestrial organic carbon may act as a refuge from visual planktivores, decreasing predation pressure and increasing production. Greater t-OC has also been demonstrated to increase zooplankton production via shading of harmful UV radiation (Williamson et al. 1994). The decline in production despite these commonly cited benefits to zooplankton productivity emphasizes the strength of physically mediated t-OC effects.

Data from our survey do not support the idea that predation strongly regulates zooplankton production. Planktivory has been shown to have strong effects on zooplankton communities and likely influences zooplankton communities in similar lakes (Carpenter et al. 1985, Carpenter and Kitchell 1987). Yet we did not observe a relationship between zooplankton production and the abundance of *Chaoborus*, the major invertebrate predator of zooplankton in these lakes, nor between zooplankton production and the presence of piscivorous

fish, which can control planktivory via top-down effects (Carpenter et al. 1985). It appears that the role of t-OC as a regulator of mixed layer depth and the poor resource quality of t-OC outweigh any top-down regulation of zooplankton production across a broad gradient in t-OC concentrations.

Increases in terrestrial resource use by zooplankton were associated with reductions in zooplankton production in our study (Fig. 2). Past studies have outlined the importance of terrestrial use within the pelagic food web, and have often suggested that allochthonous t-OC can subsidize aquatic food webs. Carpenter et al. (2005), for example, demonstrated significant support of zooplankton and fish by t-OC. Similar results were presented by Cole et al. (2006, 2011), with high proportions of zooplankton biomass coming from allochthonous origins. However, none of these studies related the level of reliance on t-OC by zooplankton to their productivity. Our results emphasize that, while allochthonous organic matter may make up a significant portion of zooplankton biomass, greater reliance on terrestrial resources appear to reduce production. Although our results do not directly address the food quality of available resources for each lake specifically, previous research has outlined the importance of an autochthonous diet in terms of EFA availability and C:P stoichiometry (Sternner 1993, Persson et al. 2007, Brett et al. 2009). Phytoplankton, relative to t-OC, are a higher quality food source because they are rich in highly unsaturated fatty acids, and are also characterized by low C:P. Greater reliance on recalcitrant terrestrial sources, either directly or through an inefficient microbial loop (Cole et al. 2002), leads to a reduction in zooplankton growth and reproduction.

Greater t-OC impacted both cladoceran and copepod zooplankton negatively, but the effect on cladocerans was stronger. Cladocerans may be impacted more significantly because of their lack of feeding selectivity, while copepods are able to more actively select algal cells (Cowles et al. 1988). Our observation that terrestrial reliance was lower for copepods than for cladocerans is consistent with this explanation (Appendix C).

The relationships between cladoceran and copepod production and t-OC ( $K_d$ ) indicate variable group-specific production at low  $K_d$ , but exclusively low production at high  $K_d$ . This suggests multiple potential controls on zooplankton production at low  $K_d$ , including contrasting upper food web structure (Carpenter et al. 2001) and competition among zooplankton (Lynch 1979). Conversely, in lakes with high t-OC inputs, the reduction in habitat through shading appears to be the strongest driver of zooplankton productivity. These data suggest a threshold of terrestrial inputs, which may decrease habitat and resource quality significantly enough to limit zooplankton production. The similar decline in production for both zooplankton groups indicates that there was no significant taxonomic

compensation when assessing the relationship between total zooplankton production and  $K_d$ .

Our observations suggest that greater t-OC concentrations in aquatic systems have a significant negative impact on aquatic consumer populations likely through simultaneous reduction in habitat and resource quality. Increasing t-OC concentrations in aquatic systems have recently been identified as a widespread environmental change (Monteith and Evans 2005, Monteith et al. 2007), which may amplify the importance and implications of our findings. A terrestrial carbon-driven reduction in zooplankton production would be expected to negatively impact recruitment and growth of fish populations, as zooplankton represent an important intermediate between aquatic primary production and higher trophic levels (Brooks and Dodson 1965, Carpenter et al. 1985). Under future environmental scenarios with lakes containing more t-OC, diminished zooplankton production may have a negative influence on the productivity of inland lake fisheries, owing to reduction in prey availability.

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#### LITERATURE CITED

- Ask, J., J. Karlsson, L. Persson, P. Ask, P. Bystrom, and M. Jansson. 2009. Whole-lake estimates of carbon flux through algae and bacteria in benthic and pelagic habitats of clear-water lakes. *Ecology* 90:1923–1932.
- Bastviken, D., J. Ejlertsson, I. Sundh, and L. Tranvik. 2003. Methane as a source of carbon and energy for lake pelagic food webs. *Ecology* 84:969–981.
- Berggren, M., L. Strom, H. Laudon, J. Karlsson, A. Jonsson, R. Giesler, A. K. Bergstrom, and M. Jansson. 2010. Lake secondary production fueled by rapid transfer of low molecular weight organic carbon from terrestrial sources to aquatic consumers. *Ecology Letters* 13:870–880.
- Brett, M. T., M. J. Kainz, S. J. Taipale, and H. Seshan. 2009. Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. *Proceedings of the National Academy of Sciences USA* 106:21197–21201.
- Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. *Science* 150:28–35.
- Carpenter, S. R., J. J. Cole, J. R. Hodgson, J. F. Kitchell, M. L. Pace, D. Bade, K. L. Cottingham, T. E. Essington, J. N. Houser, and D. E. Schindler. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. *Ecological Monographs* 71:163–186.
- Carpenter, S. R., J. J. Cole, J. F. Kitchell, and M. L. Pace. 1998. Impact of dissolved organic carbon, phosphorus, and grazing on phytoplankton biomass and production in experimental lakes. *Limnology and Oceanography* 43:73–80.
- Carpenter, S. R., J. J. Cole, M. L. Pace, M. Van de Bogert, D. L. Bade, D. Bastviken, C. M. Gille, J. R. Hodgson, J. F. Kitchell, and E. S. Kritzberg. 2005. Ecosystem subsidies: terrestrial support of aquatic food webs from  $^{13}\text{C}$  addition to contrasting lakes. *Ecology* 86:2737–2750.
- Carpenter, S. R., and J. Kitchell. 1987. The temporal scale of variance in limnetic primary production. *American Naturalist* 129:417–433.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* 35:634–639.
- Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He, and C. N. von Ende. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68:1863–1876.
- Clark, J. M., S. H. Bottrell, C. D. Evans, D. T. Monteith, R. Bartlett, R. Rose, R. J. Newton, and P. J. Chapman. 2010. The importance of the relationship between scale and process in understanding long-term DOC dynamics. *Science of the Total Environment* 408:2768–2775.
- Coe, R. 2002. It's the effect size stupid: what effect size is and why it is important. Paper presented at the Annual Conference of the British Educational Research Association, University of Exeter, UK. <http://www.leeds.ac.uk/educol/documents/00002182.htm>
- Cole, J. J., S. R. Carpenter, J. F. Kitchell, and M. L. Pace. 2002. Pathways of organic carbon utilization in small lakes: Results from a whole-lake C-13 addition and coupled model. *Limnology and Oceanography* 47:1664–1675.
- 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. *Proceedings of the National Academy of Sciences USA* 108:1975–1980.
- Cole, J. J., S. R. Carpenter, M. L. Pace, M. C. Van de Bogert, J. L. Kitchell, and J. R. Hodgson. 2006. Differential support of lake food webs by three types of terrestrial organic carbon. *Ecology Letters* 9:558–568.
- Cowles, T. J., R. J. Olson, and S. W. Chisholm. 1988. Food selection by copepods—discrimination on the basis of food quality. *Marine Biology* 100:41–49.
- Dolbeth, M., M. Cussion, R. Sousa, and M. A. Pardal. 2012. Secondary production as a tool for better understanding of aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 69:1230–1253.
- Francis, T. B., D. E. Schindler, G. W. Holtgrieve, E. R. Larson, M. D. Scheuerell, B. X. Semmens, and E. J. Ward. 2011. Habitat structure determines resource use by zooplankton in temperate lakes. *Ecology Letters* 14:364–372.
- Jones, R. I., J. Grey, D. Sleep, and L. Arvola. 1999. Stable isotope analysis of zooplankton carbon nutrition in humic lakes. *Oikos* 86:97–104.
- Jones, S. E., C. T. Solomon, and B. Weidel. 2012. Subsidy or subtraction: how do terrestrial inputs influence consumer production in lakes? *Freshwater Reviews* 5:21–35.
- Jonsson, A., G. Algesten, A. K. Bergstrom, K. Bishop, S. Sobek, L. J. Tranvik, and M. Jansson. 2007. Integrating aquatic carbon fluxes in a boreal catchment carbon budget. *Journal of Hydrology* 334:141–150.
- Kankaala, P., S. Taipale, J. Grey, E. Sonninen, L. Arvola, and R. I. Jones. 2006. Experimental delta C-13 evidence for a contribution of methane to pelagic food webs in lakes. *Limnology and Oceanography* 51:2821–2827.
- Karlsson, J., M. Jansson, and A. Jonsson. 2002. Similar relationships between pelagic primary and bacterial production in clearwater and humic lakes. *Ecology* 83:2902–2910.
- Karlsson, J., A. Jonsson, M. Meili, and M. Jansson. 2003. Control of zooplankton dependence on allochthonous organic carbon in humic and clear-water lakes in northern Sweden. *Limnology and Oceanography* 48:269–276.
- Lennon, J. T., and L. E. Pfaff. 2005. Source and supply of terrestrial organic matter affects aquatic microbial metabolism. *Aquatic Microbial Ecology* 39:107–119.

- Lynch, M. 1979. Predation, competition, and zooplankton community structure—experimental study. *Limnology and Oceanography* 24:253–272.
- Marczak, L. B., R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* 88:140–148.
- McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton in samples. Pages 232–240 in J. A. Downing and F. H. Rigler, editors. *A manual on methods for the assessment of secondary productivity in fresh waters*. Blackwell Scientific Publications, London, UK.
- Menzel, D. W., and N. Corwin. 1965. The measurement of total phosphorous in seawater based on the liberation of organically bound fractions by persulfate oxidation. *Limnology and Oceanography* 10:280–282.
- Monteith, D. T., and C. D. Evans. 2005. The United Kingdom Acid Waters Monitoring Network: a review of the first 15 years and introduction to the special issue. *Environmental Pollution* 137:3–13.
- Monteith, D. T., et al. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature* 450:537–540.
- Olsen, K. K. 2008. Multiple wavelength ultraviolet determinations of nitrate concentration, method comparisons from the preakness brook monitoring project, October 2005 to October 2006. *Water, Air, and Soil Pollution* 187:195–202.
- Pace, M. L., S. R. Carpenter, J. J. Cole, J. J. Coloso, J. F. Kitchell, J. R. Hodgson, J. J. Middelburg, N. D. Preston, C. T. Solomon, and B. C. Weidel. 2007. Does terrestrial organic carbon subsidize the planktonic food web in a clear-water lake? *Limnology and Oceanography* 52:2177–2189.
- Persson, J., M. T. Brett, T. Vrede, and J. L. Ravet. 2007. Food quantity and quality regulation of trophic transfer between primary producers and a keystone grazer (*Daphnia*) in pelagic freshwater food webs. *Oikos* 116:1152–1163.
- Plante, C., and J. Downing. 1989. Production of freshwater invertebrate populations in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1489–1498.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Preston, N. D., S. R. Carpenter, J. J. Cole, and M. L. Pace. 2008. Airborne carbon deposition on a remote forested lake. *Aquatic Sciences* 70:213–224.
- Solomon, C. T., S. R. Carpenter, M. K. Clayton, J. J. Cole, J. J. Coloso, M. L. Pace, M. J. Vander Zanden, and B. C. Weidel. 2011. Terrestrial, benthic, and pelagic resource use in lakes: results from a three-isotope Bayesian mixing model. *Ecology* 92:1115–1125.
- Sterner, R. W. 1993. *Daphnia* growth on varying quality of *Scenedesmus*—mineral limitation of zooplankton. *Ecology* 74:2351–2360.
- Welschmeyer, N. A. 1994. Fluorometric analysis of chlorophyll-a in the presence of chlorophyll-b and pheopigments. *Limnology and Oceanography* 39:1985–1992.
- Wetzel, R. G. 2001. *Limnology: lake and river ecosystems*. Third edition. Academic Press, San Diego, California, USA.
- Wilkinson, G. M., M. Pace, and J. Cole. 2013. Terrestrial dominance of organic matter in north temperate lakes. *Global Biogeochemical Cycles* 27:1–9.
- Williamson, C. E., H. E. Zagarese, P. C. Schulze, B. R. Hargreaves, and J. Seva. 1994. The impact of short-term exposure to UV-B radiation on zooplankton communities in north temperate lakes. *Journal of Plankton Research* 16:205–218.

#### SUPPLEMENTARY MATERIAL

##### Appendix A

Table containing end member stable isotope values for each lake ([Ecological Archives E095-105-A1](#)).

##### Appendix B

Table containing medians and quantiles for zooplankton terrestrial resource reliance estimates ([Ecological Archives E095-105-A2](#)).

##### Appendix C

Table containing group-specific and total zooplankton production and terrestrial resource reliance estimates for each lake ([Ecological Archives E095-105-A3](#)).