Macrophyte biomass predicts food chain length in shallow lakes

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Abstract. Food chain length provides insights into how ecosystems function and respond to global change. A recent synthesis has shown that food chain length is significantly related to both ecosystem productivity and ecosystem size. Relaxation of energetic constraints on top predators has been advanced as the primary mechanism explaining the importance of ecosystem productivity whereas the significance of ecosystem size may be related to the fact that larger ecosystems provide more refuge that stabilizes intermediate predators. Given that submerged macrophytes in lakes are known to enhance both ecosystem productivity and the amount of available refuge, we hypothesized that food chain lengths, measured as the trophic positions of top predators, would be significantly related to macrophyte biomass. We tested our hypothesis by conducting a field survey of shallow lakes across a strong macrophyte but limited morphometric gradient using a hierarchical mixed effect modeling approach. We determined that macrophyte biomass was positively related to the trophic position of numerous piscivores and to food chain length across lakes. Both lake volume and macrophyte biomass were retained as fixed predictors in our model with lowest AICc, and this model explained 85% of the variation in piscivorous fish trophic positions considering both fixed and random effects (i.e., lake and species-specific responses to lake volume). Macrophyte biomass explained 29% of the residual variation in food chain length when the effect of lake volume was removed. These results are the first to directly relate macrophyte biomass to piscivore trophic positions and food chain length. We conclude that shallow lakes with higher macrophyte biomass support longer food chains independent of ecosystem size and nutrient concentration. We suggest that loss of macrophytes largely driven by human activities reduces food chain length, with potential consequences for ecosystem function.

Key words: food chain length; macrophytes; refuge; shallow lakes; stable isotopes.

INTRODUCTION

Food chain length—the trophic position of the top predator in an ecosystem—is a simple and fundamental description of the structure of food webs. It affects a wide variety of ecosystem processes, including energy flow, trophic cascades, contaminant bioaccumulation, and response to change and disturbance (Elton 1927, Pimm and Lawton 1977, Cabana and Rasmussen 1994, Carpenter and Kitchell 1996, Duffy et al. 2005, Hansson et al. 2012). While food chain length is of great basic and applied interest to ecologists, it was difficult to measure before the widespread adoption of stable isotope methods for quantifying trophic position introduced in the...
early 1990s. Since that time, a number of empirical studies have demonstrated substantial variation in food chain lengths among ecosystems (Vander Zanden et al. 1999, Post et al. 2000).

Several hypotheses have been proposed to explain variation in food chain lengths. The first is the ecosystem disturbance hypothesis, which predicts that long food chains become truncated due to the instability of higher trophic levels, as the survival of apex predators is dependent upon the survival of all lower trophic levels (Hutchinson 1959, Pimm and Lawton 1977, Pimm and Kitching 1987, Sabo et al. 2010). Mathematical models have shown that following a disturbance, systems with longer food chain lengths exhibit longer recovery times to stable equilibrium (Pimm and Lawton 1977). In contrast, the basal productivity hypothesis is based on the second law of thermodynamics and states that the length of a food chain is dependent on the amount of basal resources available within an ecosystem because energy is lost with each trophic transfer (Hutchinson 1959, Pimm and Kitching 1987, Pimm 2002). Finally, an ecosystem size pattern has been observed, wherein larger ecosystems support longer food chain lengths, perhaps because large systems provide refuges that stabilize predator-prey interactions and permit persistence of intermediate consumers (Post et al. 2000). Similarly, longer food chains have been observed in ecosystems that are de-coupled in space or where prey refuge is present (McCann et al. 2005, Dolson et al. 2009, Tunney et al. 2012).

Of these proposed drivers of food chain length, ecosystem size and productivity have emerged through empirical tests as the most important in freshwater ecosystems because energy is lost with each trophic transfer (Hutchinson 1959, Pimm and Kitching 1987, Pimm 2002). Finally, an ecosystem size pattern has been observed, wherein larger ecosystems support longer food chain lengths, perhaps because large systems provide refuges that stabilize predator-prey interactions and permit persistence of intermediate consumers (Post et al. 2000). Similarly, longer food chains have been observed in ecosystems that are de-coupled in space or where prey refuge is present (McCann et al. 2005, Dolson et al. 2009, Tunney et al. 2012).

Of these proposed drivers of food chain length, ecosystem size and productivity have emerged through empirical tests as the most important in freshwater ecosystems. A meta-analysis conducted almost entirely on freshwater systems concluded that the mean effect of disturbance was not significantly different from zero, while the mean effects of ecosystem size and productivity on food chain length were significantly positive (Takimoto and Post 2012).

Macrophytes in lake littoral zones increase prey refuge and ecosystem productivity. The refuge provided by macrophytes is important for a wide variety of primary and secondary consumers, including zooplankton (Jeppesen et al. 1998, Burks et al. 2002, Genkai-Kato 2007), small prey fish (Savino and Stein 1982, Persson and Eklov 1995), and benthic macroinvertebrates (Diehl 1992). Consequently, refugia can dampen the effect of predators on intermediate consumers like predatory invertebrates and fish, resulting in more intermediate consumers available for top predators and less omnivory (feeding at lower levels). Thus, the trophic position of predators should increase with available refuge. In addition, macrophytes increase littoral and subsequently whole-lake productivity, particularly in shallow lakes (Brothers et al. 2013). Macrophytes increase basal resources both directly, by providing detrital organic matter to benthic food chains at the end of the growing season, and indirectly, by increasing habitat for epiphytic periphyton (Diehl and Kornijów 1998 and the references therein). Despite the widespread concern about human-mediated alterations of macrophyte assemblages (Jennings et al. 2003, Hicks and Frost 2011) and their potential to alter trophic structure in lakes (Kovalenko et al. 2012), the effect of macrophytes on piscivore trophic positions and food chain length has not been clearly shown.

Given the positive effects of macrophytes on the abundance of refuge and productivity, as well as evidence showing food chain length increases with refuge and productivity, we hypothesized that food chain length increases as a function of increased macrophyte biomass. To test our hypothesis, we measured fish trophic positions and food chain lengths in 20 small, shallow lakes that varied widely in macrophyte biomass. We related macrophyte biomass and productivity metrics (total phosphorus and epiphytic periphyton chlorophyll-\(a\) concentration) to piscivore trophic positions. We show that macrophytes are positively correlated to piscivore trophic positions and food chain length, independent of ecosystem size. These results suggest that loss of macrophytes in lakes reduce food chain lengths.

**METHODS**

**Study sites**

We quantified fish trophic positions and food chain length in 20 lakes within southeastern Quebec (Fig. 1). We focused on small, shallow lakes (<2.5 km\(^2\) surface area and <5 m mean depth) because their large variation in macrophyte biomass but small variation in total size allowed us to isolate, as much as possible, the
effects of macrophytes from ecosystem size effects per se. We captured variation in pelagic and littoral primary productivity by selecting lakes that spanned a large trophic state gradient (2.5–117 micrograms L\(^{-1}\) total phosphorus). Macrophyte biomass was unrelated to total phosphorus and lake volume, which allowed us to assess macrophyte effects independent of pelagic productivity and ecosystem size. We controlled for fish stocking effects by selecting lakes that had no record of fish stocking in the past 10 years (Québec Ministère des Ressources Naturelles, personal communication).

**Macrophyte and water quality analyses**

We estimated macrophyte biomass for all 20 lakes one to four times in August between 2006 and 2012. We chose six near-shore sampling locations at each lake using a stratified random sampling design following the methods described in Vermaire et al. (2011). Briefly, at each of the six sampling stations within a lake, we placed four quadrats approximately 5 m apart along a transect that ran parallel to shore at the depth of maximum macrophyte standing crop (n = 24 for each lake). We sampled at the depth of maximum macrophyte standing crop because Canfield et al. (1990) previously showed that mean littoral submerged macrophyte biomass was strongly related to macrophyte biomass at this depth (r\(^2\) = 0.85). We determined macrophyte wet weight from quadrats after we harvested the plants, removed roots and sediment, and spun the macrophytes using a salad spinner to remove external water. We converted plant wet weight to dry weight using the regression equation developed by Vermaire et al. (2011). We converted macrophyte biomass from depth of maximum standing crop to mean littoral macrophyte biomass using the methods outlined in Canfield et al. (1990).

In some instances macrophytes were not sampled in the same year as fish sampling and therefore we investigated if macrophyte biomass varied more across lakes than it did across years. To determine this we fit a hierarchical model with the following structure:

\[
MB_{ly} \sim \beta_{\text{rain/ℓ}}
\]
where macrophyte biomass (MB) was nested in quadrat \( i \) in lake \( l \) in year \( y \). The model only contained the intercept \( (b_{int}) \). The intraclass correlation coefficient (ICC) for lake and year was 0.4 and 0.1, respectively (an ICC ranges from 0 to 1 with 0 meaning that a group conveys no information and 1 meaning that group identity is meaningful) (Gelman and Hill 2006). Therefore, macrophyte biomass varied more across lakes than across years. As such, the mean of year replicates was used when macrophyte surveys were conducted more than once. We report mean macrophyte biomass across years in g dry weight m\(^{-2}\).

We determined epiphytic chlorophyll-\( \alpha \) concentration (hereafter referred to as periphyton) in each lake using the methods outlined in Cattaneo and Kalff (1978). We harvested macrophytes from a quadrat at three different sites in each lake and carefully placed them in sealable plastic bags. We agitated the macrophytes in a known volume of 0.45 ml filtered lake water. We then concentrated the slurry on a Whatman GF/F glass fiber filter. We used standard spectrophotometric techniques to determine phaeophytin corrected chlorophyll-\( \alpha \) concentration and to quantify total phosphorus concentration from epilimnetic water samples, these methods are described in Vermaire et al. (2011).

**Fish sampling**

We sampled fish during July and August in 2010 and 2012. We used two 60-m experimental gill nets with eight panels ranging from 25 to 152 mm stretch mesh as the primary fishing gear. We set one net perpendicular to the shore in the littoral region of each lake and the second net in the pelagic zone at or just above the thermocline. In 2010 we set nets for three hours in the afternoon and then again in the same location for an additional nine hours over night. In 2012 we set nets in the morning and removed them after dusk to comply with permit regulations. In both years each net was set for 12 hours in total. In addition, we angled with rod and reel when possible to increase fishing effort for piscivorous fish.

Relevant measurements and samples were obtained from each fish. We identified, weighed, and measured fork lengths of all piscivorous fish. We took dorsal muscle tissue from fish to determine trophic position using stable isotope analysis (SIA). We did this by either sacrificing the whole individual (2010) or via a muscle biopsy with a 4-mm dermal punch (2012). Muscle biopsies are unbiased with respect to SIA if individuals are greater than 10 cm (Schielke and Post 2010). We kept muscle samples on ice until they were frozen within 12 hours. Samples remained frozen until further analysis (see Isotope analysis). We performed SIA on muscle samples from the largest individuals of each piscivorous fish species present in each lake.

**Isotope analysis**

We used the methods of Post (2002) to calculate piscivore trophic positions. We lyophilized, homogenized and then analyzed muscle tissue for carbon and nitrogen stable isotope ratios. Analysis was done at the Idaho State University Interdisciplinary Laboratory for Elemental and Isotopic Analysis (ILEIA) using a Costech ECS 4010 elemental analyzer interfaced to a Thermo Delta V Advantage continuous flow isotope ratio mass spectrometer. All stable isotopic data are reported in standard delta notation (\( \delta^{13}C, \delta^{15}N \)) relative to the Vienna Pee Dee Belemnite (VPDB) and atmospheric N\(_2\) (air), reference standards. Analytical precision, calculated from analysis of standards distributed throughout each run, deviated less than \( \pm 0.2\% \) for both carbon and nitrogen stable isotopes, and less than \( \pm 0.5\% \) of the sample value for %N and %C. We corrected the \( \delta^{13}C \) values of all samples for lipids using the following equation from Post et al. (2007):

\[
\delta^{13}C_{\text{norm}} = \delta^{13}C_{\text{untr}} - 3.32 + C : N
\]

where \( \delta^{13}C_{\text{norm}} \) is the normalized \( \delta^{13}C \) of a consumer or baseline and \( \delta^{13}C_{\text{untr}} \) is the untreated \( \delta^{13}C \) signature of a consumer or baseline. For two *Perca flavescens*, we had samples of fin tissue but not muscle tissue. We corrected the \( \delta^{15}N \) and \( \delta^{13}C \) signature of these fin clips with regression equations that used muscle and fin samples of *Perca flavescens* from several of the study lakes \( n = 10, r^2 = 0.89 \) and 0.77 for \( \delta^{15}N \) and \( \delta^{13}C \), respectively; \( p < 0.001 \).

Following methods outlined in Post (2002), snails and mussels served as littoral and pelagic baselines for trophic position calculations. We prepared and lipid corrected the soft tissue of.
snails and mussels in the same manner as fish tissue. In St. Augustin, Sugarloaf, and Waterloo lakes we could not find any mussels and thus we adopted an approach similar to that adopted by Karlsson and Byström (2005). For Sugarloaf and St. Augustin, we estimated the pelagic baseline δ¹⁵N and δ¹³C using zooplankton samples. For Waterloo we estimated δ¹⁵N from a regression relationship with surface sediment (n = 13, R² = 0.72, p < 0.001). We used two different methods to estimate the pelagic δ¹³C value for Waterloo: (1) we used the maximum separation between littoral-pelagic carbon sources from among the lakes as a lower bound estimate of pelagic δ¹³C; and (2) we used the most negative δ¹³C signature of benthic invertebrates within this lake (i.e., indicating a high proportion of pelagic feeding) as an upper bound estimate. We used both estimates for our statistical models and in both instances the results presented below were the same.

We calculated the trophic position (TP) of an individual i using the following two source mixing model and defined food chain length as the mean trophic position of the species that had the highest trophic position within a lake (from Post 2002):

\[
TP_i = 1 + \left( \frac{\delta^{15}N_i - [\delta^{15}N_{\text{lit}} \times \alpha + \delta^{15}N_{\text{pel}}]}{(1 - \alpha)} \right) \times \frac{3.4}{\alpha} = \frac{(\delta^{13}C - \delta^{13}C_{\text{pel}}) + (\delta^{13}C_{\text{lit}} - \delta^{13}C_{\text{pel}})}{3.4}
\]

where pel and lit stand for pelagic and littoral baselines, respectively.

Statistical analyses
We used hierarchical mixed-effects regression models to describe the effects of macrophyte biomass and productivity (total phosphorus and periphyton biomass) on piscivore trophic positions. Our initial analyses demonstrated that trophic positions for one species (Perca flavescens) were strongly related to lake volume even over the relatively limited range of volumes encompassed by our study, so we included lake volume as a predictor in these models and allowed its effect to vary by species. We initially included fish length as a predictor of trophic position, but exclude it here for simplicity because trophic position was not significantly related to length over the range of lengths in our data set (95% confidence interval slope estimate for length = -0.003 to 0.005). Finally, we included lake as a random blocking factor to account for non-independence of fish from the same lake. Within this basic framework we fit several alternative models following the methods outlined in Zuur et al. (2009), and compared these models using small-sample-corrected Akaike Information Criterion (AICc) (Appendix: Table A1). To isolate the effect of macrophyte biomass on food chain length, we first removed the effect of lake volume using the species-specific intercept and volume slope parameters fit by our most parsimonious mixed effect model. We then regressed the subsequent residual variation in food chain length against macrophyte biomass. All statistical analyses were conducted in R and mixed effects models were fit using maximum likelihood in the lme4 package (Bates et al. 2012, R Development Core Team 2012).

All statistical analyses presented are based on 18 lakes and 6 taxa. We excluded Lac St-George because although larger yellow perch were observed in this lake we only had tissue samples from individuals that were significantly smaller than those used for trophic position estimates in all other lakes (ANOVA: df = 5, F = 23.58, p < 0.001; Tukey post-hoc test: all p values < 0.01 for Lac St-George comparisons) and Lac Denison because it experienced extreme bottom-water hypoxia that may have altered the mechanisms that we were considering (see Discussion). We note that length was not a significant predictor of yellow perch trophic position in our statistical analyses because the yellow perch used did not differ significantly in fork length among lakes once Lac St-George was excluded (Tukey post-hoc test all p values > 0.05). We have included Lac St-George and Lac Denison in Fig. 2 to allow readers to view these points in relation to statistical modeling results. We pooled all salmonids, Salvelinus namaycush, Oncorhynchus mykiss and Salmo trutta, into one group for analysis due to few observations of trophic positions for these species.

RESULTS
Our study lakes varied widely in macrophyte
Fig. 2. Relationship of piscivore trophic positions, macrophyte biomass, and lake volume. Parameter estimates were fit by model 4 in Table 2. This hierarchical mixed effects model accounted for individuals originating from the same lake and controlled for species specific responses to macrophytes (intercept) and volume (intercept and slope). Solid lines represent regression equations with significant slope parameters and dotted lines represent 95% confidence intervals. Lac Denison and Lac St-George, which were not included in statistical analysis, are shown as cross symbols and triangles respectively. Original lake volume data were in cubic meters.
bbiomass and food chain length as well as in the identity of the top predator species (Table 1). Macrophyte biomass varied from 1.2 to 41 g m\(^{-2}\), and food chain length varied from 3.1 to 4.8 (i.e., food chains were a full trophic level shorter in some lakes than in others). Eight different piscivorous fish species were present across all lakes, but not all of these fish were present in all lakes. The piscivorous fish species sampled were *Perca flavescens* (yellow perch), *Sander vitreus* (walleye), *Micropterus salmoides* (largemouth bass), *Esox lucius* (northern pike), *Micropterus dolomieu* (smallmouth bass), *Salvelinus namaycush* (lake trout), *Oncorhynchus mykiss* (rainbow trout) and *Salmo trutta* (brown trout). Lakes did not vary greatly in mean depth or volume (Table 1).

The trophic positions of all piscivores were positively related to macrophyte biomass, whereas only the trophic positions of yellow perch were also positively related to lake volume (Fig. 2). In contrast, trophic positions of piscivores were not related to periphyton chlorophyll-\(a\) or total phosphorus concentrations (Table 2). Model 4 provided the best description of the data, although models 5 and 6 were also plausible (\(\Delta AICc = 2\) and 3, respectively). We focus our interpretation on model 4 because it contained statistically significant fixed effects, the fixed effects explained more variation in fish trophic positions, and it was significantly better than model 5 when compared using the likelihood ratio test (df = 8, log likelihood = 4.50 and 3.50 for models 4 and 5, respectively; \(p\) value < 0.001) (Table 1). Model 4 contained lake volume and macrophyte biomass as predictor variables and allowed both the intercepts and the effect of lake volume to vary by species (Table 2, model 4). Although we considered the possibility that the effect of macrophytes may vary by species, we found that this model had a lower predictive ability compared to a common effect across species (\(\Delta AICc = 8\)). Considering both the random and fixed effects, we found that model 4 explained 85% of the variation in fish trophic positions, whereas macrophyte biomass and lake volume (the fixed effects) alone explained 36% of the variation. The fixed effect of volume alone in the same model without macrophyte biomass only explained 15% of the variation.

Macrophyte biomass consistently had a significant positive effect on food chain length, even after we accounted for the effect of volume (Fig. 3). In particular, we found that macrophyte

### Table 1. Summary of lake characteristics.

| Lake         | Longitude (DD) | Latitude (DD) | Top predator species | Volume \((10^3 \times m^3)\) | Mean macrophyte biomass \((g m^{-2})\) | Total phosphorus \((\mu g L^{-1})\) | Food chain length |
|--------------|----------------|---------------|----------------------|-----------------------------|----------------------------------------|-----------------------------------|------------------|
| Augustine    | −71.393        | 46.749        | YP                   | 3.6                         | 2.30                                   | 34.2                              | 86               |
| D’Argent     | −72.313        | 45.310        | SMB                  | 4.5                         | 9.30                                   | 15.5                              | 17               |
| Bisby        | −71.306        | 45.954        | NP                   | 2.5                         | 0.52                                   | 1.5                               | 25               |
| Bran de Scie | −72.202        | 45.406        | LMB                  | 3.9                         | 0.49                                   | 5.2                               | 17               |
| Bromont      | −72.671        | 45.266        | LMB                  | 4.5                         | 2.00                                   | 26.7                              | 18               |
| Denison      | −72.102        | 45.741        | NP                   | 1.8                         | 0.42                                   | 38.3                              | 40               |
| Français     | −71.643        | 45.080        | BT                   | 0.6                         | 0.04                                   | 1.6                               | 3                |
| Gale         | −72.694        | 45.269        | YP                   | 2.8                         | 0.06                                   | 32.1                              | 8                |
| Mckenzie     | −71.019        | 45.564        | LMB                  | 2.1                         | 1.20                                   | 10.0                              | 15               |
| Monts        | −72.186        | 45.403        | LT                   | 1.6                         | 0.35                                   | 1.2                               | 18               |
| Nick         | −72.328        | 45.211        | LMB                  | 3.0                         | 6.00                                   | 1.7                               | 24               |
| Parker       | −72.314        | 45.328        | LMB                  | 3.5                         | 1.70                                   | 14.1                              | 16               |
| PSF          | −72.037        | 45.538        | SMB                  | 1.2                         | 1.90                                   | 2.1                               | 117              |
| Roxton       | −72.652        | 45.467        | NP                   | 3.1                         | 5.80                                   | 6.7                               | 21               |
| LSG          | −71.892        | 45.645        | YP                   | 2.1                         | 2.20                                   | 25.5                              | 9                |
| Stoke        | −71.810        | 45.517        | NP                   | 4.3                         | 3.30                                   | 27.8                              | 11               |
| Sugarloaf    | −72.333        | 45.123        | SMB                  | 3.2                         | 0.67                                   | 9.1                               | 4                |
| Trois-Lacs   | −71.877        | 45.799        | NP                   | 3.8                         | 13.00                                  | 41.0                              | 22               |
| Trois-Milles | −70.919        | 45.687        | Wal                  | 1.5                         | 1.60                                   | 4.7                               | 5                |
| Waterloo     | −72.521        | 45.335        | YP                   | 3.4                         | 9.50                                   | 5.0                               | 28               |
| Range        | ...            | ...           | ...                  | 0.6–4.5                     | 0.04–13.00                             | 1.2–41                            | 3–117            |
| Mean         | ...            | ...           | ...                  | 2.9                         | 2.90                                   | 14.0                              | 24.3             |

Notes: Fish species codes are: YP = yellow perch, SMB = smallmouth bass, NP = northern pike, LMB = largemouth bass, LT = lake trout, BT = brown trout, Wal = walleye. Lake abbreviations LSG and PSF are Lac St-George and Petit Saint-Francois, respectively. Ellipses indicate not applicable.
biomass explained 29% of the residual variation in food chain length ($p = 0.02$). The most common top predators were northern pike and largemouth bass, which spanned the gradient of macrophyte biomass (Table 1).

**Discussion**

Our results demonstrate that shallow lakes featuring a greater biomass of submerged macrophytes support longer food chains, independent of ecosystem size and nutrient concentration. We attribute increased food chain length with macrophyte biomass to greater abundance of refuge and increased diversity of basal resources. Given that macrophyte biomass can be quite variable among lakes and through time due to human activities like motor boat traffic, nutrient enrichment, shoreline development and watershed land use (Scheffer et al. 1993, Asplund and Cook 1997, Radomski and Goeman 2001, Jennings et al. 2003, Vermaire et al. 2012), we suggest that macrophytes can cause variation in aquatic food chain length across space and through time. Consequently, future food web studies should consider macrophyte biomass as a driver of food chain length and the potential impacts this might have on energy flow at the whole ecosystem level.

Our work fits into an emerging appreciation for the role of habitat heterogeneity in influencing the structure and function of aquatic systems (Kovalenko et al. 2012). Two previous studies have suggested that macrophytes could be an important predictor of food chain length. The first compared the food webs of two shallow lakes with high and low macrophyte coverage and determined that the height of the food web in the low-macrophyte lake was compressed compared to the high-macrophyte lake (Rawcliffe et al. 2010). The second compared the trophic positions of piscivores in a bay of a shallow subtropical lake that had high abundance of macrophytes to the same bay after it underwent a regime shift to a turbid state and to another bay that was always in a turbid state (Xu et al. 2014). The authors found that piscivore trophic positions were greatest at sites in the clear-water, macrophyte-dominated state compared to the turbid state. While both of these earlier studies suggest macrophytes increase food chain length, here we directly relate macrophytes and food chain length to show a relationship at a larger spatial scale with enhanced replication.

Mechanistically, the relationship between food chain length and macrophyte biomass could be explained by changes in refuge, which in turn alter piscivore diets. Previous studies have shown that a loss of refuge for prey in small
ecosystems results in unstable predator-prey dynamics and consequently decreased food chain length. For example, linked food chains in spatially-compressed ecosystems (like small shallow lakes presented herein) can display unstable predator prey dynamics (McCann et al. 2005). However, omnivory (eating lower in the food chain) or prey refuge can alleviate the destabilizing effects of spatially compressed ecosystems (McCann et al. 2005, Tunney et al. 2012). As a result, small ecosystems can have lower food chain lengths due to omnivory, but refuge can buffer destabilizing effects and preserve longer food chains (Tunney et al. 2012). While we did not quantify intermediate consumer abundance in this current study, previous studies have found that enhanced macrophyte abundance results in persistence of predatory invertebrates and greater abundance of predatory fish (Blindow et al. 1993, Diehl 1993). Other forms of habitat heterogeneity that provide prey refuge, like coarse woody debris, should be investigated as drivers of food chain length (Sass et al. 2006).

An alternate or additional mechanism to explain variation in food chain lengths is productivity, whereby the loss of macrophyte-related production leads to decreased diversity in basal resources. We found that pelagic productivity and periphyton production estimates were not significantly related to food chain length. Given that all piscivore species increased in their trophic positions with macrophyte biomass, productivity likely did not increase food chain length in the classical sense of adding a trophic level to the top of the food chain. However, increased diversity of basal resources (i.e., periphyton, detrital macrophyte organic matter and phytoplankton) with macrophytes could have led to an insertion mechanism of intermediate consumers (Post and Takimoto 2007). For example, Brauns et al. (2011) showed that areas of higher resource diversity in three German lakes supported more diverse macroinvertebrate food webs, which had longer food chains.

Fig. 3. Residual variation from the food chain length (FCL)-volume relationship versus macrophyte biomass. Food chain length was calculated as the mean trophic position of a species that possessed the highest trophic position in the lake. Variation in FCL due to volume was removed using volume regression equations determined from model 4 in Table 2. Subsequent residuals were regressed against macrophyte biomass to determine if macrophytes had an effect on FCL when volume was controlled for.
Our finding of a weak volume effect on food chain length is consistent with studies that also considered a restricted range of ecosystem size. For example, Reid et al. (2012), which considered a range in size similar to our study, found no significant relationship between fish food chain length and lake size. Similarly, a subsample of lakes from Post et al. (2000) that fell within the minimum and maximum lake sizes we considered also had no relationship between lake volume and food chain length \( (n = 9, r^2 = 0.02, p = 0.32) \). However, considering much larger ranges (i.e., 3–9 times larger than the gradient presented herein), authors have detected a significant relationship between food chain length and ecosystem size (Vander Zanden et al. 1999, Post et al. 2000). In our dataset, the only species that had a significant food chain length-volume relationship was yellow perch. When we compared our slope estimate for yellow perch to those derived for other taxa by Post et al. (2000) across their full range of lake sizes, we found that yellow perch had the steepest slope in the trophic position versus volume relationship. This suggests that even over relatively small size gradients yellow perch trophic position may increase faster than other common piscivorous fish. In our data set, yellow perch occupied some of the highest trophic positions, but in these lakes other predator species such as northern pike, largemouth bass, and walleye were absent. We attribute high yellow perch trophic positions in these lakes to release from predation and competition allowing yellow perch to occupy higher trophic niches when other top predators were absent.

Whereas macrophytes provide lakes with numerous attributes that, in turn, can have positive effects on food chain length, there are several factors that could lead to negative effects and create some scatter in the food chain length-macrophyte biomass relationship. One example in our dataset was the combination of very small lake volume with high macrophyte biomass that led to large anoxic zones within Lac Denison. This lake had a large leverage on our modeling results as inclusion of this lake led to the effect of macrophytes being insignificant. Ecologically, this site was clearly an outlier as this lake differed from others because dense stands of *Elodea*, which are known to create anoxic conditions near the sediment, spanned the majority of the lake's surface area (Buscemi 1958). Our continuous oxygen measurements in a representative macrophyte stand within this lake are consistent with the literature, whereby, we observed complete anoxia within 0.5 m of the sediment during the entire 48-hour monitoring period. This anoxic zone likely had a large impact on suitable fish and invertebrate habitat because the mean depth of the lake was only 1.8 m (this lake also had the fourth smallest lake volume in our data set). Therefore, it seems reasonable to hypothesize that under certain conditions, extremely high macrophyte biomass in shallow lakes can lead to deleterious effects on food chain length due to constriction of habitable ecosystem size.

A potential caveat of our study was that the two highest food chain length estimates in our dataset came from lakes where we had to use alternative methods to estimate pelagic baselines (St. Augustin and Waterloo lakes). Given that we found a strong correlation between surface sediment and mussel isotopic signatures (an accepted pelagic baseline in the literature; Post 2002) across 13 of our lakes, we feel we were able to estimate the pelagic baseline in Waterloo accurately. In contrast, we had to rely on zooplankton to estimate the pelagic baseline of St Augustin, which is not ideal because these organisms are short-lived consumers and thus do not integrate isotopic signatures to the same extent as mussels. However, to account for this shortcoming, we used a mean isotopic value based on pelagic zooplankton samples collected from two different months in the same summer as fish collection. Karlsson and Byström (2005) also used zooplankton as their pelagic end members when mussels were not available and found little change in their trophic position estimates compared to those where both snail and mussel data were available. For completeness, we also re-ran our analysis excluding Waterloo or Augustin. Our results were robust to removal of either lake (i.e., model 4 was still the most parsimonious model and the effect of macrophytes on piscivore trophic positions were significantly positive). Removal of both lakes, however, resulted in models that contained positive effects of macrophytes on piscivore trophic positions having the lowest AICc values.
but the effects were not significantly different from zero, likely due to loss of statistical power. Overall, our results should be interpreted with some caution, as they are dependent on the assumption that our pelagic baseline estimates were adequate and that they were comparable across systems.

In an applied context, this research points to the impact land-use history can have on fresh water food webs and ecosystem function. As in many regions, agricultural phosphorus application in southeastern Quebec has increased substantially since 1951, with an estimated accumulation of >1050 kg P ha⁻¹ over the past century (MacDonald and Bennett 2009). Consistent with this observation and intensifying settlement densities, Vermaire et al. (2012) reported declines in the number of macrophyte-dominated lakes within this region. Our results suggest that this anthropogenic change likely altered food web structure via decreased food chain lengths. While many studies have focused only on biodiversity changes with loss of macrophytes, linking ecosystem functioning and biodiversity requires an understanding of how trophic ecology changes along these gradients (Duffy et al. 2005). Variation in trophic structure in the form of food chain length can affect biodiversity ecosystem functioning relationships through indirect effects like trophic cascades (Duffy et al. 2007). Therefore, an understanding of how food chain length varies with littoral structure is paramount if we are to predict how ecosystem function will change with loss of biodiversity in these systems (Srivastava and Vellend 2005).

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Table A1. Summary of statistical models considered. Trophic position of an individual $i$ of species $a$ in lake $l$ is described as a function of ecosystem size, macrophyte biomass, periphyton chlorophyll-a concentration, and total phosphorus. When mixed effects models are presented both the marginal and conditional $R^2$ values are given. Conditional values are variation explained by both random and fixed effects, whereas, marginal values are variation explained by fixed effects alone. The model with the most predictive power was model 9.

| Model                  | R²  | Effects                      | AICc |
|------------------------|-----|------------------------------|------|
|                         |     | Conditional | Marginal | Fixed | Random |
| **Macrophyte**         |     |             |          |       |        |
| (1) $TP_i = b_{int} + b_{MB} \times MB$ | ... | 0.08 | | | |
| (2) $TP_i = b_{int} + b_{Vol} \times Vol$ | ... | 0.07 | | | |
| (3) $TP_i = b_{int} + b_{MB} \times MB + b_{Vol} \times Vol$ | ... | 0.10 | | | |
| (4) $TP_{aal} = b_{TtlP(a)} + b_{MB(a)} \times MB + b_{Vol(a)} \times Vol$ | 0.63 | 0.30 | | | |
| (5) $TP_{aal} = b_{TtlP(a)} + b_{MB(a)} \times MB + b_{Vol(a)} \times Vol$ | 0.81 | 0.58 | | | |
| (6) $TP_{aal} = b_{TtlP(a)} + b_{MB(a)} \times MB + b_{Vol(a)} \times Vol$ | 0.80 | 0.57 | | | |
| (7) $TP_{aal} = b_{TtlP(a)} + b_{MB(a)} \times MB + b_{Vol(a)} \times Vol$ | 0.90 | 0.16 | | | |
| (8) $TP_{aal} = b_{TtlP(a)} + b_{MB(a)} \times MB + b_{Vol(a)} \times Vol$ | 0.85 | 0.36 | | | |
| (9) $TP_{aal} = b_{TtlP(a)} + b_{MB(a)} \times MB + b_{Vol(a)} \times Vol$ | 0.85 | 0.36 | | | |
| (10) $TP_{aal} = b_{TtlP(a)} + b_{MB(a)} \times MB + b_{Vol(a)} \times Vol$ | 0.86 | 0.15 | | | |
| (11) $TP_{aal} = b_{TtlP(a)} + b_{MB(a)} \times MB + b_{Vol(a)} \times Vol$ | 0.27 | 0.09 | | | |
| **Productivity**       |     |             |          |       |        |
| (11) $TP_{aal} = b_{int} + b_{TtlP(a)} \times TtlP(a) + b_{Vol(a)} \times Vol$ | ... | 0.15 | | | |
| (12) $TP_{aal} = b_{int} + b_{TtlP(a)} \times TtlP(a) + b_{Vol(a)} \times Vol$ | ... | 0.07 | | | |
| (13) $TP_{aal} = b_{TtlP(a)} + b_{TtlP(a)} \times TtlP(a) + b_{Vol(a)} \times Vol$ | 0.90 | 0.19 | | | |
| (14) $TP_{aal} = b_{TtlP(a)} + b_{TtlP(a)} \times TtlP(a) + b_{Vol(a)} \times Vol$ | 0.90 | 0.16 | | | |
| (15) $TP_{aal} = b_{TtlP(a)} + b_{TtlP(a)} \times TtlP(a) + b_{Vol(a)} \times Vol$ | 0.86 | 0.18 | | | |
| (16) $TP_{aal} = b_{TtlP(a)} + b_{TtlP(a)} \times TtlP(a) + b_{Vol(a)} \times Vol$ | 0.86 | 0.16 | | | |

Notes: Abbreviations are: TP = trophic position, Vol = ecosystem size (lake volume), MB = macrophyte biomass, Peri = epiphytic chlorophyll-a, Ttl P = total phosphorus, and int = intercept. Ellipses are present in cells when column headings are not applicable.

* P < 0.05.
Table A2. δ¹⁵N and δ¹³C isotope values for fish and average littoral and pelagic baselines for our 20 study lakes.

| Lake  | Sample          | δ¹⁵N | δ¹³C |
|-------|-----------------|------|------|
| BIS   | Ave Lit Baseline| 1.87 | -23.38 |
| BIS   | Ave Pel Baseline| 1.98 | -31.91 |
| BIS   | NP              | 10.16| -28.54 |
| BIS   | NP              | 9.69 | -28.82 |
| BIS   | NP              | 9.55 | -28.94 |
| BIS   | NP              | 9.04 | -29.21 |
| BIS   | NP              | 8.47 | -29.33 |
| BRA   | Ave Lit Baseline| 4.58 | -25.11 |
| BRA   | Ave Pel Baseline| 4.41 | -30.94 |
| BRA   | BT              | 9.99 | -18.63 |
| BRA   | LMB             | 10.10| -28.78 |
| BRA   | LMB             | 10.08| -26.42 |
| BRA   | LMB             | 10.82| -29.35 |
| BRA   | LT              | 10.87| -29.43 |
| BRA   | NP              | 10.18| -27.38 |
| BRA   | NP              | 10.32| -27.87 |
| BRA   | RT              | 9.97 | -22.50 |
| BRA   | RT              | 9.77 | -19.76 |
| BRA   | RT              | 9.97 | -25.64 |
| BRO   | Ave Lit Baseline| 6.89 | -23.00 |
| BRO   | Ave Pel Baseline| 6.75 | -29.15 |
| BRO   | LMB             | 14.70| -28.02 |
| BRO   | LMB             | 14.72| -31.61 |
| BRO   | LMB             | 14.60| -30.61 |
| BRO   | LMB             | 14.38| -28.66 |
| BRO   | LMB             | 13.96| -30.93 |
| BRO   | LMB             | 13.87| -30.03 |
| BRO   | NP              | 13.57| -27.87 |
| BRO   | RT              | 14.05| -30.32 |
| DAR   | Ave Lit Baseline| 5.50 | -23.19 |
| DAR   | Ave Pel Baseline| 4.57 | -31.45 |
| DAR   | LMB             | 11.40| -26.82 |
| DAR   | LMB             | 10.89| -25.04 |
| DAR   | LMB             | 10.78| -26.89 |
| DAR   | NP              | 11.51| -28.13 |
| DAR   | NP              | 10.90| -28.49 |
| DAR   | RT              | 10.49| -24.38 |
| DAR   | SMB             | 11.36| -29.69 |
| DAR   | SMB             | 10.91| -30.25 |
| DEN   | Ave Lit Baseline| 5.13 | -27.37 |
| DEN   | Ave Pel Baseline| 6.92 | -26.92 |
| DEN   | NP              | 12.51| -25.56 |
| DEN   | NP              | 12.22| -26.10 |
| DEN   | NP              | 12.47| -26.00 |
| FRA   | Ave Lit Baseline| 0.24 | -26.09 |
| FRA   | Ave Pel Baseline| 2.29 | -31.83 |
| FRA   | BB              | 7.86 | -30.76 |
| FRA   | BB              | 7.18 | -29.49 |
| FRA   | BT              | 8.07 | -28.10 |
| FRA   | BT              | 8.01 | -27.86 |
| FRA   | BT              | 7.96 | -27.93 |
| FRA   | BT              | 5.91 | -29.17 |
| GAL   | Ave Lit Baseline| 4.22 | -24.76 |
| GAL   | Ave Pel Baseline| 5.33 | -31.72 |
| GAL   | YP              | 9.12 | -28.98 |
| GAL   | YP              | 8.93 | -29.01 |
| GAL   | YP              | 9.11 | -28.31 |
| GAL   | YP              | 8.73 | -29.37 |
| GAL   | YP              | 8.27 | -29.18 |
| GAL   | YP              | 8.00 | -28.58 |
| GAL   | YP              | 7.75 | -28.49 |
| LSC   | Ave Lit Baseline| 5.52 | -21.53 |
| LSC   | Ave Pel Baseline| 6.85 | -28.94 |
| LSG   | SR              | 10.80| -26.73 |
| LSG   | SR              | 10.15| -28.90 |
| LTM   | Ave Lit Baseline| 4.31 | -31.22 |
| LTM   | Ave Pel Baseline| 10.42| -36.16 |
| LTM   | YP              | 9.18 | -37.43 |
| LTM   | YP              | 10.65| -30.98 |
| LTM   | YP              | 10.47| -30.38 |
| LTM   | YP              | 9.74 | -30.80 |
| LTM   | YP              | 9.29 | -32.49 |
| LTM   | YP              | 9.87 | -30.28 |
| MCK   | Ave Lit Baseline| 2.76 | -24.71 |
| MCK   | Ave Pel Baseline| 4.58 | -32.91 |
| MCK   | LMB             | 11.41| -30.79 |
| MCK   | LMB             | 11.10| -30.72 |
| MCK   | LMB             | 10.93| -30.54 |
| MCK   | LMB             | 10.35| -27.54 |
| MCK   | LMB             | 10.01| -28.03 |
| MON   | Ave Lit Baseline| 3.42 | -24.73 |
| MON   | Ave Pel Baseline| 2.51 | -30.08 |
| MON   | LMB             | 9.65 | -26.10 |
| MON   | LMB             | 9.27 | -26.15 |
| MON   | LMB             | 9.15 | -25.48 |
| MON   | NP              | 9.57 | -26.26 |
| MON   | NP              | 9.03 | -24.57 |
| MON   | RT              | 10.30| -18.10 |
| MON   | RT              | 10.07| -18.23 |
| MON   | RT              | 9.73 | -17.66 |
| NIC   | Ave Lit Baseline| 2.44 | -23.12 |
| NIC   | Ave Pel Baseline| 3.29 | -27.84 |
| NIC   | LMB             | 11.19| -28.62 |
| NIC   | LMB             | 10.67| -29.63 |
| NIC   | NP              | 9.53 | -27.83 |
| NIC   | NP              | 9.29 | -27.99 |
| NIC   | NP              | 8.91 | -31.12 |
| PAR   | Ave Lit Baseline| 3.30 | -30.84 |
| PAR   | Ave Pel Baseline| 4.60 | -34.79 |
| PAR   | LMB             | 11.98| -32.29 |
| PAR   | NP              | 11.60| -34.13 |
| PAR   | NP              | 11.57| -33.29 |
| PAR   | NP              | 10.93| -32.89 |
| PSF   | Ave Lit Baseline| 1.41 | -17.05 |
| PSF   | Ave Pel Baseline| 7.34 | -28.28 |
| PSF   | SMB             | 12.35| -25.86 |
| PSF   | SMB             | 12.68| -24.72 |
| PSF   | SMB             | 12.22| -24.78 |
| Lake  | Sample          | δ¹⁵N | δ¹³C |
|-------|-----------------|------|------|
| LTM   | Ave Lit Baseline| 6.23 | -21.27 |
| LTM   | Ave Pel Baseline| 6.89 | -26.46 |
| ROX   | NP              | 14.30| -26.75 |
| ROX   | NP              | 14.16| -25.51 |
| ROX   | NP              | 13.50| -26.48 |
| STA   | Ave Lit Baseline| 3.89 | -22.69 |
| STA   | Ave Pel Baseline| 4.62 | -27.98 |
| STA   | YP              | 14.27| -26.57 |
| STA   | YP              | 14.18| -26.52 |
| STA   | YP              | 14.02| -26.61 |
| STA   | YP              | 13.88| -27.20 |

ZIEGLER ET AL.

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January 2015 • Volume 6(1) • Article 5
Table A2. Continued.

| Lake | Sample       | δ¹⁵N  | δ¹³C  |
|------|--------------|-------|-------|
| STA  | YP           | 13.97 | −26.29|
| STO  | Ave Lit Baseline | 6.12  | −21.99|
| STO  | Ave Pel Baseline | 6.05  | −29.42|
| STO  | NP           | 14.90 | −29.88|
| STO  | NP           | 14.68 | −30.09|
| STO  | NP           | 13.89 | −28.51|
| STO  | SMB          | 15.65 | −29.31|
| STO  | SMB          | 14.71 | −30.04|
| SUG  | Ave Lit Baseline | 4.28  | −21.61|
| SUG  | Ave Pel Baseline | 3.24  | −30.32|
| SUG  | SMB          | 13.10 | −27.18|
| SUG  | SMB          | 12.30 | −27.65|
| SUG  | SMB          | 12.26 | −28.73|
| SUG  | SMB          | 12.20 | −28.82|
| SUG  | SMB          | 10.74 | −30.99|
| SUG  | SMB          | 9.82  | −29.65|
| SUG  | YP           | 10.17 | −29.97|
| SUG  | YP           | 9.99  | −30.84|
| SUG  | YP           | 9.82  | −29.76|
| SUG  | YP           | 9.42  | −29.51|
| SUG  | YP           | 9.16  | −30.00|
| SUG  | YP           | 8.72  | −29.35|
| SUG  | YP           | 8.43  | −29.03|
| TRO  | Ave Lit Baseline | 9.28  | −17.82|
| TRO  | Ave Pel Baseline | 8.97  | −31.30|
| TRO  | NP           | 17.00 | −27.64|
| TRO  | Wal          | 16.37 | −31.35|
| TRO  | Wal          | 16.23 | −31.34|
| TRO  | Wal          | 15.67 | −33.67|
| TRO  | Wal          | 15.33 | −26.32|
| TRO  | Wal          | 15.13 | −34.15|
| WAT  | Ave Lit Baseline | 1.02  | −23.43|
| WAT  | Ave Pel Baseline | 5.92  | −30.05|
| WAT  | SR           | 8.36  | −27.14|
| WAT  | YP           | 11.91 | −24.39|
| WAT  | YP           | 11.78 | −26.72|
| WAT  | YP           | 11.67 | −26.73|

*Note:* Fish species codes are: YP = yellow perch, SMB = smallmouth bass, NP = northern pike, LMB = largemouth bass, LT = lake trout, BT = brown trout, SR = Silver redhorse, Wal = walleye. Lake abbreviations are as follows: BIS = Bisby, BRA = Bran de Scie, BRO = Bromont, DAR = D’Argent, DEN = Denison, FRA = Français, GAL = Gale, LSG = Lac St-George, LTM = Lac Trois-Milles, MCK = McKenzie, MON = Des Monts, NIC = Nick, PAR = Parker, PSF = Petit Saint-François, ROX = Roxton, STA = St. Augustin, STO = Stoke, SUG = Sugarloaf, TRO = Trois-Lacs, WAT = Waterloo.