Regional ecosystem variability drives the relative importance of bottom-up and top-down factors for zooplankton size spectra

Kerri Finlay, Beatrix E. Beisner, Alain Patoine, and Bernadette Pinel-Alloul

Abstract: The relative effects of top-down and bottom-up drivers of zooplankton size structure were examined in three limnologically diverse regions of Quebec, Canada. Lake productivity drove biomass of small-sized zooplankton (300–1000 µm) in the Eastern Townships and Laurentian regions, which have high total phosphorus gradients, but was not significant in the low-productivity region, Gouin. Fish species composition was found to affect biomass of large-sized (>1000 µm) zooplankton and was the primary factor affecting zooplankton size structure in the low productivity region. When size structure of the zooplankton communities were described as normalized biomass size spectra, only bottom-up factors were significant, as increasing productivity resulted in higher curve peaks and increased parabola curvature. No factors were significantly related to any parameter of the Pareto distribution to describe size spectra. Overall, bottom-up forces were stronger drivers of zooplankton size structure, particularly in regions with wide ranges in lake trophy, while fish predation was more important in regions with low productivity variability.

Résumé : Nous avons examiné les effets relatifs des facteurs explicatifs descendants et ascendants de la structure en taille du zooplancton dans trois régions du Québec, Canada, qui diffèrent par les caractéristiques limnologiques de leurs lacs. La productivité lacustre explique la biomasse du zooplancton de petite taille (300–1000 µm) dans les Cantons de l’Est et les Laurentides où il existe de forts gradients de phosphore total; elle n’est cependant pas significative dans la région de Gouin qui possède une faible productivité. La composition spécifique des poissons affecte la biomasse du zooplancton de grande taille (>1000 µm) et elle est le principal facteur à affecter la structure en taille du zooplancton dans la région de faible productivité. Lorsque la structure en taille du zooplancton est présentée sous forme de spectres de taille de la biomasse normalisée, seuls les facteurs ascendants sont significatifs, car une productivité accrue a pour effet de produire des sommets plus élevés dans la courbe et d’augmenter la courbure de la parabole. Aucun des facteurs n’est significativement relié à quelque paramètre que ce soit de la distribution de Pareto qui sert à décrire les spectres de taille. Globalement, les forces ascendants sont de meilleurs facteurs explicatifs de la structure en taille du zooplancton, particulièrement dans les régions où il existe une forte étendue de trophie dans les lacs, alors que la prédation par les poissons est plus importante dans les régions de faible variation de la productivité.

Introduction

The question of whether bottom-up or top-down factors drive ecosystem dynamics has shifted in the last two decades to address instead when and under what conditions top-down or bottom-up factors dominate (Hunter and Price 1992; Power 1992). In lakes, bottom-up factors known to affect zooplankton dynamics include total phosphorus (TP) and cation concentration. Increased TP generally increases total zooplankton abundance and biomass (Hanson and Peters 1984; Yan 1986; Pinto-Coelho et al. 2005), but has often been demonstrated to disproportionately affect smaller zooplankton (Bays and Crisman 1983). Calcium is considered to be limiting for large cladocerans, and increasing cation concentration has been linked to an increase in the abundance of larger zooplankton (Tessier and Horwitz 1990; Patoine et al. 2002). Top-down predation effects of both invertebrates (Mysis spp.: Nero and Sprules 1986; Johannsson et al. 1994; and Chaoborus spp.: Kajak and Rybak 1979; Mackay et al. 1990; Ramcharan et al. 2001) and fish (Brooks and Dodson...
and the relative effects of each predator on zooplankton communities have been summarized by McQueen et al. (1986). Thus, although we currently know which factors can regulate zooplankton biomass and size structure, general trends of the relative strengths of top-down and bottom-up factors across lakes and regions remain elusive.

While a combination of both lake productivity and fish predation have been shown to be responsible for variations in zooplankton biomass and size structure, differences in the relative strengths of top-down and bottom-up factors between studies are common (e.g., Stemberger and Lazorchak 1994; Hessen et al. 1995; Pinel-Alloul et al. 1995). Differences in the relative variability of abiotic and biotic variables at different scales of observation may explain the lack of observed trends between studies and systems (Hunter and Price 1992). For example, Gasol et al. (1995) observed that heterotrophic nanoflagellates were correlated with bottom-up forces across lakes that varied greatly in resource supply, but when examining nanoflagellates within individual lakes (where variation in resource supply was lower), both bottom-up and top-down forces were important. The scale of observation has been used to explain the differences in conclusions drawn regarding the relative effects of top-down and bottom-up factors for crustacean zooplankton (Pinel-Alloul et al. 1995). Currie et al. (1999) found that resource levels most strongly affected zooplankton abundance across three regions in Quebec and Ontario, while across five regions in Quebec. Pinel-Alloul et al. (1995) found that bottom-up factors of lake chemistry were the main factors explaining zooplankton community structure. In contrast, Rodriguez et al. (1993) concluded that fish were more important when only one of the Quebec regions was studied.

The range of values for physical and chemical variables as well as for predation pressure often differs considerably within and between different regions, and thus conclusions may be influenced by the scale of observation and gradients of variability present in a particular area of interest.

Here, we examine the relative strengths of top-down and bottom-up factors on different size classes of crustacean zooplankton and test for differences among three lake districts that differ in their range of limnological characteristics. We examine a region that varies widely in TP concentration because of heavy human use (Eastern Townships), one that has moderate human activity and accordingly moderate variation in nutrient concentration, but is also characterized by highly coloured dissolved organic carbon (DOC, Laurentians), and one that has very low human impact and low nutrient variability (Gouin Reservoir). We predict that those regions with greater variation in nutrient availability will have stronger bottom-up effects than the region with lower nutrient variability.

As a secondary goal, we sought to explore the relationships between bottom-up and top-down factors on size spectra descriptors. Much previous work on size structure in aquatic systems has revolved around the construction of normalized biomass size spectra (NBSS) (Platt and Denman 1978) and Pareto distributions (Vidondo et al. 1997). These models fit to organism size data and have been used to estimate productivity and energy flow through lake food webs (Thiebaux and Dickie 1992, 1993; Sprules and Goyke 1994).

Most previous studies that have examined the effect of bottom-up and top-down drivers on size spectra shape have done so across multiple trophic levels from phytoplankton to fish (e.g., Sprules and Munawar 1986; Gaedke 1992; Zhou 2006), which is anticipated to follow different patterns than within trophic levels (Thiebaux and Dickie 1992, 1993; Sprules and Goyke 1994). Of those that have looked at zooplankton specifically, bottom-up and top-down factors have only been invoked anecdotally or by using a limited number of drivers. For example, in a comparison of the Great Lakes epilimnion and hypolimnion communities, Yurista et al. (2006) found that of temperature, conductivity, and chlorophyll concentration, temperature was the only significant factor driving size spectra in the Great Lakes. Moore and Suthers (2006) suggested that NBSS slopes may also reflect the relative contribution of top-down and bottom-up factors in communities of varying productivity and that oligotrophic systems may have steeper slopes because of control by top-down forces, but this was not tested directly. We therefore sought to determine whether there are consistent relationships between bottom-up and top-down forces and the biomass size structure, as well as the parabolic shape of NBSS in lake zooplankton.

The objectives of this study are twofold: (i) to determine the relative strengths of top-down and bottom-up factors on the biomass of different size classes of zooplankton in lakes in three regions in Quebec (Canada) that vary considerably in productivity, geology, and land use and (ii) to determine whether these same factors also affect NBSS and Pareto descriptions of zooplankton communities to facilitate future research in size spectrum theory.

**Materials and methods**

**Study sites**

We examined changes in biomass size structure in three different regions in Quebec: the Eastern Townships, Laurentians, and Gouin Reservoir. These three areas differ widely in their underlying geology, land use, and accordingly, their productivity (Table 1). Although the three regions were sampled in different years (1996, 2004, and 2005), all samples were taken during the month of July, and therefore those lakes that stratify will have done so at the time of sampling. 1996 and 2004 were average years in terms of climate (data from Environment Canada; www.climate.weatheroffice.ec.gc.ca) as the mean summer temperature and precipitation were well within the 10-year averages for Montreal. 2005, however, was a particularly warm and wet year (average temperature was 1.4 °C warmer than 1996 and 2004 and had the highest precipitation in the 10-year period).

Although interannual variability in zooplankton species dynamics can be large in some lakes (e.g., Gerten and Adrian 2002), Olden et al. (2006) found that this variability has only serious consequences when making conclusions for lakes that are similar in their habitat characteristics. Since we sampled lakes within each region in the same year, we believe that variability due to interannual differences among lakes within regions will be minimal relative to the differences among these very diverse regions.
### Table 1. Mean (range in parentheses) limnological lake characteristics in the three regions of Quebec.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Region</th>
<th>Eastern Townships</th>
<th>Laurentians</th>
<th>Gouin</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Bottom-up</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake area (km²)</td>
<td></td>
<td>2.9 (0.2–14.5)</td>
<td>1.2 (0.1–5.3)</td>
<td>0.42 (0.2–0.8)</td>
</tr>
<tr>
<td>TP (µg·L⁻¹)</td>
<td></td>
<td>16.5 (5.2–45.1)</td>
<td>19.0 (5.4–48.0)</td>
<td>7.6 (4.6–15.5)</td>
</tr>
<tr>
<td>TN (mg·L⁻¹)</td>
<td></td>
<td>0.41 (0.17–0.93)</td>
<td>0.31 (0.18–0.56)</td>
<td>0.23 (0.14–0.32)</td>
</tr>
<tr>
<td>DOC (mg·L⁻¹)</td>
<td></td>
<td>5.8 (2.3–8.9)</td>
<td>5.8 (2.1–9.3)</td>
<td>5.1 (2.8–9.5)</td>
</tr>
<tr>
<td>Secchi disk depth (m)</td>
<td></td>
<td>3.7 (0.8–9.5)</td>
<td>3.9 (1.5–8.5)</td>
<td>4.0 (2.1–6.1)</td>
</tr>
<tr>
<td>Mean Chl a (µg·L⁻¹)</td>
<td></td>
<td>5.2 (0.9–22.3)</td>
<td>2.1 (0.43–7.6)</td>
<td>2.2 (1.0–3.2)</td>
</tr>
<tr>
<td><strong>Top-down</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zₘₐₓ (m)</td>
<td></td>
<td>20.9 (1.8–61.9)</td>
<td>16.9 (4.2–45.7)</td>
<td>13 (7–23)</td>
</tr>
<tr>
<td>Fish species (n)</td>
<td></td>
<td>12.2 (6–19)</td>
<td>9.2 (5–15)</td>
<td>3.7 (1–7)</td>
</tr>
</tbody>
</table>

**Note:** Bottom-up variables included in the analyses were lake area, total phosphorus (TP), total nitrogen (TN), dissolved organic carbon (DOC), Secchi disk depth, and mean chlorophyll a (Chl a) concentration. Top-down factors included the presence or absence of common fish species (number of species (n)), the presence or absence of *Chaoborus* predators (not included in table), and maximum lake depth (Zₘₐₓ).

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**Eastern Townships lakes**

Eighteen lakes in the Eastern Townships region of Quebec were sampled in July 2004 (Beisner et al. 2006). These lakes are located 100 km east of Montréal in a well-buffered, calcareous region underlain by a sedimentary geology of the St. Lawrence lowlands and characterized by elevated pH and alkalinites.

Each lake was sampled at the deep point to reflect the deep pelagic community, but may not reflect conditions throughout the entire lake. Zooplankton samples were taken using a 0.5 m diameter, 2 m long, 100 µm mesh net from 1 m above the sediment to the lake surface during daylight hours, between 1000 and 1800. Cod-end samples were collected and preserved in 75% ethanol. Secchi disk depth, pH, TP, total nitrogen (TN), DOC, dissolved inorganic carbon (DIC), and chlorophyll a (Chl a) concentration were taken at the same time as the zooplankton samples. Details of chemical analyses can be found in Beisner et al. (2006). The presence or absence of *Chaoborus* spp. was determined by visual examination of the samples collected, but because of the low densities and different behaviour of these predators we did not attempt to quantify their abundance. Data of fish species composition were obtained from the Quebec Ministry of Natural Resources and Wildlife, who have sampled these lakes sporadically since the 1930s using a variety of gill nets. Fish in the Gouin region have been studied previously (Patoine et al. 2002). Patoine et al. (2002) examined the effect of watershed deforestation by logging and wildfires on the zooplankton communities for 3 months in each of 2 years following the perturbation, but for our study, we used only the data from July 1996 in reference lakes that were unaffected by logging or forest fires. The Gouin region intersects the Greenville and Superior geological provinces of the Canadian Shield (details of the lakes and region can be found in Carignan et al. 2000), and the lakes here are generally oligotrophic.

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Zooplankton were sampled from the deepest site in each lake using a cantilevering net (Filion et al. 1993) fitted with a 53 µm net from 1 m above the sediments to the surface. Fish in the Gouin region were sampled in 1996 and 1997 with experimental monofilament gill nets with a fishing effort between 6 and 12 nets per night, depending on lake area (St-Onge and Magnan 2000). Details of zooplankton and environmental sampling can be found in Patoine et al. (2002), who used an optical plankton counter (OPC) to analyze zooplankton samples.
Although the zooplankton were sampled using different methods in the three regions, we do not believe that these differences substantially biased our results. The cantilevering net is designed to minimize clogging and avoidance (Filion et al. 1993) and was particularly unlikely to clog in Gouin, which has low zooplankton densities. Our plankton nets used in the Eastern Townships and Laurentians had an open area ratio of 5:1, which should minimize clogging in most lakes (Omori and Ikeda 1984). Net efficiency has been shown to vary from 32% to 100% (McQueen and Yan 1993), and thus a severely clogged net may under-represent zooplankton densities by three times. Net clogging was possible in some of our very productive lakes; however, we observed ranges in large zooplankton (>1000 \( \mu \text{m} \)) densities from 0 to 1000 \( \text{m}^{-3} \), which is a difference of 1000 times. Thus we believe that the natural variability in densities between lakes overlays any potential differences that may have occurred because of a reduction in net efficiency.

The use of the OPC and LOPC is also not anticipated to contribute substantially to differences between regions. Patoine et al. (2006) compared OPC derived values with microscope estimates of zooplankton abundance and biomass, and Finlay et al. (2007) did the same comparisons for the LOPC. Thus, the output from both devices in terms of their abilities to process laboratory-fixed samples have been compared and standardized to microscope counts, and the differences between the OPC and LOPC should be minimal.

Size spectra analyses

The NBSS plots the normalized biomass of the community vs. the log biomass of the particle. The slope and intercept of the regression line or the parameters describing a parabolic curve comprising the overall size spectra (Vidondo et al. 1997). We used both the NBSS and Pareto distributions to describe size spectra, since the Pareto parameter \( c \) is an unbiased estimator of the NBSS slope and yields a better fit to the data. Furthermore, it avoids the need to group data by log size classes and avoids the problem of empty size classes that occurs with NBSS. The Pareto type II can be used to model parabolic curves comprising the overall size spectra (Vidondo et al. 1997). We used both the NBSS and Pareto descriptions of zooplankton size spectra for our analyses.

**NBSS calculations**

The LOPC provides data of the number of individuals in 15 \( \mu \text{m} \) bins. The biomass of the midpoint of each 15 \( \mu \text{m} \) bin was calculated using the following equation (Sprules and Munawar 1986):

\[
V = \frac{\Pi}{6} \left( \frac{\text{ESD}^3}{f^2} \right)
\]

where \( V \) is volume, which was converted to biomass assuming a specific gravity of 1; ESD is the equivalent spherical diameter of the particle as measured by the LOPC, and \( f \) is a ratio of length:width for the zooplankton samples. Previous work has found that a value of 1.72 provides the closest relationship between volume and biomass as determined by species-specific length–weight regressions in the Eastern Townships (Finlay et al. 2007). This \( f \) value fits in the range of values found by Patoine et al. (2006) and thus was used to calculate biomass in all three regions. The OPC data from the Gouin region were available as the density of particles in 100 \( \mu \text{m} \) ESD bins. The midpoint of each 100 \( \mu \text{m} \) bin was converted to biomass using the equation and conversions above.

Bin size was \( \log_{10} \)-transformed, and total community biomass was summed over all sizes in each 0.1 \( \log_{10} \) biomass size class. Delta biomass was calculated as the difference in biomass between each 0.1 \( \log_{10} \) size class (each bin was thus 1.259 times the size of the previous bin). Biomass size spectra are represented graphically as \( \log(\text{biomass (per m}^2) / \text{Abiomass}) \) vs. \( \log \) biomass of size class. Calculations of NBSS followed that of Gaedke (1992). Although the LOPC measures zooplankton from 100 to 3500 \( \mu \text{m} \) ESD, we analyzed only those zooplankton between 300 and 2000 \( \mu \text{m} \) ESD. We found that bubbles in the lab circulator arrangement of the LOPC prevented accurate counts below 300 \( \mu \text{m} \) ESD, and an extremely low density of larger zooplankton (because of the use of a small plankton net) made counts >2000 \( \mu \text{m} \) ESD unreliable. This also allowed for direct comparisons with the OPC, as the lower limit of detection for this is ~250 \( \mu \text{m} \) ESD (Herman et al. 2004); thus, we are confident that both the OPC and LOPC were adequately counting the smallest particles included in our analyses. The zooplankton included in this 300–2000 \( \mu \text{m} \) window ranged from small copepods to the largest daphnids, but excluded the microzooplankton, including copepod nauplii and rotifers, and larger predatory zooplankton such as *Mysis* spp. and *Leptodora* spp. (Finlay et al. 2007).

A parabolic fit was applied to these data using

\[
y = a + 0.5c(x - b)^2
\]

where \( c \) is the curvature of the parabola, and \( a \) and \( b \) are the \( y \) and \( x \) coordinates of the vertex (Sprules and Goyke 1994). Parameter \( a \) is thus considered to reflect total zooplankton biomass.

**Pareto calculations**

The density of individuals in each 15 \( \mu \text{m} \) ESD size bin (as given in the LOPC output for the Eastern Townships and Laurentian regions) and 100 \( \mu \text{m} \) bins (from the OPC output for the Gouin data) was used to construct the Pareto distributions of the size spectra following Vidondo et al. (1997). The probability that an individual is of a given size is taken as the fraction of all individuals larger than or equal to itself (Boix et al. 2004) and is plotted against the weight of that size class, using the calculations above to convert ESD to biomass. The relationship was fit with the type II Pareto model:

\[
\log[\text{prob}(s \geq S)] = c \log(K + D) - c \log(S + D)
\]

where \( \log[\text{prob}(s \geq S)] \) is the accumulated probability that the size variable \( s \) will have a value greater than the size \( S \) of the individual in question. \( c \) and \( K \) are the distribution’s shape and scale parameters, respectively, and \( D \) is an additive constant.
Statistical analyses

The data used for ordination techniques was zooplankton biomass in bins of 100 µm (Gouin) and 105 µm ESD (Eastern Townships and Laurentians, since LOPC data are only available in 15 µm groups). Principal components analysis (PCA) using zooplankton biomass in each bin was used to evaluate the similarities between lakes and regions.

The relationship between environmental variables and biomass of zooplankton in different size classes was first analyzed using data of zooplankton biomass in 100 µm (Gouin) and 105 µm (Eastern Townships and Laurentians) bins. This allows for a direct estimate of how each environmental factor affects each size class of zooplankton using redundancy analyses (RDA). Environmental variables with non-normal distributions were log-transformed, and all variables were centered and standardized prior to ordination. Significant ($P < 0.05$) predictor variables were determined using forward selection, and significance was determined by Monte Carlo permutation (999 permutations).

To separate the relative effects of different predictor variables, the significant environmental variables representing top-down and bottom-up factors were run in separate RDAs. Top-down variables included common fish species composition (those species occurring in more than three lakes) and the presence or absence of Chaoborus spp., as well as lake depth, as an increase lake depth allows zooplankton to vertically migrate and avoid fish predation (Tessier and Welser 1991; Gaedke 1992). The effect of piscivores will be different than the effect of planktivores on zooplankton size spectra, but this will be reflected in the direction of the relationships in the RDA. Planktivorous fish species will have a negative relationship with large ($>1000$ µm) zooplankton, while piscivores that create a trophic cascade will be positively correlated with large zooplankton biomass (Brooks and Dodson 1965). Chaoborus spp. feed preferentially on small zooplankton ($<1000$ µm, Wissel et al. 2003), and thus we would expect a negative relationship between these two groups in the RDA.

Bottom-up effects included lake size, TP, TN, DOC, Secchi disk depth, Chl $a$ concentration, as these all reflect potential productivity of lakes. RDAs examining both top-down and bottom-up factors together were run on the significant variables from the separate analyses. All PCAs and RDAs were performed using CANOCO version 4.5 (ter Braak 1990). The variation explained by bottom-up and top-down factors were summarized using variation partitioning (Borcard et al. 1992; Peres-Neto et al. 2006).

Relationships between environmental factors and the fitted size spectra functions were explored using multiple regression with forward selection of parameters from the NBSS ($a$, $b$, and $c$ from eq. 2) and Pareto ($c$, $K$, $D$ from eq. 3) to environmental variables (maximum depth, mean depth, volume, area, Secchi disk depth, pH, TP, TN, DOC, DIC, total Chl $a$). Critical $\alpha$ was chosen as the Bonferroni correction of 0.05/6 = 0.008 to account for multiple comparisons. To determine the effect of the presence or absence of predator species on size spectra parameters, $t$ tests were used. Multiple regressions and $t$ tests were performed using the statistical program JMP IN version 5.1 (SAS Institute Inc., Cary, North Carolina).

Results

An example of the three different size spectra analyses (biomass in 100 µm bins, NBSS, and Pareto distributions) in each of the three regions (Eastern Townships, Laurentians, and Gouin) is shown (Fig. 1). The lakes in this figure were chosen to demonstrate the range of variability in size spectra and how these differences are captured by the different analyses. Lake Waterloo in the Eastern Townships is eutrophic (total Chl $a$ concentration $= 21.9$ µg·L$^{-1}$) and has one of the highest zooplankton biomass levels of all the lakes studied; Lake Connelly in the Laurentians is oligo–mesotrophic (Chl $a = 2.03$ µg·L$^{-1}$); and Lake N84 in the Gouin Reservoir is oligotrophic (Chl $a = 1.0$ µg·L$^{-1}$). A parabola could not be fit to Lake N84, and thus the straight-line relationship is shown here.

Most of the variability in biomass in each 105 µm size fraction for the Eastern Townships and the Laurentians was seen in the small zooplankton fractions (from 300 to 825 µm; Figs. 2a, 2b), as these small size classes oriented along the first axis of the PCA with longer vectors than the large sizes classes. In contrast, the contrast, the most variability in Gouin was in the larger zooplankton fraction (1100–1700 µm; Fig. 2c). Overall, the variability in the zooplankton biomass–size relationship was comparable between the Eastern Townships and Laurentian regions, but the zooplankton in the Gouin region varied comparatively little. The PCA of zooplankton biomass in all regions together shows an overlap of lakes in the Eastern Townships and those from the Laurentians, while the lakes in the Gouin region all cluster very closely together near the origin (Fig. 2d).

Bottom-up factors affecting zooplankton biomass in 105 µm bins

TP concentration was the sole bottom-up environmental factor selected by the RDA with biomass in 105 µm bins for the Eastern Townships (Fig. 3a; $P = 0.002$, 52.2% variation explained) and demonstrates that the biomass of small zooplankton classes increases as TP increases. In the Laurentians, the results of the RDA between biomass in 105 µm bins and bottom-up factors demonstrated that an increase in TN concentration positively affected the biomass of small zooplankton ($<1000$ µm ESD) and negatively affected larger zooplankton, while the opposite relationship was found with increasing lake area (Fig. 3b). No significant bottom-up factors were found for the Gouin lakes or when all lakes were examined together in a single RDA.

In the Laurentian lakes, there was no relationship between TP and Chl $a$ concentration (linear regression, $P > 0.05$, results not shown). There was, however, a significant relationship between TP and TN (linear regression, $P = 0.01$, $R^2_{adj} = 0.26$), suggesting that TP measurements were accurate (i.e., that sample contamination was unlikely the cause for the lack of relationship between TP and Chl $a$). Moreover, there was a significant but weak relationship between TN and Chl $a$ ($P = 0.004$, $R^2_{adj} = 0.34$). In contrast, the TP–Chl $a$ relationship in the Eastern Townships has $R^2_{adj} = 0.73$ ($P < 0.0001$), suggesting that additional factors in the Laurentians were affecting primary production relationships, which likely also affected relationships further up the food web.
Fig. 1. Examples of biomass in 100 µm equivalent spherical diameter (ESD) bins (a, b, c), normalized biomass size spectra (NBSS) (d, e, f), and Pareto distributions (g, h, i) for Lake Waterloo in the Eastern Townships (left column), Lake Connelly in the Laurentians (middle column), and Lake N84 in the Gouin Reservoir (right column). These lakes represent the range of size spectra seen in these areas. Details of lake productivity and morphometry can be found in Table 1. For the NBSS and Pareto distributions, the points represent the size spectra values, and the lines represent the curves fit to the points using a parabolic curve for the NBSS and the Pareto type II distribution.

Top-down factors affecting zooplankton biomass in 105 µm bins

The presence of three fish species (rainbow smelt, Osmerus mordax; white sucker, Catostomus commersonii; and golden shiner, Notemigonus crysoleucas) were selected by the RDA of the biomass–size relationship with top-down variables alone in the Eastern Townships (Fig. 4a; $P = 0.008$, 54.5% variation explained). No top-down factors were significant in the RDAs for the Laurentians. Only top-down forces were found to significantly influence the biomass–size relationship of the zooplankton community in the Gouin region. The presence or absence of three fish spe-
cies (brook trout (Salvelinus fontinalus), fallfish (Semotilus corporalis), and unidentified cyprinids) explained 49.3% of the variation (Fig. 4b; $P = 0.002$). No top-down factors were significant when all regions were examined together.

**Relative strengths of top-down and bottom-up factors in 105 µm bins**

When the significant top-down and bottom-up factors of the Eastern Townships lakes were entered into an RDA with forward selection, only TP and the presence of white sucker remained significant ($R_{adj}^2 = 61.2\%, P = 0.01$). The results of variation partitioning for each region show that in the Eastern Townships, 30.1% of the variation was attributed to differences in TP concentration ($P = 0.003$), only 12.1% was attributed to the presence of white sucker ($P = 0.031$), 18.9% was due to multicollinearity between TP and white sucker presence, and 38.8% of the variation remained unexplained (Fig. 5a). The variation partitioning for the Laurentians and Gouin lakes was more straightforward, as these regions only had one type of environmental driver that was significant in the RDA analyses. Bottom-up factors accounted for 34.7% of the variation in the Laurentian lakes,
while 36.7% of variation was attributed to top-down factors in Gouin lakes (Figs. 5b, 5c; all $R^2$ values are adjusted).

Relative strengths of top-down and bottom-up factors on NBSS and Pareto parameters

In the Eastern Townships, parameter $a$ (the $y$ coordinate of the peak) of the NBSS parabolic curve was found to increase significantly with TP (Fig. 6a; $P < 0.0001$, $R^2_{adj} = 0.70$), and NBSS parameter $c$ (the curvature of the parabola) was significantly lower with increasing TP (Fig. 6b; $P = 0.003$, $R^2_{adj} = 0.41$). No parameter of the Pareto distribution was significantly related to any bottom-up factor. The presence or absence of the significant fish species (as determined by the

RDA analyses) did affect several parameters of both the NBSS and Pareto distributions, but this was not significant at $\alpha_{crit} = 0.008$.

In the Laurentians, parameter $a$ of the NBSS was significantly negatively related to lake maximum depth (Fig. 7a; $P = 0.001$, $R^2_{adj} = 0.40$), while parameter $c$ was found to vary
negatively with TP and positively with lake area (Figs. 7c, 7d; multiple regression $P = 0.01$, $R^2_{adj} = 0.57$). For the Pareto distribution, only parameter $K$ was found to have any significant relationship with any environmental variable, and $K$ decreased with increasing maximum depth (Fig. 7b; $P = 0.005$, $R^2_{adj} = 0.34$). No parameter values were significantly affected by the presence or absence of any fish species in this region.

Of the 17 lakes studied in the Gouin region, the size spectra of four could not be fit with a parabola, but were instead better described by a straight line. No significant relationships were found between any size spectra parameter (parabolic or linear) and any environmental variable. Data of catch per unit effort and biomass per unit effort from 1996 and 1997 were also available for the fish species communities in these lakes, but there were no significant relationships between these values and parabola parameters. When the data from all three regions were analyzed together, no significant relationships were found between NBSS or Pareto parameters and any environmental variable (all regression $P > 0.05$).

**Discussion**

Both bottom-up and top-down factors were found to affect zooplankton biomass and size structure in Quebec lakes, supporting the previous findings of Hessen et al. (1995) and Pinel-Alloul et al. (1995). However, the nature of the relationship between the two types of factors and size-structure varied between regions, and no factors could explain patterns in zooplankton size structure across all regions together. Our results demonstrate that lakes from a region that varies greatly in terms of potential productivity may implicate different forcing factors from lakes where fish predation varies more. This suggests that in cross-lake studies, researchers must take the limnological characteristics and degree of variation of their study lakes into account when determining whether bottom-up or top-down factors more greatly influence zooplankton community biomass.

Bottom-up factors were stronger drivers of zooplankton size structure than top-down factors in the two regions with large ranges in potential productivity (Eastern Townships and Laurentians), but was not a significant factor in Gouin, which had low productivity. Bottom-up drivers were best represented by TP in the Eastern Townships, and although Chl $a$ has previously been found to be related to TP in the Laurentians (Masson et al. 2000); in 2005, we found that TN and lake area were better predictors of lake potential productivity. Increased precipitation increases DOC inputs into lakes (Schindler 1998), and colour DOC can change the relationships between nutrients and primary productivity (Carpenter et al. 1998). Thus, the warm and wet year of 2005 may have caused a shift in the usual relationships between nutrients and productivity in the Laurentians. Regardless of the specific limiting factors in this region, we were able to detect the significant bottom-up effect on zooplankton size spectra. In both the Eastern Townships and the Laurentians, bottom-up effects were disproportionate on small zooplankton (300–1000 µm ESD), supporting Bays and Crisman (1983). Increased cyanobacterial abundance at high levels of production have been shown to reduce the densities of large cladoceran zooplankton because of feeding inhibition (Ghadouani et al. 2006), which may explain why small zooplankton in these lakes responded more strongly to bottom-up factors than larger zooplankton.

Top-down effects explained a substantial proportion of zooplankton variability in Gouin and a smaller proportion than bottom-up drivers in the Eastern Townships. Although particular fish species were not found to affect zooplankton size structure in the Laurentian lakes, we are reluctant to conclude that top-down drivers are not operating at all in this region because of the lack of sufficient fish data. The fish data available from government sources are not ideal, although we do believe that the government surveys used here were sufficient to provide an accurate list of common fish species in lakes that were sampled.

White sucker, the only fish that affected zooplankton size structure in the Eastern Townships (when both top-down and bottom-up factors were considered together), can drive other benthivores, such as brook trout, to planktivory to avoid competition (Magnan 1988). In Gouin, the presence of cyprinids accounted for the majority of the variability in zooplankton size structure. This result is contrary to predictions, since cyprinids are planktivores. However, with detailed catch-per-unit-effort data for these lakes, we were able...
to verify that even lakes with high densities of cyprinids had high relative biomass of large-bodied zooplankton. Although cyprinids can feed on large zooplankton, they switch diets to feed preferentially on benthic macroinvertebrates once they reach a size of ~150 mm in length (Hjelm et al. 2003), usually in midsummer. Our analyses were based on samples taken in July, and lakes in the Gouin region that contained cyprinids lacked larger fish predators (data not shown). Thus, the positive relationship between large zooplankton and the presence of cyprinids likely reflects a predation release midsummer, allowing the largest zooplankton to increase in biomass. Although a detailed analysis of seasonal changes is beyond the scope of this study, preliminary analyses here found that high cyprinid biomass in June was correlated with much lower biomass of large zooplankton, supporting the midsummer predation release hypothesis.

It is somewhat surprising that the presence or absence of Chaoborus spp. did not have a significant effect on biomass or size spectra in any region, as previous work has found strong effects of Chaoborus on zooplankton size structure (Mackay et al. 1990). Instead, the lack of effect supports the predictions of McQueen et al. (1986), who suggested that invertebrate predators only have a strong regulating effect on zooplankton communities when fish predation is absent. This is further supported by the work by Steiner (2004), whose experimental work noted that Chaoborus may not have a strong regulating effect on Daphnia spp. mean body size even in the absence of fish. All lakes studied here had at least a few fish species present, which may have lessened the impact by Chaoborus on the zooplankton. Thus, although we did find some significant top-down effects in our study lakes, it is currently very difficult to predict which fish or invertebrate predators will exert the strongest regulating control in different lakes and regions.

Although the causes for the relative strengths of bottom-up and top-down drivers across regions may be attributed to variations in physical or chemical characteristics of the lakes, they may also be explained by the relative variability of both the drivers and the response of the zooplankton community. For example, the increased importance of top-down factors in the Gouin region may be due to the increased water clarity owing to lower primary production. Clearer water would allow visual predators to feed more efficiently (Benfield and Minello 1996; Gregory 1998). Our analyses, however, suggest that bottom-up factors exert stronger regulating control over zooplankton size spectra than top-down factors over a large geographical range. The lakes in Gouin had both a small range of potential productivity and small variability in zooplankton biomass relative to the other two regions. Thus, the potential for bottom-up drivers to exert regulating effects on the zooplankton community in this region were minimized, simply because nutrient levels were uniformly low in this region. Top-down forces emerged as the primary driving factor only when productivity variability was low, but even here, the relative variability in zooplankton biomass was low compared with the other two regions. Thus, overall, bottom-up factors appear to be responsible for large changes in zooplankton size structure, but in the absence of large shifts in bottom-up factors, top-down forces can exert regulating effects over smaller variations in zooplankton biomass. This agrees with the conclusions of Carpenter et al. (1985), who suggested that primary productivity is primarily driven by nutrient levels, but trophic cascades can explain additional variability between systems. A comparison of the significant drivers and relative variability of the response variable of interest (in our case, zooplankton biomass and size structure) may aid in the comparison of studies across different systems and landscapes to obtain a hierarchy of environmental drivers.

In our study, normalized biomass size spectra parameter values were well correlated with a few bottom-up environmental drivers, while the Pareto distribution was not well described by any environmental factor. Top-down factors were never significantly related to any size spectra parameter, sug-
suggesting that these descriptions of zooplankton size spectra are less sensitive to top-down and bottom-up effects than biomass in size-binned groups.

Parameter $a$ of the NBSS reflects total biomass of the zooplankton. Thus, the significant relationship between TP and parameter $a$ for the Eastern Townships supports the considerable previous research that phosphorus concentration affects zooplankton biomass (Hanson and Peters 1984; Yan 1986). Again, increased lake colour in the Laurentian lakes is the likely explanation why TP was not found to vary with parameter $a$ in these lakes. The relationship between parameter $a$ and lake maximum depth likely reflects the effect of potential primary productivity on zooplankton biomass, as deep lakes have lower productivity per unit volume than shallow lakes. The lack of relationship in the Gouin lakes is most likely a reflection of the low variability of TP and productivity in these lakes.

Increasing TP was also correlated with increased curvature (more negative parameter $c$ values) in the Eastern Townships and Laurentians (where lake area was also significantly related to parameter $c$). Similarly, Yurista et al. (2006) found that parameter $c$ of the NBSS was more negative in Lakes Erie and Ontario, the most productive of the Great Lakes, when compared with Lakes Huron, Michigan,
and Superior. It is difficult to explain the environmental or biological drivers behind a straightening of parabolic curves with decreasing lake productivity, since a straighter line could be due to a relative increase of either larger or smaller particles or to a relative decrease in mid-sized particles.

Top-down factors did not consistently affect either the NBSS or Pareto distribution for any region. The non-significant relationships between fish and invertebrate predator species composition and parameter values could be explained by a lack of sufficient data (for the Laurentians and Eastern Townships, we have only fish species presence or absence, and these data were collected at different times of the year and in different years). However, we did have additional data on the fish community (including catch and biomass per unit effort, sampled consistently) in the Gouin region and were still unable to find significant relationships with size-spectra-fitted lines and parabolas (data not shown). Thus, the effect of fish predation may be less severe on NBSS and Pareto distributions of zooplankton communities than it is on biomass–size distributions, which may also support the conclusion that overall, lake potential productivity is a stronger factor influencing zooplankton size structure than fish predation. Future studies examining the relationships between fish community interactions and density with zooplankton size spectra in more detail would provide valuable information to advance our understanding of zooplankton size spectra variations.

These results demonstrate that NBSS of zooplankton are influenced by bottom-up factors alone, while the Pareto distribution has no consistent relationship with any bottom-up or top-down factors. At this point, we can predict that an increase in lake productivity will increase parameter \( a \) and decrease parameter \( c \) of the NBSS parabola of zooplankton, which should help guide future work using size spectra for estimates of energy flow and production. Zooplankton biomass in binned sizes thus appears to be the most sensitive approach to establishing top-down vs. bottom-up effects. The NBSS curve still retains some biological information (e.g., parameter \( a \) represents zooplankton biomass), while the parabolic fit to the Pareto distribution has no obvious biological links. A straight-line fit to either the NBSS or Pareto may be more biologically meaningful and therefore more responsive to top-down and bottom-up forces; however, in productive systems, a straight-line fit is not always appropriate.

In conclusion, we demonstrated that the zooplankton communities in regions with wide ranges of potential productivity are driven by bottom-up effects, as seen on large latitudinal gradients (Pinto-Coelho et al. 2005). Lake potential productivity appeared to be the strongest driving factor, which was either represented by TP or TN, depending on lake colour, and increasing lake productivity results in an increase in the biomass of small (300–1000 \( \mu \)m ESD) zooplankton. Top-down effects of fish appear to dominate in regions with lower variability of productivity, where there is less variability in zooplankton biomass. Size spectra descriptions of zooplankton community appear to be most strongly affected by bottom-up factors, which may be useful for analyses of energy flow through aquatic communities and may provide quick estimates of lake potential primary productivity.

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**References**


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