ARTICLE

Size spectra analysis of a decade of Laurentian Great Lakes data

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Abstract: Size spectra analysis (SSA) is used to detect changes in food webs by simplifying complex community structures through abundance-versus-biomass considerations. We applied SSA to 10 years (2006–2015) of data on Great Lakes organisms ranging in size from picoplankton to macrozooplankton. Summer pelagic size spectra slopes were near the theoretical value of −1.0, but spring slopes were steeper, reflecting seasonal differences in abundance of small and large individuals. Pelagic size spectra slopes were relatively stable over the time period we examined. Height (the predicted number of organisms at the spectra midpoint) varied among lakes and was slightly higher in summer than spring in more productive basins. Including benthic data led to shallower slopes when combined with pelagic data, suggesting benthic organisms may increase food web efficiency; height was less affected by benthic data. Benthic data are not routinely included in SSA, but our results suggest they affect slopes and therefore SSA-based predictions of fish abundance. The ability of SSA to track changes in trophic energy transfer makes it a valuable ecosystem monitoring tool.

Résumé : L'analyse des spectres de taille (AST) est utilisée pour détecter des changements dans les réseaux trophiques en simplifiant la structure de communautés complexes sur la base de considérations concernant l'abondance et la biomasse. Nous avons appliqué l'AST à 10 années (2006–2015) de données sur des organismes des Grands Lacs de tailles allant du picoplancton au macrozooplancton. Les pentes des spectres de taille pélagiques estivaux s'approchent de la valeur théorique de –1,0, mais les pentes des spectres printaniers sont plus fortes, reflétant des variations saisonnières de l'abondance des petits et grands individus. Les pentes des spectres de taille pélagiques sont relativement stables durant la période étudiée. La hauteur (le nombre prédit d'organismes au point médian du spectre) varie d'un lac à l'autre et est légèrement plus grande en été qu'au printemps dans les bassins plus productifs. L'inclusion de données benthiques produit des pentes plus faibles quand elles sont combinées aux données pélagiques, ce qui donne à penser que les organismes benthiques pourraient accroître l'efficacité du réseau trophique; l'incidence des données benthiques sur la hauteur est moins importante. Des données benthiques ne sont pas systématiquement incluses dans les AST, mais nos résultats indiqueraient qu'elles ont une incidence sur les pentes et donc sur les prédictions de l'abondance des poissons issues de l'AST. La capacité de l'AST de faire ressortir les variations des transferts énergétiques trophiques en fait un bon outil de surveillance des écosystèmes. [Traduit par la Rédaction]

Introduction

Understanding and predicting ecosystem productivity requires knowledge about the current state of the ecosystem and how it influences production of different organisms. However, ecosystem modeling is challenging because food webs, especially in aquatic environments, can be highly complex and include many trophic links. Complex and highly specialized models dependent on numerous parameters have been used to estimate production of functional groups (e.g., phytoplankton, herbivorous zooplankton, omnivorous zooplankton) in individual systems; recent examples from the Great Lakes includes Rogers et al. (2014), Kao et al. (2016), and Zhang et al. (2016). However, these models are difficult to parameterize. Therefore, there is a need for simpler models to inform ecosystem-based management (Guiet et al. 2016).

Theory and empirical analyses have shown that we can gain insights into the structure of aquatic ecosystems by studying the distribution of organismal abundance and body size. In general, larger individuals prey upon smaller individuals but exhibit slower life histories (Sprules and Barth 2016; Guiet et al. 2016; Blanchard et al. 2017). Thus, aquatic systems are structured such that small organisms are numerically abundant and larger organisms are more rare, resulting in similar total biomass across groups when summed in logarithmically increasing size bins (Sheldon et al. 1972; Blanchard et al. 2014). This predictable relationship between abundance and size is referred to as a size spectrum (Trebilco et al. 2013; Sprules and Barth 2016; Blanchard et al. 2017). The abundance size spectrum provides a simple approach to understanding ecosystem productivity and structure, which may be useful for detecting disturbances and changes in ecosystem function that might not otherwise be apparent.

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184

Can. J. Fish. Aquat. Sci. Vol. 79, 2022

Despite their potential for use as ecological indicators, empirical tests of the variability, responsiveness, and utility of size spectra parameters in large freshwater systems are uncommon (Sprules and Barth 2016). The slopes of size spectra for entire ecosystems are related to energy conversion efficiency and are often near −1.0 (based on theory and field observations; Sprules and Barth 2016). A shallower slope than theoretical suggests more larger sized animals than expected and the converse if slopes steepen. For instance, deviations from this anticipated slope have been reported in systems with large influxes of migratory species (Duplisea and Kerr 1995), substantial incorporation of allochthonous material into food webs (Perkins et al. 2018), overfishing (Robinson et al. 2017), or recent invasions of non-native species (Kopf et al. 2019; Barth et al. 2019). The intercept and (or) height (predicted number of organisms in the midpoint) of size spectra have been postulated to reflect system production (e.g., higher intercepts or heights reflect greater abundance at a given body size; Jennings and Blanchard 2004; Guiet et al. 2016). Taken together, these parameters may delineate important characteristics in aquatic ecosystems and produce estimates of production at higher trophic levels that can be more difficult to sample (e.g., fish; Yurista et al. 2014). Therefore, understanding the responsiveness of size spectra to ecosystem change could unlock their utility in a wide array of ecological applications. For example, if size spectra vary predictably among ecosystems, or over time within an ecosystem, in response to perturbations (e.g., amount of nutrient loading, temperature; Sprules and Barth 2016), they could provide indications of those perturbations.

Coupling of benthic and pelagic energy pathways can have strong effects on ecosystem function; benthic pathways can provide important subsidies to secondary and tertiary aquatic consumers, in addition to removing and sequestering pelagic production (Vadeboncoeur et al. 2002; Reynolds 2008). This is especially important when benthic organisms affect pelagic systems, such as filter-feeding bivalves in both freshwater (Karatayev et al. 2002; Higgins and Vander Zanden 2010; Mayer et al. 2014) and marine systems (Mann et al. 2009). Despite this, most size spectra analyses (SSA) have focused on more tractable pelagic food webs, with few examinations of benthic food webs. In addition, there are limited examples of how pelagic and benthic energy pathways should be incorporated into SSA (Schwinghamer 1985; Cyr and Peters 1996; Mehner et al. 2018) and how the inclusion of benthic organisms influences estimates of size spectra parameters (dos Santos et al. 2017). Thus, there is currently limited knowledge about how the inclusion of benthic organisms into SSA influences their reflection on whole-ecosystem function.

The Laurentian Great Lakes are one of the largest surface freshwater ecosystems in the world and show a range of human impacts (Danz et al. 2007; Allan et al. 2013), including altered nutrient loading, nonnative species introductions (Sturtevant et al. 2019), and impacts of fisheries (commercial, recreational, and tribal) activities (Gaden et al. 2013). In addition, climate change will further stress the region (Bartolai et al. 2015) and is already reorganizing primary producer communities (Reavie et al. 2017). While many human impacts on the Great Lakes continue to increase, nutrient loading from anthropogenic sources has generally been reduced since the 1970s (Evans et al. 2011; Bunnell et al. 2014); many of the lakes are now considered oligotrophic or even ultra-oligotrophic, although Lake Erie's western bay is still seasonally eutrophic (Sterner et al. 2017). In response to such stressors, managers have increasingly sought tools that will allow them to use ecosystem-based analyses in the Great Lakes and make informed decisions that are scientifically defensible. Size spectra may offer such a tool.

Routine sampling of a variety of organisms are taken across the Great Lakes bi-annually by the United States Environmental Protection Agency (US EPA) Great Lakes National Program Office

(Barbiero et al. 2018). These data provide a unique and long running dataset for large lakes across a range of human impact levels, serving as an ideal case study to test the feasibility of utilizing size spectra metrics to inform management. Here, we compare two size spectra metrics (slope and height of the normalized size spectrum) across lakes and through time for the available decade-long data series (2006–2015). Based on a recent review (Sprules and Barth 2016), we expected that slope estimates would be near −1.0 in the summer in all lakes and years but would be steeper in spring, when production of zooplankton lags behind smaller-bodied phytoplankton. Therefore, we hypothesize that slope would be a poor indicator of lake productivity across seasons. We further hypothesize that height would be a better indicator of system production; therefore, we expect to observe greater size spectra heights in the productive western and central basins of Lake Erie than in the other lakes, as well increasing heights over the sampling decade in Lake Erie because of increasing nutrient loading. We expect that height would remain stable or decrease in the other lakes where nutrient loading is thought to have stabilized or declined. Finally, we incorporate benthic data on a subset of the summer series for which the size structure of benthic organisms was available to us (2012–2015) and explored the effect on slope, height, and insights into higher trophic level production provided by incorporating benthic organisms in the SSA.

Materials and methods

Sampling design and data selection

Data were derived from a long-term monitoring program of offshore waters in all five of the Laurentian Great Lakes by the US EPA (Barbiero et al. 2018). Each year, the R/V *Lake Guardian* sampled each lake after ice-out (March–May, hereinafter spring) and again in the growing season (July–August, hereinafter summer). The full methods are detailed in a series of recent studies (Reavie et al. 2014; Burlakova et al. 2018; Jude et al. 2018; Kovalenko et al. 2018; Barbiero et al. 2019) and are reported here in brief. We used data from 2006–2015 for the pelagic system and from 2012–2015 for the benthic system; years for which size data on most ecosystem components (excluding fish) were available to us. For size spectra analysis, all data need to be converted to individuals·m^{-2}.

Phytoplankton were sampled using a rosette to collect water for an integrated water column sample (spring) or an integrated epilimnetic sample and discrete deep chlorophyll maximum (DCM) sample (summer); phytoplankton were preserved in Lugol's iodine solution. Soft-bodied algae analyses followed the Utermöhl (1958) method; diatoms were acid digested and then mounted on slides. All algae were measured and biovolume calculated ($\mu m^3 \cdot mL^{-1}$); details are in Reavie et al. (2014). We assumed the cells had the same density as water to convert biovolume to wet biomass. Phytoplankton data from summer sampling were not available from Lake Erie or Lake Ontario in 2006; thus, 2006 summer size spectra were not calculated for those lakes.

Phytoplankton cell abundance (cells·m^{-2}) was estimated differently for spring and summer samples because the water column is well-mixed in the spring and is typically stratified during summer. In the spring, we assumed the water column was fully mixed and that the size distribution and cell density of phytoplankton were uniform with depth; thus, we calculated the abundance of cells by multiplying the cell density (cells·m^{-3}) in the integrated sample by the depth of the station. Assessing phytoplankton abundance and size structure during the summer is more complex because of stratification and the frequent formation of DCM. The phytoplankton cell density at the DCM is likely a maximum abundance for depths below the epilimnion and is not representative of the full hypolimnion. In addition, algal cells within the DCM are typically larger than those in the

epilimnion (Bramburger and Reavie 2016; Scofield et al. 2017). Thus, for summer samples, we weighted both the size distributions and abundance of phytoplankton cells by the relative contributions of each depth stratum to total chlorophyll. Phytoplankton biovolume data were collected from both the epilimnion and the DCM during summer months (Bramburger and Reavie 2016), and these data were paired with extracted chlorophyll measurements to calculate the ratio of phytoplankton biovolume to chlorophyll for each depth layer. To estimate the relative contributions of phytoplankton biomass above and below the thermocline, we used calibrated in situ fluorometer profiles corrected for quenching (see Scofield et al. 2020), which were collected concurrently with the phytoplankton samples. Integrated chlorophyll ($mg \cdot m^{-2}$) was calculated for depths above and below the thermocline using the trapz function within the R package pracma (Borchers 2018; R Core Team 2018). We then used the phytoplankton biovolume to chlorophyll ratio for both depth layers to calculate an estimated total biovolume within each layer. Size spectrum data for the epilimnion and DCM phytoplankton samples were then weighted by the relative contribution of each depth layer (above and below the thermocline, respectively) to total water column phytoplankton biovolume. When the water column was not stratified and (or) there was no DCM phytoplankton sample collected, the size spectrum calculation was completed assuming uniform distribution throughout the water column, as in spring.

Zooplankton was collected in two ways: (1) 63-μm mesh net (hereinafter small zooplankton) and (2) 153-μm mesh net (hereinafter large zooplankton). The 63-μm mesh net was lowered to 20 m (or 2 m from bottom) and the 153-μm mesh net was lowered to 100 m (or 2 m from bottom) before being pulled to the surface at $0.5 \ m \cdot s^{-1}$. Net efficiency for each vertical tow was calculated using calibrated flow meters. Zooplankton were immediately narcotized with soda water and preserved in a sucrose formalin solution. In the lab, the samples were split with a Folsom plankton splitter until a subsample consisted of 200 to 400 animals. Animals were identified to the lowest practical taxonomic level (at least genus, mostly species). Body measurements to the nearest 0.01 mm were used to estimate dry weight from standard length–weight regressions. Details are in Barbiero et al. (2019).

We used densities from the deeper 153-μm net tows for crustacean zooplankton excluding nauplii and densities from the shallow 63-μm mesh tows for rotifers, nauplii, and veligers. For the 63-μm mesh tows, we assumed that densities of these smaller animals were negligible below 20 m (Watkins et al. 2017). Organismal abundance was calculated as $animals \cdot m^{-2}$ by multiplying the volumetric density of those organisms ($animals \cdot m^{-3}$) by the height of the sampled water column, except in the western basin of Lake Erie (W. Erie hereinafter). In W. Erie, organismal abundance was calculated by multiplying the volumetric density by the depth of lake at the sample station because the basin is shallow (mean depth 7.4 m), such that up to 25% of the water column was not sampled (the bottom 2 m). In addition, the water column is typically well-mixed at these shallow sites, so using the full water column depth was appropriate.

Mysis diluviana was collected at night with either a 1-m^2 square plankton net (2006–2011) or a 1-m diameter, 2-m long, circular net. The net's mouth was lowered until it was 2–5 m from bottom and then pulled to the surface at $0.5 \ m \cdot s^{-1}$. Net efficiency was assumed to be 100% for both nets. Captured mysids were anesthetized in soda water and preserved in a sucrose formalin solution. In the lab, *M. diluviana* were measured to the nearest 0.1 mm and their dry weights were calculated; details are in Jude et al. (2018).

For all *Mysis* and all zooplankton except rotifers, we assumed that dry weight was 20% of wet weight (Downing and Rigler 1984).

For rotifers, we assumed dry weight was 10% of wet weight (Doohan 1973), with the exception of *Asplanchna* spp., for which we assumed dry weight was 3.9% of wet weight (Dumont et al. 1975).

Benthic data

In contrast to phytoplankton and zooplankton, which are collected both spring and summer, benthic organisms are collected using triplicate Ponar grabs only during the summer (in August). Since 2012, all macrozoobenthos organisms were counted and weighed, but prior to 2012 they were not all weighed. Therefore, we could only create size spectra that included benthic data from 2012 to 2015. Samples were elutriated and sieved through a 500 μm mesh screens and all organisms and sediments were preserved in 10% formalin. Thus, our benthic samples excluded smaller benthic organisms such as ostracods, harpacticoids, and nematodes (meiobenthos). Most of the benthic organisms were combined by species (or by larger taxonomic units) and then weighed together; taxa that require mounting on slides prior to identification (Oligochaeta and Chironomidae) were weighted by size groups. Thus, all organisms from a species were assigned the same average weight in the size spectra. For dreissenids, the mussels were sorted into 5 mm bins (e.g., 0–5, 5–10, 10–15 mm) and all mussels in a size bin were weighed together to yield an average shell-on wet weight (SOWW) for each 5 mm bin. For the size spectra, we used shell-free wet weight (SFWW) calculated using the following equation: $W_{SFWW} = 0.671 \times W_{SOWW}$ (L.E. Burlakova, unpublished data). Additional details are in Burlakova et al. (2018). For all benthic organisms, densities were reported as $animals \cdot m^{-2}$ and biomass as $g \cdot m^{-2}$.

Size spectra analysis

We calculated pelagic size spectra (PSS) for Lakes Superior, Michigan, Huron, W. Erie, central basin of Erie (C. Erie), eastern basin of Erie (E. Erie), and Ontario for each season (spring and summer). Lake Erie was broken into three separate regions because of the large differences in productivity among basins (e.g., Cai and Reavie 2018; Scofield et al. 2020). Benthic size spectra (BSS) were only calculated for the summer. To calculate pelagic and benthic size spectra (PBSS) only summer data from 2012–2015 were used.

We allocated all organisms based on their wet weight into log_2-binned size classes and then averaged the abundance ($individuals \cdot m^{-2}$) of organisms in each size bin across all sites for each season. Bins were generated by doubling bin starting weight at a wet weight of 1.2×10^{-13} g (2^{-43} g) until they encompassed all organisms in the dataset (largest size 8.4 g, 2^4 g). The slope of the abundance size spectra was calculated with linear least-squares regressions between the logarithm of abundance and the midpoint of each log_2 size class. We used Cook's distance to evaluate and remove points with high leverage; points with Cook's distance greater than one were discarded from the regression (Bollen and Jackman 1990). Values with high leverage typically occurred at the smallest or largest log_2 size class in a spectrum, although in one case it occurred near the midpoint. The R code we used for our analysis is available as a supplementary file (Supplementary Material A[1]).

To test for differences in the slope of the PSS, analysis of covariance (ANCOVA) with a full model (log_2[Abundance] $\sim log_2$[middle of wet weight bin] $\times$ year $\times$ lake $\times$ season) was used. We fit the full model and all possible combinations of explanatory variables while always including log_2(middle of wet weight bin) and size spectrum type, and we used the Akaike information criterion (AIC) to select the most parsimonious model (Akaike 1973). We present only models with AIC scores < 10 units different. Contrasts were evaluated with a Tukey's post hoc test. To test the robustness of relying on AIC scores, we also ran a best linear unbiased prediction (BLUP) type analysis, wherein we examined the lake $\times$ season $\times$ year slopes from our model, and then ran a


Table 1. The minimum and maximum bin size, in wet weight (g), of $\log_2$ bins for pelagic and benthic size spectra for each lake.

	Size spectra			
	Pelagic		Benthic	
Lake	Minimum bin	Maximum bin	Minimum bin	Maximum bin
Superior	2^{-41} to 2^{-40}	2^{-3} to 2^{-2}	2^{-18} to 2^{-17}	2^{-5} to 2^{-4}
Michigan	2^{-41} to 2^{-40}	2^{-4} to 2^{-3}	2^{-19} to 2^{-18}	2^{2} to 2^{3}
Huron	2^{-41} to 2^{-40}	2^{-4} to 2^{-3}	2^{-21} to 2^{-20}	2^{3} to 2^{4}
Western Erie	2^{-41} to 2^{-40}	2^{-9} to 2^{-8}	2^{-18} to 2^{-17}	2^{-2} to 2^{-1}
Central Erie	2^{-41} to 2^{-40}	2^{-8} to 2^{-7}	2^{-19} to 2^{-18}	2^{-1} to 2^{0}
Eastern Erie	2^{-41} to 2^{-40}	2^{-5} to 2^{-4}	2^{-19} to 2^{-18}	2^{2} to 2^{3}
Ontario	2^{-43} to 2^{-42}	2^{-3} to 2^{-2}	2^{-21} to 2^{-20}	2^{2} to 2^{3}

Note: Lakes are arranged by west to east order.

Fig. 1. Example abundance size spectra plot (for Lake Superior in 2007) with minimum and maximum size ranges of different organismal groups denoted by the grey line, and the grey box denoting the location of the height measurement for the pelagic abundance size spectra. The slopes of the size spectra (summer or spring data) are fit to each line and reported on the graph in boxes. Data not used in the linear model are presented as open circles. [Colour online.]
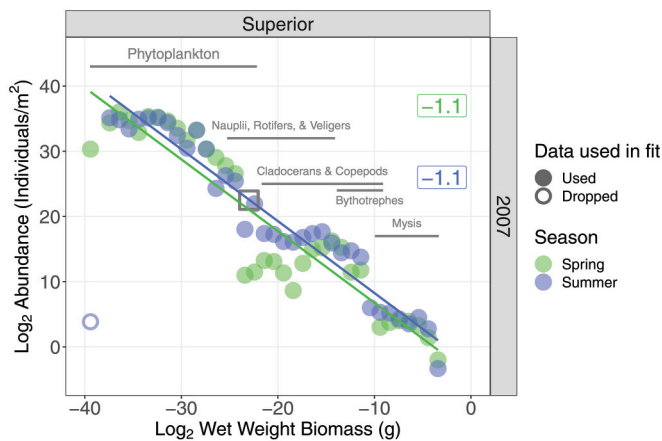
second multiple linear regression on them using AIC to look for the most parsimonious model (i.e., slope ~ lake × season × year). This analysis yielded identical preference for the most parsimonious model; therefore, we only report the results of ANCOVAs.

To detect differences in size spectra fits if benthic data were included, ANCOVAs of the size spectra data with and without benthic data were developed ($\log_2$[Abundance] ~ $\log_2$[middle of wet weight bin] × year × lake × type, where type could be "yes" or "no" if benthic data were included). Type instead of season was included because benthic data were only available for summer samples. Comparisons between models were made by analysis of variance (ANOVA) testing and AIC values, we present only models with AIC scores < 10 units different. Contrasts were evaluated with a Tukey's post hoc test.

Height is defined as the estimated abundance of organisms in a specific size bin and considered an indicator of overall system productivity. The use of height at the mid-point of the individual size spectra minimizes the issues of slopes and intercepts being correlated. However, the use of height alone can make comparisons across systems difficult because the range of size bins can vary across lakes and even sites (as it does in our dataset), and thus the midpoints are not always comparable. Therefore, we fixed height to a specific size group (size bin: 2^{-23} g; wet weight: $\sim 1.2 \times 10^{-7}$ g, primarily small zooplankton like rotifers) to make

multi-lake comparisons, as in Barth et al. (2019) (Fig. 1). Prior to further analysis, we tested the assumption that our calculation of height was uncorrelated with slope using simple linear regression. There was statistical evidence of a relationship in both seasons (Pearson correlation p = 0.003 and 0.010 for spring and summer, respectively), but the correlation was weak (R^2 = 0.12 and 0.10 for spring and summer, respectively; Supplementary Fig. S1[1]), and thus we assumed our measure of height was independent of slope. We calculated height for the PSS and used a weighted regression to detect if height differed across lakes or through time. Weights were calculated as $1/\text{SE}^2$, where SE was the standard error of the intercept calculated when ordinary least squares were fit to each PSS year, lake, and season. The weighted regression treated year as numeric (instead of factorial) with lake and season as factors (Height ~ year × season × lake). We also compared height between seasons and lakes without a covariate, using an ANOVA with weighted measures, as for the weighted regression.

Results

The PSS across all lakes spanned 38 $\log_2$ size bins (1.19×10^{-13} g to 0.065 g; Supplementary Fig. S2[1]), the BSS had 27 $\log_2$ size bins (6.25×10^{-8} g to 8.39 g), and the PBSS had 45 $\log_2$ size bins, albeit not all lakes covered all bins (Table 1). In the PSS, the smallest organisms were phytoplankton and the largest organisms were *M. diluviana* (Fig. 1). In the BSS, the smallest organisms were different in each lake but included chironomids, oligochaetes, sphaeriids, and turbellarians (Fig. 2), and the largest organisms were either dreissenids (all lakes but Lake Superior) or amphipods (Lake Superior).

Pelagic abundance size spectra

Slopes

Overall, PSS slopes were near the expected theoretical value of −1.0 in the summer, but they were steeper in spring (Table 2; Figs. 3 and 4). Testing of PSS slope differences resulted in a reduced model being identified as the most parsimonious ($\log_2$[Abundance] ~ $\log_2$[middle of wet weight bin] × season × lake + year), and no other model was within 35 AIC units (data not shown). In this reduced model, the interaction of lake and season was not significant for the slopes (df = 6, F = 1.56, p = 0.15). However, slope was steeper (−0.13 units) in spring (slope = −1.17) than summer (slope = −1.04; df = 1, F = 61.74, p < 0.0001) and varied among lakes (df = 6, F = 2.95, p < 0.0001; Fig. 4). Tukey's honest significant difference post-hoc test found that the PSS slope was significantly steeper in W. Erie than in Lake Michigan, but no other differences existed among lakes (Supplementary Table S1[1]).

There were different temporal patterns in slope among lakes. Lake Huron slopes initially became steeper (2006–2008), appeared to overcompensate (2009–2011), and then returned close to −1.0

Fig. 2. Weight frequency distribution of benthic organisms in samples taken in each lake from 2012–2015.
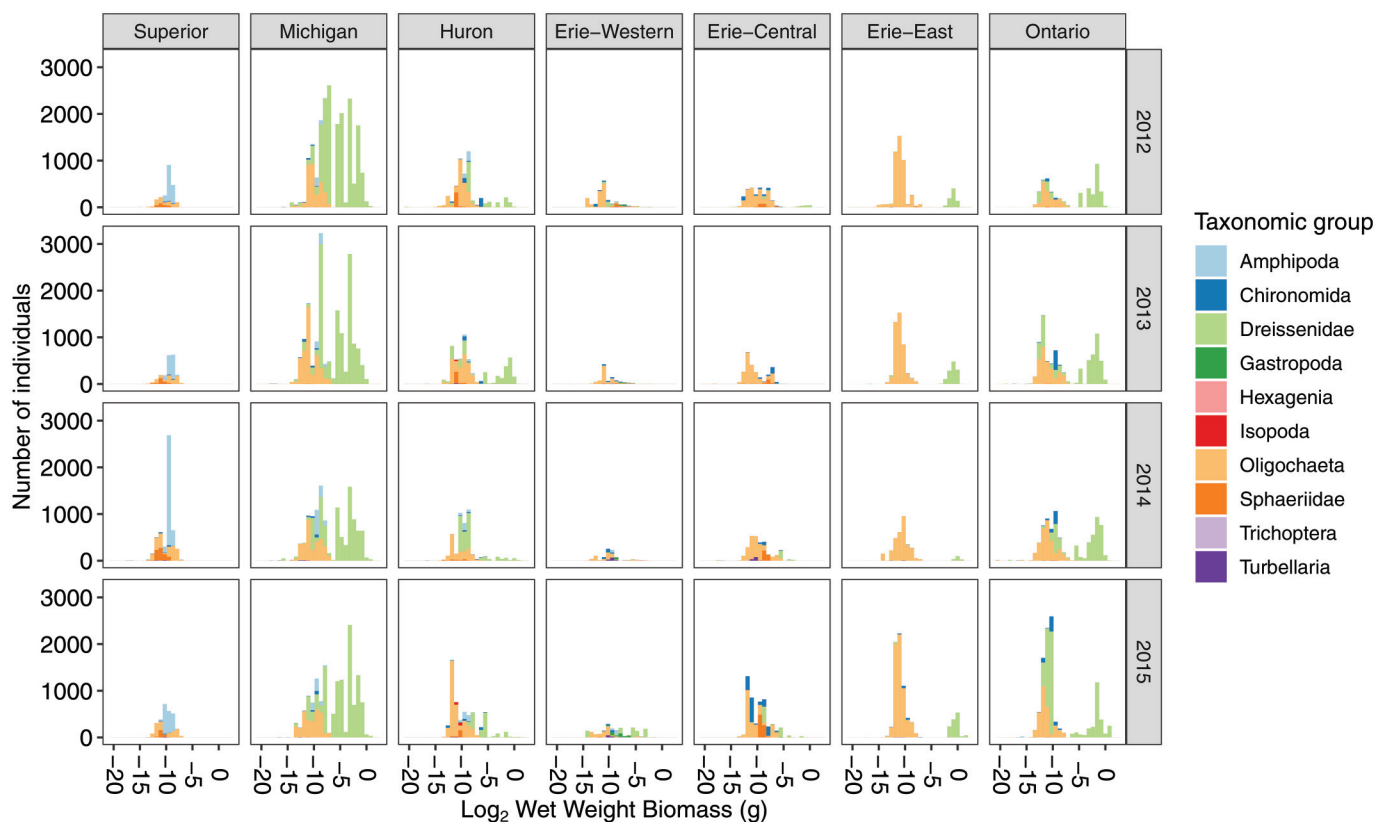
(2012–2015; Fig. 3). In Lake Erie, the PSS slopes were variable among years. All PSS slopes for W. Erie and all PSS slopes but one for C. Erie were steeper than −1.0, although slopes for C. Erie were closer to −1.0 than slopes for W. Erie (Fig. 3). PSS slopes in Lakes Michigan, Ontario, and Superior were similar in all years.

Heights

The most parsimonious height model, which was 12 AIC units different from the next best model, was: Height ∼ year + season × lake (i.e., height changed over time and independently varied among seasons and lakes). Height similarly increased over time across lakes (0.11 ± 0.26, mean ± SE; df = 1, F = 59.88, p < 0.001), but lakes differed in how heights varied between seasons (df = 6, F = 13.10, p < 0.0001). Of the possible height contrasts among lakes and seasons (91), 59 had a p value < 0.05 (Supplementary Table S3[1]). Spring observations in Lake Erie accounted for 43 of the significant 59 contrasts (Supplementary Table S3[1]; Fig. 5). Spring heights were lower than summer heights in all Lake Erie basins and Lake Ontario, but not in Huron, Michigan or Superior (Supplementary Table S3[1]; Fig. 5). In spring, the C. Erie height was higher than those in all other Lake Erie basins and Lake Huron, and in summer C. Erie height was higher than those in all other lakes except Lake Ontario (Supplementary Table S3[1]; Fig. 5).

Benthic abundance size spectra

The weights of benthic organisms in a lake were either unimodally (e.g., Lake Superior) or bimodally distributed (e.g., Lake Ontario; Fig. 2). The first mode was located near the 2^{-10} g (∼0.001 g) bin (hereinafter small benthos), and when a second mode was present it was at or near the 2^{-3} g (∼0.13 g) bin (hereinafter large benthos; Fig. 2). Note that some meiobenthic taxa (harpacticoids, ostracods, nematodes and others) were not included, as they are not sampled by the biomonitoring program. The small benthos

that were included were composed of a diverse range of organisms including chironomids, oligochaetes, amphipods, and in some lakes limited numbers of juvenile dreissenids, but the large benthos were almost entirely dreissenids (Fig. 2). Dreissenids were not found in Lake Superior, and in Lake Erie, dreissenids were rare in the western basin.

The BSS overlapped the largest size bins in the PSS (Fig. 6) and had a shallow slope (≫ −1.0, range: −0.49 to 1.12; Supplementary Fig. S3[1]); size spectra fitting to benthic data alone produced poor fits in all cases. In most cases, the addition of benthic data to pelagic data (PBSS) caused the size spectrum slope to become shallower than that of the PSS (i.e., more large organisms than expected; Fig. 7; Supplementary Fig. S4[1]). In Lake Superior, the deepest lake, benthos had a limited impact on the slope. In Lakes Michigan, Huron, E. Erie, and Ontario, benthos always caused the slope to shallow. In the shallower basins of Lake Erie (western and central), the results were mixed. The W. Erie benthos had shallower PBSS slope in some years, but not in others (Fig. 7). In C. Erie the PBSS slope was similar or steeper than the PSS slope (Fig. 7). The slope was strongly shallowed by dreissenid mussels in C. Erie and E. Erie, which were abundant and composed the largest size bins in PBSS (Fig. 2).

To explain the difference in linear fits between PSS and PBSS, the most parsimonious model included an interaction of lake and size spectra type (log₂[Abundance] ∼ log₂[middle of wet weight bin] × type × lake). There was essentially no support for including year in the model (ΔAIC > 60). The interaction of type (PSS or PBSS) and lake was not significant for slope (df = 6, F = 0.85, p = 0.53), but was for type alone (df = 1, F = 12.39, p = 0.0004); PBSS had a shallower slope than PSS (Δ = 0.067), perhaps because the combined benthic-pelagic system is more effective at capturing energy transfer from pelagic primary producers. The effect of lake on slope was also significant in the model (df = 6, F = 12.78,

188

Can. J. Fish. Aquat. Sci. Vol. 79, 2022

Table 2. Summary data for each lake and season of the slope and height in the pelagic abundance size spectra for 2006 to 2015.

Lake	Season	N	Slope			Height		
			Mean	Median	SE	Mean	Median	SE
Superior	Spring	10	−1.16	−1.15	0.03	20.63	20.76	0.62
Superior	Summer	10	−1.01	−1.02	0.07	21.50	21.72	0.71
Michigan	Spring	10	−1.11	−1.13	0.05	20.50	20.25	0.64
Michigan	Summer	10	−1.01	−1.00	0.05	21.55	21.63	0.52
Huron	Spring	10	−1.18	−1.18	0.05	19.55	19.84	0.91
Huron	Summer	10	−1.05	−1.05	0.07	20.69	21.00	0.85
Western Basin Lake Erie	Spring	10	−1.20	−1.18	0.10	17.58	17.53	1.17
Western Basin Lake Erie	Summer	9	−1.14	−1.14	0.07	21.70	21.69	0.46
Central Basin Lake Erie	Spring	10	−1.20	−1.21	0.10	20.86	20.82	1.24
Central Basin Lake Erie	Summer	9	−1.06	−1.06	0.05	22.76	22.50	0.53
Eastern Basin Lake Erie	Spring	10	−1.23	−1.22	0.08	17.33	17.50	1.25
Eastern Basin Lake Erie	Summer	9	−1.01	−0.99	0.09	21.14	21.34	1.06
Ontario	Spring	10	−1.14	−1.14	0.03	19.99	20.01	0.63
Ontario	Summer	9	−1.05	−1.03	0.03	22.41	22.48	0.38

Fig. 3. The slopes of each fit for the pelagic abundance size spectra in spring (green) and summer (blue), and the error bars are the 95% confidence intervals. No significant linear trends in slope were detected for any lake for either season ($p > 0.05$). [Colour online.]
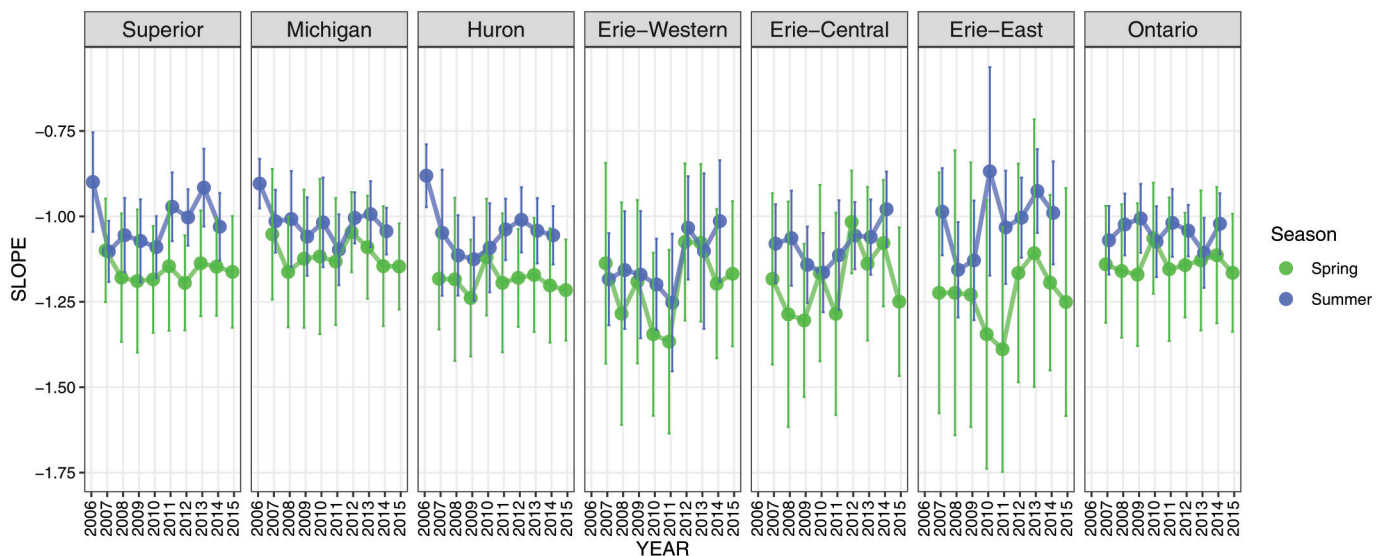
$p < 0.0001$); 6 of 21 possible lake contrasts were different (Supplementary Table S2[1]). The W. Erie slope was shallower than the slope in E. Erie and Lakes Huron, Michigan and Superior; the C. Erie slope was shallower than E. Erie and Lake Michigan.

Discussion

We compiled and compared size spectra (pelagic and benthic) using consistently sampled data for multiple lakes, years, and seasons from a wide range of lake size and system productivity (eutrophic western Lake Erie to oligotrophic Lakes Superior and Huron). Based on the comprehensive review of size spectra by Sprules and Barth (2016), our study is the most comprehensive study of large lake size spectra to date. Most prior studies that have examined size spectra in the Great Lakes have focused on a single year (Yurista et al. 2005), a few years (Yurista et al. 2014), or only a subset of the lakes (Sprules and Goyke 1994; Sprules and Stockwell 1995). The only previous large-scale size spectra analysis in the Great Lakes was developed by averaging across space and time (Sprules and Munawar 1986), obscuring differences examined here. Our data are important for testing size spectra in large lakes as well as general postulates about size spectra.

## Trends in pelagic abundance size spectra

Slopes

Size spectra slopes are postulated to reflect energy transfer efficiency across trophic levels, and changing slopes may indicate ecosystem perturbations across entire food webs (Sprules 2008; dos Santos et al. 2017; Barth et al. 2019). However, slopes may be less responsive than other metrics (e.g., height) to overall ecosystem productivity. Our results give mixed support for both hypotheses. There were few differences in PSS slopes among lakes (Fig. 4) and no clear temporal changes in PSS slope (Fig. 3). However, there was substantial variation with season: spring PSS slopes were almost universally steeper than summer slopes across lakes and years (Figs. 3 and 4). The lack of variability in slope across systems and years suggests that size spectra slopes may indeed be relatively insensitive to ecological differences among systems (Sprules 2008). Instead, they may be determined by standard metabolic rules across ecosystems (Jennings and Reynolds 2007), as suggested by the metabolic theory of ecology (Brown et al. 2007). However, the seasonal differences we observed demonstrate how the seasonal succession of organisms in lakes influences energy transfer across food webs. Spring slopes are

Fig. 4. The slopes of each fit for the pelagic abundance size spectra (2006–2015). The black line is the median, the boxes are the second to third quartiles, the whiskers are the first and fourth quartiles, and points are the individual slopes overlaid. [Colour online.]
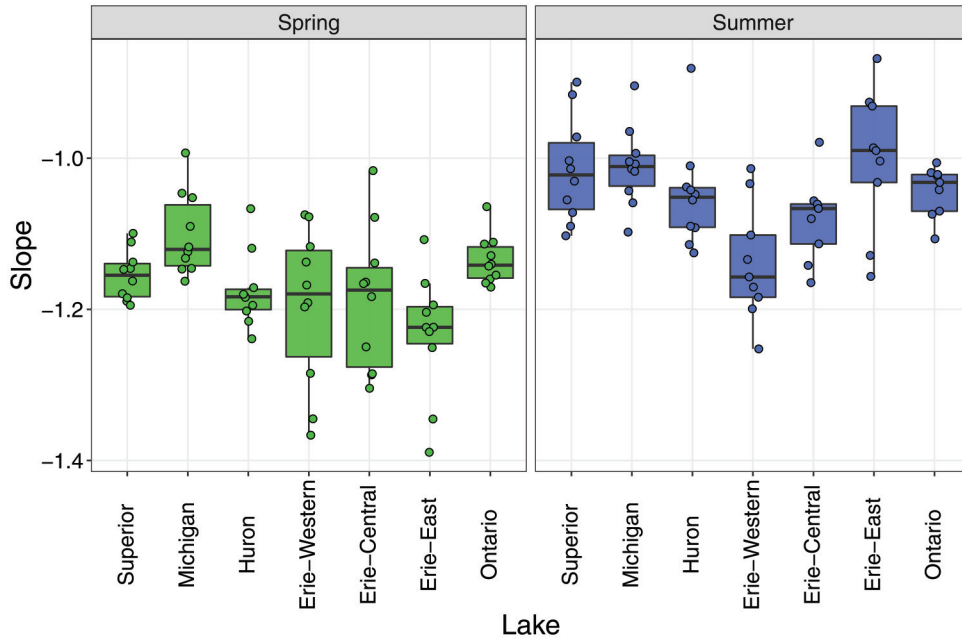

Fig. 5. The heights (defined here as the predicted number of animals in the 2^{-23} g bin) of each fit for the pelagic abundance size spectra, 2006 to 2015. The black line is the median, the boxes are the second to third quartiles, and the whiskers are the first and fourth quartiles. Groups that are different do not share a number; points are the individual heights overlaid. [Colour online.]
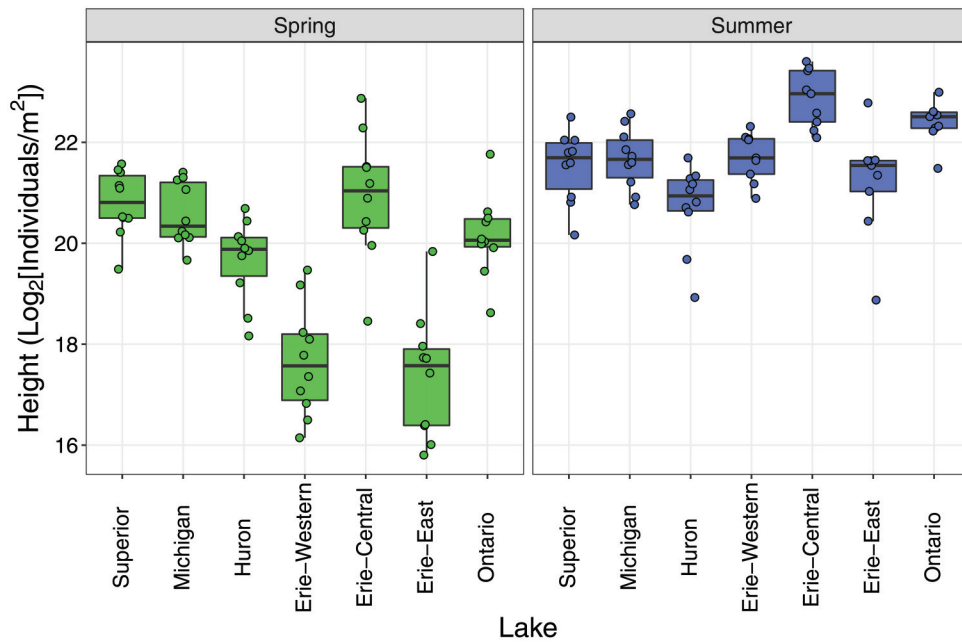

sensitive to the abundance of phytoplankton and the limited numbers of zooplankton in the lakes during this time. Growth of phytoplankton in the spring occurs before increases in zooplankton biomass (i.e., the spring bloom), and the PSS slope identified that fewer large organisms are present in spring (i.e., slope more negative than −1.0), but by summer size spectra relationships are more stable. Note that larger, longer-lived organisms will integrate across seasons, and it is likely that a size-spectra with fish would be less dependent on seasonality.

Larval fish sizes would overlap with the largest pelagic zooplankton bins in our dataset (e.g., *Mysis*), although larval fish were not included in our analysis. Larval fish densities at the lake level are low (<1 animal·m^{-2}; Nash and Geffen 1991; Martin et al. 2011; Eppehimer et al. 2019) — roughly 0.3%–2% of *Mysis* density — and larval fish are often associated with coastal habitat (Jude and Pappas 1992), which constitutes only a small percentage of lake area. As a result, larval fish would have little influence on the overall fit.

Fig. 6. The pelagic (blue circles) and benthic (gold squares) abundance size spectra for summer data in each lake and year. [Colour online.]
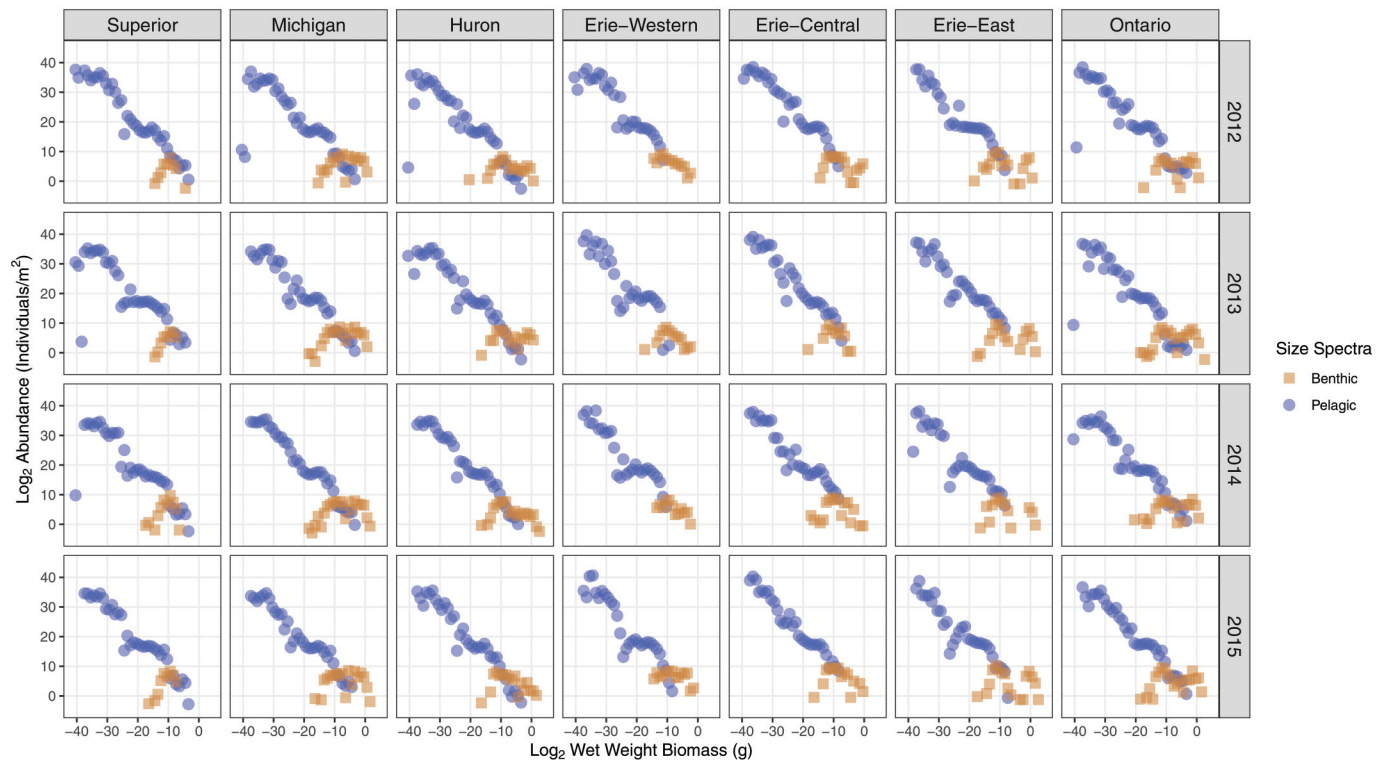
Fig. 7. The slopes from linear fits applied when benthic data were included (gold) or excluded (blue) from the summer pelagic abundance size spectra. Benthic data were not collected in a way that allowed them to be integrated into the size spectra prior to 2012. [Colour online.]
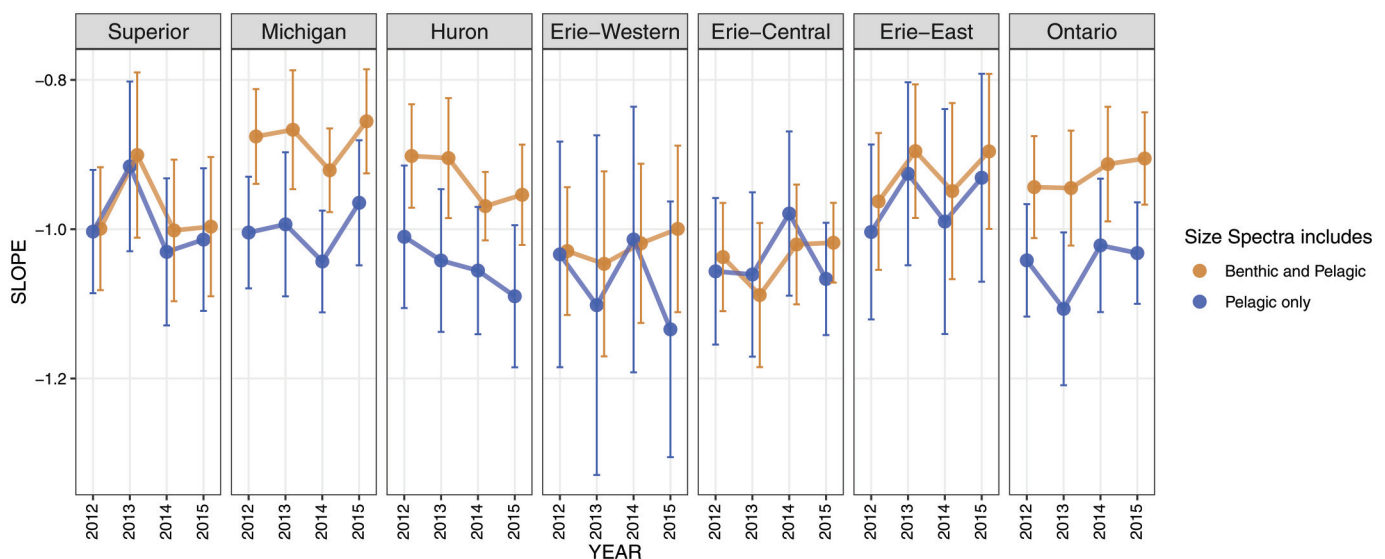
We fit our size spectra using ordinary least squares (OLS) even though more recent work has suggested the most appropriate fits are attained with maximum likelihood estimates (MLE; Edwards et al. 2017, 2020). We used OLS in this study for several reason. First, our data were collected using a wide range of approaches and expanded to density measures for comparisons across the whole size spectra. MLE have to date largely been based on data collected from individually measured organisms collected using a single approach (such as individual fish from

trawl surveys, Edwards et al. 2020). For our data, MLE may give higher influence to small size groups because the smallest bins contain such an overwhelming number of individuals (e.g., a billion cells). Second, OLS has been the primary method used both historically (Sprules et al. 1991; Vidondo et al. 1997; Hocking et al. 2013) and in more recent studies (Yurista et al. 2014; McGarvey and Kirk 2018; Barth et al. 2019); thus, using OLS allows for direct comparisons of our data with this literature. Third, we found limited effect of slope between lakes, and only large differences

between seasons that would likely be detected with either approach. However, we acknowledge that OLS may miscalculate the true confidence intervals of slope estimates (Edwards et al. 2017). More work is needed to compare OLS and MLE and to apply MLE to size spectra datasets with broad size ranges and complex collection techniques.

Height

Prior research suggests that the size spectrum height reflects system productivity (Kerr and Dickie 2001; Daan et al. 2005). In this study, heights did not always follow the expected pattern based on lake productivity (Huron < Superior = Michigan < Ontario = E. Erie < C. Erie < W. Erie). Rather, the specific order varied with season and across some regions (W. Erie, Ontario) exhibiting substantial interseasonal variation. On a broader scale, however, a general trend with productivity was apparent in height estimates — Huron, Superior, and Michigan, the three least productive lakes (Dove and Chapra 2015), also generally had the lowest height estimates, while the basins of Lake Erie (the most productive lake) typically had the highest estimates of height. These observations follow the general patterns observed in empirical and simulation modeling, which suggests that size spectra parameters reasonably reflect broad patterns in productivity (Guiet et al. 2016; Rossberg et al. 2019). However, interseasonal changes and local environmental differences among lakes may cause PSS variation that do not meet theoretical expectations. For example, rapid energetic turnover rates, strong phenological shifts between phyto- and zooplankton blooms, and high proportion of allochthonous inputs in the warm, shallow W. Erie may have driven the striking increase in height estimates between spring and summer PSS. Moreover, because we measured height at the midpoint (and therefore at a bin size representing small zooplankton), general phenological shifts between phytoplankton and zooplankton could have led to the observed increase in height from spring to summer samples across lakes. Thus, local or seasonal variability in factors affecting productivity, such as depth, temperature, and community composition (e.g., Heneghan et al. 2016), may complicate our attempts to interpret size spectra across systems with similar nutrient loads (Bianchi et al. 2000). Higher temporal resolution data are needed to track the shifts in the size spectra across seasons.

In addition to lake and season effects, we found divergent temporal trends of height across lakes, which may reflect known ecological changes occurring in each system since 2006. The productivity of Lakes Ontario and Superior has remained relatively stable over the examined time period, congruent with the relatively small change in heights we observed in these lakes. In contrast, Lake Huron total phosphorus (TP) concentrations have increased slightly since 2006 (although both TP and chlorophyll remain low; Rudstam et al. 2020), suggesting the slight increases we observed reflect increased TP. Lake Erie heights were variable and showed a range of patterns. In W. Erie, nutrient inflows have been increasing in recent years and large, often toxic, algal blooms are common in the summer (Michalak et al. 2013; Scavia et al. 2014). Central Lake Erie is sufficiently deep to form a thermocline, but the hypolimnion is small and often becomes anoxic in the summer and early fall. Annual variability in near-bottom hypoxic area may affect both internal P loading and the survival of the benthic community at deeper stations (e.g., dreissenids; Karatayev et al. 2018). Central Erie also receives variable inputs of algae and nutrients from W. Erie, due to highly variable hydrodynamics and flow between the two basins. Finally, E. Erie is the deepest basin of Lake Erie, resembling the other deeper lakes (stratified with an oxygenated hypolimnion), and it has a robust population of dreissenids (Karatayev et al. 2018); thus, it is reasonable that E. Erie size spectra has slopes and heights more similar to Lake Ontario than the other Lake Erie basins.

Inclusion of benthic data in size spectra

Pelagic components of food webs are clearly important to lake ecosystems, but benthic production can also be important in lakes (Reynolds 2008; Vadeboncoeur et al. 2008). To our knowledge, the incorporation of benthic size spectra into pelagic size spectra is rare in both freshwater (Cyr and Peters 1996; Mehner et al. 2018) and marine systems (Boudreau and Dickie 1992). How benthic data affect lake size spectra is a key knowledge gap, especially in light of drastic changes to lake food webs as a result of invasive dreissenids worldwide and associated "benthification" of lake ecosystems (Mayer et al. 2014). Mehner et al. (2018) combined benthic and pelagic size spectra (normalized biomass by areal density) from two shallow eutrophic lakes (mean depth ∼2 m) for a single year. They found good correspondence from trophic transfer efficiency models and size spectra when benthic data were included, suggesting that inclusion of benthic–pelagic coupling is important for interpreting size spectra. Our benthic data overlapped with larger zooplankton (Fig. 6) and could roughly double the numerical abundance of organisms in some size bins, often corresponding to a region of the pelagic size spectra that appeared less linear than other size ranges in the absence of benthic organisms (Fig. 6). More broadly, if size spectra are to be applied to systems with strong benthic–pelagic coupling (Boudreau and Dickie 1992), the pairing of benthic and pelagic size spectra should be seen as necessary, not simply opportunistic.

When including benthic data into our size spectra, PBSS slopes were generally shallower than −1.0, suggesting an efficient transfer of energy across trophic levels. This is not surprising given that benthic spectra were strongly influenced by dreissenid mussels (Fig. 2), which feed on smaller particles relative to their size than do large pelagic zooplankton and are effective ecosystem engineers providing strong benthic–pelagic coupling (Karatayev et al. 2002). Moreover, the influence of benthic data varied among lakes based on the prevalence of mussels and other ecological characteristics. In Lake Superior, the only Great Lake without abundant *Dreissena* spp., inclusion of benthic data into the size spectra had little impact. Lake Superior is a deep oligotrophic lake in which benthic production is higher in nearshore areas (Auer et al. 2013), which were not sampled by the EPA Great Lakes National Program Office in 2006–2015. Benthos of Lake Superior is likely representative of Lakes Huron and Michigan before dreissenid invasion. In other lakes, inclusion of benthic data had mixed effects on slope (Fig. 7). For instance, in Lakes Michigan, Huron, E. Erie, and Ontario, where dreissenids have spread throughout all depths, PBASS slopes were always shallower than PSS. Therefore, including benthic data allowed us to capture energy flow to a generally overlooked member of lentic foodwebs that are dependent on phytoplankton production (benthic fauna), while also investigating the impact of a novel member of Great Lakes food webs (*Dreissena*) on size spectra characteristics.

In W. Erie and C. Erie, the importance of benthic data varied annually. The slope was steeper with benthic data included for some years in C. Erie (2012 and 2013; Fig. 7). In general, a steeper slope will occur if size classes are added to the size spectra that contain fewer animals than expected given the PSS. This may have been caused by extenuating ecological circumstances in these years. In C. Erie, mussels and other benthic organisms should decline in years with extended hypoxia (Karatayev et al. 2018). Hypoxia was common in C. Erie in 2012–2015 (Watson et al. 2016), likely exacerbated by diatom blooms in the western and central basins in winter and spring (Reavie et al. 2016) and to a lesser extent summer cyanobacteria (Bridgeman et al. 2013; Scavia et al. 2014). In W. Erie, where harmful algal blooms are common and increasing (Sayers et al. 2019), our PSS or PBSS slopes were steeper than −1.0, suggesting an inefficient transfer to higher trophic levels. This might be expected during summer harmful algal blooms, due to the production of toxic algae that are not consumed by zooplankton or other consumers. According to a larger benthic

survey, over 98% of all *Dreissena* spp. in W. Erie in 2014 were <18 mm in length, or younger than 3 years old (Karatayev et al. 2018). Smaller mussel length in the W. Erie suggests shorter life span compared to the E. Erie, indicative of periodic mortality events affecting the entire population. Most likely, occasional episodes of severe oxygen depletion following temporary thermal stratification affects dreissenid mussel survival (Karatayev et al. 2018).

Shallower slopes observed when benthic data were included demonstrate how decisions about which taxa to include in SSA can alter our interpretation of trophic efficiency in aquatic systems. Both larval and adult dreissenids are directly consumed by many fish (Molloy et al. 1997), including invasive species such as round goby (*Neogobius melanostomus*; Kornis et al. 2012) and native species such as lake whitefish (*Coregonus clupeaformis*; Pothoven and Nalepa 2006; Fagan et al. 2012); as ecosystem engineers, dreissenids also increase the production of other benthic invertebrates and bottom algae (Karatayev et al. 2002). However, if dreissenid mussels efficiently accumulate biomass but are not readily incorporated further into food webs they may act as a shunt, sequestering energy to the benthos and making it unavailable for pelagic production (Hecky et al. 2004; Bocaniov et al. 2014). The invasion and establishment of round goby may help to alleviate this trophic "dead-end" because round goby consume large numbers of dreissenids and are in turn preyed upon by other species like lake whitefish (*Coregonus clupeaformis*), lake trout (*Salvelinus namaycush*), walleye (*Sander vitreus*) and smallmouth bass (*Micropterus dolomieu*). Thus, round gobies may increase the efficiency of energy transfer to large-bodied fish if they are able to incorporate gobies in their diets. Fish such as lake trout (Dietrich et al. 2006) and various coregonids (Madenjian et al. 2010) will be well positioned to take advantage of this increase in efficiency; pelagically oriented predators (e.g., Pacific salmonids) will likely see no increase in efficiency or even a decrease as a result of energy pathway changes. Inclusion of fish data into Great Lakes size spectra will allow testing of whether round goby is incorporating dreissenids efficiently into the food web.

Data assumptions

Although our data represent extensive sampling effort and size ranges not all groups in the Great Lakes are proportionally represented, although their overall effect on the size spectra are expected to be low based on the number and diversity of size bins sampled. For instance, meiobenthos were not included because data are not available on this group, but it occurs at abundances ~10% of similarly sized pelagic organisms where data are available (J. Connolly, Cornell University, unpublished data). Assumptions we made about our data are considered in a supplementary section (Supplementary Material B[1]).

Size spectra's relevance to aquatic food webs

The use of size spectra to detect human disturbances and shifts in food web structure in aquatic ecosystems shows promise (Sprules and Barth 2016; Blanchard et al. 2017). Prior work has demonstrated the usefulness of this tool for lakes (Sprules and Barth 2016), and recent work in streams (Hocking et al. 2013; McGarvey and Kirk 2018) shows the potential for size spectra to elucidate trophic processes and energy flows in highly disparate aquatic systems. However, size spectra have mostly been applied to marine systems to date, and few empirical studies exist to evaluate the predictability of their responses to food web perturbations (Duplisea and Kerr 1995; Robinson et al. 2017). Based on our data, size spectra analysis can provide important and broad insights into the function of large lake systems. Moreover, size spectra are responsive to differences in shallow and deep lakes when benthic data are included. Our data also suggest that changes in the Great Lakes food webs can be detected by size spectra and provide additional support to the argument that dreissenid mussels have altered food web structure.

The potential of SSA to elucidate ecosystem processes using a simple theoretical framework makes it an attractive model for ecosystem-based management. Our results highlight this potential utility while demonstrating some possible complications in using SSA, which was only possible by leveraging one of the most temporally and spatially expansive datasets available in large freshwater ecosystems. For instance, PSS slopes and (to a lesser extent, heights) adhered relatively well to predictions about ecosystem function (i.e., slopes near −1 and heights roughly following broadscale patterns in primary productivity), but they showed limited temporal responses to ecosystem change (although patterns in Lake Huron indicated some increase in efficiency from 2006–2015; Fig. 3). Examining longer time series for primary productivity, as has been done for diatoms in fossil records (Bramburger et al. 2020), would be useful for assessing the degree of perturbation required to affect average SSA observations. The strong seasonal signal we observed in PSS suggests that SSA could be used to understand phenological processes in lakes. Additionally, SSA should be responsive to large perturbations in food webs, with the caveat that SSA based on temporally or spatially limited data may only represent a snapshot of current food web construction. Lastly, we have clearly shown the importance of including often overlooked members of aquatic food webs (benthic organisms) in SSA — adding them significantly altered SSA characteristics and would substantially alter predictions of other, unobserved food web components of interest to management (i.e., fish). Our analysis also captured the large changes in lake ecosystems — more efficient transfer of energy across trophic levels — following the introduction of invasive ecosystem engineers, dreissenid mussels. In total, size spectra clearly have the potential to reflect both long-term and seasonal variation in food web structure and merit further development as a potentially powerful and integrative ecosystem monitoring tool.

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194

Can. J. Fish. Aquat. Sci. Vol. 79, 2022

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