Canadian Journal of
Fisheries and
Aquatic Sciences

Drivers of the fish community size spectrum and its utility as an indicator of fish productivity: insights from three decades of monitoring data from a small boreal lake

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Abstract

Freshwater fisheries monitoring programs require indicators of fish community and population productivity and abundance. Two potential indicators include the slope and height of the community size spectrum, which are often interpreted as proxies for trophic dynamics and community abundance (or production), respectively. Previous studies have lacked alternative estimates of fish production and abundance to compare with community spectral parameters and have had limited limnological data to understand drivers of variability in spectral parameters among lakes. Using ∼30 years of monitoring data from a boreal lake, we showed that the height of the fish community size spectrum was related to independent mark/recapture-based estimates of abundance for the dominant large-bodied species, white sucker, but not to their biomass or annual production estimates. Further, limnological properties including the duration of ice cover, light, temperature, and the biomass of zooplankton prey were associated with inter-annual variation in spectral slopes and heights, often nonlinearly. Our results indicate that spectral parameters derived from fish communities can reflect long-term environmental change and provide new insights on drivers of fish community size structure.

Key words: size spectrum, fish productivity, experimental lakes area, long-term monitoring, ecosystem indicator, white sucker

Introduction

Fish productivity, defined as biomass generated per unit area per unit time (often expressed as kg ha^{-1} year^{-1}; Ricker 1946), is a useful metric to measure the performance of a fish population or community (e.g., Boudreau and Dickie 1989; Downing and Plante 1993; Randall and Minns 2000). The value in quantifying fish productivity is due in part to the fact that it integrates information on multiple processes that alter biomass within a population, including individual fish growth, reproduction, mortality, and immigration and emigration (e.g., Wurtsbaugh et al. 2015; MacLeod et al. 2022). Indeed, fisheries management policies often discuss the protection of freshwater fish populations in terms of maintaining productivity (Arlinghaus et al. 2016). This includes Canada's *Fisheries Act*, which supports the ongoing productivity of commercial, recreational, or Indigenous fisheries, and since 2019, aims to do this via enhanced protections for fish habitat (Bill C-68, 2019). However, reliable estimates of fish productivity can be costly and time-consuming to measure, given that they require estimates of population abundance and size structure that are often derived from mark-recapture data collected from a single site over multiple years (e.g., Rypel et al. 2015). This has led to a need to understand how metrics that measure only sub-components of productivity (e.g., abundance, body condition, and growth rate) might perform as indicators of fish production, and also to develop new fish-based and ecosystem-based indicators (e.g., de Kerckhove 2015; Dey et al. 2021).

Indicators based on fish body size have been used extensively in evaluating human impacts to marine and freshwater fisheries. In marine systems, basic indicators like the mean length, weight, and mean maximum length of the different species in a catch have been demonstrated to decline in response to size-selective fish harvest (Nicholson and Jennings 2004). Similar indicators have been used in freshwater systems to detect the impacts that both angling pressure and fishing regulations have on game and non-game species (Rypel et al. 2016). While there is a direct relationship between size-selective harvest and the maximum length or weight that individuals in a targeted population can achieve, such size-based indicators have also been used to investigate the impact of other stressors on fish growth such as eutrophication, lake-use intensity, damming, and climate (Jeppesen et al. 2000; Emmrich et al. 2011, 2014; Benejam et al. 2016). These indicators are meaningful because important ecological and physiological processes that often scale with fish productivity are strongly correlated to body size (Downing and Plante 1993), including reproduction (e.g., via fecundity and maturation time), longevity, growth rate, and trophic position (e.g., Blueweiss et al. 1978; Romanuk et al. 2011; Barneche et al. 2018; MacLeod et al. 2022).

Decades of theoretical and empirical work have shown that communities are size structured, with an inverse relationship between abundance and body size (Sheldon and Parsons 1967); this pattern is found within and across trophic levels in aquatic systems (e.g., Sprules 2008; Barth et al. 2019, 2021). This phenomenon is largely attributed to the fact that energy is lost through food webs due to individual feeding and increasing metabolic costs with body size. The relationship between abundance and body size, termed the size spectrum, is often quantified by estimating the slope of a regression line fit to the log-transformed abundance or biomass of individuals on the *y*-axis within a priori selected size bins on the *x*-axis, though it can also be fit via maximum likelihood estimation of the bounded power law distribution (Edwards et al. 2017). By integrating information across species, size classes, and trophic levels, the slope of the size spectrum is thought to provide information on trophic transfer efficiencies and predator–prey size ratios (Giacomini et al. 2016), while the intercept (or “height”) of the regression can provide a relative measure of total abundance within a community (Daan et al. 2005).

In freshwater and marine systems, size spectrum analysis has also been applied strictly to fish communities. In lakes, the slope of the fish community size spectrum has been demonstrated to be an effective proxy for changes in trophic dynamics along various environmental gradients, potentially serving as an indicator of ecosystem stress. For example, Chu et al. (2018) showed that fish communities among southern Ontario lakes located in areas protected from development tended to have shallower slopes (i.e., a higher proportion of large fish) than those outside these areas, possibly due to differences in angling pressure, nutrient loading, and subsequent oxygen depletion and changes in habitat quality. Similarly, in an analysis expanded to include lakes in parts of northern Ontario, Chu et al. (2016) showed that at this spatial extent, fish size spectrum slopes were influenced by the relationship between temperature and body size whereby proportionally fewer large fish were caught in warmer climates (i.e., steeper slopes). Across several European lakes, Emmrich et al. (2011) demonstrated that fish community size spectrum slopes became steeper with increasing nutrient concentrations. While these studies have demonstrated that changes in size spectrum slopes are related to meaningful ecological processes, they have occurred over broad geographical scales with the inclusion of only limited limnological data, such that there is still uncertainty in our understanding of drivers of fish community spectral parameters (slope and height). Moreover, studies that quantify the relationship between spectral parameters and independent estimates of fish productivity based on detailed monitoring data are needed before it can be used as a reliable indicator in fisheries monitoring.

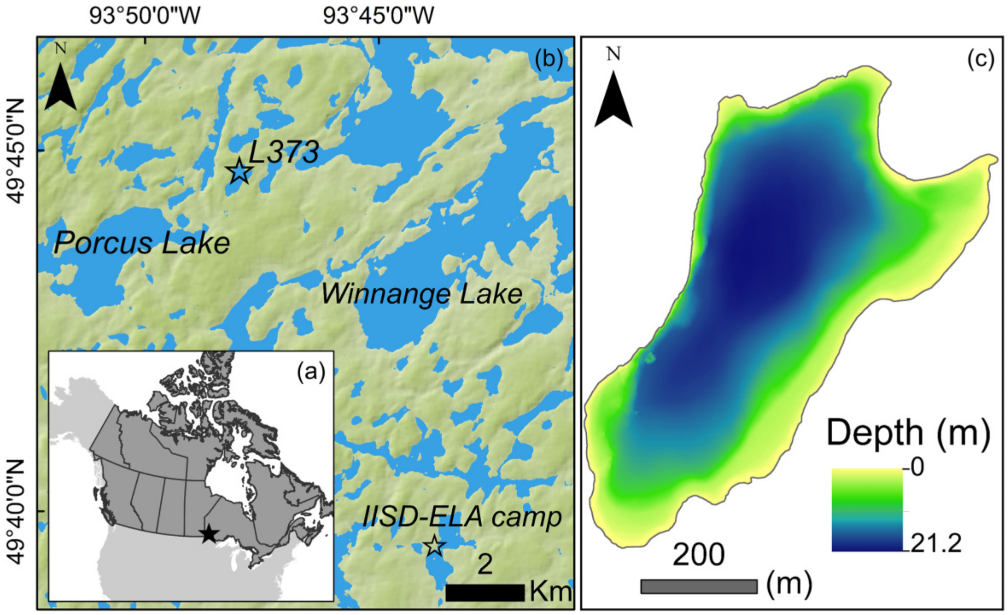
The International Institute for Sustainable Development’s Experimental Lakes Area (IISD-ELA) is a unique facility in northwest Ontario where fisheries and limnological data have been collected from lakes since its inception in 1968. These data provide the rare opportunity to investigate changes in fish community size spectra, their relationship to other measures of fish productivity, and to underlying ecosystem drivers over several decades in a single undisturbed system. Specifically, we present three decades of detailed fish and ecosystem data collected on a near-annual basis (at varying intra-annual resolutions) from Lake 373 at IISD-ELA. Our goals were to: (1) assess the utility of the fish community size spectrum height and slope as indicators of fish productivity, and (2) determine what underlying ecosystem processes drive inter-annual variability in spectral parameters. Lake 373 is an unmanipulated reference system but has experienced changes in thermal properties in response to regional warming that have been demonstrated to influence the growth and behaviour of certain fish species (Guzzo and Blanchfield 2017; Guzzo et al. 2017). Climate (temperature) and resource availability are key determinants of fish growth because of their control on metabolic demands and the amount of energy that can be allocated to somatic growth (Jobling 1997; Amundsen et al. 2007). Hence, we expected that variables related to these environmental properties would have an important influence on the size spectrum slope, as demonstrated in some previous studies (Emmrich et al. 2014; Chu et al. 2016). Because fall sampling occurs at the end of the growing season and fishes accrue body mass over this period, we also hypothesized that fall spectral slopes would be (on average) shallower than those based on spring sampling. Finally, because the height of the size spectrum is considered to represent total abundance, we expected that it would be correlated with estimates of fish abundance and productivity derived from other methods.

Methods

Study site

The IISD-ELA is situated approximately 50 km east of Kenora in northwest Ontario (Fig. 1) and consists of 58 lakes and their watersheds that are used for long-term ecological monitoring and whole-lake experimental manipulations. The public has limited access to this region, with no fishing pressure and has not been subject to impacts associated with urban or industrial development (Blanchfield et al. 2009). Briefly, the geology of this area is dominated by Precambrian Shield (granite) bedrock that is overlain by thin (<1 m) acidic soils and coniferous forests (e.g., *Pinus banksiana*, *Picea mariana*, and *Picea glauca*), typical of the Ontario Shield (Brunskill and Schindler 1971). Climate in this region is continental; mean annual air temperature (MAAT) and precipitation (MAP) recorded at IISD-ELA are 3.0 °C and 705 mm, respectively, for the period 1980–2010. Mean winter (December–February) and summer (June–August) air temperatures are −13.4 and 18.1 °C, respectively.

Fig. 1. Map of the study region and study system. (*a*) Location of the International Institute for Sustainable Development Experimental Lakes Area (IISD-ELA) relative to Canada and the northern United States, (*b*) location of Lake 373 within IISD-ELA (data from the Ontario Hydro Network, accessed under the Open Government License), and (*c*) bathymetric map of Lake 373. Map datum = WGS84, Map projection = UTM 15 N.



We utilized ca. three decades (1987–2020) of fish community and lake physical and biological data collected from Lake 373 (L373), a small (maximum depth = 21.2 m, surface area = 27.4 ha) oligotrophic (total phosphorus ~5.3 μg L^{-1}) and dimictic lake that is representative of the predominant lake type in this area. Ice-on and ice-off in the region generally occurs in late November and late April, respectively, though the period of ice cover is declining in response to climate change (Guzzo and Blanchfield 2017; Higgins et al. 2021). Mean summer surface water temperature averages ~20.1 °C. The lake has never been stocked and supports naturally reproducing populations of lake trout (*Salvelinus namaycush*), which is the top predator, and white sucker (*Catostomus commersonii*), which accounts for a large proportion of total fish biomass. Lake 373 also supports several species of small, littoral leuciscids (referred to as minnows hereafter) including northern redbelly dace (*Chrosomus eos*), finescale dace (*Chrosomus neogaeus*), and northern pearl dace (*Margariscus nachtriebi*), in addition to slimy sculpin (*Cottus cognatus*).

Annual fish sampling

The fish community in L373 has been monitored since 1987, with most of these years being sampled in both spring and fall (n = 23), while some years have spring (n = 5) or fall (n = 3) data only. Sampling generally occurs for ~2–4 weeks beginning in mid-to-late May and again in early-to-late September. We present data collected from the annual trap netting program because this method targets all species within the lake and yields a large enough sample size for reliable quantification of the fish community size spectrum in both seasons. Briefly, during each sampling campaign, 1–3 Beamish-style trap nets (Beamish 1973) with 3 mm mesh size were used to capture fish and were emptied multiple times, typically every ~2–6 days within each season. Two variations of trap nets were used; either containing a central lead set perpendicular to shore, or without a central lead where one wing was tied to the shore and set parallel to the shoreline to capture fish travelling in a single direction. Spring and fall trap netting occurred in the same general locations of the lake each year, and were placed at a water depth of ~2–3 m. Upon emptying the trap nets, all fish were enumerated and measured prior to release. For small fish (minnows and slimy sculpin), only fork lengths were taken, while both weights and lengths were recorded for white sucker and lake trout. Complete details on trap net design and sampling protocols can be found in Rennie et al. (2019) and Guzzo et al. (2014). Scientific collection permits were authorised through the Ontario Ministry of Natural Resources and Forestry, and through Animal Care Committees at Fisheries and Oceans Canada prior to 2014, the University of Manitoba in 2014 (permit #F14-007) and Lakehead University thereafter (permit #1464656).

Zooplankton, water chemistry, and physical variables

Zooplankton communities have been monitored in L373 approximately bi-weekly during the open water season (May through to October or November) since 1988. Briefly, zooplankton were sampled throughout the entire water column at seven pelagic stations across the lake, using a PVC hose calibrated for volume (Salki 1993). Samples were filtered through a 72 μm net prior to 1998 and with a 53 μm net thereafter. Comparisons of samples collected with the 53 and 72 μm nets indicated that Crustacea were collected with equal efficiency. All samples were preserved in 4% sugar-formalin after narcotization with methanol. Samples from different stations were combined into a single composite, and at least 300 Crustacea were identified to the lowest possible taxonomic category and life stage. The biomass of each taxon (μg dry mass·individual^{-1}) was estimated from measurements of zooplankton from lakes at the IISD-ELA (Malley et al. 1989; M. Paterson, unpublished data). Population and community biomass (dry mass·L^{-1}) was determined by multiplying abundance estimates by estimated taxon dry masses.

Water chemistry has also been monitored in L373 ~biweekly during the ice-free season for a suite of analytes over the same period, following standardized protocols. Water samples were collected throughout the epilimnion at a single station in the centre of the lake using an integrated water sampler (Shearer 1978). Samples were kept cool and stored in polyethylene bottles and were analyzed at the IISD-ELA Chemistry Laboratory shortly after collection following methods outlined elsewhere (Stainton et al. 1977). Photosynthetically active radiation (PAR) was measured using a model LI 192 underwater quantum sensor, while lake surface temperature was measured using an MK II digital telethermometer (Flett Research Ltd, Winnipeg, Canada) between 1987 and 2009, and an RBR XRX620 multifunction probe with integrated temperature sensor beginning in 2010. The duration of ice cover each winter was also estimated for L373. We assumed that ice-on and ice-off dates were the same as nearby Lake 239 (L239), located at the IISD-ELA field station ~10 km northwest of L373. Since 1969, ground-based visual observations have been made for ice-on date and ice-off date for L239, which were defined as 80% of the lake surface ice-covered and 80% of the lake surface ice-free, respectively (Higgins et al. 2021). Higgins et al. (2021) demonstrated that regional variation in annual ice duration throughout the IISD-ELA was driven by factors associated with lake size, with variations between L239 and L373 typically <3 days.

Construction of the fish community size spectrum

A normalized abundance size spectrum (NASS) was constructed from the fish community data in each sampling period. The NASS was constructed separately for spring and fall each year following the approach outlined in Barth et al. (2019). First, all individuals caught during a sampling campaign were placed into a $\log_2$ series of mass bins with the first bin ending at 1.25 g, while the largest size bin encompassed individuals between 1280 and 2560 g. Because minnows were only measured for fork length during trap netting, we estimated weights for these individuals based on length–weight regressions using measurements collected over seven consecutive years of small fish sampling in L373 from a different sampling program ($n = 2700$ measurements for three minnow species; Supplemental Fig. S1). The number of individuals in each mass bin were summed and subsequently divided by the linear width of the mass bin to remove the dependency of abundance on bin width, following White et al. (2008). Values across all bins were divided by the total trap net effort (the total number of net days fished) for the corresponding sampling campaign to standardize for effort. The slope of the size spectrum was determined by fitting an ordinary least squares (OLS) regression to the resulting NASS, following $\log_2$ transformation of the response variable. Identical size bins were applied to spring and fall fish data to ensure comparability between seasons.

Traditionally, the y-intercept of the OLS regression has been interpreted as a relative measure of total abundance (e.g., Sprules and Munawar 1986). Instead, we quantified the height of the size spectrum, which is defined as the normalized abundance at the centre of the log size range. This metric has been shown to provide a measure of total abundance that is not correlated to the size spectrum slope (Daan et al. 2005), and in our study, corresponded to the sixth mass bin. We note that standardizing to total effort does not change the slope of the size spectrum, but only alters the height (i.e., total abundance) and ensures that this measure is also comparable among years and seasons.

Finally, we did not use the maximum likelihood estimation (MLE) of the Pareto distribution to characterize the size spectrum (Edwards et al. 2017) given that recent studies have highlighted that ecological data may not follow a single Pareto distribution, which MLE may be more sensitive to compared to OLS (Barth et al. 2019, 2021). Moreover, the NASS facilitates the estimation of the size spectrum height, which was an explicit objective in investigating its utility as a metric for abundance and not achievable using the MLE Pareto approach.

White sucker abundance, biomass, and productivity

Given that white sucker generally account for ~90% of the fish biomass caught in trap nets during spring and fall in L373 (average 1987–2020), their abundance, biomass, and productivity was compared with size spectrum slope and height for the entire fish community to assess the utility of spectral parameters as an indicator for these different metrics. Detailed methods outlining estimation of white sucker age and population size in L373 can be found in Rennie et al. (2019). Briefly, white sucker >100 mm fork length captured in trap nets during each sampling campaign were given a dorsal fin nick that corresponded to the capture period. Pectoral fin rays were collected from newly tagged individuals and later were processed and read for age determination following methods outlined in Chalanchuk (1984). Abundance was determined for each year using the Schnabel estimator for multiple census and were performed separately using spring and fall data. Biomass was then estimated as the product of estimated abundance and the mean body weight across all sampling events within a given season. Annual production estimates for white sucker were calculated using the Instantaneous Growth Rate (IGR) method (Ricker 1946) following equation 8.47 in Hayes et al. (2007) (see Online Supplement for complete details). The IGR method requires age data to determine changes in growth and biomass of age-classes across sampling periods. Because only subsets of captured individuals were aged annually (and only for spring-caught fish), annual age-length keys were constructed to assign ages to unaged fish (Ogle 2013) which enabled all captured individuals to be included in production estimates.

Data processing and statistical analysis

To understand drivers of the fish community size spectrum slope and height, we investigated relationships with four uncorrelated predictor variables, chosen to represent climate, the lower food web of the lake, and lake physical properties. These were: (1) number of days of ice cover, (2) mean epilimnetic temperature, (3) the biomass of large, edible crustaceans, and (4) the proportion of the lake within the euphotic zone. These variables were selected because they are presumed to have an important influence on the growth and survival of planktivorous and benthivorous fish (Jackson et al. 2001). Except for ice cover, all variables represented means of samples collected during the open water period (May–October) for each year. The proportion of the lake (area) within the euphotic zone was estimated by extracting the portion of the lake bathymetry with depths less than or equal to the mean annual euphotic zone depth (Z_{eu}), which was calculated after Kalff (2002) using: $Z_{eu} = \ln 100/K_d$, where the light extinction coefficient K_d was derived from photosynthetically active radiation (PAR) measurements throughout the water column as described in Fee et al. (1996). Large crustaceans (cladocerans and copepods) were selected from the L373 zooplankton community following Rusak et al. (2002), who delineated 10 body-size and food web position-based functional groups for zooplankton communities across 22 north-temperate lakes. In our study, large edible crustaceans were defined as the sum of the biomass of adult (c6) *Epischura lacustris* (large calanoid), *Diacyclops thomasi* (large cyclopoid), and *Daphnia galeata* (large cladoceran). We also included adult *Diaptomus sicilis*, because they are an important component of the L373 zooplankton community and are known to be an important prey item for planktivorous fish (Bunnell et al. 2015).

Given that relationships among properties in aquatic systems may be nonlinear (Webb et al. 2019), we used generalized additive models (GAMs) to quantify the relationships between these key variables and annual community spectral parameters to allow for nonlinear relationships if present. Two separate GAMs were generated, using the annual spring size spectrum slope and height estimates as response variables. For each of the GAMs, predictor variables were either natural log- or square root-transformed to help improve the distribution of model residuals. Following Simpson and Anderson (2009), we investigated if year needed to be included as a continuous variable in each model by visual inspection of model residuals (vs. time) with and without its inclusion. If a temporal trend was apparent in the model residuals, year was included as a covariate in the model. Because spring fish sampling occurs almost immediately after ice off, we introduced a 1-year lag for all model covariates (except for ice-cover) when modeling spring slope and height. This meant that limnological conditions during the previous open water season predicted size spectrum slope and height for a given spring. In all models, a Gaussian error distribution was used, while restricted maximum likelihood (REML) was used as the smoothness selection method and thin plate splines were set as the basis spline, following the recommendations of Simpson (2018). To help with model selection, we applied the double penalty approach as described by Marra and Wood (2011). This procedure applies an additional penalty to the perfectly smooth components of the basis of each smooth function, in effect removing terms from the model that have no relationship to the response (Webb et al. 2019). The model covariates that are retained may or may not have a significant effect on the response, which was determined using $\alpha = 0.05$. Modeling was carried out in the R programming language (R Core Team 2021) using the *mgcv* package (Wood 2011; Wood et al. 2016). For each model, we also estimated the percent contribution of each retained predictor variable to the total deviance explained. This was done by refitting the GAMs with retained predictor variables only, and using hierarchical partitioning as implemented in the R package *gam.hp* (Lai et al. 2024).

While formal modeling was not performed using the fall data due to fewer observations (particularly after removing data from 1992 to 1993 due to low catch), potential relationships between the four covariates and size spectrum parameters were explored using Spearman's correlation coefficient on both raw and detrended (via first differences) data. Finally, we note that while leveraging a mixed model framework may have been advantageous (GAMMs; by nesting multiple limnological and trap net samples within a year), our models used annual data due to the need to pool all trap net samples within a sampling campaign to obtain a reliable number of fish to calculate the NASS.

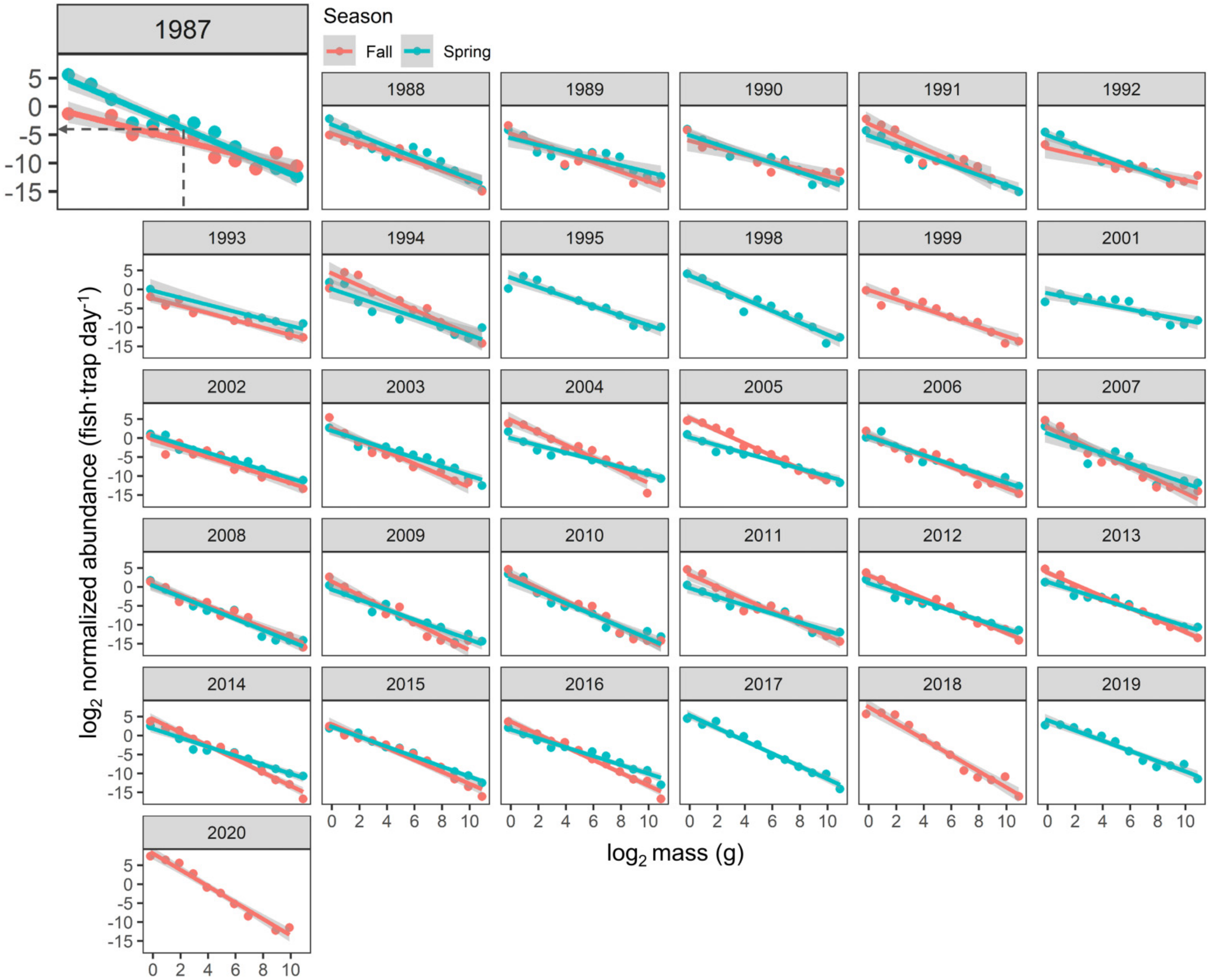
Lastly, linear regressions were used to compare spectral slopes and heights with other metrics that are commonly used to quantify fish populations. These were estimates of population size, biomass, and productivity of white sucker, which is the dominant species in our lake based on biomass. Based on plots of the autocorrelation function, there was no evidence of temporal autocorrelation in the model residuals, nor did we detect trend in model residuals with time, suggesting that this approach was adequate. For these comparisons, we only used spring data because Schnabel estimates were available at a higher temporal resolution for spring compared to fall, and because white sucker production estimates used an age-length key that was developed using individuals caught (and aged) during spring only.

Results

Fish community size spectrum

For all years, regressions on spring and fall normalized size spectra fit well, with R^2 values ranging from 0.73 to 0.98 and 0.82 to 0.98, respectively (Fig. 2). Over the period of record, mean spring size spectrum slope and height were -1.24 and -4.69, respectively, while mean fall slope and height were -1.48 and -4.98, respectively (Fig. 3). Of these four spectral parameters, spring slope tended to show the least amount of variability with a coefficient of variation (CV) of 17.5%, while CV's for the others ranged from ~22.5% to 23.5%. Spring and fall mean slopes were significantly different ($p < 0.05$), while there was no significant difference between seasons for

Fig. 2. Annual size spectra derived from fishes caught in spring (blue) and fall (red) nearshore trap net sampling in Lake 373. The dashed lines in the first panel (1987) show how height is estimated using the spring data as an example.



height. For both spring and fall, the size spectrum excluded lake trout because they represent a very small fraction of the catch in trap nets during both spring and fall; when they are targeted in the fall, it is using a different gear type (short-set gill nets; Rennie et al. 2019) and therefore impossible to standardize to the methods used here (i.e., trap net catch per unit effort). The size spectrum was constructed from all other species present in the lake; finescale dace, northern redbelly dace, pearl dace, slimy sculpin, and white sucker. The size distribution of these taxa indicated that minnows, slimy sculpin and white sucker were present through size bins 1–4 (i.e., below 10 g), while only white sucker were present in the remaining size bins (Supplemental Fig. S2). Aside from low fish counts in two falls (<50 in 1992 and 1993) and one spring (<100 in 1993), the mean total catch for fall sampling was ∼2330 (or ∼1100 excluding 2018 and 2020, which had anomalously high catches), while it was ∼900 for spring sampling (Supplemental Figs. S3 and S4). On average, minnow species and slimy sculpin were a larger numerical proportion of annual total catch in both spring and fall, relative to white sucker (means of 54 and 63% of the total number of individuals caught, respectively; Supplemental Fig. S5). In terms of biomass, white sucker dominated total catch in both spring and fall (Supplemental Fig. S6).

GAMs that used spring slope and height as response variables and time as the sole covariate indicated that some decadal-scale trends were present. Fall slope showed a consistent decline over the entire period of record, whereas spring slope showed only a subtle decline after ∼2005 (Fig. 4*a*). Fall height showed a subtle increase after ∼2010, while spring height was more variable over time, with maximum estimates occurring between ∼1995 and 2005, and minimums occurring at ∼1992 and 2010 (Fig. 4*b*).

Environmental variability and controls on size spectrum slope and height

Temporal patterns varied among the variables that we used as predictors of size spectrum slope and height. Since 1987, the proportion of the lake within the euphotic zone showed a ∼15% decline, while the duration of ice cover declined by ∼10 days (Fig. 5). The biomass of large zooplankton showed little trend over time (although interannual variability was present), while epilimnetic temperature showed maximums at ∼1998 and 2015 (Fig. 5). The GAMs that used these variables to explain spring size spectrum slope captured c. 45% of its variance, while the deviance explained for the spring height model was much higher at 81% due to the inclusion of year as a covariate (Table 1). Spring slope was most strongly related to the duration of ice cover during the preceding winter and the mean biomass of large zooplankton during the previous open water season (Table 1). Partial effects plots showed that spring slopes became shallower (proportionally more large fish) as the duration of ice cover immediately preceding sampling increased, except at the high-end of the ice duration gradient, where this relationship reversed (Fig. 6*a*). In contrast, spring slopes were steeper (proportionally more small fish) with increasing zooplankton biomass in the previous year (Fig. 6*b*). In contrast to spectral slopes, spring height was best explained by (1) the proportion of the lake within the euphotic zone (Table 1), which showed a unimodal relationship (Fig. 6*c*), and (2) epilimnetic water temperature (Table 1), which showed a positive relationship (Fig. 6*d*). The positive relationship between epilimnetic temperature and spectral height was further highlighted by pronounced low values in both variables in between 1992 and 1993 (and in the following spring of 1994 for spectral height), and in 2008 and 2009 (Figs. 4 and 5).

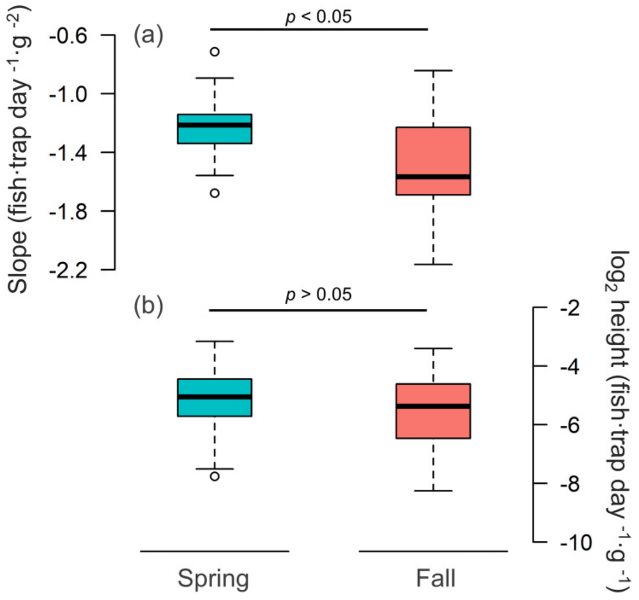
Size spectrum height and indices of fish population abundance

Fish community size spectrum heights based on spring sampling showed a significant and positive relationship with mark-recapture derived estimates of white sucker abundance, ($R^2 = 0.37$, $p < 0.05$; Fig. 7). However, we did not detect any significant relationships between either of the spectral parameters (slope and height) and white sucker biomass or production estimates (Supplemental Fig. S7).

Discussion

Our results support the use of size spectrum analysis as a tool for evaluating the effects of environmental variation on fish communities. We found that size spectra showed changes over time similar in magnitude to those reported elsewhere that examine variation among ecosystems (Marin et al. 2023). Our long-term monitoring data also demonstrated that the height of the community size spectrum was closely related to mark/recapture-based estimates of white sucker population size (the dominant species in the lake by biomass), supporting its use as a proxy for fish abundance. The size spectrum height also showed meaningful relationships with properties that may be expected to influence fish abundance including light availability and water temperature. We also found strong linkages between spectral slopes and environmental drivers, although seasonal differences in slopes did not conform to our original hypothesis that fall slopes would on average be more positive (i.e., a greater proportion of large individuals) compared to those based on spring sampling. Our results highlight that the seasonal timing of sampling has an important influence on observed fish community size structure and refines our understanding of the mechanisms that drive variability in fish community size spectra.

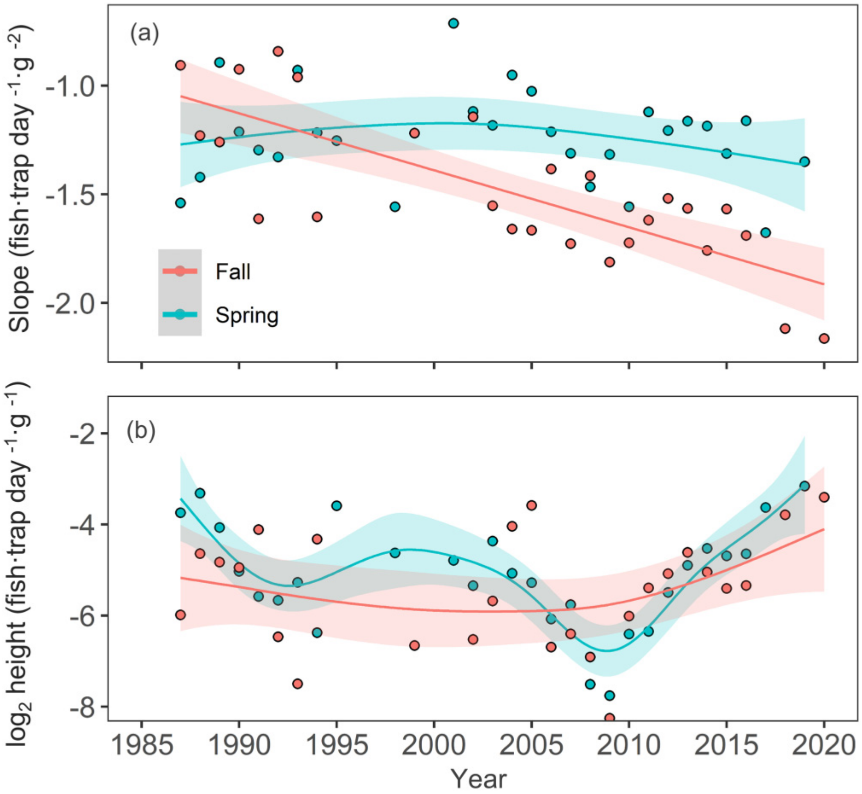
Fig. 3. Mean size spectrum (*a*) slope and (*b*) height of the fish community size spectrum in IISD-ELA Lake 373 in spring (blue) and fall (red) based on ∼three decades (1987–2020) of monitoring.



Size spectrum height as an indicator of fish abundance

We predicted that the size spectrum height would be correlated with estimates of fish abundance and productivity derived from other methods. Our data confirmed that this was true for abundance, as indicated by the significant relationship between spring height and white sucker population estimates based on annual Schnabel estimates that use mark/recapture data. Although mark/recapture population estimates for minnows were unavailable for use in this comparison, white sucker accounts for a large proportion of biomass in both spring and fall total catch (Supplemental Fig. S6), indicating that the spectral height is capturing patterns in the population size of important taxa in our study lake. We do recognize that the spectral parameters are not entirely independent from the Schnabel abundance estimates given they are derived from the same sampling effort (i.e., spring trap nets). However, to test the generality of our conclusions, we investigated if spring spectral height was also related to the (more limited) Schnabel estimates of white sucker based on fall sampling in the same year (i.e., from the same standing biomass of fish but sampled independently from the data informing spectra). The positive and significant relationship between spring spectral height and fall white sucker abundance (Supplemental Fig. S8) provides further evidence based

Fig. 4. Temporal trends in spring and fall size spectrum slope (*a*) and height (*b*) for the IISD-ELA Lake 373 fish community. Trends were evaluated using generalized additive models that used time as the sole covariate, and shaded regions represent 95% confidence intervals.



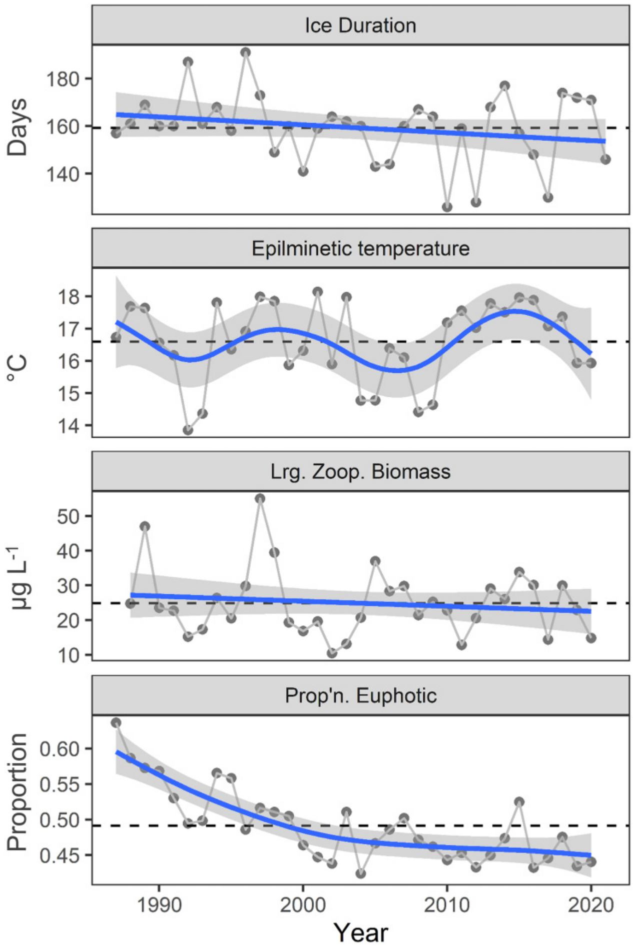
on independent sampling that size spectrum height can indeed capture interannual patterns in fish abundance.

We found that annual white sucker biomass estimates (based on spring data) were not related to spectral slope or height. We tested these relationships because the slope of the NASS changes depending on size frequency of biomass distributed within the community (i.e., higher biomass could equate to proportionally more fish in the larger size bins and shallower spectral slopes), and because abundance (as spectral height) is a key determinant of biomass. Previous studies have also found relationships between spectral slopes (as the scaling exponent of a bounded power law distribution) and fish community biomass, albeit across larger spatial scales (Robinson et al. 2017). In our study, the lack of a relationship between spectral parameters and white sucker biomass could be because the biomass estimates integrate information on abundance and body size into one measure, yet over the long-term, population sizes (abundance) of white sucker have increased at IISD-ELA while mean body size has decreased (Slongo 2022). Moreover, we were unable to account for minnow species and slimy sculpin in biomass estimates due to a lack of "true" abundance estimates for these species (no mark recapture program exists for these species given their overwhelming abundance in the catch and limited time of staff in the field). We expect that spectral parameters were not related to white sucker productivity given that productivity is a function of changes in biomass per unit time, whereas spectral slopes represent snapshots of the biomass distribution during a single sampling season. Overall, our analysis suggests that in L373 spectral height can serve as a proxy for the population size of important species, but neither slope nor height can capture the additional processes that are captured by biomass and productivity.

Drivers of size spectrum slope

We hypothesized that fall spectral slopes would be (on average) shallower than those based on spring sampling, meaning that the size structure of the population in the fall would shift towards a higher proportion of large fish. We expected this because fishes accrue body mass over the growing season, while spring sampling (after ice-off) would capture the fish community after a prolonged period of limited resource availability (reviewed in McMeans et al. 2020). Instead, we found that spectral slopes based on spring sampling tended to be shallower (and less variable) than those based on fall sampling. This pattern could have been due to a combination of overwinter mortality of small fishes, and the time at which fishes in L373 spawn. High overwinter mortality of small young-of-year (YOY) fishes is a well-documented phenomenon in lakes and occurs because small-bodied individuals do not have sufficient energy stores to endure this period of low light, cold temperatures, and limited resource availability (e.g., Biro et al. 2004). Consistent with this observation, the GAM analysis indicated that a longer duration of ice cover during the winter preceding spring sampling largely resulted in more shallow spring slopes, suggesting that longer periods of ice cover led to fewer small-bodied fishes in spring. Fur-

Fig. 5. Time series of the variables in Lake 373 that were used as explanatory variables in the fish community size spectrum slope and height. Blue lines represent temporal trends estimated via generalized additive models, and grey shading represents 95% confidence intervals. Lrg. Zoop. Biomass = the biomass of large zooplankton, Prop'n Euphotic = proportion (%) of the lake area within the euphotic zone.



ther, fall sampling would capture a higher proportion of YOY fishes relative to spring, given that white sucker and minnow species present in this lake are spring spawners and therefore would largely not yet be present in spring samples. The YOY minnows at IISD-ELA generally range from ∼20–65 mm in fork length, while YOY white sucker range from ∼50–60 mm (Rennie et al. 2019). Indeed, the trap nets used in our study lake can retain fishes > ∼20 mm (Guzzo et al. 2014). This demonstrates that both the seasonal timing of sampling and the life history traits of the fishes in the study system can have an important influence on observed spectral slopes.

The observed seasonal differences in fish community spectral slopes reported here also contrast those that have been documented based on long-term monitoring of phytoplankton and zooplankton communities. For example, using 30 years of zooplankton monitoring data from eight boreal lakes, Barth et al. (2019) showed that several systems consistently had steeper slopes early in the season (May) compared to later months—a pattern that is opposite to what we observed. Similarly, Evans et al. (2022) demonstrated that spring spectral slopes were consistently steeper than summer slopes based on ∼10 years of phytoplankton and zooplankton monitoring data from the Laurentian Great Lakes. The patterns in these previous studies are generally consistent with improved trophic transfer efficiencies later in the growing season when larger, longer-lived and more efficient grazers become abundant. The fact that we did not observe this pattern highlights that for longer lived species all within a single trophic level (i.e., planktivorous/benthivorous fishes), other processes like overwintering are likely more important in driving seasonal differences in spectral slopes.

While the differences between spring and fall slopes were unexpected, results from GAMs confirmed our expectation that resource availability influences among-year variation in spring spectral slopes. However, we found that the biomass of large zooplankton led to steeper (more negative) slopes. We believe this pattern could reflect differences in resource use between large and small-bodied species in L373. Tallman et al. (1984) found that cladocerans and detritus were among the most important dietary items for northern pearl dace in Lake 114 at IISD-ELA. In contrast, Tonin (2019) showed that littoral-benthic invertebrates and sedimentary chironomids accounted for ∼80% of adult white sucker diet in L373, while zooplankton accounted for only ∼20%. Tremblay and Magnan (1991) also showed that white sucker was heavily reliant on zoobenthos in two small Quebec lakes. Hence, a higher biomass of zooplankton prey may preferentially improve growth and reduce mortality of the smaller minnow species in our study system, which would lead to steeper (more negative) slopes. This is broadly consistent with the fact that white sucker are considered benthivores and have morphological adaptations to feed on the lake bottom, though it is important to note that zooplankton can also serve as an important prey item for this species (Saint-Jacques et al. 2000).

Drivers of size spectrum height

Spring size spectrum height was significantly (and positively) related to mean epilimnetic temperature during the preceding open water season, a relationship that could be driven by several mechanisms. For example, white sucker and the small minnows in our study lake are generally considered cool-water species (Eakins 2023), and population sizes may benefit from warming temperatures through increased recruitment, as demonstrated by Slongo (2022) for white sucker in IISD-ELA lakes. Moreover, Guzzo et al. (2017) showed that during warmer years in L373, lake trout spend less time foraging in the nearshore zone because temperatures quickly exceed their preferred range, a process that would reduce predation pressure on littoral prey fish (i.e., minnows). However, temperature may also influence fish abundance through other mechanisms. For example, warmer surface temperatures can increase littoral primary production, leading to enhanced littoral fish abundance through increased resource availability (e.g., Hayden et al. 2017).

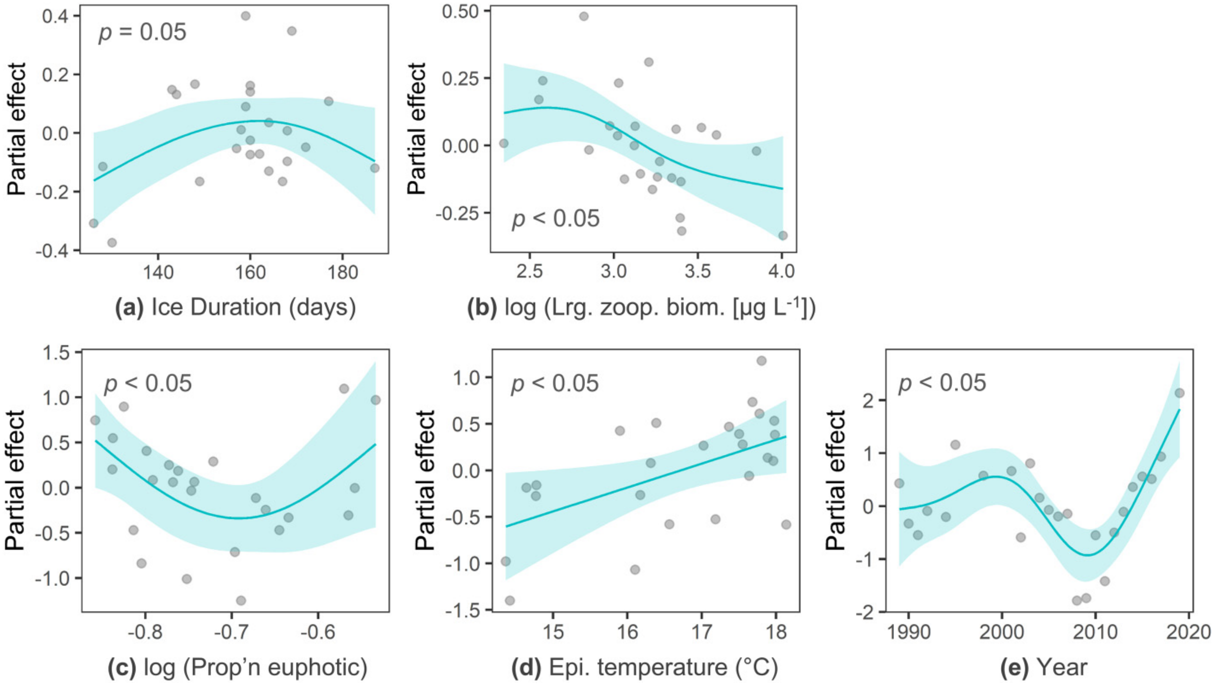
The proportion of the lake within the euphotic zone also had an important influence on spring spectral heights. This relationship was unimodal, whereby at both low and high values for relative euphotic area, spectral heights were more

Table 1. Output from the generalized additive models that assessed the relationship between key biological and physical properties and fish community size spectrum slope and height in IISD-ELA Lake 373 based on spring sampling.

Smooth term	Ref.df	edf	*F* statistic	*p*	% Contribution
Spring size spectrum slope					
f(Ice duration)	4	1.44	1.20	0.05	20
f(Epi.temperature)	4	6.3×10^{-6}	0.00	0.60	na
f(log(Lrg. zoop. biom.))	4	1.60	2.01	0.01	24
f(log(Prop'n. euph.))	4	2.24×10^{-6}	0.00	0.53	na
Intercept coefficient: −1.23 ± 0.03					
Deviance explained: 43.7%					
Spring size spectrum height					
f(Ice duration)	4	1.95×10^{-6}	0.00	0.62	na
f(Epi.temperature)	4	8.32×10^{-1}	1.24	0.01	19
f(log(Lrg. zoop. biom.))	4	1.16×10^{-6}	0.00	0.82	na
f(log(Prop'n. euph.))	4	1.48	1.52	0.03	11
f (Year)	5	3.89	5.70	<0.001	51
Intercept coefficient: −5.23 ± 0.11					
Deviance explained: 80.7%					

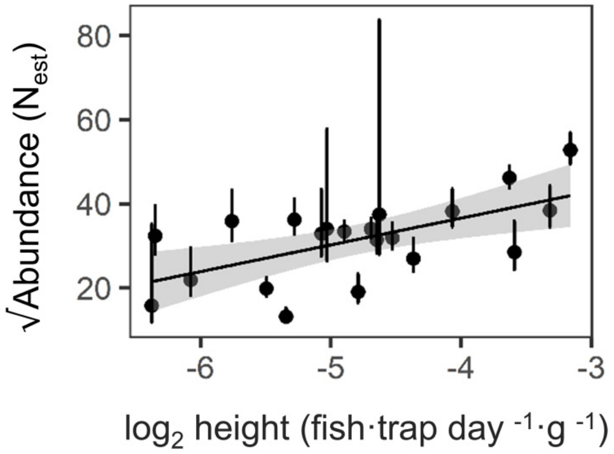
Note: Epi. temperature = mean epilimnetic temperature, Lrg. zoop. biom. = the biomass of large crustaceans, Prop'n. euph. = the proportion of the lake area within the euphotic zone. Variables with $p \leq 0.05$ are highlighted in bold. Ref. df = reference degrees of freedom, edf = effective degrees of freedom, % contribution = the relative contribution of a variable to total deviance explained. Note that variables with $F = 0$ were excluded from the final model via the double penalty approach.

Fig. 6. Generalized additive model (GAM) response patterns of spring fish community size spectrum slope in Lake 373 with (*a*) the duration of ice cover, and (*b*) the biomass of large crustaceans, and GAM response patterns of spring fish community size spectrum height in Lake 373 with (*c*) the proportion of the lake area within the euphotic zone, (*d*) mean epilimnetic temperature, and (*e*) time in years. Individual points show partial residuals for each smooth term.



positive, but lowest at middle values. This could reflect opposing mechanisms related to the effects of light on the production of invertebrate prey, and the foraging efficiency of lake trout. Tonin (2019) showed that across IISD-ELA lakes, darker systems tended to support a lower biomass of benthic invertebrates (particularly Chironomids, a key prey item for white sucker) and white sucker relative biomass compared to clearer systems. Moreover, the total area in which predatory species like lake trout are thermally excluded from the littoral zone under darker conditions due to a shallowing

Fig. 7. The relationship between spring estimated fish community size spectrum height and spring white sucker population estimates derived from mark-recapture methods. The solid line represents a linear regression and the shaded area represents the 95% confidence interval.



thermocline would also be expected to decrease (Schindler et al. 1996), increasing predation on littoral prey fish (i.e., minnows). Conversely, it is possible that darker conditions could initially increase the abundance of small fish (minnows) via reduced capture success by lake trout, which are visual predators (e.g., Mazur and Beauchamp 2003). Reduced transparency has also been associated with increased input of limiting nutrients in IISD-ELA lakes (Schindler et al. 1996), which could increase the production of benthic invertebrate prey for white sucker. Indeed, the long-term monitoring data from our study system suggested a negative relationship between relative euphotic area and total phosphorus (Spearman's $\rho = -0.63$, $p < 0.05$; data not shown). While the relative importance between these processes that influence spectral height would require further investigation, our data support the fact that light has a strong influence on aquatic ecosystem function (e.g., Tunney et al. 2018), and that changes in a single characteristic of fish habitat can affect fish abundance in several ways.

Fish community size structure and long-term environmental change

Unique to other studies evaluating fish spectral attributes, our study evaluated long-term changes in an unmanipulated lake and demonstrated that variation in regional climate is sufficient to influence spectral parameters. Ice cover on nearby Lake 239 has been reduced by ~19 days (on average) since 1970 when detailed observations began (Guzzo and Blanchfield 2017; Higgins et al. 2021), with the largest changes occurring after ~2000. Our analysis suggests this could be linked to the subtle decline in spring spectral slopes that occurs after ~2000, given that reduced ice cover favours a higher proportion of small fish. Fall spectral slopes, however, showed a different pattern having consistently declined (becoming steeper) over time. Though we did not perform formal modeling on the fall data, correlations with (non-detrended) data suggested that this consistent decline in fall slope could be linked to the decline in relative euphotic area that has occurred in L373 since ~1990 (Supplemental Table S1). For lakes at IISD-ELA, light attenuation is primarily controlled by DOC (Schindler et al. 1997), which has a strong link to precipitation patterns (Imtiazy et al. 2020). Indeed, reduced periods of ice cover and darkening of surface waters are changes that are occurring to lakes in many regions across North America and Europe (reviewed in Blanchet et al. 2022), and our results suggest that these changes may alter the size structure of fish communities.

Overall, our results indicate that the size spectrum height and slope are sensitive enough to reflect complex relationships between fish habitat and community size structure and abundance that are driven by temporal variability in climate. This is further supported by the fact that in L373, slope and height showed a similar amount of variability compared to studies of fish community spectral parameters in lakes across geographic gradients. For example, Marin et al. (2023) showed ranges of ~−2.4 to −0.8 and ~−3.3 to 2.7 for slope and height, respectively, based on fish communities across 51 lakes in France, some of which were subject to intense habitat degradation due to human activity. Additionally, the pronounced minimum in spectral height in the spring of 1994 and in epilimnetic temperature during the open water period of 1992 and 1993 coincide with a short-term global cooling event associated with the Mount Pinatubo eruption (Parker et al. 1996; Allen et al. 2015), suggesting that spectral height may be sensitive enough to respond to climatic extremes. We note that the lower degree of temporal variability in spring spectral slopes (CV = 17.5%) compared to spring and fall spectral heights (CV = ~22%) in our study is generally consistent with theory which suggests that spectral slopes should be less sensitive than height (or the intercept) to environmental change, given they are determined by fewer metabolic processes that vary consistently with body size across ecosystems (e.g., Sprules 2008).

Future directions

While the GAMs detected significant relationships among our subset of predictor variables and spectral parameters (for spring), ~50% of the variance in the spectral slope model and ~20% of the variance in the spectral height model remained unexplained. This indicates that some of our predictor variables would benefit from refinement. For example, while we leveraged available information on diet preferences for small fish at IISD-ELA (e.g., Tallman et al. 1984), the delineation of key zooplankton prey species for the various minnows in L373 would benefit from additional diet studies. Indeed, this refinement and subsequent inclusion in our predictive models may also yield additional insights on seasonal variability in trophic transfer efficiencies. In addition, eventual inclusion of annually measured isotopic signatures ($\delta^{13}C$) in lake trout fin rays, which are a more explicit indicator of their utilization of littoral minnows as prey (Guzzo et al. 2017; Kennedy et al. 2019), could improve the explanatory power of spectral model fit if included as a covariate. While such data was not available over the entire time series analyzed in this study, future work should leverage this information collected over a shorter period or across several lakes at IISD-ELA to quantify relationships (particularly those associated with top-down impacts of predation) with fish community spectral parameters.

Conclusions

Effective indicators of fish population and community abundance and health that can be measured with relative ease are required by monitoring groups, especially in response to a changing climate and an acceleration of resource development projects in boreal regions (Dey et al. 2021). Using ∼30 years of monitoring data, we showed a strong relationship between size spectrum height and independent estimates of white sucker abundance based on costly and time-consuming mark and recapture data, suggesting that spectral heights can be used as a proxy for abundance. However, our data also suggested that spectral parameters (height and slope) should not be extended to make inferences on population biomass or productivity given the additional processes (aside from abundance) that these metrics integrate.

We also demonstrated relationships between the size spectrum slope and height and key lake physicochemical variables. Even in the absence of experimental manipulation or anthropogenic stressors, these linkages were strong enough to generate long-term trends and interannual variability in fish community spectral parameters that reflect ongoing environmental change at IISD-ELA, particularly the long-term declines in both the duration of ice cover and water transparency. However, the interpretation of linkages between spectral parameters and lake properties were aided by a detailed understanding of the life history characteristics of the species in our system (e.g., spawning, diet, and thermal preferences) and may be necessary to fully understand changes in other systems. Nevertheless, this study demonstrates the utility of size spectra as an indicator of fish community response to environmental change and provides novel insights on drivers of variability in spectral parameters over time.

Acknowledgements

We would like to acknowledge the countless IISD-ELA staff, students, and external researchers who have collected fisheries, zooplankton, and limnological data in Lake 373 over the past ∼30 years, which made this work possible.

Article information

History dates

Received: 27 January 2024
Accepted: 6 October 2025
Accepted manuscript online: 24 October 2025
Version of record online: 17 December 2025

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Data availability

Data used in this study are subject to a formal data sharing agreement, and are available upon submission of a scientific data request form (https://www.iisd.org/ela/researchers/data-requests/) to IISD-ELA.

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Competing interests

The authors declare there are no competing interests.

Funding information

This work was supported by funding from Fisheries and Ocean Canada (Ocean and Freshwater Science Contribution Program to SNH), MITACS grants to GRM and HAM, the IISD Experimental Lakes Area and funding from NSERC Discovery grants and the Canada Research Chair program to MDR.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2025-0027.

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