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ARTICLE

Species-specific preferences drive the differential effects of lake factors on fish production

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Abstract: As the global human population grows, it remains a top priority for communities, managers, policymakers, and stakeholders to maintain healthy, sustainable, and productive fisheries under continued global change. Here we used a dataset consisting of fish and lake characteristics for 536 lakes across Ontario, Canada, to test whether multiple climate, human, and biological factors differentially affect fish production (i.e., population biomass per hectare per year). We tested the hypothesis that temperature is the key driver of fisheries production by testing for the effects of multiple factors on the production of three top predatory fish species: cold-water lake trout (*Salvelinus namaycush*), cool-water walleye (*Sander vitreus*), and warm-water smallmouth bass (*Micropterus dolomieu*). Using boosted regression tree analyses, we found that lake trout production was most influenced by the volume of hypolimnetic habitat, walleye production was related to other climatic variables, and smallmouth bass production was most influenced by sampling day of the year followed by Secchi depth. Our results suggest that current fish production models — that only include temperature and body size — may oversimplify important ecological complexities and thus misinform management decisions because species respond differently to environmental drivers.

Résumé : Pour faire face à la croissance démographique mondiale, les communautés, gestionnaires, décideurs et parties prenantes doivent continuer de prioriser le maintien de ressources halieutiques saines, durables et productives dans un contexte de changements climatiques. Nous avons utilisé un ensemble de données constitué de caractéristiques de poissons et de lacs pour 536 lacs en Ontario (Canada) pour vérifier si divers facteurs climatiques, humains et biologiques exercent différents effets sur la production de poissons (c.-à-d. la biomasse de la population par hectare par année). Nous avons vérifié l'hypothèse voulant que la température soit le principal facteur qui module la production des pêches en examinant les effets de différents facteurs sur la production de trois espèces de prédateurs de niveau trophique supérieur, à savoir le touladi (*Salvelinus namaycush*), une espèce d'eau froide, le doré jaune (*Sander vitreus*), une espèce d'eau fraîche, et l'achigan à petite bouche (*Micropterus dolomieu*), une espèce d'eau chaude. En utilisant des analyses par arbre de régression augmenté, nous constatons que le volume des habitats hypolimnétiques exerce la plus forte influence sur la production des touladis, que la production de dorés jaunes est associée à d'autres variables climatiques et que la date d'échantillonnage, suivie de la profondeur mesurée par le disque de Secchi, influencent le plus la production d'achigans à petite bouche. Nos résultats donnent à penser que les modèles de production de poissons actuels, qui n'intègrent que la température et la taille du corps, pourraient trop simplifier d'importantes complexités écologiques et ainsi produire des décisions de gestion non optimales découlant du fait que les espèces ne répondent pas toutes de la même manière à différents facteurs environnementaux. [Traduit par la Rédaction]

Introduction

The global human population is expected to reach 9.7 billion by the year 2050 (United Nations 2019), which will put continued stress on our freshwater ecosystems and the services they provide (Schindler 2001; Vörösmarty et al. 2000). It is estimated that the amount of protein derived from freshwater fisheries equates to the total dietary intake of 158 million people globally (McIntyre et al. 2016); however, many of the nations that depend heavily on such protein sources are not equipped to impose sustainable management strategies (Cooke and Cowx 2004). Therefore, much of our knowledge of fisheries management comes from data collected in the developed world. We rely on these data for understanding and maintaining the future of sustainable inland fisheries and thus global food security. Canada's freshwater lakes and rivers are foundational to its culture and economy, supporting world-renowned commercial, subsistence, and recreational fisheries. In Ontario alone, there are ~250 000 lakes that hold one-fifth of the world's fresh surface water and a diversity of flora and fauna (Government of Ontario 2019). Therefore, it remains a top priority for communities, managers, policymakers, and stakeholders to maintain healthy, sustainable, and productive fisheries under continued global change.

Energy flow through a lake food web starts with primary producers (e.g., phytoplankton and aquatic plants) — initiated by the microbial loop — and ends with top predators (e.g., fish; Fig. 1; Li et al. 2014). The more energy converted to new biomass, the more

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Fig. 1. Illustration of simplified lake food web with offshore (pelagic; left) and nearshore (littoral; right) energy channels (i.e., food chains). Arrows show direction of energy transfer: starting with producers (e.g., macroalgae, phytoplankton) — initiated by the microbial loop — to primary consumers (e.g., mussels, snails, macroinvertebrates, zooplankton) to secondary consumers (forage fish) to top predators (e.g., predatory fish).
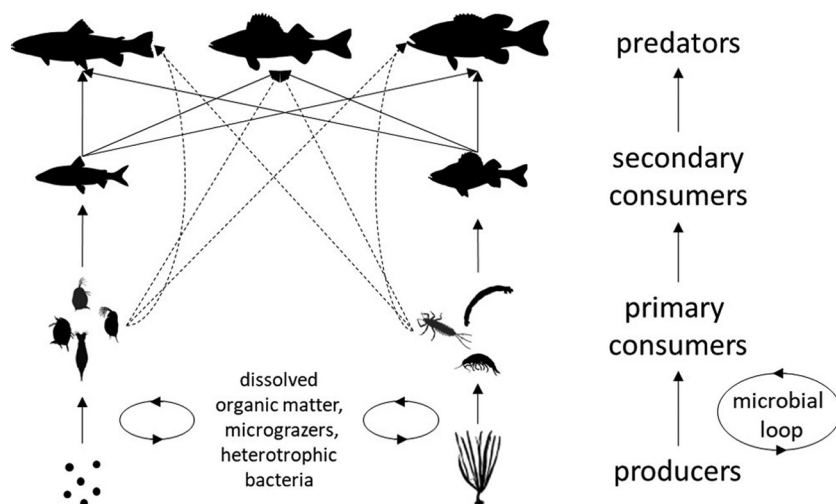

productive an ecosystem or population is said to be (Clarke et al. 1946). To ensure the sustainability and profitability of commercial, recreational, and subsistence fisheries, fisheries researchers seek to understand what drives fisheries' production; that is, what causes a fishery to produce a given amount of biomass every year (often measured as kg·ha^{-1}·year^{-1}).

With global warming of worldwide concern, the impact of temperature on fisheries production is a rapidly growing area of research (Myers et al. 2018; Till et al. 2019). Temperature drives many biological processes in freshwater ecosystems because it influences metabolic rates and thus how efficiently an individual converts resources to energy and how much resource is required for survival (or maintenance), growth, and reproduction (Kitchell et al. 1977; Hanson et al. 1997; Savage et al. 2004). This is particularly important for ectothermic fish that rely on environmental temperatures to control their internal temperatures. As such, the relationship between temperature and metabolism can provide crucial insights into how an individual's behaviour will extend to population, community, and ecosystem production. However, decades of research have shown that there are two other interesting components to this story: the first is that temperature is not the only ecological factor acting on freshwater ecosystems and thus fish production (Fig. 2; Ryder 1965; Chu et al. 2016); and the second is that temperature does not affect all fish equally (Fry 1947; Coutant 1977).

Lakes can have a diversity of fish species, each with unique physiologies and thus different temperature preferences (e.g., species better adapted for cold, cool, or warm waters; Coutant 1977; Magnuson et al. 1979; Christie and Regier 1988). Fishes also differ in their preferences for water clarity, acidity, and oxygen levels that are influenced by other factors such as landscape geology, lake morphometry, and human activities such as shoreline and agricultural development (Jackson et al. 2001; Lester et al. 2004). Each of these factors is constantly changing (Carpenter et al. 2011), and the magnitude and impacts of human activities are creating new opportunities for some fishes and fisheries while negatively influencing others (Moore and Olden 2017).

To the best of our knowledge, there has been no explicit comparison to date of the relative influences of these types of factors on the production of cold-, cool-, and warm-water freshwater fish species in lakes (though see Myers et al. 2018 for comparisons of the production of stream fish assemblages across temperature and latitudinal gradients). Therefore, our purpose was to test

Fig. 2. Schematic showing the complexity of multiple factors affecting fish production. Arrows indicate influences of one factor on another. Double arrows indicate that the factors are affecting each other. For example, habitat influences how species interact, but species interactions are also a part of an organism's habitat.
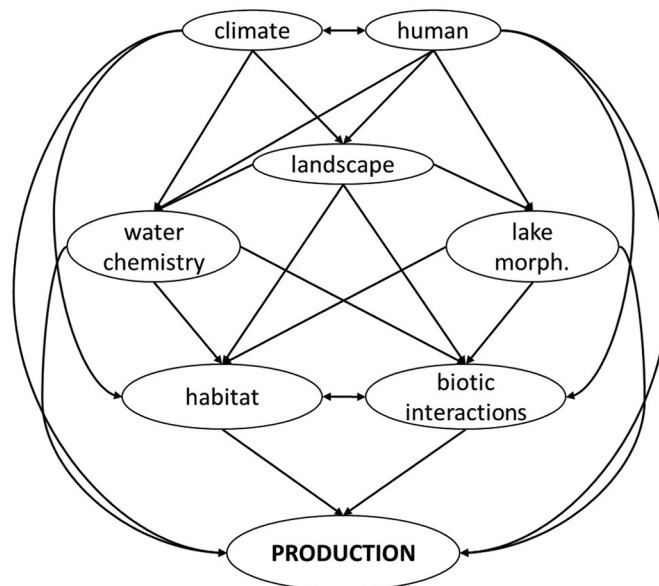
whether fish production is affected by a range of variables related to climate, water chemistry, lake morphometry, anthropogenic activity, and biological interactions and further test whether these effects differ among thermal guilds. We focus on three top predatory species that are popular sport fishes found across Ontario: cold-water lake trout (*Salvelinus namaycush*), cool-water walleye (*Sander vitreus*), and warm-water smallmouth bass (*Micropterus dolomieu*) (Shuter et al. 1980). Though different fish within a community can be classified by size, age, or diet, we chose to compare species by thermal guild because temperature preferences can spatially segregate them within a lake and thus allude to other interesting physiological and behavioural differences (Coutant 1977; Shuter et al. 1980; Christie and Regier 1988; but see Vander Zanden et al. 1999 for an example of niche overlap).

Here we used a dataset consisting of fish and lake characteristics for 536 lakes across Ontario to test for the relative influences of multiple factors on species-specific production among species with different habitat preferences. We tested the hypothesis that the temperature metrics that we have defined are key drivers of fisheries production across all species because of their influence on metabolism. However, we predicted that other climate, lake morphometry, water chemistry, anthropogenic, and biological factors also have strong influences on fish production because of their modifying effects on the amount of suitable habitat available to the different species. Our findings are relevant for fish production models that assume species uniformity across whole assemblages, which might oversimplify important ecological complexities and thus misinform management decisions if species respond differently to environmental drivers.

Methods

Study area

Our study lakes are located throughout Ontario's "northern" and "southern" regions, spanning a vast ~1 000 000 km² of land (Table 1 and Fig. 3) and large gradients of climate, land use, and fish community structure (i.e., species composition). Summers in the north are shorter than those in the south, and for our set of study lakes mean annual air temperatures range from 0.5 to 5.5 °C and 4.5 to 8.1 °C, respectively (from 2008 to 2012). Northern lakes are more isolated than southern lakes with farther proximity to roads (refer to online Supplementary materials, Fig. S1 and Fig. S2[1]). The cold, pristine waters make these lakes ideal for cold-adapted species like lake trout and other salmonids, though walleye also have a substantial northern distribution within our study lakes (Fig. 3). Our southern lakes are in more developed areas (Fig. S2[1]). These lakes tend to have higher fish abundances and hold a greater diversity of fish species, including percids (e.g., yellow perch (*Perca flavescens*) and walleye) and centrarchids (e.g., smallmouth bass and other smaller sunfish such as bluegill (*Lepomis macrochirus*)). Though we have just described the north and south as discrete areas, the range boundaries of warm- and cold- or cool-water species intersect in our dataset (Fig. 3; Chu et al. 2016).

Sampling fish communities

All data were collected following Ontario's Ministry of Natural Resources and Forestry's (OMNRF) Broad-scale Fish Community Monitoring (BsM) standardized protocol (Sandstrom et al. 2013; OMNRF 2008–2012). Standardized netting surveys were conducted between 2008 and 2012 using North American (NA1) standard large-mesh gillnets and Ontario (ON2) standard small-mesh gillnets, both benthic and horizontal in orientation. Both large- and small-mesh gillnets are used to sample whole-lake fish communities using a depth-stratified random design. Small-mesh nets are 12.5 m long horizontally, with mesh sizes that range from 13 to 38 mm and target smaller-bodied prey fishes or juveniles, while large-mesh nets are 24.8 m long horizontally, with mesh sizes that range from 38 to 127 mm and target larger-bodied predatory fish species (Bonar et al. 2009; Chu et al. 2016). All sampling occurred between June and September, once water temperatures were >18 °C, and nets were set for a target 18 h soak period. Processing the catch from the large-mesh nets involved recording the species, fork length, total length, and weight for all fishes caught in addition to the netting date (Sandstrom et al. 2013). Catches from small-mesh nets were processed for species, fork length, and total length.

Estimating population abundance and biomass

Total population abundance for lake trout, walleye, and smallmouth bass were estimated using only the large-mesh gillnet catch information and an approach adapted from Anderson (1998). The small-mesh data were not analyzed because there is currently no assessment of the selectivity of the small-mesh gillnets for different species and body sizes. The Anderson (1998) approach assumes that the likelihood of an individual fish being caught in a net is dependent on the size of the population and the probabilities of it encountering, contacting, and being retained in the net. The encounter probability is dependent on mesh size, the contact probability is dependent on fish size, and the retention probability is dependent on the combination of mesh and fish size (Anderson 1998). Mark–recapture studies on different lakes were used to estimate the encounter, retention, and contact probabilities and determine the selectivity of each mesh size across a range of fish sizes for each species (see Anderson 1998 for further detail; Giacomini et al. 2020). Therefore, using the above logic in reverse, we estimated abundance (i.e., the size of the population) given the probability of capture and the actual number of fishes caught in a given net. We then obtained total population biomass by multiplying total abundance by mean weight. Though the field data are composed of a disproportionate number of larger individuals within a population, this method — based on capture probabilities — provides a more complete representation of the size distribution of a given population and therefore a better production estimate.

Fish production

Our response variable, production (*P*), was calculated using the production–biomass ratio described by Randall and Minns (2000):

$$(1) \qquad P = B \cdot 2.64\, W^{-0.35}$$

where *P* is production (kg·ha⁻¹·year⁻¹), *B* is biomass (g·ha⁻¹), and *W* is mean body weight (g) of the species of interest. This equation uses allometric theory, which scales various biological rates (here, production) to body size (West et al. 1997). We found this equation particularly useful because only biomass and mean body size are needed to calculate production, and both are routinely measured and calculated for each BsM lake. The proportionality coefficient, 2.64, and the scaling exponent, −0.35, were taken from Randall and Minns (2000). The scaling exponent is the slope of the relationship between the production to body mass ratios and the mean weights of fish communities plotted on a log–log scale (Randall et al. 1995). The proportionality coefficient is a constant that is characteristic of a specific organism (West et al. 1997). We used values from Randall and Minns (2000) for the scaling exponent and coefficient because the life history data (fish length and age) used to derive these parameters come from a database of inland fish populations in Ontario and the lower Great Lakes. Their proportionality coefficient of 2.64 was adjusted upwards from a value of 1.32 (original equation from Randall et al. 1995) to account for the larger mean body sizes of the predatory fish species rather than a community average dominated by relatively smaller, fast-growing forage fish species (Randall and Minns 2000). Because our focus is on the production of three predatory species, we used this same approach.

Ecological variables

For our study, we selected ecological variables that may affect an organism's behaviour (e.g., habitat use, foraging) or life history characteristics (e.g., growth, reproduction). We divided the ecological variables into five main categories for comparative purposes: climate, water chemistry, lake morphometry, anthropogenic

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[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2020-0105.

Table 1. Descriptions for each of the variables used to determine the relative influence of climate (degree days, precipitation), water chemistry (Secchi depth, dissolved organic carbon, total phosphorous), lake morphometry (proportion hypolimnetic volume, proportion littoral area), human (angling activity), and biological (species richness and presence of lake trout (LT; *Salvelinus namaycush*), walleye (W; *Sander vitreus*), smallmouth bass (SMB; *Micropterus dolomieu*), and zebra mussels (*Dreissena polymorpha*)) variables on lake trout, walleye, and smallmouth bass production.

			Mean ± SD			Median			Range		
	Description	Abbrev.	Unit								
			LT	W	SMB	LT	W	SMB	LT	W	SMB
Continuous variables											
Production	New fish biomass produced	P	kg·h⁻¹·year⁻¹	1.8±1.7	2.0±2.0	2.1±2.3	1.3	1.4	1.3	0.02–12.1	0.004–12.6	0.02–14.3
Net day	Day lake was sampled	Day	Julian day number	201.1±24.66	201.6±25.27	202.3±26.3	200	200	202	155–263	151–265	151–265
Degree days above 5 °C	The number of degrees per day above 5 °C, summed for the year; temperatures based on daily averages	Dd5	Σ (degrees > 5 °C)	1618.0±168.3	1623.0±220.7	1753.0±198.0	1639	1600	1718	1232.0–2214.0	1059.0–2246.0	1239.0–2246.0
Precipitation	Rain or snowfall per year	Pcp	mm	851.6±106.7	826.8±101.9	884.6±110.2	874.5	815	902	685.0–1157.0	630.0–1152.0	685.0–1157.0
Secchi depth	Water clarity parameter measure by a Secchi disk	Secchi	m	5.0±2.0	3.5±1.8	4.4±2.0	4.7	3.2	4.1	1.5–13.4	0.1–10.5	0.50–13.4
Dissolved organic carbon	Dissolved organic carbon concentration in lake	DOC	mg·L⁻¹	5.3±2.5	8.0±3.4	6.1±2.7	4.9	7.4	5.7	0.8–14.2	1.7–19.2	0.80–16.1
Total phosphorous	Phosphorous concentration in lake	TP	μg·L⁻¹	6.7±4.0	11.2±6.7	10.1±6.9	6	9.8	8.3	1.7–43.1	2.4–52.5	2.3–52.5
Proportion hypolimnetic volume	Proportion of the total lake volume below the thermocline	Hypo		0.38±0.13	0.21±0.17	0.28±0.18	0.37	0.17	0.27	0.02–0.68	0.0–0.65	0.0–0.65
Proportion littoral area	Proportion of the total lake area shallower than 4.6 m	pLitt		0.30±0.13	0.49±0.23	0.41±0.21	0.3	0.46	0.38	0.06–0.81	0.07–1.0	0.06–0.99
Angling activity	Based on summer vessel and shore and winter hut and open-ice counts	Aa	Count·ha⁻¹	1.3±1.6	2.1±3.5	2.9±3.25	0.8	1.1	1.8	0–11.4	0.0–42.3	0.0–20.1
Species richness	Total number of species in the lake	SppRich	No. of species	11.5±4.2	11.7±4.0	12.8±4.0	11	11	13	3.00–24	3.0–25.0	4.0–25.0
Other lake characteristics											
Latitude		Lat	°N	47.69±1.70	48.08±2.11	46.77±1.83	47.42	48.54	46.49	44.54–51.41	43.06–54.33	43.06–50.65
Longitude		Long	°W	85.09±5.49	85.58±5.95	83.10±6.07	83.54	85.01	80.51	94.72–76.01	95.04–74.50	95.06–74.50
Surface area		Area	ha	1859±3637.96	2421.10±5875.59	2115.00±3569.92	719.00	1017.00	1016.00	21.00–34 518.00	25.00–90 484.00	21.00–31 370.00
Maximum depth		Depmx	m	44.31±21.52	28.54±23.23	35.17±26.35	39.60	21.40	27.25	12.00–125.95	3.00–213.50	3.00–213.50
Mean depth		Depmn	m	13.14±6.48	8.01±6.13	10.23±7.24	11.60	8.01	7.75	3.10–38.70	1.10–38.40	1.10–38.70
pH		pH	NA	6.98±0.49	7.24±0.48	7.21±0.54	6.92	7.22	7.21	5.61–8.70	5.88–8.48	5.61–8.53
Abundance		Ab	Count·ha⁻¹	11.27±13.66	21.09±50.11	23.17±33.31	6.20	13.02	11.62	0.01–935.84	0.01–935.84	0.09–231.93
Biomass		biom	g·ha⁻¹	6760.2±6120.3	5778.8±5573.9	5875.8±5711.7	5082.8	4386.3	3953.8	23.46–3733.45	23.46–37 336.45	107.9–32 288.90
Mean fish weight		Wt	g	1220.9±1146.4	499.73±495.20	451.60±321.58	810.70	352.76	324.40	137.70–7119.80	9.36–4350.00	59.00–1349.00

Table 1 (*concluded*).

Categorical variables

	Description	Abbrev.	% of lakes		
			LT	W	SMB
Lake trout presence	Species considered present if	paLt	NA	30.1	45.3
Walleye presence	its catch per unit effort	paWal	49.8	NA	79.9
Smallmouth bass presence	(CPUE) > 0 in the Broad-	paSmb	51.9	54.9	NA
Northern pike presence	scale Monitoring Program	paNp	58.6	88.7	76.3
Zebra mussel presence	data	paZm	1.7	9.5	13.5
			No. of lakes		
			LT	W	SMB
Year					
2008			72	90	71
2009			62	141	83
2010			70	102	89
2011			25	54	27
2012			10	12	4

Note: The descriptive statistics were calculated for the 239 lake trout, 399 walleye, and 274 smallmouth bass lakes used for all analyses. These data were collected between 2008 and 2012 as part of the Broad-scale Monitoring Program for Inland Lakes in Ontario, Canada (OMNRF 2008–2012).

activity, and biological community. Regional climate variables included air temperature (measured at each lake as growing degree days above 5 °C; i.e., degree days) and mean annual total precipitation. Both variables were calculated using the 1981–2010 climate normals period. Water temperature was locally represented by proportion hypolimnetic volume. Though we treated proportion hypolimnetic volume as a climate variable for organizational purposes, it should be noted that it is measured as the volume below the thermocline (measured at the time of netting; Shuter et al. 1983) and is a function of air temperature, water clarity, wind, and lake morphometry. Sampling in all lakes occurred when surface water temperatures were above 18 °C (Sandstrom et al. 2013). Water chemistry variables included dissolved organic carbon and total phosphorus concentrations (always measured during the spring and collected in the same year as the lakes were netted) and Secchi depth (measured at the time of netting). Lake morphometry variables included surface area and proportion of littoral area (proportion of lake <4.6 m deep; Pierce and Tomcko 2005). Our estimate for littoral area was a proxy because neither light attenuation data nor curves were available for each lake. Biological variables included species richness (number of species caught in the nets), the presence or absence of predatory or competing fish species (lake trout, walleye, smallmouth bass, and northern pike (*Esox lucius*)), and the presence of invasive zebra mussels (*Dreissena polymorpha*). Species richness — the number of species caught in a lake — was determined by the catch of the large- and small-mesh nets following the standardized BsM protocol (Sandstrom et al. 2013). The anthropogenic variable included in our study was angling activity, which was measured in the lake sampling year as the number of anglers per square kilometre based on angler counts from aerial surveys done during summer and winter. Summer surveys consisted of eight weekday and eight weekend flights and winter surveys included six weekday and six weekend flights (Chu et al. 2016). We also included the netting day (i.e., sampling day) and year in our analysis to account for changes in production that could be related to seasonal or annual variation in ecological conditions and thus inform future sampling protocol. Each represents the day of the year and year each lake was netted. All environmental lake and fish data were collected and provided by the OMNRF (OMNRF 2008–2012; see Table 1 for definitions, abbreviations, and descriptive statistics).

Analysis

Boosted regression tree (BRT)

For exploratory purposes we first tested for differences in production among each of our study species using a Kruskal–Wallace test for nonparametric data and accepted the null hypothesis (no significant differences among species) if $p > 0.05$ (Fig. S3[1]). Then, to test which variables influenced lake trout, walleye, and smallmouth bass production, we built models using BRT analyses, a method that has broad applications in ecological studies, such as identifying classifiers to predict fish distribution and determining species richness, among others (Leathwick et al. 2006; De'ath 2007; Elith et al. 2008).

BRT analysis is a machine learning technique that uses a series of algorithms and randomizations to test for relationships between predictor and response variables in a dataset, fit multiple models to the data, and combine this collection of models to make predictions about the response. Each new model of a BRT is built, or "boosted", from the previous one; the first model is built, or "trained" on a random sample (called the "training data"), with replacement, from the whole data set; tested using the training data; and then the values that were poorly predicted (i.e., have the most error) are weighted more heavily to be selected to train the next model. Therefore, each subsequent model achieves the best model by identifying and minimizing the error generated from the previous model.

Fig. 3. Maps of Ontario, Canada, showing the distributions of our lake trout, *Salvelinus namaycush* (*a*; *n* = 239); walleye, *Sander vitreus* (*b*; *n* = 399); and smallmouth bass, *Micropterus dolomieu* (*c*; *n* = 274) study lakes used in our analyses. Each dot represents one freshwater lake. Each lake was sampled between 2008 and 2012 as part of the Ontario Ministry of Natural Resources and Forestry's Broad-scale Monitoring Program for Inland Lakes. Map generated using GoogleMaps (2019) and desktop QGIS version 3.10.7 (QGIS 2019). Data from the OMNRF Broad-scale Monitoring Program database (OMNRF 2008–2012).
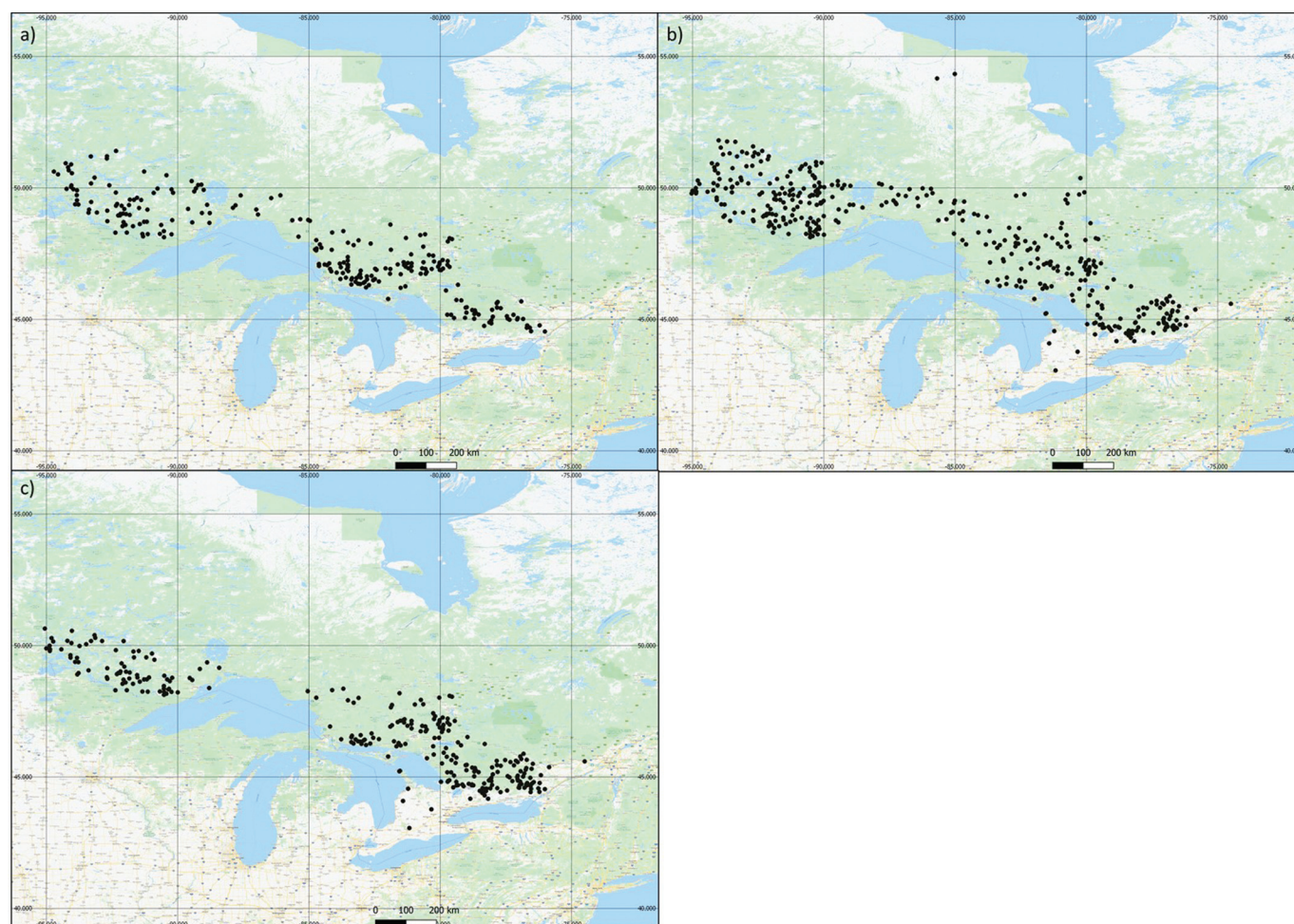
This technique is robust to non-normal distributions in predictor variables; however, the response — fish production — was $\log_2$-transformed for normality. We chose to use base-2 because of the relatively small range of production values (i.e., less than 0–100). Highly correlated continuous variables ($r < -0.6$ or >0.6) were identified using a Spearmen correlation matrix on log-transformed variables (Table S1[1]). BRTs can handle and identify interactions between predictors (De'ath 2007). All predictors were used in the BRT models developed for each species.

The BRTs for the lake trout, walleye, and smallmouth bass datasets were fit with a learning rate of 0.001, bagging fraction of 0.5, and tree complexities of 3, 2, and 3, respectively. These values were selected because they produced the models with the best predictive performances (i.e., lowest cross-validation deviance) after testing the following parameter values: learning rate = 0.0001, 0.001, 0.01, 0.1; tree complexity = 2–4; and bagging fraction = 0.5 and 0.75. Tenfold cross-validation was performed to select the optimal number of trees to use for each model and to assess their predictive performance (Leathwick et al. 2006).

Results

For our study, 239 lakes had lake trout, 399 had walleye, and 274 had smallmouth bass. Of these lakes, there were 119 lakes with lake trout and walleye, 124 with lake trout and smallmouth bass,

219 lakes with walleye and smallmouth bass, and 86 lakes with all three species (Table 2). These lakes ranged in surface area from 21 to 90 484 ha and maximum depths of 3–213 m. On average, the lakes with lake trout were the deepest but had the smallest surface area, while the lakes with walleye were the shallowest but had the largest surface area. Walleye had the greatest geographic distribution in our dataset, occurring just as far south as smallmouth bass and farther north than lake trout (Table 1; Fig. 3).

Lake trout, walleye and smallmouth bass production estimates were not significantly different ($p > 0.05$), though lake trout tended to have the lowest production rates and smallmouth bass the highest (Table 1; Fig. S3[1]). Of the three species, lake trout had the highest mean biomass (6760 ± 6120 g·ha⁻¹) followed by smallmouth bass (5876 ± 5712 g·ha⁻¹) and walleye (5779 ± 5574 g·ha⁻¹). Lake trout had the highest mean body weight (1221 ± 1146 g) compared with walleye (500 ± 495 g) and smallmouth bass (452 ± 322 g), such that they had the lowest mean abundance of the three species (Table 1). Therefore, in our study lakes the more productive species (of those studied) were those with smaller body sizes residing in relatively warmer habitats (lakes with more degree days > 5 °C; Table 1).

The best BRT models were those that explained the highest percent variance in each dataset (i.e., the highest cross-validated proportion of the total deviance explained). The best models in

Table 2. Number of lakes sampled that include each of the listed species combinations.

Species combination	A No. of lakes	B No. of lakes
LT+W	2	119
LT+SMB	20	124
LT+NP	20	140
W+SMB	25	219
W+NP	143	354
SMB+NP	12	209
LT+W+SMB	15	86
LT+W+NP	31	102
LT+SMB+NP	18	89
W+SMB+NP	108	179
LT+W+SMB+NP	71	71

Note: The species include lake trout (LT; *Salvelinus namaycush*), walleye (W; *Sander vitreus*), smallmouth bass (SMB; *Micropterus dolomieu*), northern pike (NP; *Esox lucius*). Column A is the number of lakes that include only the two predatory species listed (of the species considered here), and column B is the number of lakes that include at least the two species listed. For example, lake trout and walleye are the only two predatory species in two of the lakes sampled, but also coexist — among other species — in 119 of the lakes sampled ([LT + W] + [LT + W + SMB] + [LT + W + NP] + [LT + W + SMB + NP]). These lakes were sampled between 2008 and 2012 as part of the Broad-scale Monitoring Program for Inland Lakes in Ontario.

our study explained 22%, 40%, and 24% of the variation in the production of lake trout, walleye, and smallmouth bass, respectively (see Table S2[1] for model summary). The BRT output also lists the relative percent contribution of each ecological factor tested (i.e., each predictor variable) to predicting production (i.e., the response variable). Our results indicated that the variables that have the greatest influence on production are different among lake trout, walleye, and smallmouth bass (Table 3). Relative to all factors tested, lake trout production was most influenced by the proportion of hypolimnetic volume in the lake (19%), followed by dissolved organic carbon (14%), and the proportion of littoral area (14%). Walleye production was most influenced by annual precipitation (23%), degree days (16%), and proportion hypolimnetic volume (16%); and smallmouth bass production was most influenced by net day (17%), Secchi depth (14%), and dissolved organic carbon (10%). The biological variables had the least amount of influence on the production of all three fish species (Table 3).

Whether each factor had a positive or negative effect on production is shown in the partial dependence plots, which describe the effect of a given predictor on the response after accounting for the other predictors in the model (Figs. 4, 5, and 6; Elith et al. 2008). The partial dependence plots for the top three ecological factors for each species suggest that lake trout production increased with proportion of hypolimnetic volume but decreased with dissolved organic carbon and proportion of littoral area. Walleye production decreased with precipitation, temperature (higher degree days), and proportion hypolimnetic volume. Smallmouth bass production increased during the sampling season (end of June (~day 180) to mid-September (~day 265)) and with water clarity but decreased with increasing DOC concentration.

Discussion

Influence of temperature on production

Our study spanned 536 lakes covering an area of ~1 000 000 km² to test for key drivers of fish production for three recreationally

important top predator species, belonging to three different thermal guilds. We tested the hypothesis that temperature is the key driver of fisheries production because of its well-known effects on metabolism (Savage et al. 2004). However, our results did not support this hypothesis. We found that temperature was among the five most influential factors of those tested for all three species, but because of species-specific thermal preferences, the role of the temperature metrics in driving fish production varied by thermal guild. For cold-water lake trout, hypolimnetic volume had a greater influence on production than degree days, for walleye the influences of those variables were switched (i.e., degree days was more important than hypolimnetic volume), and for smallmouth bass, neither was among the top three most influential variables tested. These results highlight the importance of considering species-specific preferences and the roles of other interacting factors when studying production across multiple fisheries.

Species-specific effects

Lake trout production

Our results suggested that lake trout production is most influenced by the proportion of hypolimnetic volume to cold-water habitat available during summer stratification and that they are more productive in lakes with more of this optimal habitat space. This is consistent with several studies documenting that lake trout take refuge in the hypolimnion when nearshore habitats warm to temperatures that exceed their thermal tolerance (Morbey et al. 2006; Tunney et al. 2014). The presence of cold-water refugia may help explain why lake trout production increased with degree days when we expected to see the opposite given their thermal sensitivities. Our results suggest that even in warmer climates, deep, cold lake trout lakes can support high production. This may be possible because there are pelagic hypolimnetic prey available (e.g., cisco, *Coregonus artedi*) or because lake trout are capable of brief forays into the more productive nearshore habitat (Vander Zanden et al. 1999; Morbey et al. 2006). However, future lake warming and evaporation could reduce hypolimnetic refuge and prevent behavioural thermoregulation, restrict nearshore resource consumption, and negatively affect lake trout production (Mackenzie-Grieve and Post 2006; Plumb et al. 2014; Tunney et al. 2014). Projections for precipitation patterns under climate change remain highly variable, so it is uncertain whether annual precipitation will increase water levels enough to offset the effects of temperature warming and evaporation on lake trout habitat availability (Keller 2007).

We found that the second most influential factor affecting lake trout production was the concentration of dissolved organic carbon. Consistent with other studies (Karlsson et al. 2009; Hedström et al. 2017), it had a negative effect on lake trout production. Karlsson et al. (2009) and Benoit et al. (2016) also found that fish production in general decreased with dissolved organic carbon. They suggested that "brown" lakes, or those associated with high levels of phosphorous and dissolved organic carbon, had poor light penetration. Therefore, despite their higher nutrient content, there was a decline in whole-lake primary production (benthic and pelagic) that extended to higher trophic levels. Likewise, Hedström et al. (2017) highlighted the importance of winter conditions on visual predatory fish. If a lake has relatively high levels of dissolved organic carbon, light-limited winter environments can further impede foraging success, which can lead to higher winter mortality rates and lower production rates.
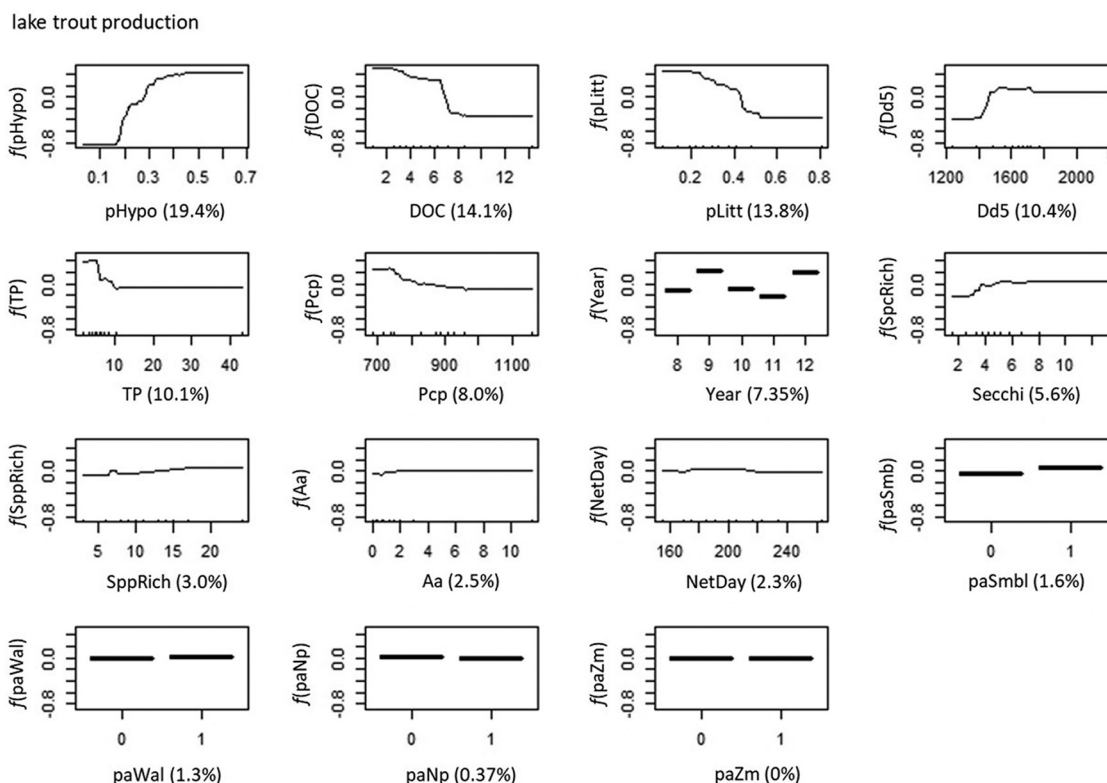
Our results showed that the proportion of littoral area was equally as influential as dissolved organic carbon, with decreased lake trout production in lakes with more littoral area. This is consistent with Tunney et al. (2012), who showed that lakes with more littoral area required too much search time for lake trout to effectively exploit nearshore resources, thus lowering consump-

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Table 3. Relative influences (%) table from the boosted regression trees (BRTs) performed on the lake trout (*Salvelinus namaycush*), walleye (*Sander vitreus*), smallmouth bass (*Micropterus dolomieu*) production data.

Lake trout		Walleye		Smallmouth bass	
Ecological factor	Relative influence (%)	Ecological factor	Relative influence (%)	Ecological factor	Relative influence (%)
Proportion hypolimnetic volume	19.35	Precipitation	22.68	Net day	16.71
Dissolved organic carbon	14.12	Degree days	16.31	Secchi	14.33
Proportion littoral area	13.81	Proportion hypolimnetic volume	15.94	Dissolved organic carbon	9.71
Degree days	10.44	Dissolved organic carbon	11.87	Angling activity	9.37
Total phosphorus	10.11	Secchi	9.84	Degree days	9.16
Precipitation	8.01	Proportion littoral area	6.21	Total phosphorus	8.60
Year	7.35	Total phosphorus	5.37	Proportion hypolimnetic volume	7.17
Secchi	5.62	Zebra mussels	3.37	Precipitation	6.30
Species richness	3.04	Angling activity	2.86	Proportion littoral area	5.58
Angling activity	2.50	Species richness	1.58	Year	4.23
Net day	2.29	Smallmouth bass	1.57	Species richness	4.18
Smallmouth bass	1.63	Net day	1.21	Lake trout	2.07
Walleye	1.33	Year	1.04	Zebra mussels	1.35
Northern pike	0.37	Northern pike	0.11	Northern pike	0.70
Zebra mussels	0.00	Lake trout	0.05	Walleye	0.54

Note: These values do not represent the amount of variability explained by the model, but rather the influence of each factor on the response (fish production) relative to all other factors included in the model. The predictors (ecological factor) are ranked from most (top) to least (bottom) influential. All data were collected between 2008 and 2012 following the Broad-scale Monitoring Program (BsM) protocol in Ontario, Canada.

Fig. 4. Partial dependence plots from the boosted regression tree (BRT) analyses performed on the lake trout (*Salvelinus namaycush*) production dataset. Each plot shows the marginal effect of the given predictor on fish production (i.e., the response). The *x* axes display predictor values and the *y* axes display the partial functions, which tell us the effect of a given predictor value on the predicted outcome of the response, with the influence of all of the other predictors averaged out. The percentages within the parentheses represent the relative influence of each predictor on fish production (also displayed in Table 3). Each predictor variable was measured once for each lake between 2008 and 2012 following the protocol for the Ontario Ministry of Natural Resources and Forestry's Broad-scale Monitoring Program for Inland Lakes.
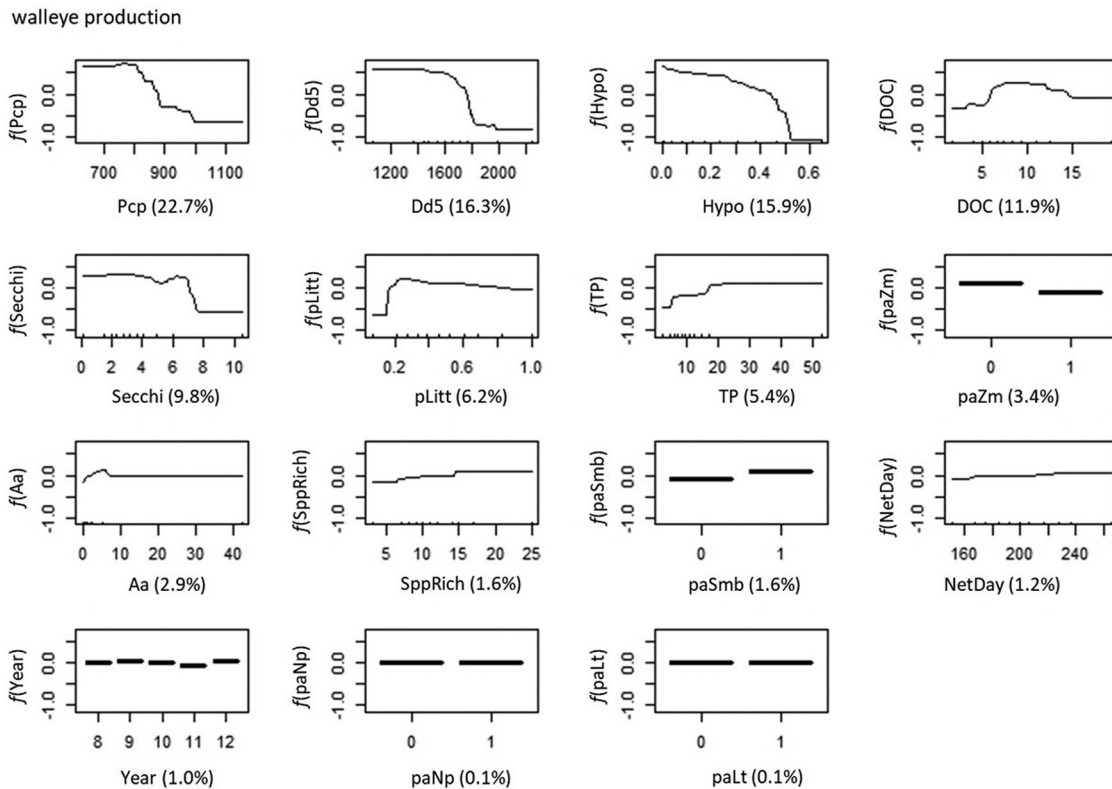

tion and productive potential from nearshore prey. Dolson et al. (2009) also showed that lake trout nearshore habitat use in summer months was lower in more reticulated lakes (i.e., convoluted, rather than smooth, shorelines) because relatively more littoral habitat space in those lakes provided more thermal refuge for prey.

Walleye production

We found that the most influential factor affecting walleye production in our study lakes was mean annual total precipitation. Our results indicated that walleye tend to be more productive in lakes with lower levels of annual precipitation, which is the opposite of what previous literature suggests. Chevalier (1977) found

Fig. 5. Partial dependence plots from the boosted regression tree (BRT) analyses performed on the walleye (*Sander vitreus*) production dataset. Each plot shows the marginal effect of the given predictor on fish production (i.e., the response). The *x* axes display predictor values and the *y* axes display the partial functions, which tell us the effect of a given predictor value on the predicted outcome of the response, with the influence of all of the other predictors averaged out. The percentages within the parentheses represent the relative influence of each predictor on fish production (also displayed in Table 3). Each predictor variable was measured once for each lake between 2008 and 2012 following the protocol for the Ontario Ministry of Natural Resources and Forestry's Broad-scale Monitoring Program for Inland Lakes.
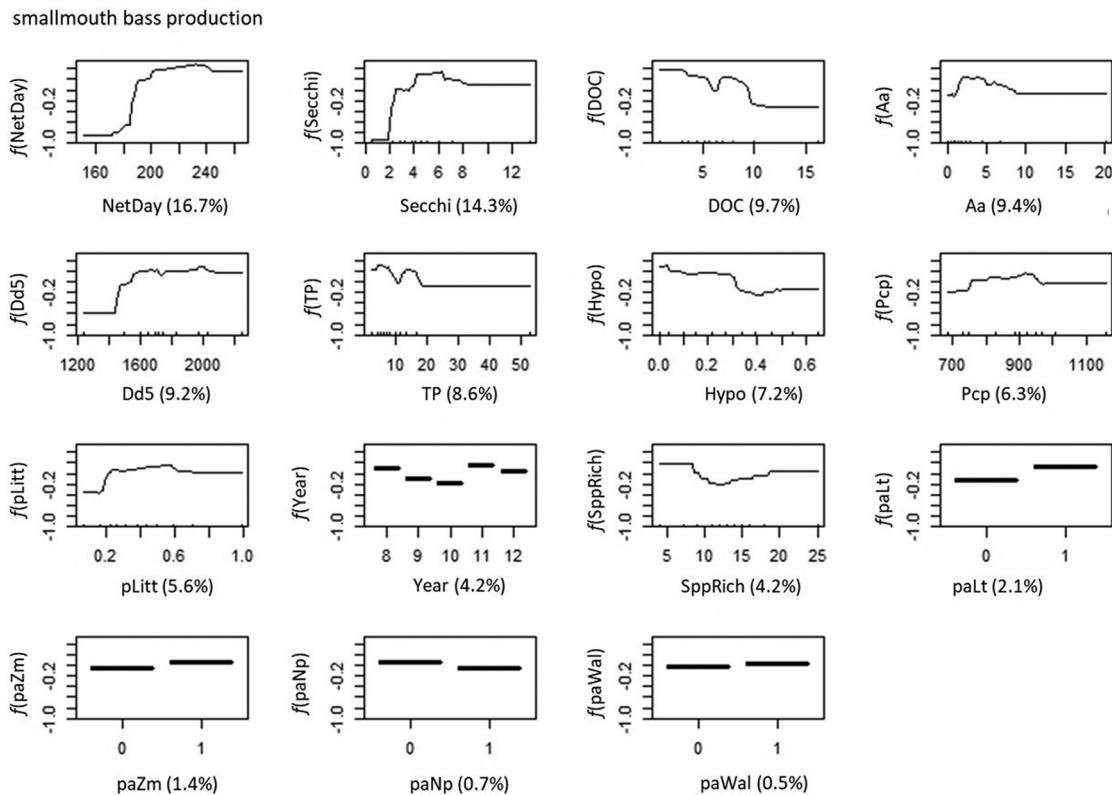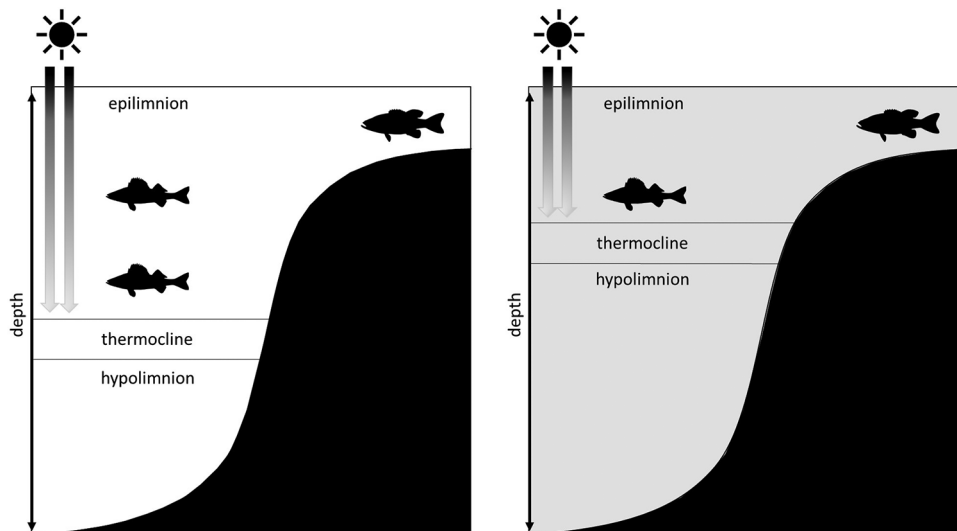

walleye production

that walleye abundance increased with spring water levels because spring flooding of gravel beaches is necessary for spawning. However, the higher-intensity precipitation events of recent years could be harmful for brood survival (Fayram et al. 2014). For walleye that spawn in the adjoining rivers of some of our lakes, it is also possible that precipitation is affecting nursery conditions via changes to riverine flow and temperature and thus walleye spawning success, brood survival, and overall production (Kitchell et al. 1977). Therefore, it remains unclear which mechanism(s) are driving the patterns observed in our data. Across our walleye lakes, precipitation was correlated with neither Secchi depth nor dissolved organic carbon, suggesting that it is unlikely that the negative effect of precipitation on walleye production was associated with their sight and foraging ability. Instead, it is possible that the strong influence of precipitation on walleye production was in part due to thermal habitat availability. Precipitation increases terrestrial run-off and surface water mixing, which could lead to reduced light penetration and shallower thermocline depths (Gauthier et al. 2014). Because walleye occupy cool waters just above the thermocline, increased precipitation could reduce the amount of walleye habitat and thus their production rates (Fig. 7). Likewise, shallower thermoclines could restrict warm-water habitats favourable for primary production and the amount of resources available to higher trophic levels (Gauthier et al. 2014). This result highlights the complexities surrounding precipitation as a driver of fish production.

We found that degree days was the second most influential factor for walleye production. Our results also showed that walleye production increased at lower degree days despite slower growth and later maturity at colder temperatures (suggestive of

lower production rates; Lester et al. 2014). Lester et al. (2014) found that walleye at 1000 degree days grew more slowly and invested less into reproduction than walleye at 4000 degree days, but estimated that natural mortality increased with degree days, suggesting a trade-off in life history traits when exposed to warmer temperatures. Our results were also consistent with Hansen et al. (2015), who found that in small lakes, walleye recruitment was more likely when degree days were relatively low (also mentioned in a review by Raabe et al. 2020). Hansen et al. 2015 argued that zooplankton resources in small lakes might be insufficient for meeting the heightened metabolic demands of juvenile walleye under higher temperatures and longer growing seasons (Johnston and Mathias 1994). It is also possible that higher degree days may hinder spawning because walleye require sufficiently cool temperatures for gonadal development (Nate et al. 2003) or that longer growing seasons increase predation of eggs by other species (Bozek et al. 2011).

Following precipitation and degree days, we found that hypolimnetic volume had the third-highest relative influence on walleye production with decreased production as hypolimnetic volume increased. As a cool-water predator with temperature preferences ranging from 20 to 25 °C (Hasnain et al. 2013), it seems intuitive that production decreased as the proportion of less suitable hypolimnetic habitat increased in our study lakes. However, because hypolimnetic volume is measured as the proportion of total lake volume below the thermocline, having more unsuitable habitat (i.e., hypolimnion) does not necessarily mean there is less suitable habitat (i.e., nearshore sublittoral or littoral) available for successful spawning and juvenile survival. For example, if two lakes have the same thermocline depth but one lake is deeper

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Fig. 6. Partial dependence plots from the boosted regression tree (BRT) analyses performed on the smallmouth bass (*Micropterus dolomieu*) production dataset. Each plot shows the marginal effect of the given predictor on fish production (i.e., the response). The *x* axes display predictor values and the *y* axes display the partial functions, which tell us the effect of a given predictor value on the predicted outcome of the response, with the influence of all of the other predictors averaged out. The percentages within the parentheses represent the relative influence of each predictor on fish production (also displayed in Table 3). Each predictor variable was measured once for each lake between 2008 and 2012 following the protocol for the Ontario Ministry of Natural Resources and Forestry's Broad-scale Monitoring Program for Inland Lakes.

Fig. 7. Simplified diagram showing hypothetical habitat availability for walleye (*Sander vitreus*) in lakes with different thermocline depths. (Left panel) Clearer lake conditions allow greater penetration of solar radiation, which means deeper thermoclines and therefore more walleye habitat (two fish above thermocline). (Right panel) Less clear lake conditions (i.e., more mixing, turbidity or colour, higher dissolved organic carbon, lower Secchi depth) reduce penetration of solar radiation, causing shallower thermocline depths and less walleye habitat (one fish above thermocline). The nearshore smallmouth bass (*Micropterus dolomieu*; one fish in each panel) indicates that their habitat space might not be affected by changing thermoclines.

than the other, the deeper lake will have relatively more hypolimnetic volume, but both lakes will have equal volume above the thermocline, all else equal. Therefore, the effect of hypolimnetic volume on walleye production might also be related to prey availability. Walleye typically spend most of their time in nearshore habitats but will make foraging forays into the hypolimnion if pelagic prey fish such as cisco are present in a lake. Having nutrient-rich cisco in their diets allows adult walleye to grow larger than they would feeding solely on littoral prey fish such as yellow perch (*Percidae flavascens*) or invertebrates (Kaufman et al. 2009). Therefore, if a lake has proportionally more hypolimnion, there might be more space for cisco to evade walleye capture, thus limiting walleye growth potential. We did not include the presence of prey fish in our analysis, but this would be an interesting avenue for future research, as would exploring whether the proportion of hypolimnetic volume in a lake affects the amount of pelagic prey incorporated into walleye diets (i.e., phenomenon known as habitat coupling; Vander Zanden and Vadeboncoeur 2002).

We found that dissolved organic carbon and Secchi depth — both indicators of water clarity — were among the top five most influential factors on walleye production. Walleye production showed a unimodal response to dissolved organic carbon (more production between 6 and 12 mg·L^{-1} dissolved organic carbon) but was greater at low Secchi depths (0–4 m). This result is not surprising because walleye have evolved subretinal tapetum lucidum that allow them to feed, grow, and reproduce at low light levels (Ryder 1977; Lester et al. 2004). Other studies have found that walleye population biomass is greater in dark lakes (Lester et al. 2004; Hansen et al. 2019).

Smallmouth bass production

For smallmouth bass, our results showed that production is most influenced by netting day. We found that smallmouth bass production was greater in lakes sampled later in the field season (i.e., end of June versus mid-September). Smallmouth bass typically nest from April to June, so it is very likely that smallmouth bass are nesting during this time, thus lowering their swimming activity and net encounter rates (Brown et al. 2009). This result emphasizes the importance of life history and habitat preferences when developing monitoring designs and interpreting results for management.

Our results also suggested that production was influenced by Secchi depth and dissolved organic carbon, with higher production in clearer lakes (deeper Secchi depths) and lower production in lakes with more dissolved organic carbon. Smallmouth bass are visual predators that are sensitive to even slight decreases in water clarity and perform better in clearer waters with high visibility (Sweka and Hartman 2003; Carter et al. 2010). This sensitivity could also make them less competitive in the presence of other species that are more tolerant of low visibility, such as largemouth bass (*Micropterus salmoides*; Carter et al. 2010).

Following Secchi depth and dissolved organic carbon, our results showed that angling activity was the fourth most influential factor driving smallmouth bass production. Interestingly, production initially increased with angling activity before falling slightly again in a unimodal relationship. Though counterintuitive, it is likely that we are seeing this effect because angling activity is higher in southern Ontario, where lakes have more primary production to fuel productivity at higher trophic levels. Another interesting possibility is that we are seeing evidence of the hydra effect, a phenomenon that describes higher growth rates with increased mortality (Abrams and Matsuda 2005). Abrams and Quince (2005) explain that such an effect can occur if mortality (e.g., harvest) of a predator population reduces exploitation of its prey, thereby increasing prey production to the point of offsetting predator mortality. This theory has yet to be tested empirically and difficulties arise in understanding the true functional re-

sponse of natural populations; however, this would be an interesting avenue to explore for management purposes.

Biological interactions

We found that across all three fish species, the biological interaction variables (presence of competing species, invasive zebra mussels, and species richness) were the least influential in our analysis. Despite evidence for altered trophic position and foraging behaviour from interspecific competition (e.g., smallmouth bass on lake trout and walleye; Vander Zanden et al. 1999; Sharma et al. 2009a, 2009b) or depression of lake nutrients by invasive zebra mussels (Nienhuis et al. 2014), our results suggested that these factors were less important in driving fish production. This is consistent with past studies that have suggested that biological interactions will appear less important on a regional dataset that includes a wide range of abiotic habitat conditions (Jackson et al. (2001). Therefore, because we did not group lakes with similar abiotic conditions prior to analysis, it is likely that biotic factors are confounded at the regional scale (Alofs and Jackson 2015), despite the robustness of BRTs to variable interactions (Leathwick et al. 2006). Likewise, MacDougall et al. (2018) conducted multivariate analyses on a similar set of inland lakes in Ontario and found that abiotic conditions strongly influenced biological interactions, potentially masking their impacts on fish species richness. They further reported that it was rare for species to interact strongly enough to the point of exclusion. With this, it is possible that we are missing the potential effects of relative abundances or size distributions of predators, competitors, or invasive species on production because we only included the presence or absence of potentially interacting species in our analyses. Unpacking these effects is an avenue for future research.

Caveats

For all three of our study species, the predictive performances of the BRT models were low, explaining 22%, 40%, and 24% of the variation in the lake trout, walleye, and smallmouth bass production data, respectively. Our data spanned one sampling "cycle" (5 years), and each lake was only sampled once during that cycle. Therefore, our study did not account for any temporal variability in production (i.e., good versus bad years). We also did not account for detailed harvest or catch data when considering angling activity, which was measured as angler density for each lake. Therefore, angling activity may not reflect which species were actually targeted on a given lake, and any effect on species-specific production could have been missed by the BRT analyses (Embke et al. 2019). Our study also lacked winter data (e.g., lake water chemistry data are only sampled in the summer, time of ice on or off), so we might be missing over-wintering or other seasonal processes that could affect winter energy storage, spawning, young-of-year (age-0) fish survival, or fish body condition (body mass) during the sampling year (Fernandes and McMeans 2019). Therefore, measures such as degree days may not account for warm winter temperatures that are still below 5 °C but are unfavourable for gonadal development and successful reproduction the following year. Nonetheless, since the summer is when most species are actively feeding and growing, we believe our analyses are still valid and informative.

Taken together, there are many interesting avenues for further study. However, given that BsM has used a standard netting protocol to sample ~700 lakes (536 analysed here) across Ontario's expansive landscape, giving us data for an unprecedented area and number of lakes sampled with identical methods, we feel that our data allowed us to meet the aim of our study: to sufficiently capture the relative influences of various factors on fisheries production and compare them among thermal guilds.

Concluding remarks

Fish are a diverse group of organisms that include species adapted for various temperatures or levels of light, nutrients, and oxygen. Reproductive and foraging ecology also vary widely; there are insectivores, piscivores, spring spawners, fall spawners, and those that do or do not invest in parental care. Each of these physiological, ecological, and life history traits are undeniably linked, partition groups of fishes in space and time, and tell us how any given species might be affected by changes to their environment. While it is often effective to find patterns in community production (Ryder 1965; Randall et al. 1995) or to study fish by size class (Chu et al. 2016), these vast differences among species cannot be ignored in fisheries management. Our study spanning hundreds of lakes and ~1 000 000 km² shows that the relative influence of climate, human, lake morphometry, and water chemistry factors on fish production differ among cold-, cool-, and warm-water species. Whether it is anticipating the demise of a traditional but poorly adapted fishery (e.g., cold-water species fisheries) or optimizing yields for a novel or expanding fishery (e.g., warm-water species fisheries), highlighting species-specific differences can improve how fisheries managers predict fish production under global change.

Data availability statement

Lake morphometric data can be found at the following link: https://www.gisapplication.lrc.gov.on.ca/FishONLine/Index.html?site=FishONLineandviewer=FishONLineandlocale=en-US. All code will be made available upon publication.

Acknowledgements

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