Thermal preferences drive behavioural responses but not biomass responses of predatory fishes to lake morphometry

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ABSTRACT

Top predators' responses to environmental conditions are now widely recognized as a key part of understanding how changing food web architecture influences ecosystem structure and stability, ultimately determining the fate of ecosystems with environmental change. Yet the ways that fundamental ecosystem properties like size and complexity impact top predators' behaviour are not well understood. We examined how lake morphometry impacts the behaviour of three key fish top predators—the cold-adapted lake trout, the cool-adapted walleye, and the warm-adapted smallmouth bass—which can each strongly shape local food web structure. We used a catch-per-unit-effort database of these key fish species in nearly 500 boreal lakes of Ontario, Canada to evaluate the role of thermal preference in driving behavioural and biomass responses to lake morphometry. We found strong evidence that species' thermal preferences influence their responses to lake size, proportion of littoral area, and mean depth, but we found limited evidence that these species respond to lake shape. However, we did not find strong evidence that lake morphology influences these species' biomasses. Our results suggest that some aspects of lake morphometry can alter habitat accessibility and productivity in ways that influence the behaviour and biomass of these top predator species depending their thermal preferences. Our results have strong implications for how the food webs of these lakes expand and contract with lake morphometry and other key abiotic factors. We argue that several key abiotic factors likely drive top predator behaviour in ways that may shape local food web structure and play in important role in determining how ecosystems respond to global environmental change.

KEYWORDS: food webs, freshwater, habitat coupling, top predator, habitat use

INTRODUCTION

We have now entered the Anthropocene, an epoch characterized by rapid and complex changes to Earth's systems caused by human activities (Vitousek et al. 1997). In response to these drastic environmental alterations, organisms across the globe are swiftly responding by altering their behaviour (Tuomainen and Candolin 2011, Bartley et al. 2019). Organisms' responses to environmental change are not only important for individual fitness and populations to persist, but they often influence food web dynamics and dictate the fate of whole ecosystems (Walther 2010). Thus, understanding how ecosystems will respond to global environmental change requires that we understand their constituent organisms' responses to changing conditions, and researchers are now documenting the various ways in which organisms are responding (Parmesan and Yohe 2003).

Many species are responding to global environmental change by altering their degree of habitat coupling (Bartley et al. in press), i.e., the linking of spatially-disparate habitats through movement and foraging (Schindler and Scheuerell 2002). Top predators in particular, which tend to be highly mobile and generalists, seem to respond to environmental conditions in ways that shape their local food webs (Cruz-Font et al. 2019, Hammerschlag et al. 2019). Habitat coupling appears to be a fundamental component of food architecture that, importantly, can stabilize food webs (Rooney et al. 2008, McCann and Rooney 2009). Consumers can rapidly switch away from low density resources and towards other, more abundant resources, creating a stable resource base from the perspective of consumers that produces relatively stable consumer densities. This switching also simultaneously culls high-density prey and relieves low-density prey from top-down pressure (McCann and Rooney 2009, Valdovinos et al. 2010). Habitat coupling can also influence the trophic biomass structure of food webs. In theory, when consumers couple distinct

habitats, they have access to a larger energy pool that can inflate in their biomass (McCann et al. 2005, McCauley et al. 2018). These changes in biomass can in turn affect a predator's ability to supress prey through top-down control, leading to top heavy food webs and impacting stability (McCann et al. 2005, McCauley et al. 2018). This theoretical prediction has some empirical support. For example, increased habitat coupling is associated with increased biomass of the predatory walleye (*Sander vitreus*) (Tunney et al. 2018). Yet, widespread empirical evidence is lacking for whether the shifts in habitat coupling exhibited by predators translate to altered predator biomasses.

Flexible habitat coupling is perhaps best documented in freshwater lakes. In these ecosystems, predatory fish consume prey that reside in macrohabitats with distinct energy sources, namely the nearshore and offshore zones powered by benthic algae and phytoplankton, respectively (Dill 1983, France 1995, Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002). This linking of offshore and nearshore food chains can stabilize aquatic food webs by allowing the preferred prey of predators to rebound when they begin to decline (Post et al. 2000, McCann et al. 2005). The degree to which predatory fish couple offshore and nearshore habitats is potentially shaped by a few key factors. One possibility is that predators respond to changes in resource abundance by shifting towards locations with abundant resources (i.e., the birdfeeder effect, see Eveleigh et al. 2007). This phenomenon has been documented in the freshwater top predator northern pike (*Esox lucius*) (Kennedy et al. 2018). However, the ability of predators to respond to resource abundances may be limited by accessibility, especially temperature (Tunney et al. 2012, 2014, Guzzo et al. 2017a). As ectotherms, the internal body temperatures of fish closely follow that of their ambient environment, forcing fish to behaviourally thermoregulate by occupying species-specific temperature ranges. These

behavioural responses are likely particularly important in temperate lakes due to seasonal cycles in water temperature and undergo thermal stratification (Wetzel 2001).

The role that habitat accessibility and resource availability play in driving behaviour likely depends on a predator species' thermal preferences (Magnuson et al. 1979). During summer, warm surface waters often exceed the temperature preferences of cold-water fish, increasing the metabolic costs associated with occupying nearshore habitats. In response, the cold-adapted top predator lake trout responds by retreating to the offshore to forage and at most accessing nearshore resources in quick forays (Guzzo et al. 2017b, Cruz-Font et al. 2019). Other cold-water fishes exhibit similar responses across natural gradients in lake temperature (Bartley et al. in press, 2018, Tunney et al. 2014), suggesting that thermal accessibility may be limiting for many species. Various morphometric factors appear to influence the accessibility of the nearshore in lakes. During summer, large and reticulate lakes likely have larger nearshore zones, and predatory fish must spend more time and travel greater distances through warm water to reach prey (Dolson et al. 2009). As a consequence, increasing lake size and complexity are associated with reduced consumption less from littoral resource pathways in lake trout (Dolson et al. 2009, Tunney et al. 2012). Importantly, these foraging shifts are associated with behavioural shifts in the form of altered habitat use (Guzzo et al. 2017b, Bartley et al. 2018). However, cool-water species such as the walleye are likely less thermally restricted than cold-water species, and so likely show weak behavioural response to changes in nearshore accessibility (Fig. 1). Furthermore, warmwater species, such as smallmouth bass, may never be thermally restricted from accessing prey in the nearshore and thus may show no behavioural responses to lake morphometry (Fig. 1).

Changes in habitat coupling by top predators likely have important consequences for lake food webs (McCann et al. 2005, Hammerschlag et al. 2019). If habitat coupling does indeed increase the overall resource pool available to predators, inflating predators' biomasses (McCann et al. 2005, McCauley et al. 2018), factors like lake morphometry may impact the ability fish predators may to supress their prey and respond to changes in resource density. There is some empirical evidence that predators' biomass responds to changes in lake size (Tunney et al. 2012, 2018, Eloranta et al. 2015). Thus, the differences in coupling responses to changes in lake morphometry that predicted here ought to produce a large reduction in energy availability for lake trout but little reduction for walleye and no reduction for smallmouth bass. Thus, these three species ought to show contrasting biomass responses to changes in lake size and complexity. Such responses would strongly suggest that lake morphometry shapes whole food webs.

Here, we use an unprecedented catch-per-unit-effort database of fishes in over nearly 500 boreal lakes of Ontario, Canada to evaluate the role of thermal preference in driving behavioural and biomass responses to lake morphometry. We predict that as lake size, complexity and proportion littoral area increase, lake trout will be caught at much deeper depths and have a strong reduction in biomass (Fig. 1). We predict that walleye will show weak behavioural and biomass responses to lake morphometry, and that smallmouth bass will show no behavioural or biomass responses to changes in lake morphometry (Fig. 1). Because these behavioural changes are thought to influence species biomass, we also predict that lake trout will show decreasing biomass with increasing lake size, complexity, and proportion littoral area. We predict that walleye will show weak biomass decreases with these lake morphometric variables, and that smallmouth bass will show no change in biomass. By evaluating the behaviour and biomass of these three key top predator species with changes in habitat accessibility, we provide further

insight into the response of a mobile generalist consumers to key ecosystem characteristics that can shape the ways that ecosystems are altered by global environmental change.

METHODS

Data Source

We used an extensive catch-per-unit-effort (CPUE) database of 721 lakes constructed by the Ontario Ministry of Natural Resources and Forestry (OMNRF) Broad-scale Fisheries Monitoring (BsM) Program (Sandstrom et al. 2013). This survey used overnight sets of a multipaneled mesh gillnets to randomly sample the fish community in each lake (Sandstrom et al. 2013) during one period of time between May and September from 2008 to 2012. This netting protocol uses a combination of North American standard multipaneled gill nets (with mesh sizes varying from 38 to 127 mm, Sandstrom *et al.* 2013) and small mesh gillnets (with mesh sizes from 13 to 38 mm, Sandstrom *et al.* 2013) set in up to eight depth strata: 1-3m, 3-6m, 6-12m, 12-20m, 20-35m, 35-50m, 50-75m, and >75m. For this study, we only included lakes with a maximum depth greater than 10 m to ensure that both nearshore and offshore habitats were present and because of the stratified netting protocol (Sandstrom et al. 2013), which left 556 lakes for our analyses.

Lake Attribute Selection

We selected seven lakes attributes to use as predictor variables in our statistical analysis following a two-step procedure. First, we retrieved 10 lake attributes available for the 556 lakes included in our analysis OMNRF's data to evaluate lake size, lake complexity, and habitat availability, but also variables to control for climatic conditions, and productivity. Lake size was measured by the surface area of the lake and lake complexity by the shoreline development index

(or SDI) computed following Dolson et al. (2009) using lake area and lake shoreline. We used growing degree days (yearly average cumulative number of degrees above 5°C from 1981 to 2010) and latitude as proxies for climatic condition; Secchi depth, total phosphorus and dissolved organic carbon to assess productivity; mean depth (based on the bathymetry of the lake), maximum depth and the proportion of littoral area (proportion of the lake less than 4.6 m) to assess habitat availability. In a second step, we transformed all these variables (see Table 1) and scaled them in order to perform a principal component analysis (PCA). Based on the results (see Fig S1, Table S1 and S2), we narrowed down the control variables to two: growing degree days for climatic conditions and Secchi depth for productivity. Because prey availability may also influence the responses of these predator species, we investigated how the proportion of prey in the offshore changes with our abiotic variables.

Species Selection and Characteristics

We selected one top predator species from each of the three thermal guilds for Canadian freshwater fishes that are well distributed across lakes of Ontario. Lake trout (*Salvelinus namaycush*) is a cold-water top predator of offshore habitats in boreal shield lakes (Hasnain et al. 2013), and much research on behavioural responses to thermal accessibility has focused on this species (Morbey et al. 2006, Dolson et al. 2009, Plumb and Blanchfield 2009, Tunney et al. 2014, Guzzo et al. 2017b, Bartley et al. 2019). Walleye (*Sander vitreus*) is a cool-adapted voracious piscivore and popular sport fish that is present in lakes across the boreal shield (Hasnain et al. 2013). Smallmouth bass (*Micropterus dolomieu*) is a warm-water adapted generalist top predator that is non-native in part of its range in Ontario (Hasnain et al. 2013, Alofs and Jackson 2015). These three species—all of which are popular sport fish for anglers

(Queen's Printer for Ontario 2015)—are among the most common species in Ontario and comprise a large portion of the average catch in the BsM database.

Catch-per-unit-effort Behavioural and Biomass Metrics

For our analysis, we used species-specific catch-per-unit-effort data converted into number of individuals per 100 metres per night (CUE, provided by OMNRF) to make catch data comparable within and across lakes. For our analysis for each species, we examined lakes that had at least 10 individuals caught. We did so to ensure that our behavioural metrics were representative of the species depth distribution in the lake. This leaves 485 lakes with at least one of our three focal species for our analyses. We used BsM catch data for each depth stratum in each lake to examine the mean depth of capture for each species, calculated as

$$SMD = \frac{\sum_{i=1}^{4} d_i \times CUE_i \times p_i}{\sum_{i=1}^{4} CUE_i}$$

where SMD is the mean depth of capture of a fish species or guild, CUE_i is the CUE of that species or guild for depth stratum i, p_i is the proportion of the lake in depth stratum i, and d_i is the middle depth of the depth range for that depth stratum. Based on shifts in the averages of this metric of average habitat use across lakes, we can infer the behavioural response of species to changing temperature. As an estimate of biomass density we calculated the biomass per unit effort (WUE) for each species in each lake, we transformed the mean fork length of each species in each lake into a mean weight using the following equations: For lake trout, weight = $10^{-5.19} *$ (fork length)$^{3.1}$; for walleye, weight = $10^{-4.79} *$ (fork length)$^{2.9}$; for smallmouth bass, weight = $10^{-4.7} *$ (fork length)^{3}. We then multiplied the CUE for each species in each lake by the estimated

mean weight to get a mean weight per unit effort in kg per 100 metres per night or WUE, hereafter referred to as 'biomass index'.

Statistical Analyses

We used multiple regressions to test the influence of physical lake characteristics on the depth of capture and biomass index of predatory fish (lake trout, walleye, and smallmouth bass) as well as the proportion of prey fish captured in the offshore of lakes, which may affect the behaviour of these predator species. For each response variable, model selection was performed using backwards selection based on AIC starting with a starting model that contained the seven predictor variables without interactions (Table 1). The predictor variables were transformed for multiple regression (Zuur et al. 2010).

RESULTS

Depth of capture

For lake trout, the top ranked model accounted for a much of the of the variation in mean depth of capture among lakes (60%) and contained the predictor variables lake surface area, lake mean depth, and growing degree days (Table 2). Scaled coefficients indicated that as each of these variables increased, lake trout were captured at deeper depths, with lake surface area and lake mean depth each having a moderate effect and growing degree days having a relatively weaker effect (Table 2, Fig. 2, 3).

For walleye the top ranked model accounted for 26% of the variation in mean depth of capture among lakes and contained the predictor variables lake surface area, lake mean depth, growing degree days, and proportion of littoral area (Table 2). Scaled coefficients indicated that

like surface area had a weak positive effect on depth of capture, while the proportion of littoral area and mean depth had strong and moderate negative effects on mean depth of capture, respectively (Table 2, Fig. 2, 3). Although growing degree days was included in the top ranked model, this variable did not have an obvious influence on depth of capture (Table 2, Fig. 2).

For smallmouth bass, the best model accounted for 24% of the variation in mean depth of capture among lakes and contained the predictor variables lake mean depth, growing degree days, proportion littoral area, Secchi depth, and shoreline development index (Table 2). Scaled coefficients indicated shoreline development index, growing degree days, and Secchi depth each had a relatively weak positive effect on mean depth of capture, while proportion of littoral area and lake depth had a strong and moderate negative effect on mean depth of capture, respectively (Table 2, Fig. 2, 3).

Biomass

For lake trout, the top ranked model accounted for 17% of the variation in biomass index among lakes and contained the predictor variables lake mean depth, growing degree days, shoreline development index, and proportion littoral area (Table 3). Scaled coefficients indicated that as each of these variables had a negative effect on lake trout biomass index, with lake mean depth and proportion of littoral area each having a moderate effect and growing degree days and shoreline development index having an intermediate and weak effect, respectively (Table 3, Fig. 2, 4).

For walleye the top ranked model accounted for 25% of the variation in biomass index among lakes and contained the predictor variables lake surface area, lake mean depth, and proportion littoral area (Table 3). Scaled coefficients indicated that proportion of littoral area and

lake mean depth had a strong and moderate negative effect on biomass index, while lake surface area had a weak positive effect (Table 3, Fig. 2, 4).

For smallmouth bass, the top ranked model accounted for 19% of the variation in mean depth of capture among lakes and contained the predictor variables lake mean depth and shoreline development index (Table 3). Scaled coefficients indicated that lake mean depth had a moderate negative effect, while shoreline development index had only a weak negative effect (Table 3, Fig. 2, 4).

Prey fish distribution

The top ranked model accounted for 24% of the variation in the proportion of the prey fish captured in the offshore among lakes and contained the predictor variables lake surface area, lake mean depth, maximum depth, growing degree days, shoreline development index, Secchi depth, and proportion littoral area (Table 4). Scaled coefficients indicated that as each of these variables except lake surface area and Secchi depth had a negative effect on the proportion of prey fish located in the offshore. The strongest influences on the proportion of prey fish located in the offshore was proportion of littoral area, which had a negative effect, and lake surface area, which had a positive effect on the offshore prey fish (Table 4).

DISCUSSION

Organisms' responses to environmental conditions are now widely recognized as a key part of understanding how food web architecture influences ecosystem structure and stability (Bartley et al. 2019). In this study, we sought to understand how lake morphometry impacts the behaviour and biomass of three key fish predators that strongly influence food web structure. By

examining three key predator species that differ in their thermal preferences, we can better understand the drivers of species behavioural responses and the consequences of these behavioural shifts for those species and for food web dynamics. Such insights are likely to be key to piecing together the fundamental factors that structure food webs, which form the backdrop for how ecosystems respond to environmental change.

We found strong evidence that species' thermal preferences influence their responses to lake size. Consistent with our predictions, lake trout behaviour is strongly influenced by lake surface area, while walleye and smallmouth bass behaviour show weak or no response to this lake characteristic, respectively. These results therefore support the accessibility hypothesis (Dolson et al. 2009, Tunney et al. 2012), with the cold-adapted lake trout driven to occupy cold, offshore waters when nearshore waters are warm and the species is not spatially constrained in small ecosystems. Our results for lake trout also strongly resonate with previous results, which show that lake trout diet predictably vary across a range of lake size (McCann et al. 2005, Tunney et al. 2012). The relatively weak response of walleye may indicate that their nearshore habitat use may be limited by thermal accessibility only when temperatures in this region get high enough, allowing them to use this region more than lake trout. In contrast, and consistent with their physiology, smallmouth bass appear to have no limitations to nearshore accessibility; however, it remains unclear whether warmwater species experience limited accessibility to the offshore. Offshore resources can be significant for some nearshore-associated predators like northern pike (*Esox lucius*) (Kennedy et al. 2018). Overall, our results are also consistent with a growing body of theory that suggests that increasing ecosystem area may impact the behaviour of predators in ways that and structure food webs in space (Eloranta et al. 2015).

We found that thermal preferences of these predator species influenced their responses to the proportion of littoral habitat in lakes. Lake trout showed no behavioural response to increasing proportion littoral area, but walleye showed a weak response and smallmouth show a strong decrease in depth of capture with increasing proportion littoral area. Because of the strong relationships between proportion littoral area, total phosphorous, and dissolved organic carbon, a larger proportion littoral area likely indicates a more productive lake. Thus, it seems likely that because walleye and smallmouth are less limited by thermal accessibility, these two species can respond to this increased nearshore productivity by moving towards the nearshore. In contrast, the thermal limitations of lake trout limit their ability to take advantage of greater nearshore resource availability (Evans 2007). Understanding the role of productivity and littoral area will be critical moving forward as human impacts alter these factors in boreal lakes through climate change and alteration of nearshore habitats via shoreline development and resource extraction (Keller 2007, Schindler and Lee 2010).

We did not find strong evidence that lake shape influences the behaviour of top predator fishes in boreal lakes of Ontario. We found only some evidence for an influence of lake shape on smallmouth bass depth of capture but no such relationship for depth of capture for either lake trout and walleye. This result is in contrast to previous work that shows a response of lake trout diet to changes in lake shape (Dolson et al. 2009). This discrepancy is potentially due to the vast differences in the ranges of lake area and other factors between our datasets since the lakes studied by (Dolson et al. 2009) are relatively small and geographically constrained to Algonquin Park in Ontario, Canada. It is possible that across large geographic area, other abiotic factors are more important in driving the behaviour of these species. It is also possible that lake shape does not present as much of a limitation to habitat accessibility as previously thought, especially when

controlling for other factors such as littoral area and lake size. The relatively high R^2 for lake trout depth of capture suggests that this species' behaviour is better explained by the abiotic factors we examined here, including lake morphometry. For walleye and smallmouth bass, a significant portion of the overall variance is not explained by the models, suggesting that factors not considered in the present study could more strongly influence these species' behaviour.

Interestingly, we found that mean lake depth was an important factor for all species behaviour. This may in part be because fish species are simple able to occupy deeper waters in deeper lakes. However, greater depth also allows for vertical habitat partitioning (Hamrin 2008). This likely has strong implications for interactions between these species, with shallower lakes potentially forcing stronger resource competition between species of differing thermal guilds (McCann et al. 2005). These interactions may be dependent on other related factors, such as the presence of preferred prey species. For example, the top-down suppression of littoral prey fish by smallmouth bass is thought to drive lake trout to retreat to deeper waters (Vander Zanden et al. 1999). Thus, both vertical and horizontal spatial axes in lakes may play important roles in shaping behaviour and food web structure in these lakes (Guzzo et al. 2016).

Despite the strong relationship between behaviour and lake morphometry, we did not find evidence that the behaviour of these species influences their biomass. Lake trout and smallmouth bass showed no significant change in biomass with lake area, although walleye did show a significant increase in biomass with lake area. Thus, our results do not simply support the theoretical prediction that habitat coupling influences the biomass of predators (McCann et al. 2005, McCauley et al. 2018). There are several possible explanations for why biomass does not respond to changes in species behaviour. The proportion of prey captured in the offshore increases with greater lake area. This shift in prey availability may counteract changes in

nearshore resource accessibility for lake trout; however, this shift in the proportion of prey in the offshore may also be a result of reduced top-down control exhibited by lake trout. Productivity is likely playing an important role in determining these species biomasses. For example, mean lake depth showed a significant relationship with each species biomass, likely because it correlates with productivity. Thus, the relationship between predator behaviour and predator biomass appears to be complex and requires further investigation than we can provide here.

Our examination of the prey fish biomass shows that the proportion of prey fish in the offshore habitat increases with increasing lake size. Importantly, this can be interpreted in multiple ways. It is possible that this increased biomass of prey offshore indicates an increased availability of resources in the offshore in larger lakes (a bottom up response). Lake trout and walleye may be responding to this change in resource density rather than habitat accessibility of the nearshore. However, this would also suggest that smallmouth bass is not responding in this manner, possibly because smallmouth bass are thermally limited in terms of utilizing the cold offshore waters. Alternatively, the increase in relative offshore prey biomass may indicate reduced top down suppression by predators despite their behavioral response to shift towards the offshore. Our analyses here cannot tease apart these possible mechanisms but understanding what is driving the behaviour of these species is critical for understanding what underlies food web structure in boreal lakes.

Our results have strong implications for how the food webs of these lakes expand and contract with lake size (Tunney et al. 2012). Previous work has shown that boreal lake trout habitat use relates to their nearshore energy use (Guzzo et al. 2017a, Bartley et al. 2019). Thus, the behavioural responses that we document here may indicate dietary shifts towards the offshore for lake trout and walleye but not for smallmouth bass. This deviation of predator habitat use

could imply a horizontal expansion of the food web rather than the a contracted and reality uniform foraging behaviour in spatially constrained environments. This flexible food web structure is probably an important aspect of the adaptive capacity of lake ecosystems (McMeans et al. 2016). Our results add to the growing evidence that various abiotic factors can drive predator behaviour in ways that may shape local food web structure.

The strong link between ecosystem size, behaviour and food web structure have strong implications for how these systems are responding to changing environmental conditions. Our work here sets the stage for understanding the context dependency of ecosystems' climate change responses; climate change and other human alterations to ecosystems take place on top of local factors like lake morphometry that shape food web structure. Understanding how these various factors interact is critical to accurately forecast the trajectories of ecosystems across the globe in the face of relentless alterations of human activities. Our work adds to a growing literature that shows how such physical properties of ecosystems as fundamental as their size determine their functioning, from individual behaviour, to food web structure, to ecosystem services.

DECLARATIONS

The authors declare no competing interests.

DATA AVAILABILITY

Data will be deposited in DataDryad upon acceptance.

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Table 1. Summary of lake characteristics. The mean, median, standard deviation (sd), minimum and maximum for each of the abiotic variables used in our analyses as well as the transformation applied to normalize each variable for statistical analysis.

Variable	Mean	Median	sd	Range	Transformation
Surface area (ha)	2555	978	6911	41–90484	log
Maximum depth (m)	35.5	28.0	24.4	10.0–213.5	log
Mean depth (m)	10.2	8.1	6.7	1.4–40.1	log
Shoreline development index (unitless)	5.3	4.3	3.4	1.3–20.9	log
Proportion littoral area (unitless)	0.39	0.37	0.19	0.06–0.99	logit
Growing degree days (˚C)	1630	1626	202	1059–2246	none
Secchi depth (m)	4.1	3.9	2.0	0.1–13.4	log

Table 2. Results of stepwise model selection of multiple regression testing for the influence of physical lake characteristics on the mean depth of capture of lake trout, walleye, and smallmouth bass in study lakes.

Species	**Variable**	**Scaled coefficient**	**se**	**t-value**	**Significance[1]**	**df**	**F-value**	**R^2_{adj}**
Lake trout	Surface area	0.3997	0.04597	7.561	***	3, 186	94.93	0.60
	Growing degree days	0.1625	0.05486	3.469	***			
	Mean depth	0.4534	0.04685	5.359	***			
Walleye	Surface area	0.2891	0.04935	5.859	***	4, 327	30.64	0.26
	Growing degree days	-0.0721	0.04796	-1.503				
	Mean depth	-0.4238	0.1031	-4.109	***			
	Proportion littoral area	-0.7743	0.1019	-7.599	***			
Smallmouth bass	Shoreline development index	0.1474	0.06072	2.427	*	5, 206	14.19	0.24
	Growing degree days	0.2778	0.06528	4.255	***			
	Mean depth	-0.3771	0.1329	-2.839	**			
	Secchi depth	0.1444	0.06743	2.142	*			
	Proportion littoral area	-0.7112	0.1326	-5.365	***			

[1]P-value significance: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table 3. Results of stepwise model selection of multiple regression testing for the influence of physical lake characteristics on the biomass index of lake trout, walleye, and smallmouth bass in study lakes.

Species	**Variable**	**Scaled coefficient**	**se**	**t-value**	**Significance**[1]	**df**	**F-value**	**R^2_{adj}**
Lake trout	Shoreline development index	-0.1249	0.06732	-1.855	.	4, 185	10.34	0.17
	Growing degree days	-0.2819	0.06778	-4.159	***			
	Mean depth	-0.4489	0.1197	-3.751	***			
	Proportion littoral area	-0.4831	0.1191	-4.057	***			
Walleye	Surface area	0.2860	0.04947	5.781	***	3, 328	38.48	0.25
	Mean depth	-0.4351	0.1037	-4.195	***			
	Proportion littoral area	-0.7689	0.1020	-7.541	***			
Smallmouth bass	Shoreline development index	-0.1844	0.06197	-2.975	**	2, 209	26.30	0.19
	Mean depth	-0.4214	0.06197	-6.800	***			

[1]P-value significance: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Table 4. Results of stepwise model selection of multiple regression testing for the influence of physical lake characteristics on the proportion of the total prey fish located in the offshore zone of each lake.

Variable	**Scaled coefficient**	**se**	**t-value**	**Significance[1]**	**df**	**F-value**	**R^2_{adj}**
Surface area	0.4437	0.05520	8.039	***	7, 546	25.21	0.24
Shoreline development index	-0.1688	0.05867	-2.876	**			
Growing degree days	-0.1470	0.03890	-3.778	***			
Mean depth	-0.2863	0.1564	-1.831	.			
Maximum depth	-0.2122	0.1013	-2.094	*			
Secchi depth	0.1771	0.04564	3.881	***			
Proportion littoral area	-0.5845	0.09757	-5.991	***			

[1]P-value significance: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

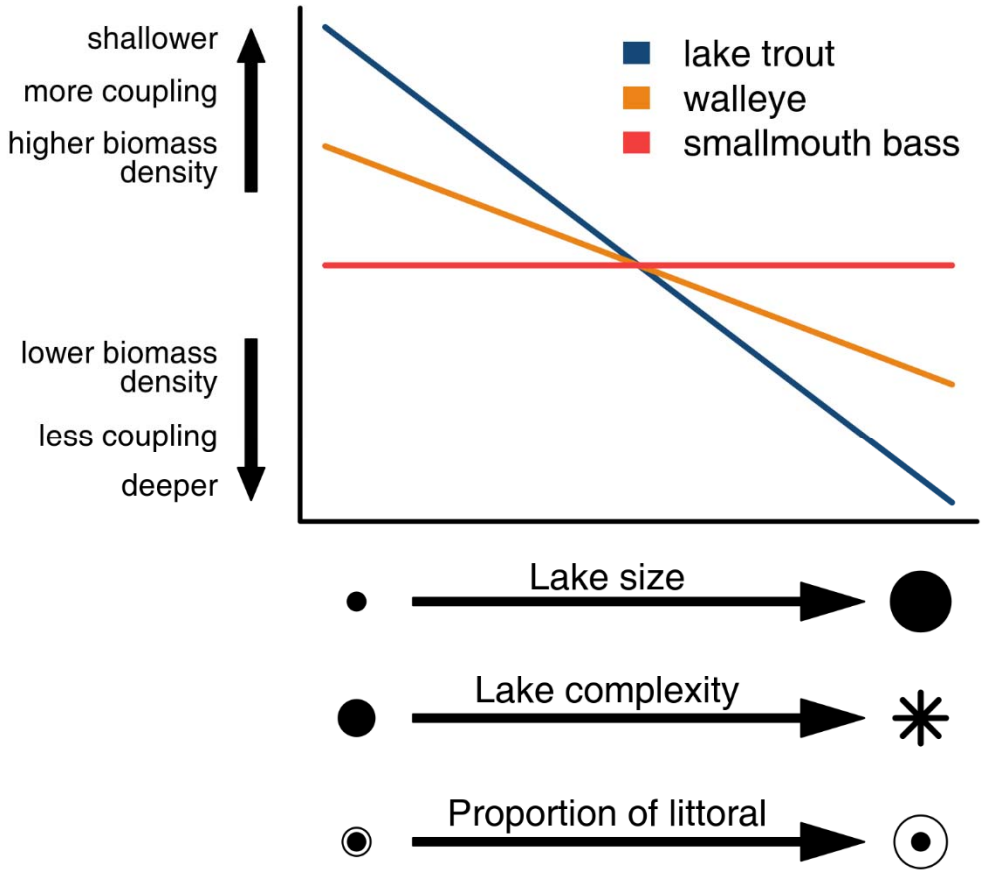

Figure 1. Predictions of the influence of lake surface area and shape (Shoreline development index) on (A-B) habitat use, (C-D) biomass.

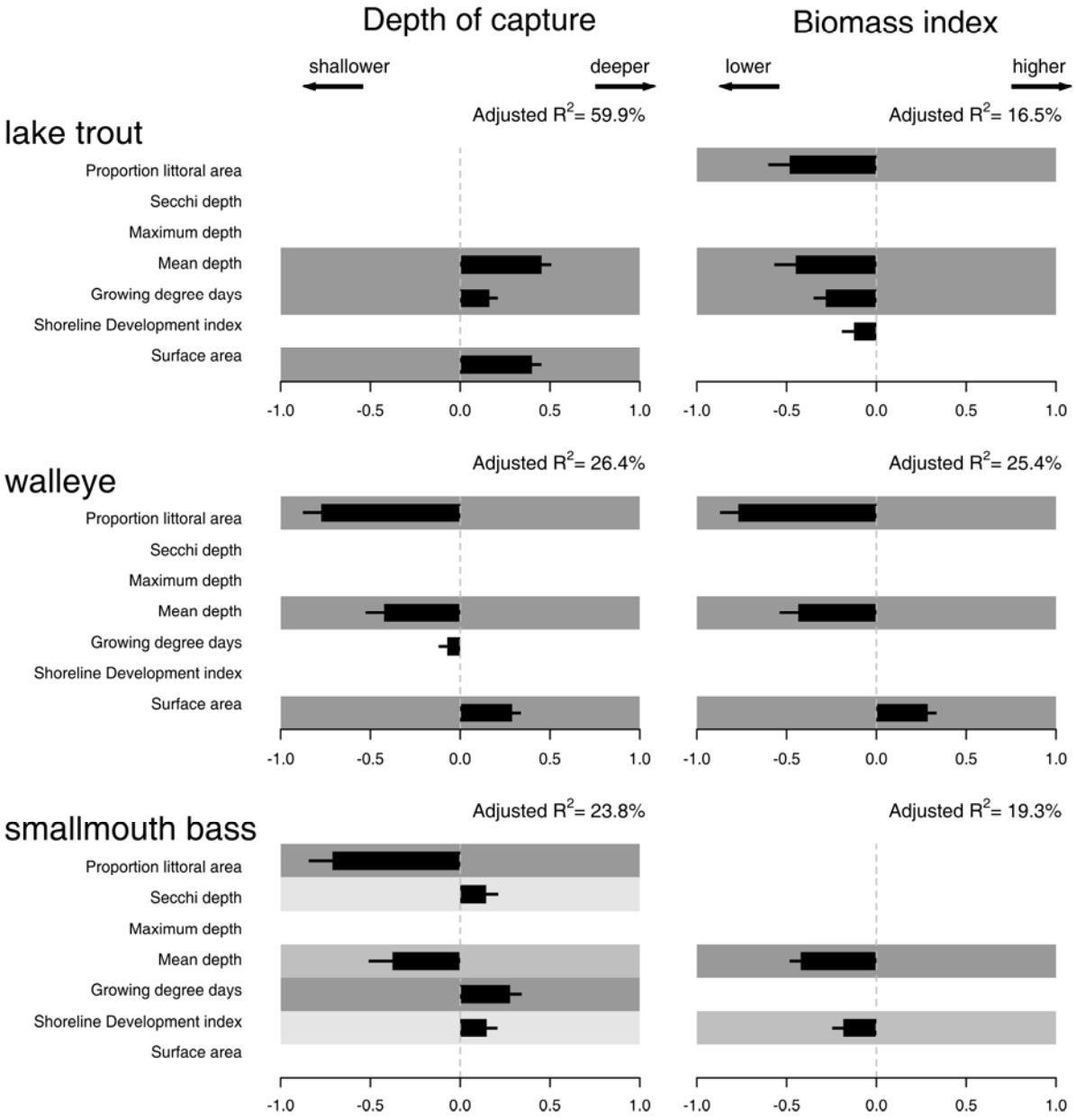

Figure 2. Impact of predictors on depth of capture (left side) and biomass (right side) for the three species. The scaled effect of each variable included in a species and the corresponding standard error are depicted with black bars. A gray background is added to all explanatory variables found statistically significant (the different p-value thresholds 0.05, 0.01 and 0.001 are colored in light, medium and dark gray, respectively).

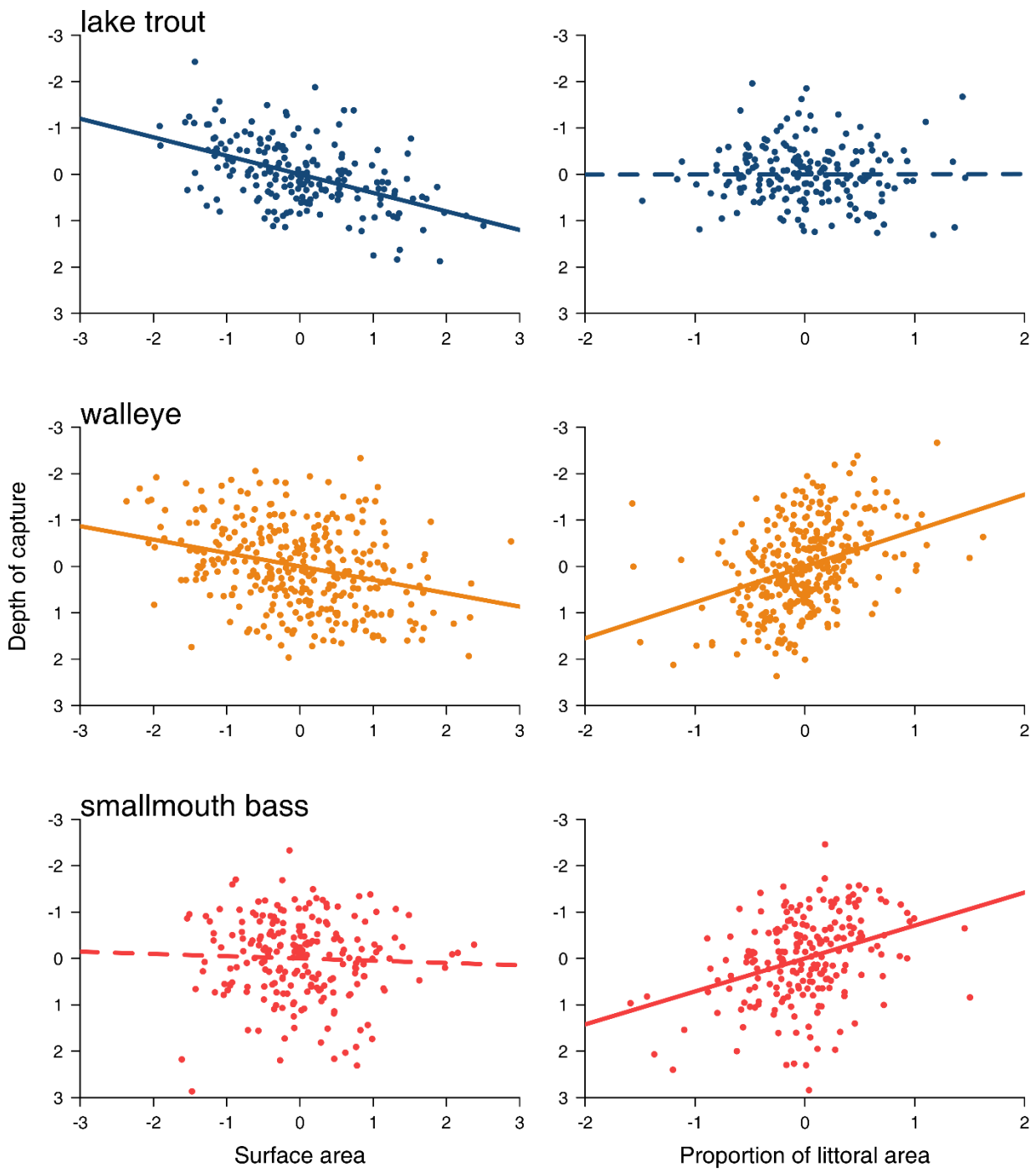

Figure 3. Added variable plots depicting relationships between mean depth of capture of lake trout, walleye, and smallmouth bass with lake surface area and proportion of littoral area in Ontario lakes.

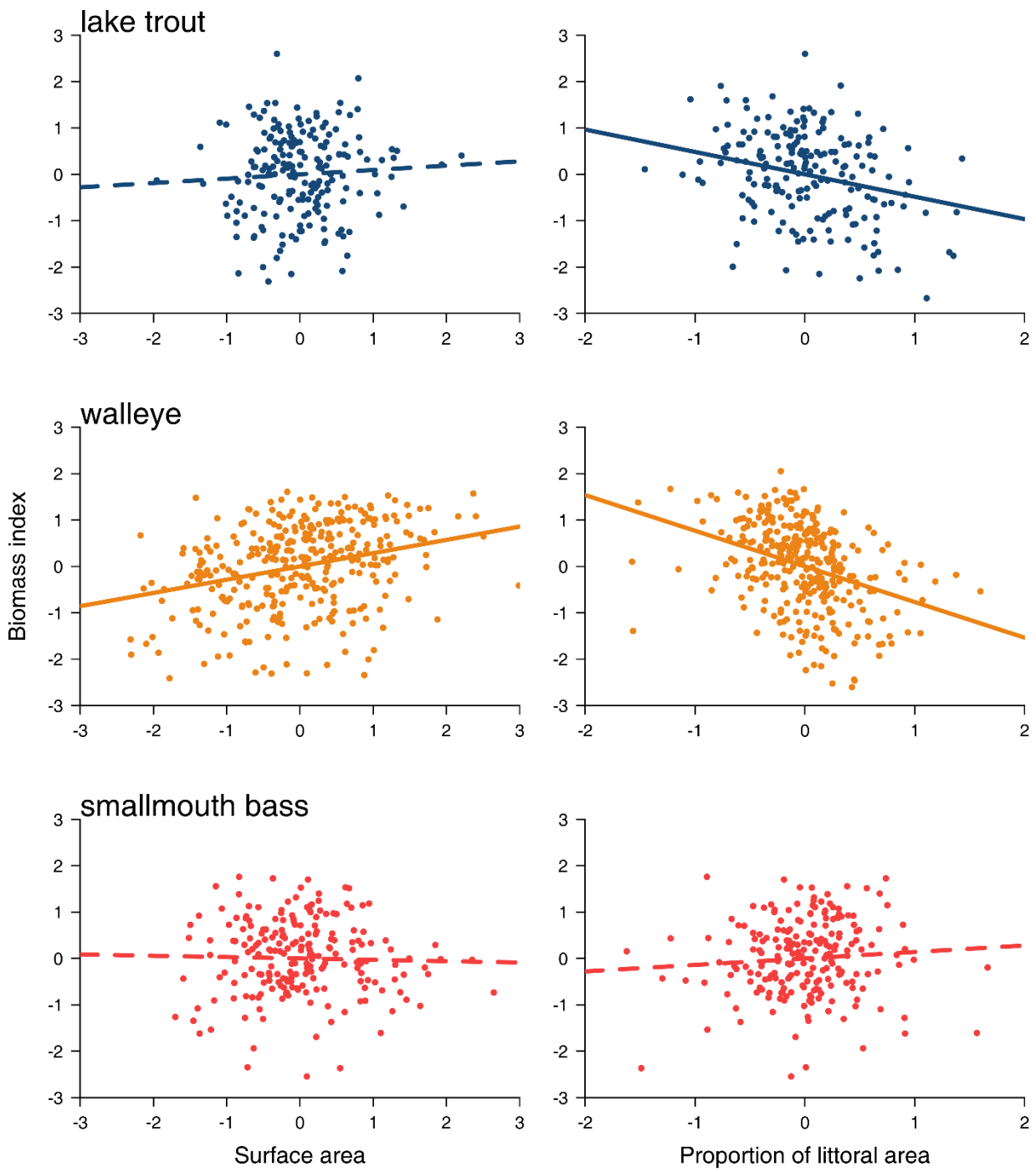

Figure 4. Added variable plots depicting relationships between biomass index of lake trout, walleye, and smallmouth bass with lake surface area and proportion of littoral area in Ontario lakes.