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Growth and Diet of Northern Pike (*Esox lucius*) in Boreal Lakes: Implications for Ecosystem Management

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Abstract: An important top-down predator, the northern pike (Esox lucius), faces harsh environmental conditions in the northern boreal ecoregion. They are often managed for recreational fishing and, more recently, to create environmental offsets; strategies aimed at balancing ecological impacts by enhancing or restoring habitats. Our study examines northern pike populations in two remote boreal lakes in northern Alberta: Steepbank and Wappau. The lakes differ in size, vegetation cover, and trophic status, providing a natural experiment for investigating northern pike growth, condition, diet, and population density. Over three years (2018–2020), northern pike were sampled using gill nets. Population metrics, including growth, condition, and stomach contents, were compared between the lakes. Steepbank, a smaller, oligotrophic lake with low vegetation cover, showed lower prey fish densities compared to the larger, eutrophic Wappau, but it did not differ in northern pike catch per unit effort. Growth rates and body condition varied significantly between the lakes, with the northern pike in Wappau exhibiting faster growth and a better condition in the older age groups, while the younger northern pike in Steepbank had higher relative weights. A diet analysis revealed significant differences in prey consumption: Steepbank northern pike displayed higher rates of conspecific predation and invertebrate consumption, particularly in the younger age classes. These findings highlight how lake characteristics and prey availability shape northern pike population dynamics, offering valuable insights for lake management approaches in northern Alberta.

Keywords: environmental management; habitat enhancement; lake ecosystem; northern boreal; fish ecology

1. Introduction

Freshwater species are in decline globally, with one in three species being listed as threatened [1–5]. These declines are attributed to various anthropogenic and environmental stressors, ranging from eutrophication to loss of genetic diversity and competition with non-native species [2,3,6,7]. Individual stressors can interact with each other creating feedback loops and background processes, like climate change, can enhance stressors further [3,8]. Habitat loss and degradation is commonly regarded as the most pressing issue for many species [9,10]. Conservation and management frameworks have been implemented in many countries and through cross-boundary treaties to counter freshwater biodiversity declines, as well as to manage aquatic



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Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/ licenses/by/4.0/). resources and ecosystem services [11–14]. Frameworks can be aimed at requiring development proponents to mitigate impacts and provide compensatory environmental benefits through offsets [12,15,16]. Other management frameworks are meant to preserve ecosystem services provided by freshwater habitats and species like recreational and sport fishing, using licensing, take limits, habitat restoration and enhancement, and often stocking [17–19].

Northern pike (*Esox lucius*) is one of the most widespread, abundant, and commonly targeted top predators in northern Canada, aside from popular species like lake trout (Salvelinus namaycush) or walleye (Sander vitreus) [20–22]. These prolific benthopelagic ambush predators can be found in lacustrine as well as riverine environments, preferring cool to warm waters $(17-24 \,^{\circ}C)$ with heavy aquatic vegetation [23,24]. Notably, northern pike growth and body condition are mainly dependent on temperature, water clarity, and prey availability [23,25,26]. The reasons behind stunted growth or low body conditions in pike populations are generally related to overpopulation and consequent competition, a lack of adequately sized prey, thus lowering their energy uptake from smaller prey items, and thermal stress in the absence of summer refugia [26]. However, given their hardiness and generalist piscivore feeding behavior, northern pike can be found in a wide range of habitats aside from their preferred ones [21,25]. Northern pike also show remarkable plasticity in prey choice and size, including consuming aquatic invertebrates, even in their adult stage, and conspecific predation as well as adaptation in high turbidity settings [25,27]. Inherent plasticity and adaptability apply to northern pike in Canada's northern boreal ecoregion, which contains an estimated 1.5 million lakes, with many northern boreal lakes being small, oligotrophic, and shallow [28]. Overall low productivity, low species richness, long winters, active fire regimes, limited organic input, and low recruitment rates (5.8 pieces of large woody debris per lake per century, e.g., through treefall or storms [29]), distinguish these lakes and resident fish populations from other more productive ones [29-33].

The northern boreal ecoregion of Canada and its freshwater habitats are exposed to both development stress, mainly through resource extraction, and recreational activities including fishing [1,20,34,35]. Approved anthropogenic impacts like logging or mining in the northern boreal ecoregion are often compensated for by creating new lakes either from the ground up or by repurposing mining pits [36]. These newly created ecosystems rely on expert knowledge to ensure trophic and community stability in the long run [36–38]. This becomes even more important given the persistent shortcomings of creating physical habitats, with high rates of project failures and uncertainty, and a lack of long-term population stability, with most mitigation policies requiring long-term or in-perpetuity functionality and provision of positive effects for the system or population [15,39–43]. Similarly, managing already existing natural lakes to ensure recreational ecosystem services for anglers will benefit from region-specific insights. Most anglers tend to target larger or trophy fish, which holds important implications for size and take limits for fish populations [44,45]. To advance our understanding of northern pike ecology and adaptation in the northern boreal ecoregion, we investigate northern pike populations and their respective prey choices in two northern boreal lakes in northern Alberta, one oligotrophic (Steepbank) and the other eutrophic (Wappau). Specifically, we have the following hypotheses:

- The growth rates (von Bertalanffy growth parameters) of northern pike will differ between Steepbank and Wappau due to differences in environmental conditions (e.g., lake size, depth, aquatic vegetation, and prey availability).
- (2) Northern pike in Wappau will exhibit a higher relative body condition compared to those in Steepbank due to a more diverse and abundant prey base, based on a prey fish catch.
- (3) Prey selection by northern pike will differ between Steepbank and Wappau, with northern pike in Steepbank relying more on conspecific predation due to limited prey diversity and a potentially lower prey fish catch.

Deepening the understanding of how top predators, like northern pike, behave and fare under different environmental conditions within the context of the northern boreal ecoregion will be of immense help to implement management measures and achieve ecosystem stability with offsets comparable to natural reference lakes, as well as the management recreational fisheries [21,37,40,46].

2. Materials and Methods

2.1. Study Lakes

Steepbank (185.4 ha, max depth 16 m) and Wappau (576.6 ha, max depth 6 m) in northern Alberta are northern boreal lakes with northern pike as the top predator (Figure 1). Steepbank is a shallow, oligotrophic lake with low vegetation cover (6.38%; Braun-Blanquet percent: 6.38% based on 24 littoral plots; Simba 0.3–5; [47]) and a summer thermocline of ~8 m. It has a Secchi depth of 2.25 m and is managed with a limit of one pike >70 cm per angler (Table 1). The fish community includes five species: northern pike, *Catostomus commersonii* (white sucker), *Notropis hudsonius* (spottail shiner), *Pungitius pungitius* (ninespine stickleback), and *Culaea inconstans* (brook stickleback).

Table 1. Study lakes in northern Alberta, including base parameters related to lake physiology and habitat characteristics. Lists each lake's size in hectares, maximum depth in meters, mean summer pH with standard deviation, mean summer temperature in degrees Celsius with standard deviation, percentage of littoral zone covered by aquatic vegetation, mean epilimnetic dissolved oxygen (DO) in milligrams per liter with standard deviation, and Secchi depth in meters during summer sampling.

Lake	Size ha	Max Depth m	Mean Summer pH	Mean Summer Temperature °C (1 m Steps)	Littoral % Aquatic Vegetation	Mean DO mg/L	Secchi Depth m
Steepbank Wappau	185.4 576.6	16 6	$\begin{array}{c} 8.23 \pm 0.47 \\ 8.66 \pm 0.03 \end{array}$	$\begin{array}{c} 18.5 \pm 0.68 \\ 18.4 \pm 0.71 \end{array}$	$\begin{array}{c} 6.38 \pm 8.95 \\ 18.04 \pm 16.94 \end{array}$	$\begin{array}{c} 8.16 \pm 0.09 \\ 8.87 \pm 1.57 \end{array}$	2.25 1.125



Figure 1. The study area, including Wappau (yellow) and Steepbank (blue) lakes, is in the northern boreal region of Alberta, Canada. Potential prey species availability for resident northern pike populations. Symbol attribution: Tracey Saxby, Kim Kraeer, Lucy Van Essen-Fishman, Integration and Application Network; Dieter Tracey, Marine Botany; ian.umces.edu/media-library. Geospatial layers are available from AHS-GIS and open.alberta.ca under 'Open Government Licence—Alberta' and are part of QGIS 3.32.2.

Wappau is larger, with more aquatic vegetation cover (18.04%), and is eutrophic. Its Secchi depth is 1.125 m and northern pike management allows for two fish per day without size limits (Table 1). Its fish community includes seven species. In addition to the fish community in Steepbank, there are *Perca flavescens* (yellow perch) and *Percopsis omiscomaycus* (troutperch). Both lakes are remote (Figure 1), with minimal human impact, and are used as models for constructing new lakes for compensatory offsetting in northern Alberta.

Variables such as lake size (ha), maximum depth (m), and mean summer pH are important to consider because they influence habitat availability and water chemistry, both of which can affect predator distribution and abundance [48]. Mean summer temperature (°C, measured at 1 m intervals) can influence predator metabolic rates and prey availability [49,50]. The percentage of littoral aquatic vegetation serves as an indicator of habitat complexity and prey refuge availability, which can affect predator foraging behavior [49,51]. Mean dissolved oxygen (DO) concentration (mg/L) was included because oxygen availability is critical for the survival and activity of aquatic organisms, especially during warmer months [52,53]. Lastly, Secchi depth (m) was used to capture water clarity, which can impact predator–prey interactions by influencing visual hunting efficiency [54]. Collectively, these variables were controlled for given their known relevance to predator ecology, helping to identify potential drivers of differences between the two predator populations.

2.2. Sampling and Study Data

The lakes in this study are routinely sampled by Alberta Environment and Parks (AEP) for walleye (Sander vitreus) and northern pike population monitoring. In August 2018 (13th–24th), 30 northern pike from each lake (n = 60) were netted with multi-mesh gill nets (18 m), set at random locations at depths of ≥ 2 m, and kept overnight (Research License: RL18-1809). Further sampling occurred in August 2019 and 2020 (14th–24th) using 23 m monofilament multi-mesh gill nets. Gill net meshes knot-to-knot for the sampling period were: 25 mm, 38 mm, 51 mm, 63 mm, 76 mm, 102 mm, 127 mm, and 152 mm; net height: 1.83 m. The use of a multi-mesh design follows standard protocols for community-based fish sampling [55,56] as well as license requirements (Research License: RL19/20-1809). Nets were deployed at depths between 2 and 6.7 m, a range that was chosen to target the primary nearshore habitat of northern pike during summer months [21,25,27,51]. Nets were set for 3 h, in compliance with research license agreements, at similar locations to 2018 to facilitate comparability between years [57].) Northern pike samples collected from Steepbank included n = 13 (2019) and n = 14 (2020), while Wappau provided n = 12 (2019) and n = 13 (2020). Sampling stopped once 12-14 voucher specimens were reached to avoid exceeding mortality limits. Specimens from all years were measured (total and fork length in mm) and weighed (g).

Northern pike CPUE was calculated as the number of pike captured per hour of sampling. Prey fish density (CPUA) was calculated as the number of prey fish per unit area sampled using 50 m seine hauls (n = 5 per year and lake), standardized over 100 m² of sampled area. Preliminary results indicated no significant differences in within-lake CPUE for northern pike or prey fish CPUA across the sampling years, allowing us to pool the data for each lake over the three years despite variations in net set times [58]. CPUE and CPUA between lakes were compared through Kruskal–Wallis rank sum tests, with eta-squared as effect size measure (η^2) and upper bound fixed at 1, which quantifies the proportion of total variance in the response variable explained by the predictor variable [59].

2.3. Age and Growth Analysis

Growth was analyzed using the von Bertalanffy Growth Function for northern pike in both lakes, using length-at-age data from 2018, 2019, and 2020, with age determined through the cleithrum [60,61]. Growth parameters, L ∞ (asymptotic length), K (growth rate), and t0 (hypothetical age at zero length), were estimated via non-linear least squares regression [61,62]. Deviations (alpha < 0.05) from expected growth were identified to examine significant differences between the lakes, identifying ages at which growth curves between the two lakes potentially differ (Wilcoxon rank sum test; [63]).

2.4. Condition Analysis

Body condition was assessed using relative weight (Wr), calculated as $Wr = W/W' \times 100$, where W is the observed weight and W' is the species-specific standard weight for a given length. Wr values were compared across age groups (2–4, 5–7, and >8 years) and lakes to determine growth efficiency differences [62,64]. Statistical comparisons (ANOVA; eta² for effect size) were conducted to assess any significant variations in condition between the lakes and age classes.

2.5. Diet and Stomach Contents Analysis

The diet of northern pike was assessed through stomach contents analysis, with samples obtained via dissection, with caught specimen being frozen after capture to preserve stomach and prey integrity. This approach allowed for a comprehensive evaluation of prey composition and feeding behaviors across different age classes and lake environments [65]. For stomach contents analysis, we categorized prey item presence and absence in individual northern pike stomachs into four groups: macroinvertebrates, conspecific northern pike, piscivorous (other prey fish), and empty stomachs. This grouping facilitated the analysis of prey group switches and differences between lakes [65]. The normalized proportion of prey types per age group was calculated, and prey choice differences between lakes were evaluated using Kruskal–Wallis rank sum tests [59]. Diet changes with age (2–4, 5-7, and >8 years) were explored to identify potential differences in prey items across lakes. Conditional probabilities were calculated to assess the likelihood of selecting one prey type given the selection of another (co-selection), stratified by lake and age. For each prey type, the probability P(PreyB | PreyA) was computed as the proportion of individuals selecting both prey A and prey B relative to the total number of individuals selecting prey A within each lake-age subgroup [66]. This approach captures age-related dietary shifts and lake-specific foraging strategies, offering insights into how individual feeding behaviors adapt in response to ecological conditions [27,67].

3. Results

3.1. Northern Pike CPUE and Prey Fish CPUA

Both lakes exhibited a median catch-per-unit-effort (CPUE) of 0.25 pike per net-hour (pike/nh; Figure 2a). The mean CPUE was slightly lower in Steepbank (0.244 pike/nh, SD = 0.237) than in Wappau (0.283 pike/nh, SD = 0.250; Table S1). The prey fish density, measured via seine net hauls, was higher in Wappau (mean = 43.4 fish/100 m², SD = 16.8) than in Steepbank (mean = 31.2 fish/100 m², SD = 6.87; p = 0.04; $\eta^2 = 0.2$; Figure 2b). The species composition of prey fish differed between the lakes, with yellow perch dominating in Wappau (81%, SD = 8%) and spottail shiner in Steepbank (85%, SD = 5%; Table S1).



Figure 2. Mean Catch Per Unit Effort (CPUE) for northern pike caught in gill net sets, standardized to catch per net hour (**a**). Prey fish catch in 50 m seine hauls standardized to fish per 100 m² (**b**). Sampling was conducted over three years (2018–2020) at Wappau and Steepbank lakes, Alberta, Canada. * Indicates significant differences for catch.

3.2. Age and Growth

Northern pike from Steepbank had an average length of 434.8 mm (SD = 144.4 mm), while those from Wappau were larger on average, with a length of 502.5 mm (SD = 206.4 mm). The growth rates were significantly higher in Wappau (55.6 mm/year) compared to Steepbank (39.1 mm/year; $p = 2.43 \times 10^{-13}$; Table S2). The predicted growth deviations occurred in older individuals (≥ 8 years), as illustrated in Figure 3.



Figure 3. Predicted growth deviations for northern pike in Steepbank and Wappau lakes based on average growth rates as estimated by Von Bertalanffy growth curves (age in years/length in mm). Average growth rate comparison (mm/age) is provided on secondary *y*-axis. Age is determined through extracted cleithra.

3.3. Condition

The relative weight (Wr) of northern pike differed significantly between the lakes (p = 0.004; $\eta^2 = 0.17$; Figure 4a) and showed an interaction between the lake and age class (p = 0.01; $\eta^2 = 0.25$; Table S3). In Steepbank, the Wr decreased with age, with mean values of 109.0 (SD = 10.7) for ages 2–4, 101.0 (SD = 8.99) for ages 5–7, and 95.4 (SD = 7.75) for ages 8–11. In Wappau, the Wr values were 96.2 (SD = 11.3) for ages 2–4, 92.0 (SD = 7.28) for ages 5–7, and 109.0 (SD = 11.9) for ages 8–11. Younger pike (ages 2–7) in Steepbank had a higher Wr than those in Wappau (p = 0.04), but for the oldest age class (8–11), the Wr was higher in Wappau (p = 0.04; Figure 4b). This interaction indicates that the condition of the pike changes with age differently in the two lakes (Figure 4).



Figure 4. Relative weight (Wr) values of northern pike across age classes (2–4, 5–7, and 8–11 years) in Steepbank and Wappau lakes, Alberta, Canada. Wr compares individual northern pike condition, using length at capture, to global reference populations (%). * Indicates significant differences for Wr (**a**). Simplified Wr trends for both lakes across age classes (**b**).

3.4. Diet and Stomach Contents

The proportion of empty stomachs and those containing piscivorous prey did not differ significantly between the lakes (Table S4; Figure 5). However, conspecific predation was higher in Steepbank, especially for age classes 2–4 (33.3%) and 8–11 (33.3%), compared to Wappau, where no conspecifics were observed in these age groups. For ages 5–7, conspecific predation was 12.5% in Steepbank and 6.67% in Wappau (p = 0.04; Table S4; Figure 5).

Invertebrate consumption also varied between the lakes (p = 0.049; Table S4). Steepbank pike consumed more invertebrates across all age classes compared to Wappau. In Steepbank, invertebrate consumption declined from 33.3% at ages 2–4 to 18.8% at ages 5–7 and 16.7% at ages 8–11. In Wappau, consumption was lower overall, with 22.2% for ages 2–4, 6.67% for ages 5–7, and no recorded invertebrate consumption for ages 8–11. These results suggest that invertebrates play a diminishing role in pike diets as they age, particularly in Wappau (Figure 5).

In Steepbank lake, prey co-selection patterns evolved across age groups. For ages 2–4 and 5–7, macroinvertebrates were the central prey type, with mutual co-selection observed between macroinvertebrates and piscivorous prey, as well as between macroinvertebrates and conspecific prey (Figure S1). However, there was no strong direct link between

piscivorous prey and conspecific prey in either age group. By ages 8–11, this pattern had shifted. The link between macroinvertebrates and conspecific prey disappeared, while a new direct link formed between piscivorous prey and conspecific prey, (33% and 50% co-selection). Additionally, individuals feeding on macroinvertebrates were highly likely to also feed on piscivorous prey (100%), with a reciprocal link from piscivorous prey to macroinvertebrates (33%). This shift suggests a growing reliance on piscivorous prey in older age groups.

In Wappau, there were no strong associations between prey types in the 2–4 and 8–11 age groups. In age group 5–7, individuals feeding on macroinvertebrates were likely to also feed on piscivorous prey, and those feeding on conspecific prey were likely to also feed on piscivorous prey (100%). However, the reverse was not true (Figure S1). This suggests that, in this age group, piscivorous feeding is more central to prey choice.



Figure 5. Diet composition of northern pike from Steepbank and Wappau lakes in Alberta, Canada, showing normalized proportion of empty stomachs, piscivorous prey, conspecific prey, and macroinvertebrates across different age classes (2–4, 5–7, and 8–11 years). * Indicates overall significant differences in prey type proportions.

4. Discussion

Our study investigated the growth rates, relative condition, and prey selection of northern pike in Steepbank and Wappau lakes to test three key hypotheses. We predicted that the growth rates of northern pike would differ between the lakes due to their contrasting environmental conditions. This was confirmed, as the northern pike in Wappau exhibited significantly higher growth rates for older specimens compared to those in Steepbank, supporting the notion that lake-specific factors such as prey availability influence growth. We also hypothesized that the northern pike in Wappau would exhibit a higher relative condition due to having a more diverse prey base. This hypothesis was partially supported, as there were significant differences in relative condition (Wr) between the lakes, but this effect varied by age class. Northern pike in Steepbank had a higher relative condition in the younger age groups, while Wappau northern pike had a higher condition in the oldest age group. Finally, we expected that prey selection would differ between the lakes, with the northern pike in Steepbank relying more on conspecific predation due to limited prey diversity. This hypothesis was supported by the findings, as conspecific predation was significantly more common in Steepbank, particularly in the youngest and oldest age classes.

4.1. Growth Rates, Condition, and Prey Choice

The observed differences in growth rates between the northern pike populations in Steepbank and Wappau reflect both environmental and ecological influences. Both lakes exhibited similar median and mean CPUEs per net hour for northern pike, suggesting a comparable northern pike abundance. However, the population differences likely stem from other factors, particularly habitat characteristics and prey availability.

The northern pike in Wappau exhibited significantly higher growth rates compared to those in Steepbank. This difference is linked to Wappau's habitat complexity, higher prey fish density (measured as prey fish CPUA), macrophyte cover, and overall lake size [23,27,67]. Wappau's shallower, vegetated habitat likely enhances lake productivity, creating abundant prey resources for northern pike [68,69]. This complex habitat supports both prey fish and ambush hunting opportunities for pike, with dense macrophytes providing cover and a rearing habitat [25,69]. In contrast, Steepbank's deeper, less complex habitat may limit prey availability and consequently, the growth potential of its northern pike [32,69,70].

Interestingly, the younger northern pike (ages 2–7) in Steepbank exhibited a higher relative condition (Wr) compared to those in Wappau. This suggests that younger pike benefit from opportunistic feeding on invertebrates [66,71]. Research indicates that young pike in environments with limited prey fish availability rely on invertebrates for sustenance, which is a pattern that was observed in Steepbank. The consistent co-selection between macroinvertebrates and piscivorous prey or conspecifics in the 2–4 and 5–7 age groups suggests that macroinvertebrates serve as an important alternative food source at younger ages. [67,71]. However, this dietary shift, while supporting the growth of younger pike, highlights a compensatory feeding strategy. The diet analysis reveals that older northern pike in Steepbank also still rely to some degree on invertebrates due to low prey fish availability. However, in older individuals (ages 8–11), the disappearance of the macroinvertebrate-conspecific relationship and the emergence of stronger links between piscivory and conspecific predation suggests that as pike grow larger, they become more efficient at predation on other pike and fish [25,58,71]. In contrast, the northern pike in Wappau shift towards prey fish as they age, emphasizing how prey abundance influences feeding behavior and diet composition. The lack of strong co-selection patterns, with the few patterns present centered around piscivory, further support the high abundance of prey fish, where individuals, regardless of age, have less need to feed on less preferred prey [71].

Older pike (>8 years) in Wappau presented with a better relative condition than those in Steepbank, likely benefiting from the higher prey fish density in Wappau [25,72,73]. Adult northern pike thrive in habitats rich in high-energy prey, and the abundance of prey fish like yellow perch provides the necessary resources for maintaining their condition and size [72,73]. Consequently, Wappau provides a more suitable environment for larger, older pike.

Despite similar CPUEs for northern pike in both lakes, the shallower, more vegetated Wappau offers greater habitat accessibility compared to the deeper, less complex Steepbank [74]. This difference in habitat complexity impacts the northern pike, especially smaller individuals, who may be confined to less favorable habitat patches in Steepbank, thus limiting their access to prey and increasing competition [75]. Larger northern pike in Steepbank may face competition and conspecific predation, which could influence their growth and distribution [76]. The stomach contents analysis reveals significantly higher rates of conspecific predation in Steepbank, with older pike preying on smaller individuals, which is likely driven by prey scarcity and habitat limitations [76].

In contrast, Wappau showed minimal conspecific predation, with no predation observed in the oldest age group. The higher conspecific predation in Steepbank reflects a compensatory feeding behavior in response to prey scarcity, with a shift towards conspecifics when alternative prey is scarce. This aligns with previous studies observing such behavior in predator populations under similar conditions [25,27]. Interestingly, white sucker, although abundant in Steepbank, do not appear to be a major prey item for pike, likely due to their larger size and rapid growth [77]. The ability of the younger pike in Steepbank to maintain a higher condition through prey switching (such as the increased consumption of invertebrates) highlights the adaptability of northern pike to changing environmental conditions [67]. However, this strategy may not be sustainable in the long term, as indicated by the stunted growth and lower condition of the older pike in Steepbank. This suggests that while younger individuals may adapt their diet, the long-term health of northern pike populations may be compromised if habitat and prey conditions remain suboptimal [26,67].

4.2. Management Implications

Our ecological findings also have practical management implications for northern pike populations, with an emphasis on enhancing trophy fisheries, improving habitat conditions, and designing new lakes for compensation efforts in the northern boreal region.

For trophy fisheries, ensuring the long-term health and growth of northern pike requires careful consideration of both habitat enhancement and fishing regulations [23,24]. The differences observed between the Steepbank and Wappau populations suggest that populations in stunted environments, such as Steepbank, would not benefit from stocking efforts alone. In such cases, stocking does not address the root cause of density-dependent bottlenecks or juvenile mortalities in the population, such as conspecific predation or a lack of prey fish. Instead, stocking may exacerbate the problem by adding more individuals to a population that is already resource-limited [78,79]. To improve northern pike populations in stunted lakes, angling regulations should focus on targeting stunted size classes. Implementing a size slot limit (where only pike within certain size ranges can be harvested) will allow smaller individuals to grow and mature, while protecting the large, fecund adults that contribute to population stability. This approach balances conservation goals with angler interests [80,81].

In areas with limited shelter for younger pike, creating refuges or adding vegetation and coarse woody structures can provide essential cover for juvenile fish [23,24]. These enhancements, in turn, support the prey fish populations that northern pike rely on [32]. While targeted interventions like habitat enhancement or stocking could improve conditions, it is important to consider whether such management aligns with the natural ecological balance [40,82]. In cases where stunted populations represent a natural state of the ecosystem, extensive management efforts might not be justified and could disrupt existing ecological processes [40,41,82].

When designing new lakes as part of compensation efforts or offsetting, it is critical to consider the unique ecological features of the northern boreal region [36,37]. Boreal lakes have a slow wood regime, meaning that they naturally accumulate little deadwood over time [29,32]. For newly designed or restored lakes, adding coarse woody habitats can accelerate the development of functional ecosystems by providing shelter and food for both prey fish and northern pike [32,83]. Similarly, riparian planting can provide an additional

habitat and contribute to the system's overall ecological health [40,69,84,85]. In lake design, factors such as the depth and surface area also play a crucial role in determining habitat connectivity, as lakes with smaller surface area to depth ratios, as seen in Steepbank, may have limited opportunities for ecological exchanges between habitat patches, while larger lakes can offer more extensive, interconnected environments for both predator and prey species [70,76,86].

The choice of prey fish should also be a key consideration in lake design. For example, while prey fish abundance is often thought to be sufficient for supporting predator populations, the species composition matters [87,88]. In Steepbank, for instance, white sucker were abundant but not heavily targeted by northern pike due to their large size and rapid growth [58,87,89]. This highlights the need to carefully select prey fish species that are appropriately sized for northern pike, such as yellow perch, which are more suitable for younger and adult pike [71,90].

Another important factor is food web interactions and connectivity. Introducing a single top predator, such as northern pike, will regulate the food web differently compared to systems where pike coexist with other top predators like walleye or bass [72,73]. This should be carefully considered when designing new systems, as the absence of competitive interactions could lead to different prey dynamics [73]. If new lakes are connected to nearby streams or other lakes within the watershed, this could alter the balance of prey and predator species, introducing both diversity, nutrients, and competition. These shifts must be carefully planned to avoid unforeseen consequences, such as the introduction of additional predators or changes in prey availability, especially in systems with naturally low species diversity [91,92].

Finally, climate stressors, such as the active fire regimes and long winters in the northern boreal ecoregion, should be factored into design plans. These environmental pressures and the associated death of both predator and prey species can exacerbate the stress on northern pike populations, particularly in newly established systems [33,93–95]. It is important to design lakes that can withstand these pressures while providing stable conditions for predator and prey populations [94,95]. Additionally, the potential overabundance of parasites and the chance for disease outbreaks in new systems, as well as algal blooms, must be monitored closely [96,97].

Monitoring should include regular evaluations of both community composition and habitat availability, as well as, and more importantly, habitat use, which has been overestimated for certain species in the past [36,98,99]. Tracking these factors over time can reveal changes in the ecosystem and fish behavior that might otherwise go unnoticed, allowing for timely interventions if needed [100–102]. Incorporating metrics that evaluate community health, such as species diversity, trophic relationships, and ecosystem resilience, will provide a more complete picture of overall ecosystem health [73,90,102].

5. Conclusions

Our study highlights the significant impact of prey availability and habitat complexity on the growth and condition of northern pike in northern boreal lakes, represented by Steepbank and Wappau lakes. Higher prey densities and more complex habitats, as observed in Wappau, support better growth and conditions compared to less complex and less productive environments like Steepbank. Younger northern pike can adapt to a lower prey availability by consuming invertebrates, but this may result in stunting for older individuals, if prey levels remain insufficient, and a higher degree of conspecific predation. For management, considering harvest slots in lakes with naturally lower prey availabilities might balance population dynamics, while more extensive interventions should be carefully weighed against natural stunting tendencies. Insights from this study also highlight that, when creating new lakes for compensatory mitigation, prioritizing prey fish availability and habitat complexity is essential for supporting productive ecosystems, especially if the goal is to enhance overall fish biomass rather than replicating regional lake conditions.

This study's focus on only two lakes and a specific timeframe limits its ability to capture seasonal or long-term variations in northern pike populations [71,103]. Future studies should include a wider range of lakes and longer monitoring periods to enhance the generalizability of these findings [72,104]. Aside from the overall spatial and temporal scope, the absence of telemetry data restricts our understanding of northern pike movements and habitat use. Incorporating telemetry could provide insights into how northern pike navigate their environments and how their movements correlate with prey availability and habitat features as done in other studies [100,105,106]. Future studies should also account for other environmental factors such as nutrient concentration, like nitrogen or phosphorus, which would provide a more comprehensive view of northern pike ecology in the region [107,108]. By addressing these limitations and exploring additional research avenues, future studies can build on our findings to develop more effective management strategies and improve our understanding of northern pike ecology for the northern boreal ecoregion.

Supplementary Materials: The following supporting information can be downloaded at: https: //www.mdpi.com/article/10.3390/hydrobiology4010001/s1, Table S1: Summary statistics for CPUE and CPUA; Table S2: Von Bertalanffy growth curve results; Table S3: ANOVA results for relative weight; Table S4: Kruskal–Wallis test results for stomach contents. Figure S1: Conditional probabilities for co-selection of prey.

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