Effects of colonizing predators on yellow perch (*Perca flavescens*) populations in lakes recovering from acidification and metal stress

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Abstract: We examined the effects of predator species on yellow perch (*Perca flavescens*) from lakes in the Sudbury mining region (Ontario, Canada), where fish communities are just beginning to recover from the effects of decades of acidification and metal stress. The predation regimes investigated included six lakes with no predators, four lakes recently invaded (≤3 years) by predators, and eight lakes with well-established (≥15 years) predator populations. Netting survey results indicated that yellow perch biomass was 69% lower in lakes with predators. In lakes recently invaded by predators, perch displayed earlier ontogenetic diet shifts from zooplankton to benthos and much poorer growth during their first growing season. Energy investment (lipid content per egg) in eggs by mature females was also less in the lakes recently invaded by predators. Growth potential in adult perch (age 1), estimated by nucleoside diphosphokinase, was highest in lakes with established predators. Body condition, controlling for size of perch, was also greatest in established predator lakes. Perch body shape in lakes with predators showed a shift from a typical streamlined, pelagic body form towards a deeper-bodied benthic body form, a change that may increase foraging efficiency for benthos or represent an antipredator strategy.

Résumé : Nous examinons l'effet des espèces prédatrices sur la perchaude (*Perca flavescens*) dans des lacs de la région minière de Sudbury (Ontario, Canada) où les communautés de poissons commencent tout juste à se remettre après des décennies d'acidification et de stress dû aux métaux. Les régimes de prédation étudiés comprennent six lacs sans prédateur, quatre lacs envahis récemment (≤3 ans) par les prédateurs et 15 lacs avec des populations de prédateurs bien établies (≥15 ans). Les résultats d'un échantillonnage au filet indiquent que la biomasse des perchaudes est de 69 % inférieure dans les lacs avec prédateurs. Dans les lacs récemment envahis par les prédateurs, les perchaudes devancent leur passage ontologique d'une diète de zooplancton à une de benthos et leur croissance durant leur première saison de développement est de beaucoup inférieure. L'investissement d'énergie dans les oeufs (contenu lipidique de l'oeuf) par les femelles matures est aussi inférieur dans les lacs récemment envahis par les prédateurs. Le potentiel de croissance chez les perchaudes adultes (âge 1), estimé par la nucléoside diphosphokinase, est maximale dans les lacs avec des prédateurs établis. La condition corporelle des perchaudes, après correction pour la taille, est aussi maximale dans les lacs avec des prédateurs établis. La forme du corps des perchaudes dans les lacs avec prédateurs change d'un aspect fuselé typique d'un corps pélagique à une forme benthique à hauteur du corps plus marquée, un changement qui peut augmenter l'efficacité de la recherche de nourriture benthique ou alors représenter une stratégie anti-prédateur.

[Traduit par la Rédaction]

Introduction

Ecologists have long recognized that predators are among the most important factors structuring aquatic communities (Reznick et al. 1990). Much of the early literature focused on the direct lethal effect of predators, but the mere presence of a predator is now widely known to exert profound indirect effects on entire prey communities (Lima 1998). Changes in the behavior of the prey to avoid detection, encounter, and capture by the predator are common indirect effects that of-

ten involve major changes in habitat use (Lima and Dill 1990). Such changes in habitat use can be quite costly to some prey species if they are forced to confine themselves to refuge areas where they initially, or eventually (because of their numbers), lack abundant or high quality food (Werner and Gilliam 1984). These indirect density-dependent effects of predation can also influence the phenotypic expression of prey communities leading to changes in survival, growth, reproductive investment, physiology, and morphology (Werner et al. 1983; Werner 1984; Fraser and Gilliam 1992). The morphology changes (i.e., changes in body form), like the habitat changes, may help reduce predation pressure by reducing encounters with predators or by allowing prey to escape after an encounter. Such morphological changes can be stimulated by visual or olfactory cues from predators (Brönmark and Miner 1992; Holopainen et al. 1997), and like many aspects of the predation effects, the morphological changes among individuals can occur very rapidly.

Yellow perch (*Perca flavescens*) and its close relative the Eurasian perch (*Perca fluviatilis*) are widely distributed in

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1414

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

the northern hemisphere and represent prey species that co-exist with many different predators. However, few studies have attempted to assess the effects of predators on a multitude of life history characteristics of perch. Controlled pond experiments have shown that small perch, vulnerable to predation, moved from open-water habitats to littoral refuges to avoid predators (Werner et al. 1983). Also, vulnerable size classes (<120 mm total length) of yellow perch showed decreased growth rates when a predator (walleye, *Sander vitreus*) was first introduced; however, growth rates increased after the predator became well established (Olson et al. 2001).

Behavioral changes related to predation pressure can influence the swimming ability in prey. Swimming performance is closely related to morphological structure and body shape but is also dependent on muscle tissue capacities for aerobic and anaerobic activities (Webb 1976; Domenici 2001; Blake 2004). Anaerobic enzyme activities, or burst swimming activity, have been commonly estimated by the activity rates of the glycolytic enzyme lactate dehydrogenase (LDH) (Sherwood et al. 2002). The enzyme activity rate of a mitochondrial enzyme, citrate synthase (CS), has also been used to assess aerobic or sustained swimming activity, but this enzyme has not been widely used in wild populations (Rajotte and Couture 2002). In addition to swimming activity, enzymatic activity rates have also been used to estimate growth potential in fishes by nucleoside diphosphate kinase (NDPK), an indicator of protein synthesis (Couture et al. 1998; Rajotte and Couture 2002). One would therefore expect low NDPK levels to occur in slow-growing stunted yellow perch populations (Olson et al. 2001).

Phenotypic divergences in terms of shape changes have been well documented in perch and consist of two rather distinct morphologies: an open-water form (including limnetic or pelagic forms) and a shallow-water form (including benthic and littoral forms) (Schluter 1996; Proulx and Magnan 2002; Svanbäck and Eklöv 2002). The shallow-water form typically has a deep body, a downwards-bending snout, and long pectoral fins. This form appears to be adapted for feeding on macroinvertebrates and other littoral zone prey. Open-water forms have an upward-pointing snout and a more slender body shape. This body conformation may decrease the amount of drag produced when swimming and is thus more energetically suitable for feeding on planktonic prey items (Svanbäck and Eklöv 2003). Such trophic polymorphisms are particularly common in fish and bird species that use their mouths to capture and hold their prey (Wimberger 1994).

This study examines the effects of predator invasion on yellow perch populations in lakes from the Sudbury area recovering from acidification. Acid and metal deposition from the mining industry that began in the 1880s caused extensive biological damage to area lakes, including the loss of many acid-sensitive predator populations (Matuszek et al. 1992). The removal of the top predator left many lakes with very simple fish communities, often consisting largely of abundant populations of yellow perch (Gunn et al. 1990). Large reductions (~90%) in sulphur and metal emissions from local smelters in recent decades have allowed chemical recovery in Sudbury lakes to occur (Gunn and Keller 1990), permitting the reestablishment of indigenous predators (such as walleye and northern pike (*Esox lucius*)). At the same time,

the expansion of smallmouth bass (*Micropterus dolomieu*) into the Sudbury area has occurred. Smallmouth bass is a warm-water invasive species at the northern edge of its distribution in the Sudbury lakes and now appears to be responding to climate-induced changes by increased overwinter survival of young (Dunlop and Shuter 2006).

Our objective was to make use of this unique opportunity to study the early stages of predator colonization in these industrially stressed lakes to assess the effects of invading predators on yellow perch populations. In lakes with predators present, we hypothesized that perch would exhibit (*i*) a decrease in the abundance, (*ii*) increased growth and investment in reproduction, (*iii*) early ontogenetic diet shifts, (*iv*) decreased swimming activity (by enzyme analysis), and (*v*) a change in body shape to reduce vulnerability by gape-limited predators.

Materials and methods

Study lakes

Yellow perch populations from 18 lakes within the City of Greater Sudbury, Ontario, were selected for this study (Table 1; Fig. 1). The lakes were relatively small (surface area 20–1079 ha; median 77 ha) and were all underlain by Precambrian Shield bedrock. However, for Shield lakes they did vary quite widely in limnological characteristics such as maximum depth (6.0–50.3 m), water clarity (Secchi 2.4–14.0 m), base cation (Ca 1.4–16.6 mg·L^{-1}) and nutrient (total P 2.7–24.3 µg·L^{-1}; DOC 1.9–8.8 mg·L^{-1}) concentrations (Table 1), and fish community composition (Table 2). With the exception of Lovering Lake (36 km from smelter), all of the lakes were within 30 km of Sudbury, in the area of high metal particulate deposition, and as a result, most lakes had metal concentrations of Cu and Ni well above the provincial water quality objectives (PWQO) (5 µg·L^{-1} Cu; 25 µg·L^{-1} Ni; Table 1). Many of the lakes were very well studied in that the history of chemical recovery (i.e., pH ↑, metals ↓) and the changes in the fish communities since 1990 were known (Keller et al. 1992; Gunn and Keller 1995; J.M. Gunn, unpublished data). Introduction of predators such as smallmouth bass and walleye occurred as a result of hatchery stocking by government agencies or by unrecorded introductions by citizen groups or by natural movements between lakes during high-water periods. Based on the results of netting surveys (discussed later), the lakes were classified into three different predator regimes: 1, lakes with no predators (Camp, Clearwater, Crowley, Linton, Lohi, and Wavy lakes); 2, lakes with recently (≤3 years) introduced predators (Daisy, Hannah, Middle, and St. Charles lakes); and 3, lakes with well-established (≥15 years) predator populations (Lovering, Massey, McFarlane, Nelson, Nepahwin, Ramsey, Vermilion, and Whitson lakes).

There were no significant differences in maximum or mean depth or Secchi depth transparency among the lake groupings (Table 1). However, the lakes with established predators had significantly larger surface area, a fact that may also explain the higher fish species richness in these lakes (Table 2). In terms of chemical conditions, the predator groupings correspond well with the stage of chemical recovery or the overall productivity of the lakes. For example, lakes that lacked predators had lower pH, P, Ca, and DOC than the lakes with established predator populations (Table 1). The

Table 1. Selected physical and chemical characteristics for the 18 study lakes from the Sudbury area grouped by predator regime.

Predator regime	Lake	Latitude (N)	Longitude (W)	Surface area (ha)	Maximum depth (m)	Mean depth (m)	Secchi depth (m)	pH 1990	pH 2004	P ($\mu g \cdot L^{-1}$)	Ni ($\mu g \cdot L^{-1}$)	Cu ($\mu g \cdot L^{-1}$)	Ca ($mg \cdot L^{-1}$)	DOC ($mg \cdot L^{-1}$)
No predators	Camp[†]	46°22′58″	81°00′10″	20	15.0	8.7	4.0	6.30*	6.69	4.0	50.6	7.4	2.4	2.6
	Clearwater	46°22′13″	81°03′01″	77	20.4	8.2	5.7	4.88	6.27	4.2	60.4	10.1	4.0	2.6
	Crowley	46°23′00″	80°59′00″	42	16.0	6.4	5.2	5.88	6.12	7.8	52.6	10.2	2.0	2.2
	Linton	46°22′00″	80°59′00″	27	16.0	6.4	5.8	5.41	5.97	6.6	55.7	10.4	1.8	2.5
	Lohi	46°23′00″	81°02′00″	41	18.5	6.2	6.3	4.92	6.28	7.1	56.3	11.0	4.0	2.8
	Wavy	46°18′00″	81°06′00″	306	34.0	15.0	3.5	4.74	5.11	3.7	34.7	5.6	1.4	2.2
	Group mean	—	—	85.5a	20.0a	8.5a	5.1a		6.07a	5.6a	51.7ab	9.1a	2.6a	2.5a
Recent predators	Daisy	46°27′00″	80°54′00″	36	14.0	5.2	14.0	4.82	6.52	6.7	62.2	8.0	2.4	1.9
	Hannah	46°27′00″	81°02′00″	27	8.5	4.0	3.3	7.06	7.32	7.6	94.7	22.1	10.8	3.8
	Middle	46°26′00″	81°02′00″	28	15.0	6.2	5.4	6.57	7.09	6.7	95.5	24.0	8.8	3.4
	St. Charles	46°26′00″	81°01′00″	41	6.0	3.0	3.5	7.11	7.12	11.6	100.0	25.7	8.9	4.1
	Group mean	—	—	33.0a	10.9a	4.6a	6.6a		7.01b	8.2a	88.1b	19.9a	7.7ab	3.3ab
Established predators	Lovering[†]	46°13′55″	80°45′12″	90	20.0	7.3	2.5	—	7.65	13.0	15.0	4.0	3.8	8.8
	Massey[†]	46°40′19″	80°51′10″	77	4.0	11.1	2.7	—	6.47	18.0	16.3	7.3	2.8	5.4
	McFarlane	46°25′01″	80°57′23″	141	20.1	5.8	2.4	7.10	7.21	21.0	53.7	8.7	15.8	4.3
	Nelson	46°43′36″	81°05′40″	316	50.3	9.3	8.2	6.43	6.64	2.7	4.6	2.1	2.2	3.0
	Nepahwin	46°27′00″	80°58′00″	128	22.0	8.6	8.2	7.71	7.58	17.0	49.2	10.5	16.6	4.3
	Ramsey	46°28′57″	80°57′01″	874	21.3	2.2	3.8	7.48	7.32	14.6	62.5	12.8	14.1	3.1
	Vermilion[†]	46°31′22″	81°23′28″	1079	13.1	4.7	3.7	—	7.31	24.3	12.0	3.2	10.1	5.2
	Whitson	46°35′00″	80°58′00″	437	16.0	7.3	3.6	5.97	6.92	14.0	92.2	19.7	8.4	2.8
	Group mean	—	—	392.8b	20.8a	7.0a	4.4a		7.14b	15.6b	38.2a	8.5a	9.2b	4.6b

Note: The chemical data was provided by OMOE from midlake epilimnetic samples collected in 2004. Available pH values from 1990 also indicated. Group means within columns followed a common lowercase letter are not significantly different (analysis of variance (ANOVA); least significant difference (LSD)). DOC, dissolved organic carbon.
*Mean of four monthly samples from summer 1992 (Wright 1995).
[†]Samples taken during summer of 2006 and analyzed at Test-Mark Laboratories in Sudbury.

1416

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

Fig. 1. Map showing the location of each study lake (except Lovering Lake, an established predator lake, which is south of the display area). The smokestack icons indicate the locations of the two active metal smelters.
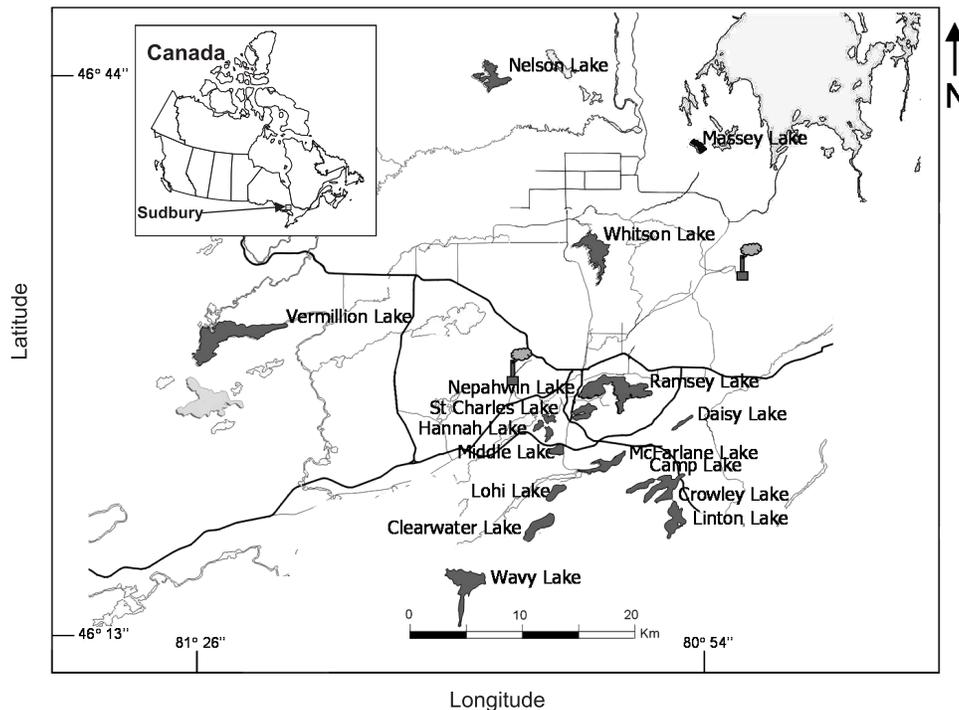
recently invaded lakes were intermediate in the variables related to acidification and overall productivity, but they did have elevated metal (Cu, Ni) concentrations compared with the other two groups. Metals may therefore have some confounding effects on the biota in the lakes where the predators first arrive (will be discussed later).

Sampling

Standard netting method

Fish community assessments of all study lakes were conducted in the summers of 2004 and 2005 using the Nordic multimesh gillnetting method (Appelberg 2000) (Table 2). This quantitative, depth-stratified method uses a geometric series of multimesh gill nets (5–55 mm) with a sampling intensity scaled for lake area and maximum depth. The nets were oriented randomly with respect to the shoreline contour between 1800 and 2000 and then were picked up the next morning between 0600 and 0800. The lifted nets were stored in plastic bins and transported to the Ontario Ministry of Natural Resources (OMNR) necropsy laboratory and processed within 8 h of lifting. Fish were enumerated, and each individual was measured for fork and total length (±1 mm) and body mass (±0.01 g). Data were used to estimate relative abundance, spatial distributions, and biomass (g·net^{-1}) for each fish species. In addition, samples of perch from the catch of each lake (target of 20 fish for every 10 mm size class) were frozen for later stomach content analysis.

Additional fall sampling

Yellow perch were collected at the end of the growing season in October 2004 from each of the study lakes to obtain samples for muscle tissue, body shape, and life history analysis, with the exception of Camp, Crowley, Linton, and Nepahwin lakes, which were only sampled for body shape and life history analysis in 2005 (Table 3). Benthic gillnets (9.5 and 12.5 mm knot-to-knot) were set in depths between 2 and 5 m for approximately 24 h. These mesh sizes were chosen to target a similar perch size range (90 to 130 mm in total length) in each lake. Captured fish were measured for total length (±1 mm) and body mass (±0.01 g).

A subsample of perch was selected for analysis of body shape by choosing the first 30 individuals between 90 and 130 mm in total length with no external physical damage (e.g., broken opercle bone). Afterwards, sex and maturity were determined by visual inspection of gonads, first in fish sampled for body shape analysis and then in additional perch (to a maximum of 20 males and 20 females) of similar size (90 to 130 mm total length) used for metabolic enzyme analysis. Muscle plugs were removed from the males ($n = 20$) and females ($n = 20$) and stored in liquid nitrogen <4 h after the perch were removed from the lake. Greater details describing the methods used for body shape and metabolic enzyme analysis will be presented later. Finally, a subsample ($n = 100$) from each lake was processed for life history analysis ensuring that an equal number of each size class (using 10 mm size classes) was collected across the available range. All mature gonads were weighed (±0.01 g wet mass), and mature ovaries were preserved in 95% ethanol for later fecundity estimates. Saggital otoliths were removed and age was interpreted by a single observer (S. Mann, Ontario Ministry of Natural Resources, Dryden, Ontario) by cracking and burning and counting winter bands (Christensen 1964).

Additional spring sampling

Mature female perch were collected just before spawn in April 2005 from a subset of the study lakes (Table 3) to as-

Table 2. Fish community characteristics for the 18 study lakes based on summer Nordic netting assessment.

Predator regime	Lake	Species richness*	Predator species†					Predator biomass ($g \cdot net^{-1}$)‡	Perch biomass ($g \cdot net^{-1}$)‡	Cyprinid biomass ($g \cdot net^{-1}$)‡	Total biomass ($g \cdot net^{-1}$)‡,§	Total no. of nets	Nordic netting assessment (month/year)
			LT	NP	SMB	SP	W						
No predators	Camp	2						0.0	759.1	0.0	760.1	16	07/2005
	Clearwater	3						0.0	1248.7	4.4	1257.9	24	08/2004
	Crowley	1						0.0	2121.2	0.0	2121.2	16	07/2005
	Linton	2						0.0	2111.4	0.0	2112.2	14	07/2005
	Lohi	3						0.0	1746.0	10.5	1757.7	16	09/2004
	Wavy	1						0.0	998.2	0.0	998.2	47	08/2004
Recent predators	Daisy	7		2			1	205.0	978.9	1.7	1343.9	16	07/2004
	Hannah	6		2	1			247.3	768.8	0.0	1940.9	16	09/2004
	Middle	7		1	1		1	286.4	382.5	0.0	675.6	16	09/2004
	St. Charles	5		7			7	840.4	648.6	0.0	1723.0	8	08/2004
Established predators	Lovering	10		1	15		30	545.8	36.5	0.0	1729.6	32	07/2004
	Massey	5		31			31	1356.4	1210.1	13.6	3543.0	16	07/2004
	McFarlane	13		12	75		25	956.8	156.9	36.0	3831.2	32	08/2004
	Nelson	11		¶	62			917.8	302.1	1.2	1547.3	48	08/2004
	Nepahwin	11		2	73	16	178	944.1	170.3	0.0	2702.0	32	07/2004
	Ramsey	8		7	49		251	886.0	80.7	0.0	1849.0	47	07/2004
	Vermilion	14	67	22	12		251	1724.5	385.2	19.8	4721.0	32	07/2004
	Whitson	7		17	1		135	1268.2	516.0	0.0	2468.2	40	07/2004

*Total number of fish species collected during the Nordic Lake survey.

†Total number of individuals collected during the Nordic survey. Predator species are represented by the following acronyms: lake trout (LT), northern pike (NP), smallmouth bass (SMB), splake (SP), and walleye (W).

‡Mean biomass calculated from the individual weights of fish captured per net during the Nordic survey.

§Total biomass included other fish species not included in predator, perch, and cyprinid biomass estimates.

¶Present in the lake but not captured during the 2004 assessment.

1418

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

Table 3. Sampling times for the 18 study lakes.

Predator regime	Lake	Yellow perch diet analysis (month/year)	Fall sampling* Life history	Metabolic enzyme	Body shape	Spring sampling Lipid
No predators	Camp	07/2005	×		×	
	Clearwater	08/2004	×	×		×
	Crowley	07/2005	×		×	
	Linton	07/2005	×		×	
	Lohi	09/2004	×	×	×	×
	Wavy	08/2004	×	×		×
Introduced predators	Daisy	07/2004	×	×	×	
	Hannah	09/2004	×	×	×	×
	Middle	09/2004	×	×	×	×
	St. Charles	08/2004	×	×	×	×
Established predators	Lovering	07/2004	×	×		
	Massey	07/2004	×	×		
	McFarlane	08/2004	×	×		×
	Nelson	08/2004	×	×	×	
	Nepahwin	07/2004	×		×	×
	Ramsey	07/2004	×	×	×	
	Vermilion	07/2004	×	×		
	Whitson	07/2004	×	×	×	

*Fall samples for detailed body shape, metabolic enzyme activity rates, and life history analyses were completed in October of the same year as the Nordic assessment, except for Nepahwin Lake, which was sampled in October 2005.

sess lipid content of eggs. The same netting procedure and sampling protocol as used during the fall period were used. Mature females were measured for total length (±1 mm) and body mass (±0.01 g). Sex and maturity were assigned by visual inspection of gonads. Ovaries were removed, weighed (±0.01 g), and frozen (–20 °C) for later lipid extraction.

Diet analysis

Perch collected during the summer Nordic lake surveys (target of 20 fish for every 10 mm size class) were frozen for later diet analysis (Table 3). Once thawed, each fish was measured for total length (±1 mm) and body mass (±0.01 g), and sex was determined. Stomachs were opened and food items were transferred to a clean Petri dish and diluted with water to determine the presence or absence of zooplankton, benthos, and fish in the diet.

Reproductive tissue analysis

Mature ovaries from the spring samples were used for lipid analysis (Table 3). Ovaries were freeze-dried for 7 days, and three subsamples of 30 freeze-dried eggs were weighed (±0.1 mg) to determine mean egg size (mg dry mass·egg^{-1}). The ovary was then ground to a powder with a mortar and pestle. Lipid extraction methods were modified from Folch et al. (1957) and Herbes and Allen (1983). Weighed subsamples (~ 0.20 g) of ground tissue were extracted twice with chloroform–methanol (2:1 by volume) solvent, and the supernatant was washed with 0.88% KCl (aqueous). The solvent layer (containing lipid) was transferred to preweighed aluminum pans. Pans were dried in a fume hood until all solvent was evaporated and then reweighed to determine mass of lipid extracted. Lipid content per egg (mg·egg^{-1}) was then

estimated as ovary lipid concentration (g extracted lipid·(g ovary subsample)$^{-1}$) multiplied by mean egg size (mg dry mass).

Enzyme analysis

Fish from lakes sampled in the fall of 2004 (Table 3) were used for muscle enzyme analysis. Samples were restricted to a single season and year to avoid potential interannual variation (Leonard and McCormick 1999). To control for variation in enzyme activity rates associated with fish size and sex (Pelletier et al. 1995), all sampled fish were between 90 and 130 mm in total length and equal sample sizes of males and females (20 each) were used. White muscle samples (~0.50 g) were removed from the left caudal region of each specimen (Leonard 1999) and immediately frozen in liquid nitrogen and stored at –80 °C prior to enzyme assays. Enzyme (LDH, CS, and NDPK) activity rates were measured in duplicate (triplicate if greater than 5% difference between replicates) for 5 min using a temperature-controlled spectrophotometer (Varian Cary 100; Varian Inc., Palo Alto, California) at 18 °C. Detailed methods are outlined in Rajotte and Couture (2002).

Shape analysis

Yellow perch sampled in the fall from four lakes within each predator regime were selected for shape analysis (Table 3). In each lake, the first 30 perch of the targeted size range (90 to 130 mm total length) removed from the nets were put aside for photography before further dissection. Each perch was placed on a mat with 1 cm^2 grids with the anterior tip of the maxilla and fork of the tail aligned as a straight line on the grid (Fig. 2). The caudal fin was gently

pressed against the grid to ensure visibility of the fork of the tail. The surface of the perch was lightly blotted with a towel to minimize glare before the photograph was taken. Digital images (Nikon COOLPIX880, 3.34 megapixels) were taken of the left lateral side of each fish. Total length (±1 mm) and body mass (±0.01 g) were measured, and sex was recorded for each individual after the image was taken. All fish preparations, photography, and specimen selection were conducted by the same person (K.A. Lippert) following a standard protocol.

Individual digital photos were appended using tpsUtil (Rohlf 2004) and imported into tpsDig (Rohlf 2005a). Sixteen homologous landmarks (Fig. 2) were chosen as common fixed morphological features of perch (Svanbäck and Eklöv 2003) and other fish species (Corti and Crosetti 1996; Hard et al. 2000; Loy et al. 2000). Landmarks were digitized for all specimens by the principal author (K.A. Lippert) and imported into tpsRelw (Rohlf 2005b) to conduct geometric morphometric analysis. Landmarks were used to create a configuration matrix where a series of translations were computed to remove differences in location, size, and rotation for each individual. Eigenvalue analysis on the configuration matrix was performed to calculate 26 partial warps and two uniform scores. To visualize the deformations in shape between groups of individuals, thin-plate splines were generated using tpsRegr (Rohlf 2003).

Statistical analysis

Physical and chemical lake properties were compared among the predator regimes using analysis of variance (ANOVA) followed by a comparison of means using Fisher's least significant difference (LSD).

Yellow perch biomass (g·net^{-1}) was compared among predator treatment groups using ANOVA. The presence or absence of prey categories (zooplankton, benthos, fish) in perch stomachs was used to generate logistic regressions for each predator regime. The presence or absence of any particular prey type was not dependent on another prey type being present or absent. Logistic regressions of the form

(1) $y = e^{a+bx}/(1 + e^{a+bx})$

were fitted for each of the three prey categories, where y is the probability of finding the prey type in the perch stomach (0 or 1), x is perch length, and a and b are fitted parameters (Tolonen et al. 1999). Models were fitted to data from individual lakes and then to pooled data from all lakes within predator regimes and used to estimate ontogenetic diet shifts (i.e., size-at-50% probability) for each food category by predator group.

Log-transformed total length (mm) was significantly correlated with log-transformed body mass (g), gonad weight (g), fecundity (number of eggs·individual^{-1}), egg mass (mg·egg^{-1}), and egg lipid content (mg·egg^{-1}) for each lake. Estimated values for each of the listed life history variables were adjusted to a common covariate total length across all lakes. Estimated life history parameters for each lake were used to test for differences among predator groupings using ANOVA. Using the fall sample, average total lengths (mm) of young-of-year (YOY) and 1- and 2-year-old individuals (calculated separately for males and females in each lake) were compared by ANOVA among the predator regimes.

Fig. 2. Landmark locations used for yellow perch morphological analysis in 12 of the study lakes. Positions of landmarks are as follows: (1) tip of the dentary; (2) operculum–isthmus overlap; (3) insertion of pelvic fin; (4) tip of pelvic fin; (5) insertion of anal fin; (6) tip of anal fin; (7) posterior–ventral edge of caudal peduncle; (8) posterior end of hypural bones; (9) posterior–dorsal edge of caudal peduncle; (10) end of soft-ray dorsal fin; (11) insertion of soft-ray dorsal fin; (12) insertion of spiny-ray dorsal fin; (13) tip of maxilla; (14) centre of eye; (15) tip of operclum spine; and (16) fork of caudal fin.
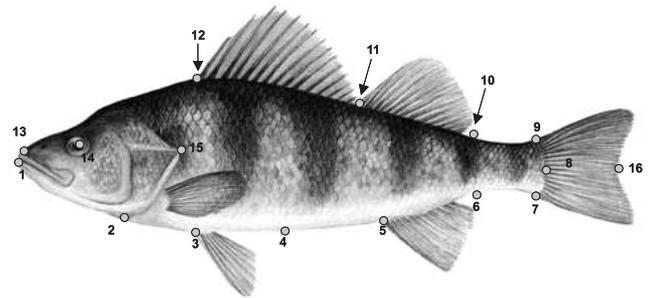
Power analysis was preformed on life history parameters where no differences among lake groups were detected.

Mean metabolic enzyme capacities (e.g., LDH, CS, and NDPK) were calculated for each lake and were used in an ANOVA to test for differences in swimming activity among the predator regimes. All enzyme activity rates were log-transformed to normalize residuals.

The morphological index (MI) is the function produced when partial warp and uniform scores were analyzed using discriminant function analysis (DFA). This methodology for calculating MI has been used to discriminate individuals belonging to different predator regimes (Proulx and Magnan 2002).

Principal component analysis was used to calculate significant explanatory factor scores for each lake using all physical and chemical variables (lake environmental characteristics) independently. The environmental factor scores, biomass estimates (yellow perch, predators, and fish community), and biological variables were compared using correlation analysis.

All statistical analyses were completed using STATISTICA software (StatSoft Inc., Tulsa, Oklahoma) and considered to be significant if $p < 0.05$.
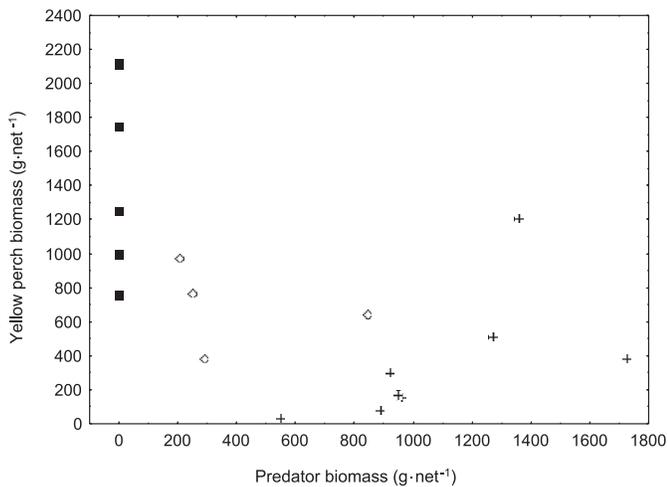
Results

Fish biomass

Yellow perch biomass was significantly lower (69%) in lakes with predators than in lakes with no predators (ANOVA, $F_{[2,15]} = 11.8$, $p < 0.001$). However, perch biomass did not differ significantly between groups of lakes with recently invaded versus established predators (Fig. 3). In the absence of predators, yellow perch biomass averaged 1497.4 g·net^{-1} (±580.4 standard deviation (SD), $n = 6$), whereas in lakes with recently introduced and established predators, the perch biomass was 694.7 g·net^{-1} (±978.9 SD, $n = 4$) and 357.2 g·net^{-1} (±380.0 SD, $n = 8$), respectively (Table 2).

Lakes with established predator populations had significantly higher total biomass than the other two predator groupings (ANOVA, $F_{[2,15]} = 5.07$, $p = 0.021$). However, to-

1420

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

Fig. 3. Relationship between yellow perch biomass (g fish·net^{-1}) and predator biomass (g fish·net^{-1}) for 18 lakes sampled in Sudbury, Ontario: ■, lakes with no predators; ◇, lakes with recently invaded predators; +, lakes with established predators.

Table 4. Predicted total lengths (mm) of yellow perch at 50% probability of finding a prey category (zooplankton, benthos, fish) in stomach contents.

Predator regime	Lake	Yellow perch length (mm)		
		Zooplankton	Benthos	Fish
No predators	Camp	132	130	183
	Crowley	163	167	209
	Linton	134	—	231
	Lohi	90	—	179
	Wavy	114	—	176
	Clearwater	139	123	198
Introduced predators	Daisy	132	95	202
	Hannah	101	78	208
	Middle	76	22	186
	St. Charles	78	—	160
Established predators	Nelson	95	—	136
	Nepahwin	138	105	—
	Ramsey	118	101	—
	Whitson	107	98	152

Note: Only those lakes with significant logistic regressions are included. Predicted lengths were derived from fitted logistic regressions for each study lake.

tal fish biomass correlated positively with predator biomass (linear regression, $R = 0.79$, $p < 0.001$; total community biomass = 1267.89 + 1.55(predator biomass)). When adjusted for predator biomass, total fish biomass did not differ across the predator regimes (analysis of covariance, ANCOVA, $F_{[2,15]} = 1.42$, $p = 0.274$).

The total biomass of forage fish for each lake was estimated from surveys by summing the biomass of yellow perch and cyprinid species in the Nordic nets. Irrespective of lake grouping, yellow perch was found to dominate (>80%) the available forage fish biomass in all study lakes. The proportion of yellow perch biomass (as a function of the total forage fish biomass) did not differ significantly across the predator regimes (ANOVA, $F_{[2,15]} = 1.03$, $p = 0.381$).

Ontogenetic diet shift

The perch from lakes with predators displayed a diet shift from zooplankton to benthos at a much smaller size (83 mm) compared with perch from lakes with no predators (140 mm) (ANOVA, $F_{[1,7]} = 7.48$, $p = 0.029$) (Table 4). We defined the point of ontogenetic diet shift as the perch length corresponding to the inflection point in the fitted logistic regressions (i.e., prey prevalence = 50%) (Table 4; Fig. 4). Ontogenetic diet shifts onto fish occurred at 200 and 217 mm in total length in lakes with no predators and recently invaded predators, respectively (Fig. 4). However in lakes with established predator populations, the predicted size (i.e., 268 mm) at which perch shifted their diet to fish was larger than the maximum size of perch sampled in this group of lakes (Fig. 4c). Therefore, perch from lakes with established predators did not completely make the last ontogenetic shift to fish.

Reproductive investment

Male perch had higher reproductive investment in the absence of interspecific predators (Table 5). The estimated testes mass (0.95 g) for a 110 mm perch in lakes with no predators was significantly higher (ANOVA, $F_{[2,15]} = 5.43$, $p = 0.017$)

than in lakes with recently introduced predators (~0.70 g) and lakes with established predators (~0.77 g).

Reproductive investment of females also varied with respect to predator status; however, the direction was opposite to that of the males. Females had higher reproductive investment in lakes with established predators compared with the other two lake groupings. Reproductive investment, defined as the weight of ethanol-preserved fall ovaries adjusted to a standard length of fish, was highest in lakes with established predators (ANOVA, $F_{[2,15]} = 12.06$, $p < 0.001$; Table 5). In lakes with established predators, the mean estimated preserved fall ovary mass for a 125 mm long perch was 0.64 g. Yellow perch from lakes with no predators and recently introduced predators had adjusted mean ovary masses of 0.43 and 0.50 g, respectively (not statistically different from each other).

Female perch were also found to make a trade-off between ovary size and the lipid content per egg (Table 5). The spring lipid content of eggs from perch in lakes with recently invaded predators was significantly lower than in perch from lakes with no predators (ANOVA, $F_{[2,5]} = 7.0$, $p = 0.036$). There was, however, no statistical difference in egg lipid content among lakes with established predators and either of the other two predator regimes, likely because of low statistical power ($1 - \beta = 0.069$, where β is the probability of a type II error) with such a small number of lakes (266 lakes are required for $\beta = 0.80$). Perch egg lipid content in lakes with no predators, recently invaded predators, and established predators was 0.040, 0.027, and 0.034 mg·egg^{-1}, respectively.

Perch length-at-age

Both male and female YOY perch in lakes with recently introduced predators were significantly smaller (13%) at the end of their first growing season than YOY perch in lakes with no predators (ANOVA, $F_{[2,25]} = 5.02$, $p = 0.015$; Ta-

Fig. 4. Total length of perch at the point where 50% of the sampled fish contained (*a*) zooplankton, (*b*) benthos, and (*c*) fish in their stomachs in lakes with no predators (solid line), lakes with recently introduced predators (broken line), and lakes with established predators (dotted line). All the fish were collected during the summer Nordic lake survey. The number of stomachs in the logistic regressions containing the diet item is indicated in parenthesis.
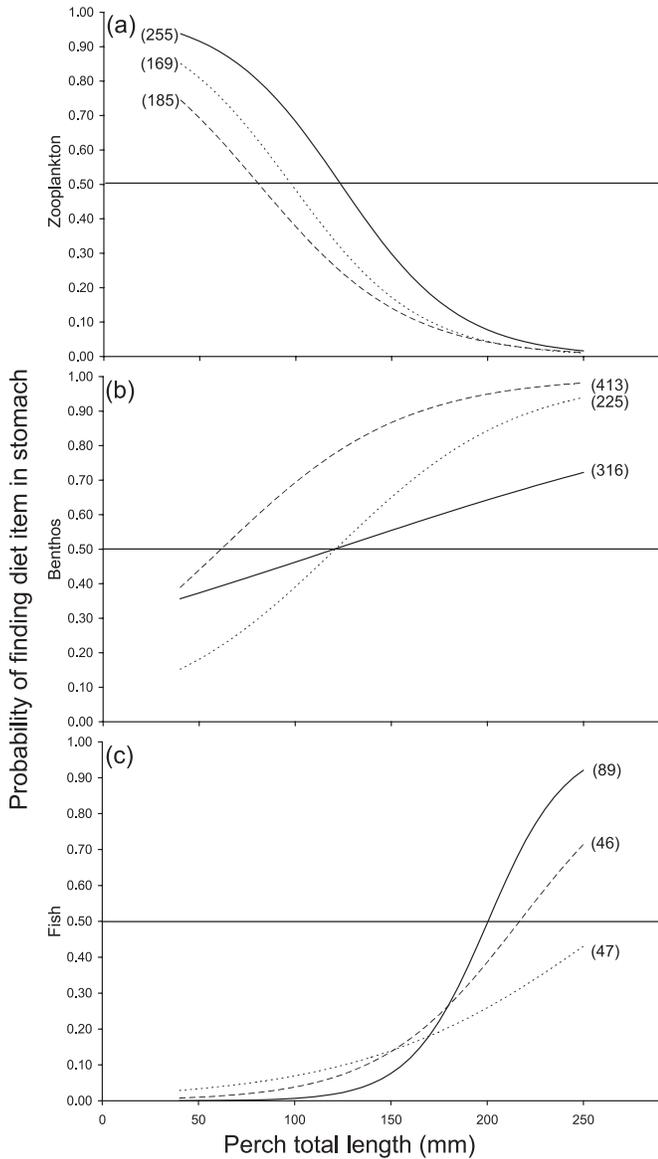
ble 5). Similar to the egg lipid effects, this response to predators also seemed transient; growth of YOY perch from lakes with well-established predator populations was not statistically different from YOY growth in lakes with no predators or recently introduced predators.

Not all lakes within a single predator grouping were sampled within the same year, so interannual variation was tested within each regime. There was no significant difference between the total length of YOY perch (males, $p = 0.477$; females, $p = 0.414$) in lakes with no predators sampled in the fall of 2004 and 2005. Similarly, no interannual differences were found for age-1 (male, $p = 0.667$; female,

Table 5. Summary of the life history and metabolic enzyme activity rates from yellow perch populations across the predation regime.

Variable	Female			Male			p
	No	Recent	Established	No	Recent	Established	
Round weight (g)	11.04a (±0.61)	10.86a (±0.84)	12.18b (±0.82)	11.61a (±0.52)	11.03a (±0.86)	12.43b (±0.74)	<0.001
Gonad weight (g)	0.44a (±0.06)	0.51a (±0.08)	0.66b (±0.09)	0.92b (±0.09)	0.69a (±0.12)	0.76a (±0.11)	0.017* <0.001*
Egg lipid content (mg·egg^{-1})	0.041b (±0.007)	0.025a (±0.009)	0.036ab (±0.033)	—	—	—	0.036†
Length-at-YOY (mm)	68b (±8)	61a (±5)	68ab (±8)	74b (±7)	61a (±4)	66ab (±8)	0.015
Length-at-age 1 (mm)	105 (±5)	108 (±11)	108 (±13)	98 (±3)	99 (±7)	105 (±13)	0.629
Length-at-age 2 (mm)	147b (±26)	139b (±21)	147b (±17)	129a (±21)	118a (±31)	125a (±15)	0.654
NDPK (IU)	15.05a (±4.73)	11.91a (±5.77)	26.27b (±7.23)	13.87a (±5.37)	13.57a (±4.76)	21.09b (±9.30)	0.007
LDH (IU)	159.49 (±95.55)	128.98 (±21.36)	127.40 (±36.79)	169.60 (±99.82)	136.42 (±37.32)	128.49 (±34.04)	0.270
CS (IU)	0.84 (±0.325)	0.69 (±0.237)	0.53 (±0.212)	1.01 (±0.639)	0.70 (±0.162)	0.60 (±0.268)	0.128

Note: Data represent means (±95% confidence intervals) from logarithmically transformed estimates using 110 mm (males) and 125 mm (females) as covariates (values determined by taking the mean of the intersecting ranges among all lakes). p values are shown for two-way analysis of variance (ANOVA) analysis with the predator regime and sex as the treatment groupings where there was no significant interaction. Statistically similar values are denoted by the same lowercase letter. YOY, young of the year; NDPK, nucleoside diphosphate kinase; LDH, lactate dehydrogenase; CS, citrate synthase; IU, international units.
*Results from one-way ANOVA analysis for each sex (there was a significant interaction between predator regime and sex in the two-way ANOVA analysis).
†Results from one-way ANOVA.

Fig. 5. Morphometric analysis. (*a*) Distribution of yellow perch morphological index (MI) (determined by discriminant function analysis of partial warp scores) from lakes with no predators (solid bars), recently invaded predators (shaded bars), and established predators (cross-hatched bars). (*b*) Deformation grids depicting shape differences for a typical perch in a lake with (*i*) no predators and (*ii*) established predators are shown. Numbers identify the landmarks used in the analysis as described in Fig. 2. The distribution of the morphological index (MI) shows that perch in lakes without predators were at the left (negative) side of the distribution, established predators were at the right (positive) side, and introduced predator exposure was intermediate between the two.
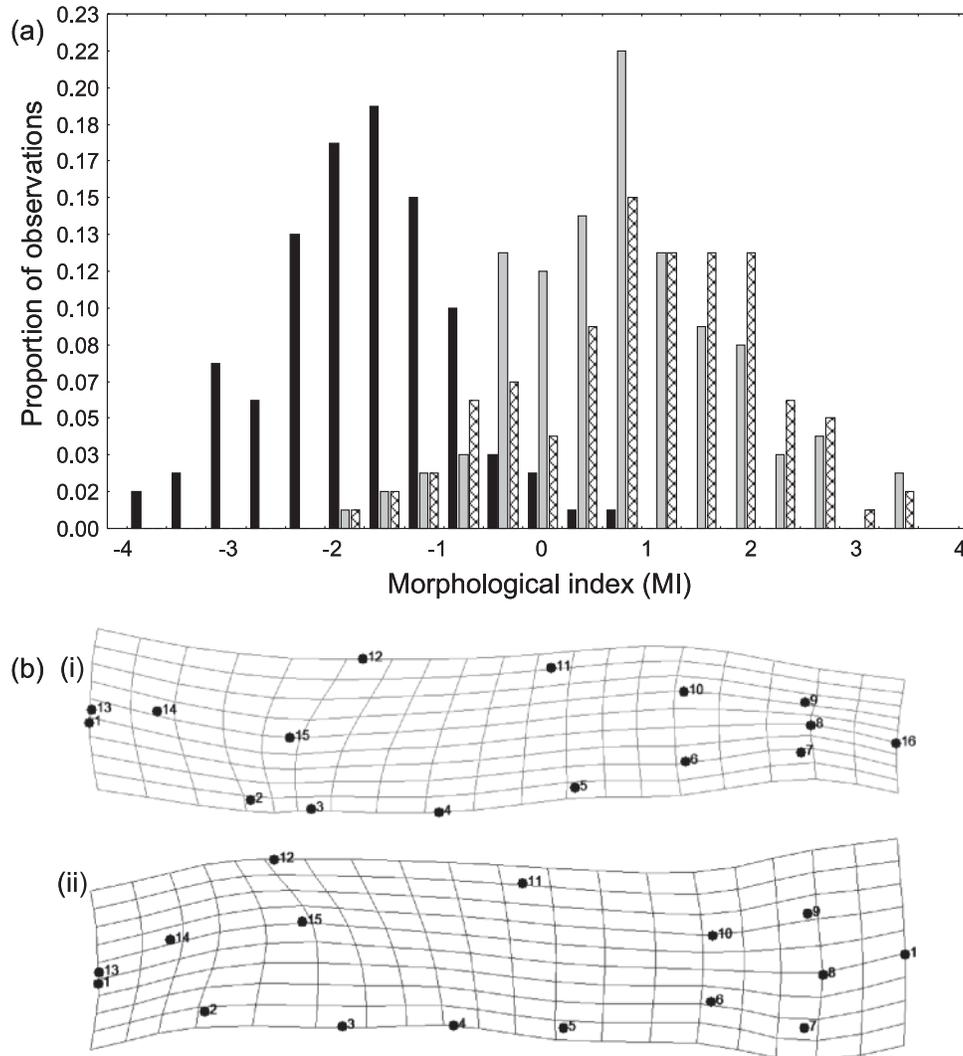
$p = 0.431$) or age-2 (male, $p = 0.364$; female, $p = 0.147$) individuals for this grouping.

In contrast to the effects seen in growth during the first year of life, size-at-age for older age classes of perch did not vary greatly across the predator regimes. At age 1+, perch size did not differ between males and females (ANOVA, $F_{[1,30]} = 2.29$, $p = 0.141$) or across the predation gradient (ANOVA, $F_{[2,30]} = 0.47$, $p = 0.629$; Table 5). By age 2, typical sexual dimorphisms in perch were established; females were 13% larger on average than males across the predation gradient (ANOVA, $F_{[2,27]} = 7.49$, $p = 0.011$; Table 5).

Metabolic enzyme activity rates and body condition

Analysis of muscle NDPK indicated that perch in lakes with established predator populations had higher growth potential than perch in lakes with either no predators or only recently introduced predators (ANOVA, $F_{[2,22]} = 6.28$, $p = 0.007$; Table 5). Mean NDPK rates were 23.44, 14.45, and

12.72 IU·(g wet mass)$^{-1}$ in lakes with established predators, lakes with no predators, and lakes with recently introduced predators, respectively.

Body condition, quantified as total body mass adjusted for length, was not statistically different between lakes without predators and recently invaded predators but was higher in males and females in lakes with established predator populations (ANOVA, $F_{[2,30]} = 10.48$, $p < 0.001$; Table 5). This trend was similar to the effect observed in growth potential as estimated by NDPK activity. The higher growth potential in lakes with established predators therefore seems to be directed towards increased weight at length (i.e., condition) rather than increased total length of fish.

Metabolic enzyme estimates for swimming activity

Yellow perch LDH rates (log-transformed) did not differ significantly among predator groupings (ANOVA, $F_{[2,22]} = 1.40$, $p = 0.270$; Table 5). On average, the LDH rates from

perch between 100 and 120 mm total length were 134.9 IU·(g tissue wet mass)$^{-1}$. Similarly, CS rates (log-transformed) of yellow perch did not differ significantly across the predator groupings (ANOVA, $F_{[2,22]}$ = 2.26, p = 0.128; Table 5). The average CS rate was 0.66 IU·(g tissue wet mass)$^{-1}$. The lack of difference in LDH and CS rates across the predator groupings suggests that the addition of interspecific predators did not change anaerobic or aerobic swimming potentials in yellow perch.

Body shape analysis

The body shape of the perch could be readily used to classify the predator regime from which they came. From the morphometric analysis, 86.1% of individuals was correctly classified into the appropriate predator regimes (Fig. 5a).

Perch in lakes without predators had shallow bodies, a slightly upturned snout region, and a thin, elongated caudal peduncle region (landmarks 6, 7, 8, 9, and 10) (Fig. 5b (i)). Perch in lakes with predators had thicker bodies with heads pointed slightly upwards and a thick, short caudal peduncle (Fig. 5b (ii)). The insertion of the spiny dorsal fin (landmark 12) was more anterior and the pelvic fin insertion (landmark 3) was more posterior compared with perch in lakes with no predators.

The population mean MI increased rapidly with predator biomass (Fig. 6a), up to approximately 200–400 g·net^{-1}. Beyond this level of predator biomass, body morphology did not change significantly. Mean population MI also decreased significantly with increasing perch biomass (Fig. 6b); however, when considered together in a multiple regression analysis, only predator biomass loaded as a significant explanatory variable for the MI (multiple regression, multiple R^2 = 0.90, p < 0.001). Perch biomass itself did not add to the explanatory power of this relationship.

## Biological responses to lake characteristics

Principal component analysis was used to identify the correlation structure among physical and chemical variables in the study lakes (Table 6). The analysis revealed three significant factors describing almost 80% of the total variability in lake characteristics. The first factor, which explained 37% of the variation, included measures of acidity and lake productivity such as pH, P, Ca, and DOC. An additional 28% of the variation was described by aqueous metal contamination of Ni and Cu (the second factor). The third factor, mostly explained by lake maximum depth, contributed a further 14% of the variation. The acidity and lake productivity factor (factor 1) was positively correlated with perch biomass and negatively correlated with the total fish community biomass, the perch morphological index, and female condition (Table 7). Predator biomass, fish community biomass, male and female condition, female ovary weight, and NDPK activity were positively correlated with the metal contamination factor (factor 2). No biological variables were correlated with factor 3 (Table 7).

Discussion

Community structure

We interpret the dramatic decrease (69%) in yellow perch biomass with increasing total predator biomass as a direct le-

Fig. 6. Relationship between yellow perch body shape (morphological index (MI)) and (a) total predator biomass (g·net^{-1}) and (b) total yellow perch biomass (g·net^{-1}) among predator regimes: lakes with no predators (■), lakes with recently invaded predators (◇), and lakes with established predators (+).
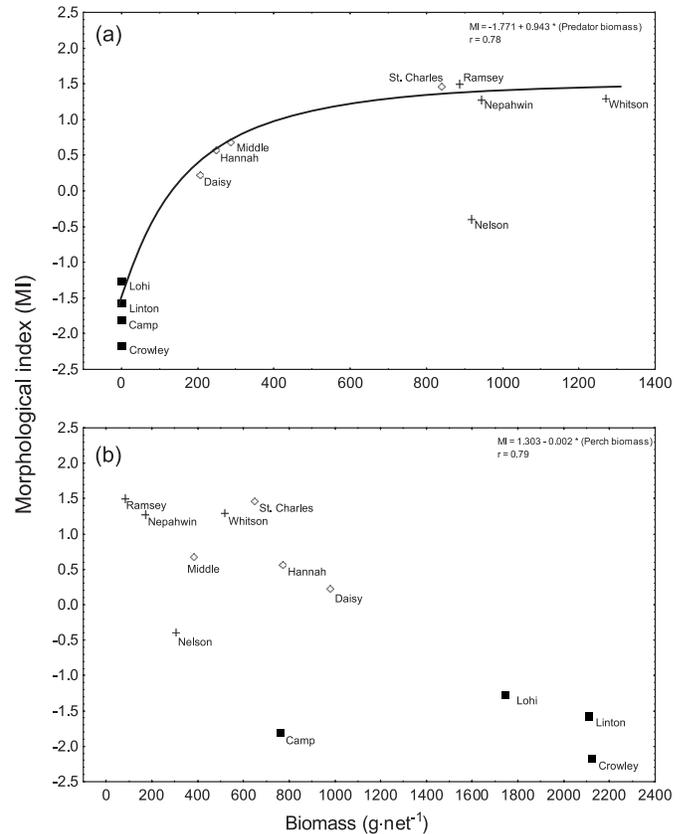
thal effect of the predators on prey populations, while the indirect effect of the presence of the colonizing predator is thought to generate most of the other life history changes observed in this study. Northern pike and walleye have been documented to feed on yellow perch (Sammons et al. 1994; Kaufman et al. 2006), and yellow perch were found in the summer diet of smallmouth bass from the study lakes (K. Lippert, unpublished data). Perch populations in Sudbury area lakes are known to decline rapidly with the introduction or the recovery of a remnant population of a predator such as lake trout (Gunn et al. 1988, 1990; Gunn and Keller 1990).

Summer diet shifts

The differences in sizes at which perch make the ontogenetic shifts from zooplankton to benthic macroinvertebrates are an important finding in this study. Perch in lakes with recently invaded predators appeared to be forced onto benthic resources at approximately half the size of perch from lakes with no predators. Such behavioral changes in prey communities in response to predators have been shown to operate over short time scales (He and Kitchell 1990). Another possible cause for the early shift to benthos could be limitations in the composition and size structure of the offshore zooplankton community. Zooplankton communities were not assessed as part of this study, but it seems unlikely that zooplankton availability would be limited in the recently in-

1424

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

Table 6. Summary of the factor loadings, eigenvalues, and percent variation explained for principal component analysis using physical and chemical lake characteristics.

Environmental (lake) variables	Factor 1	Factor 2	Factor 3
Surface area (ha)*	–0.169051	0.685943	0.436055
Maximum depth (m)*	0.499700	0.335518	0.652927
Mean depth (m)	0.645425	0.380004	–0.380004
Secchi depth (m)*	0.493481	–0.297686	–0.297686
pH	–0.847744	0.132919	0.132919
Cu ($\mu g \cdot L^{-1}$)*	–0.414682	–0.842673	–0.061108
Ni ($\mu g \cdot L^{-1}$)	–0.329173	–0.885439	0.114947
P ($\mu g \cdot L^{-1}$)	–0.756492	0.471425	–0.029749
Ca ($mg \cdot L^{-1}$)*	–0.882382	–0.037687	0.357632
DOC ($mg \cdot L^{-1}$)*	–0.670851	0.529041	–0.321756
Eigenvalue (% variation explained)	3.738 (37.4%)	2.831 (28.3%)	1.366 (13.7%)

Note: DOC, dissolved organic carbon.
*Data logarithmically transformed.

Table 7. Pearson correlations (sample size in parenthesis) for yellow perch biological variables and factor scores.

Biological variable	Factor 1	Factor 2	Factor 3
Perch biomass ($g \cdot net^{-1}$)	**0.53** (18)	–0.41 (18)	–0.34 (18)
Predator biomass ($g \cdot net^{-1}$)	–0.22 (12)	**0.63** (12)	–0.09 (12)
Total biomass ($g \cdot net^{-1}$)	**–0.52** (18)	**0.52** (18)	–0.08 (18)
Size shift from zooplankton (mm)	0.34 (14)	0.16 (14)	0.03 (14)
Size shift to benthos (mm)	0.53 (9)	0.47 (9)	–0.18 (9)
Size shift to fish (mm)	0.05 (12)	–0.51 (12)	–0.39 (12)
Egg lipid content ($mg \cdot egg^{-1}$)	0.55 (8)	0.58 (8)	0.15 (8)
Morphological index	**–0.78** (12)	–0.03 (12)	0.44 (12)
Male round weight (g)	–0.46 (18)	**0.61** (18)	–0.23 (18)
Female round weight (g)	**–0.51** (18)	**0.65** (18)	–0.11 (18)
Male testes weight (g)	0.12 (18)	–0.05 (18)	–0.24 (18)
Female ovary weight (g)	–0.39 (18)	**0.48** (18)	0.04 (18)
LDH (IU)	0.21 (14)	–0.10 (14)	–0.18 (14)
NDPK (IU)	–0.34 (14)	**0.65** (14)	–0.23 (14)
CS (IU)	0.37 (14)	0.38 (14)	0.35 (14)
Male length-at-YOY (mm)	0.08 (16)	–0.08 (16)	0.34 (16)
Female length-at-YOY (mm)	0.16 (16)	–0.03 (16)	0.38 (16)
Male length-at-age 1 (mm)	–0.23 (18)	0.13 (18)	0.19 (18)
Female length-at-age 1 (mm)	–0.19 (18)	–0.04 (18)	0.13 (18)
Male length-at-age 2 (mm)	–0.11 (16)	0.04 (16)	–0.09 (16)
Female length-at-age 2 (mm)	–0.11 (17)	0.01 (17)	0.10 (17)

Note: Significant correlations ($P < 0.05$) are noted in bold. YOY, young of the year; NDPK, nucleoside diphosphate kinase; LDH, lactate dehydrogenase; CS, citrate synthase; IU, international units.

vaded lakes given the large reduction in the biomass of perch observed.

Perch from lakes with well-established predators made the shift onto benthos at a similar size to perch from lakes with no predators. However, fish species richness was usually much higher in the lakes with established predators, suggesting that alternate forage fish prey items were available in this lake set. Alternate prey species such as cisco (*Coregonus artedi*) have been shown to buffer perch behavioral changes associated with walleye predation from similar lakes of the Sudbury region (Kaufman et al. 2006). Therefore, the size at which the ontogenetic shift was made onto benthos may

have been restored in lakes with established predators because of the buffering capacity of other forage fish species.

Reproductive investment

Males had smaller testes in lakes with predators, indicating that less energy was allocated towards reproduction when predators were present. If perch are confining themselves to less optimal habitats when predators are present, decreased energy acquisition could limit gonadal development in males. However, this trend was not observed in females, suggesting that confinement in refuge areas may not be the explanation. An alternate hypothesis is that variation

in testes mass may be correlated with perch biomass rather than predator biomass and that the males are responding to decreased intraspecific competition for females when predators have reduced overall densities. Because perch are group spawners, sperm competition would increase in lakes with higher perch biomass (Parker 1982). Therefore, males may invest more in reproduction when the density of competing males is high in the absence of predators.

Female perch in lakes with recently invaded predators showed a significantly lower egg lipid content than in lakes without predators. Egg lipids are an important energy supply for hatched larvae before they initiate feeding. Greater egg lipid content available for the hatched larvae can promote an early start to growth and would likely influence the length achieved at the end of their first growing season (Ware 1975; Johnston 1997). Where offspring habitat quality is low, the results of other studies suggest that females would invest in larger eggs with higher lipid content (Lack 1954; Parker and Begon 1986; Reznick and Yang 1993). However, in our study, females showed an opposite response and produced eggs with low lipid content when challenged by the arrival of an invading predator. This finding, as well as the observation that perch switched to benthic invertebrates at a much smaller size in these early invasion lakes, suggest that somewhat unknown but particularly stressful conditions might exist in these early invasion lakes.

Growth patterns across the predation gradient

Relatively rapid growth, indicated by body mass and NDPK activity, in yellow perch from lakes with established predators appeared to be an indication of indirect trait-mediated effect of predation in these study lakes. Predation may affect prey populations by reducing intraspecific competition, by altering activity or distribution as a behavioral modification to decrease mortality risk, or both (Werner et al. 1983). Reduced activity interpreted as a trait-mediated indirect interaction could increase the amount of energy directed towards growth and (or) reproduction (Peacor and Werner 2001). Size-selective predation may also select for fast-growing phenotypes that rapidly move through vulnerable size ranges of prey (reviewed by Colby et al. 1987; Taborsky et al. 2003). Selection for prey with a heavier mass per unit length may have the same protective effect when the predator is gape-limited.

The observed poor growth of YOY perch in the recently invaded predator lakes continues the pattern observed above, further indicating particularly stressful conditions in these lakes. Two alternate explanations for this finding are that the observed lower egg lipid content reduced growth potential for YOY perch in the lakes and (or) that limited food availability reduced early growth. Age-1 mean length did not differ among the predation regimes, suggesting that the trait-mediated effect of predation on length seen in their first summer of growth was no longer present after their second year of growth. The explanation appears to be that only those individuals with good growth potential could survive the first year of predation or overwinter starvation period. By age 2, females were larger than males, a trend common in perch populations (Scott and Crossman 1973), and this result was consistent across the predator regime. Therefore, after surviving their first year, there were no detectable effects of

predators on perch length for a given age-1 or age-2 perch across the predation gradient.

Swimming activity

There was no observed effect of predation on perch swimming behavior based on LDH and CS muscle tissue activity rates. Studies using Trinidadian guppies (*Poecilia reticula*) have shown that burst (estimated by maximum velocity) and aerobic swimming performances (estimated by oxygen consumption rates and CS activity) did not differ significantly between populations with low- and high-predation pressures (Odell et al. 2003; Chappell and Odell 2004). In addition, LDH activity rates were found to be lower in populations with high-predation pressures (Odell et al. 2003). Therefore, factors other than aerobic and anaerobic swimming activities may reduce the risk of predation to perch in these study lakes.

Body shape changes in response to predation

The morphological analysis showed that perch had pelagic body forms in predator-free lakes and littoral body forms in lakes with recently invaded and established predators, a pattern consistent with earlier research (Proulx and Magnan 2002; Svanbäck and Eklöv 2002; Olsson and Eklöv 2005). Dimorphic body forms of Eurasian perch are well documented in lake communities containing predators such as pike, roach (*Rutilus rutilus*), and vendace (*Coregonus albula*) (Svanbäck and Eklöv 2002, 2003). Different phenotypes have been shown to be differentially selected for under various predator regimes (Reimchen 1994; Walker 1997).

In the absence of predators in our lakes, perch had a relatively thin body shape, a more posterior insertion of the spiny dorsal fin, an upwards-pointing snout, and a longer and more slender caudal peduncle area compared with perch from lakes with predators. In lakes with predators present, a shift was observed in the overall body morphology showing increased similarities to the typical littoral form. In lakes with recently introduced predators, the typical shape observed was a thickened body with a short and wide caudal peduncle region, slight anterior migration of the dorsal spiny fin, and a downwards-pointing snout. Increased body thickness in crucian carp (*Carassius carassius*) in response to chemical cues from northern pike has been considered a defensive response to predation because deeper-bodied prey are more difficult for predators to handle and swallow (Hambright 1991; Brönmark and Miner 1992; Nilsson et al. 1995). If this were also true in perch, it would benefit small perch, which are susceptible to predation, to redirect energy towards increased body thickness to decrease vulnerability to gape-limited predators.

Eurasian perch show two distinct morphologies adapted for foraging in littoral and pelagic habitats. Presumably, these morphological differences would be accompanied by activity differences. In our study, we observed morphological differences among yellow perch from different lakes but found no difference in swimming activity as estimated by metabolic enzyme capacities of LDH and CS. There are three possible explanations for the findings: (*i*) changes in body shape across the predator regimes were not large enough to elicit differences in swimming activity across a predation gradient of this magnitude, (*ii*) the morphological

1426

Can. J. Fish. Aquat. Sci. Vol. 64, 2007

changes increased swimming efficiency, allowing tissue enzyme activity to remain the same, and (or) (*iii*) phenotypic changes in shape occur faster than phenotypic changes in physiology.

The anterior migration of the spiny dorsal fin may represent a defense mechanism. A greater body depth could be achieved when spines are erected in this body configuration, presenting a defense against a gape-limited predator. The erection of the dorsal spine has been shown to be the first observed response of perch to various visual and chemical cues from pike, irrespective of stimulus intensity or duration (Vainikka et al. 2005). Similar antipredator strategies have been reported in YOY perch that exhibited an increased spine length in the presence of northern pike (Magnhagen and Heibo 2004).

Relation to lake recovery

Improvements in water chemistry and productivity (pH, P, Ca, and DOC) along with declines in metal contamination (Ni and Cu) were correlated with increased fish community biomass in the Sudbury lakes. Yellow perch biomass was negatively correlated with improvements in water chemistry and productivity and unrelated to metal contamination. Predator biomass increased as metal contamination (Ni and Cu) declined but was unrelated to water chemistry and productivity. Few of the yellow perch biological parameters were correlated with factors related to improvements in water quality or metal contamination. Yellow perch shape variation was related to water chemistry and productivity concurrent with decreases in yellow perch biomass (but not overall fish community biomass). Lakes above pH 6.5 appeared to have environmental characteristics amenable to the establishment of predatory fish species. Yellow perch biomass was significantly lower in lakes with predators. The addition of predators to the fish community also triggered a change in yellow perch shape. Although we cannot negate the fact that environmental variables do play an important role in shaping community and perch phenotypes, we found that predator biomass was still the best predictor for these variables.

The elevated metal levels in the water and sediments of Sudbury lakes are, and will remain, long-term concerns (estimates of several centuries to reach background levels) in these industrially damaged lakes (Nriagu et al. 1998). From a physiological or toxicological perspective, there is little evidence that perch, a metal-tolerant species, are severely impacted by the current metal levels (Giguère et al. 2005; Pyle et al. 2005). However, it is well known that many metal-sensitive benthic invertebrate species are scarce or absent from these lakes (Borgmann et al. 2001; Iles and Rasmussen 2005), and reduced benthic availability may be a confounding factor affecting perch bioenergetics in such ecosystems.

Future studies are necessary to fully explain the repercussions of fish predator introductions in recovering lakes. Experiments involving the introduction of predators into prey-only lakes are needed to test many of the predator–prey relationships observed in this study. Detailed studies of benthic invertebrate communities, before and after predator introductions, are also needed to determine whether food limitations are severely impacting prey species in these industrially stressed lakes. For example, do predators create "trophic bottlenecks" by forcing prey into impoverished littoral areas?

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