Prey life-history and bioenergetic responses across a predation gradient

M. D. Rennie*†‡, C. F. Purchase*§, B. J. Shuter†‖, N. C. Collins*†, P. A. Abrams† and G. E. Morgan¶

Aquatic Ecology Group, Department of Biology, University of Toronto Mississauga, 3359 Mississauga Road North, Mississauga, ON, L5L 1C6 Canada, †Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, ON, M5S 3B2 Canada, ‖Harkness Laboratory of Fisheries Research, Aquatic Research and Development Section, Ontario Ministry of Natural Resources, DNA Building, 2140 East Bank Drive, Peterborough, ON, K9J 7B8 Canada and ¶Cooperative Freshwater Ecology Unit, Department of Biology, Laurentian University, Sudbury, ON, P3E 2C6 Canada

To evaluate the importance of non-consumptive effects of predators on prey life histories under natural conditions, an index of predator abundance was developed for naturally occurring populations of a common prey fish, the yellow perch *Perca flavescens*, and compared to life-history variables and rates of prey energy acquisition and allocation as estimated from mass balance models. The predation index was positively related to maximum size and size at maturity in both male and female *P. flavescens*, but not with life span or reproductive investment. The predation index was positively related to size-adjusted specific growth rates and growth efficiencies but negatively related to model estimates of size-adjusted specific consumption and activity rates in both vulnerable (small) and invulnerable (large) size classes of *P. flavescens*. These observations suggest a trade-off between growth and activity rates, mediated by reduced activity in response to increasing predator densities. Lower growth rates and growth efficiencies in populations with fewer predators, despite increased consumption suggests either 1) a reduction in prey resources at lower predator densities or 2) an intrinsic cost of rapid prey growth that makes it unfavourable unless offset by a perceived threat of predation. This study provides evidence of trade-offs between growth and activity rates induced by predation risk in natural prey fish populations and illustrates how behavioural modification induced through predation can shape the life histories of prey fish species.
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INTRODUCTION

Predator-induced mortality can influence both individual and population fitness. By directly affecting mortality, rates of predation can influence the evolution of prey life histories (Abrams & Rowe, 1996). Many organisms can also respond to predation

‡Author to whom correspondence should be addressed at present address: Fisheries and Oceans Canada Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6 Canada. Tel.: +1 204 984 8970; fax: +1 204 984 2404; email: Michael.Rennie@dfo-mpo.gc.ca

§Present address: Biology Department, Memorial University, St John's, NL, A1B 3X9 Canada

through behavioural modification (*e.g.* altering activity rates or seeking refuge), which are non-consumptive effects of predators on their prey (Peacor, 2002). As these behavioural modifications frequently influence prey growth rates, they can in turn affect other prey life-history traits such as investment in and scheduling of reproduction (Abrams & Rowe, 1996).

Two common tactics of predator-avoidance emerge frequently in the literature. If exposed to gape-limited predators (*e.g.* many species of fishes), one prey strategy is to grow rapidly through the vulnerable size range and achieve a size greater than the gape of their predators (Day *et al.*, 2002; Biro *et al.*, 2005; Urban, 2007). Such rapid growth rates typically require an increased rate of foraging and, in the absence of a spatial or temporal refuge, may increase exposure to predators for a shorter time period, but with the benefit of reaching an invulnerable size more quickly (Urban, 2007). A second tactic is for prey to modify their behaviour to reduce detection by predators. This strategy frequently involves a decrease in prey foraging rates (Peacor, 2003), though the resulting effect on prey growth and life histories may vary (Abrams & Rowe, 1996). Predator-induced changes in prey behaviour may also produce indirect effects on prey resources that can influence prey growth rates (Abrams, 1995; Bolker *et al.*, 2003). Further, changes in energy allocated to activity without an equal associated change in energy intake can influence the amount of surplus energy available for growth and reproduction (Rennie *et al.*, 2005; Johansson & Andersson, 2009).

Measuring the fitness consequences of changes in foraging behaviour can be difficult because those changes will occur in conjunction with several other factors. Traits such as food conversion efficiency may increase with decreases in prey ration (Teskeredzic *et al.*, 1995). Prey resource availability may also vary indirectly with predation risk (Abrams & Rowe, 1996) in response to changes in prey consumption and resource quality (Relyea & Auld, 2005; Olsson *et al.*, 2007). These responses to predation risk as well as potential changes in prey activity costs are all likely to affect prey growth rates.

Little is currently known about how the energetics of prey behavioural modification (through altering individual rates of energy acquisition and allocation) affect their growth rates under natural conditions. Results of empirical work to address this question have been inconsistent. Some studies have shown that increased predation can decrease prey consumption and growth rates, suggesting that the negative effect of decreased foraging is stronger than the positive effects of greater resource abundance and decreased metabolic expenditure towards activity (Nakaoka, 2000; Relyea, 2000). In an elegant mesocosm study, however, Peacor (2002) showed that potential predation by dragonflies had a net positive effect on growth of small frogs, as mediated by a decrease in the activity rates of small frogs that also contributed to an overall increase in resource availability. Other studies have demonstrated that decreased activity rates (holding ration level constant) can lead to increased growth and changes in body morphology consistent with the reduction in activity rates that occurs as a consequence of exposure to predators (Johansson & Andersson, 2009). Furthermore, prey behaviour (or their scope for behavioural modification) may also vary as a function of both prey size and sex. In many species, males and females acquire and allocate energy differently (Cox *et al.*, 2005; Isaac, 2005; Rennie *et al.*, 2008), presumably due to gender-dependent relationships between size and fitness, and, therefore, each sex may respond differently to the threat of predation.

This study examined how predation, under realistic field conditions, affected the life histories of the yellow perch *Perca flavescens* (Mitchill). Two alternative adaptive hypotheses were tested regarding the behavioural response of prey to increase in predation pressure. The first possibility is that prey increase foraging activity to grow out of the vulnerable size range quickly, where both growth and activity scale positively with predation. The second is that prey decrease activity overall, spending more time hiding and less time foraging to reduce exposure to predators. If activity is allocated primarily to foraging, then growth rates should be slower with increased exposure to predators (decline in both growth and activity with increasing predation). If, however, activity declines are such that the metabolic savings of these reductions are significant relative to energy acquisition (*i.e.* consumption), then growth rates should increase as predation exposure increases. Throughout the study, the effects on males and females were considered separately, given previous research on this species that has demonstrated sex-dependent responses for both life histories and bioenergetics (Rennie *et al.*, 2008). Freshwater fish populations in Ontario lakes (Canada) were chosen as the model system selected to explore these hypotheses.

MATERIALS AND METHODS

SAMPLING

Prey (*P. flavescens*) and their fish predators were collected in autumn using two different survey methods. The primary source of fish was from a standardized, Ontario provincial 'Fall Walleye Index Netting' programme (FWIN; Morgan, 2002). Lakes sampled using the FWIN protocol employed overnight gillnet sets at depth strata of 2–5 and 5–15 m. Each net was composed of eight panels, each one ranging in stretched mesh-size (knot to knot) from 25–152 mm. Panels increased in 13 mm increments to 76 mm mesh and in 25 mm increments thereafter. These were set in random locations, with the number of sets scaled to the surface area of the lake. The FWIN programme provided data on *P. flavescens* populations from across the province (Purchase *et al.*, 2005*a*, *b*) and formed the basis of investigations of predator effects on life histories. Four of these lakes received additional sampling to provide sufficient data for bioenergetic analyses (Table I).

A second set of six intensively studied lakes was sampled slightly differently (method B; Table I). Gillnets consisted of panels that represented only the smaller range of mesh-sizes included in the FWIN protocol (25–76 mm) and also included a 19 mm mesh panel. These nets were typically set in only the shallow (2–5 m) depth strata (Purchase *et al.*, 2005*a*, *b*). Four nets were set simultaneously, with each net composed of two gillnet panels. *Perca flavescens* were retained for analysis, while predators were measured, marked and released. Predator masses were later estimated using provincial-based total length (L_T) and mass (M) relationships for each species (Table II). Catch per unit effort (CPUE) from these lakes was estimated from a combination of short (1 to 4 h) and overnight sets. The combined catch in each simultaneous set of all four nets was used to generate standardized estimates. A complete list of lakes included in the study using both collection methods can be found in the Appendix.

LIFE-HISTORY TRAITS OF *P. FLAVESCENS*

Individual *P. flavescens* were measured for both L_T and fork length (L_F) (to the nearest mm) and weighed (to the nearest 0·1 g). All lengths reported are L_F unless otherwise noted. Sex and maturity status were determined from macroscopic examination of gonads and age was determined from the examination of annual rings on otoliths. Where possible, mean life-history traits (maturation age and size, life span, maximum size and reproductive investment)

TABLE I. Lakes in Ontario, Canada, for which bioenergetics of *Perca flavescens* were estimated

Lake	Sample method	Predator community	*Perca flavescens* vulnerability*
Ashley	B	P, W	M = 3, F = 3
Elephant	FWIN	P, W, SB	M = 4, F = 3
Lady Ruth	B	P, W	M = 5, F = 4
Melic	B	P, W	M = 4, F = 3
Mindemoya	FWIN	W, SB	M = 1, F = 1
Plastic	B	None	n/a
Round	FWIN	P, W, SB	M = 2, F = 2
Scolt	B	None	n/a
Stumpy	FWIN	W	M = 1, F = 1
Trailer	B	P	M = 5, F = 3

FWIN, 'Fall Walleye Index Netting' protocol; B, sampling method B; P, *Esox lucius;* W, *Sander vitreus*; SB, *Micropterus dolomieu.*
*Age class in bioenergetic models up to and including which *P. flavescens* were considered vulnerable to predation. M, males; F, females; n/a, not applicable, due to lack of predator species in these lakes.

TABLE II. Characterization of predator species detected in study lakes, Ontario, Canada

Predator species	Predator L_T at which piscivory on *Perca flavescens* begins (mm)*	*Perca flavescens* escape L_T from predation (mm)*	Predator L_T (mm) and M (g) regression
Esox lucius	500	150	$M = 6.27 \times 10^{-6} L_T^{2.988}$
Micropterus dolomieu	250	100	$M = 7.98 \times 10^{-6} L_T^{3.085}$
Sander vitreus	250	100	$M = 3.24 \times 10^{-6} L_T^{3.164}$

L_T, total length; M, mass.
*Estimated from Liao *et al*. (2002).

were estimated separately for each sex in each population as reported in Purchase *et al*. (2005*a*). Life span and maximum size were estimated as the mean age of the oldest and mean L_F of the largest 5% of individuals, respectively. These estimates are highly repeatable within a population across a wide range of sample sizes (Purchase *et al*., 2005*b*). Size and age at 50% maturity were determined using logistic regression. An index of female reproductive investment (I_R) was estimated as the number of eggs in an average-sized (123 g) female collected in autumn samples (Purchase *et al*., 2005*a*). Not all variables could be estimated for each population, as indicated by differences in d.f. in statistical comparisons of life-history traits with the index of predator abundance (see Appendix).

ESTIMATING PREDATION RISK

An index of predation risk was developed under the assumption that predator mortality on *P. flavescens* was positively correlated to the CPUE of piscivorous fishes, namely, pike *Esox lucius* (L.), walleye *Sander vitreus* (Mitchill) and smallmouth bass *Micropterus dolomieu* Lacepède. These predator species all undergo ontogenic diet shifts to piscivory. Therefore, the index included only those predators above a certain species-specific size limit (Table II)

deemed to be capable of consuming *P. flavescens* of the size range captured during the study. Using data from FWIN-sampled lakes, predator CPUE was estimated as the total catch of *S. vitreus*, *E. lucius* and *M. dolomieu* that were above the appropriate size threshold in each gillnet set. The index of predator abundance was estimated as the $\log_{10}$-transformed mean catch [$\log_{10}(x + 1)$] per net among sets in a lake and expressed in units of kg km^{-1} of gillnet per day. Of the original data set, 58 populations had sufficient data to allow the generation of an index of predation that was used to explore relationships with *P. flavescens* life history (Appendix). For the data collected using method B, the total catch of *S. vitreus*, *E. lucius* and *M. dolomieu* captured during each simultaneous set of four nets was used. The CPUE was estimated as the $\log_{10}$-transformed mean catch [$\log_{10}(x + 1)$] per net among sets in a lake and expressed in units of kg per gillnet per day. Because of the differences in sampling protocols, predation indices for the method B data were considered separately from FWIN-sampled populations and used only for investigations of bioenergetics.

Size limits for each predator species were determined from a comprehensive study that reported mean sizes of piscivores that were actively consuming *P. flavescens* (Liao *et al.*, 2002). The mean sizes of 'small' piscivores (defined in Liao *et al.* 2002 as *S. vitreus* <305 mm) was chosen as the size at which predator species began to inflict significant mortality on *P. flavescens* through predation (Table II). To compare the extension of the Liao *et al.* (2002) study to the study lakes included here, the mean sizes of their *S. vitreus* that were consuming *P. flavescens* were compared to unpublished estimates of mean L_F of *S. vitreus* <305 mm collected using the FWIN method from northern Ontario lakes with *P. flavescens* in their gut contents (G. Morgan, unpubl. data); the mean L_F of autumn *S. vitreus* feeding on *P. flavescens* was 257 mm in Liao *et al.* (2002) and 256 mm in northern Ontario lakes. Based on this similarity between the Ontario data and the Liao *et al.* (2002) study, and lacking similar data for *E. lucius* or *M. dolomieu* in northern Ontario, mean size estimates from Liao *et al.* (2002) were used for these other species to estimate the size at which piscivory on *P. flavescens* became significant (Table II). Because the size cut-offs were based on mean values over all seasons and years reported in the Liao *et al.* (2002) study, they were rounded down to the closest 5 mm interval for all species to provide a slightly less-conservative estimate of predator densities (Table II).

Relationships between *P. flavescens* life-history traits and the predator abundance index were investigated using linear regression (Table III). Statistical significance was assessed using a type I error rate of 0·05 (Perneger, 1998; Moran, 2003). In a larger data set including the current study lakes, growing degree days (GDD) >5° C were shown to influence *P. flavescens* life-history traits, while CPUE of *P. flavescens* was not (Purchase *et al.*, 2005*b*). The GDD were therefore considered as a possible covariate in life-history relationships with the index of predator abundance.

TABLE III. Statistical summary of *Perca flavescens* life-history relationships with predator catch per unit effort across populations

Life-history variable	Sex	d.f.	P	Direction
Maximum body size	Female	1,41	<0·05	+
Maximum body size	Male	1,34	<0·05	+
Maturation size	Female	1,47	<0·001	+
Maturation size	Male	1,27	<0·05	+
Maturation age*	Female	1,47	<0·05	+
Maturation age	Male	1,32	>0·05	
Life span	Female	1,34	>0·05	
Life span	Male	1,29	>0·05	
Reproductive investment	Female	1,19	>0·05	

*Life-history variable for which growing degree days >5° C also explained a significant component of variation.

ESTIMATING FOOD CONSUMPTION, CONVERSION EFFICIENCY AND ACTIVITY

Data from 12 populations previously examined in Rennie *et al*. (2008) were used to assess the effects of predation on *P. flavescens* bioenergetics (Table I). Two populations were excluded from the analysis: Shoe Lake due to a lack of predator density estimates and Margueratt Lake because it was atypical, being the only lake to contain only *M. dolomieu* as predators, as well as extensive macrophyte beds and submerged trees (unlike the other lakes included in the study). It was thought that this extensive cover provided additional refuge from fish predators (Eklov & Persson, 1996; Persson *et al*., 1996; Snickars *et al*., 2004), unlike the rest of the study lakes.

A contaminant and bioenergetic mass balance model (Rennie *et al*., 2008) was used to estimate rates of *P. flavescens* growth, food consumption, activity and conversion efficiency. The model combines the mass balance formulae of contaminants and *M* on a daily basis from a mercury mass balance model (MMBM) with that of fish energy budgets from a bioenergetics model (Kitchell *et al*., 1977). The MMBM models the balance of methylmercury in fishes, which is the form most readily bioaccumulated in aquatic ecosystems (Mason *et al*., 1995; Lawson & Mason, 1998; Lawrence *et al*., 1999). Fish total mercury and methylmercury concentrations were equivalent in the present study (Rennie, 2003).

Fishes in uncontaminated waters (like the lakes in this study) accumulate MeHg primarily through diet (Hall *et al*., 1997; Lawson & Mason, 1998; Leaner & Mason, 2002), and muscle [Hg] can be assumed equivalent to whole body concentrations (Becker & Bigham, 1995; Trudel *et al*., 2000; Trudel & Rasmussen, 2001). Fish MeHg accumulation is then described by:

$$\frac{dHg}{dt} = (\alpha \cdot C_d \cdot C) - (E + G + S) \cdot Hg, \tag{1}$$

where Hg is [MeHg] of the fish (μg Hg g^{-1} wet mass), α is the assimilation efficiency of MeHg from food (unitless), C_d is [MeHg] in food (μg Hg g^{-1} wet mass), C is the mass-specific food consumption rate day^{-1} at time t, E is the instantaneous elimination rate of MeHg day^{-1}, G is the mass-specific growth rate (day^{-1}) and S is the instantaneous loss rate of MeHg day^{-1} to gonads. If modelled discretely over small (*i.e.* daily) time steps, differences in variables such as E and S will be small and can therefore be treated as constants. Integration of equation 1 then yields the following (rearranged to solve for consumption):

$$C = \left[Hg_t - Hg_0 e^{-(E+G+S)t} \cdot \left[\alpha \cdot C_d (1 - e^{-(E+G+S)t})\right]^{-1}\right] \cdot (E + G + S), \tag{2}$$

where Hg_0 and Hg_t are the [MeHg] in fish at time 0 and time t, respectively. Losses due to spawning (S) are as described in Rennie *et al*. (2008).

The MMBM (equation 2) is solved over a daily time step and combined with a bioenergetics model (BM; Kitchell *et al*., 1977) through the common term, C (C above can be converted to units of J day^{-1} by multiplying C by prey energy density and M_{t-1}). The bioenergetics model can be expressed simply as:

$$M_t = M_0 + [C - (F + U + R_T)] \cdot E_D^{-1}, \tag{3}$$

where M_t is the final fish mass (g), M_0 is the initial fish mass (g), C is ingestion rate (J day^{-1}) at time t, E_D is the energy density of fish (J g^{-1}), F is losses due to egestion (J day^{-1}), U is losses due to excretion (J day^{-1}) and R_T is losses due to metabolism (J day^{-1}).

Consumption rate in the BM is a function of temperature and an allometric function describing maximum consumption determined from laboratory experiments. Losses from metabolism, R_T from equation (3), can be further subdivided into three components:

$$R_T = ACT \cdot R_s + R_d, \tag{4}$$

where R_d is specific dynamic action (SDA, J day^{-1}) which varies proportionally with C, R_s is loss due to standard metabolism (J day^{-1}) and is an allometric function of temperature and body mass and ACT is a unitless representation of energy lost to active metabolism, expressed as a multiple of standard metabolism (R_s), where $1 < ACT < \infty$.

Loss to reproduction in the BM is modelled as a one-time loss on 15 April, estimated as:

$$M_t = M_{t-1} - M_{t-1} \cdot \left(I_G \cdot E_{F(X,Y)} \right), \tag{5}$$

where M_t is the mass of fish after spawning, M_{t-1} is the mass of fish the previous day, I_G is the gonado-somatic index (proportion of total mass of the fish associated with gonads) and $E_{F(X,Y)}$ is the sex-specific ratio of gonad to whole body energy densities.

Gross growth efficiency (K) was estimated as:

$$K = G \cdot C^{-1}. \tag{6}$$

By iterating on a daily basis both equations 2 and 3 linked through the common term, C, the unique solution of C and ACT that achieved the observed final mass and [MeHg] was obtained through an optimization routine. The optimization minimized error between observed M_t and Hg$_t$ and modelled M_t and Hg$_t$, such that the average difference between observed and modelled M_t and Hg$_t$ was $<0.01\%$. The model was run for fish over age transitions 1–2, 2–3, 3–4, 4–5 and 5–6 years. These transitions represented differences in size and Hg among adjacent cohorts of fish collected during the autumn of 2001. All fish ages refer to the age at the beginning of these intervals.

MODEL PARAMETERIZATION

Stomach contents of *P. flavescens* were collected in July and September 2001, and either analysed individually or pooled among individual fish in each lake by 2 cm L_F intervals for methylmercury analysis. Up to five individual stomachs were pooled for each L_F interval, and between two to 10 intervals were analysed from each lake (average of six size intervals per lake). In total, 150 stomach content samples were analysed, of which 80 composite samples were analysed in duplicate or triplicate. Approximately 10% of individual stomachs were also analysed in duplicate for quality control and quality assurance. In September, a standard piece of epaxial muscle tissue was taken from the left side of the fish, anterior to the dorsal fin, and dorsal to the lateral line. Muscle tissue and stomach contents were frozen at $-20°$ C for Hg analysis. Fish mercury was determined either on individual fish or on composite samples of two to five fish from members of the same age class. In total, 318 individual or composite samples of tissues for mercury were analysed, 72 of which were composite samples and run in duplicate. Approximately 10% of individual samples were also run in duplicate for quality control and quality assurance. Determination was performed by acid digestion of tissues followed by analysis using cold vapour atomic fluorescence spectroscopy, as described in Rennie *et al.* (2008). Methylmercury in stomach contents was determined by organic extraction, as described in Rennie *et al.* (2008).

Water temperatures in each lake were recorded during 2001–2002 by data loggers every 8 min and were used to generate lake-specific mean daily littoral water temperatures to be used in bioenergetic analyses. All other variables for the mercury mass balance model, including inputs for fish mass, I_G and associated energy densities, [THg], diet [MeHg] and functions describing daily [MeHg] elimination, mass and [MeHg] losses to gonads are from Rennie *et al.* (2008).

EVALUATING EFFECTS OF PREDATION ON BIOENERGETICS OF *P. FLAVESCENS*

Linear regression was used to test for variation in growth rates of *P. flavescens* (as implied by size differences between adjacent cohorts sampled in 2001) and model estimates of consumption, activity and conversion efficiency that were explained by the index of predator abundance. Bioenergetic estimates were log_{10} transformed where necessary to linearize relationships. Because it was anticipated that vulnerability to gape-limited predators would affect the behaviour of *P. flavescens*, analyses were conducted separately for vulnerable and invulnerable life stages (*i.e.* small and large fish). Sexes were also considered separately, based on previous work demonstrating that male and female *P. flavescens* differ in their rates of energy allocation and acquisition and should be considered separately when considering life-history patterns (Purchase *et al.*, 2005a) and bioenergetics (Rennie *et al.*, 2008). Significance was evaluated using $\alpha = 0.05$ (Perneger, 1998; Moran, 2003).

Both absolute (g day^{-1}) and specific (g day^{-1} M^{-1}) consumption and growth rates can vary with fish size (*e.g. M* in g), making comparisons across fish of different sizes problematic (Hewett & Kraft, 1993; Jobling, 1994) unless relationships between mass-specific rates and body mass are isometric (Trudel *et al.*, 2001). These rates, however, can be compared among fish of different size if relative rates (g day^{-1}) are divided by *M* raised to the appropriate exponent describing the allometric scaling of the particular rate with *M*. Hewett & Kraft (1993) recommend an exponent of 0·8 be applied to *M* to correct for size differences in consumption, based on their analyses of *P. flavescens* and *Perca fluviatilis* L. populations. Jobling (1994) reports mass exponents of mass-specific growth rates to *M* in the range of -0.32 to -0.45, with a mean of -0.37 (0·63 converted to a scaling exponent for absolute growth rates). The original studies for these data are not cited, however, and apply strictly to salmonids. Mélard *et al.* (1996) report absolute growth rates of *P. fluviatilis* at varying body sizes raised at four different temperatures. These data were re-analysed using ANCOVA, which determined the mass exponent common across temperature treatments to be 0·58 (ANCOVA, $F_{1,15} = 963$, $P < 0.05$; test for heterogeneity of slopes, $F_{3,12} = 0.83$, $P > 0.05$).

To determine whether these literature values could be appropriately applied to the current data set, allometric exponents of absolute consumption and growth with *M* were estimated for the *P. flavescens* populations under study. While allometric exponents of absolute consumption rates (g$_{food}$ day^{-1}) with *M* (g) varied among populations (0·4–0·99), the mean of all scaling exponents was 0·74 with a s.e. of 0·06. Further, *M* scaling exponents for consumption were not different between males and females (paired *t*-test, $t_9 = 1.4$, $P > 0.05$). The scaling exponent of 0·8 proposed by Hewett & Kraft (1993) was therefore concluded to closely approximate that of the populations under study and was used to provide size-adjusted mass-specific consumption rates (g$_{food}$ day^{-1} $M^{-0.8}$). Allometric exponents of absolute growth (g$_{fish}$ day^{-1}) with *M* (g) also varied among populations (0·38–0·8) and were found to differ between male and female fish (paired *t*-test, $t_9 = 8.0$, $P < 0.05$; mean difference of 0·19). While the mass exponent for growth from Mélard *et al.* (1996) closely matched the value for male *P. flavescens* in this study (mean ± s.e. 0·548 ± 0·340), it was well outside the range of exponents for female fish (0·734 ± 0·016). Thus, the mass scaling exponent determined from Mélard *et al.* (1996) was used to provide size-adjusted mass-specific growth rates for males (g$_{fish}$ day^{-1} $M^{-0.58}$), and the mean scaling exponent among females from this study was used to provide size-adjusted mass-specific growth rates for females (g$_{fish}$ day^{-1} $M^{-0.73}$).

The importance of choosing an appropriate scaling exponent for bioenergetic comparisons of fish differing in size was revealed by sensitivity analysis. A 10% increase or decrease in the mass exponent for males resulted in a mean change in size-adjusted mass-specific growth rates of 18 and 22%, respectively, though the difference was typically <10% for the smallest age class of fish. This difference increased as the mass scaling exponent became larger; a 10% increase or decrease in the mass exponent for consumption resulted in 23 or 32% change in size-adjusted mass-specific consumption rates, respectively.

Perca flavescens vulnerability was assigned as a function of both prey size and the predator community present in a lake (Tables I and II). Using the data presented in Liao *et al.* (2002), predator-specific vulnerability limits (the size at which prey appear to escape predation, specific to each predator species) were estimated as the mean size of *P. flavescens* found in the stomachs of 'large' predators (defined in Table II). Depending on the predator

community in the lake and the size of the cohort, age classes of modelled *P. flavescens* were classified as 'vulnerable' (for ages with average sizes below the appropriate cut-off) or 'invulnerable' (Table I). Mean estimates of *P. flavescens* growth, consumption, activity and conversion efficiencies between life stages were compared using two-sample *t*-tests with a Welch's correction for unequal variance.

Because of differences in sampling protocols that made CPUE estimates for predators impossible to compare on the same scale between data sets, the effects of predation on *P. flavescens* bioenergetics in the study were analysed separately for each of the sampling protocols (FWIN and method B). Although the absolute values of predation indices differ between the two data sets, both should correctly indicate the relative effect of predation within their respective groups. Two of the lakes studied lacked predators. Because the index of predator abundance in these two lakes would have been zero regardless of the sampling protocol used, data from these two lakes were included with both the FWIN and method B data sets when examining the effects of predation index on *P. flavescens* bioenergetics.

RESULTS

EFFECTS OF PREDATION ON *P. FLAVESCENS* LIFE HISTORIES

The index of predator abundance was significantly related to life-history traits of *P. flavescens*. For both male and female *P. flavescens*, higher predator CPUE was associated with larger maximum body size [Fig. 1(a) and Table III], larger size at maturity [Fig. 1(b) and Table III] and later maturation in females only [Fig. 1(c) and Table III]. No significant relationship was found between predator CPUE with male age at maturity (Fig. 1 and Table III), life span or female reproductive investment (Fig. 2 and Table III).

There was a significant negative relationship between the predation index and GDD (linear regression, $F_{1,54} = 20.1$, $P < 0.001$). When included as a covariate, only GDD explained a significant proportion of the variation in female age at maturity (Table III; GDD: $F_{1,46} = 14.56$, $P < 0.001$; predation index, $F_{1,46} = 0.95$, $P > 0.05$), where female age at maturation was significantly and negatively related to GDD. GDD was not a significant covariate in any other relationships between predation index and life-history traits of *P. flavescens*.

EFFECTS OF PREDATION ON *P. FLAVESCENS* BIOENERGETICS

For small *P. flavescens* vulnerable to predation, predator CPUE was positively associated with size-adjusted specific growth rates for FWIN-sampled lakes only [Fig. 3(a),(b) and Table IV]. Similarly, growth of invulnerable *P. flavescens* was positively associated with size-adjusted specific growth rates, though only significantly so at the 0.05 level for FWIN-sampled lakes [Fig. 4(a),(b) and Table IV].

Perca flavescens displayed higher food conversion efficiencies as predator CPUE increased, regardless of vulnerability, though the pattern was consistently significant only for FWIN-sampled lakes [Figs 3(e),(f) and 4(e),(f) and Table IV]. No significant associations were found for predator CPUE with either adjusted specific consumption or activity rates for fish of vulnerable size, though there was a pattern of lower size-adjusted specific consumption rates and activity with increasing predation among FWIN-sampled lakes (Fig. 3 and Table IV). The pattern of declining consumption
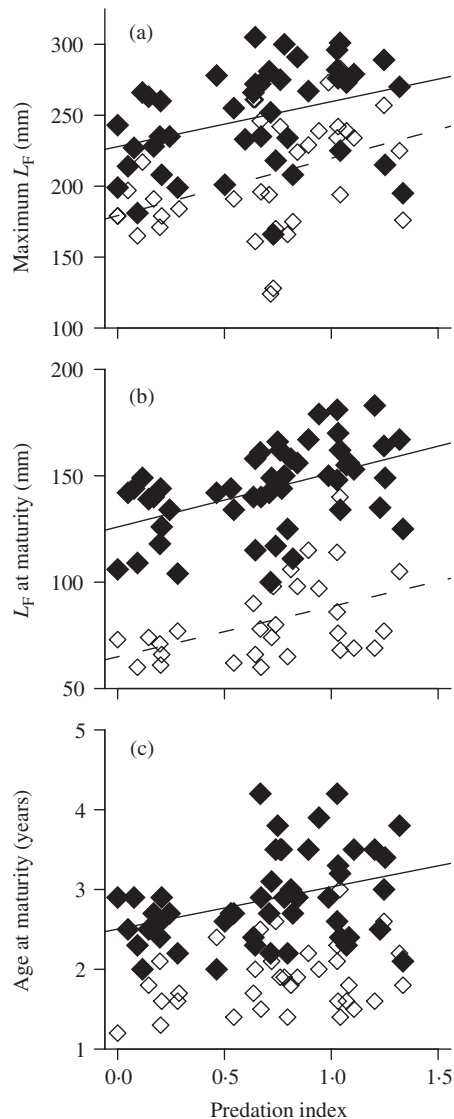
FIG. 1. Relationships between an index of *Perca flavescens* predation {estimated as the $\log_{10}$-transformed [$\log_{10}(x+1)$] mean catch per unit effort of *Esox lucius*, *Sander vitreus* and *Micropterus dolomieu* combined} with *P. flavescens* (a) maximum fork length (L_F), (b) L_F at maturity and (c) age at maturity for females (◆ —) and males (◇ - - -). Only significant relationships are shown. The curves were fitted by: (a) females $y = 31 \cdot 7x + 227 \cdot 8$ and males $y = 40 \cdot 4x + 179.2$, (b) females $y = 25 \cdot 3x + 125 \cdot 9$ and males $y = 23 \cdot 6x + 64 \cdot 9$ and (c) female $y = 0 \cdot 53x + 2 \cdot 50$.

and activity with increasing predation risk among invulnerable-sized fish tended to be more pronounced and more frequently significant statistically at the 0·05 level (Fig. 4 and Table IV).

Overall mean values for bioenergetic variables (*i.e.* size-adjusted specific consumption and growth rates, activity or conversion efficiency) did not differ significantly
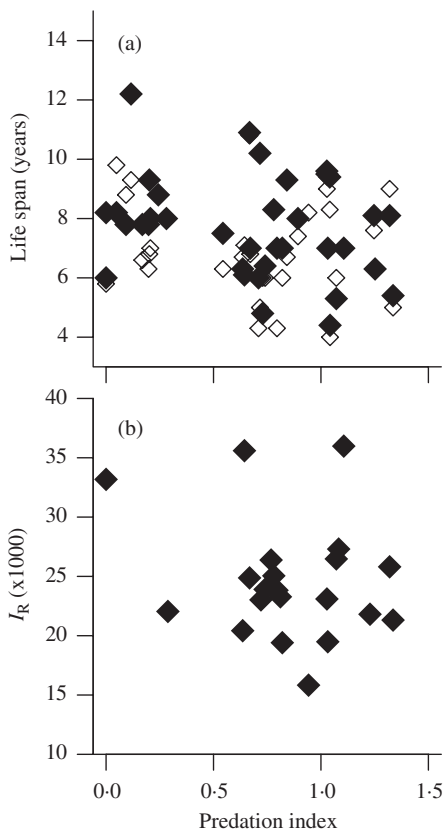
FIG. 2. Relationships between an index of *Perca flavescens* predation with (a) *P. flavescens* life span (◆, females; ◇, males) and (b) female reproductive investment (I_R).

between vulnerable and invulnerable life stages (all $P > 0.05$ for both males and females).

DISCUSSION

The results of this study, in whole, are consistent with the hypothesis that increased prey growth rates in the face of predation risk are a consequence of reduced activity. In both size classes of *P. flavescens* examined, size-adjusted specific growth rates and conversion efficiencies tended to increase, while estimated activity and size-adjusted specific consumption rates tended to decrease with increasing predation risk. Faster growth rates in lakes with greater predator densities despite lower consumption rates suggest two possible but non-exclusive causal mechanisms. One is that energetic savings resulting from reduced activity allow for a greater amount of surplus energy per unit of food consumed (Rennie *et al.*, 2005; Johansson & Andersson, 2009). Another alternative is that the relatively lower prey activity and foraging rates in lakes with greater predator densities could positively influence resource availability and quality. Realistically, both processes are probably at work in this study to some
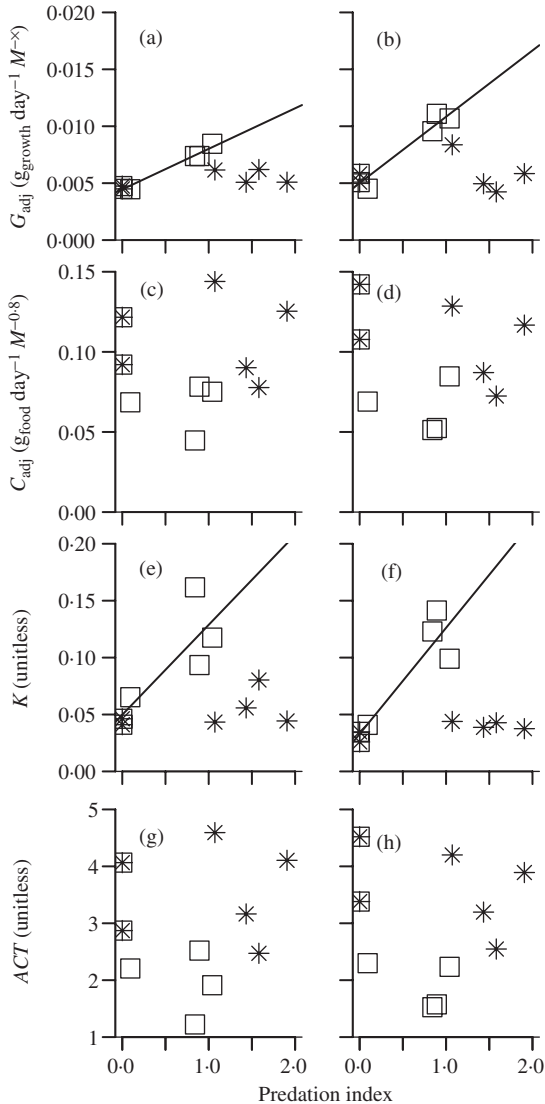
FIG. 3. Relationships between an index of predation with *Perca flavescens* (a), (b) size-adjusted specific growth rate [(a) $x = 0.73$ and (b) $x = 0.58$] (G_{adj}), (c), (d) size-adjusted specific consumption rates (C_{adj}), (e), (f) conversion efficiencies (K) and (g), (h) activity rates [ACT; expressed as a multiple of standard metabolic rates for (a), (c), (e), (g) females and (b), (d), (f), (h) males]. Results are for *P. flavescens* vulnerable to predation only. Populations sampled using 'Fall Walleye Index Netting' (□) and method B (✳). The curves were fitted by: (a) $y = 0.0036x + 0.0045$, (b) $y = 0.0058x + 0.0050$, (e) $y = 0.079x + 0.049$ and (f) $y = 0.093x + 0.033$.

degree. While direct measures of resource availability or quality do not currently exist for these study lakes, other studies show that behavioural modification in the face of increased predation risk can increase resource density (Abrams & Rowe, 1996; Peacor, 2002). Behavioural modification, however, may influence growth of

TABLE IV. Statistical summary of *Perca flavescens* bioenergetics relationships with an index of predation across populations. Relationships significant at $\alpha = 0.05$ are in bold. Direction of relationship reported for significant relationships as well as for non-significant relationships where a clear directional pattern was observed

Life stage	Variable	Sex	Lakes	d.f.	P	Direction
Vulnerable	Size-adjusted specific growth rate (g_{growth} day^{-1} M^{-X})*	**Female**	**FWIN**	**1,4**	**<0.001**	+
		Males	**FWIN**	**1,4**	**<0.01**	+
		Female	B	1,4	>0.05	
		Males	B	1,4	>0.05	
	Size-adjusted specific consumption rate (g_{food} day^{-1} $M^{-0.8}$)	Female	FWIN	1,4	>0.05	−
		Males	FWIN	1,4	>0.05	−
		Female	B	1,4	>0.05	
		Males	B	1,4	>0.05	
	Growth efficiency	**Female**	**FWIN**	**1,4**	**<0.05**	+
		Males	**FWIN**	**1,4**	**<0.01**	+
		Female	B	1,4	>0.05	
		Males	B	1,4	>0.05	
	Activity	Female	FWIN	1,4	>0.05	−
		Males	FWIN	1,4	>0.05	−
		Female	B	1,4	>0.05	
		Males	B	1,4	>0.05	
Non-vulnerable	Size-adjusted specific growth rate (g_{growth} day^{-1} M^{-X})*	**Female**	**FWIN**	**1,4**	**<0.05**	+
		Males	**FWIN**	**1,4**	**<0.05**	+
		Female	B	1,4	>0.05	
		Males	B	1,2	>0.05	+
	Size-adjusted specific consumption rate (g_{food} day^{-1} $M^{-0.8}$)	**Female**	**FWIN**	**1,4**	**<0.05**	−
		Males	FWIN	1,4	>0.05	−
		Female	B	1,4	>0.05	−
		Males	**B**	**1,2**	**<0.05**	−
	Growth efficiency	**Female**	**FWIN**	**1,4**	**<0.001**	+
		Males	**FWIN**	**1,4**	**<0.001**	+
		Female	**B**	**1,4**	**<0.05**	+
		Males	B	1,2	>0.05	+
	Activity	**Female**	**FWIN**	**1,4**	**<0.05**	−
		Males	**FWIN**	**1,4**	**<0.05**	−
		Female	B	1,4	>0.05	−
		Males	B	1,2	>0.05	−

FWIN, lakes sampled using Fall Walleye Index Netting protocol; B, lakes sampled using sampling method B.
*X, 0.58 for males and 0.73 for females.

prey independent of resource abundance. Rennie *et al*. (2005) demonstrated that in two lakes where resource availability did not differ, faster prey growth rates in the lake with predators were best explained by a reduction in energy allocated to activity, despite lower consumption rates (relative to the rates from a population in a lake without predators). A more recent study also clearly demonstrated the role of activity in altering growth and morphology of prey species, showing experimentally
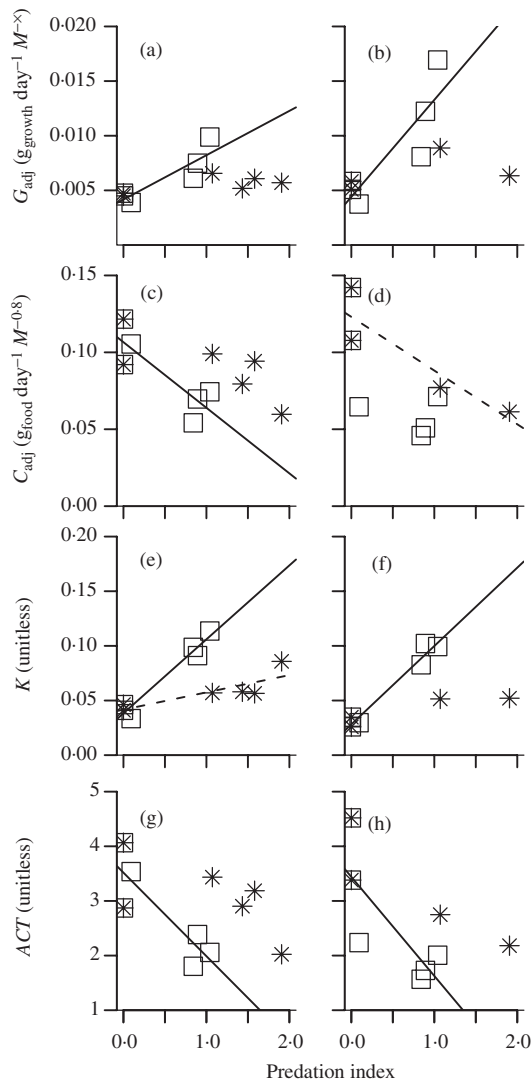
FIG. 4. Relationships between an index of predation with *Perca flavescens* (a), (b) size-adjusted specific growth rate [(a) $x = 0.73$ and (b) $x = 0.58$] (G_{adj}), (c), (d) size-adjusted specific consumption rates (C_{adj}), (e), (f) conversion efficiencies (K), and (g), (h) activity rates (ACT; expressed as a multiple of standard metabolic rates) for (a), (c), (e), (g) females and (b), (d), (f), (h) males. Results are for *P. flavescens* invulnerable to predation only. Populations sampled used 'Fall Walleye Index Netting' (☐) and method B (✳). The curves were fitted by: FWIN (a) $y = 0.0041x + 0.0042$, (b) $y = 0.0044x + 0.0089$, (c) $y = -0.043x + 0.107$, (e) $y + 0.068x + 0.038$, (f) $y = 0.072x + 0.028$, (g) $y = -1.53x + 3.52$ and (h) $y = -1.81x + 3.44$, and method B (d) $y = -0.035x + 0.123$ and (e) $y = 0.016x + 0.042$.

that reduced activity due either to perceived risk of predation or due to exclusion from water currents resulted in similar increases in growth rate and changes in body morphology (Johansson & Andersson, 2009). Daily ration in their study was a constant among all treatments. The selection for more moderate growth in the absence

of predation risk may be due to the physiological costs associated with rapid growth (Monaghan *et al*., 2009). Therefore, the trade-off in prey response to predators may be between fast growth to avoid perceived risk of predation mortality (facilitated by reduced activity) and the physiological costs of sustaining high metabolic rates (associated with rapid growth).

Overall, the relationships observed between *P. flavescens* life-history responses to increasing predation (as measured by a predation index) matched closely with theoretical predictions of predator-induced mortality in the literature (Dunlop *et al*., 2007). Using an individual-based eco-genetic model, Dunlop *et al*. (2007) simulated the harvest of young-of-year (YOY) fishes from a population and tracked the evolutionary life-history consequences of this harvest regime. In their model, harvest of small fishes closely simulates predator-induced mortality in natural systems, where gape limitations of predators often limit feeding on larger sized prey (Liao *et al*., 2002; Dunlop *et al*., 2007). As harvest rates of YOY fishes increased, size at maturation, asymptotic length and immature growth rate all increased (Dunlop *et al*., 2007). Similarly, as predation risk on *P. flavescens* in the present study increased, size at maturation, asymptotic length and size-adjusted specific growth rates all increased. While an increase in female age at 50% maturity was observed as predation increased, this pattern was not significant once the effect of GDD was accounted for.

Life-history schedules and modelled bioenergetics of *P. flavescens* reported here are also consistent with theory on the relationship between early growth rates and life-history patterns in fishes. Lester *et al*. (2004) demonstrated that maximum size is a function of early growth rate and reproductive investment. Reproductive investment in the system described here was invariant with predator abundance. As such, faster growth rates of *P. flavescens* at invulnerable life stages are expected to result in larger maximum sizes (as observed in the current study). Age at maturity was also invariant with predator abundance; though age at maturity scaled positively with predator abundance in females, the slope of this relationship was shallow (range of predicted values of only 0·7 years over the range of predator intensity observed) and was not significantly related to predator abundance after accounting for variation associated with GDD. Age at maturity is dependent on adult mortality rate (Shuter *et al*., 2005), which was also invariant with predation in the present study (as indicated by life span results). Given that adult mortality rate is relatively unaffected by predation (where predation mortality is focused primarily on smaller individuals), then age at maturation should also be relatively invariant. The combined effect of relatively invariant maturation age and faster juvenile growth rates should result in larger sizes at maturity, which were observed. In contrast, models which do not explicitly consider stage-dependent growth predict decreased maximum size and decreased size and age at maturity with faster growth rates (Roff, 1984; Jensen, 1996). The ability of a stage-dependent life-history model to explain the present results, while more simplistic models cannot, contributes to a growing body of evidence demonstrating the importance of a stage-explicit framework for understanding life-history patterns of organisms (Biro *et al*., 2006; Urban, 2007, 2008).

The lack of a significant relationship between predation and activity rates of smaller, vulnerable *P. flavescens* in the current study could be due to at least two possible causes. First, small fish may be growing as fast as possible, regardless of the presence of predators. If so, consumption and activity rates of small fish would be relatively insensitive to predation. Another possibility is that there may be limitations

in the models used in terms of how standard metabolism is characterized. Standard metabolic rate (R_s) in the bioenergetic model is a function of water temperature and body size. If prey fish exposed to predators have elevated R_s due to stress, this would not be accurately described by the model and instead manifest itself (as implemented in this study) as an increase in the activity multiplier. Thus, while activity rates in vulnerable *P. flavescens* could be declining with increased predation, increased stress levels resulting in elevated R_s could be masking this trend. Similarly, it is also possible that a loss of potential stress-related elevation in R_s of larger, non-vulnerable fish could explain why declines in activity with increased risk of predation were more clearly observable. Less-stressed larger fish, however, might be expected to be more rather than less active as the risk of being consumed declines, which is not the case for non-vulnerable *P. flavescens*.

It is unlikely that factors other than predation are responsible for the variation in life-history results reported here. While GDD was significantly associated with predation index and female age at maturity, it was not a significant predictor of any other variables. Using the same data set, Purchase *et al.* (2005*b*) found no significant relationships between life-history traits of *P. flavescens* and *P. flavescens* population density (measured as CPUE), neither was the CPUE of *P. flavescens* explained by the index of predation (linear regression, $F_{1,52} = 0.109$, $P > 0.05$). The relationship between predation index and GDD reflects the increased density of predator species with increases in latitude, probably a consequence of increased fishing pressure in the south of the province. Predator species are the main target of anglers in Ontario, and *P. flavescens* are with few exceptions ignored or of secondary interest to anglers; this is further reflected by the lack of any relationship linking *P. flavescens* CPUE with GDD (linear regression, $F_{1,55} = 1.37$, $P > 0.05$), in contrast to the pattern observed between GDD and predator CPUE.

A strategy of overall reduced activity of *P. flavescens* in lakes with more predators combined with highly variable feeding rates might also result in faster growth rates and higher conversion efficiencies. Recent work has demonstrated that fishes which were moved from a high-food to a low-food environment exhibit higher growth efficiencies than organisms exposed to either treatment alone (Gauthier *et al.*, 2008). Growth efficiencies of fishes are also highest in fishes with low food intake (Teskeredzic *et al.*, 1995; Gauthier *et al.*, 2008). Traditional bioenergetic models may not perform well when applied to situations where consumption rate is highly variable and compensatory growth results (Bajer *et al.*, 2003, 2004). Unlike traditional bioenergetic models, the current study used independently derived consumption rates from the mercury mass balance model to estimate activity using the bioenergetics model. If compensatory growth is occurring in *P. flavescens* in cases where the predator community is abundant, however, then observed reductions in activity rates could (at least in part) be due to hypothesized reductions in R_s associated with compensatory growth under variable ration levels (Bajer *et al.*, 2003). While direct observational data on activity rates to confirm the bioenergetic model output are lacking from the current study, other work on *P. flavescens* has shown that estimates of consumption and activity rates using this method correspond well with other methods of estimating fish activity (Sherwood *et al.*, 2002; Rennie *et al.*, 2005).

In summary, this study provides significant empirical evidence of predation affecting *P. flavescens* life histories through behavioural modification and supports predictions of both evolutionary models of predator-induced mortality (Dunlop *et al.*,

2007), as well as stage-dependent theoretical models of organismal growth (Lester *et al*., 2004). Further, this study provides evidence that patterns in life-history traits may be mediated through behavioural changes in activity associated with predation risk, primarily through a trade-off between growth and activity.

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APPENDIX. Lakes included in study. Note that predator indices for lakes sampled using method B are in different units and generated using different methods than those from 'Fall Walleye Index Netting' (FWIN) lakes and are not comparable between collection methods

Sampling method	Waterbody	Latitude and longitude	GDD	Predator index	Males					Females					
					N	T_m	L_m	LS	L_{max}	N	T_m	L_m	LS	L_{max}	I_R
B	Ashley	48·02° N; 80·82° W	1458	1·072	116	1·4	72	3·8	175	105	3	128	7·3	250	14 302
B	Lady Ruth	47·88° N; 80·78° W	1469	1·433	63	1·4	57	7·7	161	109	2·6	93	5·8	182	26 052
B	Margueratt	47·62° N; 80·85° W	1484	1·411	40	2·4	88	·	·	80	4·8	176	9	282	21 832
B	Melic	47·95° N; 81·03° W	1450	1·906	70	1·7	69	·	180	79	3	111	6	190	21 270
B*	Plastic	45·10° N; 78·49° W	1699	0·000	87	·	·	5·8	179	211	·	·	6·0	199	·
B*	Scolt	47·59° N; 81·03° W	1450	0·000	154	1·2	73	8·2	179	150	2·9	106	8·2	243	33 177
B	Trailer	48·00° N; 80·60° W	1495	1·581	71	1	56	·	117	138	2·1	88	5	191	37 833
FWIN	Agnew	46·35° N; 81·75° W	1643	0·288	66	1·7	·	·	184	36	·	·	·	·	22 044
FWIN	Balsam	44·58° N; 78·84° W	1825	0·201	512	1·3	61	6·8	208	729	2·6	144	9·3	260	·
FWIN	Belmont	44·48° N; 77·82° W	2004	0·145	19	1·8	74	·	·	25	2·5	139	·	263	·
FWIN	Biscotasi	47·17° N; 82·04° W	1475	0·463	28	2·4	·	·	·	83	2	142	·	278	·
FWIN	Buckhorn	44·48° N; 78·38° W	1937	0·206	222	1·6	66	7	179	657	2·9	126	8	208	·
FWIN	Burntbush	49·60° N; 79·98° W	1156	0·749	22	·	·	·	·	18	3·8	166	·	·	·
FWIN	Cameron	44·55° N; 78·75° W	1890	0·077	20	·	·	·	·	43	2·9	144	·	227	·
FWIN	Cataract	46·15° N; 83·00° W	1750	0·781	5	·	·	·	·	24	·	·	·	·	25 048
FWIN	Chemong	44·38° N; 78·38° W	1986	0·198	128	2·1	71	6·3	171	311	2·4	118	7·8	235	·
FWIN	Crotch	44·90° N; 76·80° W	2000	0·636	55	1·7	90	6·7	261	80	2·4	140	6·3	266	20 420
FWIN	Dalrymple	44·63° N; 79·10° W	1825	0·795	55	1·4	65	4·3	166	80	2·2	125	7	234	23 827
FWIN	Denbigh	45·12° N; 77·27° W	1750	0·716	68	·	·	5	124	116	2·2	100	10·2	252	·
FWIN	des Milles Lacs	48·85° N; 90·51° W	1385	1·203	35	1·6	69	·	·	26	3·5	183	·	·	·
FWIN	Dog	48·76° N; 89·54° W	1255	1·082	16	1·8	·	·	·	12	2·4	156	·	·	27 304
FWIN	Elephant	48·93° N; 93·58° W	1500	0·093	136	·	60	8·8	165	282	2·3	109	7·8	181	·
FWIN	Four Mile	44·67° N; 78·73° W	1810	0·530	26	·	·	·	·	48	2·7	144	·	·	·
FWIN	French River	45·93° N; 80·90° W	1735	0·820	110	·	·	6	175	130	2·7	111	7	208	19 409

APPENDIX. Continued

Sampling method	Waterbody	Latitude and longitude	GDD	Predator index	Males					Females					
					N	T_m	L_m	LS	L_{max}	N	T_m	L_m	LS	L_{max}	I_R
FWIN	Jack	44·68° N; 78·02° W	1825	0·243	46	·				58	3·3	170	7	276	19 488
FWIN	Jowsey	48·37° N; 81·72° W	1370	1·032	67	1·6	76	7	242	115	2·5	142	8·2	214	·
FWIN	Kasshabog	44·62° N; 77·95° W	1911	0·048	118	·		9·8	197	38	3	158	·	·	23 279
FWIN	La Cave	46·37° N; 78·75° W	1700	0·811	28	1·8	106			128	2	149	12·2	266	·
FWIN	Lower Paudash	44·97° N; 78·00° W	1750	0·116	83	·		9·3	217	89	2·2	104	8	199	·
FWIN	Madawaska	45·40° N; 76·40° W	2000	0·281	48	1·6	77			50	3·4	149	6·3	215	·
FWIN	Makokibatan	51·27° N; 87·35° W	1254	1·252	49	·				188	2·3	158	6·1	305	35 596
FWIN	Manitou	45·80° N; 82·00° W	1750	0·644	207	2		7·1	261	24	2·9	150	·	·	·
FWIN	Marian	46·77° N; 79·78° W	1629	0·987	31	·			273	·	·	·	·	·	·
FWIN	Mcfarlane	46·42° N; 80·95° W	1619	0·729	183	·	98	6	128	305	·	162	4·8	166	·
FWIN	Mindemoya	45·76° N; 82·20° W	1750	1·041	190	3	140	8·3	283	202	3·2	148	9·4	301	·
FWIN	Mink	45·56° N; 77·05° W	1961	1·027	35	2·3	114			197	2·6	134	9·6	296	·
FWIN	Mississagagon	44·87° N; 77·07° W	1825	0·544	64	1·4	62	6·3	191	129	2·7	140	7·5	255	·
FWIN	Moira	44·48° N; 77·45° W	1999	0·671	109	1·5	60	6·8	196	166	2·9	179	7	235	·
FWIN	Mountain	47·63° N; 80·22° W	1495	0·942	94	2	97	8·2	239	46	3·9	181	·	·	15 830
FWIN	Nagagamisis	49·47° N; 84·65° W	1244	1·028	206	2·1	86	9	234	195	4·2	150	9·5	282	23 097
FWIN	Nippigon	49·83° N; 88·50° W	1312	0·780	24	1·9				50	2·9	161	8·3	300	·
FWIN	Nippissing	46·28° N; 80·00° W	1659	0·668	372	2·5	78	10·8	246	437	4·2	140	10·9	272	24 873
FWIN	Pigeon	44·47° N; 78·48° W	1939	0·169	269	·		6·6	191	578	2·7	·	7·8	228	·
FWIN	Plastic	45·17° N; 78·82° W	1699	0·000	87	·		5·8	179	211	·	115	6	199	·
FWIN	Ramsey	46·28° N; 80·57° W	1613	0·645	29	·	66		161	54	·	144	·	272	·
FWIN	Rennie	48·38° N; 83·95° W	1288	0·768	17	·				54	3·5	125	·	·	26 380
FWIN	Rice	44·17° N; 78·18° W	2068	1·336	543	1·8		5	176	820	2·1	·	5·4	195	21 317
FWIN	Richard	46·43° N; 80·90° W	1618	0·502	19	·				30	2·6	·	·	201	·
FWIN	Round	48·00° N; 80·03° W	1487	0·893	196	2·2	115	7·4	229	119	3·5	167	8	267	·
FWIN	Saganash	49·04° N; 82·58° W	1333	1·320	118	2·2	105	9	225	139	3·8	167	8·1	270	25 807

APPENDIX. Continued

Sampling method	Waterbody	Latitude and longitude	GDD	Predator index	Males					Females					
					N	T_m	L_m	LS	L_{max}	N	T_m	L_m	LS	L_{max}	I_R
FWIN	Scolt	47·98° N; 81·05° W	1450	0·000	154	1·2	73	8·2	179	150	2·9	106	8·2	243	33 177
FWIN	Stormy	46·04° N; 79·46° W	1751	0·597	2	·	·	·	·	48	·	·	·	233	·
FWIN	Stumpy	47·58° N; 80·76° W	1488	0·841	65	1·9	98	6·7	224	45	2·9	156	9·3	291	·
FWIN	Thistle	46·67° N; 80·02° W	1650	0·721	42	2·1	74	·	·	27	3·1	149	·	·	23 021
FWIN	Vermillion	46·52° N; 81·38° W	1597	0·761	52	1·9	·	·	242	41	3·5	162	·	275	·
FWIN	Wabibigima	50·33° N; 86·37° W	1250	0·740	98	2·6	80	6	170	174	3·5	117	6·4	218	23 904
FWIN	Wakami	47·49° N; 82·85° W	1386	1·042	90	1·4	68	4	194	133	2·4	134	4·4	225	·
FWIN	White	48·77° N; 85·63° W	1251	1·071	53	1·6	·	6	239	69	2·3	155	5·3	273	26 474
FWIN	Whitefish	48·22° N; 90·00° W	1332	1·247	239	2·6	77	7·6	257	228	3	164	8·1	289	·
FWIN	Wildgoose	49·73° N; 87·15° W	1262	1·106	54	1·5	69	·	234	76	3·5	153	7	279	35 981
FWIN	Wolfe	44·68° N; 76·47° W	2000	0·709	61	·	·	4·3	194	88	2·7	142	6	281	·
FWIN	Wowun	49·17° N; 85·75° W	1282	1·228	9	·	·	·	·	24	2·5	135	·	·	21 809

GDD, growing degree days >5° C; N, number of fish sampled; T_m, age at 50% maturity; L_m, fork length (L_F) at 50% maturity; LS, life span (years); L_{max}, maximum L_T; I_R, index of reproductive investment; '·', no data.
*Lakes were included in life-history analyses of FWIN lakes, since predator absence was independent of sampling method.