

## Phenotypic variation of walleye, *Sander vitreus*, in Canadian Shield lakes: New insights on percid polymorphism

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### Synopsis

Literature on colour dimorphism in walleye has concerned only the blue form, *Sander vitreus glaucum* (formerly *Stizostedion vitreum glaucum*), historically found in lakes Erie and Ontario (Canada) and considered to be extinct from the fish fauna since the 1960s. In this paper, we report unusual observations of a blue form of walleye living in sympatry with the yellow form, *Sander vitreus* (formerly *Stizostedion vitreum*), in five lakes of the Canadian Shield, northern Québec. We compared head morphology, diet, and growth of the two forms to determine if there are any variations in characteristics other than colour and to examine the potential adaptive value of the two phenotypes. The blue form has a significantly longer head than the yellow form but does not differ in diet; the blue form also exhibits slower growth. The existence of a blue form of walleye in lakes of the Canadian Shield provides new insights into percid polymorphism and gives important information about their occurrence outside the Great Lakes area.

### Introduction

Phenotypic variation between populations of the same species is common in fishes, particularly in freshwater forms (Robinson & Wilson 1994). These variations are often interpreted as a result of selective pressures and are frequently associated with the initial stage of sympatric speciation (Skúlason & Smith 1995). Such phenotypic variations are well documented in Salmonid (Adams et al. 1998, Dynes et al. 1999), Gasterosteid (Schluter 1995), and Centrarchid (Robinson et al. 2000) species but are uncommon in percid fishes (Svanbäck & Eklöv 2002).

In walleye, *Sander vitreus* (formerly *Stizostedion vitreum*), the only case of phenotypic polymorphism reported in North America is in the Great Lakes, where walleye with an uncommon blue colouration were observed in the 1900s. The blue form of walleye, *S. vitreus glaucum*, com-

monly referred to as blue pike, are distinct from the usual yellow form in colour, size, growth rate, morphological features, and other biological characteristics such as a preference for deeper, cooler waters (Campbell 1987). At the beginning of the century, populations of the blue form of walleye were abundant in lakes Erie and Ontario (Canada). Due to overexploitation and environmental stress, they began to fluctuate greatly by 1915 and became extinct, with the last specimen being reported in 1965 (Campbell 1987, Wing & Glazier 1991). However, catches of this morphotype continued to be reported from this area (Morrison & King 2003<sup>1</sup>). Although the evolutionary status of the lineage had not been deter-

<sup>1</sup> Morrison, C. L. & T. L. King. 2003. Taxonomic status of blue pike *Stizostedion vitreum glaucum*: a molecular systematic comparison of nuclear and mitochondrial DNA regions. Pages 59 In Percis III, The Third International Percid Fish Symposium, Madison, Wisconsin.

mined using molecular data, the blue form of walleye was considered as a subspecies in the middle of the 20th century. However, a recent genetic study on museum specimens revealed that blue form is not a distinct species but rather a morphotype distinguishable at the population level (Morrison & King<sup>1</sup>).

In 2001, we caught walleye with the typical yellow colouration and others with an atypical blue colouration in five lakes of the Canadian Shield in northern Québec (Paradis 2004). This blue colouration was particularly dark on the dorsal surface of the fish, from the caudal peduncle to the head, and on their sides, especially above the lateral line (Figure 1). Except for colouration, both forms were visually similar and could not be distinguished *in situ* on the basis of other morphological criteria.

The objective of this study was to compare head morphology, diet, and growth of the two forms to determine if there are any variations in characteristics other than colour and to examine the potential adaptive value of the two forms.

## Materials and methods

### Study sites

We collected the data in July 2001 in five stratified headwater lakes of the Canadian Shield (Table 1). All the lakes are located within a 30,000 km<sup>2</sup> area around Réservoir Gouin, Québec (Table 1; see Carignan et al. 2000 for a detailed description of the study site). The watersheds of these lakes were undisturbed and the fish communities were generally unexploited or lightly exploited due to the limited access (all lakes were reached by aircraft). The fish communities of these lakes include northern pike, *Esox lucius*; white sucker, *Catostomus commersoni*; lake whitefish, *Coregonus clupeaformis*; yellow perch, *Perca flavescens*; and fallfish, *Semotilus corporalis*. We also found mottled sculpin, *Cottus bairdi*, in lakes CSL-2, DA-4, and K-2 while spottail shiner, *Nototropis hudsonius*, were sampled in lakes CSL-2 and DA-4 and burbot, *Lota lota*, in lakes K-1 and K-2.

### Fish sampling

We captured fish with experimental monofilament gillnets, 102.3 m long × 2.7 m deep, with stretched

mesh panels of 20, 24, 33, 36, 50, 60, 76, 90, and 100 mm (filament diameter of 0.17, 0.20, 0.20, 0.20, 0.20, 0.32, 0.32, 0.32, and 0.32 mm, respectively). We set gillnets perpendicular to the shore, with small and large meshes alternating from the shore among gillnets. We placed the nets at regular intervals around the lake, the first being randomly located using aerial photography. The fishing effort was six nets per night for lakes <50 ha, eight nets per night for lakes of 50–100 ha, and 10 nets per night for lakes of 100–150 ha (i.e., six nets per night for lakes K-1 and DA-4, eight nets per night for lakes CSL-2 and N-89, and 10 nets per night for Lake K-2). The nets fished for periods of 16–24 h, always covering the periods between 18:00 and 09:00 hours.

For each fish caught, we noted total length ( $\pm 1$  mm) and mass ( $\pm 0.1$  g); when possible, we determined sex by gonad examination. We also removed opercular bone structures for age determination. We classified walleye into three colour categories: yellow, blue, or intermediate. The yellow form was easy to classify because it has the species' typical colouration. In our study lakes, the blue colouration of some walleye was obvious (Figure 1). These walleye are covered with a blue mucus that leaves a bluish colour on one's hands after manipulation. We classified walleye with an ambiguous colouration as intermediate. We sampled 16 intermediate walleye in Lake CSL-2, 8 in Lake DA-4, 9 in Lake K-1, 25 in Lake K-2, and 14 in Lake N-89. Once classified as yellow, blue, or intermediate, we removed the specimen's stomach and head and preserved them in a 10% formalin solution for diet and morphometric analyses.

### Abundance, morphology, and diet analysis

To evaluate the abundance of the blue and yellow forms of walleye in each lake, we estimated catch per unit effort (CPUE) from gillnetting. In the laboratory, we made 10 external and two internal measurements (Figure 2) on the left side of the head with a digital caliper ( $\pm 0.01$  mm). Due to logistical constraints, namely the weight and space taken by the entire specimen in the aircraft, we restricted morphological analyses to the heads. Morphological differences between the blue and yellow forms of walleye reported by Stone (1948)



Figure 1. Colouration of blue and yellow forms of walleye: (a) general colouration of the yellow form, (b) dorsal zone of the yellow form, (c) general colouration of the blue form, (d) dorsal zone of the blue form.

for the Great Lakes were also based only on head measurements, making our comparison with the Great Lakes (the only area where this polymorphism has been reported) valuable. We classified prey from stomach contents into eight functional categories: fish, zoobenthos, zooplankton, amphipods, dipteran pupae, hirudinae, swimming insects, and terrestrial insects. The prey were dried for 12 h at 60°C before being weighed ( $\pm 0.0001$  g). We used the mean percent mass of each prey category (Hyslop 1980) to compare the diet of the two forms.

#### *Walleye age and growth*

We used the opercular bones for age determination of walleye (Babaluk et al. 1993). We placed pairs of opercular bones in a solution of soap and water overnight and then cleaned and dried them. We submerged the bone structure in immersion oil and determined age by counting true annuli at 10 $\times$  magnification on a black background according to

Pépin & Lévesque<sup>2</sup> for Québec's walleye population. We made two independent age readings. When the results were different, we made two additional readings; when there was still disagreement, we rejected the samples. Because not enough walleye were caught in lakes DA-4, K-1, and N-89 to construct body length to opercular length relationships, we made the back-calculation only in lakes K-2 and CSL-2. We measured the successive annual growth increments to the nearest 0.01 mm using a reticulated micrometer mounted on a dissecting microscope. We back-calculated body lengths at previous ages following the two proportional back-calculation methods: the scale-proportional hypothesis (SPH) and the body-proportional hypothesis (BPH) (Francis 1990). In each lake (K-2 and CSL-2), we constructed a body

<sup>2</sup> Pépin, S. & F. Lévesque. 1985. Techniques de détermination de l'âge des dorés applicables aux populations de cette espèce au Québec. Ministère Loisir Chasse et Pêche, Québec, 33 pp.

Table 1. General characteristics of the studied lakes and walleye forms.

Lake	Latitude(°N)	Longitude (°W)	Surface area (ha)	Mean depth (m)	Secchi depth (m)	Blue form		Yellow form		TL (mm) (mean ± SD)
						n	CPUE No. net <sup>-1</sup>	n	CPUE No. net <sup>-1</sup>	
CSL-2	48°51'	74°40'	84.9	10.2	2.8	27	3.38	24	3.00	327.3 ± 69.8
DA-4	48°11'	76°19'	25.9	6.7	1.6	2	—	5	0.83	400.2 ± 27.1
K-1	48°19'	75°16'	31.7	9.1	2.1	7	1.17	5	0.83	485.4 ± 105.3
K-2	48°17'	75°10'	142.2	12.2	2.4	18	1.80	33	3.30	249.9 ± 93.7
N-89	48°58'	74°02'	67.3	14.0	5.1	6	0.75	16	2.00	411.9 ± 105.3

n: sample size; CPUE: catch per unit of effort (number of fish captured per gillnet per day); TL: total fish length (mm).

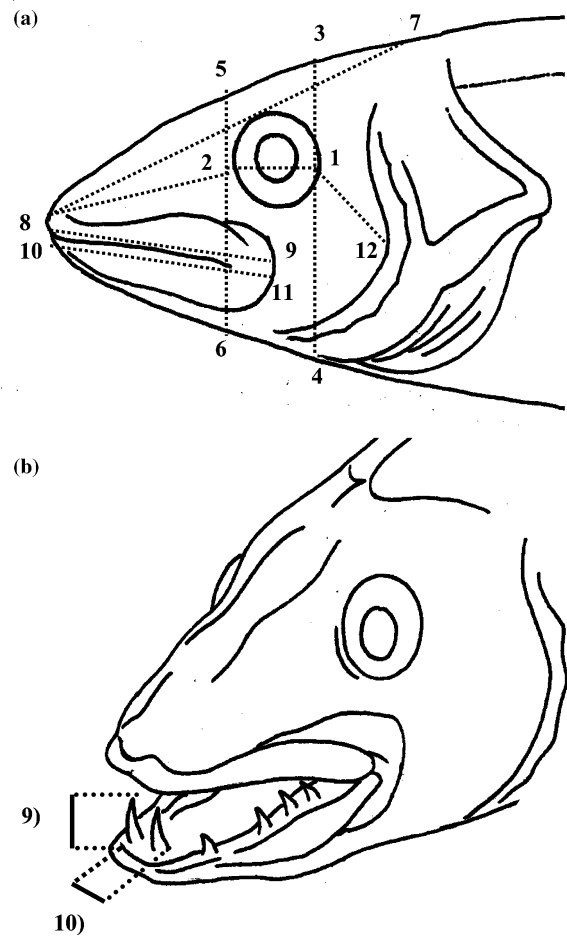


Figure 2. (a) Location of the ten external morphological characteristics measured on the head of walleye: eye diameter (1–2), postorbital head height (3–4), preorbital head height (5–6), head length (7–8), upper jaw length (8–9), lower jaw length (11–10–11), interorbital width (11), preorbital length (2–8), mouth width (11 left–11 right 1 left–1 right), and postorbital length (1–12). (b) Location of the two internal morphometric measures: canine height (9), and canine width (10).

length to opercular length relationship for the blue and yellow forms. Because the  $R^2$  values of these relationships were above 0.90 in both lakes, we found no substantial differences in fish lengths between back-calculation methods (SPH vs. BPH) (Pierce et al. 1996). In this paper, we only present the results computed with the SPH method.

#### Statistical analyses

For morphometric studies, it has been suggested that populations should be compared in terms of

shape variates, free from the effects of size variation (Reist 1986). We removed the effect of fish size and sex on head measurements with a regression technique (Fleming et al. 1994). First, we log-transformed the data of each morphological descriptor to meet conditions of regression (i.e., normality, linearity, and homoscedasticity of residuals). We then transformed each morphological character into a shape variate (regression residuals) by expressing it as the deviation of individuals from the pooled within-group regression line (blue and yellow forms) describing the relationship between that descriptor and head length (Reist 1986, Proulx & Magnan 2002). We used residual scatter plots, normal probability plots, and partial residual plots to determine if the assumptions of the regression were satisfied. These residuals are considered to be approximately independent of fish size and should reflect the variation resulting from measurement errors and biological deviations of individuals from the predicted character-length relationship (Kuhry & Marcus 1977). We used a stepwise discriminant function analysis (DFA) (with the jackknife procedure provided in SYSTAT 8.0; Wilkinson 1998) to test the hypothesis that the two forms of walleye, identified by their colour, were different on the basis of their head morphology. This also allowed us to determine the most useful descriptors for separating population groups (Legendre & Legendre 1998). We set the cut-off significance values for variable selection (i.e., *p*-to-enter and *p*-to-remove) to *p* = 0.15, as recommended in SYSTAT (Wilkinson 1998). We compared forward and backward methods of variable selection and retained only the final model with the lower *p* value. For intra-lake morphological comparisons, we computed DFAs only in lakes K-2 and CSL-2, where sample sizes were high enough to make this comparison. Walleye classified as intermediate were only available in Lake K-2 for morphological analysis. The DFA analysis was done with and without intermediates individuals in lake K-2 for comparison with lake CSL-2.

We tested if the mass of each prey category and the proportion of empty stomachs differed between the two forms with a Mann-Whitney *U*-test and a  $\chi^2$  test, respectively. Due to low sample size in lakes DA-4, K-1, and N-89, we only compared feeding habits of fish in lakes K-2 and CSL-2.

We used back-calculated lengths-at-age to compare intra-lake growth variations of the blue and yellow forms in lakes K-2 and CSL-2; the sample size was not high enough in the other lakes to make this comparison. For lakes K-2 and CSL-2, we first log-transformed the back-calculated data and then computed the mean lengths-at-age for blue and yellow forms. We then calculated the linear regression between the log of the mean back-calculated length and age for blue and yellow forms. In each lake (i.e., K-2 and CSL-2), we tested for differences in slope and intercept between the two regression lines using analysis of covariance (ANCOVA) with age as a covariate. Due to the low abundance of old walleye in our samples, ANCOVAs were computed on ages 1–7 in Lake K-2 and 1–10 in Lake CSL-2. We performed all statistical analysis using SYSTAT for Windows, version 8.0 (Wilkinson 1998).

## Results

The general characteristics of the study lakes as well as those of blue and yellow forms of walleye are given in Table 1.

### *Morphological variations*

The DFA (backward selection) of morphometric parameters yielded a significant difference between blue and yellow individuals in Lake K-2 ( $F = 3.668$ ,  $p = 0.035$ ; Table 2). Inspection of the canonical coefficients revealed that the blue form had a longer head and a larger space between canines than the yellow form. The *a posteriori* classification accuracy of the DFA (jackknife procedure) indicated that 8 of 13 (62%) blue individuals and 16 of 26 (62%) yellow ones were correctly reclassified, for an overall classification success of 62%. The DFA (backward selection) did not yield significant results when intermediate walleye were added to the analysis ( $F = 0.402$ ,  $p = 0.993$ ). The results of this analysis (not shown here) revealed that the morphology of intermediate individuals overlapped with that of the blue and yellow ones. In Lake CSL2, the DFA (forward selection) yielded a highly significant difference between the two forms of walleye ( $F = 4.680$ ,  $p = 0.007$ ;

Table 2. Results of the discriminant function analysis used to compare head morphology of yellow and blue forms of walleye.

Lake	Morphological variable (mm)	Blue	Yellow	Standard canonical coefficient	Wilk's lambda	F value	p
K2		(n = 13)	(n = 26)				
	Head length	46.31 ± 1.02	46.25 ± 1.01	1.120	0.8307	3.6679	0.035
Canine width	4.24 ± 1.06	4.16 ± 1.02	0.791				
CSL2		(n = 21)	(n = 20)				
	Head length	53.16 ± 1.01	53.12 ± 1.01	0.788	0.7249	4.6800	0.007
	Interorbital width	27.16 ± 1.01	28.29 ± 1.01	0.801			
Canine height	2.24 ± 1.03	2.44 ± 1.03	0.593				

Means ± SD (mm) were adjusted to a mean fish length of 303 mm in Lake K2 and 325 mm in Lake CSL2.

Table 2). Canonical coefficients revealed that blue form individuals had a longer head length, a shorter interorbital width, and a smaller canine height than yellow individuals. The *a posteriori* classification accuracy of the DFA indicated that 16 of 21 (76%) blue individuals and 15 of 20 (75%) yellow ones were correctly reclassified, for an overall classification accuracy of 76%. The degree of divergence between forms is illustrated by the frequency distributions of the discriminant function scores (Figure 3), showing the overlap between the blue and yellow forms.

#### Diet analysis

Blue and yellow walleye forms fed mainly on zoobenthos, swimming insects, and fish in our study lakes (Figure 4). Zooplankton, terrestrial insects, and amphipods were not observed in stomach contents while dipteran pupae and hirudinae were in low abundance. Blue and yellow forms did not show significant differences in the number of empty stomachs in lakes K-2 ( $\chi^2$  test:  $F = 0.822, p = 0.364$ ) or CSL-2 ( $\chi^2$  test:  $F = 1.569, p = 0.210$ ). Mann-Whitney tests on prey category weights showed no significant differences in the diets of blue and yellow individuals in Lake K-2 (zoobenthos:  $U = 318, p = 0.179$ ; swimming insects:  $U = 289, p = 0.552$ ; terrestrial insects:  $U = 270, p = 1.000$ ; fish:  $U = 234, p = 0.328$ ) or in Lake CSL2 (zoobenthos:  $U = 224, p = 0.243$ ; swimming insects:  $U = 301, p = 0.416$ ; terrestrial insects:  $U = 276, p = 1.000$ ; fish:  $U = 290, p = 0.719$ ) (Figure 4).

#### Growth analysis

In lakes K-2 and CSL-2, the mean age of blue individuals was  $6.8 \pm 2.9$  years (range: 4–13

years) and  $5.6 \pm 3.7$  years (range: 1–15 years) respectively while that of yellow ones was  $3.7 \pm 1.9$  years (range: 1–9 years) and  $5.5 \pm 2.3$  years (range: 3–11 years) respectively. In Lake K-2, the ANCOVA on the mean back-calculated lengths revealed no significant differences in the

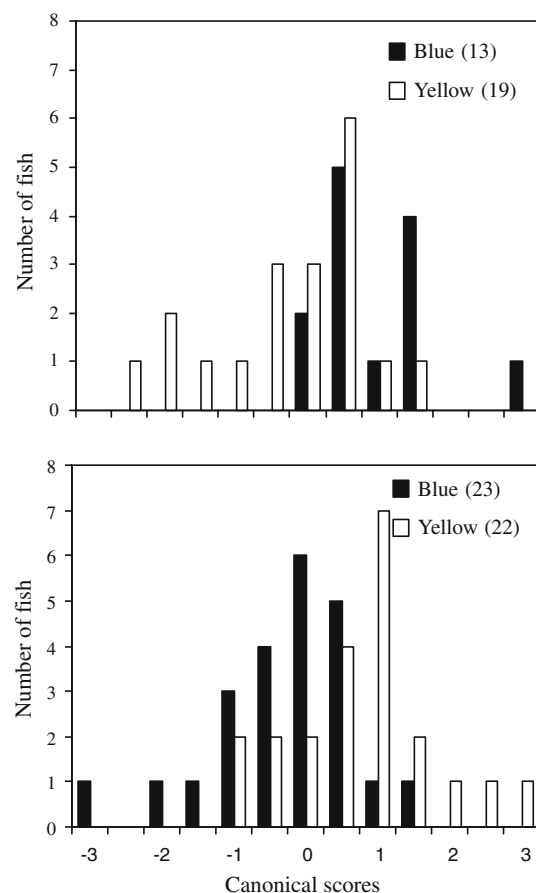


Figure 3. Frequency distribution of the discriminant scores for blue and yellow forms of walleye from lakes K-2 (a) and CSL-2 (b).

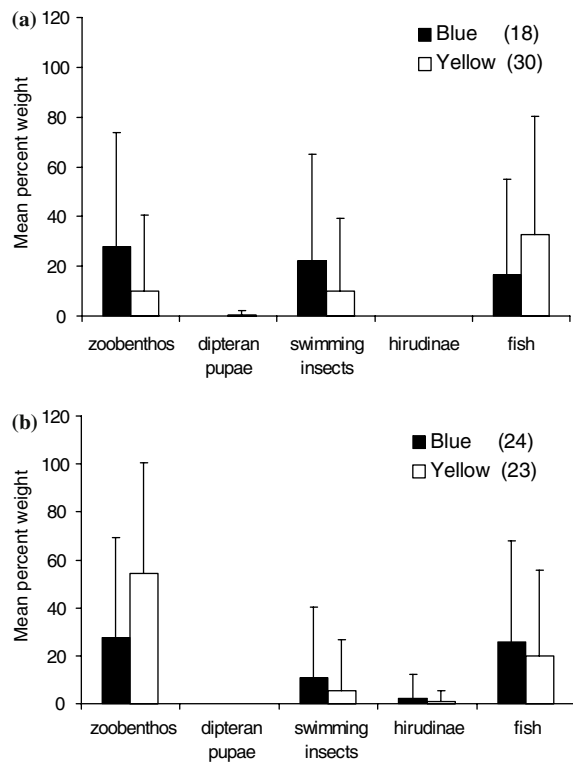


Figure 4. Mean percent weight of different food items in walleye stomachs from lakes K-2 (a) and CSL-2 (b).

slope of growth curves ( $F = 4.549$ ,  $p = 0.06$ ) but significant differences in the intercepts ( $F = 11.733$ ,  $p < 0.01$ ) between the two forms (Figure 5). In Lake CSL-2, the ANCOVA analysis of the regression line slopes indicated a significant effect of the form on walleye growth ( $F = 11.095$ ,  $p < 0.01$ ) (Figure 5). In both lakes, the slope or intercept of the regression lines indicated a longer length-at-age in the yellow form (except in ages 9 and 10 in Lake CSL-2).

## Discussion

This study is one of the first attempts to quantitatively characterize the differences in morphology, diet, and growth of yellow and blue forms of walleye outside the area of lakes Erie and Ontario (Canada). Despite the small sample size in three of our study lakes, our results indicate that the blue form was found in sympatry with the normal yellow form in five lakes; thus, this colour polymorphism is susceptible to be found in many Canadian

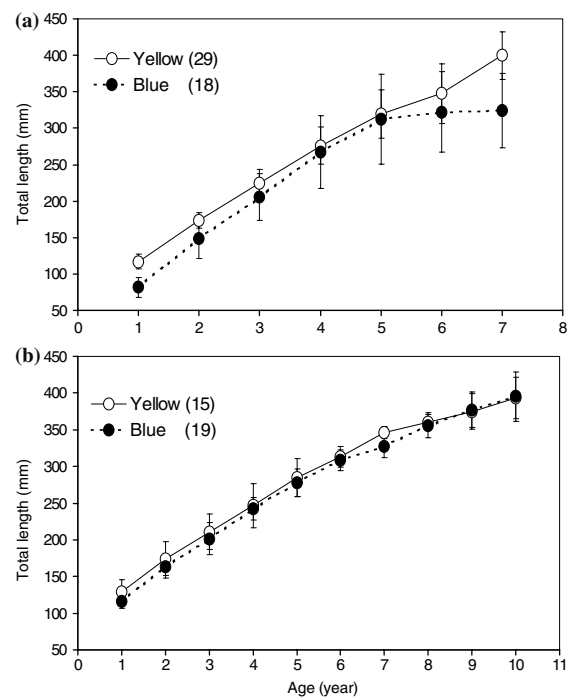


Figure 5. Mean back-calculated length-at-age ( $\pm$  standard deviation) of yellow and blue forms of walleye from lakes K-2 (a) and CSL-2 (b).

Shield lakes. Our DFA results also show that yellow and blue individuals can be discriminated quite efficiently with a few descriptors of head morphology. Results also suggest that forms do not differ in diet and that the growth of the blue form is slower than that of the yellow one. The only other study on phenotypic polymorphism of walleye was in the Great Lakes, where a blue morphotype was reported in the 1930s (Scott & Crossman 1973).

The colour of percid fishes is known to be highly variable, but the blue colouration of some walleye is not well understood. Hubbs & Lagler (1964) and Scott & Crossman (1973) reported that the blue forms of walleye in lakes Erie and Ontario were probably not identical to those found in other lakes in terms of the hue of the bluish colouration, head morphology, and growth rate. Regier et al.<sup>3</sup> and Scott & Crossman (1973) suggested that the bluish colouration of some walleye in Lake

<sup>3</sup> Regier, H., V.C. Applegate & R.A. Ryder. 1969. The ecology and management of walleye in western Lake Erie. Great Lakes Fish. Comm. Tech. Rep. 101 pp.

Nipissing (Ontario, Canada) came from a coloured mucus secretion that overlays the original yellow colouration.

The hypothesis of mucus secretion mentioned by Regier et al.<sup>3</sup> and Scott & Crossman (1973) to explain the bluish colouration of walleye in Lake Nipissing seems to be supported by our observations: the blue form of walleye in our study lakes leaves a bluish colour on one's hands after manipulation, supporting the hypothesis of a coloured mucus secretion. However, the origin of this colouration is unclear and will need further investigation. Because the great variability in colour of *Stizostedion* species depends on the habitat in which they live (Craig 2000), the blue and yellow colouration of walleye may be related to differences in habitat selection between the two forms.

Phenotypic variations in colouration, morphology, and diet are often associated with habitat segregation between benthic and pelagic forms of the same species (Robinson & Wilson 1994). Because no significant differences were observed in the diets of the yellow and blue forms, it is difficult to conclude that habitat segregation occurs between the blue and yellow forms. The blue form from the Great Lakes was known to use the deeper zone with cooler water (Campbell 1987). Because walleye in our study express the same phenotype as walleye in the Great Lakes, we hypothesize that the foraging habitat of the blue form is deeper than that of the yellow one in our lakes. Colour changes induced by coloured mucus secretion may produce a cryptic colouration in the blue form in deeper zones, which could be an advantage for approaching prey without being detected (Fujii 1993).

The analyses of morphological characters of walleye support the existence of two forms inhabiting the same lake. Walleye of Lake K-2 differed significantly in two variables (yellow forms had shorter head lengths and shorter canine widths than blue ones) while those of Lake CSL-2 differed in three morphological variables (yellow fish had shorter head lengths, larger interorbital widths, and longer canine heights than blue ones). It is generally hypothesized that the use of different resources is a major force promoting morphological diversification among individuals of a same species or between species (Schluter & McPhail 1993, Robinson & Wilson 1994). The

morphological analysis of walleye with intermediate individuals revealed that these individuals were not a distinct group from the blue and yellow walleye but overlapped with these two forms. It is noteworthy that a large number of walleye with intermediate colouration were also observed in the Great Lakes (Kendall 1920, Stone 1948). However, these intermediate individuals were not considered as a distinct group from the blue and the yellow walleye in the Kendall (1920) and Stone (1948) analyses. Intermediate individuals are probably generalists in terms of habitat selection and/or foraging strategies. Alternatively, the intermediate individuals could represent the middle of a gradient between two extreme forms. The test of these hypotheses would require a more specific sampling design.

One common discriminant variable selected by the DFA in lakes K-2 and CSL-2 is head length, which was significantly longer in the blue than in the yellow form. A longer head could be related to a higher efficiency in catching and handling larger prey (Gatz 1981). The stomach content analyses did not allow us to determine the prey size and thus it is not possible to investigate this hypothesis. However, if the blue form is more efficient at catching and handling larger prey, we should have found a higher proportion of prey fish in their diet, which was not the case. Stomach content analysis gives a short-term index (24–48 h) of feeding habits (Murphy & Willis 1996), thus a more detailed analysis of diet would be necessary to conclude on differences in the type or size of prey eaten by the blue and yellow individuals.

The only common morphometric trait discriminating the blue and yellow forms from the Great Lakes (Scott & Crossman 1973) and those in the present study is the interorbital width in Lake CSL-2, which was shorter in the blue than in the yellow form. The main difference between the two forms from the Great Lakes and the present study was the larger eye size of the blue form in the Great Lakes (Stone 1948) and the longer head of the blue form in the present study. The differences in phenotypic variation of walleye between the Great Lakes and Canadian Shield lakes may be related to intrinsic differences in available prey or habitat characteristics of the two systems (environmental component) or to genetic variations.

The growth analysis revealed that, for a given age, the yellow form is longer than the blue form. These differences in growth tend to be more important for juveniles (i.e., 1 and 2 years) than for adults (except for ages 6 and 7 in Lake K-2). Adamstone (1922) studied the growth rate of the blue and yellow forms of walleye in Lake Erie and observed a slight decrease in growth rate of the blue form during the second year of life and a very marked decrease near the fifth year. Deason (1933) observed that the blue form of walleye in Lake Erie was slower growing than the yellow form of walleye and the sauger, *Sander canadensis*. This difference in growth was interpreted as a basic physiological distinction between the two forms (Adamstone 1922). For juvenile walleyes, variations in growth are known to be related to the availability of forage fish (Craig 2000). Because walleye fingerlings and adults grow faster on a diet of fish than on a diet of invertebrates (Craig 2000), longer lengths-at-age of the yellow form in lakes K-2 and CSL-2 might be related to higher piscivory.

Slower growth in blue form juveniles can also be a consequence of a later larval emergence compared with the yellow form. In the Great Lakes, blue and yellow individuals were known to have distinct spawning habitats and spawning dates (April–June for the yellow form; May–June for the blue form) (Stone 1948). During the spawning season, the blue form exhibited offshore shoals and was found deeper than the yellow form, which spawned in nearshore shoals (Stone 1948). Like the blue form in the Great Lakes, the blue form in lakes K-2 and CSL-2 might have distinct spawning habitats and/or different spawning dates. Variability in the timing and location of spawning and reproductive behaviour is common in sympatric or parapatric fish morphs (Skúlason et al. 1989). A distinctive spatio-temporal spawning period could favour the progeny of the yellow form and thus explain the longer length-at-age of yellow fingerlings in our study. Such a reproductive isolation could also promote genetic differentiation between the two forms on an evolutionary scale.

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