Morphological and trophic differentiation of growth morphotypes of walleye (Sander vitreus) from Lake Winnipeg, Canada


Abstract: Ecologically related polymorphisms occur in many northern freshwater fish populations and are distinguished by alternate phenotypes consistently associated with differential use of habitats or resources. We tested for polymorphism in walleye (Sander vitreus (Mitchill, 1818)) in the south basin of Lake Winnipeg, where evidence suggests that “dwarf” and “normal” growth forms may coexist. Morphometric comparisons of these growth forms at similar size demonstrated significant differences in the relative sizes of head, snout, eye, and mouth, collectively suggesting dwarf individuals inhabit a more benthic niche than normal morphs. Stable isotope analysis did not support this morphometric interpretation, however, as $\delta^{13}$C and $\delta^{15}$N isotope signatures were similar between similar-sized individuals of both forms, but differed from those of large normal walleye. Walleye from Lake Winnipeg do not seem to exhibit a simple resource polymorphism where different ecotypes are associated with alternate habitats throughout their life history, nor do they exhibit characteristics of a simple mating polymorphism. We suggest the walleye from Lake Winnipeg represent two growth forms sharing a common juvenile habitat followed by the normal form shifting into an alternative adult niche.

Résumé : Des polymorphismes de nature écologique se produisent dans plusieurs populations boréales de poissons d’eau douce et se caractérisent par le fait que les différents phénotypes sont associés à une utilisation particulière des habitats ou des ressources. Nous avons vérifié le polymorphisme chez le doré (Sander vitreus (Mitchill, 1818)) dans le bassin sud du lac Winnipeg, où il y a des indications de coexistence de formes de croissance « naines » et « normales ». Des comparaisons morphométriques de ces formes de croissance à des tailles semblables montrent des différences significatives dans les tailles relatives de la tête, du museau, de l’œil et de la bouche qui, considérées conjointement, laissent croire que les individus nains occupent une niche plus benthique que les individus normaux. Une analyse des isotopes stables n’appuie, cependant, pas cette interprétation morphométrique puisque les signatures isotopiques $\delta^{13}$C et $\delta^{15}$N sont semblables chez les individus de même taille des deux formes, mais elles diffèrent de celles des dorés normaux de grande taille. Les dorés du lac Winnipeg ne semblent pas posséder un simple polymorphisme des ressources dans lequel les différents écotypes sont associés à des habitats différents pendant tout leur cycle biologique; ils n’ont pas non plus les caractéristiques d’un simple polymorphisme d’accouplement. Nous croyons que les dorés du lac Winnipeg comprennent deux formes de croissance qui partagent un habitat commun durant leur période juvénile et qu’ensuite la forme normale va occuper une niche adulte différente.

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Introduction

Unusual phenotypic variation regularly occurs within many fish taxa of northern temperate lakes, such as chars (Dynes et al. 1999; Jonsson and Jonsson 2001; Adams and Huntingford 2002; Keeley et al. 2005), whitefishes (Lu and Bernatchez 1999; Turgeon et al. 1999), sticklebacks (McPhail 1994; Kristjansson et al. 2002; Gray et al. 2005), and sunfishes (Jastrebski and Robinson 2004). Traits varying within species are often consistently associated with specific habitats or resources and include behavioural, life history, and morphological characters (Robinson and Wilson 1994; Skulason et al. 1996; Robinson and Parsons 2002). Polymorphism is most obvious when phenotypic variation is discontinuous within a population (Jonsson and Jonsson 2001), and is often thought to be maintained by some form of ecological specialization that has most likely evolved under diversifying selection. Ecological-based polymorphisms have been included as an early stage in some speciation models (Smith and Skúlason 1996; Schluter 2000; Bolnick and Fitzpatrick 2007).

One trait that frequently varies among coexisting forms is...
the rate of growth or size-at-age of the individual (Noakes et al. 1989), resulting in “normal” and “dwarf” individuals within polymorphic populations. Various models exist to explain polymorphic populations, including those composed of dwarf and normal forms. One of the more common models is that which considers the evolution of traits associated with trophic resource use (Smith and Skúlason 1996). When a population becomes free to utilize multiple resources in the absence of interspecific competitors or predators, the population undergoes ecological release which provides the opportunity for character release (Robinson and Wilson 1994), whereby forms diverge in response to selection imposed by specialization on alternate prey or habitats (Skúlason and Smith 1995). In lake fishes, feeding-related traits are often specialized for a particular niche such as benthivory, planktivory, or piscivory. Several studies have highlighted the relationship between dwarf and normal forms in a population and their trophic position (Hindar and Jonsson 1982; Chouinard et al. 1996; Guiguer et al. 2002). Dwarf forms are commonly found to inhabit an alternative niche, such as profoundal habitats where they feed on benthic resources (Hindar and Jonsson 1982; Winfield et al. 2002). Alternatively, where the benthic niche may already be occupied, the dwarf population may inhabit the pelagic habitat and feed on zooplankton (Lu and Bernatchez 1999). Explanations for the existence of differential growth forms have usually focused on the nutritional quality of different resources (Trudel et al. 2001), and intraspecific competition (Ylikarjula et al. 1999). Here, growth polymorphism is thought to be a consequence of local environment and resource conditions (Saint-Laurent et al. 2003; Andersson et al. 2005). However, in several cases, phenotypic life-history variants are accompanied by some degree of reproductive and genetic isolation suggestive of evolutionary responses to diversifying selection (Hendry et al. 2002; Proulx and Magnan 2004). These categories of proximal mechanisms reflect traditional distinctions, although polymorphisms may reflect a combination of both processes (Parsons and Robinson 2006). Phenotypes may evolutionarily diverge with respect to how their developmental systems respond to different conditions in alternate habitats.

Several mechanisms have been proposed to explain the emergence and maintenance of polymorphisms. Under the standard resource polymorphism hypothesis, the absence of interspecific competition in depauperate environments amidst strong intraspecific competition favors individuals that exploit alternate resources through frequency and density-dependent processes (Wilson and Turelli 1986; Smith and Skúlason 1996). This is expected to result in the evolution of an adaptive polymorphism where different morphs become increasingly specialized to feed in different habitats or on different prey resources. Alternatively, size polymorphism may reflect phenotypes of alternate mating forms (usually males) when their success is related to body size; examples are seen in some salmonids and in lekking species such as bluegill sunfish (Lepomis macrochirus Rafinesque, 1819) (Gross 1984). Lastly, polymorphism may represent an evolutionary or developmental response to variation in size-specific mortality in a population; for example, in a fishery, larger individuals face a greater risk of mortality than do smaller individuals.

Here, we examined a purported dwarfism that exists within a population of walleye (Sander vitreus (Mitchill, 1818)) in Lake Winnipeg, Manitoba, Canada. Lake Winnipeg is a large, shallow, and productive lake on the edge of the Canadian Shield (Evans 2000) that has supported a commercial fishery for over a century, with much of the fishing effort directed at walleye (Frazin et al. 2003). Analyses of sex-specific length-frequency distributions for each age class of walleye captured in stock assessment surveys from 1979 to 2003 indicated a bimodal size distribution in both sexes that was evident from ages four to seven inclusive (Johnston et al. 2010). This bimodality was most evident in walleye sampled in the south basin, but was weak or absent in walleye sampled farther north on the lake. The upper mode was defined as the “normal” form because it represented a size-at-age structure similar to other local, non-polymorphic populations of walleye (Johnston et al. 2010). Relatively few polymorphisms have been identified in percid populations (Svanbäck and Eklov 2002; Paradis and Magnan 2005), making the walleye from Lake Winnipeg a somewhat unique case.

Our goals in the current study were to further examine this size-based polymorphism in walleye from Lake Winnipeg and to begin to evaluate various hypotheses about its origins. We test predictions relating to the resource use hypothesis, but also discuss the evidence in the context of alternate mechanisms. Specifically, if the intraspecific diversity in walleye from Lake Winnipeg represents an adaptive resource polymorphism, then we predict that dwarf and normal forms will use distinct resources or habitats over most of their lifetimes. Because normal adult walleye are usually piscivorous and inhabit littoral environments (Craig 2000), we predicted that adult dwarf individuals will utilize benthic or planktonic resources to avoid competing with normal forms. We tested this prediction in two ways. First, we assessed whether variation in external body form corresponded to variation associated with the use of specific habitats or resources. For instance, gill raker traits (length and number) are often positively correlated with planktivory in fishes (Amundsen et al. 2004). Fish that inhabit benthic habitats often have larger heads and eyes, blunter snouts, subterminal mouths, and a less streamlined body compared with individuals occupying pelagic habitats (Schluter 1993; Skúlason and Smith 1995; Svanbäck and Eklov 2002). Second, we tested whether variation in body form was associated with a divergence in habitat use, as inferred through differences in trophic ecologies. Stable isotopes of carbon and nitrogen provide time-integrated information concerning resource use within aquatic food webs (Peterson and Fry 1987; Post 2002) and were used to compare the trophic ecologies of the two morphotypes. Finally, if this polymorphism represents adaptive optima that have evolved under diversifying selection imposed by different resources or environments, then all else being equal, the relative fitness of dwarf and normal forms should be roughly similar (Schluter 2000). In addition, phenotype should be related to fitness within each form so that individuals that possess more specialized body forms should have higher fitness than those with intermediate body forms (Robinson et al. 1996). To test these two predictions, we compared the whole body lipid concentration, as an index of fitness, between adult normal and dwarf...
individuals and also tested for an association between lipid concentration and external body form within morphs of walleye from Lake Winnipeg.

Materials and methods
Field sampling and fish processing
We sampled mature, normal walleye during the spring spawn in 2002, 2003, and 2004 near spawning shoals along the northwest shore of the south basin of Lake Winnipeg, Manitoba, Canada (51°00’N, 96°58’W). Immature, normal walleye, as well as mature and immature dwarf walleye, were sampled at this same location in the spring of 2004 only. At this time, spawning had just begun and most female walleye were unovulated (i.e., eggs not free-flowing). Large individuals (generally, >400 mm fork length) were lethally sampled using 100–150 mm stretched mesh monofilament gill nets. Dwarf individuals and smaller normal walleye were sampled using 25–62 mm stretched mesh monofilament gill nets. Subsamples of both males and females were selected haphazardly from the large mesh net samples, whereas all mature females and males and a haphazard subsample of immature fish were taken from the small mesh net samples.

Fish sampled in all years were processed following a similar protocol with a few additional steps for fish sampled in 2004. Each individual was identified for sex and maturity by visual inspection of the gonads, then weighed (total mass, ±10 g wet) and measured from the tip of the snout to the fork of the caudal fin (fork length (FL), ±1 mm). At this point, walleye sampled in 2004 were placed whole in labeled plastic bags and frozen so that they could be photographed for morphometric analyses (see below) before further processing. Carcass processing for all fish proceeded as follows. All tissue samples described below were kept in small plastic bags at −20°C once removed from the carcass. Gonads and liver were removed, weighed, and frozen for a concurrent study on reproductive ecology of the morphotypes. Carcasses were thawed, cut coarsely into pieces, and homogenized by passing three times through a commercial stainless steel meat grinder. A subsample (~25 g) of the homogenate was weighed (±0.1 g wet) into a glass vial and frozen at −20°C. Gonad, liver, muscle, and carcass homogenate subsamples were all freeze-dried for 7 days and re-weighed (±0.1 g dry) to estimate moisture contents. All freeze-dried tissues were ground to a coarse powder in a ball mill.

Ages were determined by counting annuli on sections of the sagittal otoliths. Otoliths were set in epoxy and sectioned through the nucleus and perpendicular to the longitudinal axis using a Buehler® Isomet low-speed saw. Sections were mounted in clear epoxy on a glass microscope slide and viewed under a compound microscope. The outer edge of the section was always counted as a complete annulus because fish were sampled at spawning season (i.e., near their birth dates). Individuals were classified as either dwarf or normal using criteria developed from age- and sex-specific length-frequency distributions generated from Lake Winnipeg stock assessment survey data (Johnston et al. 2010). Specifically, our criteria represented the least frequent FL value, or the midpoint in any range of least frequent values, between the two observed modal lengths in each of the age- and sex-specific length-frequency histograms. Thus, male walleye collected in this study were classified as “dwarf” if their FL was <260 mm at age four, <280 mm at age five, or <350 mm at any age older than five. Female walleye were classified as “dwarf” if their FL was <320 mm at age four or five, or <350 mm at any age older than five. Males and females that were larger at age than these thresholds were classified as “normal”. 

Analysis of body form
Morphological analysis of external body form involved the thin-plate spline (TPS) method of geometric morphometrics (Parsons et al. 2003; Adams et al. 2004). Variation in body form could either be compared between dwarf and normal fish of similar ages but different size, or between fish of similar (small) size but different ages. We used the second approach to avoid trophic differences that may arise from ontogenetic shifts in niche use. This allows a more conservative test of a standard resource polymorphism.

The right side of each individual was digitally photographed and 22 homologous landmarks covering the entire head and body (Fig. 1a) were digitized on each specimen using the software tpsDig2 (Rohlf 2007). Cartesian grid coordinates for the landmarks were then analyzed using tpsRelw (Rohlf 2007). This adjusts the geometric landmark data for variation induced by size, position, and rotation using generalized least-squares procedures (Rohlf and Slice 1990). It then estimates centroid size (a multidimensional estimate of body size) and a consensus (average) configuration used as a benchmark for comparison to each individual specimen. Shape variation of each sample is quantified as the partial warp scores of the individual compared with the consensus form. Partial warp scores represent the minimal “bending energy” required to deform the consensus form to that of each individual and are suitable for use in standard statistics. We statistically removed the allometric effects of size on shape variation by regressing partial warp scores against centroid size using tpsRegr (Rohlf 2007) and calculating residual partial warp scores.

Dwarf and normal morphotypes were treated as groups in a discriminant function analysis (DFA) of the residual partial warp scores. Discriminant scores were used as a measure of each individual’s morphology and Wilks’ λ was calculated to test the strength of evidence for group differences in external body form. Individual DFA scores were then regressed against the partial warp scores using tpsRegr (Rohlf 2007) to generate deformation grid plots allowing visualization of shape variation over the entire form.

The most anterior gill arch (closest to the operculum) was excised from the left side of each specimen after digital imaging and the total number of gill rakers including rudiments were counted. Raker length was then measured on
the axial and second longest rakers at 1.25× magnification using an ocular micrometer mounted on a dissecting scope.

We analyzed all dwarf individuals and a random subsample of normal individuals of similar size caught in 2004. Variation in gill raker traits were then analyzed using an ANCOVA model with morphotype as the class variable and FL as the covariate.

Stable isotope analysis

Stable isotope signatures were determined on the dried, ground muscle samples from 30 dwarf and 54 normal morphotype walleye sampled in 2004. Stable isotope analyses were performed with a Finnigan Mat Delta Plus continuous-flow isotope-ratio mass spectrometer connected to a Thermoquest NC2500 elemental analyzer (EA–CFIRMS). Carbon and nitrogen content were analyzed simultaneously with the elemental analyzer and converted to mole ratios of carbon to nitrogen (C/N). Stable isotope ratios were expressed as parts per mil (%δ) delta values (δ15N and δ13C) relative to international standards using the formula:

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\delta^{15}N = \frac{R_{sample} - R_{standard}}{R_{standard}} \times 1000
\]

where \( R = {^{15}N/^{14}N} \) or \( {^{13}C/^{12}C} \). The standards are atmospheric nitrogen and Pee Dee Belomnnte for nitrogen and carbon, respectively (Peterson and Fry 1987). Variation in \( \delta^{13}C \) and \( \delta^{15}N \) was analyzed by ANCOVA with morphotype as a class variable and FL as the covariate. Males and females were analyzed separately.

Body lipid analyses

Total lipid contents of the freeze-dried, homogenized tissues were determined gravimetrically using a chloroform:methanol extraction procedure modified from earlier studies. Detailed descriptions of our methods are provided elsewhere (Kaufman et al. 2007; Moles et al. 2008). Dry mass lipid concentrations were determined for the gonad, soma (body minus gonads), liver, and muscle samples of each fish. Somatic lipid concentration on a wet mass basis was estimated from the tissue moisture content and the dry mass lipid concentration and was used as our index of

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**Fig. 1.** Geometric morphometric analysis of shape differences between dwarf and normal walleye (*Sander vitreus*) captured on spawning reefs in Lake Winnipeg’s south basin in May 2004: (a) locations of the 22 landmarks used in the analysis; (b) normal and (c) dwarf morphotype shape grids as determined by canonical scores of a discriminant function analysis performed on partial warp values. Deformations of the shape grids represent the difference in body form between each morph and the mean form (the average form of all individuals combined) as represented by a grid of perfect squares. Grid deformations are exaggerated 3× for clarity.
body condition. We tested for differences in somatic lipid concentrations between morphotypes using an ANCOVA model with morphotype as the class variable and FL as the covariate.

**Results**

A total of 341 walleye were sampled from 2002 to 2004; of these, 270 were classified as normal morphotype (157 males, 113 females) and 71 were classified as the dwarf morphotype (49 males, 22 females) based on our size-at-age criteria. The dwarf group contained 11 immature individuals (2 males, 9 females), whereas the normal group included 89 immature individuals (57 males, 32 females). We captured numerous dwarf walleye that were older (≥8 years; Figs. 2a, 2b) than previously reported in Lake Winnipeg stock assessment surveys (Johnston et al. 2010). Divergence in growth trajectories between the two morphotypes was most pronounced beyond age five and was evident in both sexes (Figs. 2a, 2b).

**Variation in external body form**

External body form varied between dwarf and normal morphs of similar size (DFA, Wilk’s $\lambda = 0.312, F_{[40,152]} = 8.37, P < 0.0001$). Ninety percent of individuals were correctly assigned to their size-at-age morph classification (4 female and 11 male dwarf individuals were misclassified as the normal morph, whereas 1 female and 3 male normal individuals were misclassified as the dwarf morph). The most pronounced difference between walleye morphs was observed in the head region where dwarf individuals were characterized by a smaller, sloped head, shorter snout, and larger eyes relative to normal individuals (Figs. 1b, 1c). Dwarf individuals also had smaller mouths, with the maxillary extending only to the anterior margin of the eye, in contrast to normal individuals where the maxillary extended past the posterior eye margin. In addition, dwarf individuals had a shorter base for the first dorsal fin, a larger gap between the first and second dorsal fins, more upwardly angled pectoral fin insertions, and a shortened vertebral column relative to normal individuals.

**Variation in gill raker traits**

The number of gill rakers on the first branchial arch varied with body size in both sexes. In females, raker count increased more rapidly with body size in the normal form than the dwarf form (ANCOVA, interaction between morph and FL: $F_{[1,47]} = 18.1, P < 0.0001$). In males, this interaction was not significant (ANCOVA, interaction between morph and FL: $F_{[1,124]} = 0.80, P = 0.37$), and raker count increased with body size (ANCOVA, $F_{[1,124]} = 9.8, P = 0.002$). Mean raker count was slightly higher in dwarf males than in normal males, but the effect was not significant (ANCOVA, $F_{[1,124]} = 3.5, P = 0.065$).

Gill raker lengths did not differ significantly between walleye morphs. Raker length increased with body size in females and in males for both the apex and second longest raker (apex raker, males: $F_{[1,124]} = 33.8, P < 0.0001$; apex raker, females: $F_{[1,48]} = 39.8, P < 0.0001$; second longest raker, males: $F_{[1,124]} = 51.3, P < 0.0001$; second longest raker, females: $F_{[1,48]} = 34.9, P < 0.0001$). However, there was little evidence in either sex that the increase in raker length with body size varied between morphs (ANCOVA, interaction between morph and FL for either sex combination, all $P$ values ≥ 0.065). There was also no evidence for either sex that raker length varied significantly between dwarf and normal forms after adjusting for body size (apex raker, males: $F_{[1,124]} = 1.10, P = 0.30$; apex raker, females: $F_{[1,48]} = 0.88, P = 0.35$; second raker, males: $F_{[1,124]} = 0.58, P = 0.45$; second raker, females: $F_{[1,48]} = 0.29, P = 0.59$).

**Stable isotope variation between morphs**

Variability in both $\delta^{13}$C and $\delta^{15}$N was much higher among smaller individuals (<350 mm FL) than among larger individuals, although this did not appear to be related to morphotype (Figs. 3a, 3b). The highest observed $\delta^{15}$N values were seen in dwarf morphotype walleye (Fig. 3b). In all analyses of stable isotope ratios, interaction between morphotype and FL was not significant and the interaction term was dropped from the ANCOVA models. In female walleye, $\delta^{13}$C increased (Fig. 3a) and $\delta^{15}$N decreased (Fig. 3b) with FL (respective ANCOVAs, covariate effect: $F_{[1,40]} = 66.5, P < 0.0001$ and $F_{[1,40]} = 7.4, P < 0.001$). There was no consistent difference between morphs in either isotope ratio (ANCOVA, morph main effect: $\delta^{13}$C: $F_{[1,40]} = 0.48, P = 0.52$; $\delta^{15}$N: $F_{[1,40]} = 0.003, P = 0.96$).
Fig. 3. Comparison of muscle stable isotope ratios of (a) carbon ($\delta^{13}$C), and (b) nitrogen ($\delta^{15}$N) versus fork length (FL) relationships for dwarf (open symbols) and normal (solid symbols) morphotypes of female (circles) and male (triangles) walleye (Sander vitreus) sampled from the Hecla and Sandy Bar region of Lake Winnipeg’s south basin during the spawning period of May 2004.

Somatic lipid content

Somatic lipid concentration was lower for immature fish than mature fish for both morphotypes. Thus, morphotypes were compared separately for each sex and maturity state. Interaction between FL and morph was not significant in any analyses and the interaction term was dropped from the ANCOVA models. For immature females, somatic lipid concentration increased with fork length (ANCOVA, $F_{[1,36]} = 5.90$, $P = 0.020$), but did not differ significantly between morphotypes (ANCOVA, $F_{[1,36]} = 0.94$, $P = 0.34$). We did not conduct this analysis for immature males because of a small sample size ($n = 2$) for the dwarf morphotype. For mature females, somatic lipid concentration showed no relationship with FL (ANCOVA, $F_{[1,91]} = 0.51$, $P = 0.48$). Mean somatic lipid concentrations of the normal form were higher than those of the dwarf form (10.5% vs. 8.5%), although this difference was not statistically significant (ANCOVA, $F_{[1,91]} = 3.87$, $P = 0.083$). Finally, for mature males, somatic lipid concentration did not vary significantly with FL (ANCOVA, $F_{[1,142]} = 1.91$, $P = 0.17$) or between morphotypes (ANCOVA, $F_{[1,142]} = 1.34$, $P = 0.25$).

We further examined the relationship between condition, expressed as somatic lipid content, and body form using an alternate approach. We developed an ANCOVA model using maturity as a class variable and the DFA scores from the morphometric analysis as a covariate representing body form. The mean body form corresponds to a DFA score of zero, whereas more negative and more positive DFA scores correspond to increasingly normal and dwarf body forms, respectively. We restricted this analysis to the range in body size common to both morphotypes (<350 mm FL). In both males and females, somatic lipid content appeared to be positively related to the DFA body form score, but the trend was influenced by state of maturity (Figs. 4a, 4b). For both sexes, there was no significant interaction between the DFA score and maturity, and this term was removed from the models. For females, somatic lipid content was positively related to DFA score (ANCOVA, $F_{[1,48]} = 7.69$, $P = 0.0079$) but did not differ between maturity states (ANCOVA, $F_{[1,48]} = 0.65$, $P = 0.42$) (Fig. 4a). In contrast, for males, somatic lipid content increased with DFA score, although the trend was not significant (ANCOVA, $F_{[1,134]} = 2.13$, $P = 0.15$), and somatic lipid content was significantly higher in mature fish than in immature fish (ANCOVA, $F_{[1,134]} = 38.0$, $P < 0.001$) (Fig. 4b).

Discussion

Our results confirmed the existence of two distinct growth morphotypes of walleye in southern Lake Winnipeg, a slower-growing dwarf form and a faster-growing normal form, and shed new light on the nature of the divergence between these two morphotypes. Compared with earlier research on this population (Johnston et al. 2010), we sampled with a wider range of gill net mesh sizes and utilized ageing structures with greater resolution (otoliths rather than scales). In doing so, we examined a wider size range of the dwarf morphotype and demonstrated that it has a much greater longevity than previously reported.

Differences in external body form, especially in the head region and in fin position, suggest that the dwarf form may inhabit a more benthic niche than the normal form (Skulason and Smith 1995). However, gill raker traits did not differ markedly between the morphotypes. Gill raker morphology of these walleye suggests that neither morphotype is a significant adult planktivore (Amundsen et al. 2004). Benthivory in dwarf forms is common in other fishes such as whitefishes (Lu and Bernatchez 1999) and salmonids (Noakes et al. 1989), and is usually interpreted as indirect evidence that different morphs utilize different habitats and (or) resources (Bjørn and Sandlund 1995; Jonsson and Jonsson 2001). Benthic invertebrates are a viable alternative to fish as prey for walleye (Craig 2000; Paradis et al. 2006), and should these morphotypes be differentiated in this manner, then the Lake Winnipeg population would represent the...
The origin of the ex-
juvenile normals (Hindar and Jonsson 1982; Parker et al. 2000). Ontogenetic niche shifts are common in fishes and (or) habitat specializations. Walleye are widely consid-
ered to be littoral piscivores as adults (Lyons 1987; Craig 2000). Ontogenetic niche shifts are common in fishes (Werner and Gilliam 1984), including walleye (Craig 2000), and there is some evidence in other polymorphic species that dwarf individuals can share habitats and resources with juvenile normals (Hindar and Jonsson 1982; Parker et al. 2001; Claessen and Dieckmann 2002). The origin of the ex-
ternal body form of dwarf walleye in Lake Winnipeg may reflect neoteny whereby traits common to the early juvenile period are retained for primary use of benthic resources. Although juvenile ecology of the dwarf morphotype is largely unknown, it is unlikely that a standard resource poly-
orphism model (Smith and Skúlason 1996), whether as a function of energetic intake (Trudel et al. 2001) or habitat–
phenotype associations (Taylor 1999), describes the pheno-
typic differentiation of walleye in Lake Winnipeg.

Alternatively, the similar isotopic ratios of dwarf and small normal walleye may reflect some insensitivity of our isolate analysis. Baseline isotope ratios for different prey taxa from different lake habitats were not obtained and may have provided greater discriminatory power in our analyses (Overman and Parrish 2001; Post 2002). However, baseline isotopic information is of limited value if the origins of the fish cannot be determined. The walleye congregating to spawn at our sampling site may have arrived from widely divergent areas of the lake. Baseline isotopic signatures have been shown to vary among the basins of Lake Winni-
peg (Stewart et al. 2003), and thus, fish movements of this scale could drastically increase the observed variability in isolate ratios.

We now turn our attention to the relative performance of different walleye morphs to infer patterns of selection that may operate in this system. Body lipid concentrations are a good measure of surplus energy and performance in fishes because lipid contributes to both survival and reproductive success (Robinson et al. 1996; Adams 1999). We hypothe-
sized that if selection favoured the divergence between normal and dwarf body forms that the dwarf form would exhibit higher performance than the normal form at similar body sizes. Our analyses of body lipid content provided partial support for our prediction. After accounting for variation owing to sex, maturity, and body size, we found no significant difference in somatic lipid contents between the dwarf and normal morphotypes. However, when we restricted the analysis to fish within the size range common to both mor-
phs (<350 mm FL), we did observe a positive relationship between body lipid content and dwarf body form (represent-
ed by morphometric scores), though this was only significant for females. Thus, at small body sizes (<350 mm FL), directional selection may favor a more dwarf-like, and possibly more benthic, body form. Presumably, the more normal body form offers selective advantages at larger body sizes; traits such as larger and more terminal mouths on larger heads may be better suited for predation on large-
bodied forage fishes. This suggests selection pressures on body form of walleye may shift over the ontogeny of normal individuals, whereas dwarf forms experience more consistent directional selection. However, the relative fitness of dwarf and normal walleye will depend not only on growth and morphometric differences, but also on associated differences in reproductive strategies and mortality rates.

The possibility remains that nonresource-based mechan-
isms could be directing the polymorphism in walleye from Lake Winnipeg. Our results allow us to rule out that the ob-
served variation reflects different ontogenetic stages inhab-
iting different niches because both dwarf and normal forms contained both immature and mature fish. Our results are also not consistent with reproductive polymorphisms, such

![Graph](image-url)
as male competition for access to limited females (Gross 1984; Telnes and Saegrov 2004) that arise from differences in mating tactics, spawning site choice, or philopatry (Gross 1996). Spawning site and philopatry seem unlikely factors promoting this walleye polymorphism because spawning individuals of both forms were caught at the same time and place (Moles et al. 2010). Behavioural differences in spawning, such as “sneak” mating in males (Taborsky 1994) are often associated with variation in body form and size, but this also seems an unlikely mechanism here. Mating polymorphisms generally predict size, behavioral, and life-history differences among males but not females because small females experience no obvious reproductive advantage.

Bottom-up resource effects are the most common mechanism thought to drive polymorphism (Gross 1984; Smith and Skúlason 1996), even though top-down ecological effects, such as predation, also favor polymorphism in some birds (Galeotti et al. 2003), invertebrates (Palma and Steneck 2001; Johannesson and Ekedahl 2002), and fishes (Chipp et al. 2004; Doucette et al. 2004). Predation is not expected to impose strong selection on top predators like walleye because as adults at least, they have few natural predators. However, predation on juveniles could lead to polymorphism (Claessen et al. 2002; Klemetsen et al. 2003; Persson et al. 2004). Cannibalism is commonly observed both among (Claessen et al. 2000) and within (Li and Mathias 1982; Craig 2000) fish cohorts. Cannibalism within cohorts can reduce competition for resources and provide an energetic bonus allowing canibals to grow into abnormally large “giants”, while noncannibal conspecifics develop into smaller “dwarfs”. Alternatively, plastic developmental responses of older cohorts feeding on younger cohorts can generate a polymorphism that fluctuates if cannibalism is density-dependent (Li and Mathias 1982; Svanba¨ck and Persson 2004). The observed similarity of isotope ratios between dwarf and small juvenile normal walleye, and the relative low δ15N of the larger normal walleye, are not consistent with either of these scenarios. Furthermore, cannibalism is most frequently observed where prey fish of other species are rare or absent, and it usually results in a population with relatively few large carnivals but many small individuals. These conditions seem inconsistent with the forage fish community and the population of walleye in Lake Winnipeg.

An intriguing alternative is that fishing mortality may have contributed to polymorphism in walleye from Lake Winnipeg. The Lake Winnipeg fishery primarily employs gill nets and the minimum mesh size allowed is tightly regulated. The susceptibility of a given fish depends on its body size relative to the gill net mesh size. Fishing mortality is strongly size-selective towards larger (and faster-growing) fish. Dwarf morph walleye probably have very low susceptibility to the minimum mesh size (currently 76 mm stretched mesh for southern Lake Winnipeg) for most of their life span. Lower adult mortality, relative to the normal form, may lead to a greater number of lifetime reproductive opportunities for the dwarf form. Increasing evidence suggests that commercially exploited marine fishes often mature at a younger age or grow more slowly perhaps as a response to the higher mortality inflicted upon faster-growing and larger fish (Heino and Godo 2002; Hutchings 2005). Dwarf walleye in Lake Winnipeg may be favored if their lifetime reproductive success equals or exceeds that of normal forms. Polymorphism is maintained if diversifying selection favours both forms or if directional selection against the normal form is relaxed in space or time. For example, variable fishing pressure could periodically release normal forms from predation allowing them to increase because of their superior fecundity. Alternatively, spatially heterogeneous fishing pressure could preserve subpopulations of normal forms that, through migration or dispersal, would maintain variation in the population. Fishing effort on the percid community in Lake Winnipeg is most intense in the south basin (Franzin et al. 2003) where dwarf walleye are most common (Johnston et al. 2010).

Dwarf forms may persist if the reduction in lifetime fecundity owing to small adult size is offset by a reduction in adult mortality, also owing to small adult size. For example, Parker et al. (2001) determined the ratios of fecundity ($r$) to mortality ($\mu$) in dwarf and normal Arctic char (Salvelinus alpinus (L., 1758)) and used them to predict states that favored polymorphism versus monomorphism in high-arctic lakes. A similar approach could be taken with respect to the walleye from Lake Winnipeg. For example, the ratio of fecundity to mortality may be roughly similar between walleye forms if the superior fecundity of normal forms comes at the expense of increased mortality imposed by the walleye fishery. Estimates of fecundity suggest that normal females produce, on average, 10 times the number of eggs per spawn than dwarf females (Moles 2006). All else being equal, normal walleye would have to encounter 10 times the mortality experienced by the dwarf form for the two forms to have comparable fitnesses. But this may be an overestimate for several reasons. For instance, although dwarf individuals appear to mature at the same age, if they have longer life spans resulting in a greater number of spawns, then lifetime reproduction may approach that of normals. It also appears that dwarf forms produce higher quality eggs (Moles et al. 2010) which could increase juvenile survival and further reduce the effect of fecundity differences between forms. Accurate estimates of the relative mortality and lifetime fecundity of dwarf and normal walleye in Lake Winnipeg are required to predict the outcome of fishery-induced predation in this system.

**Conclusions**

Polymorphism in fishes predominate in fairly depauperate communities with empty niches awaiting colonization by enterprising conspecifics (Robinson and Wilson 1994). In contrast, the only known case of size and shape polymorphism in walleye occurs in Lake Winnipeg within a diverse fish community of at least 58 species (Franzin et al. 2003), particularly in the south basin, where an ecologically similar congenic species (sauger, Sander canadensis (Griffith and Smith, 1834)) is also present. Despite this community diversity, walleye exhibit divergent growth forms that are associated with different adult but not juvenile niches. Dwarf forms may have a paedomorphic origin that has either evolved under or represents a plastic developmental response to a more benthic habitat. Variation in walleye from Lake Winnipeg likely does not represent either typical life-history variation or a reproductive polymorphism. Dwarf
forms may also be a response to natural or anthropogenic predation. We suggest a theoretical framework in which to analyze growth and phenotypic variation that results from size-specific mortality imposed by a commercial fishery but conclude that any predictions rely on accurate estimates of size and age-specific mortality in both forms. If fisheries-imposed predation is a key mechanism contributing to the intraspecific divergence of walleye from Lake Winnipeg, then this would be the first case of fishery-induced polymorphism in freshwater fishes.

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