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Lazy males? Bioenergetic differences in energy acquisition and metabolism help to explain sexual size dimorphism in percids

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Summary

1. Differences in energy use between genders is a probable mechanism underlying sexual size dimorphism (SSD), but testing this hypothesis in the field has proven difficult. We evaluated this mechanism as an explanation for SSD in two North American percid species – walleye *Sander vitreus* and yellow perch *Perca flavescens*.

2. Data from 47 walleye and 67 yellow perch populations indicated that SSD is associated with the onset of maturation: typically, males of both species matured smaller and earlier and attained a smaller asymptotic size than females. Males also demonstrated equal (perch) or longer (walleye) reproductive life spans compared with females.

3. To examine whether reduced post-maturation growth in males was due to lower energy acquisition or higher reproductive costs we applied a contaminant mass-balance model combined with a bioenergetics model to estimate metabolic costs and food consumption of each sex. Mature males exhibited lower food consumption, metabolic costs and food conversion efficiencies compared with females.

4. We propose that slower growth in males at the onset of maturity is a result of decreased feeding activity to reduce predation risk. Our finding that SSD in percids is associated with the onset of maturity is supported by laboratory-based observations reported elsewhere, showing that changes in growth rate, consumption and food conversion efficiency were elicited by oestrogen (positive effects) or androgen (negative effects) exposure in *P. flavescens* and *P. fluviatilis*.

5. Researchers applying bioenergetic models for comparative studies across populations should use caution in applying bioenergetic models in the absence of information on population sex ratio and potential differences between the sexes in energetic parameters.

Key-words: sexual dimorphism, activity, consumption, reproductive investment, walleye, yellow perch.

Introduction

Sexual dimorphism is common in nature, and is thought to arise from differential selection of the sexes (Darwin 1871). If selection leads to sexual size dimorphism (SSD), a consequence should be disparity in the optimal life history strategies of males and females. Proximate mechanisms for SSD are gender differences in either energy allocation or acquisition, both of which have been observed in the animal kingdom (fish: Roff 1983; Holtby & Healey 1990; Henderson *et al.* 2003; insects: Mikolajewski *et al.* 2005; lizards: Cox, Skelly & John-Alder 2005; Fuselier *et al.* 2007; mammals: Isaac 2005). Although vertebrates typically display male-dominated SSD

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(males larger than females: Isaac 2005), female-biased SSD occurs throughout the taxa (Roff 1983; Zamudio 1998; Isaac 2005). Female-biased SSD is attributed typically to the fecundity advantage hypothesis, whereby female fitness increases more rapidly with size than does male fitness (Zamudio 1998; Henderson *et al*. 2003). The observed range of sexual dimorphism also suggests that the magnitude of these differences is both species- and population-dependent (Holtby & Healey 1990).

An example of sex differences in energy allocation is the relatively high energy investment in gonad production by female fish compared to males (e.g. Henderson, Wong & Nepszy 1996). All else being equal, this would suggest that relatively more energy should be available for growth in males. However, the sex with higher gonad investment may not necessarily invest more energy into reproduction. Energy allocation to gonads is only one aspect of reproduction, which is simple to measure and has therefore received much attention. More difficult to quantify are other 'costly' behaviours which may be related to reproduction, such as activity related to finding and competing for mates and/or reduced feeding during mating. Thus, a greater net loss of energy due to reproductive activity defined more broadly to include all the above possible costs could lead to reduced growth and/or survival of males compared to females (Henderson *et al*. 2003).

A problem faced by investigators attempting to link SSD to patterns of energy acquisition and allocation has been the difficulty of estimating key parameters in the field, particularly feeding and activity rates of wild populations. However, recent advances in ecological modelling facilitate easier estimation of these parameters. Validated contaminant mass-balance models (Rowan & Rasmussen 1996; Forseth *et al*. 1992; Madenjian, O'Connor & Nortrup 2000; Trudel *et al*. 2000) have been shown to estimate accurately consumption rates of fish. When combined with a bioenergetics model of energy allocation, a mercury mass-balance model (Trudel *et al*. 2000) has been shown to provide estimates of activity costs due to metabolic expenditures that are supported by independent field observations (Rennie *et al*. 2005a).

Walleye (*Sander vitreus* Mitchill, 1818) and yellow perch (*Perca flavescens* Mitchill, 1814) are two closely related, iteroparous, sexually dimorphic species of percids that are common in North American lakes and rivers. Though they typically differ in trophic level (walleye are primarily piscivorous, yellow perch are benthivorous/omnivorous), females commonly mature later and attain a larger asymptotic size than males in both species (Henderson *et al*. 2003; Purchase *et al*. 2005). However, a detailed comparative evaluation of SSD in these two species has not been conducted.

In this study, we used data compiled from many walleye and yellow perch populations to demonstrate that, in spite of trophic differences, SSD patterns are similar in both species. We then addressed hypotheses to account for the observation that females grow larger than males. For one species (yellow perch), data were available from a subset of lakes to model the bioenergetics of growth using a contaminant and bioenergetic mass-balance model (Trudel & Rasmussen 2001; Rennie *et al*. 2005a). Results from this modelling exercise were used to test competing hypotheses of whether reduced somatic growth in mature male percids was due to higher activity costs (Henderson *et al*. 2003) or reduced consumption and activity (Roff 1983).

Methods

DATA COLLECTION

Walleye (47 populations) and yellow perch (67 populations) data were obtained from surveys by provincial government agencies in the provinces of Ontario and Quebec, Canada (Table S1 in Supplementary material). Sampling was conducted during the autumn (water surface temperature between 10 and 15 °C) using multimesh, sinking gill nets (19–152 mm stretched measure, Morgan 2002). Fish were sampled for length, weight, sex and maturation status; age was estimated from otoliths by a single Ontario Ministry of Natural Resources Fisheries Ageing biologist.

ESTIMATION OF LIFE HISTORY PARAMETERS

For every combination of species, population and sex, we estimated age and size at maturity using logistic regression to determine the point when 50% of individuals had matured. The life span of each sex was estimated as the mean age of the oldest 5% of individuals, given that at least 50 individuals were sampled per sex (Purchase *et al*. 2005). Random sampling of data indicated that life span calculated in this manner was not correlated significantly with sample size (where sample sized ranged from 50 to 350 individuals) for either males or females (Purchase 2004; Purchase *et al*. 2005).

We used a biphasic growth model to describe prematuration and post-maturation growth patterns of each sex (Lester, Shuter & Abrams 2004; Shuter *et al*. 2005). This model assumes that growth rate prior to maturation is constant (i.e. length increases linearly with age) and that a progressive decline in growth rate occurs after maturation due to the allocation of surplus energy to reproduction. In assuming that investment in reproduction is proportional to somatic weight, the model predicts that post-maturation growth is described by the von Bertalanffy (VB) growth equation. Furthermore, parameters of the VB growth equation are interpreted in terms of energy acquisition and allocation to reproduction. Thus, the model supplies a framework for comparing male and female investments in reproduction.

For walleye populations, where age of maturity can be quite late (e.g. 10 years), it was very clear that this type of model was needed to describe the lifetime growth pattern. Examination of growth curves revealed that male and female growth was approximately linear prior to maturation and that deviation from linearity occurred once fish became mature. Because males matured earlier than females, departure from linear growth occurred at different ages and it was evident that the lifetime growth of each sex could not be described adequately by a single VB equation. The need for this biphasic model was less evident for perch, because fish matured very young and an extended period of prematuration growth could not be observed. For this reason, we used different methods to estimate growth parameters in each species.

For walleye populations, we used immature fish to estimate a prematuration growth rate:

$$L_t = h \cdot (t - t_1) \qquad \text{eqn 1}$$

where L_t is length at age t, h is the growth rate (i.e. cm year^{-1}) and t_1 is the age-intercept. We then used a VB model to describe the post-maturation growth of males and females:

$$L_t = L_\infty \cdot (1 - e^{-k(t-t_0)}) \quad \text{eqn 2}$$

where L_∞ = asymptotic length, k = Brody growth coefficient (year^{-1}) and t_0 = the age-intercept. In estimating these parameters for each sex, we used the biphasic model to justify the following constraints:

$$L_\infty = 3h/g \quad \text{eqn 3}$$

$$k = \ln(1 + g/3) \quad \text{eqn 4}$$

where g measures reproductive investment (which may differ among sexes) and h is the potential growth rate (i.e. estimated from prematuration growth) which is common among sexes. Thus, we estimated for each sex what value of g (and t_0) best described the post-maturation growth pattern. This approach assumes that the prematuration growth rate would have been sustained if energy had not been allocated to reproduction. This analysis was conducted for the 47 walleye populations using non-linear fitting methods applied to individual observations of length and age to solve for g and t_0.

The use of prematuration growth rate (h) to condition estimates of reproductive investment (g) described above could not be applied to yellow perch because prematuration growth could not be observed in most populations. In this case, it was necessary to solve for h and g simultaneously when describing post-maturation growth. This was achieved by including a Boolean effect variable ('male') so that a common h and sex-specific g could be estimated. In addition, the fitting procedure constrained estimates of t_0 based on biphasic growth theory. Lester *et al.* (2004) showed that the value of t_0 is a function of age of maturity (T), reproductive investment (g) and t_1 (from equation 1):

$$t_0 = T + (\ln(1 - (g \cdot (T - t_1)/3)/\ln(1 + g/3)) \quad \text{eqn 5}$$

We used sex-specific estimates of T and assumed $t_1 = 0$ to incorporate this constraint into each fit. We analysed 39 of the 67 yellow perch populations for which estimates of T were available for both sexes. As in the walleye analysis, non-linear fitting methods were applied to individual observations of length and age to estimate yellow perch g and h.

These analyses supplied sex-specific estimates of asymptotic length and reproductive investment to compare between males and females in both walleye and yellow perch populations.

SAMPLING FOR BIOENERGETIC ANALYSES

Twelve of the 67 yellow perch populations were sampled for estimation of bioenergetic parameters (Table S2 in Supplementary material). In early autumn, epaxial muscle was taken from the left side of the fish, anterior to the dorsal fin and dorsal to the lateral line. Stomach contents were taken from fish captured in July and September and pooled within each lake by 2-cm fork length intervals. Both fish muscle tissue and stomach contents were frozen at –20 °C for later analysis.

ESTIMATION OF CONSUMPTION AND ACTIVITY IN YELLOW PERCH

We used a contaminant/bioenergetics model described by Trudel & Rasmussen (2001) and reported in Rennie *et al.* (2005a). The model combines the mass balance formulations of contaminants and fish weight on a daily basis from a mercury (Hg) mass balance model (MMBM), with the mass balance of fish energy budgets from a bioenergetics model (BM; Kitchell, Stewart & Weininger 1977). The MMBM models the balance of methylmercury (MeHg) in the tissues of fish, as this is the form of Hg that is bioaccumulated most readily (Mason, Reinfelder & Morel 1995; Lawson & Mason 1998; Lawrence *et al.* 1999). When fish total mercury (THg) and MeHg concentrations are equivalent, as they were in this study (Rennie 2003), then [THg] is used to approximate [MeHg].

The primary mode for MeHg uptake in fish from uncontaminated waterbodies is through absorption in the gut from diet (Hall *et al.* 1997; Lawson & Mason 1998; Leaner & Mason 2002). The [Hg] in muscle and the whole body can be assumed to be equivalent (Becker & Bigham 1995; Trudel *et al.* 2000; Trudel & Rasmussen 2001). The accumulation of MeHg in fish is then described by:

$$\frac{dHg}{dt} = (\alpha \cdot C_d \cdot C) - (E + G + K) \cdot Hg \quad \text{eqn 6}$$

where Hg is [MeHg] of the fish (μg Hg g^{-1} wet weight), α is the assimilation efficiency of MeHg from food, C_d is [MeHg] in food (μg Hg g^{-1} wet weight), 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 K is the instantaneous loss rate of MeHg to gonads (day^{-1}). If modelled over small (i.e. one day) time steps, differences between parameters such as E and K will be small and can therefore be treated as constants. Integration of equation 6 then yields the following (rearranged to solve for consumption):

$$C = \frac{Hg_t - Hg_0 \cdot e^{-(E+G+K)t}}{\alpha \cdot C_d \cdot [1 - e^{-(E+G+K)t}]} \cdot (E + G + K) \quad \text{eqn 7}$$

where Hg_0 and Hg_t are the [MeHg] in fish at time 0 and time t, respectively. Losses due to spawning (K) are as described in Appendix S1 (Supplementary material).

The MMBM (equation 7) is solved over a daily time step, and combined with the BM (Kitchell *et al.* 1977; Hewett & Johnson 1992) through the common term, C (C above can be converted from units of day^{-1} to J day^{-1} by dividing C by the product of the energy density of the fish and W_{t-1}). The BM can be expressed simply as:

$$W_t = W_0 + [C \cdot ED_{prey} - (F + U + R_T)]/ED_{fish} \quad \text{eqn 8}$$

where W_t is the final fish weight (g), W_0 is the initial fish weight (g), C is ingestion rate (g day^{-1}) at time t, ED_{prey} is the energy density of prey (J g^{-1}), ED_{fish} 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}). Egestion and excretion losses are functions of temperature, body size and consumption (equation 2 in Hewett & Johnson 1992); all parameters for the BM are from Kitchell *et al.* (1977), reported in Hewett & Johnson (1992).

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 8, can be subdivided further into three components:

$$R_T = ACT \cdot R_s + R_d \quad \text{eqn 9}$$

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

Losses to reproduction are modelled as a one-time loss:

$$W_t = W_{t-1} - W_{t-1} \cdot (GSI \cdot ED_{F(X,Y)}) \quad \text{eqn 10}$$

where W_t is the fish weight after spawning, W_{t-1} is the fish weight the day previous and $ED_{F(X,Y)}$ is the ratio of the energy density of the gonads to that of the whole fish (Table 1).

By iterating both equations (linked through the common term, C) on a daily basis, the unique solution of C and ACT that achieved the observed final weight and [MeHg] was obtained through an optimization routine. The optimization minimized error between observed W_t and Hg_t, and modelled W_t and Hg_t, such that the average difference between observed and modelled W_t and Hg_t was less than 0·01%. We modelled fish from ages 1–2, 2–3, 3–4, 4–5 and 5–6 years. Hereafter all fish ages refer to the age at the beginning of these age intervals.

MODEL PARAMETERIZATION

All model parameters for the MMBM, as well as functions describing daily MeHg elimination, weight and MeHg losses to gonads, were based on equations presented in Trudel & Rasmussen (2001) and Rennie (2003). Automated loggers deployed in each lake recorded mean daily littoral water temperatures over the course of the year. We estimated model inputs for fish weight, fish [THg] and diet [MeHg] using the following procedure. (1) Lake-specific and sex-specific regression equations were calculated for weight and fish [THg] across ages 1–5 years. These regressions were used to predict mean weight and fish [THg] in a given age class. (2) Two of our lakes were studied more intensively and provided sex-specific diet [MeHg] data to test for differences between sexes (Rennie 2003). There was no sex difference in diet [MeHg], controlling for lake and size effects [analysis of covariance (ANCOVA): $F_{1,333} = 1{\cdot}61$, $P = 0{\cdot}205$]. The interaction between sex and body size was also non-significant ($F_{1,332} = 0{\cdot}99$, $P = 0{\cdot}32$). Body size was a weakly significant covariate in the model ($F_{1,333} = 4{\cdot}11$, $P = 0{\cdot}044$). Based on this finding, we assumed no sex-based differences in diet among similar-sized fish in any of the lakes. Typical yellow perch diet items increase in [MeHg] with trophic level (Tremblay & Lucotte 1997; Rennie *et al*. 2005b), as does prey size (Kerr & Dickie 2001). Thus, similar-sized males or females feeding on different-sized prey (thereby affecting foraging efficiency) would have been revealed by differences in diet [MeHg] when controlling for body size effects.

Assuming no dimorphism in diets, yellow perch stomach contents were pooled by 2 cm length intervals, and the mid-points of these length intervals were converted to weight using a common regression equation [ln weight (g) = −12·117 + 3·169 * (ln length, mm), R^2 = 98·6%, n = 16 233]. (3) Lake-specific diet [MeHg] was predicted from fish weight and used to determine diet [MeHg] in an average-sized fish at each age. (4) The Hg analysis procedures used dry tissue, but the MMBM is based on wet (fresh) weight. Water content did not vary by sex, age or lake across all samples, and therefore we used the average value of 78% water content for fish muscle tissue and 82% for stomach contents to convert [MeHg] from dry weight to wet weight concentrations. (5) We used fish weight, fish [MeHg] and diet [MeHg] estimated using the above procedures to model one year of fish growth across adjacent age classes for each sex in each lake using lake-specific littoral water temperatures. All other parameters required for the models are reported in Table 1.

[THG], [MEHG] DETERMINATION OF YELLOW PERCH MUSCLE AND DIETS

[THg] in fish muscle tissues were prepared and analysed as described in Rennie *et al*. (2005a). National Research Council (NRC, Canada) biological reference standards DORM-2 and DOLT-2 were analysed concurrently with tissues for [MeHg] and [THg] determinations, and corrected for by blank subtraction. Mean raw values of [THg] for DORM-2 and DOLT-2 for the 27 replicate digests were 4·85 and 2·35 μg Hg g^{-1} dry weight, respectively (standard errors: DORM-2, 0·17 μg g^{-1}; DOLT-2, 0·08 μg g^{-1}). These values fall within 10% of the reported NRC [THg]. Average recoveries for DORM-2 and DOLT-2 over the course of the study were 104% and 110%, respectively.

Notable deviation from the nominal values of standards occurred in nine of the 27 THg runs performed during the study. For analyses where DORM-2-values deviated by more than 15% of nominal values, corrections of [THg] were made by dividing the observed concentration by a run-specific correction factor, equal to the ratio of the average observed DORM-2-value in a digest to nominal values reported by NRC. We tested this approach by running flesh samples

Table 1. Input parameters of the mercury mass balance model and bioenergetics model

Symbol	Parameter description	Value	Source[a]
α	Assimilation efficiency	0·8	1
E	Elimination of Hg	Function[b]	2
φ	Coefficient of Hg elimination	0·0029	2
β	Allometric exponent of Hg elimination	–0·20	2
γ	Temperature coefficient of Hg elimination	0·066	2
Q_m	Ratio of Hg concentration in gonads and whole fish, males	Function[b]	12
Q_f	Ratio of Hg concentration in gonads and whole fish, females	Function[b]	3
GSI_m	Gonadosomatic index, males	0·05	4, 5, 6, 7, 12
GSI_f	Gonadosomatic index, females	0·17	4, 7, 8, 9, 10
ED_{FX}	Ratio of energy density of ovaries to energy density of the whole fish	1·2	8, 11
ED_{FY}	Ratio of energy density of testes to energy density of the whole fish	0·85	12
ED_{prey}	Energy density of fish stomach contents	3517 J g^{-1}	12

[a]1, Norstrom, McKinnon & de Freitas (1976); 2, Trudel & Rasmussen (1997); 3, Hammerschmidt *et al*. (1999); 4, Norton (1997); 5, Sulistyo *et al*. 2000; 6, Vuorinen *et al*. (1992); 7, B. A. Henderson, unpublished data, University of Toronto at Mississauga, 3349 Mississauga Road. N. Mississauga ON L5L 1C6; 8, Henderson, Trivedi & Collins 2000; 9, Nelson & Magnuson (1992); 10, Heibo & Vøllestad 2002; 11, Diana (1983); 12, Rennie (2003). [b]Functions relating gonad and tissue Hg losses provided in Supplementary material Appendix S1.

from the same fish in several different digestions. Values of fish [THg] among digestions were indistinguishable from one another after correction (Rennie 2003).

[MeHg] in fish stomach contents were prepared and analysed as described in Rennie *et al.* (2005a). The average value for DORM-2 over all organic Hg analyses, based on 22 runs, each consisting of two to five replicate digests, was 4·06 μg Hg g^{-1} dry weight (± 0·14 standard error), which is within 10% of the nominal value reported by NRC.

MODELLING PROCEDURE TO EVALUATE BIOENERGETIC SEXUAL DIMORPHISM

In each of our 12 lakes, we modelled five age-class cohorts of fish for both sexes (see 'Model parameterization' above), each yielding five parameter estimates for each lake (Table S2 in Supplementary material). Among lakes, yellow perch are exposed to different thermal regimes as a consequence of microclimate. Most fish bioenergetic parameters are either directly or indirectly temperature- and size-dependent, and often in a non-additive fashion. In order to remove size and lake-specific (i.e. temperature) effects statistically among lakes, we first separated data for all fish by lake. Then, within each lake, we regressed each bioenergetic parameter (joules day^{-1}) against body mass (g) using data from both sexes (linear regression on $\log_{10}$ transformed variables). Thus, one relationship for each of the five bioenergetic estimates (C, G, R_T, F, U), was generated in each of the 12 lakes (60 relationships in total) based on data from both sexes (10 observations per relationship, five males and five females). Lake-specific residuals around relationships between bioenergetic measures and fish mass were then estimated for each age and sex class by subtracting back-transformed predicted values from observed bioenergetic estimates. These lake-specific residuals were used as the basis for our analyses of gender- and age-specific differences with lake and body size effects removed, assuming that males and females within the same lake experience similar thermal regimes. To estimate food conversion efficiency (FCE) between males and females controlling for food intake and lake effects, we used an approach identical to that outlined above but instead regressed growth estimates on consumption (rather than on body mass).

This residual-based approach was chosen to describe sex-based differences because it best resembled the manner in which bioenergetic models were developed. Submodels of consumption and respiration were parameterized originally under the assumption that males and females have comparable physiology (Kitchell *et al.* 1977). Thus, assuming sex ratios of the fish used to generate submodel regressions were close to equal, differences between sexes in fish contributing to the original submodel regressions (were this information available at the time) would be reflected in their residuals.

To determine the effects of sex and fish age on energy acquisition and allocation patterns in yellow perch, we used two-factor analyses of variance (ANOVAs) considering age (five categories, 1–5), sex (two categories, male and female) and their interaction for each set of bioenergetic residuals. Sequential Bonferroni corrections (Rice 1989) were performed to adjust critical P-values for multiple comparisons.

Results

SEXUAL DIMORPHISM IN LIFE HISTORIES OF WALLEYE AND YELLOW PERCH

Growth curves for walleye and yellow perch indicate that growth rates of both sexes are similar in young fish, but sexual size dimorphism (SSD) exists in older individuals (Fig. 1). In walleye, this discrepancy becomes obvious when total length exceeds 38 cm. In perch, the discrepancy becomes obvious at a smaller size (i.e. 13 cm). This difference is correlated with size of maturity (Fig. 2): in most walleye populations, males are mature at 38 cm and in most perch populations males are mature at 13 cm. These observations support the conclusion that SSD in these species is related to maturation.

In both species, males matured earlier than females and, because prematuration growth rates were similar, males matured at a smaller size (Fig. 2). Walleye males matured almost 2 years earlier (1·8 years on average, paired t-test, $t_{46} = 15{\cdot}0$, $P < 0{\cdot}0001$) and an average of 97 mm smaller than females (paired t-test, $t_{46} = 19{\cdot}6$, $P < 0{\cdot}0001$), roughly 75% the size and age of females (Fig. 2a,c). In perch, this ratio was approximately 60% (Fig. 2b,d); male yellow perch matured on average 1·1 years earlier (paired t-test, $t_{41} = -11{\cdot}46$, $P < 0{\cdot}0001$) and 59 mm smaller (paired t-test, $t_{35} = -14{\cdot}85$, $P < 0{\cdot}0001$) than females. In walleye populations, male life span was not significantly different from that of females (Fig. 2e, paired t-test, $t_{46} = -0{\cdot}71$, $P > 0{\cdot}05$). In yellow perch populations, male life span was only slightly shorter (0·7 years on average) than that of females (Fig. 2f, paired t-test, $t_{35} = -2{\cdot}67$, $P < 0{\cdot}01$). Because males matured approximately 1 year earlier than females this difference implies reproductive life span was the same in both sexes for yellow perch, and that male walleye reproductive life span was approximately 2 years longer than that of female walleye.

After maturation, growth rates declined more rapidly in males than in females, resulting in males having a smaller asymptotic size (L_∞, Fig. 3a,b). Walleye male L_∞ was 75% that of females (Fig. 3a, paired t-test, $t_{46} = 11{\cdot}16$, $P < 0{\cdot}0001$). A nearly identical pattern was observed for asymptotic sizes of male and female yellow perch (Fig. 3b, paired t-test, $t_{38} = 4{\cdot}85$, $P < 0{\cdot}0001$). Implied male reproductive investment (g) was 1·3 times that of females in walleye (Fig. 3c, paired t-test, $t_{46} = -13{\cdot}79$, $P < 0{\cdot}0001$), and 1·2 times that of females in yellow perch (Fig. 3d, paired t-test, $t_{38} = -8{\cdot}43$, $P < 0{\cdot}0001$).

BIOENERGETIC COMPARISONS BETWEEN MALE AND FEMALE YELLOW PERCH

The observation that growth diverged only after maturity was also reflected in our bioenergetic analyses of yellow perch; controlling for body size and lake-specific effects, male and female energy allocation to growth was similar at ages 1–2 years, but female growth was significantly greater than that of males for ages 3 years and older ($F_{4,110} = 33{\cdot}18$, $P < 0{\cdot}0001$, $P_{crit} = 0{\cdot}008$; Fig. 4a). Higher growth rate in females could have been due to higher consumption, lower metabolic activity, or a combination of both factors. Our analysis indicated that females consumed significantly more than males ($F_{1,110} = 13{\cdot}70$, $P = 0{\cdot}0003$, $P_{crit} = 0{\cdot}017$). Although a plot of the data suggests increased consumption in older females (Fig. 4b), there was no significant interaction between age and sex using corrected critical P-values ($F_{4,110} = 2{\cdot}95$, $P = 0{\cdot}023$, $P_{crit} = 0{\cdot}017$). Relative FCE (expressed as the lake-specific

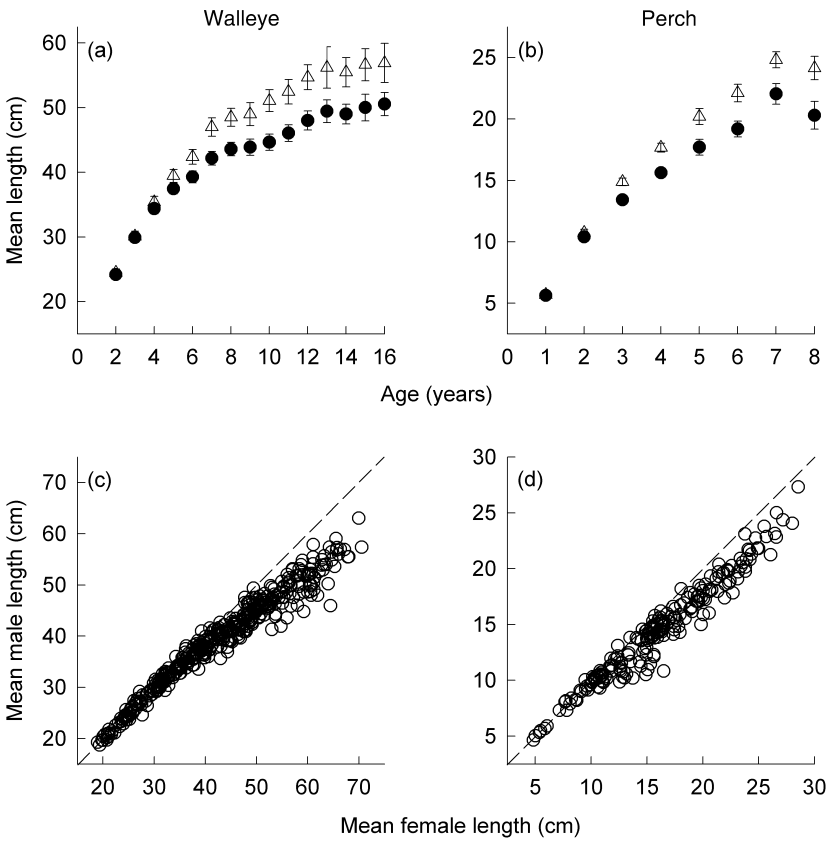

Fig. 1. Sexual growth dimorphism of walleye (panels a, c) and yellow perch (b, d). Top panels (a, b) are mean length at age of males (circles) and females (triangles). Each datum is the mean across populations, where $n \geq 4$ populations per sex and age class and $n \geq 4$ individuals per sex and age class per population. Vertical bars are 1 standard error and represent among-lake variation. Bottom panels (c, d) show mean length of males vs. mean length of females compared to the 1 : 1 relationship (dashed), where male and female data are paired by population.

residuals of a growth vs. consumption regression) was greater in females than in males at ages 3–5 years, but similar at ages 1–2 years ($F_{4,110} = 12{\cdot}26$, $P < 0{\cdot}0001$, $P_{crit} = 0{\cdot}01$; Fig. 4c). The interaction between age and sex on total metabolic costs (R_T) was insignificant ($F_{4,110} = 1{\cdot}59$, $P = 0{\cdot}18$), but R_T costs were higher for females than males ($F_{1,110} = 6{\cdot}77$, $P = 0{\cdot}01$, $P_{crit} = 0{\cdot}025$; Fig. 4d). The following modelled metabolic rates are reported but not shown in figures. The effect of gender on excretion rates was significant, with females excreting more than males ($F_{1,110} = 6{\cdot}77$, $P = 0.\ 0{\cdot}01$, $P_{crit} = 0{\cdot}0125$), and the interaction with age was near significance ($F_{4,110} = 3{\cdot}29$, $P = 0{\cdot}013$, $P_{crit} = 0{\cdot}0125$). Egestion rate was also significantly higher in females (ANOVA: $F_{1,110} = 7{\cdot}77$, $P = 0{\cdot}006$, $P_{crit} = 0{\cdot}05$).

Discussion

Patterns of sexual dimorphism in walleye and yellow perch were very similar, suggesting that comparable evolutionary forces and/or constraints may be acting on the life histories of both these closely related fishes. This is noteworthy, given the ecological differences between the species; walleye are primarily piscivorous and on average live twice as long as perch, which are typically benthivorous/zooplanktivorous. This similarity in sexual dimorphism between species suggests that bioenergetic differences between male and female yellow perch described here also probably apply to walleye, and perhaps other species demonstrating similar life histories (Roff 1983).

Our results do not support a previous hypothesis (Henderson *et al*. 2003) that reduced male growth efficiency is due to increased activity associated with reproduction. Considering growth characteristics alone, one might conclude that males invest more in reproduction relative to females because estimates of male *g*-values were 1·2–1·3 times higher than those observed in females. For walleye and yellow perch (as well as other fish species), it has been shown that estimates of female *g* based on the biphasic growth model are correlated with (and approximately equal to) female gonadosomatic index (Shuter *et al*. 2005). Because gonad production is a major energetic cost of reproduction in females, estimates of female *g* seem to provide a good measure of reproductive investment. A logical extension of this argument is that growth-based estimates of male *g* reflect reproductive costs of males. Thus, one might conclude that males attain a smaller asymptotic size because energetic losses associated with reproduction are higher for males than for females. If this were the case, then a bioenergetic analysis should reveal higher metabolic activity in post-maturation males. This was not supported by our study; bioenergetic results for yellow perch indicate that the sex-related differences in growth rate are due to reduced energy acquisition and assimilation in males relative to females at the onset of maturity. Reduced male growth rate in sexually mature yellow perch and walleye cannot be explained by an activity hypothesis (i.e. more active males) because estimates of male total metabolic costs were lower than in females.

Our observation of decreased consumption and metabolic activity in male perch is consistent with Roff's (1983) hypothesis that smaller male size in teleosts relative to females (in the

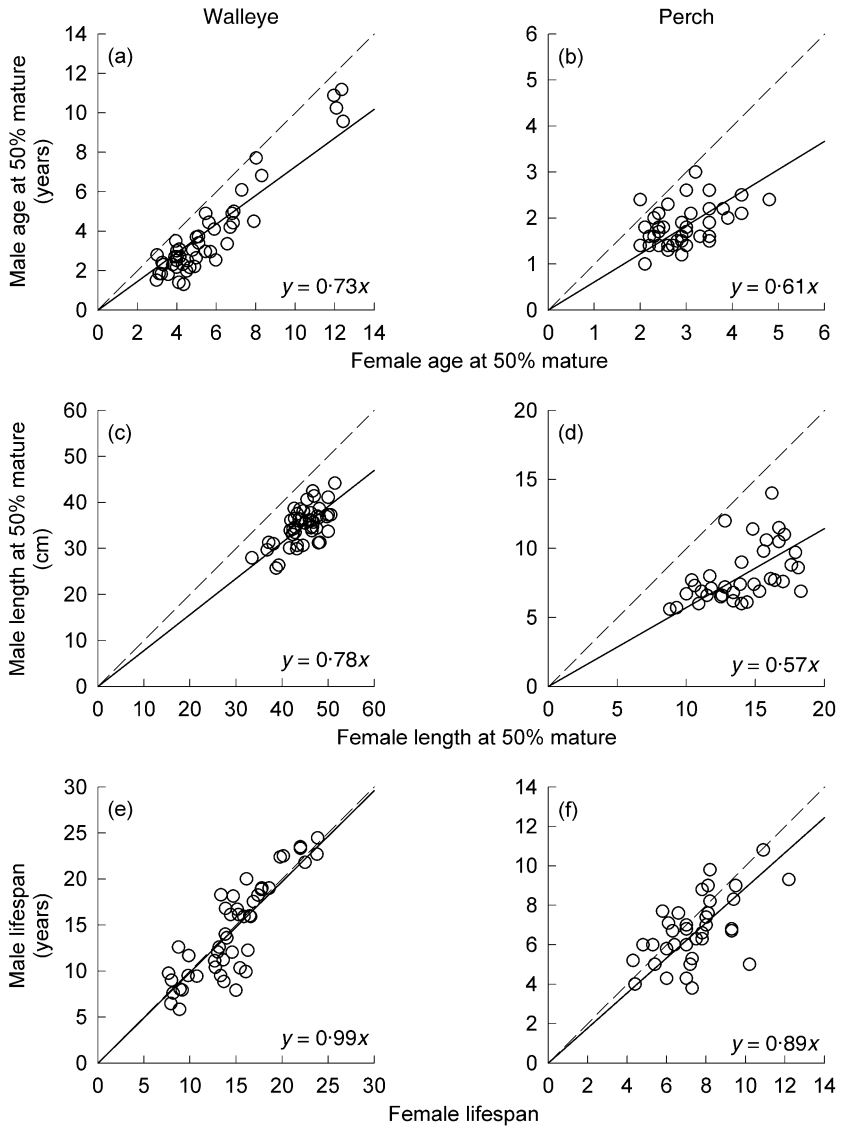

Fig. 2. Sexual dimorphism of walleye and yellow perch at the age of 50% maturity (panels a, b), length at 50% maturity (c, d), and life span (e, f). Male and female data are paired by population. Shown on each panel are the fitted linear regression line (solid, through origin), equation of the fitted regression line, and the 1 : 1 relationship (dashed) for comparison.

absence of territorial behaviour or parental care) is a selective response to increase survival by reducing foraging activity, presuming that increased activity entails increased predation risk. A previous application of the mercury mass-balance model also reported higher activity in female *Esox lucius* (Trudel *et al*. 2000). The difference was not significantly greater than in males, but was based on a relatively small sample of populations. Similarly, an application of a ^{137}Cs model also reported higher activity in female *E. lucius* and *Salvelinus namaycush* based on a small (one to three) number of observations (Rowan & Rasmussen 1996). Another study that examined mercury concentrations between genders in four species of centrarchid fish concluded that male foraging rates declined relative to those of females at the onset of maturity (Nicoletto & Hendricks 1988). Our findings may also apply more generally to species where the smaller sex (male or female) displays reduced activity and foraging. For example, larger male *Anax junius* (damselflies) were found to be more active than smaller females during foraging trials (Fuselier *et al*. 2007).

However, the hypothesis presented by Henderson *et al*. (2003) is not without support in the literature. Reproductively active male gerrids (hemipteran water striders) exhibited greater activity than immatures or mature females, but were also the poorest foragers (Blanckenhorn & Perner 1996). Also, female *Coenagrion puella* (damselflies) were less active than males in the presence of food and predators, and emerged at larger sizes (Mikolajewski *et al*. 2005). Given literature support for both the reduced foraging hypothesis (Roff 1983) and the increased activity hypothesis (Henderson *et al*. 2003), feeding and activity budgets should be considered together when attempting to explain proximate mechanisms of SSD.

Our results indicate that the onset of sexual maturity plays a major role in generating SSD in percids. Bioenergetic differences between male and female yellow perch were obvious only after the onset of maturity, when many organisms experience changes in endocrine activity. Laboratory experiments by Malison *et al*. (1985, 1988) demonstrated that consumption and FCE differences between male and female yellow perch

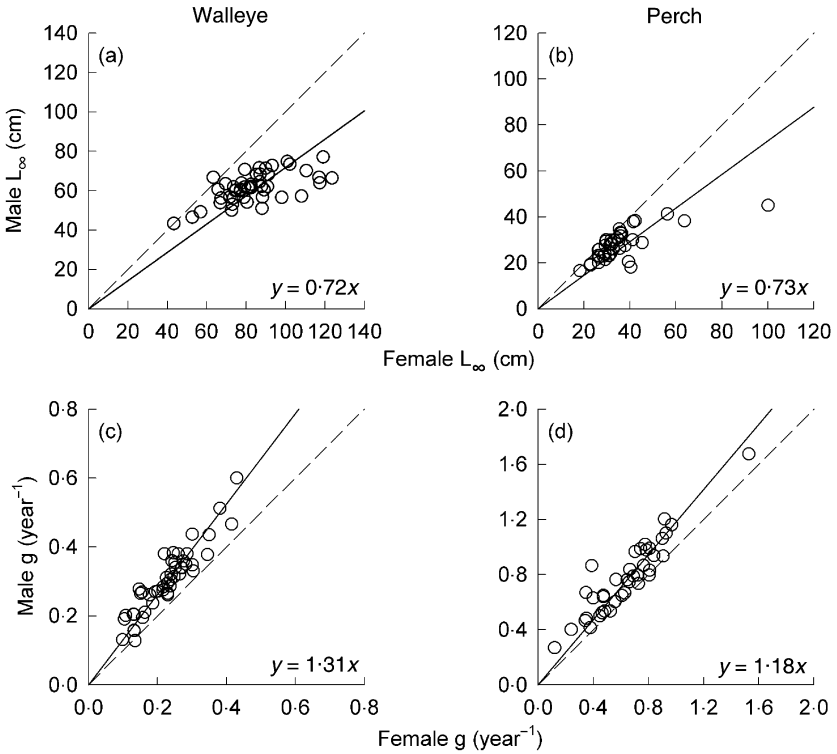

Fig. 3. Sexual dimorphism of walleye and yellow perch in asymptotic length (L_∞, cm; panels a, b) and reproductive investment (g; panels c, d). Male and female data are paired by population. Shown on each panel are the fitted linear regression line (solid, through origin) and the 1 : 1 relationship line (dashed) for comparison.

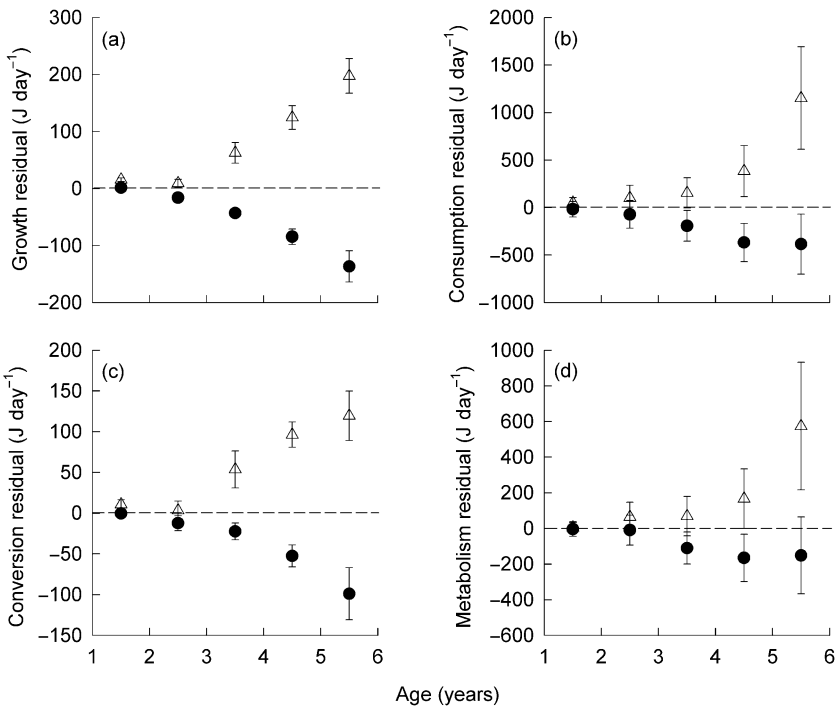

Fig. 4. Relative differences in male (circles) and female (triangles) yellow perch (a) growth (b) consumption (c) conversion efficiency and (d) total metabolic cost. Lake and body size influences have been removed from bioenergetic estimates using lake-specific regressions on body mass, and averaged residuals from these relationships are shown. Vertical bars are 1 standard error and represent among-lake variation in relative sex differences.

probably result from differential hormonal effects on males and females at the onset of maturation. In yellow perch, ovarian oestrogens stimulated and testicular androgens inhibited growth (Malison *et al.* 1985). However, the effect was observed only in larger juveniles, suggesting that the action of these hormones would manifest in fish where a certain maturational status had been achieved. Growth and consumption of larger juvenile male and female yellow perch fed *ad libitum* both increased when individuals were exposed to oestrogens (Malison *et al.* 1988). Consistent with our bioenergetic results, Malison *et al.* (1988) observed faster female growth, higher consumption and higher FCE relative to males regardless

of oestrogen exposure level. Analogous negative effects of androgens on consumption and FCE have been documented in juvenile Eurasian perch (*P. fluviatilis*; Mandiki *et al*. 2004; Mandiki *et al*. 2005), where consumption rates increased in females exposed to oestrogens and decreased in males exposed to androgens. The action of both these hormones (positive effect of oestrogens on female growth, negative effects of androgens on male growth) and the dependence of hormone action on perch developmental stage corresponds with our observed onset of SSD in yellow perch and walleye at sexual maturation. Hormonal activity has also been tied to changes in maturation status, SSD and metabolic rate in other taxonomic groups (Cox *et al*. 2005; John-Alder, Cox & Taylor 2007; Wudy, Hartman & Remer 2007).

Bioenergetic submodels of consumption and respiration were parameterized originally under the assumption that males and females have comparable physiology (Kitchell *et al*. 1977), and potential gender differences in these submodels have not been evaluated. Although published accounts show that standard metabolism and assimilation efficiencies can differ between males and females (Shillington 2005; Valle *et al*. 2005), sufficient data are currently lacking to parameterize accurately gender-based submodels for consumption and metabolism in percids. However, our analysis best reflects the evaluation of gender differences between male and female fish given the manner in which these submodels were parameterized, as we examined residual differences of bioenergetic patterns from the common slope (across both sexes) with body weight. Clearly, this work calls for investigations into the dependence of bioenergetic and contaminant allometries on gender. In the absence of this information, our findings suggest that investigators use caution in interpreting bioenergetic results from models applied to both males and females in the absence of information regarding population sex ratio.

One aspect of our bioenergetic analysis that remains difficult to resolve is that relative differences in FCE residuals between males and females are greater than would be expected by the male–female differences in bioenergetic residuals of loss terms. Total metabolism, egestion and excretion residuals were all higher in females than in males, after controlling for body size and temperature differences among sexes and lakes, which seems inconsistent with the greater observed growth per unit energy consumed in females. The reason for this apparent discrepancy is not clear; however, it suggests further that conventional mercury accumulation or bioenergetics models may be incapable of accurately modelling gender differences, as these models do not reflect potential physiological differences between sexes (e.g. Malison *et al*. 1985, 1988; Mandiki *et al*. 2004, 2005). Gender differences in assimilation could explain some of the discrepancy outlined above; if the assimilation of energy (and/or Hg) from diet is higher in males under the influence of hormones associated with the onset of maturity (e.g. Valle *et al*. 2005), then consumption estimates for males would be overestimated. A reduction in male consumption estimates would reduce the observed difference in FCE residuals between male and female perch and help to resolve this apparent discrepancy. Similarly, if standard metabolic rates (i.e. weight exponent of standard metabolism) were higher in males than in females (e.g. Shillington 2005), total metabolic costs of males in this study might be underestimated. Another possibility is that females are experiencing compensatory growth as a response to more variable intake relative to males. Fish undergoing compensatory growth due to variable intake have higher growth efficiencies and/or assimilation than those with constant intake (Skalski *et al*. 2005). Also, bioenergetics models applied to fish exposed to variable intake have underestimated consumption (Whitledge *et al*. 1998). However, it is not clear why female perch might demonstrate more variable intake patterns than males.

In summary, our study provides a test of two competing hypotheses for the explanation of female-biased SSD in two species of fish, and highlights the importance of measuring both consumption and activity costs in evaluating proximate mechanisms for SSD. Our study and the literature reviewed here suggests that sex-specific bioenergetics models are warranted. Further, we provide a detailed comparison of SSD in yellow perch and walleye, and demonstrate important similarities between these species that transcend the trophic differences that separate them.

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Supplementary material

The following supplementary material is available for this article.

Table S1. Lake information for walleye and yellow perch populations in this study.

Table S2. Bioenergetic model input and output for yellow perch populations.

Appendix S1. Description of Hg elimination and allocation of Hg to reproductive tissues.

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