



Linking lake whitefish (*Coregonus clupeaformis*) condition with male gamete quality and quantity

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ABSTRACT

Sexual-selection theory predicts males will increase investment in ejaculates if there is an increase in the level of sperm competition. Production of ejaculates is energetically costly, so males in better condition should be able to produce ejaculates of higher quality than individuals in poorer condition. We examined how ejaculate investment (i.e., relative testes mass) and sperm quality (i.e., sperm swimming speed) in lake whitefish (*Coregonus clupeaformis*) were related to residual soma mass, fork length, and fish age using data collected from Lake Michigan and Bay of Quinte (Lake Ontario). Populations from both lakes had positive relationships between relative testes mass and residual soma mass. Fork length was the most important predictor of sperm swimming speed with larger males from both lakes tending to have faster swimming sperm than smaller fish. Testis asymmetry, which is a commonly observed phenomenon in other animals but which has only recently been reported in fishes, was found to occur in the majority of examined lake whitefish with the left testes typically larger than the right.

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Introduction

Declines of lake whitefish (*Coregonus clupeaformis*) growth and body condition in Lake Michigan have been associated with the invasion of dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) to the lake (Nalepa et al., 1998; De Bruyne et al., 2008). Through filter feeding on phytoplankton, dreissenid mussels divert energy from pelagic to benthic food webs and this has been linked with declines in abundance of *Diporeia* spp., an important prey of lake whitefish (Nalepa et al., 1998; De Bruyne et al., 2008). Dreissenid mussels are now the main component of lake whitefish diets in lakes Michigan, Ontario, and Erie (Hoyle et al., 1999; Cornelius, 2000; Pothoven et al., 2001). Because dreissenid mussels are less energetically valuable than

Diporeia, the switch in resource use may have led to declines in growth and body condition of lake whitefish observed in lakes Ontario, Huron, and Michigan (Pothoven et al., 2001; McNickle et al., 2006; Lozano et al., 2001).

Reductions in condition of fish have been linked to poor recruitment (Marshall and Frank, 1999; Pangle et al., 2004; Kamler, 2005) at least partially because poor gamete quantity and quality can lower fertilization success (the percentage of ova fertilized during a spawning event) (e.g. Rätz and Lloret, 2003). Ova fertilized by males in good condition have been found to have higher rates of survival than those fertilized by fish in poorer condition (Wedekind and Müller, 2004). Recently, Burness et al. (2008) showed that ejaculate investment (i.e., relative testes size) in lake whitefish in the Bay of Quinte (Lake Ontario) was related to fish condition, which suggests that lake whitefish in good condition may have a reproductive advantage over other fish. The goal for this project was to determine if similar relationships between sperm quality (relative testes mass, sperm swimming speed) and fish condition existed for Lake Michigan and Bay of Quinte (Lake Ontario) lake whitefish given that the foodwebs in both lakes have been heavily impact by dreissenid mussel invasion. Rather than simply comparing our results to those of

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Burness et al. (2008), we reanalyzed the Bay of Quinte data to account for likely heteroscedasticity in ejaculate investment data.

Methods

Sampling and study sites

Adult male lake whitefish were sampled during fall spawning from two sites (Naubinway and Saugatuck) in Lake Michigan during 2004 (Fig. 1 A). For each collected individual, fork length ($FL \pm 1$ mm) and body mass (± 1 g) were measured, and sperm was extracted by abdominal massage and collected in 1-mL syringes. Left and right testes were removed by dissection and weighed (± 1 g). Otoliths were removed for aging. Details of how fish were aged are presented in Muir et al. (2008).

Sampling of Bay of Quinte (Lake Ontario) lake whitefish (Fig. 1 B) is described in detail in Burness et al. (2004, 2008). Briefly, fish were collected by trap nets in fall 2002 during peak period of spawning. Similar to Lake Michigan sampling, fork length (± 1 mm) and body mass (± 1 g) of collected individuals were measured, and sperm was extracted by abdominal massage. Left and right testes were extracted by dissection and weighed (± 1 g) and sagittal otoliths were extracted and used to age individuals (Burness et al., 2008).

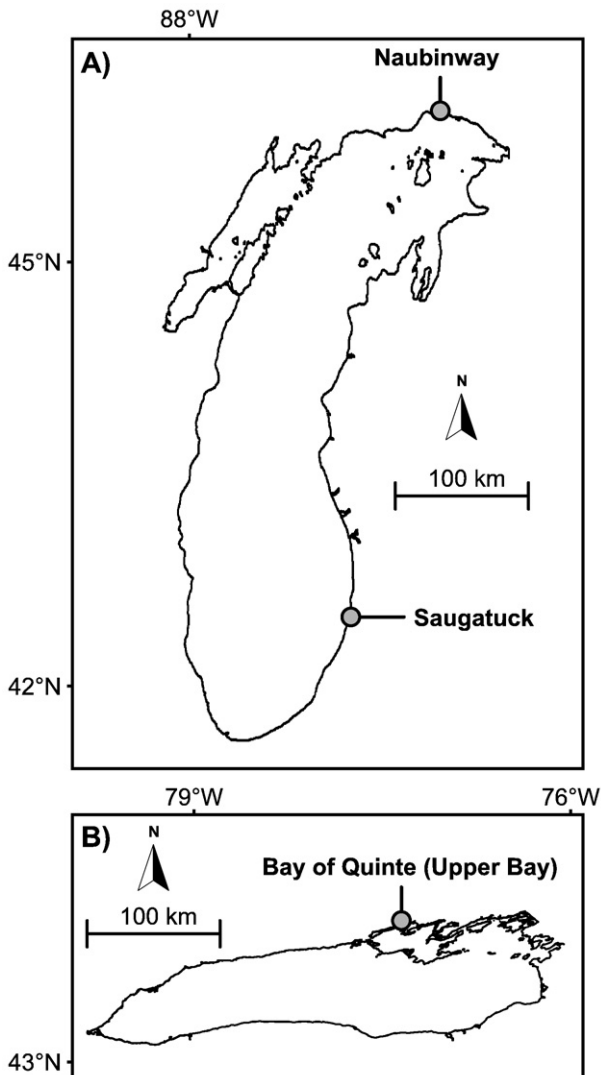


Fig. 1. Lake whitefish (*Coregonus clupeaformis*) sampling sites in Lake Michigan (A) and in the Bay of Quinte (B), Lake Ontario.

Sperm quality

Tail lengths of sperm collected from Lake Michigan lake whitefish were measured by first placing a drop of milt from each fish on a clean glass slide and diluting with a drop of distilled water. The sperm sample was then spread thinly across the slide and allowed to air dry. Tail lengths of 10 intact spermatozoa for each fish were measured under 400-times magnification using ImageJ (v1.33, available at <http://rsbweb.nih.gov/ij/>) digital imaging software. Each sperm tail was measured from the base of the sperm head to the tip of the tail, using a Wacom Intuos graphics tablet, calibrated using a standardized scale.

Sperm behaviour was videotaped in the field within an hour of collection. A sample ($<1 \mu\text{L}$) of milt from each fish was placed on a haemocytometer with a slip cover. The sample was viewed at 100-times magnification under a negative-phase contrast microscope (Olympus CH30) attached to a video camera (Sony model XC-ST50, Hamilton-Thorne Research, Beverly, Massachusetts, USA). Sperm were activated by flooding the slide with lake water with an average temperature of 6 °C. Sperm activity was recorded until all spermatozoa stopped moving. Because sperm swimming speed varies with temperature, water temperature on the slide was maintained using a modified Peltier plate. Lake temperatures were relatively consistent across the sampling sites as a result of a time lag between northern and southern collections.

The videotapes of sperm behaviour were analyzed using a CEROS video sperm analysis system (v. 12, Hamilton-Thorne Research). Smoothed average sperm velocity (VAP, $\mu\text{m/s}$) was measured for a minimum of 25 spermatozoa from each male at 10 s after sperm activation. Smoothed average sperm velocity was calculated using a smoothing algorithm that reduces the effect of lateral head displacement on the estimate of sperm swimming speed, and thus mimics the most natural path of travel by a spermatozoon (Casselmann et al., 2006). For each male, the VAP at 10 s after activation (VAP10) was used for analysis because the majority of fertilizations have been reported to occur within the first few seconds following emission in externally fertilizing fishes (Vladic and Järvi, 1997; Hoysak and Liley, 2001). To minimize the effects of outliers and the typical skewness of sperm speed distributions, we performed all analyses using median VAP10 values for each male (Casselmann et al., 2006).

Similar methods to those described above were used by Burness et al. (2008) to obtain sperm swimming speeds and sperm tail lengths for Bay of Quinte lake whitefish. The major difference in sperm handling between the two studies was that Burness et al. (2008) added an extender to the sperm sample prior to activation to facilitate the tracking of spermatozoa swimming speed. The use of an extender for the Lake Michigan samples was not necessary because of improved handling and tracking methodologies. The other major difference in handling techniques between the two studies was that the temperature of the lake water used to activate sperm samples from Bay of Quinte fish was 7 °C (Burness et al., 2008), which was a slightly warmer temperature than that used for Lake Michigan samples.

Data analysis

Condition of Lake Michigan and Bay of Quinte lake whitefish from which sperm samples were collected was indexed using residual soma mass. Residual soma mass was estimated by regressing \log_{10} soma mass (soma mass = body mass – total testes mass) versus \log_{10} FL and calculating the residuals or differences between predicted and observed Soma mass (Burness et al., 2008; Schulte-Hostedde et al., 2005). The residuals from this regression equation provides an indication of whether an individual's soma mass is greater or less than the conditional mean relationship between soma mass and fork length and helps control for body size differences in soma mass (Jakob et al., 1996).

Prior to analyses, two outliers were removed from the Bay of Quinte lake whitefish data. One of the outliers was a 16-year-old fish

that was both the oldest fish in the sample and in very poor condition. The second outlier was a fish that had very small testes for his body size, indicating that he was likely not in breeding condition (see Burness et al., 2008 for further details). Additionally, one outlier was removed from the Lake Michigan dataset. This individual had a recorded total testes mass that was approximately 2.5 times greater than the average testes mass for the population. We chose to delete this observation from the dataset as we believed this was likely a typographical error that occurred during data entry.

We initially tested for differences in morphological and ejaculate traits of Lake Michigan and Bay of Quinte lake whitefish using *t*-tests. All variables were \log_{10} transformed prior to testing. We used weighted least-squares multiple linear regression to relate ejaculate investment (relative testes mass) and sperm quality (sperm swimming speed) to lake whitefish condition. Relative testes mass was calculated as the residuals from a simple linear regression model relating \log_{10} testes mass to \log_{10} FL (Burness et al., 2008). Fork length and fish age were also included in the models as predictor variables to determine if variability in relative testes mass and sperm swimming speed could be related to these variables. Separate models were constructed for the Bay of Quinte and Lake Michigan populations. For the Lake Michigan populations, an indicator variable was used to distinguish Naubinway and Saugatuck site effects.

The weights used in fitting the weighted regression models were estimated by first fitting the regression models by unweighted least squares and calculating the standardized residuals of these models (Neter et al., 1996). The weights for the weighted regression models were set equal to the inverse of the absolute value of the standardized residuals. Stepwise variable selection was used as a model selection process for determining how relative testes mass and sperm swimming speed were related to condition, fork length, and age. The site indicator variable also was included in the stepwise selection for the Lake Michigan dataset. The significance level for a variable to enter the model was set at $\alpha=0.25$, while the significance level for a variable to leave the model was set at $\alpha=0.10$. Multicollinearity among the variables included in the final regression models was assessed by calculating pairwise Pearson correlation among the variables. None of the predictor variables included in any of the final regression models had correlations greater than 0.30; as a result, we do not believe collinearity among predictor variables affected our conclusions. All analyses were performed using either JMP 7.0 or R 2.8.0 (R Development Core Team, 2008).

Results

Morphological and ejaculate traits

Morphological and ejaculate traits of lake whitefish were largely similar between Lake Michigan and Bay of Quinte (Table 1). There

were no statistically significant differences in mean age, fork length, right and left testes mass, and sperm tail lengths between the lakes. There were however differences in body mass and sperm swimming speeds between the populations. Body mass of lake whitefish from Lake Michigan was significantly greater than that of fish from Bay Quinte, while sperm swimming speed was significantly lower (Table 1).

As described in Burness et al. (2008), 81% of Bay of Quinte lake whitefish had a larger left testis than the right, with the average difference in mass of approximately 2.68 g. We found a similar difference in testis mass for Lake Michigan. Approximately 76% of lake whitefish had a larger left testis than the right, with the average difference in mass of approximately 2.56 g. Testing of the differences in testis mass by paired *t*-tests indicated that the differences in testis mass for the Lake Michigan samples were significant ($P<0.0001$) as were the differences in testis mass for the Bay of Quinte samples (Burness et al., 2008).

Relative testes mass

The final regression model for relative testes mass for Lake Michigan lake whitefish included fork length and residual soma mass as predictor variables (Table 2). The coefficient estimates for lake whitefish age and the indicator variable for Naubinway and Saugatuck site effects were not retained by the stepwise variable selection process. Based on the estimated standardized coefficients, fork length and residual soma mass had positive relationships with relative testes mass, indicating that relative testes mass generally increased in larger and better condition lake whitefish. The coefficient of determination for the final selected model was 0.87, which indicated that fork length and residual soma mass explained substantial variation in relative testes mass for Lake Michigan lake whitefish.

For Bay of Quinte lake whitefish, lake whitefish age, fork length, and residual soma mass were included in the final regression model for relative testes mass (Table 2). As was found for Lake Michigan, the coefficient for fork length and residual soma mass were positive, indicating that as these variables increased so did relative testes mass. The coefficient estimate for lake whitefish age was negative, meaning that younger fish generally had lower relative testes mass than older fish. The coefficient of determination for the final selected model was 0.90, which again indicated that substantial variation in relative testes mass of Bay of Quinte lake whitefish was explained by the predictor variables.

Sperm swimming speed

The final regression model for sperm swimming speed (VAP10) for Lake Michigan lake whitefish included fork length and residual soma

Table 1
Descriptive statistics for morphological and ejaculate traits of male lake whitefish (*Coregonus clupeaformis*) from Lake Michigan and Lake Ontario (Bay of Quinte). The median was estimated for sperm length and sperm speed (VAP10). All the morphology and ejaculate traits for the Bay of Quinte have been published in Burness et al. (2008). *T*-tests and Mann-Whitney tests were used to assess significance; the *p*-values from the *t*-tests are indicated.

| Trait | Lake Michigan | | | Bay of Quinte | | | <i>t</i> -test |
|-------------------------|-------------------|------------|----------|-------------------|-------------|----------|-----------------|
| | Mean \pm SE | Range | <i>n</i> | Mean \pm SE | Range | <i>n</i> | <i>p</i> -value |
| <i>Morphology</i> | | | | | | | |
| Sample Age (years) | 8.31 \pm 0.25 | 6–12 | 35 | 8.8 \pm 0.3 | 5–12 | 45 | 0.91 |
| Fork length (mm) | 452.2 \pm 3.76 | 375–550 | 66 | 452.9 \pm 5.0 | 360–538 | 47 | 0.96 |
| Body mass (g) | 1099.1 \pm 28.2 | 697–1986 | 66 | 1001.9 \pm 38.1 | 472–1712 | 47 | 0.02 |
| Left testis mass (g) | 9.46 \pm 0.50 | 4–27 | 66 | 8.38 \pm 0.56 | 3–19 | 47 | 0.48 |
| Right testis mass (g) | 8.08 \pm 0.62 | 3–37 | 66 | 6.74 \pm 0.46 | 3–19 | 47 | 0.78 |
| <i>Ejaculates</i> | | | | | | | |
| Sperm length (μ m) | 38.5 \pm 0.4 | 31.7–45.7 | 53 | 38.4 \pm 0.4 | 30.4–44.7 | 47 | 0.66 |
| VAP10 (μ m/s) | 83.5 \pm 2.4 | 52.0–129.2 | 66 | 112.5 \pm 2.0 | 108.5–116.8 | 23 | <0.01 |

Table 2

Standardized coefficient estimates and *P*-values for tests of whether the coefficient estimates were significantly different from zero for the relative testes mass regression models for Lake Michigan and Bay of Quinte. The regression models were fit using weighted least-squares regression and stepwise variable selection.

| Variable | Std. coefficient estimate | <i>P</i> -value |
|----------------------|---------------------------|-----------------|
| <i>Lake Michigan</i> | | |
| Fork Length | 4.17 | <0.001 |
| Residual soma mass | 2.29 | <0.001 |
| <i>Bay of Quinte</i> | | |
| Age | −2.05 | 0.02 |
| Fork length | 7.71 | <0.001 |
| Residual soma mass | 8.85 | <0.001 |

mass as predictor variables (Table 3). Based on the direction of the coefficient estimates, sperm swimming speeds were positively related to fork length, but was negatively related to residual soma mass. Compared to that of relative testes mass, the final regression model explained a smaller amount of the total variability of sperm swimming speed for Lake Michigan lake whitefish. The coefficient of determination for the sperm swimming speed model equaled 0.59.

For the Bay of Quinte, the final regression model for sperm swimming speed only included fork length as a predictor variable (Table 3). The coefficient estimate for fork length was positive, again indicating that sperm swimming speed was greater in larger fish. The coefficient of determination for the final regression model was only 0.31, meaning that nearly 70% of the observed variability in sperm swimming speed was left unexplained.

Discussion

Positive relationships between relative testes size and body condition have mainly been reported in non-fish taxa (e.g., Simmons and Kotiaho, 2002). As far as we are aware, Burness et al. (2008) provided the first evidence in fish of testes size (relative testes mass) being positively related to body condition (residual soma mass). We show here that a positive relationship exists between testis size and body condition (residual soma mass) for lake whitefish in Lake Michigan (Table 2). In other taxa, fitness benefits have been found to occur in individuals with larger testes. In yellow-pine chipmunks (*Tamias amoenus*), individuals with larger testes were found to have higher rates of reproductive success than individuals with smaller testes (Schulte-Hostedde and Miller, 2004). Whether such a relationship also holds in fishes remains unclear. Although, some studies have documented links between condition and reproductive success in species such as lake whitefish (Wedekind and Müller, 2004) and Atlantic cod (*Gadus morhua*) (Rakitin et al., 1999), other studies have not found such relationships (Coward et al., 2002). Even for those species where linkages between condition and reproductive success have been established, the physiological mechanisms governing the relationships are not well understood. Given the ecological and

Table 3

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| Variable | Std. coefficient estimate | <i>P</i> -value |
|----------------------|---------------------------|-----------------|
| <i>Lake Michigan</i> | | |
| Fork length | 5.73 | <0.001 |
| Residual soma mass | −3.30 | <0.001 |
| <i>Bay of Quinte</i> | | |
| Fork length | 22.25 | <0.001 |

economic importance of lake whitefish to the Great Lakes, clearly establishing the reproductive benefits of improved condition may assist fishery managers in formulating management decisions that can affect lake whitefish stocks.

Although a relationship between sperm quality (i.e., sperm swimming speed) and fish condition was detected for Lake Michigan lake whitefish, a similar relationship was not found for the Bay of Quinte. Positive relationships between sperm swimming speed and fork length were detected in both populations, which suggests that larger individuals may have a distinct reproductive advantage over smaller individuals. This observed relationship between sperm swimming speed and fork length may come as a surprise to some. Negative associations between sperm swimming speed and factors such as fish age and body size may have been expected as a result of larger individuals having better access to females because of a size-related dominance over smaller individuals, which might allow larger individuals to invest less energy into sperm energetics. Such an argument may not hold for lake whitefish, however, as the species is a broadcast spawner, and size-related dominance might not be expected to confer reproductive advantages over smaller individuals. Reduced sperm swimming speed in males in better condition may be the result of a trade-off between a male's investment in current body condition and growth, rather than into reproduction (Casselman and Montgomerie, 2004). Recent studies have identified sperm swimming speed as an important determinant of fertilization success in Atlantic salmon (Gage et al., 2004), so the negative relationship between sperm swimming speed, and size may have important consequences for male fitness, particularly in light of changes in growth and condition of Great Lakes lake whitefish.

Age was found to be negatively related to testes size in the Bay of Quinte population, but similar relationships were not detected in Lake Michigan (Table 2). This discrepancy in results between the Bay of Quinte and Lake Michigan populations possibly was related to differences in age distributions for the different samples. Although, there was not a significant difference in mean ages between the Bay of Quinte and Lake Michigan samples (Table 1), the age distribution for the samples from Lake Michigan were generally skewed towards younger age classes for the Naubinway site and towards older age classes for the Saugatuck site. A relationship between age and sperm characteristics may have been more apparent had the Lake Michigan age structure of the sample been more similar to that of the Bay of Quinte.

Variability in growth rates between the two Lake Michigan stocks may also have masked age effects because the slow growing northern Naubinway stock was pooled with the relatively faster growing southern Saugatuck stock (Muir, 2008). An additional factor that may have compounded comparisons among basins was that reproductive tradeoffs between male testis size, sperm quality, age, and body condition may have been occurring in Lake Michigan. For example, coregonids use lipids and proteins stored in the body tissues during active feeding to yield energy for growth and reproduction during the fall (Dabrowski, 1982). In the case of Lake Michigan fish, where growth and body condition has declined dramatically over the past decade (Pothoven et al., 2006), males may have been in poorer condition as a result of making greater reproductive investment to maintain sperm quality. Similar tradeoffs were proposed by Muir (2008) to explain patterns of female lake whitefish reproductive investment from the same populations from Lake Michigan.

The slight differences in sperm handling techniques and approaches for measuring sperm swimming speeds between our study and the Burness et al. (2008) study may have contributed to the discrepancies that were observed for Lake Michigan and the Bay of Quinte. The ambient *in situ* water temperature in the Bay of Quinte was slightly higher than in Michigan which could in part account for the higher sperm swimming speeds (Table 1) (e.g., Alavi

and Cosson, 2005). Such variation between sites in environmental parameters (including water chemistry) is a challenge when making broad geographic comparisons. Although it could be argued that sperm should be activated in distilled water of a constant temperature, this would not reflect the natural conditions experienced by the fish.

In both lakes, we aimed to collect males of similar age classes (Table 1) at the peak of spawning. This task was complicated by the fact that the spawning season and the water temperature during spawning for lake whitefish vary both spatially and temporally (Hart, 1930). For example, lake whitefish in the Bay of Quinte have been shown to spawn from late-October to early November where the water temperature ranged from 4.5 °C to 10.0 °C (Hart, 1930). However, there are reasons to believe that slight differences in the timing of sample collection during spawning did not affect our results. In general, male lake whitefish are the first to arrive on the spawning shoals and tend to mature sooner than females and remain ripe for a longer duration, primarily because less energy is required to maintain mature testis (Wootton, 1998). Furthermore, the spawning period lasts seven to ten days (Hart, 1930) and ripe males are present on the shoals throughout this period. Finally, in the family salmonidae, males are generally capable of fertilizing multiple females, and this is likely true for lake whitefish, which are broadcast spawners (Scott and Crossman, 1973).

Testis asymmetry has previously been reported in birds and frogs (Møller, 1994), and Burness et al. (2008) provided the first evidence from fishes, in their study of lake whitefish from the Bay of Quinte. We report here a similar asymmetry in lake whitefish populations from Lake Michigan, with the left testis most often larger than the right. Previous studies (e.g. Scharer et al., 2004) of invertebrates have shown that individuals with large testes produce sperm at higher rates. If a similar pattern were to be present in fish, then the larger size of the left testis in whitefish from the Bay of Quinte and populations from Lake Michigan would suggest that the left testis would make a greater contribution to sperm production than the right testis. Burness et al. (2008) also showed that the heavier left testis were a better predictor of sperm ATP stores per spermatozoon than was the smaller right testes, suggesting that testis size asymmetry may be related to production of high-quality sperm. Previous research has linked testis asymmetry in whitefish (*Coregonus lavaretus*) to environmental pollution (Liedtke et al., 2009), it presently is not known whether pollution could be a contributing factor to the testis asymmetry observed in Lake Michigan and Bay of Quinte lake whitefish.

In summary, we found that body size and condition (residual soma mass) of lake whitefish from Lake Michigan and Bay of Quinte (Lake Ontario) were important predictors of ejaculate investment (testes size) and sperm quality (swimming speed). Further work is necessary to determine whether body size and condition may be related to other measures of ejaculate quality, such as sperm density, motility, and ATP stores. Further work in the form of controlled laboratory experimentation is also needed to determine how variability in body condition influences sperm quality, and how this relationship can be affected by environmental or individual characteristics of a fish.

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