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Analysis of the larval swimming performance of two Great Lakes fish species:

Hydrodynamic & genetic effects on swimming

by

Sarah R.A. Humphrey

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Analysis of the larval swimming performance of two Great Lakes fish species:

Hydrodynamic & genetic effects on swimming

by

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DECLARATION OF CO-AUTHORSHIP

I hereby declare that this thesis incorporates material that is the results of joint research undertaken in collaboration with my co-supervisors, Dr. Dennis Higgs and Dr. Yingming Zhao of the Ontario Ministry of Natural Resources, who co-authored each chapter of my thesis. While I was the primary researcher to develop the key ideas, experimental design, data analysis and interpretation, the work could not have been completed without the contribution and dedication of Drs. Dennis Higgs and Yingming Zhao, as well as the financial support of the Ontario Ministry of Natural Resources and MITACS Accelerate. As my supervisors, they were essential to the proper development of techniques and data acquisition and provided statistical advice, as well as financial support.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from my co-authors to include the above materials in my thesis.

I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work, completed during my registration as a graduate student at the University of Windsor.

I declare that, to the best of my knowledge, my thesis does not infringe upon anyone’s copyright nor violate any proprietary rights and that any ideas, techniques, quotations, or any other material from the work of other people included in my thesis, published or otherwise, are fully acknowledged in accordance with the standard referencing practices. Furthermore, to the extent that I have included copyrighted material that surpasses the bounds of fair dealing within the meaning of the Canada Copyright Act, I certify that I have obtained a written permission from the copyright owners to include such materials in my thesis.

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ABSTRACT

The retention of eggs and larvae in suitable habitat through periods of strong current is necessary for growth and development of many fish species. This thesis examines abilities of eggs and larvae to withstand current driven advection and investigates morphological and genetic drivers behind possible retention. In the first study, the water velocities required to remove walleye eggs from substrates and larvae from station were investigated. Substrate type had an effect on egg retention, and swimming speed increased throughout development. Morphology predicts 59% of variation in swimming ability of larval walleye. The second study utilized a full-factorial breeding design to examine the effects of parentage on the swimming performance of lake trout. Swimming ability differed across families and a female effect was determined. Together, these studies provide insight into the role of current in egg and larval advection and broadens the knowledge of parental effects on swimming performance in fish.

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CHAPTER I

INTRODUCTION

Population sizes of many fish species are plastic and fluctuate with varying conditions. Some of the factors responsible for these fluctuations are food availability (Hjort, 1914; Lasker, 1981), predation (Quist *et al*., 2003; Crowder, 1980) and hydrodynamic forces (Matlock, 1987; Walker *et al*., 1991). These factors can be especially important for species with a pelagic larval stage when fish are more likely to be vulnerable to their surroundings. Johan Hjort (1914) proposed the "critical-period hypothesis", suggesting that the amount of prey available to first-feeding larvae can control their year-class strength: during the years with abundant prey, year-classes will be large but when prey are scarce, year-class strength will be weak. This hypothesis has been the source of much controversy among fisheries biologists. Marr (1956) disputed the existence of a "critical period", claiming there is little evidence proving mass mortality due to starvation in the sea among larvae which had recently started exogenous feeding (as cited by Li & Mathias, 1987). More recently proposed is the match-mismatch hypothesis, proposing that resources are patchily distributed and fish must encounter these patches to survive and recruit to the population (Cushing 1975). Prey abundance and the encounter rate of these young fish with the patches of food resources was first thought to be most important for young fish beginning exogenous feeding, but has since been expanded to include the entire larval stage (Cushing, 1990 as cited by Li & Mathias, 1987).

The arrival of larvae to suitable areas can be a strong determinant of year-class strength (Nelson *et al*., 1977; Sinclair *et al*., 1985; Roseman *et al*. 2005), as these supply the developing larvae with proper resources for growth: abundant prey, adequate temperatures (Checkley *et al*., 1988), and proper substrates and vegetation (Nagelkerken *et al*., 2001; Keckeis *et al*., 1997; Lehtiniemi, 2005). Temperature has a great effect on egg and larval development (Pepin, 1991), as warmer waters can reduce stage duration by increasing growth rates (Otterlei *et al.*¸1999; Pepin, 1991; Pepin *et al*., 1997), thus decreasing the risk of mortality due to predation (Miller *et al.*, 1988; Hare & Cowen 1997). The nursery habitats of freshwater species are often small and shallow, and because of this, they are vulnerable to temperature fluctuations (Houde, 1994) which can impact the survival of the developing larvae (Houde *et al.*, 1988). Checkley *et al*., (1988) suggest that Atlantic menhaden (*Brevoortia tyrannus*) has evolved to spawn in winter storms near warm currents that the larvae utilize as shoreward transportation. However, many species' spawning habits are not adapted to these conditions, and eggs and larvae can be carried by strong currents away from nursery areas. Deviation of physical processes away from those that the fish have been adapted to may explain variation in fish recruitment.

Observations of high mortality rates and the loss of cohorts due to single catastrophic storm events have been recorded in marine systems (Matlock, 1987; Walker *et al*., 1991; Moring, 1996; DiBacco *et al*. 2001; Martins *et al*. 2007). Similarly, large storm events can also have profound effects on the population dynamics of freshwater species (Shuter & Post, 1990; Zhao *et al*. 2009), and may cause mortality during the early life stages of fish. Eggs, larvae and nutrients can be removed from the vital spawning and nursery habitats by strong storm-generated currents and transported to unsuitable areas (Bishai, 1960; House, 1969; Lasker, 1975; Clady, 1976; Ventling-Schwank & Livingstone, 1994).

The vast majority of studies exploring the swimming abilities of larval fish utilize marine species as models; specifically coral reef fishes, as many of these species lead a pelagic larval phase. The larval pelagic phase is when dispersion occurs, determining the spatial scales of population connectivity and geographic size of the fish populations (Cowen, 2002; Sale, 2004). The focus of these studies is largely to determine the factors affecting the fluctuating population size and structure (Doherty & Williams, 1988 as cited by Stobutzki & Bellwood, 1997). Initially, researchers accepted the idea that larvae are passive particles, incapable of self-directed movement (Williams *et al*. 1984; Roberts, 1997), leaving the fish susceptible and helpless to their hydrodynamic environment. However, hydrological patterns alone are incapable of predicting observed larval distributions (reviewed by Leis, 1991), leaving larval behaviour as the determining factor. As such, more studies focused on this have been conducted, and have shown that some reef species are capable of withstanding currents and their behaviours play an active role in recruitment (Leis, 1982; Armsworth, 2000; Fisher *et al.*, 2000; Fisher *et al.*, 2005; Stobutzki & Bellwood, 1994; 1997). Many of these larvae are capable of swimming for long periods at speeds equal to or greater than ambient currents in their environment (Fisher *et al.*, 2005). A study by Fisher *et al.* (2005) measured the critical swimming speeds of 89 species of coral reef fish larvae, reporting swimming velocities ranging from 5.5 cm s^{-1} to 100 cm s^{-1}, demonstrating the strong swimming abilities of these fish. Stobutzki & Bellwood (1997) measured the sustained swimming performance of 9 families of late-stage reef fish larvae, with some larvae swimming several hundred hours and over 100kms in a single session. *In situ* swimming speeds of some coral reef fish larvae revealed velocities ranging from 1.8 cm s^{-1} to 65.5 cm s^{-1}, with nearly all species having mean swimming speeds greater than the ambient current (Leis & Carson-Ewert, 1997). Based on these numerous studies, it is clear then that many marine reef larvae are exceptional swimmers and their behaviour has an impact on their dispersal.

Despite the clear importance of larval swimming to marine reef fish populations, much remains to be learned about this relationship in freshwater species as studies in this field are lacking (Kekalainen *et al*., 2010; Huuskonen *et al*., 2009; Fuiman 1986; Hale, 1999; see review by Wolter & Arlinghaus, 2003). Fuiman (1986) determined that Zebrafish (*Danio rerio*) larvae can burst-swim against currents between 1.8cms^{-1} and 2.4 cms^{-1}. The burst swimming speeds attainable of 3 salmonid species (*Salmo trutta, Oncorhynchus kisutch* and *O. tshawytscha*) are much higher than those of *D. rerio,* attaining swimming speeds of 13-60 cms^{-1}, 14-100 cms^{-1} and 16-100 cms^{-1}, respectively (Hale, 1999). Endogenously feeding whitefish larvae (*Coregonus lavaretus*) are able to swim for 20-40s at 6.2 cm s^{-1} (Huuskonen *et al*., 2009), while those at 7 days post-hatch can swim between 100s and 150s at 6.2 cm s^{-1} (Kekalainen *et al*., 2010). As is clear from the few species that have been examined, freshwater fish have the potential to withstand current-driven advection but until more focused studies are conducted it will remain unclear how important these abilities are in a natural recruitment context.

Numerous studies exist exploring the role of parental effects on various larval characteristics including first feeding success (Huuskonen *et al.*, 2009), yolk-sac volume (Bang *et al.*, 2006; Kekalainen *et al.*, 2010), survival (Pitcher & Neff, 2007; Rudolfsen *et al.*, 2005; Butts & Litvak, 2007) and length and weight (Bang *et al.*, 2006; Saillant *et al.*¸2001; Butts & Litvak, 2007). Whitefish larvae from highly-ornamented dams have greater yolk volume and increased total lengths when compared to larvae from lesser ornamented dams (Kekalainen *et al.*, 2010). Also, a sire effect on the first feeding success in whitefish is apparent, with larvae from males having large breeding tubercles ingesting more prey than larvae from males with smaller tubercles (Huuskonen *et al.*, 2009). Parental effects can be separated into additive and non-additive effects, wherein lie the "good genes" and the "compatible genes" hypotheses, respectively. The good genes hypothesis is prevalent in non-resource based mating systems (reviewed in Kokko *et al*., 2003; Mead & Arnold, 2004), where females receive only gametes from their chosen mate and do not benefit directly (Hoglund & Alatalo, 1995; Payne 1984; Gibson and Bradbury 1985). Because there are no direct benefits for the female, she is thought to choose her mate based on his genetic quality, conferring increased survivorship to her offspring (Kokko *et al*., 2003). In these situations, additive genetic effects are responsible for the variation in characteristics throughout the population. The compatible genes hypothesis proposes that offspring fitness is increased because of favourable gene-gene interactions between sire and dam (Zeh & Zeh, 1996; Zeh & Zeh 1997). These compatible genes show non-additive genetic variation. The contribution of the female to her offspring can be both genetic and non-genetic. Non-genetic (maternal) effects have been noted across taxa (Roach & Wulff, 1987; see reviews by Mousseau & Dingle, 1991 and Price, 1998; Valenzuela, 2001) and can be the result of nutrient partitioning (Dzialowski & Sotherland, 2004), the presence of stress hormones (McCormick, 1999; Saino *et al*., 2005), and habitat choice (Hendry *et al.*, 2001; Iles & Sinclair, 1982), among others. There is a strong influence of maternal effects found in a variety of fish species including brook trout (*Salvelinus fontinalis*) (Robison & Luempert, 1984), pink salmon (*Oncorhynchus gorbuscha*) (Beacham, 1989), Arctic char (*Salvelinus alpinus*) (Nilsson, 1992), whitefish (*Coregonus lavaretus*) (Kekalainen *et al.*, 2010) and rainbow trout (*Oncorynchus* mykiss) (Wangila & Dick, 1996).

Although it is clear that offspring characteristics can be determined by parentage, very few studies have concentrated on the physical performance of larvae, more specifically swimming performance. Presently, there are 5 published studies which have determined the genetic component of larval and juvenile (7 days to 6 months post-hatch) swimming with contradictory results. Interfamily differences in burst swimming capacity have been seen in the threespine stickleback (*Gasterosteus aculeatus*) (Garenc *et al*., 1998). Whitefish exhibit maternal effects on sustained swimming speed (Huuskonen *et al*. 2009), and sire, dam and sire x dam effects on swimming performance (Kekalainen *et al*. 2010). Anemonefish (*Amphiprion melanopus*) (Green & McCormick 2005) show maternal effects on critical swimming speed. Although genetic and maternal effects are important in whitefish, anemonefish and sticklebacks, sockeye salmon (*Oncorhynchus nerka*) do not show parental effects on swimming performance (Nadeau *et al*. 2009). Based on the limited and contradictory results of studies examining the genetic role in swimming performance in freshwater species thus far, it seems probable that genes do play an important role in swimming performance and that these effects may be species- or stage-specific.

Although it is clear that genetic effects on growth and development exist, many conservation and management programs responsible for supplementing wild populations with the intention of creating a sustainable population or for recreational use often ignore sexual selection, producing and releasing fish with characteristics that may or may not occur in wild natural populations. These characteristics may be the result of altered genotypes which may contain deleterious alleles, harmful or fatal to the wild populations. Frequently, hatchery management teams breed individuals with desirable phenotypic traits such as increased growth rate, early reproductive performance or early maturation

(Gall & Huang, 1988a, 1988b; Su *et al*., 1999). These desirable traits are not necessarily advantageous to the fish once they are released into natural habitats where they can undergo high rates of mortality due to poor foraging (Brown & Laland, 2002; Johnsen &Ugedal, 1989) and predator avoidance skills (Berejikian, 1995; Johnsson *et al*., 1996). Wild populations can be spatially distinct, and this morphological and ecological divergence reflects local adaptation. After generations in hatcheries, fish often differ from their wild counterparts as seen in hatchery-reared brook trout (*Salvelinus fontinalis*), which show decreased swimming stamina as compared to their wild counterparts (Green, 1964). Although supportive breeding programs are introduced with good intention, the result may not be as hoped for. If wild populations have reached an optimal trait distribution shaped by selection in the natural environment, the introduction of captive-bred individuals may reduce the mean fitness of the population if reproduction between the exogenous and wild fish occurs. As an example, Pacific salmonids bred in captivity are under inadvertent selection for behavioural and morphological traits that are suboptimal upon release to wild habitats (Reisenbichler & McIntyre, 1977; Fleming & Gross, 1993). Although stocking local waterways and supporting natural populations appears benevolent, the actual toll taken on natural populations could be harmful and further action must be taken to ensure the genetic integrity of natural populations.

Thesis Objectives

Hydrodynamic forces play a crucial role in determining the life history of many fish species (Clady, 1976; Houde, 1989; Roseman *et al.*, 2001), and this is especially true during the egg and larval stages. Demersal eggs may be swept from the spawning habitat to unsuitable areas (Roseman *et al*., 2001; Roseman *et al.*, 2005) and larvae removed from nursery grounds (Roseman *et al*., 2001; Roseman *et al*., 2005), both resulting in reduced recruitment. The swimming capabilities of larval freshwater fish species is largely unknown, and the possibility of a genetic determinant of swimming performance is understudied in freshwater species. The primary objective of my thesis was to determine the water velocities necessary to remove walleye eggs from substrate and larvae at different stages of growth from station, and explore the possibility of a genetic component to swimming ability in lake trout.

My data chapters consist of three objectives. The first objective (Chapter 2) examined the water current velocity required to remove walleye eggs from varying different substrates over time. The second objective (Chapter 2) of my research examined the maximum velocity walleye larvae were capable of holding station against using a water flume apparatus. The third objective (Chapter 3) of my thesis examined the genetic effects on swimming ability using a full factorial design cross of lake trout.

To my knowledge, this is the first study to directly quantify the water current velocities required to remove freshwater fish eggs from their spawning substrate, and one of few studies examining the swimming performance of freshwater fish larvae and the role of genetics in larval swimming. Thus, my thesis serves an important function in broadening our current knowledge on the effects of hydrodynamic forces on freshwater fish eggs and larvae and their ability to remain in suitable habitat. It provides insight into the understudied area of freshwater fish swimming and the role of parental effects on larval swimming performance.

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CHAPTER II

HYDRODYNAMIC FORCES IMPACTING WALLEYE (*SANDER VITREUS*) RECRUITMENT AND RETENTION IN NURSERY AREAS

INTRODUCTION

For many fish species, larval survival is dependent upon the time of arrival at, and retention in, suitable nursery areas (Nelson *et al.*, 1977; Sinclair *et al.*, 1985; Roseman *et al*. 2005), as these habitats supply the larvae with proper and adequate resources required for their survival and growth. Physical environments can affect the development and survival of fish eggs and larvae, and ultimately result in large fluctuations in year-class strength (Clady, 1976; Colby *et al*., 1979; Sinclair *et al.*, 1985; Houde, 1989; Roseman *et al.*, 2001). Fish prefer suitable conditions for spawning, hatching and nursing activities and the conditions can vary greatly by time, space and fish species. These conditions include substrate type, vegetation cover (Nagelkerken *et al*., 2001; Keckeis *et al.*, 1997), temperature, and current velocity (Keckeis *et al.*, 1997). Temperature plays an important role in egg and larval development (Pepin, 1991), as warmer waters accelerate development (Otterlei *et al.*¸1999; Pepin, 1991; Pepin *et al*., 1997) and potentially decrease the mortality from predation in both egg and larval phases (Miller *et al.*, 1988; Hare & Cowen 1997).

In marine ecosystems, there have been numerous accounts of single catastrophic storm events or water current changes which resulted in high mortality rates during fish early life stages and even the loss of entire cohorts (Matlock, 1987; Walker *et al*., 1991; Moring, 1996; DiBacco *et al*. 2001; Martins *et al*. 2007). Similarly, large storm events have profound effects on the population dynamics of freshwater species as well (Shuter &

Post, 1990; Zhao *et al*. 2009). Fish eggs and larvae can be removed from vital spawning and nursery habitats by strong, storm-generated currents and transported to unsuitable areas (Bishai, 1960; House, 1969; Lasker, 1975; Clady, 1976; Ventling-Schwank & Livingstone, 1994), although studies focused on quantifying the current speeds required to remove eggs from substrate simply do not exist in the literature.

Previous studies investigating the impacts of water current dynamics on fish recruitment have been driven, at least partly, by the hypothesis that fish larvae are passive particles and capable only of limited self-directed movements (Williams *et al*. 1984; Roberts, 1997). Recent research on marine species suggest that this hypothesis is oversimplifying larval fish behaviours and fish larvae have clear ability to withstand current-driven advection (Leis, 1982; Armsworth, 2000). The ability to actively modify dispersal patterns has been demonstrated by the larvae of many coral reef fish species (Fisher *et al.*, 2000; Fisher *et al.*, 2005; Stobutzki & Bellwood, 1994; 1997). Some species are also capable of vertical migration which can act as an additional method of horizontal migration through self-selection of appropriate current regimes, ultimately altering dispersal trajectories during the larval stage (Sponaugle *et al.*, 2002; Paris & Cowen, 2004; Hare *et al*., 1999).

For most fish species, the pelagic larval phase is likely when dispersion occurs and may determine the spatial scales of population connectivity and geographic size of the fish populations (Cowen, 2002; Sale, 2004). Therefore, successful arrival at, and retention in, suitable nursery habitat has a substantial impact on the life history of these larvae. If larval fish are indeed capable of withstanding current-driven advection to remain in suitable habitat, as now seems likely at least for some marine species (Fisher *et al.*, 2000; Fisher *et al.*, 2005; Stobutzki & Bellwood, 1997; Stobutzki & Bellwood, 1994), nursery retention can no longer be considered a passive process. The dispersal patterns of warm-water marine fish larvae have been studied extensively; however, information about larval swimming for species inhabiting cool/cold-water environments are largely lacking in this regard. As it has been observed that there are large effects of temperature on the larval swimming (Green & Fisher, 2004; Koumoundouros *et al.*, 2002), much work remains to be completed to better understand the relationships between lake or river hydrodynamics and fish larval recruitment.

Body morphology has been shown to be correlated with swim performance in several species (Webb & Weihs, 1986; Sambilay, 1990; Fisher *et al.*, 2000), even during development (Bainsbridge, 1958; Wardle, 1977). Using these morphological measurements, predictions regarding the swimming capabilities of several species of mature fish (Langerhans, 2008) and larvae (Fisher & Hogan, 2007) have been made. Since individual variation in morphology exists in larval fish (Koumoundouros *et. al.*, 2002), it is possible that some individuals may be more suited to certain habitats when compared to other individuals. By incorporating the predicted swim performance of larvae into traditional practices, hatcheries may be capable of increasing survivorship of larvae upon release to their stocking habitats.

In the current study, I used walleye (*Sander vitreus*) as a model species to study the role of water current in egg retention and larval swimming performance. Walleye is an important species for Lake Erie's commercial and recreational fisheries, with a total allowable catch limit of 2.45 million fish in 2009 (Lake Erie Committee Walleye Task Group, 2010). The abundance of walleye eggs and larvae is heavily impacted by water currents in spawning grounds and retention in nursery areas (Roseman *et al.*, 1996; Roseman *et al*., 2001; Roseman *et al*., 2005) and early growth and survival of walleye is the primary determinant of year-class strength (Carlander & Payne, 1977; Forney, 1980). Walleyes are broadcast spawners preferring to spawn their adhesive eggs over rocky substrates in water <5m deep (Roseman *et al.*, 1996), leaving the demersal eggs vulnerable to removal from strong wind and wave action, possibly leading to higher mortality rates and lower recruitment (Johnson, 1961; Roseman *et al*., 1996). Lake Erie exhibits a patchy distribution of several resources necessary for walleye survival such as zooplankton (Watson, 1976) and water temperature and clarity (Bolsenga & Herdendorf, 1993; Roseman *et al*., 1999). Because of this distribution, walleye must be able to reach and maintain position in areas of high productivity, resisting out-advection via active locomotion. I examined egg retention and larval swimming and used the latter to develop a predictive model based on larval morphology.

METHODS

All walleye eggs and larvae were housed at the White Lake Fish Culture Station operated by the Ontario Ministry of Natural Resources in Sharbot Lake, Ontario. Newly hatched larvae were kept indoors during endogenous feeding, and then moved outdoors to large ponds, where they were sampled using bag seines. Larvae captured for trials were held in a 10L white bucket for the duration of trials per day, and eventually moved to a 75L aquarium stocked with zooplankton to remain overnight.

All trials were performed in a plexiglass flume, measuring 45x26x4.5 cm, featuring 3 swim chambers with areas measuring 18x7x4.5 cm (Fig. 2.1). The swimming area was sectioned using mesh screen to avoid loss of subjects, and plastic drinking straws were adhered near the inflow to provide laminar water flow to the chambers (Stobutzki & Bellwood, 1994). Water was delivered to the flume by a ½ horsepower submersible sump pump (Burcam Model # 300700P). Velocity was controlled using a rheostat (Powerstat®) and ball valves on the in- and out-flow tubes of the flume. Water velocity in the swim chambers was calibrated using a dye tracer, in the absence of fish. A dilute solution of methylene blue was released into the swim chamber and dye travel was video recorded. The time needed for this plume to travel a measured distance was quantified and converted to velocity (cm s^{-1}) for each rheostat setting used.

Broodstock at the White Lake Fish Culture Station originated from the eggs and milt of wild mature fish from the Bay of Quinte (Lake Ontario), haphazardly sampled in 2001. Eggs from 2 haphazardly chosen females were fertilized with milt from one haphazardly chosen male, and this procedure was replicated once. Each replicate of fertilized eggs was poured over experimental tiles in 2 aquaria and the eggs allowed to adhere to the substrate. The tiles were 5.1 cm^2 glazed porcelain tiles (Daltile Corporation) covered with aquarium stones, sand or left untreated. These tiles were placed haphazardly in the bottom of each aquarium, with each aquarium having equal numbers of tiles from the 3 treatments: stone, sand and smooth. Trials were run at 1, 3, 5, 8, 24, and 48 hours post fertilization, placing 1 tile from each treatment into the swim chambers. Water velocity was incrementally increased every 2 minutes, recording the time and speed when eggs were first removed (primary removal) and when approximately 90% of eggs were removed (secondary removal) from their respective substrates. It was not possible to estimate intermediate levels of egg removal as this would require disruptions in the water flow regime, likely leading to inaccurate results.

Walleye larvae were produced from 120 family pairings, with each parent weighing an average of 1kg. Swim trials began immediately after hatching when larvae measured approximately 8mm total length. One larva was placed into each swim chamber, and left to acclimate in still water for 5 minutes. Once the trial was started, water temperature was kept constant by exchanging water from large supply bin with fresh water. Water current was increased every 5 minutes until maximum velocity was attained. The last velocity at which the fish retained station was recorded, and deemed the maximum swimming velocity, after which the fish were removed individually and euthanized via overdose of tricaine methane sulphonate (MS-222 Sigma). The larvae were then fixed in 4% paraformaldehyde and transported back to the University of Windsor for morphological analysis using Northern Eclipse imaging software (Empix Imaging Incorporated, www.empix.com). Morphological measurements of each larva were recorded (total length, body depth, caudal peduncle depth, caudal fin depth and caudal fin area), combining several measurements to produce morphometric ratios (see Fisher & Hogan, 2007). The aspect ratio (AR) was produced by dividing the caudal fin depth by the square root of the caudal fin area, and the square of the caudal peduncle depth factor (CPDF) was calculated as the caudal peduncle depth divided by the body depth. Using these morphological parameters (TL, AR and CPDF^2), the swimming performance of each larvae was predicted based on the protocol of Fisher & Hogan (2007).

Data gathered from egg removal experiments were analyzed using nonparametric 2-way ANOVA with hours post-fertilization and substrate as fixed effects, with Tukey post-hoc analysis where appropriate. My experimental apparatus was unable to reach velocities fast enough to achieve secondary removal of eggs from the control and stone treatments, so an arbitrary velocity (40 cm s^{-1}) was utilized in cases where eggs remained adhered to the substrate. This arbitrary maximum velocity was chosen because it well exceeds the maximum attainable velocity from the experimental apparatus and statistical analyses showed that speeds of 40cm s^{-1} and greater gave similar results. Therefore, I used the nonparametric statistical approach to analyze the egg data. Data from larval swim trials were analyzed using curvilinear, exponential and piecewise regressions to examine developmental changes in swimming speed. The Akaike information Criterion corrected by sample size was used to select among the three models. The observed larval swimming speed was first categorized into 12 intervals by larval length (mm): 6.5-8.5, 8.5-10.5, 10.5-12.5, 12.5-14.5, 14.5-16.5, 16.5-18.5, 18.5-20.5, 20.5-22.5, 22.5-24.5, 24.5-26.5, 26.5-28.5, 28.5-30.5. The mean swimming speed and the mean length for each length interval were used for the regression and model selection. Multiple regression and multivariate tests were used to test the predictive ability of the morphometric model (TL, AR and $CPDF^2$), the difference in morphology between individuals that swam and those that did not as well as identifying any distinct morphological groups. The relationship between the raw morphological measures and swimming performance was further investigated using discriminant function analysis. Predicted swimming speeds were calculated using the equation $Y = A(TL) + B(AR) + C(CPDF^2) + error$, and were plotted against the observed swimming speeds of the larvae that swam. Residual analyses were used to develop a size-independent measure of the influence of the aspect ratio on swimming performance.

RESULTS

For the egg removal trials, a 2-way ANOVA using the ranked values of primary removal velocity revealed that there was a significant effect of treatment type on the speed at primary removal (Table 2.1, Fig. 2.2, $F_{2, 90} = 21.73$, $p < 0.001$) though there was no effect of time post-fertilization nor the interaction of time post-fertilization and treatment (Table 2.1, Fig. 2.2, $F_{5, 90} = 1.26$, $p = 0.29$ and $F_{10, 90} = 0.72$, $p = 0.71$, respectively). Tukey post-hoc analysis showed that the control and stone treatments were both significantly different from the sand treatment ($p < 0.001$ for both treatments), with eggs being easily removed from the sand treatment at an average velocity of 11.23 ± 0.87 cm/s for primary removal. There was no difference in current speed at primary removal ($p = 0.78$) between the control and stone treatments (18 ± 1.05 cm/s and 18.5 ± 0.83 cm/s, respectively). A 2-way ANOVA using the ranked scores of the velocity at secondary removal again revealed that there was a significant effect of treatment type on secondary removal (Table 2.1, Fig. 2.3, $F_{2, 90} = 49.012$, $p < 0.001$), though there was no effect of time post-fertilization nor the interaction of time post-fertilization and treatment (Table 2.1, Fig. 2.3, $F_{5, 90} = 1.23$, $p = 0.30$ and $F_{10, 90} = 1.23$, $p = 0.28$, respectively). Tukey post-hoc showed that the control and stone treatments were both significantly different from the sand treatment ($p < 0.001$ for both treatments), although they did not differ from each other ($p = 1.00$).

I used three different regression models (curvilinear, exponential and piecewise) to test the relationship between total length of the fish and their respective swimming performance. The corrected AIC selected the piecewise regression to be the model of best fit with an AIC value of 2.87. There was minimal change in swimming performance with time until the fish reached 21mm in length, after which the swimming speed significantly increased (Fig. 2.5).

Multiple linear regression showed that the 3-parameter morphological model as found by Fisher & Hogan (2007) was also a significant predictor of swimming performance for walleye larvae ($F_{3, 353} = 114.41$, $p < 0.001$, $R^2 = 0.49$), though more variation was explained when using only fish that swam ($F_{3, 62} = 31.974$, $p < 0.001$, $R^2 = 0.59$).

The morphology of larvae that swam significantly differs from those that did not swim (Wilk's λ: $F_{9, 347} = 6546.37$, $p < 0.001$), where total length, body depth, caudal fin height, caudal peduncle depth, caudal fin area, caudal fin perimeter, caudal fin diameter and aspect ratio were significantly different between groups ($p < 0.001$, $p < 0.001$, $p < 0.001$, $p < 0.001$, $p < 0.001$, $p < 0.001$, $p < 0.001$, $p = 0.003$, respectively): however the caudal peduncle depth factor did not differ significantly between groups ($p = 0.474$) (Table 2.2).

To investigate the relationship between morphology and swimming performance further, I explored the contribution of aspect ratio and total length on swimming speed. As these two attributes are likely correlated, I developed a size-independent measure of the influence of aspect ratio on swimming speed using the residuals from a regression of aspect ratio on total length. Residual analysis demonstrated that aspect ratio independent of the influence of total length was also a significant predictor of swimming speed ($F_{1, 64} = 6.916$, $p = 0.011$, $R^2 = 0.083$).

Since piecewise regression is the model of best fit, this indicates the existence of 2 morphologically distinct groups based on the observed length: the group with total length less than 21 mm and the group larger than 21 mm. A stepwise discriminant function analysis on the 9standardized morphological variables confirmed the presence of the 2 distinct morphological groups (Table 2.3, Wilk's $\lambda = 0.135$, $F_{8, 348} = 278.79$, $p < 0.001$).The 4 morphological variables: body depth, caudal fin height, caudal peduncle depth and caudal fin area were selected at the final steps as main factors creating the two groups identified by the piecewise regression. The resultant discriminant function essentially indicated the magnitude of the contrast between caudal peduncle depth and caudal fin area, and body depth and fin height (Table 2.3). A cross-validation study showed that the discriminant function was able to successfully separate the two groups (chi-squared statistic = 702.941, df = 8, $p < 0.001$) with only one individual being classified incorrectly, and that the hit ratios for the two groups were 99.72 and 83.47, respectively. The overall Mahalanobis distance between the two group means was 46.2 (Table 2.4).

DISCUSSION

The present study utilized walleye to investigate the water velocity required to remove eggs from different spawning substrates and remove larvae from their station, and to my knowledge is the first to directly quantify the velocity needed to remove fertilized eggs of any fish species from their spawning substrate. Egg retention experiments demonstrate that once walleye eggs are adhered to a suitable substrate, the chances of removal by water currents do not change over time during the first 48 hours of the incubation period. The smooth (control) and stone covered tiles allowed for the greatest retention of eggs, and the average speed of first removal for both tiles was approximately 18cm/s. In fact, none of the velocities used in this study were able to dislodge the majority of eggs in the control or stone treatments, demonstrating the suitability of rocky substrates for walleye hatching conditions.

During the typical spawning season in Lake Erie (April-May), bottom current velocity measurements recorded at 7.5m in depth range from 0.1 cm/s to 40 cm/s, averaging at 7.3 cm/s (Zhao pers. comm.). Surface current measurements recorded velocities ranging from 0.5 cm/s to 44 cm/s, with an average velocity of 8.4 cm/s. These current velocities are based on recordings during the spring of 2010, and may not be indicative of the average conditions in Lake Erie, although this is the only available current data to date. The Lake Erie walleye population utilizes shallow mid-lake reefs for spawning at depths < 5m (Busch *et al*., 1975; Roseman *et al*., 1996). The reefs consist of gravel/rubble, silt and combinations of these substrates, and all are utilized by walleye with a high degree of the eggs spawned over silty areas (Roseman *et al*., 1996). Retention of the eggs is highest on gravel/rubble substrates (Johnson, 1961). The average bottom current velocities are largely incapable of removing a small amount of eggs from rocky substrates. Current velocity measurements rarely reach velocities greater than 30 cm/s (the maximum speed attainable in this study's apparatus), indicating that a large portion of eggs will remain adhered to rocky substrates. This has strong implications for walleye recruitment in Lake Erie. The results from the current study indicate sand to be of poor suitability for retaining walleye eggs, with egg retention likely similar to silt substrate: As such, it is very likely that eggs are easily removed from silty substrates, resulting in loss of the eggs and reduced recruitment. Additionally, high rates of sedimentation in Lake Erie during early spring (as cited by Busch *et al.*, 1975) likely reduce the survival of the early-spawned eggs, because fine, silty substrates could potentially suffocate the eggs and reduce adherence. Such conditions favour those walleye that spawn later in the season since sediment deposited in early spring is likely cleaned from the reef substrates via wave-action. According to my data, eggs will remain adhered to sandy substrates under calm conditions, however any deviation away from the norm, whether through storm events or changes in water level, increases the likelihood that the eggs will be removed from their sandy/silty substrate and swept away. There was an increase in the current velocity required for primary and secondary removal of eggs from the sand treatment at the 48 hour post-fertilization time period, however it is unclear whether this is biologically important or simply an artifact. The results from the current study also suggest that the estimates of the number of walleye eggs retained in the spawning grounds could be biased if using number of walleye spawners or the number of the eggs spawned as a predictor and ignoring substrate types. For example, eggs spawned in sandy or silty areas are more easily removed and swept away by water currents than those on gravels, rubbles or even rock surfaces.

A large number of larvae immediately post-hatch did not swim against the opposing current. This could be due to a number of factors. Though handling prior to experimentation was limited, walleye larvae become easily stressed (T. Drew, personal communication). A study by Tarby (1981) showed the adult walleye (>0.35m) refused to swim against current in energy expenditure experiments. This could be the case for the larvae as well, as prior to the application of the currents, larvae were observed to be actively swimming in their holding tank and inside the swim chamber during acclimation but to refuse to swim when some levels of water current were applied. It is also possible that larvae with yolk sacs are incapable of proper swimming, as the large yolk sac may impede motion (Bishai, 1960).

Although newly hatched larvae often did not swim against the current, there was an increase in the number of individuals that swam past approximately 15mm in total length. As such, the current study adds to the growing number of publications in support of the ability of larval fishes to actively swim against water currents. The swimming abilities of reef fish larvae vary greatly: at 12 hours post-hatch, the ambon damselfish (*Pomacentrus amboinensis*), coral cardinal (*Sphaeramia nematoptera*) and anemonefish (*Amphriprion melanopus*) all had some level of critical swimming ability, ranging from

1.8cm s^{-1} to 4.6 cm s^{-1} (Fisher *et al*. 2000). Critical swimming speeds of these species also increased throughout ontogeny, ranging from 10.9 cm s^{-1} to 30.3 cm s^{-1} (Fisher *et al*., 2000). Stobutzki & Bellwood (1994) found that pre-settlement reef larvae were capable of swimming more than 40 cm s^{-1}, though some species are capable of 75 cm s^{-1} (Fisher *et al*., 2005). Walleye larvae have a swimming ability falling within the range of coral reef fish larvae, though attainable speeds for the older/larger larvae could have been higher had the maximal speeds not been constrained by the experimental apparatus. It is possible that walleye larvae differ from fast-swimming reef species in swimming ability because their environments are considerably different. Marine reef larvae are exposed to a more constant and stronger current, and have likely evolved to these conditions by increasing their swimming speeds, whereas many lake-dwelling freshwater species are only exposed to these conditions infrequently and thus have a lower maximal swimming speed. How the swimming performance of walleye compares to other temperate freshwater species is hard to determine, as there are very few studies measuring this (Kekalainen *et al*., 2010; Huuskonen *et al*., 2009; Fuiman 1986; Hale, 1999; see review by Wolter & Arlinghaus, 2003). Zebrafish larvae, *Danio rerio*, measuring 3.6mm total length, are able to burst-swim against currents between 1.8cms^{-1} and 2.4 cms^{-1} (Fuiman 1986), while 3 salmonid species (*Salmo trutta, Oncorhynchus kisutch* and *O. tshawytscha*) are able to attain burst-speeds of 13-60 cms^{-1}, 14-100 cms^{-1} and 16-100 cms^{-1}, respectively (Hale, 1999). Whitefish larvae (*Coregonus lavaretus*) with yolk-sacs are able to swim for 20-40s at 6.2 cm s^{-1} (Huuskonen *et al*., 2009), and whitefish larvae 7 days post-hatch can swim between 100s and 150s at 6.2 cm s^{-1} (Kekalainen *et al*., 2010). Clearly, the lack of information regarding the swimming abilities of larval freshwater fish species warrants more attention so that comparisons across species can be made and their applications in fisheries management utilized.

Since fish larvae appear to be passive during early ontogeny and most are incapable of swimming against even minor currents, storm events would be catastrophic if currents carry them to unsuitable habitats (Roseman *et al*., 2001). At approximately 15mm total length (approximately 2 weeks post-hatch), walleye larvae are capable of withstanding currents between 10 cm s^{-1} and 15 cm s^{-1}, which are speeds greater than the average surface speeds recorded in Lake Erie (8.4 cm/s). Under regular conditions, these larvae are capable of resisting advection from the nursery habitat. When larvae are 25mm in total length, they are able to swim against currents between 20 cm s^{-1} and 30 cm s^{-1} and possibly even faster speeds. These speeds are much higher than the average surface current velocity in Lake Erie, indicating that these larvae also have to ability to resist advection, but at much higher velocities. The larvae will thus have a greater chance of retention in nursery habitats if storms occur several weeks post-hatch, after the yolk-sac has been absorbed and the larvae show greater swimming ability. Zhao *et al.* (2009) developed a hydrodynamic-ecological model to explore how currents affect walleye recruitment in western Lake Erie assuming that the larvae were passive particles without self-directed mobility. According to the present study, this assumption is only justifiable for walleye larvae less than 15mm in total length. When those larvae measure total lengths greater than 15mm in total length, they are no longer passive particles and are capable of self-directed movement. As such, swimming performance data should be incorporated into the coupled model to obtain more accurate predictions of larval transport. The utilization of individual-based models can provide more information to researchers than models based on averaged values, especially when investigating factors related to size. Individuals of a species can vary in their size during the same developmental period, and these subtle differences can equate to differences in their recruitment success.

Consistent with previous research, the current study found that the total length of fish larvae was significantly related to their swimming ability (Fisher *et* al., 2000; 2005). The morphological model incorporating the total length, aspect ratio and caudal peduncle depth factor of each larva revealed that of those fish that swam, 59% of the variation in swimming ability could be explained by these measures alone, indicating that morphology is an important predictor of swimming performance of walleye larvae. The finding could be applicable to other freshwater fish species. The current data demonstrate similar findings to those of Fisher and Hogan (2007) who used 26 different families of pre-settlement juvenile reef fishes and concluded that the same morphological model used in the current study accounted for 69% of variation in swimming ability for these species. Similarly, a morphological model using aspect ratio and standard length explained 77% of variation in attainable swimming speeds of 63 species of fish (Sambilay, 1990). The unexplained variation of larval walleye swimming speeds observed in the current study may be due to differences in less obvious characteristics, such as genetic differences (Garenc *et al.*, 1998; Green & McCormick, 2005; Huuskonen *et al.*, 2009; Kekalainen *et al.*, 2010; Chapter 3) or intraspecific variation in physiological measures. However, the effects of these characteristics on the swimming speeds of fish larvae remain to be understudied. A significant difference in morphology was found between those larvae that swam and those that did not, providing further evidence that morphology is a good predictor of the swimming ability of fish larvae, although we recognize that the factors mentioned above could also be contributing to the tendency of some fish to not swim in our experimental setup.

Throughout development, larval morphology is constantly changing to meet the demands of the fish during a specific time period. After endogenous feeding commences, larval fish must be able to forage and swim efficiently in order to capture prey or evade predators, which are considered the main modes of larval mortality (Bailey & Houde, 1989). The results of discriminant function analysis show 2 distinct morphological groups, separated by body depth, caudal fin height, caudal peduncle depth and caudal fin area. According to the weights, there is a contrast in the thrust and drag forces generated by these morphological features, indicating that walleye greater than 21mm total length experience a shift in those structures which generate thrust and drag. A deep caudal peduncle and increased caudal fin area can create more thrust (Webb, 1982). The increase in caudal fin height allows for a greater amount of water to be affected by caudal propulsion (Webb, 1982) and when coupled with a small caudal peduncle depth, can reduce drag (Webb & Weihs, 1986). Drag can also be reduced by decreasing the caudal fin area by scooping out the centre area (Lighthill, 1975). Therefore, the changes we saw in walleye with area and depth should have signif impacts on thrust and drag. larvae have rounded caudal fins that begin to fork during development, allowing for the observed increase in swimming speed in the current study. A deep body is characteristic of slow-swimming fish, as there is greater resistance to acceleration with an increase in body depth (Webb & Weihs, 1986). Further exploration into other morphological ratios and features not measured in this study could yield interesting results.

In summary, the current study demonstrates significant effects of water current on walleye egg and larval retention in spawning and nursery habitats, and these effects differ with the life stages and the substrate types of the spawning grounds. The study also suggests that some current modelling approaches that assume larvae are passive particles and that all eggs regardless of spawning substrate have equal viability may be inadequate. Incorporation of more specific information on egg viability and swimming dynamics into recruitment models may lead to more accurate assessments of year-class strengths, especially considering the increased current speeds and wave action common during storm events in walleye habitats (Roseman *et al*., 2001).

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Table 2.1 ANOVA analysis using the ranked scores of current velocity at primary and secondary removal showed a significant effect of treatment type but no significant effect of hours post-fertilization nor the interaction of treatment and hours post-fertilization in either primary or secondary removal of eggs. Abbreviations are as follows: T – treatment type, HPT – hours post-fertilization and T x HPT – treatment x hours post fertilization.

		MS	**df**	**F**	**Sig.**
Primary Removal					
	T	14840.91	2	21.73	<0.001
	HPT	857.06	5	1.26	0.29
	T x HPT	490.24	10	0.72	0.71
	Error	683.06	90		
Secondary Removal					
	T	11833.37	2	49.02	<0.001
	HPT	297.92	5	1.23	0.30
	T x HPT	297.92	10	1.23	0.28
	Error	241.41	90		

Table 2.2 MANOVA analysis revealed a significant difference in total length (TL), body depth (BD), caudal fin height (CFH), caudal peduncle depth (CPD), caudal fin area (CFA), caudal fin perimeter (CFP), caudal fin diameter (CFDiam), and aspect ratio (AR) between larvae that swam and those that did not, and no difference between the 2 groups in the square of the caudal peduncle depth factor ($CPDF^2$).

		MS	**df**	**F**	**Sig.**
Wilks Lambda (λ)				6546.37	< 0.001
Group					
	TL	4066.57	1	193.7	< 0.001
	BD	138.01	1	170.65	< 0.001
	CFH	135.34	1	158.28	< 0.001
	CPD	29.02	1	174.7	< 0.001
	CFA	2285.39	1	228.52	< 0.001
	CFP	5086.35	1	209.29	< 0.001
	CFDiam	308.12	1	242.29	< 0.001
	AR	0.16	1	9.12	0.003
	$CPDF^2$	0.005	1	0.51	

Table 2.2 Continued

		MS	df
Error			
	TL	21.00	355
	BD	0.81	355
	CFH	0.86	355
	CPD	0.17	355
	CFA	10.00	355
	CFP	24.30	355
	CFDiam	1.27	355
	AR	0.02	355
	CPDF^2	0.01	355

Table 2.3 Results from MANOVA analysis revealed the presence of 2 distinct morphological groups. Subsequent weights and loadings from discriminant function analysis indicate the importance of each variable on the separation of the 2 groups.

	Value	**F**	**Numerator df**	**Denominator df**	**Sig.**
Wilks Lambda (λ)	0.135	278.79	8	348	< 0.001

Variable	**Weight**	**Loading**
Body Depth	-1.32	0.88
Caudal Fin Height	-1.56	0.89
Caudal Peduncle Depth	1.04	0.90
Caudal Fin Area	5.70	0.98
Caudal Fin Perimeter	-1.25	0.92
Caudal Fin Diameter	-0.16	0.92
Aspect Ratio	0.34	0.34
Caudal Peduncle Depth Factor	-0.23	0.16

Table 2.4 The importance of variables for discriminating between the groups was determined using backwards selection. The discrimination between the groups is measured by the total sum of all of the Mahalanobis distances. The naive ranking indicates which variables resulted in the largest change to the total sum of Mahalanobis distances when removed.

Variable	Mahalanobis Distance	Naïve Rank
Body Depth	45.27	5
Caudal Fin Height	44.44	2
Caudal Peduncle Depth	45.67	6
Caudal Fin Area	25.55	1
Caudal Fin Perimeter	45.08	4
Caudal Fin Diameter	46.14	8
Aspect Ratio	45.03	3
Caudal Peduncle Depth Factor	45.87	7

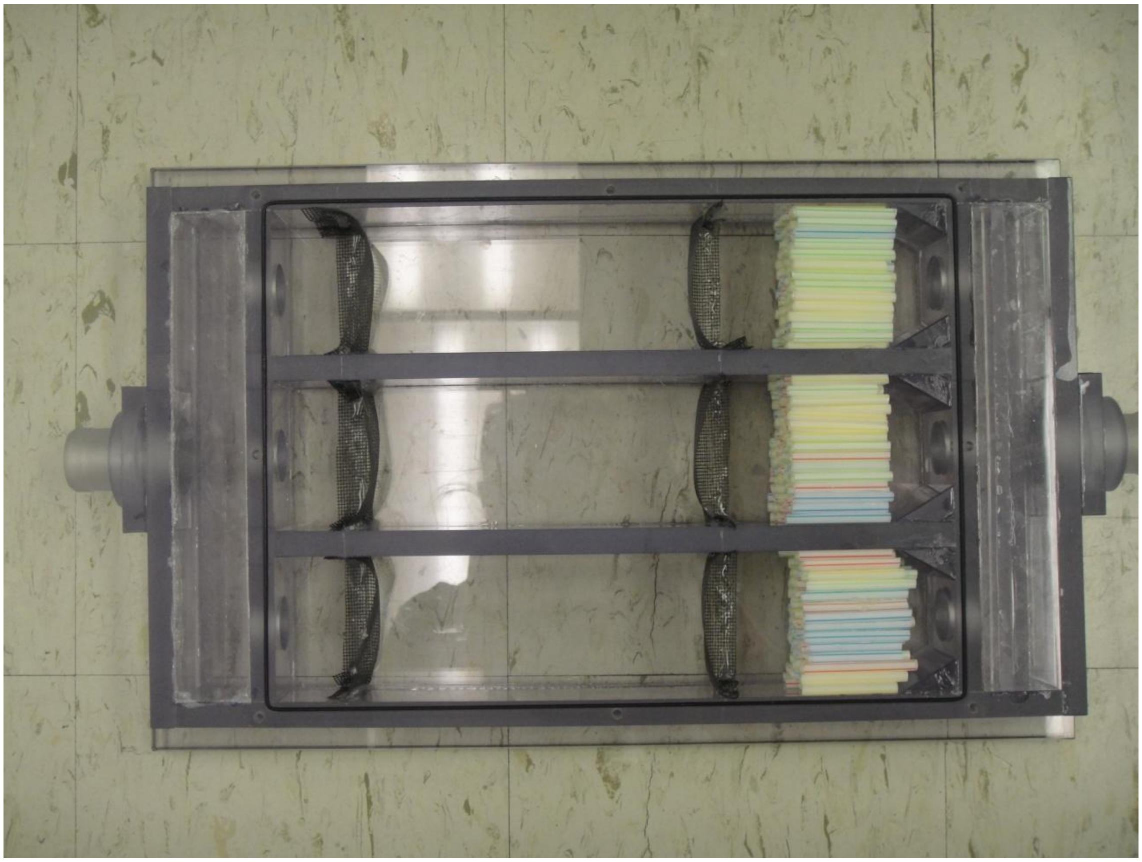

Figure 2.1 Photograph of the experimental flume. Swim chambers measure 45x26x4.5 cm, featuring 3 swim chambers with areas measuring 18x7x4.5 cm. The swimming area was sectioned using mesh screen to avoid loss of subjects, and plastic drinking straws were adhered near the inflow to provide laminar water flow to the chambers.

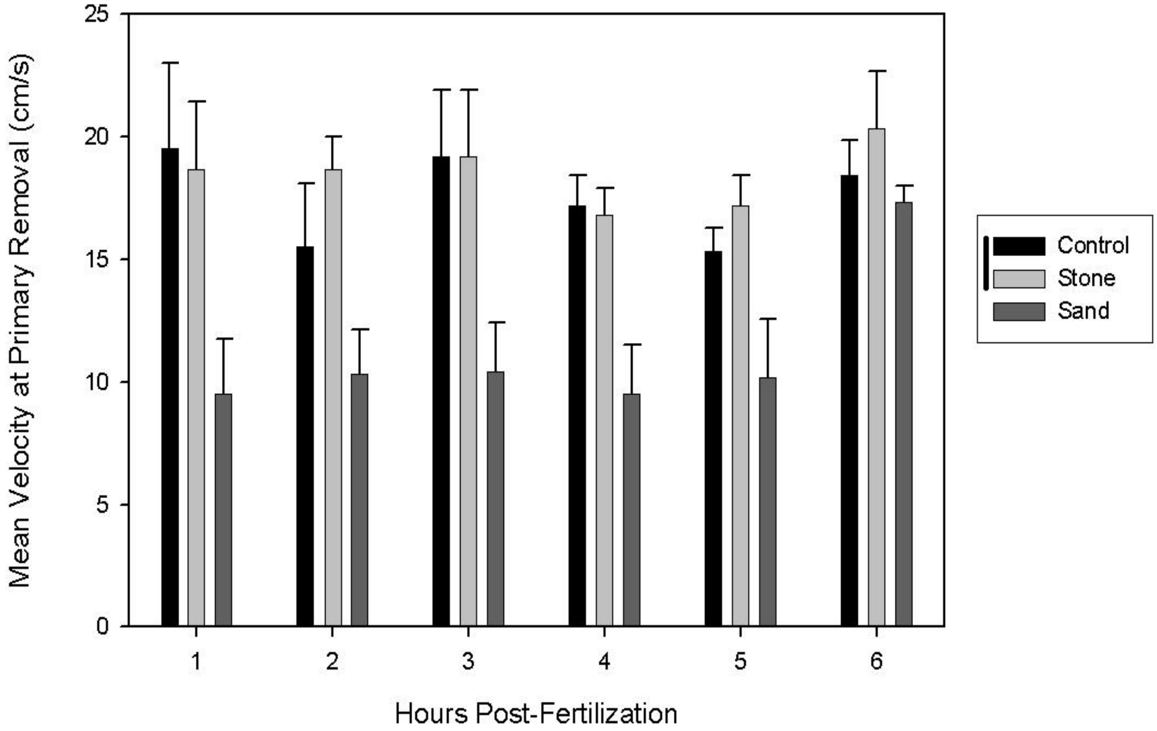

Figure 2.2 Results of primary egg removal trials from 3 substrates (control, sand and stone) at 6 different time periods (1, 3, 5, 8, 24, 48 hours post-fertilization) show a significant effect of treatment type on egg removal ($F_{2,\ 10.06} = 23.51$, $p < 0.001$), though no significance of hours post-fertilization nor the interaction of treatment and hours post-fertilization ($F_{5,\ 10.03} = 2.14$, $p = 0.14$ and $F_{10,\ 90} = 0.6$, $p = 0.81$, respectively). The control and stone treatments were both different from the sand treatment ($p < 0.001$), though not different from each other ($p = 0.78$). Infrequently, our experimental setup was unable to attain velocity capable of primary removal of eggs: For statistical purposes, we designated an arbitrary velocity (40cm/s) as the velocity required for primary removal of eggs.

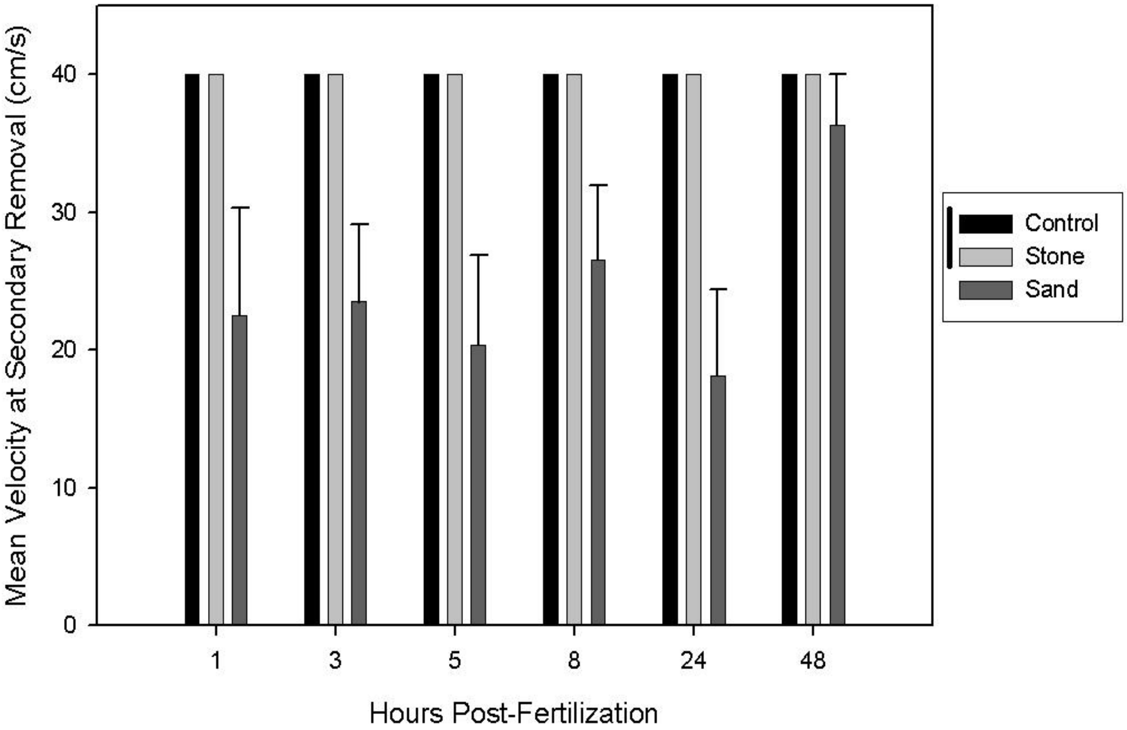

Figure 2.3 Results of secondary egg removal trials from 3 substrates (control, sand and stone) at 6 different time periods (1, 3, 5, 8, 24, 48 hours post-fertilization) show a significant effect of treatment type on egg removal ($F_{2,\ 10.03} = 33.99$, $p < 0.001$), though no significance of hours post-fertilization nor the interaction of treatment and hours post-fertilization ($F_{5,\ 10.02} = 0.1$, $p = 0.47$ and $F_{10,\ 90} = 1.14$, $p = 0.34$, respectively). The control and stone treatments were both different from the sand treatment ($p < 0.001$), though not different from each other ($p = 1.00$). Our experimental setup was unable to reach a maximal velocity capable of removing 90% of the eggs: For statistical purposes, we designated an arbitrary velocity (40cm/s) as the velocity required for secondary removal of eggs.

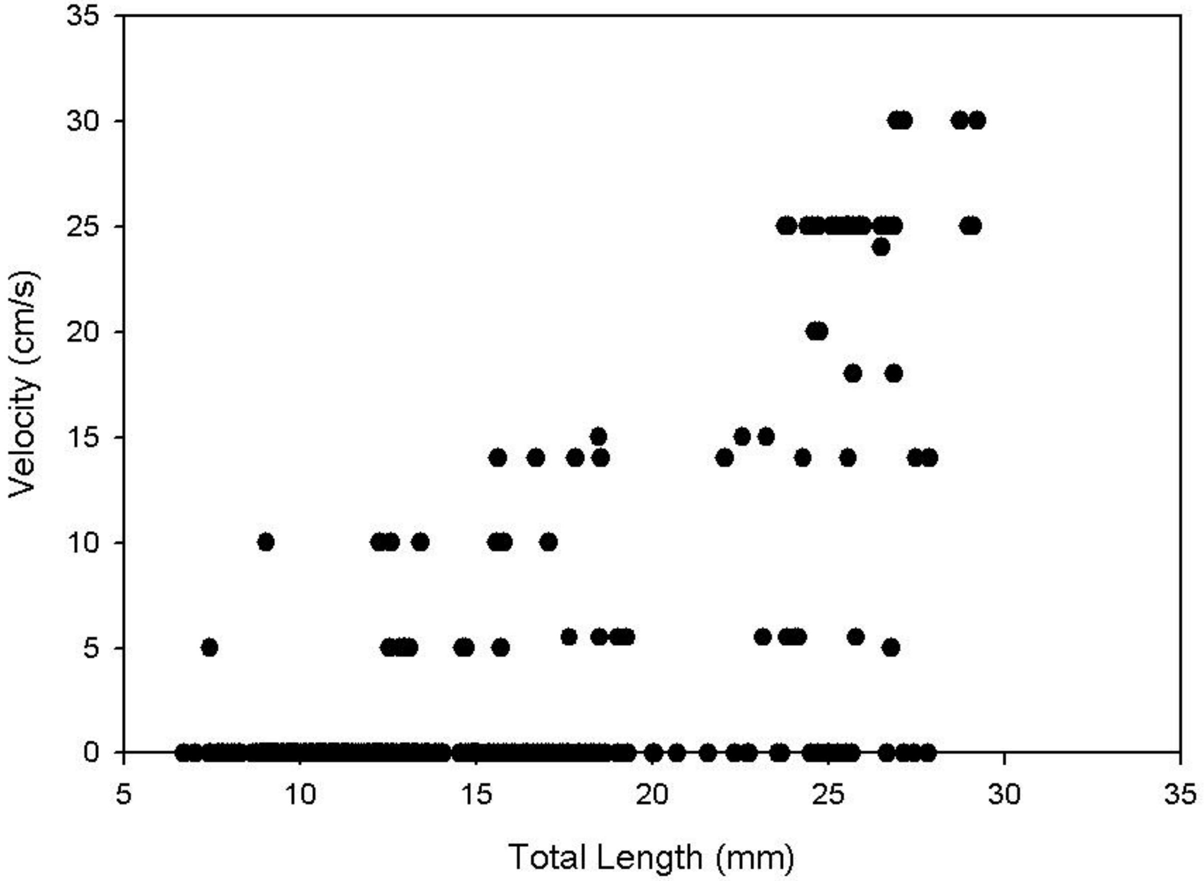

Figure 2.4 Scatter plot of all individual larvae and their respective maximum swimming velocity.

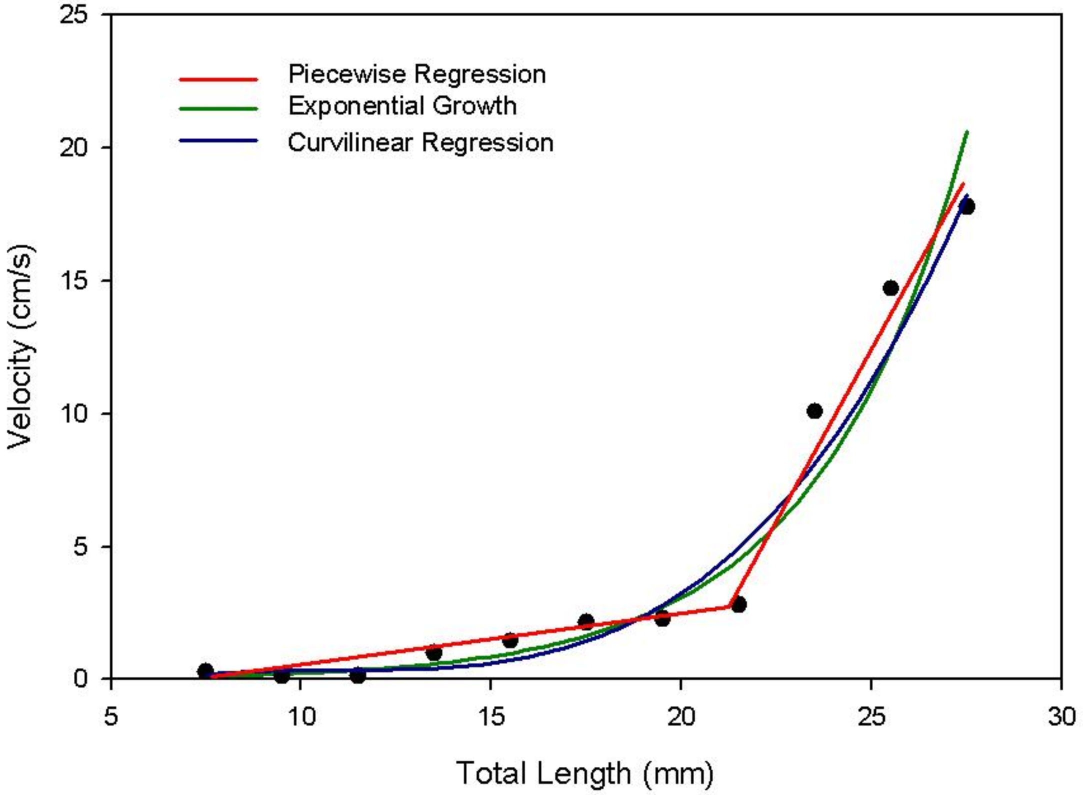

Figure 2.5 A visual comparison of the 3 models used to explore the swimming performance data. Each individual data point represents multiple individuals in 2 mm increments. AIC analysis showed that piecewise regression is the model of best fit (AIC = 2.87) with AIC values for exponential growth and curvilinear regression being 5.04 and 7.91, respectively.

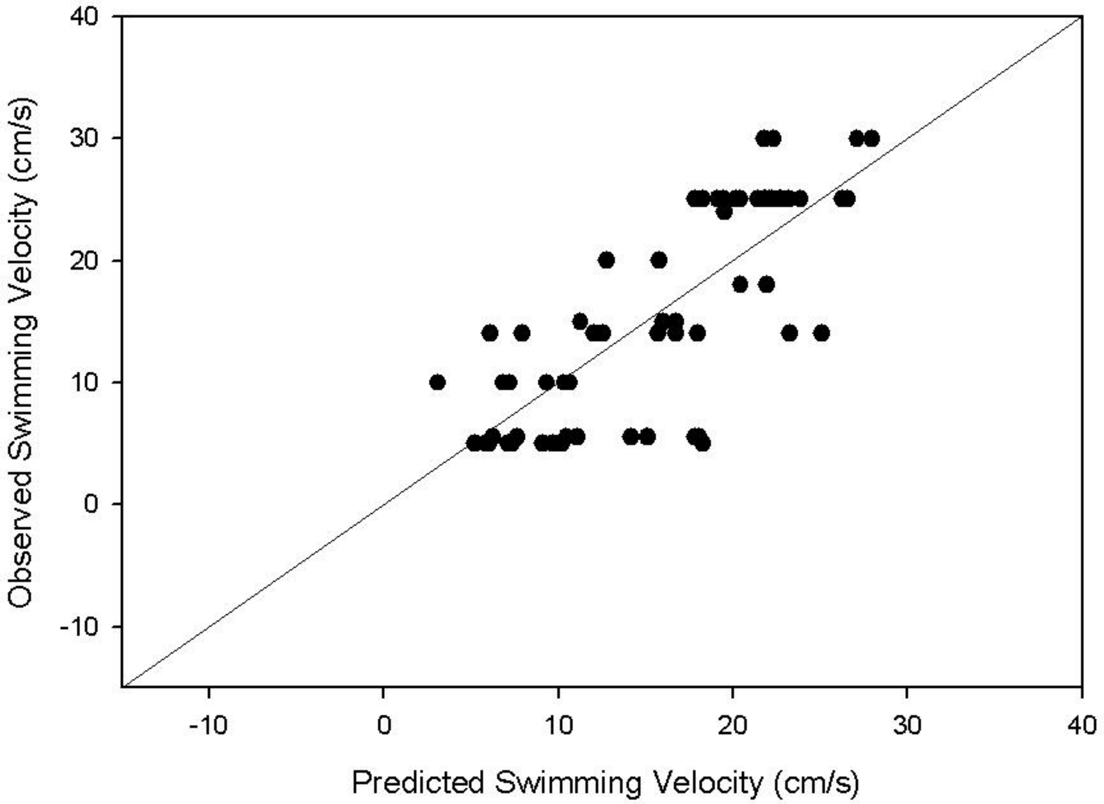

Figure 2.6 A visual representation of the fit between observed and predicted swimming speeds of larval walleye. The solid line represents a relationship of 1:1. Predicted swim performance was calculated by inserting the unstandardized coefficients from a multiple regression of total length, aspect ratio and caudal peduncle depth on velocity and their respective errors into a multiple regression equation.

CHAPTER III

MATERNAL EFFECTS ON THE SWIMMING PERFORMANCE OF LARVAL LAKE TROUT (*SALVELINUS NAMAYCUSH*)

INTRODUCTION

In fish, there is extensive evidence for parental effects on various features and characteristics of offspring (Kekalainen *et al*., 2010; Pitcher & Neff, 2007) and these effects can vary over time (Mousseau & Fox, 1998; Heath *et al*., 1999). Strong evidence exists for paternal additive genetic effects in Atlantic herring (*Clupea harengus*) (Hoie *et* al., 1999a,b), haddock (*Melanogrammus aeglefinus*) (Rideout *et* al., 2004) and brown trout (*Salmo trutta*) (Vollestad & Lillehammer, 2000). Female contributions to offspring fitness can be genetic or non-genetic. Maternal genetic effects have been found across teleosts (e.g. brook trout (*Salvelinus fontinalis*) (Robison & Luempert, 1984), pink salmon (*Oncorhynchus gorbuscha*) (Beacham, 1989), Arctic char (*Salvelinus alpinus*) (Nilsson, 1992), whitefish (*Coregonus lavaretus*) (Kekalainen *et al*., 2010) and rainbow trout (*Oncorynchus mykiss*) (Wangila & Dick, 1996)) and can represent an important component to overall offspring fitness (Robison & Luempert, 1984; Beacham, 1989; Kekalainen *et al*., 2010). Non-genetic maternal effects include nutrient provisioning during vitellogenesis (Bang *et al*., 2006; Lombardi, 1996), hormone release (McCormick, 1999), and spawning and nest habitat (Hendry *et al*., 2001; Iles & Sinclair, 1982). The genetic compatibility hypothesis proposes that offspring fitness is increased because of favourable gene-gene interactions between sire and dam (Zeh & Zeh, 1996; Zeh & Zeh 1997). In fish, such non-additive effects have been noted in Chinook salmon (Pitcher & Neff, 2007), Atlantic cod (*Gadus morhua*) (Rudolfsen *et al*., 2005), Alpine lake whitefish

(Wedekind *et* al., 2001), Atlantic salmon (*Salmo salar*) and Rainbow trout (Rye *et* al., 1990). Regardless of whether good genes or compatible genes mechanisms are at play in a given mating system, it now seems clear that genetic composition can have measurable impacts on offspring growth, survival, and perhaps performance.

Despite the clear evidence for genetic effects on growth and development as outlined above, and the evidence for active female mate choice in the wild (Zuk *et al.* 1989; Kokko *et al.* 2003; Milinski & Bakker, 1990), many conservation and management programs that supplement wild natural populations with captive bred individuals ignore sexual selection in the breeding designs (McLean *et al*., 2005; Lynch & O'Hely, 2001; Hankin *et al*., 2009). The heritability of phenotypic traits has been the basis of many production hatchery programs (Hankin *et al*., 2009; McLean *et al*., 2005), and mating is random or effort is placed into mating dissimilar individuals to increase genetic diversity, bypassing sexual selection (Hankin *et al*., 2009; McLean *et al*., 2005). Aquaculture operations may breed individuals who have desirable qualities from a production standpoint; such as growth rate, increased reproductive performance or early maturation (Gall & Huang, 1988a, 1988b; Su *et al*., 1999) but these qualities may not translate to success once fish are released to the wild. Hatchery-reared fish released into natural habitats show increased mortality which can be attributed to poor foraging (Brown & Laland, 2002; Johnsen &Ugedal, 1989) and predator avoidance skills (Berejikian, 1995; Johnsson *et al*., 1996). Often, the purpose of stocking local lakes and rivers has the conservation goal of producing a self-sustaining population, a goal that is compromised if released fish do not perform as well as their wild counterparts. While it is clear that hatchery rearing conditions can affect some aspects of viability (Maynard *et al*., 1995, 1996), potential genetic effects also must be considered when designing crosses for hatchery spawning (Bang *et al*., 2006; Pitcher & Neff, 2007; Butts & Litvak, 2007; Kekalainen *et al*., 2010.

A plethora of studies exist that focus on the role of genetics in several larval characteristics, including survivorship (Pitcher & Neff, 2007; Butts & Litvak, 2007), and growth (Bang *et al*., 2006; Pitcher & Neff, 2007; Kekalainen *et al*., 2010). However, very few studies have concentrated on the physical performance of larvae; more specifically swimming performance. Currently, there are 5 published studies exploring the potential genetic basis of swimming ability of fish larvae and juveniles, but the 5 have contrasting results. Threespine sticklebacks (*Gasterosteus aculeatus*) (Garenc *et al*., 1998) show interfamily differences in burst swimming capacity, whitefish (Huuskonen *et al*. 2009) and anemonefish (*Amphiprion melanopus*) (Green & McCormick 2005) show maternal effects on sustained and critical swimming speed, respectively, and whitefish larvae (Kekalainen *et al.* 2010) show sire, dam and sire x dam effects on swimming ability. In contrast, parentage is a poor predictor of swimming performance in sockeye salmon (*Oncorhynchus nerka*) (Nadeau *et al*. 2009). Based on the limited and contradictory studies thus far, it seems clear that genetic effects may play some role in swimming performance but these effects may be either species- or stage-specific. Until more analyses are conducted, it will remain unclear to what extent genetic effects can explain performance variation among and even within species.

In the current study, we used a 7 x 7 full factorial design cross of lake trout (*Salvelinus namaycush*) to partition genetic variance in offspring critical swimming performance among additive, non-additive and maternal effects. Lake trout are an important recreational and commercial fish (OMNR 2007), and are commonly produced in hatcheries for stocking local lakes and waterways (OMNR 2007). Incorporating the importance of genetic quality into supportive breeding programs could help lead stocked populations to becoming self-sustaining through increased larval survival upon release.

METHODS

In October 2009, a 7x7 full factorial design cross was produced at the Codrington Research Facility (Peterborough, Ontario). All adults used for the 7x7 cross originated from wild spawn collections from Kingscote Lake in Algonquin Park in 1999 and 2000. Founding data for all families were recorded (male and female parents) to facilitate subsequent rearing and data collection. All wild adults used for the 1999 and 2000 wild spawn collections were marked with a fin punch to prevent accidental re-use for gametes, and fin punches were individually kept for potential future DNA analysis. Any marked fish that were recaptured within or between years were excluded from additional gamete collection, to prevent unintentional inbreeding.

All males used in the cross and one female were from the 1999 cohort, and the remaining seven females were from the 2000 year class/cohort. Three males from the 1999 year-class (individuals from lots K-35, K-36, and K-37) were maternal half-siblings (R=0.25), as their family lots were founded from the same wild female in 1999 as part of the original breeding design for the captive population. All other captive adults that were used from the 1999 and 2000 year classes were unrelated, other than to the potential extent of shared ancestry within a wild finite population. As a result, parental relatedness and offspring inbreeding coefficients were nil for all families, and would not have influenced the hatching success of fertilized eggs.

Eggs and milt were collected by applying gentle pressure on the abdomen. Caution was taken during gamete collection to avoid getting eggs or milt wet, as this can activate sperm and induce water hardening, rendering gametes ineffective during fertilization. Fertilized eggs were then placed in Heath trays where they remained until hatching, at which point they were placed into large bins. Water temperature during development fluctuated from approximately 4-7^{0}C. Swimming trials were performed in late March shortly after exogenous feeding had begun when fish measured 26 ± 0.34 mm. All trials were performed in a plexiglass flume (Fig. 2.1), measuring 45x26x4.5 cm, featuring 3 swim chambers with areas measuring 18x7x4.5 cm. The swimming area was sectioned using mesh screen to avoid loss of subjects, and plastic drinking straws were adhered near the inflow to provide laminar water flow to the chambers. Water was delivered to the flume by a ½ horsepower submersible sump pump (Burcam Model # 300700P). Velocity was controlled using a rheostat and ball valves on the in- and out-flow tubes. Calibration of water velocity in the swim chambers was done using a dye trace, in the absence of fish. A dilute solution of methylene blue was released into the swim chamber and dye travel was video recorded. The time needed for this plume to travel a measured distance was quantified and converted to velocity (cm s^{-1}) for each rheostat setting used. Six juvenile lake trout were randomly selected from each of the 49 families for swim trials. One fish was placed into each swim chamber and allowed to acclimate for 5 minutes with no flow. Current velocities were increased in 2-minute intervals up to the maximum speed or when all fish had been exhausted and were removed from station. The last velocity the fish swam successfully was recorded, after which fish were removed individually and euthanized via overdose of tricaine methane sulphonate.

Data were analyzed using parametric one-way and two-way analyses of variance (ANOVA) with female identity (dam), male identity (sire), and the interaction (dam x sire) all entered as random factors as this is common statistical protocol found in pertinent literature. Additionally, nonparametric one-way and two-way Kruskal-Wallis analyses were conducted since normality could not be achieved, even with transformation. Both types of tests resulted in similar findings however, and parametric tests proved to be robust to non-normality: As such, all reported values are from parametric tests as these tests made it possible to also calculate variance components. Any negative variance components were assumed to be zero (Searle *et al*., 1992). Statistical analyses included only fish that swam against the water current, as analyses used require minimal to no zeroes present in the dataset. Non-swimming larvae may have been injured during the handling process or had morphological deformities that may have impeded swimming performance (Basaran *et al.*, 2007).

RESULTS

A total of 294 juvenile fish from 49 families were swum in the flume and all were of approximately equal total length (26 mm ±0.34). Mean critical swimming speed differed significantly across families ($F_{38, 98} = 1.745$, p=0.015), ranging from 1 (± 8.48) to 24.7 (± 4.89) cm/s (Fig. 3.1). Despite the overall difference in swimming ability, post hoc pairwise comparisons showed no difference in swimming ability between even the fastest (family 47) and slowest (family 18) swimming families (t = 1.09, df = 1, p = 0.474).

Lake trout swimming speed was significantly affected by the identity of the maternal female ($F_{6, 27.5} = 6.21$, $p < 0.001$, Table 3.1, Fig. 3.2) but not by the identity of the male ($F_{6, 28.69} = 1.362$, p = 0.263, Table 3.1, Fig. 3.2), nor the interaction between male and female ($F_{25, 99} = 0.89$, p = 0.623, Table 3.1). For the main effect of female, there were significant pairwise differences between females 6 and 7 ($p < 0.001$), 7 and 4 ($p < 0.001$), 7 and 3 ($p = 0.002$), 7 and 2 ($p = 0.012$), 1 and 7 ($p = 0.038$) and 4 and 5 ($p = 0.006$), with offspring from females 5 and 7 swimming faster than those from other families. Overall, the maternal effect in swimming performance explained 18% of the total variance in swimming speed, while the paternal and interaction effects were negligible (Table 1). A non-significant relationship between female body size and offspring swimming performance was found ($p = 0.244$, $R^2 = 0.110$).

DISCUSSION

The present study used a fully crossed quantitative genetic breeding design to quantify the genetic effects on larval offspring swimming performance during the early exogenous feeding stage. My results add to the growing number of studies on fishes that demonstrate the genetic components in larval swimming ability. Consistent with our study, Green & McCormick (2005) and Kekalainen *et al.* (2010) found maternal influences on swimming performance of larval fish, although the former study did not partition maternal effects into additive and non-genetic components, and the latter, in addition to maternal effects, also found significant paternal and interaction effects on swimming performance. It is interesting to note that current results differed from studies on another salmonid species, *O. nerka* (Nadeau *et al.* 2009) which found that maternal identity did not significantly affect burst swimming performance. This contradiction could be due to the fact that Nadeau *et al.* (2009) tested on juvenile fish, having fed exogenously for at least 4 months, and it is possible that the maternal effects were no longer expressed since it is possible that expression decreases over time (Mousseau & Fox, 1998; Heath *et al*., 1999). This decrease in maternal effects through ontogenetic progression has been demonstrated in a number of salmonid species (Gjerde & Refstie, 1984; Robison & Luempert, 1984; Beacham, 1989; Nilsson, 1992; Wangila & Dick, 1996), though in early life stages maternal effects were strong. The broad term "maternal effects" is comprised of genetic and non-genetic components, and there numerous ways for the dam to influence the condition of her offspring without the effects of her DNA. Non-genetic maternal effects can vary temporally and spatially, as there is a positive relationship between the amount of energy invested in offspring and maternal age (Berkeley *et al.*¸2004), and the specific environment chosen for egg deposition also has an effect on various performance characteristics of offspring (Hendry *et al.*, 2001; Ilse & Sinclair, 1982). In larval fish, offspring condition has been linked to numerous variables including egg size (Pepin *et al.*, 1997) exposure to hormones McCormick, 1999) and contaminants (Billard *et al.*, 1981), nutrient partitioning during oogenesis (Bang *et al.*, 2006; Lombardi, 1996) and nest site selection (Schaffer & Elson, 1975). The influences of these variables are not applicable to all species and the effects are likely species-specific. Although maternal influence can have a great effect on offspring condition, paternal identity has also been shown to have profound effects on offspring viability and various characteristics.

The lack of significant sire or dam x sire effects in our study could be explained by a change in expression over time as well. Paternal effects in survivorship of winter flounder (*Pseudopleuronectes americanus*) larvae increased with time post hatch (Butts & Litvak, 2007), however in haddock (Rideout *et. al.*, 2004), strong paternal effects on standard length were prevalent at hatching and decreased with time, though Probst *et al.* (2006) found paternal effects on yolk area and eye diameter to increase at 5 days post hatch. In brown trout, significant paternal effects were found on larval length at hatching but this relationship was insignificant at the time of death due to exogenous starvation (Vollestad & Lillehammer, 2000). Rideout *et al*. (2004) suggested that during the early life stages of fish, paternal effects, which are solely genetic, may be masked by maternal effects which are composed of nuclear and mitochondrial DNA as well as environmental effects. This can make paternal effects appear unimportant, although the time at which they are most influential seems to vary among species. It is clear that the current literature regarding parental effects and the times these effects predominate during development report conflicting findings, indicating that results are likely species and time specific. As such, had the current study taken place at an earlier or later time in development, the resultant parental effects may have differed.

The current study is one of very few in the growing field of genetic effects in larval swimming performance. As shown by the contradictory results of previous studies, the role of genetics in swimming performance remains unclear, perhaps due to differences in species but also because of differences in life history stage tested or methodological differences. In order to make comparisons across studies and species, it would be beneficial for researchers to adopt similar protocols and measures of performance such that reliable inferences can be made about the importance of genetic and environmental impacts on the development, and therefore fitness, of larval fish. At this time, researchers are employing whichever measure of swim performance is most convenient for their study, and may be dependent upon the budget, man-power and the time necessary to perform various swim trials. Burst swimming trials (Garenc *et al*., 1998; Nadeau *et al*., 2009), when fish are subjected to short bouts (<20s) of high velocity current (Beamish, 1978), are suited to studies with large sample sizes or those which are trying to minimize time. Critical swimming speed studies (Green & McCormick, 2005) which follow the method proposed by Brett (1964) utilize a post-handling recovery period of 8-12h in the flume, and although recent research has shown that 1-2h is sufficient for the fish to recover (Kolok, 1991; Peake *et al*., 1997), this is still time consuming. Although the use of exact procedures across species may not be possible, adopting similar methodologies and protocols would allow for comparisons of swim performance across species.

By utilizing the data from swim performance trials, aquaculture management teams may be able to produce more viable offspring, and increase release survival rates. Although breeding dissimilar individuals or breeding for traits that are beneficial from a production standpoint is common, it is not necessarily advantageous to the fish or practical in creating a self-sustaining wild population. Captive fish in a hatchery setting can lose characteristics that confer an advantage in the wild. A quantitative genetic model produced by Ford (2002) predicts that low gene flow from a captive to a wild population will shift the wild population's phenotype towards the optimal captive phenotype. This model also shows that introducing wild individuals into a captive population will not entirely eliminate this phenotypic shift. This domestication has been shown to hinder the success of hatchery-reared fish upon release to wild habitats via deviations in predator avoidance skills and agonistic behaviours (reviewed by Resisenbichler & Rubin, 1999), as well as decreased reproductive success (reviewed by Berejikian & Ford, 2004 as cited by Araki *et al.*, 2008). As this field grows and more data become available, comparisons across species may allow researchers and hatcheries to infer the abilities of their species of interest. Although there are only a handful of studies on the genetic effects of swimming performance to date, it is an important field that constitutes further study.

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Table 3.1 Paternal, maternal and interaction influences on the swimming performance of lake trout. Variance components and percent contributions were calculated using mean squares and corresponding error terms as described in Graham & Edwards (2001).

Source	**df**	**SS**	**F**	**P**	**Variance**	**Relative Contribution (%)**
Sire	6	519.702	1.362	0.263	1.135	1.285
Error	28.69	1824.78				
Dam	6	2364.788	6.212	< 0.001	15.98	18.09
Error	27.5	1744.79				
Interaction	25	1577.713	0.886	0.623	0	0
Error	99	7050.633			71.219	71.219

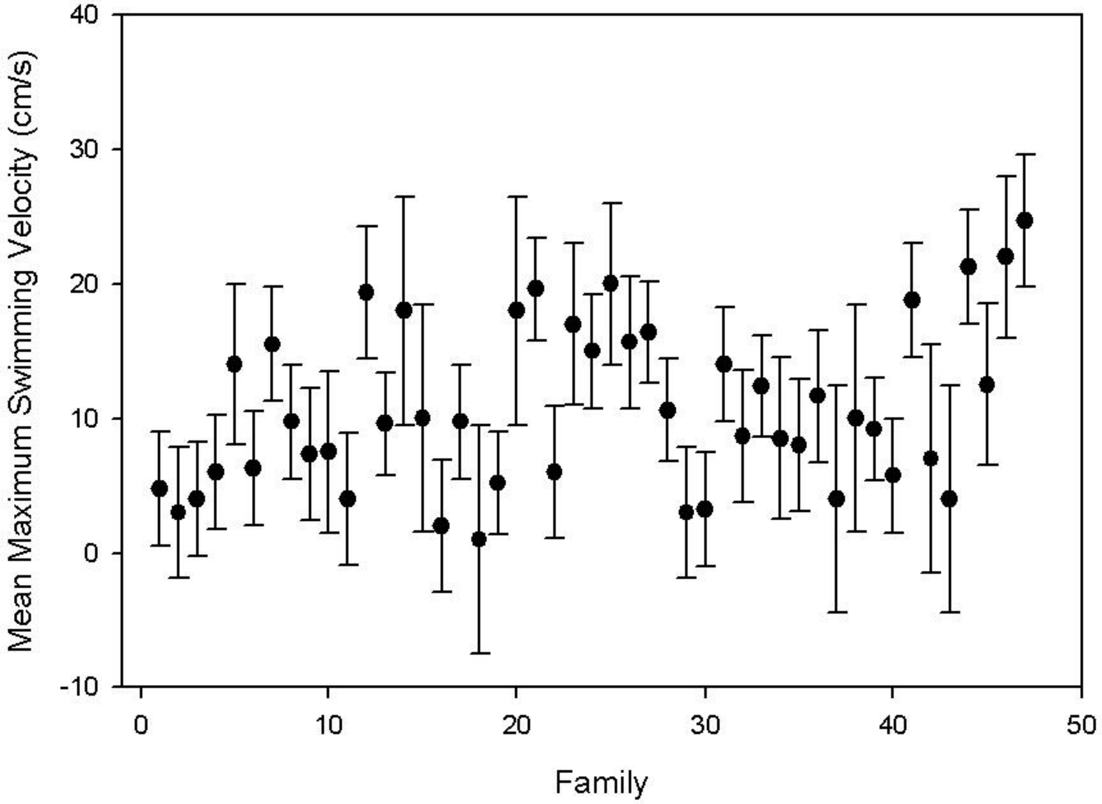
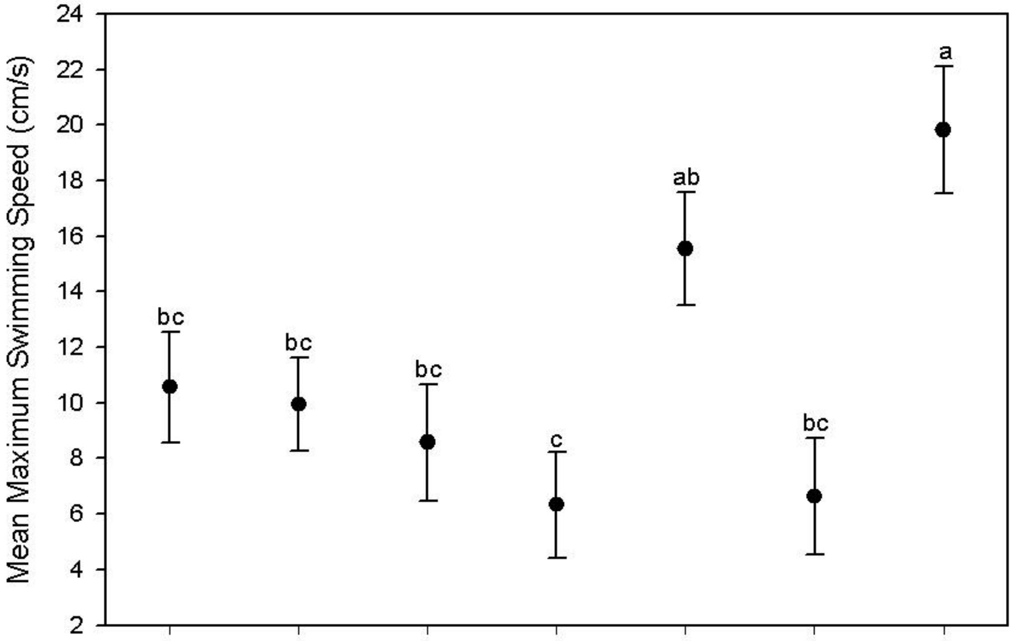
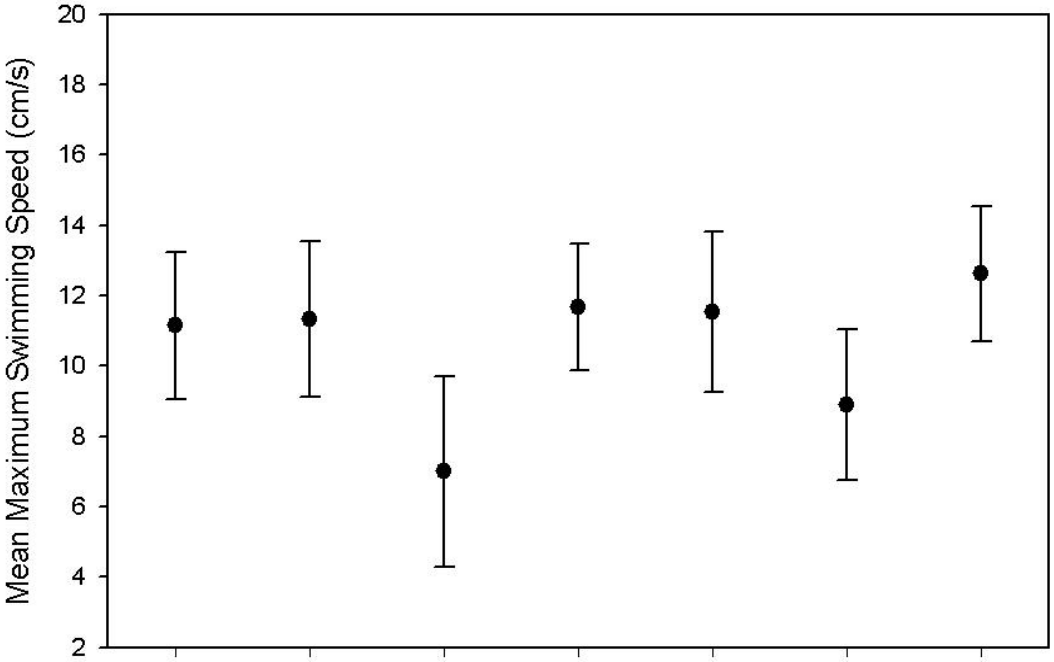


Figure 3.1 The relationship between swimming speed and family identity in lake trout. Of the possible 49 created families, 2 families lacked any larvae who swam. As such, the 47 plotted families each had at least one larvae which swam. A significant family effect on swimming performance was found (F = 1.745, df = 38, p=0.015).



Female Number (N)	1(19)	2 (29)	3 (17)	4 (21)	5 (19)	6 (17)	7 (15)
Body Weight (kg)	2.89	3.101	3.524	3.529	3.846	4.074	4.491
Total Length (cm)	63.7	61.2	64.2	65.9	65.7	72.8	69.4

Figure 3.2 The relationship between swimming speed and maternal identity. Female number has been plotted in ascending order of body weight. A significant maternal effect on swimming performance was found (F = 6.212, df = 6, $p < 0.001$).



Male Number	1	2	3	4	5	6	7
Body Weight (kg)	3.2	3.450	3.89	3.952	4.041	4.059	4.755
Total Length (cm)	67.0	66.6	68.7	65.8	69.5	71.0	72.0

Figure 3.3 The relationship between swimming speed and paternal identity. Male number has been plotted in ascending order of body weight. No significant paternal effect on swimming performance was found (F = 1.36, df = 6, p=0.0.26)

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