Life History and population dynamics of Eastern Sand Darter (*Ammocrypta pellucida*) in the lower Thames River, Ontario

by

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AUTHOR'S DECLARATION

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

Eastern Sand Darter (*Ammocrypta pellucida)* is listed as Threatened under the Canadian *Species at Risk Act*. Canadian populations are declining primarily due to the siltation of sandy depositional areas, the preferred habitat of the species. Little other relevant biological information is available for most Canadian populations and only limited information is available for populations in the United States. To supplement the paucity of information, this study collected biological information on *A. pellucida* during field surveys in 2006- 2007 from 10 sites located around the Big Bend Conservation Area in the lower Thames River, Ontario, Canada. Collected data were used to estimate critical life history traits including: longevity, fecundity, clutch size and number, growth, survival, age-at-first-maturity and cohort age structure. Longevity was 3+ years, with age-at-first-maturity being 1+ for both sexes. A minimum of 2 clutches, were laid per year with an average clutch size of 71 eggs. Average density within in the study area was 0.36 ± 0.11 *A. pellucida*/m^2. Quantitative comparison of lower Thames River biological information with a more southerly *A. pellucida* population in the Little Muskingum River, Ohio, demonstrated little latitudinal variation between the populations. Data comparison suggests that localized environmental factors are affecting biological characteristics, in particular water temperature that may be controlled by differences in riparian cover and/or groundwater input. Field derived life history information was used to create a Leslie matrix model which was used for population viability analysis. Perturbation analyses of reproductive scenarios involving changes in clutch numbers and size and age-at-first maturity found large variations in the finite rate of population growth. Elasticity analyses further indicated that 0+ survival and 1+ fertility were the limiting life history parameters. Thus allowing fish to survive until first reproduction would have the largest overall impact on improving population viability. Inclusion of environmental stochasticity in the model facilitated estimation of extinction probabilities in the range of 0.13 to 0.21

within 100 years. Based on the above, it is recommended that management activities for protection and restoration of *A. pellucida* focus on habitat protection of nursery and spawning areas. Further and improved biological data are also required to permit extension of basic population viability analysis to other *A. pellucida* populations.

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Chapter 1
Background Information

1.1 Species at Risk Act

Freshwater fishes in North America face many anthropogenic threats including: altered hydrologic regimes from channelization and impoundment activities, increased nutrient and sediment loads due to agricultural practices and deforestation of riparian areas, introduction of toxic contaminants from municipal and industrial sources, and the invasion of non-native species (Richter et al. 1997; Ricciardi & Rasmussen 1999; Olden et al. 2007). Due to these threats, Ricciardi & Rasmussen (1999) estimated that the number of temperate freshwater taxa are declining at a rate of 4% per decade. Within Canada, protection of endangered species is offered through the 2002 *Species at Risk Act (*SARA), that aims to protect species at risk from extinction through the creation and implementation of recovery strategies and associated management action plans (Rosenfeld & Hatfield 2006; Environment Canada 2009). Currently 47 freshwater fish species have been listed under SARA and recovery strategy development is ongoing. Development of mandated recovery strategies for these species requires increased knowledge of species' life history traits and the identification of critical habitat (Rosenfeld & Hatfield 2006; Environment Canada 2009), with the latter being defined as "the habitat required for the survival or recovery of a listed species" (SARA section 2).

1.1.1 Research Challenges for Species at Risk

For many of the listed species, limited biological information is available about life history parameters, habitat preferences, population dynamics or limiting factors. Habitat and population surveys are necessary to fill biological knowledge gaps, but must be conducted with minimal harm to

studied populations due to their listed status (Rosenfeld & Hatfield 2006). Sampling permits for species at risk specifically require non-lethal sampling techniques, thereby increasing the challenges associated with obtaining the life history and population information necessary for the development of recovery strategies.

Using the lower Thames River Eastern Sand Darter (*Ammocrypta pellucida)* population, the M.Sc. research discussed here used non-lethal sampling methodologies to fill biological knowledge gaps identified in the Recovery Strategy for Eastern Sand Darter in Canada (RSESDC) that was developed in consultation with federal and provincial agencies (Edwards et al. 2007). In particular, the research addresses the stated general aims of the recovery strategy by augmenting available population demographic information and using the information to better understand *A. pellucida* population dynamics via the construction and experimentation of a population model specifically calibrated to a Thames River, Ontario, population. When possible, demographics and population dynamics were coupled with habitat information to better understand the importance of habitat features as drivers of observed differences in population densities.

1.2 Focus Species: *Ammocrypta pellucida*

A. pellucida is listed as a Threatened species by the Committee of the Status of Endangered Wildlife in Canada (COSEWIC), SARA (Edwards et al. 2007) and the Committee on the Status of Species at Risk in Ontario (COSSARO) (OMNR 2009). Globally, *A. pellucida* are listed as rare (NatureServe 2009). In the United States, *A. pellucida* populations have not been actively protected by federal law, however, many U.S. states have listed the species under state endangered species legislation (Grandmaison et al. 2004).

A. pellucida have an adult size range of 46 - 71 mm and are most commonly associated with sandy substrate in rivers and lakes (Scott & Crossman 1973; Trautman 1981). Populations of *A. pellucida* are thought to be declining throughout their range due to habitat destruction, primarily via

the siltation of sandy bottoms from bank erosion and altered stream channels (Scott & Crossman 1973; Daniels 1993; Holm & Mandrak 1994; Holm & Mandrak 1996; Dextrase et al. 2003). Point and non-point contamination, invasive species (e.g., Round Goby (*Neogobius melanostomus))*, lack of genetic variation, baitfish harvest-related mortality and the pet trade are also thought to have contributed significantly to population declines (Holm & Mandrak 1996; Cudmore et al. 2004; Edwards et al. 2007). Based on historical population surveys, it has been estimated that 45% of Ontario's *A. pellucida* populations have disappeared during the past 50 years (Holm & Mandrak 1996).

1.2.1 Biology and Ecology of *A. pellucida*

The habitat associated with *A. pellucida* is shallow water (< 0.5m) with water velocities < 0.2 m/s and sand substrate (Daniels 1993). *A. pellucida* are not limited to this habitat, as they have been found in lacustrine environments over silt, gravel, detritus and clay substrates (Holm & Mandrak 1996; Facey 1998; Facey & O'Brien 2003). Nevertheless, Daniels (1993) noted that the best locations to find *A. pellucida* were the shallow depositional areas downstream of bends in meandering rivers. Anecdotal evidence from a tagging study in the Thames River suggests that *A. pellucida* do not migrate between depositional areas during the spring and summer (S.E. Doka, M.A. Koops, Fisheries and Oceans Canada, personal communication), but seasonal migration from sandy depositional areas to deeper pools for overwintering may occur (Simon & Wallus 2006). Larval *A. pellucida* may also undergo a pelagic phase involving passive floating with water currents (Simon & Wallus 2006), possibly as a means of dispersal.

A. pellucida display a fossorial, or burying behaviour that has been suggested as a predator avoidance tactic (Jordan & Copeland 1877). Burying behavior, however, has also been associated with improving the efficacy of prey ambush (Trautman 1981; Daniels 1989) and minimizing the

energetic costs of holding station in flowing water (Simon 1991). The lack of a developed swim bladder, in particular, enables *A. pellucida* to remain in close contact with the substrate (Evans & Page 2003). Burying as a tactic with evident physiological benefit has been questioned as a result of the reduced dissolved oxygen levels within substrates that may increase respiration costs (Holm & Mandrak 1994). Associated declines in temperature within substrates during the summer, however, may allow buried *A. pellucida* to lower metabolic rates in comparison to fish in surrounding waters (Simon & Wallus 2006), thereby increasing energy allocated to growth.

Maximum observed age in Ohio *A. pellucida* populations has been set at 2+ years, with female age at first maturation occurring at age 1+ (Spreitzer 1979). Recent aging analysis of specimens from the Thames River, Ontario, noted some individuals may reach 4+ (Drake et al. 2008). Little, or no, aging information is available from other studied populations, most notably those from southern Québec, northern Vermont and New York State.

The breeding behaviour of *A. pellucida* has not been observed in the wild and can only be inferred from anecdotal information. Spawning and fecundity estimates have been derived from laboratory studies, or inferred from sampling mortalities (Johnston 1989). Spreitzer (1979) found the sex ratio to be 1:1. It appears that the spawning season is protracted throughout the summer. Timing probably differs between geographic locations occurring when water temperatures reach 20.5 - 23°C (Spretizer 1979; Johnston 1989; Facey 1998). Ontario populations are thought to spawn from late June to late July (Holm & Mandrak 1994). Females may spawn multiple egg clutches throughout the season, as eggs in various stages of development have been found in the ovaries of females collected in Ohio (Williams 1975; Spreitzer 1979; Johnston 1989). Mean total fecundity has been reported as 343.1 ova for Ohio populations, with possible clutch sizes in the range of 30 - 170 ova (Spretizer 1979). Fertilized eggs with an average diameter of 1.4 mm are laid by females and then buried in the substrate (Simon & Wallus 2006). Gestation is thought to last 4 to 5 days at water temperatures of

20.5 - 23°C (Simon & Wallus 2006). Newly hatched *A. pellucida* are approximately 5.5 mm and remain in substrate interstitial spaces until the yolk-sac has been absorbed. Following absorption, larvae float in the water column before becoming benthic at about 7.4 mm (Simon & Wallus 2006; Simon et al. 1992). Further information detailing morphological development of larval *A. pellucida* can be found in Simon & Wallus (2006).

Young-of-the-year partition most of their energy towards growth as they obtain approximately 82% of their adult length in their first year (Drake et al. 2008). During subsequent years, most energy is partitioned towards reproduction (Drake et al. 2008). Growth of 0+ individuals has been positively correlated with the dominance of sand substrate and annual channel discharge Sand substrates are preferred for burying as finer substrates (e.g., silt) may cause clogging of gill filaments and decreased growth, while higher annual channel discharge values may increase growth rates as silt is flushed from the river (Drake et al. 2008).

Stomach content analysis has shown chironomid larvae are the most important prey item for Ohio populations (94.4%), with oligochaetes and cladocerans composing the rest of the diet (Spreitzer 1979). Recent dietary analyses of lower Thames River individuals using stable isotope techniques have indicated less reliance on chironomids, with larger dietary contributions from ostracods, oligochaetes and cladocerans (Finch et al. unpublished data).

Limited biological information is available for *A. pellucida*; with the unpublished study of Salt Creek populations (Spreitzer 1979) providing the most comprehensive study of life history characteristics to date. Subsequent studies of *A. pellucida* have primarily focused on: 1) determining presence/absence for purposes of preparing population status reports (Holm & Mandrak 1994; Holm & Mandrak 1996; Facey 1998; Grandmaison et al. 2004); 2) description of preferred habitat use (Daniels 1993; Facey & O'Brien 2003); and 3) the conduct of laboratory studies on fossorial behaviour (Daniel 1989; Simon 1991), and captive reproduction and larval development (Johnston

1989; Simon et al. 1992; Simon & Wallus 2006). Most of these studies have been descriptive in nature and have not provided the detailed quantitative data needed for the development of recovery strategies and management action plans.

1.2.2 Geographic Range of *A. pellucida*

A. pellucida are currently found in the St. Lawrence River watersheds of Québec, Vermont and New York, tributary watersheds of Lake Erie, Lake St. Clair and southern Lake Huron and the watersheds of the Ohio River from New York to Illinois and south to Kentucky (Page & Burr 1991; Edwards et al. 2007). Grandmaison et al. (2004) give a detailed description of the U.S. distribution, while Holm and Mandrak (1996) and Edwards et al. (2007) provide information on the Canadian distribution. *A. pellucida* were once abundant and ubiquitous throughout the geographic extent of their range. Contemporary surveys indicate the current distribution to be patchy as a result of the extirpation of numerous populations (Holm & Mandrak 1996; Grandmaison et al. 2004; Edwards et al. 2007); with the eastern and western portions of the range now clearly disjunct (Figure 1.1). The isolation of populations in the disjoint Canadian distribution does not allow for site re-colonization should local extinctions occur. Coupled with the overall decline of *A. pellucida* populations, population isolation provides a strong rationale for listing *A. pellucida* as a species at risk (Edwards et al. 2007).

As the Canadian *A. pellucida* populations are located at the northern extent of the geographic range for the species (Figure 1.1), it is expected that population characteristics (e.g., mean size at age) and vital rates (e.g., survival probabilities) will differ from those documented for more southerly populations. For example, at the edge of the geographic range it may be more difficult for individuals to locate the water temperatures that optimize growth and the vital rates (e.g., fecundity) that ultimately control population dynamics (Power & van den Heuvel 1999). As most of the research on

A. pellucida has focused on populations located in the mid or southern portion of the range, it is evident that more Canadian life history information is needed for the appropriate design of recovery strategies and assessments (Edwards et al. 2007).

1.3 Study Location- Thames River, Ontario

Anecdotal evidence has suggested that the Thames River has the largest population(s) of *A. pellucida* in Canada (Edwards et al. 2007), making it an ideal location for the study of population dynamics. On the basis of repeated sampling of the populations, Holm and Mandrak (1996) have concluded that while the range of *A. pellucida* populations within the Thames River basin has not been reduced, abundance is on the decline.

1.3.1 Description of Thames River Watershed

The Thames River is the second largest river in southwestern Ontario and drains an area of 5285 km^2. The river is composed of two branches, the upper branch and the middle branch, which join to form the lower Thames River at the Forks of the Thames in London, Ontario and then flows into Lake St. Clair (see inset of Figure 1.2). Approximately half a million people live in the watershed, but the majority of the watershed consists of rural agricultural lands (Cudmore et al. 2004; Upper Thames River Conservation Authority 2009). The watershed is located within the Carolinian forest ecosystem that has the warmest climate, mildest winters and the most diverse flora and fauna in Canada (Wilcox et al. 1998; Cudmore et al. 2004; Taylor et al. 2004; Carolinian Canada Coalition 2009). Further promoting diversity within the aquatic environment of the Thames River are the physical and hydrological processes that promote fluctuating water levels and high nutrient loads (Cudmore et al. 2004; Taylor et al. 2004). Detailed information regarding general landscape features, soil composition, riparian cover and geology within the Thames River basin can be found in Wilcox

et al. (1998). Given the high aquatic diversity within the Thames River basin, human settlement and land-use changes, it can be assumed that anthropogenic changes may have contributed to the species-at- risk listing of *A. pellucida* and 11 other endemic fish species within the watershed (Cudmore et al. 2004).

1.3.2 Previous *A. pellucida* Surveys in the Thames River

Sampling surveys of *A. pellucida* in the lower Thames River have been conducted by Fisheries and Oceans Canada since 2004. Surveys in 2004 and 2005 examined migration and density with visual implant elastomer (VIE) tagging studies. Tag recapture was low, but available evidence suggests that *A. pellucida* were not migrating between depositional areas during the summer months and that *A. pellucida* abundances were high in the Thames River, especially around the Big Bend Conservation Area (S.E Doka, M.A. Koops, Fisheries and Oceans Canada, personal communication). Parallel analyses of individual and cohort growth indicated positive correlations between growth and the dominance of sand substrates and growth and discharge, while other environmental factors including: channel depth and width, water temperature and transparency, overhead and macrophyte cover and water velocity were found to have no significant relationship in the Thames River (Drake et al. 2008).

Grandmaison et al. (2004) noted that consistent and repeated sampling of the same populations is necessary when conducting population dynamic studies. Therefore, sampling methodologies and study sites from the previous *A. pellucida* Thames River surveys (Figure 1.2) were incorporated into the present study to provide the best time series data for population dynamics analysis.

1.4 Exploring Population Dynamics using Matrix Modelling

Matrix population modelling is a common tool used in the conservation and management of endangered species (Crouse et al. 1987; Burgman et al. 1993; Beissinger & Westphal 1998; Reed et al. 2002; Akcakaya et al. 2004). Age-based matrix models use age-class specific information on fecundity and survival probabilities, derived from life-tables or cross-sectional surveys of the population of interest, to determine future abundances and age-class structure (Leslie 1945; Caswell 2001). Arrangement of fecundity and survival information in a specialized matrix termed the projection matrix (L) allows prediction of age-class abundances N(t +m) in any future time period, *m*, given a vector of initial age-class abundances, n(t), as:

$$1)\ n(t + m) = L^m\, n(t)$$

The dominant eigenvalue of the projection matrix estimates the intrinsic rate of population increase (r) from which the finite rate of population increase (λ) may be determined as:

$$2)\ \lambda = e^r$$

The right and left eigenvectors of the projection matrix also provide information on the stable stage distribution and age-class reproductive contributions. Combined, the eigenvalues and eigenvectors provide valuable information on population status and viability useful for understanding how management action might help to minimize future extinction risks (Crouse et al. 1987; Caswell 2001; Morris & Doak 2002). Incorporating environmental and demographic stochasticity into matrix models permits examination of temporal population variability and yields more realistic predictions of future intrinsic rates of population increase (Caswell 2001; Morris & Doak 2002). However, characterization of demographic stochasticity presumes knowledge of density-dependent processes acting on the population that are not always available for a species at risk. Nevertheless, use of elasticity and sensitivity measures derived from matrix models provides significant insight into how

sensitive a population is to changes in key demographic parameters (e.g., survival probabilities) that affect population growth and fluxes (Crouse et al. 1987; de Kroon et al. 2000; Caswell 2001; Morris & Doak 2002). Population viability analysis (PVA) describes when these elasticities and sensitivity measures are used to determine the limiting age-classes that should be the focus of future management and recovery activities (Crouse et al. 1987; Beissinger & Westphal 1998; Morris & Doak 2002; Reed et al. 2002). Overall, matrix models can be an effective way of determining population viability and examining the implications of proposed management strategies aimed at ensuring long-term population viability.

1.5 Objectives of Masters Thesis Research

While recent studies of *A. pellucida* populations on the lower Thames River have provided some insights into the basic biology and ecology of the species, information remains scarce on many aspects of this species' life history, population dynamics and habitat associations. To address the basic and environmental linkage knowledge gaps, this Master's research project focuses on the estimation of Eastern Sand Darter *(Ammocrypta pellucida*) life history parameters using field and laboratory study data, the construction of a suitable life history model and the use of population viability analysis. Specifically the aims of the research are:

1) Survey *A. pellucida* populations in the lower Thames River to improve locally available biological information on densities, fecundity (clutch size), age-at-maturity, growth, cohort age structure, and longevity.
2) Compare biological information from *A. pellucida* in the lower Thames River with *A. pellucida* in the Little Muskingum River, Ohio. This comparison will test whether there are geographical differences in key biological traits between populations and will help determine

the feasibility of using vital rate information from other populations when population-specific information is limited.

3) Construct a Leslie matrix model of lower Thames River *A. pellucida* populations using acquired field-based estimates of vital rates and biological traits.
4) Use the Leslie matrix model to predict the long-term viability of the lower Thames River *A. pellucida* population, identify limiting life stages and vital rates and investigate how differing life history strategies (e.g., multiple clutches and earlier age at maturity) may alter population trajectories.
5) Investigate correlations between population abundances and measured habitat variables (e.g., substrate composition, velocity, depth) to determine *A. pellucida* microscale habitat preferences.

The second chapter will focus on objectives 1, 2 and 5. Biological characteristics of the lower Thames River *A. pellucida* population will be investigated and compared to data available for Little Muskingum River populations collected by Dr. Joe Faber in 2001 and 2005. The third chapter will use information collected in the second chapter to create the Leslie matrix model as outlined in objective 3 and will describe and study different biological scenarios for *A. pellucida* to investigate local population dynamics as outlined in objective 4. The third chapter will make recommendations on possible conservation measures for Canadian *A. pellucida* populations. Chapter 4 summarizes the knowledge gained during the completion of the M.Sc. study, discusses how the new information might be incorporated into *A. pellucida* management strategies and suggests possible future *A. pellucida* research projects.

1.6 Figures

Source: Al Dextrase (2008)

Figure 1.1. Global distribution of Eastern Sand Darter (*Ammocrypta pellucida*) illustrating the disjoint nature of the distribution.

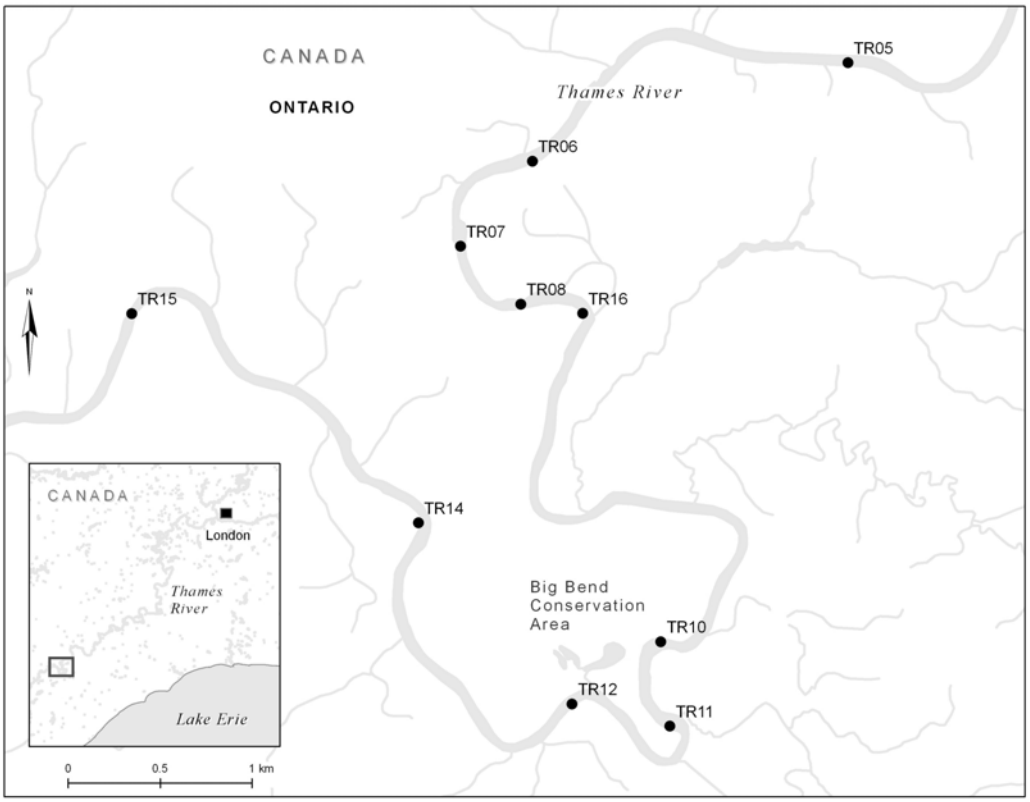


Figure 1.2. Map of the lower Thames River, Ontario showing the 2006 and 2007 sampling sites.

Chapter 2
Biological characteristics of Eastern Sand Darter (*Ammocrypta pellucida*)

2.1 Introduction

Many fish species listed under Canada's *Species at Risk Act* (SARA) are at the northern edge of their distribution (Rosenfeld & Hatfield 2006). The biological characteristics of many populations at the periphery of their range are known to differ substantially from populations located elsewhere in the range (Conover & Present 1990; Conover 1992), with environmental factors such as temperature having a more pronounced influence on growth at the edge of the range (Power & van den Heuvel 1999). Thus species at the northern edge of their distribution generally have shorter reproductive seasons, exhibit slower growth, have smaller eggs and increased longevity (Paine 1990; Johnson & Hatch 1991; Blanck & Lamouroux 2007). Therefore, when developing the recovery plans and strategies required for a species at risk, it is important to understand how biological traits (e.g., fecundity) may vary among populations and how environmental variation may affect the relative viability of southern and northern populations.

In the case of Eastern Sand Darter (*Ammocrypta pellucida*), listed as a Threatened species in Canada, limited biological information exists (Edwards et al. 2007). *A. pellucida* were originally distributed along a latitudinal gradient (38 - 46°N) that extended from southern Kentucky and the southern reaches of the Ohio River watershed to southern Lake Huron, but now exist in a more restricted, disjunct distribution, particularly along the original northern fringe of the Canadian distribution (Figure 2.1; Trautman 1981; Page & Burr 1991; Holm & Mandrak 1994; Grandmaison et al. 2004). Throughout the existing range, populations are declining due to habitat destruction, primarily as a result of the siltation of sandy substrates from bank erosion and altered stream channels (Scott & Crossman 1973; Daniels 1993; Holm & Mandrak 1994; Holm &

Mandrak 1996; Dextrase et al. 2003). Point and non-point water contamination, invasive species (e.g., Round Goby (*Neogobius melanostomus*)), lack of genetic variation, baitfish harvest related mortality and the pet trade are also thought to have contributed to population declines (Holm & Mandrak 1996; Cudmore et al. 2004; Edwards et al. 2007). In addition to the paucity of biological information on *A. pellucida,* there is limited detail on geographical variation among populations. The single best source of biological information on *A. pellucida* is an unpublished M.Sc. dissertation focusing on a population from Salt Creek, Ohio (Spreitzer 1979). Subsequent studies on *A. pellucida* have focused largely on: 1) determining presence/absence for population status reports (Holm & Mandrak 1994; Holm & Mandrak 1996; Facey 1998; Grandmaison et al. 2004); 2) description of preferred habitats (Daniels 1993; Facey & O'Brien 2003); and 3) conducting laboratory studies on fossorial behaviour (Daniels 1989; Simon 1991), captive reproduction and larval development (Johnston 1989; Simon et al. 1992; Simon & Wallus 2006). Most of the studies have been descriptive in nature, providing only limited insights into the aspects of population dynamics (e.g., fecundity, cohort structure) needed to quantify extinction risks or develop suitable recovery plans.

Given the paucity of population-specific biological data, this study uses data obtained from two seasons of field studies on *A. pellucida* populations in the lower Thames River, Ontario, to estimate important biological traits (e.g., fecundity, maturity, growth) and describe microscale habitat associations. As a secondary objective, some biological traits of the lower Thames River population were compared to those of a more southerly population from the Little Muskingum River, Ohio (Figure 2.2), to determine possible geographic variability in *A. pellucida* population characteristics.

2.2 Materials and Methods

2.2.1 Lower Thames River

The lower Thames River is a regulated 7th order river with channel widths of 40 - 50 m. The river is flashy, turbid and highly productive, flowing predominately through agricultural land from the confluence of its north and south branch tributaries to Lake St. Clair, Ontario (Figure 2.2; Upper Thames River Conservation Authority 2009). Based on comparison with historic sampling surveys, Holm & Mandrak (1995) and Edwards et al. (2007) have suggested the lower Thames River has the largest *A. pellucida* population(s) in Canada.

The designation of *A. pellucida* under Canada's *Species at Risk Act* (SARA), necessitates the use of non lethal sampling methodologies, a fact which restricts lethal sampling to accidental mortalities. All *A. pellucida* capture and handling was approved through the Fisheries and Oceans Canada Species at Risk permitting process and the Animal Care Committee sampling protocol approval process in accordance with the Canadian Council of Animal Care guidelines.

A. pellucida sampling took place in the lower Thames River during the summer months (June - August) of 2006 (n = 2) and 2007 (n = 3). For purposes of sampling consistency, study sites and protocols were the same as those described in Drake et al. (2008). Briefly, sampling was conducted in what was considered ideal *A. pellucida* habitat - the large, sandy, shallow depositional areas in the Big Bend reaches of the lower Thames River (Figure 2.2). *A. pellucida* were collected at 10 depositional areas and at multiple sites (n = 5) within each depositional area to account for possible local distributional heterogeneity. *A. pellucida* were captured using a 10 m bag seine having 1.8 x 3.7 m wings, 64 mm mesh, and 1.8 x 1.8 x 1.8 m bag, with 32 mm mesh. Seines were hauled in three passes for purposes of estimating densities following Zippin (1956, 1958). Captured individuals were sedated using clove oil, weighed (g), and measured for total length (mm). *A. pellucida* were examined for the presence of either a distended ova depositor or enlarged belly (♀) or the release of milt under slight pressure (♂), and scales were

removed from the left mid-dorsal region for aging. *A. pellucida* were revived in oxygenated river water and released back into the river at the capture location. Incidental *A. pellucida* mortalities were retained on ice and frozen for subsequent analyses.

For all sites, catch per unit effort (CPUE) per sampling event was computed as the total number of fish captured divided by the number of seine hauls. Annual average CPUE per site was computed as the mean of all site CPUE values in a given year. Differences in CPUE by year were examined using analysis of variance (ANOVA) followed by multiple comparison of means using the conservative Tukey- Kramer HSD *post hoc* test.

The numbers of fish captured in each seine haul were used to estimate site-specific population abundances using the three pass maximum likelihood estimator of Junge & Libosversky (1965):

$$1)\ N_t = \frac{(6x^2 - 3xy - y^2 + y(y^2 + 6xy - 3x^2)^{0.5}}{18(x - y)}$$

Where, N_t is the population at time t, $x = 2y_1 + y_2$, $y = y_1 + y_2 + y_3$ and y_1, y_2, y_3 are respectively, the number of fish captured in the first, second and third samples. Abundance estimates were divided by measured habitat area to obtain density estimates expressed as number of fish per m^2 to standardize for differences in sample site areas. The constant probability of capture assumption of the Zippin based N_t estimate was tested using a χ^2 based statistic as described in Seber (1982).

Survival probabilities (S_i) were calculated from 2005 to 2007 catch information using Chapman Robson methods (Chapman & Robson 1960; Robson & Chapman 1961). S_i is calculated from age-related abundance information from catch data as:

$$2)\ S_i = \frac{X}{n + X - 1}$$

Where n is the total number of fish sampled, beginning with the first fully vulnerable age-class in the catch, x = either 0+ or 1+ based on sampling season, and X is determined from the age-at-catch data as $X = \sum_{x=0}^{k} xN_x$, with k equaling the total number of age-classes and N_x equaling the number of individuals of age-classs x captured.

Following fish collection, water depth (m) and velocity (m/s) at the bottom and middle of the water column were measured at each site with a Global Water Flow Probe FP 201. Additional habitat measurements taken at the middle of each seine area included: pH, dissolved oxygen, conductivity, total dissolved solids, turbidity, and water temperature, measured with a Hydrolab datasonde 4A, and substrate composition estimates. Substrate composition was estimated using a grab sample that was qualitatively assessed *in-situ* using a modified Wentworth scale (Bain 1999): gravel (> 2.0 mm), sand (0.0625 – 2 mm) and clay/silt (< 0.0625 mm). Recorded habitat values were averaged across each sampling transect to provide a value for the entire depositional area.

Habitat associations were examined by correlating CPUE with measured habitat variables. The significance of each correlation was tested using the Spearman rank correlation coefficient. All statistical analyses were performed with JMP 7.02 (SAS Institute Inc) using an $\alpha = 0.05$ significance level.

Ages were estimated by mounting sampled scales between 2 glass slides and counting the number of annuli at magnification (10x) under a compound microscope (Beamish & McFarlane 1987). Age-at-maturity was determined by relating estimated age to field observations of gravid females and males (i.e., presence of extended ovidepositors or expression of milt when gently squeezed). For all incidental mortalities identified as 0+ fish, saggitae and lapellae otoliths were removed and mounted sulcus side up using cyanoacrylate glue and analyzed for daily growth patterns at the Bedford Institute of Oceanography, Otolith Research Laboratory (Campana 2009). Data were used to calculate larval emergence dates from which spawning dates were inferred

assuming a 5-day incubation period as found in laboratory studies where temperatures were typical of field conditions (e.g., 20.5 – 23 °C ; Simon & Wallus 2006).

Weight (W) and length (L) data were used to estimate regression models of the form $W = aL^b$ (Le Cren 1951), after appropriate logarithmic transformation of the data. Isometric growth was tested by examining the growth parameter, b, and its associated 95% confidence intervals.

For each of the 2006 and 2007 data sets, total length and ages were used to estimate von Bertalanffy growth models of the form $L_t = L_\infty (1-e^{-k(t-t0)})$, where L_t defines length at time t, L_∞ the asymptotic length, k the growth coefficient measuring the rate at which asymptotic size is obtained, and t_0 is the theoretical age at zero length (Beverton & Holt 1957).

Gravid *A. pellucida* females used for fecundity analysis were obtained from incidental mortalities, or through retrieval of specimens from predator gut contents during the week of June 4-8th, 2007. Using a dissecting microscope, ovaries were dissected, weighed (mg) and immersed in Gilson's fluid. Gonadosomatic Index (GSI) was calculated by expressing wet ovarian mass as a percentage of wet body mass (Bagenal & Braum 1968). All ova were counted and diameters (mm) measured using Northern Eclipse Image Analysis Software (Version 7. Empix Imaging, Mississauga, Ontario). The resulting frequency histogram of egg diameter measurements was examined for composite distributional structure and decomposed into component normal distributions using Bhattacharya's method (Bhattacharya 1969). The resulting component distributions were then used to identify developmental egg clutches necessary for inferring the presence or absence of multiple clutches. Correlations between total length and fecundity were examined using linear regression to estimate standard fecundity- length (F- L) models of the form $F = aL^b$ (Bagenal & Braum 1968).

2.2.2 Little Muskingum River

Faber (2006) collected *A. pellucida* from August 2000 - July 2001 (n = 186) and from June - October 2005 (n = 79) from the Little Muskingum River, Washington County, Ohio. The

Little Muskingum River is a narrow (< 15 m wide), clear, non-glaciated stream with steep banks, an intact riparian zone and large groundwater inputs located in a largely agricultural area adjacent to the Wayne National Forest (2.2). The study area, located in the middle of the species distribution range (Figure 2.2), consisted of the last 1.2 km of riffles and pools in the Little Muskingum River prior to its confluence with the Ohio River. Samples of *A. pellucida* were collected with 1/8" and 1/16" mesh ace style seines, fixed in 10% formalin and stored in 70% ethanol for subsequent laboratory analyses (Faber 2006). Samples were used to estimate fecundity, mean egg diameter, age at maturity, breeding season, survivorship, growth, longevity, parasite infestation and diet composition. Detailed information on the Little Muskingum River study, including materials and methods and results, can be found in Faber (2006).

2.2.3 Comparison Studies

To determine possible geographic variation in population characteristics, data collected in the Thames River were compared to data collected from the Little Muskingum River, Ohio. Available data on *A. pellucida* from the two sites permitted direct statistical comparison of growth (mean size at age, von Bertalanffy growth models), clutch size, egg diameters, mature female size and gender ratio. Differences between most population traits were established using two sample t-tests, adjusted for differences in variances as described in Zar (1999). Differences in gender ratios were examined using Fisher's exact test (Zar 1999). Other biological detail including, longevity, age at maturity, gonadosomatic index and spawning times could only be descriptively compared.

Lower Thames River von Bertalanffy growth curves for 2006 and 2007 estimated using nonlinear regression techniques were compared between years for significant differences to similarly estimated curves for the Little Muskingum population. Differences were assessed using analysis of residual sum of squares as follows (Chen et al. 1992; Haddon 2001):

$$3)\ F = \frac{\left(RSS_p - \sum_{i=1}^{m} RSS_i\right) \Big/ \left(DF_p - \sum_{i=1}^{m} DF_i\right)}{\left(\sum_{i=1}^{m} RSS_i\right) \Big/ DF_i}$$

where RSS_p defines the residual sum of squares derived from the von Bertalanffy model estimated using the pooled age-length data from all compared populations, DF_p is the degrees of freedom associated with the pooled model, RRS_i is the residual sum of squares from the *i* th compared population von Bertalanffy model, DF_i, is the associated degrees of freedom for the *i* th population-specific growth models and m is the number of models compared (Hadden 2001).

Fecundity in the Little Muskingum population was determined following Heins & Machado (1993) and Heins et al. (1992)'s classification of ovary development, with clutch size determined by counting the largest cohort of ova from mature (MA), mature ripening (MR) and ripe (RE) females (Faber 2006). For the lower Thames River population, fecundity was determined from the ovaries of incidental mortalities collected in June. Mature and mature ripening individuals were assessed on the presence of a prominent ovidepositor and ovaries that occupied a large portion of the body cavity (Heins 1985). Clutch size was calculated by counting all eggs over 0.7 mm, typically considered to be the size at which egg maturity is reached (Simon & Wallus 2006). Fecundity, based on MA and MR counts, and mean clutch and egg size for both populations were then compared using two-sample t-tests, adjusted for differences in variance as necessary (Zar 1999). As elsewhere, all statistical analyses was performed using JMP 7.02 (SAS Institute Inc) and using an $\alpha = 0.05$ significance level.

2.3 Results

2.3.1 Lower Thames River Populations

A total of 1924 *A. pellucida* were captured during sampling, 795 (41.3%) in 2006 and 1129 (58.7%) in 2007. A sub-sample of sexed individuals (n = 145) collected during June and July 2007 found that females dominated the catch, with an overall female to male ratio of 2.54:1. Mean *A. pellucida* catch per unit effort (CPUE ± standard error) across all sampling sites was 2.58 ± 0.43 in 2006 and 2.07 ± 0.62 in 2007 and did not differ significantly between years (ANOVA $F_{1, 140} = 0.16$, $P = 0.69$). Some differences in site-specific CPUE were observed (Figure 2.3), with significant inter-annual differences at sites TR12 (ANOVA Tukey-Kramer HSD $F_{1, 10} = 9.30$, $P = 0.01$) and TR15 (ANOVA Tukey-Kramer HSD $F_{1, 16} = 5.33$, $P = 0.03$).

Local abundances could not be estimated for all sites owing to low catches and violation of the common probability of capture assumption required of Zippin population estimators (Seber 1982). Where local population abundances could be estimated (n = 4), the associated density estimates ranged from 0.23 ± 0.01 to 0.49 ± 0.03/$m^{2,}$,with a coefficient of variation of 27.35% among sites.

River reach annual survival rate ± standard deviation was 0.48 ± 0.03 between 2006 and 2007, while 2007 seasonal site specific Chapman-Robson survival estimates ranged from 0.36 ± 0.06 - 0.42 ± 0.04 (Figure 2.4).

A. pellucida CPUE was significantly correlated to the percentage of sand in the substrate (Spearman $\rho = 0.44$, $P < 0.001$), increasing as the percentage of sand increased. Abundances were negatively related to the percentage of gravel in the substrate, depth and mid-column and bottom velocities, but increased significantly with dissolved oxygen and pH (Table 2.1). Significant relationships explained 20 - 44 % of the variation in the data. Temperature, conductivity, and the percentage of silt in the substrate had no apparent effect on relative abundance (Table 2.1).

A. pellucida captured in 2006 and 2007 ranged in length from 19 – 65 mm, with a mean and standard deviation of 45.9 mm and 0.21 mm, respectively. Comparison of the estimated weight-length regression model slope coefficients to the theoretical isometric value of three, confirmed isometric growth for all the individuals caught in 2006 and 2007. Site-specific weight-length models for the high abundance sites provided evidence of among-site differences (Table 2.2), revealing significantly different slope coefficients (ANCOVA, $F_{3, 1022} = 11711.92$, $P < 0.001$) among sites. Fish from TR14 and TR16 exhibited isometric growth, while TR15 and TR11 fish exhibited allometric growth with TR15 individuals becoming heavier for length (more rotund) and TR11 individuals becoming lighter for length (less rotund).

Four age classes (0+, 1+, 2+, 3+) were identified based on the examination of scales from 743 individuals (n = 272, 2006 and n = 471, 2007). Males were identified up to 2+, whereas females were identified to 3+. Mature individuals for both sexes were observed in the 1+ age-class, indicating age-at-first-maturity occurs during the second summer after birth. Age-class size ranges were not discreet, as overlap in length by age was noted: 0+ (9 – 55 mm, n = 535); 1+ (35 - 65 mm, n = 319); 2+ (45 – 64 mm, n = 169) and 3+ (52 – 64 mm, n = 11). Within season variation in population size structure was evident (Figure 2.5) as noted in the 2007 length-frequency histograms, with shifts to lengths dominated by 0+ individuals evident as the birth cohorts for the year grew in size.

von Bertalanffy growth models estimated for 2006 and 2007, respectively, were:

$$(1)\quad \text{Length (mm)} = 54.26\,(\,1 - e^{-1.58\,(\text{age} + 0.49)}\,)$$

$$(2)\quad \text{Length (mm)} = 57.46\,(\,1 - e^{-1.60\,(\text{age} + 0.45)}\,)$$

With r^2 in 2006 and 2007, respectively, equalling 0.72 and 0.79. All estimated parameter P values < 0.001. Analysis of residual sum of squares indicated no significant difference between the annual models ($F_{2, 19} = 1.23$, $P = 0.34$).

Daily aging of 0+ individuals (n = 27) estimated ages from 50 - 83 days, with a mean age ± standard deviation of 61.67 ± 10.67 days. Based on these data, first emergence varied from early May to the end of June for these individuals. Assuming a five day average incubation period (Simon & Wallus 2006), spawning appears to start as early as late April and to continue until late June, although the majority of the examined individuals were spawned in late May or early June in both 2006 and 2007 (Figure 2.6).

Ten gravid, 2+ females, average length ± standard deviation of 54.30 ± 0.79 mm, were used for fecundity estimates. The average gonadosomatic index ± standard deviation of 0.10 ± 0.02 was significantly correlated with length (n = 8, $r^2 = 0.53$, $P = 0.04$). An average ± standard deviation of 131.9 ± 30.1 eggs per individual was found, with a mean diameter ± standard deviation of 0.74 ± 0.28 mm. Measured egg diameters (n = 1320) showed a bi-modal size frequency distribution (see Figure 2.7) decomposed using Bhattacharya's method into normal distributions described by mean ± standard deviation, respectively, of 0.51 ± 0.17 mm (n = 654) and 0.98 ± 0.16 (n = 666). Means of the decomposed distributions differed significantly (t = -53.99, df = 1319, $P < 0.001$), but variances did not ($F_{1, 1319} = 1.16$, $P = 0.04$). Given that multiple sized eggs were present in all individuals, the distributions were treated as descriptive of individual clutches having differing maturation schedules. No significant correlation was found between logarithmic transformed female total length and total fecundity (n = 10, $r^2 = 0.09$, $P = 0.41$), however sample size was small.

2.3.2 Geographic Comparison of Populations

Comparison of biological characteristics between the Thames River and Little Muskingum River populations suggest that *A. pellucida* in the Thames River live longer, grow faster, mature faster and have smaller eggs than Little Muskingum River *A. pellucida* (Table 2.3). Analysis of residual sum of squares indicated a significant difference between the population-specific von Bertalanffy growth models ($F_{2, 39} = 5.42$, $P < 0.001$). Although both populations

reach maximum length in the ≈ 55 mm range, *A. pellucida* from the Thames River grew at a quicker rate (Figure 2.8). Thus differences in mean size at age were found at 0+ ($t = 3.98$, $df = 560$, $P < 0.001$) and 1+ ($t = 3.41$, $df = 199.27$, $P < 0.001$), but not at 2+ ($t = 1.90$, $df = 92.70$, $P = 0.06$).

The gender ratio differed significantly between populations (Fisher exact test, $P < 0.001$) with the lower Thames River having a higher proportion of females. No differences were noted in age at first maturity among males (1+) in the two populations. First maturity observed in females differed, with females in the Thames River maturing at 1+ and females in the Little Muskingum River maturing at 2+. Similar gonadosomatic index values were found for both populations.

Mature ova clutch size in the lower Thames River varied from 35 -123 ova with a mean ± standard deviation of 71.5 ± 22.7 ova per female and an average ova diameter of 0.94 ± 0.01 mm. Variation was noted for the Little Muskingum River, where mature ova clutch sizes ranged from 16-97 ova with a mean ± standard deviation 61.5 ± 8.2 ova per female and an average ova diameter of 1.08 ± 0.01 mm. There was no significant difference in either mean clutch size ($t = 1.13$, $df = 26$, $P = 0.112$) or clutch size variance ($F_{1, 27} = 1.64$, $P = 0.211$) between the two populations, but average ova diameter was significantly smaller in the Thames ($t = -13.12$, $df = 888$, $P < 0.001$). Ova diameters from lower Thames fish, however, did approximate the 0.99 mm value reported for an earlier study of Salt Creek, Ohio fish (Spreitzer 1979). Gravid female total length was not significantly different between populations ($t = -1.53$, $df = 26$, $P = 0.131$) and there was no significant correlation between clutch size and total length in either population (Thames: $P = 0.11$, Little Muskingum: $P = 0.07$).

2.4 Discussion

Given the paucity of population-specific biological data and the large number of *A. pellucida* individuals sampled in this study, it has been possible to comprehensively catalogue for

the first time many of the important biological characteristics for the species in the lower Thames River, Ontario including: growth, longevity, survival, maturation, fecundity, clutch and egg size. Significant microscale habitat associations were documented, with those related to substrate composition being strongest. The data assembled also facilitated direct statistical comparison of the lower Thames population to data available for a more southerly population in the Little Muskingum River, Ohio. Comparisons indicated similarities in growth and eventual size, but differences in longevity and egg size that may have implications for respective population dynamics. Overall there was no general evidence to suggest significant latitudinal variation in biological characteristics between these populations.

A. pellucida population densities in the lower Thames River (0.23 – 0.49/m^2) are high compared to reported densities of 0.12 - 0.29/m^2 in the Poultney River, New York, although lower densities in the Poultney River may be related to higher channel velocities (Grandmaison et al. 2004).

Relationships between CPUE and environmental variables, primarily substrate, concur with those reported in other studies. Sandy depositional areas have been widely documented as preferred habitat due to fossorial behaviour (Daniels 1993; Holm & Mandrak 1995; Facey & O'Brien 2003; Grandmaison et al. 2004). Areas of low water velocity (< 0.1m/s) have also been associated with high abundances and increased juvenile growth (Walsh & Perry 1998; Drake et al. 2008). Basic river hydrology suggests that sand substrates exist only where velocities are low and finer substrates cannot be actively flushed (Bain 1999). However, not all suitable substrate areas were equally populated, with a greater than eight-fold difference in CPUE between the high and low populated depositional areas studied here (Figure 2.3). A positive correlation between abundance and dissolved oxygen, therefore suggests concurrent selection for preferred velocity and oxygen levels when selecting substrate sand habitats for use. Selection of habitats that maximize respiration potential and facilitate predator avoidance via burrowing (Daniels 1989;

Simon & Wallus 2006; Drake et al. 2008) would tend to minimize energy expenditure and maximize growth potential.

While substrate, velocity and oxygen variables can help explain abundance, there is some plasticity surrounding localized processes that affect densities, survival and growth patterns (Figure 2.4; Table 2.2). Differing site specific growth patterns (Table 2.2) indicate that *A. pellucida* fitness may be related to variation in other habitat components not measured in this study including: prey quality and quantity, abundance of predators, landscape cover and proximity of point source contamination (e.g., Labbe & Fausch 2000; Heins 2001; Claireaux & Lefrançois 2007).

Although CPUE did not vary between years across all sites, there were marked differences between years for some sites. Tagging studies have suggested that *A. pellucida* do not actively migrate between suitable habitat sites (S.E. Doka, M.A. Koops, Fisheries and Oceans Canada, personal communication). Nevertheless, fluvial processes can alter depositional patterns between years, varying habitat suitability in the process (Bain 1999). Anecdotal evidence showed that at TR12, a large sand bar not present in 2005 was evident in 2006 and much reduced in 2007 as a result of subsequent erosion. Such changes are likely to result in abundance redistribution and local habitat availability differences among sites between years. *A. pellucida* are thought to have a drift period prior to benthic settling (Simon & Wallus 2006). It is possible that 0+ dispersal occurs as a result of passive larval drift or as an active response to increased habitat densities. Both processes are likely to account for some of the site-specific inter-annual variability observed in this study.

A. pellucida in the Thames grow quickly, with 0+ individuals reaching lengths in the range of 50 mm by the end of the first growing season (Spreitzer 1979; Drake et al. 2008). Quick growth yields large overlap in size at age, making the determination of mature from immature individuals on the basis of length almost impossible by late August. Age 0+ individuals also make up the largest part of the catch, particularly after July when gear selectivity biases are

reduced. The numerical importance of 0+ individuals in the population suggests that *A. pellucida* populations will be responsive to environmental variation favouring the species, but will be prone to rapid abundance declines should non-optimal conditions be encountered. The described population response has been documented in other fish species (e.g., Pacific Sardine (*Sardinops sagox)*, Pacific Herring (*Clupea pallasii pallasii),* Bay Anchovy (*Achoa mitchilli),* Atlantic Silverside (*Menidia menidia*)) and is often associated with opportunistic strategists and r-selected species. Given the short life cycle, early maturation, frequent reproduction and rapid larval growth of the species (Winemiller & Rose 1992; King & McFarlane 2003), *A. pellucida* is probably best classified as an opportunistic strategist.

Significantly, the estimated growth rate of Thames River fish exceeded that of the more southerly Little Muskingum fish, although eventual asymptotic lengths do not appear to differ. Differences may relate to the prevailing thermal and turbidity regimes in the two rivers. Both rivers can be classified as warm water sites with summer temperatures exceeding 24ºC (Stoneman & Jones 1996), however the Thames River reaches this temperature threshold earlier in the season (late May) due to minimal groundwater inputs compared to the Little Muskingum (early July), although both rivers have a similar season duration. Given the importance of temperature for increased growth in many fish species (Mann et al. 1984; Braaten & Guy 2002; Heibo et al. 2005); higher early season temperatures in the lower Thames River would trigger faster growth assuming that increased temperature-dependant metabolic demands could be met (i.e., food resources). Increased growth rates in the Thames River may also be related to relative predator risk. Juvenile estuarine fishes experience increased growth in turbid waters due to decreased predation pressure from visual predators (Blaber & Blaber 1980). High turbidity in the Thames (secchi disk = 0.05 m) versus the Little Muskingum River (secchi disk > 1 m) may limit loss of larger *A. pellucida* to predation and affect the computed growth rates because of relative differences in the abundance of larger individuals in the Thames.

A. pellucida spawning takes place earlier in the lower Thames River than previously thought for Canadian populations. Holm & Mandrak (1996) inferred spawning dates of late June to late July through investigation of archived museum specimens. However, daily aging analysis of 0+ individuals indicates that emergence occurs from early May to late June (Figure 2.6), with spawning taking place from late April to mid June based on a five-day incubation time. Although spawning has never been observed in the wild, spawning is believed to occur when water temperatures are in the 14.4 – 24.4 °C range, with 20.5 - 23°C being ideal (Spreitzer 1979; Johnson 1989; Holm & Mandrak 1996; Facey 1998). Information from temperature loggers placed in the river showed that temperatures reached the lower end of the required range in April in 2006 (C. Chu, Trent University, personal communication). Early spring spawning may be facilitated by multiple clutches that allow lower Thames River fish to exploit favourable thermal conditions. Such an opportunistic strategy can maximize population growth and is used by other darters including, *Etheostoma microperca* and *Etheostoma caeruleum* (Johnson & Hatch 1991; Winemiller & Rose 1992; Fuller 1998; Vila-Gispert et al. 2002).

Whether the earlier spawning is typical of the species or exclusive to this population cannot be determined from studies of short duration, and the possibility remains that the inferred spawning dates in 2006 were driven by abnormal drought conditions. Decreased water levels in 2006 caused increased river water temperatures, especially in the shallow areas targeted during sampling. In contrast, all the museum specimens used in the study by Holm & Mandrak (1996) were collected in June and July from various locations in southwestern Ontario with lower recorded water temperatures (< 21°C) than prevail in the lower Thames River.

Although first age at maturity was estimated at 1+ for males in both populations (Spreitzer 1979, Faber 2006), females in Ohio are not believed to reproduce until age 2+ (Faber 2006). Given that the mature 1+ fish in the lower Thames River were caught in June and July, the short incubation period and the documented June emergence dates, there is solid evidence to suggest spawning by 1+ individuals in the lower Thames River. Populations at increasing

latitudes typically show an older age at first maturity as cooler early season temperatures do not allow for sufficient growth in earlier years to facilitate gonad development (Mann et al. 1984; Braaten & Guy 2002). Faster first year growth in the Thames, facilitated by warmer temperatures, could allow 1+ individuals to both successfully grow and mature.

Comparisons of mean clutch size estimates among populations suggests the characteristic does not vary geographically, being approximately the same for the studied lower Thames, Little Muskingum (Faber 2006) and Salt Creek (Spreitzer 1979) populations. The lack of variation contrasts with findings for other darter species where clutch size has been shown to vary geographically (Guill & Heins 1996; Heins 2001; Heins et al. 2004), probably as result of differences in food availability, environment and genetics (Bagenal 1971; Heins 2001). Female size is also usually correlated with clutch size for other darter species, including other *Ammocrypta* (Heins 1985; Heins et al. 2004), but there was no apparent association in any of the studied *A. pellucida* populations for which data were available (Spreitzer 1979; Faber 2006). Variability among individuals and sample sizes, however, may have hampered abilities to establish meaningful statistical relationships for *A. pellucida.*

Observed differences in mean ova size fit with general trends toward smaller eggs at increased latitudes (Winemiller & Rose 1992; Vila- Gispert et al. 2002). Given that the gonadosomatic index is similar for both populations, smaller egg size may represent a trade-off against egg number. While mean clutch size did not differ between populations, the possibility exists that by virtue of earlier spawning that Thames River *A. pellucida* have a larger number of clutches than Little Muskingum populations. Differences in egg size and number of clutches among fish populations has been suggested to represent local adaptations that can vary seasonally and annually with environmental conditions (Fleming & Gross 1990; Quinn et al. 1995; Heins et al. 2004).

Relatively few detailed biological studies have been completed on *A. pellucida* populations. Until now insufficient detail on populations from across the distributional range has

been available for comparative population analyses and/or determination of how environment and genetics might act alone, or in concert, to affect population characteristics. Data gathered as part of this study has allowed some of the first geographic comparisons to be made and suggests limited latitudinal variation among populations. Differences in egg size and early growth rates among populations suggest possible trade-offs between egg size, maturation schedule, number of clutches and growth rate, reflective of adaption to local environmental conditions. However, detailed data are still lacking for the development of a comprehensive understanding of the mechanisms that might give rise to trait differences among *A. pellucida* populations. It also appears that Canadian populations are more significantly affected by localized differences in environment, such as turbidity, temperature and potentially food availability, than latitude. The result has implications for the management of other fish species at risk in Canada, as latitudinal differences alone may not be the most important consideration when developing an understanding of variation in key biological characteristics (e.g., maximal size, age, fecundity). Thus, detailed life history studies probably remain the best way of examining the implications of trait variation for fish species at risk and developing the information base necessary to wisely and appropriately manage the remaining populations. The challenge ahead then becomes developing ways in which to optimize data collection, without unduly impacting the populations that need to be protected.

2.5 Tables and Figures

Table 2.1. Habitat variables measured at sampling sites and the associated Spearman rank coefficient (ρ) for the habitat variables and *A. pellucida* CPUE. Significant correlations are denoted by * $P < 0.05$ and ** $P < 0.001$.

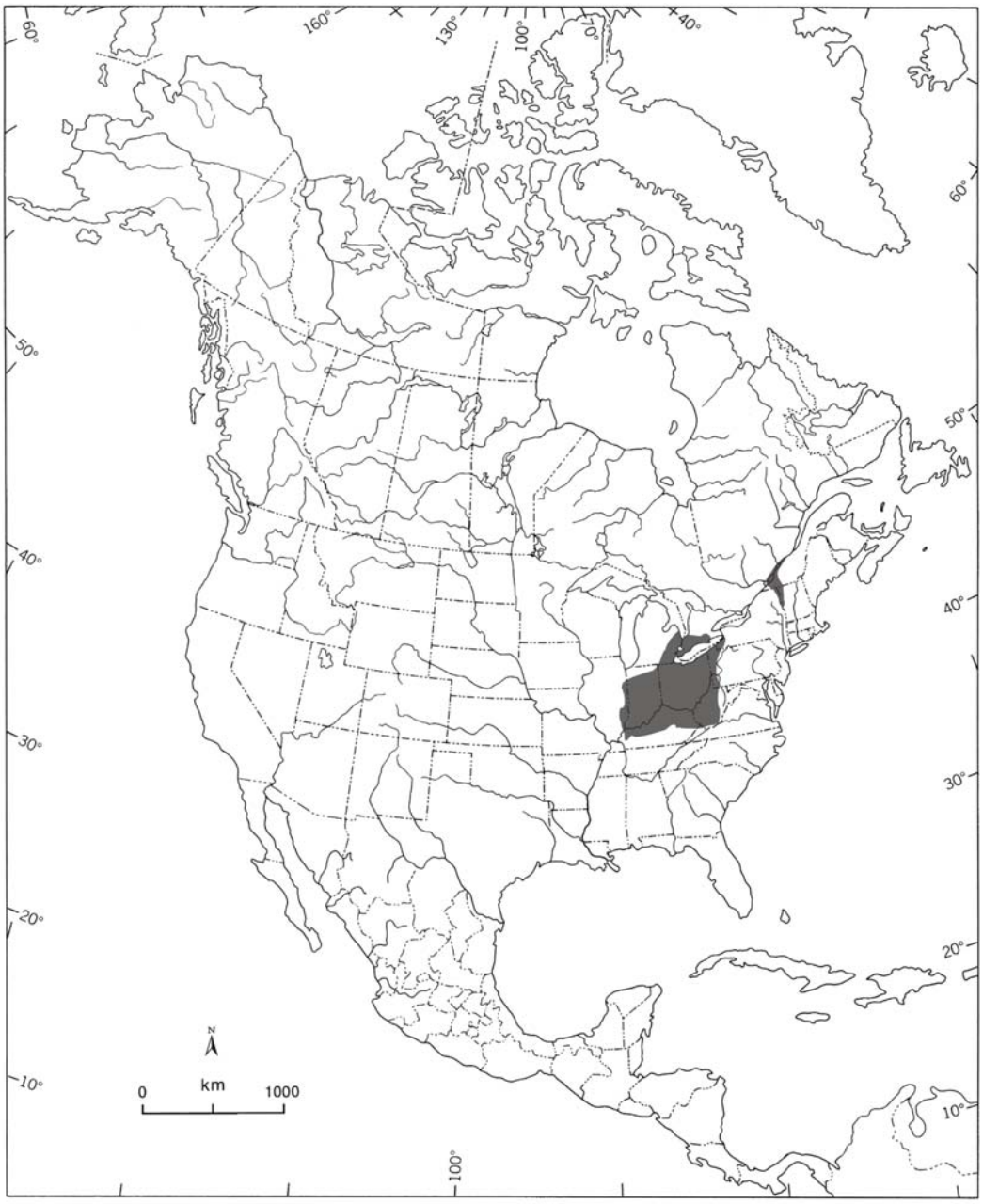
	Mean	SD	Minimum	Maximum	N	Spearman Rank (ρ)
Temperature (ºC)	24.18	2.198	19.57	28.9	48	0.10
pH	8.27	0.188	7.89	8.68	40	0.21*
Conductivity (mS/cm)	663.34	63.194	476.67	764.3	40	-0.12
Dissolved oxygen (mg/L)	8.91	1.129	6.99	12.28	48	0.35*
Bottom Velocity (m/s)	0.14	0.078	0.02	0.32	44	-0.23**
Mid water column velocity (m/s)	0.21	0.126	0.04	0.63	44	-0.20**
Depth (m)	0.43	0.143	0.16	0.82	46	-0.22**
Gravel substrate (%)	16.0	21.1	0	98.33	48	-0.40**
Sand substrate (%)	57.0	32.5	0	100	48	0.44**
Silt substrate (%)	14.0	19.0	0	73.33	48	0.12

Table 2.2. Weight-Length regression models of the form LnWeight = intercept + b LnLength for lower Thames River *A. pellucida* population (all regressions $P < 0.001$). Growth pattern is determined by comparing the slope coefficient b (± 95% confidence intervals) to the theoretical value of three indicating isometric growth.

Weight-Length Model	Intercept	Slope coefficent b (95% CI)	r^2	Growth Pattern
All individuals	-12.09	2.97 (2.92 - 3.02)	0.87	Isometric
TR11	-10.12	2.47 (2.31 - 2.63)	0.76	Allometric
TR14	-11.91	2.94 (2.71 - 3.17)	0.88	Isometric
TR15	-12.63	3.14 (3.05 - 3.23)	0.92	Allometric
TR16	-12.26	3.03 (2.94 - 3.12)	0.93	Isometric

Table 2.3. Biological characteristics of *Ammocrypta pellucida* samples from the Little Muskingum (Faber 2006) and the lower Thames rivers**.** Lengths are given as mean ± standard deviation. k defines the von Bertalanffy growth parameter, L_∞ the estimated asymptotic size and t_0 is the theoretical age at zero length. All growth parameters provided include ± standard error. Comparable measures that differ significantly between populations are denoted by ** P<0.001.

Biological Characteristic	Thames River, Ontario	Little Muskingum River, Ohio	Significant Difference
Reproduction			
Female age at first maturity (years)	1+	2+	
Male age at first maturity (years)	1+	1+	
Mature Ova size range (mm)	0.70 - 1.57mm	0.68 - 1.51mm	
Average ova diameter (mm)	0.94 ± 0.01 mm	1.08 ± 0.01mm	**
Clutch range	35 - 123	16 - 97	
Average clutch size	71.5 ± 22.7	61.2 ± 8.2	
Gonosomatic Index	0.10 ± 0.02	0.10 ± 0.02	
Average length of gravid female (mm)	54.3 ± 0.8	55.8 ± 0.6	
Gender ratio (female to male)	2.54 : 1	1.16 : 1	**
Spawning season	Late April to late June	Late May- early July	
Growth			
0+ total length (mm)	36.20 ± 6.34	31.35 ± 7.03	**
1+ total length (mm)	50.29 ± 4.83	48.27 ± 6.34	**
2+ total length (mm)	55.70 ± 3.29	54.92 ± 2.06	
3+ total length (mm)	59.45 ± 3.96		
k	1.59 ± 0.51	1.35 ± 0.36	
$L_?$ (mm)	55.81 ± 1.57	55.35 ± 2.89	
t_0	-0.48 ± 0.21	-0.31 ± 0.12	
Longevity			
Maximum age (years)	3+	2+	
Survival	0.48 ± 0.03		
Density (m^{-2})	0.36 ± 0.11		



Source: Al Dextrase (2008)

Figure 2.1. Global distribution of Eastern Sand Darter (*Ammocrypta pellucida*) illustrating the disjoint nature of the distribution

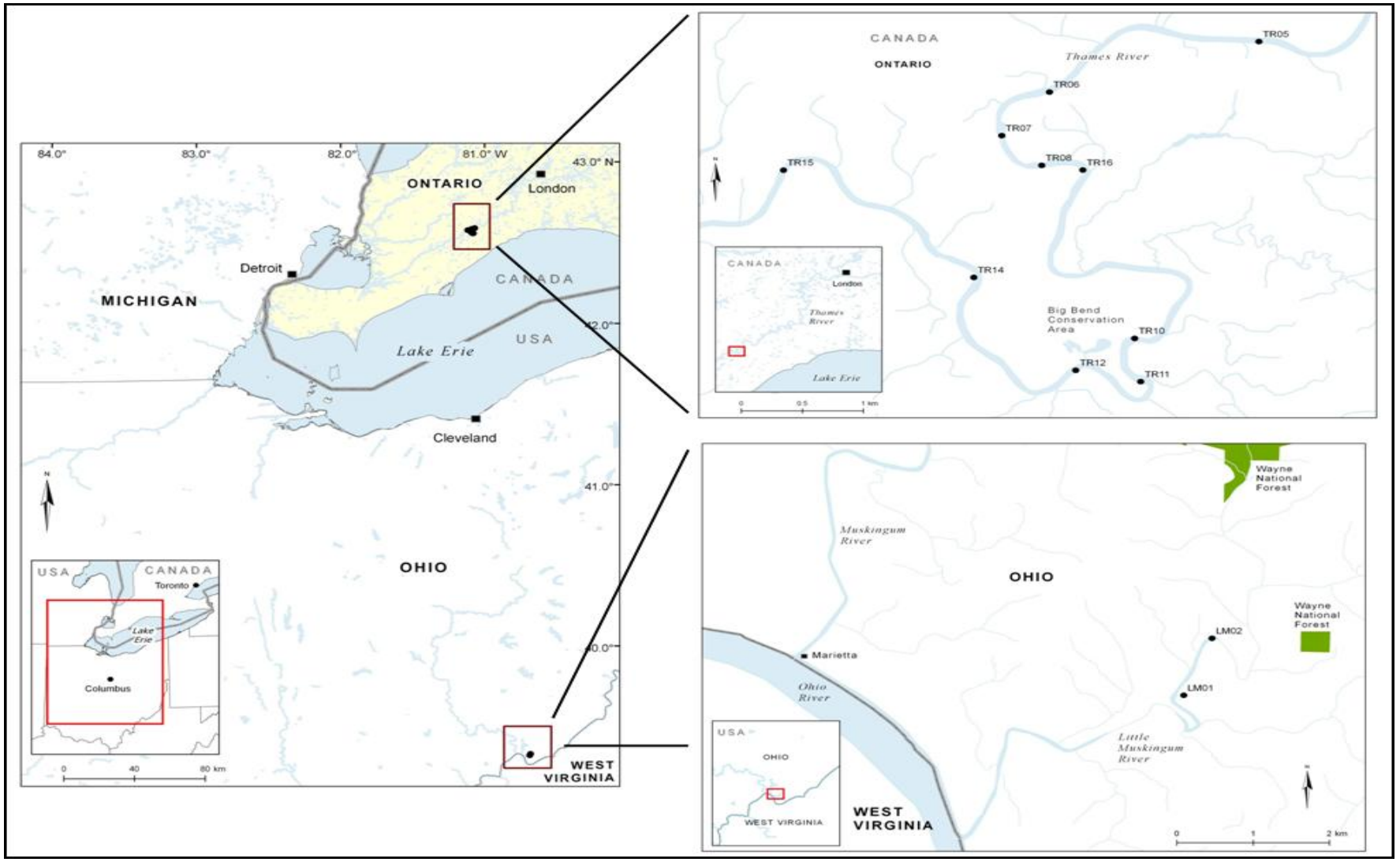


Figure 2.2. Map showing the *A. pellucida* sampling sites located in the Lower Thames River, Ontario and the Little Muskingum River, Ohio.

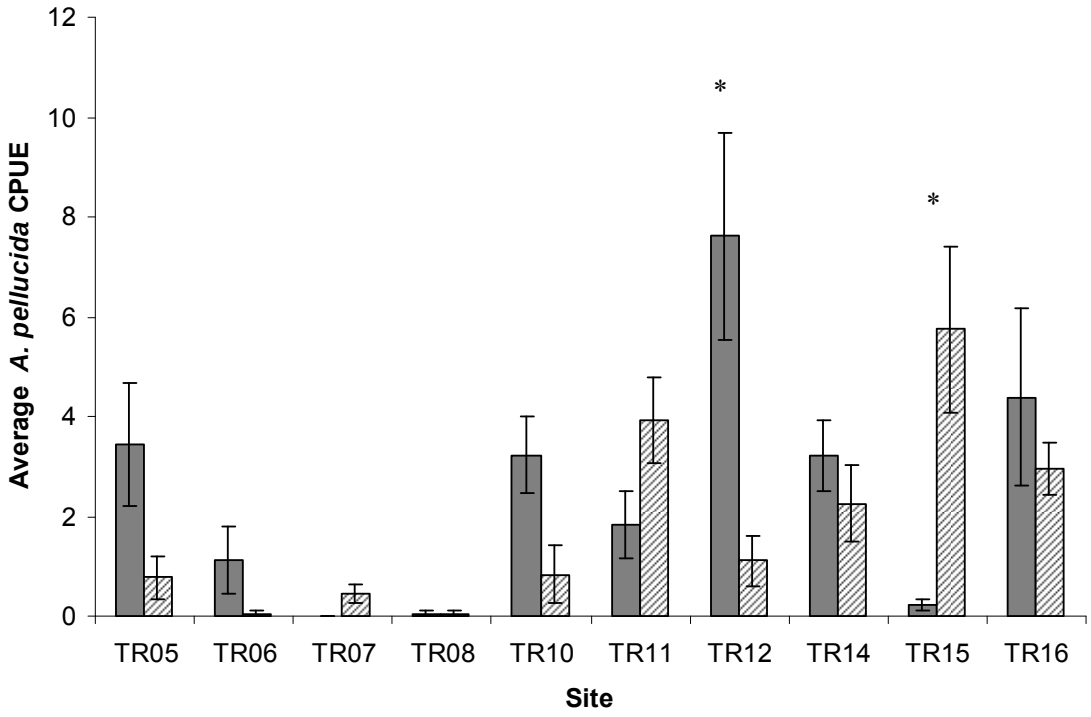


Figure 2.3. Average catch per unit effort (CPUE) ± standard error of *Ammocrypta pellucida* at the 10 lower Thames River sampling sites during 2006 (grey bars) and 2007 (striped bars), sites that exhibited significant differences in CPUE between years are denoted with an asterisk *.

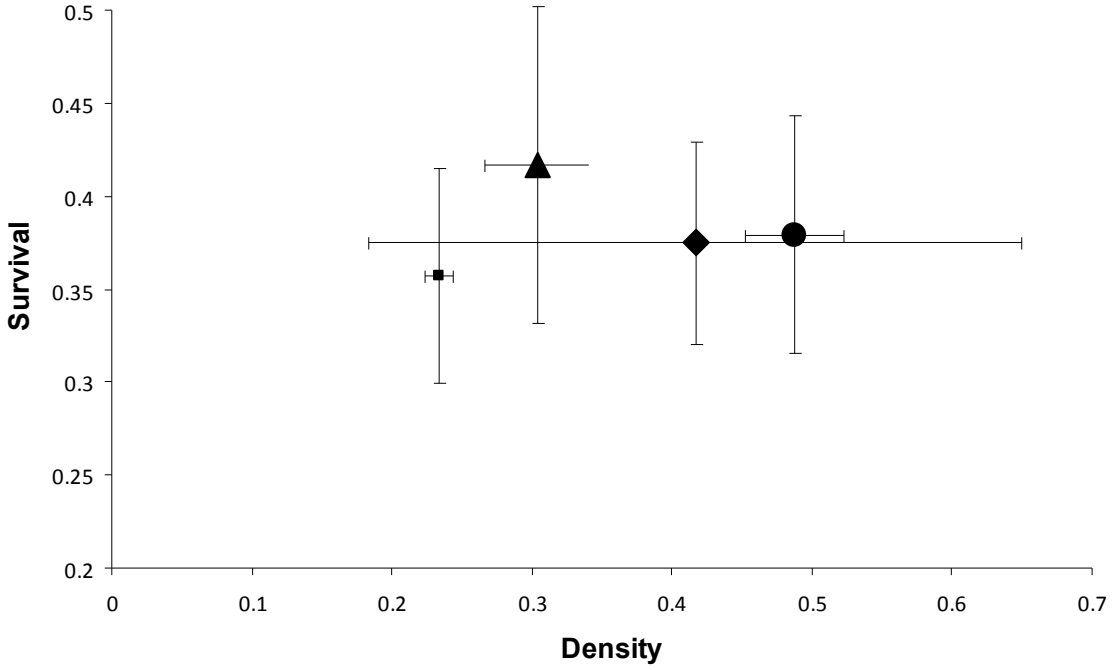


Figure 2.4. Density (m^{-2}) and survival (yr^{-1}) estimates of *A. pellucida* in four lower Thames River sampling sites (TR11: ♦, TR14: ■, TR15: ●, TR16: ▲). Horizontal and vertical bars define 95% confidence intervals for the estimates.

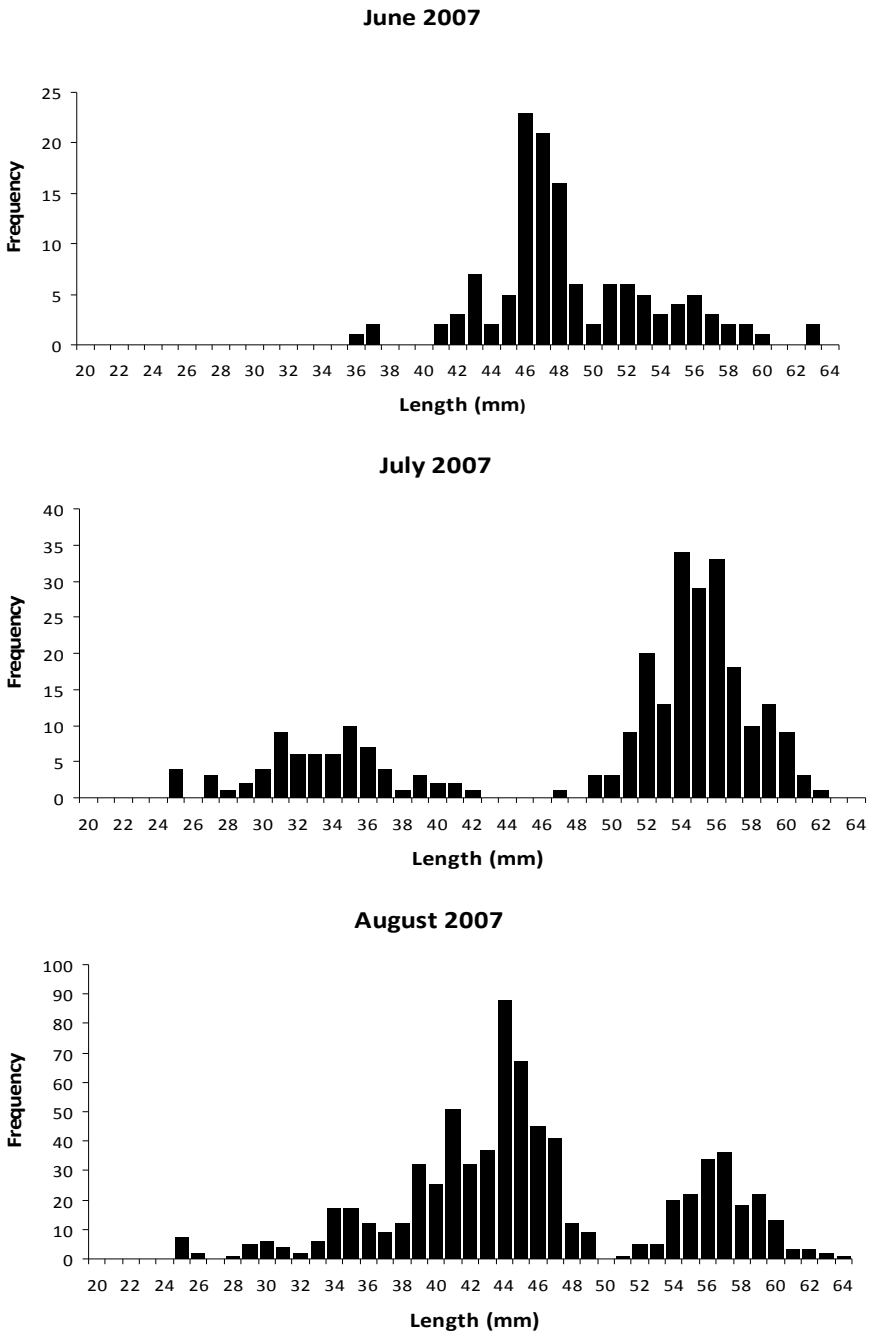


Figure 2.5. Length frequency distribution of *Ammocrypta pellucida* individuals collected during sampling dates in 2007. Left hand modes consist of 0+ individuals. Right hand modes consist of individuals aged 1+ to 3+.

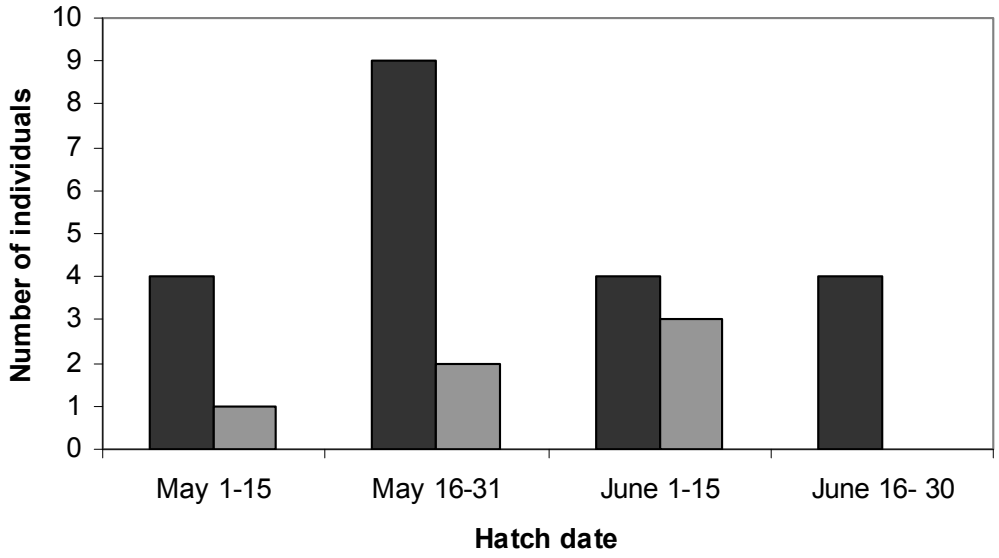


Figure 2.6. Hatch date of lower Thames River *Ammocrypta pellucida* 0+ individuals as calculated from daily aging analysis for 2006 (black) and 2007 (gray) sampling years.

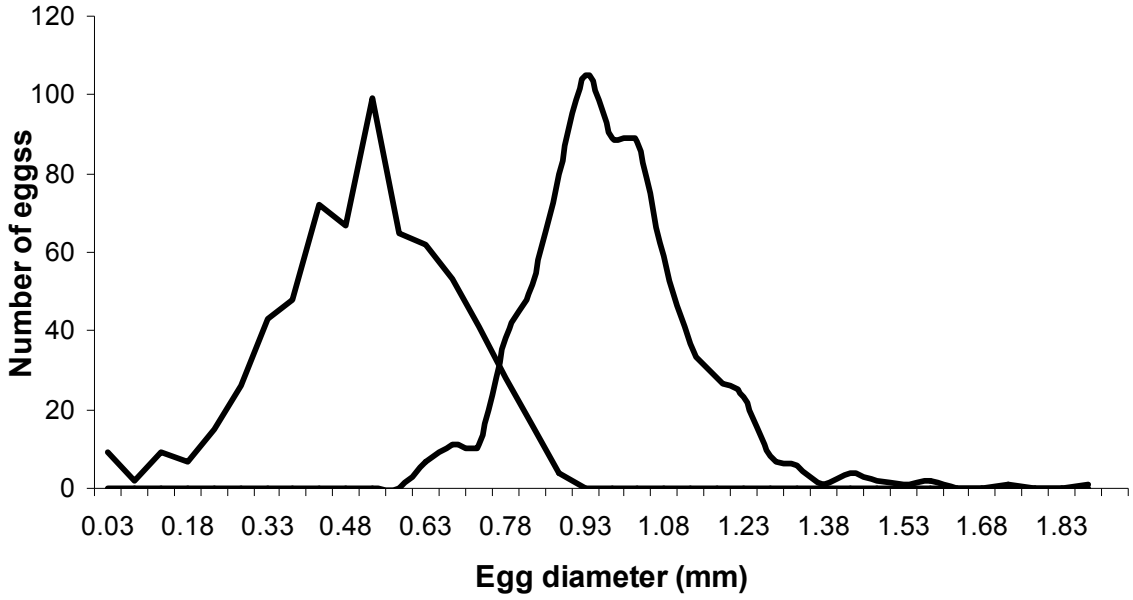


Figure 2.7. Distributions of 1320 *A. pellucida* egg diameters from 10 individuals. Distributions were identified using statistical decomposition techniques and interpreted as representative of separate clutches with differing maturation schedules. Distributions differ significantly from one another.

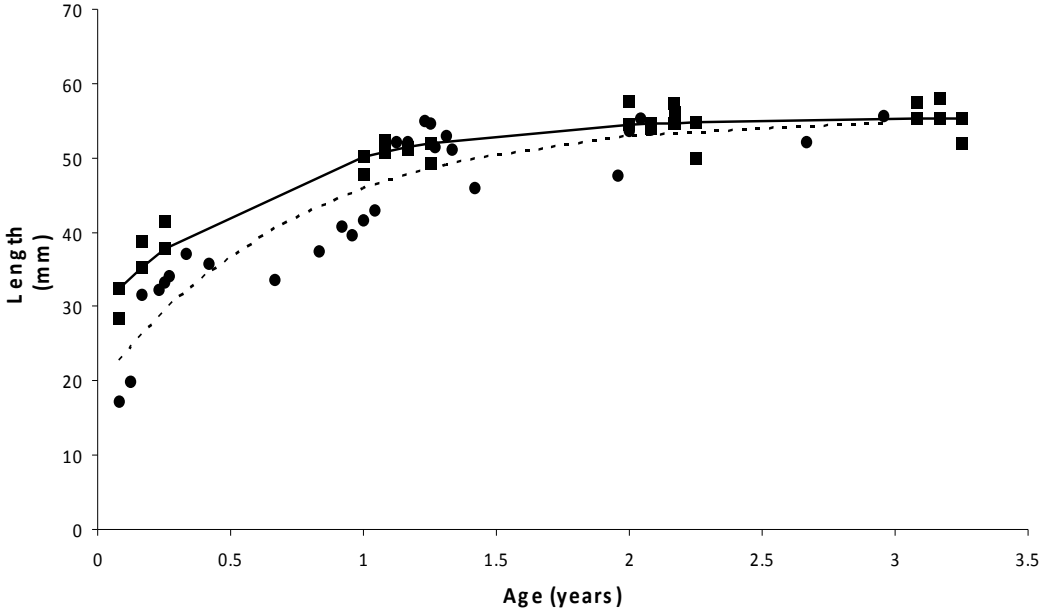


Figure 2.8. Age-specific length data and resulting von Bertalanffy growth curves estimated for the lower Thames River (black square, solid line) and Little Muskingum River (black circles, dotted line) *A. pellucida* populations. Curves differ significantly ($P < 0.001$).

Chapter 3
Population viability and perturbation analyses for lower Thames River Eastern Sand Darter *(Ammocrypta pellucida)*

3.1 Introduction

Matrix population modelling is a common tool used in the conservation and management of endangered species (Crouse et al. 1987; Burgman et al. 1993; Beissinger & Westphal 1998; Reed et al. 2002; Akcakaya et al. 2004). Matrix models use age or stage-specific information on fecundity and survival, derived from life-tables or cross-sectional surveys of the population of interest, to determine population growth rate, future abundances and population structure (Leslie 1945; Caswell 2001). Matrix models and the analyses of the resulting eigenvalues and eigenvectors can be incorporated into population viability analyses (PVA) used to estimate future population viability, determine limiting life stages, and infer how differences in population vital rates may affect population growth rate (Beissinger & Westphal 1998; de Kroon et al. 2000; Morris & Doak 2002; Morris et al. 2002). Knowledge of environmental and demographic stochasticity can increase PVA realism by accounting for uncertainty in population trajectories (Caswell 2001; Fieberg & Ellner 2001; Morris & Doak 2002). Additionally, perturbation PVA analyses can be used to better understand the implications of potential management and recovery plans by changing vital rates to simulate a proposed plan and then examine resulting population outcomes (Ehrlén & van Groenendael 1998; Caswell 2000; Heppell et al. 2000).

The ability of PVA to incorporate uncertainty into quantitative models suits the approach to studying endangered species, especially when minimal biological information (i.e., fecundity, survival rates) is available and collection of such information is constrained by logistical difficulties

and the necessity of using non-lethal sampling techniques (Caswell 2001; Morris & Doak 2002; Akcakaya et al. 2004; Norris 2004). To date, PVA has been successfully used to project possible population futures for a variety of endangered aquatic organisms including turtles (Crouse et al. 1987; Enneson & Litzgus 2008), amphibians (Zambrano et al. 2007), invertebrates (Grady & Valiela 2006; Rogers-Bennett & Leaf 2006;) and fishes (Williams et al. 1999; Cortés 2001; Robertson 2005; Vélez-Espino 2005; Vincenzi et al. 2008).

Eastern Sand Darter *(Ammocrypta pellucida*), a species listed as Threatened under Canada's *Species at Risk Act* (SARA), is an ideal candidate for matrix modelling and PVA. Limited biological information for Canadian populations currently hampers the realistic development of required recovery strategies and management programs (Rosenfeld & Hatfield 2006; Edwards et al. 2007). *A. pellucida* is also a globally rare percid that has experienced notable declines in its historic distributional range (NatureServe 2009). Once distributed from southern Kentucky and the southern reaches of the Ohio River watershed to southern Lake Huron (Grandmaison et al. 2004; Edwards et al. 2007), the current distribution is now more restricted and disjunct (Figure 3.1). *A. pellucida* prefer sandy substrates in lakes and rivers due to their fossorial behaviour. Thus, population declines have been attributed to habitat destruction, primarily via the siltation of sandy bottoms from bank erosion and altered stream channels (Jordan & Copeland 1877; Scott & Crossman 1973; Daniels 1993; Holm & Mandrak 1994; Holm & Mandrak 1996; Dextrase et al. 2003; Facey & O'Brien 2003). Point and non-point contamination, invasive species (e.g., Round Goby (*Neogobius melanostomus))*, lack of genetic variation, baitfish harvest-related mortality and the pet trade are also thought to have contributed to population declines (Cudmore et al. 2004; Edwards et al. 2007).

To date few detailed population studies for *A. pellucida* have been completed, the most comprehensive of which is an unpublished thesis focusing on an Ohio population that estimated key

life history attributes including: longevity, age-at-maturity, total fecundity and clutch size (Spreitzer 1979). Subsequent studies have suggested a doubling of reported longevity from 2+ to 4+ years (Drake et al. 2008), delayed female maturation (2+ versus 1+) and smaller clutch sizes (16-97 versus 30-170) (Faber 2006), a reported relationship between female age and clutch size (Heins 1985) and evidence for multiple spawning events (Johnston 1989; Winemiller & Rose 1992; Simon & Wallus 2006). Individually, such differences in population vital rates are likely to hold significant implications for population viability. Collectively, they suggest variability in population-specific vital rates likely to complicate the prediction of population status, even with detailed knowledge of the anthropogenic and natural stresses affecting the population.

As most of the available life history information for *A. pellucida* have been derived from the study of southern populations, further research to determine vital rates and estimate associated population projections for Canadian populations is warranted. Appropriate development of future population scenarios for *A. pellucida* will also require consideration of the implication of parameter uncertainty. In that regard the availability of a controlled experimental frame in which the effects of life history unknowns may be explored is vital. The use of a Leslie matrix model driven PVA is one means by which limited biological information and the effects of parameter uncertainty can be systematically explored to aid in the development of population-specific risk estimates and scientifically sound recovery strategies.

The goal of this study was to construct a Leslie matrix model using available field based population-specific information from the lower Thames River *A. pellucida* population. The specific objectives were: 1) to identify the limiting life stages and vital rates using PVA analyses; 2) to investigate how differing life history strategies (e.g., multiple clutches and earlier age at maturity)

and parameter uncertainty affects the population growth rate by using perturbation analyses; and 3) to predict the long term viability of the population by incorporating environmental stochasticity.

3.2 Material and Methods

3.2.1 Field Sampling

Field sampling of *A. pellucida* populations occurred in the vicinity of Big Bend Conservation Area in the lower Thames River, Ontario during the summers of 2006 and 2007 (June - August). Additional demographic information from a 2005 field survey (Drake et al. 2008) was used to create a 3-year dataset, the minimum size necessary for estimating population survival rates (Beissinger & Westphal 1998). Sampling followed the protocols described by Drake et al. (2008). Briefly, *A. pellucida* were collected from 10 depositional areas, typically sand-dominated point bars, using a three-pass seining method with a 10 m bag seine (1.8 m x 3.7 m wing with 0.64 cm mesh size and a 1.8 m x 1.8 m x 1.8 m bag with 0.32 cm mesh size). Seine hauls were completed at multiple sites (n = 5) along each point bar to account for possible within bar distributional heterogeneity.

Captured *A. pellucida* individuals were sedated using clove oil and measured for total length (mm). Scales were removed from the left mid-dorsal region for aging analysis. *A. pellucida* were revived in oxygenated river water and then released back to the river at the capture location. Incidental *A. pellucida* mortalities were retained on ice and frozen for subsequent analyses. *A. pellucida* capture and handling was approved under the Fisheries and Oceans Canada Species at Risk permitting process and internal federal Government of Canada animal care committee regulations.

Ages were estimated by mounting scales between 2 glass slides and counting the number of annuli at magnification (10x) under a compound microscope (Beamish & McFarlene 1987). Age-at-maturity was determined by relating estimated age to field observations of probable spawning readiness. In the field, female spawning readiness was assessed by the presence of extended

ovidepositors (Faber 2006), while male readiness was assessed by the release of milt when the dorsal ventral area was lightly squeezed. For all incidental mortalities identified as 0+ fish by length (< 40mm), saggitae and lapellae otoliths were removed and mounted sulcus side up using cyanoacrylate glue and analyzed for patterns of daily growth at the Bedford Institute of Oceanography, Otolith Research Laboratory (Campana 2009). Data on daily aging were used to calculate larval emergence dates and infer approximate spawning dates.

3.2.2 Model Structure

A deterministic, density-independent, Leslie matrix model was constructed using demographic information on age-at-first maturity, longevity, and mean survival and fertility rates for each age-class (Leslie 1945; Bessinger & Westphal 1998; Caswell 2001). Use of fertility and survival information in the projection matrix (L) allows future prediction of age-class abundances n(t+m), given an initial age-class abundance vector, n(t), at any period in the future (m) as:

$$1)\ n\ (t+m) = \mathbf{L}^{\mathbf{m}} n(t)$$

The dominant eigenvalue of the projection matrix defines the intrinsic rate of population increase, r, from which the finite rate of population increase, λ, may be determined as (Caswell 2001):

$$2)\ \lambda = e^{r}$$

The right (ω) and left (v) eigenvectors of the projection matrix also provide information on the stable age distribution and reproductive contributions by age-class. Combined, the eigenvalues and eigenvectors provide valuable information on population status and viability useful for understanding how management actions might help minimize future extinction risks (Crouse et al. 1987; Caswell 2001; Morris & Doak 2002). Commercially available software, RAMAS© Metapop: Viability Analysis for Stage-structured Metapopulations Version 5.0 software (Applied Biomathematics,

Setauket, NY) was used to implement all variants of the Leslie Matrix modelling framework used for analytical purposes in this study.

3.2.3 Parameter Estimation

As population surveys occurred following spring spawning, a post-breeding model consisting of 4 age-classes (ages 0+ through to 3+) was utilized here. Figure 3.2 illustrates the model, where F_i represents the mean reproductive output of the *i*th age-class and P_i represents the transition probability associated with surviving from age-class *i* to *i* +1 (Caswell 2001).

Age-class survival probabilities, P_1 and P_2 were calculated from 2005 to 2007 catch information using Chapman Robson methods (Chapman & Robson 1960; Robson & Chapman 1961).

$$3)\ P_i = \frac{X}{n + X - 1}$$

Where n is the total number of fish sampled, beginning with the first fully vulnerable age-class in the catch, *x* is either 0+ or 1+ based on sampling season, and X is determined from the age-at-catch data as $X = \sum_{x=0}^{k} xN_x$, with k equaling the total number of age-classes and N_x equaling the number of individuals of age-classes *x* captured. Differences in survival between years were calculated using analysis of variance (ANOVA) followed by comparisons of means using the conservative Tukey-Kramer HSD *post hoc* test.

Limited information on first year survival for *A. pellucida* made it impossible to quantify P_0 values directly from either field studies or literature sources. Therefore P_0 was calculated by assuming that the population was in stable equilibrium ($\lambda = 1.0$), with P_0 obtained as the value necessary to yield a finite population growth equal to one (Vaughan & Saila 1976; Caswell 2001; Morris & Doak 2002; Rogers-Bennett & Leaf 2006).

Fertility values for each age-class (*i)* were calculated following Morris & Doak 2002 as:

$$4)\ F_i = m_i q_i P_i c_i f_i$$

where m_i is the number of female offspring per female assuming that the sex ratio for the parents is the same as that for the offspring, q_i is the proportion of the population that is reproducing, P_i is the survival of the individuals within the ith age- class, c_i is the number of clutches laid per season and f_i is the number of eggs per clutch (Morris & Doak 2002; Vélez-Espino 2005). Fecundity and clutch size were based on ova counts from gravid females that were collected either as incidental mortalities or through predator gut contents. The number of clutches was determined by looking at egg diameter distributions and 0+ emergence dates based on daily 0+ aging analysis (see chapter 2) The proportion of females reproducing was calculated using the percentage of females over 42 mm, the minimum size for reproduction found by Spreitzer (1979).

Limiting life stages and the relative contributions of model parameters were determined using controlled model simulations and through the computation of parameter elasticities (e_{ij}) that express the proportional change in λ resulting from a known proportional change in a matrix parameter (a_{ij}) as follows (Benton & Grant 1999; Caswell 2001; Morris et al. 2002).

$$5)\ e_{ij} = \frac{a_{ij}}{\lambda}\frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i, \omega_j}{< \omega, v >}$$

Where <ω, v> represents the scalar product of the right (ω) and left (v) eigenvectors of the Leslie projection matrix (de Kroon et al. 1986; Caswell 2001), a_{ij} is the perturbed projection matrix element (e.g., age-class fertility, age-class survival), and ∂a_{ij} is the simulation change in a_{ij}. Elasticities sum to 1.0 thereby allowing for the relative contribution of each model parameter to λ to be easily established (de Kroon et al. 1986)

3.2.4 Perturbation Analyses

Perturbation analyses used to investigate changes in λ in relation to changes in the deterministic base model vital rates were performed in four different ways. First, survivorship for each age-class was systematically manipulated, while holding the rest of the model parameters at their original value. The original base model survival values were systematically varied from a 50% decrease to a 150% increase in percent increments and the resulting λ values were calculated. Secondly, reproduction was investigated using scenarios based on life history information gathered from studies of other *Ammocrypta spp.* populations (Spreitzer 1979, Heins 1985; Johnston 1989; Winemiller & Rose 1992; Faber 2006; Simon & Wallus 2006). The reproduction scenarios were broadly classified into three categories: 1) variation in the number of clutches per individual; 2) variation in the proportion of individuals participating in reproduction; and 3) variation in clutch size. See Table 3.1 for information detailing each reproduction scenario. Thirdly, the theoretical range of λ for the lower Thames River *A. pellucida* population was estimated using the maximum and minimum F_i and P_i values observed in this study. A best case matrix was created using the highest F_i and P_i values, while a worst case scenario was created using the lowest observed values. Finally, a simplistic, density-independent, stochastic model simulating environmental variation was used to estimate extinction rates, minimum expected abundance and associated population trajectories.

Many fish populations persist over long periods of time and are thought to be regulated by negative relationships between population growth rate and density that ensures that growth rate increases when abundances are low and declines when abundances are high (Hassell & May 1990). More recently it has been suggested that many populations are governed by concave relationships between population growth rate and density where population growth rates are relatively high at low abundance, but decline rapidly to a constant as abundance increases (Sibly et al. 2005). An important

implication of this finding is that many populations spend much of their time at, or above, carrying capacity and experience changes in abundance unlikely to be directly reflected in changes in population growth rates. Given the lack of correlation between density and survival rates for *A. pellucida* in the lower Thames River (see chapter 2), and the prevalence of concave population growth rate abundance relationships for many fish species (Sibly et al. 2005), a standard linear density-dependant relationship could not be assumed for *A. pellucida.* Accordingly, density dependence was not assumed for this population and demographic stochasticity was not included in the model.

Environmental stochasticity, however, was included and modelled by including specific consideration of parameter (e.g., age-class fertility) variability in the analysis. Stochasticity was considered over a 100 year period using an annual time step and 10 000 iterations of the model. Pertinent vital rates were randomly sampled from vital rate parameter distributions, assumed by default to be normal, using routines built into the RAMAS software (Akcakaya et al. 2004). Survival parameter standard deviations necessary for defining parameter distributions were estimated directly from available field data or, for $P_{0,}$ were calculated based on the mean variation observed for the other age-class survival probabilities. Given that fertility rates include both survival rates and fecundity estimates, standard deviations for F_1, F_2, and F_3 were computed following Monte Carlo methods (Law & Kelton 1991) with n = 10 000 replications under the assumption that m_i, q_i, c_i remained constant. Initial population size for the stochastic model was estimated based on site-specific sampling densities obtained from field studies (e.g., chapter 2) corrected for a standardized 10 000 m^2 area.

3.3 Results

3.3.1 Field Sampling and Parameter Estimation

A total of 1924 *A. pellucida* were captured during the 2006 (n = 795) and 2007 (n = 1124) sample seasons with data on an additional 1305 individuals from 2005 available from the Drake et al. (2008) study of the same population. Mean catch per unit effort (CPUE ± standard error) declined between 2005 and 2007, but there were no significant differences (Figure 3.3) among the years (ANOVA, $F_{2, 226} = 1.23$, $P = 0.29$).

Chapman-Robson survival rate estimates ± standard deviation for P_1 and P_2 varied across sites and sampling years from 0.277 ± 0.022 to 0.507 ± 0.016, with a mean survival rate of 0.386 ± 0.075 (n = 12) and a coefficient of variation of 19.87%. The majority (n = 5) of the survival estimates were obtained from the 2007 sampling season, but sufficient data for 2006 (n = 3) allowed comparison of survival between years that showed no significant differences (ANOVA, $F_{1, 6} = 2.12$, $P = 0.20$). Insufficient data existed to test differences between the sites.

Four age classes (0+, 1+, 2+, 3+) were identified based on the examination of scales of 743 individuals from the 2006 and 2007 sampling seasons. Mature individuals for both sexes were observed in the 1+ age-class, indicating age-at-first maturity occurs during the second summer after birth. Only 10 of 112 (8.9%) 1+ individuals were found to be below 42 mm, the spawning length threshold suggested by Spreitzer (1979). None of these 10 individuals showed signs of maturation when examined for the presence of an extended ovidepositor or expression of milt.

Ten gravid females were used to estimate fecundity. Average total fecundity ± standard deviation was 130.1 ± 30.1 eggs based on direct egg counts. Variation in egg size within individuals was apparent, with statistical decomposition (Bhattacharya 1967) revealing distinctive bimodality in the egg size distribution (Figure 3.4). Egg size modes were interpreted as representative of two

separate clutches with differing maturation schedules. Clutch size ranged from 35-123 eggs with an average 71.5 ± 22.7 eggs per clutch. No significant correlation was found between log-transformed female total length and total fecundity (n= 10, r^2= 0.086, *P*= 0.41). Fertility rates (27.60) for age-classes 2 and 3 were computed using a mean clutch size of 71.5 eggs, assuming 2 clutches per individual per year, 100% of all individuals participating in spawning and a sex ratio of 50:50. The mean fertility value for age-class 1 (25.15) was similarly computed, assuming that all 91.1% of the age 1 individuals that reached the minimum required maturity length spawned.

3.3.2 Population Viability Analyses

Assuming population equilibrium ($\lambda = 1$) and calculating P_0 from the other matrix entries (Caswell 2001), the resulting lower Thames River *A. pellucida* population projection matrix (L):

$$L=\begin{bmatrix} 0 & 25.15 & 27.60 & 27.60 \\ 0.025 & 0 & 0 & 0 \\ 0 & 0.386 & 0 & 0 \\ 0 & 0 & 0.386 & 0 \end{bmatrix}$$

The stable age distribution (right eigenvector, *w)* indicates that 0+ individuals make up the majority of the population (Table 3.2). Reproductive values (left eigenvector, *v)* are highest at the age of first reproduction, declining only marginally as fish age (Table 3.2).

The highest elasticity was associated with P_0 (Figure 3.5), indicating that small changes to Age 0+ survival have the largest affect on λ. High elasticities were also associated with F1 (0.255) and P_1 (0.150). The lowest elasticities (0.042) were found for F_3 and P_2, indicating that changes in these parameters had little effect on λ.

3.3.3 Perturbation Analyses

Increases and decreases in survival over the range of -50% to 150% resulted in monotonic changes in the finite rate of population growth, with maximum increases in λ occurring with a 150% increase in P_0 and maximal decreases occurring with a 50% decrease in P_0 (Figure 3.6). In the range of -25% to 25% only minor variations in λ were observed (± 10%).

Varying the number of clutches over the range from 1 to 4 resulted in a 24% reduction in population growth rate when all age-classes produced a single clutch, up to a 33% increase in λ when all age-classes produced four clutches relative to the base case of two clutches per year. Differing the size of clutches caused a variation of ± 44% in λ when the lowest (16 ova) and highest (343 ova) reported clutch sizes were utilized relative to the base case of 71 ova. When only 2+ individuals participated in spawning, a -36% decrease in λ was noted compared to when all age-classes participated in reproduction (Table 3.1).

The population growth for the lower Thames River *A. pellucida* population based on the worse and best case scenario (using the lowest and highest P and F values) indicated that λ could range between 0.703 and 1.311, a total variation of 60.8%. Inclusion of environmental stochasticity yielded *A. pellucida* extinction probabilities within the next 100 years in the range of 13.25 – 20.87% (Table 3.3). Population abundance trajectories appear to remain relatively stable (Figure 3.7), with the minimum expected abundance in excess of 1600/10 000 m^2 in all considered scenarios (Table 3.3).

3.4 Discussion

The Leslie matrix model constructed using acquired field data demonstrated the dependence of *A. pellucida* population dynamics on 0+ survival rates and the sensitivity of the finite population growth rate on reproductive assumptions, including clutch size and number. Age-at-maturity

assumptions while affecting λ, are less important for conclusions about the eventual success of *A. pellucida* populations. Environmental stochasticity acting on all life-history parameters poses real risks for the continued viability of lower Thames River populations, with significant chances of local extinction predicted on the basis of what is currently known about those populations.

A. pellucida management activities legislated under Canada's *Species at Risk Act* include habitat protection for all life stages, but have not made specific allowances for possible life-stage specific requirements. In particular, previous assessments have lacked information on which life stage may be most vulnerable to habitat degradation, or which life stage is most critical for continued viability of the population (Edwards et al. 2007). Based on the elasticity results from this study, the limiting life-stage vital rates are P_0 and F_1 (Figure 3.5). The importance of P_0 and F_1, as determined from their elasticities combined with the domination of 0+ individuals in the stable age distribution (Table 3.1), suggests that variation in the survival of *A. pellucida* individuals from egg to their first spawning are the key drivers of λ. Based on modelling results, therefore, management activities should focus on strategies designed to ensure successful spawning and improvement of 0+ survival rates. Conservation and restoration of juvenile and spawning habitats have been suggested as a means of protecting freshwater teleosts (Vélez-Espino et al. 2006) and based on the present study should be an important component of *A. pellucida* recovery activities.

Given that *A. pellucida* has a demonstrated preference for shallow, slow moving waters over sand substrates typical of river depositional areas, it is necessary to ensure that the hydrological processes governing the creation of these areas are maintained (Daniels 1989; Holm & Mandrak 1996; Cudmore et al. 2004; Edwards et al. 2007). To that end, water abstraction, diversion and impoundment activities known to alter flow regimes, flushing events and thermal regimes hold potentially serious consequences for *A. pellucida* populations. For example, while *A. pellucida*

spawning events have never been observed in the wild, optimal spawning conditions are thought to exist when water temperatures are between 20.5 - 23ºC (Johnston 1989; Simon & Wallus 2006). Non-optimal water temperatures in other darter species have been linked to decreased P_0 values with increased water temperatures causing larval and egg mortality due to fungal infections and decreased water temperatures inhibiting egg release and larval growth (Bonner et al. 1998; Poly 2003).

Increased protection of suitable depositional areas is likely to benefit 0+ individuals. Drake et al. (2008) found that 0+ growth was negatively correlated to percent silt substrate composition but positively correlated to percent sand substrate composition. In contrast no correlation was found for adult phases. Correlations suggest that 0+ individuals are more sensitive to variations in substrate composition and it is reasonable to assume P_0 would be compromised as substrate siltation rates increase. Mechanisms for reducing P_0 in habitats with a greater percentage of silt in the substrate include increased physiological costs associated with respiration when engaged in burying behaviour (Daniels 1989; Holm & Mandrak 1996; Grandmaison et al. 2004; Simon & Wallus 2006; Drake et al. 2008) and the loss of access to the more productive sand substrates (Riznyk & Phinney 1972; Wulff et al. 1997).

Another consideration with respect to increased protection for 0+ individuals is the suggestion that *A. pellucida*, like many other darter species, have a larval pelagic phase during which larvae might be transported downstream of their natal sites (Freeman & Freeman 1994; Rakes et al. 1999; Slack et al. 2004; Simon & Wallus 2006). Research on other small bodied fishes has suggested possible meta-population reliance on upstream populations as a source of recruits for downstream populations (Labbe & Fasch 2000; Bennett et al. 2008). Concentration on localized larval habitat features alone, therefore, may not suffice to ensure protection of *A. pellucida* populations within a single river reach. Landscape level processes such as disturbance, dispersal and habitat patch mosaic

structure have been found to influence populations of Arkansas Darter, *Etheostoma cragini* (Labbe & Fausch 2000) and similar factors could also have implications for the lower Thames River *A. pellucida* population. Local variations in P_0, therefore, might be offset by downstream larval drift and facilitated by natural disturbance regimes that create and re-distribute habitat and refugia within the broader landscape (e.g. Bisson 1995; Reeves et al. 1995). The importance of P_0 for a specific-population, therefore as determined here does not account for recruitment effects and improved efforts at refining understanding of larval drift and/or inter-population adult migration are warranted.

The reproduction scenarios examined here and the resulting sensitivity of λ to reproduction related assumptions highlight the need for further detailed reproductive studies. In particular, improved understanding of clutch numbers, size and the period over which spawning occurs is required. Temporal variations in spawning readiness, clutch size and the apparent wide variety of vital rates suggests spawning may occur over a protracted period of time from early May until late June. Spawning dates can vary with age in fishes, with older mature individuals spawning earlier in the season (Bagenal 1971). Information on reproductive tactics available for this study suggested a wide variety of plausible reproductive scenarios. The variation may have been driven by the paucity of information. Alternatively the variation and its associated impacts on λ may simply reflect population growth rate plasticity. Such plasticity is often observed in species living in unpredictable environments where environmental conditions such as floods and droughts can compromise population survival (Vinyoles & De Sostoa 2007). The ability to produce extra clutches under favourable environmental conditions can compensate for periods when reproductive output (e.g., decreased clutch size and number of clutches) declines in the face of environmental constraints (Pianka 1970; Winemiller & Rose 1992; King & McFarlene 2003; Vinyoles & De Sostoa 2007).

Reproductive plasticity combined with dependence on juvenile survival classifies *A. pellucida* as an opportunistic strategist. Opportunistic strategists are typically small bodied, short-lived fishes where rapid larval growth, early maturation (typically) and frequent reproduction facilitate rapid population growth and turnover rates (Winemiller & Rose 1992; Vélez-Espino et al. 2006). These mechanisms can also make opportunistic strategists more susceptible to extinction when exposed to prolonged periods of natural or anthropogenic stresses (Olden et al. 2007). As noted here, even under fairly optimistic reproduction and survival scenarios, extinction rates were high. Coupled with evidence for declining CPUE and suggestions that existing population numbers are at historic lows (Holm & Mandrak 1995), an evolutionary susceptibility to extinction under stress suggests the future viability of the lower Thames River *A. pellucida* population is far from assured. Accordingly, when taking these factors into account, caution must be taken when interpreting the projected stable population trajectory (Figure 3.7).

To date, limited research on *A. pellucida* population dynamics has impeded the ability of resource managers to develop management strategies. Population models such as the one described here provide one means of exploring *A. pellucida* population dynamics. Nevertheless, detailed studies on reproduction and the life history characteristics of the species are still needed to properly understand and rank the factors influencing λ. In the absence of such studies, it is evident that with the predicted high extinction probability for *A. pellucida*, management activities must focus on suitable habitat protection to increase P_0 and ensure future population viability. Ultimately population viability will depend on whether the anthropogenic stressors associated with habitat degradation can be removed in time to allow for the successful recovery of the lower Thames River *A. pellucida* population.

3.5 Tables and Figures

Table 3.1. Summary of perturbation scenarios involving reproductive strategies reported or suggested for *Ammocrypta spp.* and the resulting impact on the λ for the lower Thames River *A. pellucida* population. For each reproductive scenario group, details of the simulation experiment are described. The column new matrix value defines the parameter value used for the simulation scenario described, with the new parameter values listed in order in which they are defined in the simulation column. λ defines the resulting finite rate of population growth. Difference compares the scenario estimate of λ = 1, as obtained in the base case, an increment of 0.01 representing a 1% change in population abundance**.**

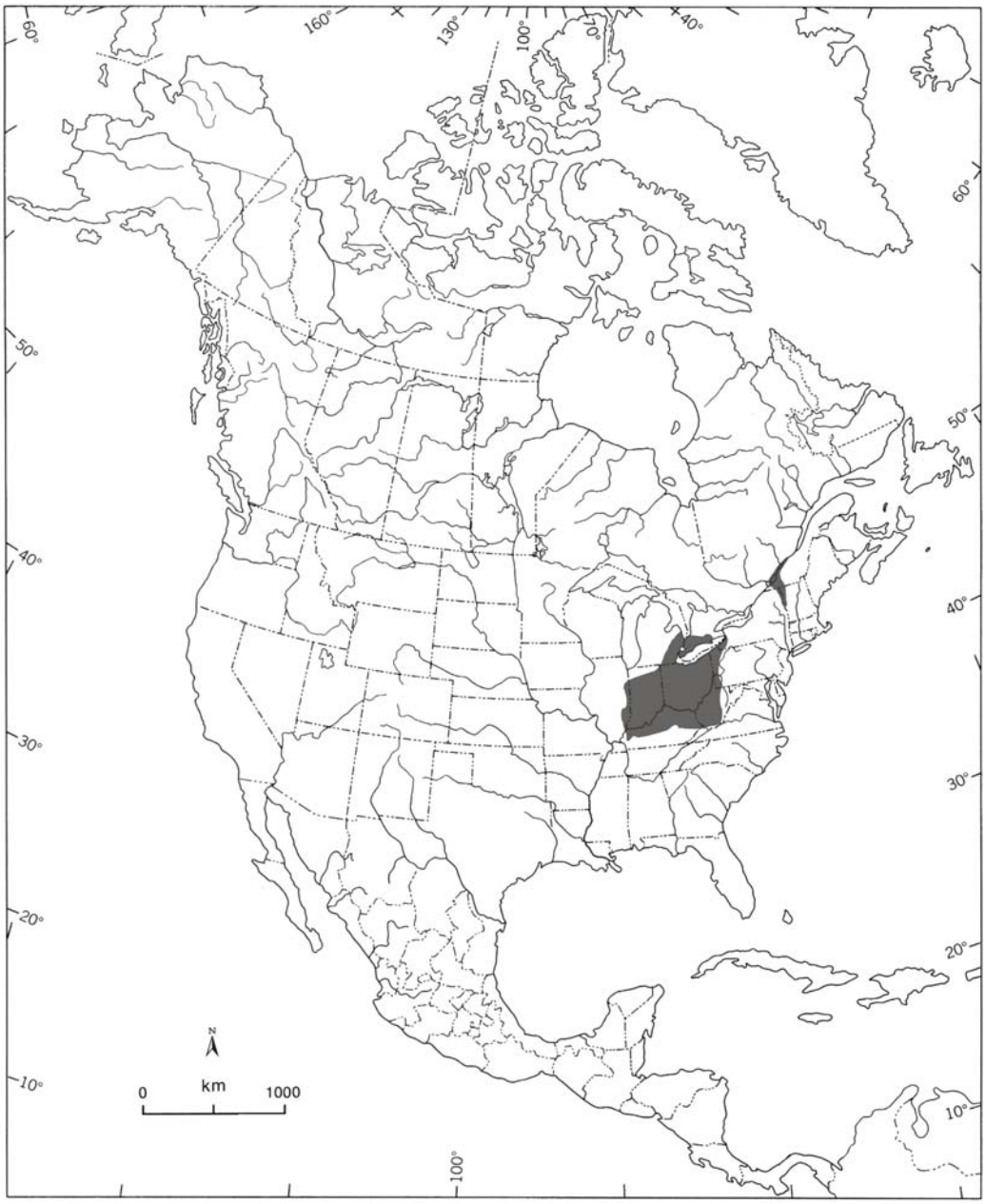
Reproduction Scenario	Simulation	New Matrix Value	λ	Difference
Number of clutches (Heins 1985; Johnston 1989; Winemiller & Rose 1995; Simon & Wallus 2006)	4 clutches for F1, F2, F3	50.30, 55.21, 55.21	1.332	+ 0.332
	4 clutches for F3 individuals	55.21	1.038	+ 0.038
	3 clutches F1, F2, F3	37.72, 41.40, 41.40	1.180	+0.180
	3 clutches for F3 individuals	41.40	1.020	+0.020
	3 clutches for F2 individuals	41.40	1.050	+0.050
	1 clutch for all age classes	12.59, 13.80, 13.80	0.761	-0.239
	1 clutch for F1	12.59	0.870	-0.130
Individuals participating in reproduction (Spreitzer 1979; Faber 2006)	Age-at-maturity of 2+ (no F1 spawning)	0	0.740	-0.260
	Population longevity of 2+ (No F3 spawning)	0	0.954	-0.046
	Only reproductive stage is F2	0, 27.60, 0	0.644	-0.356
	All 1+ individuals reproducing	27.6	1.024	+0.024
	25% decrease in the number individuals involved in reproduction	18.86, 20.70, 20.70	0.891	-0.109
Clutch size range (Spreitzer 1979; Faber 2006; current study)	Highest clutch size of Thames River	43.26, 47.48, 47.48	1.250	+0.250
	Lowest clutch size for Thames River	12.31, 13.51, 13.51	0.754	-0.246
	Highest clutch size for Little Muskingum River (Ohio)	34.11, 37.45, 37.45	1.132	+0.132
	Lowest clutch size for Little Muskingum River (Ohio)	5.63, 6.18, 6.18	0.564	-0.436
	Spreitzer's fecundity estimate of 343.1 eggs per individual (Salt Creek, Ohio)	60.00, 65.87, 65.87	1.436	+0.436

Table 3.2. Right and left eigenvector values from Leslie model matrix analysis representing the stable age distribution and age-specific reproductive values for the lower Thames River A. pellucida population.

Age Class	Stable age distribution ω	Reproductive values v
0	0.963	1.00
1	0.024	39.97
2	0.009	38.29
3	0.004	27.62

Table 3.3. Probability (95% confidence interval) of extinction and the expected minimum abundance (*A. pellucida*/10 000 m^2) of A. *pellucida* in the next 100 years using low, average and high initial population abundance scenarios

	Abundance Estimates (95% CI)	Extinction probability (95% CI)	Expected Minimum Abundance
Low Density	2234 (2111 - 2333)	20.87% (19.50 - 23.05%)	1648.1
Average Density	3602 (2486 - 4104)	16.38% (15.49 - 17.27%)	2617.9
High Density	4874 (4555 - 5222)	13.25% (12.36 - 14.14%)	3691.4



Source: Al Dextrase (2008)

Figure 3.1. Global distribution of Eastern Sand Darter (*Ammocrypta pellucida*) illustrating the disjoint nature of the distribution.

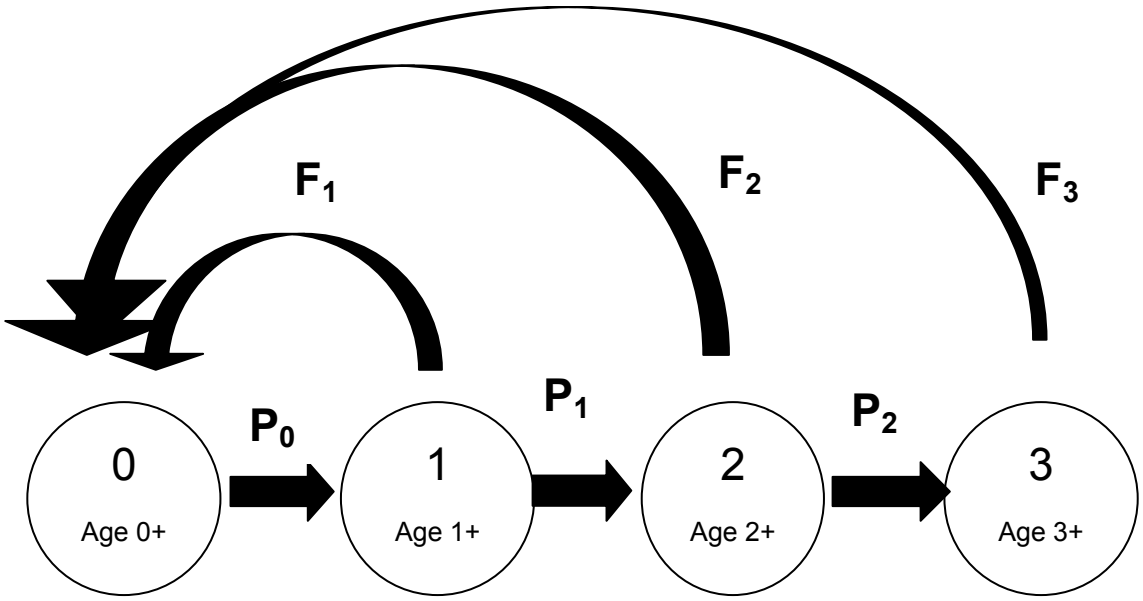


Figure 3.2. *A. pellucida* life cycle diagram for the post breeding deterministic Leslie matrix model. Circles indicate age-class, Fi defines mean age-class fertility rate; while P_i represents the probability of an individual in age-class i surviving for one year (modified from Caswell 2001).

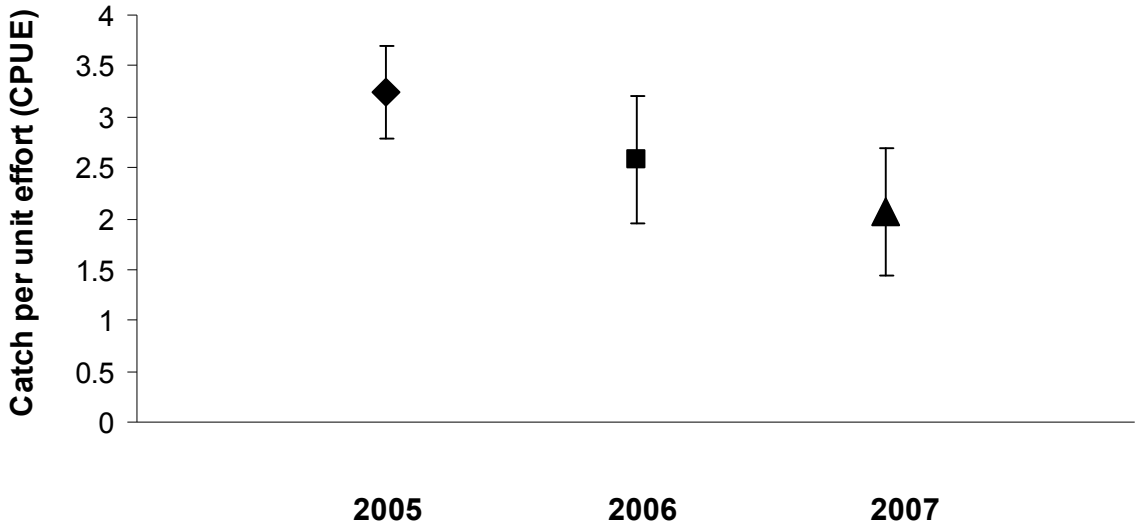


Figure 3.3. Annual catch per unit effort ± standard deviation for each sampling year for *A. pellucida* from the lower Thames River. Catch per unit effort did differ significantly among years (ANOVA, $F_{2, 226} = 1.23$, $P = 0.29$).

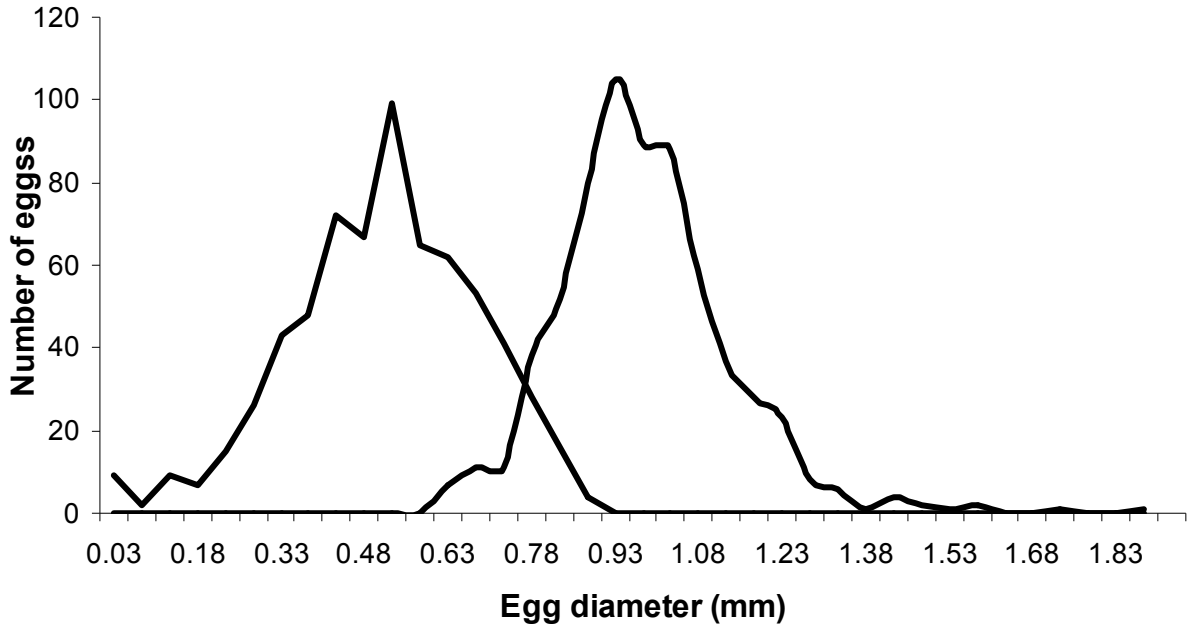


Figure 3.4 Distributions of 1320 *A. pellucida* egg diameters from 10 individuals. Distributions were identified using statistical decomposition techniques and interpreted as representative of separate clutches with differing maturation schedules.

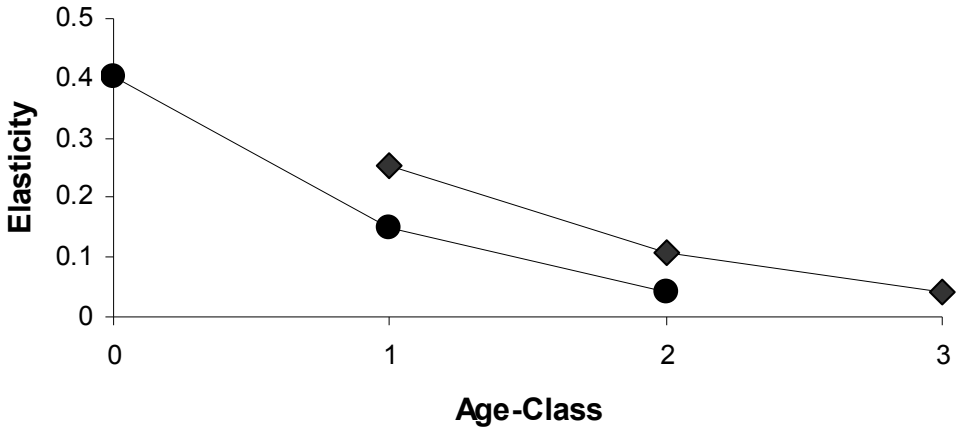


Figure 3.5. Estimated fertility F_i (♦) and survival P_i (●) elasticities for the *A. pellucida* Thames River population Leslie matrix model. Elasticities sum to 1.0, thereby allowing statements about the relative importance of parameter changes for the finite rate of population growth.

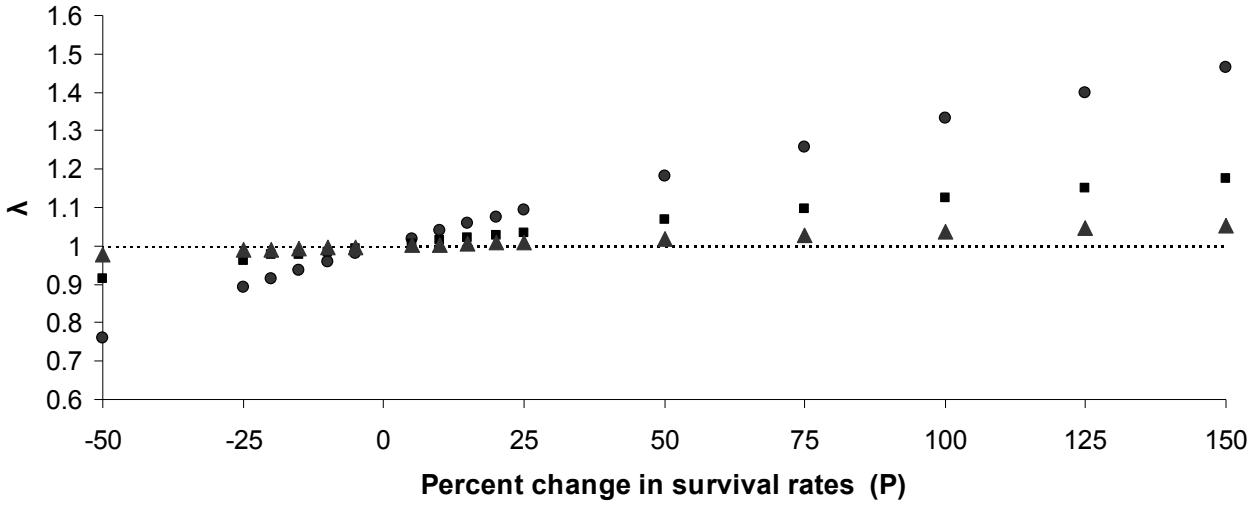


Figure 3.6. Simulation of changes in survival and the resulting population growth (λ) for the lower Thames River, Ontario *A. pellucida* population. Circles represent P_0 values, squares are P_1 values and triangles are P_2 values. The dotted line indicates equilibrium population growth (λ= 1).

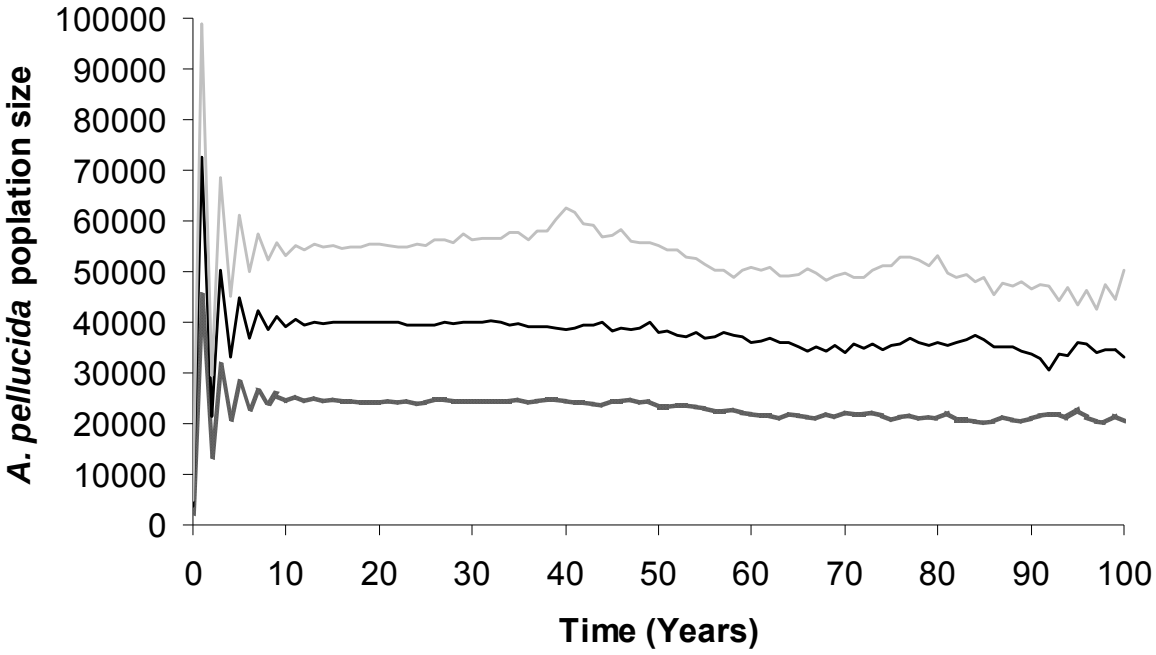


Figure 3.7. Mean estimated population trajectory for *A. pellucida* population (*A. pellucida*/10 000 m^2) in the lower Thames River over the next 100 years based on stochastic projections generated for: low (doted line), average (black line) and high (grey line) initial population estimates.

Chapter 4
General conclusions and future research directions

The Recovery Strategy for Eastern Sand Darter (*Ammocrypta pellucida*) in Canada was drafted in response to the listing of *A. pellucida* as a Threatened species under Canada's *Species at Risk Act* (SARA). Included in the strategy was a synopsis of the current and historical distribution of the species in Canada, suggested reasons for population decline and species recovery goals and objectives (Edwards et al. 2007). Highlighted was the paucity of information on life history traits, population dynamics and critical habitat requirements for the Canadian populations. This M.Sc. project was undertaken to help scientifically address some of the identified knowledge gaps.

This study marks the first time that a comprehensive life-history study has been completed for a Canadian *A. pellucida* population. Using time series information from field surveys conducted in 2006 and 2007 in the lower Thames River, Ontario, biological information on longevity, fecundity, clutch size, growth, age cohort structure, survival, density and age-at-first-maturity were investigated. At the local habitat scales, *A. pellucida* abundances were positively associated with sand substrates and high dissolved oxygen and pH levels and negatively associated with the presence of gravel substrates and increased velocities. Detailed description of both local habitat preferences and life history characteristics as described has increased the ecological knowledge of Canadian *A. pellucida* populations.

When life history values from this study were compared with populations from the Little Muskingum River, Ohio, the lower Thames River *A. pellucida* population was shown to have greater longevity and lower age-at-first-maturity, increased first year growth and to spawn multiple clutches

of eggs (Spreitzer 1979; Faber 2006; Simon & Wallus 2006). The comparison study further suggested that observed population differences are more likely due to localized environmental conditions rather than latitudinal effects. The suggestion has implications for Canadian species-at-risk resource managers as it means that in the absence of Canadian population data, it is not feasible to accurately predict life history values based on other populations without detailed knowledge of local habitats and an understanding of how environmental factors may act to condition population dynamics through possible adaptation.

Investigation of population dynamics through the creation of a Leslie matrix model in Chapter 3 found that 0+ individuals were the most important determinates of population structure and growth rate. Elasticity analyses found that the population limiting vital rates were 0+ survival and 1+ fecundity. Further evidence for the reliance of population growth on 0+ individuals was demonstrated by the presence of a large 0+ cohort. Therefore knowing how to minimize the factors that most influence juvenile mortality factors and facilitating the survival of individuals to first breeding would have the largest positive impact on the finite rate of population growth (λ) and suggests that management activities should focus on improving survival probabilities at this life stage. Suggested management activities include protecting spawning and nursery habitats and ensuring that the hydrological processes governing the creation of sandy depositional areas are maintained. Model-based population trajectories showed a high probability of extinction within the next 100 years. Decreasing trends in catch per unit effort (CPUE) also question the future viability of *A. pellucida* populations. When fecundity scenarios involving differing numbers of clutches and clutch sizes were modelled, large variations in λ were noted. The variation has implications for recovery, as it suggests that λ can quickly change in response to environmental perturbations that affect egg production or survival. Responsiveness to changes in reproductive output when combined with the opportunistic

habitat use strategy demonstrated for the species (Daniels 1989; Simon 1991; Holm and Mandrak 1994) means that population recovery could be rapid should anthropogenic stresses be minimized and habitat quality improved.

The Eastern Sand Darter Recovery Strategy is scheduled to be revised in 2010 and I am hopeful that the results of this study will provide the information needed to reduce the knowledge gaps outlined in the previous strategy drafts. The modelling framework created for this study can be used to test other population scenarios and possible habitat modifications, thereby allowing potential management scenarios to be investigated for efficacy prior to implementation (e.g., Vélez-Espino & Koops 2009). While this study has provided much of the needed information on a Canadian *A. pellucida* population, there are still many areas were additional research could be focused. Future research ideas include:

1) Continued times series sampling of the lower Thames River population could provide more concrete information on density-dependence and demographic stochasticity, allowing for strengthened population viability estimates. The use of standardized sampling methods would also provide a better time series database for increased understanding of demographic vital rates.

2) Examination of daily growth analyses data could be used to investigate the impact of maternal investment. In particular the data generated from this study could determine whether 3+ individuals spawn large eggs earlier in the season giving rise to 0+ individuals that have increased survival probabilities (Bagenal & Braum 1971).

3) Metapopulation analyses using genetic information could provide increased knowledge of larval drift and migration. Such data could provide important information on population

sources and sinks and the associated habitats as well as providing a picture of the overall importance of multiple populations for meta-population viability (e.g. Bennett et al. 2008).

4) Laboratory studies, investigating spawning and 0+ growth and survival would increase the ecological knowledge of the most vulnerable life stages. Results would provide more insight into clutch size and the number of spawned clutches, parameters both vital to accurate population viability analysis. Additional work could include temperature, turbidity, and siltation manipulations to test how these factors are related to fecundity and larval growth and survival. Laboratory studies might also test the feasibility of maintaining *A. pellucida* stocks in captive breeding programs for possible future supplementation of existing wild populations, or the reintroduction of the species into extirpated areas (e.g., Rakes et al 1999).

5) Comparison of the lower Thames River population life history characteristics to the traits of another Ontario population (e.g., Grand River or Sydenham River) would also provide more insight into how localized environmental factors may impact Canadian populations and would help to identify potential stressors for each population. A comparative study of this nature would further help to determine whether life history values estimated for the Thames River population were potentially representative of other Canadian populations or if environmental variability between systems plays a large role as suggested in this study.

6) Increased habitat and larval surveys are needed to identify nursery and spawning habitat. Additionally habitat surveys should also investigate localized effects of point and non point source contaminants on *A. pellucida* abundances.

A potential implication of this study for other Canadian species-at-risk small-bodied fish is that in the absence of population-specific life history information, the use of analogue information from

other populations is not necessarily valid. However, as demonstrated, non-lethal sampling techniques (e.g., collection of scales for aging analyses) can provide information on the biological characteristics of a population and matrix models can provide a useful quantitative means of testing potential life history strategies with minimal harm to the study population.

During this study of *A. pellucida*, a fish relatively unknown to the general public, I was often asked about the "importance" of the study. When providing answers about the importance of biodiversity and how species richness is important to the sustainability of ecosystems, I began to question the necessity, validity and feasibility of spending resources to study a single species. I find it amazing to think that so little is known about the biology and ecology of a species living in such a heavily populated area as southern Ontario. Improvement of that information base is one reason for this study however, the most important reason lies in the bigger ecological picture. The recovery of *A. pellucida* requires habitat rehabilitation and the maintenance of appropriate hydrology regimes, activities that will benefit all species inhabiting the lower Thames River (including humans) and, in my opinion that is the ultimate importance of this study.

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Chapter 1

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