University of Alberta

Effects of Predator Presence on Fathead Minnow Life History

by

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Abstract

The presence of predators may alter life history strategies of prey populations. I examined how predator presence shapes life history traits of the fathead minnow (*Pimephales promelas*) by comparing characteristics of minnows from lakes that differed in the risk of predation by northern pike (*Esox lucius*). Predator presence was linked to differences in length distribution, age-at-maturity, and timing of the spawning season of minnow populations. To examine if these differences had a genetic component, I stocked minnows from two lakes (with and without pike) into experimental ponds. Nest size and duration, level of parental care, egg incubation time, egg and hatchling survival, and offspring size differed between the two populations, suggesting at least a temporary mismatch between traits and environment while the predator-experienced population adjusted to changed predation pressure. Understanding fish species' responses to predator community changes should be incorporated into management options, such as stocking of piscivorous sport fish.

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Chapter 1: GENERAL INTRODUCTION

Life history theory seeks to explain an organism's lifecycle, from its growth rate and age at maturity to its reproductive effort and lifespan (Stearns 1992). Through natural selection and the resulting evolutionary responses, in combination with various constraints on adaptation, life history traits are thought to optimize the success and fitness of individuals in a given environment; thus, the set of life history traits seen at the population level, such as age or size at maturity, reproductive investment, and lifespan, should maximize fitness under a given set of selective pressures (Gadgil and Bossert 1970). As such, populations of the same species existing under different conditions, with differing selective pressures, should vary in their life history traits.

Life history traits are bound together, however, by a series of trade-offs, where a beneficial change in one trait is often linked to a sub-optimal characteristic in another (e.g., Roff 2000, Roff *et al.* 2006). Likewise, in certain environments, a trait that has beneficial effects early in life may be favourably selected even if it reduces vigour later in life (Williams 1957, Roff 2000). The specific selective pressures encountered by a population should determine the trade-offs among life history traits. A short-term change in the environment could result in phenotypic responses, a within-generation change in traits among cohorts (Endler 1986). The range of variation, or plasticity, within a phenotype covers the range of tolerance within a genotype for a given environmental condition (Lynch and Gabriel 1987). When the same pressures are regularly experienced by a population over time, the life history traits selected to maximize fitness in that environment may become the norm. Gradually, these phenotypes and, in turn, the related genotypes will increase in frequency across generations (Wootton 1990). Variation in environmental conditions influences the ranges of tolerance of the genotypes; high levels of variability in the environment selects for adaptation to a broad range of conditions, resulting in a broader range of tolerance and, therefore, selects for phenotypic plasticity (Lynch and Gabriel 1987).

Selective pressures on a population include abiotic conditions, such as temperature, nutrient availability, oxygen levels, and pH, as well as biotic factors, such as food availability, competition, and predation. Predation, in particular, has been shown to affect prey species in a number of ways. Effects of predation can include modifications to behaviour, physiology, and morphology. Modifications to behaviour can include vertical migrations of plankton to avoid predators (Stich and Lampert 1981) or abandonment of territorial defenses and subsequent concealment in the presence of predators in fish (Jones and Paszkowski 1997). Prey may also avoid predators through physiological means, such as producing chemicals to make themselves unappealing to predators (Kerfoot 1982). Colouration changes may make the organism more cryptic to the predator, whereas other changes could also occur that make the organism less cryptic, e.g., to advertise the unpalatable chemicals discussed above. Changes in colouration may also direct attacks to specific areas of the body; for example, Gray treefrog (*Hyla chrysoscelis*) tadpoles have darker tail colouration in the presence of predatory dragonfly (*Aeshna umbrosa*) larvae (McCollum and Leimberger 1997), which directs attacks toward the tail rather than the more vulnerable head, reducing tadpole mortality. A change in the morphology of organisms can also be induced through predator presence. Such changes often make the prey item more difficult to handle, as is the case with

Daphnia ambigua adults that develop a pronounced helmet and spines on the carapace in the presence of *Chaoborus* spp. (Hebert and Grewe 1985). This change in morphology results from a shift in energy allocation, as documented in males of the green swordtail (*Xiphophorus helleri*), which have shorter swords in habitats with piscivorous fishes as more energy is put into somatic growth to attain larger body sizes (Basolo and Wagner 2004).

Predation can also act as a selective force on life history traits, affecting growth rate, age and size at maturity, reproductive effort, and lifespan. The direction of the effects on life history traits depends on the selective nature of the predator on prey. For example, invertebrate predators of cladoceran species are size-limited in their prey selection such that predation decreases as prey size increases until a maximum prey size threshold is reached, beyond which predation does not occur. Thus, in the presence of such size-limited predators, populations of small-sized cladoceran species, which are vulnerable to predation throughout their lifespans, accelerate their reproductive effort early in life; often, large offspring are produced at an early age, which minimizes juvenile mortality and increases fitness. In contrast, large-sized cladoceran species may delay maturity and allocate their energy to high growth rates that allow them to quickly reach a size not vulnerable to predation, after which reproduction occurs (Lynch 1980). Studies of Utah chub (*Gila atraria*) found that populations coexisting with size-limited predators exhibited the predicted trade-off between growth and reproduction, including increased growth and larger adult size, but delayed and decreased reproduction. These populations also had longer lifespans compared to populations without predators (Johnson and Belk 1999). Reznick and Endler (1982) similarly found a larger size at maturity and decreased reproductive effort in Trinidadian guppies (*Poecilia reticulata*) experiencing size-limited predation; in contrast, in the presence of predators that selected larger prey, guppies had a smaller size at maturity but increased reproductive allocation, maximizing reproductive success within a shortened lifespan. These differences in life history strategies can be attributed to the selection by predators of juveniles in the case of the Utah chub (Johnson and Belk 1999) and of adults in the latter guppy example (Reznick and Endler 1982).

Both high and low levels of predation pressures can occur on fishes in Alberta lakes. Lakes in northern Alberta frequently experience low oxygen levels under the ice (Danylchuk and Tonn 2003). Large-bodied piscivores, such as northern pike (*Esox lucius*), have relatively low tolerance for such conditions (Robb and Abrahams 2003), and may experience over-winter mortality or be excluded from the lakes that regularly experience such conditions (Robinson and Tonn 1989). Many small-bodied forage fishes are more tolerant of low oxygen levels (Klinger *et al.* 1982) and are often found in lakes prone to these harsh abiotic conditions (Robinson and Tonn 1989). However, such species are vulnerable to predation by large-bodied piscivores (Robinson 1989, Jones and Paszkowski 1997), which generally prevents the co-occurrence of the two groups. As a result, fish assemblages in small, northern Alberta lakes are often dominated either by small-bodied or large-bodied fishes (Robinson and Tonn 1989). Occasionally, however, lakes can be found in which large-bodied piscivores and small-bodied prey fishes co-occur. These mixed assemblages could be the result of variable conditions, including the opportunity for large-bodied piscivorous fishes to re-populate and/or re-colonize more inhospitable lakes via intermittent inlets (Tonn and Magnuson 1982).

I examined whether the presence of piscivorous fish leads to changes in life history traits of fathead minnow (*Pimephales promelas*) and, if so, documented the nature of these changes, by comparing life history characteristics of populations from lakes where this predation risk does and does not exist. In Chapter Two, I focus on this comparison of life history characteristics between these populations; age and growth as well as reproductive characteristics of populations were examined. A second objective of my study was to determine if observed differences in life history traits between populations are caused by genetic or environmental influences. To address this question, I carried out a common-garden experiment by introducing minnows from two lake populations (one where minnows coexist with piscivorous fish and one where they do not) into experimental ponds at Meanook Biological Research Station (MBRS). In Chapter Three, I focus on the reproductive effort of these experimental populations through comprehensive monitoring of their nesting activities, looking at whether differences in life history traits persist in the common environment.

The results of this study will help us to understand the role of predation in shaping the life history of the fathead minnow and the ability of the minnows to respond to a change in predation pressure. The predatory pressure experienced by a prey population may fluctuate due to various causes. As alluded to above, fish community composition in many boreal lakes is driven by the abiotic conditions of a lake, including over winter hypoxia and is limited to species tolerant of the conditions (Robinson and Tonn 1989). Colonization of lakes by less tolerant species, including large-bodied piscivores, can occur through connectivity to other water bodies (Tonn and Magnuson 1982); thus, even generally harsh lakes with intermittent inlets may be temporarily colonized by species less suited to the environment (Robinson and Tonn 1989; DeBates *et al.* 2003). Changing climatic conditions can affect the abiotic condition of lakes (e.g., Magnuson *et al.* 1997; Mooij *et al.* 2007), which can shift fish community composition; climate change may also affect water levels, altering the connectivity of lakes and allowing predators to colonize lakes that have historically been predator-free or excluding predators from lakes to which they currently have access. The introduction of non-native fish species can also result in new selective pressures on the native fish community (Latta *et al.* 2007). These changes to the lake environment and fish community will influence predatory pressures through space and time. It is important to understand how prey species will respond to such changing ecological conditions; the ability to alter life history strategies under changing environments has important implications for population persistence.

Study Organism

Fathead minnow is one of the most widely distributed fishes across northern Alberta (Nelson and Paetz 1992). It is tolerant to environmental conditions that are unsuitable to many other species and in the absence of potential competitors and predators, is often abundant in these harsh environments (Nelson and Paetz 1992). The distribution of the fathead minnow among boreal lakes (Robinson and Tonn 1989) and behavioural studies of its responses to the presence of northern pike (Jones and Paszkowski 1997a,b) suggest, however, that the fathead minnow is extremely susceptible to predation by pike.

The spawning behavior of fathead minnow allows for detailed information to be obtained on key life history traits, such as reproductive activity and recruitment of young.

Typically, a female spawns adhesive eggs to a site selected by a male, such as the undersurface of vegetation, woody debris, or rocks in water less than 1m (Nelson and Paetz 1992); fathead minnows will also readily use artificial spawning substrates (e.g., Grant and Tonn 2002), which increases our ability to study their nests. In northern Alberta, the spawning season generally begins in late May or early June, when temperatures reach 15.6-17.8°C, and extends to August (Dobie *et al.* 1956, Nelson and Paetz 1992). The incubation time of eggs is temperature-dependent, however, 4.5-6 days is typical (Scott and Crossman 1985). Female fathead minnows are fractional spawners, releasing approximately 400 eggs per session and up to 10,000 eggs over the summer (Gale and Buynak 1982).

Aided by these favourable biological characteristics, techniques have been developed locally to quantify the life history traits of fathead minnows in both natural populations (Danylchuk and Tonn 2006) and whole-pond field experiments (e.g., Danylchuk and Tonn 2001, Grant and Tonn 2002). Because of its sensitivity to predation and its favourable traits, fathead minnow is therefore an excellent model with which to examine the effects of predation on the life history of a boreal Alberta fish.

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Chapter 2: EFFECTS OF PREDATOR PRESENCE IN NATURAL FATHEAD MINNOW POPULATIONS.

Introduction

Life history theory states in general that traits should be selected to increase fitness under the prevailing set of ecological conditions (Roff 1992). Predation acts as a selective force (e.g., Crowl and Covich 1990, Belk 1998, Heibo and Magnhagen 2005), and can affect prey species in multiple ways, including modifications to behaviour, physiology, morphology, and life history (e.g., Hebert and Grewe 1985, Jones and Paszkowski 1997, McCollum and Leimberger 1997).

Life history traits affected by predation include growth rate, age and size at maturity, reproductive effort, and lifespan. Therefore, in lakes where large-bodied piscivorous fishes and small-bodied forage fishes co-occur, the selective pressures experienced by the prey species could lead to differences in their life history traits compared to traits found in piscivore-free environments. For many of these traits, however, the direction of the effect can be influenced by the size-related selection of prey by the resident predators. Studies of bluegill sunfish (*Lepomis macrochirus*) found that populations coexisting with abundant populations of size-limited predators exhibited increased growth rates early in life and larger adult size, but delayed and decreased reproduction (Belk and Hales 1993). Johnson and Belk (1999) found these same results when studying Utah chub (*Gila atraria*) exposed to gape-limited predators; these chub populations also had a longer lifespan compared to populations without predators. On the other hand, when larger-sized prey are selected for and adult mortality is increased, more energy is allocated to reproduction rather than to growth. Reznick and Endler (1982) found a smaller size-at-maturity and increased reproductive effort in Trinidadian guppies (*Poecilia reticulata*) experiencing intense size-selective predation. Understanding how piscivorous fishes shape the life history strategies of prey species can provide insight into the ability of fishes to adjust in ways that optimize their fitness and improve probability of persistence under different selective pressures (Hutchings 1993).

Small lakes in northern Alberta regularly experience low oxygen levels during winter, due to the lakes' high productivity, shallow depths, long periods of ice cover, and isolation from other surface waters (Danylchuk and Tonn 2003). Large-bodied piscivorous fish species have relatively low tolerances for such conditions and, as a result, may experience over-winter mortality or be excluded from lakes that regularly experience such conditions (Robinson and Tonn 1989). Many small-bodied forage fishes, in contrast, are more tolerant of low oxygen levels (Klinger *et al.* 1982) but are vulnerable to predation by piscivorous species (Robinson 1989, Jones and Paszkowski 1997). As a result of the differing tolerance levels and vulnerabilities among species, fish assemblages in small, northern Alberta lakes are often dominated either by small-bodied forage fishes or large-bodied piscivorous fishes (Robinson and Tonn 1989). Occasionally, however, lakes can be found in which these two groups co-occur. As a result of the presence of the piscivores, forage fishes in these lakes will be exposed to predation at levels they would not experience in their more common piscivore-free habitat.

The purpose of this study was to investigate whether sympatry with piscivorous northern pike (*Esox lucius*) leads to changes in life history characteristics of fathead minnow (*Pimephales promelas*) in small, northern Alberta lakes. To achieve this, I examined the life history characteristics of fathead minnow populations in lakes with and without northern pike. Fathead minnows are highly vulnerable to predation by northern pike (Robinson 1989) and can be a significant food source for northern pike (Sammons *et al.* 1994). The optimal prey size for pike, from a cost-benefit standpoint, is approximately 25% of body length (Nursall 1973, Hart and Connellan 1984); thus, for minnow-sized prey, most pike should select larger-bodied individuals, increasing mortality of adult fathead minnows. With increased adult mortality and, thus, a shorter expected life span, life history theory predicts selection for early maturity and increased allocation of resources to reproduction (Stearns 1992), as this selection will maximize lifetime reproductive success by increasing the number of viable offspring produced (Williams 1966). Consequently, I predicted that fathead minnows in lakes co-occurring with northern pike would mature at a younger age and smaller adult size, invest more energy into reproduction, and thus display increased reproductive effort than minnows allopatric to pike. Since early maturation and reproduction is favoured by increased juvenile growth (Hutchings 1993), I also predicted that minnows co-occurring with pike would reproduce earlier in the spawning season; this earlier seasonal reproduction leads to greater growth potential for young-of-year, resulting in a positive feedback loop (Danylchuk and Fox 1994). Belk (1995) found no detectable differences between bluegill sunfish from predator-experienced and predator-naïve populations when raised in a common environment, suggesting that differences were mainly influenced by environmental differences; as such, I expected to find that traits in the minnow population of a lake that recently became piscivore-free would be similar to those in a population from a lake lacking pike.

Research Methods

Study Systems

Several lakes in north-central Alberta were surveyed early in the 2005 field season to locate minnow populations sympatric with and allopatric to piscivorous fish. Three suitable lakes were found, located within 50 km of each other: Armstrong Lake, Duck Lake and Sara Lake (Table 2-1). Following the selection of these lakes, more thorough fish population surveys were conducted in these lakes in May 2005 and 2006 using a combination of overnight sets of unbaited Gee minnow traps and multi-mesh gill nets (45m net, 6.25-75mm square mesh sizes).

Armstrong Lake supported populations of both pike and fathead minnow as recently as 2003 (Robinson and Tonn 1989, Jones and Paszkowski 1997, Paszkowski *et al.* 2004, K. Norris, University of Alberta, personal communication); however, no pike were found in Armstrong Lake in 2004 (C. Davis, Alberta Sustainable Resource Development, personal communication), or during my surveys in 2005-2006 when the fish assemblage consisted only of fathead minnow and brook stickleback (*Culaea inconstans*). The fish assemblage in Duck Lake included both pike and fathead minnow, as well as white sucker (*Catostomus commersoni*), yellow perch (*Perca flavescens*) and brook stickleback. Sara Lake contained only small-bodied fish species: fathead minnow, brook stickleback and finescale dace (*Phoxinus neogaeus*).

Since avian predators could not be controlled, a lake-perimeter survey was conducted on each lake in 2005 to account for the potential differences in this guild. All lakes had similar assemblages of piscivorous birds, including nesting Black Tern (*Chlidonias niger*), Common Loon (*Gavia immer*), and Red-necked Grebe (*Podiceps* *grisegena*); as well, American white pelican (*Pelecanus erythrorhynchos*) were irregular visitors on Duck and Armstrong lakes, while black-headed gull species (*Larus* spp.) sometimes visited Armstrong and Sara lakes.

To assess environmental conditions among lakes, a temperature data logger (HOBO, Onset Corp., Pocasset, MA, USA) was placed in each lake, 0.25 – 0.3 m below the water surface. Data loggers were set from May/June until the end of August, and temperature readings were taken every hour. Water samples were collected from just under the water surface for analysis of conductivity, total dissolved nitrogen, total phosphorous, and chlorophyll *a*. These samples were analyzed by the University of Alberta's Meanook Biological Research Station Water Quality Laboratory, using standard laboratory protocols (see Appendix a).

Life History Characteristics

Prior to the onset of reproductive activity in the 2005 field season, fathead minnows from the study lakes were sampled to examine life history characteristics, following previously developed protocols (Danylchuk 2003). Minnows were collected using unbaited Gee minnow traps, set at random locations around the shore of each lake and recovered approximately 24 hours later. A subsample of 150-350 minnows per lake was euthanized with clove oil and frozen for later analysis. Following this large collection, trapping continued bi-weekly throughout both the 2005 and 2006 spawning seasons; a subsample of approximately 20 fish per lake was euthanized from each trapping session and frozen for later analysis.

For all preserved samples, fish were thawed under cold tap water before processing. I measured total length (TL, to the nearest mm) and wet weight (to the nearest 0.001 g), determined gender based on secondary sexual characteristics, and determined level of maturity through examination of the gonads during dissection. Individuals were considered mature if the testes were white and enlarged or the ovaries contain yolked eggs. In mature female minnows, ovaries were removed and weighed (to the nearest 0.001 g) to calculate the gonadosomatic index (GSI; (gonad weight/total body weight)*100) as a measure of reproductive allocation. For approximately 30 randomly selected females from each lake, I measured the diameter (to the nearest 0.1 ocular micrometer unit, converted to the nearest 0.001 mm) of 10 of the largest eggs in the ovaries to represent egg size at spawning. Both lapilli otoliths were removed from sacrificed fish for aging (Danylchuk 2003).

After cleaning, each otolith was mounted whole on the end of a glass microscope slide in a thin layer of thermoplastic cement (Buehler #40-8100), warmed on a hot plate at ~50°C. After the slide cooled and the thermoplastic cement hardened, I sanded the otoliths until the primordium was visible. This was done using a succession of progressively finer sandpaper (600, 1200 and 1500 grit) and finally diamond paste (8000 mesh equivalent) with a felt polishing cloth. A thin layer of molten thermoplastic cement was then spread over the mounted otoliths to ensure the mount was secure.

The otoliths of 25 fish in each life history class (males, females, and juveniles) from each lake in both 2005 and 2006 were analyzed to obtain age and growth information for the populations. The mounted otoliths were photographed in transmitted light at 20x magnification with an LM CCD digital camera (Optronics MacroFire LM-

OCCD). The distance to each annuli and the otolith radius (OR) were measured along a straight path from the primordium to the edge of the otolith using on-screen caliper software calibrated to the scale of the photo (Screen Calipers 3.2, Iconico Inc., New York, NY, USA). I determined a TL-OR relationship using linear regression for each lake in each year and, using these relationships, I back-calculated the length-at-age using the Fraser-Lee method (Bagenal and Tesch 1978). By computing the mean back-calculated length at each age, I determined instantaneous growth rates [ln(TL at age x+1) – ln(TL at age x)] between consecutive ages for each sex from each lake population, with all individuals of age x from both years combined. The proportion of mature fish at each age was calculated for both sexes to identify the age- and back-calculated size-at-maturity for each population. The approximate life span of fathead minnows in each lake was determined by examining the age-frequency distributions of the samples.

Reproductive Activity

The spawning behavior of fathead minnows facilitates detailed monitoring of reproductive activity. Reproductively mature males establish nesting territories on the undersurface of vegetation, woody debris or rocks in water less than 1m (Nelson and Paetz 1992), on which ≥1 females spawn buoyant, adhesive eggs; fatheads will also readily utilize artificial spawning substrates (e.g., Grant and Tonn 2002).

I monitored reproductive activity of the fathead minnow populations in the three study lakes in 2005 and 2006 by placing artificial nesting substrate (nestboards) along the shore of each lake in the spring. Nestboards were made of fence boards (0.14 x 1.6m), covered in black tarpaulin for easier egg detection, floating on the water's surface; the boards were anchored in place with approximately 1m of tarred twine attached to a brick buried in the sediment. In each lake, 15 nestboards were set out in groups of three boards placed approximately 3 m apart at five randomly selected locations along the shore. Nestboards were checked twice weekly in 2005 and weekly in 2006; on each date, the number of nests per board was recorded. From these data, the time of peak spawning activity and the end of the spawning season were estimated. To adjust for any missing nestboards, the time of peak spawning activity was determined by the date on which the mean number of nests per board was highest for each lake; the end date of the spawning season was determined by the date of the last nestboard surveys for which eggs were present. When no nests were present on any board within a lake for a period of two weeks, I stopped surveying nestboards.

Statistical Analyses

Data were tested for normality using the Kolmogorov-Smirnov test and for homogeneity of variance using Levene's test (Zar 1999). If data met or could be transformed to meet the assumptions, parametric statistics such as the *t*-test or analysis of variance (ANOVA) were used (Zar 1999); differences in mean size-at-age, age-specific growth rates, GSI (arcsine-square root transformed), and egg diameters were analyzed using these tests. Differences in the length-at-age of individuals from Armstrong Lake during times of predator presence and absence were examined with a t-test. Because pike were known to have disappeared during the 2003-2004 winter, I compared back-calculated lengths at ages 1 and 2 of fish that co-occurred with pike, i.e., individuals that were 3 (2005 only), 4, and 5 years old at the time of the study (predator present), to the lengths at ages 1 and 2 from fish that were in those age-classes when pike were absent. Peak spawning time and end of the spawning season were both mean-adjusted for differences between years by subtracting the mean Julian date for each year from the observed values for the respective year; these data were also analyzed by ANOVA. When the assumptions of parametric statistics could not be met, non-parametric statistics were employed (Zar 1999). Catch-per-unit effort was calculated from 2006 biweekly trapping; mean number of fish caught per hour per trap was compared among lakes for each sampling period using Kruskal-Wallis tests with pairwise Mann-Whitney *U*-tests used to determine where differences occurred on each date. Differences in total lengths among lakes were evaluated in a similar fashion, using a Kruskal-Wallis test with pairwise Mann-Whitney *U*-tests. The length-frequency distributions of the three pairs of lakes were compared using two-sample Kolmogorov-Smirnov tests. To analyze trends in reproductive allocation, the GSI-frequency distributions of the three pairs of lakes were compared in the same manner; to account for any post-spawning or transitionally mature individuals, GSI values below 10% were removed from the analyses. Statistical analyses were carried out using SPSS 16.0 for Mac (SPSS Inc., Chicago, IL, USA). Significance levels for analyses were set at $\alpha = 0.05$, but were Bonferroni-adjusted to $\alpha' = 0.05/3 = 0.017$ for the analysis of pairwise Mann-Whitney *U*-tests of CPUE and total length.

Results

Population Characteristics

Catch-per-unit-effort (CPUE) of fathead minnows was significantly lower in Duck Lake than in Sara and Armstrong lakes during most of the summer (Kruskal-Wallis tests: $p \leq 0.01$; Mann-Whitney *U*-tests: $p < 0.01$; Figure 2-1); however, Sara's CPUE was the lowest (significantly lower than Armstrong; Mann-Whitney *U*-test: $p < 0.001$) during the first two weeks of June. Subsequently, Armstrong and Sara lake CPUEs displayed similar temporal patterns. In the initial collection from May 2005, total lengths and length-frequency distributions differed among the lakes (Kruskal-Wallis test: $\chi^2 = 79.78$, df = 2, $p < 0.001$; Kolmogorov-Smirnov $Z = 1.53$-1.84, $p = 0.002$-0.018; Figure 2-2). Fathead minnows were smallest in Sara Lake and largest in Armstrong Lakes (Mann-Whitney *U*-tests: $p < 0.001$); total lengths did not differ between Duck and Armstrong lakes.

Life History Characteristics

The maximum age of fathead minnows in all three populations was 5+ years, except for males from Sara Lake, which had a life span of 4+ years (Figure 2-3). Size-at-age differed between sexes (t-tests, $p<0.001$) for Armstrong Lake (ages 1-5), Duck Lake (ages 1-4), and Sara Lake (ages 2-4); thus, back-calculated size-at-age was examined separately for each sex. Mean back-calculated size-at-age differed in females among lakes at ages 1, 2 and 3 (one-way ANOVAs, $p<0.001$; Figure 2-3a). Females were larger in Armstrong Lake than in Duck and Sara lakes (Tukey's HSD, $p<0.005$). Back-calculated size-at-age of males also differed among lakes (ages 1-4; one-way ANOVAs, $p<0.001$; Figure 2-3b). Armstrong Lake males were largest while Sara Lake males were smallest at age 1; by age 4, males from Duck Lake were largest while Sara Lake males remained smallest. In Armstrong Lake, mean back-calculated sizes at ages 1 and 2 were larger for those individuals coexisting with pike at that age (52 mm and 56 mm, respectively) compared to individuals of the same ages (48 mm and 51 mm) following the elimination of pike from the lake (independent sample t-tests: $t_{132} = 8.12$, $p < 0.001$ (age 1); $t_{124} = 7.94$, $p < 0.001$ (age2)).

During their first year of life, fathead minnows from all lakes had much higher growth rates than at all subsequent ages. Age-specific growth rates differed among populations for both males (ages 0-5) and females (ages 0-4; one-way ANOVAs, $p<0.02$; Figure 2-4). In their first year, fathead minnows of both sexes from Armstrong Lake grew fastest while those from Sara Lake grew slowest (Tukey's HSD, $p<0.001$). By the second year, growth in Armstrong Lake fell below the rates from Duck and Sara lakes. After this point, both males and females from Duck Lake grew at least as fast or faster than minnows from Sara Lake.

Fathead minnows matured at an earlier age in Duck Lake than in Armstrong and Sara lakes, with ≥ 90% of individuals from Duck Lake being mature by age 2 (Figure 2-5). This level of maturity was reached only at age 4 for both sexes in Armstrong Lake and for males in Sara Lake; Sara Lake females reached this proportion at age 5. However, the age of maturity, when 50% of individuals were mature, was age 3 in both Armstrong and Sara lakes (Figure 2-5).

Gonadosomatic index (GSI) varied widely in females from each lake population, ranging from 10% to greater than 50%. Pairwise differences in the GSI-frequency distributions between Armstrong Lake and Sara Lakes were significant (Kolmogorov-Smirnov $Z=1.42$, $p=0.03$; Figure 2-6); however, no differences were found between Duck Lake and either Armstrong or Sara lakes (Kolmogorov-Smirnov $Z=1.14$-1.26, $p=0.08$-0.15). Although mean GSI values did not differ between lakes (one-way ANOVA:

$F_{2,288}$=1.72, p=0.182), the range and peak of values were smaller for Sara Lake (range: 13-36%, mode = 22-23%) than for Armstrong (range: 10-40%, mode = 28-33%) or Duck (range: 12-52%, mode = 26-27%) lakes (Figure 2-6). There was no difference in mean (±SE) egg sizes among the Armstrong (1.06 ± 0.01 mm), Duck (1.03 ± 0.03 mm), and Sara (1.03 ± 0.02 mm) lake females (one-way ANOVA: $F_{2,98}$=0.488, p=0.616).

Reproductive Activity

The initiation of the spawning season could not be accurately estimated, as nests were present in all lakes on the date of first check after deployment of the nestboards in late-May and early-June; thus, duration of the spawning season could not be calculated and the Julian date of the final nestboard check with eggs present was used to determine timing of spawning season. The peak spawning time was 2 weeks earlier in Duck Lake than in Sara Lake, although differences were not significant (one-way ANOVA: $F_{2,5}$ =2.578, p=0.223; Table 2-2). The end of the spawning season, however, was marginally different among lakes (one-way ANOVA: $F_{2,5}$=6.205, p=0.086; Table 2-2); spawning in Duck Lake ended approximately 2 weeks earlier than in Armstrong or Sara lakes.

Discussion

In lakes where the two species co-occur, fathead minnows are a primary prey of northern pike (Sammons *et al.* 1994), which select larger minnows (Duffy 1998). As a result of this size-selective predation, I expected to find that fathead minnows in Duck Lake, co-occurring with northern pike, would exhibit increased juvenile growth, mature at a younger age and smaller adult size, and have a shorter lifespan than minnows in Armstrong and Sara lakes (see Introduction). To achieve the increased juvenile growth rate, I also expected to find spawning activity earlier in the season to provide greater growth potential for young-of-year in Duck Lake than in either of the other two lakes (Divino and Tonn 2007).

The results of this study were consistent with several of the predictions. Both males and females from Duck Lake matured at an earlier age; my data were also consistent with the predicted earlier timing of spawning in Duck Lake, with an earlier (albeit non-significant) peak and earlier end to the spawning season than in Armstrong or Sara lakes. One- and two-year-old fathead minnows in Armstrong Lake grew faster when coexisting with pike that after the pike had been extirpated. However, fathead minnows from Duck Lake exhibited a slower or intermediate juvenile (ages 0-1) growth rate, although following this initial year they exhibited a faster growth rate than minnows from Armstrong and Sara lakes and grew to a larger adult size than minnows from the other populations.

The differences in growth rates among populations could be driven by food availability or life history tradeoffs (Ruttenberg *et al.* 2005). A probable effect of predation on the growth rate of prey results from the decreased density of prey in these environments, as indicated in this study by lower catch-per-unit-effort in Duck Lake. Because predation removes individuals from the population, per capita resource availability is increased (Abrams 2004); this decreased competition and increased food availability can lead to higher growth rates (Heibo and Magnhagen 2005) compared to growth rates in populations at higher densities in lakes lacking piscivorous fish. Indeed, Smith *et al.* (1978) documented increased fathead minnow size with increased food rations. Alternatively, growth rates could be influenced by life history tradeoffs between growth and reproduction; however, in Duck Lake, increased growth rates occurred following early maturity. The observed trend is contrary to the general association between early reproduction and high juvenile growth rate, although some exceptions have been noted and still explained by life history theory (Hutchings 1993). For example, life history theory predicts that populations with higher adult mortality will have an earlier age at maturity; under high risk of adult mortality, a population with slow juvenile growth may still exhibit early maturation (Hutchings 1993). This latter explanation could explain the slow juvenile growth and early maturation observed in Duck Lake, but does not explain the increased adult growth following maturation. This explanation also only seems plausible if a population typically exhibits slow juvenile growth under its most commonly experienced conditions, with predation pressure directly influencing the early timing of maturation rather than the juvenile or adult growth rates; thus, I would suggest that density-dependent resource availability is the driving factor of growth rates in this study for individuals in populations both coexisting with and without piscivorous fish.

Increased growth can be advantageous for individuals living sympatrically with predators. Even if fathead minnows cannot grow to escape the gape size of northern pike and all sizes of fathead minnow in Duck Lake are vulnerable to predation, increased body size can offer advantages, such as increased swimming speed (and therefore ability to escape predators) and increased nest guarding ability (Peterson *et al.* 2007). Increased size for females of course results in increased fecundity (e.g., Hutchings 1993, Heibo and Magnhagen 2005).

When the risk of mortality is high, individuals that accelerate maturity and are able to reproduce before they die will be favoured (Haugen and Vollestad 2000, Peterson *et al.* 2007). Larger and faster growing individuals, as were found in Duck Lake after age 1, have been reported to mature at an earlier age in several fish species (e.g., Reznick *et al.* 1990, Fox 1994, Heibo and Magnhagen 2005). Early maturation of fathead minnows in Duck Lake provided increased chances of reproductive success for individuals in that environment, thereby maximizing age-specific (Hutchings 1993, Belk 1998, Heibo and Magnhagen 2005) and lifetime fecundity (Williams 1966); in addition, parents that mature early may produce offspring that also mature at an early age (Scheuerell 2005), providing a positive feedback that increases reproductive success. Indeed, the early maturing females from Duck Lake did have higher maximum gonadal investment values than females from Armstrong and Sara lakes, although no difference was seen in the mean values.

The observed spawning season in Duck Lake appeared to peak approximately 2 weeks sooner and ended significantly earlier than the spawning seasons in Armstrong and Sara lakes. This is consistent with the predicted earlier spawning in the presence of predators, and could be a result of the larger sizes of the older age groups of Duck Lake minnows, which should be ready to spawn earlier in the season due to increased energy reserves after the winter (Danylchuk and Tonn 2003). Earlier spawning, in turn, can influence the age-at-maturity of young-of-year individuals hatched earlier in the season; Divino and Tonn (2007) found more early-hatched individuals showing signs of maturity in their second summer (i.e., at age 1) compared to late-hatched cohorts. Thus, spawning earlier in the season can contribute to an earlier age at maturity in offspring.

Armstrong Lake has had a northern pike population intermittently over the last 20 years, however, at the time of this study, no pike had been reported in the lake for 2 years. Both male and female minnows from Armstrong Lake had a high growth rate from age 0 to 1 and larger body sizes at age 1; their growth rate then slowed and body size was similar to either Duck or Sara lake individuals at the same ages. Half of the individuals from Armstrong Lake reached maturity at age 3, the same age as those from Sara Lake, and 1 year later than Duck Lake individuals. The timing of the spawning season was also similar between Armstrong and Sara lakes. Detailed information on the life history of the Armstrong Lake fathead minnow population during years of predation pressure would be necessary for a more definitive statement, however, the similarities in the Sara Lake and Armstrong Lake minnow populations suggested a shift in the life history of the predator-free Armstrong Lake population towards that seen in Sara Lake, which has had no history of pike presence in the past 40 years (D. Gullion, Alberta Sustainable Resource Development, personal communication). As further support for such a shift, I found that individuals that had co-existed with pike at ages 1 and 2 were smaller than similarly aged individuals that had never co-existed with pike, consistent with the size differences observed between young minnows in Duck Lake (with pike) and Sara Lake (without pike). Belk (1995) found that when populations of bluegill sunfish living with and without largemouth bass (*Micropterus salmoides*) were put in a common environment, life history differences between populations disappeared, indicating that differences observed in native habitats were not evolved adaptations but primarily a result of environmental differences, including those due to predation. Although a similar phenomenon cannot be confirmed for Armstrong Lake without further study, temporal changes associated with the presence and absence of pike, the similarities between the Armstrong and Sara lake populations following extirpation of the pike in Armstrong Lake, and differences between these lakes and Duck Lake suggest that these life history traits may be driven more by environmental influences and phenotypic plasticity than by genetic differences.

Because this was a natural comparative study, variables were not controlled; therefore, interpopulation differences, although largely consistent with effects of piscivory, cannot be attributed solely to differences in predation pressures. Confounding factors, such as abiotic factors, resource availability, and competition could also influence life history strategies (Johnson and Belk 1999). The temperature regime was similar in the three lakes of this study, but the chlorophyll-*a* concentration in Duck Lake was higher than in the other two lakes. This could suggest greater productivity and higher food availability, which can lead to increased growth and body sizes in minnows (Smith *et al.* 1978). The forage fish assemblage also differed among lakes, which could lead to additional pressures on the fathead minnow populations. Sara Lake contained finescale dace in addition to the ubiquitous brook stickleback. Potential competition from finescale dace in Sara Lake could reduce resource availability and limit growth of the fathead minnow population. Manipulations though common-garden, transplant or laboratory experiments should help untangle the potentially confounding variables.

Natural studies, such as this one, are able to provide information on how life history strategies respond to different environmental pressures, allowing for population persistence. In Alberta, as elsewhere, predatory pressure can fluctuate due to changes in the fish community composition of a lake, as colonization occurs through connections to other water bodies or winterkill selectively affects the more sensitive predator species (Tonn and Magnuson 1982, DeBates *et al.* 2003). Both of these factors can be affected by changes in climatic conditions or land use (e.g., Magnuson *et al.* 1997; Mooij *et al.* 2007). The introduction of non-native fish species can also result in new selective pressures (Latta *et al.* 2007). Although comparative studies can show us realized responses of populations to these increasingly frequent changes, additional manipulative studies are also needed to eliminate confounding factors and possible lake effects, and to investigate the genetic and phenotypic basis for life history differences among populations.

Table 2-1. Characteristics of study lakes, including location, water chemistry, and fish assemblage. Surface area data were determined using Google Earth Pro (Google Earth 4.2.0205.5730, Google Inc., Mountainview, CA, USA). Depth data are from D. Gullion (Alberta Sustainable Resource Development, personal communication). Conductivity, total dissolved nitrogen (TDN), total phosphorus (TP) and chlorophyll-*a* data are from 2006 analyses. Mean daily temperature was calculated from all daily temperature readings available (over both 2005 and 2006) for each lake. Fish species: BS = brook stickleback, FM = fathead minnow, FD = finescale dace, NP = northern pike, WS = white sucker, YP = yellow perch.

Lake	**Latitude (°N)**	**Longitude (°W)**	**Surface Area (ha)**	**Max. Depth (m)**	**Conductivity (µS/cm)**	**TDN (µg/L)**	**TP (µg/L)**	**Chlorophyll-*a* (µg/L)**	**Daily Temperature (°C; x̄ ± SE)**	**Fish Species Present During Study[a]**
Armstrong (historical presence)	54.23.19	113.38.54	215	4.5	400	1581.48	213.5	5.577	19.0 ±0.2 (n = 203 days)	BS, FM
Duck (pike present)	54.38.36	113.56.59	150	1.6	191	1314.2	120.9	7.772	18.4 ± 0.3 (n = 111 days)	BS, FM, NP, WS, YP
Sara (pike absent)	54.37.49	114.13.21	140	6.0	237	1007.13	57.8	4.397	20.6 ± 0.3 (n = 91 days)	BS, FM, FD

[a] Historically, Armstrong Lake contained white sucker from 1986 until the mid-late 1990s and yellow perch (without suckers) from ca. 1999 until 2003.

Table 2-2. Mean-adjusted timing of spawning activity (mean ± SE; range in parentheses) for fathead minnow populations from Armstrong Lake, Duck Lake and Sara Lake in 2005 and 2006. Mean-adjustment of values indicates how far dates from each lake deviate from the overall (among-lake) mean (see Research Methods: Statistical Analyses for details). Julian date at peak reproduction: $\bar{x}_{2005} = 169.0$, $\bar{x}_{2006} = 176.7$. Julian date at end of spawning season: $\bar{x}_{2005} = 214.7$, $\bar{x}_{2006} = 218.7$.

Lake	Mean-adjusted peak spawning time	Mean-adjusted end of spawning season
Armstrong Lake	-2.8 ± 5.2	4.3 ± 2.0
(historical presence)	(-8.0-2.3)	(2.3-6.3)
Duck Lake	-5.8 ± 1.2	-9.2 ± 4.5
(pike present)	(-7.0-(-4.7))	(-13.7-(-4.7))
Sara Lake	8.7 ± 6.3	4.8 ± 2.5
(pike absent)	(2.3-15.0)	(2.3-7.3)

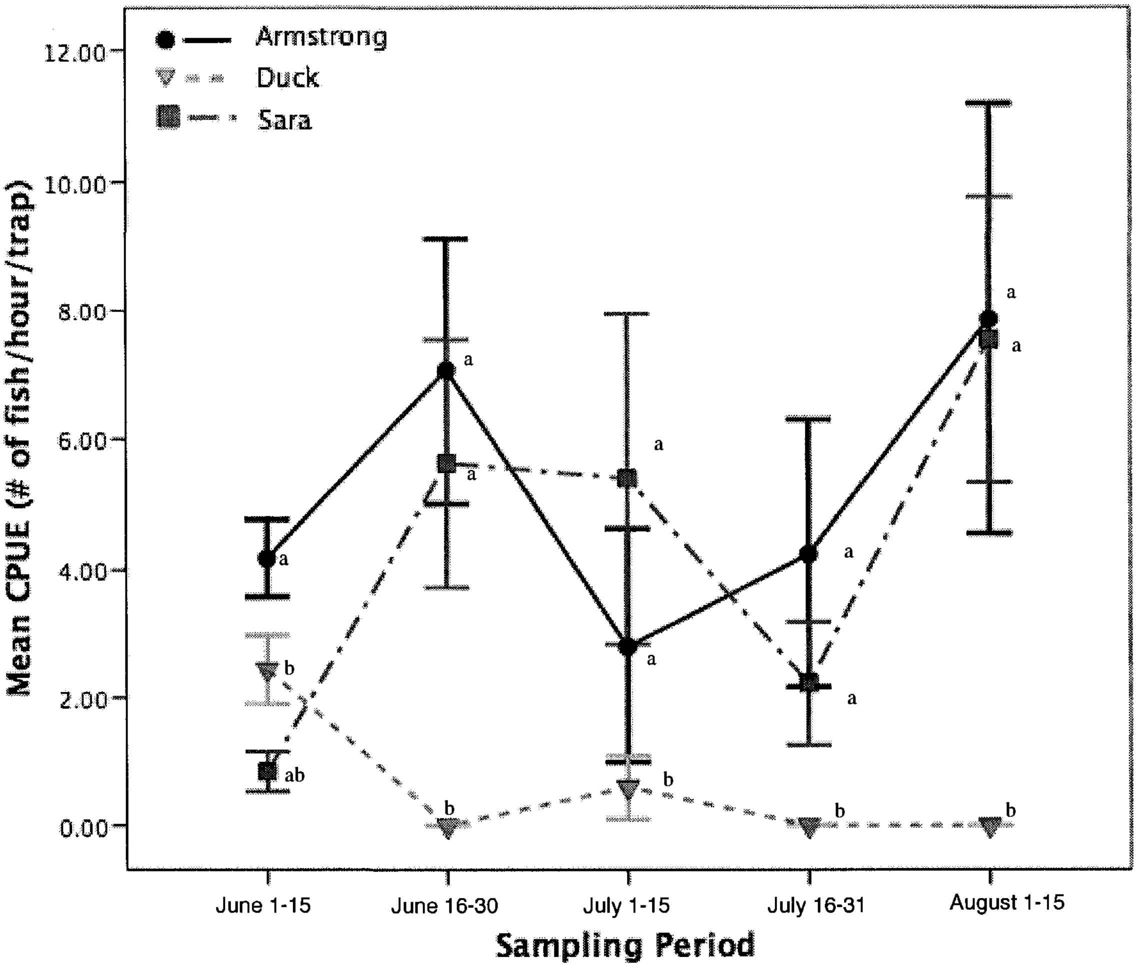

Figure 2-1. Mean (± SE) catch-per-unit-effort (CPUE) over time of fathead minnows in the Armstrong (historical presence of pike), Duck (pike present) and Sara (pike absent) lakes. Means were calculated from all minnow traps (n=3-34) set within two-week time periods throughout the summer of 2006. Letters indicate significant differences for each sampling period between lakes (Mann-Whitney *U*-tests, *p*<0.04).

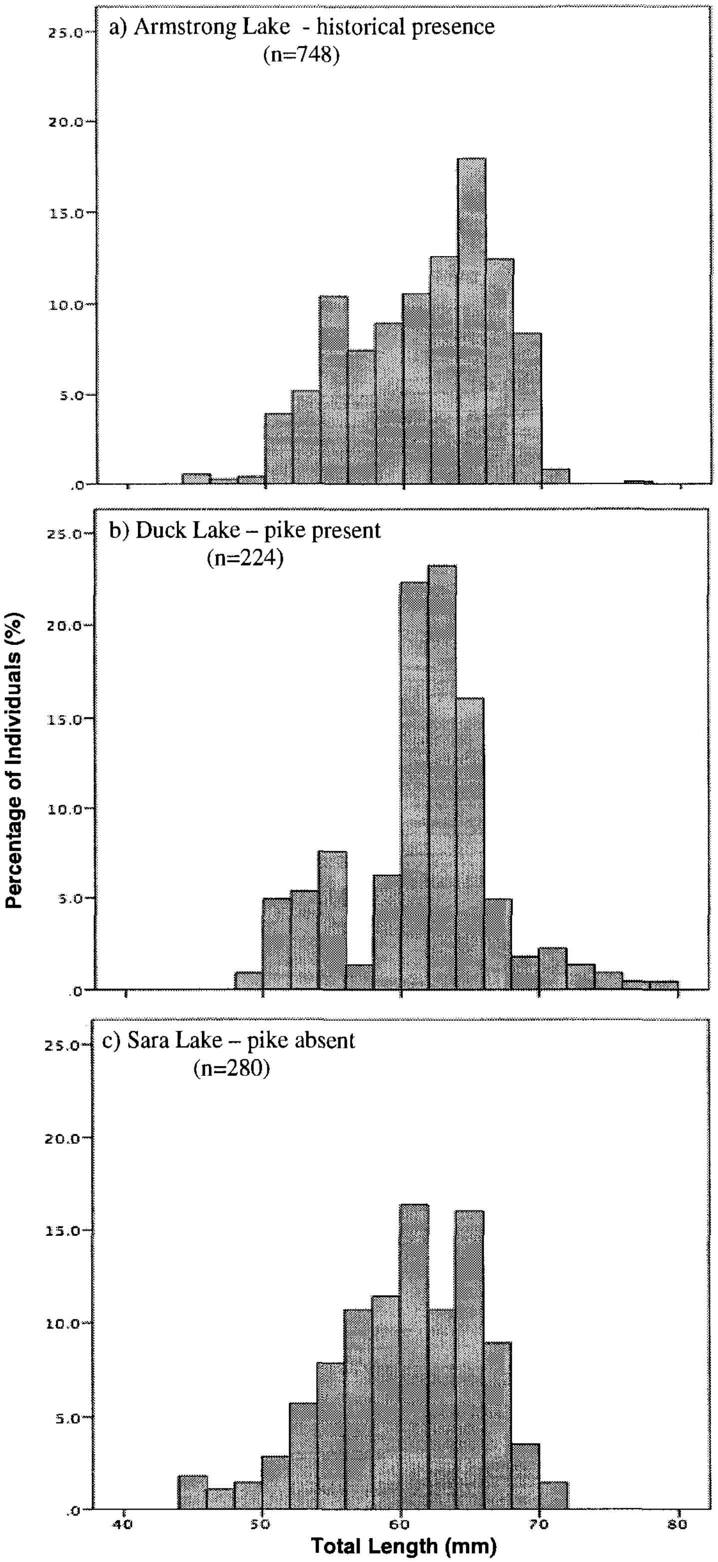

Figure 2-2. Length-frequency distributions for fathead minnows in (a) Armstrong, (b) Duck, and (c) Sara lakes. Lengths taken from the initial (May 2005) sampling period.

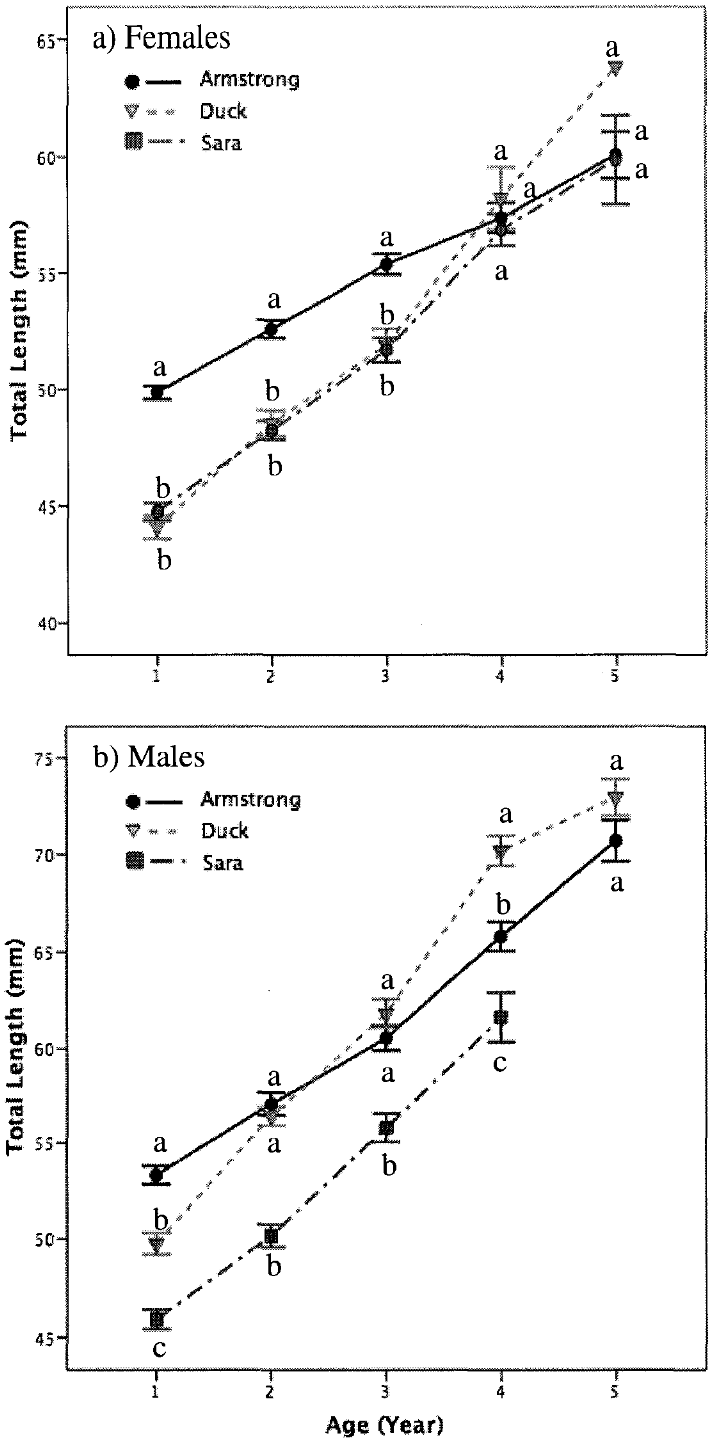

Figure 2-3. Back-calculated total length-at-age (x̄ ± SE) for (a) female and (b) male fathead minnows in Armstrong (historical presence of pike), Duck (pike present), and Sara (pike absent) lakes, calculated from all individuals of age *x* in 2005 and 2006 combined (n = 1-50; sample sizes are higher at ages 1-3 (n ≈ 30-50) and decline at ages 4-5 (n ≈ 1 – 25)). Letters indicate significant differences for each age between lakes (Tukey's HSD, p<0.03).

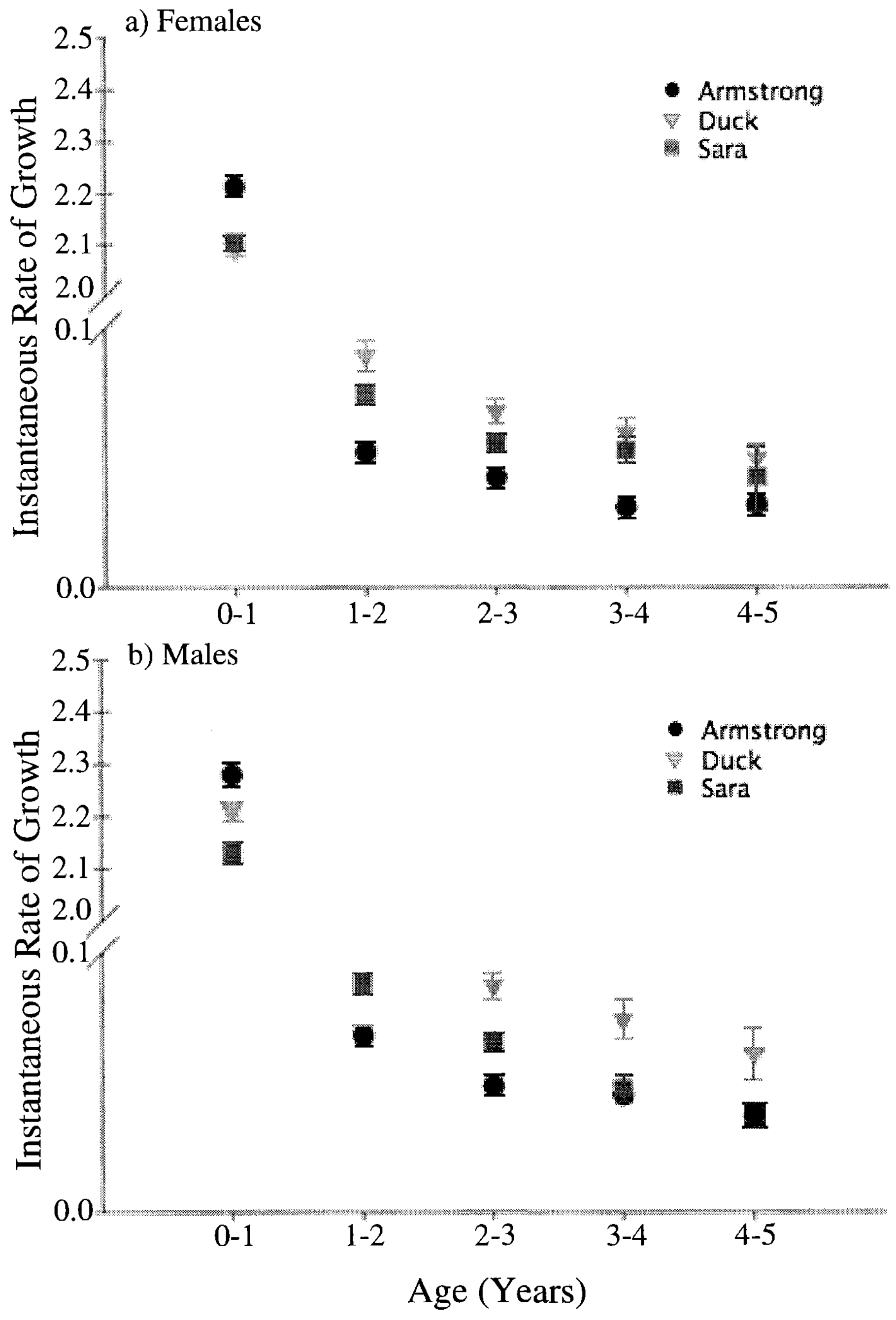

Figure 2-4. Age-specific rate of growth (x̄ ± SE) for (a) female and (b) male fathead minnows in Armstrong (historical presence of pike), Duck (pike present) and Sara (pike absent) lakes, calculated from all samples taken in 2005 and 2006 combined (n = 1-50; sample sizes are higher at ages 1-3 (n ≈ 30-50) and decline at ages 4-5 (n ≈ 1 – 25)).

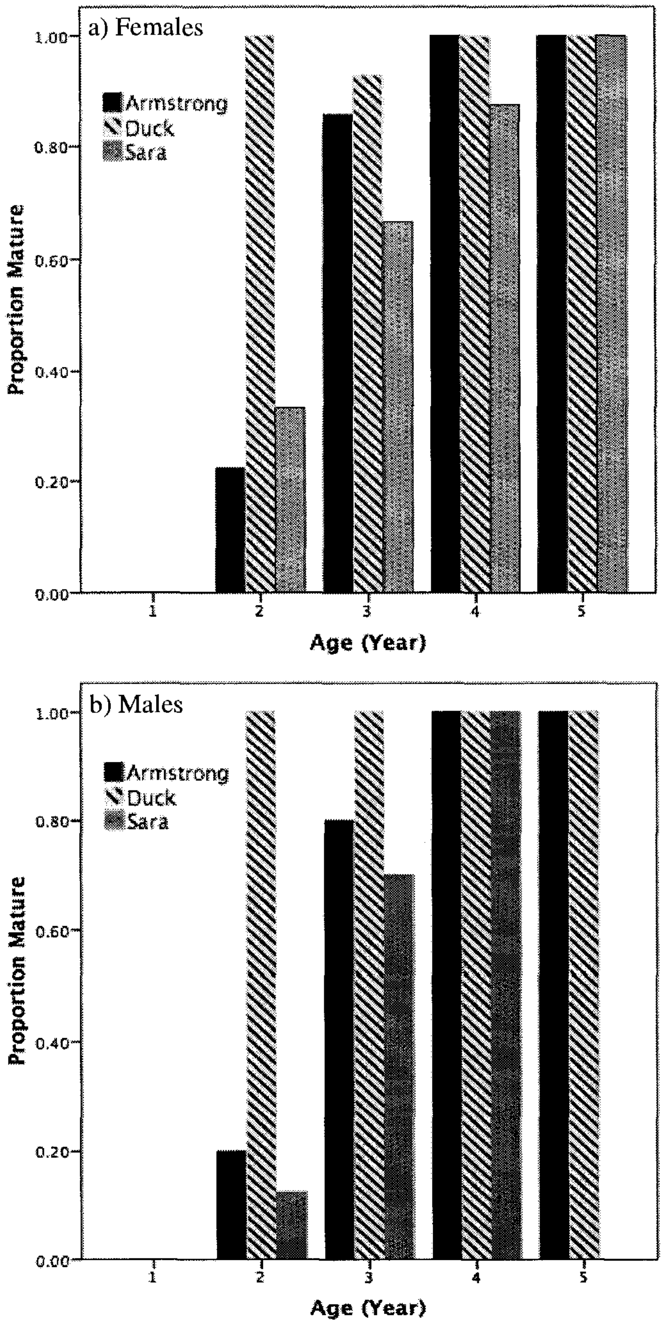

Figure 2-5. Proportion of individuals mature at age for (a) female and (b) male fathead minnows in Armstrong (historical presence of pike), Duck (pike present) and Sara (pike absent) lakes, calculated from samples taken over 2005 and 2006 (n = 1-25; sample sizes are higher at ages 3-4 (n ≈ 12-25) and lower at ages 1,2, and 5 (n ≈ 1 – 12)).

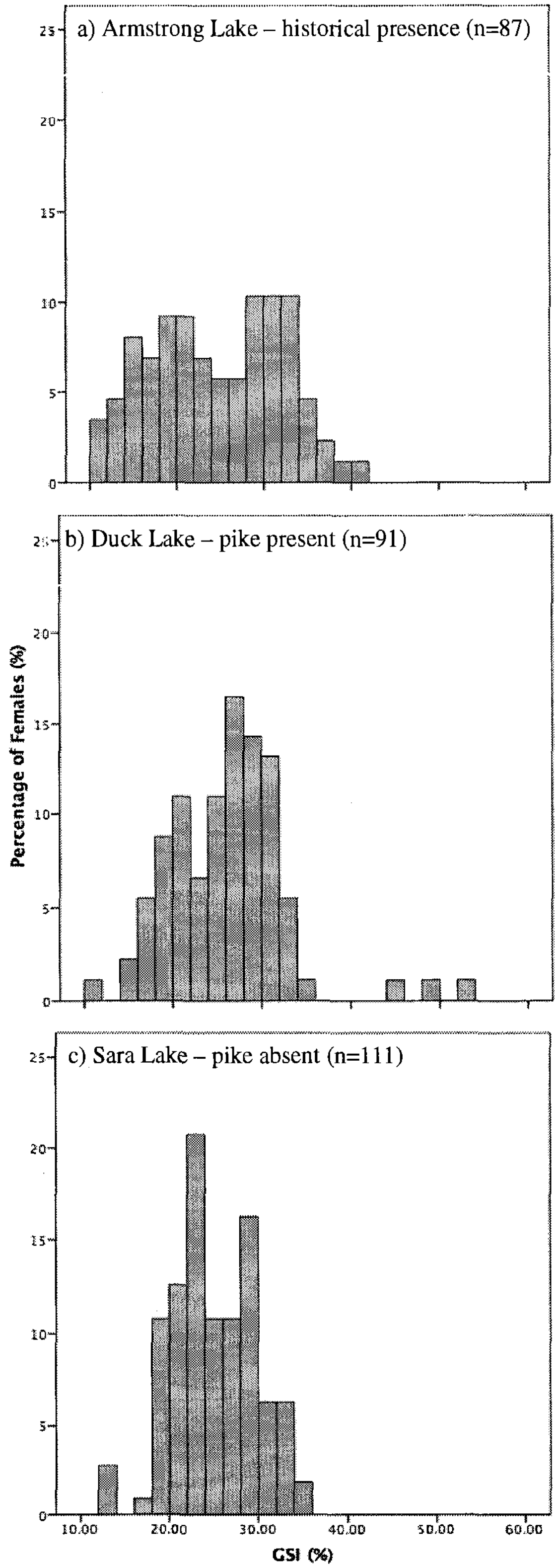

Figure 2-6. Gonadosomatic index-frequency distributions of females in (a) Armstrong Lake, (b) Duck Lake, and (c) Sara Lake in 2005 and 2006 combined.

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Appendix a. Meanook Biological Research Station Water Quality Laboratory water chemistry analyses protocols for chlorophyll *a*, conductivity, total dissolved nitrogen, and total phosphorous.

Chlorophyll a

Collect chlorophyll *a* samples in opaque (brown) 1 to 2L Nalgene bottles and filter within 4 hours. Filter 50-500ml of lake water, depending on cell density, through Gelman A/E filters. Analyze samples within 2 weeks of collection by ethanol extraction procedure described by Bergmann and Peters (1980).

Conductivity

Place the probe in the well-shaken sample and move the probe up and down several times to remove air bubbles. Using a thermometer, record the temperature and then the conductance of the sample (dial reading). A correction factor is applied to adjust the temperature to 25°C and the conductivity is expressed as umhos/cm (Gardiner and Dackombe 1983).

Total Dissolved Nitrogen

Store samples at 5°C from the time of collection. Filter sample through a Gelman A/E filter and photocombust (within 48 hours) in a UV digester. Total dissolved nitrogen is analyzed using the Technicon AutoAnalyzer.

Total Phosphorous

Collect samples in 1-L acid washed Nalgene bottles. Within 4h of collection, prefilter sample (after Dillon and Rigler 1974) and transfer to culture tubes. Add one scoop (0.4g) potassium persulfate to the sample; digest and analyze the sample by Menzel and Corwin's (1965) method as modified by Prepas and Rigler (1982).

Chapter 3: UNTANGLING GENETIC AND ENVIRONMENTAL INFLUENCES OF PREDATION ON FATHEAD MINNOW REPRODUCTIVE CHARACTERISTICS.

Introduction

Life history theory seeks to explain the features of an individual's life cycle in relation to the selective environmental pressures on that individual and its population (Stearns 1992). If different populations of the same species encounter different selective pressures, different adaptations, including life history traits, could develop across generations and be visible by comparisons between populations (Stearns 1992). However, when an environment is spatially or temporally variable, individuals of the same species experiencing different conditions can also develop differences in life history traits as a result of non-genetic responses to the environment, a phenomenon known as phenotypic plasticity (Reznick *et al.* 1990, Wootton 1996). In fact, when there is high spatial and/or temporal variance, selection for more broadly adapted genotypes, i.e., selection for phenotypic plasticity, can occur, resulting in a broader range of tolerance in a given genotype (Lynch and Gabriel 1987).

Age- or size-specific mortality can be an important selective force leading to differences in life history patterns. Because predation is often size-dependent, it can cause differential mortality of juvenile or adult size classes (Endler 1986). For example, Reznick and Endler (1982) found that Trinidadian guppies (*Poecilia reticulata*) experiencing high adult mortality due to size-selective predation had smaller adult sizes and increased reproductive effort. In contrast, populations experiencing high juvenile mortality from size-limited predation were characterized by larger adult sizes and decreased batch-specific reproductive effort.

As a result of contrasting environmental conditions, small lakes in northern Alberta are typically dominated either by small-bodied forage fish species or large-bodied piscivorous fish species; fish assemblages comprising both forage fishes and piscivorous fishes are rare (Robinson and Tonn 1989). There are, however, some exceptions, in which mixed assemblages of piscivorous and forage fishes co-exist; these mixed assemblages could be the result of lake conditions, such as partial winterkills in lakes containing the piscivore assemblage (thus allowing prey species to coexist) or the opportunity for limited colonization of piscivore-free lakes by the more sensitive piscivores via intermittent inlet streams (Robinson and Tonn 1989). The presence of piscivores in these mixed assemblages likely results in different pressures on forage fish populations, compared to their more typical predator-free habitats. This, in turn, could lead to the development of different life history strategies in populations with and without piscivorous fish. When life history differences exist between populations, it is important to tease apart genetic-based adaptations from environmental influences to determine the responsiveness of individuals to changes in their environment.

This study was designed to determine if observed differences in life history patterns between populations of a small-bodied prey species existing with and without piscivorous fish are the result of selection or phenotypic plasticity. I employed a 'common-garden' design to minimize environmental variation. By stocking populations of fathead minnow (*Pimephales promelas*) from contrasting predatory regimes into comparable adjacent ponds, I was able to examine whether life history differences observed in lakes persist in a common environment. I showed in Chapter 2 that the fathead minnow population of a lake with an intermittent, but currently extirpated, piscivore population was similar in several traits to the population from a piscivore-free lake. In addition, in the lake with the intermittent piscivore population, back-calculated total lengths showed that fathead minnows that had co-existed with piscivorous fish early in their lives achieved larger size-at-age than individuals of the same population that had never co-existed with piscivores, with the change occurring over a period as short as 1 year. This apparent rapid response to the presence of predators suggests a strong environmental basis and thus phenotypic plasticity of these life history traits. Based on this, I predicted that differences in life history traits observed in the natural populations would not persist, or would not be as great, in the common environment. The use of small experimental ponds allowed for detailed observation of spawning and reproductive activity, including egg production, parental care, and hatching success.

Methods

Study Populations

Robinson and Tonn (1989) surveyed small Alberta lakes to describe their fish assemblages; they found that Duck Lake (54°38'N, 113°57'W) contained a mixed assemblage of both fathead minnow and northern pike. Nearby, Sara Lake (54°37'N, 114°13'W) was devoid of piscivorous fish and contained only forage fish species, including fathead minnow. I documented several differences in the life history traits between these two minnow populations (see Chapter 2), therefore I used fathead minnows from Duck Lake and Sara Lake in my experiment.

Study Site

This study was carried out using three experimental ponds at the University of Alberta's Meanook Biological Research Station (MBRS; 55°37'N, 113°35'W), located near Athabasca, Alberta, Canada. Each pond was divided in half (pond-half surface area ($\bar{x} \pm$ SE) =141.0 ± 8.1m^2) with a polyethylene tarpaulin to help control for between pond differences in the treatments. These dividers were fitted with four Nitex screens (mesh = 560μm; total area ≈ 1.5m^2) to equalize hydrostatic pressure between the pond halves. All natural spawning substrate, including coarse woody debris and aquatic vegetation, was removed from the ponds prior to stocking. Artificial spawning substrate (nestboards) was placed around the perimeter of each pond half. Each nestboard consisted of a fenceboard (0.14 x 1.6m), covered in black tarpaulin for easier egg detection; the boards were floated on the water's surface and were anchored approximately 0.5m off shore by tarred twine attached to a brick buried in the sediment. The shoreline of each pond half was lined with 11 evenly distributed nestboards. One half of each pond received either Sara Lake stock or Duck Lake stock, for a total of three replicates of each stock.

To assess similarity of abiotic conditions among ponds, one temperature data logger (HOBO, Onset Corp., Pocasset, MA, USA) was placed in each pond, approximately 0.5m below the water surface. Temperatures were recorded bihourly, from the beginning of June through late August/early September. Conductivity and pH were measured approximately 0.1m below the surface in late July (ECTestr Low & pHTestr 10, Oakton Instruments, Vernon Hills, IL, USA).

Experimental Procedure

I collected fathead minnows from Duck and Sara lakes in spring using unbaited Gee minnow traps. Minnows were transported from the lakes to MBRS, where they were segregated by sex, held in shaded outdoor holding tanks, and fed daily maintenance rations of standard commercial flaked food. Total length-frequency distributions for males and females were used to determine small, medium and large size classes (3-mm classes; Table 3-1) for each population. The fish from each lake were batch-marked according to size-class using subcutaneous injections of acrylic paint (Danylchuk and Tonn 2001).

On June 27, 2006, 48 (±1) fish were stocked in each pond half; fish were stocked in identical ratios of sexes and size-classes across ponds (Table 3-1). Minnows found dead within 1 week of stocking were replaced with fish of the same sex and size class from the same source population to account for stocking-induced mortalities; any mortality after this time was assumed to be natural and was not replaced.

I inspected nestboards daily throughout the spawning season; detailed censuses were taken of all nests present. For each nest, date of initiation, location on the nestboard, and the total number and developmental stage of eggs were recorded. Developmental stage was assigned based visual characteristics according to a 3-stage classification system (sensu Vandenbos *et al.* 2006). In the third and final stage, eggs had an observable golden tint and hatched within 24-48 hours. Eggs were therefore considered hatched if they disappeared from the nest within this time; eggs that disappeared prior to the third stage were considered depredated. Diseased eggs were identifiable by the presence of a white fungus (Vandenbos *et al.* 2006) and the number of infected eggs in each nest was recorded. Each egg was ultimately accounted for as preyed upon, diseased or hatched.

I used the nestboard data to investigate differences in timing of spawning, and size and development of nests. Incubation time of eggs and the time spent at each stage of development were determined for the first batch of eggs in each nest. On each day, I also recorded the presence or absence of a male defender; if one was present, I recorded his size class and aggression level. When I intruded upon their territories during my daily nestboard inspections, males that displayed agonistic behaviours (e.g., biting or charging; McMillan and Smith 1974) were characterized as aggressive, whereas males that either circled their territory or left and returned following the disturbance were labelled as passive defenders (Divino 2005). Ultimately, the nest defense behaviour (i.e., undefended, passively defended, or aggressively defended) was classified as the highest defense behaviour observed at a given nest.

In September 2006, remaining adults were removed from the ponds using intensive minnow trapping. Once minnow trapping no longer yielded minnows, the pond halves were drained to a depth of 0.25-0.5m and width of approximately 3m. Any remaining adult minnows and all young-of-year (YOY) were removed by repeated seining (seine: 4 x 1.2 m, 2 mm mesh). The minnow population from each pond half was considered removed when three consecutive seine sweeps produced zero fish. All YOY minnows were counted, measured, and weighed.

Statistical Analyses

For analyses involving individual nests, I used unpaired, two-tailed *t*-tests to compare data between Duck Lake and Sara Lake halves of each pond; when the assumptions of parametric statistics could not be met, I used Mann-Whitney *U*-tests. To examine overall differences between Duck and Sara lake pond populations in individual nest duration, length of incubation, batch size, maximum nest size, nest days defended, and YOY size, I used Fisher's combined probability (*CP*) tests for each metric (Gotelli and Ellison 2004); for each trait, this test combines the results of the separate per-pond *t*-tests or *U*-tests by summing the natural logarithms of the probabilities from the per-pond tests and comparing the sum to a χ^2 distribution. I also used CP tests to look for differences between populations in both egg survival to hatch and YOY survival to fall; in these cases, χ^2 tests were used to determine the per-pond probabilities for both egg and YOY survival. I used a paired, two-tailed *t*-test to compare the duration of spawning season between Duck and Sara lake populations, and a Wilcoxon sign-rank test to examine differences between populations in the percentage of nests that failed. Prior to analysis, data for the duration of the spawning season and batch size were square-root transformed, and percentage of nest days defended and percentage of nests failed were arcsine square-root transformed to better meet the assumptions of parametric statistics. I analyzed the number of nests per pond (square-root transformed), the number of eggs laid per pond half, and the estimated hatchlings per pond using a two-factor, model III analysis of variance (ANOVA) to test for differences between treatments (with lake as the fixed factor); pond was set as the random factor in this analysis. Relative frequencies of paternal defense behaviour of the Duck and Sara lake populations were compared using a G-test. Statistical analyses were carried out using SPSS 16.0 for Mac (SPSS Inc., Chicago, IL, USA). Significance levels for all analyses were set at $\alpha = 0.05$; $0.10 > \alpha > 0.05$ was considered marginally significant.

Results

Reproductive activities among the Duck and Sara lake pond halves lasted from June 29 to July 29, 2006 (31 days) and from July 2 to August 17, 2006 (47 days), respectively (Figure 3-1). On a per-pond basis, the one-week difference in the duration of the reproductive season between Duck Lake (23 ± 3 days) and Sara Lake (30 ± 3) pond halves was not significant (paired *t*-test: $t_2 = -1.260$, $p = 0.335$; Table 3-3). Overall, 29 nests were produced in Duck Lake pond halves while 17 nests were produced in Sara Lake pond halves; the mean number of nests per pond did not differ (two-factor model III ANOVA: $F_{1,2} = 6.784$, $p = 0.121$; Table 3-3). The mean duration of individual nests was approximately twice as long in Sara Lake pond halves as compared to Duck Lake pond halves ($CP = 20.40$, df = 6, $p = 0.002$; Table 3-3). Although the number of days spent in any of the three individual stages of development did not differ, the total incubation time of eggs in the Duck Lake pond halves was significantly shorter than in Sara Lake pond halves ($CP = 19.29$, df = 6, $p = 0.004$; Figure 3-2).

Approximately 30,000 and 34,000 eggs were laid in the combined Duck and Sara lake pond halves, respectively (Figure 3-1); the number of eggs laid per pond half did not differ between treatments (two-factor model III ANOVA: $F_{1,2} = 0.327$, $p = 0.625$; Table 3-3). Although mean batch size, based on new eggs laid, was marginally larger for Duck versus Sara lake pond halves ($CP = 11.18$, df = 6, $p = 0.08$; Table 3-3), the maximum nest size was higher in the Sara Lake pond halves (*CP* = 17.82, df = 6, $p = 0.007$; Table 3-3).

The percentage of total nest days when male defenders were present was lower in Duck Lake (32.4% ± 4.3) than in Sara Lake (56.3% ± 6.7) pond halves (*CP* = 17.32, df = 6, $p = 0.008$; Table 3-3). The relative frequencies of paternal defense behaviour (undefended, passively defended or aggressively defended) also differed between the Duck and Sara lake pond halves (G-test: $G_2 = 9.31$; $p = 0.010$; Figure 3-3). The high proportion of undefended nests in the Duck Lake pond halves relative to Sara Lake pond halves was the proximate cause of this difference. Correspondingly, Duck Lake pond halves had 31.8% nest failure (i.e., 0% hatching success), while Sara Lake pond halves had no nest failures (Wilcoxon signed rank test: $Z = -1.60$, df = 2, $p = 0.109$; Table 3-3).

In turn, egg survival in Sara Lake pond halves (75.5 % ± 11.8) was two times higher than in Duck Lake pond halves (37.2 % ± 15.4; *CP* = 41.45, df = 6, $p < 0.001$; Figure 3-4). Overall, approximately 13,000 and 26,000 hatchlings were estimated across all of the Duck and Sara lake pond halves, respectively; however, the number of hatchlings per pond did not differ between treatments (two-factor model III ANOVA: $F_{1,2} = 1.47$, $p = 0.350$; Table 3-3). In contrast, survival from hatch to fall sampling was higher in Duck (46.5 % ± 22.7) vs. Sara lake pond halves (24.3 % ± 5.7; *CP* = 37.29, df = 6, $p < 0.001$; Figure 3-4). As a result, the number of young-of-year removed in the fall did not differ between Duck (1215.0 ± 316.5) and Sara (1781.3 ± 423.0) lake pond haves (paired *t*-test: $t_2 = -2.565$, $p = 0.124$). At the time of removal, the young-of-year minnows from the Duck Lake pond halves were larger than those from the Sara Lake pond halves (*CP* = 55.26, df = 6, $p<0.001$; Figure 3-5).

Discussion

When faced with changes in environmental conditions, populations can respond in various ways, including modifications to life history traits. Predation directly removes individuals from a population, often selectively. With minnows as prey, northern pike select larger individuals (Nursall 1973, Hart and Connellan 1984). As a result, because the chances of long-term survival are lower for organisms at risk of predation, life history theory predicts that minnows co-occurring with northern pike would allocate less energy to growth (and therefore future reproduction) and more to current reproduction (Hutchings 1993), relative to populations allopatric with pike. Increased reproductive effort would be seen through increased numbers of eggs per batch as well as per nest, and an increased number of nesting males (and therefore an increased number of nests).

In this study, several metrics of life history traits of the fathead minnows differed, depending on the origin of minnow populations, while others showed tendencies to differ ($p \approx 0.1$) despite low sample sizes (n = 3 pond halves per treatment). Fathead minnows in the pond halves stocked from Duck Lake exhibited an increased reproductive effort in regards to some of the reproductive traits; there was a trend to produce more nests (suggesting an increased number of nesting males), and batch size was increased. Although the maximum size of nests was smaller in Duck Lake pond halves and the number of eggs laid per pond half did not differ these could also be effects of decreased paternal care that was observed in Duck Lake pond halves (see below).

Jones and Paszkowski (1997a) found a higher number of fathead minnow nests in areas of lower pike density, likely as a result of the males' choice of breeding areas where the risk of predation is low. In the experimental ponds, the risk of predation was removed, thus, the predator-experienced individuals from Duck Lake may have perceived the risk of predation to be low and increased their nesting activity. While female fathead minnows demonstrate a preference for spawning in active nests already containing eggs (Sargent 1988), when exposed to predatory cues, some females will deposit eggs in close available nests, perhaps simply to reduce body weight and increase probability of escape from a predator (Jones and Paszkowski 1997b). Although no predatory cues were present in my experiment, it could be that predator-experienced females are "programmed" to dump their eggs when spawning opportunities are available to increase chances of a quick escape from potential predators in the near future. This would likely provide the opportunity for less-experienced males to recruit females to their nests. The pressures experienced by both the males and the females to invest in current reproduction over future reproduction could increase the number of nests found in predator-experienced populations of fathead minnows.

Based on the higher number of stage one eggs in nests, batch sizes were somewhat larger in the Duck Lake pond halves. This greater number of eggs laid by a female at one time could again be a demonstration of the Duck Lake females' increased investment in current reproduction. Studies of other species have also found an increase in batch size under predation pressure; for example, predator-naïve daphnids increased their initial batch size when exposed to fish kairomones (Latta *et al.* 2007).

Although there was a larger average batch size, nests in the Duck Lake pond halves were smaller in terms of the maximum number of eggs each nest contained. Other studies have found similar results for fathead minnows in the presence of pike (Jones and Paszkowski 1997a) or crayfish (*Orconectes* spp.; Sargent 1988), with fewer eggs per nest than in the control treatment. This discrepancy between the number of eggs laid per batch and the overall nest sizes could be a result of reduced paternal care in these nests; Divino (2005) found that defended nests were close to twice as large as undefended nests, while aggressively defended nests were greater than 50% larger than passively defended nests. When males are absent, their nests are more vulnerable to egg predators, including conspecifics (McMillan and Smith 1974), as supported by the trend for increased nest failure in the Duck Lake pond halves.

Egg survival in Duck Lake ponds halves was less than half of that in Sara Lake pond halves, and several nests in Duck Lake pond halves failed completely. It is thus no coincidence that I observed undefended nests significantly more often in Duck Lake pond halves than in Sara Lake pond halves, as nest failure and egg survival is strongly related to the intensity of paternal care (Unger and Sargent 1988, Divino 2005). When disturbed or threatened, individuals often favour shelter over 'risky' activities such as foraging or nest defending to minimize the threat of predation (Sargent 1988, Jones and Paszkowski 1997a); thus, the predator-experienced Duck Lake minnows appear "programmed" for reduced activity, including reduced paternal care, even in the predator-free 'common garden' of the experimental ponds. A second explanation for the decreased egg survival is Sargent's (1988) suggestion that the number of eggs in a nest must exceed a minimum size threshold in order for males to provide sufficient paternal care to increase hatching success; although Sargent (1988) was dealing with small nest sizes, the same relationship between paternal care and nest size may exist as nests get larger. Thus, males with smaller nests (as seen in the Duck Lake pond halves) may provide less care, resulting in decreased egg survival.

Nests in the Duck Lake pond halves had a lower overall nest duration, from the time of first eggs laid to the time of last eggs hatched. The eggs in these nests also had a faster development time to hatch. Interestingly, fathead minnow eggs also exhibited a decreased time to hatch when exposed to virile crayfish (*Orconectes virilis*) fed on minnow eggs (Kusch and Chivers 2004), while Jones and Paszkowski (1997a) similarly found older fathead minnow eggs in controls compared to predator treatments. That faster egg development was maintained by Duck Lake minnows even in the predator-free 'common garden' suggests that faster development time of eggs has been selected for in populations of predator-experienced fathead minnows, and may not always be driven by predatory cues in the environment. Males also reduce defense activity as eggs get older (Jones and Paszkowski 1997a); therefore, with faster development of eggs, males would be able to reduce time spent performing activities that make them vulnerable to predation in favour of time spent in refugia from piscivores. The reduced development time of eggs also reduces the possibility of nest failure by decreasing the amount of time the eggs are vulnerable to predation, cannibalism, and disease if a defending male is depredated.

Spawning in the Duck Lake pond halves began 3 days earlier than in Sara Lake pond halves and had a shorter duration, lasting ~30 days compared with ~50 days for Sara Lake across all pond halves. The earlier spawning could relate to the larger size of males in the Duck Lake pond halves; these larger males have higher energy reserves coming out of winter (Danylchuk and Fox 1994), and, therefore, have more resources available to allocate to spawning earlier in the season (Danylchuk and Tonn 2006). This earlier spawning time in populations exposed to a risk of predation could, in turn, increase seasonal growth potential and result in larger body sizes of young-of-year fathead minnows; Divino and Tonn (2007) found that fry hatched earlier in the spawning season were larger by fall and remained larger through the second year of their lives than fry hatched later in the season. The condensed spawning season could also be associated with the adult fathead minnows attempting to minimize their own vulnerability to predation. Reproductive activity and paternal care of nests expose minnows to predation risk, as demonstrated by the suppression of these activities in the presence of predators and predator cues (e.g., Sargent 1988, Jones and Paszkowski 1997b). By limiting these 'risky' activities through the curtailment of the spawning season, the adult fathead minnows should reduce their vulnerability to predation, while the larger batch sizes allow comparable overall reproductive success relative to fish from predator-naïve populations.

The larger size of the Duck Lake young-of-year minnows in the fall could again be a result of the earlier hatching time and longer growing season (Divino and Tonn 2007). The increase in growth could also be partly caused by the low hatching success and correspondingly low number of offspring in these pond halves. Vandenbos *et al.* (2006) found that young-of-year growth was greater in populations with lower densities of hatchlings. The lower density of young-of-year minnows reduces intra-cohort competition, making more energy available for growth (Smith *et al.* 1978).

A higher percentage of young-of-year minnows survived from hatch to fall in the Duck Lake pond halves compared to the Sara Lake pond halves. This increase in survival could also result from the lower density of the young-of-year minnows. Vandenbos *et al.* (2006) found that the proportion of fathead minnow young-of-year surviving from hatch to fall was inversely related to the number of minnows hatched. As well, increased food resources due to nutrient enrichment increased the number of young-of-year surviving from hatch to fall (Grant and Tonn 2002). Although Divino and Tonn (2007) found that fry hatched earlier in the season exhibited lower survival to fall, likely due to increased time of exposure to potential risk factors, the density-dependent food availability seems to have been a stronger mechanism driving young-of-year survival in my study.

Shifts in life history strategies due to predation pressure have been documented in many fish species (e.g., Reznick and Endler 1982; Tonn and Paszkowski 1986; Belk and Hales 1993). When populations experience consistent environmental pressures, such as predation, over the long term, life history traits that increase success in that environment should be selected (Stearns 1992). Alternatively, when populations experience variable environmental pressures, selection should favour adaptable phenotypes able to respond quickly to the current environment (Belk 1995), leading to a within-generation change in traits among cohorts (Endler 1986). The ability to respond to changes maximizes success within a variable environment.

In this study, I found that some differences observed in the lake populations of fathead minnows (Chapter 2) persisted when individuals were introduced to the common environment of the experimental ponds. Although in consistent with Belk's (1995) findings in a similarly designed study with a larger, longer-lived species, the persistence of differences in some life history, and corresponding demographic traits, could indicate that the differences in those traits between the Duck Lake and Sara Lake populations are a result of genetic adaptation to their respective environments. To more conclusively untangle the genetic and environmental influences on the life history strategies a longer term study is necessary, following responses made within a cohort over its lifespan. I found that fathead minnows from a population co-existing with predators were generally not able to adjust life history traits related to reproductive success over the short term. This suggests that when exposed to a change in predation pressure in their natural environment, there may be a lag in optimizing the life history of a population while minnows adjust to the new conditions.

Table 3-1. Fathead minnow size class definitions and stocking distribution of sexes and size classes.

	Duck Lake (piscivore-experienced)			**Sara Lake** (piscivore-naïve)		
	Size Classes (mm)			**Size Classes (mm)**		
	Small	*Medium*	*Large*	*Small*	*Medium*	*Large*
Males (M)	63-66	67-70	71-74	55-58	59-62	63-66
Females (F)	52-55	56-69	60-63	53-56	57-60	61-64

	Number of Fish Stocked							**Number of Fish Stocked**						
	Small		**Medium**		**Large**			**Small**		**Medium**		**Large**		
	M	*F*	*M*	*F*	*M*	*F*	*Total*	*M*	*F*	*M*	*F*	*M*	*F*	*Total*
Pond 3	11	6	19	3	4	6	49	11	7	16	3	4	6	47
Pond 5	12	6	17	2	3	7	47	12	6	17	2	3	7	47
Pond 6	12	6	17	3	4	6	48	12	6	17	3	4	6	48

Table 3-2. Abiotic conditions of experimental ponds at Meanook Biological Research Station during the summer, 2006. Temperature values are mean (± SE) daily temperatures during spawning activity in each pond ($n_{\text{pond 3}} = 81$ days; $n_{\text{pond 4}} = 93$ days; $n_{\text{pond 5}} = 105$ days); pH and conductivity values reported are the mean (± SE) of three measurements taken in each pond half (n = 6 per pond).

	Pond 3	**Pond 5**	**Pond 6**
Mean Temperature (°C)	21.4 ± 0.3	19.1 ± 0.3	19.7 ± 0.3
Mean pH	8.3 ± 0.3	9.3 ± 0.0	8.9 ± 0.2
Mean Conductivity (μS/cm)	350.0 ± 28.9	231.7 ± 1.7	266.7 ± 12.0

Table 3-3. Reproductive characteristics of Duck Lake and Sara Lake fathead minnow populations stocked in experimental ponds at Meanook Biological Research Station. All values reported are $\bar{x}$ ± SE (n). Nest failure is the percent of nests with 0% hatching success. ** $p < 0.01$ for differences between treatments.

	Duck Lake (piscivore-experienced)	**Sara Lake (piscivore-naïve)**
Nesting season duration (d)	23.0 ± 3.2 (3)	30.3 ± 3.5 (3)
Number of nests	9.7 ± 2.0 (3)	5.7 ± 1.2 (3)
Nest duration (d)**	7.8 ± 0.7 (20)	13.9 ± 1.3 (17)
Total number of eggs	9995.3 ± 1945.1 (3)	11233.3 ± 3458.1 (3)
Batch size (number of eggs)	428.4 ± 34.6 (70)	362.4 ± 32.8 (93)
Maximum nest size (number of eggs)**	926.9 ± 94.6 (29)	1299.2 ± 181.2 (17)
Nest days defended (%)**	32.4 ± 4.3 (29)	56.3 ± 6.9 (17)
Incubation (d)**	3.8 ± 0.2 (29)	4.9 ± 0.2 (17)
Nest failure (%)	31.8 ± 12.0 (3)	0 (3)
Estimated number of hatchlings produced	4267.7 ± 2520.3 (3)	8698.3 ± 3081.2 (3)

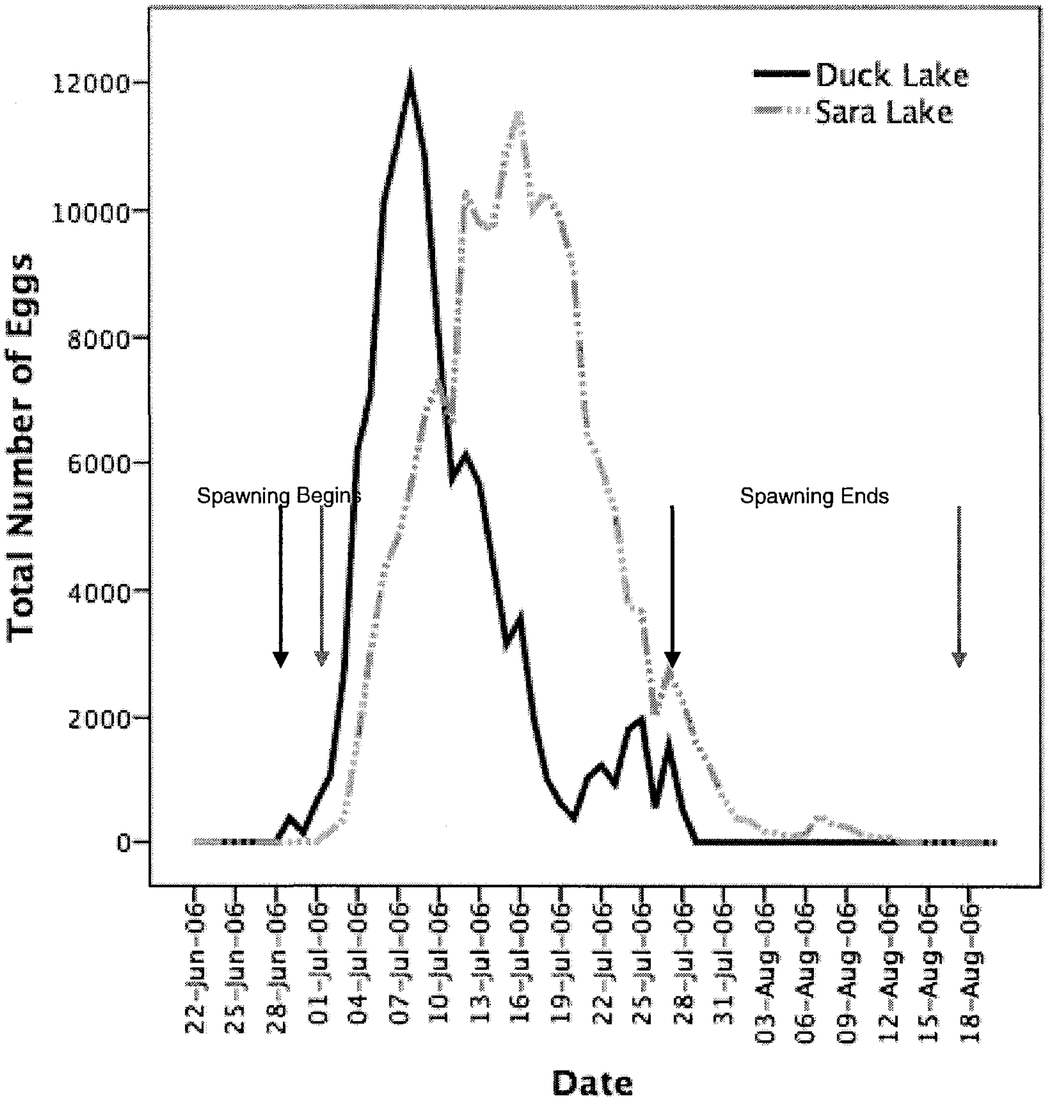

Figure 3-1. Total number of eggs over the spawning season in all Duck (piscivore-experienced) and Sara (piscivore-naïve) lake pond halves combined. Start and end of spawning season are indicated for each population, as the dates of the first and last days for which eggs were present on nestboards.

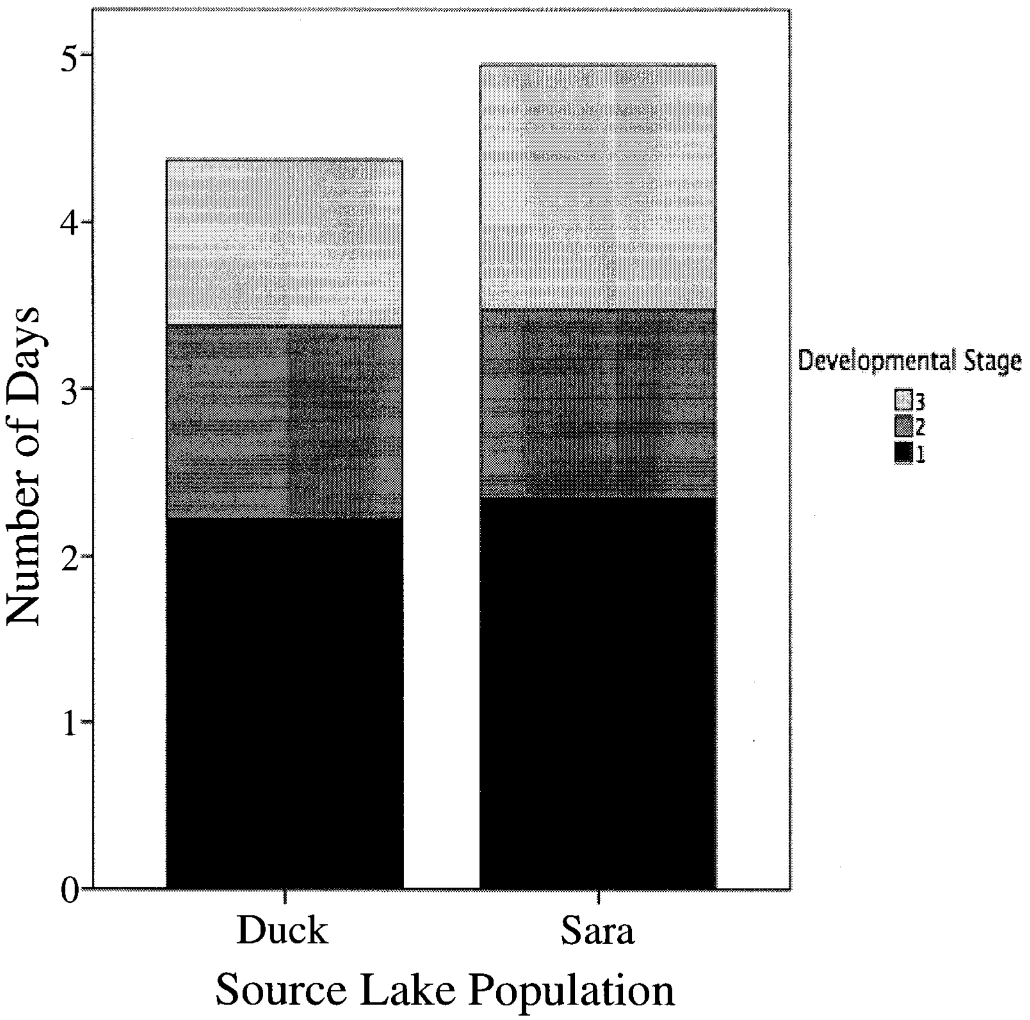

Figure 3-2. Mean development time (days) of eggs in the first batch of each nest from Duck Lake (piscivore-experienced; n=3) and Sara Lake (piscivore-naïve; n=3) pond halves. Total incubation time is divided into the mean number of days spent in each developmental stage.

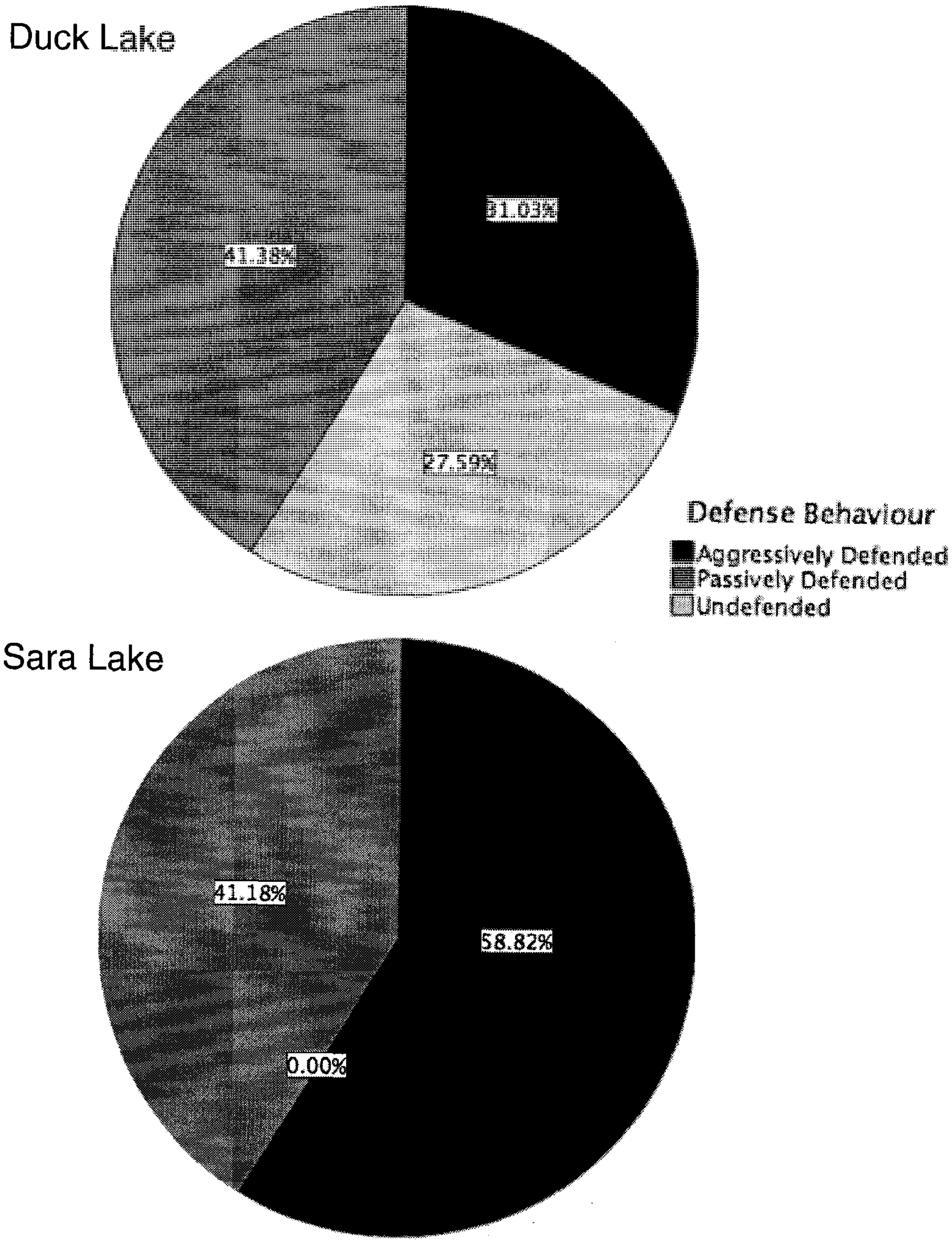

Figure 3-3. Distribution of male defense behaviours in the Duck Lake (piscivore-experienced; n=29) and Sara Lake (piscivore-naïve; n=17) pond halves. This distribution is based on the highest observed defense behaviour at each nest.

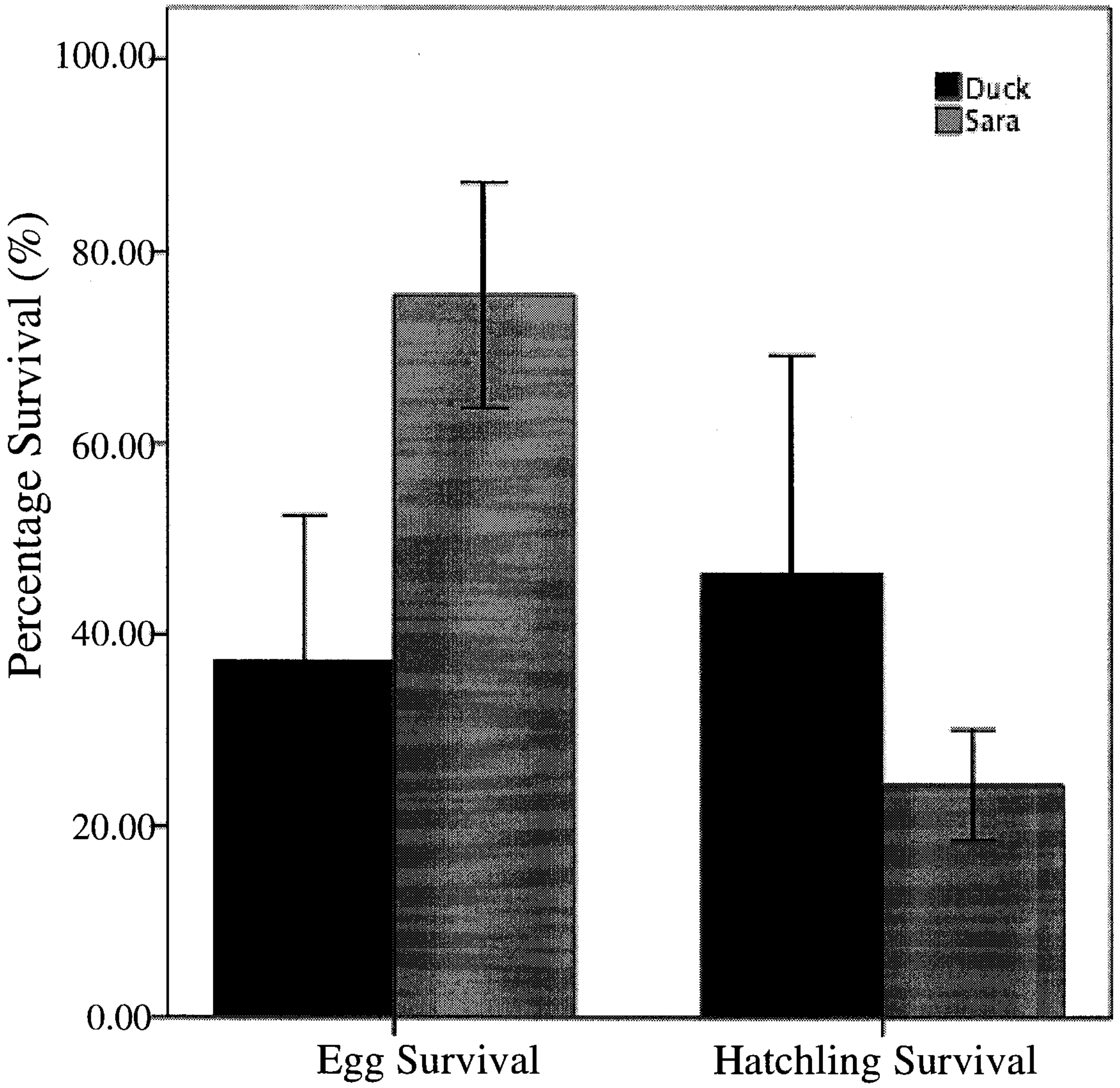

Figure 3-4. Mean egg survival from spawning to hatch and hatchling survival from hatch to fall in Duck Lake (piscivore-experienced; n=3) and Sara Lake (piscivore-naive; n=3) populations raised in separate halves of common ponds. Error bars indicate standard error.

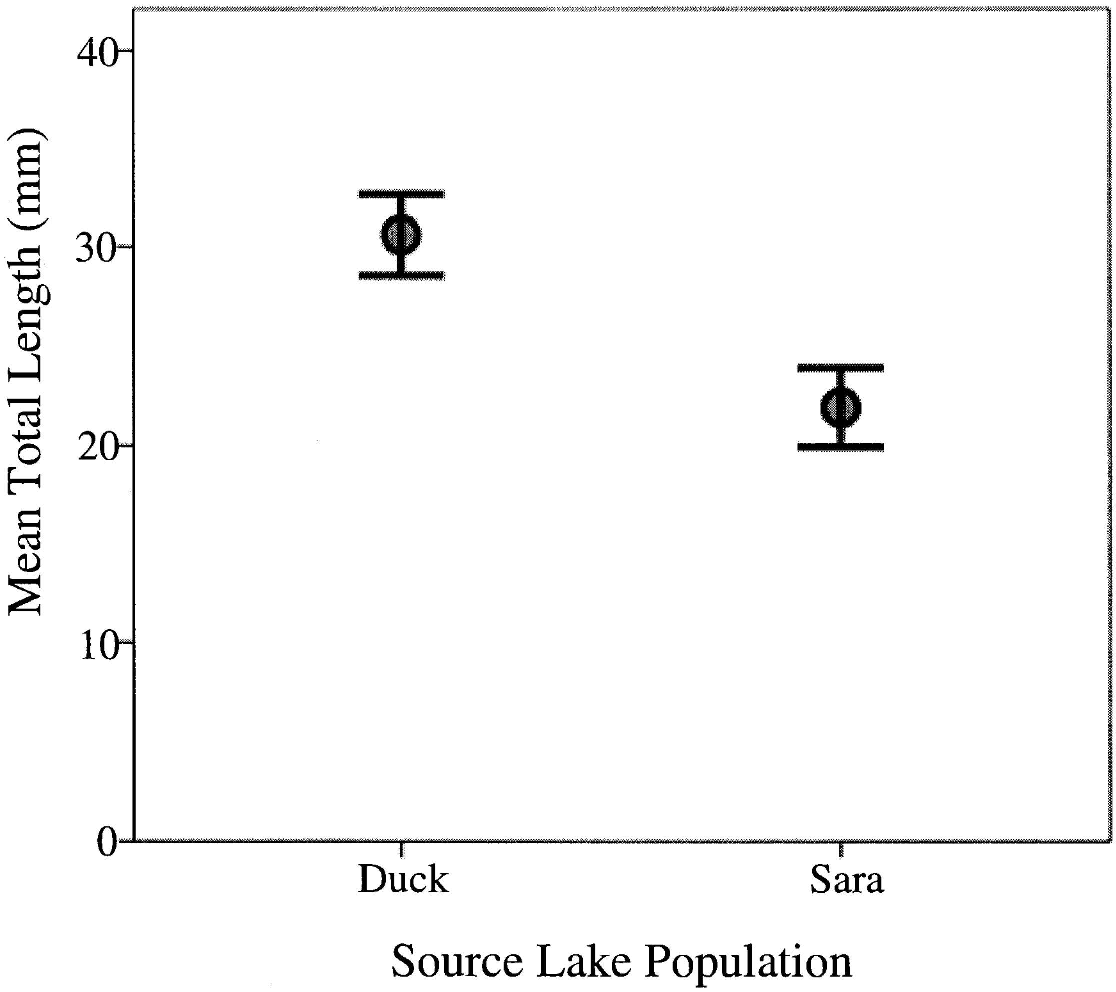

Figure 3-5. Mean (± SE) total length of young-of-year fathead minnows in the fall sampling from Duck (piscivore-experienced; n=3) and Sara (piscivore-naïve; n=3) lakes raised in separate halves of common ponds.

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Chapter 4: GENERAL DISCUSSION

Both biotic and abiotic conditions influence the occurrence of fish species in a lake. The species present in a given lake are limited to those that can access the lake, which can be constrained by factors such as habitat connectivity and dispersal ability (e.g., Tonn and Magnuson 1982, Eadie and Keast 1984). These species are further filtered by abiotic conditions (Tonn and Magnuson 1982, Rahel 1984, Tonn 1990) and biotic interactions, including competition and predation (Rahel 1984, Tonn and Paszkowski 1986, Robinson and Tonn 1989). The combination of these factors drives fish assemblages found in small, boreal lakes in Alberta, with assemblages generally consisting of either small-bodied forage fish species or large-bodied species, including piscivores (Robinson and Tonn 1989). Occasionally, colonization by less tolerant species, including large-bodied piscivores, of abiotically harsher lakes that are normally restricted to tolerant small-bodied fish, can occur through connectivity to other water bodies (Tonn and Magnuson 1982), resulting in mixed assemblages of small- and large-bodied species.

My study suggests that the presence of northern pike (*Esox lucius*) in mixed assemblages alters the life history of the fathead minnow (*Pimephales promelas*). A minnow population co-existing with pike exhibited earlier spawning, slower juvenile growth with faster adult growth and larger adult sizes, earlier maturity, and higher overall reproductive effort than minnows from a lake lacking piscivorous fish. Natural selection as a result of predation by northern pike is a likely explanation of the observed life history patterns, however, other possible factors cannot be ignored.

Because other variables were not controlled, such interpopulation differences in life history strategies cannot be attributed solely to differences in predation pressure. Confounding factors such as temperature and other abiotic factors, competition, and resource availability could also influence life history strategies (Johnson and Belk 1999).

Changes to life history strategies can occur via two non-exclusive processes. Phenotypic plasticity of traits operates within a single generation, adjusting traits within a range of tolerance to the environmental conditions experienced, while the genotype remains unchanged (Lynch and Gabriel 1987). When the same pressures are experienced over a longer time scale, the life history traits selected to increase fitness in that environment may become the norm (Stearns 1992). Gradually, these phenotypes and the genotypes that produce them will increase in frequency and change the gene pool of the population through this evolutionary response (Wootton 1990). Although differences in some life history traits between populations remained when fathead minnows from predator-experienced and predator-free populations were stocked into a common environment (Chapter 3), to further examine the phenotypic plasticity of those traits, the response of a cohort of fathead minnows should be monitored throughout its lifespan. The results of this study suggest that several traits seem to respond to the current environment in a relatively short amount of time (i.e., 1-2 years), however differences between populations did persist in a common environment over a period of 3 months. This indicates that there may be a lag in the optimization of fitness in individuals experiencing a removal of predation pressure while those individuals adjust to the changed conditions.

In habitats where predation pressure is variable as a result of changing environmental conditions, selection may favour the evolution of phenotypically plastic traits, allowing individuals to optimize fitness under a range of environmental conditions within their tolerance limits (Lynch and Gabriel 1987, Stearns 1992). Armstrong Lake has an intermittent population of northern pike; at the time of this study, no pike had been reported in the lake for the previous 2 years. By comparing the life history strategies of fathead minnows from Armstrong Lake (with a historically intermittent but currently absent population of northern pike) to those from Duck (with pike present) and Sara lakes (with only small-bodied fish), I was able to evaluate longer-term, although more-or-less still within-generation, changes. Many similarities were found between the life histories of the Armstrong Lake and Sara Lake individuals, potentially indicating a shift in strategies by the Armstrong Lake population towards strategy observed in predator-free Sara Lake (Chapter 2). To correlate the life history strategies with the predatory pressure, however, it is necessary to document the full range of conditions experienced by the population (Tonn and Paszkowski 1986); this would require detailed life history data from years of predator presence in Armstrong Lake. However, using the available data, a comparison of back-calculated total lengths at ages 1 and 2 during times with and without pike present in Armstrong Lake also indicated a shift in minnow length-at-age, with the same patterns observed in the presence and absence of pike in Armstrong Lake as seen in the comparison of fish from two separate lakes with and without pike.

The effects of predation on the fathead minnow can be used as a model for other fish species that experience similar predation. Additionally, since piscivory is often size-selective or size-limited, its effects on life history can be extrapolated to other pressures that would result in a similar selective removal of individuals from the population. Fishing pressure, for example, is almost always non-random. Both recreational and commercial fishing are often size-selective through personal preference or gear type, generally selecting for larger and, therefore, older or faster-growing individuals (Law 2000). In addition to size-selection, harvesting, like piscivory, reduces the stock densities, which in turn allows density-dependent factors to influence growth and other life history traits of a harvested population (e.g., Law 2000, Vandenbos *et al.* 2006). Many traits observed in both the lakes and the ponds in this study could be partly due to density-dependent processes.

An awareness of the roles of predation and other size-selective influences is important for the understanding of both natural and human disturbances. Determining how fish species respond to changes in the predator community will help us predict the impact of such occurrences resulting from changing environmental conditions (e.g., Magnuson *et al.* 1997), or species introductions (e.g., DeBates 2003) and removals. This knowledge will aid our understanding and should be considered by policy-makers and managers when considering management options, such as the stocking of piscivorous sport fish.

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