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Contents

Diet and divergence of introduced smallmouth bass, *Micropterus dolomieu*, populations

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Abstract

We examine the degree and causes of divergence in growth and reproduction in two populations of smallmouth bass (*Micropterus dolomieu*) introduced a century ago. Despite a common source, the Provoking Lake population now has a higher population density and slower growing individuals than the Opeongo Lake population. Using this system, we test the predictions of life history theory that delayed maturation and reduced reproductive investment are expected in high density populations with slow individual growth rates. Observations on both populations run directly counter to the aforementioned expectations. Instead, Provoking males have smaller sizes/younger ages at nesting and higher gonad masses than Opeongo males; Provoking females have smaller sizes at maturity, larger egg sizes, and higher ovarian dry masses than Opeongo females. Temperature, food availability, diet ontogeny, newborn mortality, and adult mortality were examined as plausible contributors to the divergence. Results suggest that low food availability, likely caused or mediated by intra-specific competition for prey, and lack of large-sized prey in the diet are contributing to the slow growth, increased reproductive investment, and higher mortality following reproduction in Provoking. This study provides insight into the processes that produce rapid divergence of life history in a species exhibiting parental care.

Keywords: growth; maturation; reproductive investment; phenotypic plasticity; diet ontogeny.

Introduction

Rapid divergence of life history traits can occur between recently colonized and subsequently isolated populations. Such divergence can be the result of phenotypic plasticity or may involve an evolutionary shift in response to selective forces in the new environment (e.g. Reznick et al. 1990; Haugen and Vøllestad 2000). Recent studies have observed evolutionary divergence in growth and maturation within a century in separated grayling (*Thymallus thymallus*) populations (Haugen and Vøllestad 2000; Koskinen et al. 2002) and in 25-30 generations in partially isolated chinook salmon (*Oncorhynchus tshawytscha*) populations (Unwin et al. 2000; Quinn et al. 2001). Studies of divergence provide a rare and important glimpse at the processes creating widespread life history variation among populations and the natural evolution of new populations.

In the present study, we characterize the degree and possible causes of divergence in the individual growth and reproductive traits of two populations of a paternally nest guarding fish, the smallmouth bass (*Micropterus dolomieu*). The two populations, from Provoking and Opeongo Lakes in Ontario, were introduced in the early 1900s from the same source (Christie 1957; Orendorff 1983; Kerr and Lasenby 2000), but since introduction have diverged in life history. In the 1980s, the Provoking population was reported to have a high density and slow-growing individuals relative to the Opeongo population; these slower growth rates were a likely consequence of high intra-specific competition for food (Orendorff 1983).

Life history theory predicts delayed maturation and reduced reproductive investment in populations such as Provoking, with slow individual growth and high population density (Gadgil and Bossert 1970; Pianka 1970; Ylikarjula et al. 1999; but see Abrams and Rowe 1996). We tested this simple prediction on the Opeongo and Provoking populations. In Opeongo, not all

mature males actually breed each year and the relationship is negatively density-dependent (Ridgway et al. 2002). Those that do breed when density is high are the larger individuals (Ridgway et al. 2002), probably because smaller males do not have enough energy reserves for the costly nest-guarding period (Mackereth et al. 1999). Given these observations, Provoking bass may delay maturation until they are older/larger in the high density environment and because smaller bass tend to have lower energy reserves (Mackereth et al. 1999), may have less energy available for gonadal investment.

In nature, the forces driving life history can be complex and discrepancies between simple theoretical expectations and observed life history patterns may arise when multiple, often confounding, variables are influencing life history traits (Reznick et al. 2002). Also, the theoretical predictions of models may vary depending on the functions and measures of fitness (i.e. intrinsic rate of population growth versus expected lifetime reproduction) used (i.e. see discussions in Mylius and Dieckmann 1995 and Abrams and Rowe 1996). Consequently, not all empirical observations have supported the prediction of delayed maturation and reduced reproductive investment in high density populations containing slow growing individuals; Fox (1994) found the opposite pattern: an association between early maturity, increased gonadal investment and high density in Ontario pumpkinseed (*Lepomis gibbosus*) populations. Mortality rates are a force capable of influencing life history and can themselves modify resource availability, population density and somatic growth (Abrams and Rowe 1996). High mortality, particularly at adult stages, can select for earlier maturation and higher reproductive investment (Hutchings 1993; Reznick et al. 1996; Lester et al. 2004). Differential mortality rates between the Provoking and Opeongo environments may have contributed to the divergence (e.g. Haugen and Vøllestad 2001) and may modify the expected life history patterns.

Other factors, most notably diet ontogeny, may have contributed to the divergence of the Provoking and Opeongo populations. A de-pauperate prey field can limit or prevent the ontogenetic diet shifts that a predator typically exhibits as it increases in body size and can result in slower individual growth rates (Pazzia et al. 2002; Sherwood et al. 2002); preliminary work suggests that the diet of Provoking bass is lacking in large-sized prey (Orendorff 1983). Water temperatures are also important in determining individual growth in bass and should be examined as a possible driver of divergence (Shuter and Ridgway 2002).

The purpose of this study is three-fold. First, we test the predictions of traditional life history theory that individuals from the higher-density Provoking population exhibit a slower lifetime growth pattern, depleted somatic energy, delayed maturation and reduced reproductive investment. Second, we examine evidence that the divergence in life history was driven by the density difference, through its impact on food availability. We do this by documenting diet of bass from both populations and by conducting a transplant experiment to assess the degree to which the observed diet and growth differences are plastic responses to the feeding environment. Third, we document inter-population differences in other factors that could have contributed to the observed life history divergence. Specifically, we document differences in: (i) ontogenetic diet shifts and the correspondence between those shifts and changes in the lifetime growth pattern; (ii) newborn and adult mortality; (iii) water temperature.

Although several studies have examined the correlates of between-population differences in growth and maturation (e.g. Hutchings 1993; Fox 1994; Reznick et al. 2001), studies of recently diverged populations are rare (but see Haugen and Vøllestad 2000 and Quinn et al. 2001) and can provide insight into the processes that create variation. Our study makes a significant contribution to this body of work because: (i) it characterizes rapid divergence in the wild of a fish species that exhibits parental care; the presence of parental care significantly affects the

tradeoffs between growth, reproduction, and survival (Mackereth et al. 1999; Ridgway et al. 2002) and studies of divergence in such species should provide instructive new tests of this body of theory; (ii) our characterization of divergence in reproductive traits is comprehensive; (iii) our evaluation of possible mechanisms driving divergence is also comprehensive and we demonstrate the importance of factors that have received little attention in previous work–particularly diet ontogeny.

Methods

The study lakes

Provoking Lake (45°30'N, 78°29'W) and Opeongo Lake (45°42'N, 78°22'W) are located 10 km apart and about 400 km northwest of Toronto, Ontario in Algonquin Provincial Park. Provoking Lake has an area of 1.1 km^2 and the only other fish, in addition to smallmouth bass, are splake (*Salvelinus namaycush* x *Salvelinus fontinalis*) and yellow perch (*Perca flavescens*). Opeongo Lake is larger (58.6 km^2) and has many fish species including yellow perch (*P. flavescens*), pumpkinseed (*L. gibbosus*), lake trout (*Salvelinus namaycush*), numerous species of cyprinids (family Cyprinidae) and many others (see Martin and Fry 1973 for a complete list). Both smallmouth bass populations were introduced between 1900 and 1920 (Christie 1957; Orendorff 1983), from an Ontario hatchery as part of the provincial railway stocking program (Kerr and Lasenby 2000). In 1981-1982, Orendorff (1983) estimated adult population densities using mark-recapture and Chapman's modified version of the Petersen method (Ricker 1975). The Provoking population had a higher density (3741 adults per km^2) and slower individual growth rates while the Opeongo population had a lower density (82 adults per km^2) and faster growth rates (Orendorff 1983). For the current study, we compared Provoking and Opeongo data

from two time periods: (i) 1975-1985; (ii) 1993-2003. A third smallmouth bass population, from Bridle Lake, was also examined in the 1980s as part of a transplant experiment. Bridle Lake ($45^{o}40'N$, $78^{o}09'W$) is located in Algonquin Provincial Park and contains a low-density smallmouth bass population (250 adults per km^2) made up of individuals that are faster-growing than the Opeongo population (Orendorff 1983).

Field sampling

The mean daily littoral temperatures were compared between lakes in order to evaluate the role of temperature in influencing the growth differences. Littoral zone temperatures (1-1.5 m depths) were monitored from spring through fall of 2001 in eight locations in Provoking and ten locations in Opeongo using Stowaway (Onset Corporation; Maine, USA) temperature loggers.

To characterize the differences between smallmouth bass in Provoking and Opeongo, population sampling was done in the fall of 2000, prior to the spawning period in spring 2001, and in the summer of 2002. Trap-nets (24 hour sets, 4-6 foot nets), minnow traps (24 hour sets), and angling were used to capture smallmouth bass. Body lengths were measured and scales taken for aging purposes from all fish. Samples caught from the various gear types were pooled because our estimates (i.e. growth, diet, maturation) were compared between populations relative to body size/mass and thus required representative samples from all age/size classes. The effects of gear selectivity and sampling effort will be minimal for the estimates we used. The 2000-2001 sampling data were used to characterize lifetime growth patterns, age/size at maturation, and reproductive investment, while the 2002 summer sampling data were used to assess diet and somatic/gonadal energy content. Summer sampling was chosen to measure diet and energy because, at this time of year, temperature differences between the two lakes were minimal and potentially confounding spawning and nest-guarding activities were completed. Sampling to

assess lifetime growth patterns and diet was also conducted on the Provoking and Bridle populations in 1981-1982 using angling, gill-nets, and trap-nets and on the Opeongo population in 1975-1985 using an annual creel survey (described in Shuter et al. 1987).

Smallmouth bass display paternal care in the form of an extended nest guarding period in the spring. To estimate mortality and the age/size at reproduction in nesting males, mark-recapture surveys were done on Opeongo Lake in 1993-2003 and Provoking Lake in 2000-2003. Both lakes were monitored frequently by snorkelers throughout the nesting season to locate smallmouth bass nests. Male nest-guarders were captured with fishing rods, had 3-6 scales removed for aging purposes, were given dorsal spine clips and tags (external t-tags in all years and passive integrated transponder tags since 1997) and were released back onto their nests within 1-5 minutes of first capture (see Ridgway et al. 1991 for detailed methods). Dorsal spine clips were permanent and their presence was easily visible to snorkelers who could thus identify those males that were sampled in a previous year. For Opeongo Lake, Jones Bay (the primary spawning area of the population - see Ridgway et al. 1991) was sampled and for Provoking Lake, the entire perimeter of the lake was sampled for nests. On Opeongo, from 1993-1997, all nesting males in all sections of Jones Bay were sampled and, from 1998-2003, all males in only the south section of Jones Bay were sampled. For Provoking, smallmouth bass nest in specific, concentrated areas and it is possible to sample most nesting males in these locations. Also, all males on both lakes that were identified as nesters from a previous year (i.e. those with clips) were captured and sampled again. Smallmouth bass show extremely high nest-site fidelity – 94% of experienced males return to within 200 m and 35% return to within 20 m (the modal distance category) of their original nest site (Ridgway et al. 2002). Therefore, by sampling the same areas on each lake across years and by capturing all previously clipped fish, it was possible to

determine how many males did not return to nest in a subsequent year. Similar nesting surveys were completed on Opeongo and Provoking in 1981-1982.

Growth and energy density

Individual growth rates

Back-calculations of lengths-at-ages (Francis 1990) were performed by a single researcher on smallmouth bass five years old and younger using the population scale samples that were collected in 2000-2001. Individuals older than 5 years were not used because of the potential bias in the back-calculated sizes of older fish (Casselman 1987). For bass caught in trap-nets, only those with fork lengths greater than 20 cm were used to ensure full recruitment to the gear (i.e. to exclude size-classes that are usually too small to be captured by the trap-nets). Back-calculated lengths-at-ages one through five plus actual lengths for all ages captured (except trap-netted fish < 20 cm) were used to construct mean size-at-age curves for each population. Individual growth rates were also measured for Provoking bass captured in 1981-1982 and Opeongo bass captured in 1975-1985; these were used to construct mean size-at-age curves following similar methodology to 2000-2001. The aging and back-calculation techniques were validated using tagged, recaptured Opeongo smallmouth bass sampled over a 10 year period and using multiple aging structures (scales, spines, opercula) of smallmouth bass from both Provoking and Opeongo Lakes.

Growth plasticity: Reciprocal transplant experiment

A reciprocal transplant experiment was carried out in Provoking and Bridle Lakes in 1981-1982 to test the hypothesis that the slow growth in Provoking is a plastic response to a high density/low food environment. We chose Bridle Lake because its smallmouth bass population consists of fast-growing individuals like Opeongo, and it has a small size (0.2 km^2). Opeongo

Lake was not used in the transplant experiment because of its large size; recapture rates of transplanted individuals in such a large lake would have been too low.

In the fall of 1981, 45 smallmouth bass (15-19.5 cm fork lengths) and 43 smallmouth bass (20-25 cm fork lengths) were captured in Provoking and released in Bridle while 45 smallmouth bass (> 25 cm body lengths) were captured in Bridle and released in Provoking. Transferred bass were predicted to enter the next size category by the following summer in Bridle but not in Provoking. Different size ranges were transferred for each lake because the size at maturation is larger in Bridle (25 cm) than in Provoking (20 cm). All transferred fish were given a one-half left pelvic clip and external plastic disc tags applied posterior to the dorsal fin using polypropylene line. The transferred bass were recaptured in the summer of 1982 using angling and gill-nets to measure diet using gastric lavage (Foster 1977) and then re-released. The transferred bass were again captured (using angling and gill-nets) for a final comparison one year after initial transfer, and scales were removed to measure growth. In total, 13 non-native smallmouth bass were recaptured in Bridle and 5 non-native smallmouth bass were recaptured in Provoking in the fall of 1982 (i.e. one year after initial transfer). At the same time, native smallmouth bass were also captured from each population. The mean scale increment was measured for the prior year of growth in both natives and non-natives in each lake. Two-tailed *t* tests were used to compare mean scale increments for native versus non-native transplanted bass of similar size. As scale growth is closely linked to body growth (Ricker 1992), we could determine if growth of the transplanted bass shifted in the predicted direction (i.e. slower in Provoking; faster in Bridle).

Somatic energy density

To more fully understand how resource limitation has influenced growth and reproductive investment, we measured somatic energy density. Individual bass collected and frozen in summer 2002 were removed from the freezer, thawed and the gonads removed. The whole body

of each bass, minus the gonads, was homogenized. A sub-sample (approx. 100 g) of the homogenized tissue was placed in a drying oven at 110 ^{o}C until it reached a constant mass. Dry mass was recorded, and the dry homogenized tissue was ground to a consistent powder and stored frozen in sealed bags. Energy density of the somatic tissue was determined using isoperibol bomb calorimetry. The relationship between energy density and body mass for individuals from each population was described using a polynomial function.

Reproduction

Age and size at maturation

Smallmouth bass captured during the fall 2000 population sampling were dissected to determine reproductive status on the day of capture; assessment of maturity was based on visual examination of gonads. Fitted logistic functions (of age or body size versus reproductive status) were used to determine the age and length at which 50% of the males and females were mature (the age/size at 50% maturity). The ages used for the logistic functions were the observed ages plus one year because the stage of development of the gonads in the fall indicated whether the fish was preparing to spawn the following spring. The lengths used were the observed lengths because little growth is expected during the winter months (Shuter and Post 1990). Generalized linear models using a likelihood ratio test (McCullagh and Nelder 1989) in STATISTICA (Statsoft; version 6.1) were used to assess between-lake differences in the age/size at 50% maturity. To account for possible type I errors with multiple tests, Bonferroni corrections (Quinn and Keough 2002) were performed for between-lake tests of either length or age at 50% maturity.

The age and body length distributions of breeding adults were characterized by using sampled nest-guarding males. Analysis of variance (ANOVA) was done in STATISTICA to compare distributions between populations for both time periods (1981-1982, 2000-2003).

Reproductive investment

We used gonad mass, ovary egg size, and fecundity as measures of reproductive investment (Roff 1992). Mature males and females sampled in spring 2001 were brought back to the laboratory and their body and gonad masses were measured on the same day as capture. To estimate egg size and fecundity, ovaries were preserved in a fixative (1 part glacial acetic acid, 1 part formalin, 1 part glycerol, 3 parts ethanol, 5 parts distilled water) and within 2 months, removed from the fixative and blotted dry. Excess tissue was removed and the ovaries were divided into four sections. Each section was weighed and one section was randomly chosen for further analysis. For each female, we measured the diameter of 50 randomly selected eggs and calculated the mean ovary egg diameter. To estimate fecundity, the following relationship was assumed

$$\frac{N_S}{N_T} = \frac{M_S}{M_T} \tag{1}$$

where N_S is the number of eggs in the sampled ovary section, N_T is the total fecundity, M_S is the mass of the sampled ovary section, and M_T is the total mass of the ovary. N_S was estimated by sub-sampling as follows: (i) eggs were placed in a single layer in a 1 cm^2 gridded dish; (ii) the mean number of eggs per grid was calculated by averaging the number of eggs counted in three grids; (iii) the mean number of eggs per grid was multiplied by the total number of grids to give N_S. Equation (1) was then rearranged to solve for fecundity (N_T). Variables (gonad mass, mean ovary egg diameter, fecundity) were natural log transformed (to linearize relationships) and regressed against body mass. To compare between-lake differences relative to body mass (i.e. to account for the confounding influence of body size), analysis of covariance (ANCOVA) was

done in S-Plus (Insightful Corp.; version 6.0) using body mass (g) as the covariate and either gonad mass (g), egg size (mm), or fecundity (number of eggs) as dependent variables. The ANCOVA assumption of statistically homogenous slopes was also tested in S-Plus for all variables (Quinn and Keough 2002).

We conducted one additional comparison of reproductive investment based on ovary dry matter content from female bass sampled in both lakes in summer 2002. Frozen fish were thawed and their ovaries were removed, weighed, homogenized and placed in a drying oven at 110 ^{o}C until they reached a constant mass. The proportion dry mass was estimated by dividing the dry mass by the wet mass of the ovary. There was no relationship between proportion dry mass of ovaries and body wet mass ($F_{1,23} = 4.2$; $P > 0.05$; $N = 25$) and proportion dry mass was compared between populations using Mann-Whitney (M-W) tests (Quinn and Keough 2002) performed in STATISTICA. We used M-W tests because the distribution of proportion dry mass was non-normal.

Diet

Diet was assessed for Provoking and Opeongo smallmouth bass captured and frozen in the summer of 2002. Each bass was thawed and we measured mass of stomach contents, length of each prey item, and percent occurrence of prey items in the stomach. For each population, the mean percent occurrence of prey items and the percent of empty stomachs were calculated. Stomach content mass and prey length were natural log transformed for normality and ANOVA was used to test for between-lake differences; ANCOVA with body mass as the covariate, was also performed to test for differences between lakes. M-W tests were performed to test for between-lake differences in the amount of each prey type in the diet (because of non-normality in prey type).

Diets were also measured in the Provoking and Opeongo populations in 1981 from processed fish and in the Provoking and Bridle populations in 1982 using pulsed gastric lavage of live fish (Foster 1977). The mean percent occurrence of prey items in the diet and the percent of empty stomachs were calculated and between-lake differences in the amount of each prey type were tested using M-W tests. Bonferroni corrections (Quinn and Keough 2002) were done for each time period to account for potential type I errors with multiple tests.

Mortality

Nesting males

Mortality for first-time nesting male smallmouth bass was estimated by dividing the number of males that did not return to spawn in a subsequent year by the total number of males clipped for that age. We pooled the 1991-1998 cohorts to obtain representative sample sizes, and for Opeongo, only used males captured within the south section of Jones Bay (because the south section was sampled every year). To test for between-lake differences in the number of first-time nesting males that returned with those that did not return, Chi-square tests were done in STATISTICA and Bonferroni corrections were done to account for type I errors. Two potential sources of bias in using return rate as a measure of mortality are straying of nesters and skipped spawning. While it is possible that some males strayed to nest in unsampled areas of the lake in subsequent years, the number is likely low given the high nest site fidelity of smallmouth bass (Ridgway et al. 2002). Since 'straying' is not a problem in the Provoking samples (the entire shoreline was sampled), its only impact would be on the Opeongo mortality estimates, where it would inflate them slightly. Similarly, although skipped spawning does occur in this species, the incidence appears low enough to not have a large influence on our estimate of return rate: only 11 males (out of a total of 359 tagged) were observed to skip spawning (i.e. skipped the year after they first spawned but returned to spawn in another year) since 1997 in Opeongo.

Newborns: Removal experiment

To estimate relative predation pressure on newborns, we conducted a removal experiment of nest-guarding males in 2003. We randomly chose ten nests in Jones Bay, Opeongo and eleven nests in Provoking for the experiment; all nests had new, fresh eggs. The number of eggs in each nest was counted and the nest-guarding male was permanently removed from the nest. The number of eggs was counted 1 and 24 hours following removal of the male. We used the proportion of eggs removed from the nest as a relative measure of predation rate over a fixed period of time. Between-lake differences were tested using ANOVA.

Results

Water temperatures

In 2001, littoral water temperatures were similar for Provoking and Opeongo Lakes in the summer with the mean difference between them being 0.44 °C. Provoking was slightly warmer in the spring (mean difference of 1.8 °C) and cooler in the fall (mean difference of -1.8 °C). The number of days with littoral temperatures above 10 ^{o}C was 152 for Provoking and 154 for Opeongo, above 15 ^{o}C was 122 for Provoking and 111 for Opeongo and above 20 ^{o}C was 66 for Provoking and 56 for Opeongo. Thus, the number of warm days was higher for Provoking than for Opeongo. Since the lakes are only 10 km apart, climatic differences are expected to be minimal.

Growth and energy density

Individual growth rates

The lifetime growth patterns of bass from Provoking and Opeongo were different in 2000-2001 (Fig. 1). Growth was similar for the first 3-4 years of life, after which the growth of

Provoking individuals was considerably less than Opeongo individuals. Opeongo bass also reached a greater maximum body length than Provoking bass. For both lakes, males and females showed similar lifetime growth patterns (mean female fork length divided by male fork length for each age ranged from 0.89-1.11 for Provoking and 0.94-1.08 for Opeongo). A similar pattern of slower growth in Provoking after age 3-4 was also found in 1975-1985 (Fig. 1).

Growth plasticity: Reciprocal transplant experiment

Provoking bass that were transplanted to Bridle grew at greater rates than their counterparts that remained in Provoking; Bridle bass transplanted to Provoking grew at slower rates than their counterparts that remained in Bridle. The mean scale increment for transplanted Provoking bass was significantly greater than the mean scale increment for resident Provoking bass and the mean scale increment for transplanted Bridle bass was significantly lower than the mean scale increment for resident Bridle bass (Table 1). Although sample sizes of recaptured fish were low, the differences in growth between transplanted and native fish were significant and in the predicted direction. Also, although the size range of bass used was different for the two lakes, the *t* tests compared bass of similar lengths.

The diet of transplanted Provoking bass resembled the diet of native Bridle bass. Transplanted Provoking bass (N = 24) contained more fish and crayfish and had less empty stomachs (14% versus 30% empty stomachs) than resident Provoking bass of the same size. Only five of the transplanted Bridle bass were captured in Provoking Lake for the diet study and all stomachs were empty.

Somatic energy density

Substantial differences were observed between the pattern of energy content of Provoking and Opeongo smallmouth bass. The somatic energy density was similar between lakes for smaller body sizes but then decreased in Provoking as body size increased (Fig. 2). For larger body sizes,

the somatic energy density of individuals in Opeongo was greater than for those in Provoking (Fig. 2).

Reproduction

Age and size at maturation

Provoking bass matured at smaller sizes than Opeongo bass. In 2000, Provoking bass had significantly smaller sizes at 50% maturity than Opeongo bass (Table 2). Provoking nesting males were significantly smaller than Opeongo nesting males in 2000-2003 (Fig. 3a; $F_{1,458}$ = 327.0; $P < 0.01$; Provoking: mean = 25 $\pm$ 3.7 cm, N = 218; Opeongo: mean = 32 $\pm$ 4.9 cm, N = 342) and in 1981-1982 ($F_{1,155}$ = 30.7; $P < 0.001$; Provoking: mean = 26 $\pm$ 3.4, N = 90; Opeongo: mean = 30 $\pm$ 5.4 cm, N = 67). Nesting Provoking males also had a smaller minimum size than nesting Opeongo males in both sampling periods (Fig. 3a).

The differences in the age at maturation were less pronounced. The estimated age at 50% maturity was similar in 2000 for females in both lakes, but was significantly younger for Opeongo males than for Provoking males (Table 2). Provoking nesting males were significantly younger than Opeongo nesting males in 2000-2003 (Fig. 3b; $F_{1,458}$ = 29.7; $P < 0.001$; Provoking: mean = 6.2 $\pm$ 1.4 years, N = 218; Opeongo: mean = 6.8 $\pm$ 1.5 years, N = 342) and in 1981-1982 ($F_{1,155}$ = 10.7; $P < 0.01$; Provoking: mean = 6.3 $\pm$ 1.5 years, N = 90; Opeongo: mean = 7.2 $\pm$ 1.6 years, N = 67).

Reproductive investment

To compare reproductive investment, gonad mass was plotted against body mass (Fig. 4a) and ANCOVA was used to test for significance. For mature male gonad mass, the ANCOVA was significant ($F_{1,31}$ = 14.4; $P < 0.001$; N = 34) and the assumption of homogenous slopes was met ($F_{1,30}$ = 0.0001; $P > 0.90$; N = 34); therefore, Provoking males had greater gonad masses than

Opeongo males of similar body mass. For mature female gonad mass (Fig. 4a), the ANCOVA ($F_{1,58}$ = 2.9; P = 0.09; N = 61) and the test for homogenous slopes ($F_{1,57}$ = 3.2; P = 0.08; N = 61) were close to significant (i.e. P values were between 0.05 and 0.10); the fitted regression lines suggest that small Provoking females invest more in gonad mass than small Opeongo females whereas investment by larger females is similar (Fig. 4a).

Ovary egg size and fecundity were also plotted against body mass and compared between lakes (Figs. 4b-4c). The assumption of homogenous slopes was met for both egg diameter ($F_{1,38}$ = 2.1; P > 0.10; N = 42) and fecundity ($F_{1,38}$ = 1.9; P > 0.10; N = 42). The ANCOVA was significant for mean gonad egg diameter ($F_{1,39}$ = 31.4; P < 0.001; N = 42) but not for fecundity ($F_{1,39}$ = 1.8; P > 0.10; N = 42); therefore, Provoking females had significantly larger egg diameters but similar fecundities relative to Opeongo females of similar body mass. Figure 4b (egg diameter versus body mass) is shown on the same scale as Figure 4a (gonad mass versus body mass) to highlight that although there is a significant difference in egg diameter between populations (insert in Fig. 4b), this does not translate into a large, observable difference in gonad mass (on the scale we used in Fig. 4a) between populations. This explains why similar fecundities but different egg diameters are translated into only small differences in gonad mass between populations.

For the proportion dry mass of mature ovaries, the M-W test was significant (Z = -2.0; P < 0.05; N = 25), indicating that Provoking females had higher gonad proportion dry weights than Opeongo females (Fig. 5).

Diet

There were substantial differences between populations in the amount and types of prey consumed. In 2002, 33% of all Provoking and 29% of all Opeongo smallmouth bass had empty stomachs. For adults, the percent of empty stomachs was 40% for Provoking and 35% for

Opeongo. The stomach contents of Provoking bass weighed significantly less ($F_{1,87} = 10.3$; $P < 0.01$; Provoking: mean = 1.9 g, Standard error, SE = 1.0, N = 25; Opeongo: mean = 4.3 g, SE = 1.2, N = 43) and prey items had significantly shorter body lengths ($F_{1,57} = 5.0$; $P < 0.05$; Provoking: mean = 25.1 mm, SE = 6.0, N = 29; Opeongo: mean = 37.7 mm, SE = 4.5, N = 30) than Opeongo bass. These differences were also significant when using body mass as a covariate (stomach content mass ANCOVA: $F_{1,86} = 12.3$, $P < 0.001$; prey length ANCOVA: $F_{1,56} = 5.7$, $P < 0.001$; slopes were homogenous for stomach content: $F_{1,85} = 0.24$, $P > 0.10$; slopes were homogenous for prey length: $F_{1,55} = 1.3$, $P > 0.10$). Opeongo bass had significantly more crayfish in their stomachs than Provoking bass; in contrast, Provoking bass had significantly more insects in their stomachs than Opeongo bass (Table 3).

Similar differences were observed in 1981 between Provoking and Opeongo bass in the types of prey consumed (Table 3). As in 2002, the major difference between the populations in 1981 was that crayfish made up a large proportion of the Opeongo bass diet whereas insects were the major component of the Provoking bass diet. In 1982, the Bridle population had higher proportions of crayfish and lower proportions of insects in their diet than the Provoking population (Table 3).

As body size increased, so also did the difference in diets between Provoking and Opeongo bass (Table 4). The diet of 5-10 cm bass in both populations consisted of small-bodied prey such as plankton and insects. As bass size increased, the proportion of insects in the diet dropped in Opeongo but remained high in Provoking. In Opeongo, large-bodied prey such as fish and crayfish first appeared in the diet of 10-15 cm and 15-20 cm bass and the percentage of crayfish in the diet increased until it made up 71% of the diet in the largest bass. Even the large size-classes of the Provoking bass consumed a low proportion of large-bodied prey. Also, the percent of empty stomachs increased in both populations as bass got larger, but was considerably

higher in Provoking bass than Opeongo bass in the largest size-class (Table 4). The growth rates of bass in Provoking started to fall behind Opeongo at the size (15-20 cm) when crayfish first appeared in the Opeongo diet.

Mortality

Nesting males

Return rates of first-time nesting males were lower for Provoking than Opeongo across all ages (Table 5). Between-lake differences were significant for ages five and seven (Table 5). This suggests that following reproduction and nest-guarding, Provoking males suffer greater mortality than Opeongo males.

Newborns: Removal experiment

One hour after removal of the male, there was no between-lake difference in the reduction of eggs in the nest (Fig. 6; $F_{1,19} = 2.2$; $P > 0.10$). After 24 hours, significantly more Opeongo eggs were removed from the nest relative to Provoking (Fig. 6; $F_{1,19} = 17.5$; $P < 0.001$). Wind and wave action during the course of the experiment was minimal in both lakes – therefore it is reasonable to infer that the observed egg losses were due to predation and that over fixed period of time the predation rates appear higher in Opeongo than Provoking.

Discussion

Since introduction, the Provoking and Opeongo smallmouth bass populations have shown considerable divergence in life history traits. Our data from the latest study period (1993-2003) demonstrate the following: (i) Provoking newborn bass likely experience lower mortality from predators than Opeongo newborns; (ii) juvenile bass (ages<=4) in both populations have similar individual growth rates; (iii) Provoking males have slower adult growth rates, younger

ages/smaller sizes at nesting, older ages/smaller sizes at maturity, higher gonadal investment, and greater mortality following reproduction than Opeongo males; (iv) Provoking females have slower adult growth rates, similar ages/smaller sizes at maturity, higher ovarian dry matter content, similar relative fecundities, and larger egg sizes than Opeongo females.

The apparent contradiction between an older age at 50% maturity in Provoking males, but a younger nesting distribution relative to Opeongo, can be explained as follows. The observed age distribution of nesters suggests that more young mature males are successful in acquiring nests and broods in Provoking than in Opeongo. This is consistent with the fact that in Provoking, size at maturity is similar between sexes (minimum length at maturity is 20 cm for males versus 19 cm for females; length at 50% maturity is 22 cm for males versus 21 cm for females), while, in Opeongo, male size at maturity is substantially less than female size at maturity (minimum length at maturity is 18 cm for males versus 24 cm for females; length at 50% maturity is 24 cm for males versus 26 cm for females). Given that smallmouth bass mate size assortatively (Ridgway et al. 1991; Mackereth et al. 1999), in Provoking, small mature males have small mature females to mate with and hence appear in the age distribution of nesting males; however in Opeongo, small/young males have no small females to mate with and hence do not appear in the age distribution of nesting males. These interesting patterns were uncovered because we were able to characterize both the ages/sizes at which gonads become developed (i.e. mature) and the ages/sizes at which individuals actually breed (i.e. nest); this type of detailed characterization is relatively rare in studies of fish life history.

Numerous factors (i.e. food availability, diet ontogeny, mortality, temperature) could have contributed to the divergence of life history traits between the Provoking and Opeongo populations, however, some can be eliminated from consideration. Warmer water temperatures promote higher growth rates in smallmouth bass (e.g. Shuter and Post 1990) but Provoking has

more warm days (i.e. days above 15 and 20 ^{o}C) than Opeongo despite slower growth rates; this observation coupled with the overall similar temperature patterns between lakes rules out temperature as a primary factor driving the divergence. Likewise, higher parasite loads, perhaps associated with the high densities in Provoking, could force lower growth rates, however, Orendorff (1983) compared parasite loads between the two populations and found no evidence that they had an impact on growth or body condition.

Instead, we propose that differences in the foraging environment supported by the two lakes could have played a major role in driving the divergence in life histories. The slow-growing adult smallmouth bass in Provoking are more likely to have empty stomachs, eat smaller prey, and have fewer grams of food in their stomachs than the bass in Opeongo. Provoking individuals have low somatic energy reserves and, when transferred into a lower density population, their diet changed and growth increased. These observations suggest that food availability in Provoking is lower than in Opeongo, a likely consequence of intra-specific competition caused by high population densities.

In addition to prey availability, the types of prey being consumed in Provoking and Opeongo have likely contributed to the differences in growth. It is common for many species of fish, including smallmouth bass, to switch to eating larger prey as they grow (Carlander 1977). An inability to switch to larger prey types has been proposed as an explanation for slow growth in yellow perch (*P. flavescens*) (Sherwood et al. 2002). Smallmouth bass typically switch from eating small prey such as insects when young, to eating larger prey such as fish and crayfish as they become adults (Olson and Young 2003; Shrader and Weldon 2004). Crayfish are the preferred food of adult bass in many systems (e.g. Olson and Young 2003), including Opeongo, and are in small quantity in the diet of Provoking bass. In Opeongo, fish first appear in the diet when bass reach sizes between 10 and 20 cm, and crayfish first appear in the diet when bass

reach sizes between 15 and 20 cm. These are similar to the body sizes at which the somatic energy density begins to drop in Provoking (i.e. 12-17 cm), suggesting that the lack of large-sized prey is depleting the available somatic energy reserves. At body sizes just beyond the drop in somatic energy, the growth rates in Provoking start to fall behind Opeongo (i.e. 15-20 cm), indicating that the inability to switch to larger prey has depleted the somatic energy reserves and likely contributed to the growth rate drop in Provoking.

The decline in growth rate and somatic energy that accompany continued reliance on smaller prey in Provoking may be attributed to increases in the cost of feeding activity. As a predator grows, it requires increasing rations to maintain positive growth rates (Kerr 1971). If large-sized prey are not available, the number of small prey needed to maintain positive growth will increase with predator body size and the amount of energy required to obtain increasing numbers of small prey will also rise (Sherwood et al. 2002). In Provoking, the absence of larger prey would act jointly with low prey availability (i.e. due to high population density) to force reduced somatic energy density and slower growth rates on older bass.

The production of large eggs in Provoking is in concordance with theoretical expectations that it is advantageous to produce larger eggs in environments where food availability is low (Hutchings 1991; Roff 1992). Larger eggs typically produce larger larvae with larger energy stores--such larvae can feed more efficiently, better endure food shortages and are better able to avoid predators (Marteinsdottir and Steinarsson 1998; Zhao et al. 2001). Experimental research has shown that females can manipulate offspring size in response to food availability (Reznick and Yang 1993), which may be the case in the Provoking bass. We acknowledge, however, that not all fish species show the expected production of large progeny in growth-limited environments (e.g. Quinn et al. 2004), suggesting that the generality of this pattern may not hold.

Our measures of direct reproductive investment suggest that both sexes in Provoking invest more energy in reproductive products than their counterparts in Opeongo. Spring gonad weights are higher for both sexes: among males, this holds across the observed weight range; among females, it appears to hold for the lower half of the observed weight range. In addition, our observations of lower somatic energy density and higher ovary proportion dry matter content in Provoking reinforce the conclusion that Provoking fish invest relatively more of their available energy directly into reproductive products. Since gonad energy density varies with gonad dry matter content (Henderson et al. 2000), higher gonad energy densities coupled with lower somatic energy densities imply that the ratio of gonadal energy to somatic energy among Provoking adults exceeds that in Opeongo.

Despite resource limitation, the slow-growing Provoking adults are investing more energy in reproduction than their faster growing counterparts in Opeongo. Intuitively, and given simple theoretical predictions to the contrary (Gadgil and Bossert 1970; Pianka 1970; Ylikarjula et al. 1999), this may seem surprising, however, an increase in reproductive investment by itself can lead to a lower somatic growth rate for adults (Lester et al. 2004). Also, high reproductive investment could be a viable strategy for dealing with a foraging environment that only provides low densities of smaller prey. If prey density is low and large-sized food unavailable, somatic energy may drop systematically with size (Fig. 2) and breeding males, particularly, may suffer additional mortality following the energetically costly nest-guarding period (Table 5). Therefore, in resource-poor environments, males will have fewer breeding opportunities over their shorter lifetimes and, as a consequence, may invest more energy into each breeding opportunity that remains to them. Findings consistent with this idea have been reported in several studies of related centrarchids: Fox (1994) found an association between high gonadal investment, early maturation and high population density in pumpkinseed (*L. gibbosus*) populations and Aday et al.

(2002) found that stunted bluegill (*Lepomis macrochirus*) populations had younger, smaller nesting males. The presence of parental care (or other reproductive behaviors that incur high costs) may produce discrepancies between observed patterns and the expectations of simple theory.

Theoretical (Gadgil and Bossert 1970; Law 1979; Lester et al. 2004) and empirical (Hutchings 1993; Reznick et al. 1996; Shuter et al. 2005) research show that high adult to juvenile mortality rates select for younger ages at maturation and increased reproductive investment. Our observations of reproductive investment in Provoking and Opeongo bass concur with these previous studies; they also match our observations of mortality as follows. First, juvenile mortality rates appear higher in Provoking than in Opeongo. This is supported by our removal experiment, where the relative predation pressure of newborns per unit time is lower in Provoking than Opeongo and by the fact that there is a lack of species that prey on young life stages of bass in Provoking. The only other littoral species in Provoking is yellow perch whereas Opeongo has many littoral species (mean number of individual fish other than smallmouth bass caught per trap-net in 2001 was 3.2 in Provoking and 12.6 in Opeongo). Second, mortality following reproduction is higher for Provoking males than for Opeongo males, as we have shown, but this is not due to fishing mortality because less than 3% of the Provoking population is removed annually by anglers (Orendorff 1983). Third, Orendorff (1983) reported higher natural mortality rates for ages 6-12 in Provoking bass (35%) relative to Opeongo bass (27.5%), measured using catch-curve analysis. The above three observations suggest that the ratio of adult mortality to juvenile mortality may be higher in Provoking than in Opeongo, which, according to theory (Gadgil and Bossert 1970; Law 1979), would predict younger ages at maturation and increased reproductive investment. However, although we observed higher reproductive investment in Provoking, the age at 50% maturity was similar between populations, at least for

females (but note that Provoking nesting males had younger age distributions). An explanation for the absence of an effect on age at maturity is that the differences in mortality may reflect a much greater cost of reproduction in Provoking due to severe resource limitation. Expectations of life history theory may breakdown if higher mortality is a consequence of the 'decision' to reproduce, rather than simply an aspect of the environment that influences optimal reproductive strategy.

Rapid phenotypic divergence in life history traits can be environmentally-induced and/or genetically based responses to factors such as resource availability and mortality (Heath and Roff 1987; Haugen and Vøllestad 2001; Reznick et al. 2001). The Provoking/Bridle transplant experiment demonstrates that the slow growth of Provoking smallmouth bass has a significant environmentally-determined component since the growth rates of Provoking and Bridle individuals responded quickly (within a year) to changes in their feeding environment. We should note, however, that in our transplant experiment, fish were not grown in a common environment (as in a traditional common garden experiment) and as a result, it is not possible to completely discount a genetic difference. Instead, our experiment provides support for the hypothesis that the slow growth of the Provoking population has a significant environmental component. If genetic differences do exist, they would reinforce the environmental effects of density and food on growth (Unwin et al. 2000).

This study provides insight into the rapid divergence of life history traits that can occur in introduced populations. The two bass populations described here were stocked from the same source approximately 20 generations ago (Christie 1957; Orendorff 1983; Kerr and Lasenby 2000), and thus, did not originally differ in life history. The slow adult growth rates, small sizes at maturation, and diet differences observed in Provoking have persisted since at least the early 1980s (4 generations before present) and there is evidence in old Algonquin Park records

(Department of Lands and Forests records, 1947-1948) that Provoking smallmouth bass were exhibiting small body sizes in the 1940s (12 generations before present). Thus, the divergence of growth between Provoking and Opeongo smallmouth bass occurred at most, within eight generations of introduction.

This raises the question of why the two introductions proceeded rapidly to two quite different, apparently steady states: one characterized by high densities and low adult growth rates and the other characterized by low densities and relatively high adult growth rates. An answer to this question may lie with the very low diversity of the Provoking fish community: predators on all life stages are rare and competitors for the adults are absent. The higher egg and larval survival rates permitted by the absence of predators would allow the Provoking population to expand rapidly and the absence of competitors would permit the expansion to continue until low resource availability imposed sufficient reductions in fecundity and/or increases in mortality to end population growth. In Opeongo, predation-driven high mortality rates on egg and larvae would ensure that population stability could be achieved with less suppression of adult growth and fecundity and thus at lower adult densities.

Rapid divergence of life histories has been observed in other isolated fish populations, most commonly in response to differential mortality rates (e.g. Reznick et al. 1990; Haugen and Vøllestad 2001). Our study provides evidence of the rapid divergence of somatic growth and reproductive traits that can occur in a parental care species and it suggests that the additional costs associated with parental care may shape some of the patterns of life history response.

Table 1. Comparison of native and transplanted bass from the reciprocal transplant experiment of 1981-1982. Significant differences were found in growth (i.e. in units of scale growth) between transplanted bass and those that remained in the native lake (two-tailed *t* tests; $P < 0.01$).

	Source population	
	Provoking Lake	Bridle Lake
Mean scale growth in native lake $\pm$ 1 standard error	15.66 $\pm$ 0.54	18.56 $\pm$ 1.25
Mean scale growth in non-native lake $\pm$ 1 standard error	19.21 $\pm$ 1.31	7.25 $\pm$ 0.77
Body size range for comparison (cm)	19-28	30-36

Table 2. Maturation patterns of smallmouth bass, *Micropterus dolomieu*, in fall 2000. Log likelihood and Chi-square (X^2) statistics used to test between 50% estimates for each sex are shown (* is a significant difference at $P < 0.05$ and † is a significant difference at $P < 0.0042$ after Bonferroni correction).

	Provoking males	Opeongo males	Provoking females	Opeongo females
Fork Length				
# mature/immature used in estimates	34/41	42/29	35/32	99/44
Mean size of mature/ immature (cm)	25/19	30/21	25/17	32/23
Standard error of mature/immature	0.5/0.5	0.8/0.5	0.7/0.5	0.5/0.5
Minimum length at maturity (cm)	20	18	19	24
Length at 50% maturity (cm)	22	24	21	26
Log likelihood/X^2	-46/4.6*		-44/46*†	
Age				
# mature/immature used in estimates	34/41	41/28	35/32	98/41
Mean age mature/ immature (years)	6/4	6/4	7/4	7/4
Standard error mature/immature	0.3/0.2	0.3/0.2	0.3/0.2	0.2/0.2
Minimum age at maturity (years)	3	3	4	4
Age at 50% maturity (years)	5	4	5	5
Log likelihood/X^2	-57/9.2*†		-47/0.2	

Table 3. A comparison of the diets of smallmouth bass, *Micropterus dolomieu*, from Provoking, Bridle, and Opeongo Lakes. Shows the mean percent occurrence of prey items in the diet, the percent of empty stomachs, and the sample size (N) for pooled juvenile and adult smallmouth bass. Standard errors are shown in brackets under each prey category. The between-lake P values from Mann-Whitney (M-W) tests are shown (* is a significant difference at $P < 0.05$ and † is a significant difference at $P < 0.012$ after Bonferroni correction).

Lake	% Crayfish	% Insects	% Fish	% Other	% Empty	N
Provoking summer 1981	14 (0.02)	61 (1.3)	16 (0.07)	8 (1.4)	50	138
Opeongo summer 1981	74 (0.15)	11 (0.07)	14 (0.05)	1 (0.05)	23	97
1981 M-W test	$P < 0.001^{*\dagger}$	$P < 0.01^{*\dagger}$	$P > 0.50$	$P > 0.50$		
Provoking summer 1982	10 (0.04)	72 (1.4)	14 (0.3)	4 (0.08)	30	64
Bridle summer 1982	45 (0.2)	28 (0.4)	15 (0.2)	9 (0.2)	13	63
1982 M-W test	$P < 0.001^{*\dagger}$	$P < 0.05^{*\dagger}$	$P > 0.50$	$P > 0.50$		
Provoking summer 2002	2 (1.5)	62 (6.6)	3 (1.9)	32 (5.5)	33	60
Opeongo summer 2002	43 (7.5)	10 (4.2)	16 (5.5)	31 (5.8)	29	62
2002 M-W test	$P < 0.001^{*\dagger}$	$P < 0.001^{*\dagger}$	$P > 0.10$	$P > 0.50$		

Table 4. Diet for Provoking (Pro) and Opeongo (Op) Lake smallmouth bass, *Micropterus dolomieu*, in 2002. Includes the mean percent occurrence of prey items (% fish, crayfish, insects, plankton, other), the percent of empty stomachs (% Empty), and the sample size (N) used for different body lengths (underlined lengths) of smallmouth bass. Standard errors are in brackets below each mean percent occurrence estimate.

	5-10 cm		10-15 cm		15-20 cm		20-25 cm		>25 cm	
	Pro	Op	Pro	Op	Pro	Op	Pro	Op	Pro	Op
% Fish	0	0	0	43	0	8	0	11	22	14
	(0)	(0)	(0)	(18)	(0)	(6.9)	(0)	(8.3)	(7.2)	(8.3)
% Crayfish	0	0	0	0	0	44	4	50	6	71
	(0)	(0)	(0)	(0)	(0)	(15)	(3.4)	(12)	(1.6)	(11)
% Insects	12	28	57	21	85	14	65	5	44	0
	(11)	(24)	(20)	(13)	(7.2)	(9.2)	(11)	(4.2)	(13)	(0)
% Plankton	25	72	41	7	4	6	6	6	17	4
	(22)	(24)	(20)	(6.3)	(3.7)	(4.6)	(4.5)	(4.2)	(4.8)	(3.1)
% Other	62	0	1	28	10	28	25	28	11	11
	(21)	(0)	(1.2)	(16)	(6.5)	(12)	(11)	(11)	(3.2)	(6.6)
% Empty	20	0	28	22	28	31	33	44	50	26
N	5	4	7	9	18	13	18	16	12	19

Table 5. Mortality (M) for first-time nesting male smallmouth bass estimated by dividing the number of males that did not return to spawn in a subsequent year by total number (N) of males clipped for that age. To test between-lake differences, results (statistic and P-value) of Chi-square tests are presented (* is a significant difference at $P < 0.05$ and † is a significant difference of $P < 0.01$ after Bonferroni correction).

Age	Provoking		Opeongo		Chi-square test	
(years)	M	N	M	N	Chi	P
4	1	14	0.8	10	3.05	0.08
5	0.92	39	0.71	26	7.02	0.008*†
6	0.70	44	0.64	120	0.57	0.45
7	0.86	28	0.46	41	10.98	0.0009*†
8-10	1	5	0.55	11	3.31	0.069

Fig. 1. Mean size-at-age ± 1 standard deviation for Provoking and Opeongo smallmouth bass, *Micropterus dolomieu*, in 2000-2001 (closed circles for Provoking; open circles for Opeongo) and 1975-1985 (solid line for Provoking; broken line for Opeongo). Sample sizes: 312 Provoking (2000-2001), 301 Opeongo (2000-2001), 715 Provoking (1981-1982), 549 Opeongo (1975-1985).

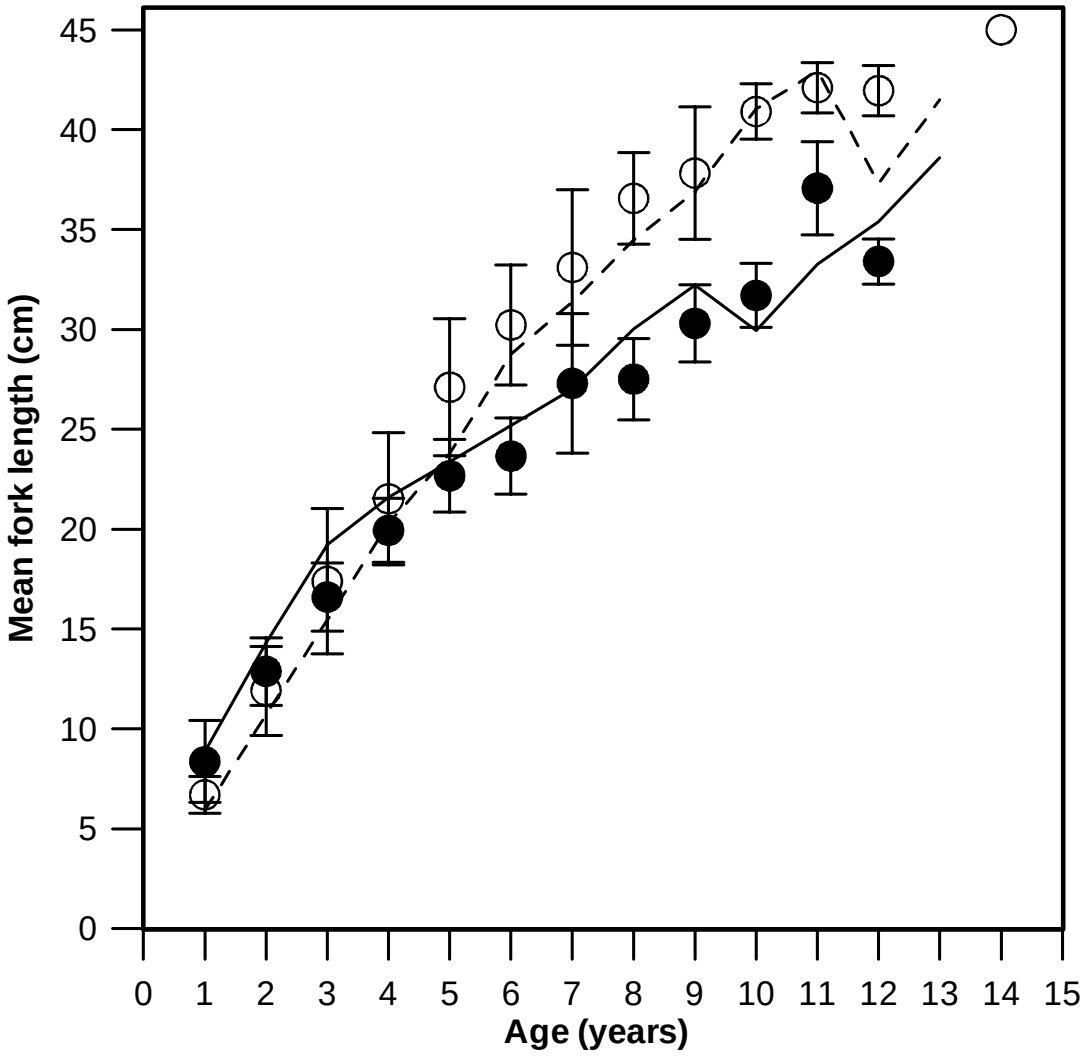

Mean fork length (cm)
0
5
10
15
20
25
30
35
40
45
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
Age (years)

Fig. 2. Somatic energy density relative to fork length in Provoking (closed circles and solid line; $y = 5598 – 51.1x + 0.6x^2$) and Opeongo (open circles and dashed line; $y = 5111 + 9.6x - 0.2x^2$) smallmouth bass, *Micropterus dolomieu*.

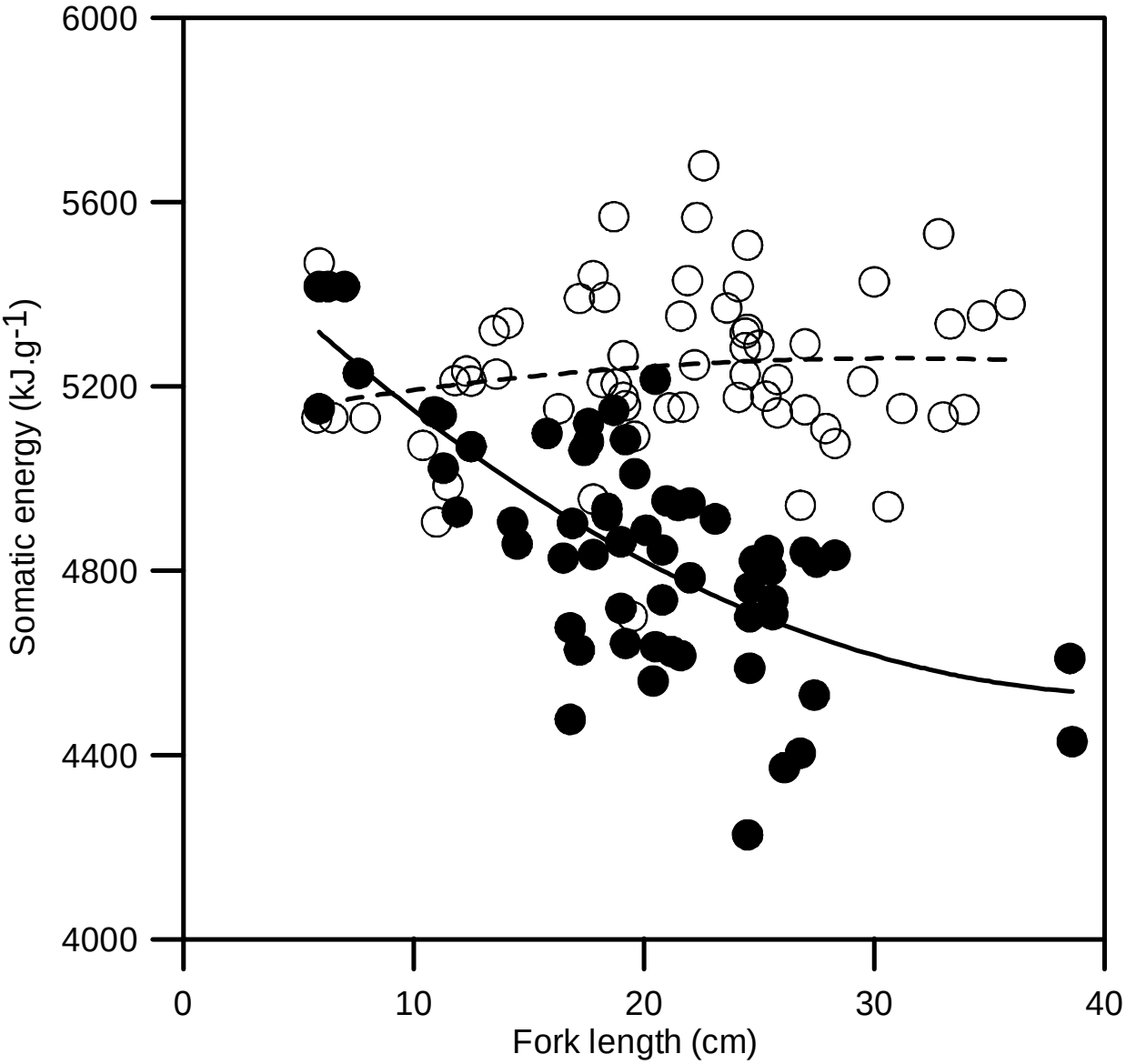

6000
5600
5200
4800
4400
4000
Somatic energy (kJ.g-1)
0
10
20
30
40
Fork length (cm)

Fig. 3. (a) Fork length and (b) age distributions for Provoking (solid) and Opeongo (thatched) nesting male smallmouth bass, *Micropterus dolomieu*, in 2000-2003. Range (lines) and means (squares) shown above for Provoking (solid) and Opeongo (thatched) in 1981-1982.

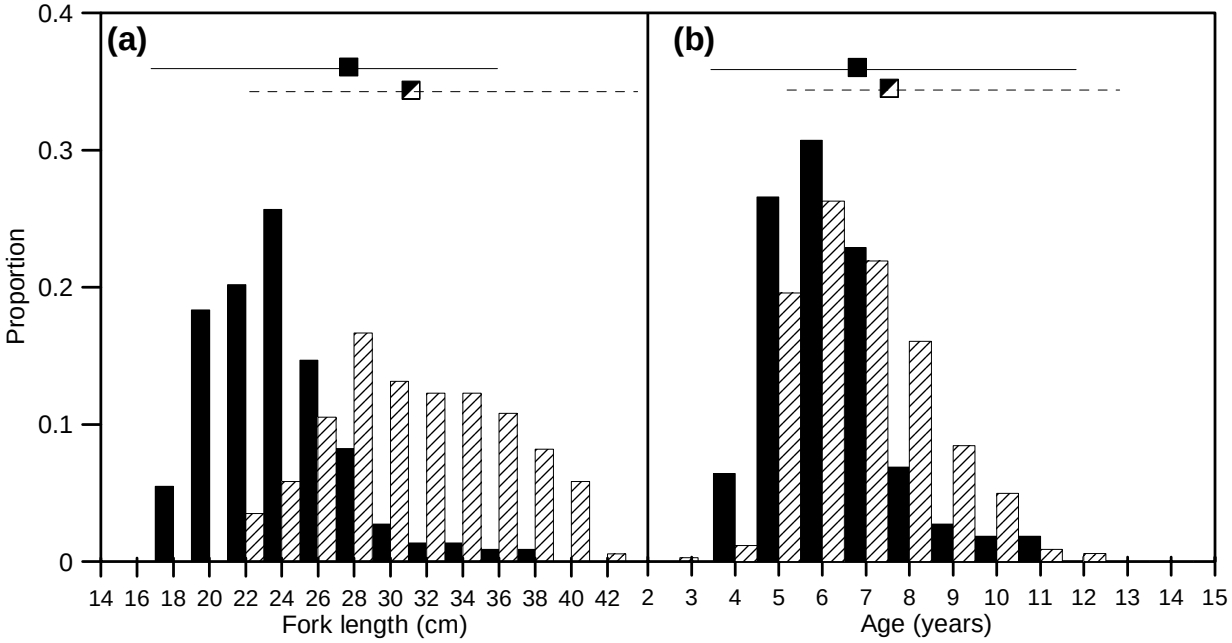

(a)
(b)
Proportion
0.4
0.3
0.2
0.1
0
14 16 18 20 22 24 26 28 30 32 34 36 38 40 42
Fork length (cm)
2 3 4 5 6 7 8 9 10 11 12 13 14 15
Age (years)

Fig. 4. Reproductive investment relative to body mass (soma + gonad mass) for mature 2000-2001 Provoking (closed symbols; solid lines) and Opeongo (open symbols; dashed lines) smallmouth bass, *Micropterus dolomieu*. Females are squares, males are triangles. (a) Gonad mass relative to body mass for Provoking females ($\ln y = 1.0\ln x - 3.1$, $r^2 = 0.66$) and males ($\ln y = 1.5\ln x - 7.2$, $r^2 = 0.90$) and Opeongo females ($\ln y = 1.4\ln x - 5.2$, $r^2 = 0.82$) and males ($\ln y = 1.5\ln x - 7.6$, $r^2 = 0.87$). (b) Mean gonad egg diameter relative to body mass for Provoking ($\ln y = 0.08\ln x + 0.5$, $r^2 = 0.1$) and Opeongo ($\ln y = 0.08\ln x - 0.28$, $r^2 = 0.17$). Insert at top right corner is a magnification to highlight the difference in egg diameter but at a finer scale. (c) Female fecundity relative to body mass; solid line is both populations combined ($\ln y = 0.93\ln x + 3.3$, $r^2 = 0.66$).

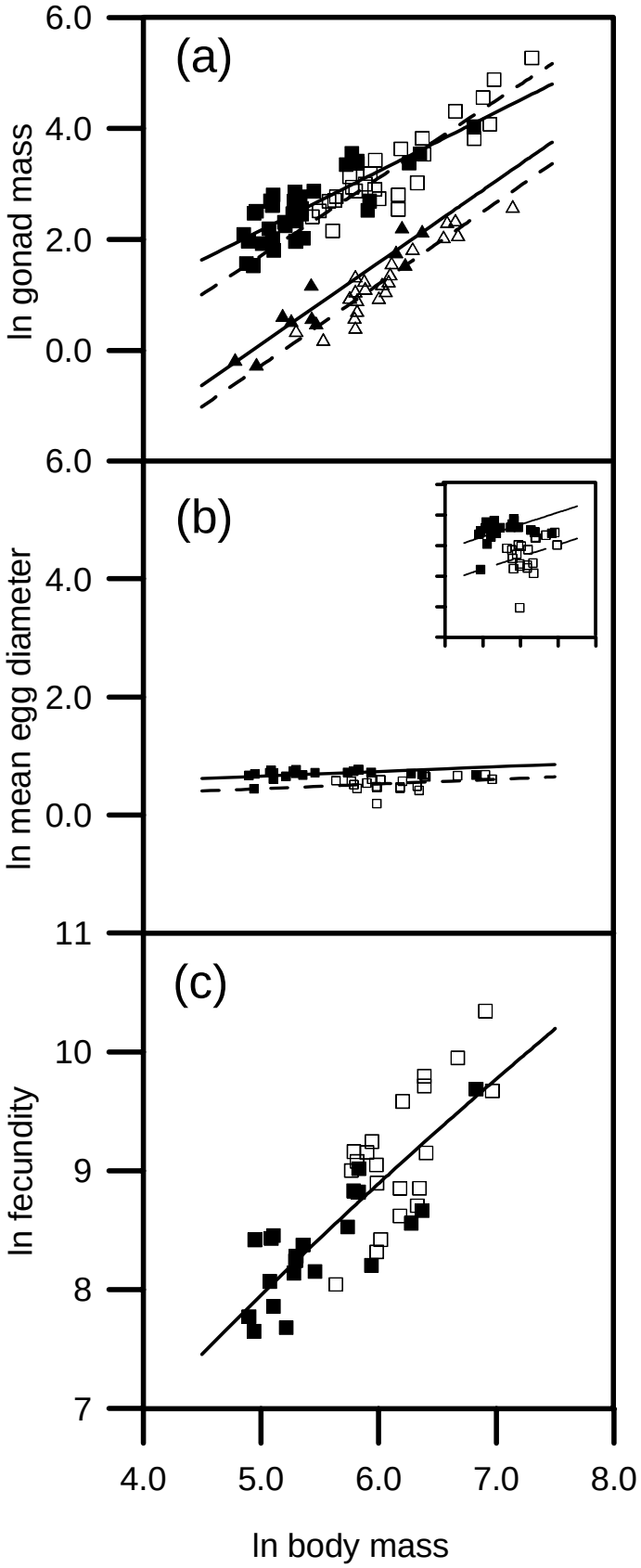

(a)
(b)
(c)
ln gonad mass
ln mean egg diameter
ln fecundity
ln body mass
6.0
4.0
2.0
0.0
6.0
4.0
2.0
0.0
11
10
9
8
7
4.0
5.0
6.0
7.0
8.0

Fig. 5. Proportion dry mass of the ovaries of mature Provoking (solid) and Opeongo (thatched) smallmouth bass, *Micropterus dolomieu*.

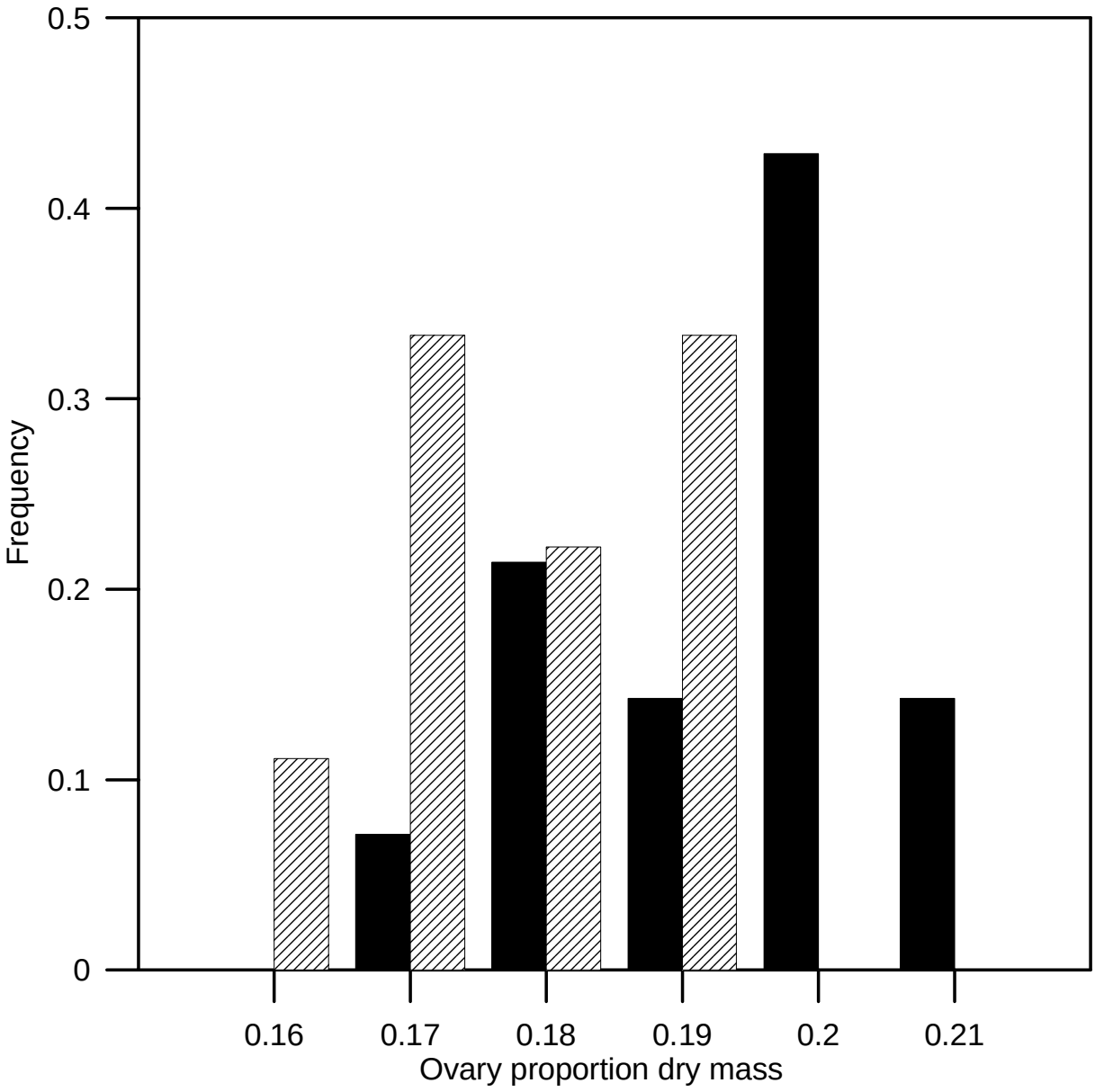
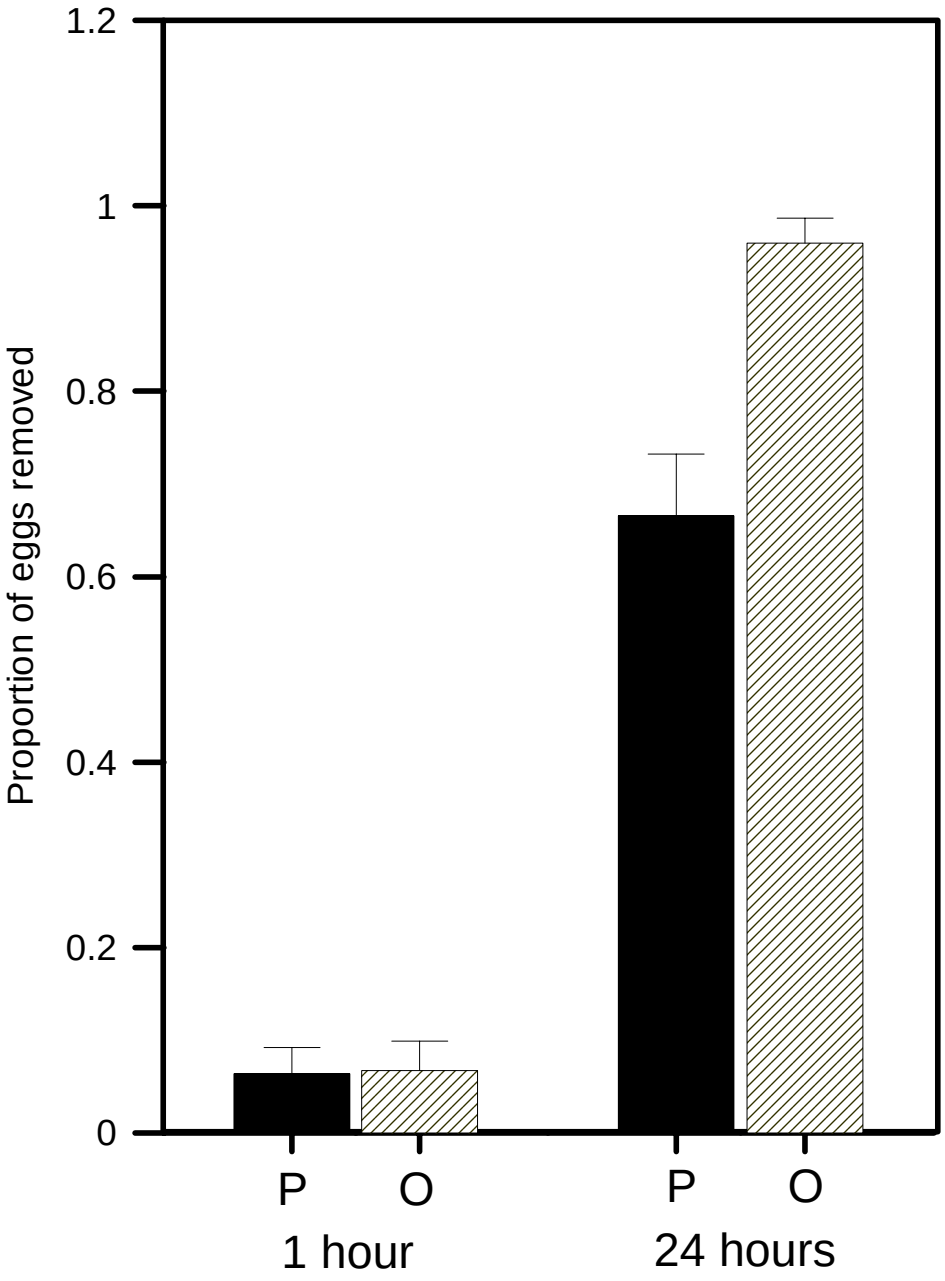

0.5
0.4
0.3
0.2
0.1
0
Frequency
0.16
0.17
0.18
0.19
0.2
0.21
Ovary proportion dry mass

Fig. 6. The proportion of eggs removed by predation ± 1 standard error, 1 hour and 24 hours after removal of the nest-guarding male in Provoking (P) and Opeongo (O) Lakes.


1.2
1
0.8
0.6
0.4
0.2
0
Proportion of eggs removed
P
O
P
O
1 hour
24 hours

Acknowledgments

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