

Isolating the influence of growth rate on maturation patterns in the smallmouth bass (*Micropterus dolomieu*)¹

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Abstract: In this study, we examine the divergence in growth and maturation between two populations of smallmouth bass (*Micropterus dolomieu*) introduced from a common source a century ago. To determine if the divergence in maturation is simply a plastic response to differences in growth rate, we use a new approach to estimate and then compare the probabilistic maturation reaction norms (PMRNs) for each population. The PMRNs for 5-year-old males are similar in the two populations, suggesting that the observed divergence in maturation is largely a plastic response to growth rate differences. For one population, we document the time course of maturation changes for the 60-year period from 1937 through 1990; while the mean length at maturation for 5-year-old males exhibits a steady downward trend (beginning at 31 cm and ending at 26 cm), their PMRNs vary over a much narrower range (25–27 cm) and do not exhibit a consistent temporal trend. These observations are consistent with the hypothesis that most of the observed change in maturation since introduction is a product of phenotypic plasticity, driven by environmentally based differences in growth rate. Our study provides an instructive example of how the PMRN approach can be used to isolate the role of growth rate variation in generating life history differences.

Résumé : Nous avons étudié la divergence dans la croissance et la maturation chez deux populations d'achigans à petite bouche (*Micropterus dolomieu*) introduites d'un même point d'origine il y a un siècle. Afin de déterminer si la divergence dans la maturation est simplement une réaction plastique à des différences de taux de croissance, nous avons utilisé une nouvelle méthodologie pour estimer et comparer les normes probabilistes de réaction (PMRN) de la maturation dans chaque population. La norme PMRN est semblable chez les mâles de 5 ans des deux populations, ce qui laisse croire que la divergence observée dans la maturation est en grande partie une réaction plastique aux différences de taux de croissance. Dans une des populations, nous avons tracé l'évolution chronologique des changements dans la maturation pour la période de 60 ans qui va de 1937 jusqu'aux années 1990; alors que la longueur moyenne à la maturité chez les mâles de 5 ans décline de façon constante (de 31 à 26 cm), leurs PMRN varient sur une gamme beaucoup plus étroite (25–27 cm) et ne montrent pas de tendance temporelle. Ces observations s'accordent avec l'hypothèse qui veut que la majeure partie du changement observé depuis l'empoissonnement est le résultat de la plasticité phénotypique, causée par des différences de taux de croissances reliés aux conditions environnementales. Notre étude fournit donc un exemple instructif de l'utilisation de la méthodologie PMRN pour circonscrire le rôle de la variation des taux de croissance dans la production de différences démographiques.

[Traduit par la Rédaction]

Introduction

Age at maturity, size at maturity, and growth rate are key life history traits that often vary among populations and are important to characterize because they influence population

dynamics and resilience to overexploitation (Roff 1992; Heino and Godø 2002). Variation in life history traits among populations will reflect some combination of plastic and evolved responses to environmental and ecological differences. For example, differences in growth rate and matura-

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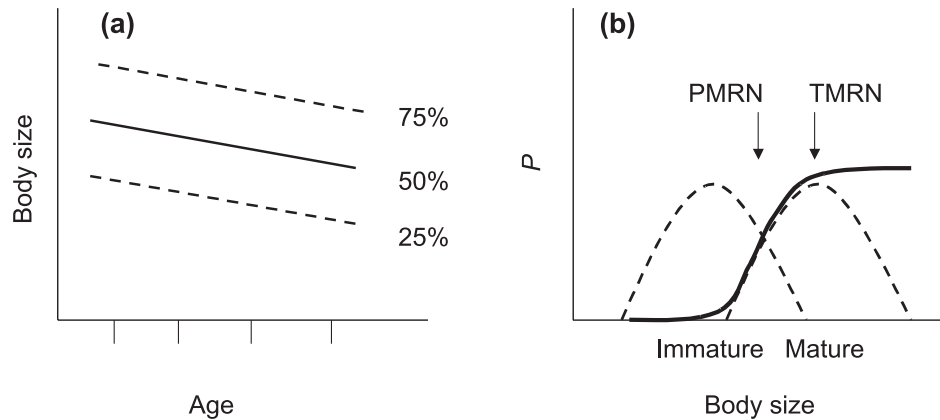
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Fig. 1. Schematic diagram of the probabilistic maturation reaction norm (PMRN) concept. (a) The 25%, 50% (midpoint), and 75% probability positions of the PMRN. Note that the PMRN is shown as a continuous line, although position is calculated discretely for each age. (b) The body-size distributions (broken lines) of immature and newly mature individuals and the fitted logistic regression (solid curve) used to estimate the PMRN for a single age; P is the probability of maturing. The traditional maturation reaction norm (TMRN) is estimated as the mean size of newly mature individuals.



tion can result from a plastic response of the phenotype to changes in food availability, or, over time, may evolve in response to selective mortality (Law 2000; Hutchings 2004). Furthermore, recent research suggests that evolutionary responses can occur within just a decade in harvested populations (e.g., Olsen et al. 2005), much faster than was previously thought. A complete understanding of the processes that create life history variation requires knowledge of the relative contribution to the overall response of both phenotypic plasticity and evolved changes.

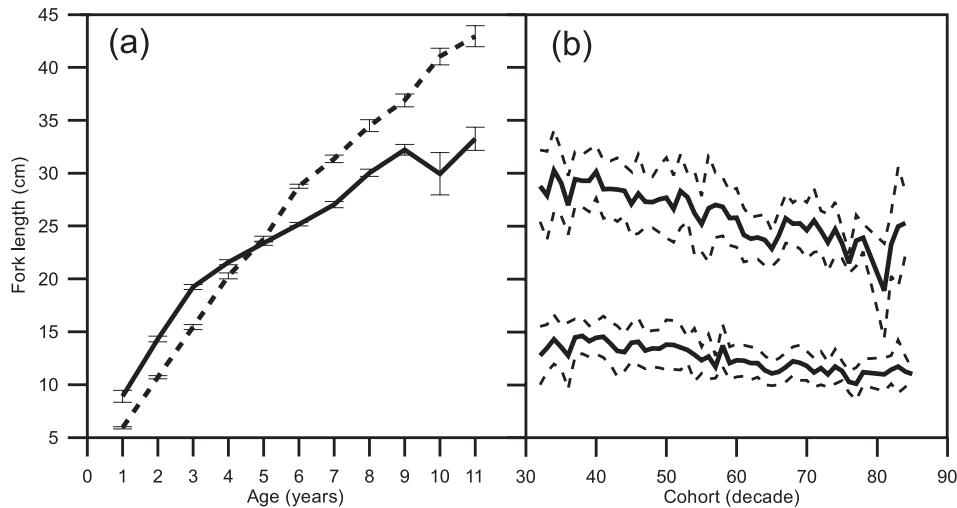
Unfortunately, it can be difficult to determine whether phenotypic changes in a population, or among populations, are plastic or evolved. Generally, common garden-rearing experiments or DNA analyses are used to test for evolved differences (e.g., Haugen and Vøllestad 2000; Koskinen et al. 2002); however, these methods can be expensive and are logistically difficult to use for species with long generation times. Therefore, in our study we chose to use maturation reaction norms (MRNs) as a tool to distinguish between phenotypic plasticity and changes that may be indicative of evolved responses.

The MRN for a population is the relationship between age at maturity and size at maturity for the individuals within the population. If individuals are part of a genetically distinct population but exhibit different growth rates because they vary in their experience of a specific environmental variable (e.g., food availability), the relationship between age and size at maturity expresses a classic reaction norm (Stearns and Koella 1986; Roff 2002; Ernande et al. 2004) (i.e., the systematic change in the expression of a phenotype in response to variation in a specific environmental variable (Schmalhausen 1949)). Abrams and Rowe (1996) and Abrams et al. (1996) investigated models in which the realized growth rate is determined, in part, by a behavioural or developmental trade-off between higher growth rate and greater mortality; age at maturity also changes adaptively in these models and, together with growth rate, determines size at maturity. Their analyses demonstrate that the optimal relation between age and size at maturity (i.e., the MRN) depends on which environment factor (e.g., food availability,

predator abundance, temperature) drives variation in realized growth rate. Thus, a change in the MRN of a population over time may reflect a change in the genetic character of the individuals in the population (an evolved response), but it may also reflect a change of the environmental factor that is driving the variation in realized growth rate. Conversely, genetically distinct populations could in theory exhibit similar MRNs, but only if different environmental factors elicit identical MRNs from the different genomes involved. Although this is theoretically possible, the level of coincidence required for it to occur seems high enough to make it an unlikely event. In addition, common garden-rearing experiments (e.g., Reznick 1993; Haugen 2000) show that different MRNs evolve in genetically divergent populations. Thus, it seems reasonable that a comparison of population MRNs will lead to one of the following conclusions: (i) if two populations exhibit identical MRNs or if a single population exhibits no change in its MRN over time, the most parsimonious explanation is that there is no difference in the genetic traits that underlie the observed MRNs; (ii) a demonstration of differences, or changes, in MRNs raises the real possibility that evolved differences in genetic traits do exist; however, an assessment of the environmental sources of the observed variation in growth rates is required to confirm this.

A new method has been developed (Heino et al. 2002) to estimate MRNs probabilistically. Traditionally, a MRN was often estimated from the mean size of the maturing individuals in each age group (e.g., Reznick 1993). The estimator describes the relationship between growth rate and age–size at maturity and we will refer to it as the traditional estimator for the maturation reaction norm (TMRN). In contrast to the TMRN, the probabilistic estimator for the maturation reaction norm (the PMRN) is based on a direct estimate, for each age group, of the probability that an individual of a particular size will mature and requires information on immature individuals in the population (Fig. 1). A probabilistic descriptor of the maturation process is likely realistic in wild populations where maturation is often stochastic, owing to variable and complex environmental influences (Bernardo

Fig. 2. (a) Size-at-age (mean \pm 1 standard error) of smallmouth bass, using data collected in 1975–1985 in Opeongo Lake (broken line) and 1981–1982 in Provoking Lake (solid line). (b) Mean size (solid lines) \pm 1 standard deviation (broken lines around means) at age 2 (lower lines) and age 5 (upper lines) for Opeongo cohorts sampled during the creel survey of 1937–1990 (i.e., 30–90).



1993). Heino et al. (2002) have argued that (i) a probabilistic representation of the reaction norm is a more accurate depiction of how this trait is likely to be expressed in the wild; (ii) an estimator (i.e., the PMRN) that explicitly recognizes the probabilistic character of this trait will be unbiased in the face of changes in growth rate, while the TMRN will exhibit significant bias in the face of growth rate changes; (iii) thus, the PMRN should be used when attempting to isolate how the observed maturation schedule for a population is shaped by plastic responses to changes in growth rate.

Given that maturation in the wild is likely probabilistic, the following reasons are given for the interdependence of the TMRN on growth. First, maturation at young ages will often occur at small sizes if there are no individuals in the population with growth trajectories steep (i.e., fast) enough to intersect the upper bounds (i.e., the 75th percentile of the PMRN in Fig. 1a) of the MRN. Second, maturation at old ages will often occur at larger sizes if there are no individuals in the population with growth rates shallow (i.e., slow) enough to intersect the lower bounds (i.e., the 25th percentile of the PMRN in Fig. 1a) of the MRN. Consequently, the TMRN, estimated as the mean size at maturation for each age, could be biased low for young ages and biased high for old ages, depending on the individual growth rates in the population. If the average growth rates of a population change, the TMRN estimate may also change even though the actual MRN (and the PMRN) remain unchanged. To differentiate between changes in maturation that are due to growth (i.e., plastic responses) versus changes in maturation that reflect an evolutionary response, it is important to use a MRN estimator that does not vary with growth. In this paper we assess the above contentions by comparing the relative effectiveness of the TMRN and PMRN estimators in isolating the role played by growth rate variation in generating differences in the observed maturation schedules for two introduced populations of smallmouth bass (*Micropterus dolomieu*).

Our two study populations are from Provoking Lake and Opeongo Lake, located in Algonquin Provincial Park, Ontario. Smallmouth bass were introduced into each lake be-

tween 1900 and 1920 from the same source population (Christie 1957; Orendorff 1983). Since introduction, the populations have diverged in both their growth trajectories and their apparent maturation schedules: Provoking bass grow more slowly after age 5 (Fig. 2a) and have smaller sizes and younger ages at breeding than Opeongo bass (Orendorff 1983). Interlake-transfer experiments demonstrated that at least a portion of the growth reduction exhibited by the Provoking population is a plastic response to low food availability; however, the higher natural mortality rates suffered by Provoking adults (Orendorff 1983) may have produced an evolved response toward earlier maturation at smaller sizes (Reznick et al. 1990). In Opeongo, body sizes have undergone a declining trend since introduction (Fig. 2b) and maturation patterns may have changed accordingly. Since both populations have undergone considerable shifts in density and growth (Orendorff 1983; Shuter and Ridgway 2002), they provide ideal case studies for assessing the effectiveness of the PMRN estimator in identifying possible contributions of plastic and evolved changes to shifts in maturation patterns. In this study, we compare the current TMRN and PMRN for both populations, and we quantify temporal variation in the PMRN for the Opeongo population over the period 1937–1990. To date, the PMRN approach has been primarily used as a tool to examine temporal variation within populations (e.g., Grift et al. 2003; Olsen et al. 2004a) and we provide evidence that the approach can be used to study divergence between populations. PMRNs are being increasingly used to argue that evolution has occurred in harvested populations (e.g., Barot et al. 2004b; Olsen et al. 2005) and tests of their utility and robustness are required.

Methods

Background

Provoking and Opeongo are oligotrophic lakes located approximately 10 km apart. Provoking is considerably smaller than Opeongo (1.1 versus 58.6 km² in area) and supports just three fish species: smallmouth bass, yellow perch (*Perca*

flavescens), and splake (*Salvelinus namaycush* × *Salvelinus fontinalis*). Opeongo contains numerous fish species including smallmouth bass, lake trout (*Salvelinus namaycush*), cyprinids (Cyprinidae), yellow perch, and pumpkinseed (*Lepomis gibbosus*).

There were three objectives to our study: (i) to describe the variation in growth rates of breeding males within the two populations and document the divergence in growth rates and maturation between them; (ii) to estimate and compare the current position of both the TMRN and the PMRN for each population; and (iii) to estimate temporal variation in the TMRN and PMRN for the Opeongo population. Data from three different field surveys were used to meet these objectives: (i) breeding-male surveys conducted from 1993 to 2003 on Opeongo and from 2000 to 2003 on Provoking; (ii) direct population sampling conducted from 2000 to 2002 on both lakes; and (iii) harvest sampling from an annual creel survey that has been conducted on Opeongo since 1936.

Breeding-male surveys

Smallmouth bass display paternal care in the form of an extended nest-guarding period in the spring and early summer. A long-term study of Opeongo guarding males has been conducted from 1980 to the present (Shuter et al. 1980; Ridgway et al. 1991). The study site for this work (Jones Bay) is located in the south arm of Opeongo, has a perimeter of 5 km, and is divided into three sections: south, central, and north. The study involves monitoring smallmouth bass nests frequently throughout the nesting period. Male nest-guarders are captured, measured, marked with tags, and released back onto their nests within 1–5 min of first capture. Body length of male nest-guarders is measured and 3–6 scales are removed for aging purposes. From 1993 to 1997, all the nesting males in all sections of Jones Bay were captured, measured, and released. From 1998 to 2003, all the nesting males in the south section and all previously tagged males in the central and north sections of Jones Bay were sampled. From 1993 to 2003, all nesting males were tagged with external T-bar tags (Hallprint, Victor Harbour, South Australia) placed beneath the soft dorsal fin and were given dorsal-spine clips. From 1997 to 2003, all nesting males were also tagged with internal passive integrated transponder (PIT) tags (Biomark, Boise, Idaho) placed in the cheek. Dorsal-spine clips are permanent and can be used to determine which fish have been tagged previously. Individual smallmouth bass that spawn repeatedly show high nest-site fidelity, with 94% of experienced males returning to within 200 m and 35% of experienced males returning to within 20 m (the modal distance category) of their previous nest site (Ridgway et al. 2002). Therefore, from 1993 to 2003, it was possible to determine which males were likely first-time nesters (males without clips) and which males had nested in a previous year (those with clips). As the rate of PIT-tag loss was low (M. Ridgway, unpublished data), it was also possible to identify most individual males in each year that they nested.

A similar survey of nesting males was conducted on Provoking from 2000 to 2003. The entire shoreline of Provoking was monitored frequently by snorkelers throughout the nesting period to locate smallmouth bass nests and cap-

ture males. All males that were identified (by the presence of easily visible dorsal-spine clips and (or) external T-bar tags) as nesters from a previous year were captured, sampled again, and released back onto their nests. Smallmouth bass nest in specific concentrated areas on Provoking (Orendorff 1983) and it is possible to sample most nesting males in these concentrated areas. Return rates for males nesting on Provoking are low for all ages (mean return rate 10%), and therefore most males sampled that were not captured in a previous year (as identified by clips) were most likely first-time nesters.

Direct population sampling and creel-survey sampling

Direct population sampling was conducted on Provoking and Opeongo in the late summer (September) of 2000, spring (May) of 2001, and late summer (end of August to early September) of 2002. Trap-netting (24-h sets), minnow trapping (24-h sets), and angling were used to capture individuals. For all captured smallmouth bass, fork length was measured, scale samples were taken for aging and back-calculation, sex was recorded, and the state of maturity was assessed by internal examination.

Sampling of the angler harvest on Opeongo was carried out through a point-access creel survey that has been run annually on the lake since 1936 (for details see Shuter et al. 1987). Harvested fish were examined by survey staff, scale samples for aging and growth back-calculation were taken, and fork length, weight, sex, maturity status, and data on diet were recorded. Annual sample sizes typically exceeded 100 fish.

Reconstructing individual growth histories

The individual growth history of each captured nesting male was reconstructed by back-calculating its fork length at each age from the distance to each annulus identified on its scale sample (Francis 1990). The aging and back-calculation techniques were validated using tagged, recaptured Opeongo smallmouth bass sampled over a decade, as well as multiple aging structures (scales, spines, opercula) from both populations. The same back-calculation techniques were used to estimate individual growth histories for 4-, 5-, and 6-year-old fish sampled during the creel survey. Scale samples from at least 40 fish from each cohort born over the period 1932–1985 were processed in this way. Multivariate analysis of variance (MANOVA) was used to test between-lake differences in growth histories (i.e., size at age) for each age at first nesting and within-lake differences in growth histories among ages at first nesting.

Estimation of age and size at breeding

Males captured on nests were used to give direct estimates of age and size at breeding. The age and length distributions of first-time nesting males sampled in 2001–2003 were compared between populations using analysis of variance (ANOVA). Those years were selected because 2000 was the first year of tagging in Provoking and recaptures could therefore be identified in 2001. The mean size of first-time nesting males at each age was also estimated by cohort, and between-lake differences among pooled cohorts were tested using ANOVA.

Estimation of TMRNs and PMRNs

The TMRN for a particular age is estimated as the mean size of individuals breeding for the first time at that age. The procedure for estimating a PMRN is considerably more complex because it requires a representative sample of body sizes for both the newly mature and the immature fish in each of the age groups to be included in the PMRN. Logistic regression is then applied to the data for each age group to estimate the length at which the probability of maturing is 50% (Fig. 1). These estimated sizes form the age-specific midpoints of the PMRN, and other percentiles (e.g., 25%, 75%) can also be estimated (Fig. 1). In our analyses of the Opeongo and Provoking data, we could only develop reliable estimates for the PMRN of age-5 males because (i) the number of younger males that mature in either population is so small that we were unable to collect sufficient data to obtain reliable PMRN estimates for those age groups, and (ii) for older males, it was impossible for us to reliably distinguish between newly mature fish and fish that had matured in previous years.

For the direct population sampling in Opeongo in the late summer of 2000 and 2002, and for the creel-survey sampling from 1937 to 1990, we assumed that the 5-year-old males that were classified as mature fell into one of two categories: (1) those that had reproduced for the first time at age 5 in the spring of their year of capture, and (2) those that were preparing to reproduce for the first time at age 6 in the spring following their year of capture. To construct the PMRN for 5-year-olds, we needed to remove the males of category 2 from the estimate. This was done by using a discriminant function to separate category 1 and 2 fish, based on their growth histories. The discriminant function was based on the back-calculated growth histories (ages 1–4) of two groups of nesting males sampled from the 1991–1998 cohorts in Opeongo: group 1 included just those fish known to have spawned for the first time at age 5 and group 2 included just those fish known to have spawned for the first time at age 6. The discriminant function was developed using the relative change in body length (R_i) for age groups 1–4, calculated as follows:

$$R_i = \frac{\Delta F_i - \overline{\Delta F}_i}{S_i}$$

where ΔF_i is the change in fork length from age i to age $i + 1$, $\overline{\Delta F}_i$ is the mean change in fork length from age i to age $i + 1$, and S_i is the standard deviation of the change in fork length from age i to age $i + 1$. R_i rather than ΔF_i values were used in the discriminant function to allow for extraneous differences in body size that might exist between populations and through time. The discriminant function was constructed to identify membership in group 1 or group 2 based on values for R_1 , R_2 , R_3 , and R_4 . The discrimination was significant ($F_{[4,258]} = 21.7$, $P < 0.0001$, $N = 263$; correct classification 73%). This function was applied to the R_i values calculated for all mature age-5 males collected from either the late-summer direct population samples or the creel survey, in order to classify these fish into one of the two categories defined above: category 1 males were those that had spawned for the first time at age 5 in the spring of their year of capture, and category 2 males were those that would spawn for

the first time at age 6 in the spring following their year of capture.

To estimate the PMRN for age-5 males, the size distribution of both immature and newly mature 5-year-old males is required. The size distribution of maturing 5-year-olds was derived by pooling (i) the back-calculated lengths at age 5 for all category 1 males identified by the discriminant analysis; (ii) observed late-summer and fall lengths of 4-year-old males that had developed mature gonads — since very few individuals spawn at age 4, we assumed that these fish were preparing to spawn for the first time at age 5; and (iii) observed spring lengths of 5-year-old males that had developed mature gonads. The size distribution of immature fish was derived by pooling (i) the back-calculated lengths at age 5 for all category 2 males identified by the discriminant analysis; (ii) observed late-summer and fall lengths of 4-year-old males that did not exhibit any gonadal development; and (iii) observed spring lengths of 5-year-old males that did not exhibit any gonadal development. The same procedure, using the Opeongo discriminator, was applied to the Provoking males taken during the direct sampling of that lake over the period 2000–2002. The PMRN for 5-year-old males was then estimated for each population by running a simple logistic regression on the length data from these representative samples of immature and newly matured individuals. The logistic regression was used to estimate the size at which the probability of maturing was 25%, 50%, and 75%. The significance of each logistic regression was tested using a χ^2 test.

In the case of the creel-survey estimates, individuals were pooled by decade in which they were born and the 1930s and 1940s cohorts were combined to obtain adequate sample sizes. A generalized linear model using a log-likelihood ratio test (McCullagh and Nelder 1989) was used to test for between-lake differences in the 2000–2002 PMRNs and for temporal changes in the Opeongo PMRNs from the cohorts of the 1930s to the 1980s.

TMRNs were estimated for 5-year-old males in both populations using the direct population sampling in 2000–2002. A time series of TMRN estimates was obtained for the Opeongo population using data from creel-sampled males captured over the period 1937–1990 (TMRN estimated by decade of birth as was done for the PMRN). For both cases, the TMRN was estimated as the mean size of newly mature 5-year-old males, and differences between lakes and within Opeongo were tested using ANOVA. All statistical tests were done in STATISTICA® (version 6.1; Statsoft Inc. 2003).

Results

Variation in individual growth rates within and between populations

In both populations, the faster growing members of a cohort bred first. This difference was clearly evident for the 1995 Opeongo cohort (Fig. 3; MANOVA for growth rates through age 4 compared across groups that breed first at ages 4–8: $F_{[4,16]} = 257.3$, $P < 0.001$, $N = 92$) and was typical of other Opeongo cohorts. In Provoking, those that nested at early ages (e.g., age 5) had higher growth rates (Fig. 3); however, the difference among all ages was not significant (MANOVA: $F_{[4,12]} = 0.8$, $P > 0.5$, $N = 56$). Also, Opeongo

Fig. 3. Size-at-age (mean \pm 1 standard error) of first-time nesting male smallmouth bass from the 1995 cohort in Opeongo (a) and Provoking (b). The shaded area in b represents the range from Opeongo shown in a. Each symbol represents the growth history for a different age at first nesting.

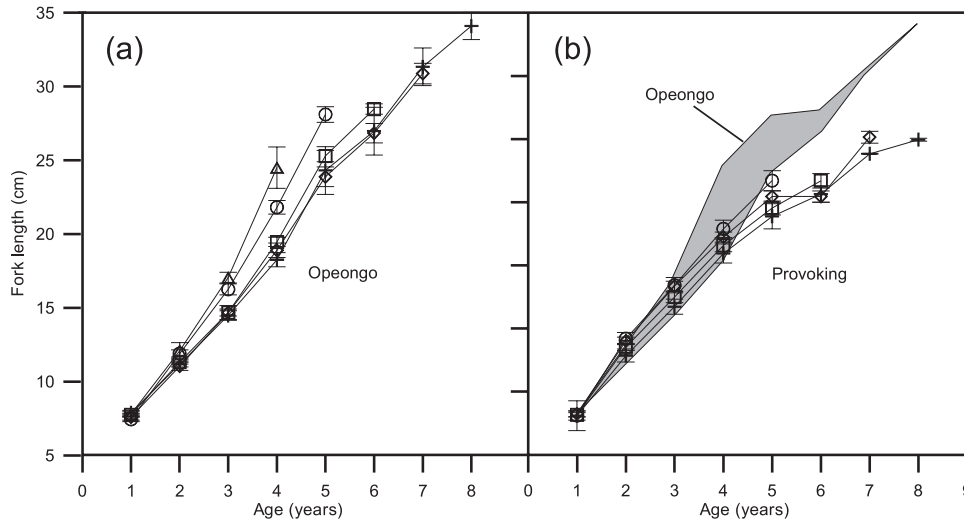
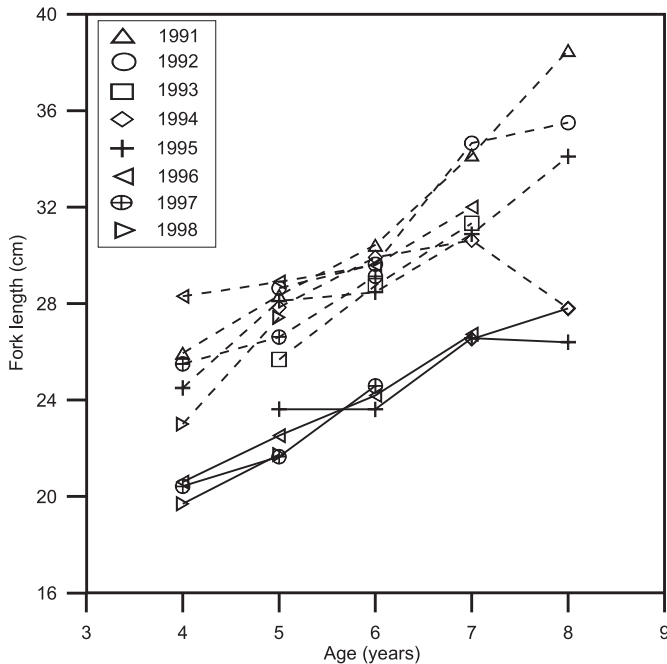


Fig. 4. Mean size of first-time nesting males by age for the 1991–1998 cohorts in Provoking (solid lines) and Opeongo (broken lines). Each symbol represents a different cohort.



nesting males had significantly higher growth rates than Provoking males at ages 5–7 (Fig. 3; MANOVA, age 5: $F_{[5,33]} = 14.4$; age 6: $F_{[6,55]} = 31.2$; age 7: $F_{[7,33]} = 15.5$; $P < 0.001$, $N = 142$). Although growth rates at age 8 were higher for Opeongo than for Provoking, sample sizes were likely too small for statistical significance (MANOVA: $F_{[3,1]} = 14.0$, $P = 0.19$, $N = 5$).

Variation in age and size at breeding between populations

Provoking nesting males had smaller sizes both before (ANOVA: $F_{[1,458]} = 327.0$, $P < 0.01$, $N = 460$; 24.6 ± 3.6 cm

(mean \pm SD) for Provoking and 32.3 ± 5.0 cm for Opeongo) and after (ANOVA: $F_{[1,306]} = 174.4$, $P < 0.01$, $N = 308$; 24.0 ± 3.3 cm for Provoking and 29.1 ± 3.4 cm for Opeongo) removal of experienced nesters (i.e., recaptures from a previous year) relative to those in Opeongo. Before experienced nesters were removed from the analysis, Provoking males nested at significantly younger ages than Opeongo males (ANOVA: $F_{[1,458]} = 29.7$, $P < 0.001$, $N = 460$; 6.0 ± 1.4 years for Provoking and 7.0 ± 1.6 years for Opeongo). However, after experienced nesters were removed, the age distribution of first-time nesting males was not significantly different between populations (ANOVA: $F_{[1,306]} = 0.3$, $P > 0.5$, $N = 308$; 6.0 ± 1.3 years for Provoking and 6.0 ± 1.0 years for Opeongo). The mean size of first-time nesting males was significantly greater in Opeongo than in Provoking across all ages and cohorts (Fig. 4; ANOVA: $F_{[1,517]} = 237.0$, $P < 0.001$, $N = 519$).

Variation in TMRNs and PMRNs between populations and within Opeongo

The strong association between rapid growth prior to maturation and early maturation (Fig. 3) was the basis for the discriminant function that we used to construct the mature and immature size distributions needed for our PMRN estimates. The effectiveness of this discriminant function in accurately identifying males that were maturing for the first time at age 5 was demonstrated by the fact that the mean size of males identified by the function from the direct population samples in 2000–2002 was similar to the mean size of 5-year-old first-time spawners in both populations (26 versus 27 cm in Opeongo; 23 versus 22 cm in Provoking).

The TMRNs (i.e., the mean sizes at maturation derived from the 2000–2002 direct population sampling) differed between the populations but the PMRNs were similar. As was observed for nesting males, the mean size of newly mature males (TMRN) was significantly greater in Opeongo than in Provoking (Fig. 5; Table 1). The logistic regressions used to estimate the age-5 PMRNs for 2000–2002 were significant ($P < 0.01$) for both populations (Table 1); however, the posi-

tions of these PMRNs did not differ (Fig. 5; log-likelihood test: log likelihood = -42.5 , $P > 0.50$). The sample sizes used for the PMRN estimates were fairly low for both populations (Table 1), and this reduces their precision (Barot et al. 2004a); however, both logistic curves provided visually good fits to the data, were statistically significant, and were essentially identical for the two populations (Fig. 5).

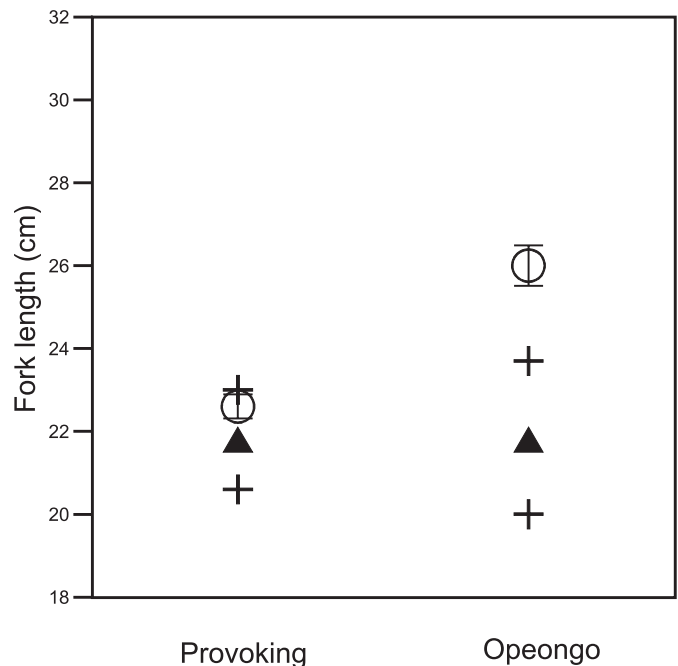
The TMRN for 5-year-old males derived from the Opeongo creel survey showed a consistent and significant (ANOVA: $F_{[5,175]} = 27.0$, $P < 0.001$) trend through time. It decreased dramatically from the 1930s to the 1950s cohorts and then stabilized for the 1960s to the 1980s cohorts (Fig. 6). The logistic regression used to estimate the position of the Opeongo PMRNs from the creel survey data was significant for all pooled cohorts (Table 1). The PMRN estimate decreased from the 1930s to the 1950s and then increased from the 1960s to the 1980s but the overall change was not as large as that observed in the TMRN (Fig. 6). There was a significant cohort effect, indicating that differences in the position of the PMRN over time were significant (log-likelihood test; log likelihood = -272.5 , $P < 0.001$). The TMRNs for the early cohorts lie above the 75th percentile of the PMRNs, but they tend to fall within the 25th and 75th percentiles for the more recent cohorts.

It should be noted that (i) the 2000–2002 PMRNs were derived from a direct population sampling program that employed a range of gear designed to provide representative samples of the size distributions of all 4- and 5-year-old fish in both lakes, and (ii) the Opeongo PMRN time series was derived from samples taken by a size-selective angling fishery. Although Shuter et al. (1987) found no evidence of changes in the size selectivity of 5-year-olds over the life of the creel survey, the harvest of 4-year-olds and, to a lesser degree, 5-year-olds was biased toward larger fish. Since immature 5-year-olds tend to be smaller than maturing 5-year-olds (Fig. 3), size-selective sampling will produce a positive bias in the estimated size distribution for immature 5-year-olds, shifting it toward larger sizes and this will cause the Opeongo creel-based PMRNs to overestimate the true PMRNs by a small but relatively consistent amount. Thus, the creel-based time series of Opeongo PMRN estimates (Fig. 6) cannot be directly compared with the 2000–2002 PMRN estimate (Fig. 5) derived from the direct sampling program. However, although the creel-based estimates may be biased toward large sizes, the temporal changes in the PMRN (Fig. 6) are relative and therefore readily interpretable.

Discussion

The analysis of changes in the MRN can help identify whether observed differences in maturation schedules are likely the product of evolved or plastic responses to ecological differences: temporal stability in the MRN suggests that the observed differences are largely the product of plastic responses; systematic change in the MRN raises the possibility that the observed differences may be the product of evolved responses (Heino 2002; Ernande et al. 2004; Stearns and Koella 1986). Downward trends in the MRN (and shifts to younger, smaller breeders) have been documented in commercial fish populations (Grift et al. 2003; Olsen et al. 2005) and suggest evolved responses to harvest; such trends will

Fig. 5. The TMRN (mean \pm 1 standard error) (\circ) and midpoint of the PMRN (\blacktriangle) for Provoking and Opeongo age-5 males captured in 2000–2002. The plus signs (+) represent the 25th (lower) and 75th (upper) percentiles of the PMRNs.



likely cause a reduction in body sizes in the catch and a decline in the quality of the fishery (Ernande et al. 2004). Moreover, evolved responses may be difficult to reverse (Law 2000) and it is therefore important for managers to detect such responses as soon as possible so that they can act to ameliorate them. This requires effective procedures for estimating the MRN.

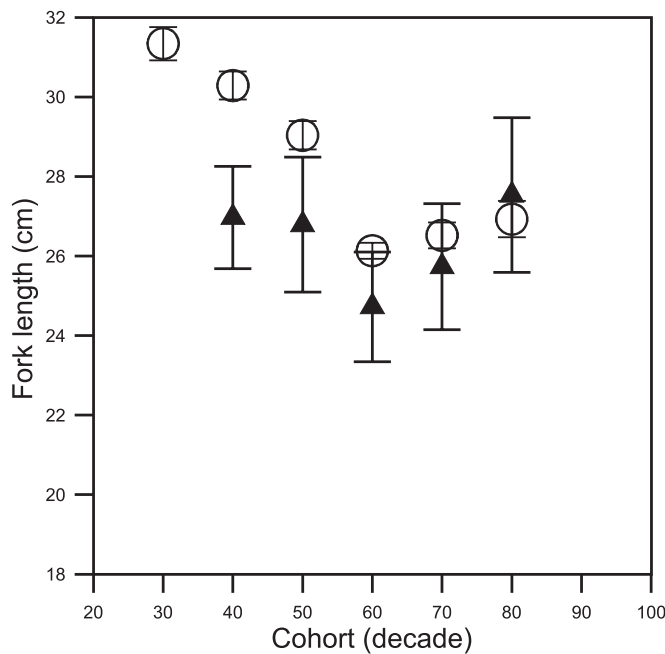
Traditional estimation of the MRN (e.g., the TMRN) was often done by plotting the relationship between age and size at maturity without considering data on immature individuals (e.g., McKenzie et al. 1983; Reznick 1990). However, an explicitly probabilistic estimator (the PMRN) should be superior to the TMRN because the position of the TMRN will be strongly affected by the mean somatic growth rate characteristic of the population (Heino et al. 2002). Our comparison of TMRN and PMRN estimates of the Provoking and Opeongo MRNs provides a strong confirmation of this assertion: the PMRN estimates were unresponsive to both the growth rate difference between Opeongo and Provoking fish and the temporal shift in the growth rates of Opeongo fish; the TMRN estimates varied directly with these growth rate changes – lower growth rates were always associated with lower TMRN values. As Heino et al. (2002) highlight, this is a necessary consequence of the inherently probabilistic character of the MRN. Given that (i) there is an age-specific range of sizes over which maturation can occur, and (ii) the probability of maturing increases from zero at the lower bound of the range to 1 at the upper bound, then, when the mean growth rate is low, only a few fish can reach the lower end of the maturation size range and thus the TMRN estimate derived from the small fraction of those fish that do mature will sit near the lower bound of the maturation size range. In contrast, when the mean growth rate is high, most

Table 1. Results of the logistic regressions used to estimate the probabilistic maturation reaction norms (PMRN) for Provoking Lake and Opeongo Lake cohorts of smallmouth bass (*Micropterus dolomieu*) sampled in 2000–2002 (1990s) and from the creel survey (1930s to 1980s).

Population and cohort	N	Reaction norm		Body size (cm)			
		χ^2	P	Immature		Newly mature	
				Mean	SE	Mean	SE
Provoking							
1990s	62	12.3	<0.001	21.1	0.22	22.6	0.29
Opeongo							
1990s	34	10.4	<0.01	22.4	0.90	26.0	0.49
1980s	79	21.6	<0.00001	23.7	0.32	26.9	0.46
1970s	147	69.0	<0.00001	22.2	0.25	26.5	0.33
1960s	304	160	<0.00001	22.4	0.15	26.1	0.20
1950s	84	48.3	<0.00001	24.1	0.50	29.0	0.35
1930s to 1940s	94	38.7	<0.00001	26.6	0.53	30.5	0.29

Note: Sample sizes (N) used in estimating the PMRNs and results of the χ^2 analysis (χ^2 and P value) used to test for significance of the logistic regressions are shown. The mean size and standard error (SE) are shown for immature and newly mature 5-year-old males used in estimating the PMRNs.

Fig. 6. The TMRN (mean \pm 1 standard error) (○) and the midpoint of the PMRN (▲) for 5-year-old males in the 1930–1980 (i.e., 30–80) cohorts in Opeongo measured from the creel survey. The vertical bars above and below the solid triangles indicate the 75th and 25th percentiles, respectively.



fish will reach the upper end of the maturation size range and the TMRN estimate derived from the large fraction of those fish that do mature will sit near the upper bound of the maturation size range. Hence, the TMRN must vary with growth rate even when the MRN (and its PMRN estimate) remains unaltered.

Our study illustrates the usefulness of mark–recapture data in MRN research. The mark–recapture data permitted us to differentiate newly matured males from previously matured males and thus show that a large and significant difference in the age distributions of all the breeding males in

Opeongo (older) and Provoking (younger) disappeared when experienced spawners (i.e., recaptures) were removed from both age distributions. Thus, we could conclude that the initial difference in age distributions was largely driven by the higher mortality rate in Provoking (Orendorff 1983) rather than by a difference in maturity schedules. Since experienced spawners have endured the growth and mortality costs of reproduction for varying periods of time, their contribution to the overall size and age distribution of mature fish will cause these distributions to reflect an ill-defined mixture of both the maturation schedule of the population (the primary focus of an MRN study) and the post-maturation growth and mortality rates suffered by mature individuals. Hence, in an MRN study, it is always desirable to identify and separate first-time breeders from experienced breeders. In situations where experienced adults cannot be identified and separated from inexperienced ones, alternative approaches to PMRN estimation based on maturity ogives have been proposed by Barot et al. (2004a) but they suffer from some potentially limiting assumptions when data on mortality are lacking.

In fishery science, two common indices used to describe maturation patterns are age and size at 50% maturity (e.g., Gangl and Pereira 2003; Olsen et al. 2004b). These measures involve running a logistic regression using either age or size as the predictor variable and maturation status as the binary response variable and are commonly referred to as maturity ogives. The maturity ogives can be used to estimate the length or age at which 50% of the population is mature. This is distinct from the PMRN estimates, which determine the body size at which the probability of becoming mature is 50%. PMRN estimates are superior to maturity ogive estimates for two reasons: (i) they summarize maturation patterns in a single descriptor rather than requiring two separate estimates for age and size, and (ii) they are not subject to the growth and survival costs incurred during and after the reproductive event itself. The main distinction is that the maturity-ogive estimate includes data from individuals that have matured at previous ages (i.e., includes experienced breeders) and is thus subject to the same bias caused by mortality that we see in the TMRN estimate. This is substantiated by the smaller size at 50% maturity (calculated using

the direct population sampling in 2000) for Provoking versus Opeongo males (22 versus 24 cm) and females (21 versus 26 cm). The between-lake differences in maturity ogives, unlike those in the PMRNs, are significant (at a 5% level using a log-likelihood ratio test) and correspond to the direction of growth rate patterns observed in the two populations.

For the Opeongo population, temporal variation in our time series of TMRN values differed significantly from the variation exhibited by our PMRN values: the TMRN values declined progressively over a 5-cm range, while the PMRN values varied erratically over a 2-cm range. These patterns of variation were accompanied by a general decline in the mean somatic growth rate of the population and a pattern of abundance variation characteristic of an introduced population — abundance rose rapidly, peaked, and then contracted somewhat and appeared to stabilize (Shuter and Ridgway 2002). The relative stability of the PMRN values suggests that the observed changes in the Opeongo maturation patterns were largely plastic responses to growth rate changes. This finding contrasts with recent work on North Sea plaice, *Pleuronectes platessa* (Grift et al. 2003) and northern cod, *Gadus morhua* (Olsen et al. 2004a), where strong downward trends in PMRN values were observed and interpreted as reflecting evolved responses to high fishing-mortality rates. The absence of such trends in the Opeongo time series could reflect the lower fishing-mortality rates experienced by this population (Shuter et al. 1987) than by the marine populations studied to date.

Our comparison of Opeongo and Provoking MRNs also suggests that the observed differences in maturity schedules between these populations was largely a plastic response to differences in growth rate: both growth rate and TMRN estimates for Provoking were significantly lower than those for Opeongo; however, the PMRN values for the two populations were essentially identical. In environments with highly size-selective mortality of adults, evolution favours those that mature earlier at smaller sizes (e.g., Reznick et al. 1990). Although natural mortality rates of adults are higher in Provoking than in Opeongo (Orendorff 1983), their ages at maturation are similar and, at least for 5-year-olds, their PMRN values are very similar. The interpopulation difference in growth rate, which seems to be driving the maturity difference, seems itself to be a plastic response to a difference in food availability (Orendorff 1983). This is strongly suggested by the results from a 1982 experiment where smallmouth bass transferred from Provoking to a lake supporting a low-density, high-growth smallmouth bass population increased their growth rates, while bass transferred from the high-growth population to Provoking decreased their growth rates (Orendorff 1983).

The PMRN approach to disentangling plastic from evolved responses that we present here assumes that variation in growth is environmentally based (Bernardo 1993) and caused by the same factors (i.e., fast-growing individuals in one population grow fast for the same reason as individuals in the other population) (Abrams and Rowe 1996). This may not always be the case because growth rates themselves can evolve (Conover and Munch 2002) and individuals may exhibit different relations between growth and age–size at maturity, depending on the kind of environmental factor that drives variation in growth (Abrams and Rowe 1996). How-

ever, our overall conclusion (i.e., differences in maturation between bass in Provoking and Opeongo are the result of phenotypic plasticity) seems reasonable because (i) growth rates in these populations have a significant and common food-driven component as suggested by a transplant experiment where Provoking bass increased their growth when transplanted to a low-density population and fast-growing bass transplanted to Provoking decreased their growth (Orendorff 1983); and (ii) the lack of a clear temporal trend in Opeongo PMRNs and the similar position of the PMRNs between Provoking and Opeongo suggests that there has been no underlying change in other factors (e.g., growth evolution and behaviour) that may influence maturation.

There are a growing number of studies utilizing PMRNs to argue that evolution has occurred in commercially important fish populations (e.g., Barot et al. 2004b; Olsen et al. 2005) and tests of the PMRN approach, such as the one we present here, are needed. To date, PMRNs have been used primarily to study temporal changes in maturation within harvested populations (e.g., Grift et al. 2003; Olsen et al. 2004a). Our study demonstrates how PMRNs can be used to isolate the influence of growth on maturation when characterizing divergence between populations in response to ecological differences.

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