

Integrating the effects of fish exploitation and interspecific competition into current life history theories: an example with lacustrine brook trout (*Salvelinus fontinalis*) populations¹

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Abstract: We used data from 17 populations of lacustrine brook trout (*Salvelinus fontinalis*) of the Canadian Shield, southern Quebec, to test whether early maturity (in males and females) and high reproductive effort (in females) are associated with increased (i) fish exploitation (sportfishing) and (ii) interspecific competition through their effects on growth and survival. The age at maturity of males and females was inversely related to the intensity of both fishing and interspecific competition. Fishing and interspecific competition affect the age at maturity through their effect on adult survival but not on growth, supporting predictions of life history models based on survival. In contrast, we did not find consistent effects of interspecific competition and fishing on the gonadosomatic index of females, which was directly related to survival (in all populations) and to the age at maturity (in exploited populations). These latter results are contrary to the predictions of life history models under the assumption that survival is directly related to growth rate. Our results suggest that reproductive effort and age at maturity are not dependent on growth when survival is independent of growth, as is the case in exploited and sympatric populations experiencing low adult survival but high growth.

Résumé : Nous avons utilisé les données de 17 populations lacustres d'omble de fontaine (*Salvelinus fontinalis*) du bouclier canadien, du sud du Québec, pour tester l'hypothèse qu'une maturité précoce (chez les mâles et les femelles) et un effort reproducteur élevé (chez les femelles) sont associés à une augmentation de (i) l'exploitation par la pêche sportive et (ii) la compétition interspécifique via leurs effets sur la croissance et la survie. L'âge à maturité des mâles et des femelles était inversement relié à l'intensité de la pêche et de la compétition interspécifique. La pêche et la compétition interspécifique ont affecté l'âge à maturité par leurs effets sur la survie des adultes mais non sur la croissance, supportant les prédictions des modèles de stratégies de vie basés sur la survie. Par contre, nous n'avons pas trouvé d'effets cohérents de la compétition interspécifique et de la pêche sur l'indice gonado-somatique des femelles, lequel était directement relié à la survie (pour toutes les populations) et l'âge à maturité (pour les populations exploitées). Ces derniers résultats sont contraires aux prédictions des modèles de stratégies de vie qui assument que la survie est directement reliée à la croissance. Nos résultats suggèrent que l'effort reproducteur et l'âge à maturité ne sont pas dépendants de la croissance lorsque la survie est indépendante de la croissance, comme c'est le cas des populations sympatriques et exploitées par la pêche, dont la survie des adultes est faible mais la croissance élevée.

Introduction

Current life history theories suggest that the reproductive investment and age at maturity of animals vary in response to age-specific survival rates if the expectation of producing future offspring is a selected trait (Schaffer 1974; Stearns 1976; Hutchings 1993). In this context, an individual should trade off between present fecundity and future survival if

one assumes that age-specific fecundity does not change with age-specific survival (Charlesworth 1980; Hutchings 1993). Growth is also expected to be involved in this trade-off because of its direct influence on age-specific fecundity (Schaffer 1974; Hutchings 1993). This is especially true for species with indeterminate growth like fish, where fecundity is positively related to body size (Køzlowski and Uchmanski 1987). Growth rate could also be indirectly re-

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lated to environmental factors associated with mortality and thus act as a signal to individuals about impending mortality (Stearns and Koella 1986). Different mathematical models have been suggested to predict the variations in reproductive effort and age at maturity from an organism's growth and survival (Roff 1984; Stearns and Koella 1986; Hutchings 1993). These models predict that high adult survival favours low reproductive effort and delayed reproduction, whereas increased juvenile growth rate favours high reproductive effort and early reproduction. The models of Roff (1984) and Stearns and Koella (1986) do not distinguish juvenile from adult growth rates, whereas that of Hutchings (1993) considers that the ratio of juvenile to adult growth is more significant than growth rate per se when predicting life history strategies.

Direct empirical support of the above theoretical predictions was provided by Hutchings (1993), who found that high juvenile to adult growth and survival ratios were associated with high reproductive effort and early maturity in three populations of unexploited brook trout (*Salvelinus fontinalis*) inhabiting small streams. Fox and Keast (1991) found that pumpkinseed (*Lepomis gibbosus*) populations experiencing high overwinter mortality exhibited earlier maturity and higher reproductive investment than populations in low-mortality environments. Fox (1994) also found that large and fast-growing juveniles, and to some extent high juvenile to adult growth ratios, favoured early maturity and high gonadal investment in a study of 27 populations of lacustrine pumpkinseed. In a metaanalysis of 85 marine and freshwater fish species, He and Stewart (2001) found a non-linear negative relationship between the von Bertalanffy growth coefficient (K) and the age at first reproduction ($T - r$). These predictions were also indirectly supported by studies relating potential for growth and survival to geographical gradients and environmental factors (Leggett and Carscadden 1978; Fleming and Gross 1990; Duchesne and Magnan 1997).

Few studies have been designed to explicitly test the effects of both competition and fish exploitation on variations of life history traits of a species in the same system. Growth and survival appear to be the driving factors that explain variations in reproductive effort and age at maturity. It is thus important to first understand the effects of exploitation and competition on growth and mortality before predicting their effects on reproductive effort and age at maturity. Based on current fishery theories, fish exploitation has a direct negative impact on adult survival (Jennings and Kaiser 1998; Hall 1999; Rochet et al. 2000). The effect of fishing on growth is more difficult to predict. Sustained removal of larger and fast-growing animals will select for small-sized, slow-growing individuals (Rochet et al. 2000). On the other hand, harvesting may release populations from density regulation, and consequently, individuals can undergo growth compensation as the intraspecific competition declines (Jennings and Kaiser 1998; Hall 1999; Rochet et al. 2000). So, the growth trajectory will depend on the species' intrinsic potential for growth (i.e., slow- versus fast-growing species) and the fishing intensity. Regarding interspecific competition, it has been shown that survival and growth of juvenile pumpkinseed are reduced in the presence of blue-

gills (*Lepomis macrochirus*) (Mittelbach 1988; Osenberg et al. 1992). Persson and Greenberg (1990) also observed a reduction in growth of age-0+ and age-1+ perch (*Perca fluviatilis*) with increasing roach (*Rutilus rutilus*) density in an enclosure experiment. However, as for fishing, increased mortality associated with competition could also involve growth compensation through a decrease in intraspecific competition. Thus, one can predict that fish exploitation and interspecific competition will promote high reproductive effort and early reproduction through their negative effect on survival. However, fish exploitation and interspecific competition will affect reproductive effort and age at maturity in different ways, depending on their effect on growth trajectories.

The first goal of this study was to test these predictions with data from 17 populations of lacustrine brook trout of the Canadian Shield, southern Quebec. This species provides a good model to study the effects of both competition and fish exploitation on the life history of a freshwater fish because unexploited and exploited populations, living with and without competitors (cyprinid and catostomid species), occur in adjacent lakes of the same area. Furthermore, the effects of competition from cyprinids and catostomids on the ecology of brook trout are well documented in this system (Magnan 1988; Tremblay and Magnan 1991; Lacasse and Magnan 1992). The second objective of the study was to explore how interspecific competition and fish exploitation affect growth and an index of survival with the aim of better understanding the mechanisms underlying the observed variations in reproductive effort and age at maturity.

Materials and methods

Study lakes

The 17 study lakes are located in two adjacent study areas in the province of Quebec (Canada): Lakes Arlequin, Belle-rive, Ford, Franciscains, Grillon, Lajoie, Michelin, Petit, Sauterelle, Vautour, and Vert are situated in the Mastigouche Reserve (46°34'N, 73°34'W), and Lakes Alphonse, Archange, Baie-verte, Formont, Sud-est, and Theode are in La Mauricie National Park of Canada (46°46'N, 73°00'W). These lakes are typical oligotrophic temperate-zone lakes with respect to surface area, mean depth, conductivity, Secchi disk transparency, and thermal stratification (Magnan 1988; Environnement Canada 1990; Lacasse and Magnan 1992). Four of these brook trout lakes were unexploited and contained allopatric populations, four were unexploited with sympatric populations, three were exploited by sportfishing with allopatric populations, and six were exploited with sympatric populations (Table 1). Exploited brook trout populations had been subject to sportfishing for at least 20 years, and their exploitation is carefully controlled by governmental agencies (Mastigouche Reserve, Ministère des Ressources Naturelles et de la Faune (Faune Québec), and La Mauricie National Park of Canada, Parks Canada). Fishery managers tend to keep the maximum annual yield of these lakes in equilibrium with the mean fish weight and fishing success, which should correspond to the maximum sustainable yield (Ricker 1975). However, lakes from La Mauricie National Park of Canada tend to be underexploited for conservation purposes.

Table 1. General characteristics of allopatric, sympatric, exploited, and unexploited brook trout (*Salvelinus fontinalis*) populations in the 17 study lakes (Canadian Shield, southern Quebec).

Lake	Surface area (ha)	Length at 2 years old (mm) ^a		GSI (g·g ⁻¹) ^b	Mean age at maturity (years)		Maximum age (years)	Fishing yield (kg·ha ⁻¹) ^c	Other fish species (BPUE) ^d		
		Females	Males		Females	Males			Se	CaCo	CaCa
Arlequin	6	189	205	0.113	2.2	2.7	3	—	—	—	—
Bellerive	10	200	210	0.076	3.1	2.7	4	—	—	—	—
Baie-verte	10	197	195	0.090	4.0	3.3	6	—	—	—	—
Theode	18	166	168	0.076	4.2	3.5	7	—	—	—	—
Franciscains	7	190	156	0.032	2.6	2.1	3	7.43	—	—	—
Petit	8	210	183	0.052	2.3	2.3	3	6.90	—	—	—
Vautour	7	160	173	0.069	2.7	2.4	3	6.55	—	—	—
Grillon	5	189	205	0.096	2.7	2.8	4	—	0.68	—	—
Sud-est	14	211	241	0.065	4.8	3.6	7	—	0.04	—	—
Michelin	8	201	203	0.116	3.3	3.2	4	—	0.69	4.84	—
Ford	32	201	216	0.058	2.8	2.7	4	—	—	3.67	0.37
Alphonse	13	196	200	0.093	4.1	4.3	6	3.69	0.02	—	—
Archange	17	163	174	0.088	4.5	4.3	6	1.87	0.10	—	—
Formont	22	223	207	0.092	4.0	4.8	5	2.46	0.10	—	—
Lajoie	10	183	173	0.045	2.7	2.3	4	3.28	—	1.50	—
Sauterelle	6	229	253	0.064	2.6	2.2	3	2.25	—	3.86	—
Vert	16	207	205	0.019	2.2	2.1	3	2.39	0.01	7.31	—

^aBack-calculated length (see text).

^bGSI, gonadosomatic index (ratio of gonad mass to total body mass).

^cSee Materials and methods.

^dBPUE, biomass per unit of effort (kg fish-gill net⁻¹·day⁻¹); Se, *Semotilus* spp. (creek chub (*Semotilus atromaculatus*); pearl dace (*Margariscus margarita*, formerly *Semotilus margarita*)); CaCo, white sucker (*Catostomus commersoni*); CaCa, longnose sucker (*Catostomus catostomus*).

In addition to brook trout, sympatric populations contained creek chub (*Semotilus atromaculatus*), pearl dace (*Margariscus margarita*, formerly *Semotilus margarita*), white sucker (*Catostomus commersoni*), longnose sucker (*Catostomus catostomus*), or a combination of these (Table 1). In this system, the intensity of interspecific competition varies from zero (allopatric brook trout populations) to intermediate (in sympatry with cyprinids) to high (in sympatry with catostomids) (see Bourke et al. 1999). So, the study lakes provided good gradients in the intensity of both fishing and interspecific competition (Table 1).

Fish sampling

Lakes in the Mastigouche Reserve were sampled from 5 to 23 September 1984 and those in La Mauricie National Park of Canada were sampled from 23 September to 13 October 1999. These differences in sampling year and site may have introduced some variation in the response variables and statistical analyses. We did not use a dummy variable coding for sampling year and study site in the statistical analyses described below because (i) we could not distinguish the variation related to the sampling year from that related to the study site (although the Mastigouche Reserve and La Mauricie National Park of Canada are adjacent and part of the same hydrographic system) and (ii) we would have had an unbalanced sample size between study sites (of our 17 study lakes, only six were in La Mauricie National Park of Canada). To examine this, we performed all statistical analyses described below with and without the second data set from La Mauricie National Park of Canada (Table 1). The

results were comparable, indicating that there was no observable effect of sampling date or study site.

Fish were captured with experimental multifilament gill nets (1.8 m deep × 38 m long with stretched mesh of 25, 32, 38, 51, 64, and 76 mm). The nets were set randomly, perpendicular to the shore, with small (25 mm) and large (76 mm) meshes alternating from the shore among gill nets. We varied the number of nets used (between 4 and 12) among lakes to capture a minimum of 100 brook trout within 4–5 days (it took 1–2 days to get this sample size with four nets in allopatric populations compared with 4–5 days with 12 nets in brook trout – white sucker lakes). Fishing took place for 16–24 h and always covered the period between 1800 and 0900 local time. Fish were kept on ice until processed in the laboratory, which occurred on the same day. All fish captured were identified, weighed (±0.1 g), and measured (±1 mm total length). Each brook trout was classified as mature or immature, and mature females were weighed (±0.1 g) with and without their gonads. Scales and otoliths were sampled in 1984 and 1999, respectively, for age determination (see details on age determination below). Scales from the left side of brook trout, between the dorsal fin and lateral line, were mounted between acetate sheets (Magnan and FitzGerald 1983).

Dependent variables

We used four dependent variables to test our hypotheses: indices of survival and growth, age at maturity, and gonadosomatic index (GSI) (ratio of gonad mass to total body mass) as a surrogate of reproductive effort by females.

Because of the sampling gear used (low catchability of ages 0+ and 1+), it was not possible to estimate the true survival rate (S) (Ricker 1975). We used catch per unit of effort (CPUE) (number of fish captured per gill net per day of fishing) to determine if brook trout survival is affected by fishing and interspecific competition and thus if these latter factors affect reproductive effort and age at maturity of trout through their effects on survival. When using CPUE to determine if brook trout survival is affected by fishing and interspecific competition, we assume that all lakes have roughly the same density of juveniles and subadults. If this assumption is true, we predict that the effects of exploitation and interspecific competition will be additive on CPUE of brook trout (see Results). It is important to note that such a use of CPUE as an index of survival related to fishing and interspecific competition does not give any information about the other causes of natural mortality. It has been shown that the presence of white sucker decreases the CPUE of juvenile and adult brook trout (Lachance and Magnan 1990; Venne and Magnan 1995) and that fish exploitation imposes a direct mortality on larger individuals in a population (Jennings and Kaiser 1998; Hall 1999).

We used the back-calculated length at ages 1 and 2 as indices of juvenile and adult growth, respectively. Length at age 1 was selected for juvenile growth because no individuals mature before 1 year of age in brook trout (Power 1980). Length at age 2 was used for adult growth because many populations had mature 2-year-old individuals (Table 1). A detailed description of the methods used to prepare the scales and otoliths and determine brook trout age can be found in Magnan and FitzGerald (1983). These authors showed that the two structures give comparable results when estimating the age of brook trout. The first author of the present paper (P. Magnan) was involved in age determinations of the two samples (1984 and 1999) to insure uniformity in the interpretation of these bone structures. Age was estimated by two readers. When the first two readings differed, two other readings were completed; the sample was discarded if there was still no agreement. Back-calculations were made following Magnan and FitzGerald (1983). For the 1984 samples, the growth increments were measured to the nearest 0.01 mm from marks drawn on a line from a clear chamber mounted on a dissecting microscope with a digitizing table interfaced with the DISBCAL-1989 software (Missouri Department of Conservation, Fisheries Division, Jefferson City, MO 65102-0180, USA). For the 1999 samples, growth increments were also measured to the nearest 0.01 mm but using an image analyzer (Cohu color camera, 8210 Series NTSC/Y-C; Cohu, Inc., San Diego, CA 92123-1827) mounted on a dissecting microscope connected to a computer and interfaced with the Sigma Scan Pro[®] program (version 4.0). We back-calculated body lengths at previous ages following the two proportional back-calculation methods: the scale-proportional hypothesis and the body-proportional hypothesis (Francis 1990). Because we got some negative back-calculated lengths when using the scale-proportional hypothesis method, we used back-calculated lengths computed with the body-proportional hypothesis method (Francis 1990).

Age at maturity of male and female brook trout were considered separately in this study, whereas reproductive effort

was estimated only for females. We used the mean age of mature individuals as an index of age at maturity (i.e., age when 50% of the individuals are mature). This was necessary because the life span of many of our exploited populations was very low (3–4 years) (Table 1), and thus, it was not possible to accurately determine the cumulative frequency of mature individuals needed to estimate the size and age at maturity from probit analyses or the first occurrence at 50% maturity (Trippel and Harvey 1991). The estimation of age at maturity from probit analyses was possible in only four of our populations. Simple age structure effects will cause the mean age of mature fish to decrease as adult mortality increases. However, the short adult life span of brook trout should ensure that most of our observed variation in mean age of mature fish results from real differences in the age at maturity. This contention is confirmed by the fact that among females, the youngest age group exhibiting a level of maturity equal to or greater than 50% was highly correlated with the mean age of mature females ($r = 0.76$, $p < 0.001$, $n = 17$). Such a comparison was not possible for males because the youngest male age group exhibiting a maturity rate greater than 50% was very similar across all populations (either 2 or 3 years). So, we considered that the mean age of mature individuals was a good index for representing the among-lake variability in age at maturity for both males and females. In the computation of mean age at maturity, we set the age of mature individuals as well as their maximum age at the end of their growing season because if not captured, these fish would have completed this growth when spawning (e.g., an age-1+ individual that was mature at the moment of capture would have reproduced at 2 years old, some weeks later). Finally, the GSI should be a good approximation of reproductive allocation in brook trout because females do not provide parental care (Power 1980; Hutchings 1993).

Independent variables

We used four independent variables to predict the age at maturity and reproductive effort of brook trout from the 17 study lakes: CPUE of brook trout as an index of survival (described above), lengths at ages 1 and 2 as indices of juvenile and adult brook trout growth, respectively (described above), mean annual brook trout yield (kilograms per hectare) of the last 5 years as a measure of fish exploitation (described above), and biomass per unit of effort (BPUE) (kilograms per gill net per day) of competing species as a measure of interspecific competition. We used the BPUE instead of CPUE for competing species because the different density – body size relationships among these (small cyprinids versus large catostomids) could bias the estimation of the overall impact of competitors on the available resources and thus on brook trout (see Brodeur et al. 2001). We also used in independent models the adult to juvenile growth ratio instead of length at ages 1 and 2 as growth indices (see Statistical analyses) to test the hypothesis suggested by Hutchings (1993) that the adult to juvenile growth ratio, not growth rate per se, is the more significant parameter when predicting life history strategies. The adult to juvenile growth ratio was computed as the back-calculated length of adults from the beginning to the end of their second year of life divided by the length of juveniles at the end of their first year of life. We also used CPUE and mean annual yield of

brook trout and BPUE of competing species as independent variables in other models to predict growth of male and female brook trout (juveniles and adults).

Statistical analyses

Even though the basic design of our study was suited to testing with a two-way analysis of variance (ANOVA) (i.e., comparison of response variables in allopatric versus sympatric and exploited versus unexploited brook trout populations), we instead used multiple linear regressions to predict the age at maturity (males and females) and reproductive effort (females) from all of the independent variables described above. This was done to determine the independent contribution of growth, survival, fishing, and interspecific competition on age at maturity and reproductive effort, considering that a part of growth and survival could be explained by fishing and interspecific competition. Furthermore, linear regression is more powerful than ANOVA to test for the main effects of fishing and interspecific competition in our study: with the ANOVA, we would have used these independent variables as categorical variables, which is less sensitive than using the raw data of mean fishing yield and BPUE of competing species (which are continuous variables). We also used multiple linear regressions to predict growth parameters of brook trout from survival, fishing, and interspecific competition to better understand factors that affect these parameters. Finally, we used simple linear regressions to test whether reproductive effort (GSI) was inversely related to age at maturity, a current prediction of life history models. All models involving growth parameters (back-calculated length at 1 and 2 years) were also run with the adult to juvenile growth ratio instead of length at 1 and 2 years (see above).

All variables that were not normally distributed were log transformed. In the stepwise procedure of the multiple linear regression, we used both the forward and backward variable selection procedures when more than two independent variables were used in the models (i.e., models predicting growth parameters, age at maturity, and GSI). In most cases, the same regression equation was obtained by both approaches, but in case of disagreement, preference was given to the best model, as indicated by the highest R^2 and the lowest mean square error associated with the estimate. Collinearity between the independent variables was evaluated by examination of the pairwise correlation coefficients. The independent variables that were highly correlated (e.g., $r = 0.7-1.0$) were not considered simultaneously in the regression analysis. After variable selection was completed, models were also screened for multicollinearity by examination of the tolerance level of individual variables (Tabachnick and Fidell 1996). The tolerances of individual variables were greater than 0.80 in all final equations. Residual scatterplots, normal probability plots, and partial residual plots were used to determine if the assumptions of the multiple linear regression were satisfied (i.e., normality, linearity, and homoscedasticity of residuals; Tabachnick and Fidell 1996). To determine if the variable selection obtained with the stepwise procedure gave the most plausible model, we compared models obtained with this procedure with the set of all possible models containing two or more independent variables. Akaike's Information Criterion (AIC) corrected for small

samples (AIC_c) was used to compare and rank all of the candidate models (Burnham and Anderson 2002). This approach for model selection helps to avoid both under- and over-fitting of the data and thus provides an objective way of selecting the model that accounts for the most variation with the fewest variables. The AIC_c was used to select the best model (i.e., the one having the smallest AIC_c value) by deriving the relative plausibility of each fitted model (Burnham and Anderson 2002). All analyses were done with SYSTAT version 8.0 software (Wilkinson 1998).

Results

The comparison of all possible candidate models developed with the AIC procedure revealed that the models produced with the stepwise variable selection in the multiple regression analyses were the most plausible models. Therefore, only the results of this latter procedure will be presented here.

CPUE and BPUE of male and female brook trout

The CPUE of brook trout females was inversely related to the intensity of fishing ($p = 0.050$) and to the BPUE of competing species ($p = 0.003$) (Table 2; Fig. 1). Fishing yield and BPUE of competing species explained 15.1% and 38.8%, respectively, of the variation in CPUE of brook trout females (Table 2). The regression model explaining the CPUE of males was marginally significant ($p = 0.071$) and showed the same trend as that of females (i.e., negative effects of fishing yield and BPUE of competing species on the CPUE of brook trout) (Table 2; Fig. 1). As for CPUE, the BPUE of brook trout females was inversely related to the intensity of fishing ($p = 0.002$) and to the BPUE of competing species ($p < 0.001$) (Table 2; Fig. 1). Fishing yield and BPUE of competing species explained 24.7% and 51.2%, respectively, of the variation in BPUE of brook trout females (Table 2). The regression model explaining the BPUE of males was significant ($p = 0.004$) and explained 54.4% of the variation (Table 2; Fig. 1). This model retained only the BPUE of competing species as a significant determinant ($p = 0.002$) and the fishing yield as a suppressive variable (i.e., an independent variable that is not significantly correlated with the dependent variable but that is useful in the model because it suppresses some variance in the other independent variable; Tabachnick and Fidell 1996). This model also showed negative effects of BPUE of competing species and fishing yield (although this latter effect was not significant, $p = 0.066$) on the BPUE of brook trout males (Table 2).

Growth

None of the models predicting the growth of male and female juvenile and adult brook trout were significant (Table 2). Only the regression model predicting the growth of adult males was marginally significant ($p = 0.053$) (Table 3; Fig. 2). This model explained a total of 34.1% of the variation in growth of adult males and retained the fishing yield as a significant determinant ($p = 0.040$) and the CPUE of brook trout as a suppressive variable. This model showed negative effects of fishing yield and CPUE of brook trout (although this latter effect was not significant) on growth of adult males (Table 3; Fig. 2).

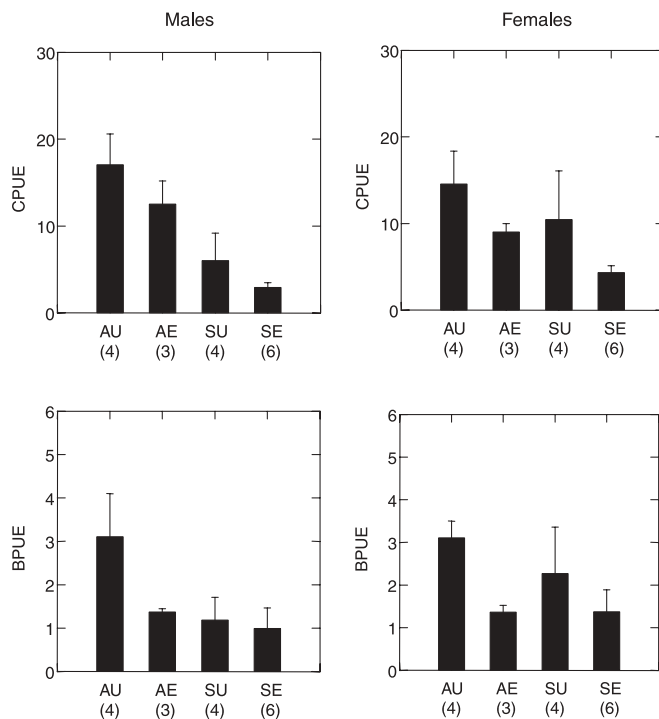
Table 2. Best regression models predicting catch and biomass per unit of effort (CPUE and BPUE) of male and female brook trout (*Salvelinus fontinalis*).

Model	<i>p</i>	SE	<i>R</i> ²	Adjusted <i>R</i> ²	<i>S</i> _{xy}
Males					
CPUE	0.071 ^a		31.4	21.6	0.87
0.11	0.595	0.21			
-0.19	Fishing yield	0.22	3.8		
-0.52	BPUE-COMP	0.21	27.6		
BPUE	0.004 ^a		54.4	47.9	0.71
-0.06	0.715	0.17			
-0.35	Fishing yield	0.18	13.0		
-0.65	BPUE-COMP	0.17	41.4		
Females					
CPUE	0.004 ^a		53.9	47.3	0.57
0.28	0.065	0.14			
-0.30	Fishing yield	0.14	15.1		
-0.51	BPUE-COMP	0.13	38.8		
BPUE	<0.001 ^a		75.9	72.4	0.51
0.27	0.043	0.12			
-0.47	Fishing yield	0.13	24.7		
-0.72	BPUE-COMP	<0.001	51.2		

Note: The partial *R*² associated with each variable was calculated as the standardized regression coefficient times the correlation coefficient between the dependent variable and this independent variable (Tabachnick and Fidell 1996). SE, the standard error of the coefficients; *S*_{xy}, the standard error of the estimate; BPUE-COMP, biomass per unit of effort of cyprinids and catostomids.

^aProbability associated with the entire model.

Fig. 1. Catch and biomass per unit of effort (CPUE (no.·gill net⁻¹·day⁻¹) and BPUE (kg·gill net⁻¹·day⁻¹) of brook trout (*Salvelinus fontinalis*) in allopatric (A), sympatric (S), exploited (E), and unexploited (U) brook trout populations in the 17 study lakes (Canadian Shield, southern Quebec). Data are means (bars) + standard errors (vertical lines above bars). The number of lakes in each category is given in parentheses.



Age at maturity

The multiple regression analyses revealed that ages at maturity of males ($p = 0.038$) and females ($p = 0.051$) were inversely related to mean fishing yield and competitor biomass and, to some extent, the CPUE of brook trout (significant in the regression model for males and as a suppressor variable in that of females; Table 4). These models explained 46.5% and 43.9%, respectively, of the variation in the age at maturity of male and female brook trout (Table 4). No models were significant ($p > 0.05$) or improved when using the adult to juvenile growth ratio instead of growth of juveniles and adults as independent variables.

Reproductive effort

The multiple regression analysis indicated that the GSI of females was positively related to the CPUE of brook trout ($p = 0.014$) (Table 4). This model explained 45.4% of the variation in the GSI of females and also retained juvenile growth as a suppressor variable (Table 4). Again, no models were significant or improved when using the adult to juvenile growth ratio instead of juvenile and adult growth as independent variables. Simple linear regressions also revealed that the GSI of females was positively related to their age at maturity in exploited lakes (exploited lakes: $p = 0.003$, $R^2 = 0.73$; unexploited lakes: $p > 0.05$) (Fig. 3). Although not significant, the GSI of females tended to be inversely related to their age at maturity in unexploited lakes.

Discussion

The CPUEs of male and female brook trout were significantly lower in sympatric than in allopatric populations and in exploited than in unexploited lakes, supporting that the effects of these factors were additive and thus that brook trout

Table 3. Best regression models predicting growth of male and female juvenile (back-calculated length at 1 year) and adult (back-calculated length at 2 years) brook trout (*Salvelinus fontinalis*).

Model		<i>p</i>	SE	<i>R</i> ²	Adjusted <i>R</i> ²	<i>S</i> _{xy}
Males						
Juvenile growth		0.462 ^a		17.4	0.1	0.80
–0.18		0.410	0.21			
–0.17	Fishing yield	0.435	0.21	9.4		
0.26	BPUE-COMP	0.381	0.29	5.2		
0.43	CPUE-SAFO	0.296	0.38	2.8		
Adult growth		0.053 ^a		34.1	24.7	0.71
–0.04		0.814	0.18			
–0.40	Fishing yield	0.040	0.17	19.9		
–0.39	CPUE-SAFO	0.104	0.23	14.2		
Females						
Juvenile growth		0.281 ^a		24.7	7.3	0.80
–0.28		0.410	0.21			
–0.05	Fishing yield	0.435	0.21	0.4		
0.43	BPUE-COMP	0.381	0.29	15.2		
0.71	CPUE-SAFO	0.296	0.38	9.2		
Adult growth		0.441 ^a		11.0	0.1	0.67
–0.19		0.274	0.17			
–0.06	Fishing yield	0.710	0.16	1.0		
–0.27	CPUE-SAFO	0.214	0.21	10.0		

Note: The partial *R*² associated with each variable was calculated as the standardized regression coefficient times the correlation coefficient between the dependent variable and this independent variable (Tabachnick and Fidell 1996). SE, the standard error of the coefficients; *S*_{xy}, the standard error of the estimate; BPUE-COMP, biomass per unit of effort of cyprinids and catostomids; CPUE-SAFO, catch per unit of effort of brook trout.

^aProbability associated with the entire model.

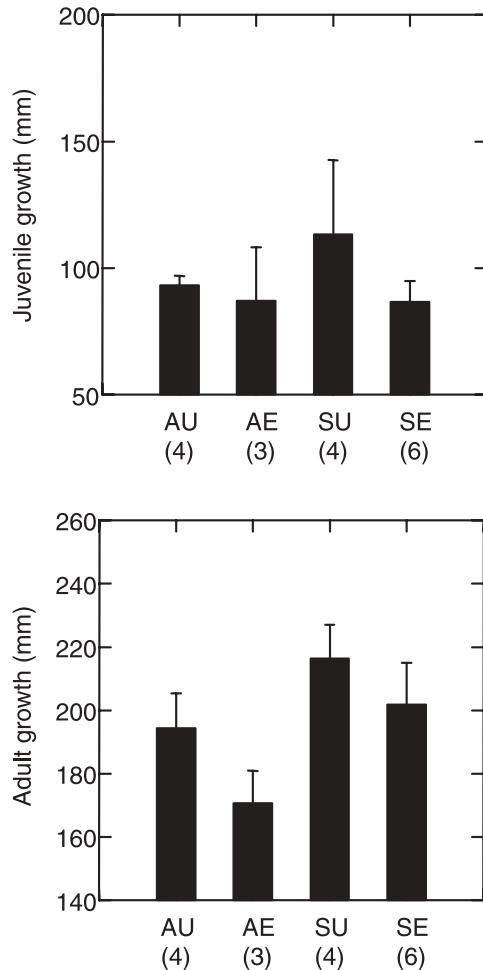
survival is lower in exploited and sympatric populations. The fact that we considered replicates of each treatment level prevented us from interpreting outlier or atypical populations (e.g., stunted populations). It is well documented that fishing, through the harvesting of larger individuals, decreases adult survival (Jennings and Kaiser 1998; Hall 1999). Studies done in our system also indicate that mortality associated with competition occurs in both juvenile and adult brook trout. Venne and Magnan (1995) found that young-of-the-year brook trout (captured in June) were 90% less abundant in five lakes containing white sucker than in five others containing allopatric brook trout, indicating that there is an important bottleneck on juvenile brook trout survival in the presence of white sucker. Furthermore, Lachance and Magnan (1990) observed that the recoveries (creel census) of stocked age-1+ and age-2+ brook trout (wild, domestic, and hybrid strains) were 75% lower in three lakes with white sucker than in three allopatric lakes.

One prediction of life history models is that low adult survival will favour early maturity (Roff 1984; Stearns and Koella 1986; Hutchings 1993). Based on the tenets of these models, we predicted that interspecific competition and fish exploitation would promote early maturity through their negative effects on adult survival. This prediction was supported by our data on lacustrine brook trout populations of the Canadian Shield: the ages at maturity of males and females were inversely related to the intensity of both fishing and interspecific competition by cyprinids and catostomids. In an analysis of 84 populations of 49 species, Rochet et al. (2000) found that increasing fishing pressure decreases age at maturity. However, the inverse relationship between the age at maturity and CPUE of brook trout (significant for

males and as suppressive variable for females) is more difficult to interpret. In these models, CPUE of brook trout (when significant) explained a given proportion of the variation in the age at maturity, after the effects of fishing and interspecific competition were accounted for in the regression models. If CPUE of brook trout is a good index of the other causes of mortality, then this component of mortality does not support the current hypothesis that low adult survival will favour early maturity. However, one must be cautious when interpreting CPUE of brook trout as an index of survival in this context (i.e., in a model considering simultaneously the effects of fishing, interspecific competition, and other causes of mortality) because fishing and interspecific competition might drive mortality of brook trout in this system.

Life history models also predict that high juvenile growth will favour early maturity (Roff 1984; Stearns and Koella 1986; Hutchings 1993). We did not find any significant effect of fishing and interspecific competition on growth of juvenile or adult brook trout. Furthermore, the regression model predicting the age at maturity did not retain any growth parameters. It was difficult to predict the effect of fishing and interspecific competition on growth trajectories and thus on the age at maturity of brook trout. In some cases, it has been shown that growth is reduced in the presence of competing species. For example, juvenile pumpkinseed growth is reduced in the presence of bluegills (Mittelbach 1988; Osenberg et al. 1992), and Fox (1994) showed that these decreases in growth were associated with delayed maturity and lower reproductive effort in pumpkinseed. However, factors other than juvenile growth may have contributed to the observed differences in life histories between sympatric and

Fig. 2. Growth of juvenile (back-calculated length at 1 year) and adult (back-calculated length at 2 years) brook trout (*Salvelinus fontinalis*) males in allopatric (A), sympatric (S), exploited (E), and unexploited (U) populations in the 17 study lakes (Canadian Shield, southern Quebec). Data are means (bars) + standard errors (vertical lines above bars). The number of lakes in each category is given in parentheses.



allopatric pumpkinseed populations, like differences in adult compared with juvenile survival, environmental factors among lakes, and piscine predators (Fox 1994). Brodeur et al. (2001) found that competitive release from white sucker, through mass removal, significantly improved juvenile and adult brook trout growth in the lakes where white sucker removal was highest. We thus expected a similar growth compensation in sympatric and exploited populations owing to the effect of competitive release at the intraspecific level (as both fishing and interspecific competition decrease brook trout abundance). It is possible that when they are at equilibrium with competition and fishing exploitation, sympatric and exploited brook trout populations experience growth similar to allopatric and unexploited populations. Despite this, there is still an incongruity with respect to the current prediction of life history models: after controlling for the effects of interspecific competition and fishing, the multiple regression did not retain any growth parameters as factors explaining the age at maturity.

Finally, life history models predict that low adult survival and high juvenile growth will be associated with high reproductive effort (Roff 1984; Stearns and Koella 1986; Hutchings 1993). The analysis by Rochet et al. (2000) on 49 exploited species supported the hypothesis based on survival: decreased survival (associated with increased fishing pressure) was related to increased reproductive effort. We did not find any significant effect of interspecific competition or consistent effect of fishing on the GSI of females. Female GSI was directly related to an index of adult survival (in all populations) and with the age at maturity (in exploited populations). These results are opposite to the predictions of life history models under the assumption that survival is directly related to growth. Hutchings (1993) suggested that a positive association between growth and survival is not a prerequisite for the prediction of life history models to be true. Anadromous salmonids provide an example of how the selective benefits of high reproductive effort can overcome the selective disadvantages of high adult mortality. Compared with freshwater habitats, the marine environment provides a rich food resource for salmonids and allows for rapid growth with a concomitant high reproductive effort, despite the significantly higher mortality experienced at sea (Hutchings 1993). Such a phenomenon might also occur in freshwater ecosystems. Compared with the growth of many freshwater brook trout populations (Scott and Crossman 1973; Power 1980; Hutchings 1993), our populations are among the fast-growing ones. This high growth is probably related to habitat type (individuals from lake populations are usually larger than individuals from small streams) and latitude (low latitudes provide better conditions for growth than higher ones through the effect of latitude on the length of the growing season; Venne and Magnan 1989; Conover 1992; Duchesne and Magnan 1997). So, it is possible that, over a given juvenile growth rate, the benefits of high reproductive effort can overcome the advantage of delaying reproduction and reducing reproductive effort even when adult survival is high (i.e., observed positive relationship between GSI and the index of female survival). It is also possible that in a fast-growing population, survival, not growth, would be the main determinant of the age at maturity and that the reproductive effort would not be a main issue (because rapid growth is concomitant with high reproductive effort, and thus, reproductive effort will be high in any case). In the context of fast-growing populations, the difference in growth related to competition and fishing might not be detectable, but the rapid growth of juveniles is still related to high reproductive effort and thus conforms to the life history predictions. There might not be enough variation in growth in these populations to observe any effect of this parameter on the age at maturity and reproductive effort.

The above hypothesis about fast-growing populations could explain why the adult to juvenile growth parameter was not a better predictor than length at ages 1 and 2 in our statistical analyses because in this case, both juveniles and adults are fast growing. This hypothesis could also explain why we did not observe any compensatory growth response of brook trout in sympatric and exploited lakes due to the decrease in intraspecific competition. Juvenile and adult growth may be high enough to prevent any growth response given the level of competitive release. Finally, our results

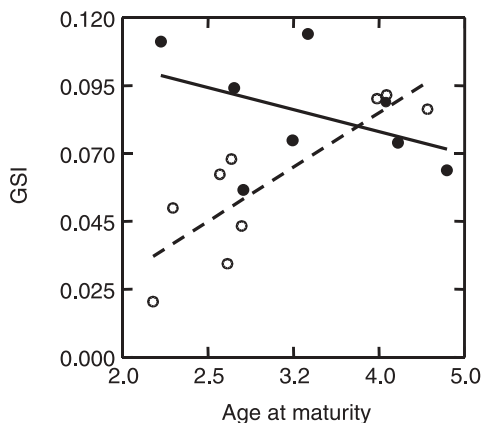
Table 4. Best regression models predicting the age at maturity of male and female brook trout (*Salvelinus fontinalis*) and the gonadosomatic index (GSI) of females.

Model	p	SE	R^2	Adjusted R^2	S_{xy}
Males					
Age at maturity	0.038 ^a		46.5	34.2	0.83
-0.02	0.906	0.20			
-0.46	Fishing yield	0.041	0.21	19.7	
-0.58	CPUE-SAFO	0.047	0.24	13.4	
-0.70	BPUE-COMP	0.012	0.25	13.4	
Females					
Age at maturity	0.051 ^a		43.9	31.0	0.84
0.36	0.143	0.23			
-0.57	Fishing yield	0.032	0.24	11.8	
-0.77	CPUE-SAFO	0.072	0.39	16.5	
-0.81	BPUE-COMP	0.014	0.29	15.6	
GSI	0.014 ^a		45.4	37.6	0.67
-0.11	0.546	0.17			
0.51	CPUE-SAFO	0.034	0.22	32.0	
0.38	Juvenile growth	0.084	0.21	13.4	

Note: The partial R^2 associated with each variable was calculated as the standardized regression coefficient times the correlation coefficient between the dependent variable and this independent variable (Tabachnick and Fidell 1996). SE, the standard error of the coefficients; S_{xy} , the standard error of the estimate; BPUE-COMP, biomass per unit of effort of cyprinids and catostomids; CPUE-SAFO, catch per unit of effort of brook trout.

^aProbability associated with the entire model.

Fig. 3. Relationship between the gonadosomatic index (GSI) ($\text{g}\cdot\text{g}^{-1}$) and the mean age at maturity (years) of females in exploited (broken line, open circles) and unexploited (solid line, solid circles) lakes of the Canadian Shield, southern Quebec. Note that the figure shows untransformed data on logarithmic scales.



suggest that survivorship is more important than growth in predicting age at maturity. Fox (1994) reached this conclusion with pumpkinseed and discussed the importance of mortality relative to growth in the evolution of life histories. There are often exceptions to the predictions of life history models (early maturity associated with slow growth and delayed maturity associated with high growth; see Hutchings 1993; Fox 1994), but these exceptions are most often explained by variations in survivorship. In contrast, predictions based on survival usually support life history models. The current life history models assume that survival is directly related to growth. However, reproductive effort and age at maturity would not be dependent on growth when survival is

independent of growth, like in exploited and sympatric populations that experience low adult survival but high growth.

Whether the differences in age at maturity of the brook trout observed in our system are under genetic control or related to phenotypic plasticity of individuals cannot be determined from our experimental design. The results of Fox and Keast (1991) and Fox (1994) showed that pumpkinseed populations co-occurring with bluegills did mature significantly later and at larger sizes and tended to have lower gonadal investment than populations living in systems without bluegills. Their observations, based on winterkill events in beaver ponds and a transplant enclosure experiment, suggested a high phenotypic plasticity in the age at maturity and reproductive investment in pumpkinseed. Both brook trout fishing and the presence of cyprinids and catostomids, through bait fish introductions (Magnan 1988), are recent in our system (within the last century). The work of Brodeur et al. (2001) suggests that brook trout growth is under phenotypic control in this system: a 3-year mass removal of white sucker significantly improved juvenile and adult brook trout growth in the lakes where white sucker removal was highest. So, it is possible that early maturity in brook trout populations experiencing higher adult mortality, through interspecific competition and fishing, would be within the reaction norm of individuals.

In conclusion, our results suggest that fast-growing populations that experience high adult mortality (here through interspecific competition and fishing) exhibit life history strategies comparable with those of slower growing populations when predictions are based on survival (i.e., early maturity and high reproductive effort are associated with high adult mortality). However, the inverse relationship between growth and survival is such that growth would not be a driving factor in the evolution of life history strategies of these populations. These results thus highlight the often overriding

importance of survival in influencing life history traits. It will be important to formalize the different growth trajectories associated with fishing and interspecific competition in future mathematical models to better understand and predict their effects on life history strategies of fishes. Such models would be useful in managing exploited species and those experiencing interspecific competition, or both.

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