

Plasticity in maturity and fecundity of yellow perch, *Perca flavescens* (Mitchill): comparisons of stunted and normal-growing populations

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Maturity, fecundity, and egg size of a stunted (mean length at age 5: 13.5 cm) and normal-growing (21.8 cm) population of yellow perch (*Perca flavescens* Mitchill) were studied in central Alberta, Canada. Stunted perch matured at a younger age and at a much smaller size than normal perch. Minimum size at initial maturation in stunted females was the smallest recorded in the literature for either perch (*Perca*) species. Relative fecundity, the slope of the fecundity-weight regression, and the gonado-somatic index were significantly higher in stunted perch. Mean dry weight of eggs, percentage connective tissue, gonad energy content, and gonad weight specific fecundity were similar for perch from both populations. Reproductive parameters of stunted perch are discussed in the context of life-history theory.

1. Introduction

Although numerous studies have dealt with the biology and ecology of perch (*Perca flavescens* Mitchill and *P. fluviatilis* L.), relatively little information exists on the fecundity and age at maturation of these species, particularly *P. flavescens*. From both a basic ecological and a management perspective it is, however, important to know whether gonadal production is divided into many or few eggs in order to better understand the dynamics of perch populations and to obtain more reliable estimates of early juvenile mortality. Fecundity may vary greatly between (Tsai & Gibson 1971, Thorpe 1977a) and

within populations among years (Bagenal 1973, Sztramko & Teleki 1977, Craig 1982, Makarova 1986), and also between individual fish of similar size (Muncy 1962, Stehlik 1968, Sheri & Power 1969, Craig 1980, Wells & Jorgenson 1983). Nevertheless, most of the available data indicate that fecundity in perch is positively correlated with fish size (Muncy 1962, Sheri & Power 1969, Tsai & Gibson 1971, Mann 1978, Treasurer 1981, Viljanen & Holopainen 1982), and, somewhat less so, with age (Tsai & Gibson 1971, Brazo *et al.* 1975, Treasurer 1981, Schneider 1984). A few studies on other fish species have documented a negative correlation between fecundity and egg size (see summaries

in Bagenal 1978 & Wootton 1979, Fleming & Gross 1990) indicating that, in accordance with life-history theory, a trade-off exists between egg size and egg number. For perch, such a relationship has not been clearly documented, although Muncy (1962), Sztramko and Teleki (1977), and Treasurer (1981) reported no obvious variation of egg size with fecundity, whereas fish length and fecundity were positively correlated.

Both *P. flavescens* (e.g. Schneider 1984, Boisclair & Leggett 1989) and *P. fluviatilis* (e.g. Alm 1946, Tesch 1955) exhibit considerable variation in growth patterns, and thus offer an opportunity to evaluate how maturity and fecundity respond to differences in growth. Improved growing conditions as a result of, for example, higher temperatures (Thorpe 1977a), eutrophication (Hartman 1975, Lang & Lang 1983), and exploitation (Healey 1975, 1978) have been proposed to increase the rate of maturation in fish. However, this relationship is not always straight forward in perch. Alm (1959) noted that in most cases sexual maturity occurs earlier with good growth, but under very unfavourable environmental conditions slower growing perch (*P. fluviatilis*) may also mature earlier and at a smaller size (Alm 1952, Tesch 1955 & Alm 1959). Furthermore, the relationship between growth, age and maturity is possibly constrained by a minimum size threshold for first maturation (Holčik 1969, Thorpe 1977a, Malison *et al.* 1986).

In order to test the hypotheses that size and age at first sexual maturity is positively related to growth rate, and that a minimum length of 80 mm is necessary before sexual maturity can be attained in *P. flavescens* (Malison *et al.* 1986), growth and maturity schedules of a stunted and a normal growing population of *P. flavescens* from the same geographical area were compared. A further objective of this study was to determine the relationships between fish length, weight or age and fecundity or egg weight, and to evaluate the existence of a trade-off between egg-size and egg number.

2. Material and methods

2.1. Description of the study area

Yellow perch populations in Narrow Lake (54°45'N, 113°37'W) and Baptiste Lake (54°45'N, 113°33'W) in central Alberta represent examples of a stunted (mean length at age 5: 13.5 cm) and a 'normal'-growing (21.8 cm) popula-

tion, respectively (Jansen & Mackay 1991). Throughout this paper, these fish are referred to as 'stunted' and 'normal' perch. Both lakes are located within the same geographical area, the southern mixed-wood boreal forest. Narrow (1.1 km²) and Baptiste Lake (9.8 km²) are above average size compared to other lakes in that region and have similar mean depths of 14.2 m (Narrow L.) and 9.3 m (Baptiste L.). Baptiste Lake has historically been eutrophic (mean summer total phosphorus in south basin 49 mg × m⁻³; Mitchell & Prepas 1990), whereas Narrow Lake is a mesotrophic lake (mean summer total phosphorus 10.5 mg × m⁻³; Prepas & Trimbee 1988) with a relatively small littoral zone. Other than yellow perch, the fish community of both lakes consists of northern pike (*Esox lucius*), burbot (*Lota lota*), brook stickleback (*Culea incostans*), and Iowa darter (*Etheostoma exile*). In addition, Baptiste Lake provides habitat for walleye (*Stizostedion vitreum*), white sucker (*Catostomus commersoni*), cisco (*Coregonus artedii*), ninespine stickleback (*Pungitius pungitius*), and spottail shiner (*Notropis hudsonius*).

2.2. Fish sampling

Between May 5, 1986 and March 24, 1989, yellow perch were collected from Narrow and Baptiste Lake at regular intervals. Sampling gear consisted of Windermere perch traps, Fyke nets, a 15.2 × 1.8 m floating bag seine with 6 mm (stretched) knotless mesh, a 56 × 3 m sinking bag seine with 9 mm knotless mesh, and hook and line. The latter were used exclusively for ice-fishing in January and March. During the spawning season between April and June, sampling by seine (see below) was conducted biweekly and traps and Fyke nets (see below) were checked every second day over a 6-week period.

On each sampling occasion, approximately 40 fish (if available) age-0+ and older were kept, representing as nearly as possible the observed size range of the total catch. Upon capture, fish were killed with a 0.2% aqueous solution of 2-phenoxyethanol, then immediately stored on ice, and transported back to the laboratory. There, perch were kept at 0.5°C and wet weight (± 0.01 g), total length (TL; ± 0.1 cm) and sex were recorded within 2 d of capture. Sex was determined by the macroscopic appearance of the gonads. In perch, the female gonads of perch fuse to form a single ovary early during larval development, while in males the testes remain paired (Malison *et al.* 1986). To determine age, both opercular bones of each fish were removed, cleaned from attached tissues, and the number of growth rings (annuli) were determined, following a technique similar to Le Cren (1947).

2.3. Size and age at first sexual maturity

The size and age of first sexual maturity of perch was determined from fish caught during and at the end of the spawning season between the end of April and the beginning of June. At this time, based upon visual inspection of the gonads and plots of the gonadosomatic index, *GSI*, (gonad weight × body weight⁻¹ × 100) ripe and spent mature females (Fig. 1), and males could be easily distinguished from immatures. However, only relatively small numbers of fe-

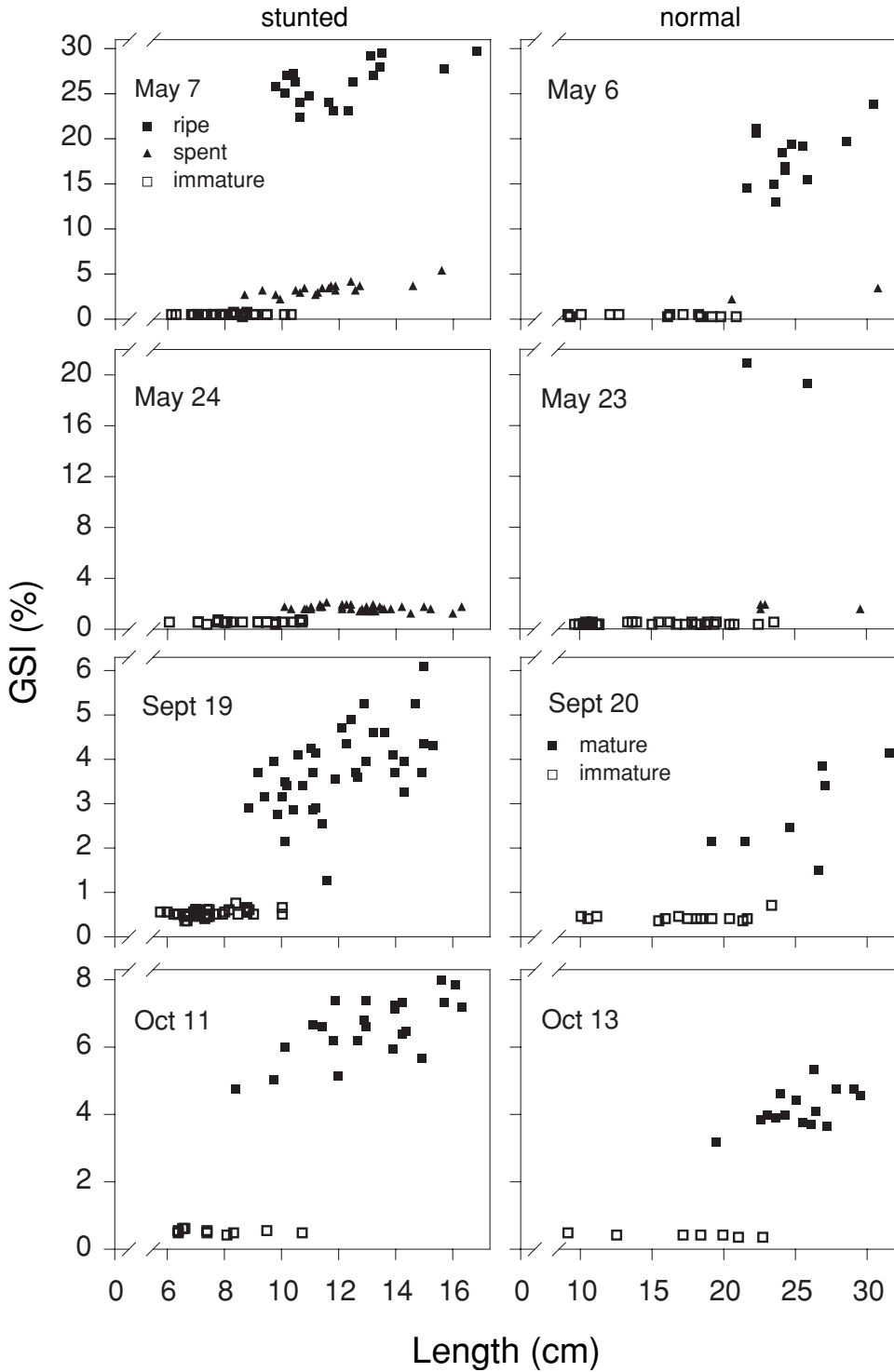


Fig. 1. Relationship between gonado-somatic index (GSI) and fish length for stunted and normal female yellow perch (*Perca flavescens*). Selected dates represent the situation immediately before (early May) and at the end (late May) of the spawning season, and at the time of rapid gonadal development in September and October.

males were caught during the spawning period. In order to increase sample size, females and males caught between September and March were also used in the analysis of age at maturity. During this latter period, gonadal growth, particularly in males, progressed rapidly, and maturity could be assessed based on the value of the *GSI* (Fig. 1). Mean age at sexual maturity was defined according to L'Abée-Lund *et al.* (1990) as the age at which 50% of the female and male perch, respectively, were mature. This age was estimated by linear interpolation between the two ages at which 50% maturity would occur.

2.4. Fecundity and egg size

Fecundity was determined from 28 stunted and 29 normal females caught in May 1987, and March–April 1988 from Narrow and Baptiste Lake, respectively. According to Mance (1988), maximum potential fecundity in *P. flavescens* is modulated downward by preovulatory atresia, but the actual number of oocytes produced does not change past January. To estimate absolute fecundity, the total weight (± 0.0001) of the gonads was recorded. After removal and weighing (± 0.0001) of the peritoneal layer and the tunica (Treasurer & Holliday 1981), which are further referred to as 'connective tissue', three subsamples of exactly 300 eggs each were counted and weighed (± 0.0001 g). Egg subsamples, the remainder of the gonad, and the connective tissue, were separately dried to a constant weight (± 0.00001) and fecundity was calculated by multiplying by 300 the ratio of the total weight of the gonad (excluding removed connective tissues) to the average weight of the three subsamples. Egg size was expressed in terms of dry weight. To determine the reliability of the method to estimate fecundity, all eggs present in the ovaries of six perch were counted. In all cases, the estimate based on the three subsample counts was within 2% of the total count. In addition, two measures of weight specific fecundity were obtained. Relative fecundity (Bagenal 1978) was calculated as the number of eggs $\times g^{-1}$ total body weight. The number of eggs $\times g^{-1}$ gonad weight described the relationship between gonad size and fecundity.

As a further estimate of egg size, yolk diameters were measured (± 0.04 mm) under a dissecting microscope equipped with an ocular micrometer. Thirty eggs each from the anterior end, the centre, and the posterior end of the ovaries of three stunted and normal perch each were measured. These fish were captured in May, shortly before spawning. To determine if eggs differed in energy content among perch populations, 1 g of gonad without connective tissue was combusted in a bomb calorimeter (Parr, Model 1241) for 12 perch from each lake.

2.5. Statistical analysis

Differences in reproductive parameters between stunted and normal perch were tested by analysis of variance (ANOVA) and linear regression, using the Statistical Analysis System

(SAS 1984). A probability of $P \leq 0.05$ was considered significant. Homogeneity of variances was tested applying Hartley's F_{\max} -test (Sokal & Rohlf 1981). Stepwise linear regression procedures were applied to test the significant contribution of fish length, weight, gonad size, and age in explaining variation in fecundity or egg weight. Differences in the slopes of significant regression equations between stunted and normal perch were evaluated by analysis of covariance (ANCOVA).

3. Results

3.1. Age and size at maturity

Out of the 483 stunted males analyzed for maturity status, almost all fish had reached maturity by the time they were two years old, and one male reached maturity after the first growing season (Table 1). This perch measured 5.9 cm and weighted 1.71 g (Table 2), which was the smallest weight of any mature stunted male measured. One of the 2-year old mature males was 5.8 cm long. In contrast, the smallest mature male from the normal population measured 10.0 cm and weighted more than 10 g (Table 2). The average age of maturity (1.61 years)

Table 1. Percentage of mature stunted and normal-growing yellow perch from Narrow and Baptiste Lake, respectively. Only perch captured between September and May were used to determine maturity status. No perch older than age 7 were caught from Narrow Lake and all perch older than age 7 from Baptiste Lake were mature.

Age	Stunted		Normal	
	N	% mature	N	% mature
Females				
1	164	0.0	144	0.0
2	140	6.4	91	0.0
3	142	69.0	100	3.0
4	93	98.9	121	9.1
5	23	100.0	87	70.1
6	7	100.0	22	95.5
7	3	100.0	18	100.0
Males				
1	128	0.8	112	0.0
2	161	96.9	129	25.6
3	117	100.0	103	91.3
4	56	100.0	132	100.0
5	13	100.0	98	99.0
6	6	100.0	29	100.0
7	2	100.0	9	100.0

of stunted males was nearly 1 year less than that of normal males (2.52 years). The largest immature females from the stunted population attained just over 10% of the weight of the smallest normal females which had reached maturity (Table 2). Moreover, every mature normal perch was considerably larger than even the biggest stunted perch (for weights, see Fig. 2). The smallest stunted female was 8.4 cm long and weighed 5.52 g (Table 2). At an average age of 2.84 years, stunted females matured exactly 2 years earlier than their normal conspecifics (4.84 years).

3.2. Fecundity and egg size

Mean fecundity of 28 stunted females, 9.8–16.8 cm, was 3 992 eggs (range: 1 910–11 812). The corresponding value for 29 normal perch (20.0–30.5 cm) was 22 658 eggs (range: 10 639–55 592). For both populations, fecundity was positively correlated with fish weight (Fig. 2), length, and age, with weight being the best predictor, explaining 89% and 84% of the variability in fecundity of normal and stunted perch, respectively (Table 3). Furthermore, in a stepwise regression using weight, carcass weight (total body weight minus the weight of gonads, liver, and gastro-intestinal tract), length, and age as independent variables, only fish weight contributed significantly to the regression equation in normal perch. For the stunted fish, carcass weight ($P = 0.001$) and age ($P = 0.05$) also were significant in explaining variability in fecundity beyond the contribution of total weight. The slopes of linear regressions describing the relationship between weight and fecundity were significantly different for female stunted and normal perch (ANCOVA, $P < 0.05$), and indicated that fecundity of stunted perch increased faster with increasing fish weight (Fig. 2). Although the weight range of stunted and normal perch did not overlap and values had to be extrapolated for stunted fish, the above relationship between fecundity and weight was used to calculate the fecundity of a 100 g 'standard' perch. For the stunted population this hypothetical fish produced approximately 5 000 more eggs ($16\,556 \pm 710$) than a corresponding female from the normal population ($11\,327 \pm 2\,245$).

Mean egg dry weight (stunted: 0.224 g, normal: 0.239 g), percentage connective tissue (5.11% for both groups), and caloric content (985 and $956 \text{ cal} \times \text{g}^{-1}$ wet weight) of the ovaries did not differ in stunted

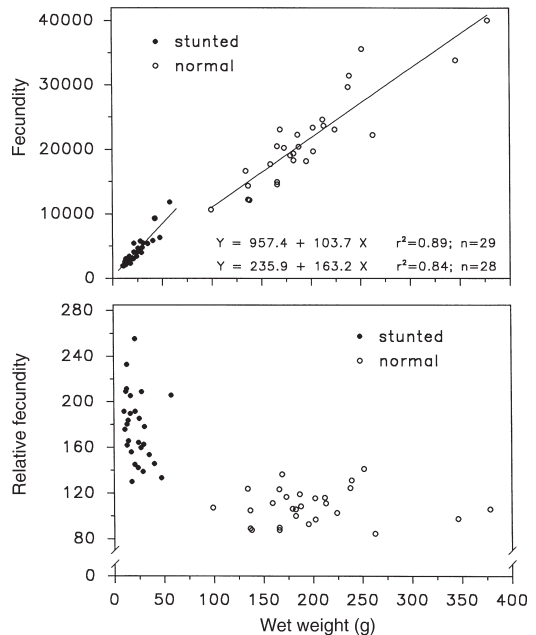


Fig. 2. Relationship between fecundity and relative fecundity to fish wet weight for stunted and normal yellow perch (*Perca flavescens*). Significant regression equations are indicated.

and normal perch (Fig. 3). The number of eggs per gram gonad weight (766 and 740) was also similar for fish of both populations (Fig. 3). However, mean *GSI* (Fig. 3) and relative fecundity (Figs. 3 and 4B) were significantly (ANOVA, $P < 0.0001$) higher in stunted perch than in normal conspecifics. Mean yolk diameters in

Table 2. Lengths (mm), weights (g) and age at spawning of the smallest mature and largest immature stunted and normal growing yellow perch from Narrow and Baptiste lakes, respectively. Only perch captured between January and May of each year were used to determine maturity status.

Population	Length (mm)	Weight (g)	Age
		♂♂, smallest mature	
Stunted	58	1.71	1
Normal	100	10.62	3
		♂♂, largest immature	
Stunted	72	3.57	3
Normal	161	45.49	3
		♀♀, smallest mature	
Stunted	84	5.52	2
Normal	193	91.46	3
		♀♀, largest immature	
Stunted	107	10.05	3
Normal	264	254.08	6

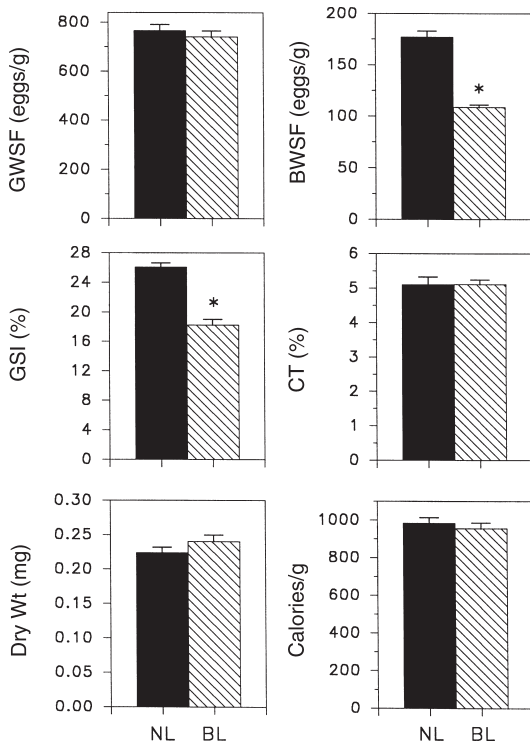


Fig. 3. Mean (\pm S.E.) gonad weight specific fecundity (GWSF), body weight specific fecundity (BWSF), gonado-somatic index (GSI), percentage contribution of the connective tissue to gonad weight (CT), egg dry weight, and energy content of gonadal tissues of stunted (dark bars, NL) and normal (patterned bars, BL) yellow perch (*Perca flavescens*). Asterisks indicate significant ($P < 0.0001$) differences between stunted and normal fish.

stunted perch (0.96 ± 0.05 mm) were significantly ($P < 0.01$) smaller than those of normal perch (1.07 ± 0.04 mm). No difference in egg size could be found between the different areas of the gonad. However, there was significant (ANOVA, $P < 0.05$) variation in yolk diameters among the three fishes analyzed from each population.

Gonad weight explained 89% of the variance in fecundity for both stunted and normal perch (Table 3). Relative fecundity was not significantly correlated with fish size in either stunted or normal perch (Fig. 2), a necessary condition for the unbiased use of this parameter for comparisons between populations (Bagenal 1978). Relative fecundity decreased with increasing age in stunted perch (Fig. 4B), although not significantly (ANOVA, $P = 0.07$). In normal

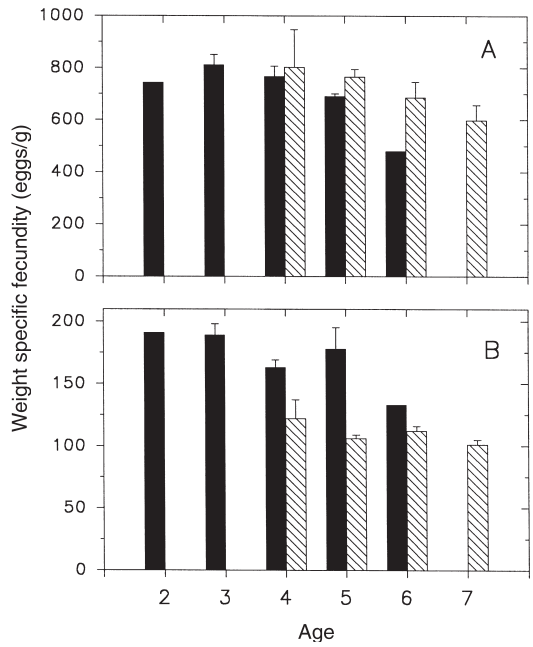


Fig. 4. Gonad weight specific (A) and body weight specific (B) fecundity for age-classes 2–7 years of stunted (dark bars) and normal (patterned bars) yellow perch (*Perca flavescens*). No ripe females 3 years or younger were found for normal perch, no ripe female older than 6 years could be obtained for stunted perch.

perch, relative fecundity remained stable over all age classes for which data were available (Fig. 4B). Gonad weight specific fecundity decreased significantly ($P < 0.05$) with increasing age for individuals from both populations (Fig. 4A). Connective tissue weight increased linearly and significantly ($P < 0.0001$) with increasing gonad weight in both populations, but did not show any significant relationship with age or size for either stunted or normal perch.

Fecundity showed no significant relationship to egg dry weight in stunted perch, but increased with egg weight in normal perch (Table 3). The residual variance in this regression, however, was substantial. Furthermore, if one perch (with the highest fecundity and the smallest egg weight) was excluded from the analysis of stunted perch, the relationship between fecundity and egg weight also became positive ($P < 0.05$), i.e., stunted and normal perch did not basically differ in the way total egg number and egg weight were related. However, when relative fecundity (RF) and egg dry weight ($EDWt$) were correlated, a negative linear relationship existed in both

stunted ($RF = 297.4 - 535.8 \text{ EDWt}$; $r^2 = 0.46$; $P < 0.0001$) and normal perch ($RF = 147.8 - 165.4 \text{ EDWt}$; $r^2 = 0.12$; $P < 0.05$). As indicated by a significant difference in slopes (ANCOVA, $P < 0.01$), this relationship was much more pronounced in stunted fish, thus suggesting that differences in egg weight are mainly responsible for the large range in weight specific fecundity found in stunted perch (Fig. 2).

Egg dry weight was positively related to age in stunted ($\text{EDWt} = 0.148 + 0.021 \text{ age}$; $r^2 = 0.19$, $P = 0.01$) and in normal perch ($\text{EDWt} = 0.122 + 0.022$; $r^2 = 0.16$, $P < 0.05$). Stepwise regression including length, weight, and age as independent variables within the model, indicated that for normal perch only weight contributed significantly to explaining the variance in egg dry weight, and that age had no additional effect. For stunted perch, this situation was exactly reversed, i.e., only age was significant.

4. Discussion

4.1. Age and size at maturity

The data presented here document distinct differences in a number of reproductive parameters between stunted and normal perch. First sexual maturity occurred almost one year earlier in stunted males and exactly two years earlier in stunted females, com-

pared with normal conspecifics. Within populations and age classes, slow growing individuals usually mature later than faster growing ones (Röper 1936, Alm 1946, 1952, Jobes 1952, Tesch 1955, Treasurer 1981, Schneider 1984, Persson 1990). To my knowledge, Alm (1952, 1959) is the only other author documenting earlier maturation in slow growing compared to faster growing perch (*P. fluviatilis*) populations, although in the same study stunted perch also matured at the same or an older age than normal perch (Alm 1959). Other direct evidence for a very young age at maturity of stunted perch has been presented by Lake (1959, cited in Thorpe 1977a) for *P. fluviatilis* and by Ridgeway and Chapleau (1994) for *P. flavescens*. The latter authors state that males mature at age 0+ and females at age 1+. However, because of Ridgeway and Chapleau's (1994) method of defining age at maturity, these values must be considered minimum ages, and the mean age of maturity for both sexes was probably similar to that of stunted perch from Narrow Lake. Deelder (1951) and Trautmann (1981) also provide some circumstantial evidence for early reproduction in stunted *P. flavescens* and *P. fluviatilis*, respectively.

Other observations on stunted perch do not indicate precocious sexual maturity (Nyberg 1979 and Rask 1983 for *P. fluviatilis*, and Heath & Roff 1987

Table 3. Coefficients and their standard errors (S.E.) for the regressions of fecundity (*Fec*) with weight, length, age, gonad weight and egg dry weight of stunted ($n = 28$) and normal ($n = 29$) perch. All regression equations were calculated using untransformed data, except for length (*Lth*) which was described by: $\log Fec = \log a + b \log Lth$. The notation *n.s.* indicates that the probability for H_0 : Parameter = 0 is > 0.10 .

Population	Slope	S.E.	Intercept	S.E.	r^2
Weight (g)					
Stunted	163.2	13.6	235.9	<i>n.s.</i>	0.841
Normal	103.7	6.9	957.4	<i>n.s.</i>	0.890
Length (cm)					
Stunted	2.823	0.226	0.489	0.246	0.852
Normal	3.604	0.359	-0.650	<i>n.s.</i>	0.781
Age (years)					
Stunted	1 665	295	- 2 132	1 117	0.533
Normal	7 997	2 096	- 19 532	11 154	0.326
Gonad weight (g)					
Stunted	575.3	39.2	842	250	0.886
Normal	397.0	26.8	9 368	1 076	0.888
Egg dry weight (mg)					
Stunted	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	<i>n.s.</i>	-
Normal	131 042	45 237	- 8 610	<i>n.s.</i>	0.209

for *P. flavescens*). Males of *P. flavescens* (Hasler 1945, Jobes 1952, Herman *et al.* 1959, Shafi & Maitland 1971, Wells & Joergensen 1983) and *P. fluviatilis* (Laskar 1945, Healy 1954, Tesch 1955, Nyberg 1979, Jellyman 1980, Treasurer 1981, Rask 1983, Linløkken *et al.* 1991, Jamet & Desmolles 1994) typically spawn at age 2, although in some populations of *P. fluviatilis* almost all fish mature during their first year of life (Holčík 1969, Craig 1974a, Jellyman 1980, Lang & Lang 1983), and in one reported case most male *P. flavescens* mature at age 1 (Vogel & June 1987). Generally, females mature 1 or more years later than male *P. fluviatilis* (Alm 1952, 1959, Tesch 1955, Holčík 1969, Craig 1974a, Nyberg 1979, Jellyman 1980, Rask 1983) or *P. flavescens* (Jobes 1952, Muncy 1962). This can be as early as during the second year of life (Brazo *et al.* 1975 for *P. flavescens*, Stehlik 1968, Craig 1974a, Jellyman 1980, Lang & Lang 1983, Persson 1990, Sandström *et al.* 1995, for *P. fluviatilis*). More commonly, though, females are 3 or 4 years old at first maturity (Laskar 1945, Healy 1954, Hartmann 1975, Mann 1978, Nyberg 1979, Rask 1983, Jamet & Desmolles 1994 for *P. fluviatilis*, and Hasler 1945, Kennedy 1949, Jobes 1952, Muncy 1962, Sheri & Power 1969, Wells & Jorgenson 1983, Vogel & June 1987 for *P. flavescens*), and in some populations it may take on average 5 years to become mature (Lind *et al.* 1974).

The minimum length and weights recorded for stunted females and males at spawning time are the smallest values found in the literature for either perch species. Perch normally reproduce for the first time at sizes similar to those recorded for fish from Baptiste Lake (e.g. Laskar 1945, Alm 1946 for *P. fluviatilis*, Jobes 1952, Wells & Jorgenson 1983 for *P. flavescens*). The only other study reporting minimum lengths of mature *P. flavescens* similar to the ones from Narrow Lake is that of Schneider (1984), although these perch were most likely not stunted. In the fall prior to spawning, Vogel & June (1987) found a single male of 54 mm fork length to be sexually mature, whereas most of the other mature 1-year males measured between 75 and 107 mm. The very young mature 'stunted' perch (*P. flavescens*) studied by Ridgeway and Chapleau (1994) apparently grew rapidly during their first year of life, reaching a total length of at least 81 mm. Rask (1983) and Craig (1974b) found female *P. fluviatilis* to first spawn as small as 9.3 and 10 cm, respectively, the

smallest sizes recorded for this species. For male *P. fluviatilis* this size is 6.3 cm (Craig 1974b) or possibly smaller. Sandström *et al.* (1995) reported the smallest maturing males to measure 'about 55 mm' in the fall, and Treasurer (1981) found that 'most males of 6 cm length and above were maturing!'

Holčík (1969) first suggested the possibility of a size threshold (115 mm) below which female *P. fluviatilis* would not mature. Thorpe (1977a) restated this idea in a more general form, and Malison *et al.* (1986) proposed that the attainment of a minimum body size of 80–100 mm and 5–10 g is more important than either environmental stimuli or chronological age in determining the initiation of vitellogenesis and spermatogenesis of *P. flavescens*. Contrary to these findings, the large number of ripe male perch in the size range 60–80 mm consistently found at Narrow Lake, suggest that, if such a threshold exist in natural populations, it does at a smaller size. Either the laboratory environment prevented the expression of the potential physiological repertoire or stunted perch from Narrow Lake differ from the genotypes used by Malison *et al.* (1986), allowing greater plasticity in the onset of maturation. Data on the size of maturing males obtained from other populations of *P. flavescens* (Schneider 1984) and *P. fluviatilis* (Craig 1974b, Treasurer 1981) provide further evidence that the proposed size threshold does not hold for all natural populations.

4.2. Fecundity and egg size

The largest stunted perch for which fecundity could be assessed in this study was more than 3.5 cm smaller and weighted less than half of the smallest mature normal perch. Nevertheless, the stunted fish produced more eggs of similar weight. Based on estimates from the fecundity-weight regression, a hypothetical 100 g 'standard' perch from Narrow Lake would have the second highest fecundity recorded for any perch population (Table 4). Only fast growing 'standard' perch (*P. flavescens*) from Lake Michigan produced more eggs (Brazo *et al.* 1975). Normal growing *P. flavescens* from Baptiste Lake have a relatively low fecundity compared to literature values for that species (Table 4). Although the information in Table 4 is limited to those data sets allowing the required calculations, it suggests that *P. flavescens* is perhaps generally more fecund than

its sister species.

Absolute fecundity was positively related to fish size (length and weight) in both stunted and normal perch, stunted fish showing a greater increase in fecundity with increase in size. Compared to published values (summary in Thorpe 1977a, Papageorgiou 1977, Mann 1978, Schneider 1984, Lappalainen *et al.* 1988, Mance 1988, Linlokken *et al.* 1991, Sandström *et al.* 1995), the exponent for the (log transformed) fecundity-length regression is close to the average value for normal perch and among the highest recorded for stunted perch. The exponent for stunted perch was almost identical to the one for a smaller sample of females ($n = 9$) obtained by Mance (1988) from Narrow Lake in 1984, thus indicating that the relationship between fecundity and fish length has remained stable for this population over a period of 6 years.

In contrast to normal perch, age contributed sig-

nificantly to the observed variability in fecundity of stunted perch once body weight was accounted for, i.e., for fish of equal size, the older females produced more eggs. Many authors have documented increases in absolute fecundity with age in *P. flavescens* (Sheri & Power 1969, Tsai & Gibson 1971, Brazo *et al.* 1975, Szramko & Teleki 1977) and *P. fluviatilis* (Stehlik 1968, Treasurer 1981). However, the relation was usually weak, and length or weight proved to be better predictors of fecundity. In the above studies, the effect of age on fecundity, beyond the contribution of weight or length was not evaluated. When this was done, age did not have a significant effect on fecundity (Tsai & Gibson 1971, Schneider 1984).

Relative fecundity showed no relationship to fish size in both perch populations, but it decreased with age in stunted perch. A number of authors have found changes in relative fecundity with increasing size of perch (Stehlik 1968, Papageorgiou 1977, Jellyman

Table 4. Summary of data from the literature on fecundity for *Perca flavescens* and *P. fluviatilis*, and corresponding values for total length (Length) of perch. Values for fish length, absolute and relative fecundity (number of eggs \times g⁻¹ total body weight) represent ranges except for data on relative fecundity separated by a semicolon. These numbers represent lowest and highest values for absolute fecundity for cases where data on relative fecundity were not provided by the authors. 'Standard' fecundity has been calculated for a 100 g perch applying the fecundity-weight regression provided by the authors; asterisks indicate values where no fecundity-weight regression was available, and the (provided) fecundity-length regression and length-weight regression were used in combination to calculate 'standard' fecundity. ¹⁾pers. comm. in Thorpe 1977a.

Absolute Fecundity	'Standard' Fecundity	Relative Fecundity	Length (mm)	<i>n</i>	Location	Source
<i>Perca flavescens</i>						
10 654–157 594	18 844	130;232	190–354	96	L. Michigan US	1
1 910–11 812	16 556	130–255	98–168	28	Narrow L. CDN	2
3 035–61 465	14 757	112;199	135–257	48	L. Ontario CDN	3
5 266–75 715	13 632	82;184	174–411	112	Patuxent R. US	4
9 300–136 000	13 131	–	173–355	49	L. Michigan US	5
10 639–55 592	11 327	85–141	200–305	29	Baptiste L. CDN	6
12 641–135 848	–	132;157	156–353	194	L. Erie CDN	7
4 600–109 000	–	–	173–358	30	Chesapeake Bay USA	8
<i>Perca fluviatilis</i>						
9 277–74 124	12 400	50–146	176–324	15	L. Kinord & Davan GB	9
2 080–24 488	12 065	69–216	115–210	92	L. Agios Vasilios GR	10
–	12 034	–	–	–	Baltic Sea	11
1 000–30 500	9 227*	52–188	98–278	49	Slapton Ley GB	12
3 752–7 496	8 968*	–	141–191	31	L. Broborvann N	13
2 657–63 858	8 656*	33–141	145–422	66	L. Pounui NZ	14
6 710–144 000	–	91–317	115–330	61	L. Klíčava CSSR	15

1) Brazo *et al.* 1975, 2) Present study, 3) Sheri & Power 1969, 4) Tsai & Gibson 1971, 5) Wells & Jorgenson 1983, 6) Present study, 7) Szramko & Teleki 1977, 8) Muncy 1962, 9) Treasurer 1981, 10) Papageorgiou 1977, 11) Grahn & Aneer 1975¹⁾, 12) Craig 1974, 13) Linlokken *et al.* 1991, 14) Jellymann 1980, 15) Stehlik 1968.

1980, Makarova & Shatunovskiy 1984, Sandström *et al.* 1995). Either fecundity does not increase as fast as body weight, or fecundity increases faster than body weight in the largest individuals (Papageorgiou 1977). In the latter situation, caution should be applied when comparing relative fecundity between different places or populations (Bagenal 1978).

The decrease in the number of eggs produced per gram body weight in the older stunted perch, coincided with a reduction in egg numbers per gram ovary weight. This may suggest that as females senesce, the proportion of connective tissue in the ovary increases (Hickling 1940, Gerking 1959, both cited in Woodhead 1979, Wootton 1979). The presence of such a process is indirectly supported by data for a number of other fish species in which fecundity increases disproportionately to the gonad weight, without a concomitant increase in egg size (Woodhead 1979). However, for the perch studied here, particularly those from Narrow Lake, the reduction in gonad weight specific fecundity with increasing age at least partially reflects the larger egg size of older fish, and, is probably not a result of increasing proportions of connective tissue in the gonad. Although I did not measure all of the gonadal connective tissue, the highly significant linear relationship between tunica weight and gonad weight provides some direct evidence for this assumption.

Egg dry weight showed a significant positive relationship to fecundity in both stunted and normal fish. Bagenal (1978) concluded that because large eggs produce larger (and healthier) larvae than do small eggs, there must be a trade-off between egg size and egg number, and that these two parameters should be negatively correlated. However, this argument only fully applies, if the amount of energy invested into reproduction is fixed. If, as suggested by the seasonal energy budget for perch from Narrow Lake (W. Jansen, unpubl. data), (additional) energy is allocated to reproduction instead of growth, a high reproductive investment may result from increasing both egg numbers and egg weight. Furthermore, like in other species egg size changes with developmental stage in *P. flavescens* (Mance 1988) and *P. fluviatilis* (Treasurer & Holliday 1981). It is therefore difficult to measure egg size in a way to allow unbiased comparisons between different studies and perhaps has contributed to the inconsistent findings in the relationship between egg size and fecundity or fish size. Egg size, although commonly

used as a measure of investment, may not be such a good indicator. Energy is generally considered the most appropriate currency of performance of organisms and systems (Van Valen 1976). Unfortunately, to my knowledge, size and caloric content have not been measured on the same eggs. The relationship of egg dry weight, a useful estimator of energy content, and yolk diameters is quite variable (W. Jansen, unpubl. data). Furthermore, egg and yolk diameters of perch differ substantially between studies (Mansueti 1964, Stehlik 1968, Sztramko & Teleki 1977, Thorpe 1977b, Jellyman 1980, Treasurer 1981, Sandström *et al.* 1995), whereas the only other published value for egg dry weight (0.243 g, Treasurer 1983) is almost identical to the weights recorded in the present study. Thus, caution should be applied before using egg size to compare reproductive investment between perch populations, and, if data on energy content are not available, dry weights should be used.

Finally, the increase in egg weight with increasing fecundity found in the present study must be put in perspective. For stunted perch, it became marginally significant ($P = 0.05$) only after one 'outlier' was omitted from the analysis, and for normal perch it was also marginally significant. Thus, it could be argued that egg weight, and thus energy content, remains relatively stable at an optimal value over the whole fecundity range, and in a situation where larval mortality is mainly affected by density independent factors a higher reproductive effort is best invested into increasing egg numbers instead of egg size.

4.3. Relationship between maturity and fecundity

Alm (1959) proposed that early maturity of stunted perch either resulted from a genetically fixed maturation age, or reflected a change in environmental conditions from good opportunities for growth during early life to poor conditions after reaching maturity. Based on the considerable range in the age of sexual maturity seen both within and between populations of *P. fluviatilis* (Röper 1936, Laskar 1945, Alm 1946) and *P. flavescens* (Wells & Jorgenson 1983), and the known response of age at first reproduction to environmental factors like temperature (Thorpe 1977a, Sandström *et al.* 1995) and nutrient levels (Hartmann 1975, Lang & Lang 1983), a strictly ge-

netic basis for the onset of maturity seems unlikely in perch. Furthermore, pronounced changes in feeding, and thus growing conditions were not apparent in Narrow Lake between 1985 and 1990, and perch growth rates remained similar for the same age class during different years and between different age classes during the same year (W. Jansen, unpubl. data). Therefore, obvious clues concerning the ultimate cause of the precocious sexual maturity of stunted perch in Narrow Lake are lacking.

The optimal life-history strategy allocates resources to maintenance, growth, and reproduction in a way that maximizes individual fitness (Leggett & Carscadden 1978), i.e., age specific fecundity and survivorship. Consistent with arguments by Stearns and Crandall (1984), under conditions of reduced juvenile growth, stunted perch seem to alter age and size at maturity along a trajectory that minimizes the reduction of fitness caused by slower growth and that maximizes surplus power (*sensu* Ware 1982). These fish reproduce earlier during their life in order to decrease the risk of mortality before reaching maturity. Furthermore, as indicated by the steep slope of the fecundity-body weight regression and the similar egg size and energy content compared to normal perch, stunted perch from Narrow Lake are able to reduce the impact of the trade-off between early maturity and low fecundity without sacrificing egg quality. As indicated by the consistent influence of age on measures of fecundity and egg size in stunted, but not in normal perch, concomitant with the more uniform timing in the age of first sexual maturity of stunted females, these perch live closer to their physiological limits and senescence occurs more predictably. Thus, as a likely consequence of this strategy of early and high reproductive effort under poor growing conditions, stunted perch experience poor somatic condition and a reduced life expectancy (Jansen & Mackay 1991). Similar reproductive plasticity has recently been documented for a population of *P. fluviatilis* faced with elevated water temperatures during times of unfavourable feeding conditions (Sandström *et al.* 1995). These fish adopted an energy-saving strategy, and reduced fecundity or even restrained from reproducing in the year(s) following the year of first reproduction in order to reduce the high mortality risk associated with this considerable energy investment into gonadal production. In summary, the data presented here suggest that the stunted growth in perch, and possibly other

fish species, should not be perceived as an expression of ecological failure, but as a consequence of an adaptive reproductive strategy that maximizes fitness.

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