SOME DETERMINANTS OF MATURATION IN BROOK TROUT, *SALVELINUS FONTINALIS*

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ABSTRACT

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·Size, age, growth rate and photoperiod were examined for their effects on the timing of maturation and the proportion of mature male and female brook trout (*Salvelinus fontinalis*). Photoperiod completely entrained the gonadosomatic index and the timing of functional maturation (spermiation and ovulation). High feed and delayed photoperiod conditions resulted in a greater proportion of mature individuals of each sex in their first year, with percent maturation higher for males. The results indicated that (1) given a positive growth rate, age and growth rate are less important than size in determining maturation of brook trout, and (2) the maturation response to size is sexually divergent. A conceptual model depicting the effects of environmental factors on size and the initiation of maturation is presented.

INTRODUCTION

Although age at first maturity is most commonly reported in studies of natural populations, Alm (1959) concluded that size and growth rate were more important determinants of salmonid maturation. An understanding of salmonid demography depends, in part, on our ability to differentiate between size, age and growth rate as determinants of maturity. In addition, management of domestic salmonids can be facilitated through manipulation of maturation. Since feeding rate and diet influence both size and growth rate, but not age, maturation may to some degree be controlled by culture methods (Alm, 1959). Photoperiod may also be used to control the timing of maturation of domestic salmonids (Billard et al., 1978).

While investigating the effect of size, age and photoperiod on osmoregulation in brook trout, *Salvelinus fontinalis* (McCormick and Naiman, 1984a,b), we found feeding and photoperiod influenced the timing and degree of maturation. Knowledge of the determinants of brook trout maturation may offer substantial insight into salmonid reproduction. Since brook

trout most often complete their life cycle in freshwater (Power, 1980), their reproductive physiology will be uncomplicated by complex physiological changes associated with oceanic migrations. Furthermore, Hoar (1976) has suggested that the genus *Salvelinus* is most similar to the earliest salmoninae, a 'primitive archetype' upon which greater specializations were made by *Salmo* and *Oncorhynchus*. The objective of this paper, therefore, is to investigate the effects of size, age, growth rate and photoperiod on maturation in brook trout, a representative of the genus *Salvelinus*.

MATERIALS AND METHODS

Twenty thousand brook trout eggs from the Massachusetts State Fish Hatchery at Sandwich were fertilized on 28 October 1980. Fertilized eggs were transported to the Woods Hole Oceanographic Institution's Shore Lab facility and supplied with 10—11°C well water. Eggs were randomly divided into two annually cycling photoperiods corresponding to a latitude of 42°N; one photoperiod cycle corresponded to the normal calendar date (longest day 21 June, shortest day 21 December), while the other was 3 months delayed from the norm (longest day 21 September, shortest day 21 March; Fig. 1). Day length was changed every 5 days. Sunrise and sunset were simulated each day by a 15 min period of gradual illumination or dimming of incandescent bulbs. Beginning and end of daylight period were delayed 2 h from Eastern Standard Time. Vita-Lite spiralux fluorescent bulbs and incandescent bulbs were used to simulate daylight.

After first feeding fish were transferred to 1000 l flow-through tanks which received supplemental aeration. Within 1 week after feeding fish were divided randomly, within each photoperiod treatment, into two feeding groups. For 4 weeks after first feeding, fish in each group were fed equal amounts. Afterward, one group was fed commercial fish pellets ad libitum following common hatchery procedures (Leitritz and Lewis, 1976). The low feed group was fed approximately half the amount, per unit body weight, fed the high feed group. Every 6—8 weeks at least 25% of the fish from a 1000 l tank in each feeding group in the normal photoperiod were weighed. Only 10% of the fish in each feeding group in the delayed photoperiod were weighed. Fish were dip-netted, anesthetized, blot-dried on a moist chamois cloth, fork length was measured to the nearest mm and fish were weighed to the nearest 0.01 g.

Specific growth rates (G_w) were calculated using the formula

$$G_w = [(\ln W_t - \ln W_0)/t] \times 100$$

where W_t is the weight at time t, W_0 is the weight at time 0 (the time at which weight was last measured) and t is time in days. In order to compare growth rates of animals of different sizes, the ln G_w of a fish of unit size (ln $G_w{}'$) was calculated (Jobling, 1983) using the equation
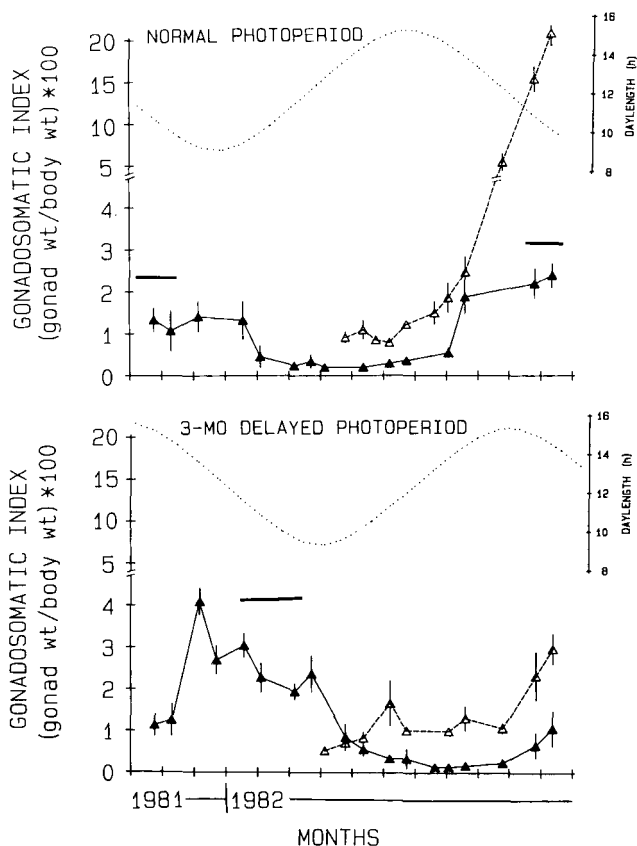
$$\ln G_w{}' = \ln G_w - b \ln W_t$$

Fig. 1. Gonadosomatic index of males (closed triangles) and females (open triangles) in the high feed group as a function of time. Values are the mean (± 1 SE) of 4—12 fish per sampling period. Horizontal bars correspond to the period of spermiation under each photoperiod treatment. Period of final maturation in females (when eggs could be extracted by pressing the body walls) occurred within the same period but usually began 1—2 weeks later. GSI of females is shown only in 1982 because of the low number of mature females in 1981.

where b is the slope of the linear relationship between $\ln G_w$ and $\ln W_t$. An experimentally derived value of $b = -0.47$ was used in all calculations of $\ln G_w$, [b is the slope of the regression between $\ln G_w$ and $\ln W_t$ in high feed fish, 0.06—367.9 g; normal photoperiod $b = 0.47$ ($r = 0.96$), delayed photoperiod $b = 0.48$ ($r = 0.90$)] . A generalized value of $b = -0.41$ for salmonids was reported by Brett (1979).

Gonads of fish which were periodically sacrificed were weighed to the nearest 0.01 g and gonadosomatic index (GSI) calculated [(gonad weight/ body weight) $\times$ 100]. Determinations of the state of maturation of individual fish (i.e., mature or immature) were made between the longest and shortest daylengths in each photoperiod (e.g., 21 June—21 December in

normal photoperiod). Males were determined to be mature when gonads were wider than 3 mm (Jones, 1959). Females were determined to be mature when egg diameter was greater than 1.0 mm and the ovary took up more than 1/2 the length of the body cavity (Vladykov, 1956). Condition factor was calculated as (weight/length^3) × 100.

Contingency tables and 3- and 4-way log-linear contingency tables were used to determine significant differences among the proportion of mature individuals in experimental groups (Dixon, 1981).

RESULTS AND DISCUSSION

Photoperiod entrainment of maturation

Relative to the normal photoperiod, gonadal development (Gonadosomatic index) in mature males and females was shifted by approximately 3 months in the delayed photoperiod (Fig. 1). Under normal photoperiod conditions the period in which milt could be easily exuded from mature males (spermiation) corresponded to the normal spawning time of brook trout at 42°N (latitude of Woods Hole; Power, 1980). The mid-point of spermiation in the delayed photoperiod was slightly more than 3 months after that of the normal photoperiod.

Previous investigations have shown photoperiod to be an effective Zeitgeber of several physiological and hormonal cycles of teleosts, including maturation (Henderson, 1963; Clarke et al., 1978; Billard et al., 1978). Eriksson and Lundqvist (1980) found that the rate of change in daylength, rather than daylength per se, was responsible for entraining maturation in precocious Atlantic salmon (*Salmo salar*). Despite the ability of photoperiod to entrain maturation in our experiments, the 3-months delayed photoperiod failed to shift the plasma thyroxine cycle that occurred under normal photoperiod conditions (McCormick and Naiman, 1984a), even though several lines of evidence suggest that the thyroid plays a role in teleost maturation (see Leatherland, 1982, for review). Nevertheless, these results indicate that a seasonal cycle of plasma thyroxine (characterized by high 'spring' levels) is not required for gonadal development in brook trout.

Growth

The weight and specific growth rate per unit weight (ln G_w ') of fish in high and low feed groups in each photoperiod are shown in Fig. 2. Wet weight is used to represent body size with the knowledge that length is an equally valid measurement highly correlated with weight. Reduced rations in low feed groups resulted in smaller body size for a given age and lower growth rates in the first year. Similar growth rates for high and low feed groups in 1982 possibly reflect a growth—ration relationship that changes with body size, though little is known of this process (Ricker, 1979). Growth
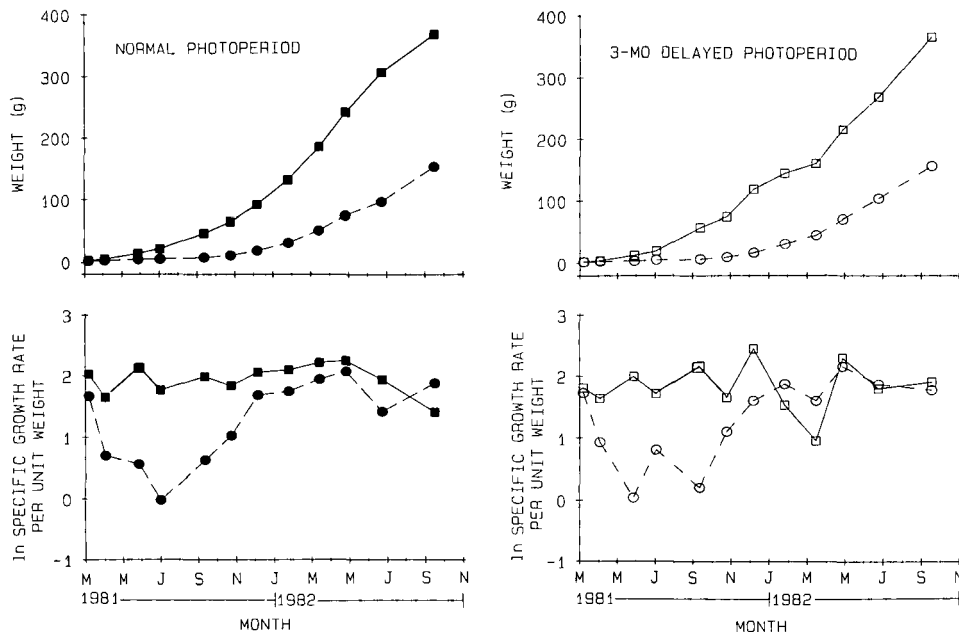
Fig. 2. Effect of feeding treatment on wet weight and growth rate. High feed (squares) and low feed (circles) fish in normal (solid) and 3-months delayed (open) photoperiods as a function of time. Weights are the mean value of 40—125 fish.

as a function of feeding treatment was similar between photoperiods. Since the delayed photoperiod shifted developmental timing, fish in this group were larger at every point in the maturation cycle, including the time at which the 'decision' to initiate maturation was made. For instance, high feed fish in the delayed photoperiod were 36.3 g heavier than normal photoperiod fish on the equivalent photoperiod day 3 months earlier in 1981 (Table I).

Since diet composition was constant and growth rate was positive for all experimental groups throughout the study, we assume the nutritional state was satisfactory for all groups. Mean condition factor was always greater than 0.96 (low feed groups 0.96—1.36; high feed groups 1.09—1.41).

Determinants of maturation

Year 1. Feeding in combination with photoperiod treatment had a significant effect on the proportion of mature individuals in both sexes in their first year ($P < 0.01$, 3-way log-linear contingency tables; Table I). Within each photoperiod there was a significantly greater ($P < 0.01$) percentage of mature males in the high feed group than in the low feed group. Size and growth rate, but not age, differed between these two groups (Table I).

TABLE I

Percentage of individuals of each sex which became mature in their first and second year as a result of feeding and photoperiod treatments. Mean wet weight, age and growth rate shown in each treatment are those which occurred on the sampling date closest ($\pm$ 14 days) to the longest photoperiod day (e.g., first day of summer in normal photoperiod). Numbers in brackets are the sample size for males and females, respectively. Parenthetical growth rates are those calculated from the first weighing period (86 days old, mean weight 0.53—0.60 g)

Feed regime	% Mature		Size (g)	Age (d)	Growth rate ln Gw	
	males	females				
Year 1						
Normal photoperiod						
Low [21,23]	0	0	4.0	196	0.53	(1.26)
High [70,34]	44	3	13.7	196	1.91	(2.28)
3-months delayed photoperiod						
Low [41,41]	7	5	7.3	301	0.15	(1.13)
High [75,60]	72	38	50.0	301	2.11	(2.56)
Year 2						
Normal photoperiod						
Low [20,23]	86	92	96.7	582	1.30	(2.19)
High [17,31]	96	100	306.3	582	1.94	(2.91)
3-months delayed photoperiod						
Low [41,41]	95	100	157.7	665	1.67	(2.36)
High [75,60]	100	100	367.2	665	1.78	(2.88)

In the high feed treatments, the 3-months delayed photoperiod produced a greater porportion of mature males than the normal photoperiod (72% and 44%, respectively), and were 36.3 g heavier and 90 days older on the longest photoperiod day. Since growth rate was similar for high feed fish in each photoperiod (Table I), size or age must be responsible for the difference in the proportion of mature individuals in the normal and delayed photoperiods. Because size or growth rate is responsible for differences between feeding groups, and size or age is responsible for differences between normal and delayed photoperiods, only size can explain all of the results.

The pattern of maturation of females in their first year was similar to that of males with a significantly greater proportion of females becoming mature under high feed, delayed photoperiod conditions (38%) than under low feed or normal photoperiod conditions ($\leqslant$ 5%; $P < 0.01$, 3-way log-linear contingency table; Table I). As with male maturation, size most easily explains these results. The proportion of mature females, however, was significantly lower than that for males ($P < 0.01$, 4-way log-linear contingency table). This is particularly evident in the high feed groups where the percentage of mature females was one-fifteenth and one-half that of mature males in the normal and delayed photoperiods, respectively. If, as hypoth-

esized, size is of overriding importance in determining maturation in brook trout, a sexually divergent response to size is a logical extension of this hypothesis that explains male-female differences in maturation. A larger size at first maturation for females may reflect the greater limitations imposed by size on egg production relative to sperm production (Darwin, 1871).

Year 2. In year 2 the proportion of mature individuals varied between 86% and 100% and did not differ by sex, feeding level or photoperiod treatment ($P > 0.10$, 4-way log-linear contingency table; Table I). In accordance with our interpretation of the importance of size, it would appear that a minimum size (97 g on the longest photoperiod day; Table I) has been reached by all experimental groups in their second year.

The relationship of size to the proportion of mature individuals across all experimental groups for both sexes is shown in Fig. 3. Regression of percent maturation on log wet weight on the longest photoperiod day had values of $r^2 = 0.99$ and 0.97 for males and females, respectively (Fig. 3). The area between the curves represents the degree of sexual divergence in the response of maturation to size. For example, in order to achieve 50% maturation under the present experimental conditions, males must be 21.9 g and females 45.8 by the longest photoperiod day.

The importance of size in maturation of brook trout is in substantial agreement with Alm (1959), who found a greater number of mature individuals among larger, faster growing brook trout and several other salmonid species. There is growing evidence that size-determined developmental
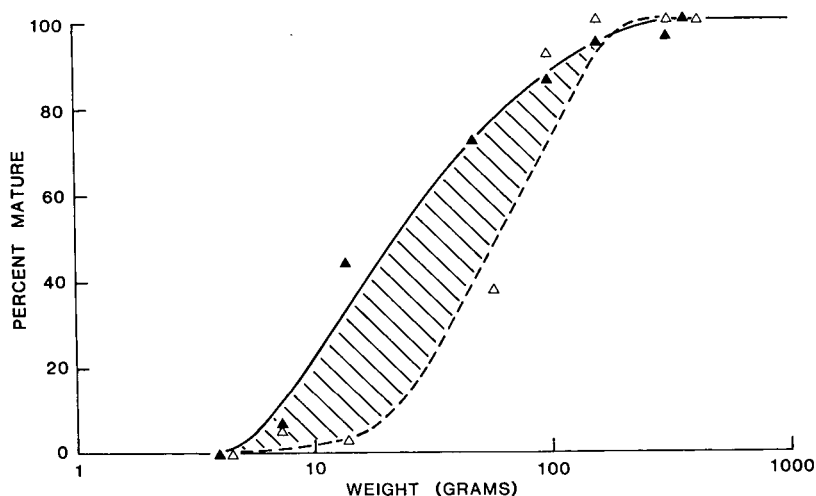

Fig. 3. Percent maturation of males (closed triangles) and females (open triangles) as a function of wet weight (g) on the longest photoperiod day. Curves were fitted using third order polynomial regressions ($r^2 = 0.99$ and 0.97 for males and females, respectively). Shaded area represents sexual differences in the response of maturation to size.

events (maturation included) occur in many teleosts (Policansky, 1983). The results presented here and shown schematically in Fig. 4 indicate that at high growth rates, size alone can increase the proportion of mature brook trout. Factors other than feeding levels, such as temperature, also influence size and have the potential to affect maturation. Furthermore, temperature, and perhaps other environmental factors, may have a direct effect on salmonid maturation (Saunders et al., 1983).

Although these results indicate that size is an important determinant of maturation in brook trout, certain levels of growth rate, nutrition and health are probably required for maturation to occur (Fig. 4). It may be necessary to achieve several physiological thresholds before maturation is initiated. Furthermore, the biological property triggering the maturation process may not be size per se, but a factor (or factors) strongly correlated with size, such as energy reserves or lipid storage. Minimum lipid : body mass ratios have been hypothesized to be responsible for variations in the onset of puberty in human and primate females (Reiter and Grumbach, 1982). Such a threshold mechanism would account for the importance of size in brook trout maturation, and would explain variations in spawning schedules which, for example, occur every other year in northern, food-limited populations (Vladykov, 1956).
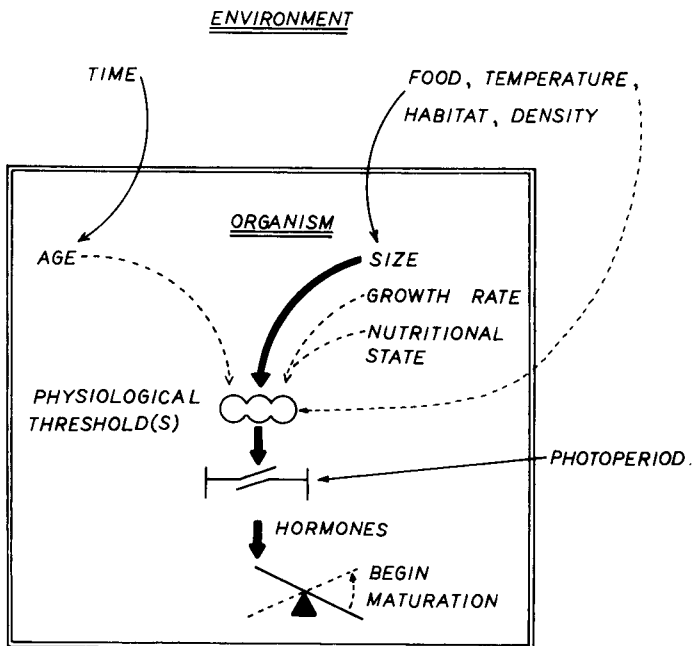
ENVIRONMENT

Fig. 4. Schematic representation of the environmental effectors and biological determinants of maturation. Thick lines emphasize size dependent maturation found for brook trout.

ACKNOWLEDGEMENTS

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