Photoperiod Control of Parr—Smolt Transformation in Atlantic Salmon (*Salmo salar*): Changes in Salinity Tolerance, Gill Na+,K+-ATPase Activity, and Plasma Thyroid Hormones

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Atlantic salmon (*Salmo salar*) were subjected to artificial photoperiods to determine the manner and extent of photoperiod control of the parr—smolt transformation. Exposure to continuous light (L24) at first feeding and maintained throughout the rearing period inhibited increases in salinity tolerance and gill Na+,K+-ATPase activity that occurred in spring in fish raised under simulated natural photoperiod (SNP). Fish reared under continuous light and returned to SNP in October (L24OCT) underwent normal increases in salinity tolerance and gill Na+,K+-ATPase activity, whereas those returned in December (L24DEC) underwent delayed and intermediate increases. Plasma thyroxine peaks occurred simultaneously in all groups but were diminished in the L24 and L24DEC groups. Plasma 3,5,3'-triiodo-L-thyronine levels were not affected by any photoperiod treatment. Inhibition of the parr—smolt transformation decreased the potential for growth in seawater. In spite of changes in the timing of the transformation induced by photoperiod treatment, salinity tolerance and gill Na+,K+-ATPase activity were strongly correlated; correlation between changes in salinity tolerance and plasma thyroid hormones were, by comparison, weak. The results demonstrate that continuous light applied early in ontogeny and maintained throughout the rearing period inhibits osmoregulatory changes associated with parr—smolt transformation, whereas increasing day length during winter—spring stimulates transformation.

On a soumis des saumons de l'Atlantique (*Salmo salar*) à des photopériodes artificielles afin de déterminer comment et dans quelle mesure la photopériode régit la transformation d'un tacon en smolt. L'exposition continue à la lumière (L24) au moment de l'alimentation initiale et pendant toute la période de croissance a bloqué l'augmentation de la tolérance à la salinité et de l'activité du Na+,K+-ATPase dans les ouïes qui est observée au printemps chez des poissons soumis à une photopériode naturelle simulée (PNS). Chez les poissons gardés en milieu continuellement éclairé et exposés à une PNS en octobre (L24OCT), on a observé des augmentations normales de la tolérance à la salinité et de l'activité du Na+,K+-ATPase dans les ouïes; par contre, les poissons exposés à une PNS en décembre (L24DÉC) ont montré des augmentations intermédiaires et retardées. Les teneurs en thyroxine plasmatique ont atteint des pointes simultanément chez tous les groupes mais étaient réduites chez les groupes L24 et L24DÉC. Les teneurs en 3,5,3'-triiodo-L-thyronine plasmatique n'ont pas été touchées par les modifications de la photopériode. L'inhibition de la transformation tacon—smolt a réduit le potentiel de croissance en milieu marin. Malgré des variations du moment de la transformation induites par la photopériode, la tolérance à la salinité et l'activité du N+,K+-ATPase dans les ouïes étaient fortement corrélées. En comparaison, la corrélation entre les variations de la tolérance à la salinité et les hormones thyroïdiennes plasmatiques était faible. Les résultats révèlent qu'une illumination continue appliquée au début de l'ontogenèse et maintenue pendant toute la période de croissance paralyse les changements osmorégulatoires liés à la transformation tacon—smolt tandis qu'une augmentation de la longueur de la journée en hiver et au printemps stimule la transformation.

The life history of anadromous Atlantic salmon (*Salmo salar*) is characterized by a rapid, synchronous seaward migration of juveniles in spring. The migrant juvenile, known as a smolt, can be distinguished from the riverine parr by its larger size, absence of vertical pigmented bars (parr marks), blackening of the paired and caudal fins, and intense silvering of the skin and scales which is the result of guanine and hypoxanthine deposition (Johnston and Eales 1967; Wedemeyer et al. 1980). The parr—smolt transformation is characterized by a number of changes in osmoregulatory

physiology that occur in freshwater and result in increased salinity tolerance (see reviews by Hoar 1976; McCormick and Saunders 1987). Prominent among these preparatory physiological adaptations are increases in the activity of gill Na+,K+-ATPase, an enzyme which plays a central role in active ion transport (Maetz and Garcia-Romeau 1964; Silva et al. 1977). Circulating levels of thyroid hormones also increase during transformation (Dickhoff et al. 1978, 1982), though their role with regard to osmoregulatory changes has yet to be established.

Several studies have implicated photoperiod in controlling the timing of the parr—smolt transformation in Atlantic salmon and other anadromous salmonids (Saunders and Henderson

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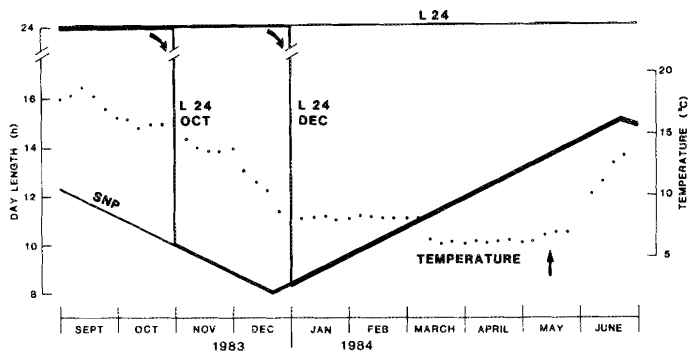*Can. J. Fish. Aquat. Sci., Vol. 44, 1987*

FIG. 1. Changes in day length and temperature during experimental photoperiod treatment. Vertical arrow indicates time at which fish were transferred to sea cages.

1970; Zaugg and Wagner 1973; Wagner 1974a; Komourdjian et al. 1976; Clarke et al. 1978, 1985; Saunders et al. 1985). The nature of this control has not been established, nor has a practical method for the temporal manipulation of the parr—smolt transformation been developed. Saunders et al. (1985) found that exposure of juvenile Atlantic salmon to continuous light in autumn increased growth rate but had a deleterious effect on salinity tolerance in spring and inhibited other aspects of the transformation. The present study was initiated to determine how and to what extent photoperiod controls the parr—smolt transformation. We also hoped that environmental manipulation of the transformation would shed light on temporal changes in salinity tolerance, gill Na^+,K^+-ATPase activity, and thyroid hormone levels.

Materials and Methods

Experiment I

Atlantic salmon of mixed river stock were incubated and hatched at the North American Salmon Research Center and brought to the St. Andrews Biological Station just prior to first feeding. They were reared in 1-m-diameter tanks supplied with freshwater at 12 $L \cdot min^{-1}$. Coincident with first feeding (May 25, 1983), fish were divided into four groups of approximately 1000 fish (two replicate tanks per group). Three of the groups were exposed to continuous light (24 $h \cdot d^{-1}$) and the remaining group was subjected to simulated natural photoperiod (SNP). Standard fluorescent bulbs provided light intensities at the water surface of 430–540 lx. On October 31, one group (L24OCT) was returned to SNP (Fig. 1). On December 31, a second group (L24DEC) was returned to SNP. A third group remained under continuous light (L24). Water temperature fluctuated seasonally (range 6–18°C) except during the period of physiological testing (January–May 1984) when it was relatively constant (6–8°C). During the laboratory phase of the study (May 1983–May 1984), salmon were fed commercial dry pellets (EWOS) to satiation (adjusted for temperature and body size (Saunders et al. 1985)) at half-hour intervals during daylight hours of the SNP group.

On December 21, fish smaller than 12.5 cm were removed from each group (approximately 25% of the fish in each tank) so as to reduce crowding and provide fish sufficiently large to undergo smoltification. Fish smaller than 10.3 cm (reared previously under SNP) were placed in a separate tank at the same thermal and photoperiod regimes as the SNP group and

were designated the PARR group.

At monthly intervals, 50% of the fish in each tank were sampled randomly for measurement of length and weight. The fish were anaesthetized (1% tert-amyl alcohol), weighed to the nearest 0.1 g, and measured for fork length to the nearest 0.1 cm. No mortalities resulted from this procedure, and fish resumed feeding within hours.

Monthly between January and March and biweekly from April through May, 8 salmon from each group were killed for blood and tissue sampling, and 10 fish per group were subjected to high salinity. Salinity tolerance was measured by direct transfer of fish to 40‰ seawater for a period of at least 96 h as described by Saunders et al. (1985). For blood and gill sampling, fish were starved overnight prior to sampling between 12 30 and 15 00 Atlantic Standard Time. After measuring length and weight, anaesthetized fish were blotted dry, the caudal peduncle was severed, and blood was collected in two heparinized microhematocrit tubes which were centrifuged for 5 min at 5500 rpm. Plasma was removed and stored at $-17°C$. Gill arches were removed immediately after blood collection as described below.

Over a 2-wk period beginning May 11, 250–350 fish from each group (except PARR) were gradually acclimated to 30‰ seawater. On May 22 they were given pelvic and/or adipose fin clips to distinguish the four groups and were transported to a commercial salmon farm at Grand Manan Island, New Brunswick. The four groups were placed in a 20-m^2 floating net enclosure. Fish were fed moist pellets containing ground herring and groundfish supplemented with vitamins. Between May and November, temperature and salinity ranged from 6 to 12°C and 28 to 30‰. On October 11, 1984, at least 60 fish per group were anaesthetized and measured for length and weight. On November 8 and 25, blood and gills were sampled as described above with the exception that blood was sampled from the dorsal aorta with a heparinized syringe.

Analytical Techniques

Primary gill filaments (0.05–0.20 g wet weight) were trimmed from gill arches (ceratobranchials), placed in 1.0 mL of SEI buffer (0.3 M sucrose, 0.02 M disodium ethylenediaminetetraacetate, and 0.1 M imidazole at pH 7.1) and stored for 1–4 wk at $-80°C$. Gill Na^+,K^+-ATPase activity was determined by the method of Zaugg (1982) with the following modifications. Gill homogenates were incubated in 115 mM NaCl, 55 mM KCl, 17 mM MgCl$_2$, and 85 mM imidazole at 37°C and pH 7.0. Inorganic phosphate was determined by the method of Heinonen and Lahti (1981). Protein determination was performed by the method of Miller (1959) using bovine serum albumin as standard. Gill Na^+,K^+-ATPase activity was expressed as micromoles inorganic phosphate per milligram protein per hour. Intra- and interassay coefficients of variation of pooled and separated gill samples were 3.3% ($n = 4$) and 11.8% ($n = 4$) with two to four replicates each, respectively.

Plasma samples were stored for up to 6 mo at $-17°C$. Thyroxine (T4) and 3,5,3'-triiodo-L-thyronine (T3) concentrations were measured by radioimmunoassay (Dickhoff et al. 1978; McCormick and Naiman 1984). Charcoal-stripped Atlantic salmon plasma was used to make all standards. Intra- and interassay coefficients of variation for these assays were 5–13 and 9–12%, respectively. Plasma osmolarity was measured with a Wescor vapor pressure osmometer; all samples
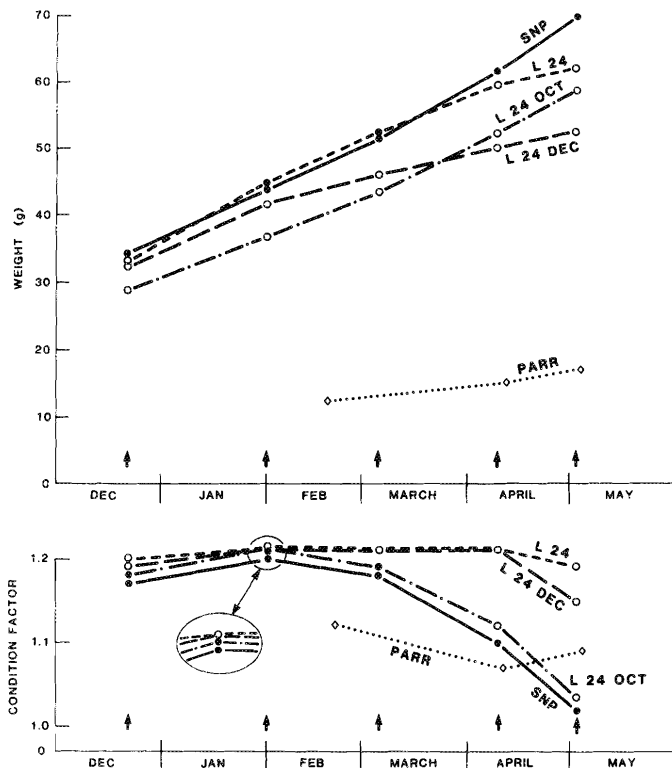
FIG. 2. Weight and condition factor of Atlantic salmon subjected to various photoperiod regimes. Values are the mean of 200–250 fish per group. Standard errors were less than 1% of the mean in each group (contained within the symbol for each mean). Significant changes in weight and condition factor over time occurred in each group ($p < 0.001$, one-way ANOVA). Open symbols represent a significant difference from the SNP group at a given time interval ($p < 0.05$, one-way ANOVA, Student–Newman–Keuls procedure).

were measured in one assay in which the intraassay coefficient of variation was 0.8% ($n = 5$).

Statistical comparisons of photoperiod treatment effects were performed with two-way analysis of variance. Interactions between photoperiod treatment and time were not significant. Differences among treatment groups at any time and changes over time within each treatment group were compared by Student–Newman–Keuls procedure. Statistical analysis of proportions (percent survival) was by Brownlee's test (Brownlee 1960). A significance level of $p < 0.05$ was used to establish statistically significant differences. All values are reported as mean and standard error (SE) unless otherwise stated. Condition factor is defined as ((weight/length^3)·100) with weight expressed in grams and length in centimetres.

Results

Experiment I

Photoperiod and growth

In mid-December, fish in each group (except PARR) that were smaller than 12.5 cm were removed from the study so as to provide fish large enough to undergo transformation. After grading, the L24OCT group was 20% smaller ($p < 0.05$) than the SNP group (indicating a lower growth rate in the period prior to grading), but grew at a similar rate thereafter (Fig. 2).
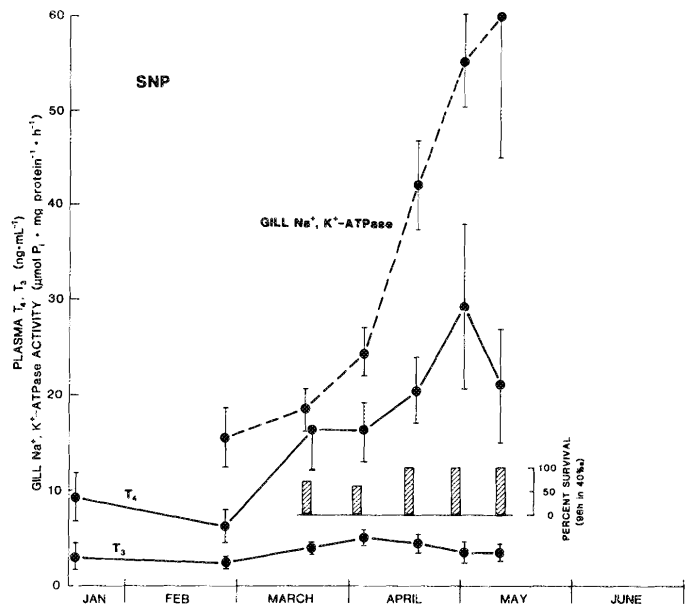

FIG. 3. Changes in gill Na$^+$,K$^+$-ATPase activity, plasma thyroid hormones, and salinity tolerance (percent survival for 96 h in 40‰ seawater) of Atlantic salmon exposed to SNP. Values are the mean ± 95% confidence interval of 8–10 fish at each sampling interval.

Beginning in mid-March and for the remainder of the study, the rate of change in weight of the L24DEC group was lower than that of the SNP and L24 groups. In each of these cases, a decline in day length (change from continuous light to simulated natural photoperiod) resulted in lower growth rates relative to SNP and L24 fish. In the case of the L24OCT group, this decline in growth rate was of short duration. L24 and SNP fish were of similar size (within 5% of one another) until the last weighing interval (early May).

Condition factor was similar in all photoperiod groups until the April–May period, when substantial decreases (>15%) occurred in both the SNP and L24OCT groups (Fig. 2). A slight decrease also occurred in the L24DEC group in May, while the L24 group remained nearly constant throughout the experiment. Condition factor of the PARR group, which in February was lower than the other groups, remained relatively constant between February and May.

Photoperiod and physiological change during parr–smolt transformation

Significant changes in salinity tolerance, gill Na$^+$,K$^+$-ATPase activity, and plasma thyroid hormones occurred between January and May under SNP (Fig. 3). Salinity tolerance had already reached 70% survival after 96 h in 40‰ seawater by mid-March, reached a maximum of 100% by mid-April, and remained at 100% through mid-May. Gill Na$^+$,K$^+$-ATPase activity rose steadily from late February to mid-May, increasing by 300% over this period. Plasma T4 also rose from a low mean value of 6.3 ng·mL^{-1} in late February to a peak of 29.5 ng·mL^{-1} in early May and subsequently declined to 7.1 ng·mL^{-1} in mid-May. Absolute and relative changes in plasma T3 were smaller than changes in plasma T4, though significant increases did occur. Plasma T3 rose from a low mean value of 2.6 ng·mL^{-1} in late February to a peak of 5.2 ng·mL^{-1} in early April and subsequently declined to 3.5 ng·mL^{-1} in early and mid-May.

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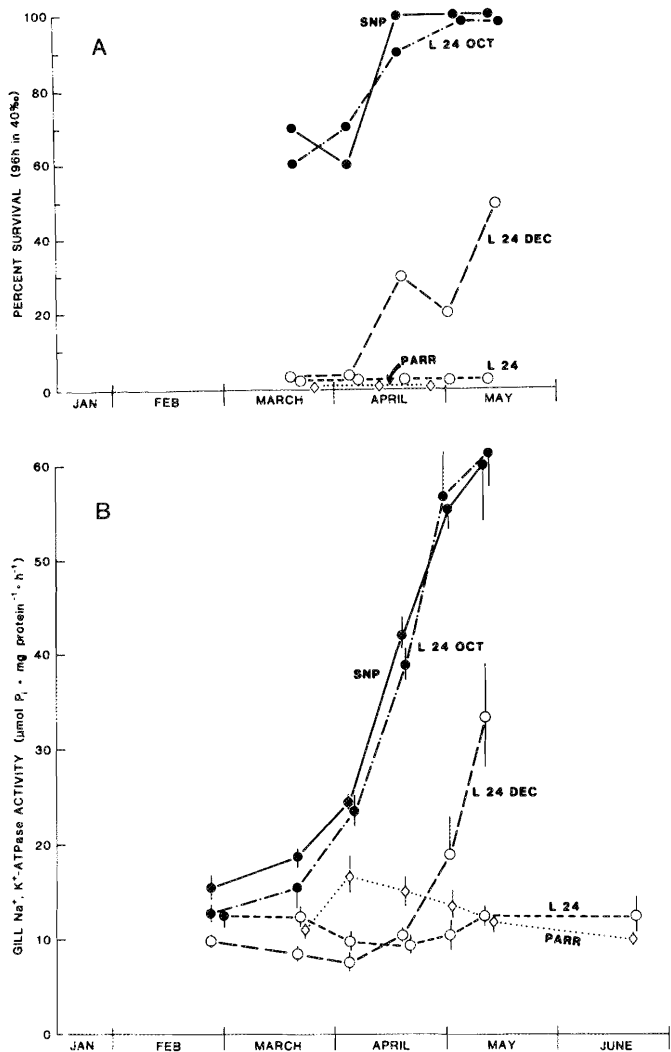*Can. J. Fish. Aquat. Sci., Vol. 44, 1987*

FIG. 4. (A) Percent survival after 96 h in 40‰ seawater of Atlantic salmon exposed to photoperiod treatment. Ten fish per group were used at each time interval. Open symbols represent a significant difference from the SNP group at a given time interval ($p < 0.05$, Brownlee's test). (B) Gill Na^+,K^+-ATPase activity of Atlantic salmon exposed to photoperiod treatments. Eight fish per group were used at each time interval. There was a significant effect of photoperiod treatment and date of sampling on gill Na^+,K^+-ATPase activity ($p < 0.05$, two-way ANOVA). Significant changes over time occurred in all groups except L24 ($p = 0.05$, one-way ANOVA). Open symbols represent a significant difference from the SNP group at a given interval ($p < 0.05$, one-way ANOVA, Student–Newman–Keuls procedure).

Salinity tolerance levels in both the SNP and L24OCT groups rose from 60–70% in mid-March to 100% by early May and were not significantly different from one another at any time (Fig. 4). No fish in either the L24 or PARR group was able to survive as long as 96 h in 40‰ seawater at any time between March and May. Salinity tolerance in the L24DEC group was 0% through early April, but increased to 50% by mid-May, indicating a delayed and perhaps diminished development of salinity tolerance in this group relative to the SNP group.

Changes in gill Na^+,K^+-ATPase activity in response to photoperiod treatment (Fig. 4) were similar to those for salinity
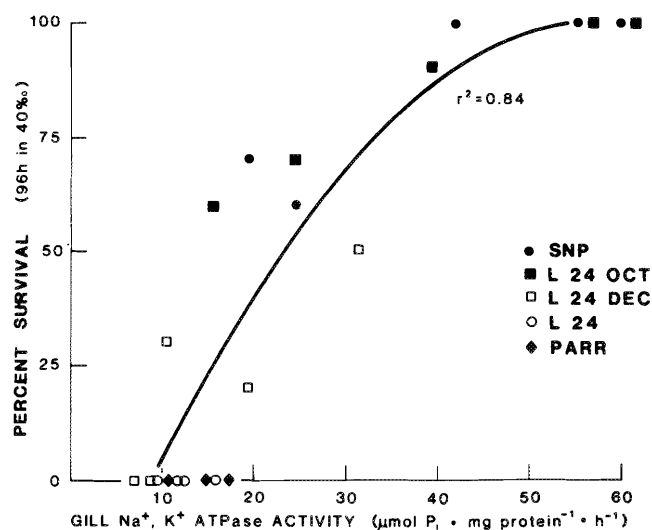

FIG. 5. Correlation between salinity tolerance and gill Na^+,K^+-ATPase activity for all photoperiod treatments at each sampling period. Each point represents the mean values reported in Fig. 4 and 5. Regression curve was fitted using a second-order polynominal with the following equation: $y = -0.042x^2 + 4.9x - 41.1$.

tolerance. Gill Na^+,K^+-ATPase activity levels increased steadily between late February and mid-May in the SNP and L24OCT groups and were not significantly different from one another at any time. Gill Na^+,K^+-ATPase activity of the L24 group was not significantly different from the SNP and L24OCT groups in late February, but did not increase significantly throughout the freshwater sampling period ending in late June. A significant increase did occur in the PARR group between mid-March and mid-April, but this increase was slight (40%) relative to the 300% increase in the SNP and L24OCT groups. Gill Na^+,K^+-ATPase activity of the L24DEC group was significantly lower than the SNP group at all times, but increased by 200% between early April and mid-May, again demonstrating delayed development. Significant correlation ($r^2 = 0.84$) existed between the development of gill Na^+,K^+-ATPase activity and salinity tolerance (Fig. 5).

Plasma T4 levels increased in all groups in spring (Fig. 6). Highest mean plasma T4 levels were found consistently in the SNP group. Differences in plasma T4 can be most easily compared among groups by examining early May values when plasma T4 (as well as salinity tolerance and gill Na^+,K^+-ATPase activity) in the SNP group was at its peak. At this time, plasma T4 levels in the L24OCT group were not significantly different from SNP, while L24DEC, L24, and PARR had significantly lower levels. However, whereas a developmental shift occurred in the timing of increases in salinity tolerance and gill Na^+,K^+-ATPase activity of the L24DEC group, no such temporal shift occurred in their plasma T4 levels. In addition, whereas no salinity tolerance developed in the L24 and PARR groups, there were significant increases in plasma T4 in these two groups (albeit to a lesser degree and for the PARR group at a later time).

Plasma T3 levels were not significantly affected by photoperiod treatment (excluding the PARR group; Fig. 6). With the exception of lower levels in the PARR group, no consistent differences in plasma T3 were observed among the groups. The absence of concurrent changes in plasma T3 and other physiological changes is exemplified by comparison of the

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TABLE 1. Length, growth, and osmoregulatory parameters of Atlantic salmon (subjected to prior photoperiod treatment) after 5 mo in sea cages. Values are expressed as mean (SE); length in cm, growth rate in mm·d^{-1}, osmolarity in mosm/L, gill Na$^+$,K$^+$-ATPase activity in µmol P$_i$·mg protein^{-1}·h^{-1}, and thyroid hormones in ng·mL^{-1}. Significant differences ($p < 0.02$) in plasma thyroid hormone levels were found among prior photoperiod treatments; groups with different letter designations were significantly different from one another ($p < 0.05$, Student—Newmand—Keuls procedure).

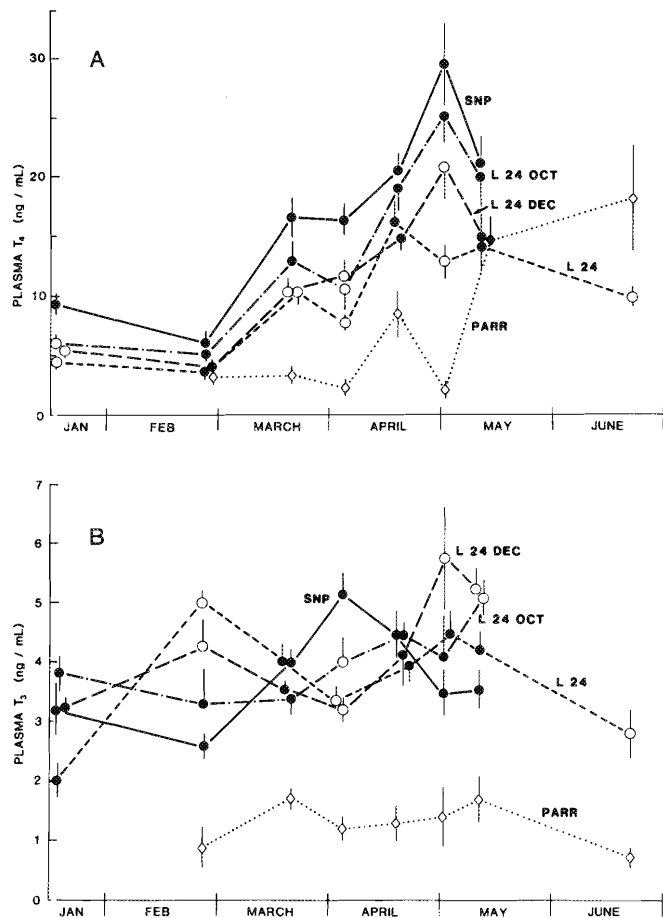| Prior photoperiod treatment	Initial length (May) (n = 350–400)	Final length (October) (n = 60–66)	Growth rate	Plasma osmolarity (n = 8)	Gill Na$^+$,K$^+$-ATPase activity (n = 6)	Plasma T3 (n = 8)	Plasma T4 (n = 8)
SNP	18.9 (0.05)	35.1 (0.3)	1.0	339 (3.5)	29.4 (3.7)	6.1^a (1.0)	10.2^a (1.6)
L24OCT	17.8 (0.05)	33.0 (0.2)	0.9	345 (2.9)	—	3.1^b (0.5)	9.6^{ab} (2.3)
L24DEC	16.5 (0.05)	30.0 (0.3)	0.8	341 (4.2)	—	3.6^b (1.0)	5.6^{bc} (1.1)
L24	17.2 (0.06)	23.2 (0.5)	0.4	335 (4.0)	33.9 (3.9)	1.6^b (0.5)	4.3^c (0.7)

FIG. 6. Plasma T4 and T3 in Atlantic salmon exposed to photoperiod treatments. Eight fish per group were used at each time interval. There was a significant effect of photoperiod treatments and date of sampling on plasma T4 ($p < 0.05$, two-way ANOVA), but no significant effect of photoperiod treatment (excluding the PARR group) on plasma T3 ($p > 0.2$). Significant changes over time occurred in plasma T4 and T3 in all groups, except for plasma T3 in the L24OCT and PARR groups. Open symbols represent a significant difference from the SNP group at a given time interval ($p < 0.05$, one-way ANOVA, Student—Newman—Keuls procedure).

SNP and L24OCT groups which had identical patterns of increase in salinity tolerance and gill Na$^+$,K$^+$-ATPase activity but which were dissimilar in their plasma T3 changes over time.

After completion of the laboratory phase of the study, salmon from each group (except PARR) were gradually acclimated to seawater and transferred to a sea cage. No mortalities occurred during acclimation or transport. During 5 mo, growth rates in the SNP, L24OCT, and L24DEC groups were similar, whereas growth rate of the L24 group was half that of the other groups (Table 1). Plasma osmolarity in early December was not significantly affected by prior photoperiod treatment, nor were there significant differences in gill Na$^+$,K$^+$-ATPase activity between SNP and L24 fish. Plasma T4 and T3 were highest in the SNP group and lowest in the L24 group and were significantly different from one another. Plasma T3 was also significantly lower in both the L24OCT and L24DEC groups relative to the SNP group, in spite of their similar growth rates.

Discussion

Exposure of Atlantic salmon to continuous light from first feeding did not increase growth rate relative to those exposed to normal photoperiod. The change from continuous light to normal photoperiod (a decrease in day length) resulted in decreased growth (Fig. 2). In contrast, exposure of juvenile Atlantic salmon to continuous light starting in November (increase from 9 to 24 h day length) resulted in increased growth during the next 6 mo (Saunders et al. 1985). It appears that it is not continuous light *per se* that has a beneficial effect on growth, but rather an increase in day length.

Under conditions of SNP, Atlantic salmon undergo increases in salinity tolerance, gill Na$^+$,K$^+$-ATPase activity, and plasma T4 levels in spring (Fig. 3). Continuous light, when applied from first feeding or in autumn, inhibits increases in salinity tolerance and gill Na$^+$,K$^+$-ATPase activity (Fig. 4; Saunders et al. 1985). These results are in apparent conflict with those of Wagner (1974b) in which seawater survival and hypo-osmoregulatory ability of steelhead (*Salmo gairdneri*) maintained under continuous light was similar to that of fish raised under normal photoperiods. In Wagner's experiments, fish were either (1) exposed to continuous light soon after hatching but were challenged with seawater at small sizes (<10 cm, a size too small for this species to undergo transformation) or (2) challenged at larger sizes but only after exposure to continuous light late in the year when the fish may have been developmentally prepared to perceive and respond to continuous light as an increase in day length. The size dependence of spring increases in salinity tolerance and gill Na$^+$,K$^+$-ATPase activity in salmonids has been demonstrated before (Parry 1960; Conte and Wagner 1965; Clarke et al. 1978; Boeuf et al. 1985).

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Species and/or experimental differences, such as our use of 40‰ to test salinity tolerance versus the 30–32‰ used by Wagner (1974b), may also account for the dissimilar results between studies.

Other experiments indicate that conditions of constant day to night ratio do not inhibit behavioral or physiological changes associated with the parr–smolt transformation. Eriksson and Lundqvist (1982) subjected 1+-yr-old Atlantic salmon to a 12:12 day:night cycle. Body silvering and fin margin darkening, condition factor, and growth rate cycled with an endogenous rhythm of 10 mo. Our results indicate that continuous light applied early in ontogeny prevents an endogenous rhythm associated with parr–smolt transformation. Continuous light may act directly on the pineal and other photoreceptors to cause arhythmia. This inhibition is reversible, since Atlantic salmon returned to normal photoperiod underwent normal transformation, albeit with a significant lag period in the L24DEC group. Sexual maturation of presmolt male Atlantic salmon, which is also under photoperiod control in salmonids (Eriksson and Lundqvist 1980), is not inhibited by exposure to continuous light (R. L. Saunders, unpubl. data).

Photoperiod manipulation alters the timing of the parr–smolt transformation in several salmonid species, indicating that increasing day length is a zeitgeber (time-keeping device) for transformation. Decreasing or increasing the rate of change in day length retards or accelerates, respectively, increases in gill Na^+,K^+-ATPase activity and downstream migratory behavior in steelhead (Zaugg and Wagner 1973; Wagner 1974b). Sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon respond to increasing daylength with increased hypoosmoregulatory ability but show no change under constant or decreasing photoperiod (Clarke et al. 1978). Doubling the rate of increase in day length advanced the seasonal cycle of hypoosmoregulatory ability of a Baltic Sea stock of Atlantic salmon by 1 mo (Clarke et al. 1985).

Our results also support the role of increasing day length in stimulating transformation. Atlantic salmon exposed to continuous light from first feeding and returned to normal photoperiod in late October underwent increases in salinity tolerance and gill Na^+,K^+-ATPase activity the following spring, concurrent with fish under SNP. Fish returned to SNP in late December also had increases in these parameters but with a delay of 1 mo (Fig. 4). This "lag" period may have resulted from the decrease in day length experienced by these fish when returned to normal photoperiod from continuous light. Atlantic salmon larger than 14 cm which were raised under normal photoperiod and then exposed to continuous light in January (change from 9 to 24 h day length) responded with increased gill Na^+,K^+-ATPase activity (S. D. McCormick and R. L. Saunders, unpubl. data). Similarly, Komourdjian et al. (1976) found that when photoperiod was changed from 8 to 16 h day length in mid-December, salinity tolerance, apparent activity of pituitary somatotropes, growth, and smolt appearance of Atlantic salmon (>13 cm) occurred 2 mo earlier than in fish maintained under SNP.

The present experiments do not indicate whether rate of change in day length, a threshold day length, or some combination of the two is necessary to stimulate the parr–smolt transformation. Clarke et al. (1978) concluded that effects of photoperiod on growth and seawater adaptation in underyearling sockeye and coho salmon were not related to the accumulated hours of day length but to the direction and rate of change in day length. These authors also suggested that sensitivity to

photoperiod changed with season or prior photoperiod experience. This hypothesis may explain the results of our current study, but we cannot exclude the possibility that a threshold day length is also involved in the parr–smolt transformation of Atlantic salmon.

Simultaneous measurements of salinity tolerance, gill Na^+,K^+-ATPase activity, and thyroid hormones during environmental manipulation of the parr–smolt transformation have not been reported previously. Our results indicate that inhibition or phase-shift of increases in salinity tolerance is accompanied by similar changes in gill Na^+,K^+-ATPase activity (Fig. 4). The strong correlation between these parameters (Fig. 5) is necessary but not sufficient to establish a causal relationship. This correlation underscores the utility of measuring gill Na^+,K^+-ATPase activity as an indicator of salinity tolerance and potential for growth in seawater. However, changes in salinity tolerance can occur rapidly, especially in warmer water (R. L. Saunders, unpubl. data), and this correlation may not hold when entrance into seawater is preceded by a lengthy migration (Ewing et al. 1985). Changes in condition factor (Fig. 2) were also affected by photoperiod treatment, decreasing concurrently with increases in salinity tolerance and gill Na^+,K^+-ATPase activity. The value of condition factor as a smolt criterion has been previously demonstrated by Farmer et al. (1978) and may reflect a complex interaction between growth and metabolism (McCormick and Saunders 1987).

Plasma T4 levels were influenced by photoperiod treatment, and some relationship between plasma T4 levels and osmoregulatory changes was apparent. When plasma T4 was at its peak in the SNP and L24OCT groups, levels in the L24DEC and L24 groups were significantly lower. However, the shifts in salinity tolerance and gill Na^+,K^+-ATPase activity in the L24DEC group were not accompanied by a shift in their plasma T4 levels. Furthermore, the inhibition of osmoregulatory changes by continuous light was not accompanied by an inhibition of the seasonal plasma T4 cycle. Plasma T3 levels were not affected by the photoperiod treatments, nor were changes in plasma T3 correlated with increases in salinity tolerance and gill Na^+,K^+-ATPase activity.

Exogenous thyroid hormones do not increase gill Na^+,K^+-ATPase activity or result in permanent increases in salinity tolerance that are independent of hormonally induced increases in body size (Miwa and Inui 1985; Saunders et al. 1985; Omeljaniuk and Eales 1986). A direct causal role of thyroid hormones in triggering the parr–smolt transformation, analogous to their role in inducing amphibian metamorphosis (see Freiden 1967), remains to be demonstrated. A more likely role for thyroid hormones is a permissive or synergistic one involving interactions with other neuroendocrine factors (see Dickhoff and Sullivan 1987). In support of this hypothesis, Miwa and Inui (1985) found that T4 and growth hormone administered together increased salinity tolerance and gill Na^+, K^+-ATPase activity of Amago Salmon to a greater extent than growth hormone alone. Similar evidence for a permissive or synergistic role for thyroid hormones in control of growth and development has been reviewed by Donaldson et al. (1979).

In addition to the dramatic seasonal increase in salinity tolerance of smolts, seasonal changes in seawater adaptability may occur throughout salmonid ontogeny (Hoar 1965, 1976; Wagner 1974b; Saunders and Henderson 1978; Langdon and Thorpe 1985; McCormick and Saunders 1987). In the present study, the PARR group exhibited a 40% increase in gill Na^+,K^+-ATPase activity in April which declined steadily

thereafter. Although this increase was small relative to that observed in larger fish, it suggests that a seasonal increase in gill Na$^+$,K$^+$-ATPase activity does occur in parr. No change in salinity tolerance was detected in the PARR group during this period, perhaps due to the high salinity used in the present study. Spring increases in salinity tolerance have been observed in small (10–12 cm) presmolt steelhead (Conte and Wagner 1965). Plasma T4 concentrations of the PARR group in late spring rose to levels that were two-thirds that of the SNP group 6 wk earlier (Fig. 6). A similar spring increase in circulating thyroid hormones has also been observed in pre-smolt coho salmon and was hypothesized to be an important "maturational" event influencing transformation the following spring (Dickhoff et al. 1982; Dickhoff and Sullivan 1987).

Inhibition of increases in gill Na$^+$,K$^+$-ATPase activity and salinity tolerance by exposure to continuous light did not preclude gradual adaptation of the L24 group to 30‰ seawater. Although survival and capacity to maintain plasma osmolarity after 5 mo in seawater was not significantly different from the other groups, the growth of the fish during this period was halved. This reduction in growth is due to salinity, since we have recently found that poor growth does not result if L24 fish are maintained in freshwater (S. D. McCormick and R. L. Saunders, unpubl. data). It seems likely that endogenous and environmental factors which affect changes in osmoregulatory physiology during the parr–smolt transformation will also affect growth in seawater.

Acknowledgments

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