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# THE EFFECT OF ORALLY ADMINISTERED 3,5,3′-TRIIODO-L-THYRONINE ON GROWTH AND SALINITY TOLERANCE OF ATLANTIC SALMON (*SALMO SALAR* L.)

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## ABSTRACT

Saunders, R.L., McCormick, S.D., Henderson, E.B., Eales, J.G. and Johnston, C.E., 1985. The effect of orally administered 3,5,3′-triiodo-L-thyronine on growth and salinity tolerance of Atlantic salmon (*Salmo salar* L.) *Aquaculture*, 45:143—156.

Atlantic salmon (*Salmo salar*) juveniles were fed diets containing 0, 10, 20 and 100 ppm 3,5,3′-triiodo-L-thyronine ($T_3$) to test the effect of this hormone on growth, salinity tolerance and smoltification. Two 6-month feeding experiments, beginning in summer (experiment A) and winter (experiment B), were conducted under simulated natural photoperiods and temperatures. In each experiment, $T_3$-supplemented diets significantly elevated plasma $T_3$ levels and growth rates in a dose-dependent manner. $T_3$ administration increased relative opercular and fin growth, resulting in severe morphological abnormalities at the highest dose. The proportion of precociously mature males in experiment A was decreased by $T_3$ treatment. $T_3$ treatment significantly increased salinity tolerance in mature males but not in immature fish. In fish acclimated to sea water in spring (experiment B), $T_3$ treatment increased seawater survival for the first 2 months, but had no effect thereafter. $T_3$ did not change lipid content, moisture content or gill $Na^+$—$K^+$-ATPase activity in fresh water. We conclude that, while $T_3$ supplemented diets are effective in promoting growth, there was no demonstrable direct effect on smoltification.

## INTRODUCTION

Parr—smolt transformation of Atlantic and Pacific salmon occurs concurrently with marked increases in thyroid activity (Hoar, 1939; Dickhoff et al., 1978). The dramatic action of exogenous thyroid hormones on tadpole metamorphosis (see Rosenkilde, 1979) have suggested their use to induce salmonid smoltification. While thyroid hormones have been implicated in the behavioral, physiological and morphological aspects of smolting (Fontaine and Hatey, 1950; LaRoche and Leblond, 1952; Bagger-

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man, 1960; Piggins, 1962), much confusion remains as to the role of thyroid hormones in initiating smoltification (Eales, 1979).

Exogenous administration of the two major thyroid hormones, 3,5,3'-triiodo-L-thyronine ($T_3$) and to a lesser extent L-thyroxine ($T_4$), has a clear anabolic effect on most teleosts, including smolting and non-smolting salmonids (Higgs et al., 1977, 1982). While salinity tolerance of coho (*Oncorhynchus kisutch*) and Atlantic salmon (*Salmo salar*) can be increased by oral administration of $T_3$ (Fagerlund et al., 1980; Refstie, 1982), it is unclear whether $T_3$ can promote long-term salinity tolerance and other aspects of the parr—smolt transformation. The effective use of $T_3$ to promote salinity tolerance and smoltification will require knowledge of the constraints imposed by ontogeny and environmental conditions. In addition, the response of juvenile Atlantic salmon to $T_3$ administration may provide insight into the normal function of thyroid hormones in the parr—smolt transformation. The present study investigates the effects of $T_3$-supplemented diets on growth, salinity tolerance and smolt physiology of underyearling and yearling Atlantic salmon.

## MATERIALS AND METHODS

### *Experiment A*

On 15 May 1980, 800 laboratory-reared 14-month-old Atlantic salmon parr of Saint John River stock were divided into four groups of 200 and placed in 1-$m^2$ Swedish-style rearing tanks. Fish for this study were chosen from the lower range (8—10 cm) of the population size distribution. The tanks were supplied with fresh water at 12 $l \cdot min^{-1}$ from 15 May to 2 December and natural sea water (30‰ salinity) thereafter. Photoperiod simulated the natural cycle at latitude 45°N. Overhead lighting was by standard fluorescent bulbs which provided light intensities at the water surface of 430—538 lx. Water temperatures ranged from 10 to 18°C from May to August, and fell to 8°C from September to December. During the period December to January, temperatures were maintained at about 10°C by addition of warm water. Temperature among groups was maintained within ± 0.5°C.

Fish were fed commercial pellets (Ewos) containing $T_3$ at four levels (0, 10, 20, and 100 ppm). Appropriate amounts of $T_3$ were dissolved in alkaline 70% ethanol (33 ml 95% ethanol—12 ml 0.1*N* NaOH/kg food) and the hormone solution was sprayed on the food (Higgs et al., 1979). Food for the control group was sprayed with the same solution without the addition of $T_3$. Following addition of $T_3$, the food was stored in a freezer and the amount required for daily feeding removed each morning. Samples of food were withdrawn on 25 August and 25 November 1980 and $T_3$ content was determined by the method of Higgs et al. (1979). Feeding rates were adjusted weekly as water temperatures and body weight

changed so that fish were fed to satiation with minimal waste (2.0 to 3.0% of wet body weight/day). Food was dispensed by placing weighed amounts in automatic feeders adjusted to feed the daily ration during daylight hours.

After 3 months (25 Aug.) and 6 months (25 Nov.), blood samples were collected from 15 fish taken randomly from each group for measurement of plasma $T_3$. After severing the caudal peduncle and artery, blood was collected in heparinized centrifuge tubes, centrifuged for 5 min at 4000 r.p.m., and the plasma frozen and stored at −20°C. Plasma $T_3$ was measured by radioimmunoassay (Brown and Eales, 1977).

Measurements of fork length (cm) and wet weight (g) were made on 15 May 1980, and at approximately monthly intervals until 20 January 1981. Condition factor was calculated as 100·wet weight (g)/fork length $(cm)^3$. On 25 November 1980, 15 fish from each experimental group were randomly selected for fin and opercular measurements. Opercular measurements were from the back of the eye to the end of the operculum. The caudal fin was measured from the posterior end of the caudal peduncle to the fork of the caudal fin. Each pair of opercula, pectoral and pelvic fins was measured and an average length used. Fish with obvious fin deterioration were not used for fin measurements.

Survival was monitored daily throughout the experiment. Fork length and wet weight of dead fish were measured; fish were sexed and state of maturation determined. Fish were considered mature if gonads were milky white and ⩾2mm thick. After 49 days in sea water (20 January 1981) all remaining fish were killed and measurements listed above were made. Percent mature males (number of mature males/number of males) included survivors and those that died during the experiment.

*Experiment B*

On 21 January 1981, 9-month-old laboratory-reared Atlantic salmon parr of Waweig River stock were divided into four groups of 400. Fish for this study were chosen from the lower range (<10 cm) of the population size distribution. The parr were placed in 1-$m^2$ Swedish-style rearing tanks supplied with fresh water at a rate of 12 $l \cdot min^{-1}$ from January to June. Beginning 12 June 1981 salt water was gradually added to the tanks until the salinity reached 30‰ (12 July), at which level it was maintained thereafter. Photoperiod simulated the natural cycle at latitude 45°N. Water temperatures were held at 5—6°C until late March after which they were allowed to follow seasonal patterns of the laboratory supply. Sea water temperature ranged from a high of 13.6°C in September 1981 to a low of 1.2°C in March 1982. Temperature among groups was maintained within ± 0.5°C.

Food for experimental and control diets was prepared as in experiment A. Feeding rates were adjusted weekly, as water temperatures and body weight changed, and ranged from 1.0 to 2.5% of wet body weight/day.

Food was dispensed by placing weighed amounts in automatic feeders adjusted to feed the daily ration during the daylight hours.

On 24 March, 23 April and 2 June, five fish per group were randomly removed from tanks and analyzed for moisture and lipid content. Moisture content was determined by drying the whole body to a constant weight at 80°C. Lipid assays were conducted on the total dried carcass by the method of Bligh and Dyer (1959). On 10 June, ten fish were taken at random from each group for determination of gill $Na^+$—$K^+$-ATPase activity. The methods used for preparation of samples and analysis are described by Johnston and Saunders (1981). ATPase activity is expressed as $\mu$mol $P_i \cdot mg\ protein^{-1} \cdot h^{-1}$.

Initial measurements of length and weight were made on 28 January and subsequent measurements were made on 20 March, 24 April, 4 June, 29 June, 21 July, and 2 September. Survival was monitored daily throughout the experiment and dead fish were examined as in experiment A. After 8.2 months in sea water (18 March 1982) the experiment was terminated.

## RESULTS

### *Experiment A*

The concentrations of $T_3$ present in food were 53—99% of the calculated levels (Table I). Although the effective $T_3$ dose was smaller than intended, the relative difference between the experimental diets remained roughly the same (0.01:1:2:10). Plasma $T_3$ concentrations (measured on two occasions) were elevated in a dose-dependent manner but with declining effectiveness (non-linear) at increasing dose levels (Table I).

After 2 months of $T_3$ administration, length (but not weight) was sig-

TABLE I

$T_3$ in food and plasma of Atlantic salmon fed $T_3$-supplemented diets. Plasma $T_3$ values are the arithmetic mean (S.E.) of 8—15 fish per group

| | Control | 10 ppm | 20 ppm | 100 ppm |
|---|---|---|---|---|
| $T_3$ in feed ($\mu$g/g) | | | | |
| 25 Aug. 1980 | 0.05 | 9.93 | 12.33 | 52.74 |
| 25 Nov. 1980 | 0.05 | 6.85 | 14.93 | 66.10 |
| $T_3$ in plasma (ng/ml)[1] | | | | |
| Experiment A | | | | |
| 25 Aug. 1980 | — | 3.0 (0.6) | 5.4 (1.3) | 27.2 (4.6) |
| 25 Nov. 1980 | 2.0 (0.1) | 4.7 (0.9) | 5.9 (1.0) | 9.8 (1.3) |
| Experiment B | | | | |
| 2 June 1981 | 0.5 (0.1) | 1.4 (0.4) | 2.9 (1.1) | 8.6 (1.4) |

nificantly greater in $T_3$-treated fish ($P < 0.05$, one-way ANOVA). After 4 months, growth of $T_3$-treated fish in both length and weight was increased in a dose-dependant manner ($P < 0.05$, one-way ANOVA, Fig. 1). After 6 months of $T_3$ treatment, weight was increased 6, 21 and 49% over controls for the 10, 20 and 100 ppm diets, respectively ($P < 0.01$, one-way ANOVA). Condition factor from July onwards was depressed at the highest dose, but was nearly the same as controls for intermediate doses (Fig. 2).

After 3—4 months of $T_3$ treatment, severe morphological abnormalities occurred at the 100 ppm feeding level. These abnormalities were primarily the result of relative increases in opercular and fin growth (Table II, see

TABLE II

Fork length, wet weight, condition factor, and relative opercular and fin length (100·opercular or fin length/fork length) of yearling Atlantic salmon fed $T_3$-supplemented diets (experiment A). Values are the arithmetic mean (S.E.) of 15 fish per group sampled randomly on 25 Nov. 1980. Measurements with different superscripts are significantly different (one-way ANOVA, $P \leq 0.05$; Duncan's test, $P = 0.05$)

| | Control | 10 ppm | 20 ppm | 100 ppm |
|---|---|---|---|---|
| Fork length (cm) | $17.7^{a}$ (0.5) | $18.2^{a}$ (0.7) | $18.3^{a}$ (0.5) | $20.4^{b}$ (0.4) |
| Weight (g) | $64.9^{a}$ (4.5) | $72.0^{a}$ (7.5) | $69.7^{a}$ (4.7) | $94.4^{b}$ (5.4) |
| Condition factor ($(g/cm^3)\cdot 100$) | 1.15 (0.02) | 1.14 (0.02) | 1.13 (0.02) | 1.10 (0.03) |
| Operculum (% body length) | $9.9^{a}$ (0.3) | $11.3^{b}$ (0.2) | $14.8^{c}$ (0.3) | $14.5^{c}$ (0.4) |
| Pectoral (% body length) | $14.0^{ab}$ (0.3) | $13.0^{a}$ (0.5) | $14.7^{b}$ (0.4) | $16.7^{c}$ (0.3) |
| Pelvic (% body length) | $11.9^{a}$ (0.3) | $11.9^{a}$ (0.3) | $12.5^{a}$ (0.2) | $14.7^{b}$ (0.3) |
| Dorsal (% body length) | $11.9^{a}$ (0.2) | $12.3^{ab}$ (0.3) | $12.3^{ab}$ (0.2) | $12.7^{b}$ (0.2) |
| Adipose (% body length) | $6.6^{a}$ (0.1) | $6.6^{a}$ (0.1) | $6.7^{a}$ (0.2) | $7.2^{b}$ (0.2) |
| Anal (% body length) | $11.4^{a}$ (0.2) | $11.6^{a}$ (0.3) | $12.2^{a}$ (0.4) | $14.7^{b}$ (0.2) |
| Caudal (% body length) | $6.0^{a}$ (0.2) | $6.5^{ab}$ (0.2) | $6.8^{b}$ (0.2) | $8.5^{c}$ (0.2) |

photograph fig. 4D in Higgs et al., 1982). The opercula of fish in the 100 ppm feeding group were distinctly more flared and abnormally shaped than those of all other groups. While morphological abnormalities were not obvious among fish at the 20 ppm feeding level, the relative sizes of the opercula and caudal fins were significantly greater than controls (Table II).

After 6 months of feeding $T_3$-supplemented diets in fresh water, Atlantic salmon were returned to normal diets and exposed to 30 ppt sea water

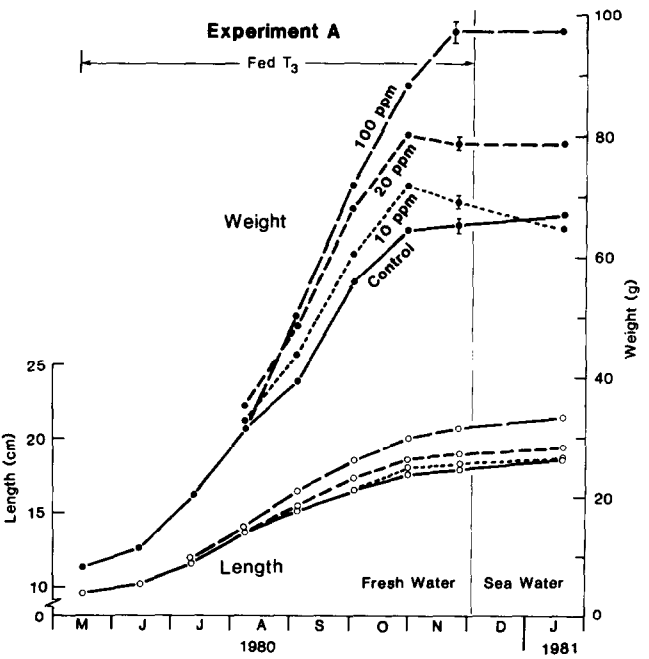


Fig. 1. Fork length and wet weight of yearling Atlantic salmon fed $T_3$-supplemented diets (experiment A). Values are the arithmetic mean of all fish in each group (67—200 fish); ± 1 S.E. of weight is shown for the last measurement in fresh water. Standard error of mean length is contained within each point.

TABLE III

Percent mortality after 49 days in sea water of yearling Atlantic salmon fed $T_3$-supplemented diets (experiment A). Asterisks denote percent mortalities that are significantly different from controls (Brownlee's test, $P \leq 0.05$). Sample size of each group is given in parentheses. No mature females were found under these experimental conditions

| | Control | 10 ppm | 20 ppm | 100 ppm |
|---|---|---|---|---|
| All fish | 28.8 (104) | 12.8* (109) | 8.4* (107) | 3.1* (96) |
| Mature males | 65.0 ( 40) | 26.7* ( 30) | 28.6* ( 28) | 11.5* (26) |
| Immature males | 7.1 ( 14) | 9.5 ( 21) | 3.3 ( 30) | 0.0 (25) |
| Immature females | 6.0 ( 50) | 6.9 ( 58) | 0.0 ( 49) | 0.0 (45) |

in late autumn for a period of 49 days. Percent mortality during seawater exposure for fish at all $T_3$ treatment levels was significantly lower than for controls (Table III). The primary effect of $T_3$ treatment on salinity tolerance was through mature males; seawater survival of control mature males was poor (65% mortality), but was significantly increased at all $T_3$

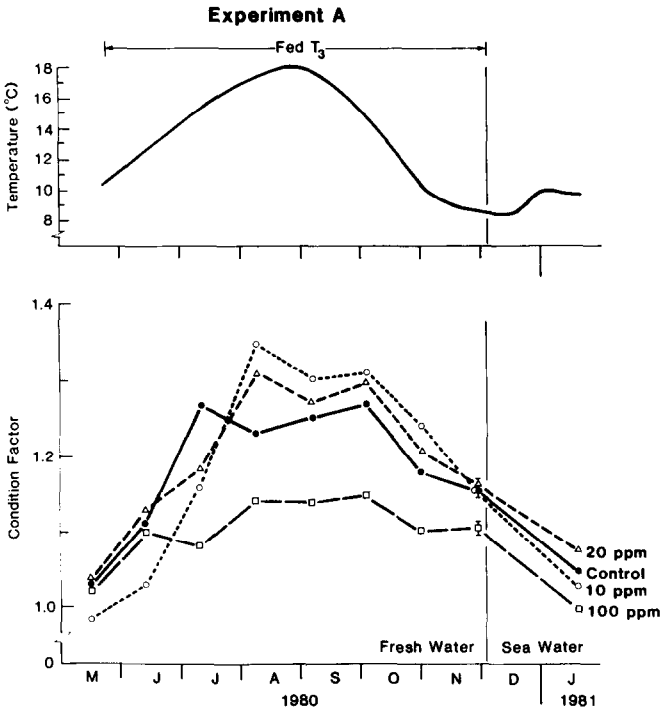


Fig. 2. Thermal regime and condition factor of yearling Atlantic salmon fed $T_3$-supplemented diets (experiment A). Values are the arithmetic mean of all fish in each group (67—204 fish); ± 1 S.E. of condition factor is shown for the last measurement in fresh water.

TABLE IV

Length and weight of mature male and immature (male and female) Atlantic salmon fed $T_3$-supplemented diets. A subsample of 40—50 fish for each dietary group was taken on 25 Nov. State of maturation was determined by external examination. Values are mean (S.E.)

| | Control | 10 ppm | 20 ppm | 100 ppm |
|---|---|---|---|---|
| Length (cm) | | | | |
| Mature males | 16.4 (0.22) | 15.6 (0.25) | 17.5 (0.25) | 18.4 (0.40) |
| Immature males and females | 18.6 (0.16) | 19.0 (0.16) | 19.5 (0.16) | 21.4 (0.14) |
| Weight (g) | | | | |
| Mature males | 54.2 (2.12) | 46.7 (2.12) | 65.1 (2.78) | 71.9 (4.30) |
| Immature males and females | 72.0 (1.87) | 77.1 (2.20) | 84.5 (2.20) | 106.3 (1.97) |

feeding levels. It should be noted that just prior to seawater exposure (25 Nov.) mature males were significantly smaller than immature fish in all groups ($P < 0.01$, Students $t$-test, Table IV). Owing to the high seawater survival (>90%) of immature fish, we could not detect a significant effect of $T_3$ treatment on salinity tolerance of immature fish of either sex.

The percentage of males which matured 'precociously' (age 1+) during the study was 74.1, 58.8, 48.3 and 51.0% for control, 10, 20 and 100 ppm groups, respectively; proportions for 20 and 100 ppm groups were significantly lower than for controls ($P < 0.05$, Brownlee's test).

*Experiment B*

Underyearling Atlantic salmon fed 10, 20 and 100 ppm $T_3$ diets were significantly longer and heavier than controls after 4 months of experimental feeding (Fig. 3, $P < 0.01$, one-way ANOVA). Growth response to $T_3$ treatment was dose-dependent and was maintained for the final 2 months of $T_3$ administration during which the fish were exposed to brackish and full-strength sea water. As in experiment A, condition factor of fish fed the 100 ppm $T_3$ diet was depressed relative to controls (Fig. 4). Condition

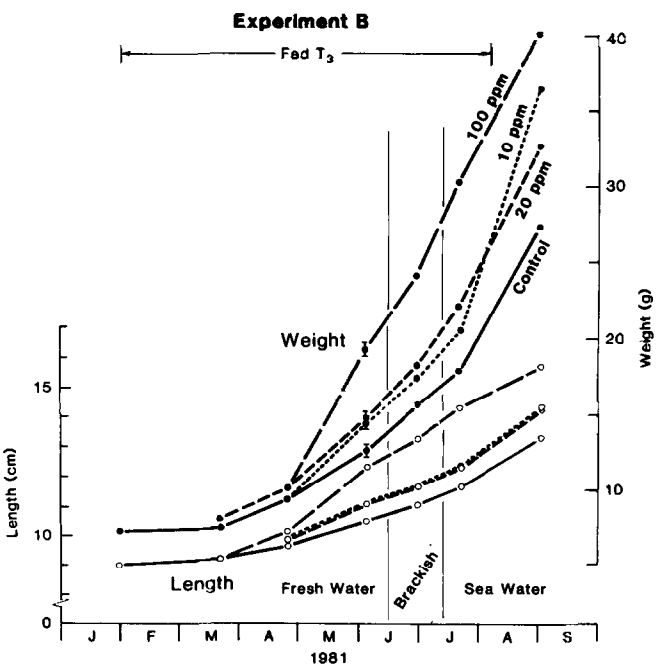


Fig. 3. Fork length and wet weight of underyearling Atlantic salmon fed $T_3$-supplemented diets (experiment B). Values are the arithmetic mean of all fish in each group (124—400 fish); ± 1 S.E. of weight is shown for the last measurement in fresh water. Standard error of mean length is contained within each point.

factors of fish at intermediate doses (10 and 20 ppm) were similar to controls until seawater exposure when the condition factor of controls declined sharply.

Morphological abnormalities in the 100 ppm feeding group were less frequent and less marked than those observed in experiment A.

After 4.5 months of $T_3$ administration (which continued for 6 months), Atlantic salmon in each group were gradually exposed to salt water beginning 12 June 1981. Survival in sea water was monitored for 8.5 months (Fig. 5). For the first 3 months in sea water the lowest mortality occurred in the 100 ppm group and the highest for the control group. In late autumn mortality was low and similar for all groups. In mid-winter the rate of mortality rose for all groups but was greatest in fish previously fed the 100 ppm $T_3$ diet. Mortality remained high in all groups for the remainder of the experiment.

Lipid and moisture content and gill $Na^+$—$K^+$-ATPase activity were examined as indicators of smoltification (Table V). Lipid and moisture content measured on three occasions (24 March, 23 April and 2 June 1981) were not significantly altered by $T_3$ treatment at any level ($P > 0.05$, two-way ANOVA). Sampling date, however, had a significant effect; lipid content increased and moisture content decreased in each group on the 2 June

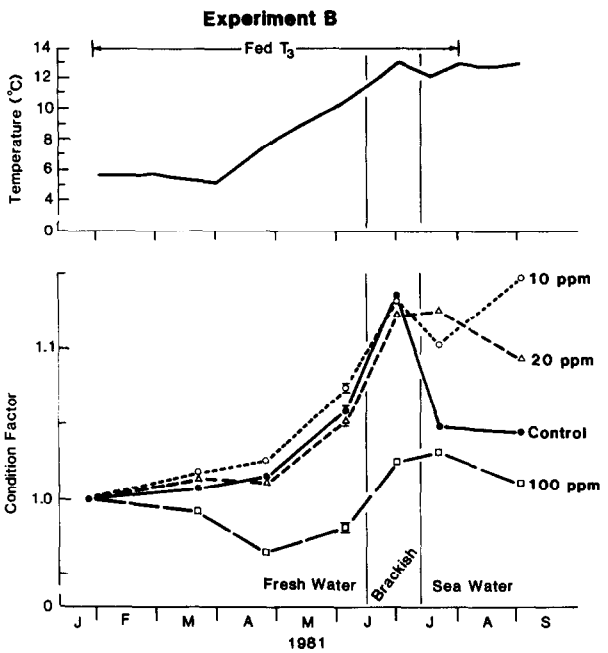


Fig. 4. Thermal regime and condition factor of underyearling Atlantic salmon fed $T_3$-supplemented diets (experiment B). Values are the arithmetic mean of all fish in each group (124—400 fish); ± 1 S.E. of condition factor is shown for the last measurement in fresh water.

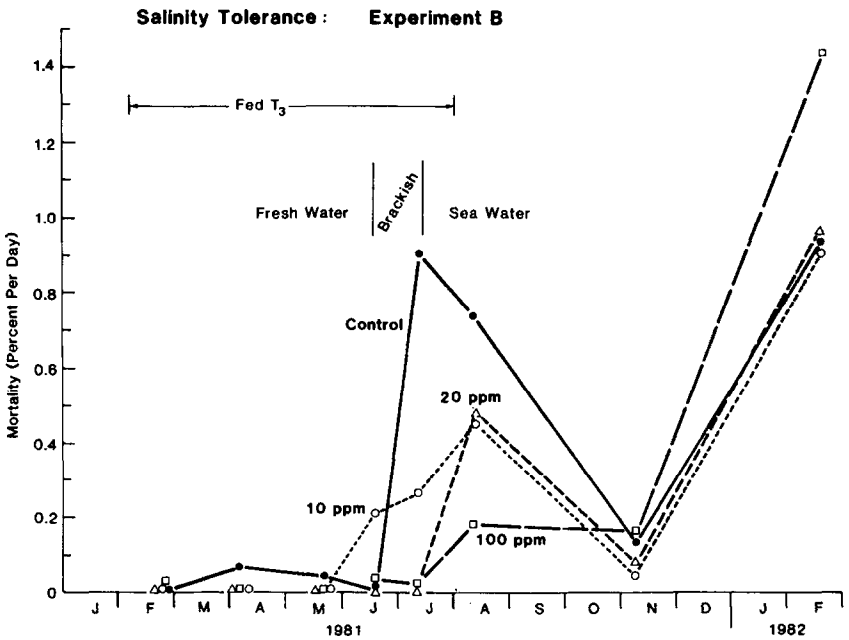


Fig. 5. Freshwater and seawater mortality of underyearling Atlantic salmon fed $T_3$-supplemented diets (experiment B). Mortality (percent per day) for each time interval was calculated as: 100 (number dead in each interval/number dead and surviving in each interval)/number of days per interval, and is plotted at the mid-point of the interval.

sampling date ($P < 0.01$, two-way ANOVA). Gill $Na^+$—$K^+$-ATPase activity of freshwater fish measured on 10 June was not significantly influenced by $T_3$-supplemented diets (Table V).

## DISCUSSION

### *Growth*

The normal role of the thyroid in teleost growth is thought to be a 'permissive' one in which thyroid hormones act in conjunction with other anabolic hormones (Eales, 1979). Nonetheless, exogenously administered $T_3$ can increase growth in most teleosts (Higgs et al., 1982). Our results indicate that both underyearling and yearling Atlantic salmon will increase growth in response to $T_3$-supplemented diets and that this will occur irrespective of season. These results contrast with those of Refstie (1982), who found that 10 ppm $T_3$ in food increased growth of 7-month-old but not 19-month-old Atlantic salmon. It should be pointed out that, in hormone feeding studies such as the present one, the actual hormone dosage received by a fish is dependent on feeding rate, which is in turn temperature dependent. Lower temperature culture conditions will require higher doses of the hormone in food to increase plasma $T_3$ levels to the same extent, and vice versa.

TABLE V

Mean moisture and lipid content (% wet weight) and gill $Na^+$—$K^+$-ATPase activity ($\mu$mol $P_i$·mg protein$^{-1}$·h$^{-1}$) of Atlantic salmon fed $T_3$-supplemented diet and sampled in fresh water on several dates in 1981 (experiment B). Values are the arithmetic mean (S.E.) of 5—10 fish for each time interval and experimental group. For both lipid and moisture content, two-way ANOVA indicated there was no significant ($P > 0.05$) effect of $T_3$ treatment level, while date of sampling was significant. There was no significant effect of $T_3$ feeding level on gill $Na^+$—$K^+$-ATPase activity ($P > 0.05$ one-way ANOVA)

| | 24 March | 23 April | 2 June |
|---|---|---|---|
| Moisture content | | | |
| Control | 77.3 (0.3) | 77.1 (0.5) | 74.2 (0.3) |
| 10 ppm | 76.2 (0.6) | 76.3 (0.3) | 74.3 (0.2) |
| 20 ppm | 76.4 (0.3) | 76.5 (0.4) | 74.5 (0.5) |
| 100 ppm | 76.4 (0.4) | 77.2 (0.3) | 75.8 (0.4) |
| Lipid content | | | |
| Control | 4.01 (0.27) | 4.20 (0.45) | 6.70 (0.27) |
| 10 ppm | 4.93 (0.50) | 4.96 (0.33) | 6.54 (0.16) |
| 20 ppm | 4.46 (0.21) | 5.02 (0.42) | 6.88 (0.60) |
| 100 ppm | 4.65 (0.43) | 4.83 (0.27) | 6.56 (0.15) |
| | 10 June | | |
| Gill $Na^+$—$K^+$-ATPase | | | |
| Control | 12.9 (0.6) | | |
| 10 ppm | 12.0 (1.2) | | |
| 20 ppm | 10.5 (0.6) | | |
| 100 ppm | 10.6 (0.9) | | |

Severe morphological abnormalities occurred at the highest dose (100 ppm) in experiment A and to a lesser extent in experiment B. Abnormalities in skull structure were observed in coho salmon (*Oncorhynchus kisutch*) at doses of 20 ppm and above (Higgs et al., 1979). Aberrant morphological changes are commonly observed after administration of large amounts of thyroid hormones to teleosts (see Donaldson et al., 1979). Abnormal morphological development will preclude the routine use of high doses of $T_3$ and will limit the potential uses of $T_3$-induced growth in salmonid culture.

Changes in condition factor and relative growth of opercula and fins as a result of $T_3$ administration (even at low doses) suggest that thyroid hormones may play a role in normal morphological development. Thyroid hormones have been implicated in both normal and abnormal bone growth (Barrington and Rawdon, 1967; Higgs et al., 1982). The parr—smolt transformation is characterized by several morphological changes including decreased condition factor, lengthening of the caudal peduncle and changes in relative fin size (Evropeitseva, 1957; Fessler and Wagner, 1969). The high thyroid activity during this period (Hoar, 1939; Dickhoff et al., 1978) may be partially responsible for inducing such morphological changes.

*Salinity tolerance*

Salinity tolerance of mature males in experiment A was relatively poor but was significantly improved by prior $T_3$ treatment. While mature males in the two highest dose groups were significantly larger than controls, mature males from the 10 ppm group were smaller (not significantly, $P > 0.05$) than the controls (Table IV). However, salinity tolerance of mature males from the 10 ppm group was significantly greater than that of controls (Table III). $T_3$ administration may have affected the maturation process directly, which in turn influenced seawater survival. Survival of mature male brook trout (*Salvelinus fontinalis*) in sea water is lowest during the spawning period at the height of gonadal development (McCormick and Naiman, 1984). Ikuta et al. (1985) have recently shown that methyltestosterone incorporated into the food of masu salmon (*Oncorhynchus masou*) decreases salinity tolerance and the appearance of smolt characteristics. In the present experiments, prior $T_3$ treatment may have increased seawater survival by affecting the timing or degree of maturation of Atlantic salmon, though this was not apparent from inspection of gonads.

Survival of underyearling Atlantic salmon for the first several months in sea water was increased by $T_3$ administration in a dose-dependent fashion. Similar results concerning the effects of $T_3$ treatment on salinity tolerance were obtained by Fagerlund et al. (1980) for coho salmon and Refstie (1982) for Atlantic salmon. In feeding studies such as the present one, it is difficult to determine whether increased salinity tolerance is a direct effect of the hormone or a secondary effect of increased size which itself increases salinity tolerance. In the present study, removal of $T_3$ from the diet several weeks after seawater exposure did not result in increased mortality, suggesting that increased size of $T_3$-fed fish is the agent responsible for improved seawater survival.

Irrespective of this interpretation, however, long-term survival of underyearling Atlantic salmon in sea water was not improved by $T_3$ treatment. All experimental groups experienced high mortality in winter. Poor seawater survival of salmonids of low temperatures ($<0°C$) reported by Saunders et al. (1975) may partially explain these results. Poor initial (summer) and winter survival may also indicate that none of the experimental groups had undergone smoltification, as discussed below.

*Smoltification*

Normal smoltification of Atlantic salmon is accompanied by decreased lipid and increased moisture content (Farmer et al., 1978). Increased lipid and decreased moisture content observed at all $T_3$ levels and in the control group (experiment B, Table V) in early summer are characteristic of parr rather than smolts. Fagerlund et al. (1980) found that $T_3$-supplemented diets (4 and 20 ppm) did not alter whole body moisture or lipid content of

coho salmon. The multitude of conflicting results in this regard, however, suggests that the response of proximate body composition to thyroid hormone treatment is dependent on dose, diet, nutritional state and other environmental conditions (Higgs et al., 1982).

Gill $Na^+$—$K^+$-ATPase activity was also unaffected by $T_3$ treatment (Table V). Activity levels of 10—12 $\mu$mol $P_i \cdot mg\ protein^{-1} \cdot h^{-1}$ found in the present study are similar to levels found for parr and are less than half the level found for smolts under similar environmental conditions and assay technique (Johnston and Saunders, 1981). We conclude that none of the $T_3$ feeding groups or controls underwent smoltification, a result which is probably due to the small size of fish in all groups, a size that is below that at which Atlantic salmon normally undergo smoltification (Johnston and Saunders, 1981). These results indicate that $T_3$-supplemented diets cannot induce smoltification in Atlantic salmon that have not achieved the proper developmental stage (size) for such a transformation.

*Prospectus*

The present experiments indicate that dietary $T_3$ is effective in promoting growth in both underyearling and yearling Atlantic salmon. $T_3$ treatment also increased short-term salinity tolerance of yearling mature males and underyearlings, but it appears that this effect is primarily the result of size differences induced by $T_3$. Nonetheless, $T_3$-supplemented diets may be efficacious in promoting smoltification by increasing growth such that a minimum size for smolting is achieved during spring. In future work with oral administration of $T_3$ to smolting salmonids, it will be important to determine whether $T_3$-induced increases in growth permit normal development and completion of the parr—smolt transformation.

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