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Physiological Smolt Characteristics of Anadromous and Non-anadromous Brook Trout (*Salvelinus fontinalis*) and Atlantic Salmon (*Salmo salar*)[1]

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Anadromous brook trout, *Salvelinus fontinalis*, of rivière à la Truite, Quebec, were examined for physiological changes associated with smoltification, and compared with non-anadromous brook trout from the adjacent Matamek River. There were no statistical differences in plasma thyroxine concentration, gill Na^+,K^+-ATPase activity, hematocrit, or osmoregulatory ability between the populations. Moisture content was different between the populations, but both had the same pattern of declining moisture content as summer progressed. Silver coloration of brook trout in rivière à la Truite was associated with larger fish and higher gill Na^+,K^+-ATPase activity, but not with changes in plasma thyroxine concentrations, moisture content, hematocrit, or condition factor. Brook trout at high-salinity estuarine sites had greater gill Na^+,K^+-ATPase activity and hypoosmoregulatory ability than those from low-salinity sites. Silvering of Atlantic salmon (*Salmo salar*) in rivière à la Truite was associated with larger fish, higher gill Na^+,K^+-ATPase activity, and higher plasma thyroxine. Gill Na^+,K^+-ATPase activity of highly silvered freshwater Atlantic salmon was greater than that of highly silvered brook trout. Estuarine Atlantic salmon had significantly higher plasma thyroxine concentration and gill Na^+,K^+-ATPase activity than estuarine brook trout. Based on these physiological factors, we conclude that smoltification is undeveloped in brook trout and that estuarine residence is important for salt water acclimation and eventual seaward migration.

Les modifications physiologiques associées à la smoltification chez l'omble de fontaine (*Salvelinus fontinalis*) anadrome peuplant la rivière à la Truite (Québec) ont été étudiées et comparées à l'état physiologique de l'omble de fontaine non anadrome vivant dans la rivière Matamek avoisinante. Il n'y avait aucune différence statistique entre les populations pour ce qui est des concentrations de thyroxine dans le plasma, de l'activité du Na^+-K^+-ATP-ase dans les ouïes, de l'hématocrite et de la capacité osmorégulatoire. La teneur en humidité variait entre les populations, mais les deux montraient le même régime de décroissance de la teneur au cours de l'été. Une livrée argentée chez l'omble de fontaine de la rivière à la Truite était associée à de gros poissons et à une activité élevée du Na^+-K^+-ATP-ase dans les ouïes mais non à des variations de la concentration plasmatique de thyroxine, de la teneur en humidité, de l'hématocrite ou du facteur de condition. Les individus présents aux sites estuariens à forte salinité avaient une activité du Na^+-K^+-ATP-ase dans les ouïes et une capacité hypoosmorégulatoire plus élevées que ceux qui peuplaient les sites à faible salinité. L'argenture du saumon atlantique (*Salmo salar*) dans la rivière à la Truite était associée à de gros poissons, à une activité élevée du Na^+-K^+-ATP-ase dans les ouïes et à une concentration plasmatique élevée de thyroxine. L'activité du Na^+-K^+-ATP-ase dans les ouïes de saumons atlantiques dulçaquicoles à livrée très argentée était plus importante que chez les ombles de fontaine semblables. Les saumons atlantiques pêchés en estuaire avaient une concentration plasmatique de thyroxine et une activité du Na^+-K^+-ATP-ase significativement plus élevées que les ombles de fontaine provenant d'estuaires. D'après ces facteurs physiologiques, les auteurs formulent la conclusion que la smoltification n'est pas développée chez l'omble de fontaine et que la stabulation en estuaire est importante pour l'acclimatation à l'eau salée et la migration finale en milieu marin.

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The process of parr–smolt transformation in anadromous salmonids has received much attention in recent years owing, in part, to the realization that some aspects of artificial production may limit returns of hatchery reared smolts (Wedemeyer et al. 1980). Although comparative studies have been conducted on smolting in the genera *Salmo* and *Oncorhynchus* (see Hoar 1976 for a review), little has been reported on the possible smolt status of charrs[4] (genus *Salvelinus*). The outward signs of smolting (silvering and seaward migration), however, occur in many populations of anadromous brook trout, *Salvelinus fontinalis*, and Arctic charr (*S. alpinus*) (White 1940; Wilder 1952; Black 1981; Castonguay et al. 1982;

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[4]The spelling differs from that (char) used in *A List of Common and Scientific Names of Fishes from the United States and Canada* (American Fisheries Society Special Publication No. 12).

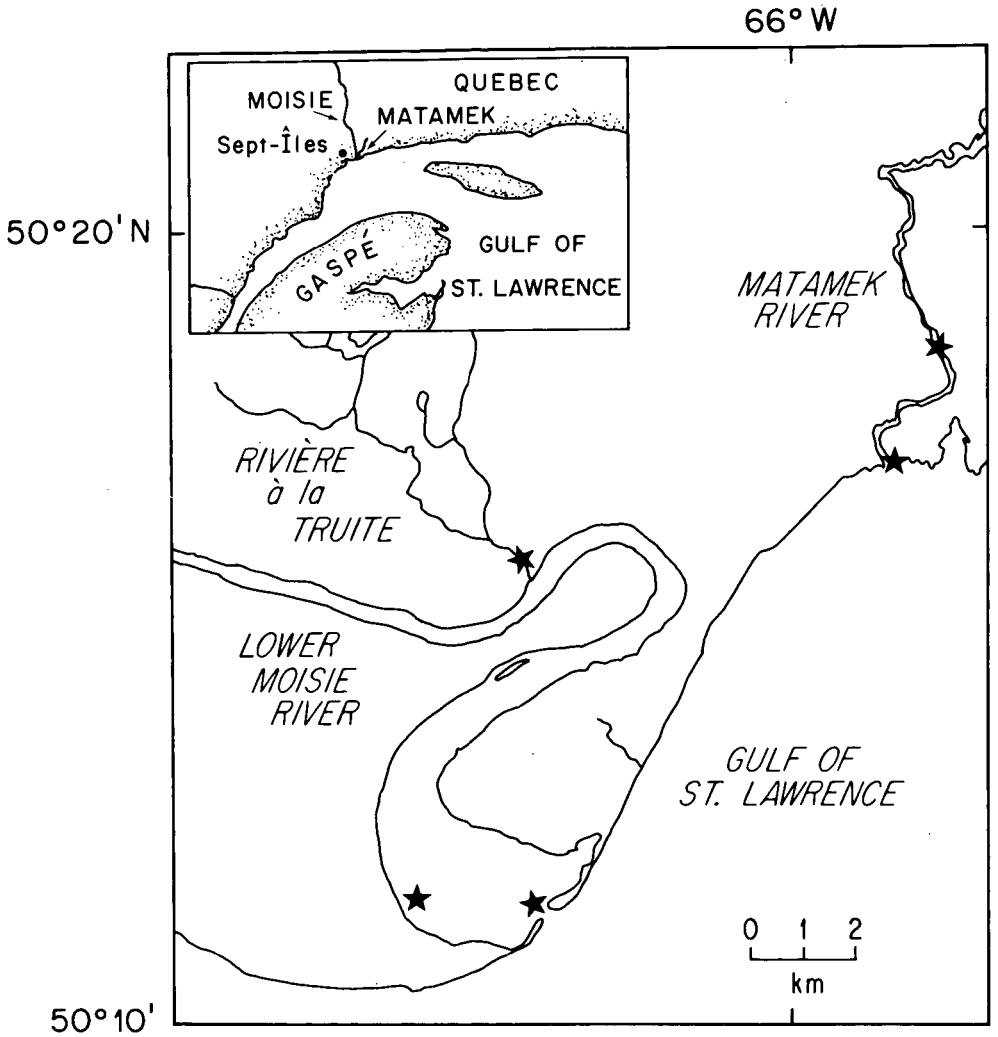

FIG. 1. Freshwater and estuarine brook trout sampling sites. Anadromous fish were captured at rivière à la Truite and at two sites in the Moisie River estuary. Non-anadromous brook trout were captured at the base of the 2nd and 3rd Falls of the Matamek River.

Nordeng 1983). The charrs are thought to be similar to the earliest anadromous salmonids (Rounsefell 1958).

Seaward migration of anadromous brook trout in northern latitudes is characterized by downstream movement in spring, residence in estuarine or coastal waters for 2–4 mo, followed by upstream migration in autumn (White 1940; Castonguay et al. 1982). Montgomery et al. (1983), studying sea-run brook trout of rivière à la Truite, found seaward migration to be temporally synchronous among individuals. In the southern portion of their range, the timing and duration of seaward migration is more variable (Mullan 1958; Smith and Saunders 1958). In addition to seasonal aspects of migration, size-dependent migration has been reported for all sea-run brook trout populations (White 1940; Wilder 1952; Smith and Saunders 1958; Dutil and Power 1980; Castonguay et al. 1982). Size-dependent and seasonal seaward migration are characteristic of all smolting salmonids (Hoar 1976). Smolting involves environmentally cued (Komourdjian et al. 1976; Grau et al. 1982), hormonally regulated changes in morphology, behavior, biochemical composition, and osmoregulatory physiology, which are presumably adaptive for seawater entry (see Hoar 1976; Folmar and Dickhoff 1980; Wedemeyer et al. 1980 for reviews). For this investigation, a smolt is defined as a freshwater salmonid that has undergone metamorphic and physiological changes preparatory for seawater entry. Prominent among these characteristics are increases in hypoosmoregulatory ability (salinity tolerance), gill Na^+,K^+-ATPase activity, plasma thyroxine (T_4), deposition of guanine and hypoxanthine on skin and scales (silvering), changes in lipid–moisture dynamics, and decreases in condition factor (Wedemeyer et al. 1980).

Knowledge of physiological changes preparing brook trout for entry into seawater would aid our understanding of anadromy in brook trout in particular, and salmonids in general, as well as upgrade the technology for sea ranching and farming of brook trout (Whoriskey et al. 1981). Our objectives were to determine if physiological changes associated with smoltification occur in northern anadromous brook trout, and if these changes are preparatory for seawater entry.

Study Sites

The Moisie and Matamek rivers empty into the Gulf of St. Lawrence approximately 22 and 36 km east of Sept-Îles, Quebec, respectively (Fig. 1). Rivière à la Truite is a 4th-order stream with an average width of 10 m and a maximum midsummer depth of 2 m that enters the Moisie River 14 km

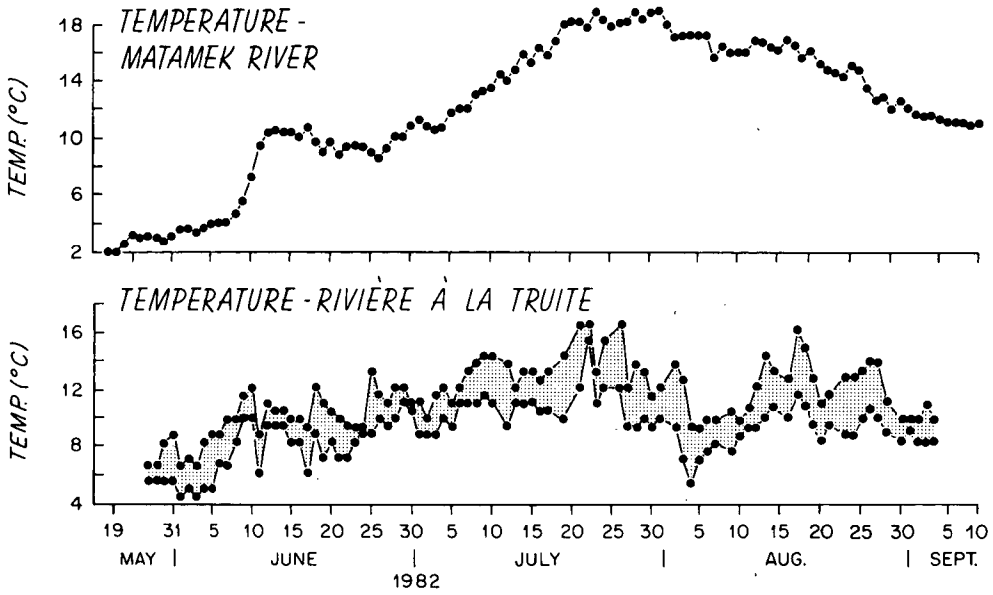

FIG. 2. Temperature profiles of rivière à la Truite (daily maximum and minimum) and the Matamek River (single day time reading) from May 19 to September 3, 1982. Ice-off occurred on May 13 and May 3 for rivière à la Truite and the Matamek River, respectively.

upstream of the Gulf of St. Lawrence. Our study site on rivière à la Truite was located 0.4 km upstream of its confluence with the Moisie River. The Moisie River broadens into a 2-km-wide estuary with sandbars restricting confluence with the Gulf of St. Lawrence to 0.25 km. Two sites were chosen in the Moisie River estuary: one 2 km upstream of the Gulf of St. Lawrence and the second at its confluence with the Gulf (Fig. 1). The Moisie River confluence site is characterized by higher salinities than the upstream site (Table 1; Montgomery 1980).

The Matamek River (6th order) averages 52 m wide and passes over five waterfalls from Matamek Lake to the Gulf of St. Lawrence (9.6 km). The 1st Falls is a barrier to upstream migration of brook trout (Haedrich 1975). Sampling of brook trout in the Matamek River occurred at the base of the 2nd and 3rd Falls. The Matamek River estuary averages 80 m wide; saline water can intrude nearly to the base of the 1st Falls. Brook trout in the Matamek River estuary have been washed over the 1st Falls and do not contribute reproductively to the river population (Haedrich 1975).

Materials and Methods

In rivière à la Truite, two fyke nets, with wings spanning the river, were placed so that one faced upstream and one faced downstream. Nets were checked and emptied daily. Details of capture methodology are reported in Montgomery et al. (1983). Fish in the Matamek River were captured by fyke nets (checked and emptied daily or every other day) or by beach seine. Seasonal temperature changes in rivière à la Truite and Matamek River are detailed in Fig. 2. Sampling of brook trout in the Moisie River estuary was accomplished with beach seines during daylight within 2 h of high tide. In the Matamek River estuary, brook trout and Atlantic salmon were sampled with beach seine at night within 2 h of high tide.

Fish were examined for degree of silvering, fork length (FL) was measured to the nearest 0.1 cm, and fish were weighed to the nearest 0.1 g. Condition factor (CF) was calculated as

$$CF = 100 \cdot \text{wet weight (g)}/\text{fork length (cm)}^3.$$

TABLE 1. Physical characteristics of Moisie River estuary and Matamek Rivery estuary sampling sites. Moisie River and Matamek River estuaries were sampled from July 2 to August 31 and June 4 to July 29, respectively. Although no salinity change was detected at the Moisie River estuary upstream site, some salt water intrusion occurs at this site and beyond (Montgomery 1980).

	Moisie River estuary		
	Upstream	Mouth	Matamek River estuary
Temperature (°C)	12–17	10–16	10–15
Salinity (‰)	0	0–27	5–27
Maximum depth (m)	6–7	6–7	5–6
Tidal influence	Yes	Yes	Yes

Degree of silvering was determined by inspection using the following criteria: (1) no silvering; (2) partial silvering, >20% of body surface reflective and silver, but parr marks or vermiculation pattern on dorsal surface clearly visible; (3) full silvering, >80% body surface is reflective and silver, parr marks or vermiculation pattern not clearly visible.

Analytical Techniques

Fish were sampled in the field within 15 min of removal from nets. Due to the difficulty of obtaining sufficient blood from small fish, only those >8.5 cm FL were used in physiological analyses. Fish were anesthetized in 0.4 mL/L phenoxyethanol solution for 30–60 s. Anesthesis for this brief period did not influence measured characteristics relative to animals stunned by a blow to the head (S. D. McCormick, unpubl. data). After anesthetization, the caudal fin was severed and blood collected into two ammonium heparinized capillary tubes. Gill arches were removed and 0.05–0.2 g (wet weight) of gill filament was trimmed from gill arches and placed in 1 mL of sucrose–EDTA–imidazole (SEI) solution (0.3 mmol/L sucrose, 0.02 mmol/L disodium ethylenediaminetetraacetate, and 0.1 mmol/L imidazole adjusted to a final pH of 7.1 with HCl). Blood and gill

samples, and fish carcasses, were placed on ice and transported within 30 min to the laboratory. Hematocrit tubes were centrifuged for 5 min at 5500 rpm, hematocrit read (percent red blood cells), and plasma removed. Duplicate 25-μL plasma samples and gill samples were stored at −17°C for later analysis of T_4 concentration and gill Na^+,K^+-ATPase activity.

Plasma osmolarity was measured immediately after centrifugation using a Wescor vapor pressure osmometer (intraassay coefficient of variation ±1.0%). Body moisture content (percent water) was determined by drying the central portion of the body (excluding head and tail but including viscera) at 60°C to a constant weight. Plasma T_4 was analyzed by competitive binding radioimmunoassay (Dickhoff et al. 1978). Gill Na^+,K^+-ATPase activity was determined by the method of Zaugg (1982). Details of these techniques can be found in McCormick and Naiman (1984a).

Seawater Challenge

We used a 24-h seawater challenge test (Clarke and Blackburn 1978) to measure hypoosmoregulatory ability. Gulf of St. Lawrence seawater (28‰) was supplemented with Instant Ocean salt to a salinity of 32‰ in order to provide sufficient salinity stress. Seawater challenges were conducted in a 400-L aquarium maintained at 10 ± 0.5°C, an average spring temperature for both rivers and their estuaries. To avoid overcrowding, no more than 12 fish were used in the aquarium at one time. Total ammonia levels were checked periodically and did not exceed 0.1 mg/L. Fish were transported to the laboratory within 15–45 min of capture and placed directly in the seawater aquarium. Care was taken to prevent temperature changes (±1°) or oxygen depletion during transport. After 24-h (±15 min), fish were removed from the aquarium, anesthetized in phenoxyethanol–seawater solution, and blood samples taken and analyzed as previously described.

Statistical Methods

To determine the statistical significance of physiological differences between brook trout populations, we used two-way analysis of variance (ANOVA). To determine significant differences within river populations over time, differences among fish based on silvering characteristics, and differences among estuarine brook trout and Atlantic salmon, we used one-way ANOVA. To establish homogeneity of sample variances, we used the F_{max} test. In cases where variances were heterogeneous, the data were log transformed to produce homogeneous variances. The Scheffé method was used in a posteriori tests of differences among means. Confidence level for all statistical tests was 95%, unless otherwise stated.

Results

Freshwater Studies

There was no silvering in non-anadromous brook trout of the Matamek River whereas marked silvering was observed in fish leaving rivière à la Truite ($p < 0.01$; Fig. 3). Moisture content was significantly greater in rivière à la Truite brook trout ($p < 0.01$). There were no significant differences, however, in plasma T_4, gill Na^+,K^+-ATPase activity, or hematocrit between fish from the two rivers ($p > 0.10$; Fig. 3).

Within each river, several significant changes in brook trout physiology occurred over time. Plasma T_4 levels of brook trout in rivière à la Truite were significantly higher during periods of downstream movement (May and June) than during July and August. Matamek River brook trout did not display a significant change in plasma T_4 over time. Moisture content and hematocrit had a similar pattern for fish in each river; moisture content declined with time, while hematocrit increased with time (Fig. 3). Gill Na^+,K^+-ATPase activities of brook trout in both rivers decreased over time as river temperatures increased.

To compare "smolt" appearance with "smolt" physiology, we divided brook trout from rivière à la Truite captured during the period of peak downstream migration (May 20 to June 30) into three groups based on the degree of silvering (Fig. 4). Brook trout possessing more silvering were larger ($p < 0.01$) and had higher gill Na^+,K^+-ATPase activity ($p < 0.02$). There were no significant differences in plasma T_4, moisture content, hematocrit, or condition factor among brook trout grouped by silvering ($p > 0.10$). Hematocrit and moisture content of downstream migrating fish were correlated with date of capture (day 1 = May 20, $r = 0.61$ and -0.31, $p < 0.01$ and 0.05, respectively) and were significantly correlated with one another ($r = -0.28$, $p < 0.05$, $N = 51$). With the exception of silvering, fork length did not significantly correlate with any of the measured physiological variables.

Atlantic salmon captured in rivière à la Truite were also examined for physiological smolt characteristics (Table 2). Atlantic salmon with high silvering were significantly larger and had significantly greater gill Na^+,K^+-ATPase activity and plasma T_4 than fish with intermediate and no silvering ($p < 0.05$). Hematocrit was significantly lower in highly silvered Atlantic salmon. Moisture content and condition factor were not significantly different between the two groups.

Seawater Challenge — Freshwater Fish

In rivière à la Truite, downstream migrating brook trout between 9.5 and 19.5 cm FL (13.5 ± 1.0, x ± SE) captured between June 8 and 24 were subject to a 24-h seawater challenge. Brook trout from the Matamek River (14.0–20.2 cm FL, 17.5 ± 0.7) captured between August 2 and 29 were also seawater challenged. Mean plasma osmolarity of rivière à la Truite brook trout after 24 h in seawater was 442 ± 15.7 mosmol/L ($N = 10$). This level of plasma osmolarity was not significantly different from seawater-challenged Matamek River fish (459 ± 1.35 mosmol/L; $N = 9$). Plasma osmolarity and FL of seawater-challenged fish were not significantly correlated ($p > 0.10$) in either river.

Estuarine Studies

Brook trout at the upstream site of the Moisie River estuary were significantly smaller than those from the downstream site (Fig. 5). This resulted from size dependent migration (Montgomery et al., unpubl. data). Brook trout at the mouth of the Moisie River estuary, and brook trout and Atlantic salmon in the Matamek River estuary, did not differ significantly in size (range 10.9–23.0 cm FL; Fig. 5). All fish captured at estuarine sites had silvering (either category 2 or 3); there was no significant difference in brook trout silvering between estuarine sites.

Several smolt characteristics were significantly different for brook trout and Atlantic salmon captured in estuaries. Plasma T_4 concentrations were the same for brook trout from all estuarine locations, but were significantly lower than those of Atlantic salmon from the Matamek River estuary (Fig. 5). Similarly, gill Na^+,K^+-ATPase activity was 2–3 times higher in Atlantic

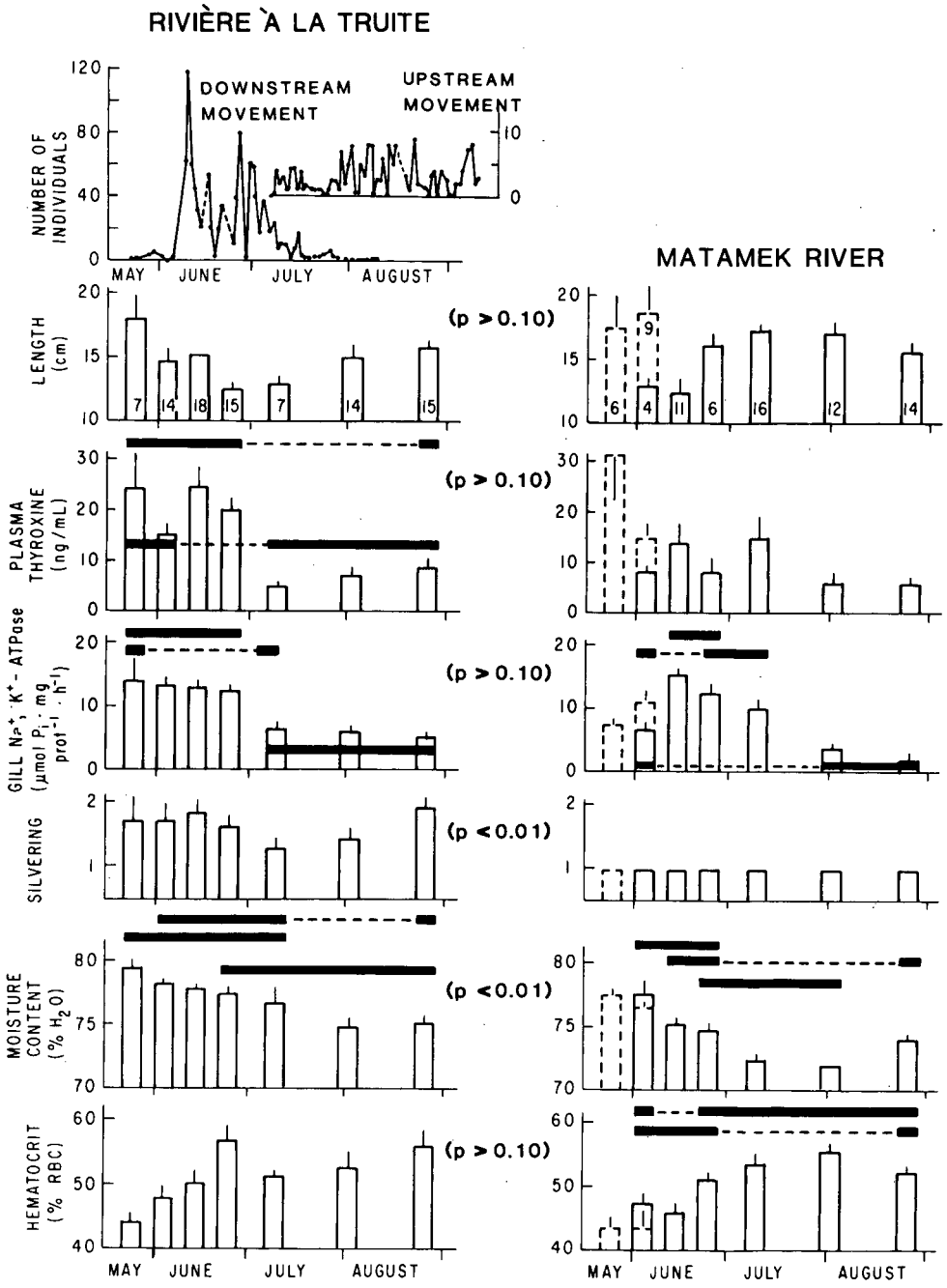

FIG. 3. Movements and physiology of anadromous brook trout in rivière à la Truite and nonmigratory brook trout of the Matamek River. Downstream and upstream movements of brook trout are daily captures of upstream and downstream facing nets. Broken lines indicate periods when the net was washed away by high water. Brook trout sampled in rivière à la Truite from late May to mid-July were moving downstream; those sampled in late July and August were moving upstream. Catches in the Matamek River did not vary greatly over the 3.5 mo of sampling, averaging one fish per day. Brook trout were divided into seven time intervals by date of capture (four 10-d, one 20-d, and two 25-d intervals), so that each time interval had approximately equal sample sizes. Dotted histograms (Matamek River) were fish captured below the 2nd Falls; solid histograms were those captured below the 3rd Falls. Only brook trout captured below the 3rd Falls were used for statistical comparisons. Sample size for each time interval is listed in the length histogram. Values are reported as $\bar{x} \pm$ SE. Statistical significance of physiological differences between brook trout populations (two-way ANOVA) is denoted by p values (in parentheses). Horizontal bars represent a posteriori differences among time interval means within rivers; intervals not connected by horizontal bars are significantly different from one another ($p < 0.05$).

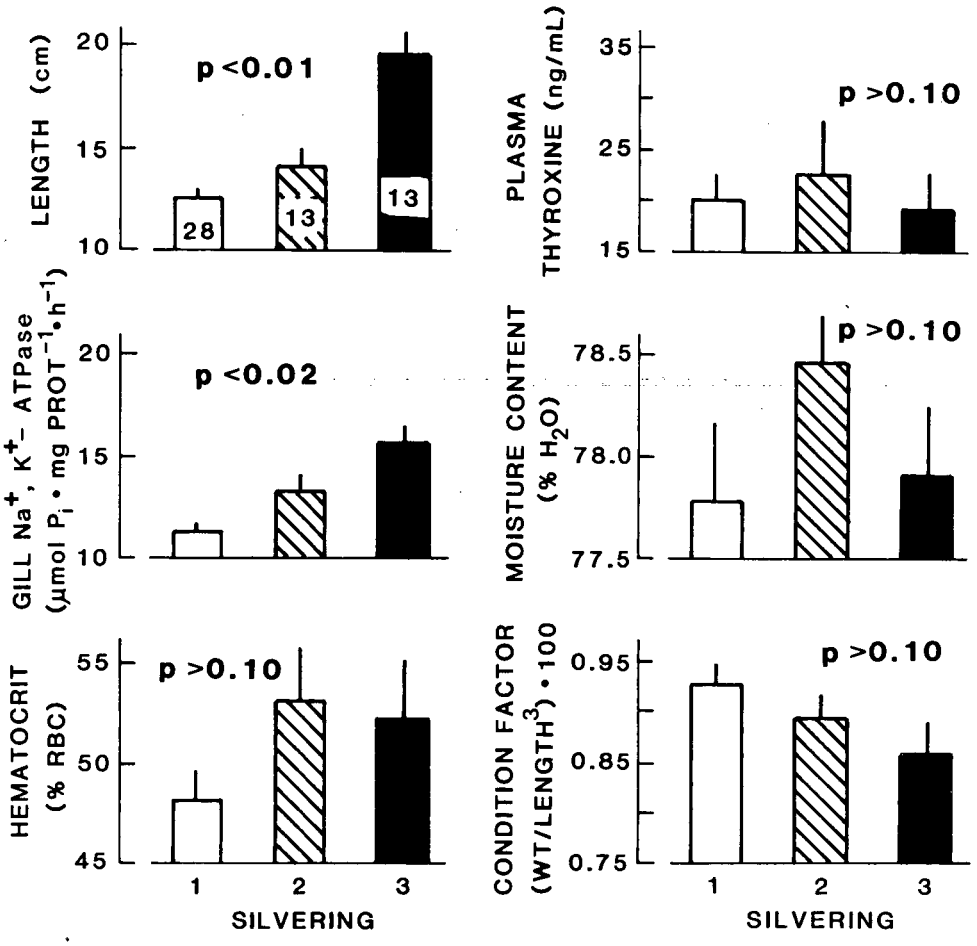

FIG. 4. Physiological comparison of brook trout migrating downstream in rivière à la Truite from May 20 to June 30. Fish were divided into three classes on the basis of silvering and compared using one-way ANOVA. Sample size is listed in the length histogram; values are reported as $\bar{x} \pm$ SE.

TABLE 2. Physiological comparison of Atlantic salmon migrating downstream in rivière à la Truite between June 6 and 29. Fish are divided into high (3) and low (1 and 2) degree of silvering on the basis of visible inspection. Values are reported as $\bar{x}$ ($\pm$ SE). Asterisks indicate significant differences between means of high and low silvering groups at $*p \leq 0.05$ and $**p \leq 0.01$ using Student's t-test.

Degree of silvering	Fork length (cm)	Gill Na^+,K^+-ATPase (μmol $P_i \cdot$mg protein$^{-1} \cdot h^{-1}$)	Plasma thyroxine (ng/mL)	Hematocrit (% RBC)	Moisture content (% H_2O)	Condition factor $(W/L^3) \cdot 100$
Low (N = 8)	10.3	13.2	7.7	57	77.66	0.943
	(0.7)	(2.4)	(3.1)	(1.6)	(0.33)	(0.018)
High (N = 6)	12.9*	26.3*	22.7*	49**	77.94	0.928
	(0.6)	(2.4)	(6.1)	(2.4)	(0.36)	(0.008)

salmon than in estuarine brook trout. Figure 6 presents a conceptual summary of differences in gill Na^+,K^+-ATPase activity, plasma T_4, and hypoosmoregulatory ability between brook trout and Atlantic salmon.

Physiological differences also occurred among brook trout at the different estuarine sites. Gill Na^+,K^+-ATPase activities of brook trout at high-salinity sites were greater ($p < 0.05$) than at the low-salinity site. Plasma osmolarity of brook trout at the mouth of the Moisie River estuary was significantly higher than that of brook trout at the upstream Moisie River estuary site and the Matamek River estuary. Moisture content was significantly lower in brook trout at the Moisie River estuary mouth than in brook trout from the Matamek River estuary. We suggest that brook trout from the Moisie River estuary mouth were experiencing osmotic imbalance due to seawater acclimation, a process more nearly complete in brook trout from the Matamek River estuary.

Seawater Challenge — Estuarine Fish

Plasma osmolarity of brook trout from the upstream site of the Moisie River estuary was significantly higher, after seawater

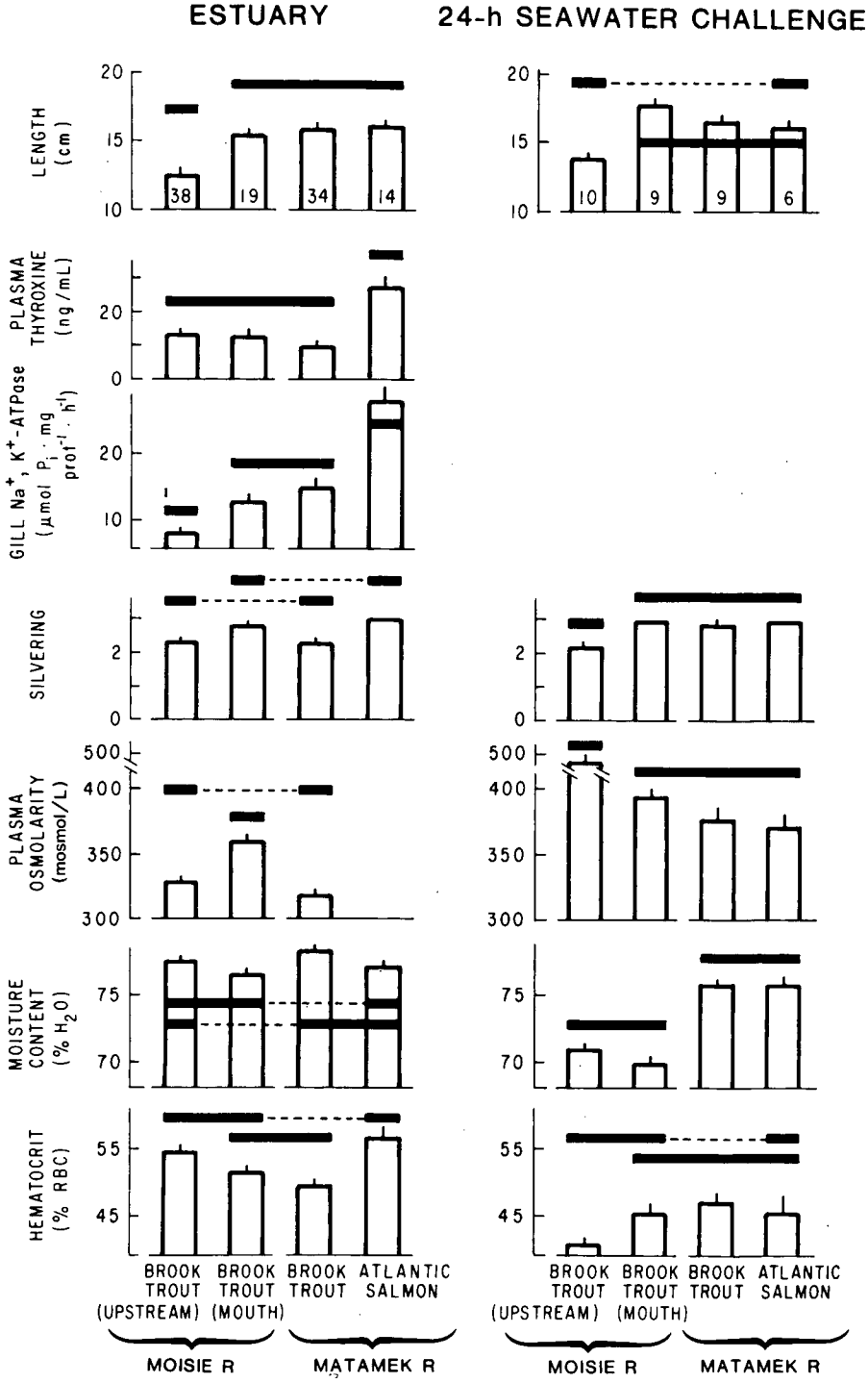

FIG. 5. Physiological comparison of brook trout and Atlantic salmon captured at estuarine sites. Brook trout were captured at one low-salinity site (Moisie River estuary, upstream) and two high-salinity sites (Moisie River estuary, mouth; Matamek River estuary). Atlantic salmon were captured in the Matamek River estuary only. Panels on the left represent sampling immediately after capture. Panels on the right report physiological changes after 24-h of exposure to seawater. Horizontal bars represent a posteriori comparison among means; groups not connected by horizontal bars are significantly different from one another ($p < 0.05$). Sample size is listed in the length histogram and is the same for all measurements. Values are reported as $\bar{x} \pm$ SE.

challenge, than that of brook trout and Atlantic salmon from the mouth of the Moisie River estuary and the Matamek River estuary (Fig. 5). Plasma osmolarity after seawater challenge was not correlated with FL for any estuarine group ($p > 0.10$). FL was significantly correlated with plasma osmolarity after seawater challenge when brook trout from all freshwater and estuarine sites were considered ($r = 0.34$, $p < 0.01$, $N = 55$). This may reflect, in part, the fact that larger fish were found at high-salinity sites. Moisture content after seawater challenge of brook trout at both Moisie River estuary sites was significantly

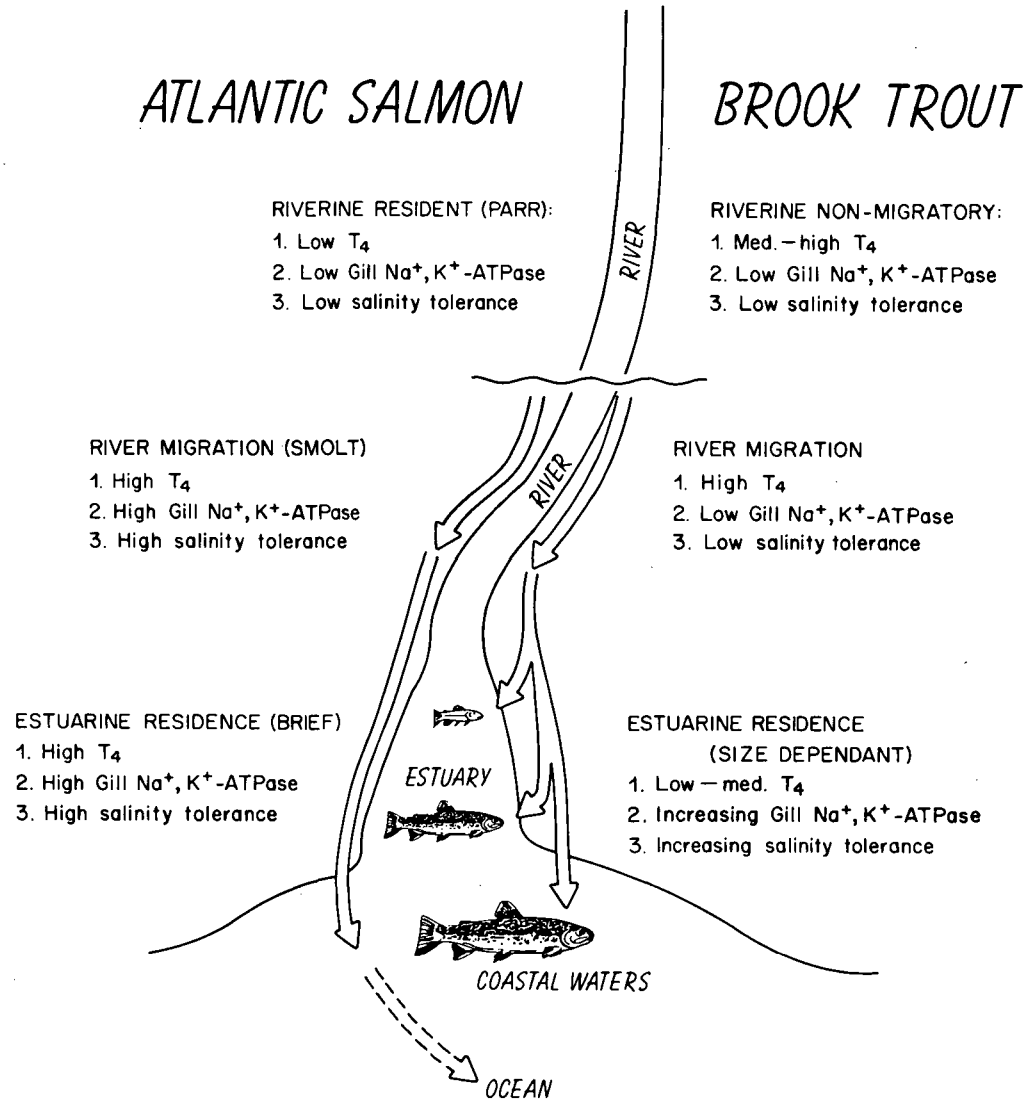

FIG. 6. Conceptual model of changes in plasma T_4, gill Na^+,K^+-ATPase, and salinity tolerance of Atlantic salmon and brook trout during freshwater residence, river migration, and estuarine residence.

lower than that of brook trout and Atlantic salmon from the Matamek River estuary ($p < 0.05$).

Discussion

Wilder (1952) and McGlade and MacCrimmon (1979) studied electrophoretic, meristic, and morphometric differences of several eastern Canadian brook trout populations and concluded that anadromous and non-anadromous brook trout were a single taxonomic unit. Although Matamek River and Moisie River brook trout were found to be genetically distinct, they had greater genetic similarity than freshwater populations of brook trout examined over a broader greographic area. While these studies addressed general taxonomic characters, physiological factors associated with seaward migration may undergo stronger selection pressure resulting in genetic differences in smolt physiology.

With the exception of coloration, we found no evidence of differences in smolting physiology between anadromous and non-anadromous brook trout. Seasonal changes in plasma T_4 concentration, with high springtime values coinciding with migration, occurred in anadromous brook trout, but these changes were not significantly different from non-anadromous brook trout. Gill Na^+,K^+-ATPase activity of migratory brook trout was not different from that of non-anadromous brook trout. Salinity challenge tests of the two freshwater populations are not strictly comparable, since brook trout for this portion of the study were obtained 2 mo apart. Nonetheless, anadromous brook trout captured during the peak of migration do not appear to possess greater hypoosmoregulatory ability than non-anadromous brook trout in August, a period when the latter would not be expected to have exceptional salinity tolerance.

Although moisture content was significantly different in brook trout from rivière à la Truite and the Matamek River, each had a similar trend of decreasing levels with time. Smoltification was probably not responsible for between-river differences in moisture content. Falling moisture content and increasing hematocrit occurred through the summer, indicating that both intracellular and extracellular compartments had lower water content. Since moisture content of teleosts is inversely related to

lipid levels (Phillips 1969), reduction in moisture content over time in the two populations may have resulted from greater fat deposition as food supply increased.

A seasonal cycle of high spring levels of plasma T_4 has been found in laboratory-reared brook trout that do not smoltify (McCormick and Naiman 1984a). From the absence of differences in plasma T_4 concentrations between anadromous and non-anadromous brook trout, or between anadromous brook trout of differing degrees of silvering, we suggest that the seasonal cycle of this hormone regulates functions other than migration or silvering of brook trout. We cannot rule out, however, the possibility that T_4 regulates different functions in different populations of brook trout. White and Henderson (1977) hypothesized that the seasonal T_4 cycle is involved in maturation. McCormick and Naiman (1984a, 1984c) found, however, that a 3-mo-delayed photoperiod caused a 3-mo shift in maturation but not in the T_4 cycle. Thyroxine levels were higher in fish fed maximally, and were positively correlated with differences in growth rate. Thyroid hormones have been shown to be both growth-promoting and responsive to feeding in a variety of salmonids (Flood and Eales 1983; Higgs et al. 1982). In the wild, spring increases in plasma T_4 concentration may play a role in, or result from, increased feeding or somatic growth.

Gill Na^+,K^+-ATPase activities of both rivière à la Truite and Matamek River brook trout decreased as summer progressed. Such a change in enzyme activity may be a response to increasing water temperature. Using a similar method of enzyme activity determinations, McCarty and Houston (1977) found decreases in gill Na^+,K^+-ATPase activities of rainbow trout (*Salmo gairdneri*) acclimated to high temperatures.

Of the physiological characteristics investigated, only the degree of silvering showed a clear distinction between brook trout populations in the Matamek River and rivière à la Truite. Greater silvering in rivière à la Truite brook trout is associated with greater size and increased gill Na^+,K^+-ATPase activity, characteristics that are typical of smolting salmonids (Zaugg and McLain 1972; Lasserre et al. 1978; Saunders and Henderson 1978; Buckman and Ewing 1982). The difference in gill Na^+,K^+-ATPase activity between high and no silver groups, however, was only 25%, a small value relative to differences found between salmon parr and smolt, normally 100–400% (Table 2; Folmar and Dickhoff 1980).

Black (1981) used the marine trematode *Brachyphallus crenatus*, a brook trout parasite, as an indicator of seawater residence. Brook trout captured upstream in the Moisie River estuary, though highly silvered, had only a 3% incidence of infection. Fish from the mouth of the Moisie River estuary had an 86% infection rate. Black (1981) concluded that silvering was unrelated to eventual entry into seawater. In our study, brook trout captured at the upstream Moisie River estuary site had marked silvering, but low gill Na^+,K^+-ATPase activity and hypoosmoregulatory ability. Since brook trout in the upper Moisie River estuary are similar in size to silvered fish emigrating from rivière à la Truite, it is possible that silvering is acquired during residence in the Moisie River estuary and is retained over the winter. Silvering was induced in a Matamek River brook trout maintained in 32‰ for 2 mo (S. D. McCormick, pers. obs.), and is apparently induced in brook trout washed over the 1st Falls into the Matamek River estuary.

In contrast with brook trout, Atlantic salmon captured in rivière à la Truite, and divided on the basis of silvering, showed clear indications of smoltification (Table 2). Gill Na^+,K^+-ATPase activity in highly silvered Atlantic salmon was approximately 2 times greater than Atlantic salmon with intermediate or no silvering, and plasma T_4 was 3 times greater. Plasma T_4, however, was as high for all silvering categories of rivière à la Truite brook trout as it was for highly silvered Atlantic salmon. Perhaps increased growth or activity of brook trout, irrespective of degree of silvering, can explain high plasma T_4 of brook trout during this period. Although moisture content is higher and CF is lower in highly silvered versus less silvered Atlantic salmon, the differences are not significant (Table 2). Failure to detect significant differences in these smolt characteristics may reflect differences in feeding or other environmental variables that are held constant in laboratory investigations of smolting but that are not controlled under natural conditions.

Interpretation of the estuarine physiology of brook trout must be made in light of the size-dependent migration that occurs in the Moisie River estuary. Brook trout at the Moisie River upstream site are significantly smaller than at the downstream site (Fig. 5). Brook trout >15 cm FL are rare in the Moisie River estuary, and none are >18 cm FL (Montgomery et al., unpubl. data). Large brook trout apparently leave the estuary, enter the Gulf of St. Lawrence for 2–3 mo, and return to the river in autumn. Salinity tolerance of brook trout is size dependent (McCormick and Naiman 1984b). Size-dependent salinity preference and salinity tolerance coincide in other salmonids (McInerny 1964; Weisbart 1968), and a similar phenomenon in brook trout would explain their size-dependent distribution in the Moisie River estuary.

Tagging studies have shown that Atlantic salmon smolts reside in the Matamek River estuary only 3–4 d (Gibson 1978). Coloring, body form, and physiological characteristics (Fig. 5) indicate that Atlantic salmon are fully smolted as they enter the estuary. Plasma T_4 concentrations and gill Na^+,K^+-ATPase activities of Atlantic salmon are significantly higher than estuarine brook trout. The preparatory physiological changes associated with smoltification of Atlantic salmon appear adaptive for rapid seawater acclimation and brief estuarine residence.

Gradual acclimation to seawater significantly increases seawater survival of brook trout (S. D. McCormick, unpubl. data). Activities of gill Na^+,K^+-ATPase are elevated and hypoosmoregulatory ability is greater at high-salinity estuarine sites (Fig. 5), suggesting that seawater acclimation is occurring. Whereas increases in gill Na^+,K^+-ATPase activity (and other hypoosmoregulatory mechanisms) of smolting salmonids occur wholly in freshwater, these mechanisms are apparently induced in brook trout <18 cm by estuarine residence. We suggest that the estuary is an important site for acclimation of brook trout, which ultimately permits their entry into seawater.

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References

BLACK, G. A. 1981. Metazoan parasites as indicators of movements of anadromous brook charr (*Salvelinus fontinalis*) to sea. Can. J. Zool. 59: 1892–1896.

BUCKMAN, M., AND R. D. EWING. 1982. Relationship between size and time of entry into the sea and gill (Na^+,K^+)-ATPase activity for juvenile spring chinook salmon. Trans. Am. Fish. Soc. 111: 681–687.

CASTONGUAY, M., G. J. FITZGERALD, AND Y. CÔTÉ. 1982. Life history and movements of anadromous brook charr, *Salvelinus fontinalis*, in the St. Jean River, Gaspé, Québec. Can. J. Zool. 60: 3084–3091.

CLARKE, W. C., AND J. BLACKBURN. 1978. Seawater challenge tests performed on hatchery stocks of chinook and coho salmon in 1977. Can. Fish. Mar. Serv. Tech. Rep. No. 761.

DICKHOFF, W. W., L. C. FOLMAR, AND A. GORBMAN. 1978. Changes in plasma thyroxine during smoltification of coho salmon, *Oncorhynchus kisutch*. Gen. Comp. Endocrinol. 36: 229–232.

DUTIL, J. D., AND G. POWER. 1980. Coastal populations of brook trout, *Salvelinus fontinalis*, in Lac Guillaume-Delisle (Richmond Gulf), Quebec. Can. J. Zool. 58: 1828–1835.

FLOOD, C. G., AND J. G. EALES. 1983. Effects of starvation and refeeding on plasma T_4 and T_3 levels and T_4 deiodination in rainbow trout, *Salmo gairdneri*. Can. J. Zool. 61: 1949–1953.

FOLMAR, L. C., AND W. W. DICKHOFF. 1980. The parr–smolt transformation (smoltification) and seawater adaptation in salmonids. A review of selected literature. Aquaculture 21: 1–37.

GIBSON, R. J. 1978. Salmon studies. *In* R. J. Gibson [ed.] Matamek Annual Report for 1977. Woods Hole Oceanogr. Inst. Tech. Rep. 78-92.

GRAU, E. G., J. L. SPECKER, R. S. NISHIOKA, AND H. A. BERN. 1982. Factors determining the occurrence of the surge in thyroid activity during smoltification. Aquaculture 28: 49–57.

HAEDRICH, R. L. 1975. Sea trout, p. 43. *In* R. J. Gibson [ed.] Matamek Annual Report. Woods Hole Oceanogr. Inst. Tech. Rep. 75-62.

HIGGS, D. A., U. H. M. FAGERLUND, J. G. EALES, AND J. R. MCBRIDE. 1982. Application of thyroid and steroid hormones as anabolic agents in fish culture. Comp. Biochem. Physiol. 73B(1): 143–176.

HOAR, W. S. 1976. Smolt transformation: evolution, behavior, and physiology. J. Fish Res. Board Can. 33: 1234–1252.

KOMOURDJIAN, M. P., R. L. SAUNDERS, AND J. C. FENWICK. 1976. Evidence for the role of growth hormone as a part of a 'light-pituitary axis' in growth and smoltification of Atlantic salmon (*Salmo salar*). Can. J. Zool. 54: 544–551.

LASSERRE, P., G. BOEUF, AND Y. HARACHE. 1978. Osmotic adaptation of *Oncorhynchus kisutch* Walbaum. I. Seasonal variations of gill Na^+,K^+-ATPase activity in coho salmon, 0+-age and yearling, reared in freshwater. Aquaculture 14: 365–382.

MCCARTY, L. S., AND A. H. HOUSTON. 1977. Na^+:K^+- and HCO^{3-}-stimulated ATPase activities in the gills and kidneys of thermally acclimated rainbow trout, *Salmo gairdneri*. Can. J. Zool. 55: 704–712.

MCCORMICK, S. D., AND R. J. NAIMAN. 1984a. Osmoregulation in the brook trout *Salvelinus fontinalis*. I. Diel, photoperiod and growth related physiological changes in freshwater. Comp. Biochem. Physiol. 79A: 7–16.

1984b. Osmoregulation in the brook trout *Salvelinus fontinalis*. II. Effects of size, age and photoperiod on seawater survival and ionic regulation. Comp. Biochem. Physiol. 79A: 17–28.

1984c. Some determinants of maturation in the brook trout *Salvelinus fontinalis*. Aquaculture 43.

MCGLADE, J., AND H. MACCRIMMON. 1979. Taxonomic congruence of three populations of Quebec brook trout, *Salvelinus fontinalis* (Mitchill). Can. J. Zool. 57: 1998–2009.

MCINERNY, J. E. 1964. Salinity preference: an orientation mechanism in salmon migration. J. Fish. Res. Board Can. 21: 995–1018.

MONTGOMERY, W. L. 1980. Tides and water movements in the Moisie River estuary. *In* R. J. Naiman [ed.] Matamek Annual Report for 1979. Woods Hole Oceanogr. Inst. Tech. Rep. 80-31.

MONTGOMERY, W. L., S. D. MCCORMICK, R. J. NAIMAN, F. G. WHORISKEY, AND G. A. BLACK. 1983. Spring migratory synchrony of salmonid, catostomid and cyprinid fishes in Rivière à la Truite, Québec. Can. J. Zool. 61: 2495–2502.

MULLAN, J. W. 1958. The sea-run or "salter" brook trout (*Salvelinus fontinalis*) fishery of the coastal streams of Cape Cod, Massachusetts. Mass. Div. Fish Game Bull. No. 17.

NORDENG, H. 1983. Solution to the "char problem" based on Arctic char (*Salvelinus alpinus*) in Norway. Can. J. Fish. Aquat. Sci. 40: 1372–1387.

PHILLIPS, A. M. 1969. Nutrition, digestion and energy utilization, p. 599–675. *In* W. S. Hoar and D. J. Randall [ed.] Fish physiology. Vol I. Academic Press, New York, NY.

ROUNSEFELL, G. A. 1958. Anadromy in North American salmonidae. U.S. Fish Wildl. Serv. Fish. Bull. 58: 171–185.

SAUNDERS, R. L., AND E. B. HENDERSON. 1978. Changes in gill ATPase activity and smolt status of Atlantic salmon (*Salmo salar*). J. Fish. Res. Board Can. 35: 1542–1546.

SMITH, M. W., AND J. W. SAUNDERS. 1958. Movements of brook trout, *Salvelinus fontinalis* (Mitchill), between and within fresh and salt water. J. Fish. Res. Board Can. 15: 1403–1449.

WEDEMEYER, G. A., R. L. SAUNDERS, AND W. C. CLARKE. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Mar. Fish. Rev. 42: 1–14.

WEISBART, M. 1968. Osmotic and ionic regulation in embryos, alevins, and fry of the five species of Pacific salmon. Can. J. Zool. 46: 385–397.

WHITE, H. C. 1940. Life-history of sea-running brook trout (*Salvelinus fontinalis*) of Moser river, Nova Scotia. J. Fish. Res. Board Can. 5: 176–186.

WHITE, B. A., AND N. E. HENDERSON. 1977. Annual variation in the circulating levels of thyroid hormones in the brook trout, *Salvelinus fontinalis*, as measured by radioimmunosassay. Can. J. Zool. 55: 475–481.

WHORISKEY, F. G., R. J. NAIMAN, AND W. L. MONTGOMERY. 1981. Experimental sea ranching of brook trout, *Salvelinus fontinalis*, Mitchill. J. Fish Biol. 19: 637–651.

WILDER, D. G. 1952. A comparative study of anadromous and freshwater populations of brook trout (*Salvelinus fontinalis* (Mitchill)). J. Fish. Res. Board Can. 9: 169–203.

ZAUGG, W. S. 1982. A simplified preparation for adenosine triphosphatase determination in gill tissue. Can. J. Fish. Aquat. Sci. 39: 215–217.

ZAUGG, W. S., AND L. R. MCLAIN. 1972. Changes in adenosinetriphosphatase activity associated with parr–smolt transformation in steelhead trout, coho, and spring chinook salmon. J. Fish. Res. Board Can.29: 167–171.