Anadromous Brook Charr, *Salvelinus fontinalis*: Opportunities and Constraints for Population Enhancement

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Introduction

Success of enhancement programs depends largely on the efficient use of natural factors rendering a species suitable for a particular form of culture and management (Bardach et al., 1972). Most efforts to enhance anadromous species have been directed toward commercial species with proven marketability. These species, however, are not necessarily the most efficient in dealing with vagaries of the natural environment. Inability to control natural environmental factors introduces significant unpredictability into fisheries enhancement and aquaculture.

Anadromous brook charr, *Salvelinus fontinalis*, have some characteristics favorable for enhancement and aquaculture which will be reviewed in this article. Throughout most of their natural range, they enter salt water, where accessible, and grow rapidly while at sea. They have well developed homing abilities, migrating seasonally at precise periods. At sea they stay near their natal river, remaining in salt water for periods usually no greater than 4-5 months. Within their native freshwater range, they do not appear to compete significantly with native salmon or trout for space and resources. Lastly, charr are popular recreational fishes and could have some commercial potential. At present, brook charr are of importance in recreational freshwater fisheries and aquaculture, but their enhancement and utilization in marine systems remains largely unexplored (Power, 1980).

The objectives of this article are to summarize studies initiated by Gibson and Whoriskey (1980) on anadromy in brook charr, and continued by us, on the North Shore of the Gulf of St. Lawrence near Sept-Iles, Quebec; to compare our results with those reported for other populations; and to make recommendations for enhancement of the fishery. For 5 years we have examined the ecology of anadromous and freshwater populations of brook charr, and have experimentally explored their growth and survival in seawater. Aspects of this study have been presented elsewhere on induction of anadromy and experimental sea ranching (Gibson and Whoriskey, 1980; Whoriskey et al., 1981a, b), parasites (Black, 1981; Black et al., 1983), migration and ecology (Montgomery et al., 1983), and osmoregulatory physiology (McCormick and Naiman 1984a, b, 1985a, b; McCormick et al. 1985). These studies, combined with previous ecological in-

ABSTRACT—We present an overview of studies conducted during 1978-84 on anadromous brook charr, Salvelinus fontinalis, *near Sept-Iles, Quebec, Can. Studies on experimental sea ranching are integrated with those on the biology of anadromous stocks, results are compared with those reported for other anadromous and nonanadromous stocks, and recommendations are made for population enhancement. Anadromous brook charr exhibit short but synchronized migratory movements, can enter brackish water at a small size, remain in coastal waters, grow rapidly while at sea, home effectively, and provide a potentially high yield to recreational and commercial fisheries. We suggest that anadromous brook charr, and possibly other members of the genus* Salvelinus, *are reasonable candidates for local enhancement of coastal or estuarine salmonid fisheries and for sea ranching in northern latitudes.*

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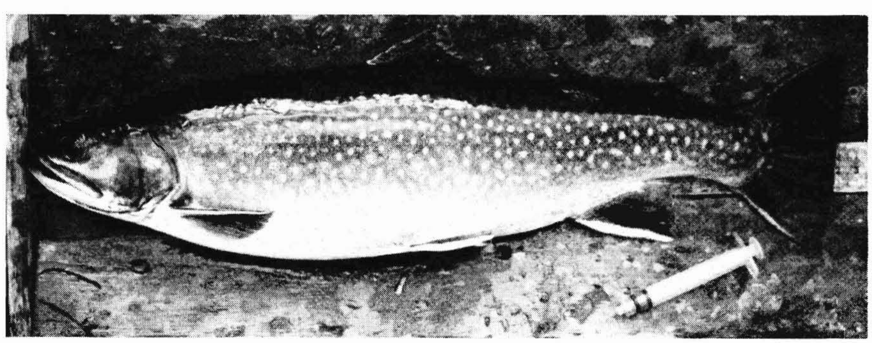

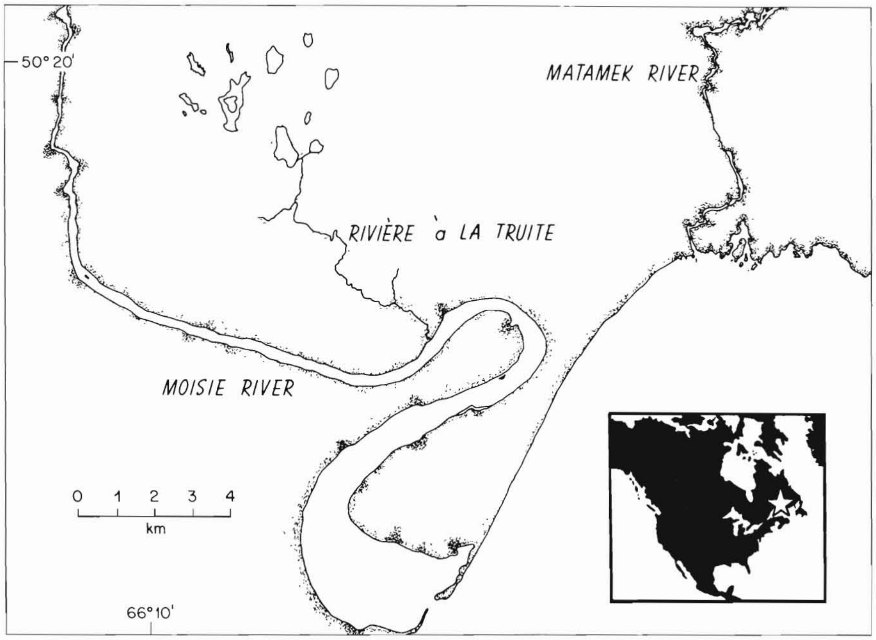

Figure 1.—Location of principal study sites.

Table 1.—Physiochemical characteristics of the study sites.

Parameter	Rivièire à la Truite	Matamek River	Moisie River
Stream order	4	6	9
Watershed area (km^2)	36	673	19,871
Mean width (m)	15.6	51.7	208.7
Mean depth (m)	<1.0	1.8	2.5
Mean annual discharge (m^3/sec.)	1.5	13.7	466.1
Substrate	Gravel	Gravel/cobble	Sand/cobble
Temperature range (°C)	0.1-16.0	0.1-22.0	0.1-21.8
Annual degree days (°C/year)	2,000	2,225	2,219
pH range	?	4.8-6.0	6.3-7.1
Alkalinity (as CaCO in mg/L)	?	0-0.5	0-2.1
Forest canopy development	Mostly open	open	open

vestigations of freshwater brook charr in the same watersheds and with information from the literature, provide the basis for evaluating the opportunities for, and constraints upon, the population enhancement of anadromous brook charr.

General Life History

Brook charr are endemic to North America, distributed under natural conditions from the Atlantic provinces south to Long Island, N.Y., in the Appalachian Mountains south to Georgia, west in the upper Mississippi and Great Lakes drainages to Minnesota, and north to Hudson Bay (Scott and Crossman, 1973). They have been introduced successfully throughout the world. Brook charr inhabit well-oxygenated streams and lakes, preferring temperatures below 20°C. They spawn in late summer or autumn, the date varying with latitude and temperature, over gravel beds in headwater streams and rivers. Mature fish may travel a considerable distance upstream to reach the spawning grounds. Unlike lake charr, *Salvelinus namaycush*, and artic charr, *Salvelinus alpinus*, brook charr are short-lived with wild individuals seldom attaining 5 years of age. Sexual maturity is usually reached at age 3, but some individuals may mature at age 2. Maximum size is about 5 kg. In general, brook charr are carnivorous, feeding on a wide range of organisms, depending upon their size and the size of available prey.

Although most populations of brook charr are restricted to fresh water, many coastal rivers in their native territory of northeastern North America contain anadromous brook charr. In northern latitudes, brook charr migrations are characterized by spring emigrations of 2 to 4-year-old fish whose coastal sea residence lasts 2-4 months (White, 1940; Wilder, 1952; Dutil and Power, 1980; Castonguay et al., 1982). In the southern portion of its range, the timing of emigration is more variable, often occurring in the fall (Mullan, 1958).

Assessment of Potential for Enhancement

Initial Experiments

An experiment to induce anadromy in a population of nonanadromous wild brook charr was conducted in 1978 and 1979 near Sept-Iles. This area is a subarctic boreal forest biome (mean annual temperature = 1°C) composed of black spruce, *Picea mariana*; white spruce, *P. glauca*; and balsam fir, *Abies balsamea*. The rivers are ice covered from about November to April. There is a strong freshet in April and May when ~50 percent of the annual discharge occurs. The aquatic growing season is short (~105 days), and the rivers accumulate only about 2,100 degree-days annually (Table 1).

Brook charr from two river systems were chosen for study: An anadromous population from the lower Moisie River and its tributary Rivière à la Truite, and a freshwater population from the Matamek River (Fig. 1). The Matamek River population does not migrate to sea due to a large waterfall, 0.7 km from the ocean, blocking upstream movement to suitable spawning areas, thus precluding anadromous habits. The three rivers differ significantly in physical dimensions but not in most chemical characteristics (Table 1; Naiman et al., 1987) or seasonal timing of environmental events (Naiman, 1982, 1983).

Initially, nearly 1,800 brook charr, age 1+ to 5+, were captured from the Matamek River (identified with serially numbered Carlin tags if >10 cm fork length (FL) or fin clipped if ≤10 cm FL), transported to the Matamek River estuary from late May to early July, and released (Gibson and Whoriskey, 1980; Whoriskey et al., 1981b). The mean number of days at liberty for different age classes ranged from 63 to 98. Fish were recaptured in autum (late August and September) as they returned to fresh water. Over 2 years, 34.0 percent of the released fish were recaptured. Best returns were in the 2+ and 3+ age classes with 38.0 and 62.1 percent recaptured, respectively. Movement of transplanted fish to other nearby rivers was <1 percent; predation by birds and other fish was not evaluated. All age classes included sea-run brook charr, but the largest percentages of sea-run charr occurred in older and larger fish. Growth was substantially better in sea-run charr than in fish remaining in freshwater (Fig. 2), presumably a function of increased food supply at sea. Tagging severely stunted growth, especially in younger and smaller fish, and probably suppressed anadromy. Nevertheless, tagged sea-run charr grew between 0.8-3.5 percent d^{-1}, which was clearly superior to tagged fish in the freshwater population (0.4 percent day), and they had greater condition factors than their freshwater counterparts. Gonadal maturation was suppressed in sea-run charr compared with fish remaining in fresh water, and there was a significantly larger percentage of female sea-run charr.

These results suggested that an integrated research program could demonstrate the viability of this technique where moderate enhancement of native salmonid production was desired. In 1980 we begun a program investigating movements, feeding, growth, survival, production, reproduction, and physiological adaptation to seawater for wild anadromous brook charr.

Movements

Anadromous northern populations of brook charr tend to leave streams and move to estuaries and coastal marine waters immediately after the peak in the spring freshet (White, 1940; Wilder, 1952; Dutil and Power, 1980; Castonguay et al., 1982). Nevertheless, movements to and from rivers correlate variously with temperature, river discharge (particularly spring floods), lunar cycles, tides, and migrations by other species. In the Moisie River the duration of emigration appears to vary with the pattern of discharge. In 1980, when discharge rose to an early maximum and then declined steadily, the migration was largely completed within 2 weeks; in 1982, when rains caused three secondary discharge peaks following the early June maximum, the migration was extended over 5 weeks (Montgomery et al., 1983). Movements of brook charr into cool, spring-fed creeks of Cape Cod, Mass., seemed to correlate with high summer temperatures of estuarine waters (Mullan, 1958). Migratory activity of brook charr on the Gaspé peninsula, Quebec, correlates with lunar cycles (Castonguay et al., 1982). Migrations of Moisie River charr to coastal waters coincide with simultaneous movements of several other species (Montgomery et al., 1983), suggesting that environmental cues may be similar for all species. Water temperatures in the river and the sea are similar at this time (~8-10°C), reducing the thermal barrier to migration.

Although it is apparent that movements are often rapid and directional, details of migratory behavior are sparse. Our own studies (Montgomery et al.[1]) are typical, involving capture, marking and recapture at a single trap site in the river and at several locations in the estuary. In the Moisie River system, one fish travelled from Rivière à la Truite to the estuary (~15 km) in <2 days, while several others were recaptured in the estuary after <10 days. Anadromous arctic charr and whitefish, *Coregonous* sp., in the coastal Beaufort Sea have a net movement of 3-6 km d^{-1} along the shore (Craig, 1984). Sockeye salmon, *Oncorhynchus nerka*, smolts travel 10-15 km d^{-1} in Babine Lake, B.C., and at much greater rates in rivers (Brett, 1983). It seems unlikely that the trip to the Moisie River estuary would require more than 2 days if movements were strongly directional.

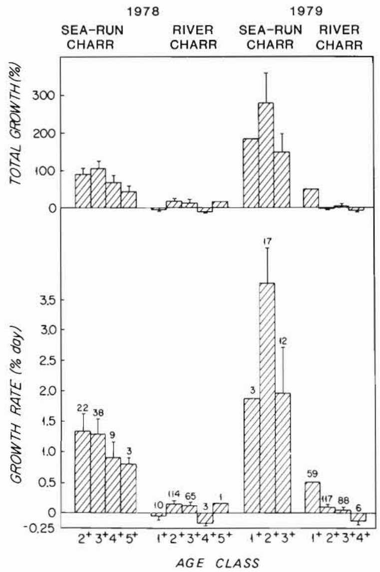

Figure 2.—Growth, expressed as percentage increase of body weight, and mean daily growth rate are shown by age group for tagged brook charr for 1978 and 1979. The 1978 sea-run charr data are calculated from Gibson and Whoriskey (1980). Vertical lines above bars represent one S.E.; numbers are the sample size. Negative values result from handling and tagging stress. Adapted from Whoriskey et al. (1981b).

Data on total distances traversed by migrants are similarly tentative. Records indicate that anadromous brook charr move 30-50 km upriver in the Moisie River (MacGregor, 1973), and Castonguay et al., (1982) sighted schools of anadromous brook charr 48 km upstream from the mouth of the St. Jean River, Quebec. Moore (1975) found migratory Arctic charr a maximum of 50 km upriver on Baffin Island, N.W.T.

Studies indicate that brook charr at sea remain close to their natal rivers. Castonguay et al. (1982) recorded only two strays to adjacent rivers 19 and 45 km from the tagging location in the St. Jean River. During 2 years of experimental tagging only three recaptures (<1 percent of total recaptures) were made away

[1]Montgomery, W. L., R. J. Naiman, S. D. McCormick, F. G. Whoriskey, and G. Black. Biology of anadromous brook charr (*Salvelinus fontinalis*) in the Moisie River, Quebec. Unpubl. manuscr. W. L. Montgomery, Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011.

from the tagging site in the Matamek River estuary (Gibson and Whoriskey, 1980; Whoriskey et al., 1981b). All were recaptured from an intense recreational fishery in the Moisie River and had moved 12-39 km. White (1941) and Smith and Saunders (1958) took most of their recaptures within 5-8 km of the river mouths. Fish generally moved <10 km from tagging sites in Richmond Gulf (Dutil and Power, 1980). The brook trout's square tail with a low aspect ratio is not designed for efficient high speed swimming; the more slender somewhat forked tails of other charr are better adapted for long migrations and pelagic cruising (Power, 1980). This information, in concert with the observations by White (1942) that brook charr wander in schools in shallow waters along shore, suggests that anadromous brook charr remain inshore and close to their river of origin.

As in arctic charr (Craig, 1984) the tendency of brook charr to remain close to home rivers may be influenced by pockets of brackish (5-28‰) and relatively warm (8°-13°C) water along the coastline during the open-water season. This estuarine band varies in width and depth with freshwater input to coastal waters, prevailing winds, and topographic features. In shallow waters (2-3 m) the entire water column is usually brackish; in deeper waters a two-layered system develops, with a lens of surface brackish-water overlying a wedge of colder marine water. A variety of factors (e.g., wind, topography) influence how far the warm, brackish-waters and the brook charr extend seaward, but in most cases we have observed the seaward limit is <10 km (Naiman et al., personal observation).

Table 2.—Comparisons of brook charr feeding by the percent volume of taxa in stomach contents for regions of the Matamek River system. Indicated taxa are major components of diet. Streams are presented in increasing order of size. Fish were sampled in June and July.

	Stream				Lake			Estuary
Taxa/group	S[1]	G	T	M5	R	B	M	E
No. fish	28	51	32	111	9	24	29	18
Fork length (cm)	10-15	10-15	10-15	8-18	10-15	15-20	10-20	15
Zooplankton					19			
Insects								
Simuliidae, l[2], p	4	2	14	16				
Chironomidae, l, p	1	6	11			1		
Chaoborus, l					25			
Total Diptera, l, p	5	11	26	19	25	6	7	1
Trichoptera	40	27	12	36	9	4	14	1
Ephemeroptera	4	11	5	5	16	45	36	1
Plecoptera	6	4	14	3			2	
Total insect	55	53	57	63	50	55	59	3
Terrestrial insects	20	35	52	7		1	16	2
Amphipoda								45
Fish						30	5	46

[1]Abbreviations and data sources: S = Sherry Creek, G = Gallienne Creek, T = Tchinicamen (O'Connor, 1974); M5 = Matamek River below 5th Falls (Gibson, 1973); R = Lake MacRae (Carscadden, 1970); B = Lake Bill (O'Connor, 1971); M = Lake Matamek (Saunders, 1969), and E = Matamek River estuary (Whoriskey et al., 1981b).
[2]l = larvae, p = pupae

Feeding

Brook charr are visual, opportunistic predators, whose food habits change in relation to seasonal prey abundance, foraging locality, and effects of agonistic interactions with other fishes (Power, 1980). When brook charr fry emerge from the spawning gravel, they initially feed on minute drifting prey (Williams, 1981; Walsh et al., In press). Subsequently, they feed during daytime along stream edges, consuming increasingly diverse prey as they grow. Cladocera and copedoda constituted 9-31 percent of the food volume in June of emerging brook trout fry from the Matamek River (Williams, 1981). Dipteran larvae, mainly simuliidae and chironomidae, constituted 42-67 percent of the food volume. In July and August the diet shifts to organisms captured at the water surface, including both winged aquatic insects and terrestrial insects (Morin et al., 1982, and unpublished data).

The diets of juvenile and adult brook charr differ between stream, lake, and estuarine environments (Ricker, 1932a, b; Carlander, 1969). These differences in feeding are reflected in Table 2 based on studies throughout the Matamek River system. Diptera larvae and trichoptera are major components of diets in streams. In 3rd to 5th order streams (Strahler, 1957), brook charr of all sizes consume mainly terrestrial invertebrates at the water surface, particularly in late summer. In large streams such as the Moisie River, brook charr are more piscivorous and depend less upon organisms at the water surface (Montgomery et al.[1]).

Prey consumed by brook charr in saline waters differ in size and probably nutritional value from those in freshwater. Freshwater foods are dominated by small aquatic insect larvae and terrestrial or aquatic insect adults, both of which have considerable refractory exoskeletal materials. In sea water, brook trout feed mainly on fleshy foods such as fishes (particularly sand lance, *Ammodytes* sp.), mysids, and amphipods (Table 2; Whoriskey et al. 1981b; Montgomery et al.[1]). Other dietary studies of brook charr in salt water generally report piscivorous feeding (White, 1942; Greendale and Hunter, 1978; Dutil and Power, 1980). White (1940, 1942) reported that brook charr in the Moser River estuary relied heavily on young eels and saltwater isopods, while amphipods, nereid worms, and freshwater insects constituted the remainder of the diet while those in salt water consumed at least seven species of marine fishes.

Differences between fresh and saltwater feeding also relate to the abundance and seasonal availability of prey. Studies in Quebec indicate that resident fish in rivers feed regularly or heavily only during the 6-week mid-summer period of insect growth and emergence (Gibson and Galbraith, 1975). In contrast, anadromous brook charr have extensive food reserves available throughout their residence in coastal waters. Whoriskey et al. (1981b) found substan-

Table 3.—Comparison of age-weight and growth increments for freshwater and adjacent estuarine populations of brook charr. Weight is shown in grams with instantaneous weight increments in parenthesis.

Location	Lat.	Mean weight and instantaneous weight increment						
		2+		3+		4+		5+
Richmond Gulf, Quebec[1]	56°N							
River		19	(0.8)	42	(0.5)	71		
Estuary		51	(1.3)	181	(0.8)	399	(0.5)	647
Sept-Iles, Quebec[2]	50°N							
Matamek Lake		22	(1.0)	59	(0.6)	110	(0.5)	188
Matamek River		42	(0.7)	85	(1.0)	221		
Matamek River estuary		66	(0.7)	126	(0.6)	227		
Moisie River estuary				160	(0.8)	346	(0.7)	718
Moser River, Nova Scotia[3]	45°N							
River		62	(0.4)	90	(0.7)	174	(0.6)	309
Estuary		129	(0.7)	249	(0.3)	348	(0.6)	657

[1]Data from Dutil and Power (1980); length converted to weight using, for river fish, a condition factor of 1.1

[2]Data from Saunders and Power (1970), Whoriskey et al. (1981b), and Montgomery et al. (text footnote 1).

[3]Data from White (1940).

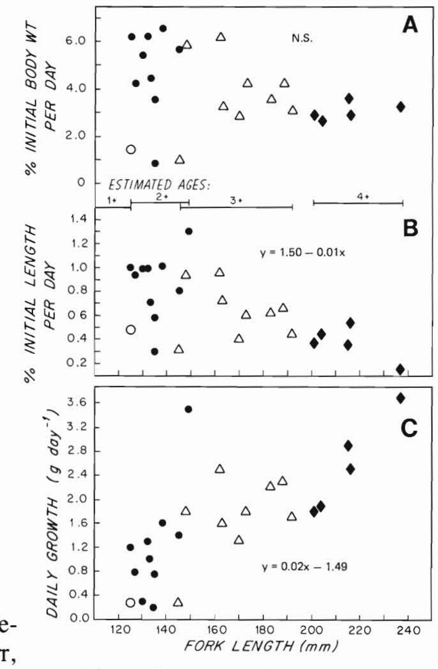

Figure 3.—Growth rate, by weight (A) and length (B), of anadromous brook charr in the Moisie River are presented as a function of initial size and age. Average daily growth (C) is presented as a function of fork length and age. The relationship between growth in weight and fork length (A) is not significant ($P > 0.1$; $r = -0.28$), but the relationships between growth in length (B), daily growth (C), and fork length are significant ($P < 0.05$; $r = -0.58$ and 0.71, respectively). Circles = 1+, dots = 2+, triangles = 3+, and diamonds = 4+.

tial numbers of amphipods and sand lance in the Matamek River estuary, and both foods were available in great abundance in the Moisie River estuary from April to October (Montgomery et al.[1]).

Flesh color of anadromous charr reflects food habits, and may serve as an indicator of perceived quality for human consumption. Increasing age of sea-ranched charr from the Matamek River was accompanied by increasing frequency of yellow or pink flesh and correlated with increased dependence on marine foods (Gibson and Whoriskey, 1980). All 1+ aged fish, 78.3 percent of the 2+, 57.4 percent of the 3+, and 11.8 percent of the 4+ fish had white flesh. In the 2+, 3+, and 4+ age classes the percentages with yellow flesh were, consecutively, 3.1, 7.0, and 5.9; with pink flesh, 14.9, 28.7, and 58.8; and with deep pink flesh, 3.7, 7.0, and 23.5. Larger specimens of anadromous charr from the Moisie River also had colored flesh, although no quantitative data were collected. Arctic charr with red flesh have the greatest market demand in Labrador, followed by charr with pink flesh; charr with white flesh are only used locally (Andrews and Lear, 1969).

Growth and Survival

Brook charr at sea exhibit enhanced growth typical of anadromous salmonids. Table 3 illustrates this pattern by comparing growth in adjacent sea-run and freshwater charr populations. In extensive reviews of the growth of brook charr, Bigelow (1963) and Carlander (1969) reported that sea-run charr attain a maximum weight of about 4.5 kg, no greater than their maximum size reported from freshwater. Unfortunately, no data were available on the age of such fish. In general, growth data are sparse for larger and older brook charr (>1 kg, >6 years of age) and for southern populations, particularly the anadromous populations that once inhabited Long Island, N.Y. and the large New England rivers (Power, 1980). However, instantaneous growth increments between age classes (Table 3) are highest for anadromous brook charr of Hudson Bay and the northern Gulf of St. Lawrence. These regions have shorter growing seasons and colder marine conditions than in the more southerly range of brook charr. The high growth rates in this area, however, may be an artifact of size and age since northern freshwater populations are smaller at any given age than southern populations. An increase in growth rate (due to anadromy) will result in greater growth rates of smaller fish and greater weight increments at any age.

Growth rates were calculated in 1980 for tagged Moisie River brook charr at large for more than 30 days between tagging and recapture, as growth was suppressed during shorter intervals by the tagging procedure (Montgomery et al.[1]). Rates of growth relative to both length and weight declined with increasing initial size and age (Fig. 3B), although absolute rates (g/day) increased significantly ($P > 0.01$) with length (Fig. 3C). These data provide a conservative evaluation of growth since sampling constraints prevented study under fully marine conditions. The daily growth rates from the Moisie River study compare favorably with results from the Matamek River, and are significantly greater than growth rates in fresh water (Saunders and Power, 1970; Gibson, 1973). Tagged brook charr introduced to the Matamek River estuary grew at 0.8 - 3.5 percent/day by weight while tagged brook charr remaining in freshwater grew at 0.4 percent/day (Fig. 2).

Several studies (Wilder, 1952; Dutil and Power, 1980; Whoriskey et al. 1981b; Castonguay et al., 1982) indicate that, at least for some age or size classes, brook charr experience enhanced growth through anadromy by feeding on marine foods. Exceptions to this trend are usually found in younger (1+, 2+) or smaller fish (Fig. 2, 3A, B, C). Moisie River brook charr consistently enter saline water after they attain a length of ≥15 cm FL (Montgomery et al.[1]). Virtually all growth rates for the smaller 1+ and 2+ fish are below means predicted from rates determined for fish ≥15 cm FL. This indicates that size classes which remain in essentially fresh water, despite being in the estuary, fail to attain the expected rapid rate of growth. In addition, fish ≤9 cm FL are rarely captured in the estuary, although they are common in the river. These apparent limitations in size at migration correspond to the known size limitations of brook charr salinity tolerance (discussed below). Considered together, these data indicate that 0+ fish remain in the river, while larger 1+ and older animals move to the estuary and constitute the sea-run component of brook charr in anadromous populations (Montgomery et al.;[1] Whoriskey et al., 1981b).

The survival of anadromous brook charr has not been extensively studied. However, a number of sources suggest that it may be favorable in comparison with freshwater populations. Saunders and Smith (1964) reported that yearling brook charr stocked in estuaries yielded an average return to anglers of 28 percent compared with an average of 13 percent for yearlings and 4 percent for younger charr stocked in the stream. Dutil and Power (1980) recaptured 56 percent of tagged fish during studies in Richmond Gulf, and White (1941) reported returns of 9-40 percent for different size classes of sea-run brook charr in the Moser River, Nova Scotia.

Survival of sea-run charr of the Moisie River was estimated from tagged fish at large at the end of 1980, and recaptured over the following 3 years by anglers (Montgomery et al.[1]). Calculations were made according to Ricker (1975) assuming constant angling pressure between years. Nine hundred sixty-four fish were tagged and released; 557 were 101-150 mm FL, 251 were 151-200 mm FL, and 156 were 201-350 mm FL. The efficiency of the fishery (μ) was estimated to be 22 percent for 101-150 mm fish, 45 percent for 151-200 mm fish, and 31 percent for all sizes. Survival rate(s) between years was estimated to be 31, 20, and 25 percent for the three size groups, respectively.

Estimates of survival for the sea-run population of the Moisie River compare favorably with data from unexploited freshwater charr populations in the Matamek watershed and with seasonal return rates for sea-ranched char in the Matamek estuary. Gibson (1973) estimated minimum survival to be 46 and 16 percent based on recovery of brook charr marked in a previous year at two sites in the lower Matamek River. The lower estimate (16 percent) was attributed to a greater proportion of tagged yearlings which were thought to incur higher mortality during winter. O'Connor and Power (1976) estimated survival from year-class structures of four stream populations of brook charr in the Matamek watershed. Survival rates between successive year classes of charr aged 1 year and older ranged between 17 and 37 percent. In our induced anadromy experiments, minimum recovery rates over 2 years were 29 and 40 percent for charr released in the Matamek River estuary (Gibson and Whoriskey, 1980; Whoriskey et al., 1981b).

Production

The growth attained in our induced anadromy project is particularly interesting since growth and production in the Matamek River drainage network are among the lowest reported throughout the geographic range of brook charr (Saunders and Power, 1970; O'Connor and Power, 1976; Power, 1980). Charr production in lakes of the Matamek River watershed ranges from only 0.5 to 2.2 kg/ha/year (Carscadden, 1970; Saunders and Power, 1970; O'Connor and Power, 1973) and in streams leading into Matamek Lake it is 14.5-66.4 kg/ha/year (O'Connor and Power, 1976). The growth of charr in the Matamek River is most rapid during the first 2 years of life, accounting for 70-90 percent of total population production.

Despite the apparent abundance of flowing waters in northern watersheds, only a small fraction of those waters actually contribute to fish production, making the marine phase of brook charr life history even more significant. Fish are absent from first and second order streams and sparse in third order streams on the North Shore of the Gulf of St. Lawrence (Naiman et al., 1987; Morin and Naiman, unpubl. data). These streams are subject to nearly complete freezing in winter and experience substantial variations in flow and temperature during summer. First to third order streams constitute 23 percent of the total surface area of streams in the Moisie River system (Naiman, 1983), but have negligible fish production. Significant fish production in the Matamek system occurs only in streams ≥4th order (O'Connor and Power, 1976). These constitute 70 percent of the stream surface area in that system, but even this is an overestimate of productive habitat. Given the depth distribution and habitat requirements of fry and yearling, significant charr production is possible in <40 percent of the total lotic surface area. In short, these northern river systems cannot normally support highly productive salmonid populations; anadromous populations circumvent to some degree the limitations of food, space, and temperature (Gibson and Galbraith, 1975; Gibson et al., 1976; O'Connor and Power, 1976; Walsh et al., In press) during critical mid-summer periods by moving to coastal areas.

To evaluate the viability of an enhancement program, it is essential to know, first, the biological productivity of anadromous brook charr populations and second, how much of that production can be successfully harvested. Neither determination has been made for an anadromous brook charr population. Nevertheless, given the observed growth rates of brook charr aged 2+ to 7+ in the Moisie River estuary, production of those year classes in freshwater populations (e.g., O'Connor and Power, 1976) could approximately double if they moved to sea and incurred similar mortality. Such an estimate is based only on the difference between sea and freshwater growth and does not include possible increases in recruitment by anadromous charr due to increased growth, fecundity, and spawning frequency. Measures of yield from northern commercial and native fisheries on anadromous populations of Atlantic salmon, Arctic charr, brook charr, and whitefish (Power, 1966, 1980; Power and LeJeune, 1976; MacCrimmon and Gots, 1980) also suggest that this estimate of potential for enhanced production is conservative.

Table 4.—Age-specific maturity for Matamek River brook charr from the Second and Fifth Falls, and from the Moisie River. Values in percent; M = male, F = female. Numbers in parentheses are sample sizes.

	Age							
	1+		2+		3+		4+	
Site	M	F	M	F	M	F	M	F
Matamek River[1]								
Second Falls		0 (5)	29 (17)	29 (17)	73 (26)	91 (32)	50 (12)	100 (6)
Fifth Falls	41 (49)	0 (29)	37 (43)	81 (37)	69 (13)	100 (24)		88 (8)
Moisie River[2]								
Anadromous only	20 (10)	0 (4)	50 (20)	52 (25)	80 (5)	72 (18)	100 (3)	100 (5)
Freshwater and anadromous	10 (197)	3 (163)	33 (93)	27 (94)	67 (6)	67 (21)	100 (3)	100 (5)

[1]From Gibson et al. (1976).
[2]From Montgomery et al. (text footnote 1).

Reproduction

Despite extensive observations, we were unable to detect any significant differences in choice of spawning site, reproductive behavior, fertility, early ontogeny, or early life history between anadromous and nonanadromous stocks of brook charr (unpublished data). Power (1980) has described these reproductive aspects in detail. Our discussion here centers around maturation schedules, fecundity, and life history strategies.

While age is often reported as a correlate of maturation, other factors also influence its onset. Under laboratory or hatchery conditions, size is a more important determinant of maturation in brook charr than either age or growth rate, explaining 97-99 percent of the variation in maturation (McCormick and Naiman, 1985b). Under accelerated growing conditions, brook charr mature and spawn in their first autumn, at an age of 10 months and a weight of 60 g (Carlson and Hale, 1973; McCormick and Naiman, unpubl. data). Other physiological features (e.g., nutritional state and health) also influence time of maturation. Schedules of maturation normally differ between sexes, with the proportion of mature males greater at small sizes than that of mature females (Carlson and Hale, 1973; Power, 1980; McCormick and Naiman, 1985b). This difference is characteristic of many fishes and other poikilothermic vertebrates, and may relate to the nature of mating systems and to differential energetic investment in reproductive products (Bell, 1980).

Brook charr mature over a wide range of sizes and ages. This probably results from genetic differences between stocks combined with phenotypic responses to environmental variation. Environmental factors such as food, habitat, population density, temperature, and salinity, may act indirectly (through size or growth rate), or directly, on the onset of maturation. In highly productive streams, brook charr mature as early as 1+ or 2+ years of age; in northern or unproductive rivers maturation begins at ages >3+ (Power, 1980). Relatively late maturation also characterizes anadromous brook charr (White, 1940; Castonguay et al., 1982), and anadromous and experimentally transplanted brook charr show signs of delayed gonadal development upon reentering freshwater (White, 1940; Whoriskey et al. 1981b). Dutil and Power (1980) observed that final ripening of gonads of anadromous brook charr occurs in freshwater.

Reproduction by anadromous brook charr in the Moisie River system is largely delayed until the fish attain age 2+ and return to spawning tributaries at lengths >15 cm FL (Montgomery et al.[1]). Females lagged behind males in attaining maturity (Table 4). Similar patterns were observed in Moisie River fish that had not been tagged. It is surprising that maturity schedules for tagged fish from the Moisie River are comparable to those for tagged Matamek River charr (Gibson et al., 1976), as maturation was much lower in tagged Matamek River fish of the same age (Whoriskey et al., 1981b). The only clear difference between the two populations was that Matamek River females tended to lead males in percentage maturation at ages greater than 1+ (Table 4).

Power (1980) found little difference in interpopulation weight-specific fecundity of brook charr. Only the anadromous stock from the Koksoak River, Ungava Bay, Quebec, seems to increase fecundity more rapidly than other populations, and that only occurs at lengths >40 cm FL. However, when slopes of fecundity-weight regressions are compared for freshwater and anadromous brook charr in the same region, the slopes for Moisie River fish (2.8 in 1972, in MacGregor, 1973; 3.0 in 1980, Montgomery et al.[1]) exceed those reported for fish from lakes and streams in the Matamek River drainage (1.7-2.4; Fig. 4). Thus, anadromous charr may gain an advantage in terms of increased fecundity beyond that predicted from simple increases in body size (Fig. 4).

Freshwater brook charr in northern regions have different life history strategies than anadromous stocks (Power, 1980). In northern streams the fish grow slowly, not all fish mature at the same age, and there is the possibility of multiple spawning so that the reproductive potential of a year class is spread over more than one year (Fig. 5A). Sex ratios shift in favor of females in the older age groups. A few males are long lived, and the oldest fish in a population may often be a large male (Power, 1980).

With the addition of a migratory phase to the life cycle and a separation of spawning and nursery areas from feedings grounds, a life cycle of the type in Fig. 5B is found in anadromous populations. Anadromous migration provides more living space and results in better growth, possible lower mortality, larger fish, and better fecundity. Annual spawning usually occurs once maturity is

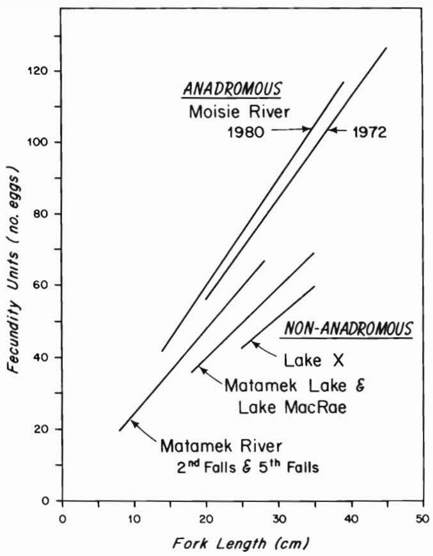

Figure 4.—Size-related increases in fecundity for Quebec brook charr. All intercepts of linear regression equations for fecundity on FL have been adjusted to zero. Projection of lines on abcissa gives the size range of fish used for regression. Data sources are: Moisie River, 1972 (MacGregor, 1973); Moisie River, 1980 (Montgomery et al., text footnote 1); Lake X and Lake MacRae in Matamek River watershed (O'Connor, 1971); and Matamek River (Gibson et al., 1976).

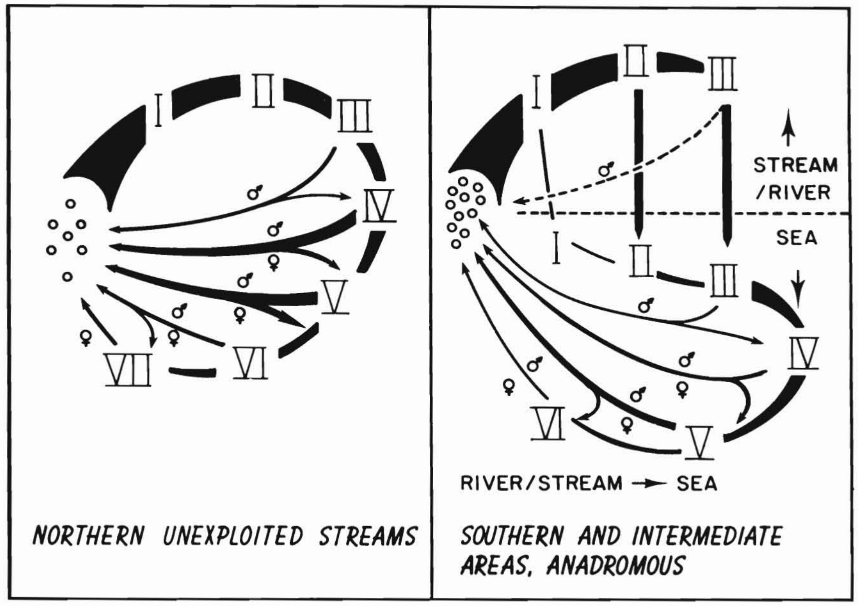

Figure 5.—The life history strategy of nonanadromous brook charr in northern streams is contrasted with that of an anadromous stock in the same area. Adapted from Power (1980).

attained. Multiple spawning is normal so that the reproductive potential of a year class is spread over 2-3 years. In combination, these factors make anadromy an important alternate life history strategy for brook charr with oceanic access.

Physiological Adaptation to Seawater

Movement of brook charr from fresh water to salt water requires not only a behavioral (migratory) impetus but also a physiological tolerance to salinity. The latter depends primarily on the ability to regulate plasma ions in a hyperosmotic medium. For a variety of teleosts, including salmonids, salinity tolerance and hypoosmoregulatory ability have been shown to change as a function of size and life history stage (Parry, 1958; Conte and Wagner, 1965; Conte et al., 1966; Nordlie et al., 1982).

McCormick and Naiman (1984b) demonstrated that survival of brook charr between 6.0 and 32.0 cm FL in 32‰ seawater was size dependent ($r^2 = 0.77$), as was the ability to regulate plasma ions (Na^+, Cl^-, K^+, Mg^{+2}) and plasma osmolarity (Fig. 6). Age, by itself, had no significant influence on seawater survival of brook charr. Size dependent hypoosmoregulation may be the result of more favorable surface area-to-volume ratios in larger fish. Although seawater survival increases throughout all sizes tested (6.0-32.0 cm FL), fish >15 cm FL achieved a near-maximum rate of survival.

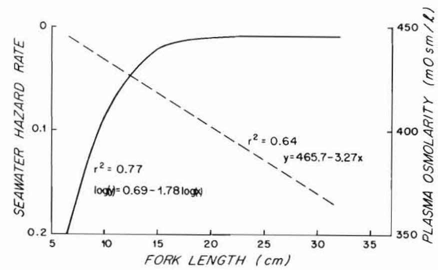

Figure 6.—Size dependent survival after 20 days (—) and plasma osmolarity after 4 days (—) of exposure to 32‰ seawater. Seawater hazard rate is a measure of the probability of survival (number of deaths/days at risk), with survival rate increasing as hazard rate approaches zero. Data originally presented in McCormick and Naiman (1984b).

In addition to ontogenetic changes associated with size, hypoosmoregulation is also affected by gonadal maturation of males (McCormick and Naiman, 1985a). Seawater survival of mature males is lower than that of mature females or immature fish of similar size in spring, summer, and autumn (mature brook charr were not tested in winter). Furthermore, mean survival time of mature males in seawater is reduced by >50 percent in autumn during the normal spawning period. The ability of mature male brook charr to regulate plasma ions (Cl^- and Mg^{+2}) and osmolarity in seawater during autumn is significantly reduced relative to that of mature females. Mature females and immature brook charr of both sexes exhibit no such decline in autumnal seawater survival.

The decreased salinity tolerance of males during gonadal maturation signi-

Table 5.—Phylogenic comparison of size-dependent salinity tolerance and seaward migration in salmonids.

Species	Salinity tolerance				Size at seaward migration (cm)	References[1]
	Salinity (ppt)	Method of acclimation	Duration (days)	Size at 75% survival (cm)		
Oncorhynchus						
Pink salmon	32	Direct	>14	<6.0	2.5-4.0	(1, 2)
Chum salmon	32	Direct	>14	<6.0	3.2-7.0	(1, 2)
Chinook salmon	30	Direct	30	6.5	6.0-10.0	(3, 4)
	30	Gradual	30	4.2		
Coho salmon	30	Direct	30	7.0	10.0-11.0	(5, 4)
Salmo						
Atlantic salmon	29	Direct	44	13.8	12.7-15.2	(6, 2)
Steelhead trout	30	Direct	30	16.0	15.0-20.0	(7, 8)
Salvelinus						
Brook charr	32	Gradual	20	19.0	15.0-18.0	(9, 10)

[1]1 = Weisbart, 1968; 2 = Scott and Crossman, 1973; 3 = Wagner et al., 1969; 4 = Healey, 1980; 5 = Conte et al., 1966; 6 = Johnston and Saunders, 1981; 7 = Conte and Wagner, 1965; 8 = Wagner et al., 1963; 9 = McCormick and Naiman, 1984b; 10 = Montgomery et al., text footnote 1.

fies a potential negative effect on males in enhancement programs. In fact, poor seawater survival (or preference) may explain the existence of greater female: male sex ratios in most populations of anadromous and sea-ranched brook charr (White, 1940; Wilder, 1952; Whoriskey et al., 1981b; Castonguay et al., 1982; Montgomery et al.[1]).

The influence of seasonal daylengths on developmental events has a substantial impact on the osmoregulatory physiology of salmonids. Photoperiod entrains the timing of maturation in salmonids (Billard et al., 1978; McCormick and Naiman, 1985b) and will therefore influence seawater survival of brook charr through male maturation (McCormick and Naiman, 1985a). In Atlantic salmon, *Salmo salar*, and Pacific salmon, *Oncorhynchus* spp., the transition from resident parr to migratory smolt is cued by photoperiod, presumably acting through the hypothalmus-pituitary system. Known as smoltification, this process includes seasonal (usually springtime) changes in appearance, behavior, morphology, and body composition, and increases in gill Na^+, K^+-ATPase activity and hypoosmoregulatory ability (see reviews by Hoar, 1976; Folmar and Dickhoff, 1980; Wedemeyer et al., 1980; and McCormick and Saunders, In press). Some of these changes may be mediated by surges in plasma thyroxine (Folmar and Dickhoff, 1980). Anadromous brook charr often possess the silver coloration and migratory behavior characteristic of salmon smolts (White, 1940; Wilder, 1952), but silvering of brook charr does not indicate imminent seawater entry (Black, 1981). Unlike smolting salmonids, brook charr do not display photoperiod-induced increases in gill Na^+, K^+-ATPase activity or hypoosmoregulatory ability (McCormick and Naiman, 1984a, b). Furthermore, there are no significant differences ($P > 0.05$) in gill Na^+, K^+-ATPase activities or plasma thyroxine levels between anadromous and nonanadromous brook charr from adjacent rivers (McCormick et al., 1985). From these and other results we have concluded that physiological changes preparatory for seawater entry that are observed in smolting salmonids are undeveloped in brook charr.

While photoperiod appears to affect salinity tolerance of brook charr only through maturation, other environmental factors will have direct impact. Though largely unexplored in brook charr, the interaction of temperature and salinity affects ion transport in other salmonids (Rao, 1969). Ionic equilibrium of presmolt Atlantic salmon after seawater exposure was achieved more quickly at an acclimation temperature of 10°C than at 1.5°C (Virtanen and Oikari, 1984). Poor osmoregulatory capacity at low temperature could explain high mortality of brook charr and Arctic charr overwintered in seawater net pens (Saunders et al., 1975; Wandsvik and Jobling, 1982).

Method of seawater acclimation also affects survival. Brook charr acclimated for 1-2 weeks at intermediate salinities (10-25‰) before transfer to 32‰ sea water had only 18 percent mortality after 20 days vs. 85 percent mortality for those transferred directly (McCormick, unpubl. data). This is in agreement with our observations that brook charr may spend up to a month in an estuary before migrating to sea (Montgomery et al.[1]), and that at estuarine sites characterized by high salinity, gill Na^+, K^+-ATPase activity and hypoosmoregulatory ability are elevated (McCormick et al., 1985). In addition, relatively small increases in salinity (e.g., 28‰ vs. 32‰) can have dramatic effects on salmonid survival (Jackson, 1981).

Because the decision to use brook charr in enhancement programs for anadromous salmonids will undoubtedly be made relative to the use of other salmonids, it is instructive to compare the relative salinity tolerances of salmonids (Table 5). Size dependent hypoosmoregulatory abilty is a common feature of all salmonids (Parry, 1958; Conte and Wagner, 1965; Conte et al., 1966; Weisbart, 1968; Farmer et al., 1978). As might be expected, the size at which salinity tolerance is achieved is similar to that at which normal seaward migration occurs (Table 5). Species of the genus *Oncorhynchus* have relatively greater salinity tolerance at any size than *Salmo* sp. (e.g., Atlantic salmon and rainbow trout), followed by *Salvelinus* sp. (see Rounsefell, 1958). We have hypothesized that greater exploitation of the sea has been accompanied by adaptations to decrease the impact of size dependent ion transport in a hyperosmotic environment (McCormick and Naiman, 1984b). Other things being equal, enhancement of anadromous brook charr will require longer rearing in fresh water so that a larger body size is achieved before introduction to seawater.

Exploitation of Anadromous Brook Charr

For at least 5,000 years northern peoples have fished for brook charr (MacCrimmon and Gots, 1980). Nevertheless, throughout their native range, there are only four historical records of anadro-

Table 6.—Perceived positive and negative aspects associated with the enhancement of anadromy in brook charr.

Parameter	Positive aspects	Negative aspects
Life history traits	1 Short, synchronized migrations 2. Remain in coastal areas 3. Rapid growth at sea 4. Multiple spawnings after age 2+ 5. Minimum straying	1 Must be close to seawater for anadromy 2. Requires overwinter habitat in northern rivers 3. 2-3 yrs before migration in northern latitudes
Physiology	1 Tolerance to low pH and low temperatures 2. Ability to enter brackish water at a small size	1 Difficulty adapting to full-strength seawater until 15-18 cm FL 2. Poor salinity tolerance of mature males
Genetics	1 Genetically plastic throughout range; possibility for selective breeding	1. None known
Economics	1 Low costs for fishery development and maintenance 2. Potentially high yield for recreational fishery 3. High quality fish 4. Improved social situation for rural communities 5. Available to anglers with average incomes	1. Typical resource management problems associated with anadromous fisheries

mous brook charr being harvested commercially. In the 1800's they were netted in the ocean near the Magdalen Islands, Quebec, during summer and pickled for export to the West Indies where, if in choice condition, they brought a higher price than Atlantic salmon (Perley, 1852; Lanman, 1873). Anadromous brook charr were also commercially exploited in Ungava Bay, Quebec, in Laborador by the Hudson's Bay Company in the 19th Century (G. Power[2]) and in Richmond Gulf, Quebec, between 1962 and 1964 (Power and LeJeune, 1976). On the Koksoak River, Quebec, the native harvest has been estimated at 15,500 kg/year[3]. Anadromous charr currently are netted for local consumption wherever they are present in sufficient numbers, but they are not generally numerous enough to be of widescale commercial importance, since most natural populations consist of only a few thousand fish.

The main economic value of anadromous brook charr probably lies in providing recreation. In contrast to occasional commercial and native exploitation, anadromous charr have consistently been a favorite with anglers, notably in New England and the Maritime region of Canada (Perley, 1852; Bigelow, 1963). In the past, much of the recreational angling in eastern Canada and the northeastern United States was provided by Atlantic salmon. However, the worldwide catch had declined 42 percent between 1967 and 1982 despite a severalfold increase in fishing effort (RASA, 1983), and the decline continues. Some 41 percent of coastal streams in New Brunswick have sea-run charr in sufficient quantities to provide a sport fishery. In Newfoundland, anadromous brook charr are second only to Atlantic salmon as a quarry for anglers (Scott and Crossman, 1964). Moreover, in recent years, about 21.7 million brook charr have been distributed annually from government hatcheries in the United States and Canada to meet public demand for recreational fishing (MacCrimmon and Gots, 1980). In coastal areas the angling effort for anadromous brook charr can be substantial. For example, in the Moisie River, Quebec, 18 percent of the fish tagged as part of our migration study in this remote area were returned by anglers (Montgomery et al.[1]).

Summary

We suggest that anadromous brook charr and other members of the genus *Salvelinus*, have inherent traits making them reasonable candidates for enhancement programs (Table 6). In northern latitudes they make short, synchronized migrations to coastal areas during the ice-free season, they remain close to shore where they are not subject to interception by foreign vessels, they undergo rapid growth while at sea, they begin reproduction at about 2 years and reproduce every 1-2 years thereafter, and they exhibit the strong homing ability characteristic of other salmonids (Fig. 7). Brook charr are able to tolerate a wide variety of environmental conditions including low food levels and low water temperatures, and are more resistant to low pH than other salmonids (Muniz and Grarde, 1974). Moreover, they appear to have population dependent differences in life histories suggesting a genetic plasticity which offers substantial opportunities for selective breeding. These positive factors are essential for potential use of this species for enhancement and for commercial sea ranching efforts.

There are, however, some negative aspects to consider (Table 6). First, brook charr must be close to seawater to induce anadromy. Apparently they do not make long (>75 km) migrations to sea. They require overwintering habitat in fresh water and rearing habitat for 2-3 years before migration from northern rivers. Second, brook charr have difficulty in adapting to full-strength seawater before reaching a size of 15 cm FL. Three factors appear to exert the strongest limitations on the salinity tolerance of brook charr: 1) Size is of primary importance; brook charr $\leq$15 cm FL will probably not survive well at salinities greater than 25‰. 2) Gradual acclimation at intermediate salinities eases osmotic stress and increases survival. 3) The negative effect of male maturation on salinity tolerance is likely to preclude introduction of mature fish into seawater, particularity in autumn. Spring releases of juveniles may circumvent some or all problems associated with poor seawater survival of mature males. Eventually, development of late-maturing stocks, sex control, or sterilization may prove advantageous. The greater degree of size dependent salinity tolerance in brook charr requires a longer freshwater rearing phase than for other anadromous salmonids. Since freshwater

[2]Geoff Power, Department of Biology, University of Waterloo, Waterloo, Ontario N2L 3G1, Canada. Personal commun.

[3]N.Q.I.A. 1976. Research to establish present levels of harvesting by native peoples of northern Quebec. Part II. A report on the harvests by the Inuit of northern Quebec. 230 p.

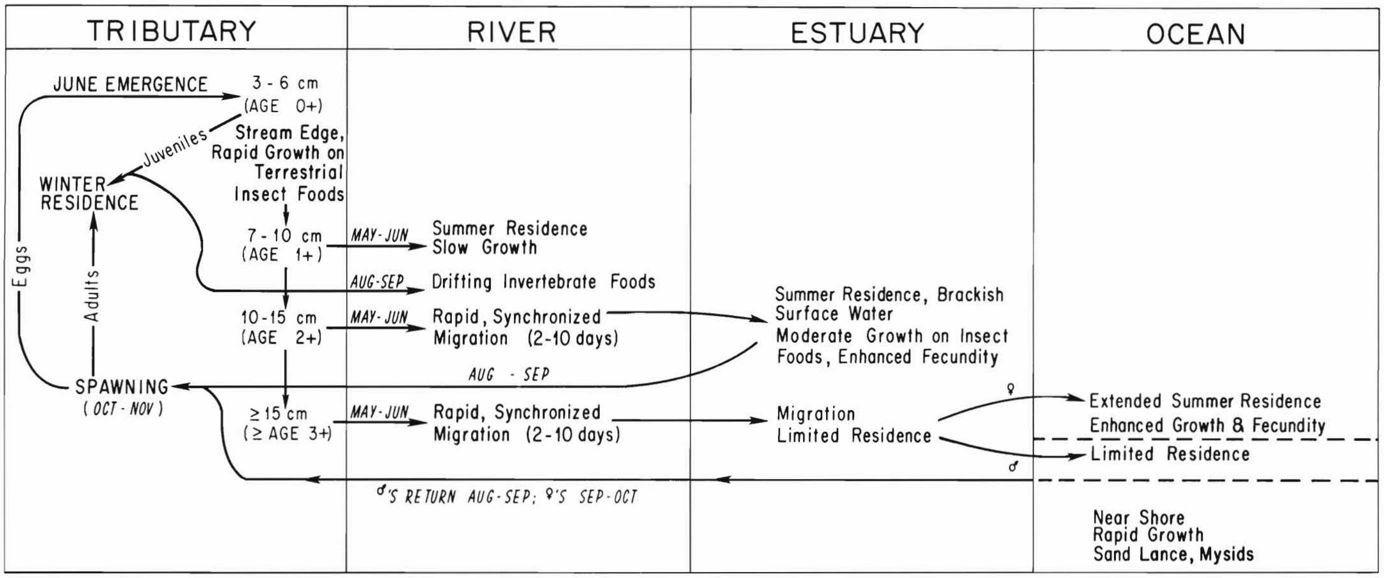

Figure 7.—The life history of anadromous brook charr studied by our group near Sept-Iles, Quebec, is summarized. See text for explanation.

rearing is often limiting or costly, this is an important consideration in choosing a species for enhancement. It will be necessary to judge the limitations of salinity tolerance in brook charr against other merits for enhancing salmonid production to properly evaluate their potential. Finally, there are the typical resource management problems associated with anadromous fisheries where fish often use habitats under the jurisdiction of several agencies with different management priorities.

Considering both the positive and negative factors, we recommend that anadromous brook charr be used in local enhancement programs where the objective is to provide a high quality recreational fishery. This may include habitat improvement, supplemental stocking to aid previously overexploited populations, improved management to protect the seasonal movements and reproduction of the population, or the development of a hatchery (or genetic) program to exploit life history characteristics that appear useful for population enhancement. For instance, the initial experiments with inducing anadromy (sea ranching) demonstrated the potential for using brook charr in a moderate effort, high yield enhancement technique (Gibson and Whoriskey 1980; Whoriskey et al. 1981b). However, certain aspects can be modified to improve the production and return of anadromous charr. These modifications are applicable to both population enhancement for the purpose of expanding fisheries potential and to commercial sea ranching.

Survival could be improved by gradual acclimation to seawater, releasing fish only during the period of natural migration to sea, using large estuaries with the proper geomorphology (mixed vs. stratified water, etc.), and using fish in good condition. Harvesting fish could be improved by recapture at a counting fence, or some other structure that concentrates individuals soon after reentry into fresh water in autumn. Growth rates at sea could possibly be enhanced by choosing marine sites having physical attributes to insure abundant food resources and by selective breeding of an anadromous stock. Although we are not aware of any negative genetic aspects, genetics could have major consequences and should be considered. At this point we recommend that enhancement be limited to the use of local stocks. Two basic enhancement strategies are habitat restoration of streams where anadromous brook charr once flourished and use of local native populations for hatchery stock to supplement existing populations.

However, several characteristics of brook charr will, in our judgment, make them a relatively poor choice for commercial net pen culture in high salinity. Relative to other species, brook charr require a longer rearing period in fresh water prior to entrance into seawater. Gradual acclimation to seawater in commercial net pen culture would in many cases be costly or infeasible. The poor performance of mature males in sea water and the relatively small size of maturation in both sexes will limit the period of seawater culture. These factors will work against the economic viability of net pen culture.

One final consideration is that in the southern part of the brook charr's range (i.e., near Cape Cod, Massachusetts), faster growth could reduce the length of freshwater residence. However, in those areas they would face increased numbers of competitors, warmer marine waters which they do not tolerate well, and habitat degradation. North of Cape Cod, conditions are more favorable for enhancement of anadromous brook charr. We suspect that enhancement will be limited to that region.

In summary, from our research and experience we believe that anadromous brook charr, and possibly other members of the genus *Salvelinus*, are candidates for enhancement programs in suitable regions. At present, their potential has not been fully explored. Based on information presented here, we suggest that brook charr be considered for relatively low-effort, high-yield enhancement programs in suitable areas, with economic gains accruing to the local populace.

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