



Variations in juvenile growth, energy allocation and life-history strategies of two populations of Arctic charr in North Norway

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Within the populations of Arctic charr *Salvelinus alpinus* in Storvatn and Rungvatn, Norway, fish that attained the largest size in the late parr stage migrated as 4+ smolts, fish that attained a medium size became 5+ smolts, and the smallest parr became lake residents. Within the last 2 years of the parr stage, those that became anadromous had a lower growth rate during the winter and early summer than those that became resident, and vice versa in late summer. Thus, anadromous fish grew faster in the parr stage, but in years prior to migration, their growth pattern seemed to differ from that of parr that became resident. Due to early size differences between parr that became anadromous or resident, it is suggested that some of the basis for the decision to smoltify or not in charr depends on the growth rate through the whole parr stage, but with significant modification by the local environment. Rungvatn parr had a significantly higher population density ($5 \times$), higher lipid content and mortality, an earlier maturation, a lower rate of growth, and only one-third the degree of anadromy than those from Storvatn. It is suggested that the two charr populations have evolved different life-history adaptations due to unequal growth, energy allocation and competition opportunities in the lakes.

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Key words: Arctic charr; *Salvelinus alpinus*; growth; energy allocation; anadromy; life-history strategies.

INTRODUCTION

The growth rate of juvenile salmonids is assumed to influence life-history strategies of individuals within a population (Alm, 1959; Thorpe, 1987; Jonsson & Jonsson, 1993; Presa *et al.*, 1996; Duston & Saunders, 1997; Thorpe *et al.*, 1998). Arctic charr *Salvelinus alpinus* (L.) display both anadromous and resident life-history strategies (Nordeng, 1961, 1983; Sandlund *et al.*, 1992; Kristoffersen *et al.*, 1994; Rikardsen *et al.*, 1997). The two morphs coexist in the same lake and the individuals belong to the same gene pool (Nordeng, 1983; Hindar *et al.*, 1986; Reist, 1989). However, the relative abundance of anadromous v. resident individuals (the degree of anadromy) varies greatly among populations (Johnson, 1980; Svenning *et al.*, 1992; Strand & Heggberget, 1994; Rikardsen *et al.*, 1997), even within a restricted geographical area (Kristoffersen *et al.*, 1994). This may be due partly to different growth potential between and within the lakes (Kristoffersen *et al.*, 1994; Rikardsen *et al.*, 1997).

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In populations with both anadromous and resident charr, the fast-growing parr usually migrate to sea, while slow-growing individuals often remain resident (Svenning *et al.*, 1992; Kristoffersen *et al.*, 1994; Strand & Heggberget, 1994; Rikardsen *et al.*, 1997). In a laboratory experiment with Atlantic salmon *Salmo salar* L. parr, Rowe & Thorpe (1990) found that not only the growth rate, but also the variation in juvenile growth during the last year of the parr stage, was of vital importance for the individual life-history decision to mature, or not, in the parr stage. The same seems to be true for the life-history decision to smolt, or not, as indicated in several laboratory experiments (Thorpe, 1987; Huntingford *et al.*, 1992; Jonsson & Jonsson, 1993; Thorpe *et al.*, 1998). Rapidly growing individuals in a population often have a higher metabolic rate than slower-growing individuals (Jobling, 1994; Forseth *et al.*, 1999). They usually use most of their surplus food consumption for protein production with little going to energy reserves in the form of lipid stores (Jonsson & Jonsson, 1998). These fish may be energy constrained earlier in their life if food is limited in the freshwater environment (Jonsson & Jonsson, 1993). This constraint may necessitate decisions about niche shifts such as migration to the sea v. residency (Jonsson & Jonsson, 1993; Kristoffersen *et al.*, 1994; Rikardsen *et al.*, 1997). If so, anadromous parr may be expected to have better growth than resident parr through summer, but poorer growth in the autumn and winter prior to migration because of food limitation when temperature decreases and the available food is reduced.

In an earlier study of the charr population in Storvatn, North Norway, Rikardsen *et al.* (1997) found that the youngest smolts seemed to be recruited from fast-growing parr in the littoral zone, while older and more slow-growing smolts may have been recruited from all habitats in the lake. However, this study was restricted to a comparison of size-at-age for ascending smolts and lake-dwelling fish (residents) in the spring, and did not consider variation in growth over time in the parr stage. Other studies on growth and anadromy in salmonids were done similarly (Strand & Heggberget, 1994), or performed in laboratories (Thorpe, 1987; Beckman *et al.*, 1998), or utilized back-calculation from otoliths or scales (Svenning *et al.*, 1992; Erkinaro *et al.*, 1997; Jonsson *et al.*, 1998). No studies have therefore shown an actual growth variation of wild individuals in the years prior to smolting or residency.

To extend the study of Rikardsen *et al.* (1997), the present study was performed in the same lake (Storvatn), but over a longer time period. The objectives were: (i) to follow individual charr of one year class through their last years prior to smolting or residency, and to determine directly if juvenile growth varied between fish that migrated to sea or became resident in the lake during this period; (ii) to compare life-history strategy of Storvatn charr with those of another small lake, Rungavatn, and to see if these strategies could be correlated with unequal stock characteristics, such as energy allocation, growth, mortality and density.

MATERIALS AND METHODS

STUDY AREA

Storvatn (70°39'48" N) and Rungavatn (69°47'60" N) are oligotrophic and monomictic lakes in northern Norway (Fig. 1). Storvatn is 8 m above sea level in Hammerfest town

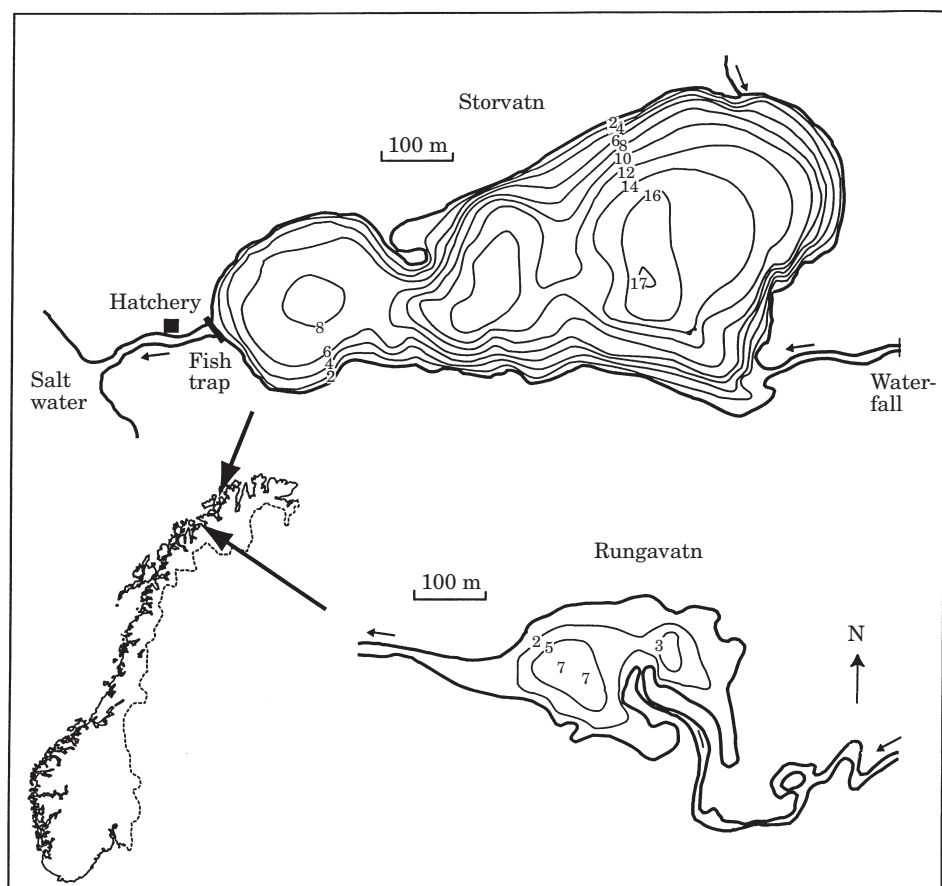


FIG. 1. Location of Storvatn in Hammerfest and Rungavatn in Nordreisa, North Norway. The depth contour lines (m) are indicated.

(Fig. 1), and has an area of 0.23 km^2 with a catchment area of 41 km^2 . Average depth is 9 m, maximum depth 17 m, and the water renewal time is *c.* 9 days in summer and 38 days in winter (Rikardsen *et al.*, 1997). The lake is covered with ice from November until late May/early June. Water temperatures through the whole water column are close to zero during winter ($0\text{--}1^\circ \text{C}$), and increase rapidly in June to a maximum of *c.* 12°C in July. The outlet stream is 200 m long and passage is uninhibited for migratory fish. Storvatn is the only habitat for charr, because they are prevented from moving upstream by waterfalls in the two inlet streams.

Rungavatn is 50 m above sea level in Nordreisa municipality, and has an area of only 0.06 km^2 with a catchment area of 15 km^2 , while the whole watercourse has a catchment area of 24 km^2 . Average depth is 2 m, maximum depth 7 m, and the water renewal time is only *c.* 1.5 days in summer and 5 days in winter. Like Storvatn, Rungavatn is covered with ice from November until late May/early June. Water temperatures during winter are stable from 0.2°C at the surface (ice cover) to 3.5°C at the bottom (7 m), with an average of 2°C . After the ice break up, the temperature increases rapidly during June to a maximum of *c.* 13°C in July. The outlet stream is 3.5 km long with many small rapids and few pools, but passage is easy for migratory fish. Rungavatn is the main habitat for charr, but they can move *c.* 2 km upstream in the inlet river before further migration is prevented by waterfalls. The first 800 m of this river is slow flowing, narrow (1.5–5 m) and deep (0.5–1.8 m), where fish can hide and feed in the summer.

Arctic charr is the dominant fish species in both lakes, but they also support brown trout *Salmo trutta* L. and three-spined sticklebacks *Gasterosteus aculeatus* L. Storvatn also contains eels *Anguilla anguilla* L. and a few Atlantic salmon. In both lakes, anadromous charr migrate downstream in early May and June, and upstream from late June to the end of August. In contrast to the charr in Storvatn, that spawn close to the shore around the lake, most charr in Rungavatn seem to spawn in the inlet river. The charr spawn from the middle of September to the middle of October in both lakes.

DEFINITIONS

It is difficult to distinguish resident charr, smolts and sea-run charr only by their morphology (Rikardsen *et al.*, 1997). The different life stages of the charr in Storvatn and Rungavatn were therefore defined using the following criteria.

- (i) Anadromous or sea-run charr: fish that had been to sea one or more times.
- (ii) Smolts: descending fish with smolt characteristics (Damsgård, 1991; Staurnes *et al.*, 1992) that were not infected by marine parasites (Kristoffersen, 1991; Kristoffersen *et al.*, 1994), and not previously caught in the traps in the outlet streams.
- (iii) Resident charr: charr ≥ 5 years old that had not migrated to sea. This age limit was set because very few smolts were older than 5 years (2.2% in Storvatn and 4.0% in Rungavatn).
- (iv) Parr: charr ≤ 4 years old found in the lake, that had not been recorded in the traps in the outlet streams (1997 and 1998), or ≤ 4 -year-old fish without marine parasites that were caught after all smolts and sea-run charr had left the lake in 1996 (see later text).
- (v) Lake-dwelling charr: resident charr and parr caught in the lake. Note that the parr (see above) include both potential anadromous and resident charr.

SAMPLING AND TAGGING

Lake-dwelling charr (10–20 cm) were caught with funnel traps and gillnets, and tagged from July 1996 to May 1998 (Rungavatn) or to June 1998 (Storvatn) (Table I). Ascending and descending charr (>10 cm) were caught through the summer of 1997 and 1998 in fish traps in the outlet streams of the two lakes.

Wire funnel traps (cylindrical, length 90 cm, diameter 50 cm, see detailed description in Amundsen *et al.*, 1993) were used in all tagging periods in the littoral and profundal zone of both lakes. They were baited with cod roe, enclosed in small perforated bags so that the fish could not feed on the bait. The traps were fished for 5–12 days before tagging started. They were very efficient in Rungavatn, both under the ice and during the ice-free season, but in Storvatn catches were sufficient only during the first weeks after the ice break. Therefore standard gillnets were used in the ice-free season to increase the number of fish in each period in Storvatn, and to some extent in Rungavatn. The gillnets were used in the littoral, profundal and pelagic zones, and raised every hour to prevent the fish from being seriously exhausted or injured. To ensure that fish caught by gillnets were healthy, they were kept in captivity for 2 days before tagging, and for another day after tagging.

The charr were anaesthetized and tagged individually with the Floy FTF 69-tag (fingerling tag) or the soft Visible Implant alpha-numeric tag (henceforth called the VI-tag). The VI-tag is a new soft version of the former rigid type described in Bergman *et al.* (1992), and is implanted in the adipose post-ocular eyelid of salmonid fishes. The FTF-69 (henceforth called the Floy-tag) is inserted by a needle through the cartilage tissue of the dorsal fin. These two types of tags can be used on small fish, but can have somewhat different retention rates depending on fish size (personal observation). Both types were therefore used to obtain sufficient data. To identify tag-loss, the charr were also batch tagged with Alcian Blue dye using a Panjet inoculator (Herbinger *et al.*, 1989) to show the tagging period and type of tag used. This batch marking technique has been shown to have no effect on growth of small salmon fry (Metcalf *et al.*, 1992).

To ensure that only lake-dwelling charr were tagged, the first tagging period was carried out in July 1996, after the smolts and anadromous fish were assumed to have left the lake (Table I). In periods 2–5, when the anadromous fish had returned to the lake, fish with marine ectoparasites were not tagged. Furthermore, charr that had been to sea

were usually >20 cm (Rikardsen *et al.*, 1997), and fish in this category were therefore also not tagged in these periods, as they may have been to sea. This was not a problem in periods 6–8, because then it was known if a charr had been to sea, as every ascending sea-run charr in 1997 was marked by clipping the adipose fin when it was caught in the traps in the outlet stream of the two lakes.

The traps in the outlet streams of the lakes were maintained daily after ice break and throughout the summer. The Storvatn trap (Fig. 1) consisted of two fyke nets of vinyl with collecting pens, one in each direction, connected with a wire fence (Hubert, 1983; Templeton, 1995). The Rungavatn trap was placed 2.5 km downstream and built as a Wolf grid-type (Mills, 1989), where descending fish pass over a grid into a trough and swim into a collecting pen. All ascending fish were caught with a fyke net, as in Storvatn. A high flow in Rungavatn in June 1997 broke down parts of the trap, and only some of the descending smolts were caught. The trap was then repaired, and all tagged post-smolts (not caught while descending) were sampled while ascending.

All descending smolts, that had been tagged as parr in the lake and caught in the traps, were sampled and killed. Those from the 1993 year class were used in subsequent analyses (Table II). This was the dominant and most complete year class in the samples. Untagged descending smolts were tagged individually and released to monitor the return rate of sea-migrating fish. After the anadromous charr had left the lakes in 1998, an extensive fishing with funnel traps and gill nets was conducted in July and August 1998 to catch the resident tagged charr that were left in the lakes (Table II).

ESTIMATIONS AND ANALYSIS

The lake-dwelling fish sampled after the anadromous charr had left the lake in 1998, together with the smolts sampled in the river in 1997 (age 4+) and 1998 (age 5+), were used for the determination of size-at-age retrospectively at the point of tagging or later recording (fish tagged in one period and recaptured and recorded in a later period) (Table II), and hence the change in length and weight from one tagging period to another could be estimated. In the present study, length or weight at age is therefore used indirectly to describe growth between the different tagging periods (Fig. 2). As individual fish usually could not be followed between the tagging periods, only mean specific growth rate for the change in size could be estimated by: $G = 100(\ln W_2 - \ln W_1) (t_2 - t_1)^{-1}$, where W_2 and W_1 are mean body weights on days t_2 and t_1 , respectively.

As samples of fish, previously tagged in periods 2–5, were small, data from periods 2+3, and 4+5 were pooled (Table II) to enlarge the first autumn and spring samples, respectively. Fish that were recaptured in periods 3 and 5, and had been tagged in periods 2 and 4, respectively (number in parentheses in Table I), had an average gain in length of only 0.00–0.25 mm, and an average loss in weight of only 0.05–1.2 g between the pooled periods in both lakes (t -test, d.f. = 12–86, $P > 0.64$). Therefore period 3 was treated as an autumn sample together with period 2, and periods 4 and 5 were combined as spring samples (Table II).

All tagged and sampled fish were measured (fork length L_F) to nearest mm and weighed to nearest 0.1 g. All sampled fish were sexed and the degree of maturation was described according to Dahl (1917). The relationship between weight and length was estimated according to Fulton's condition factor $K = 100 W L_F^{-3}$. Otoliths were analysed to determine age, as described by Nordeng (1961) and Kristoffersen & Klemetsen (1991).

The stock of lake-dwelling charr (N) (10–20 cm) in the lakes was estimated by Petersen's method (Seber, 1982), by comparing the number of tagged (including fish that had lost their tag) and untagged charr from one to the next tagging periods using the equation: $N = [(M+1)(C+1)](R+1)^{-1} - 1$, where M = number of fish tagged in period t , C = total number of fish captured in period $t+1$ and R = number of tagged fish from period t recaptured in period $t+1$. Fish that immigrated to the lake between periods 1 and 2 (sea-run charr) were not included in C . The emigration of smolts from the lake took place between periods 5 and 6 (and after period 8) (Table I), and, therefore, stock estimates between these periods were not calculated. An average of the different estimates between the periods provided the final estimate (Table III). 95% CL (Poisson

CL) were estimated from a method described by Krebs (1989). Fish density was estimated by stock size/surface area (in hectare) of the lake.

The degree of anadromy was estimated as the proportion of fish that were tagged in the spring before the smolt migration started, that were larger than the average smolt length for the lakes (i.e. ≥ 18 cm in Storvatn and ≥ 14 cm in Rungavatn, Table IV), and migrated to the sea in the same year. Smaller fish were excluded from the estimation because there was a high probability that some of these fish that did not migrate to the sea in the present year, would do so in the following year, and therefore underestimate the degree of anadromy.

The mortality of lake-dwelling charr (10–20 cm) was estimated for the period from October 1996 to May 1997, by comparing the proportions of fish tagged in July 1996 that were recaptured in October and May 1997. The reduction in recapture rate from October to May was assumed to correspond to the mortality rate. It was not possible to estimate the mortality rate for the rest of the year, because of insufficient catch per unit effort data in the summer.

Total lipid content (% wet body weight), from a random sample of 18–30 immature parr in May, June, July and October in Rungavatn and July and October in Storvatn, was determined after hydrolysis of the tissue samples in a drying cabinet for 12 h, followed by an extraction with petrol-ether as a solvent (Anonymous, 1987). After removal of lipid and water, protein was determined as the weight difference between fat-free samples and the ash after combustion (12 h at 550°C) (Gardiner & Geddes, 1980).

Paired *t*-tests were used to test for significant differences in lipid, protein and water content between the charr in the two lakes (Table IV), and for differences in size at age retrospectively within the 1993 year class of fish that migrated as 4+ smolts in 1997, as 5+ smolts in 1998, or became resident in 1998 (Fig. 2). The 95% CL for mean specific growth rate for the 1993 year class (Table V) was estimated by analysis of independent samples when $\sigma_1 \neq \sigma_2$ after a method described in Snedecor & Cochran (1967). No overlap in CL indicated significant differences.

RESULTS

In both lake systems, smolts were larger than charr that remained resident, irrespective of tagging time [Fig. 2(a), (b), (d) and (e)]. Within the populations, fish that had attained the largest size in the 2 last years of the parr stage, migrated as 4+ smolts, fish that attained a medium size became smolts at 5 years old, and the smallest parr became residents. Except for the first tagging period, these differences in size were significant between all three groups in all tagging periods in Rungavatn [Fig. 2(d) and (e)]. In Storvatn the differences between the groups were less than in Rungavatn and 4+ smolts in Storvatn were significantly larger than the resident fish throughout the premigratory year. The 5+ smolts were significantly larger than the resident fish 1 year before migration, but the resident fish had almost caught up the difference in size when the 5+ smolts migrated [Fig. 2(a) and (b)]. The 4+ smolts were always larger than the 5+ smolts in the parr stage in Storvatn, but these differences were not significant. Between the two charr populations, differences in size at the same age were highly significant, irrespective of tagging time and group of fish (*t*-test, $P < 0.001$).

Both 3+ and 4+ parr that became smolts had a generally higher specific growth rate than the resident parr in the summer, but a lower growth rate in the winter (Table V). The only exception was in the summer of 1997 in Storvatn, where the resident parr grew better than the parr that became 5+ smolts in the following spring. However, differences in growth rate were only significant

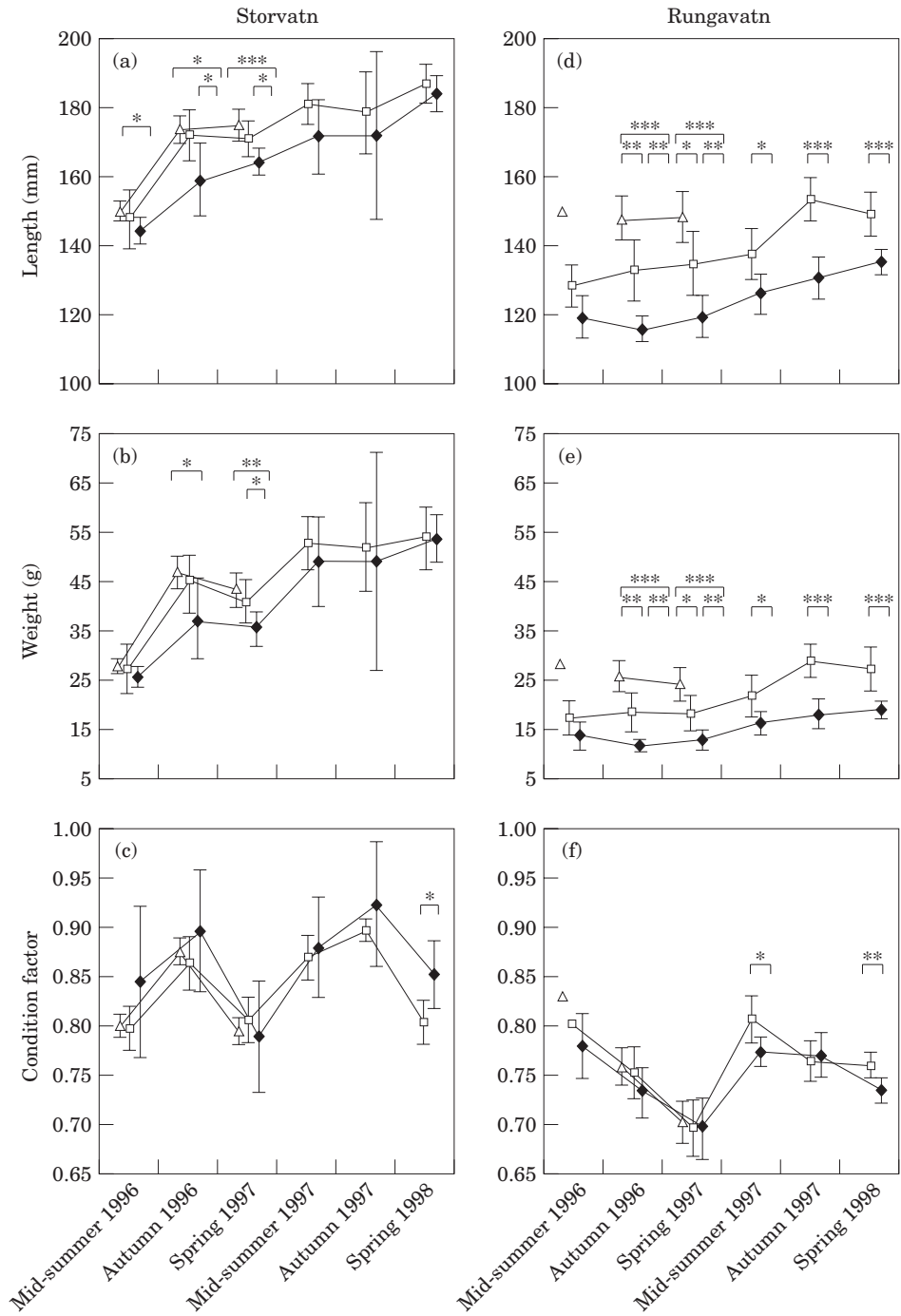


FIG. 2. Mean length (a), (d), weight (b), (e) and condition factor (c), (f) with 95% CL for 4- (△) and 5-year-old smolts (□) and resident (◆) immature charr of the 1993 year class in the different tagging periods in Storvatn and Rungavatn. Asterisks indicate significant differences between the groups (*t*-test, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

TABLE I. Number of charr tagged with Floy- and VI-tags in the different tagging periods

Tagging period:	1	2	3	4	5	6	7	8	Total
Storvatn:									
Date:	11 Jul. 1996	14 Oct. 1996	15 Mar. 1997	4 May 1997	24 Jun. 1997	19 Jul. 1997	1 Oct. 1997	17 Jun. 1998	—
VI-tag:	167	82 (19)	46 (11)	30 (13)	78 (32)	251 (37)	66 (9)	341 (32)	1061 (153)
Floy-tag:	101	34 (3)	9 (3)	27 (12)	62 (13)	19 (23)	0 (3)	50 (9)	302 (56)
Rungavatn:									
Date:	15 Jul. 1996	17 Oct. 1996	4 Mar. 1997	1 May 1997	22 Jun. 1997	22 Jul. 1997	6 Oct. 1997	29 May 1998	—
VI-tag:	170	295 (33)	65 (47)	165 (87)	32 (19)	175 (39)	220 (45)	211 (81)	1333 (270)
Floy-tag:	155	194 (27)	72 (29)	159 (46)	38 (23)	78 (63)	57 (59)	180 (60)	933 (307)

Number of recaptures from earlier periods is given in parentheses. Fish that had lost their tag are not included.

TABLE II. Total number of tagged charr from the 1993 year class that were recaptured in the river (smolts) or the lake (residents) in the summers of 1997 (4+ smolts) and 1998 (5+ smolts and residents)

Time of year: Age at tagging (years): Tagging period:	Mid-summer 1996 3+ 1	Autumn 1996 3+ (2+3)	Spring 1996 4 (4+5)	Mid-summer 1997 4+ 6	Autumn 1997 4+ 7	Spring 1997 5 8	Summer 1997/98 5 8	Total recaptured
Storvatn								
Residents:	4	7 (5+2)	18 (0+18)	8	3	17	57	
5+ smolts:	16	8 (6+2)	14 (1+13)	27	6	23	94	
4+ smolts:	56	25 (20+5)	20 (1+19)	—	—	—	101	
Rungavatn								
Residents:	4	15 (3+12)	9 (7+2)	6	21	33	88	
5+ smolts:	2	10 (7+3)	12 (9+3)	17	13	42	96	
4+ smolts:	1	21 (11+10)	24 (6+18)	—	—	—	46	

The times of the year when these fish were first tagged (mid-summer 1996 to spring 1998) and their age at tagging are also given. These fish were used for the analyses summarized in Fig. 2. The combined tagging periods for Autumn 1996 and Spring 1997, and the respective number of tagged fish from the 1993 year class recaptured from these periods, are given in parentheses.

TABLE III. Stock estimations (*n*) with 95% CL of lake-dwelling charr (10–20 cm) in Storvatn and Rungavatn from different tagging periods (TP) and the following recapture periods (RP)

Lake	TP	RP	M	C	R	<i>n</i> (95% CL)
Rungavatn	1	2	496	1001	111	4446 (4103–6128)
	2	3	649	351	83	2724 (2227–3375)
	3	4	171	518	44	1984 (1494–2731)
	4	5	338	136	8	5008 (2916–10 838)
Average			414	502	62	3541 (2618–4286)
Storvatn	1	2	280	156	22	1918 (1325–2987)
	4	5	57	205	3	2987 (1312–6572)
	6	7	270	79	7	2710 (1467–5058)
Average			202	147	11	2538 (1498–4820)

The average of the different results provided in final estimate (see Estimations in Materials and Methods).

between the populations in the late-summer period in 1996 (not overlapping CL, $P < 0.05$), but not significant between any of the groups within the lakes (overlapping CL, $P > 0.05$).

In general, the parr in Rungavatn had a significantly lower condition factor than the parr in Storvatn [Fig. 2(c) and (f)]. Within the populations, the condition factor increased rapidly from spring to mid-summer in both lakes, but started to decrease earlier in Rungavatn (after mid-summer) than in Storvatn (after autumn). There were no significant differences in the condition factor between the anadromous and resident charr in the early parr stage. However, the anadromous parr in Storvatn seemed to have a generally lower condition factor than the resident fish, but this was only significant for 5-year-old smolts and resident parr in spring 1998. In Rungavatn the situation may have been the opposite, as anadromous parr had in general a higher condition factor than the resident parr, but this was only significant for anadromous and resident parr in mid-summer 1997 (4+ parr) and spring 1998 (5-year-old pre-smolts and residents).

The density of lake-dwelling charr (10–20 cm) was estimated to be over five times higher in Rungavatn than in Storvatn (respectively 97 and 18 fish ha⁻¹, Tables III and IV). Furthermore, the degree of anadromy was significantly lower in Rungavatn (21%) than in Storvatn (56%) (Table IV). Values for the degree of anadromy were minimum estimates, as some of the fish used in the estimations, that did not migrate in the current year, may have migrated the following year or died between the tagging and the smolt migration (see Estimations and Analysis). Despite that, the smolts had a significantly larger size at the same age in Storvatn than in Rungavatn (Fig. 2), there were no differences in average smolt age, smolt sex ratio or return rate from the sea between the populations (Table IV). However, none of the smolts sampled was maturing in Storvatn, in contrast to Rungavatn where 20% of the females and 17% of the males were maturing (Table IV). There was a higher

TABLE IV. Different characteristics of the charr population in Storvatn and Rungavatn with the number of fish used for estimations (n); the statistics used to test the different parameters between the lakes are given with P -values

Stock characteristics	Storvatn	n	Rungavatn	n	Statistics	P
Ascending anadromous population 1997:	1260 (16–60 cm)	1260	1650 (10–49 cm)	1650	$\chi^2=52.20$	<0.001
Degree of anadromy:	56% (≥ 18 cm)	62	21% (≥ 14 cm)	168	$\chi^2=27.67$	<0.001
Smolt:						
Average length (cm \pm s.d.) 1997, 1998:	17.7 \pm 1.29, 18.7 \pm 2.25	97, 130	14.2 \pm 2.49, 14.6 \pm 1.73	67, 133	$t_{162,261}=6.7, 12.3$	<0.001
Average age (year \pm s.d.) 1997, 1998:	4.0 \pm 0.34, 4.7 \pm 0.60	97, 130	4.0 \pm 0.90, 4.5 \pm 0.74	67, 133	$t_{162,261}=0.5, 1.5$	>0.05
Females:	54%	285	53%	244	$\chi^2=0.20$	>0.5
Returned from sea 1997 (tagged):	32%	808	28%	140	$\chi^2=0.97$	>0.1
Maturing:						
Smolts (females, male):	0, 0%	227	20, 17%	244	$\chi^2=21.1, 17.7$	<0.001
Lake-dwelling females (3, 4, 5, 6 years old):	0, 0, 10, 15%	193	0, 4, 19, 45%	130	$\chi^2=17.8$	<0.001
Lake-dwelling males (3, 4, 5, 6 years old):	4, 10, 31, 69%	189	28, 35, 39, 66%	121	$\chi^2=25.9$	<0.001
Lake-dwelling charr (10–20 cm):						
Population density:	18 fish ha ⁻¹	(2538)	97 fish ha ⁻¹	(3541)		
Mortality (October–May):	17%	280	30%	1202	$\chi^2=18.9$	<0.001
Lipid (% \pm 95% CL):						
May:	—	—	1.00 \pm 0.35	29		
June:	—	—	0.49 \pm 0.11	18		
July:	0.69 \pm 0.19	24	2.10 \pm 0.28	30	$t_{52}=8.2$	<0.001
October:	2.28 \pm 0.49	20	2.79 \pm 0.44	30	$t_{48}=1.5$	0.070
Protein (% \pm 95% CL):						
May:	—	—	17.22 \pm 0.32	29		
June:	—	—	16.59 \pm 1.58	18		
July:	18.48 \pm 0.25	24	18.03 \pm 0.44	30	$t_{52}=1.8$	0.043
October:	19.43 \pm 0.34	20	18.07 \pm 0.42	30	$t_{48}=5.0$	<0.001
Water (% \pm 95% CL):						
May:	—	—	79.00 \pm 0.57	29		
June:	—	—	79.61 \pm 0.36	18		
July:	78.19 \pm 0.32	24	77.34 \pm 0.48	30	$t_{52}=2.7$	0.004
October:	75.73 \pm 0.66	20	76.57 \pm 0.66	30	$t_{48}=1.7$	0.048

TABLE V. Mean specific growth rate with 95% CL for parr from the 1993 year class that became smolts or residents

Season:	Late summer 1996	Winter 1996/97	Early summer 1997	Late summer 1997	Winter 1997/98
Time interval: Number of days (Storvatn, Rungavatn): Age of fish (years):	11 Jul.–17 Oct. 93, 95 3+	14 Oct.–24 Jun. 264, 260 3+/4	22 Jun.–22 Jul. 26, 30 4+	19 Jul.–6 Oct. 64, 67 4+	1 Oct.–17 Jun. 257, 238 4+/5
Storvatn:					
temperature range:	3.0–9.1+	3.0–0.2 (0.7)	3.0–11.5 (6.9)	6.5–13.5 (10.7)	0.05–6.5 (2.8)
residents:	0.40 ± 0.29	– 0.01 ± 0.10	1.20 ± 1.04	0.00 ± 1.43	0.05 ± 0.40
5+ smolts:	0.55 ± 0.19	– 0.03 ± 0.06	1.09 ± 0.60	– 0.03 ± 0.40	0.01 ± 0.08
4+ smolts:	0.57 ± 0.09	– 0.03 ± 0.04	—	—	—
Rungavatn:					
temperature range:	1.4–7.2+	2.0–5.2 (2.3)	5.2–11.5 (7.3)	3.6–13.2 (9.6)	1.8–3.6 (2.1)
residents:	– 0.09 ± 0.14	0.02 ± 0.17	0.85 ± 0.26	0.17 ± 0.21	0.03 ± 0.17
5+ smolts:	0.06 ± 0.30	– 0.01 ± 0.25	0.68 ± 0.35	0.43 ± 0.23	– 0.02 ± 0.16
4+ smolts:	—	– 0.03 ± 0.16	—	—	—

The time intervals correspond with the times between the periods given in [Table II](#) and [Fig. 2](#). The water temperature range is given in °C with mean temperature in parentheses. Maximum and mean temperature for late summer 1996 could not be estimated, because measures were not taken continuously through the first 2 months of this period.

proportion of maturing lake-dwelling charr in Rungavatn than Storvatn (respectively 26 and 8% in total), with a dominance of maturing males in both lakes (Table IV).

The lipid and protein content of the immature parr in both lakes increased rapidly through the summer, while the water content decreased simultaneously. However, the parr in Rungavatn had a significantly higher total lipid content than the Storvatn parr in July but not in October, and a significantly lower protein content than the parr in Storvatn in both July and October (Table IV).

DISCUSSION

INDIVIDUAL GROWTH AND ANADROMY

The most important conclusion from the present study is that within the populations, fish that attained the largest size in the final 1 or 2 years of the parr stage usually migrated as 4+ smolts, fish that attained a medium size became 5+ smolts, and the smallest parr remained residents at 5 years old. This result was most obvious for the Rungavatn charr. However, within the last 2 years of the parr stage in both lakes, parr that became anadromous had a lower specific growth rate during the winter and early summer than the parr that became resident, while the situation was the opposite in late summer (except for the 4+ parr in the late-summer period in Storvatn). Although these differences in growth rate were not significant, the trends were generally the same, which indicates that this may be a valid result. Thus, the anadromous fish had faster overall growth in the parr stage, but in the years prior to migration, they seemed to have a different growth pattern to that of the parr that became resident.

Earlier laboratory studies on other salmonid species indicate that the individual life-history decision to smolt or mature is made in the previous year, and is influenced by growth rate, metabolic rate, lipid stores and social status of the fish (Thorpe, 1987; Metcalfe *et al.*, 1990; Metcalfe, 1991; Rowe *et al.*, 1991). The same may apply to the wild charr populations in the present study. However, the early difference in size between the charr parr that became anadromous or resident in Storvatn and Rungavatn may indicate that some of the basis for the later life-history decision, to smolt or not in wild Arctic charr, is established several years prior to the observed life-history change, and that this decision is strongly influenced by several ecological factors in the local environment (see later discussion). This hypothesis is supported by a recent study, where back-calculated lengths at the end of the first growth season in wild Atlantic salmon differed significantly between parr smolting at age 1, 2 and 3 years (Jonsson *et al.*, 1998). One possible explanation for the early variation in parr growth within the populations, is that some individuals may either inherit a higher growth rate than others, or for some other reason attain a higher rate shortly after hatching, which in turn would affect the variation in individual growth within the populations (Metcalfe *et al.*, 1992; Forseth *et al.*, 1999). This also corresponds to the predictions from a new model developed by Thorpe *et al.* (1998), that life-history events in salmonids are triggered by a combination of the physiological state of the individual fish (e.g. lipid content or body mass) and the rate of change of state, with genetic thresholds (a genotype-environment interaction).

Rapidly growing individuals in a population may generally have a higher metabolic rate than slower growing individuals (Metcalf *et al.*, 1992; Jobling, 1994). This accords with a recent study of juvenile migration in brown trout, where the fast growing trout migrated first, allocated most energy to growth and had the highest metabolic costs (Forseth *et al.*, 1999). It is suggested that different metabolic requirements for fast- and slow-growing parr lead to situations where the fast growers may be energy-constrained earlier in life by the food limitations of a freshwater habitat, and thus have to migrate to the sea to maintain the high growth and food intake (Jonsson & Jonsson, 1993; Økland *et al.*, 1993; Rikardsen *et al.*, 1997). The results from Storvatn and Rungavatn may give support to this theory. It is therefore hypothesized that the fast-growing parr that became anadromous in both lakes, had poorer growth rate through the winter and spring prior to the migration, compared with the parr that became resident, because local food limitations in the lakes retain further growth in these fast-growing parr, due to their high metabolic requirements. Parr with low growth may not have been energy-constrained in the same way, and became resident. Furthermore, the parr must then be able to measure, through some physiological mechanism, their rate of acquisition of surplus energy available for growth (metabolic needs), as suggested by Thorpe (1986, 1987).

LIFE-HISTORY STRATEGIES

The degree of anadromy was almost three times higher in Storvatn (56%) than Rungavatn (21%), which may be related to the growth opportunities in the lakes and the stock characteristics. The charr in Storvatn had the highest parr growth, and were on average twice as heavy at the age they migrated to the sea than those from Rungavatn. The Storvatn charr therefore had an advantage when migrating to the sea, where the mortality is strongly correlated to smolt size (Bohlin *et al.*, 1993; Finstad & Heggberget, 1993, 1995; Rikardsen *et al.*, 1997; Ward & Slaney, 1998). The population difference in growth may be explained by the much higher density of lake-dwelling charr in Rungavatn than Storvatn. Therefore the parr growth in Rungavatn may be strongly density limited compared with the parr growth in Storvatn, because high densities depress the growth rate of juvenile fish in other salmonid species (Elliott, 1994). This assumption is supported by the fact that the parr in Rungavatn had both a significantly higher mortality and lower condition factor than the parr in Storvatn, which, together with the reduced growth, are common effects of interspecific competition in high density populations (Wootton, 1990; Elliott, 1994). Despite this, the individual variation in growth was higher in Rungavatn than in Storvatn. This indicates that the resources are divided unequally between the fish, probably because of different individual competition abilities of parr in the lake. Wootton (1990) describes this as intraspecific contest competition, which may result in depressed growth and high mortality of low-ranking individuals within the population. Further support for this assumption is provided by several studies which have shown that the dominance status of salmon parr may influence the life-history tactics adopted by individuals through its impact on competitive ability and growth rate (Metcalf *et al.*, 1990, 1992, 1995; Metcalf, 1991; Cutts *et al.*, 1998; Johnsson *et al.*, 1999).

The condition factor of the parr increased rapidly from spring to mid-summer in both lakes, but decreased after mid-summer in Rungvatn, while it continued to increase until autumn in Storvatn. The situation with decreasing condition factor in both lakes, may indicate starvation and/or a negative energy budget (Forseth *et al.*, 1994), which seems to last in Rungvatn for 3 months longer than in Storvatn. In addition, the average water temperature in winter in Rungvatn was almost 2° C higher than in Storvatn, which in turn will have made the metabolic cost of starvation higher in Rungvatn than in Storvatn. However, the parr in Rungvatn seem to allocate more of their surplus food consumption to lipid storage and less to protein production, compared with the parr in Storvatn. Fat is an easily mobilised energy reserve which can be used when the energy uptake is extremely low (Bull *et al.*, 1996; Jonsson & Jonsson, 1998), or as the primary energy reserve upon which fish draw for the energetic costs of reproduction (Rowe *et al.*, 1991; Adams & Huntingford, 1997). As the parr in Rungvatn seem to have a negative energy budget for a longer period than the parr in Storvatn, lipid stores may be of vital importance for these parr to survive through the winter. Recently this has been found to be important also for juvenile Atlantic salmon and brown trout (Bull *et al.*, 1996; Bull & Metcalfe, 1997; Berg & Bremset, 1998). However, by having a rapid protein growth, like the parr in Storvatn, the young fish are gradually decreasing their vulnerability towards predators and increasing their competitive ability in situations of interference, but to a smaller degree need to prepare for periods of starvation (Jonsson & Jonsson, 1998). Food is thought to be plentiful at sea (Gross, 1987; Gross *et al.*, 1988), and stored energy reserves from fresh water are probably less significant than muscle mass and a large size for the smolts when they enter the sea (Jonsson & Jonsson, 1998).

There was a higher proportion of both parr and smolts that matured in Rungvatn than Storvatn. This may explain partly the differences in growth between the two populations. Maturing parr of salmonids allocate more of the energy from food consumption to lipid stores and less to protein production in the year before the actual maturing occurs (Thorpe, 1987; Rowe *et al.*, 1991). The early maturing of the charr in Rungvatn may therefore be correlated with the higher lipid allocation in these fish, and may be an adaptation to maximize the lifetime reproductive success due to low growth (Stearns, 1992). Whether the high allocation of fat in the parr stage in Rungvatn is an adaptation to starvation, with the consequence of early maturation, or is an effect of ongoing maturation, cannot be ascertained from the observations. A combination of these factors may be possible. The fact that about 20% of the smolts in Rungvatn were maturing, may also indicate that in some populations of Arctic charr, maturation does not necessarily inhibit smolting, as described in other charr populations or salmonid species (Thorpe, 1987; Dellefors & Faremo, 1988; Jonsson & Jonsson, 1993; Staurnes *et al.*, 1994; Rikarsen *et al.*, 1997).

In conclusion, it seems that the populations in Rungvatn and Storvatn have evolved different life-history adaptations. The charr in Rungvatn may give preference to lipid allocation due to unfavourable feeding and competition conditions, but then grow slower and mature earlier, and have a disadvantage when migrating to the sea because of their small size, compared to the charr in

Storvatn. Despite this, one consequence of the fact that many fish in Rungavatn do migrate to the sea, is increased total production of charr, and reduced competition, within the lake. The charr in Storvatn, however, may give preference to protein growth and a larger size, and thus have an advantage when migrating to the sea compared to the charr in Rungavatn. This may explain the higher degree of anadromy in Storvatn than in Rungavatn.

Developmental rates (growth, smolting, maturation) in salmonids are heritable, but operate under environmental instruction (Thorpe, 1987; Elliott, 1989, 1994; Näslund, 1993; Roff, 1996; Thorpe *et al.*, 1998). Genetic variations may, therefore, also influence the difference in degree of anadromy between populations. However, although only two lakes were compared in the present study, it has indicated that not only growth, but also population density and energy allocation, may influence anadromy variation among populations. The present study therefore provides another example to support the conclusion that Arctic charr have a very flexible life history, which is closely adapted to local conditions.

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