

# Life-History Traits of Charr, *Salvelinus alpinus*, from a High Arctic Watercourse on Svalbard

ODD A. GULSETH<sup>1,2,3</sup> and KJELL J. NILSSEN<sup>1</sup>

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**ABSTRACT.** Three arctic charr (*Salvelinus alpinus*) morphs coexist within the Dieset watercourse (79°10'N, 11°20'E) on Spitsbergen, Svalbard. Small freshwater resident charr exhibited a very slow growth rate, while large freshwater resident charr grew at a rate comparable to that reported for cannibalistic charr elsewhere. First-time sea migrants of the anadromous charr were similar in size to their more southern-living Norwegian conspecifics, but on average two years older. The average number of sea runs before first-time spawning was 3.6 for males and 4.4 for females. Veteran migrants displayed growth comparable to that of anadromous charr from more southern populations. In all three morphs, sex ratio did not differ from unity. The short-lived small residents matured from an age of 4 years, 3 to 4 years earlier than did large residents and anadromous charr. The majority of small resident and anadromous charr spawn a maximum of three times, while large resident charr may spawn up to seven times. Although 69% of large resident charr were older than 15 years, only 5.7% of reproductive anadromous charr exceeded this age. This divergence may indicate different reproductive strategies between the two morphs. There was no evidence of reproductive isolation between these High Arctic charr morphs.

**Key words:** anadromous, Arctic charr, High Arctic, life-history, resident, *Salvelinus alpinus*, Spitsbergen, Svalbard

**RÉSUMÉ.** Trois variétés d'omble chevalier (*Salvelinus alpinus*) coexistent à l'intérieur du cours d'eau Dieset (79° 10' de latit. N., 11° 20' de long. E.) au Spitzberg, dans l'archipel du Svalbard. Le petit omble d'eau douce résident affichait un taux de croissance très lent, tandis que le gros omble d'eau douce résident grossissait à une vitesse comparable à celle rapportée ailleurs pour l'omble cannibale. Les spécimens d'omble anadrome qui migraient pour la première fois vers la mer avaient une taille analogue à celle de leurs congénères norvégiens vivant plus au sud, mais avaient en moyenne deux ans de plus. Le nombre moyen de voyages vers la mer avant le premier frai était de 3,6 pour les mâles et de 4,4 pour les femelles. Les anciens migrateurs affichaient une croissance comparable à celle de l'omble anadrome appartenant à des populations plus méridionales. Chez les trois variétés, la proportion des sexes ne différait pas de la valeur 1. Les petits résidents ne vivaient pas longtemps et devenaient adultes à partir de l'âge de 4 ans, c'est-à-dire 3 ou 4 ans plus tôt que ne le faisaient les plus gros résidents et l'omble anadrome. La plupart des petits résidents et de l'omble anadrome frayaient un maximum de trois fois, tandis que le gros omble résident peut frayer jusqu'à sept fois. Si 69 p. cent des gros ombles résidents avaient plus de 15 ans, seulement 5,7 p. cent des ombles anadromes reproducteurs dépassaient cet âge – divergence qui pourrait indiquer des stratégies de reproduction différentes pour chaque variété. Rien ne semblait indiquer un isolement reproducteur entre ces variétés d'omble de l'Extrême-Arctique.

**Mots clés:** anadrome, omble arctique, Extrême-Arctique, cycle biologique, résident, *Salvelinus alpinus*, Spitzberg, Svalbard

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## INTRODUCTION

Freshwater systems within the High Arctic Svalbard archipelago (74–81°N) may be covered by ice from the end of September until the beginning of the next August. Organic production is very limited, and some lakes are described as ultra-oligotrophic, with a primary production among the lowest in the world (Lund, 1983). Exploitation of these rigorous environments, therefore, requires the ability to survive long-lasting periods of darkness, low water temperatures, and food shortages. The only vertebrate found to inhabit and reproduce under such conditions is the arctic

charr (*Salvelinus alpinus*) (Gullestad, 1975; Hammar, 1985; Svenning, 1993; Nilssen et al., 1997).

Recent studies of the glacial history of Spitsbergen Island, the largest island within the Svalbard archipelago, provide evidence that the northwestern coastal zones may not have been glaciated for at least 45 000 years (Salvigsen, 1977; Boulton, 1979). It is therefore possible that today's arctic charr on Spitsbergen may have an ancient history (Hammar, 1985), with an origin 30 000 to 35 000 years earlier than that of their counterparts in northern Norway. It would be interesting from a developmental aspect to compare life-history traits of this polar charr population,

<sup>1</sup> Brattøra Research Center, Department of Zoology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway

<sup>2</sup> Norwegian Polar Institute, N-9296 Tromsø, Norway

<sup>3</sup> Corresponding author: odd.gulseth@chembio.ntnu.no

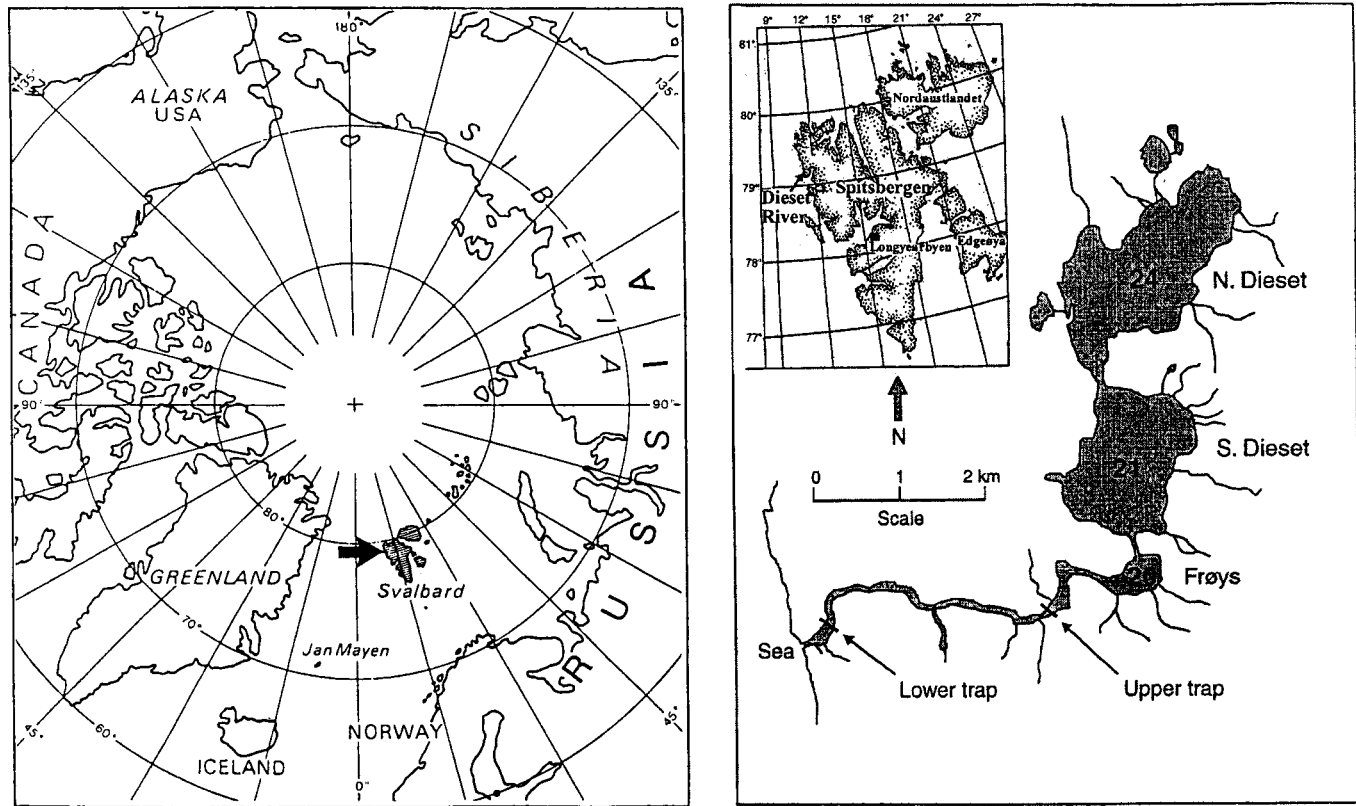


FIG. 1. Location of the study site and fish traps in the Dieset River on Spitsbergen Island within the Svalbard archipelago.

which is possibly of ancient origin, with traits documented for conspecifics of more recent origin.

Morphotypes, which frequently coexist in freshwater systems, are reported to differ in body proportions, growth rates, habitats, feeding, and spawning habits, as well as in age, size, and color at sexual maturity (Nordeng, 1961; Johnson, 1980; Sparholt, 1985; Riget et al., 1986; Jonsson et al., 1988; Walker et al., 1988; Reist et al., 1995).

In this study, we documented the coexistence of three charr morphs within the High Arctic Dieset watercourse on Spitsbergen, Svalbard. We examined their growth, migration, and reproductive strategy and compared these results with results obtained from more southern living charr populations.

## METHODS

### Study Area

The Dieset watercourse on Spitsbergen Island (79°10'N, 11°20'E, see Fig. 1) consists of a main river and seven lakes and has a total length of 10 km. The catchment area is 57.3 km<sup>2</sup>, of which 31% is covered by glaciers. The largest lakes are North Dieset Lake (2.2 km<sup>2</sup>, maximum depth 33 m) and South Dieset Lake (1.8 km<sup>2</sup>, maximum depth 18 m). The Dieset River (Fig. 1) is 4 km long, 5–40 m wide, and 0.1–1.5 m deep. Water starts to flow in river meltwater channels during the second week of June (1991–93). Maximum water flow was estimated at 20 m<sup>3</sup>·s<sup>-1</sup> at the

end of June, decreasing to 3 m<sup>3</sup>·s<sup>-1</sup> during July, then to 0.3 m<sup>3</sup>·s<sup>-1</sup> in late August or early September. River water temperature increased from a low of 0.1°C in June to a maximum of 8°C in mid-August and then declined to below 2°C during the first half of September. Both river and lakes started to freeze by mid-September, and in all years a solid ice cover had formed before the beginning of October. The rivers remain frozen solid to the bottom for about nine months of the year.

### Fish Capture

Fish traps (funnels with steel frames and seine netting; mesh size 10 mm) were established in the Dieset River, both in the upper part, below Frøys Lake, and in the lower part, 200 m upstream from the open sea (Fig. 1). The traps were connected with a two-winged seine netting fence (mesh size 10 mm) that covered the full width of the river. We monitored the traps, which caught both ascending and descending charr (larger than 10 cm), from late June (depending on ice conditions) to mid-September (depending on river closing time). Fish traps were emptied twice a day. Fish were anaesthetized (metomidate 5 mg·l<sup>-1</sup>) and tagged individually with numbered Floy-tags (T-Bar Anchor Tag), using the techniques described by Dell (1968). The charr were allowed to recover in cages (3 m<sup>3</sup>) for 24 hours before being released in their migratory direction. No mortality was registered prior to release.

During the second week of September in 1992 and 1993, charr were caught with nylon gillnets in Frøys and South Dieset Lakes (Fig. 1). The bottom nets and the pelagic gillnets were 1.5 m and 4 m deep, respectively, and consisted of 11 sections, each 5 m long with bar mesh sizes ranging from 10 to 64 mm (Jensen, 1990). The bottom nets were set perpendicular to the shoreline in the littoral zone of both lakes (1–10 m depth) and offshore in South Dieset Lake at depths of 10 to 15 m (only 18% of the lake area is deeper than 12 m). The pelagic nets were used offshore (0–8 m) over areas 8 to 15 m deep in South Dieset Lake and 8 to 11 m deep in Frøys Lake. All nets except the pelagic nets in Frøys Lake were pulled and reset in new localities after 12 to 18 hours of fishing.

#### *Measurements and Registrations*

Wet weight (g) and total length (mm) were recorded for all fish. Sacrificed individuals were aged and sexed; the degree of sexual maturation was determined using the criteria of Dahl (1943). Fish from stage IV to stage VII were considered to be spawners of the year. Nonmigrating fish were classified either as small resident ( $N = 233$ ) or large resident ( $N = 57$ ) charr on the basis of a combination of external morphological characters and coloration (Nordeng, 1961; Hindar and Jonsson, 1982). Small resident fish were under 16 cm long and pale grey in colour, with weak parr marks along the flanks, dull spawning coloration, and a blunt snout with big eyes and an overshot or terminal mouth. Larger nonmigrating fish were longer than 20 cm and dark on the back, with either grey or silvery flanks (immature) or dark, orange-yellow or red markings (spawning coloration), a relatively big head with powerful jaws, and an undershot or terminal mouth.

Charr with a proven seawater stay (captured in the lower trap upon their ascent from the sea) were termed anadromous. In all years (1991–93), all ascending anadromous charr were caught in the lower trap, and all untagged charr were tagged. Anadromous first-time migrants included three categories: (1) charr that were tagged during their descent to the sea and sacrificed in the same year upon their ascent from the sea; (2) charr tagged on their first ascent from the sea and sacrificed after their second or third return from a summer seawater stay (body measurements and age refer to their first year of ascent); and (3) untagged charr sacrificed upon their ascent from the sea during the second or third year of trapping. Using the criteria of Nordeng (1961), we assumed that the first seawater stay of the anadromous first-time migrants corresponded with their first wider (relative to the previous years) opaque otolith zone.

Fish age was determined from otoliths, using the criteria of Nordeng (1961), Christensen (1964), and Kristoffersen and Klemetsen (1991). Age at first seaward migration and number of sea runs were checked against opaque zone formation in the otoliths. Relatively wide zones in the central part of the otolith correspond to the

juvenile stage of the fish. In anadromous charr, one or more broader zone(s) after the parr stage indicate growth at sea (Nordeng, 1961).

Mature fish showing a narrow otolith edge zone in their spawning year, different from the wider zones laid down in the previous years, were recorded as first-time spawners.

Body length increase from year to year was estimated from the mean length data of each age group.

#### *Statistics*

All statistical analyses of the samples were performed using the SPSS program version 6.1.3 software for Windows. Nonparametric Mann-Whitney U-tests were used to test for differences in age and size between sexes within different morphs. Chi-square tests were used to determine whether sex ratios differed significantly from unity. A pseudo-probability test (Zaykin and Pudovkin, 1993) was used to test for heterogeneity between the morphotypes with respect to age composition of mature specimens. One-way ANOVA analysis was used to test for significant differences between males and females in mean age at maturity. *P*-values at or below 0.05 were considered significant.

## RESULTS

#### *Distribution of the Catch*

The gillnet fishing showed that arctic charr were not homogeneously distributed within the lakes at the time when spawning began (early September of both years). The majority ( $N = 505$ ) of fish within every morph were caught in the littoral zone (2–6 m). Only a very few ( $N = 18$ ) immature and spent fish were caught in the pelagic zone (down to 8 m depth), and not one was captured offshore at the bottom.

#### *Body Length*

The total catch of resident charr showed a distinctly bimodal length frequency distribution, with many small fish ( $N = 233$ ; mean length 12.1 cm; range 9.1–15.0 cm) and relatively few large ones ( $N = 57$ ; mean length 34.5 cm; range 19.9–49.3 cm) (Fig. 2). Anadromous charr ( $N = 381$ ) caught during net fishing ( $N = 233$ ) or sacrificed when ascending the river ( $N = 148$ ), exhibited a mean length of 35.4 cm (15.0–65.3 cm).

#### *Age, Growth and Sex*

The age-length relationship (Fig. 3) clearly demonstrates the superior growth of anadromous charr (mean annual growth of 4.8 cm from age 6 to 11 years) compared with that of the large resident fish (whose most rapid mean growth of 3.0 cm occurred from age 12 to 18 years) and

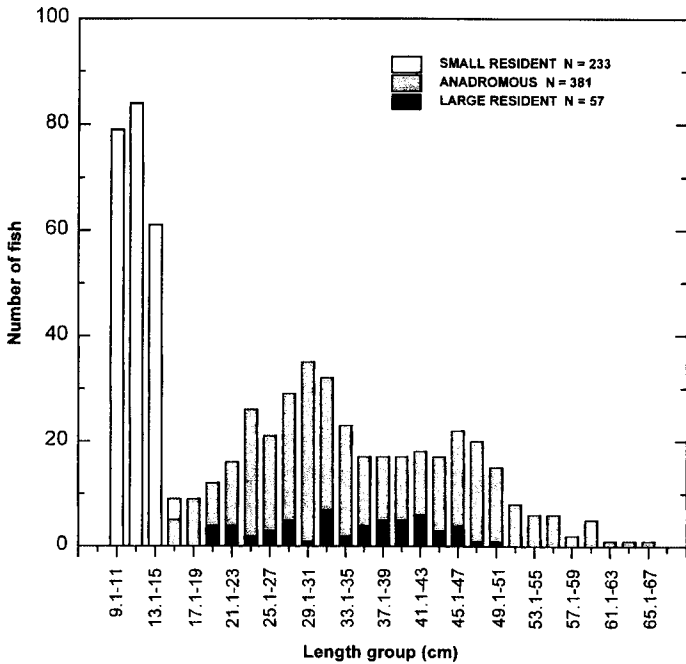


FIG. 2. Length-frequency distribution of arctic charr captured with gillnets in the Dieset lakes or sacrificed ( $N = 148$ ) when ascending the Dieset River on Spitsbergen Island.

small resident fish (mean annual growth of 1.6 cm until age 8). There were large variations in length within age groups for both anadromous and resident charr. However, the only significant length differences between sexes at the same age were found in anadromous charr at age 6 ( $p = 0.03$ ) and age 10 ( $p = 0.01$ ): in both cases, females were larger. For all morphs, sex ratios did not differ significantly from unity.

#### First-time Migrants

Most first-time migrants (91.8%) were 6 years of age or older (Table 1). No significant differences between sexes in length at age were found for ages 5–8 years, except that age 6 females were significantly ( $p = 0.003$ ) longer than males. The pooled data showed no significant differences in length between age classes from 5 to 9 years. The mean length of ascending first-time migrants was 24.2 cm (Table 1). This figure is consistent with the mean length of returning fish tagged when descending on their first seaward migration in 1992 ( $24.0 \pm 3.4$  cm,  $N = 69$ ) and in 1993 ( $24.5 \pm 2.7$  cm,  $N = 50$ ). The sex ratio for first-time migrants did not differ significantly from unity.

#### First-time Spawners

Sexually mature fish of all morphs were caught in the narrow littoral zone (2–6 m depth). First-time spawners represented 44.3% of total spawners in the anadromous group, 17% of large resident spawners (males only), and 50.9% of small resident spawners (Tables 2 and 3). Mean age in years of first-time spawners was 9.7 (males) and

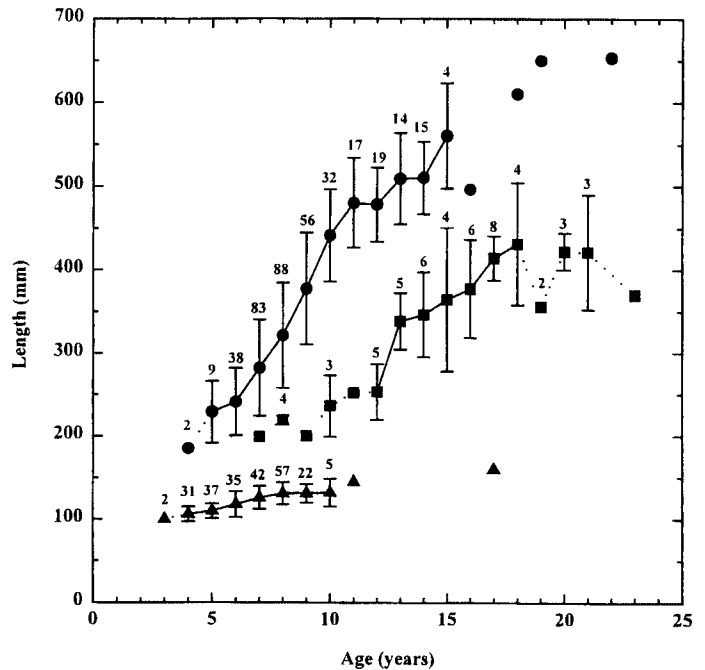


FIG. 3. Age and total length of anadromous (●), large resident (■) and small resident (▲) arctic charr captured in the Dieset watercourse on Spitsbergen Island. Values are given as mean (dot)  $\pm$  SD (vertical line). Numbers = sample size.

10.3 (females) for the anadromous group, 10.4 for the large residents (males only), and 6.6 (males) and 7.1 (females) for the small residents. For anadromous first-time spawners, body lengths and weights differed ( $p = 0.01$ ) between sexes: mean lengths were 41.7 for males and 46.5 cm for females (Table 2), and weights were 730 g for males and 997 g for females. Female first-time spawners exhibited a significantly ( $p = 0.02$ ) higher number of sea runs than males (4.4 vs. 3.7; Table 2). For resident first-time spawners, average body length was 23.8 cm for large residents (males only), 12.3 for small resident males, and 12.2 cm for small resident females. Irrespective of morph, sex ratios for first-time spawners did not differ significantly from unity.

Age distribution of male first-time spawners differed significantly among all three morphotypes ( $p = 0.0003$ ), and this was also true for their mean age at maturity ( $F(2,43) = 27.12$ ,  $p < 0.0001$ ). However, no significant difference was found between the mean ages at first maturity of large resident and anadromous males.

#### Spawners

Numbers of spawners vs. nonspawners in the total catch were 110 vs. 123 for small resident charr, 29 vs. 28 for large resident charr, and 70 vs. 311 for anadromous charr.

For mature anadromous charr of all age classes combined, no significant differences in age and length were found between sexes (Table 3). The combined mean values (for both sexes pooled) were 11.8 years for age and 48.7 cm for length. Mature large resident females were

TABLE 1. Age and total length of first-time sea migrants of arctic charr captured in the Dieset watercourse on Spitsbergen Island in 1991–93. Values are given as mean ( $\pm$  SD).

Age (years) <sup>1</sup>	4	5	6	7	8	9	10	11	12	17	Total
Males; N		7	33	36	18	4		3	1	1	103
Length (cm)		22.4	22.8	24.5	24.2	28.9		28.2	32.0	34.3	24.1
(SD)		(3.9)	(3.3)	(3.7)	(2.2)	(4.9)		(1.3)			(3.7)
Females; N	2	6	33	18	14	1	3	1	2		80
Length (cm)	18.5	22.6	25.1	22.6	25.2	23.0	26.4	32.6	26.5		24.3
(SD)		(2.7)	(2.6)	(3.1)	(3.5)		(2.7)				(3.4)
Pooled; N	2	13	66	54	32	5	3	4	3	1	183
Length (cm)	18.5	22.5	24.0	23.8	24.6	27.4	26.4	29.3	28.3	34.3	24.2
(SD)		(3.4)	(2.9)	(3.5)	(2.8)	(4.9)	(2.7)	(2.4)	(4.4)		(3.6)

<sup>1</sup> No fish between age 12 and 17 years, and none older than 17 years were sampled.

older and larger than males (all age classes combined), although the difference was not significant. Small resident female spawners were significantly ( $p = 0.04$ ) older (7.8 years) than males (7.3 years), although there was no significant difference in length between the sexes when all age classes were combined (Table 3).

The age distribution of spawners of both sexes differed significantly among all three morphotypes ( $p < 0.0001$ ): while 95.5% of small resident spawners were younger than 10 years, 69% of large resident spawners (but only 5.7% of anadromous spawners) were older than 15 years (Table 3). We tested for heterogeneity between large resident and anadromous spawners having a similar age-span. Heterogeneity in the age distribution of both males ( $p = 0.0032$ ) and females ( $p < 0.0001$ ) between these two morphs was highly significant.

About 50% of captured anadromous and small resident charr had matured by age 12 and 7 years, respectively, while all anadromous, large, and small resident charr were mature by age 16, 19, and 10 years, respectively (Table 3).

The percentage of arctic charr spawners older than age of sexual maturity indicates that resident charr may spawn every second year (large resident females may spawn more frequently), while anadromous charr may spawn less frequently (Table 4).

Among anadromous spawners, 18.5% remained in freshwater during the summer preceding spawning. Of these, 61.5% were males.

## DISCUSSION

The study verified the coexistence of anadromous, large, and small resident charr in the High Arctic Dieset watercourse. The size distribution of resident charr was bimodal and comparable to that reported for the Salangen River system in northern Norway (Nordeng, 1961, 1983). The resident Dieset charr showed large variations in length at age. Small resident charr exhibited a growth rate comparable with that reported for some of the slowest-growing landlocked charr populations (MacCallum and Regier,

1984), including small bottom-feeding arctic charr from Thingvallavatn, Iceland (Sandlund et al., 1992). Growth of large resident charr was comparable to that of cannibalistic charr from arctic lakes where food availability was low and charr was the only fish species present (Skreslett, 1973; Klemetsen et al., 1985; Sparholt, 1985; Riget et al., 1986).

Although inherited characteristics have been reported (Hindar et al., 1986; Skúlason et al., 1989; Svedäng, 1990; Hartley et al., 1992), the variations in life-history traits between coexisting morphotypes of arctic charr have, to a large extent, been reported to depend upon environmental factors (Savvaitova, 1973, 1980; Skreslett, 1973; Hindar and Jonsson, 1982; Jonsson and Hindar, 1982; Nordeng, 1983; Sparholt, 1985; Riget et al., 1986; Hindar and Jonsson, 1993; Griffiths, 1994). Ripe, running, and spent individuals of the three morphs were caught side by side in the narrow littoral zone (down to 6 m) of the extremely turbid and shallow South Dieset Lake. No fish were caught offshore at the bottom, while a very few immature and spent fish were caught in the pelagic zone. This pattern suggested that there is no reproductive isolation between anadromous and resident charr in this High Arctic system.

Ecological polymorphism in charr has been suggested to result from variations in growth conditions between different habitats (Hindar and Jonsson, 1993). Lake morphology (habitat heterogeneity) affects the size of different habitats and thus the number of available niches, which in turn influences segregation into different morphs and life history strategies (Hindar and Jonsson, 1982, 1993; Klemetsen et al., 1985; Sandlund et al., 1987; Jonsson et al., 1988; Northcote, 1992; Griffiths, 1994). The degree of isolation of sympatric groups in lakes varies, depending on the size, depth, and age of the waterbody, trophic conditions, and the presence of spawning grounds (Savvaitova, 1995). All three Dieset morphs were caught together in the extremely turbid South Dieset and Frøys Lakes, where only 18 and 15% of the lake areas were deeper than 12 and 6 m, respectively. Thick layers of glacial sediments covered most of the lake bottoms, limiting the spawning habitat to a narrow part of the littoral zone. The zoobenthos was

TABLE 2. Age and total length of small and large resident and anadromous first-time spawners of arctic charr captured in the Dieset watercourse on Spitsbergen Island in 1991–93, and number of sea runs for anadromous first-time spawners. Values are given as mean ( $\pm$  SD).

Age (years) <sup>1</sup>	4	5	6	7	8	9	10	11	12	13	14	Total
<b>Small resident</b>												
Males; N	2	3	6	8	7							26
Length (cm)	11.8	10.2	11.8	12.6	13.1							12.3
(SD)		(0.6)	(1.8)	(1.2)	(1.9)							(1.7)
Females; N		2	6	10	11	1						30
Length (cm)		10.8	11.7	12.5	12.5	10.8						12.2
(SD)			(1.2)	(1.3)	(1.0)							(1.1)
<b>Large resident</b>												
Males; N					2		1		1		1	5
Length (cm)					21.7		19.4		28.6		27.5	23.8
(SD)												(4.03)
<b>Anadromous</b>												
Males; N					3	5	4	1	1	1		15
Length (cm)					38.3	42.1	38.2	45.6	55.4	46.7		41.7
(SD)					(4.7)	(4.1)	(6.7)					(6.3)
No. sea runs					2.7	3.8	3.3	4.0	6.0	5.0		3.7
(SD)					(0.5)	(0.7)	(0.4)					(1.0)
Females; N					3	4	5			1	3	16
Length (cm)					44.3	46.7	46.4			45.5	48.7	46.5
(SD)					(3.2)	(2.7)	(2.8)				(3.0)	(2.9)
No. sea runs					4.0	4.3	4.6			5.0	4.3	4.4
(SD)					(0)	(0.4)	(0.5)				(0.5)	(0.5)

<sup>1</sup> No fish older than 14 years were sampled.

totally dominated by chironomids, which were most abundant down to 5 m depth; no zoobenthos were found deeper than 11 m (Hansen, 1983). Thus, the very low growth rate of the small resident charr could reflect the extreme lake environment of Dieset, which has one of the worlds poorest primary productivities ( $1.6\text{--}2.2\text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ , according to Lund, 1983), while the more typical growth of large resident charr may reflect the occurrence of cannibalism, as we frequently discovered small charr (10–15 cm) in the stomachs of the large resident charr. Cannibalism normally occurs among charr larger than 20 cm (L'Abée-Lund et al., 1992; Svenning and Borgstrøm, 1995). Low food availability for much of the year in species-poor habitats favours cannibalism, which also increases with higher latitudes (Griffiths, 1994). Hammar (1989), supported by studies from Greenland (Sparholt, 1985; Riget et al., 1986), suggested that a switch to cannibalism was required to maintain growth in older age classes of charr. We suggest that these two factors—low food availability and cannibalism—could have been the driving forces in sustaining the different growth characteristics of the two resident morphs in the extreme Dieset environment.

A recent study demonstrated an active riverward migration of Dieset parr (age 2–8 years) a few days after ice breakup, suggesting a migrational strategy to improve growth (Gulseth and Nilssen, 1999). The river-migrating parr had a significantly higher length-at-age than the lake-dwelling parr (age 0–4 years) captured in the shallow littoral zone (down to 0.5 m depth). Because only a portion of the parr population migrates into the river, an alternative

strategy may exist for the remainder of the population, similar to that reported from a partially lakeward migrating Atlantic salmon (*Salmo salar*) parr population (Hutchings, 1986). Thorpe (1987, 1989) hypothesized that an intermediate juvenile growth rate should favour salmonid anadromy, whereas a very rapid juvenile growth rate should favour residency. Improved feeding opportunities in freshwater may also increase the proportion of residents in hatchery-reared arctic charr (Nordeng, 1983). In nature, however, no clear-cut pattern exists as to whether fast growers migrate or mature and remain as residents. Within wild populations of arctic charr from northern Norway, there is some evidence that the fastest growing parr become sea migrants (Strand and Heggberget, 1994; Kristoffersen, 1995), corresponding to brown trout from western Norway (Jonsson, 1985). However, growth under these particular environmental conditions is considered to be insufficiently rapid to favour residency, as predicted by Thorpe's hypothesis (1987, 1989). If valid, these arguments would in time imply that, in habitats representing poor freshwater environments for growth and development, a change in habitat leading to increased growth should favour anadromy. In juvenile Atlantic salmon, the physiological decision of whether or not to migrate in a given spring is made some nine months beforehand: after this time, first-time sea migrants have higher appetites and growth rates than those that will defer migration for a further year (Metcalf et al., 1986, 1988). This has led to the development of a bimodal size distribution (Thorpe, 1977). The bimodal segregation of the Dieset parr population

TABLE 3. Age and total length of small and large resident and anadromous arctic charr spawners captured in the Dieset watercourse on Spitsbergen Island in 1991–93. Numbers of spawners and nonspawners are expressed as percentages of total number in each age class (given in Fig. 3). Values are given as mean ( $\pm$  SD).

Age (years)	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	Total	
<b>Small resident</b>																						
Males; N	2	3	6	12	15	8															46	
Length (cm)	11.8	10.2	11.8	12.4	13.1	13.0															12.5	
(SD)		(0.6)	(1.8)	(1.5)	(1.3)	(1.1)															(1.5)	
Females; N		2	6	13	27	11	5														64	
Length (cm)		10.8	11.7	12.7	12.9	13.1	13.2														12.7	
(SD)			(1.2)	(1.2)	(1.3)	(1.1)	(1.7)														(1.3)	
Spawners (%)																						
Males	6.5	8.1	17.1	28.6	26.3	36.4																
Females		5.4	17.1	31.0	47.4	50.0	100															
Nonspawners (%)																						
Males	64.5	43.2	28.6	14.3	7.0	4.5																
Females	29.0	43.2	37.1	26.2	19.3	9.1																
<b>Large resident</b>																						
Males; N					2		1		1		1	1	1	2	2				1		1	13
Length (cm)					21.7		19.4		28.6		27.5	27.6	46.7	43.8	39.3				41.3		37.0	33.7
(SD)																						(10)
Females; N								1			2	1	4	1	2	3	2					16
Length (cm)								24.6			43.7	34.6	40.3	47.4	35.6	42.2	42.5					39.9
(SD)															(1.8)	(2.2)						(6.1)
Spawners (%)																						
Males					50.0		33.3		20.0		16.7	25.0	16.7	25.0	50.0				33.3		100	
Females								20.0			50.0	16.7	50.0	25.0	100	100	66.7					
Nonspawners (%)																						
Males						100	33.3		20.0	80.0	66.7		50.0	25.0								
Females					50.0		33.3	100	40.0	20.0	16.7	25.0	16.7		25.0							
<b>Anadromous</b>																						
Males; N					3	5	5	3	5	8	1	2					1					33
Length (cm)					38.3	42.1	37.9	53.2	48.0	53.8	55.0	53.8					65.0					47.6
(SD)					(4.7)	(4.1)	(5.9)	(6.8)	(5.3)	(5.2)												(8.7)
Females; N					3	4	8	1	4	4	9	1	1		1					1		37
Length (cm)					44.3	46.7	47.5	46.5	51.8	48.3	51.2	55.3	49.6		61.0					65.3		49.7
(SD)					(3.2)	(2.7)	(3.8)		(2.6)	(2.8)	(3.6)											(5.0)
Spawners (%)																						
Males					3.4	8.9	15.6	17.6	26.3	57.1	6.7	50.0					100					
Females					3.4	7.1	25.0	5.9	21.1	28.6	60.0	25.0	100		100					100		
Nonspawners (%)																						
Males					46.6	37.5	31.3	47.1	26.3	7.1	13.3	25.0										
Females					46.6	46.4	28.1	29.4	26.3	7.1	20.0											

suggested that the lacustrine parr migrated to sea at an older age than the faster-growing migrating parr, or may in fact have stayed and been recruited to the resident population.

Before their first entry into seawater, charr from Svalbard were slower growing than charr from northern Norway. Furthermore, our results showed a large age range (4–12 years) for first-time sea migrants within a High Arctic system and a mean smolt age of 7 years, which was 2 years older than that of their conspecifics at 67–70° N in northern Norway (Nordeng, 1961; Jensen, 1994; Strand and Heggberget, 1994). Dieset charr larger than 20 cm have a fully developed seawater tolerance before entering the marine environment (Nilssen et al., 1997), while river-migrating parr smaller than 15 cm lack adequate hypo-osmoregulatory capacity (Nilssen and Gulseth, 1998). A threshold size for seawater tolerance for some arctic charr stocks has been reported to be between 15 and 18 cm (Delabbio et al., 1988), a figure consistent with the lower

TABLE 4. Percentage of arctic char spawners older than age at first maturity. N = total number of fish (mature and immature) within each sex older than age at first maturity.

	Small resident	Large resident	Anadromous
Mature males % (N)	54.3 (81)	40.7 (27)	38.5 (78)
Mature females % (N)	62.0 (100)	75.0 (20)	41.0 (83)

part of the size range (15–27 cm) of descending first-time migrants from northern Norway (Nordeng, 1961; Berg and Berg, 1989; Jensen, 1994; Finstad and Heggberget, 1995).

During their short marine residence, anadromous arctic charr have been reported to grow more rapidly (Mathisen and Berg, 1968; Johnson, 1980; Berg and Berg, 1989; Finstad and Heggberget, 1993) than most resident charr forms (Nordeng, 1961; Nordeng and Skurdal, 1985). Anadromous Dieset charr less than 30 cm long (of which 90% were larger than 20 cm) more than doubled their body

weight and showed a mean length increase from 3.1 to 4.6 cm during 32–40 days at sea (Gulseth and Nilssen, unpubl. data), showing an exceptional growth potential at sea. Our results and those from northern Norway (Nordeng, 1961, 1983) support the suggestion that size differences between anadromous and resident forms are more pronounced at high latitudes, where the marine productivity greatly exceeds that of freshwater (Gross, 1987; McDowall, 1987; Gross et al., 1988). The age-length distribution indicates that the mean annual length increment of the anadromous Dieset charr lies within the mid-range of those previously reported for anadromous charr from more southern Arctic localities (Grainger, 1953; Dempson and Green, 1985). However, variations in growth increments between populations may have been caused by size-dependent emigration to the sea of varying components of the populations, making an exact comparison difficult.

The small resident Dieset charr reached sexual maturity at an age of 4–5 years, 3 to 4 years earlier than the large resident and anadromous morphs. Small resident charr were much shorter lived than large resident charr. A link is often suggested between mortality and the age at which sexual maturation occurs: the heavy energetic cost of early reproduction may cause individuals that mature first to die early (Wootton, 1985). Cannibalism, as was seen in another study on Spitsbergen (Svenning and Borgström, 1995), may be another factor limiting the age-range of the small resident charr population in Dieset. However, if mortality was high, it would have been advantageous to have a high reproductive output early in life, because later opportunities might not have occurred (Wootton, 1985). Thus, the short life span of the small resident charr could have been due to a combination of predation and reproductive depletion of energy reserves at an early age.

Prior to first-time spawning, anadromous males and females had, on average, 3.6 and 4.4 sea runs, resulting in smaller mature males than females. The fact that males mature first, and at a smaller size than females, is a general finding that has been reported for several more southerly anadromous arctic charr populations (Nordeng, 1961; Johnson, 1980; Dempson and Green, 1985; Jensen, 1994).

In contrast to Nordeng's (1961, 1983) results, we could not demonstrate sex ratios that departed from unity, irrespective of morph or category of spawner. Sex ratios in the nonspawning segment of a charr population tended to approach unity (Johnson, 1980). A tendency of equality in sex ratios in the spawning segment of anadromous charr was shown by Grainger (1953) and Moore (1975). In other systems, migrating females have greatly outnumbered males (Johnson, 1980, 1989; Nordeng, 1983), theoretically because a large proportion of males stay in freshwater the year of spawning. We noted, however, that 18.5% of reproductive, anadromous charr had matured without leaving the freshwater system in the summer preceding spawning, and males only slightly outnumbered females.

Our results showed that among large residents, recruitment of first-time spawners was significantly lower than

that observed in the other two morphs. There was no difference in mean age at first maturity between males of the large resident and anadromous morphs. However, despite the similar maximum life-span of the two morphs, a significant difference was found in the age distribution of spawners in both males and females: only 5.7% of reproductive anadromous charr were over 15 years of age, whereas 69.0% of the large resident charr were above this age. Dutil (1986) found that the energy investment in reproduction in anadromous arctic charr increased as the length increased, and recovery potential tended to decline as length (age) increased. The combination of these relationships could result in senescence and mortality (Dutil, 1986). Therefore, the shorter life span of anadromous Dieset charr versus large residents may indicate that anadromous charr lose their capacity to recover after spawning two to three times, and they may experience high mortality due to senescence.

Nordeng (1961) suggested that both anadromous and resident charr in northern Norway were able to spawn annually, reaching maxima of 10 for small residents, 13 for large residents, and 7 for anadromous charr. In contrast, Dutil (1986) reported that anadromous post-spawners needed more than one summer to replenish their depleted reserves. The estimated spawning frequency of the Dieset morphs indicated spawning in alternate years at best, as reported in other investigations on both anadromous (Grainger, 1953; Johnson, 1980; Dutil, 1986) and resident charr (Skreslett, 1973; Sparholt, 1985; Riget et al., 1986; Parker and Johnson, 1991). The estimated spawning frequency of the Dieset morphs, combined with the age distribution of spawners in each morph, indicated that the majority of small resident and anadromous charr spawn three times at most, while large resident charr may spawn up to seven times.

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