Size, age and spawning frequency of landlocked arctic charr *Salvelinus alpinus* (L.) in Svartvatnet, Svalbard

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This contribution reports the analysis of a sample of landlocked arctic charr collected with gillnets in Svartvatnet, Svalbard, 1964. This is the first scientific sample from a landlocked charr population from Svalbard. We found a very prominent modal group of large, old and sexually adult fish of both sexes. Their length ranged from 15 to 62 cm, but 92% of the fish were longer than 40 cm and 62% of them fell in the 45 to 54 cm interval. The age range was 7 to 31 years, but 93% were 14 years or older and represented 18 year-classes. The length-at-age of the charr seemed to increase steadily until they reached the size and age of the modal group. The growth rate decreased sharply after that. The mortality rates within the age span of the modal group seemed to be low. The ages at first spawning for most of the charr in the sample were between 7 and 9 years and spawning cycles of two years were indicated.

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Introduction

The northernmost European populations of arctic charr are found in the arctic archipelago of Svalbard where it is the only permanent freshwater fish. Both anadromous and landlocked populations are found (Gullestad 1975). There are about 15 anadromous populations and probably more than 100 non-anadromous populations (Svenning 1993). Both occur along the whole latitudinal range of the archipelago and are mostly found along the western and northern coasts. Many of the non-anadromous populations are landlocked because their upstream migration is physically blocked. New charr localities are still being officially recorded (Hindrum 1994). The fishing pressure on the Svalbard charr has increased in recent decades because of increasing tourism and motorised transport. The charr populations are vulnerable to increased exploitation, and although unexploited populations can still be found, their numbers are decreasing. There is an increasing interest in studying charr in Svalbard because it is the only fish species in systems of low diversity and because the charr, even this far north, seem to exhibit large genetic, phenotypic, demographic and life history variation (Klemetsen et al. 1985; Svenning 1993; Svenning & Borgstrøm 1995). In this paper we report the results of analyses of a sample of large arctic charr from a landlocked population in Svartvatn, in southern Spitsbergen, from 1964. This appears to be the oldest sample from a landlocked charr population on Svalbard. It provides valuable information because the population was largely undisturbed by exploitation at that time.

Characteristic modes of large fish have been found in several populations in the Arctic regions, including Greenland (Sparholt 1985; Riget et al. 1986), Bjørnøya (Klemetsen et al. 1985), Spitsbergen (Svenning & Borgstrøm 1995) and Ellesmere Island, Canada (Parker & Johnson 1991; Reist et al. 1995). Such modes of large charr typically consist of old and sexually adult fish of both sexes with relatively uniform sizes but highly different ages. Their demographic structures seem to be stable if they are unperturbed by exploitation (Johnson 1983, 1995). Arctic charr populations at high latitudes tend to spawn at intervals of two years or more (Johnson 1980). Restrictions on growth because of low temperatures, short seasons and low food availability have been postulated as reasons for this tendency. In a well-documented study of the anadromous population of the Nauyuk system in arctic Canada, Dutil (1986) found that postspawners needed at least two summers to recover and build up enough energy reserves to spawn again. For non-migratory charr at lake H in Borup Fjord, Ellesmere

Island, Parker & Johnson (1991) found that the frequencies of post-spawners were about 0.1 in females and 0.2 in males. These values may indicate very long intervals between spawnings in the population, and also that males spawn twice as frequently as do females.

The 1964 sample from Svartvatn provided a good opportunity to test whether this unexploited, landlocked population had a structure that confirmed findings from elsewhere in the Arctic. We predicted that there would be a defined mode of large and sexually adult fish with a relatively narrow range of sizes and a wide range of ages. We also predicted that spawning intervals among the large charr of Svartvatn would be longer than one year but that males would spawn at shorter intervals than females would. The aim of this study was to test these predictions by describing the size and age structure and analysing the growth pattern, condition factors and spawning frequencies of the sample.

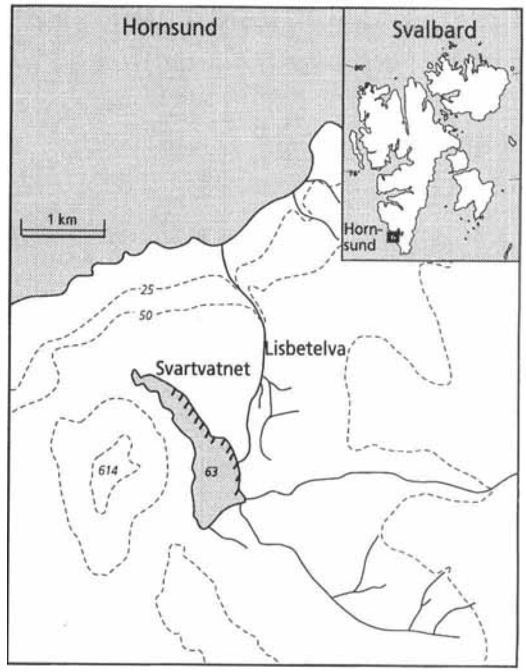

Fig. 1. Map of Svartvatn in the Hornsund area, SW Spitsbergen. The hatching indicates the area of gillnet sampling. Altitudes in m a.s.l.

Materials and methods

Svartvatnet is an oligotrophic lake situated about 3.5 km from the sea at an elevation of 63 m a.s.l. on the southern side of Hornsund, in southwest Spitsbergen (Fig. 1). The surface area is about 0.8 km^2. To the west, the bottom forms a steep gradient and the substrate is dominated by rocks and boulders. To the east, the depth of the lake increases gradually and the bottom substratum is predominantly sand. The upper part of the outlet stream, the Lisbetelva, has a gentle slope and several shallow pools. The lower part forms a number of small rapids and waterfalls and drops steeply about 50 m before entering Hornsund. The steep rise in the lower part of the stream makes it impassable to ascending fish.

The lake is influenced by glacial melt water and is usually open from late July or early August to the end of September. In 1964 the last ice on the lake disappeared on 13 August.

A total of 194 charr were caught with nylon gillnets during two rounds of sampling in 1964, 143 on 3–5 August and 52 on 11–13 August. The nets were placed singly or in pairs along the eastern shore of the lake. Knot to knot mesh sizes of the nets were 20, 25, 29, 35, 40 and 45 mm. This series catches charr longer than 17 cm fork length with approximately equal efficiency (Jensen 1984). The same effort was used in both rounds of sampling. One small charr was caught with a handnet in a stream pool close to the outlet.

All fish were measured for total length, weighed and sexed. Scale samples and otoliths were preserved dry. External colouration and flesh colour were noted. The development of the gonads was scored according to the seven-stage scale of Dahl (1943) as modified for male charr by Gullestad (1975). Fish at stages >III were considered to be spawners of that year.

Otoliths were used for age reading by employing the grinding technique of Nordeng (1961). The innermost spawning imprint in the otoliths was used to estimate the age at first spawning (Nordeng 1961).

Results

The net catches from Svartvatnet consisted of arctic charr ranging in length from 15 to 62 cm. Large fish predominated; 92% of the catch

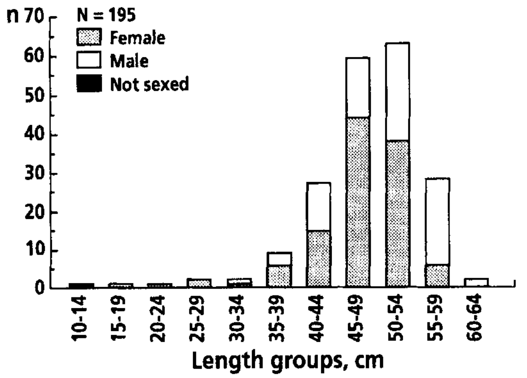

Fig. 2. Length distribution of landlocked arctic charr, Svartvatn 1984.

Table 1. Length distribution of charr in two consecutive net catches, Svartvatn 1964

	Length groups, cm						
	<35	35–39	40–44	45–49	50–54	>55	total
4–5 August	1	2	23	41	47	28	142
11–13 August	5	6	5	18	15	3	52

consisted of fish above 40 cm and 62% of these fell in the 45 to 54 cm interval (Fig. 2). Only six fish in the sample were smaller than 35 cm (Table 1). The largest female fish was 58 cm long and weighed 1680 g, and the largest male was 62 cm long and weighed 2495 g. Most fish were dark green on the back with strong yellow or orange spawning colours on the belly. Except for three fish shorter than 30 cm that had white-coloured flesh and one large fish with yellowish flesh, all charr in the sample (98%) had red-coloured flesh.

The first sample (3–5 August) contained larger fish than the second sample did. There were significantly more fish shorter than 40 cm and fewer fish longer than 54 cm in the second sampling (2% and 23% fish shorter than 40 cm and 19% and 6% longer than 54 cm, respectively, for the two samples; chi-square test, $P < 0.001$, Table 1).

Significantly more females than males were caught overall (112 females, 82 males, chi-square test, $P < 0.05$). However, males were most frequent among the very largest fish in the sample: 26 out of 30 fish longer than 55 cm were males (chi-square test, $P < 0.001$).

The fish in the net samples were 7 to 31 years old (Fig. 3). The single fish caught by hand from the stream pool was 4 years old. As many as 93% of the fish were 14 years or older, representing 18 year-classes. The bulk of the sample (87%) consisted of 13 consecutive, well-represented year-classes (14–26 years). The females were up to 29 years old and the males up to 31 years old (Table 2). The total life span, therefore, did not differ much between the sexes, but there were significantly more males than females among the oldest fish above 26 years (chi-square test, $P < 0.01$).

The sexes showed no important length for age differences. The growth data were therefore pooled. Length for age data indicated a slow but steady growth in the Svartvatn charr up to age 13 and a mean length of about 45 cm (Fig. 4). After age 13, a marked reduction in growth was evident, but there was appreciable size variation in individual fish within each year-class. The range in length for 22-year-old fish, for instance, was 40 to 59 cm. On average, a slight increase in length was indicated among the first six of the dominating year-classes. After age 18, no length-at-age increase was apparent. The weight for age data

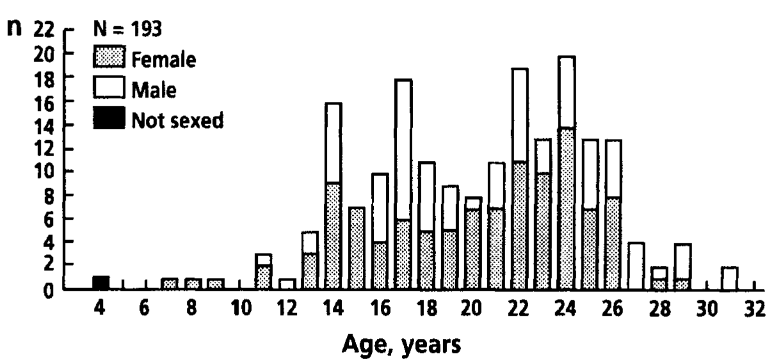

Fig. 3. Age distribution of landlocked arctic charr, Svartvatn 1964.

Table 2. Numbers of spawning and nonspawning adult charr of different ages in Svartvatn 1964

		Age classes (years)																					
		11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	total	%
Females	spawners			1	3	4	1	2	3	1	6	4	7	4	10	1	6		1	1			55	51,9
	nonspawners	2		2	6	3	3	4	2	4	1	3	4	6	4	5	2						51	48,1
Males	spawners				1		1	3	4		1	4	3	1	1	4	3	1		1			28	34,6
	nonspawners	1	1	2	6		5	9	2	4			5	2	5	2	2	3		2		2	53	65,4

showed a similar picture; there was a clear retardation in the average growth after age 13, no average growth after age 18, and a large and highly overlapping size variation in the dominating year-classes (Fig. 5).

The condition of these charr showed a high variation, with Fulton Q-values from 0.5 to 1.3. Most were between 0.7 and 1.0 (Fig. 6). All very low values (<0.7) were from large fish. These were predominantly males with unripe gonads, presumably spent fish from the year before.

Spawning marks in the otoliths were found for 164 (85%) of the fish. The majority of these (83%) matured at 7 to 9 years of age (Fig. 7). The lowest age at first spawning was 5 years and the highest 11 years. There was no apparent sex difference in the age of first spawning.

The gonad maturation pattern showed that only some of the sexually adult fish were ripening to spawn in 1964. The sample covered 21 successive year-classes (Table 2). The youngest spawning female was 13 years old and the youngest spawning male, 14 years old. Above these ages, non-spawners and spawners occurred in most age-classes of the sample. The few exceptions to this are presumably the result of stochastic variations because there were few fish in some year-classes. The frequency of female spawners above the age of first spawning was not significantly different from 0.5 (chi-square test, P = 0.75). The frequency of male spawners above the age of first spawning did differ significantly (P < 0.01) from 0.5 but not from 0.33 (P = 0.80).

Discussion

The lower part of the outlet stream from Svartvatn, the Lisbetelva, is too steep for fish to

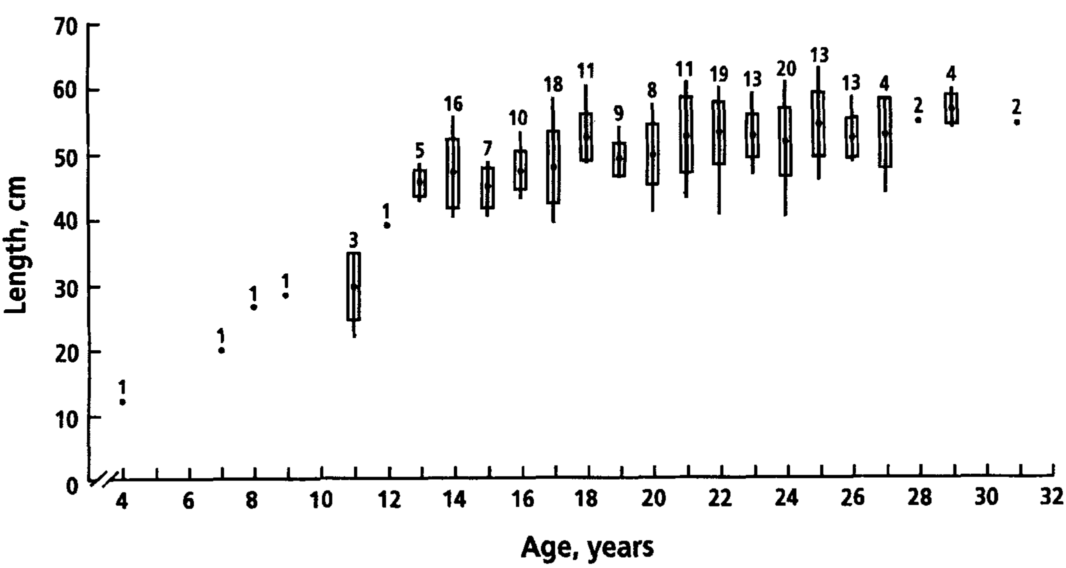

Fig. 4. Length-at-age for landlocked arctic charr, Svartvatn 1964.

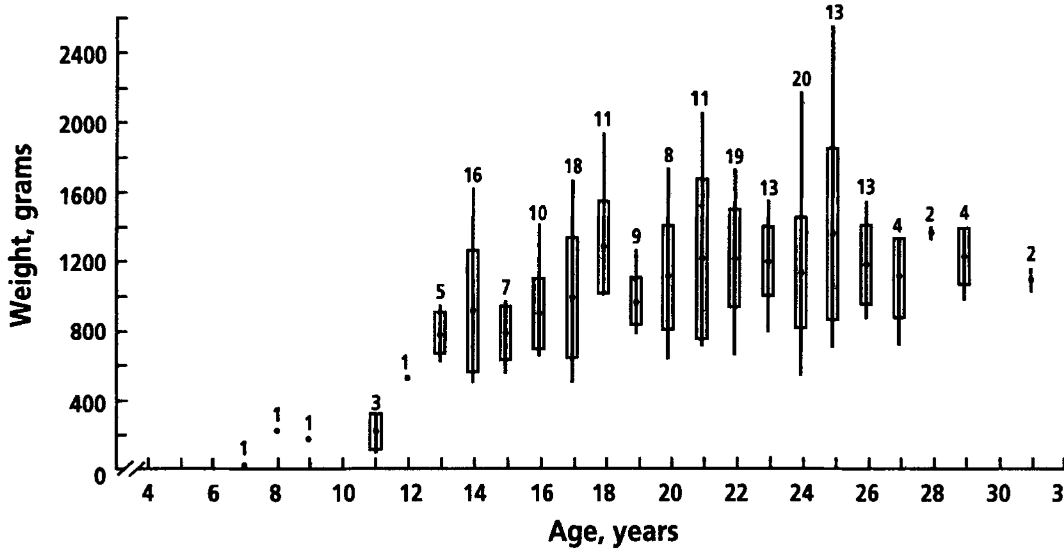

Fig. 5. Weight-at-age for landlocked arctic charr, Svartvatn 1964.

ascend. It cannot be ruled out that small fish are occasionally taken downstream past the rapid stretch and out to sea, but these fish would be lost to the population. An anadromous life cycle is therefore not possible in the Svartvatn system, and the population is essentially landlocked. The term "landlocked" is used to distinguish this situation from charr systems that are physically open to anadromous migration but in which the population (or part of it) is nevertheless non-migratory.

The prediction that the Svartvatn population would have a major mode of large and old fish comprising many accumulated year-classes was confirmed. As many as 18 year-classes were represented in the 40 to 60 cm size range and 13 of these year-classes made up the bulk of charr in the sample. The overlap in fish size between year-classes was extensive. The year-class strength within the major mode showed some variation but no more than could be accounted for by stochastic variation. We assume that the fishing mortality in the years prior to 1964 was very low in Svartvatn. Personnel from the Polish research station at Isbjørnhavna across Hornsund (pers. comm. to N.

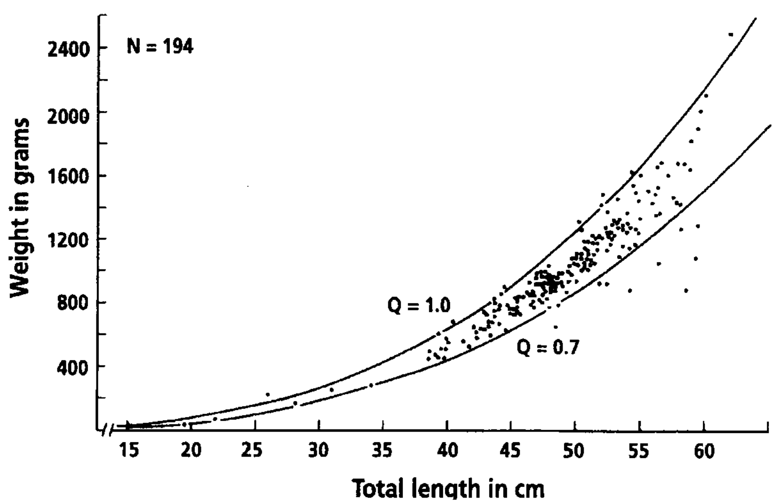

Fig. 6. Length–weight relationships of landlocked arctic charr, Svartvatn 1964. Graphs for Fulton condition factors of 0.7 and 1.0 are shown.

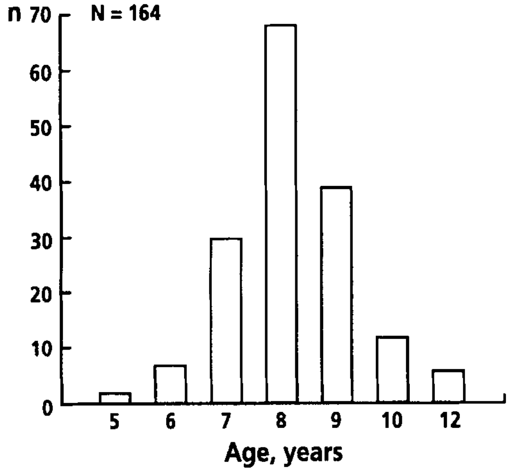

Fig. 7. Age at first spawning for landlocked arctic charr, Svartvatn 1964. Sexes are pooled.

Gullestad, 1964) had visited Svartvatn, but the fishing pressure had been light. Landlocked charr of this size have practically no natural predators on Svalbard. Therefore, the present sample describes the size and age structure of a pristine charr population in the High Arctic with very low mortality rates over a long period of time. In 1991, the Governor of Svalbard took another sample of charr from Svartvatn (Nilssen & Gulseth 1992). This sample was small and biased because only 40-mm nets were used, but it confirms the presence of a mode of large charr, similar to the results from 1964, nearly 30 years earlier. This supports results from Arctic Canada that unperturbed arctic charr populations tend to have stable age and size structures over long periods of time (Johnson 1983, Reist et al. 1995).

Strikingly similar demographic structures have been found in several populations of landlocked arctic charr in the Arctic. In Greenland, Sparholt (1985) reported a major mode of large charr in the Iterlaa lakes with lengths up to 52 cm (one fish of 62 cm) and ages up to 19 years; and Riget et al. (1986) found a large mode that peaked at 38 cm and comprised several year-classes of up to 24 years in Lake Tasersuaq. On Ellesmere Island (Canada), Parker & Johnson (1991) reported a mode of large fish in Lake H, Borup fjord, that were 14 to 22 years old and about 30 to 50 cm long. Lake Hazen on Ellesmere was found to have an upper mode of large charr that were 30 to 70 cm long, most of which were 11 to 28 years old (Reist et al. 1995). One fish was 35 years old, certainly one of the oldest arctic charr known. On Svalbard, Klemetsen et al. (1985) found a mode of large charr ranging from 29 to 50 cm and from 8 to 25 years in age in Ellasjøen, Bjørnøya, and Svenning (1993) found a mode of large charr that ranged from 26 to 56 cm in length and from 16 to 31 years in age in Arresjøen, north-west Spitsbergen. There is some variation in size and age ranges between the populations, but they all have the characteristic mode of large and mature fish of uniform size and varying age. The 1964 sample from Svartvatn confirms what seems to be a common pattern in landlocked arctic charr populations in the Arctic.

Many allopatric charr populations with an accumulated mode of large charr also have a dense mode of small but sexually mature charr in the population. Bimodality tends to increase with latitude (Griffiths 1994). There were no small charr in the present gillnet sample, which is to be expected since the nets used only caught charr above 17 cm effectively. Small fish were observed in high densities in pools in the upper part of Lisbetelva. These fishes are probably a regular part of the Svartvatn population and move into the stream in the summer to find food or to avoid predation, or both. Several of the large Svartvatn charr had small charr in their stomachs. This may indicate that the population has a bimodal structure that is sustained by cannibalism like in Arresjøen (Svenning & Borgstrøm 1995), but this needs confirmation by closer studies.

The otoliths indicated that the most common ages at first spawning were 7 to 9 years. Only a fraction of the sample had gonads that were ripening for spawning in 1964, but all had the characteristic colours of sexually adult charr. This strongly suggests that the large Svartvatn charr did not spawn annually. If the reciprocal of the frequencies of spawners are taken to indicate spawning intervals (Parker & Johnson 1991), the results may indicate that female Svartvatn charr tend, on the average, to spawn every second year while males spawn every third year. This is, however, based on defining all stage III fish in early August as non-spawners of the year. This may not always be correct for males. The development of the testes can be difficult to assess in August, and the seasonal development may differ between individual fish. There were 19 stage III males in the sample (Table 2). If only four of these were in fact going to spawn that year, then the ratio of male spawners and non-spawners was no longer significantly different from 0.5 (chi-square test, $P < 0.05$). The indication that males spawned less frequently than females therefore needs confirmation by a sample taken closer to spawning time, when gonad maturation can be assessed with certainty. We conclude that both sexes of the large charr in Svartvatn spawned, on the average, every second year and that the prediction that males spawned at shorter intervals than females was not supported.

Non-annual spawning has been demonstrated for other charr populations in the Arctic, for instance, by Gullestad (1975), Sparholt (1985) and Riget et al. (1986). Dutil (1986) found that postspawners in Nauyuk Lake, in Arctic Canada, were heavily depleted of somatic energy reserves. These are anadromous fishes that spend nearly two years in freshwater during the spawning run because of the special run-off conditions in the system (Johnson 1980). Dutil concluded that energetic constraints in arctic environments are the reason for spawning cycles of more than one year in length in arctic charr. This is presumably also the case in Svartvatn, which is a low productivity system with a short ice-free season. The low condition factors of several specimens indicate that maturation and spawning takes a heavy toll and that these large charr cannot find enough energy in one short season to be able to spawn annually.

Johnson (1983) published a classic analysis of single fish stocks in arctic lakes from Canada and discusses this in a series of papers (see Johnson 1994a,b,c and Vanriel & Johnson 1995, and references therein). A brief account is given by Johnson (1995). Johnson concludes that the fish in arctic lakes – very often single stocks of arctic charr – occupy the dominant position in the ecosystem. The uniformly sized fish of variable age form an establishment that imposes top-down stability on the rest of the system. A steady state in which stochastic environmental variability is absorbed by the population has been reached in these undisturbed, isolated systems. Johnson compares this situation to the climax concept in plant ecology. His studies have put undisturbed arctic lakes systems on the agenda as natural history documents of considerable theoretical interest. Svartvatn supports the Johnson hypothesis that populations of landlocked arctic charr in arctic lakes form dominant modes of large fish that are stable over a long time if undisturbed. The lake is situated within the South-Spitsbergen National Park (CAFF 1994). We hope that the present results will contribute to the establishment of a suitable management regime for the valuable charr population of Svartvatn.

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