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The population, survival, growth, reproduction and food of arctic charr, *Salvelinus alpinus* (L.), in four unexploited lakes in Greenland

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The material comprised 1205 arctic charr caught by gillnets and electrofishing in the ice-free season 1982 in four interconnected lakes. The lakes were similar in biotic and abiotic factors and the arctic charr populations were therefore treated as one population. Two size groups of fish older than three years, called ' small charr ' and ' large charr ', were found. The two groups differed in feeding habits, growth rates, age of maturity and spawning frequencies. However, they did not differ in the frequencies of the F- and S- serum esterase alleles, and were in accord with the model proposed by Johnson (1976) which states that the ' small charr ' and ' large charr ' are two different forms of the same population. 'Small charr ' recruit to the ' large charr ' by entering a period of fast growth. In the investigated lakes this occurred when the ' small charr ' were 3–10 years old. Some indications of rematuration of the ' small charr ' when entering the group of ' large charr ' were found.

I. INTRODUCTION

The arctic charr is the most common freshwater fish in Greenland and occurs both as non-migratory and anadromous populations. While some studies have been done on anadromous populations (Nielsen, 1961; Mortensen, 1982) little is known of the populations resident in lakes in Greenland. Recreational fisheries exploit the populations in some lakes, but most of the lakes are undisturbed by human activities.

II. STUDY AREA

The four unnamed lakes, identified according to their altitude as Lake 306, Lake 318, Lake 332 and Lake 345, are located on the same watercourse in the Iterlaa area in Paamiut/Frederikshåb county (62°15′N, 49°10′W) (Fig. 1). The catchment area is a mountain plateau mostly 300–500 m high except for the last 2 km of the river from Lake 306, where there are several waterfalls of up to 50 m in height. The vegetation is a tundra heath with patches of bare rocks and snow beds are a common feature. The rocks consist of migmatitic gneisses (Rivalenti & Rossi, 1972). The lake basins are regular with narrow littoral zones and steep sublittorals except at the stream inlets where sand and gravel are deposited. The maximum depths of the lakes are 50–100 m. There are scattered submerged patches of vegetation consisting of *Callitriche palustris* L. and the substrate of the littoral is stones, gravel and sand. The surface area of the lakes are from 0·6 to 2·5 km^2 and the catchment is about 70 km^2. Discharge from Lake 306 is 30–40 $Mm^3\ yr^{-1}$. In the lakes, ice breaks up at the end of June and forms again at the end of October. The maximum temperature measured in the lakes was 13·5° C. In the years 1980 and 1982, a

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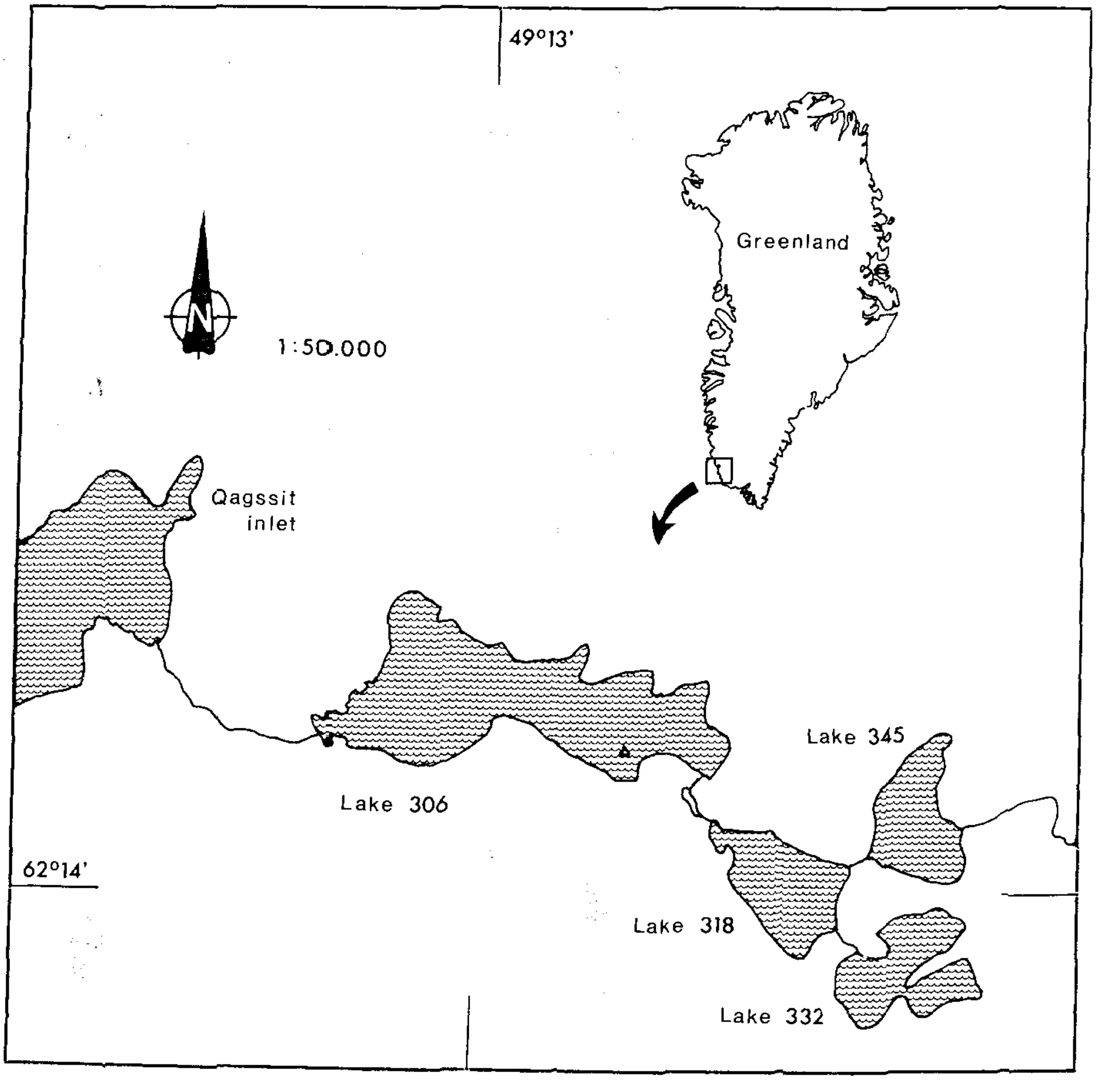

FIG. 1. The geographical situation of the Iterlaa area, southwest Greenland, and the four investigated lakes: Lake 306, Lake 318, Lake 332 and Lake 345.

thermocline at 10–20 m was found. The lake water was poor in electrolytes, with conductivity 9–10 μmho cm^{-1} (at 20° C), and pH was 6·2–6·3. The secchi depth varied from 12 to 18 m.

Dinobryon bavaricum, D. cylindricum, Volvox sp. and *Staurodesmus* cf. *subtriangularis* dominated the phytoplankton. The zooplankton was dominated by *Leptodiaptomus minutus*. However, *Holopedium gibberum, Bosmina coregoni obtusirostis, Cyclops strenuus mediatus* and the rotifera *Asplancna* sp. were frequently observed. The chironomids totally dominated the profundal fauna. The two genera *Heterotrissocladius* (*H. hirtapex, H. oliveri* and *H. changi*) and *Micropsectra* were common. The littoral mainly contained chironomids especially *Heterotrissocladius* sp., *Coryneura* sp., *Pseudosmittia* sp. and *Orthocladius* sp. The Trichoptera *Apatania zonella* and the benthic daphnia *Eurycercus glacialis* were also common. The arctic charr was the only fish present in the lakes.

III. MATERIALS AND METHODS

Gray monofilament gillnets were used for fish sampling. Each net was 96 m long and 1·5 m deep. It was composed of 3 series of 8 subunits each 4 m in length of different mesh sizes in a random order. The mesh sizes (knot to knot) and the thread diameter are shown

TABLE I. The mesh sizes and thread diameters used

mesh size (mm)	10	12·5	16	22	25	30	38	45
diameter (mm)	0·12	0·12	0·15	0·15	0·15	0·17	0·17	0·20

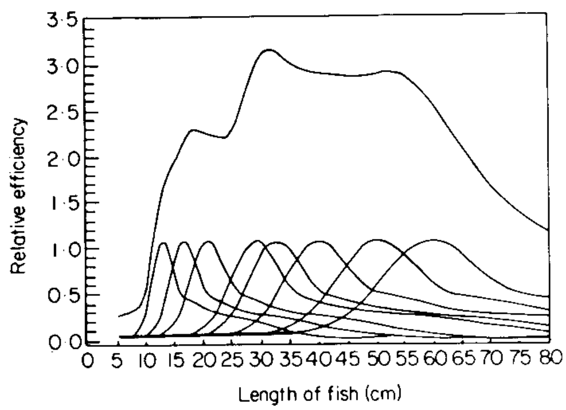

FIG. 2. Gillnet selectivity of each mesh size and of the gillnet as a whole.

in Table I. The total fishing effort with bottom nets was 400 h and with floating nets 150 h. The bottom nets were used only in the littoral from 0 to 20 m depth, except one net which on one occasion was fishing 24 h at 90 m depth. Fishing with floating nets were done at the water surface in the pelagic zone. The gillnets were set day and night from 26 June 1982 to 12 July 1982 and from 28 August 1982 to 9 September 1982. Gillnet selectivity was calculated according to Jensen (1977). The material used consisted of 1166 arctic charr caught in the gillnets during the investigation period. Several mathematical approximations to the gillnet selectivity, S_1, can be used (Hamley, 1975), but a linear combination of a skew normal and a normal distribution fit the data best:

$$s_1 = A_1\left[\frac{1}{\sigma_1\sqrt{2\pi}}e^{-(\ell-m_1)/2\sigma_1^2}.\left\{1-0{\cdot}5\ q\sigma_1^{3/2}\left(\frac{\ell-m_1}{\sigma_1}-\frac{(\ell-m_1)^3}{3\sigma_1^3}\right)\right\}\right]$$

$$+A_2\left[\frac{1}{\sigma_2\sqrt{2\pi}}e^{-(\ell-m_2)/2\sigma_2^2}\right].$$

where ℓ = fish length divided by the modal length of the mesh size of the net in which the fish was caught. This mathematically normalizing procedure brings the selection curves of all 8 mesh sizes together in one curve (Jensen, 1977), to which the formula is an approximation. m_1 = mode of the skew normal distribution, m_2 = mode of the normal distribution, σ_1 = variance of the skew normal distribution, σ_2 = variance of the normal distribution, q = skewness, A_1 = constant and A_2 = constant. The parameters were found by the method of least squares. The selectivity for a given fish of a given mesh size can be derived directly from the formula by inserting the length of the fish divided by the modal length of the mesh size as ℓ. The selectivity of each mesh size and of the whole series of mesh sizes in the gillnets used is shown in Fig. 2. The gillnet did not catch fish shorter than 9 cm. Electrofishing was used to sample smaller fish near the banks; NaCl was added to the water to increase the conductivity of the water. Echo sounder equipment similar to that described by Lindem & Nunnallee (1978) was used to obtain information of the arctic charr in the pelagic zone below a depth of 5 m.

The fish were measured to nearest lower mm, weighed to the nearest g and sexed. In the later sampling period, gonad development was recorded. The fish were classified as mature if they would spawn the same year. The eggs from some mature females were preserved in a modified Gilson's fluid (Bagenal & Braum, 1968) and counted. The diameter of 50 randomly selected eggs from each female were measured to 0·1 mm. Age estimates were obtained from otoliths read in the laboratory in 1–2-propandiol according to Nordeng (1961) and Filipsson (1967).

Plasma esterase gene frequencies of the F- and S- alelles were analysed by electrophoresis according to the method described by Nyman (1967).

The dominant food item in each stomach was noted and some stomachs were preserved in 4% formaldehyde within 3 h after capture and later analysed in the laboratory. The four lakes were similar in both biotioc and abiotic factors and only minor differences in the arctic charr populations were observed. The arctic charr populations were treated as one population.

IV. RESULTS

CATCH AND LENGTH DISTRIBUTION

The mean number of arctic charr caught per net h (C/E number) was 2·32 (S.D. = 1·80). No difference between day and night in C/E was observed (*t*-test, $P = 66\%$). The mean weight of the individuals was 189 g or, if corrected for net selectivity to compensate for the underrepresentation of small charr in the sample, 139 g. The total catch corrected for net selectivity shows a distinctly bimodal length distribution with many small fish ($L = 10–14$ cm), few intermediate fish ($L = 14–26$ cm) and many large fish ($L = 26–38$ cm) (Fig. 3a). The largest fish caught was 61 cm. The arctic charr were not homogeneously distributed within the lakes. Fish of intermediate size ($L = 22–38$ cm) dominated the pelagic zone (Fig. 3b); small arctic charr ($L = 10–14$ cm) and very large arctic charr ($L = 46–61$ cm) were only caught in the littoral (Fig. 3c).

GROWTH

The length distribution of each age class corrected for net selectivity indicated a complex growth pattern with a ramification in two length groups starting in age classes 3+ and 4+ with a few large fish but more obvious in age classes 5+, 6+ and 7+ (Fig. 4). Accordingly, the arctic charr of age 3+ and older are split into ' small charr ' and ' large charr ' by the dividing line shown in the figure. The two growth curves (Fig. 5) have been approximated separately by von Bertalanffy growth curves (Ricker, 1975):

$$\ell_t = L\infty(1 - e^{-K(t - t_o)})$$

where ℓ_t is the length of a fish of age t, $L\infty$ the asymptotic length, K the Brody growth coefficient and t_o the hypothetical age at which the fish would have been zero in length if it had always grown in the manner described by the equation. The parameters are shown in Table II.

MORTALITY

The age distribution of the population was calculated on the basis of the corrected length distribution and the observed age distribution in each length class (Fig. 6a). This was to avoid underestimation of the younger fish due to decreasing net efficiency with decreasing fish length. Only arctic charr older than 2+ were included, as many younger fish were smaller than 9 cm and not caught in the gillnets. Provided that recruitment and mortality is constant every year, the

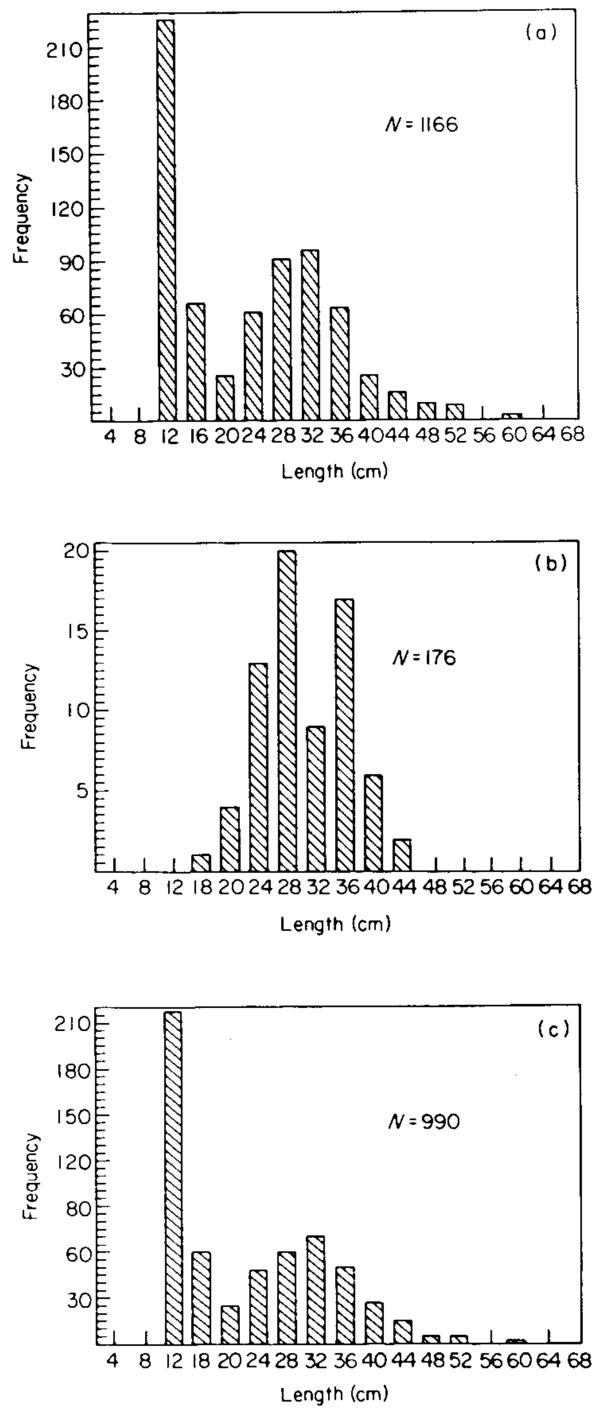

FIG. 3. Catches corrected for net selectivity. Length frequency of (a) total catch, (b) catch in floating nets in the pelagic zone and (c) catch in bottom nets in the littoral and sublittoral zones in Iterlaa, southwest Greenland, 1982. Frequency in an arbitrary scale and all catches are corrected for net selectivity.

mortality of each age class will be reflected in the decrease in number with increasing age. The instantaneous death rate, z, and the survival rate, s, can be calculated according to Ricker (1975):

$$\text{instantaneous death rate } z = (\ln N_o - \ln N)/(t - t_o)$$
$$\text{survival rate } s = e^{-z}$$

where N_o and N are the number of fish at age t_o and t. The mean survival rate from age 3+ to 20+ was 0·77 year^{-1}.

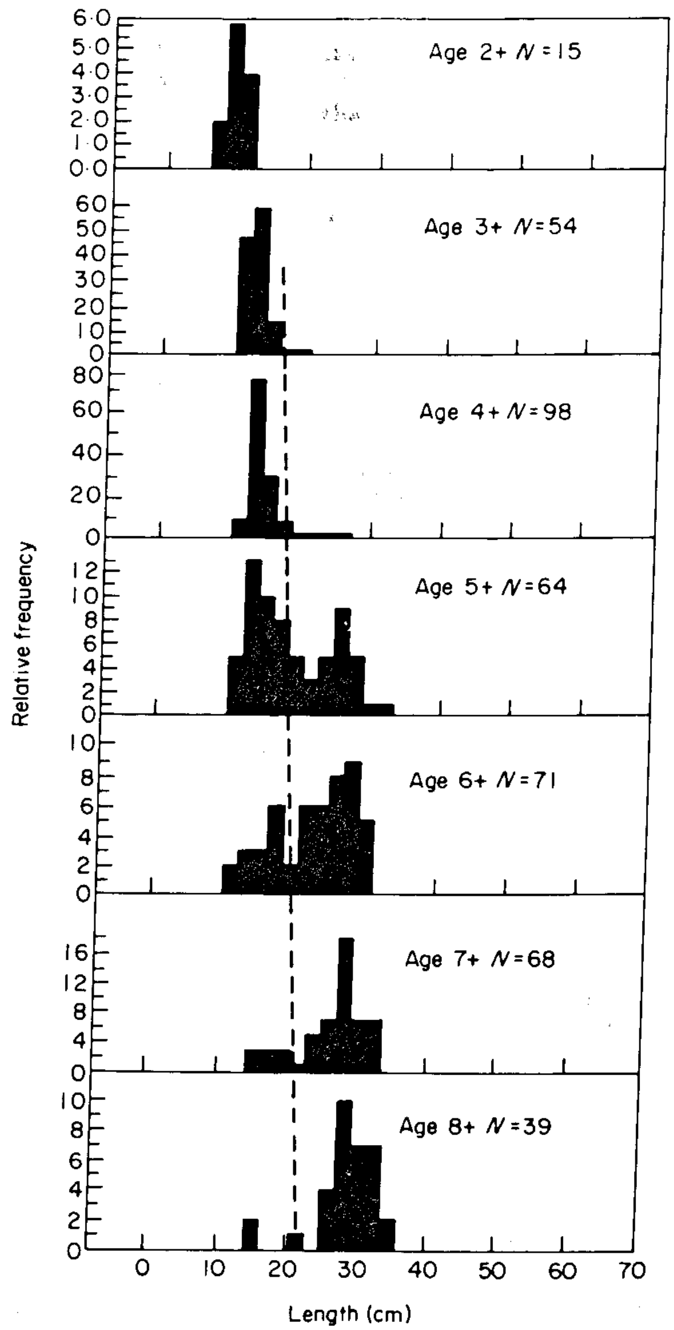

FIG. 4. Length frequency of each age class of arctic charr from age 2+ to age 8+ years. N is the number of specimens aged in each class. The broken line indicate the dividing line used to separate the ' small charr ' and the ' large charr '.

These are natural mortality rates as there is no fishing in the lakes. Splitting the fish into ' small charr ' and ' large charr ' showed that the number of ' small charr ' fell from age 4+ to 10+ while the ' large charr ' increased in number in the same age interval (Fig. 6b).

LENGTH-WEIGHT RELATIONSHIP AND CONDITION

No difference between the two forms of arctic charr in length-weight relationship was found and both forms were therefore treated together. The length–weight relationship was determined by linear regression to be $\log_{10}$ (weight in g) = ($-2{\cdot}04 \pm 0{\cdot}01 + (2{\cdot}89 \pm 0{\cdot}01)$ $\log_{10}$ (length in cm) in June–July and to be $\log_{10}$

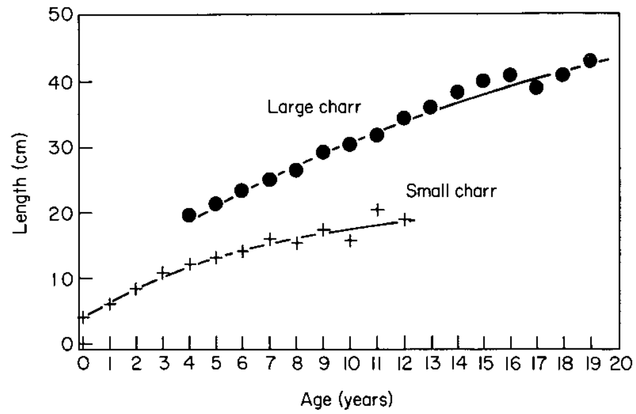

FIG. 5. The mean length of each age class of arctic charr from Iterlaa based on age determination of 576 'large charr' and 286 'small charr'. Von Bertalanffy growth equations have been fitted by the method of least squares to 'large charr' and 'small charr' separately.

TABLE II. The parameters which gave the best approximation by least squares method of the von Bertalanffy growth curves for 'small charr' and 'large charr' respectively from Iterlaa, 1982

	$L\infty$	K	t_o
'small charr'	22·295	0·138	−1·445
'large charr'	61·603	0·055	−2·643

(weight in g)=(−1·88±0·02)+(2·80±0·02) $\log_{10}$ (length in cm) in August–September (±indicates 95% confidence limits). The two lines were significantly different (successive test, variance equal, slopes unequal, P less than 0·1%) with the June–July line lying under the August–September line for L less than 60 cm. The condition thus increased during the summer for fish less than 60 cm, especially for the smallest fish. As the exponent was less than 3 in both periods the condition factor, CF (Ricker 1975), was decreasing with increasing length.

SEX RATIO

The number of males was higher than the number of females in the lakes for both 'small charr' and 'large charr', but the difference was only significant for the 'small charr' (Table III). The arctic charr were split into two groups according to their habits and there was a majority of males among arctic charr in the littoral and sublittoral zones whereas the sex ratio was not significantly different from 1:1 in the pelagic zone.

AGE OF MATURITY

No arctic charr younger than 3+ were mature. Males of the 'small charr' started to mature at age 3+ and females at age 4+ (Fig. 7). The percentage of mature specimens in each age class after these ages averaged 63% for the males and 44% for the females. Males of the 'large charr' started to mature sexually at age 4+ and females at age 9+. The percentage of mature specimens in each age class after these ages was almost constant and averaged 24% for the males and 20% for the females and was significantly different from the values for the 'small

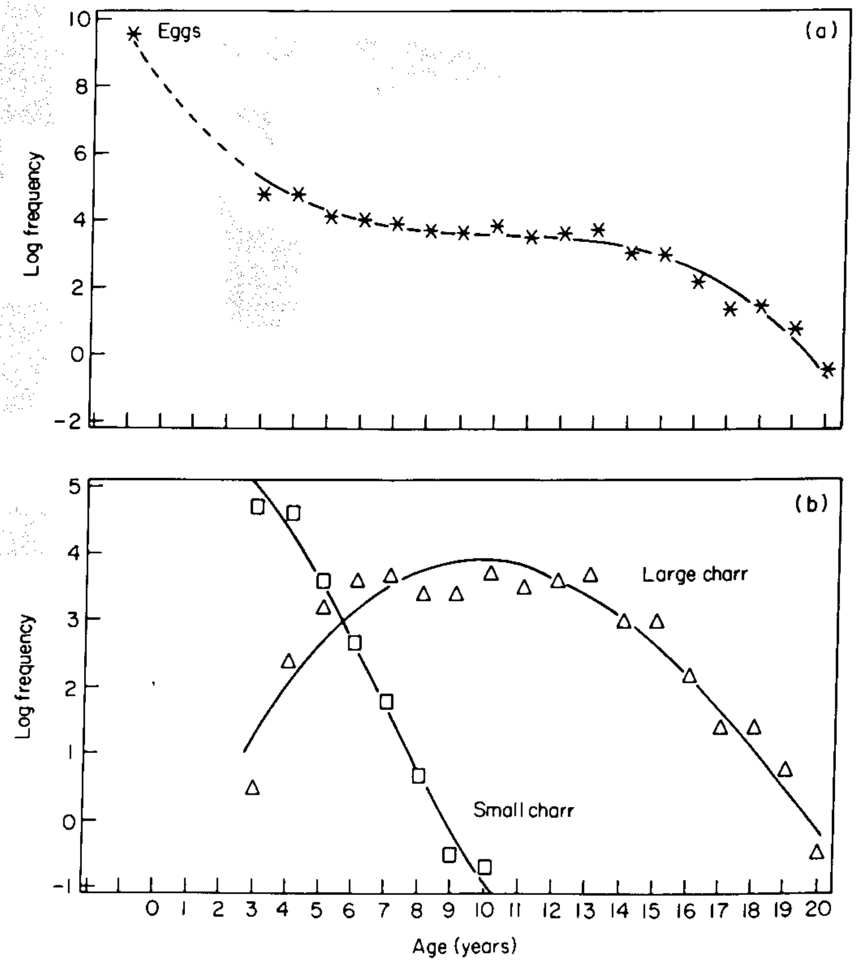

FIG. 6. Survival curves for arctic charr in Iterlaa. In (a) all fish are pooled together and in (b) the 'small charr' and 'large charr' are separated. The curves are approximated by 3 degree polynominals by the method of least squares. Frequency in an arbitrary scale. 'Eggs' represents the number of eggs in prespawning females in the period from 28 August 1982 to 9 September 1982.

TABLE III. Sex distribution of arctic charr from Iterlaa, 1982. A 1:1 distribution is tested by a binomial test

	male	female	male:female significantly different from 1:1
'large charr'	523	470	No (5% < P < 10%)
'small charr'	124	88	Yes (1% < P < 5%)
Charr from the littoral	566	469	Yes (1% < P < 5%)
Charr from the Pelagic zone	81	89	No (50% < P < 60%)

charr' (chi-squared test, P less than 0·1%). Several 'large charr' females classified as immature because of unripe gonads must have spawned previously as they had retained eggs from the last spawning season. It thus seems that at least the 'large charr' do not spawn every season but spend several years between two spawnings.

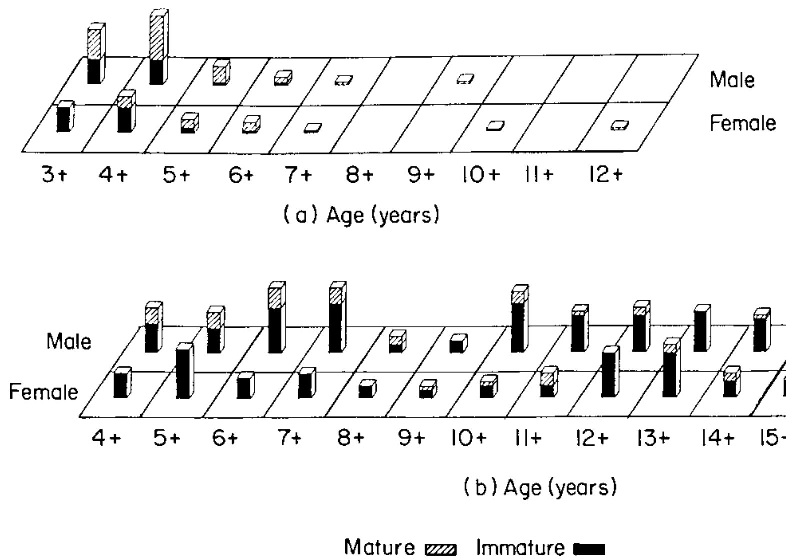

FIG. 7. Sexual maturity vs. age of (a) 'small charr' and (b) 'large charr' from Iterlaa, 28 August–9 September. $N=91$ for 'small charr' and $N=217$ for 'large charr'.

TABLE IV. Fecundity of arctic charr from Iterlaa 28 August–8 September 1982. Calculated constants with 95% confidence limits and correlation coefficients (r) for the equation $\log_{10}$ (number of eggs) $= \log_{10} a + b \log_{10}$(length in cm)

	n	range in cm	$\log_{10} a$	b	r
'small charr'	11	11·6–23·4	$-2{\cdot}42 \pm 0{\cdot}67$	$3{\cdot}67 \pm 1{\cdot}30$	0·87
'large charr'	18	26·2–37·6	$-1{\cdot}13 \pm 0{\cdot}97$	$2{\cdot}52 \pm 0{\cdot}65$	0·87

GONAD WEIGHT, EGG DIAMETER AND FECUNDITY

The gonads from arctic charr caught from 28 August to 8 September 1982 were weighed. Mature males of 'small charr' had gonads weighing 3·2%–12·5% (mean 7·1%) of the total body weight, mature 'small charr' females 3·2%–16·6% (mean 10·1%), mature 'large charr' males 1·3%–4·8% (mean 2·4%) and mature 'large charr' females 3·8%–14·3% (mean 8·4%). The precise spawning time is unknown, but a few 'small charr' and 'large charr' caught in September had running gonads, and the two types of arctic charr are tentatively assumed to spawn at the same time. The mean ovum diameter from 'small charr' females was $3{\cdot}5 \pm 0{\cdot}2$ mm (95% confidence limits, $n=11$) and from 'large charr' females $3{\cdot}6 \pm 0{\cdot}2$ mm (95% confidence limits, $n=18$). No correlation between ovum diameter and length of fish was observed ($r=0{\cdot}22$, $P=26\%$).

The relation between fecundity and length of females was analysed for 'small charr' and 'large charr' females separately by *GM*-regression of the expression $\log_{10}$ (egg number) $= \log_{10} a + b \log_{10}$ (length in cm), where a and b are constants (Table IV).

The absolute number of eggs produced per year could not be calculated, as the absolute number of fish in each age class was unknown. However, a relative number of eggs in each age class could be calculated as the following facts are known.

TABLE V. The distribution of arctic charr from Iterlaa according to dominating food item, and this item's volume percent of total stomach content

Food item	Volume of total stomach content (%)						No. of charr
	100–90	89–80	79–70	69–60	59–50	49–0	
Zooplankton	7	1	1				9
Eurycercus glacialis		1					1
Chironomidae larvae	4	3		1	1		9
Chironomidae pupae	26	2			1		29
Trichoptera larvae					1		1
Coleoptera	2	1					3
Terrestrial insects	1		1				2
Pisidium sp.					1		1
Total	40	8	2	1	4	0	55

The relationship between the length of the mature females and the number of eggs (Table IV).

The percentage of mature females in each age class (Fig. 7).

The relationship between length and age.

The relative age distribution (Fig. 6b).

The relative number of eggs produced per year was calculated separately for 'small charr' and 'large charr'. The number of eggs produced was approximately 130 times the number of fish of age 3+ (Fig. 6a).

FOOD

All of the 55 stomachs analysed in the laboratory from arctic charr caught between 1 July and 7 September were at least half full. In 40 stomachs, the volume of the dominant food item was greater than 90% of the total stomach content and it was not less than 50% in any fish (Table V). The arctic charr in Iterlaa, thus, seem highly selective in their food choice. From 26 June to 6 July, the dominant food item was chironomid larvae and pupae in all length groups of arctic charr and very few stomachs were empty (Table VI). In the following week, 8–13 July, chironomid larvae and pupae were still important but zooplankton was also often dominant, especially in fish of intermediate size ($L=15$–35 cm). Moreover, Trichoptera and terrestrial insects dominated in several stomachs and cannibalism became more common, especially in the very large fish ($L=40$–61 cm). Few stomachs were empty. In the late summer, 30 August–5 September, chironomids were less important and Crustacea were the main food item, except in the very small fish ($L=4$–10 cm) where chironomids and Crustacea (Daphniidae and Ostracoda from the littoral zone) were equally common. Fish of intermediate size ($L=15$–35 cm) had ingested the large benthic Daphnia *Eurycercus glacialis* from the littoral and sublittoral zones and planktonic Copepoda. Among the large fish ($L=40$–61 cm) cannibalism was, at this time, common. The frequency of empty stomachs was significantly higher than in the two previous periods (chi-squared test, P less than 0·1%). Of the mature fish, 51% ($n=100$) had empty stomachs in this period while the frequency of empty stomachs in the immature fish was 9% ($n=264$), i.e. nearly the same as in the two previous periods.

PRODUCTION/BIOMASS RATIO

In the present investigation it was not possible to estimate population size, absolute production (P) and biomass (B) of the arctic charr population. However, their relation, i.e. the P/B ratio could be calculated applying the principles of Allan's graphical method (Chapmann 1968) using relative numbers instead of absolute numbers and based on estimated mortality rates and age-weight relationship for fish older than age 2+. The assumptions are as follows.

All deaths from one age to the next happen when the weight of the fish is the mean of the weight of the two age classes.

All 'small charr' and all 'large charr' of the same age have the same weight.

Fifty percent of the 'small charr' females and 67% of the 'small charr' males spawn in a given year and they become mature at age 4+ and 3+; 20% of the 'large charr' females and 25% of the 'large charr' males spawn in a given year and they become mature at age 9+ and 4+.

The production of eggs is 8% of the body weight of females and the production of sperm is 4% of the body weight of males.

The P/B ratio of 'small charr' was 0·34 per year (Table VII) and of 'large charr' 0·20 per year and for the population as a whole 0·21 per year.

GENOTYPES

Table VIII shows the serum esterase allele frequencies observed. The two forms of arctic charr have the same allele combination (chi-squared test, $P=26\%$) and the combination of each of the two forms and their common allele combination all conform to the Hardy-Weinberg equilibrium. In the total population the frequency of the F-allele was 0·46.

V. DISCUSSION

The arctic charr population in the lakes is assumed to consist of many small fish ($L<14$ cm), few of intermediate size ($L=14$–26 cm) and many large fish ($L=38$–61 cm). The only possible sampling bias that could explain this bimodal length distribution of the total catch (Fig. 3) seems to be that the 'missing' fish of intermediate size ($L=14$–26 cm) might concentrate in the pelagic zone more than 1·5 m below the water surface, where no fishing was done. However, the echo-sounding survey in September did not show fish in the zone from 5 m below the surface to the bottom, when the catches simultaneously in the littoral exhibited the mentioned bimodal pattern. Similar length distributions have been observed in landlocked arctic charr populations in Scandinavia and on Jan Mayen (Klemetsen *et al.*, 1972; Skreslet, 1973), in Canada (Hunter, 1970) and in several lake trout and whitefish populations in arctic Canada (Johnson, 1976; Power, 1978).

The bimodal length distribution in age classes 5+, 6+ and 7+ implies a complex growth pattern where part of the population consists of small and slow growing fishes, while the rest are large and fast growing. Alternatively, it may be

Table VI. The dominant food item in arctic charr from Iterlaa, by percent in three periods: 26 June–6 July (I), 8 July–13 July (II) and 30 August–5 September (III) 1982. The empty positions represent 0% and '—' indicates no fish in the period of the given size

		Fish length (cm) 0–4·9	5–9·9	10–14·5	15–19·9	20–24·9	25–29·9	30–34·9	35–39·9	40–44·9	45–
zooplankton	I	—	—			8	6	9			—
	II	—	—	8	16	26	30	16	5		
	III			8	14	37	56	58	30		
Eurycercus glacialis	I	—	—								—
	II	—	—								
	III			35	36	21	21	11			
Crustacea (littoral)	I	—	—								—
	II	—	—								
	III	35	45								
Chironomidae (larvae)	I	—	—	38	50	28	45	73	100		—
	II	—	—	50	32	26	30	32	26	14	
	III	6		9	7	5			10		
Chironomidae (pupae)	I	—	—	23	50	32	21	5			—
	II	—	—	15	26	24	14	23	32	43	
	III	59	41				2	2			
Trichoptera (larvae)	I	—	—								—
	II	—	—	8	11			1	5		
	III			1	3						

Tirchoptera (pupae)	I	—	—								—	
	II	—	—	5		6	9	9	11			
	III											
terrestical insects	I	—	—							—		
	II	—	—		5	18	10	1				
	III		9									
arctic charr	I	—	—					5			—	
	II	—	—		5		4	7	5	29	33	
	III							7	20	50	33	
other	I	—	—							100	—	
	II	—	—							7		
	III			2								
indeterminable	I	—	—	38		32	21	5			—	
	II	—	—	13	5			4	5			
	III			16	18		2		10			
empty	I	—	—				6	5			—	
	II	—	—	3			4	6	11	7	67	
	III		5	26	21	37	19	24	30	30	67	
Total of percentages	I	—	—	99	100	100	99	102	100	100	—	
	II	—	—	102	100	100	101	99	100	100	100	
	III	100	100	97	99	100	100	102	100	100	100	
number of stomachs	I	0	0	13	2	25	33	22	8	1	0	$\Sigma = 104$
	II	0	0	40	19	34	80	69	19	14	6	$\Sigma = 281$
	III	17	22	85	28	19	43	45	100	2	3	$\Sigma = 365$

TABLE VII. Estimation of the P/B-ratio for ‘small charr’ and ‘large charr’ from Iterlaa. The number of ‘small charr’ of age 3+ is arbitrarily set to 1000 and the number of each age class is expressed relative to this

Age	Relative number of fish	a = number at age $n+\frac{1}{2}$	w = mean weight at age $n+\frac{1}{2}$	Biomass (B)	Δw from age $(n-1)+$ to $n+$	Production		
						$a \cdot \Delta w$	Eggs	Sperm
‘small charr’								
3+	1000	853	12·1	10,236	5·5	692	150·5	112·9
4+	705	528	17·0	8976	4·7	482	122·9	92·2
5+	350	240	22·0	5280	5·3	272	71·1	53·4
6+	129	87	27·1	2358	4·9	426	30·9	23·2
7+	45	30	32·4	972	5·6	168	12·7	9·5
8+	15	11	38·0	418	5·6	62	5·4	4·0
9+	6	5	42·8	214	4·0	20	2·7	2·0
10+	4	3	46·2	139	2·8	8	1·7	113
11+	2	2	48·3	97	1·5	3	1·2	0·9
12+	1							
Total				28,690		9133	399·1	299·4
				P/B = (9133 + 399·1 + 299·4)/28,690 = 0·34				
‘large charr’								
3+	31	33*	30·5	946	16·1	1770		15
4+	64	52*	45·3	2899	13·6	3580		18
5+	116	76*	62·3	7227	20·4	7876		42
6+	192	95*	84·5	16,224	23·9	13,747		83
7+	287	53*	110·6	31,742	28·4	14,765		131
8+	350	57*	139·2	48,720	28·8	18,835	375	188
9+	407	20*	167·0	67,969	32·7	17,035	477	239
10+	427	407	201·9	82,173	31·2	12,698	505	253
11+	387	360	234·7	84,492	34·3	11,422	503	252
12+	333	296	269·5	79,772	35·4	9169	446	223
13+	259	217	303·9	65,946	33·8	5881	335	167
14+	174	145	338·6	49,097	35·9	4164	248	124
15+	116	94	374·3	35,184	35·6	2528	167	84
16+	71	56	408·1	22,854	31·9	1308	104	52
17+	41	31	433·0	13,423	18·0	378	56	28
18+	21	16	451·3	7221	17·4	191	30	15
19+	11	9	468·5	4217	15·8	95	17	9
20+	6							
Total				620,106		118,116	3263	1923
				P/B = (118116 + 3263 + 1923)/620106 = 0·20				

*It is assumed that all fish in the age class survive and that the recruited fish come from the ‘small charr’.

explained by the co-existence of two separate fish populations with separate growth characteristics. According to Nyman (1972), at least three sibling species of arctic charr within the *Salvelinus alpinus* (L) complex can be distinguished in Scandinavia. In numerous lakes these sibling species live sympatrically (Nyman *et al.*, 1981). Two of these are generally dwarves with a littoral or benthic way of

TABLE VIII. Observed genotype distribution and calculated frequencies of serum esterase in Iterlaa arctic charr. F=' fast' allele, S=' slow' allele (Nyman 1972). The last two columns give the chi-square deviation and the P values between observed genotype distribution and the Hardy-Weinberg equilibrium

	Observed genotypes			allele freq. of F	95% conf. int. of F-freq.	χ^2 deviation	P(%)
	FF	FS	SS				
' small charr '	4	14	7	0·44	0·14	0·324	85
' large charr '	22	51	29	0·47	0·07	0·017	99
Total	26	65	36	0·46	0·06	0·115	94

life, whereas the ' normal ' charr is more pelagic. They differ in frequencies of the F-allele as well as in growth, food habits, spawning time, spawning frequency, age of maturation etc. (Nilsson & Filipsson, 1971; Klemetsen *et al.*, 1972). Several of these differences were observed for the two groups of arctic charr in Iterlaa. The ' small charr ' were exclusively littoral or benthic and only ' large charr ' were pelagic (Fig. 4). This was also reflected in the food habits in the summer where the ' small charr ' were feeding on chironomid larvae and littoral Crustacea while the ' large charr ' mainly consumed zooplankton, chironomid pupae and terrestrial insects. Spawning frequency and age of maturation were markedly different, frequency of mature ' small charr ' was twice as high as of the ' large charr ' and they were sexually mature one to several years before the ' large charr '. Nevertheless, the method outlined by Nyman & Filipsson (1972) to determine if more than one species of arctic charr inhabits a lake did not reveal difference between the two groups as their F-allele frequencies were identical. This does not disprove the existence of two populations and a straightforward explanation could be that the mature ' small charr ' belong to one population and the immature ' small charr ' are juveniles of another population including the ' large charr '. The relative gonad weights and the frequency of spawning suggest that the ' small charr ' have relatively higher reproductive investments than the ' large charr ' and this could be reflected in different growth and survival patterns. However, no difference in age/length relationship between mature and immature fish was observed and both groups showed the same ramification in two length groups. Furthermore, if the ' small charr ' and the ' large charr ' are separate populations where immature ' small charr ' are juveniles of the ' large charr ', the number of juveniles appears to be low for sustaining the population of ' large charr '. A death rate of almost zero from age 3+ to age 13+ is a consequence, and this seems unrealistic. Furthermore, the survival curve (Fig. 6b) of the ' small charr ' and ' large charr ' indicated recruitment to the ' large charr ' from the ' small charr ' at age 3+ to 10+. Thus, it seems that there are indications for assuming that all arctic charr in Iterlaa belong to the same population.

The population model proposed by Johnson (1976, 1983) seems to explain the complex growth pattern. Johnson claims that the group of ' large charr ' exerts a pressure on the ' small charr ' and only allows them to pass through the ' filter ' or suppressive mechanism as mortality in the 'large charr' reduces the pressure on the 'small charr'. The 'small charr' passing through the filter grow quickly in the first 1–3 years and become members of the group of 'large charr'. The length distributions of the age classes indicate that the youngest 'small charr' pass through the filter at age 4+, and that recruitment reaches a peak at age 5+, 6+ and 7+ years. At higher age classes, the recruitment must be small as few 'small charr' of these ages were caught. The way in which this suppressive mechanism is exerted could be through predation or through behavioural exclusion from the pelagic zone and the zooplankton food resource.

The fact that most of the 'small charr' had ripe gonads while most of the large charr were immature might be explained by a shift from a reproductive period to a growth period when the 'small charr' are recruited to the group of 'large charr'. Such shifts were reported by Skreslet (1973) for arctic charr in Lake Nordlaguna, Jan Mayen, where he could distinguish between growth zones and spawning zones in the otolith annuli. Likewise, Nordeng (1983) showed from rearing experiments that dwarf, normal and large charr can exist in one population and that dwarves can shift to normal forms and normal forms to large forms.

The growth and size of the juvenile arctic charr from age 0+ to age 3+ and of 'small charr' from age 3+ to age 12+ are like those found by Skreslet (1973) for mature small arctic charr and a little less than those found for small arctic charr by Klemetsen & Grotnes (1980) in Lake Båtsvatn, in which the sizes of age 0+, 1+ and 2+ are probably overestimated, as fish less than 9 cm cannot be caught in the gillnets used. Both Lake Nordlaguna and Lake Båtsvatn experience similar climatic condition as the Iterlaa lakes. Comparison of age classes 0+, 1+, 2+ and 3+ with juveniles of anadromous populations of arctic charr in Greenland shows a growth rate and size equal to the more slow growing populations (Nielsen, 1961; Mortensen, 1982).

The growth rate and size of 'large charr' are a little less than those found in normal arctic charr in Lake Båtsvatn but a little greater than those found in Keyhole Lake in arctic Canada (Hunter, 1970) where only one arctic charr form is described. It can, be stated that the growth rate and size of arctic charr from Iterlaa are roughly similar to arctic charr from lakes in Scandinavia and arctic Canada in the same climatic conditions.

The condition of the 'small charr' was similar to the small charr from Lake Nordlaguna. However, contrary to the response of this population, the condition of Iterlaa arctic charr decreases with increasing length. In lakes in arctic Canada both increasing (Hunter, 1970) and decreasing condition (Furniss, 1974; McCart *et al.*, 1972; Craig, 1977) with increasing length are seen. The condition was improved during the summer, more for the 'small charr' than the 'large charr'. The condition must decrease correspondingly through the winter, probably because of the loss of spawning products and reduced food intake during the winter.

In early summer the small ($L<15$ cm), intermediate ($L=15$–30 cm) and large arctic charr ($L>35$ cm) occupy roughly the same food niche. During the midsummer, there is an increasing segregation and in the autumn they occupy three clearly different food niches consisting of benthic macroinvertebrates, zooplankton and fish. Similarly Nilsson (1955) found that arctic charr and trout became progressively more segregated into different food niches during the ice-free season, and Henricson & Nyman (1976) observed the same pattern between two sibling species of arctic charr in Lake Fättjaure. The high frequency of empty stomachs among mature arctic charr in autumn compares with anadromous arctic charr which are known not to eat prior to spawning (Sparholt, 1983; Hansen, 1983).

The production/biomass ratio was 0·21 year^{-1} for the population of fish older than 2+ years. Hunter (1970) estimated a mean stock of 1302 kg of arctic charr in Keyhole Lake with a stabilised fishing mortality at 0·64 year^{-1} and a yield at 299 kg. This corresponds to a P/B ratio of 0·23 year^{-1}. Compared with P/B ratios in temperate lakes of 0·5 year^{-1} (Winberg *et al.*, 1975) this low ratio for arctic charr reveals a different population structure with a low production and a high standing stock.

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