Evidence of trophic polymorphism in Lake Randsfjorden, Norway? Analyses of morphology, stable isotopes and mercury concentrations in Arctic charr (*Salvelinus alpinus*).

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II. Abstract

A study of the Arctic charr (*Salvelinus alpinus*) in Lake Randsfjorden was performed to determine if two or more morphs are present. The analysis of 12 size corrected morphological measures showed that there were no significant differences between charr with subterminal (SUB) and terminal (TERM) mouth positions, a conspicuous character used to group the fish before succeeding analyses. However, significant morphological differences between the genders, independent of their mouth position, demonstrated sexual dimorphism. Size-at-age, mercury (Hg) concentrations and the large spread in size within each year class of sexually mature individuals expressed charr with different growth rates. Stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$), stomach contents and mercury concentrations revealed that all the analysed charr were piscivorous. Evidence of cannibalism was not found in the analysed material. A negative correlation between $\delta^{13}C$ and age, length and weight suggests that SUB individuals undergo a niche shift from bentic to pelagic environments. There were no significant differences in $\delta^{15}N$ and $\delta^{13}C$ between SUB and TERM charr. This, in combination with the niche shift in the SUB individuals, indicates that lower growth rate in the SUB charr is caused by lower food availability.

III. Sammendrag

En undersøkelse av røye (*Alpinus salvelinus*) i Randsfjorden ble gjennomført for å stadfeste tilstedeværelsen av to eller flere morfer. Røyenes munnstilling ble benyttet til å dele materialet inn i to grupper før videre undersøkelser fant sted. Analysen av 12 morfologiske mål justert for lengde viste at det ikke var morfologiske forskjeller mellom røyer med overbitt (SUB) og underbitt (TERM). Det ble funnet signifikante morfologiske forskjeller mellom hunner og hanner uavhengig av munnstilling, en indikasjon på kjønnsdimorfi. Størrelse ved alder, kvikksølvkonsentrasjoner og stor spredning i størrelse innefor hver årsklasse av kjønnsmoden røye viste at det er forskjeller i vekstrate i populasjonen. Analyser av stabile isotoper ($\delta^{15}N$ og $\delta^{13}C$), mageinnhold og Hg-konsentrasjoner viste at de analyserte røyene var fiskespisere. Det ble ikke påvist kannibalisme i det undersøkte materialet. Negativ korrelasjon mellom $\delta^{13}C$ og alder, lengde og vekt kan indikere at SUB røye foretar et nisjeskift fra bentiske til pelagiske områder. Det ble ikke påvist forskjeller i $\delta^{15}N$ og $\delta^{13}C$ mellom SUB og TERM røye. Dette kan, i kombinasjon med nisjeskiftet hos SUB røye, indikere at den lavere vekstraten hos SUB røye skyldes dårligere næringstilgang.

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Introduction

The Arctic charr (*Salvelinus alpinus*) is a species that shows considerable morphological variation within and among locations throughout its circumpolar distribution (Hindar & Jonsson 1982; Riget *et al.* 1986; Walker *et al.* 1988; Snorrason *et al.* 1994; Alekseyev *et al.* 2002; Guiguer *et al.* 2002). Several characters have been studied to distinguish sympatric morphs, such as differences in external colouration, flesh colour, morphological traits, body size and age at sexual maturity, feeding ecology, parasitic fauna, habitat use, segregation in spawning time and localities (Jonsson & Jonsson 2001). As many as four sympatric morphs have been described (Sandlund *et al.* 1992), but Arctic charr usually exhibits two morphs when distinct forms coexist. One morph that occupies the epibenthic zone and feeds on zoobenthos and one morph that reaches a larger size and utilizes the limnetic zone, commonly referred to as dwarf and normal charr, respectively (Hindar & Jonsson 1982). Allopatric and sympatric speciation, genetic inertia, piscivory, inter- and intraspecific competition and alternative life styles are all hypotheses that have been proposed to explain such bimodality (Griffiths 1994). Consequently, the phenotypic differences are induced both genetically and environmentally, but the relative emphasis seemingly differs between studied cases (Skulason & Smith 1995).

Trophic polymorphism is the occurrence of discrete intraspecific morphs showing differential niche use, usually through differences in feeding biology and habitat use (Skulason & Smith 1995). Trophic polymorphism in Arctic charr has been demonstrated in several Norwegian lakes (Hindar & Jonsson 1982; Nordeng 1983; Knudsen *et al.* 1997; Telnes & Saegrov 2004), but not in Lake Randsfjorden. Local anglers have reported two morphological distinct forms of Arctic charr, one large form with silvery sides and orange flesh colour and another small form with black head and white coloured flesh. Analysis of morphological measures can establish if statistically significant differences between two or more morphs exist. However, such data do not establish the ecological basis for the differences. Assumptions of the ecological basis can be made by analysis of stomach content, but it provides limited information of the material actually assimilated by an organism over time (Vander Zanden *et al.* 1997). Measurement of naturally occurring stable isotopes of nitrogen (^{15}N) and carbon (^{13}C) can overcome this problem. The ratio of stable isotopes of nitrogen (^{15}N / ^{14}N; $\delta^{15}N$) can be used to estimate trophic position because the $\delta^{15}N$ signature of a consumer is typically enriched by 3-4‰-points relative to its diet (Vander Zanden *et al.* 1999). The ratio of carbon

isotopes ($^{13}C/^{12}C;\delta^{13}C$) changes little between trophic levels, and can be used as an indicator of sources of primary production (Hobson & Welch 1995). By the application of $\delta^{13}C$ signatures, it is possible to distinguish between two major sources of available energy in lentic environments. Littoral detritus and primary producers tend to be more enriched in ^{13}C relative to the pelagic phytoplankton (Post 2002). The measurement of nitrogen and carbon isotopes combined with conventional dietary analysis can reveal different feeding ecology within polymorphic Arctic charr populations that would be difficult to obtain if only one of the methods was used (Hobson & Welch 1995; Guiguer *et al.* 2002; Power *et al.* 2005).

The aim of this investigation was to study the possible existence of trophic polymorphism within the Arctic charr population of Lake Randsfjorden. The study therefore stated the hypothesis that two or more discrete morphs of charr occurred. The predictions arising from the hypothesis were that (a) morphological traits must show significant differences among the morphs and (b) the distinct morphs exhibit different feeding ecology. The predictions were tested by analyses of morphological characters, stomach contents, mercury concentrations and stable isotopes.

Materials and methods

Study area

Lake Randsfjorden, 135 m a.s.l. and 140 km^2, is located in Oppland County in the south eastern part of Norway (60^{o}25´N; 10^{o}24´E) (Fig. 1).

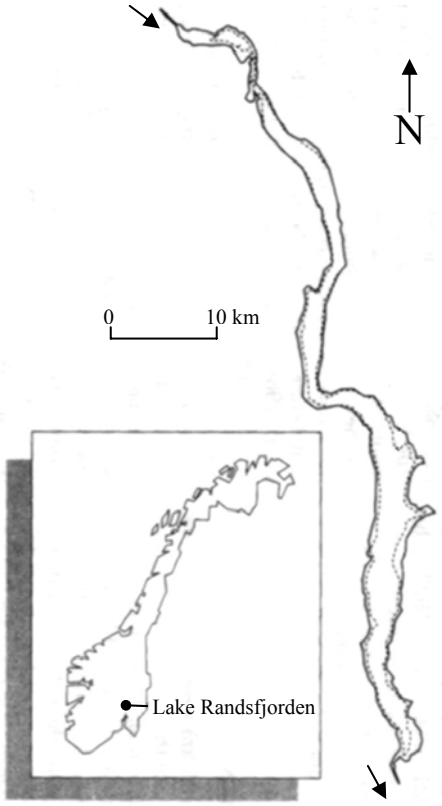


Fig. 1: *The location of Lake Randsfjorden with arrows indicating main inlet (north) and outlet (south).*

The glacial fjord-like lake has a maximum depth of 131 m (anonymous 2006), the mean depth being 44 m, and with a catchment area of 3665 km^2 (Løvik *et al.* 2005). A shallower northern basin, Flubergfjorden, is partly divided from the main basin by a sill (Styrvold *et al.* 1981). Randsfjorden Lake was last regulated in 1951, and the regulation height was set to 3.2 m (Styrvold *et al.* 1981). The lake is oligotrophic (Løvik & Andersen 2000; Løvik *et al.* 2005), and receives water mainly from Etna and Dokka rivers in the north, Lomdalselva and Vigga rivers from the west and east, respectively. The lake drains south into Lake Tyrifjorden through Randselva River, and further through Drammenselva River to the Drammen Fjord. The fish fauna comprises European whitefish (*Coregonus lavaretus*), Arctic charr (*Salvelinus alpinus*), brown trout (*Salmo trutta*), pike (*Esox lucius*), perch (*Perca fluviatilis*), three-spined

stickleback (*Gasterosteus aculeatus*), nine-spined stickleback (*Pungitius pungitius*), European smelt (*Osmerus eperlanus*), European minnow (*Phoxinus phoxinus*) and lamprey (*Lampetra sp.*) (Styrvold et al. 1981).

Fish sampling and handling

In July and August 2004 and 2005, local anglers obtained the 55 Arctic charr used in this study, which in 10 were immature. The charr were mainly caught by trolling assorted lures 14-25 m below the surface of water, and to some extent by gill netting (N=3). In addition, data (age, length, weight) from another 13 mature charr caught during 2004 were provided by Rustadbakken. The fish were killed by a blow to the head. The anglers noted the date, depth, position and fishing method for each Arctic charr they caught, and all fish were packed in separate plastic bags and frozen as soon as possible.

In the laboratory, Arctic charr were defrosted overnight. Three photographs were taken of each fish using a digital camera (Canon 350D). Two photographs portrayed the left side, one close-up of the head and one constituting the whole fish, and one the ventral side. Each charr were weighed (g) and fork length measured (nearest mm), and their sex and maturity status (I-VII/II) were determined. Weigth(W)-length(L) relationships were estimated from wet weights (g) and fork lengths (mm) by a quadratic regression model: $W=(bL+c)L+a$.

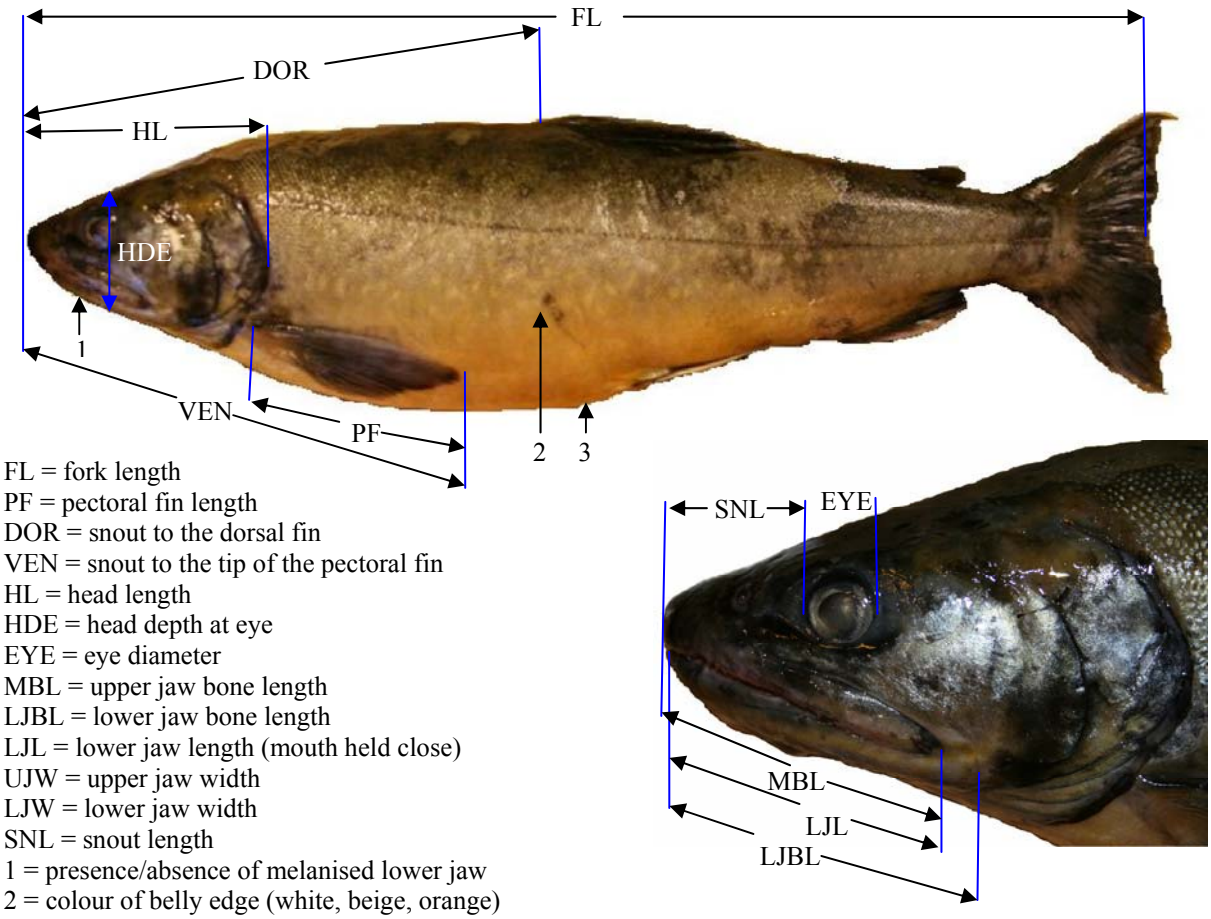
Otholiths were removed for age determination and read using a stereoscopic magnifier (Leica MS 5). The otholiths were read whole when possible, or after they had been divided and burnt, according to the methods described in Borgstrøm (2000). Stomach contents were removed, placed in separate plastic bags, and frozen before diet analysis was conducted. The thawed stomach contents were analysed in the laboratory. Prey-fish were identified to the level of species, weighed (g) and fork length measured (nearest mm) if the state of digestion allowed. Other prey items were identified to the level of order (Trichoptera and Ephemeroptera) or family (Chironomidae). Prey occurrence was determined by recording prey presence/absence for each individual charr, allowing a pattern of percent occurrence to be constructed (Hyslop 1980).

Morphological measures

The charr showed apparent differences in colouration and mouth positions. Some charr had melanised lower jaws and a tendency towards subterminal mouth positions (i.e. short lower jaw) (SUB), while others had white lower jaws and more terminal mouth positions (i.e. long lower jaw) (TERM) (Fig. 2).

Fig. 2: *An Arctic charr (Salvelinus alpinus) with subterminal mouth position and melanised lower jaw (left), and a charr with terminal mouth position and white lower jaw (right) (Photo: G. Engdahl).*

Although the differences seemed to be continuous, the charr were grouped for subsequent analyses based on their mouth positions. Patterns of colouration were recorded, including flesh colouration (white, orange), and twelve morphometric traits, known to define polymorphism in some Arctic charr populations (Sandlund *et al.* 1992; Adams *et al.* 1998; Fraser *et al.* 1998; Alexander & Adams 2004), were measured (nearest mm) using a calliper (fig 3).



FL = fork length
PF = pectoral fin length
DOR = snout to the dorsal fin
VEN = snout to the tip of the pectoral fin
HL = head length
HDE = head depth at eye
EYE = eye diameter
MBL = upper jaw bone length
LJBL = lower jaw bone length
LJL = lower jaw length (mouth held close)
UJW = upper jaw width
LJW = lower jaw width
SNL = snout length
1 = presence/absence of melanised lower jaw
2 = colour of belly edge (white, beige, orange)
3 = colour of belly (white, beige, orange)

Fig. 3: *Colouration and the morphological traits that were measured. UJW and LJW (not shown) were measured at the widest part of the jaws (Photo: G. Engdahl).*

Prior to comparative analyses of the morphological traits, the measures had to be standardised for size (fork length), using the equation of Senar *et al.* (1994):

$$Y'_i = \log_{10}Y_i - b(\log_{10}L_i - \log_{10}L)$$

L_i= fork length for fish *i* (mm)

L= mean fork length (mm) for all sexually mature Arctic charr

Y'_i= size-corrected morphometric variable value for fish *i*

Y_i= the uncorrected variable value for fish *i* (mm)

b= the pooled regression coefficient of $\log_{10}Y$ on $\log_{10}L$ for all sexually mature Arctic charr combined

The standardised measures were controlled by ensuring that they were not correlated with fork length. Morphological comparisons were conducted on sexually mature fish only (n=45, stadium III or higher) based on the possibility of different allometric relationships between young and mature fish in the population (Sandlund *et al.* 1992).

Mercury and stable isotope analyses

To obtain the muscle tissue needed for mercury and stable isotope analyses, the dorsal skin on the left side of the charr was removed, exposing the axial muscle from the area above the lateral line and between the dorsal and adipose fin (Rosseland *et al.* 2002). The darker, superficial muscle layer was removed by scraping with a scalpel. About 5 g (wet weight) of muscle tissue for analyse of mercury was taken out from the distant exposed area and put into a white scintillation tube. Approximately 1 g (wet weight) of the dorsal muscle tissue posterior to the dorsal fin was obtained for stable isotope analysis, and put on top of the tissue sample for mercury. In cases where small charr did not provide the right amount of muscle tissue needed, muscle from the same area on the opposite side were added. The samples from each charr were frozen immediately after they were obtained. Scalpel blades were changed and the instruments used for dissection were thoroughly cleaned in ethanol between each dissection.

Thirty Arctic charr were selected for mercury analysis based on size and age. In addition to the largest and oldest fish, the heaviest and lightest individual in each year class were chosen. The remaining selection was spread equally on SUB and TERM individuals. The charr analysed for mercury were also analysed for stable isotopes. In addition, 10 individuals with subterminal mouth positions were analysed because of a misunderstanding at the laboratory. The mercury and stable isotope analyses were conducted at the Isotope Laboratory, Norwegian University of Life Sciences.

Statistical analyses

All data were controlled prior to further analyses by the Anderson-Darling test to meet the assumption of normality required for parametric tests. To test for association between groups and morphological traits, a chi-square test was used. A two-tailed t-test or a Mann-Whitney U-test was used when two groups were compared. One-way analysis of variance (ANOVA) with Tukey´s comparison method or the Kruskal-Wallis test was used when more than two groups were compared. To assess trends in the material or within a group, regression analysis

or Spearman rank correlation was applied. The significant level was set to ≤ 0.05 for all statistical tests. All data were analysed using MINITAB® Release 14 statistical software, except Spearman rank correlation, which was made available through VassarStats.

Results

The size-frequency distribution of the 68 Arctic charr did not reveal any bimodality. However, a majority of the fish had fork lengths between 19 and 45 cm (Fig. 4).

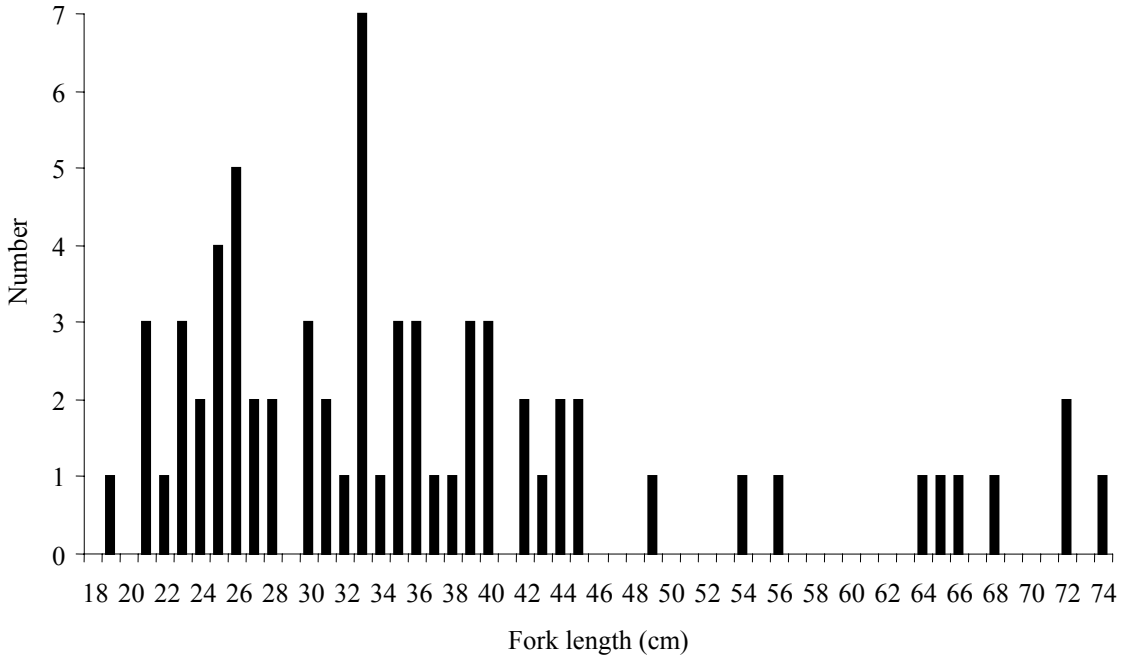


Fig. 4: *Fork length (cm) frequency of 68 Arctic charr (Salvelinus alpinus) from Lake Randsfjorden 2004 and 2005. Fifty-five charr were collected for this study. In addition, Rustadbakken provided data from another 13.*

This material, derived from 68 Arctic charr, ranging in size from 73 to 6000 g wet weight and from 192 to 735 mm in fork length, exhibited a typical weight-length relationship (Fig. 5).

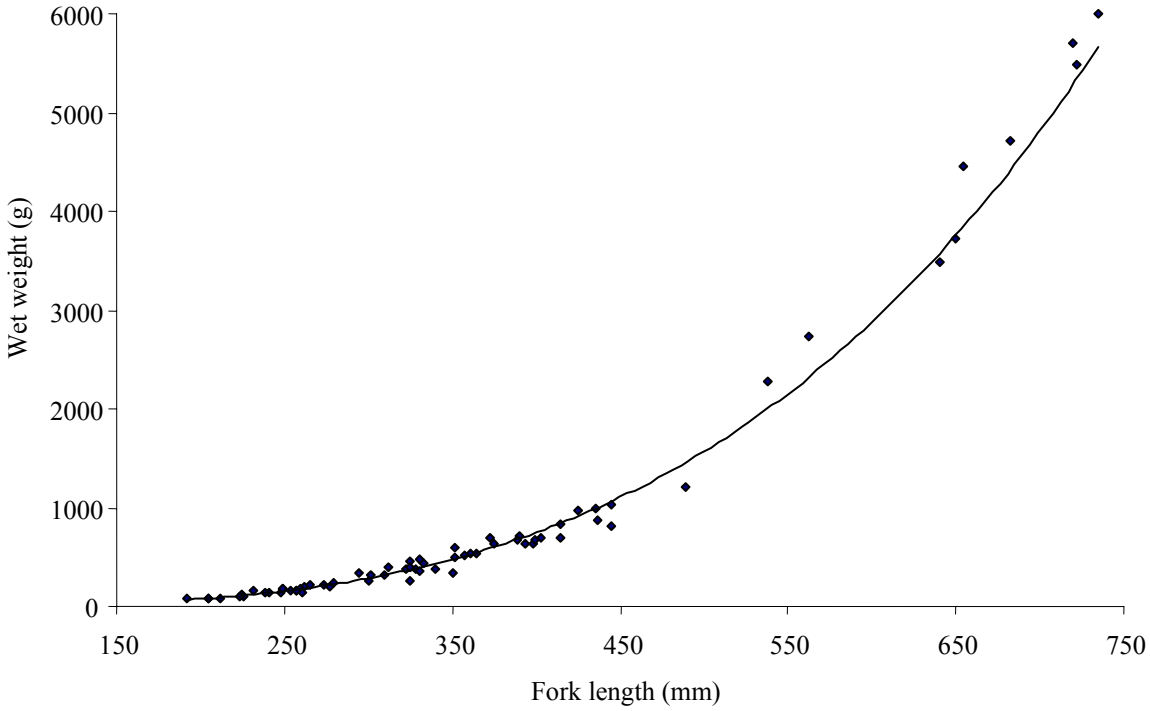


Fig. 5: *The relationship between wet weight (g) and fork length (mm) in Arctic charr (Salvelinus alpinus) from Lake Randsfjorden 2004/2005; y=(0.024x-11.53)x+1564.0, r^2=0.99, F=4406.8, d.f.=67, p<0.001. Fifty-five charr were collected for this study. In addition, Rustadbakken provided data from another 13.*

The material showed an apparent difference in colouration and mouth positions. Some charr had melanised lower jaws and a tendency towards subterminal mouth positions, while others had white lower jaws and more terminal mouth positions. The charr were grouped for subsequent analyses based on their mouth positions. Charr with terminal (TERM) and subterminal (SUB) mouth positions were not spatially segregated, as both categories were caught by the same method at approximately the same depth (20.6±1.8 m, mean±s.d.) at the same time of the year (July and August). Out of three gill netted charr caught in the same net during the same night, two individuals had subterminal mouth positions and melanised lower jaws, and the third had terminal mouth position and white lower jaw. There was no association between mouth position and gender among the mature charr (χ^2=0.80, d.f.=1, p=0.37), neither was there any significant difference between the mean ages of charr in the two groups (t=-0.78, d.f.=41, p=0.44) or between mean ages of the genders (U=563.0, N(♀)=25, N(♂)=20, p=0.79). It was evident that the material expressed charr with different growth patterns, and there was a significant difference in mean fork lengths (±s.d.) between

mature SUB (317.5±65.3 mm) and TERM (434.0±151.0 mm) charr (t=-3.01, d.f.=19, p=0.007) (Fig. 6).

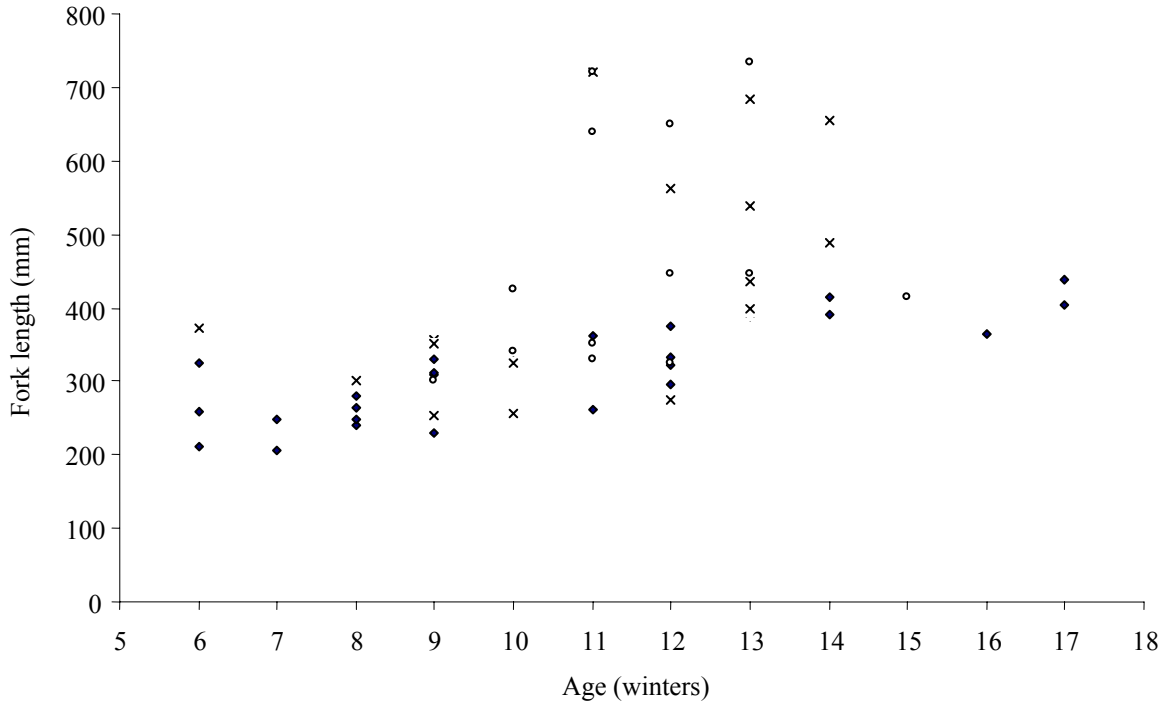


Fig. 6: *The relation between age calculated from otolith annuli, and fork length (mm) for mature Arctic charr (Salvelinus alpinus) from Lake Randsfjorden 2004/2005 (subterminal mouth position=black diamonds, terminal mouth position=crosses). Forty-five mature charr were collected for this study. In addition, Rustadbakken provided data from another 13 (open circles).*

There was a stronger correlation between fork length at age in SUB individuals ($y=16.4x+146.0$, $r^2=0.66$, $F=51.0$, d.f.=27, $p<0.001$) than in TERM individuals ($y=34.5x+50.0$, $r^2=0.29$, $F=6.1$, d.f.=16, $p=0.03$).

Statistical analyses of the 12 standardised morphological measurements did not reveal any significant differences between mature SUB and TERM charr, but there was a tendency towards wider upper jaws (UJW) in TERM individuals (U=528.0, N(SUB)=28, N(TERM)=17, p=0.06) (Table 1).

Table 1: *Means of 12 size corrected morphological measures of mature Arctic charr (Salvelinus alpinus) captured in Lake Randsfjorden 2004/2005, with subterminal (N=28) and terminal (N=17) mouth positions. P-values denote significance of t-tests or Mann-Whitney U-tests between the two groups. Pectoral fin length (PF), snout to the dorsal fin (DOR), snout to the tip of the pectoral fin (VEN), head length (HL), head depth at eye (HDE), eye diameter (EYE), upper jaw bone length (MBL), lower jaw bone length (LJBL), lower jaw length (LJL) measured with mouth held close, upper jaw width (UJW), lower jaw width (LJW), snout length (SNL).*

Character	$Mean_{sub}$(±s.e.)	$Mean_{term}$(±s.e.)	Test statistic	d.f.	p
PF	1.77 ± 0.0054	1.76 ± 0.0090	t = 0.81	27	0.42
DOR	2.14 ± 0.0030	2.14 ± 0.0066	t = 1.10	22	0.28
VEN	2.21 ± 0.0022	2.21 ± 0.0027	t = -1.11	35	0.27
HL	1.93 ± 0.0026	1.93 ± 0.0050	t = -0.82	24	0.42
HDE	1.62 ± 0.0038	1.63 ± 0.0057	U = 574.0	-	0.43
EYE	1.11 ± 0.0048	1.12 ± 0.0051	t = -0.20	38	0.84
MBL	1.67 ± 0.0043	1.67 ± 0.0092	t = -0.28	23	0.79
LJBL	1.74 ± 0.0035	1.74 ± 0.012	t = -0.10	18	0.92
LJL	1.66 ± 0.0039	1.66 ± 0.0085	t = -0.44	22	0.67
UJW	1.49 ± 0.0056	1.50 ± 0.0053	U = 528.0	-	0.06
LJW	1.39 ± 0.0069	1.40 ± 0.0072	t = -1.39	38	0.17
SNL	1.43 ± 0.0039	1.44 ± 0.0095	t = 1.04	21	0.31

To control for confounding effects, the same analyses were performed comparing females and males independent of their mouth positions. These analyses showed significant differences between the genders (Table 2).

Table 2: *Means of 12 size corrected morphological measures of mature female (N=25) and male (N=20) Arctic charr (Salvelinus alpinus) captured in Lake Randsfjorden 2004/2005. P-values denote significance of t-tests or Mann-Whitney U-tests between the two groups. Pectoral fin length (PF), snout to the dorsal fin (DOR), snout to the tip of the pectoral fin (VEN), head length (HL), head depth at eye (HDE), eye diameter (EYE), upper jaw bone length (MBL), lower jaw bone length (LJBL), lower jaw length (LJL) measured with mouth held close, upper jaw width (UJW), lower jaw width (LJW), snout length (SNL).*

Character	$Mean_{female}$(±s.e.)	$Mean_{male}$(±s.e.)	Test statistic	d.f.	p
PF	1.75 ± 0.0057	1.79 ± 0.0061	t = -3.93	41	< 0.001
DOR	2.13 ± 0.0039	2.15 ± 0.0034	t = -4.55	42	< 0.001
VEN	2.20 ± 0.0024	2.21 ± 0.0021	t = -2.49	42	0.02
HL	1.92 ± 0.0033	1.94 ± 0.0028	U = 430.0	-	0.001
HDE	1.62 ± 0.0042	1.63 ± 0.0041	t = -3.38	41	0.002
EYE	1.12 ± 0.0057	1.11 ± 0.0035	t = 1.02	38	0.32
MBL	1.66 ± 0.0042	1.69 ± 0.0060	t = -4.74	35	< 0.001
LJBL	1.73 ± 0.0065	1.76 ± 0.0053	U = 378.0	-	< 0.001
LJL	1.64 ± 0.0039	1.67 ± 0.0056	t = -4.43	34	< 0.001
UJW	1.49 ± 0.0057	1.50 ± 0.0057	U = 467.0	-	0.09
LJW	1.39 ± 0.0071	1.40 ± 0.0076	t = -0.18	40	0.86
SNL	1.42 ± 0.0042	1.45 ± 0.0069	t = -3.46	32	0.002

Males showed higher mean values than females, except for EYE, which was one of three measurements that did not differ significantly. One-way analysis of variance (ANOVA) with *post hoc* test (Tukey´s) revealed that SUB males and females had lower, but not significantly different, LJW mean values than TERM males and females (F=0.85, d.f.=43, p=0.48), SUB males showing the lowest (1.38±0.039), and TERM males showing the highest values (1.41±0.032) (mean±s.d.). Kruskal-Wallis test revealed that SUB females had the narrowest UJW values (z=-2.42) and TERM males the widest (z=1.56), with SUB males (z=0.53) and TERM females (z=0.79) in between (H=6.36, d.f.=3, p=0.10). The latter result confirms the tendency of wider upper jaw widths (UJW) in charr with terminal mouth position (Table 1).

There was a significantly higher number of SUB charr with melanised lower jaws, but this character was present among the TERM charr as well (two females and seven males) (Table

3). The most conspicuous difference in character between SUB and TERM charr were the occurrences of white coloured flesh among the SUB individuals (Table 3).

Table 3: *Number of mature Arctic charr (Salvelinus alpinus) caught in Lake Randsfjorden 2004/2005 with subterminal or terminal mouth positions, and χ^2-tests of independence of score distribution and classification.*

Character	Scores	Subterminal charr	Terminal charr	Tests of association
Melanised	+	26	9	$\chi^2 = 9.75$
lower jaw	-	2	8	p = 0.002
Belly	White	4	3	$\chi^2 = 2.79$
edge	Beige	22	10	p = 0.25
	Orange	2	4	
Belly	White	9	5	$\chi^2 = 0.06$
	Beige	10	6	p = 0.97
	Orange	9	6	
Flesh	White	6	0	$\chi^2 = 4.20$
	Orange	22	17	p = 0.04
Number of fish		28	17	

The SUB charr with white flesh comprised three females and three males between six and eleven winters old, weighing 79 to 210 g, and with fork lengths between 205 and 265 mm. There were two TERM charr with white flesh in the material, but they were both immature individuals; one female (9 winters old, 197 g, 277 mm) and one male (6 winters old, 162 g, 257 mm).

Analysis of discontinuous variables between females and males independent of their mouth positions, revealed a significant difference in belly edge colouration, where males tended to have stronger colouration than females (Table 4).

Table 4: *Number of mature Arctic charr (Salvelinus alpinus) caught in Lake Randsfjorden 2004/2005 categorized by gender, and χ^2-tests of independence of score distribution and classification.*

Character	Scores	Females	Males	Tests of association
Melanised	+	18	17	$\chi^2 = 1.09$
lower jaw	-	7	3	p = 0.30
Belly	White	6	1	$\chi^2 = 6.26$
edge	Beige	18	14	p = 0.04
	Orange	1	5	
Belly	White	9	5	$\chi^2 = 3.30$
	Beige	10	5	p = 0.19
	Orange	6	10	
Flesh	White	3	3	$\chi^2 = 0.09$
	Orange	22	17	p = 0.77
Number of fish		25	20	

There were no apparent differences in belly, lower jaw or flesh colouration between the genders (Table 4).

The mercury analysis demonstrated a strong correlation between mercury concentration (mg Hg/kg wet weight) and age (winters) (Fig. 7).

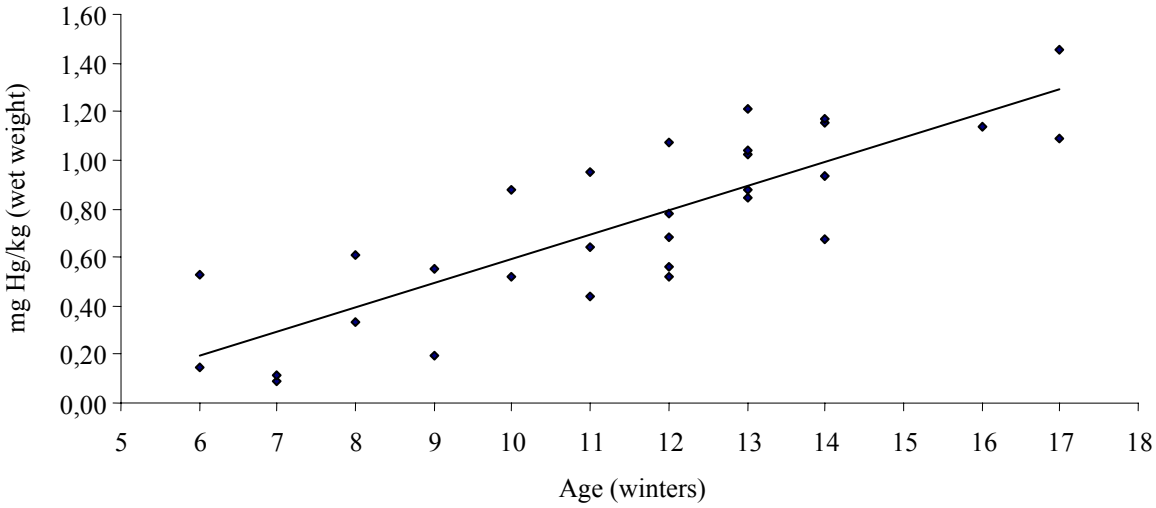


Fig. 7: *The relationship between mercury concentration (mg Hg/kg wet weight) and age (winters) in 30 Arctic charr (Salvelinus alpinus) from Lake Randsfjorden 2004/2005 ($y=0.10x-0.41$, $F=68.1$, $r^2=0.71$, $d.f.=29$, $p<0.001$).*

There were no significant differences in mercury concentrations between SUB females, SUB males, TERM females and TERM males ($F=0.26$, $d.f.=(3, 27)$, $p=0.85$), but the spread of values was greater among the SUB individuals (Tables 5 and 6).

Table 5: *Summary of basic biological data, mercury concentrations (mg Hg/kg wet weight), and stable isotope signatures (‰) of Arctic charr (Salvelinus alpinus) by mouth position (subterminal and terminal), Lake Randsfjorden 2004/2005. Numbers in parentheses denote number of charr analysed for stable isotopes.*

	Fork length* (mm)	Weight* (g)	Age* (winters)	mg Hg/kg** (wet weight)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Subterminal (27)						
Mean	310.9	389.9	10.3	0.73	13.0	-28.1
S.E.	13.1	46.7	0.6	0.11	0.2	0.1
Min.	205.0	79.0	6.0	0.09	11.1	-31.4
Max.	437.0	863.0	17.0	1.45	14,8	-27.4
Terminal (13)						
Mean	462.2	1866.4	11.5	0.75	12.8	-28.0
S.E.	44.3	525.4	0.7	0.06	0.2	0.3
Min.	257.0	161.0	6.0	0.52	11.6	-29.5
Max.	722.0	5482.0	14.0	1.04	13.8	-26.2

**Values based on charr analysed for stable isotopes.*

***Values based on 17 charr with subterminal and 13 charr with terminal mouth positions.*

Table 6: *Summary of basic biological data, mercury concentrations (mg Hg/kg muscle tissue wet weight), and stable isotope signatures (‰) of Arctic charr (Salvelinus alpinus) by gender, Lake Randsfjorden 2004/2005. Numbers in parentheses denote number of charr analysed for stable isotopes.*

	Fork length* (mm)	Weight* (g)	Age* (winters)	mg Hg/kg** (wet weight)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Female (21)						
Mean	339.7	555.8	11.0	0.74	12.8	-28.2
S.E.	18.9	107.5	0.7	0.09	0.2	0.2
Min.	212.0	80.0	6.0	0.12	11.1	-31.4
Max.	538.0	2272.0	17.0	1.45	14.7	-26.2
Male (18)						
Mean	394.3	1292.5	10.6	0.78	13.1	-28.0
S.E.	37.5	415.4	0.6	0.09	0.2	0.2
Min.	205.0	79.0	6.0	0.09	12.0	-29.5
Max.	722.0	5482.0	14.0	1.21	14.8	-26.2

**Values based on charr analysed for stable isotopes.*

***Values based on analyses of 18 females and 11 males.*

The spread of values was greater among SUB (1.36 mg Hg/kg wet weight) than among TERM charr (0.52 mg Hg/kg wet weight), and the wider interval among SUB individuals influenced the spread within the genders (females 1.33 and males 1.12 mg/kg wet weight) (Table 5 and 6). There were positive correlations between the mercury concentration in SUB charr and fork length ($y=0.005x-1.03$, $r^2=0.91$, $F=159.5$, d.f.=16, $p<0.001$), weight ($y=0.002x+0.05$, $r^2=0.87$, $F=102.3$, d.f.=16, $p<0.001$) and age ($y=0.12x-6.46$, $r^2=0.85$, $F=86.7$, d.f.=16, $p<0.001$). There were no significant correlations among TERM charr equivalent to the findings for SUB charr, but there was a tendency towards a positive correlation between mercury concentration and age ($y=0.042x+0.27$, $r^2=0.25$, $F=3.62$, d.f.=12, $p=0.08$) (Fig. 8).

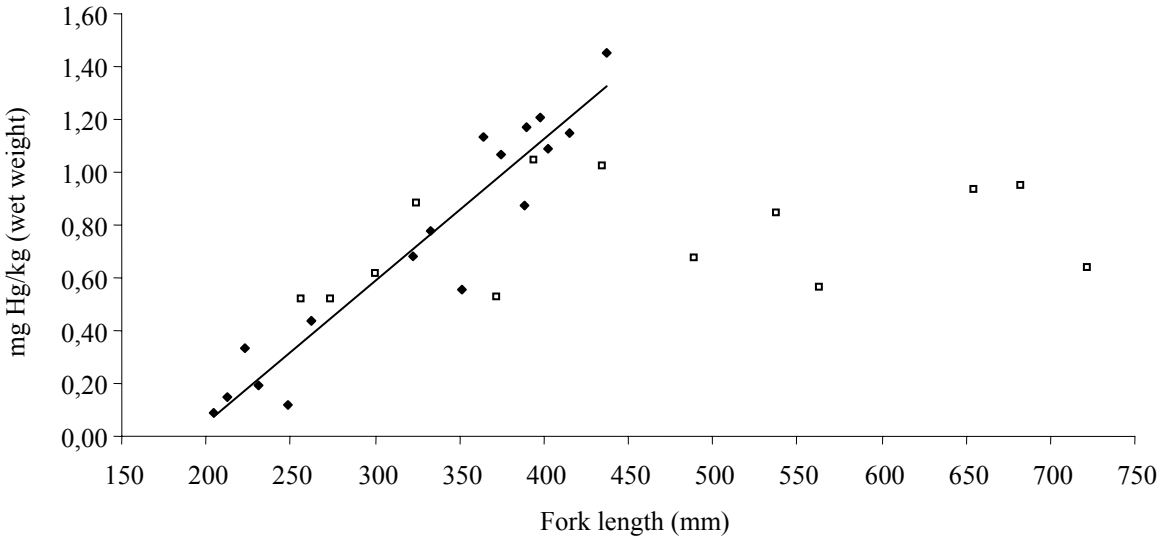


Fig. 8: *The relationship between mercury concentration (mg Hg/kg wet weight) and fork length (mm) in Arctic charr (Salvelinus alpinus) from Lake Randsfjorden 2004/2005. A significant positive correlation (y=0.005x-1.03, r^2=0.91, F=159.5, d.f.=16, p<0.001) was demonstrated among the individuals with subterminal mouth position (black diamonds), hence the regression line. No such correlation existed among the individuals with terminal mouth position (N=13) (open squares).*

The females, independent of mouth position, had a positive correlation between mercury concentration and fork length (y=0.003x-0.31, r^2=0.48, F=14.5, p=0.002), and both genders showed positive correlation between mercury concentration and age (females: y=0.092x-0.31, r^2=0.71, F=38.5, p<0.001, males: y=0.15x-0.98, r^2=0.75, F=27.6, d.f.=10, p=0.001). The absences of correlations regarding mercury concentration versus weight (both genders) and fork length (males) arose from the influence the larger specimens among the TERM charr acted upon the results (Tables 5 and 6). The charr with fork lengths above 450 mm (2 females and 4 males) showed no correlation between mercury concentration and fork length (y=0.0005x+0.45, r^2=0.09, F=0.4, d.f.=5, p=0.58), nor between mercury concentration and weight (y=0.00003x+0.66, r^2=0.09, F=0.4, d.f.=5, p=0.57) (Fig. 8).

There was no dietary segregation between SUB (N=36) and TERM (N=19) charr based on the analysis of stomach contents (Fig. 9).

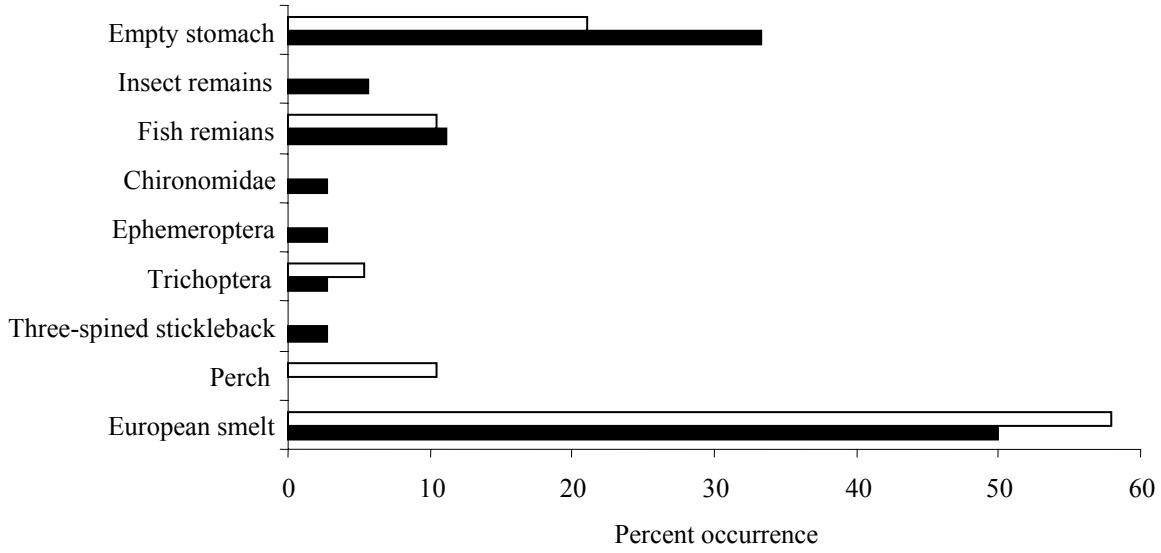


Fig. 9: *Percent occurrence of identified prey items in the stomachs of Arctic charr (Salvelinus alpinus) with subterminal (black bars, N=36) and terminal (white bars, N=19) mouth positions, Lake Randsfjorden 2004/2005. Blank entries indicate zero occurrences of the prey item.*

A considerable number of stomachs were empty, but it was evident that both forms relied upon other fish species as their predominant prey (Fig. 9 and 10). European smelt occurred in stomach contents of both forms, but perch occurred in two TERM individuals only, a female and a male of 2272 and 2732 g, respectively. A three-spined stickleback was present in the stomach of a SUB charr (Fig. 9). Insects and their remains were to a much lesser degree present, and only in aquatic stages. Trichoptera was the only insect order found in TERM stomachs (N=1).

Fig. 10: *An Arctic charr (Salvelinus alpinus) weighing 3842 g, from Lake Randsfjorden. The stomach contained 83 perch (Perca fluviatilis). This specimen was not a part of the material in this study (photo: E. Ovnerud).*

There were no significant differences in mean $\delta^{15}N$ signatures between SUB females, SUB males, TERM females and TERM males ($F=1.19$, d.f.=(3, 37), $p=0.33$) (Tables 5 and 6). The SUB individuals had a wider spread of $\delta^{15}N$ signatures (3.7 ‰-points) than the TERM charr (2.2 ‰-points) did, and this influenced the spread within the genders (females 3.6 and males 2.8 ‰-points) (Tables 5 and 6). No significant correlations existed between $\delta^{15}N$ signatures and fork lengths ($y=-0.001+13.3x$, $r^2=0.02$, $F=0.73$, d.f.=39, $p=0.40$), weights ($y=-0.0001x+13.1$, $r^2=0.03$, $F=1.28$, d.f.=39, $p=0.27$) or ages ($y=0.03x+12.7$, $r^2=0.01$, $F=0.38$, d.f.=39, $p=0.54$) in the material (Fig. 11).

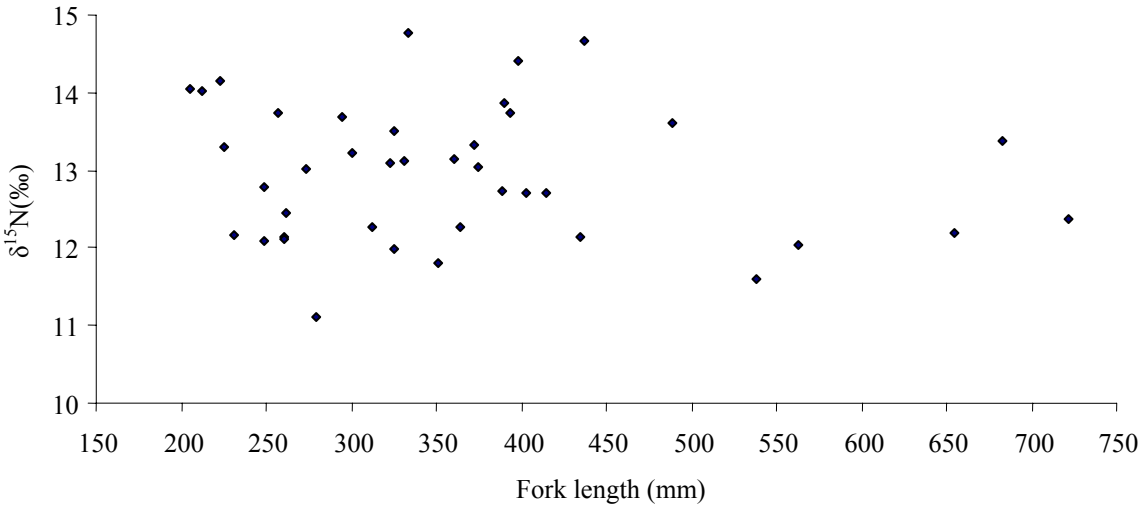


Fig. 11: *$\delta^{15}N$ signatures (‰) and fork lengths (mm) in Arctic charr (Salvelinus alpinus) from Lake Randsfjorden 2004/2005 (N=40).*

No relationships were found between $\delta^{15}N$ signatures and fork lengths ($y=0.002x+12.4$, $r^2=0.02$, $F=0.57$, d.f.=26, $p=0.46$), weights ($y=0.0006x+12.8$, $r^2=0.03$, $F=0.75$, d.f.=26, $p=0.40$) and ages ($y=0.06x+12.4$, $r^2=0.05$, $F=1.19$, d.f.=26, $p=0.29$) in SUB, nor in TERM individuals ($\delta^{15}N$ =-0.002*length+13.6, $r^2=0.13$, $F=1.66$, d.f.=12, $p=0.22$, $\delta^{15}N$ =-0.0001*weight+13.0, $r^2=0.11$, $F=1.36$, d.f.=12, $p=0.27$, $\delta^{15}N$ =-0.07*age+13.6, $r^2=0.04$, $F=0.50$, d.f.=12, $p=0.49$). No correlations were evident when the same procedure was performed upon females ($\delta^{15}N$ =0.0005*length+12.6, $r^2=0.002$, $F=0.04$, d.f.=19, $p=0.84$, $\delta^{15}N$ =-0.0002*weight+12.9, $r^2=0.008$, $F=0.15$, d.f.=19, $p=0.70$, $\delta^{15}N$ =0.05*age+12.3, $r^2=0.03$, $F=0.64$, d.f.=19, $p=0.44$) and males ($\delta^{15}N$ =-0.002*length+13.8, $r^2=0.10$, $F=1.81$, d.f.=17, $p=0.20$, $\delta^{15}N$ =-0.0002*weight+13.3, $r^2=0.12$, d.f.=17, $p=0.16$, $\delta^{15}N$ =0.01*age+13.0, $r^2=0.001$, $F=0.02$, $p=0.88$) independent of their mouth position.

No significant differences were found in median $\delta^{13}C$ signatures between SUB females, SUB males, TERM females and TERM males ($H=3.59$, d.f.=3, $p=0.31$) (Tables 5 and 6). There were not any significant correlations between $\delta^{13}C$ signatures and fork lengths ($r_s=0.28$, $N=40$, $p=0.08$), weights ($r_s=0.27$, $N=40$, $p=0.10$) or ages ($r_s=-0.10$, $N=40$, $p=0.53$) in the material (Fig. 12). The females displayed the largest spread of $\delta^{13}C$ signatures (5.2 ‰-points), but the result was largely influenced by the lightest $\delta^{13}C$ signature measured (-31.4 ‰) among the analysed charr (Table 6).

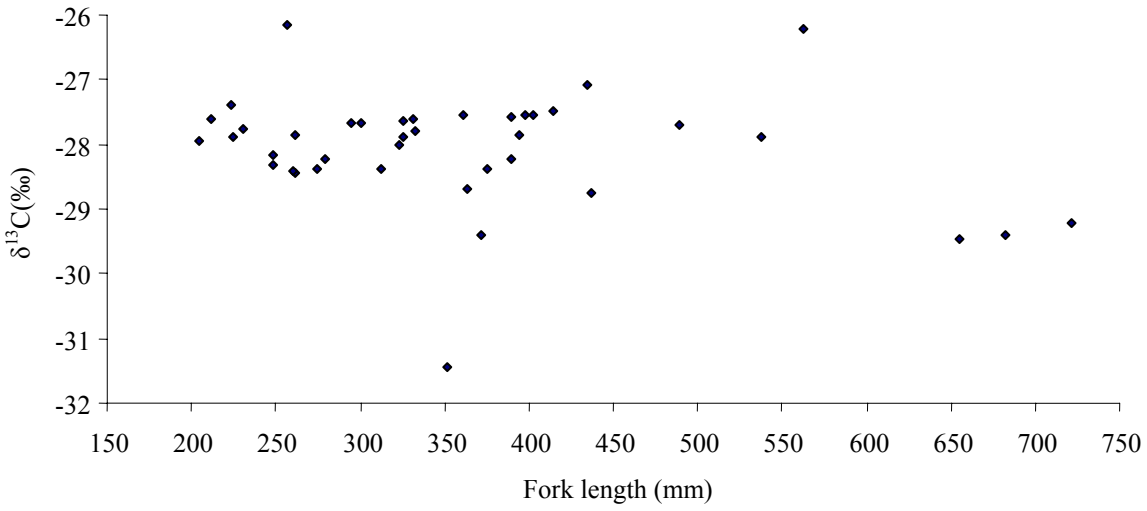


Fig. 12: *$\delta^{13}C$ signatures (‰) and fork lengths (mm) in Arctic charr (Salvelinus alpinus) from Lake Randsfjorden 2004/2005 (N=40).*

There were significantly negative correlations between $\delta^{13}C$ signatures and fork length (r_s=-0.40, N=27, p=0.04), weight (r_s=-0.42, N=27, p=0.03) and age (r_s=-0.59, N=27, p=0.01) among the SUB charr. The TERM individuals did not reveal similar correlations ($\delta^{13}C$ =-0.003*length-26.5, r^2=0.22, F=3.15, d.f.=12, p=0.10, $\delta^{13}C$ =0.02*age-28.2, r^2=0.002, F=0.02, d.f.=12, p=0.90), but there was a tendency towards negative correlation between $\delta^{13}C$ values and weights (y=-0.0003x-27.4, r^2=0.28, F=4.27, d.f.=17, p=0.06). Female charr showed a negative relationship between $\delta^{13}C$ values and ages (r_s=-0.44, N=20, p=0.05) independent of mouth position, but no correlations were found between $\delta^{13}C$ signatures and fork lengths (r_s=-0.06, N=20, p=0.79) and weights (r_s=-0.03, N=20, p=0.90). Males revealed a negative correlation between $\delta^{13}C$ signatures and weights (y=-0.0003-27.7, r^2=0.30, F=6.84, d.f.=17, p=0.02), neither fork lengths (y=-0.002-27.2, r^2=0.15, F=2.74, d.f.=17, p=0.12) or ages (y=-0.004-27.9, r^2<0.001, F<0.001, d.f.=17, p=0.95) showed any relationship with $\delta^{13}C$ signatures. There was no correlation between $\delta^{15}N$ and $\delta^{13}C$ signatures in the material (r=0.20, N=40, p=0.21) (Fig 13).

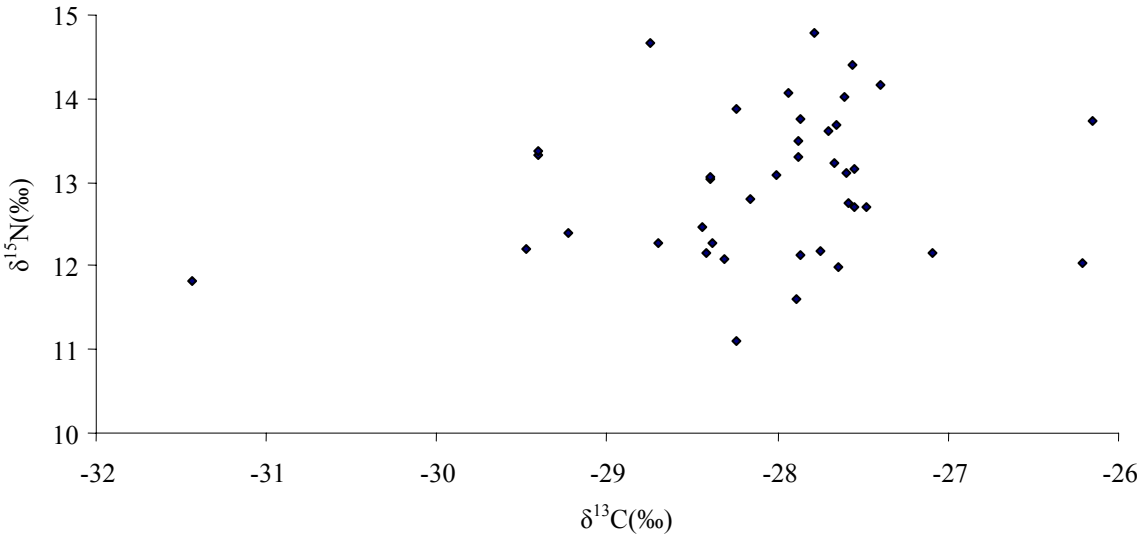


Figure 13: *Nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) signatures in Arctic charr (Salvelinus alpinus) from Lake Randsfjorden 2004/2005 (N=40).*

Discussion

The present study showed that the Arctic charr in Lake Randsfjorden exhibits body-size polymorphism. Analyses of morphological size-corrected measures did not reveal any morphological differences between sexually mature SUB and TERM charr, but a significantly higher number of SUB individuals expressed melanised lower jaws and white flesh colour. However, the results stated that sexual dimorphism accounted for the morphological differences found within the population when the measures were adjusted for size. The analyses of stomach contents, stable isotopes and mercury concentrations could not reveal if the size polymorphism were caused by differences in feeding ecology, but the $\delta^{13}C$ signatures suggested that the SUB individuals had a shift towards more pelagic food sources with increasing size and age. The reported mercury concentrations were closely correlated with age, and they emphasised the different growth rates within the charr population.

This is the first study of trophic polymorphism in Arctic charr carried out in Lake Randsfjorden. Nevertheless, throughout the years, local anglers have reported findings of two forms of charr, and Pethon (1998) mentions that Lake Randsfjorden is inhabited by one form, which he calls "kolmule", that reaches weights up to 10 kg, and another deep living, grey coloured form which attain an asymptotic length of 20 cm.

The differences in body sizes among the sexually mature charr cannot be explained with body-size variation determined by gender even though 6 out of 8 charr with lengths above 50 cm were males. The SUB and TERM groups had sex ratios of approximately the same size, and both genders comprised individuals with large spread in size within each year class. Bimodality caused by domination of one or more strong year classes seems unlikely since the age distribution is similar for SUB and TERM individuals (Griffiths 1994). Bimodal size-frequency distribution have been frequently reported in salmon (*Salmo salar*) and trout populations were individuals adapt to different life-histories; early gonadal development and maturation at small sizes or increased growth and deterred maturation (Klemetsen *et al.* 2003). If deferred maturation were the reason for increased growth rate and size within the charr population in Lake Randsfjorden, it would be predicted that the larger individuals would comprise the older fish (Adams *et al.* 2003). The material showed that the largest specimens (fork lengths >50 cm) were between 11 and 14 winters old. Young individuals were unfortunately absent in the material. However, 6 winters old sexually mature charr comprised

individuals that differed 16 cm in fork length, the smallest a SUB female and the largest a TERM female. In addition, all the sexually immature charr were small specimens (192-249 mm in fork length) with ages ranging from 6-9 winters. Consequently, increased growth at the expense of deterred maturation seems not to cause the body-size morphism in this study. Trudel *et al.* (2001) studied the different energy budgets between sympatric morphs of lake whitefish (*Coregonus clupeaformis*). Their results showed that earlier maturation and shorter life span in the small morph were caused by higher metabolic rate. This is probably not the case in Lake Randsfjorden, because of the relative high numbers of small, elderly charr in the material. Even though the material was too scarce to reveal bimodality, i.e. discontinuous size distribution with no overlap, it was evident that the charr expressed different growth rates.

Although not studied in this thesis, inherited genetic difference in growth rate could be an explanation of the variation in size. This has been demonstrated in artificially bred offspring of the large and small charr morphs from Lake Vangsvatnet and Lake Stora Rösjön, respectively (Svedäng 1990; Hindar & Jonsson 1993). In a corresponding experiment, Klemetsen *et al.* (2002) came to the opposite conclusion. The offspring from the small profundal morph in Lake Fjellfrøsvatn grew faster than the offspring from the large pelagic morph when reared under similar conditions. Another result from the rearing experiment performed by Hindar and Jonsson (1993) was that the parr marks along the flanks of the fish, one characteristic of the small morph, were dependent of body size and not parental morph. This might explain the significantly higher number of the smaller SUB charr with melanised lower jaws in the present study, a trait that also occurred among the TERM individuals.

Sexual dimorphism explained the morphological differences when adjusted for size. Phenotypic differences between genders have gained little attention in the studies of trophic polymorphism (Ehlinger 1990; Kristjansson *et al.* 2002; Proulx & Magnan 2004). Proulx and Magnan (2004) demonstrated that the environmental factors explained 15% of the variation between littoral and pelagic brook charr when sex was not accounted for. When the effect of sex was controlled, the environmental factors explained 26% of the variation between the morphs. The significantly stronger belly edge colouration among the males in the present study is a secondary sexual character that displays the quality of the bearer (Jonsson & Hindar 1982). Females, especially the larger ones, have orange and red bellies. The duller colouration of the belly edge might reduce aggressive encounters, as spawners are aggressive towards red objects (Jonsson & Hindar 1982; Jonsson & Jonsson 2001).

The stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) have been widely used in ecological studies to estimate the trophic positions of and carbon flow in food webs. To establish a consumer's trophic position, it is necessary to have an isotopic baseline (Post 2002). This is achieved by using the isotopic signatures from appropriate primary consumers.(Post 2002). However, one of the aims of this study was to examine if different feeding ecology were the cause for polymorphism in the charr population, not to depict the food chain in Lake Randsfjorden. The $\delta^{15}N$ signatures were within the 3-4‰ range that defines one trophic level (Hobson & Welch 1992; Vander Zanden *et al.* 1999; Rognerud *et al.* 2002). This implies that all the analysed charr were piscivorous, and that piscivority appeared at lengths below 20 cm fork length. Although an isotopic base line and stable isotope analyses of the whole fish community in the lake would establish the exact trophic level, the increase in Hg-concentrations with size in the SUB individuals combined with the high mean Hg-concentrations and the presence of European smelt in the stomachs within each form could only be explained by piscivority. It is demonstrated that cannibalism, the consumption of co specifics, can structure the length and year class distribution in Arctic charr populations (Svenning & Borgstrøm 1995). The $\delta^{15}N$ signatures of the larger charr in the material were lower than the $\delta^{15}N$ signatures of many of the smaller specimens. This implied that the different size distribution in the analysed material could not be explained by cannibalism, but the absence of younger and smaller individuals made it impossible to rule out the occurrence of cannibalism entirely.

The $\delta^{13}C$ signatures ranged from -31.4 to -26.2 ‰, and suggested that the organic carbon sources were of planktonic and deeper bentic origin (Meili *et al.* 1993; Hecky & Hesslein 1995). The TERM individuals showed little change in values, but the SUB charr showed depletion of $\delta^{13}C$ signatures with increasing age, weight and length. .The negative correlation of $\delta^{13}C$ values with age and size in the SUB charr could indicate a shift in habitat from bentic to pelagic environments (France 1995; Post 2002). Ontogenetic niche shifts is common in Arctic charr (Klemetsen *et al.* 2003). The charr usually utilise epibentic food resources when young and small, and often in the profundal zone (Hindar & Jonsson 1982; Sandlund *et al.* 1992). The niche shift to pelagic waters occurs when the charr reach 13-18 cm in length (L´Abée-Lund *et al.* 1993). However, this threshold is not absolute. L´Abée-Lund *et al.* (1993) reported that a habitat shift was a trade-off between food demand and risk of predation.

The scarce material and the biased sampling method made it impossible to reject the presence of other charr morphs in Lake Randsfjorden. The possibility of a genetic basis of differences in growth rate remains to be tested, although, the present study suggests that the size polymorphism within the Arctic charr population arises from differences in food availability between SUB and TERM piscivorous individuals.

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Appendix A: *Basic biological data, mercury concentrations (mg Hg/kg wet weight) and stable isotope signatures(‰).*

Fish nr.	Mouthposition/gender	mg Hg/kg (ww)	δ-15-N	δ-13-C	Weight (g)	Forklength (mm)	Age
R16	Subterminal male	0.09	14.056	-27.934	79	205	7
R20	Subterminal male	0.78	14.778	-27.79	426	333	12
R37	Subterminal male	0.88	12.741	-27.584	676	389	13
R26	Subterminal male	1.21	14.4	-27.556	629	398	13
R45	Subterminal male		12.075	-28.317	173	249	8
R55	Subterminal male		12.151	-28.415	169	260	6
R44	Subterminal male		13.107	-27.593	474	331	9
R43	Subterminal male		13.149	-27.549	525	361	11
R24	Subterminal male		13.302	-27.875	111	225	7
R50	Subterminal male		13.499	-27.884	451	325	6
R41	Subterminal male		13.69	-27.658	337	295	12
R3	Subterminal female	0.12			145	248	7
R51	Subterminal female	0.15	14.012	-27.607	80	212	6
R40	Subterminal female	0.19	12.175	-27.753	152	231	9
R46	Subterminal female	0.44	12.456	-28.442	205	262	11
R42	Subterminal female	0.56	11.816	-31.441	592	351	9
R28	Subterminal female	0.68	13.087	-28.007	371	323	12
R30	Subterminal female	1.07	13.054	-28.39	625	375	12
R48	Subterminal female	1.09	12.695	-27.548	702	403	17
R18	Subterminal female	1.13	12.269	-28.698	543	364	16
R49	Subterminal female	1.15	12.701	-27.485	841	415	14
R31	Subterminal female	1.17	13.871	-28.242	706	390	14
R1	Subterminal female	1.45	14.668	-28.742	863	437	17
R36	Subterminal female		11.112	-28.237	231	279	8
R35	Subterminal female		12.27	-28.385	398	312	9
R25	Subterminal female		12.789	-28.155	169	249	9
R13	Subterminal unknown	0.33	14.156	-27.394	105	223	8
R39	Subterminal unknown		12.118	-27.868	139	261	7
R47	Terminal male	0.52	13.027	-28.396	221	274	12
R32	Terminal male	0.56	12.041	-26.217	2732	563	12
R54	Terminal male	0.64	12.382	-29.226	5482	722	11
R52	Terminal male	0.93	12.192	-29.473	4456	655	14
R53	Terminal male	0.95	13.385	-29.4	4707	683	11
R33	Terminal male	1.02	12.144	-27.093	986	435	13
R12	Terminal male	1.04	13.748	-27.867	631	394	13
R19	Terminal male	0.52	13.744	-26.155	161	257	10
R29	Terminal female	0.53	13.32	-29.41	696	372	6
R6	Terminal female	0.61	13.228	-27.67	307	301	8
R27	Terminal female	0.67	13.607	-27.697	1211	489	14
R38	Terminal female	0.85	11.593	-27.89	2272	538	13
R34	Terminal female	0.88	11.978	-27.642	401	325	10

Appendix B: *Mouth positions, gender, fork lengths (mm) and the 12 measures (mm) that were adjusted for size.*

Fish nr.	Mouthposition/gender	FL	PF	DOR	VEN	HL	HDE	EYE	MBL	LJBL	LJL	UJW	LJW	SNL
R1	Subterminal female	437	72	170	205	99		14						34
R2	Subterminal female	310	48	117	133	70	34	12	38	46	37	25	21	21
R3	Subterminal female	248	40	93	112	62	27	10	30	37	29	19	15	17
R18	Subterminal female	364	58	133	157	85	45	13	47	55	46	30	25	26
R21	Subterminal female	328	51	118	136	74	34	13	38	48	37	25	20	23
R23	Subterminal female	239	39	91	107	57	27	12	30	34	29	18	15	17
R28	Subterminal female	323	45	118	141	77	35	13	39	49	38	26	24	23
R30	Subterminal female	375	57	137	164	84	39	13	47	56	45	30	24	26
R31	Subterminal female	390	67	154	169	92	43	14	50	56	48	31	24	28
R35	Subterminal female	312	48	117	138	71	36	12	38	46	37	28	22	23
R36	Subterminal female	279	45	111	123	64	30	11	34	41	33	22	17	19
R46	Subterminal female	262	40	102	114	61	29	11	32	39	31	20	16	18
R48	Subterminal female	403	65	151	176	91	46	14	52	58	50	36	28	29
R49	Subterminal female	415	68	157	179	94	48	13	52	60	51	35	28	31
R51	Subterminal female	212	34	83	94	52	23	12	26	30	25	15	11	14
R40	Subterminal female	231	39	86	100	55	26	13	28	35	28	21	17	16
R16	Subterminal male	205	35	79	91	49	23	11	26	31	25	16	12	14
R20	Subterminal male	333	56	132	151	81	38	13	46	54	44	28	21	26
R26	Subterminal male	398	79	166	182	98	48	14	60	67	55	36	29	32
R37	Subterminal male	389	64	154	173	94	46	13	51	63	50	33	26	29
R41	Subterminal male	295	47	112	126	71	35	12	40	46	39	24	20	23
R43	Subterminal male	361	59	140	165	86	42	13	47	55	43	31	24	27
R44	Subterminal male	331	57	136	152	78	38	12	46	54	44	28	23	25
R45	Subterminal male	249	37	96	110	57	27	11	31	37	30	19	15	16
R50	Subterminal male	325	54	125	143	76	39	13	40	48	39	27	20	24
R55	Subterminal male	260	41	100	117	60	30	11	32	38	31	17	13	17
R4	Subterminal male	265	43	104	117	64	29	11	34	41	32	22	17	19
R42	Subterminal female	351	50	128	156	79	38	13	43	52	41	29	23	24
R7	Terminal female	357	53	130	154	82	40	13	45	52	44	32	24	26
R14	Terminal female	254	40	93	114	60	28	12	32	40	30	20	16	19
R19	Terminal female	257	39	99	115	66	31	12	34	41	33	22	18	18
R27	Terminal female	489	73	181	221	112	57	16	61	74	59	43	35	37
R29	Terminal female	372	51	130	161	85	43	12	43	53	42	33	26	26
R34	Terminal female	325	46	107	142	70	36	12	37	45	37	26	22	21
R38	Terminal female	538	88	203	244	124	64	16	68	61	66	54	42	42
R6	Terminal female	301	46	108	139	68	34	12	37	42	35	24	18	21
R12	Terminal male	394	66	154	174	98	47	13	56	69	54	35	27	32
R15	Terminal male	352	55	135	156	87	42	13	48	56	47	33	26	29
R17	Terminal male	399	74	170	181	100	50	13	62	70	59	35	29	37
R32	Terminal male	563	92	211	264	128	68	15	73	85	70	57	50	42
R33	Terminal male	435	78	172	198	106	52	14	65	74	62	40	32	37
R52	Terminal male	655	119	269	317	163	95	15	99	112	97	74	61	60
R53	Terminal male	683	136	297	329	165	98	17	111	123	104	75	63	70
R54	Terminal male	722	125	289	329	175	91	17	105	121	102	73	56	66
R47	Terminal male	274	45	104	121	63	32	12	33	39	32	21	17	19