Life History Trade-offs in Anadromous Burbot Lota Lota (*Linnaeus 1758*) from Rickleån and Sävarån, Northern Sweden

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Abstract

Anadromous burbots Lota lota (*Linnaeus 1758)* from two similar rivers in the Gulf of Bothnia area, Sävarån and Rickleån, Northern Sweden, were compared. The aim was to test for and explain differences in ecology. Spawning burbots in Sävarån were smaller, younger, grew slower and were more densely populated. The positive correlations between individual size, and gonad- and liver indexes which were found in Rickleån, were weaker or absent in Sävarån. The positive correlations of rapid growth in regard of liver tissue growth and *K*, were weaker in Sävarån than in Rickleån. *K* in Sävarån were not correlated with individual size, and were also lower in general, than in Rickleån. The majority of spawning burbots had empty stomachs, 73 % in Sävarån, and 58 % in Rickleån. "Rest year" strategies, which were correlated to both organ (except gonads) indexes, and *K,* where common in Rickleån, but almost absent in Sävarån. Almost all burbots, even those smallest, found in the stomachs of bigger individuals, where fully mature with high gonad index. The size group histogram and normal probability analyses, indicated that there were large numbers of even smaller individuals present at the spawning sites in Sävarån, not possible to sample with the gear used. As a whole, burbots in Sävarån exhibited precocity, favouring early spawning on the expense of growth and/or higher fecundity in future spawnings. I also found that many of the differences confirmed between the populations, were also present within both populations, between males and females. Males exhibited a more precocious reproduction, while females exhibited a more delayed reproduction.

[1] The differences between the populations in age at spawning, individual size, growth, allocations to different organs and foraging, were presumably due to both

    a) trade-offs favoured by selection due to differences in mortality related to human harvest, and
    b) density-dependent effects [2].

[2] The population densities differed, assumably due to two abiotic factors,

    a) higher summer temperatures in the littorals outside Sävarån and
    b) more significant episodical acidity in the spring in Rickleån.

[3] The demise of the largest and oldest burbots in these rivers, as well as the whole Sweden, was a different problem. The climate change seemed to be the most plausible explanation. A climatologic and thermal threshold for burbots may have been exceeded.

Whenever a new discovery is reported to the scientific world, they say first, "It is probably not true." Thereafter, when the truth of the new proposition has been demonstrated beyond question, they say, "Yes, it may be true, but it is not important." Finally, when sufficient time has elapsed to fully evidence its importance, they say, "Yes, surely it is important, but it is no longer new."

Michel de Montaigne (1533-1592)

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Front page: Sea Pool, a burbot spawning site in Rickleån (Bothnian Bay in the background), July 28th 2012. Small photos from left-right: Female gonads; female (top) and male (below) burbots; otolith. By author.

1. Introduction

1.1 Why have the large burbots decreased in Sweden the last decades?

It seems to be a generally accepted fact among Swedish lotaphiles, that there are fewer large burbots Lota lota (Linnaeus 1758) around nowadays, than for instance in the 1990s. The trend is landwide, from north to south. What has happened with the large burbots? Naturally, we can not go back in time, and see what really happened, and why. In this study, I address the question by studying two similar rivers, in regard of biotic and abiotic factors, Rickleån and Sävarån. They both have thriving burbot populations, and experience the same decline in large burbots, as in the country in general. However, there are differences. The burbots in Sävarån are smaller and more numerous, and this difference had been present for decades. If we can explain these differences, we may also address the question on a grander scale. But first, let us repeat what we already know about this fascinating species, which thrives, beneath meter-thick ices, in mid-winter, when other organisms struggle to survive.

1.2 The burbot Lota lota (Linnaeus 1758)

1.2.1 Palaeontological records, classification and present distribution
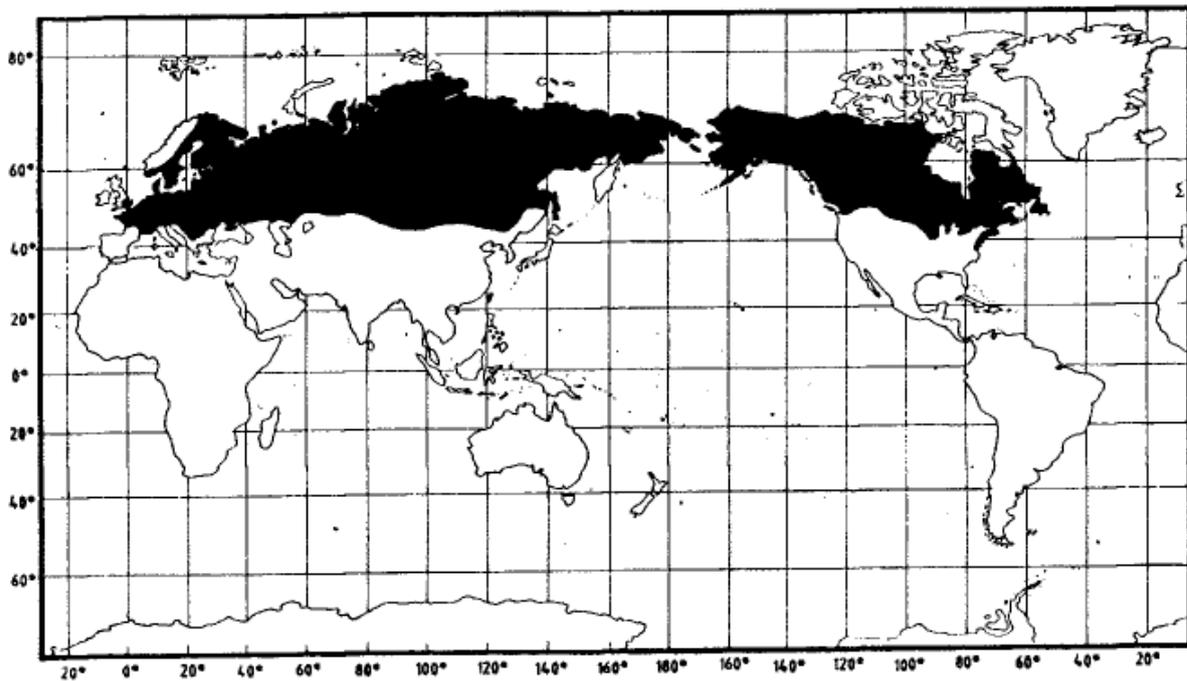
Figure 1. Burbot distribution (Cohen et al 1990).

The burbot Lota lota (Linnaeus 1758) is the only freshwater species in the family Lotidae (tab. 1). It has a circumarctic distribution in fresh- and brackish water, from Canada and northern US, through Alaska, Russia and Europe between $40^{\circ} – 78^{\circ}$ N (fig. 1; Cohen et al 1990; Froese et al 2009). The species is native in 30 countries, and introduced in one, Italy (Froese et al 2009). The burbot lineage, genus Lota, separated from other members of subfamily Lotinae around 10 MYR ago. It was present in Europe in Early Pliocene (5.3-3.4 MYR) and colonized North America in Early Pleistocene (1.8 MYR-0.73 MYR) [Van

Hoydt et al 2003]. While the nearctic populations survived climatic oscillations in different refuges, the palearctic burbot went close to extinct. The present palearctic distribution range was re-colonized during Late Pleistocene (130.000-10.000 YBP) [Van Hoydt et al 2003], contemporary with the Eurasian settlement of Homo sapiens. Based on the genetical divergence that resulted, two subspecies are suggested, L. l. lota in Eurasia and Alaska, and L. l. maculosa in North America south of Great Slave Lake (Van Hoydt et al 2003; 2005).

Table 1. Burbot Lota lota (L. 1758) classification (Froese et al 2015), Jacobs et al 2009, Myers et al 2015).

Taxon	Classification	Common name	Comments
Class	Actinopterygii	Ray-finned fishes	~ 42 orders, ~ 431 families, ~ 24.000 species
Order	Gadiformes	Cods and hakes	10 families, 475 species
Family	Lotidae	Tusk, lings, hakes and burbots	6 genuses, 21 species
Species	Lota lota (Linnaeus 1758)	Burbot	

1.2.2 General anatomical and behavourial characteristics

Figure 2. Anadromous burbots from Location 1 in Rickleån March 11th, 2007. Above, female, age 6 years, 53 cm TL, 965 grams, immature. Below, male, age 6 years, 58 cm TL, 1.155 grams, immature.
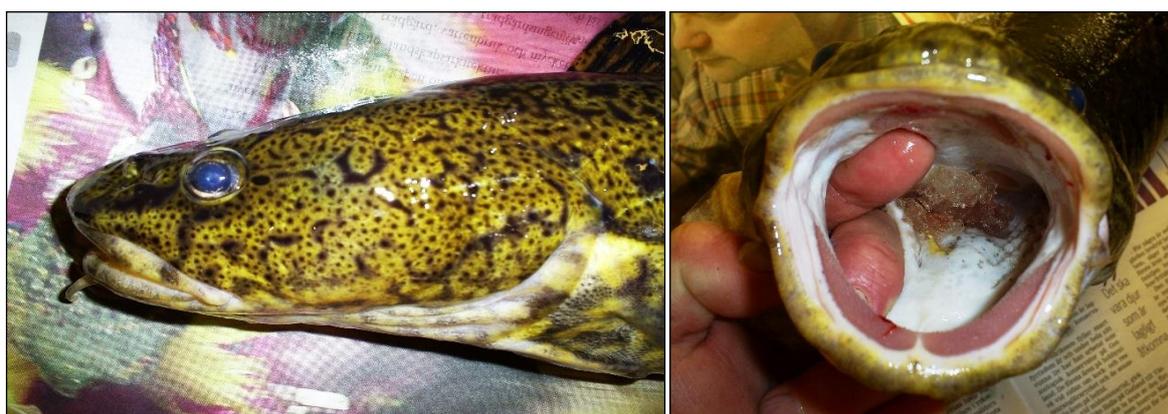
Figure 3. a) Chin barbel and pairwise nostril barbels on a male, 59 cm TL and 1.285 grams; b) teeth plates on a female, 68.5 cm and 2.285 grams

Burbots are elongate fishes with cylindrical bodies (fig. 2). Heads are flattened with rather large mouths, one single chin barbel and two pairwise nostril barbels (fig. 3a). Colouration

is greyish, olive green and yellow, overlaid with brown and black patterns and spots, and lighter belly. All fins are spotted (author´s own observation), with large, paddle-like pectorals, small pelvic fins located anterior, long anal fin (58-79 rays) and rounded caudal fin (40 rays). There are two dorsal fins, the anterior one is short and a long posterior dorsal fin (67-96 rays)[Cohen 1990, Jacobs et al 2009]. Regular teeth are absent, instead the burbot has got teeth plates in the upper and lower jaws, consisting of hundreds of small teeth (fig. 3b). The scales are small and cycloid. Maximum life span has been reported to 20 years (Muus et al 1968). Maximum size has been reported to 152 cm and 34 kg, from Siberia (Morrow 1980). The burbot is a predominantly demersal and stenothermal predator, with crepuscular and nocturnal foraging periods (Froese et al 2009, Jacobs et al 2009). It ambushes or stalks prey of various kinds (Bengtsson 1973, Jacobsson et al 1976, this study). The burbot rely mainly on olfactory, taste and acoustic stimuli when detecting, encountering and capturing prey. Even blind burbots, with eyes long-time absent (wounds fully healed) seem to maintain functionality and condition (author´s own observations).

1.2.3 Life history of anadromous burbots

a) Egg and young-of-the-year: Ontogeny and descent of juveniles

Burbot roe show similar survival, 91 %, in freshwater, oligohaline and slightly mesohaline water, with salinity between 0-6 ‰ (Jäger et al 1981). The roe is stenothermal. In laboratory conditions, embryonic development only occurs between 1-7 $^\circ$ C with an optimal temperature around 4 $^\circ$ C (Jäger et al 1981). Burbot roe during incubation is able to withstand low pH levels but newly hatched larvae are very sensitive (Kjellman et al 1996, Kjellman 2003). This is a matter of interest in the Gulf of Bothnia area since many of the rivers are episodically acidified. The first larvae, around 3-4 mm long (Ryder et al 1992, Fischer 1999), are found in the end of April in low-current streams/pools in rivers (Hedin 1983; Hudd et al 1983), but hatching may continue at least until the third week in May (Hudd et al 1983). During laboratory conditions, larvae starts to inflate the swim bladder after three days, and both yolk sac and oil droplet are fully resorbed after 15 days, when all larvaes are feeding exogenously. The mortality is high, 60 %, during this period (Palińska-Żarska et al 2014). After yolk sac atrophy, fry has been reported to forage diurnally and pelagically, sometimes in small schools, on copepods and cladocerans (Ryder et al 1992). In laboratory conditions, larvae do not feed unless water temperature reaches 8 $^\circ$ C (Jäger et al 1981), and show similar survival in the range between 8 $^\circ$ C -20 $^\circ$ C (Jäger et al 1981). Preferred habitats are deeper parts of rivers (Ryder et al 1992; Hedin 1983; Johnson 1981). After reaching 30 mm, burbot fingerlings become solitary and benthic, and switch to nocturnal foraging (Ryder et al 1992). This was contradicted by Solem (1973), who found the diel rhythm somewhat desynchronized until late July, 50-60 mm TL. After late July, Solem (1973) observed a nocturnal and crepuscular diel rhythm. The growth of young-of-the-year burbots indicate positive temperature-dependence. Kjellman et al (2002) found correlations between 0+ growth and increasing water surface temperatures between 4-18 $^\circ$ C. Hofmann et al (2003) concluded that food consumption rate in juveniles (age 0) during experimental conditions were at maximum at 17.9 $^\circ$ C, while maximum growth was achieved at 16.0 $^\circ$ C. The juveniles reach around 90-100 mm in late autumn (fig. 4; Eriksson et al 1982, Kjellman et al 2002, Lawler 1963, Hanson et al 1980, Sandlund et al 1985), but decreasing water temperatures slow down the growth rate (Eriksson et al 1982, Kjellman 2002). Anadromous juveniles descend to the Gulf of Bothnia between the end of August (52-92 mm TL) to the end of January (62-127 mm TL), with peaks in late autumn

and early winter (Hedin 1983; Johnson 1981, Eriksson et al 1982). Descent is nocturnal (Eriksson et al 1982). Lunar cycle seems to affect descent of juveniles, with increased number of migrants around new moon (Eriksson et al 1982, Müller et al 1982, Müller 1983). Lunar periodicity is maintained beneath a meter of snow and ice, in clear or cloudy weather. The mechanisms of this lunar periodicity is still unknown (Müller et al 1982).
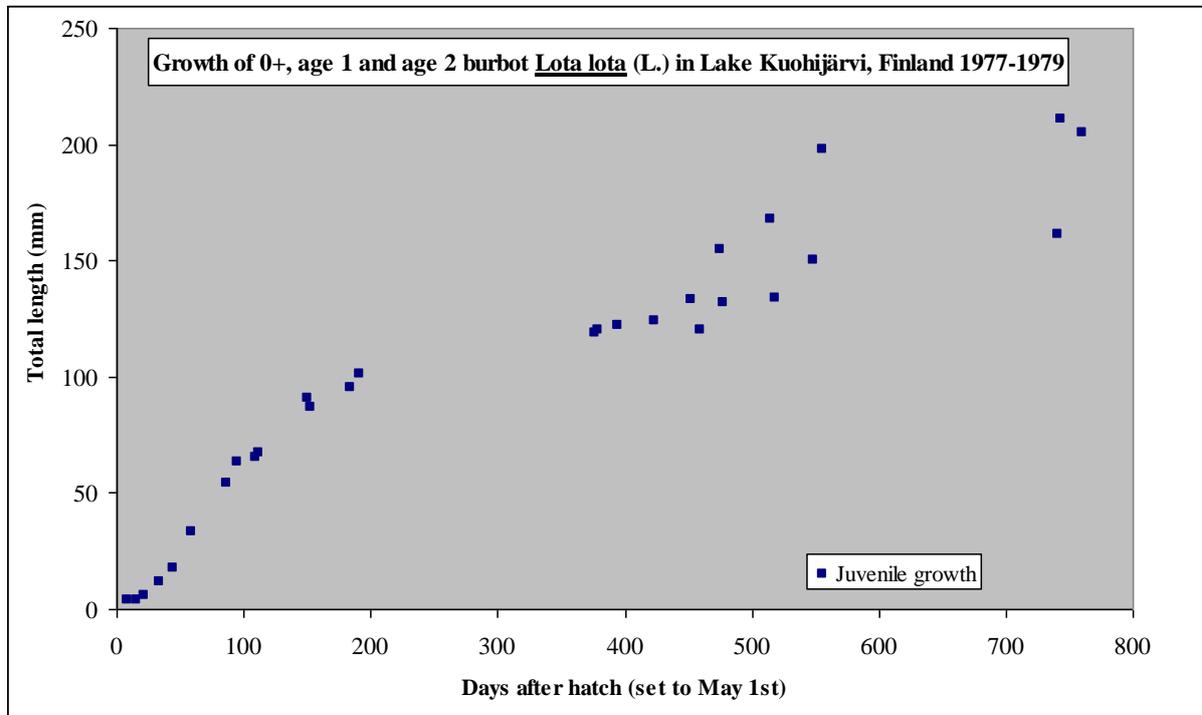
Figure 4. Burbot juvenile growth in Lake Kuohijärvi 1977-1979 (After Kjellman et al 2002).

b) Age 1 and older

Smaller burbots, age 1-2 years, forage mainly on fish and fish roe, crustaceans and benthic insects (Lawler 1963, Bailey 1972, Hanson et al 1980, Sandlund et al 1985). Older burbot, age 3 years and above, maintain a broad diet, but with a higher prevalence of fish (Clemens 1951). Temperature preference is lower for older burbots than for 0+ individuals. For age 1 year, this has been calculated to between 11.4 ^{o} C (Hofmann and Fischer 2002) and up to 13.5 ^{o} C (Hardewig et al 2004) or 14.2 ^{o} C for age 2 year (Hofmann and Fischer 2002). Large water bodies, like the Gulf of Bothnia, heat up and cool off slower. This enable the burbots to utilize the richer littorals and shallow bays for a longer period during the summers (Müller 1987). As a comparison with potamodromous populations, Hardewig et al (2004) found that burbots in River Oder, Germany, endured high summer temperatures by endogenously lowering metabolic rate. This was done by down-regulation of enzymes involved in aerobic metabolism. In Lake Opeongo, Canada, burbots exhibited lower swimming activity in summers (Carl 1995). Generally, all-year-around growth in burbot is enabled through metabolization of energy-rich liver tissue from July-October, and synthesis of liver reserves from October-December and from March-July (Pulliainen et al 1990, Holker et al 2004). Burbot, as many other gadiform fishes, have a limited amount of intramuscular or subcutaneous fat tissue. Instead, fat is stored in the liver, and serves as energy store during poor conditions. Hence, the total condition status in burbots in Gulf of Bothnia is at its lowest levels between July-October (Pulliainen et al 1990; 1993). The

beginning of this period coincide with maximum surface water temperatures in the area (Eriksson et al 1982, SMHI 2009), and forces the burbot to desert the shallows for the poorer and cooler profundal zones further out from the coast (Boström 2006, Müller 1987; Hudd et al 1987). The warmest summer months are spent off the coastal areas within a 10-20 km radius from the spawning stream (Müller 1987; Hudd et al 1987). Documented burbot prey species in this habitat are herring Clupea harengus and smelt Osmerus eperlanus (Pulliainen et al 1992, Lehtonen 1973). Generally, riverbound populations do not mix, and the burbot does not enter the open sea (Hudd et al 1987; Müller 1987; Müller et al 1982). Salinity in the Gulf of Bothnia and the main part of the Baltic Sea as a whole does not seem to be a limiting factor. Mesohaline salinity approaching 6-7 ‰ is evidently tolerable for the adult burbot as large specimens are regularly caught in Kalmarsund, between the mainland Sweden and the island Öland (SMHI 2006; The Swedish Anglers Association 2006). This contradicts statements made by Jäger et al (1981).

c) Maturity and migrations

Age at maturity in anadromous burbots in the Gulf of Bothnia is 3-5 years (Müller 1987). For comparisons, this is similar to Lake Erie (Clemens 1951b), and slightly later than for instance Lake Superior (Bailey 1972), Lake Simcoe (McCrimmon et al 1954) and Lake Winnipeg (Bailey 1972). On the other end of the scale, burbots mature at age 7-8 years in Vilyuy River Basin, Siberia (Kirillov 1988). Anadromous burbot in the Gulf of Bothnia exhibit homing behaviour, and ascends their birth rivers from late August-January. The peak is in January, later than earlier findings (Hedin 1983; Johnson 1981, Müller 1987). Navigation to birth rivers seems to be guided by olfactory stimuli only, as long-distance displacement experiments can disrupt homing behaviour (Müller 1987). The ascending rate is quite rapid, and has been estimated to 0.7-2.5 km/day, where migration was faster during the new moon phase (Hedin 1983, Müller 1987). Migration activity increases after sunset, with most fishes entering the river at midnight (Hedin 1983; Müller 1987). The enhanced numbers of ascending (and descending, see 1.1.3d) individuals after dusk (Hedin 1983, Müller 1987) indicates crepuscular and nocturnal activity periods throughout the entire year. These habits are also indicated elsewhere (Carl 1995). Somewhat contradictory, Müller (1969, 1973) found that burbots in alpine Lake Messaure, northern Lapland, changed diel rhythm twice a year, diurnal between November to spawning, and nocturnal after spawning to October.

d) Spawning and descent

Spawning in rivers in connection with Gulf of Bothnia occurs between the first and third week of February, with the peak around the second week in February, one or two weeks later than earlier findings (Bengtsson 1973; Müller 1970). Sandy substrate is preferred (Müller 1970; Bengtsson 1973). The burbot mating system seems to be neither competitive nor territorial. Spawners form a spinning globular mass with females in the center, and release gametes collectively (Bengtsson 1973, Froese et al 2006, Jacobs et al 2006). After spawning, the burbot descends after not more than a couple of weeks with some few individuals as late as May-June (Johnson 1981, Müller 1987, Hedin 1983). Some of the adult burbots present at the spawning sites in winter and spring are immature, but these are not in lesser physiological condition than the mature ones (Pulliainen et al 1990; 1993).

1.3 Burbots and humans in Sweden: Fisheries, attitudes and legislation

The burbot was formerly mainly considered as a food and game fish. They are catchable, potentially large, nutritious and offering recreational angling with an old cultural heritage. Even the sapmi people stocked burbot in many mountain lakes in Lapland in order to provide a secure protein source (Andersson 2008, Englund 2008, pers. comm.). In the 1940s, there was an intense harvest for Swedish household consumption. In the 1950s it was lower, but especially in the north, it increased strongly in the 1960s-1980s, due to Finnish market interest (Andersson 2007, Rönnberg 2007). From mid-end of the 1970s and onwards, many anglers started targeting large burbots (fig. 6; app. 2). This inspired the improvement of angling methods and localization of new undisturbed populations (Brugård 2006, pers. comm.). Consequently, the number of game fish registrations increased. From mid-1990s and on, despite maintained interest and efforts among anglers (fig. 5; app. 1), the number of registrations have declined nationwide (fig. 6; app. 2). Recreational inland fisheries in general harvest around fifteen times more than the commercial inland fisheries (fig. 5; app 1.). I failed to find specific burbot data, but as being more popular as game than market fish, I assume that the recreational burbot harvest exceeds the commercial catch.
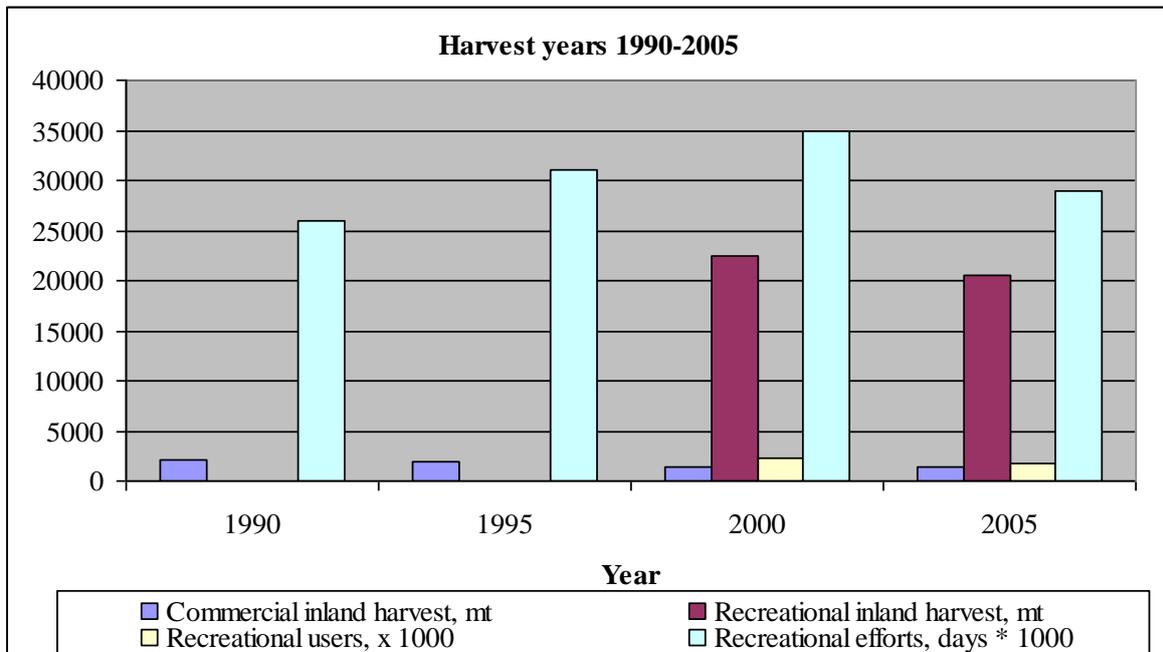
Figure 5. All-species commercial versus recreational inland harvest (mt = metric tonnes = 1.000 kg). Also, the number of recreational users and efforts, year 1973-2005 (app. 1; The Swedish Board of Fisheries 2005).
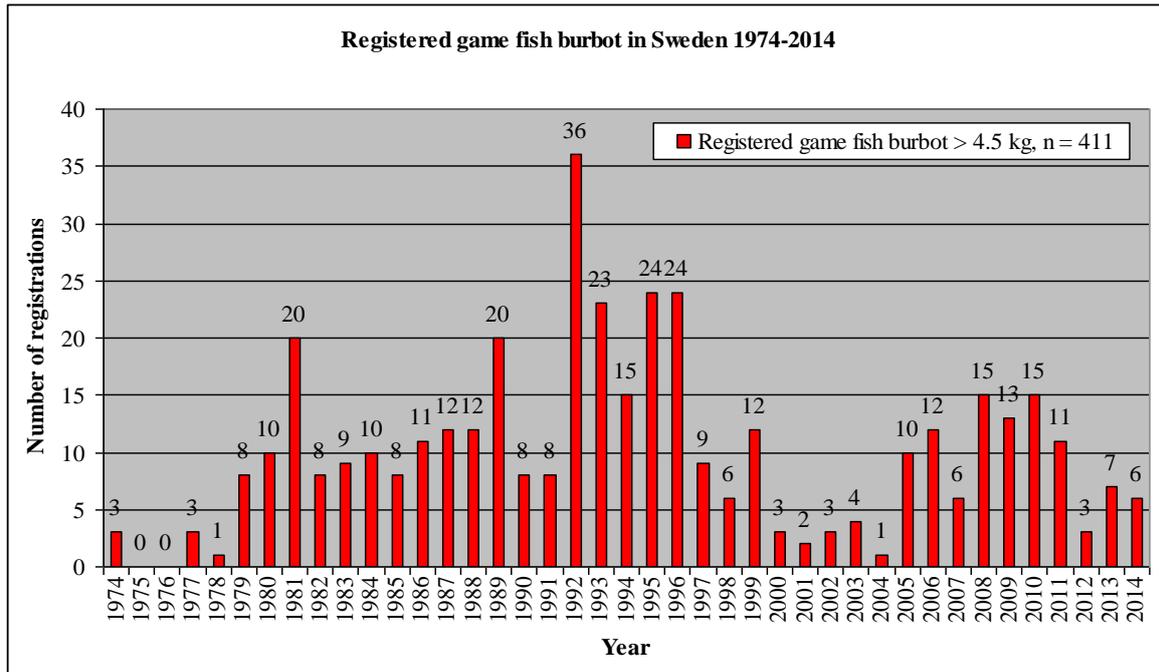
Figure 6. Game fish burbots 1974-2014 (app. 2; Swedish Association of Anglers, The Game Fish Register).

The human impact is further enhanced due to:

a) Burbot spawning behaviour

Burbots aggregate in high densities at spawning sites well before spawning, and are easy to catch (fig. 7).

b) Legislation/regulations

Figure 7. One angler, 4 hrs, 58 burbots.

Burbots have not been protected. There have been no restrictions regarding season, bag or size limits. Until 2010, the burbot has been the only freshwater species where methods when the hooks intentionally are jerked anywhere into the fish (fig. 8) are allowed (The Swedish Board of Fisheries 2009). This has been a very common practise in the large lakes, like Vänern and Vättern, and caused many lethal or disabling injuries on burbots (author´s own observations). Before 2010, the only exceptions were in some private fishery management areas where it was banned (Nyman 2009).
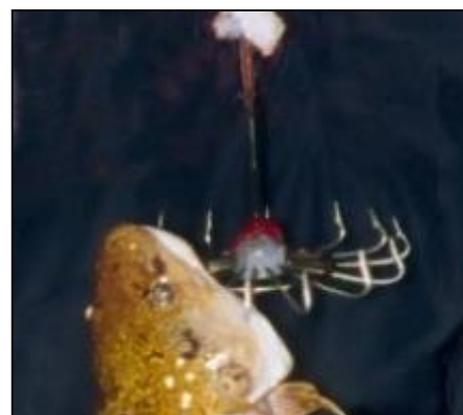
Figure 8. Fishing with "kräggla".

c) Human attitudes

Many anglers regard burbot as a junk fish or pest species, "that threaten more valuable fish species and their roe". Many burbots are killed and discarded annually (author´s own observations).

1.4 Populations in the study

The general national trend, decreased abundance of large burbots from mid-1990s and onwards, is also appearing in two anadromous populations in the Gulf of Bothnia area, in the rivers Sävarån and Rickleån (fig. 9). Both rivers are medium-sized mesothropic rivers with forestal and agricultural catchment, modest slope, similar discharge, some hydro-electrical power plants, sparse human habitation and industry, and similar fauna and flora. They are both episodically acidified without liming, but Sävarån has been limed since 1991, and rarely reach pH levels below 6.3. On the contrary, in spring the unlimed Rickleån regularly reach pH levels down to 5.8 or possibly even lower. Measurements have not been made during the highest water levels (Västerbotten County Administrative Board 2009). Recreational burbot angling is more substantial in Sävarån (Bengtsson 1973, author´s own observations 1988-2014). There are also at least two commercial fisheries around Sävarån (Andersson and Rönnberg 2007), but none recently around Rickleån (Boström 2007).
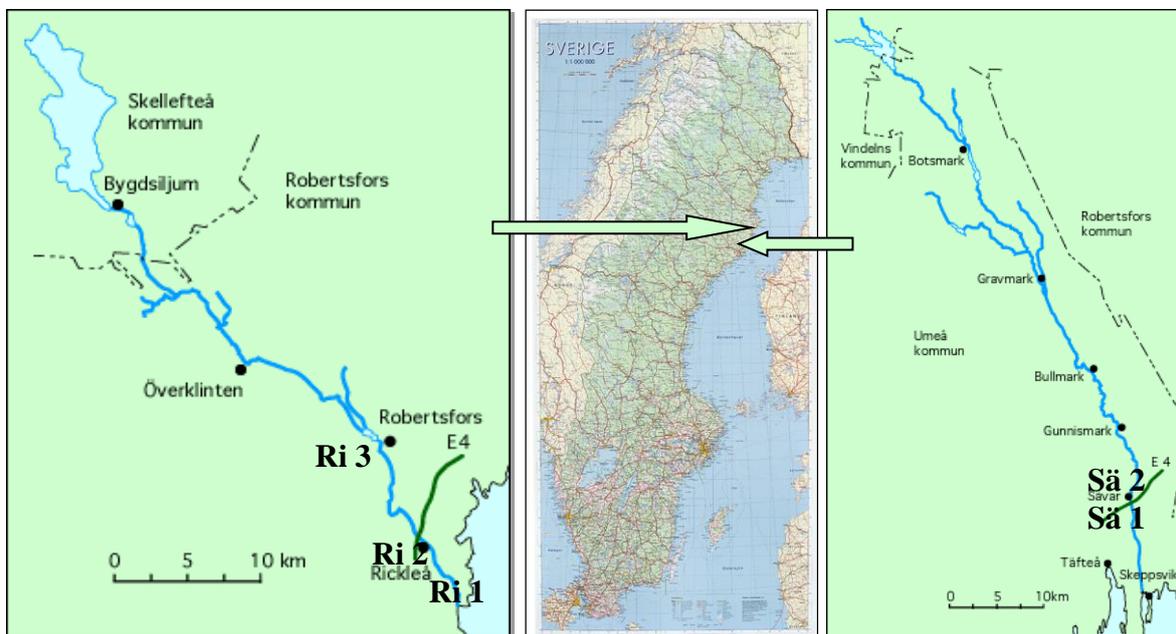
Figure 9. The rivers in the study, with sampling locations (Sigvardsson 2007). More info in 2.1 and 2.2.3.

1.5 Aim of study

Primarily, I wished to find out if the spawning populations differed in

a) Age structure, otolith appearance and annuli formation
b) Body size, growth, length-per-age, organ weights (indexes) and fish condition.
c) Timing of spawning and indications of former spawning events
d) Sex ratio and sexual dimorphism
e) Stomach content, food preferences and foraging activity
f) Parasitic infestation of liver and liver colour
g) Relative population density (CPUE)
h) Activity periods correlated to moon phases

Secondly, I wished to explain detected differences, and third, summarize conclusions and make management recommendations.

2. Material and methods

2.1 The rivers

2.1.1 Rickleån (blue field in all tables)

Table 2. Comparisons between Rickleån and Sävarån (Västerbotten County Administration 2009).

PARAMETER	Rickleån	Sävarån
Catchment area (km2)	1649	1161
Source lake	Bygdeträsket-Göksjön	Lossmenträsket
Percent lakes (%)	8,9	6,3
River length (km)	48	103
Slope (m)	131	262
Environment		
Landscape	Forestal, agricultural	Forestal, agricultural
Bedrock	Mainly gneiss	Mainly gneiss
Soils	Upper parts: Mainly wetlands and moraine; Lower parts: Increased occurence of bare bedrock, glacial sediments and fine lake and sea sediments.	Mainly wetlands and moraine; esker, riverine sediments and fine marine sediments, sparsely acid sulfate soils.
Hydroelectrical plants	4	2
1st plant location	15 kms upstream	12 kms upstream
Flood (m3/sek)	90-190	70-150
Flow, normal (m3/sek)	18	12,5
Flow, low (m3/sek)	2-4,5	1,2-2,5
pH levels in spring	Regularly below 6.0	Limed. Normally above 6.3

Rickleån´s (tab. 2; fig. 9) water catchment area is 1649 km^2. Lakes represents 9 % of the area, with Bygdeträsket and Göksjön as the largest. The bedrock is mainly composed of gneiss, some granite or gabbro upstream Bygdeträsket. In the upper parts, moraine and wetlands dominate. In the lower reaches, downstream Bygdeträsket, the bare bedrock, glacial sediments and fine-grained lake and sea sediments increase. Hydro-electrical power plants are situated in four locations, one in Älglund and three in Robertsfors, where fish ladders were constructed in 2002 and improved in 2006. The main river is not limed, and is episodically acidified, regularly reaching pH below 6.0 in spring. The river contains sea trout Salmo trutta L., Baltic salmon Salmo salar L., European grayling Thymallus thymallus (L.) and common whitefish Coregonus lavaretus (L.). There are also burbot Lota lota (L.), roach Rutilus rutilus (L.), ide Leuciscus idus (L.) and Eurasian minnow Phoxinus phoxinus (L.), the petromyzontids European brook lamprey Petromyzon planeri Bloch 1784 and European river lamprey P. fluviatilis (L.), Eurasian perch Perca fluviatilis L., northern pike Esox lucius L., bullhead Cottus gobio L. and European crayfish Astacus astacus L.. Possibly, European smelt Osmerus eperlanus (L.) occurs in the lower reaches (author´s own observation). Ruffe Gymnocephalus cernuus (L.) and vendace Coregonus albula (L.) are found in other locations in the water catchment area, like Lake Bjursjön. Freshwater pearl

mussel <u>Margaritifera margaritifera</u> (L.) occurs in the upper parts of the water catchment area but not in Rickleån (Västerbotten County Administration 2009).

2.1.2 Sävarån (yellow in all tables)

Sävarån (tab. 2; fig. 9) is a Natura 2000 area and of national environmental concern. The source lake is Lossmenträsket. Other large lakes are Stor-Sävarträsket and Lill-Sävarträsket. The water catchment area is 1.161 km^2. The river falls 262 meters on the 103 km towards the Bay of Bothnia. The upper parts are quite flat and rich in lakes, while the lower parts are more rapid and with few lakes. The proportion of wetlands is 22 %, forest 68 % and lakes 6.3 %. Gneiss is the main constitution of the bedrock. Main soils are peat bog and moraine. Downstream the highest postglacial coastline, the moraine is affected by sea movements. Sävarån partly follows an esker, but cuts also through riverine sediments. Fine marine sediments, some of them acid sulfate soils, occur sparsely. Hydro-electrical power plants are situated in two locations, in Kroknäs and Sävar. A fish ladder was constructed in Kroknäs in 1998. Sävarån was heavily affected of acidification in the 1980s, with occasional pH levels below 5.0. Hence, a liming programme in the main river started in 1991. The ichthyofauna is similar to the one in Rickleån, but with more numerous anadromous spawning spring migrations of ide <u>Leuciscus idus</u> (L.), roach <u>Rutilus rutilus</u> (L.) and freshwater bream <u>Abramis brama</u> (L.). Sävarån also differs from Rickleån since there is common dace <u>Leuciscus Leuciscus</u> (L.), and a more sparse population of European river lamprey <u>P. fluviatilis</u> (L.) . The Baltic salmon <u>Salmo salar</u> L. population is considered as valuable and the sea trout <u>Salmo trutta</u> L. is slightly increasing. Moreover, the river contains a viable population of freshwater pearl mussel <u>Margaritifera margaritifera</u> (L.). The European crayfish <u>Astacus astacus</u> L. population is sparse, despite efforts to re-establish the species.

2.1.3 Reference populations

In addition to the two study populations, I also sampled burbots, or utilized burbots sampled by Umeå University or Västerbotten County Board Administration, and friends, from 13 other watersheds and lakes. These were used as reference populations. Tavelån river, ten kilometers south of Sävarån, was chosen in order to see general patterns of otolith formation in anadromous burbots, as well as to compare other parameters in the study. One was either entirely brackish, or anadromous (Västerviken, outside Ånäset). This sample was chosen in order to study the period March-September, for instance the marine diet of burbots. One population could be defined as landlocked and riverbound (Kalix river above Jokkfall), nine were potamodromous lake populations within 80 kms radius from Umeå, and also, one subalpine lake, Landösjön, was included as reference (tab. 4). Landlocked riverine or lacustrine potamodromous populations were compared with anadromous populations, and were also used to gather information from even younger individuals, in this case down to 1+ (fig. 10).

Nr	Location	Type	n
1	Abborrtjärn	Lake	3
2	Bjärten	Lake	3
3	Kalix river	River	1
4	Landösjön	Lake	8
5	Långviskasjön	Lake	1
6	Mjösjön	Lake	4
7	Mörtsjön	Lake	4
8	Stensvattnet	Lake	1
9	Stor-Holmsjön	Lake	1
10	Sunnansjö	Lake	4
11	Tavelån	River	22
12	Vångsjön	Lake	2
13	Västerviken	Sea	27
	TOTAL		81

Figure 10. Reference populations in the study. Nine lakes in the boreal coastland, one sup-alpine lake, one bay in Gulf of Bothnia, one landlocked riverine, and one anadromous riverine.

2.2 Sampling

2.2.1 Sample size, gear and sampling methods

Figure 11. Main gear

888 burbots were sampled during the study between years 2001 and 2014, and 807 of these in Rickleån and Sävarån. With the burbot, a voracious and cold-active omnivore predator detecting prey primarily with lateral line and olfactory reception, regular ice angling gears (fig. 11) can enable high CPUE with low selectivity. Some details needed to be addressed, although. Hook and bait type and size, as well as angling technique, needed to be adapted for the purpose. I chose single hook, 5/0, and 6-8 cm^2 large filets of herring/whitefish. The spoons were moved continuously, gentle to enable catch of small individuals. During the study, this method produced a CPUE of 2.4 individuals/person/hour, as well as a size range from 100 grams (25 cm) – 2.285 grams (69.5 cm). Moreover, hand-held equipment do not become saturated, and sampling is equally efficient the entire sampling period. During ice-free periods, rod, reel and bottom-fishing with sinker, herring bait and hook was used. Each rod represented one angler. A total of 829 burbots (449 in Rickleån, 357 in Sävarån, 22 in Tavelån and 1 in Kalix river, were sampled with these techniques. In the remaining reference populations, other methods had been used, like electro-fishing, fyke- and gillnets. I chose fyke net samples, as gill nets are more selective. Also, I used their longest sample period and largest sample size. The burbots I caught were consumed after data collection.

2.2.2 Period and time of day

Sampling in the two rivers, was carried out in 121 days, 102 in Rickleån and 19 in Sävarån, between years 2001-2014, except 2010-2012. Rickleån was sampled September 23rd-April 7th, and Sävarån December 27th-March 10th, during the riverine phase of anadromous burbots. Reference populations were sampled mainly by other actors, and methods, between years 2006-2008 and 2014. About time of the day Müller (1970) found distinct

activity peaks in burbots after sunset, between around 18:00 to 20:00, something that is also testified by many anglers. Hence, sampling was carried out mainly between 18:00-22:00.

2.2.3 Locations

Among a number of tested locations, I chose slow-current reaches and pools in each watershed, all well-known burbot angling spots (fig. 9):

Site Ri 1, *Rickleån*, "Sea Pool", upstream rivermouth, slow-medium current, depth 1-3 m.
Site Ri 2, *Rickleån*, slow-current reach between the E4 and Ricklea bridge, depth 1-3 m.
Site Ri 3, *Rickleån*, slow-current reach 300 meter downstream the lowest hydro-electrical power plant, downstream Robertsfors township, depth 1-3 m.
Site Sä 1, *Sävarån*, "Water sewage treatment plant", slow-current reach at the water sewage plant 400 m downstream highway E4, depth 1-3 m.
Site Sä 2, *Sävarån*, "Church Pool", at Sävar Church, slow-medium current, depth 1-3 m.

All sampling locations were located within 15 kms from rivermouth and upstream, and downstream the first hydro-electrical power plant (fig. 9).

2.3 Collection of data

2.3.1 Age

I started with a study visit at the Institute of Freshwater Research in Drottningholm, Stockholm, where I received a first-class crash course in the basics of otolith reading, by PhD Johan Hammar and PhD Eva Bergstrand. With this inspiring new knowledge, as well as some kindly donated equipment, I was ready to go. One pair of *sagitta* otoliths was collected from each individual as soon as possible, cleaned, dried, stored in paper envelopes and labelled. Before ageing, I stored otoliths in 70 % ethanol to enhance annuli visibility. At least a few days of ethanol storage facilitated readings. Otoliths that were difficult to read, were grinded with a wet-stone on the distal side. I put the otolith pairs in black embryo bowls with 1,2-propanediol. Annuli were counted on the proximal sagittal plane of the otoliths, using a dissecting microscope set between 6.9 - 40 X magnification. Reading was performed in different directions, particularly towards the dorsal, anterior and posterior edge (Stuby 2000). Comparisons were made between the two otoliths in each pair, then I chose the best one for further counting/measuring. Moreover, each otolith pair was age estimated at least twice, to clarify the repeatability. As hatching occurs between the end

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How condition, liver and stomach, correlated with otolith increments

Pulliainen et al (1990) showed that intestine tissue decrease in burbots from Gulf of Bothnia, from June-September. Also liver tissue decreased, from July-October. Furthermore, they found the highest occurrence of empty stomachs in July-September (41-60 %). This is also the timing for ascending rivers, which cost energy and limits foraging. Pulliainen et al (1990) also found that intestine tissue increases again between September-November, and correspondingly that liver tissue increase from October to December. This corresponds with the spawning of salmonids, and ascent of river lamprey Petromyzon fluviatilis (L.), which provides both salmonid rye and fish to forage on. In January-March, Pulliainen et al (1990) found that liver index decreased again, when final allocations to gonads are made.
From March-June, between spawning/descent, and late summer warmth, liver tissue increase (Pulliainen et al 1990). Holker et al (2004) found that burbots in River Oder used energy stores in the liver during the summer and replenished the liver reserves in the winter. Also in Oder, a hyaline field should be deposited during late summer.

Notes 1. Condition vs. otoliths increments.

of April until the third week of May (Hudd et al 1983), May 1st was chosen as a baseline for hatching for further age calculations. Burbot otoliths show rather distinct annuli (fig. 12-20), with alternating hyaline rings and opaque fields. Rings that appear hyaline in reflected light indicate periods of poorer conditions, and opaque fields the opposite (Panfili et al 2002). The annuli can contain either single or double hyaline rings. When there are double hyaline rings, I found that the inner (closer to the core) hyaline ring normally is formed from late summer-early autumn, followed by a thinner opaque field, maybe affected by the ascent of the preferred prey and the salmonid deposition of roe. The second, outermost hyaline field is finalized in October-November. It seems that there is a delay between the feeding/starvation, and the actual increment (Hammar 2006, pers. comm.). The thicker opaque field grows from November-May/June. This corresponds to the

findings of Pulliainen et al (1990), who found that feeding was most intense in late winter until June, and September /October. Bailey (1972) also used a reflected light against black background, and found opaque otolith edges during December-May, while hyaline edges appeared between June-November. Bengtsson (1973) found that the average volume of stomach content increased in January-February,

Ind	Age (yr)	TL (cm)	TW (g)
Mj1001	2+	17.5	35.0
Mj1002	1+	13.8	13.5
Mj1003	1+	11.5	8.0
Mj1004	1+	10.1	5.7

Figure 12. Mj1001-1004 (June 27th)

compared to March-December. Although these earlier findings were not entirely in accordance with mine, it was clear that winter starving was not the issue in anadromous burbot. True validation of age-estimation procedures was preferable (Beamish et al 1983), but too demanding for this limited study. Instead, I carried out semi-direct validation by estimating relative marginal distance (RMD). I did this by using a dissecting microscope with binocular ruler, set on 40 x magnification, measuring Absolute Marginal Distance (AMD) and the width of the last completed annuli, $D_{i,i-1}$ (modified from Panfili et al 2003). AMD is the distance from the end of the last translucent zone to the margin (fig. 13b); $D_{i,i-1}$ is the distance from the end of the second last fulfilled translucent zone to end of the last fulfilled translucent zone (fig. 13a). Then I divided AMD with $D_{i,i-1}$. This calculation estimated the percentage (%) of a completed annuli that AMD represented, without the possible biases due to individual differences in growth rates. Also, the bias related to the asymptotic decrease of growth rate with age, was minimized. I measured on the distal surface, both on the anterior/ posterior side and the dorsal side. The anterior side, used by some scientists, were

Fig. 13. Ri2002 (Dec 28th); a = $D_{i,i-1}$; b = AMD

frequently too unrepresentative, due to common irregularities on the otolith on the anterior side. The depositions of fields were more representative for the entire otolith on the posterior and the dorsal sides, even if those were denser. Annuli were still readable on the otolith edges, since few burbots were older than nine years. To further semi-validate otolith reading, and to compare growth rates between populations, I measured the widths of each annuli. This was made from the core and to the margin of the outermost hyaline field, then every subsequent annuli. Finally, I measured otolith lengths and widths, using a dissecting microscope with binocular ruler, set on 6.9 X magnification. Split hyaline rings may indicate earlier ascent (Hammar 2006, pers. comm.), and I also assumed that it indicated earlier spawning events. During the study I found that this was not true, since also immatures developed split hyaline rings (fig. 18-20).

Figure 14. Individual Ri1106, caught 2007-09-23, 64.5 cm/1.690 g, otolith length 12.8 mm, female, gonad index 0.015, estimated age 7 years and 4 months (8 years at spawning). October is the end of late summer-autumn starvation, and is seen as the completion of another annuli, comprised by one broad opaque field and a double hyaline field. Last double hyaline field almost fully deposited.
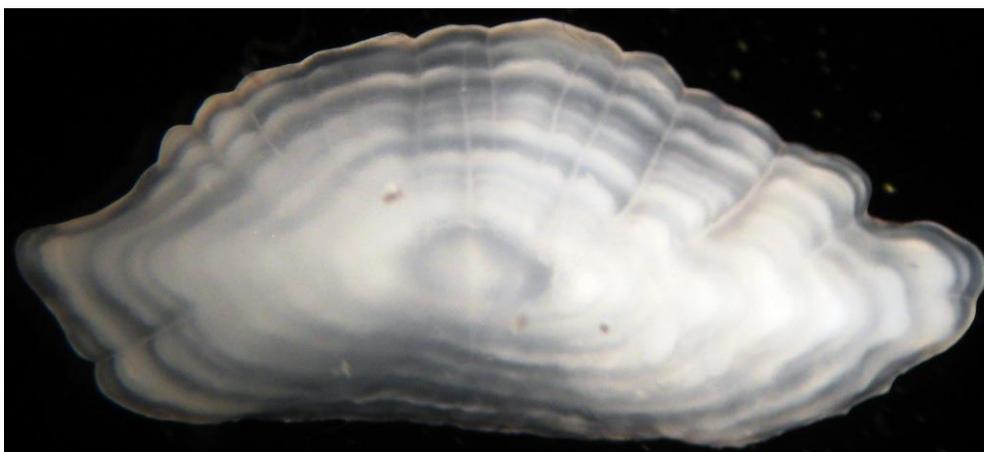
Figure 15. Individual Ri3026, caught 2008-10-05, 46.5 cm/545 g, otolith length 10.5 mm, female, gonad index 0.025, and increasing, estimated age 6 years and 5 months (7 years old at spawning). Here, last double hyaline field is fully deposited.
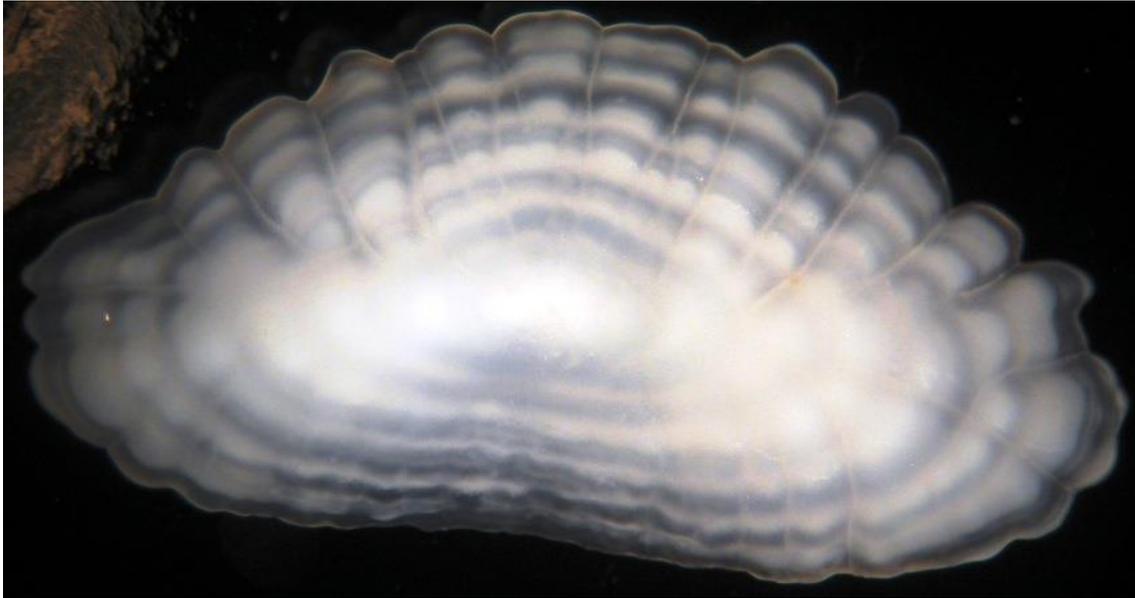
Figure 16. Individual Ri2044, caught 2008-12-14, 62 cm/1.480 g, otolith length 12.1 mm, female, gonad index 0.06, and increasing, estimated age 6 years and 7 months (7 years old at spawning). The opaque field in margin is now beginning to be deposited.

Figure 17. Individual Sä1045, caught 2008-02-06, 32 cm/150 g, otolith length 7.5 mm, male, gonad index 0.03 (spent), estimated age 2 years and 9 months (3 years). Young individual, faster midwinter growth field, only slightly weakened by spawning.

Figure 18. Individual Ri1086, caught 2007-02-25, 32 cm/185 g, otolith length 7.2 mm, female, gonad index 0.003 (immature), estimated age 2 years and 9 months (3 years). Fast midwinter growth field.

Figure 19. Individual Ri1101, caught 2007-04-01, 60 cm,/1.710 g, otolith length 12.2 mm, female, gonads 0.007 (immature), estimated age 6 years and 11 months (7 years). Half of the big opaque field now deposited.

Figure 20. Individual Ri1102, caught 2007-04-07, 68.5 cm/2.245 g, otolith length 13 mm, female, gonads 0.0003 (!, immature), estimated age 7 years and 11 months (8 years). More than half of the broad opaque field is deposited. Fast growth all years.

2.3.2 Size and growth

I measured total length (TL) from the tip of the snout to the end of the tail, using a measuring cradle, and total weight (TW) with a Pesola spring balance (scaled 0-2.500 grams). The accuracy of the balance (and reader) was regularly confirmed with an electronic Mettler Toledo PM 3000 scale (app. 3). When available, the Mettler scale was used directly. Growth was measured with length-at-age (cm), the "historical" growth of the individual throughout its lifespan. This was also correlated with indexes, per age group.

2.3.3 Organs and condition

In gonads, sex (male = yellow; female = blue, in tables), weight and reproductive stages, mature/spent/immature, were determined 2005-2014. Males and females are quite easily differentiated in all stages. Immature female gonads are orange/yellow in colour and with somewhat granular texture. Immature male gonads are beige/creamlike in colour, and fine-textured (fig. 21-25). Immatures found in the period around spawning had much higher liver index than matures and spent, since it is the liver tissues, more than feeding, that are used for development of gonads. Gonads are further resorbed after spawning, but liver tissues are naturally synthetized or metabolized at a slower rate, which facilitates determination of reproductive stages in the period I sampled, September-April.
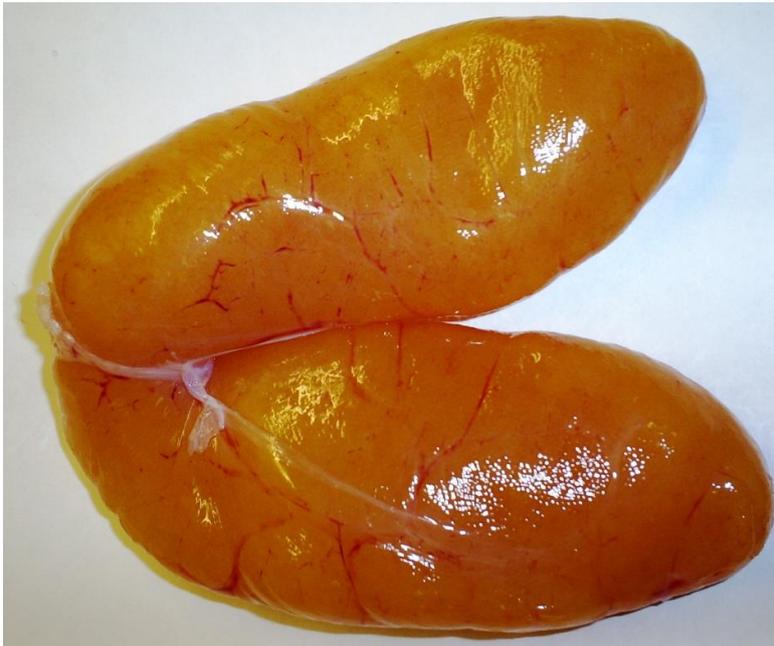
Figure 21. Ind. Sä1098, 2009-01-31, female, 63.5 cm/1.890 g, est. age 9, gonad index 0.15, liver index 0.21.
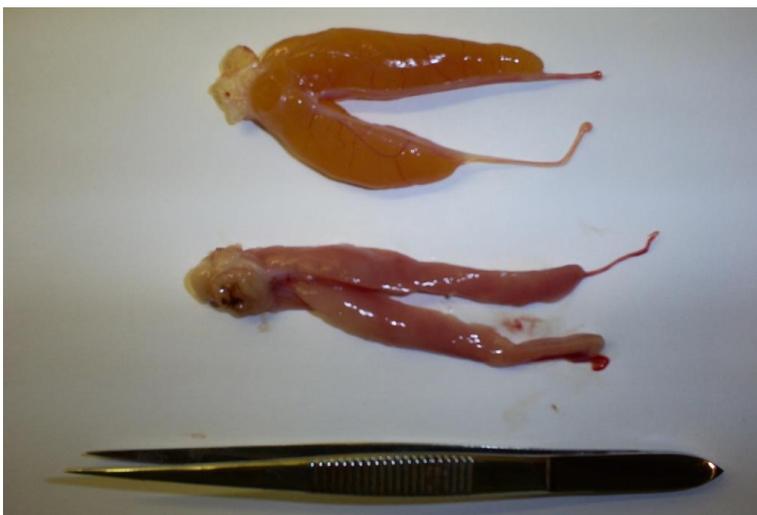
Figure 22. Two individuals, female Ri1091 and male Ri1092, caught 2007-03-11, female 53 cm/965 g, male 46 cm/640 g, both estimated age 6 years. Female gonads on the top, male gonads below. Whether these individuals were immature or spent was difficult to determine, since I have no information about the livers.
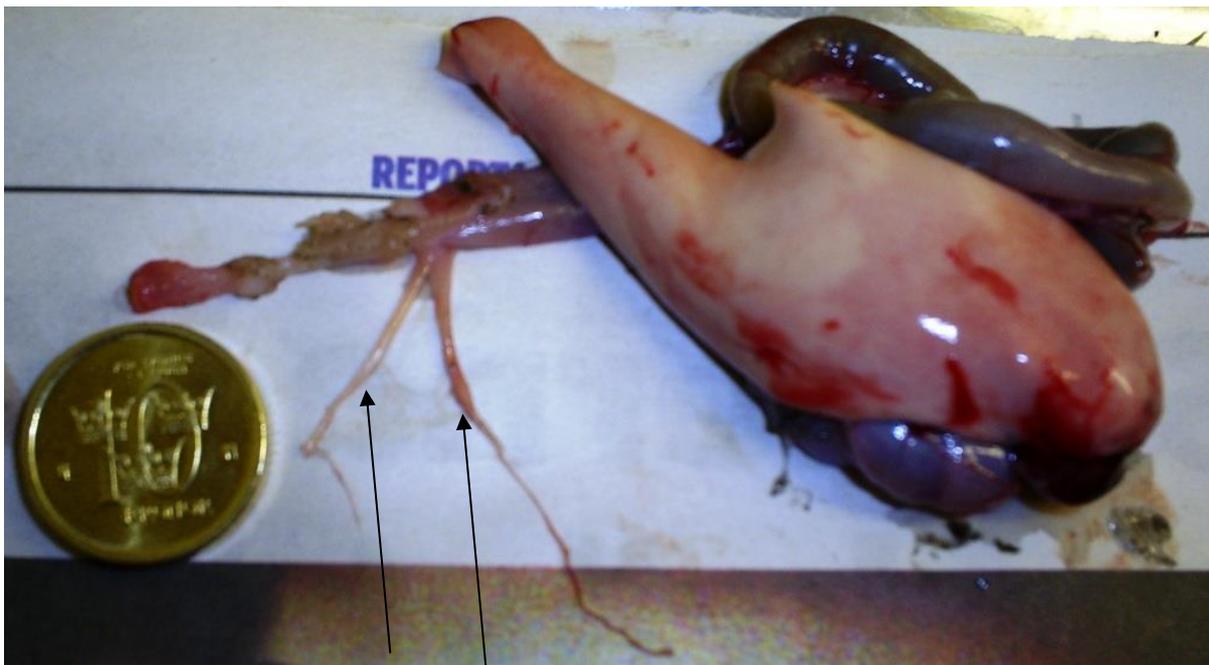
Figure 23. Individual Ri1097, caught 2007-03-24, 55 cm/1.040 g, est. age 7 years, immature male. Gonads are threadlike (arrows). Very large liver, although not indexed.
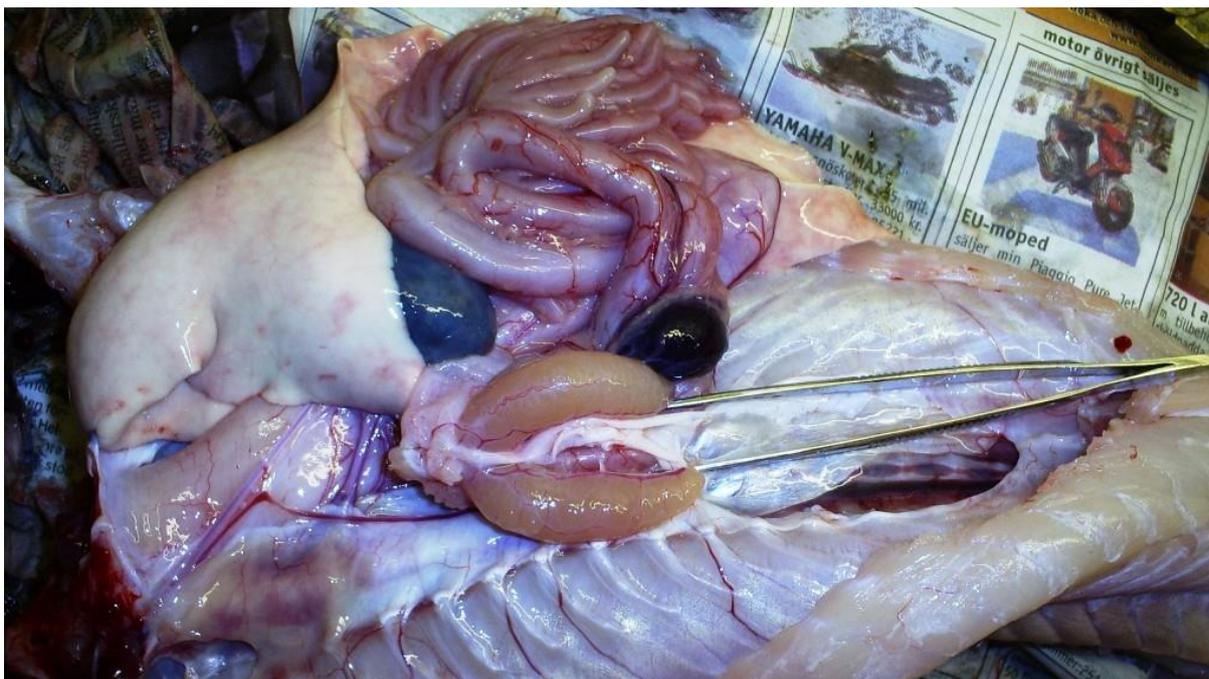
Figure 24. Individual Ri1100, 2007-03-31, 57 cm/980 g, est. age 7 years, immature female gonads. Although partly developed, some individuals do that. Very large liver, although not indexed.

In livers, I registered weight (2007-2014) and occurrence of parasites (2005-2014). I also registered liver colour deviation, from the standard white-beige (fig. 24).

In stomachs, I weighed both intact and emptied stomach (2009-2014), but used only intact stomachs in the results. The stomach contents were identified, and if possible, counted (2005-2014). Fish was identified to species level, invertebrates mainly not more than to

order level. When identification of prey item was impossible, terms as "fish", or "insects" were used.

With the organ weights, I calculated four organ indexes (*I*), gonad, liver, intact and emptied stomach, and also *K*, using intact body weight, with Fulton's (1902) proposed mathematical formula (also Misimi et al 2007; Pulliainen et al 1990):

K or *I* = 10^NW / L^3 where
K = Fulton's Condition Index (*K* was used in results)
N = Chosen value that brings *K* or *I* close to unity, in these cases N = 5 or 6
W = Weight in grams (for calculation of *K*, total weight; for *I*, organ weight)
L = Total length in millimeter

2.3.4 Population density

For relative population density estimations, I used catch-per-unit-effort (CPUE), calculated as number of anglers (or equipments) x hours, with data from year 2001-2014. These data were used for general population density estimates, but also for analyses of patterns of spawning, ascent, descent and their correlations with moon phases. The moon phases used, quantifying the moon light intensity, were new moon = "1", half moon (first and last quarter = "2" and full moon = "3". Capture dates were correlated with the nearest moon phase. In five sampling occasions (of 121), the date was exactly in the middle between two phases. These data were ignored. CPUE in my statistics, were either per interval, for example two weeks, or per sampling occasion. This depended on the analysis at hand.

2.3.5 Climate

I compiled and analysed annual average temperature (AAT, C ^{o}) data from The Swedish Meterological and Hydrological Institute (SMHI) and the Swedish Environmental Agency. Some of these data were also correlated with burbot data.

2.4 Statistical Analysis

I began with examining if my raw data exhibited the properties of normal distribution (Hesse 1998). With normally distributed data, I used Welch´s approximation of t for unequal variances, two-tailed P; [d(f)] = (n-2). In text, I only wrote "n", "t" and "P", and only *significant* results. In case of another distribution than normal distribution, I used Mann-Whitney´s U test. Correlations were made with Pearson´s r, expressed "r" in the text. [d(f)] = (n_{pairs} − 2). Significance of the Pearson's r value was calculated by transfer of "r" to t, using the formula by Miles 2015:

$$t = \frac{r \times \sqrt{n-2}}{\sqrt{1-r^2}}$$

The p value was then retrieved with Microsoft Excel (Miles 2015), typing "=tdist(t;df;2)", where the number "2" states "Two-tailed distribution of t". The final p-values were received with a free p-value calculator for correlation coefficients (Soper 2015).

3. Results

3.1 Age

3.1.1 Age estimates were accurate

My assumption was that the period from late autumn and into early summer, before late summer water temperatures force burbot further out in sea, generally represented a main growth period for the burbot, with exception of the period shortly before and during spawning. I also assumed that late summer to mid-autumn was the main starvation period, including both temperature-avoiding migrations to deeper areas in the Gulf of Bothnia, and ascent into rivers. I found the assumption to be accurate (fig. 25-26). The broadest opaque zones increased from October 5th and until my latest spring samples, on April 7th. In the individuals caught in September, these opaque fields were finalized, and single or double hyaline rings were found outside this. For simplicity I defined the start of the large opaque field to the end of the two hyaline rings, with a thin opaque field in between, one "annuli". Relative Marginal Distance, RMD (Panfili et al 2002), increased from an average of 9 % in October to 87 % in September (fig. 25; fig. 13). There were also strong correlations between individual's capture dates and relative marginal distances (fig. 26; $n = 213$; $r = 0.65$; $t = 12.4$; $P < 0.001$). The new annuli, after fulfilment of the outermost hyaline zone, began in month shift September-October (fig. 25; fig. 14-15). Deposition of largest opaque zone began in October, and spawning did not interrupt this field (fig. 14-20).
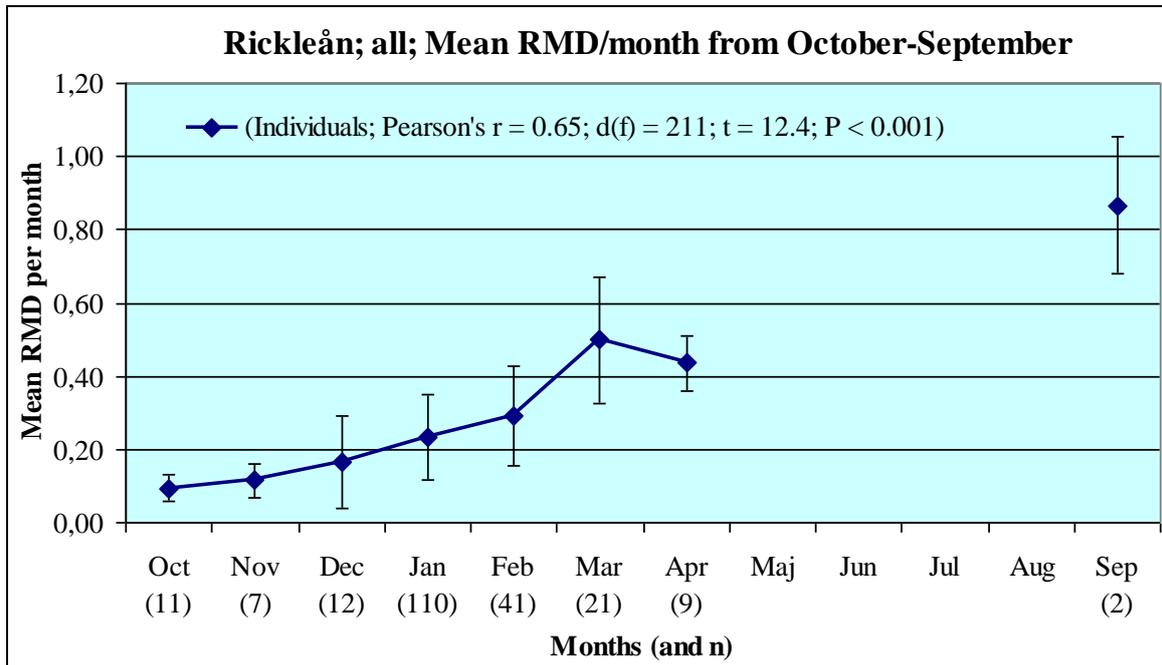
Figure 25: Relative Marginal Distance, Rickleån, montly average with StD. No data May-Aug (n = 213).
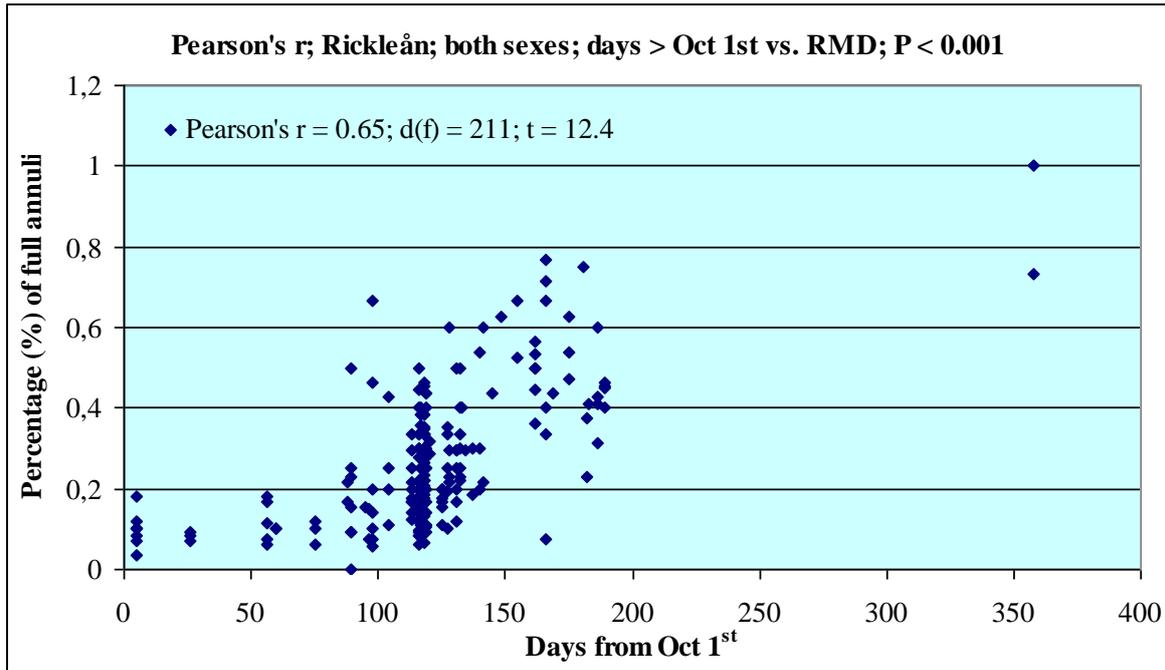
Figure 26: Pearson´s r, Rickleån, individual RMD vs. sample date from October 1st, all individuals (n = 213).

3.1.2 Otolith size and broadness were well correlated with fish sizes and condition

There were strong correlations between otolith size (mm) and total length (cm) in both rivers and both sexes (fig. 27; app. 4).
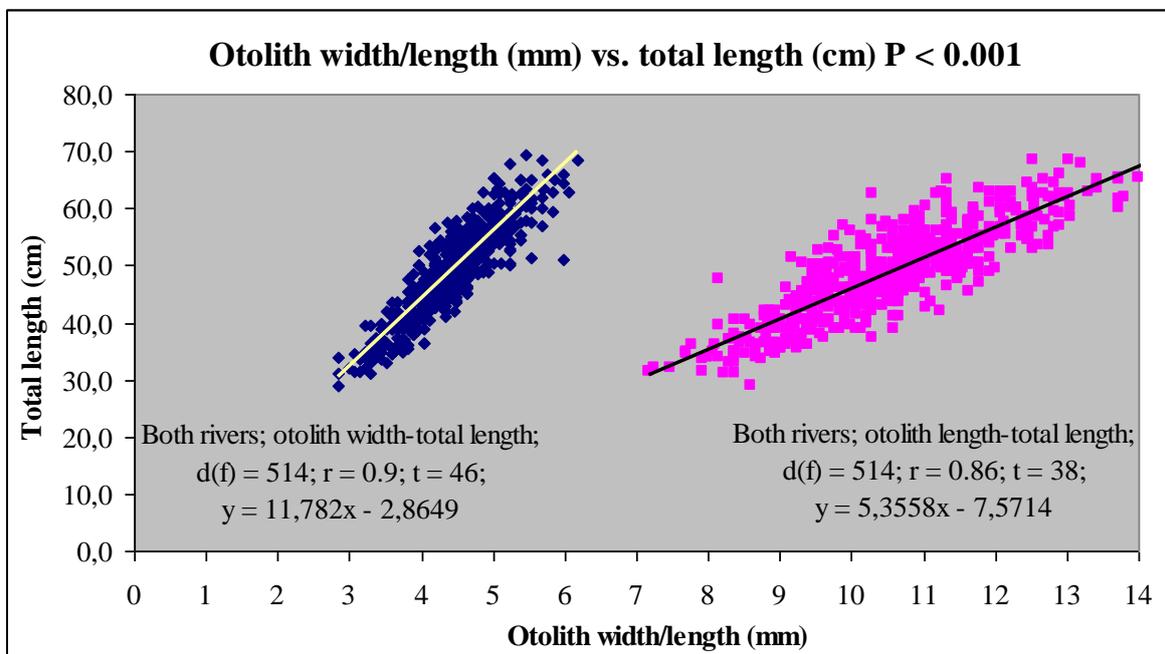
Figure 27. Otolith width and length (mm) against total length (cm). Both rivers compiled (app. 4).

There were also strong correlations between both ratio otolith width/otolith length (otolith "broadness") versus total length (cm), and liver and condition index (app. 5). This proves that a) larger individuals grew otoliths with broader appearance, and b) that burbots in better condition grew broader otoliths. Consequently, as expected from the size and condition differences, burbots in Rickleån had broader otoliths than in Sävarån (app. 6).

3.1.3 Spawners were older in Rickleån than in Sävarån, and females older than males

Spawners in Rickleån were older than in Sävarån (fig. 28; app. 7; Both sexes; Rickleån 6.8 years; Sävarån 6.4 years). Spawning males in Rickleån were also older than spawning males in Sävarån, and a similar result in females (app. 7; males Rickleån 6.6 years; males Sävarån 6.2 years; females Rickleån 7.1 years; females Sävarån 6.7 years). Females were also generally older than males at spawning (fig. 29; app. 7; Both rivers; males 6.3 years; females 6.8 years).
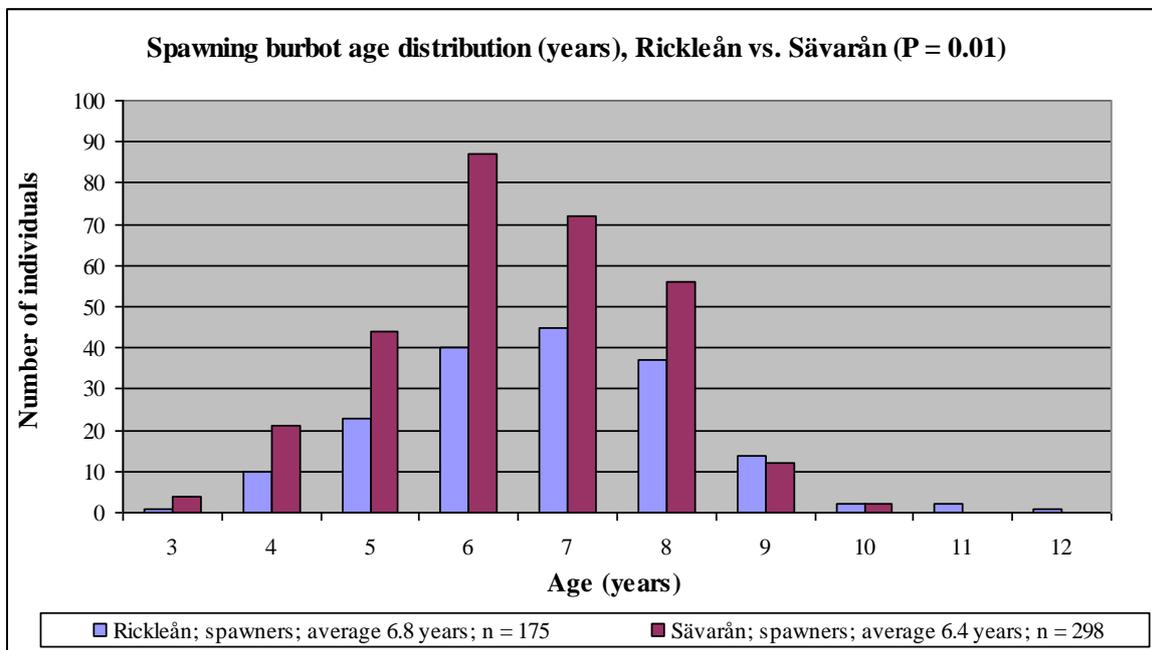
Figure 28. Age distribution in spawners (mature/spent), Rickleån vs. Sävarån (app. 7).
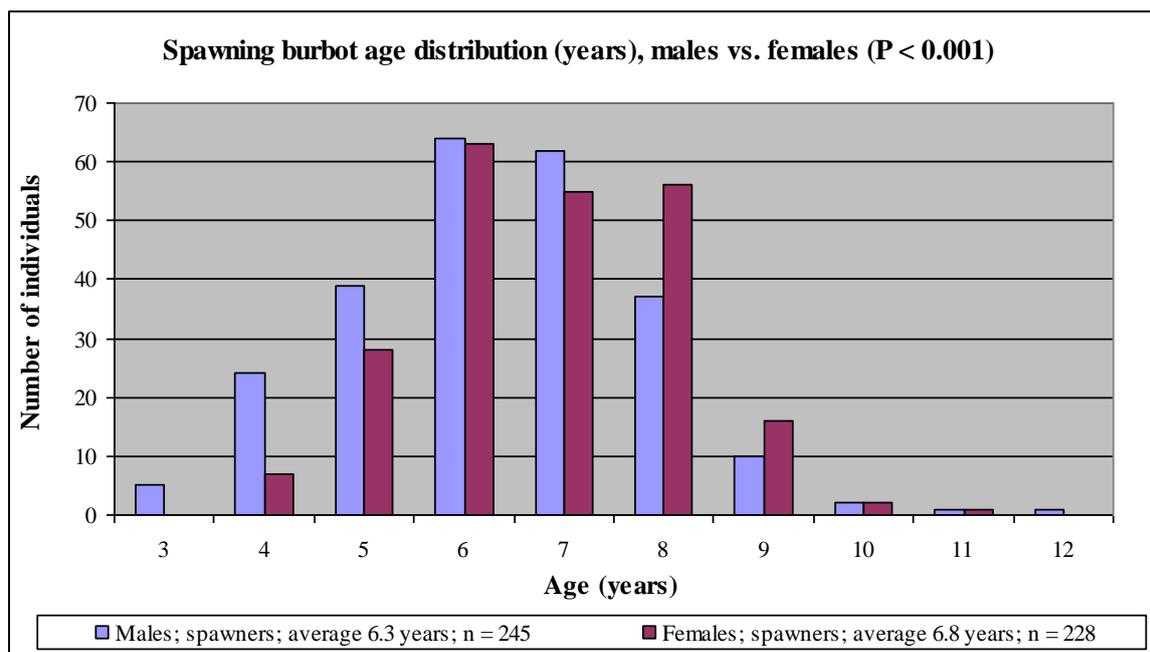
Figure 29. Age distribution in spawners (mature/spent), males vs. females (app. 7).

3.2 Size

3.2.1 Burbots were smaller in Sävarån than in Rickleån (and Tavelån)

Burbots were smaller in Sävarån (fig. 30-31; app. 8; all; TL Rickleån 51.9 cm; TL Sävarån 46.7 cm; TW Rickleån 933 g; Sävarån 625 g). Differences were maintained in matures Sep 23rd-Feb 17th, and in matures Jan 18th-Feb 17th (app. 8). Also, burbots in Sävarån were smaller than in Tavelån (app. 8). Size groups 40.5-50 cm/351-850 g dominated in Sävarån, while in Rickleån size groups 50.5-60 cm/601-1100 g dominated. In Sävarån, only 38 individuals (11 %) reached above 55 cm, while 269 (61 %) were below 40.5 cm (fig. 30-31). The differences were maintained throughout the study period (app. 11).
I also found indications that there were a considerable numbers of even smaller spawners present at spawning sites in Sävarån, although absent in my sample (fig. 31). Median total weight (g) in Sävarån were 11 % lower than average (app. 8). When plotting normal distribution, data in both ends dropped below the trendline, especially in Sävarån. This together proved that both the smallest and the largest individuals were under-represented in the sample (Hesse 1998). In the size-spectrum diagram using Total Weight, the distribution of data indicates that there are a large proportion of size class 0-100 g missing in my sample (fig. 31). This is further indicated by the fact that one very small individual (20 cm/45 g) found in a burbot stomach, was fully mature with high gonad index.
In general, females were larger than males (app. 9; all; males 47.6 cm; females 50.4 cm. However, length-at-age analysis confirmed that this was due to the age difference and not sexual dimorphism per sé (fig. 32; app. 10).
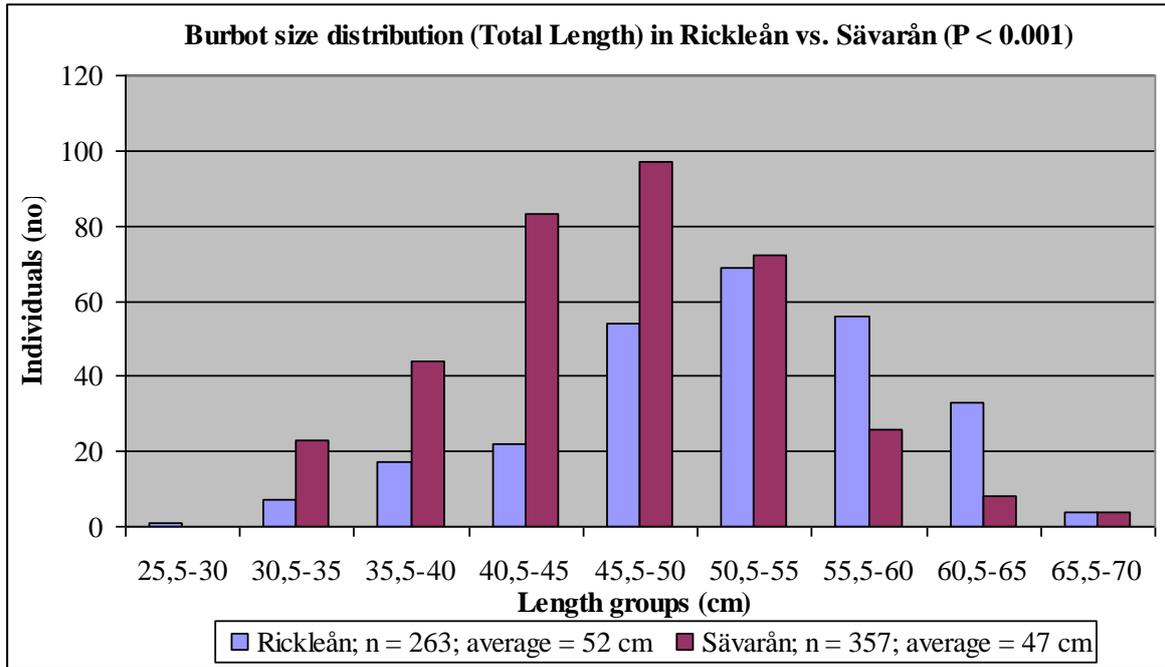
Figure 30. Size-spectrum diagram; Total Length (cm); Rickleån vs. Sävarån; full sample (app. 8).
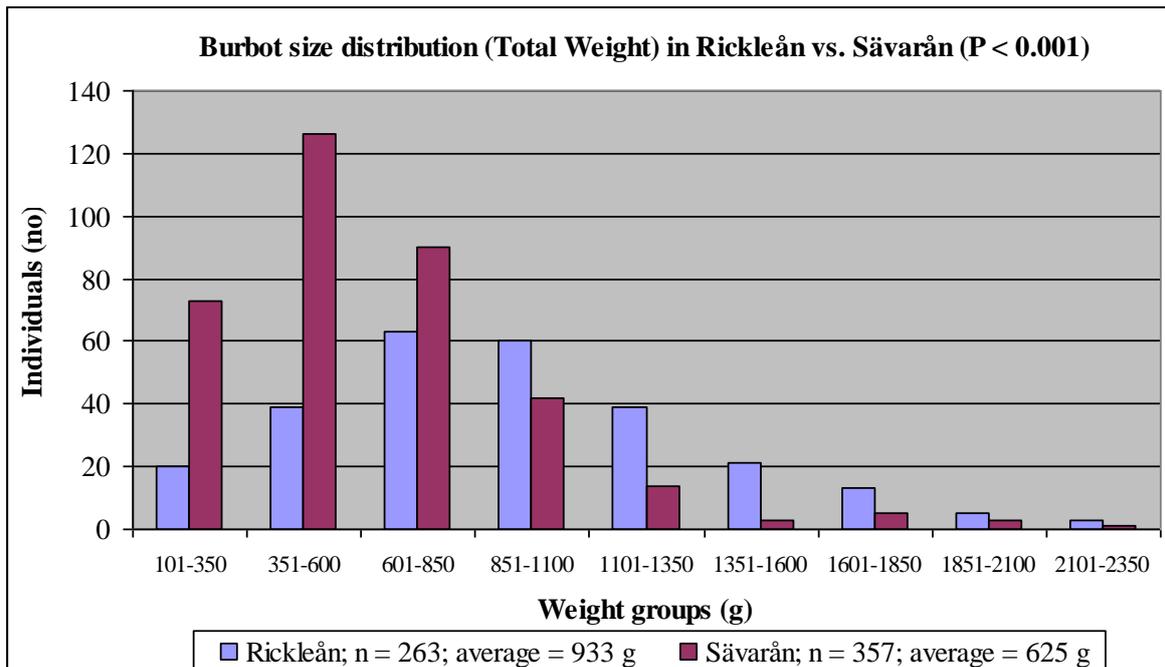
Figure 31. Size-spectrum diagram; Total Weight (g); Rickleån vs. Sävarån; full sample (app. 8).
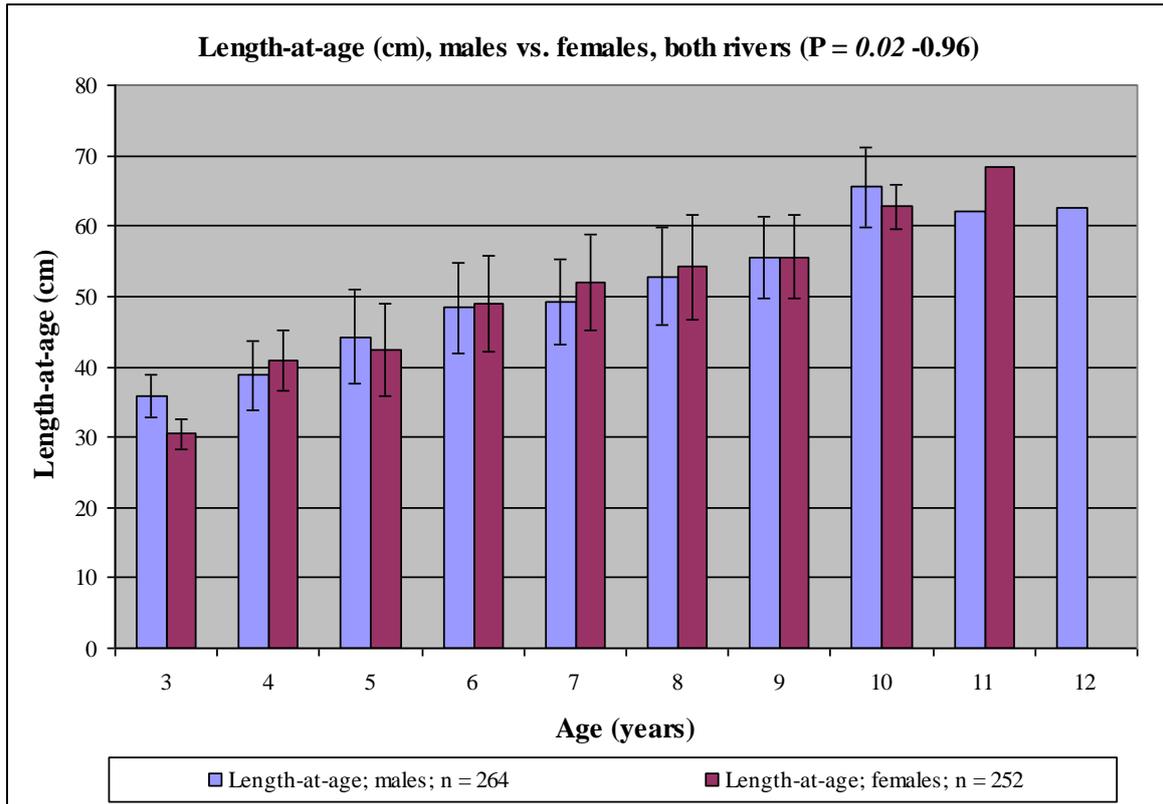
Figure 32. Length-at-age (cm); males vs. females; both rivers compiled (app. 10).

3.2.2 Burbots in Rickleån were smaller around spawning than in autumn/spring

Total length (cm) in Rickleån was larger before and after, than close to spawning. January differed from April and from November (fig. 33; app. 12). This indicated that large individuals ascended rivers first, and the smaller individuals ascended closer to spawning. Ascending individuals in spring were large and immature, foraging near rivermouth. Sävarån was only sampled between December 27th-March 10th, and could not be compared.
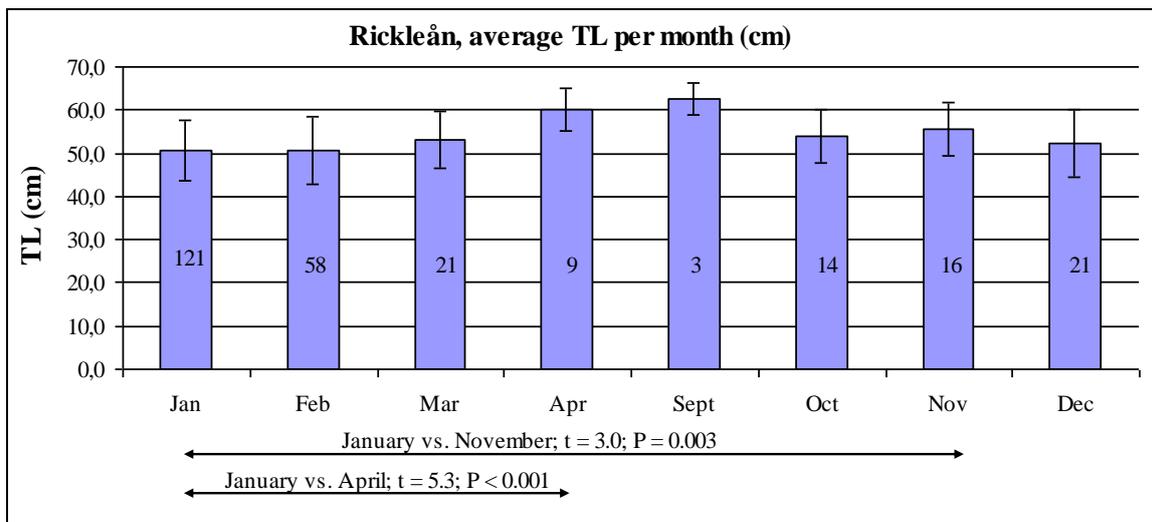
Figure 33. TL per month in Rickleån, with StD. TL in Jan differs from, respectively, Nov and Apr (app. 12).

3.3 Growth (Length-at-age)

3.3.1 Burbots in Rickleån grew faster in age 5-8 years than in Sävarån

Burbots in Rickleån had larger length-at-age (cm) in age groups 5-8 years. I found no burbots older than 10 years in Sävarån (app. 13; age 5-8 years; Rickleån TL 47.1-57.9 cm; Sävarån TL 41.2-50.3 cm). Immatures, common in Rickleån, grew faster (app. 14; age 5-7 years; TL immatures 52.3-56.7 cm; matures 46.0-52.4 cm). Since the ratio [aged immatures/total aged sample] differed (Rickleån 41/216 = 19 %; Sävarån 2/300 = 0.7 %), I needed to exclude immatures. In this analysis, burbots in Rickleån still grew faster (fig. 34; app. 15; age 5 and 7-8 years; Rickleån 46.0-57.4 cm; Sävarån 41.2-50.3 cm).
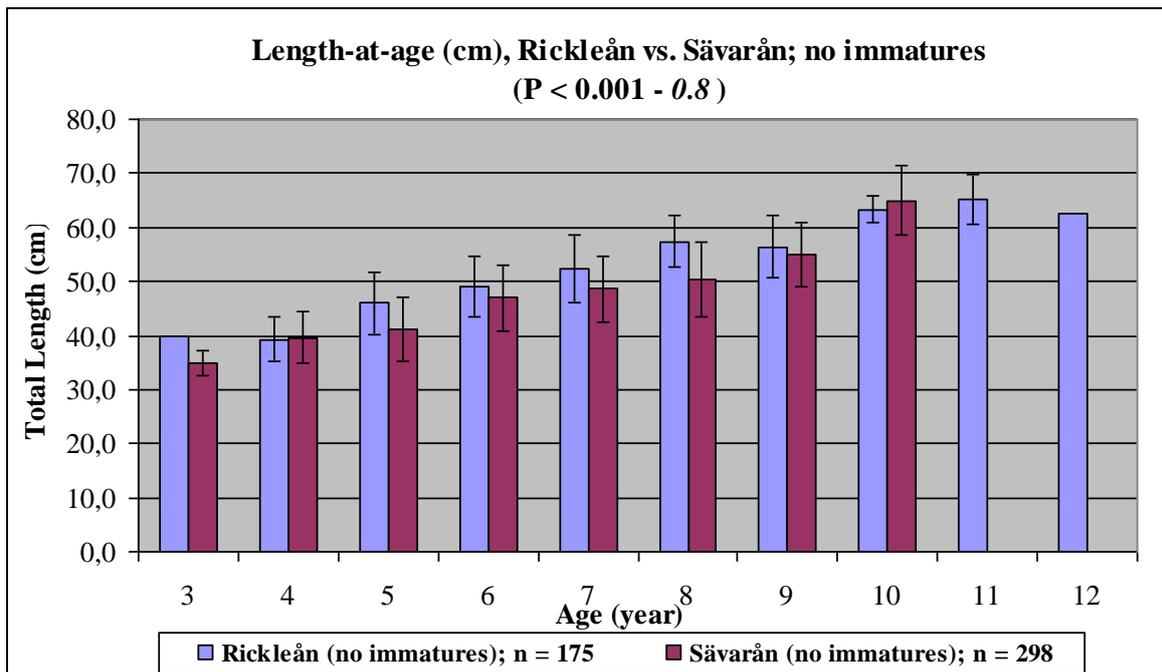
Figure 34. Length-at-age (cm); Rickleån vs. Sävarån; immatures excluded (app. 15).

3.3.2 Anadromous burbot in Gulf of Bothnia grew rapidly in comparisons

I analysed length-at-age data from a wide range of authors and locations, worldwide. This indicated that anadromous life strategies in the Gulf of Bothnia area were beneficial for burbot growth (fig. 35; app. 16). For example in Rickleån, where length-at-age in age 4-9 years (Bengtsson 1973) were larger than all compared populations. Also, the four populations with fastest growth, Rickleån (Bengtsson 1973), Simo (Pulliainen et al 1993), Rickleån (this study) and Lappfjärds å (Kjellman et al 1993), were all anadromous and/or brackish populations in the Gulf of Bothnia area (fig. 35; app. 16). Tavelån (n = 22) had similar growth tendencies. On the contrary, inland or landlocked riverine populations, had slower growth. Bengtsson (1973) also found that burbots grew faster in Rickleån than in three of the four largest lakes in Sweden, Vänern, Mälaren and Hjälmaren. Same tendency was found in Norway's largest lake, Mjösa, where average TL in 9 year old burbot still was smaller than 50 cm (Sandlund et al 1985). Bengtsson (1973) also found that landlocked burbots in Rickleån, upstream the hydroelectrical dams in Robertsfors, grew slower than the anadromous population. When comparing Rickleån now and in 1969-1971 (Bengtsson

1973), the data indicated that growth was slightly slower now, in all age groups (fig. 35; app. 16). Unfortunately this could not be tested, since I only had Bengtsson's (1973) average TL per year. The growth of burbots in Sävarån was slower than many other anadromous populations. Kjellman et al (1993) found that Sävarån had the slowest growth of all the compared burbot populations in the Gulf of Bothnia area. In my study, length-at-age was clearly higher in Sävarån, than in their study. Their length-at-age averages seemed less representative for Sävarån (age 3-9 years, were between 30-40 cm), and sampling occurred only in one year, 1984 (Kjellman et al 1993). Consequently, I excluded these data.
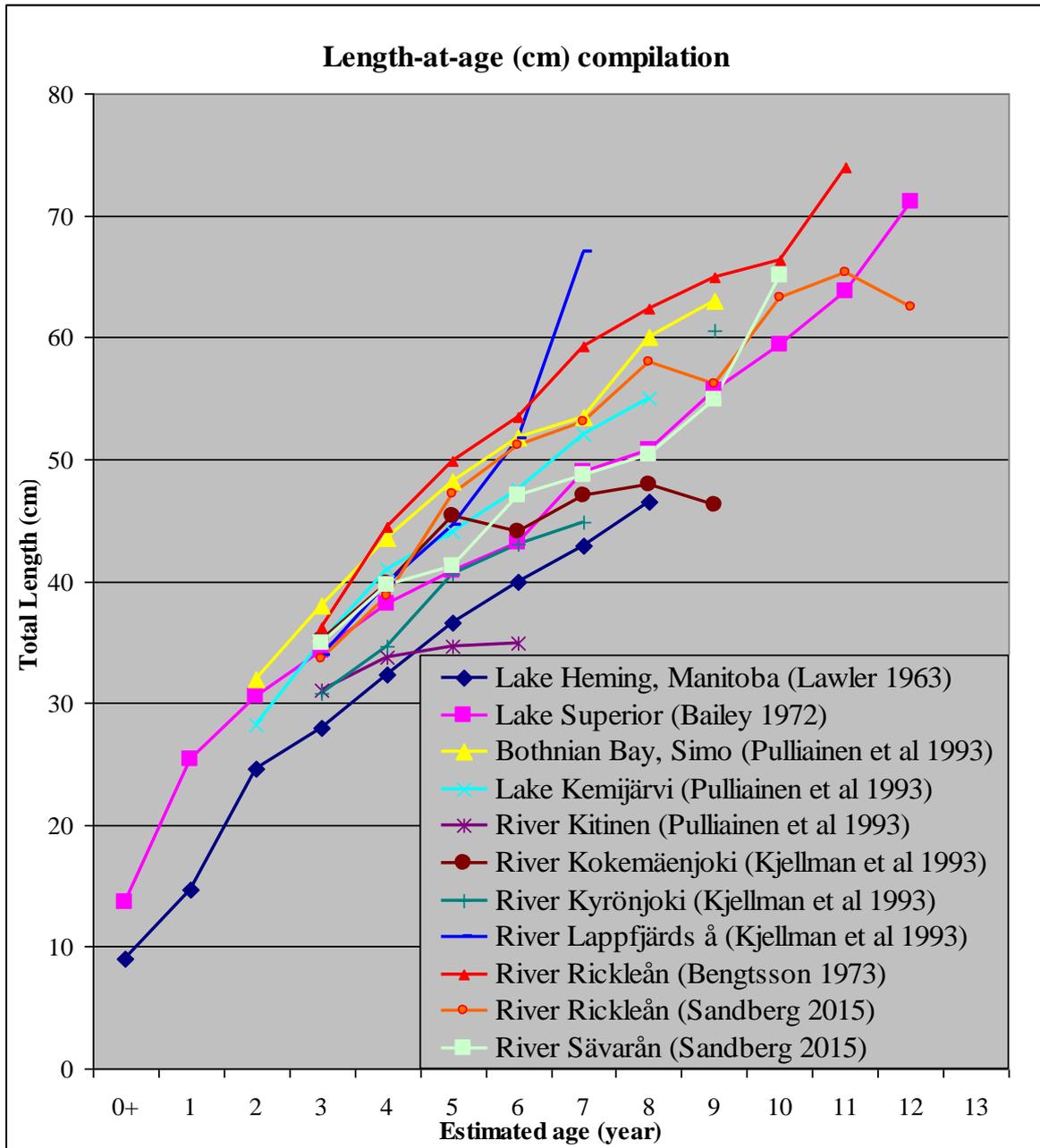
Figure 35. Length-at-age in two north-american boreal lakes compared with 8 lakes, rivers and brackish areas in the Bothnian Bay area. (app. 16; n = 67-1441).

3.4 Organ and condition cycles

3.4.1 Organ indexes and condition factor positively correlated, except gonads

All indexes (except gonad) and K increased after spawning and until late summer, decrease until November, increased slightly in November-December, then dropped until spawning. Gonad index was lowest between March-August, then increased until spawning. The sample proportion of immatures increased in March-April, which may have biased the liver index and K positively in these months. Also, bigger sample in July/August may had provided a better fit (fig. 36; app. 17).
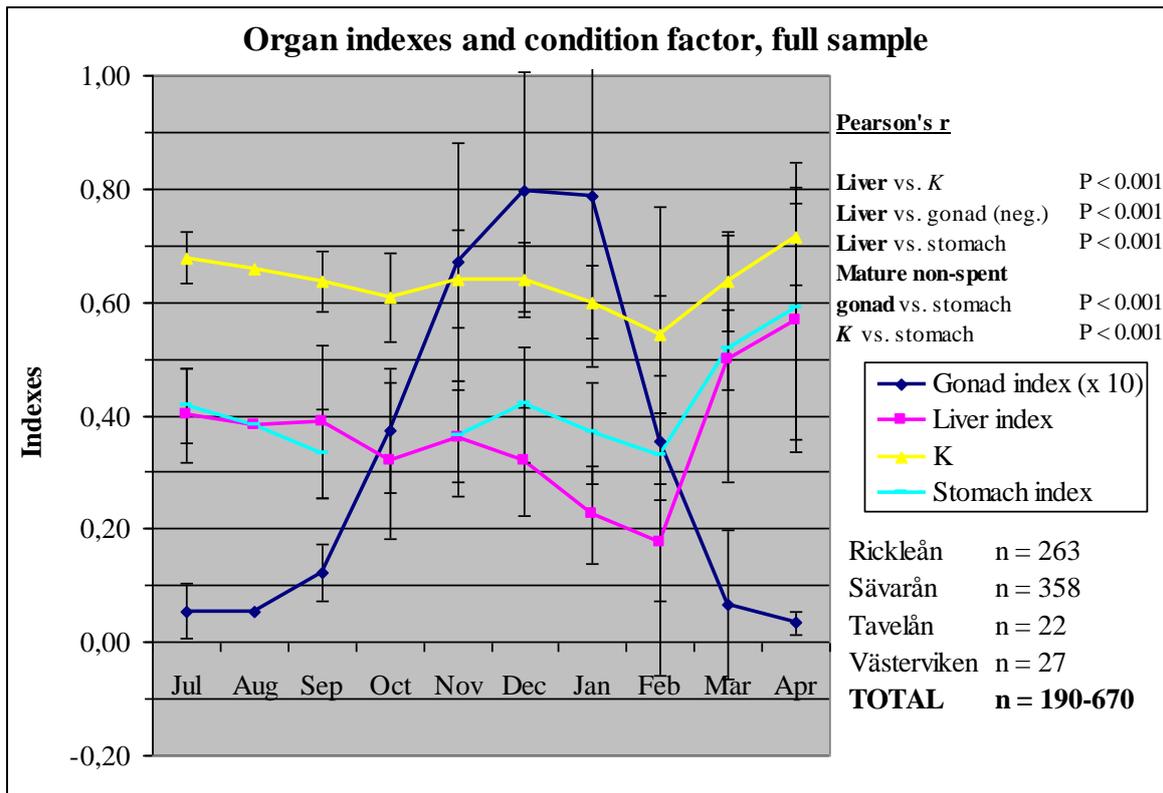
Figure 36: Organ indexes and K in anadromous/coastal burbot (Rickleån, Sävarån, Tavelån and Västerviken), per month, with StD. Samples from May and Jun is missing, also stomach content from Oct (app. 17-18; n[gonad] = 664; n[liver] = 419; n[condition] = 670; n[intact stomach] = 190; n[emptied stomach] = 190).

3.4.2 Foraging increased all indexes, and liver tissues were used for gonads

In correlations between gonad and liver, I could only use non-spent individuals, since the rapid loss of gonad tissue at spawning provides a bias. Here, I found a negative correlation between liver indexes and gonads (fig. 36; app. 18). This confirmed that liver tissue were used to develop gonad tissue. Correlations between gonad index and stomach indexes could only be done during the period when gonads grew (fig. 36), naturally excluding immatures. These indexes were also correlated (fig. 36; app. 18). This confirmed that the late autumn foraging had a positive effect on gonad development. The annual cycle of K was correlated with all organ indexes except gonads. Finally, liver index was correlated with stomach indexes. This proved that burbots enhanced feeding to build liver tissue, which from late summer was used for gonad growth.

3.5 Gonads

3.5.1 Gonad indexes did not differ between Rickleån and Sävarån, but between sexes

I excluded spent/immature burbots in gonad comparisons between rivers (ratio of spent/all in Rickleån was 13/263 = 5 %; Sävarån 112/357 = 31 %). Gonad indexes did not differ between Sävarån and Rickleån in the unstructured comparison (app. 19). Females, per size group, had higher gonad index (fig. 38; app. 21-22), and larger individuals (except males in Sävarån; fig. 39) had higher gonad index (app. 23). Since the sex ratios differed between rivers, and since burbots in Rickleån were larger, I compared the rivers per size class and sex, in the comparable time interval. Still, no differences were found (fig. 37; app. 20).
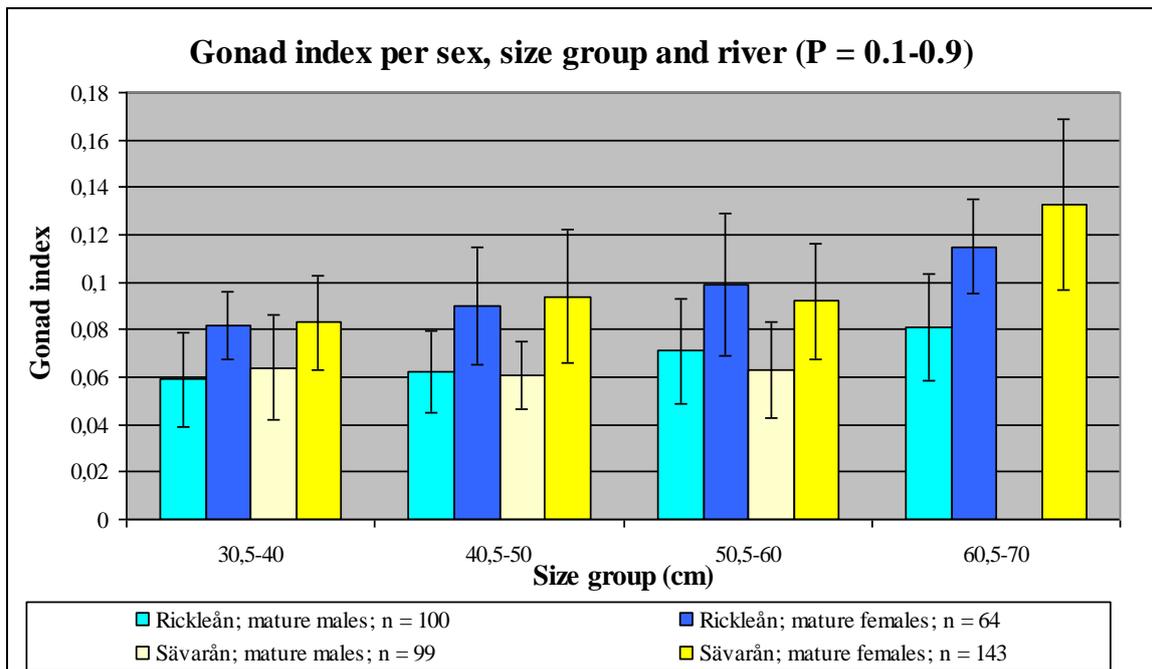
Figure 37. Gonad index, Rickleån vs. Sävarån, mature, Dec 27th-Feb 17th , per sex and size class (app. 20).
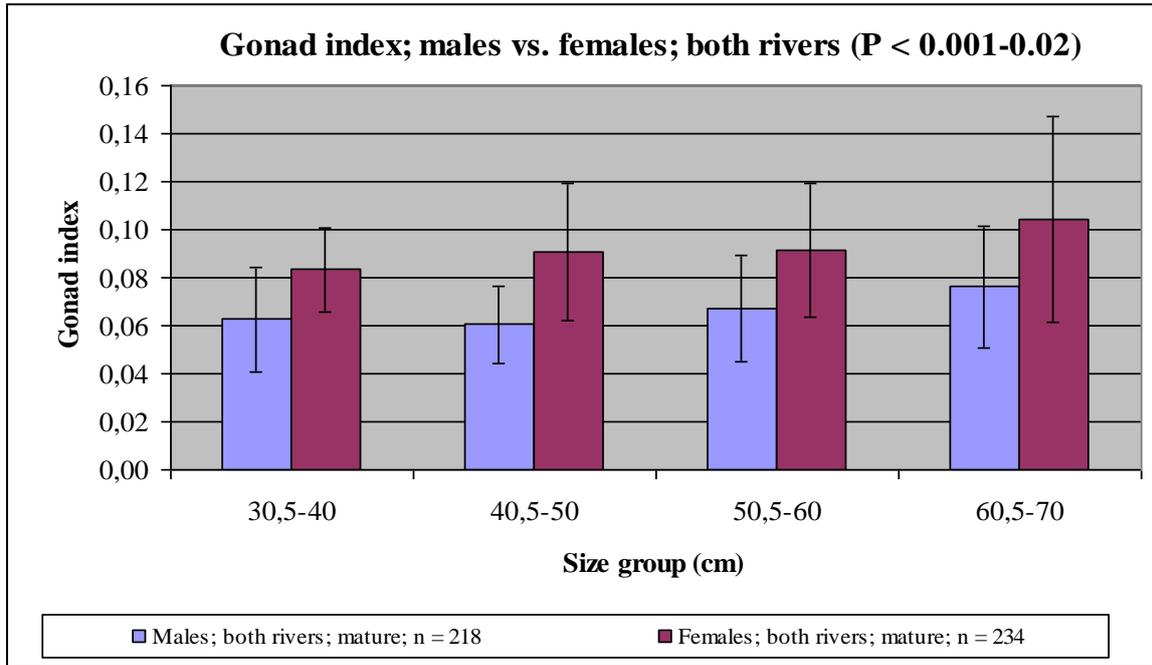
Figure 38. Gonad index; males vs. females; both rivers; all mature non-spent Sep 23rd-Feb 17th (app. 21).
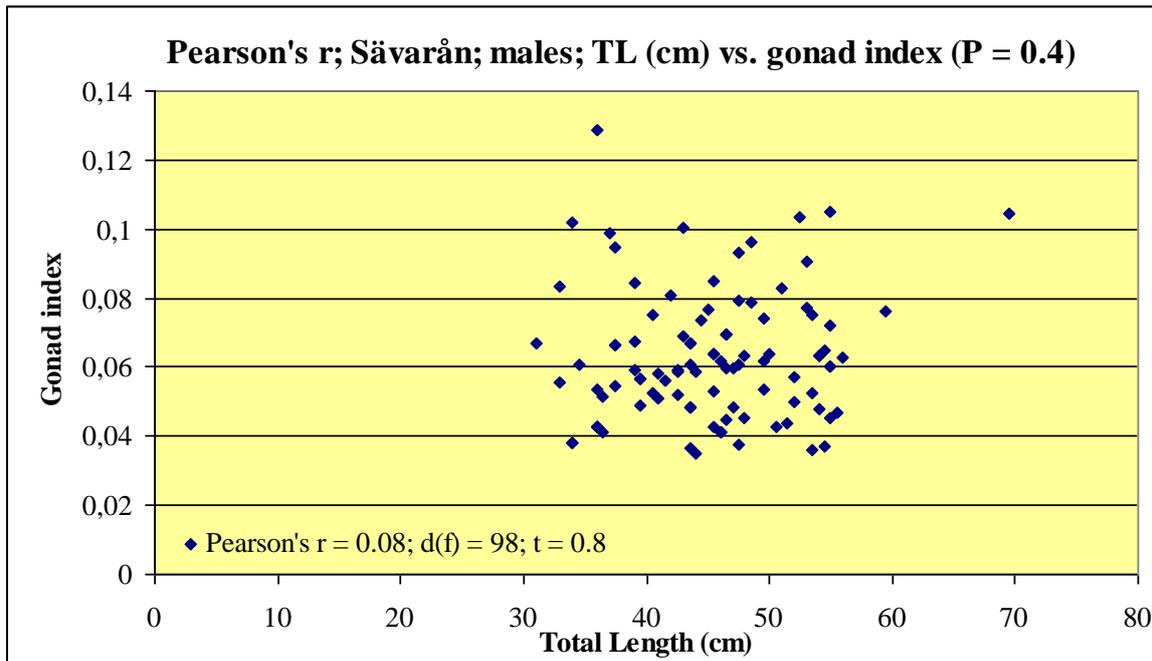
Figure 39. Pearson´s r, gonad index vs. TL (cm); Sävarån males; mature, Dec 27th-Feb 17th (app. 23).

3.5.2 Male gonads reached full maturity earlier than female gonads

Males achieved full gonad development earlier than females, already in November. Females continue to develop gonads until spawning. In mid-February, gonad index dropped due to spawning (fig. 40; app. 24). This contradicts earlier findings where both male and female gonads reached maximum development in mid-January (Bengtsson 1973).
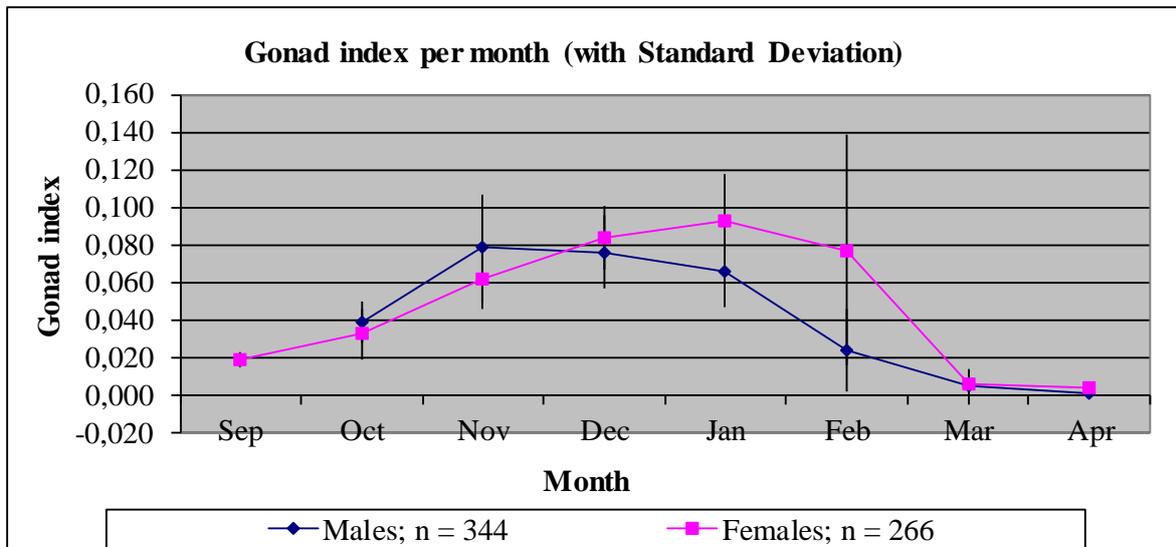
Figure 40. Male and female gonad indexes, per month Sep-Apr, rivers compiled. Immatures before and during spawning excluded, after spawning included (app. 24).

3.5.3 Growth and gonad indexes were positively correlated

Growth, measured as length-at-age, and gonad indexes were positively correlated in spawners, strongest in Sävarån (tab. 3; Sävarån; TL; age 7-9 years; TW; age 4 and 6-9 years; Rickleån; TL; No correlations; TW; age 6-7 years and 9 years).

Table 3. Pearson's Correlation, gonad index vs. TL (cm) or TW (g). Mature, non-spent Dec 27th-Feb 11, per river and per age group.

PEARSON'S CORRELATION, GONAD INDEX VS. TOTAL BODY WEIGHT OR TOTAL LENGTH								
Dec 27th-Feb 17th	Pearson's r	Pearson's r	n	df	$t_{total\ length}$	$t_{total\ weight}$	$P_{total\ length}$	$P_{total\ weight}$
Age (yrs)	Total length (cm)	Total weight (gr)	(pairs)	(pairs)	Welch's app of t		Two-tailed P	
4	-0,23	-0,12	8	6	0,6	0,3	0,6	0,77
5	0,20	0,34	19	17	0,8	1,5	0,41	0,16
6	0,25	0,32	38	36	1,6	2,1	0,13	0,047
7	0,26	0,42	27	25	1,3	2,3	0,20	0,03
8	-0,04	0,18	26	24	0,2	0,9	0,84	0,39
9	0,53	0,64	14	12	2,1	2,9	0,053	0,01
TOTAL RICKLEÅN			132					
3	-0,11	0,44	3	1	0,1	0,5	0,94	0,71
4	0,45	0,57	14	12	1,8	2,4	0,10	0,03
5	-0,02	0,01	40	38	0,1	0,8	0,92	0,43
6	0,10	0,23	77	75	0,9	2,1	0,40	0,04
7	0,31	0,40	45	43	2,2	2,9	0,04	0,01
8	0,29	0,38	47	45	2,0	2,8	0,049	0,01
9	0,74	0,83	11	9	3,3	4,5	0,01	0,001
TOTAL SÄVARÅN			237					

3.5.4 "Rest year" strategies, common in Rickleån, rare in Sävarån

The ratios of immatures/full sample were in Rickleån 41/263 = 16 %; in Sävarån 2/357 = 0.6 %. The sex ratio males/females in immatures was 19/22 in Rickleån and 0/2 in Sävarån. "Rest year" strategies enable faster growth, higher liver index and higher K (fig. 41a-b).

Figure 41. a) <u>Individual Ri1102</u>; April 7th, 2007; female; 8 years; 2.245 g/68.5 cm (fast growth); GI 0.0003 (yellow ring; very low); Liver index 0.75 (very high, annual average 0.29); b) <u>Individual Ri1109</u>; February 4th, 2008; female; 6 years; 1.585 g/62.5 cm (fast growth); GI 0.004 (low); Liver index 0.59 (high). Salmonid roe in stomach, which confirms active foraging on the onset of spawning for other burbots.

3.6 Liver

3.6.1 Liver indexes did not differ between Rickleån and Sävarån , but between sexes

Rickleån was liver-indexed between September 23rd-April 7th, and Sävarån only between December 27th-March 10th (only one individual in March). Immature burbots had much higher liver indexes than spawners, and were frequent in Rickleån but almost absent in Sävarån. Hence, these had to be excluded in the comparison (app. 31). Since liver index vary during the year (fig. 36; app. 17-18), I compared the populations both around spawning and monthly. At first, in the size- and sex-unstructured comparison, spawners in Sävarån had higher liver index Dec 27th-Feb 17th (app. 25, top). But sex ratios in the liver index samples differed and females had higher liver index (fig. 43; app. 25-28). When I compared the rivers per sex, no differences remained (app. 25, below). Larger individuals, except females in Sävarån (fig. 44; app. 29), had higher liver index (app. 29). Since burbots were bigger in Rickleån, I compared rivers per sex and size class. I found no differences in liver index between populations, except that males in Sävarån had larger liver index in size class 50.5-60 cm (fig. 42; app. 30).
I also compared liver indexes per month, all liver-indexed individuals. At first, Sävarån had lower liver indexes in February (tab. 4 part [1]; Rickleån 0.21; Sävarån 0.16). This differences were partly due to different sex ratios in February (Rickleån 33/19 = 1.7; Sävarån 101/15 = 6.7), and females had larger liver indexes than males (app. 25-28). Also, there were different proportions of spent burbots (tab. 4 part [2]; Rickleån 8/52 = 15 %; Sävarån 105/116 = 91 %). I found indications that the actual spawning decrease liver index (tab. 4 part [3]; February; mature/immature 0.21; spent 0.16; mature 0.18; spent 0.16). Hence, the liver index did not differ between the rivers when spent/mature/immature were separated (tab. 4 part [2]); Rickleån 0.17-0.18; Sävarån 0.16-0.18).
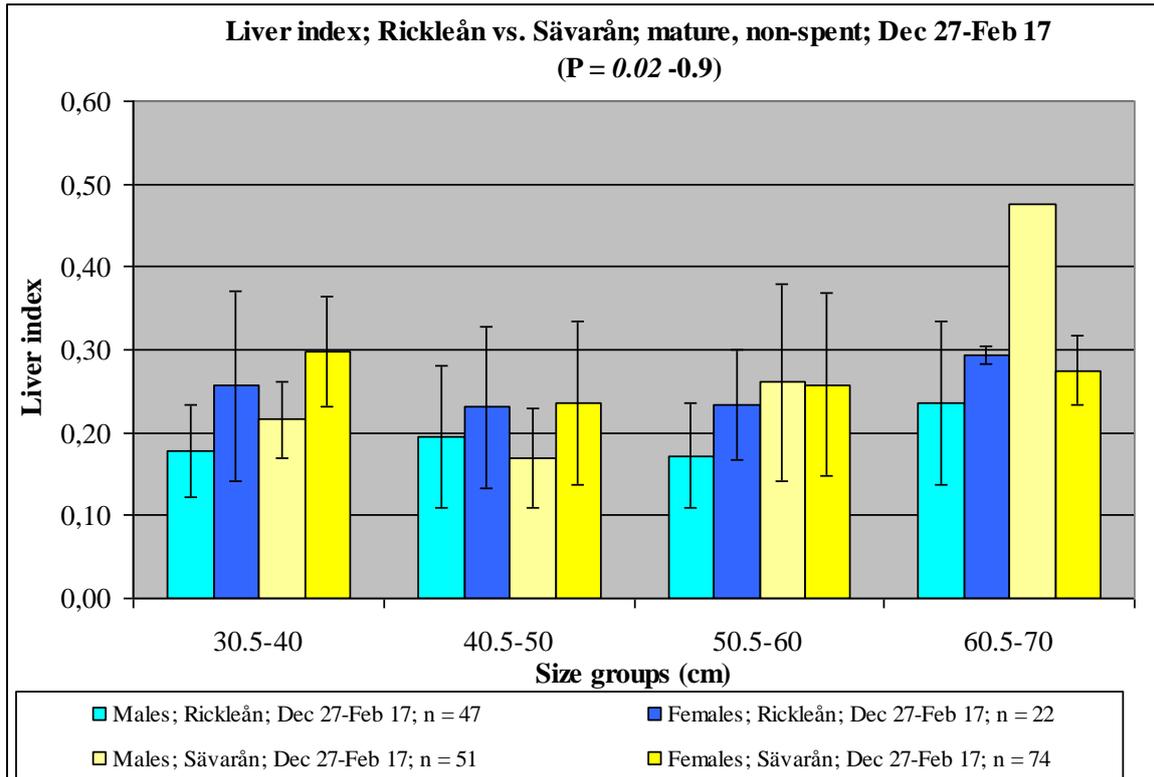
Figure 42. Liver index; Rickleån vs. Sävarån; mature, unspent; Dec 27-Feb 17; per sex/size group (app. 30).
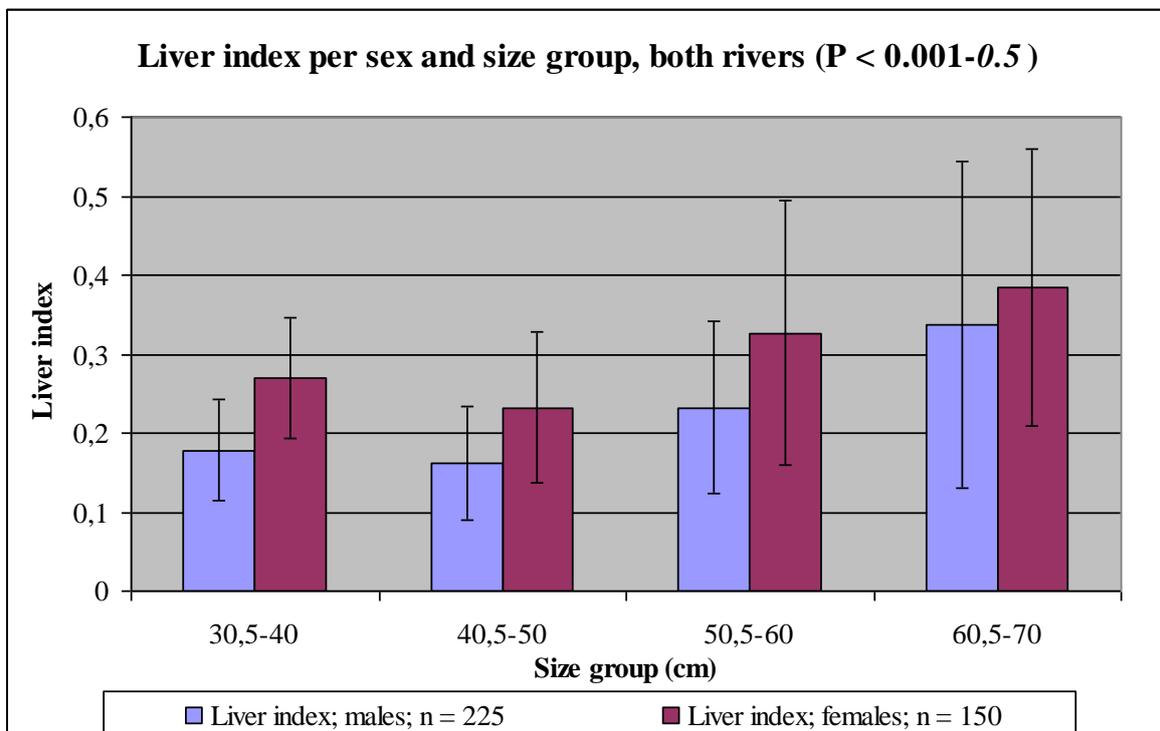
Figure 43. Liver index; males vs. females; both rivers compiled (app. 27).
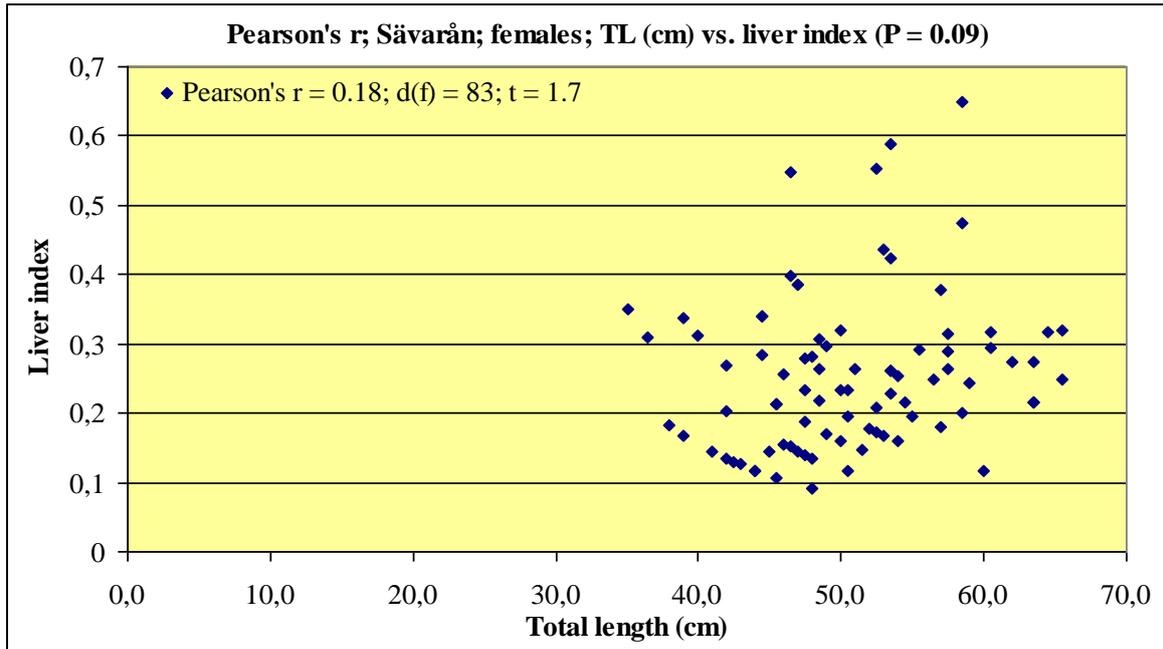
Figure 44. Pearson's Correlation, liver index vs. TL (cm); females in Sävarån (app. 29).

Table 4. Liver index, Rickleån vs. Sävarån [1] per month, all individuals. [2] February, reproductive stadium separated [3] Mature and/or immature vs. spent, both rivers compiled, February.

	LIVER INDEX	Rickleån			Sävarån			Total		t	2-tailed p
	Month, sample	n	Mean	Var	n	Mean	Var	n	df		Welch´s app
1	January, all	29	0,25	0,014	90	0,22	0,006	119	117	1,4	0,171
	February, all	52	0,21	0,018	116	0,16	0,007	168	166	2,3	0,024
	March, all	7	0,36	0,007	1	0,65		8			
	April, all	9	0,61	0,033				9			
	September, all	3	0,41	0,002				3			
	October, all	14	0,32	0,019				14			
	November, all	16	0,36	0,010				16			
	December, all	12	0,29	0,009	26	0,33	0,009	38	36	1,2	0,250
	TOTAL, ALL	**142**	**0,29**	**0,026**	**233**	**0,20**	**0,010**	**375**	**373**	**5,7**	**< 0,001**
2	February, spent	8	0,17	0,002	105	0,16	0,005	113	111	0,5	0,6
	February, mature	41	0,18	0,005	10	0,18	0,011	51	49	0,2	0,8
	February, immature	3	0,66	0,025	1	0,55		4			
	FEBRUARY, TOTAL	**52**	**0,21**	**0,018**	**116**	**0,16**	**0,007**	**168**	**166**	**2,3**	**0,024**

		Mature/immature			Spent			Total		t	2-tailed p
3	Feb, both rivers	n	Mean	Var	n	Mean	Var	n	df		Welch's app
	Mature vs spent	51	0,18	0,006	113	0,16	0,005	164	162	1,9	0,058
	Mature/immature vs. spent	55	0,21	0,020	113	0,16	0,005	168	166	2,8	0,006

3.6.2 Liver indexes were correlated with growth, more in Rickleån

With full sample, liver indexes were positively correlated with growth (tab. 5; all; TW; Rickleån 5-8 years; Sävarån 4 and 6-8 years; <u>TL</u>; Rickleån 6-8 years; Sävarån 7-8 years). I ignored age 3 years in Sävarån due to small sample.

Table 5. Pearson's Rank Correlation, liver index vs. TW (g) or TL (cm), all, per river and age.

PEARSON'S CORRELATION, LIVER INDEX VS. TOTAL BODY WEIGHT OR TOTAL LENGTH								
	Pearson's r	Pearson's r	n	df	$t_{total\ body\ weight}$	$t_{total\ length}$	$P_{total\ body\ weight}$	$P_{total\ length}$
Age	Total weight	Total length	(pairs)	(pairs)	Welch's app of t		Two-tailed P	
Rickleån	**TOTAL n (pairs)**		**93**					
3			1					
4	-0,16	-0,06	5	3	0,3	0,1	0,78	0,93
5	0,49	0,42	17	15	2,2	1,8	0,045	0,09
6	0,64	0,53	17	15	3,2	2,4	0,01	0,03
7	0,68	0,51	26	24	4,5	2,9	< 0,001	0,01
8	0,72	0,51	23	21	4,8	2,7	< 0,001	0,01
9	0,32	0,22	4	2	0,5	0,3	0,68	0,78
Sävarån	**TOTAL n (pairs)**		**174**					
3	0,94	1,00	4	2	4,0	68,7	0,06	< 0,001
4	0,53	0,36	21	19	2,7	1,7	0,01	0,11
5	0,43	0,30	20	18	2,0	1,4	0,06	0,19
6	0,63	0,42	20	18	3,4	2,0	0,003	0,06
7	0,55	0,44	46	44	4,3	3,2	< 0,001	0,002
8	0,47	0,31	52	50	3,8	2,3	< 0,001	0,03
9	-0,18	-0,26	11	9	0,6	0,8	0,56	0,44

3.7 Stomachs and feeding habits

3.7.1 No stomach index difference between Rickleån and Sävarån, but between sexes

Rickleån was stomach-indexed a longer period, Sep 26th-Feb 14th, compared to Sävarån, Jan 31st-Feb 23rd. Hence, comparisons were possible only in January and February, when burbots forage less, and concentrate on spawning (fig. 36; app. 17). I found no differences (app. 32). I also compared the sexes between rivers, per month during January and February, since sex ratios in the sample differed (Rickleån 30/27 = 1.1; Sävarån 87/19 = 4.6), and females had higher stomach index than males (fig. 46; app. 34; app. 35). No differences were found in this comparison either (fig. 45; app. 33). There were no correlations between Total Length (cm) and stomach index, and even a negative one, in Rickleån (fig. 47; app. 36). Rickleån was stomach-indexed a longer period, but this did not bias. Stomach indexes were similar, if not even higher, in autumn than at spawning (app. 32-33), and autumn burbot were bigger (fig. 33; app. 12). Also, stomach-indexed fish in December had more stomach content than in January-February (app. 37).
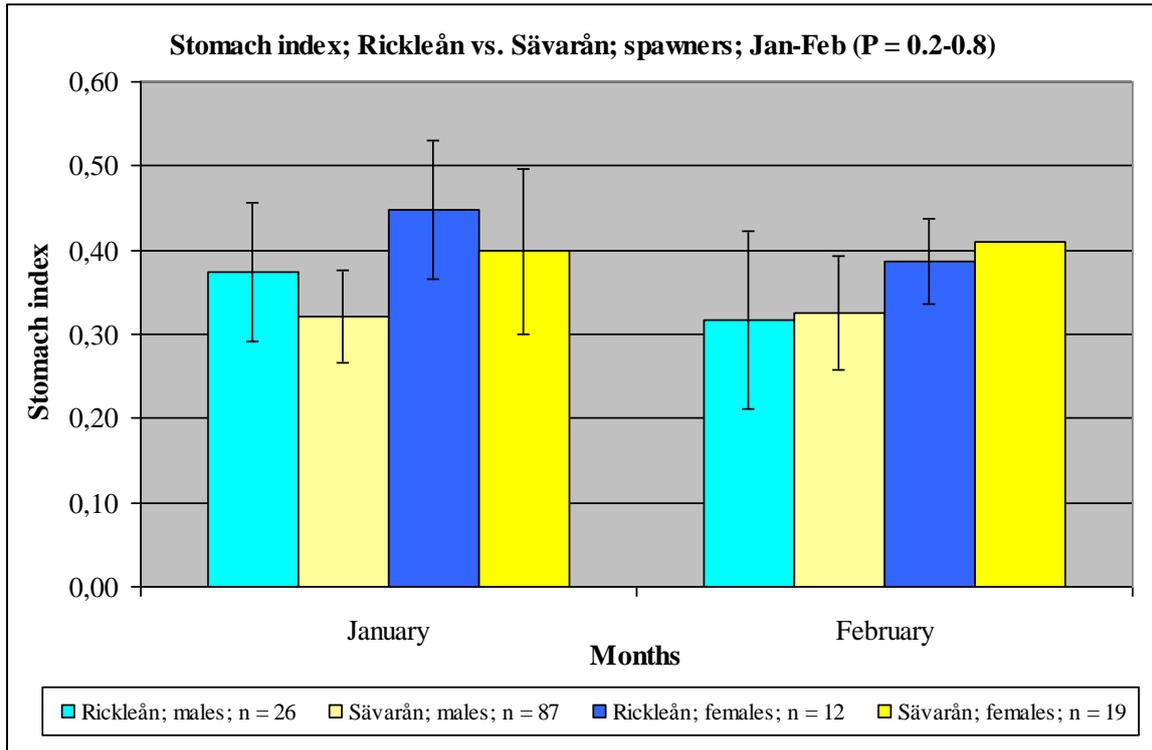
Figure 45. Stomach index; Rickleån vs. Sävarån; sexes separated; Jan-Feb (app. 33).
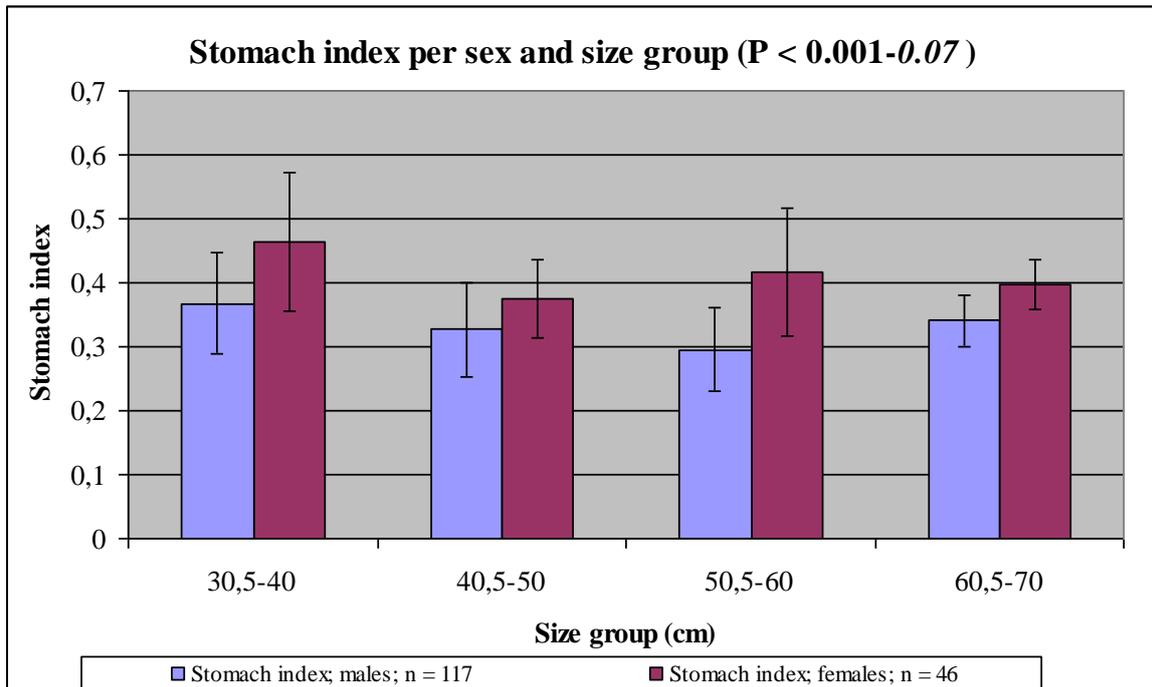
Figure 46. Stomach index per sex and size group; both rivers compiled (app. 34).
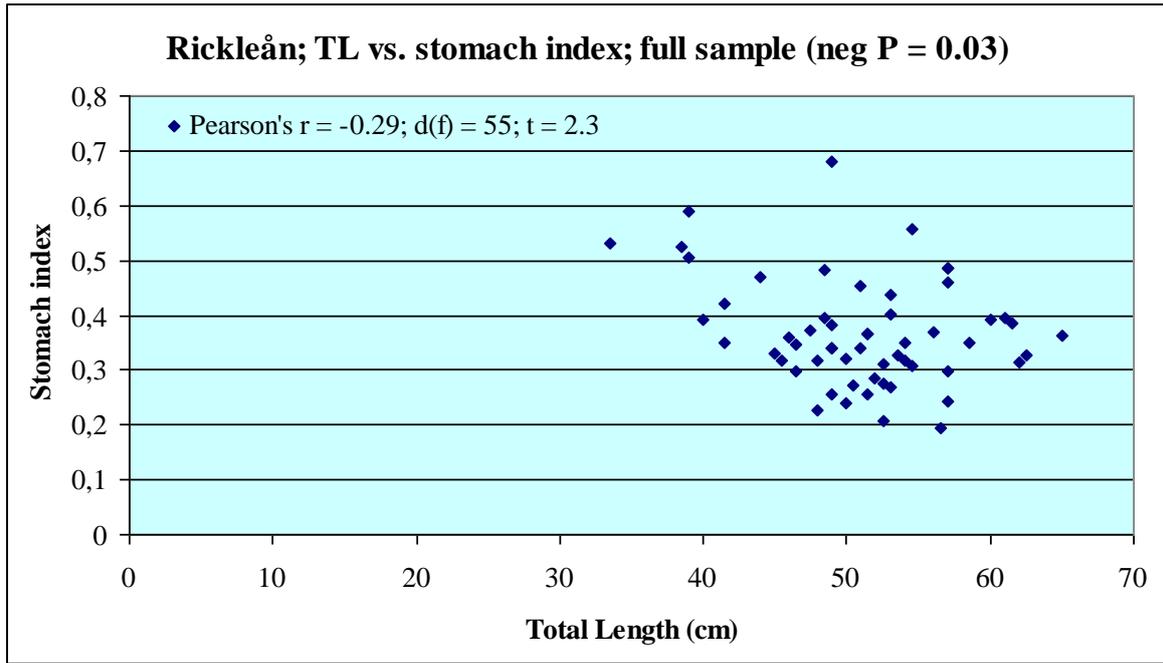
Figure 47. Pearson's r; Rickleån; TL vs. stomach index; full sample (app. 36).

3.7.2 No correlation between stomach index and growth

I found no correlations between intact stomach index and either length-at-age (cm) or weight-at-age (g). Total weight in age 6 years was ignored due to small sample (tab. 6).

Table 6. Pearson's Rank Correlation, intact stomach index vs. length- or weight-at-age, all populations.

PEARSON'S RANK CORRELATION, INTACT STOMACH INDEX VS TOTAL BODY WEIGHT OR TOTAL LENGTH							
	Pearson's r	Pearson's r	n	df	$t_{total\ body\ weight}$	$t_{total\ length}$	$P_{total\ body\ weight}$	$P_{total\ length}$
Age	Total body weight	Total length	(pairs)	(pairs)	Welch's approximation of t		Two-tailed P	
4	0,53	0,46	10	8	1,78	1,45	0,11	0,19
5	-0,02	0,00	13	11	0,06	0,02	0,95	0,98
6	0,53	0,51	7	5	1,39	1,33	0,22	0,24
7	-0,56	-0,68	4	2	0,96	1,30	0,44	0,32
8	0,10	-0,07	18	16	0,40	0,27	0,69	0,79
9	0,54	0,49	4	2	0,90	0,79	0,46	0,51

3.7.3 Most (67 %) stomachs were empty in the river, but females fed more than males

67 % of the burbots in the rivers had empty stomachs (app. 38; Rickleån 58 %; Sävarån 73 %), my own bait excluded. 24 % contained very small amounts, and 9 % a more significant content (10-50 g). This deviates from Bengtsson's findings (app. 38; 1969-1971). Bengtsson (1973) also found that stomach contents increase January-February, compared to March-December, where this study found the opposite result (fig. 36; app. 17; app. 37; app. 39). Either this was due to low-foraging behaviour in the river, or deficit of prey. My stomach-indexed data (2009-2013) indicates even less feeding at present (app. 37; Rickleån 75.4 % empty; Sävarån 97.2 %). Males have more empty stomachs (app. 39; Total; Rickleån; males; 65.5 %; females; 48.8 %; Sävarån; males; 78.2 %; females; 65.2 %

empty). In the diet, as expected of a demersal predator, bottom-dwellers like European river lamprey <u>Lampetra fluviatilis</u> (5.3 % in Rickleån, 2.2 % in Sävarån), common frog <u>Rana temporaria</u> (3.8 %/1.7 %) and bullhead <u>Cottus gobio</u> (3.8 %/0.3 %), were the main targets. Cannibalism was comparably rare (0.4 %/0.8 %). Salmonid roe in stomachs occurred rarely, just a couple of eggs, at most twenty eggs, in 8 % or 3.4 % of burbots in Rickleån and Sävarån, respectively (fig. 48; app. 38). It seemed that these roe just happened to whirl up while the burbot was foraging other prey. Salmonids cover their roe well. Burbots were able feed on large prey. One 58.5 cm/1.285 g burbot contained one pair of 4.03 mm broad cyprinid (assumably ide <u>Leuciscus idus</u> [Linnaeus, 1758]) otoliths, indicating ide size of 35 cm or around 500 grams.

Figure 48. Prey occurrence (not volume or weight) in stomachs (% of) in burbots in Rickleån (app. 38).

3.7.4 Spent descend instead of feeding in the river, but immatures ascend to feed

Spent males had higher intact stomach indexes than mature males in February (tab. 7; Both rivers; matures 0.29; spent; 0.33). I had too few data in order to analyse females-they leave the spawning site rapidly after spawning. It seemed that burbots enhance feeding as soon as spawning is completed. This was a bias, maybe due to small mature sample. Almost all spent burbots had empty stomachs (in total 106 out of 125 = 85 %), and leave the river soon after spawning (fig. 51-53; app. 47; app. 49). In March-April, immatures in Rickleån ascended upstream rivermouth in Rickleån. Of a total 29 immature spring ascenders, 14 had significant stomach contents (app. 39). Four of these had fed on burbot roe. Although overall occurrence of this food item was low, 1.5 % in Rickleån (app. 38), these individuals contained large amounts, which indicated foraging ascent.

Table 7. Both rivers, intact stomach index, mature versus spent males.

INTACT STOMACH INDEX		Mature			Spent			Total		t statistics	2-tailed p
Month	Individuals	n	Mean	Var	n	Mean	Var	n	df	Welch's app of t	
February	Males, both rivers	23	0,29	0,004	62	0,33	0,006	85	83	2,29	0,02

3.8 Condition

3.8.1 *K* were higher in Rickleån, and females had higher *K* than males

K could only be compared between Rickleån and Sävarån between December-February, since the sampling periods differed and since both mean TL (fig. 33; app. 12) and *K* in Rickleån were larger than average in November, December, March and April (app. 40). Testing the full sample per month, burbots in Rickleån had higher *K* than in Sävarån in January-February (app. 40 part [1]). But there were four biases. 1) Burbots were larger in Rickleån (fig. 30-31; app. 8) and size was correlated to *K* in Rickleån but not in both sexes in Sävarån (app. 41; ** below). 2) The proportion of spent burbots was higher in Sävarån, and spent burbot had the lowest liver index (tab. 4 part [3]) and *K* (app. 42). 3) Rickleån also had a higher proportion of immatures, who have higher liver indexes (app. 31) and *K* than matures (app. 43). Consequently, I only used mature burbots caught in December-February, sorted in size classes. Still, in this sample, the sex ratios were different, and 4) females had higher *K* (app. 44-45; * below). Hence, I tested matures December-February, per sex and per size group. The final analysis confirmed a higher *K* in Rickleån (fig. 49; app. 46; <u>males; 40.5-50 cm</u>; Rickleån 0.58; Sävarån 0.56; <u>females 40.5-60 cm</u>; Rickleån 0.63-0.64; Sävarån 0.60-0.61). * As mentioned above, females had higher *K* than males (app. 44-45). Differences remained, when I added the size factor and truncated spent individuals, as the many spent males in Sävarån were a bias (app. 45). ** Total length (cm) and K were positively correlated in Rickleån (app. 41), but not per sex in Sävarån. Growing large seemed less beneficial in Sävarån.
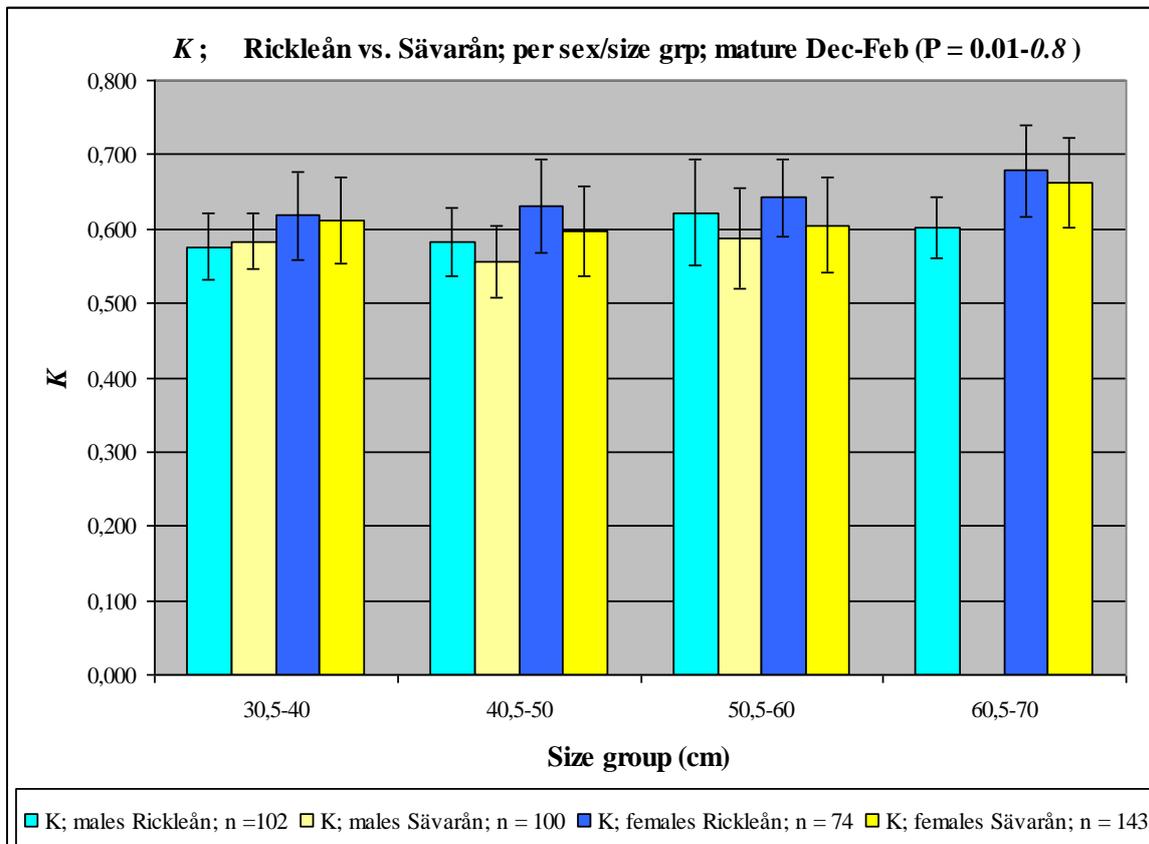
Figure 49. *K*; Rickleån vs. Sävarån; per sex and size group; mature Dec-Feb (app. 46).
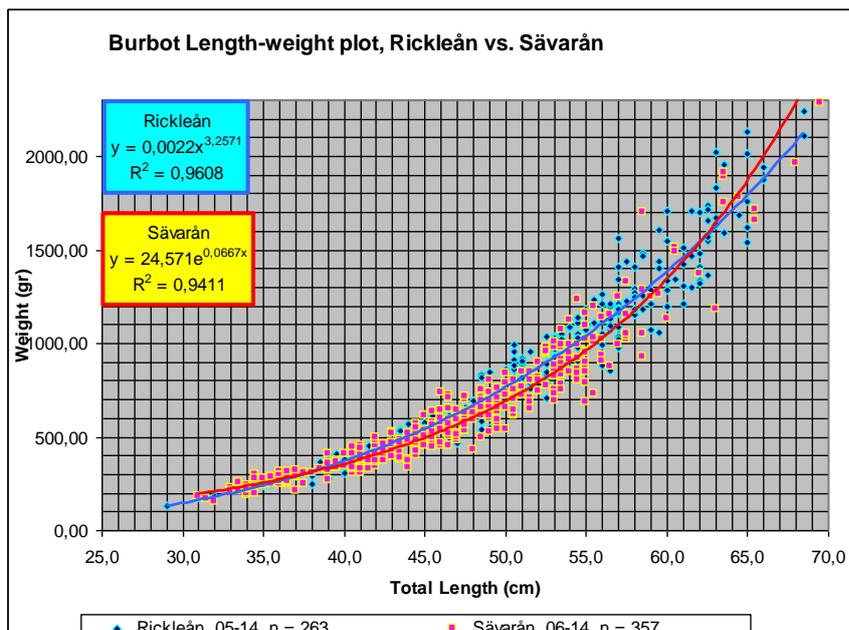
Figure 50: Weight-Length plot, Rickleån (blue, potence trendline), Sävarån (red, exponential trendline).

3.8.2 *K* was correlated with growth, more in Rickleån

Growth was positively correlated with *K* (tab. 8; <u>total weight-at-age</u>; Rickleån; age 5-9 years; Sävarån; age 4 and 6-9 years; <u>total length-at-age</u>; Rickleån; age 6-7 years; Sävarån; age 7 years). Rapid growth was more beneficial in Rickleån, than in Sävarån.

Table 8. Pearson's Correlation, *K* vs. total weight-at-age (g) or total length-at-age (cm) in Rickleån and Sävarån, full aged sample, mature/immature/spent.

PEARSON'S CORRELATION, FULTON'S C.F VS. TOTAL BODY WEIGHT OR TOTAL LENGTH								
	Pearson's r	Pearson's r	n	df	$t_{total body weight}$	$t_{total length}$	$P_{total body weight}$	$P_{total length}$
Age	Total weight	Total length	(pairs)	(pairs)	Welch's app of t		Two-tailed P	
Rickleån			211					
3	-0,92	-0,92	3	1	2,3	2,4	0,3	0,3
4	0,35	0,14	13	11	1,2	0,5	0,2	0,6
5	0,56	0,35	28	26	3,4	1,9	0,002	0,07
6	0,59	0,44	54	52	5,2	3,5	< 0,001	0,001
7	0,71	0,49	54	52	7,3	4,0	< 0,001	< 0,001
8	0,46	0,04	44	42	3,3	0,3	0,002	0,8
9	0,67	0,46	15	13	3,2	1,9	0,006	0,08
Sävarån			298					
3	0,87	0,65	4	2	2,5	1,2	0,1	0,3
4	0,46	0,17	21	19	2,3	0,7	0,03	0,5
5	0,09	-0,12	44	42	0,6	0,8	0,5	0,4
6	0,39	0,05	88	86	4,0	0,5	< 0,001	0,6
7	0,56	0,32	73	71	5,7	2,8	< 0,001	0,006
8	0,37	0,12	56	54	3,0	0,9	0,005	0,4
9	0,63	0,37	12	10	2,5	1,3	0,03	0,2

3.9 Relative population density during the year

3.9.1 Lower relative population density in Rickleån

CPUE between Jan 1st 2001-Feb 13th 2014 proved lower relative population density in Rickleån (tab. 57; Rickleån; mean CPUE = 1.8; Sävarån; 7.1). I also compared with the zero's truncated, which gave similar results (tab. 9; Rickleån; CPUE = 2.3; Sävarån; 8.0).

Table 9. CPUE (catch in number/anglers/hours); 2001-2014; a) full sample; b) with "zero" results excluded.

CPUE per sampling occasion, all			CPUE per sampling occasion, no "zero's"		
River	Rickleån	Sävarån	River	Rickleån	Sävarån
Period	010101-140203	060123-140213	Period	010101-140203	060123-140213
$n_{individs}$	441	357	$n_{individs}$	441	357
Min	0	0	Min	0,3	0,5
Max	12,5	20	Max	12,5	20
Mean	1,8	7,1	Mean	2,3	8
Median	1,2	4,1	Median	1,7	6,5
Variance	4,9	45	Variance	5,1	43,2
n_{effort}	102	19	n_{effort}	79	17
d(f)	119		d(f)	94	
t statistics	3,4		t statistics	3,5	
2-tailed P	0,001		2-tailed P	0,001	

3.9.2 Ascent from October-January, spawn 2nd week of February and rapid descent

In *Rickleån*, CPUE indicated that there were a few individuals at some locations in September, but the main migration started from October and November (fig. 51; app. 47). Large individuals ascended earlier (fig. 33; app. 12). The second half of January had higher mean CPUE than other periods (app. 48; [1] CPUE Jan 16-31 = 3.76 vs. CPUE Dec 16-Jan 15 = 1.36; [2] CPUE January 16-31 = 3.76 vs. February 1-15 = 1.73). This proved that ascent continued until spawning. The first spent individuals in Rickleån was caught February 8th. From February 11th only one mature individual was found. This indicated a peak of spawning around February 10th, one or two weeks later than what Bengtsson found (1973). Burbots had a highly synchronized spawning event, and returned to sea soon after spawning. A second migration pattern appeared after spawning, when immature individuals ascended to forage, not the least burbot roe (fig. 51; fig. 53; app. 39; app. 47; app. 49). These are recognized by distinctively larger liver indexes (app. 31) and high *K* (app. 43). In *Sävarån*, (fig. 52; app. 47), the first two intervals, December 16th-January 15th, represented only two sampling occasions, and could have been biased. 12 of the 19 sampling occasions were carried out between January 18th and February 14th, during which 74 % (265 of the total 357) of the burbots were sampled. CPUE remained rather constant during this period (app. 47; CPUE = 6.27-6.99). I caught the first spent individual January 31st. Main spawning event occurred between February 6th-February 12th. I found only four mature, in a total of 90, from February 13th and onwards. From February 13th and onwards, only five out of 98 caught individuals, were females. Females evaded spawning sites rapidly. Males descended within two weeks after spawning (app. 47; February 16th-March 15th; CPUE = 0.89).
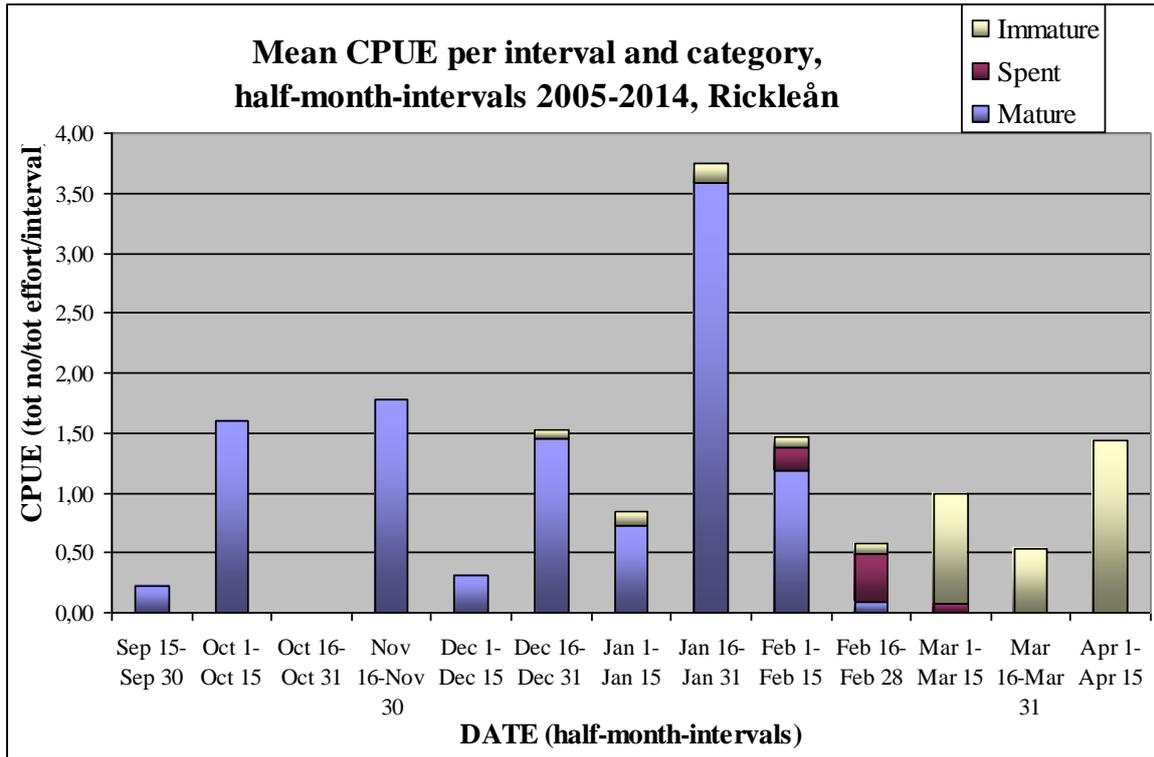
Figure 51. Catch-per-unit-effort per group (mature, spent, immature), per half-month-interval, in Rickleån in years 2005-2014. n $_{Individuals}$ = 255; n$_{Sampling\ occasions}$ = 67; n$_{anglers*hours}$ = 171 (app. 47).
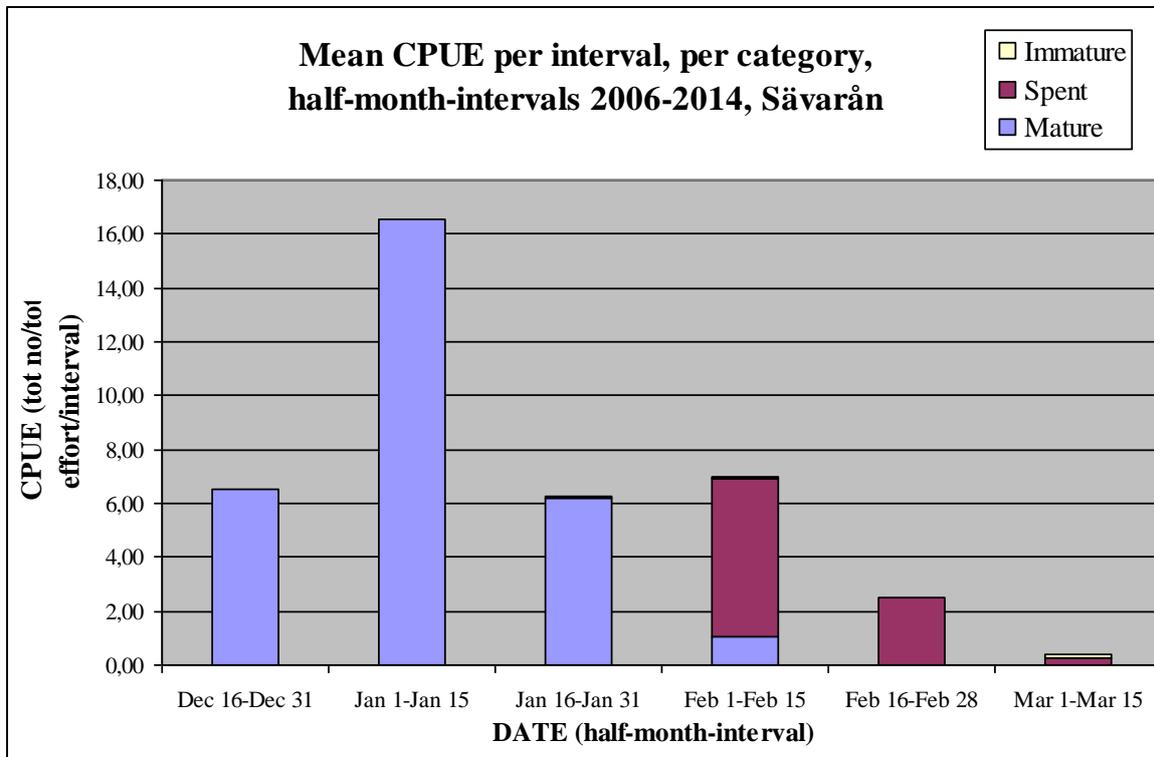
Figure 52. Catch-per-unit-effort per group (mature, spent, immature), per half-month-interval, in Sävarån in years 2006-2014; n $_{Individuals}$ = 357; n$_{Sampling\ occasions}$ = 19; n$_{anglers*hours}$ = 56.25 (app. 47).
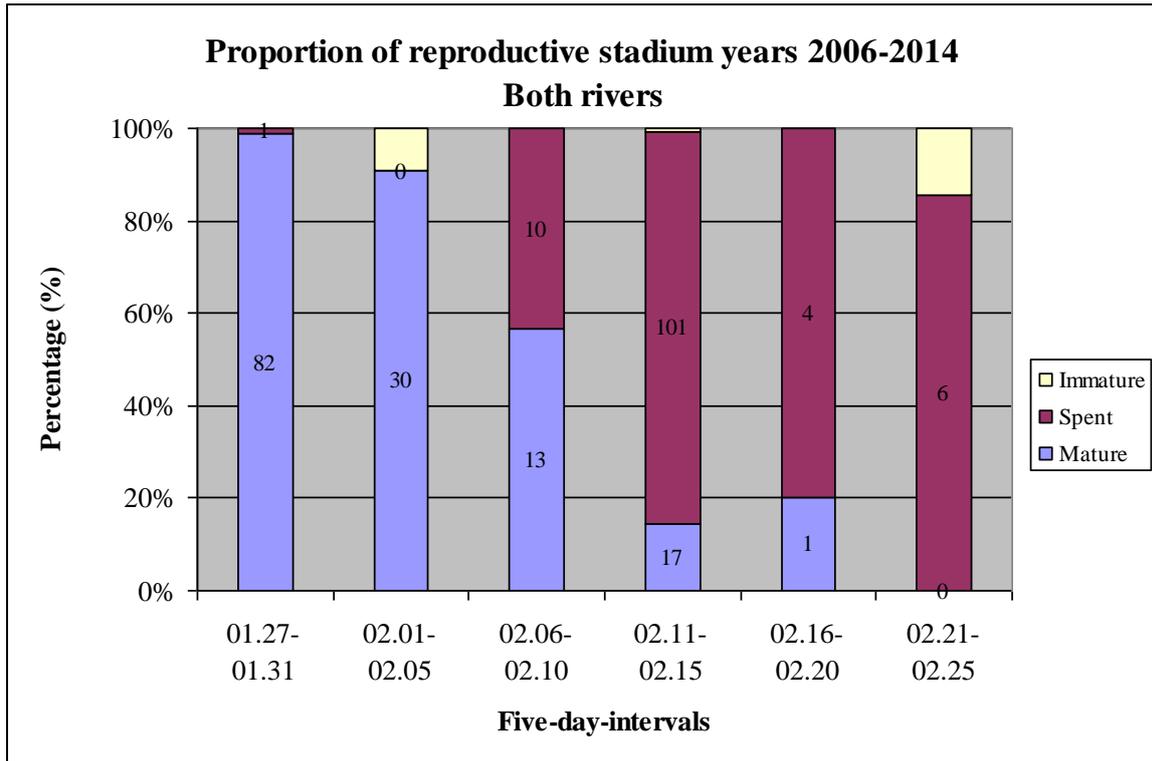
Figure 53. Both rivers compiled; percentage of individuals per reproductive stadium; Jan 27-Feb 25 (app. 49).

3.9.3 Catch-Per-Unit-Effort data were not correlated with moon phases

I also analysed moon phases and their possible effect on CPUE. The time periods were Jan 1st 2001-Feb 3rd 2014 in Rickleån, and Jan 23rd 2006-Feb 13th 2014 in Sävarån. I found no correlations (app. 51). The value of CPUE did not differ between moon phases with highest versus lowest CPUE either (app. 52; Rickleån; Full moon, CPUE = 1.3 vs. 2nd Quarter, CPUE = 2.3; Sävarån; New moon, CPUE = 3.4 vs. Full moon, CPUE = 10.4). This indicates that moon phases does not affect the activity/feeding patters in adult burbots.

3.10 Liver parasites more frequent in Sävarån, but with no effects on indexes

63 % (390 of 622 burbots) had liver parasites (fig. 54). In Rickleån 54 % (142 of 263 burbots) and in Sävarån 69 % (248 of 357 burbots). This difference was expected, since population density was higher in Sävarån (tab. 9; app. 47). There were no differences in organ or condition indexes between individuals with or without liver parasites (app. 53).

Figure 54. Liver parasites, individual Sä1119 (Sävarån), Jan 31st, 2009. Individual data (mean values for burbots in January in parenthesis). Age 8 years, male, 55cm/900 g, gonad index 0.045 (0.079), liver index 0.27 (0.23), *K* 0.54 (0.60), intact stomach index 0.24 (0.37).

3.11 Climate

3.11.1 The 1990s were warmer than previous decades, and the 2000s warmest

When comparing every two decade with each other, the annual average temperature (AAT, ^{o} C) in northern Sweden was significantly higher during the 1990s than in the 1960s and 1980s (app. 54; AAT years 1990s´ = 3.73 ^{o} C; 1960s´ = 2.3 ^{o} C; 1980s´= 2.85 ^{o} C). The temperature in the 2000s was significantly higher than all the other four decades (app. 54; AAT years 2000s´ = 4.32 ^{o} C; 1960s´ = 2.3 ^{o} C; 1970s´ = 3.05 ^{o} C 1980s´= 2.85 ^{o} C; 1990s´ = 3.73 ^{o} C) [Developed from Swedish Environmental Protection Agency 2009 and SMHI 2009]. When viewing AAT in all of Sweden during years 1860-2014, and comparing with the average AAT in the period 1961-1990, around 4.7 ^{o} C, there are only two years between 1988-2014 which are colder than this average (fig. 55).
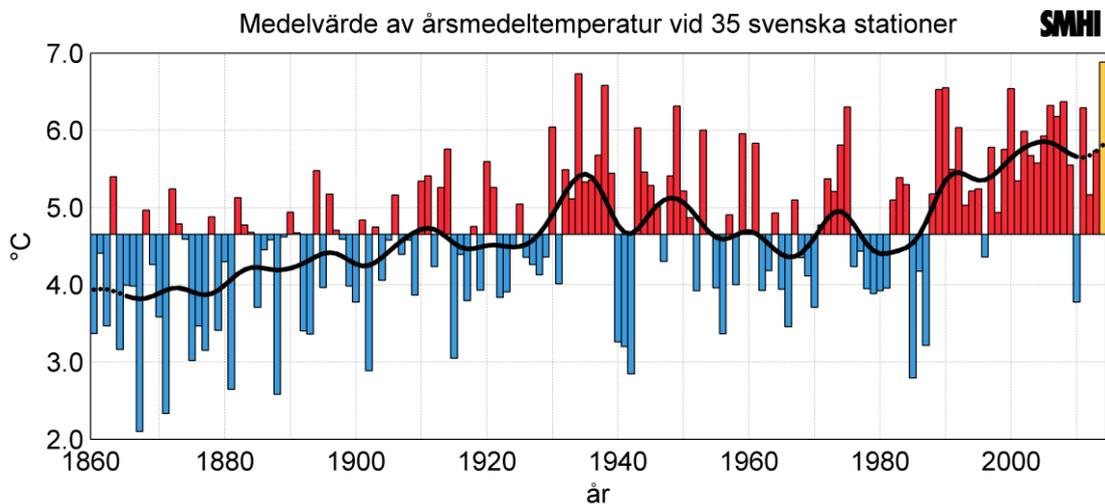
Figure 55. Annual Average Temperature (AAT, ^{o} C) in whole Sweden, yrs 1860-2014. Deviation staples, red = positive and blue = negative, from AAT 1961-1990 (around 4.7 ^{o} C) . 1987-2014, mainly red (SMHI 2015).

3.11.2 No correlations between annual average temperature (^{o} C) and burbot data

I correlated Swedish annual average temperatures [year x] (AAT, ^{o} Celsius) versus data from mature, non-spent burbots from autumn year x until spawning year x + 1 alternatively from autumn year x+1 until spawning year x+2 (tab. 10; app. 55). This mode was chosen because I assumed that preceding temperatures, rather than present, were potentially more influential on these factors. I found few correlations (tab. 10).

Table 10. Pearson's Rank Correlation, AAT (^{o}C) in Sweden year x vs. the five factors TL (cm), gonad index, liver index, intact stomach index and K. I used two periods per factor; either from autumn year x until spawning year x + 1 (named "x + 1" in table) or autumn year x + 1 until spawning year x + 2 (app. 55).

Factors year x + 1 or x + 2 vs. AAT (°C) year x (only mature non-spent)						
River	Factor and period		n	Pearson's r	t stat	2-tailed P
Rickleån	Total Length (cm)	x + 1	7	0,7	2,3	0,07
		x + 2	7	0	0,1	0,92
Rickleån	Gonad index	x + 1	7	-0,1	0,3	0,78
		x + 2	7	0,5	1,2	0,27
Rickleån	Liver index	x + 1	5	0,3	0,5	0,66
		x + 2	5	0,3	0,5	0,63
Rickleån	Intact stomach index	x + 1	4	-0,43	0,7	0,56
		x + 2	4	0,89	2,7	0,11
Rickleån	Fulton's Condition Factor	x + 1	7	0,09	0,2	0,84
		x + 2	7	0,62	1,8	0,14
Sävarån	Total Length (cm)	x + 1	5	-0,3	0,6	0,59
		x + 2	5	-0,1	0,2	0,85
Sävarån	Gonad index	x + 1	5	0,4	0,7	0,51
		x + 2	5	-0,3	0,5	0,65
Sävarån	Liver index	x + 1	4	1	4,5	0,047
		x + 2	4	0,7	1,4	0,3
Sävarån	Fulton's Condition Factor	x + 1	5	0,4	0,8	0,46
		x + 2	5	0,6	1,4	0,25

4. Discussion

4.1 Main differences between burbots in Rickleån and Sävarån

First step was to quantify differences between burbots in Sävarån and Rickleån.

[1] Burbots in Sävarån were smaller than those in Rickleån.
[2] Spawners in Sävarån were younger than those in Rickleån.
[3] Length-at-age in spawners in Sävarån were smaller than in Rickleån.
[4] Total Length was not correlated with gonad index in males in Sävarån.
[5] "Rest year" strategies, which enabled better condition, were rare in Sävarån.
[6] Total Length was not correlated with liver index in females in Sävarån.
[7] Rapid growth affected liver indexes less in Sävarån.
[8] Spawners in Sävarån foraged less than those in Rickleån.
[9] Fulton's Condition Factor's (*K*) were lower in burbots in Sävarån than in Rickleån.
[10] *K* was not correlated with Total length in males and females in Sävarån.
[11] Rapid growth affected *K* less in Sävarån.
[12] Population density was higher in Sävarån.

Second step was to explain why. I chose to discuss life history trade-offs and abiotic/density-dependent/parasitological factors and their effects, apply this on conclusions on the disappearance of large burbots in Sweden, and finally, make recommendations of management and further studies. When referring to the results above, I use numbers [1-12].

4.2 Life history trade-offs in burbots in Rickleån and Sävarån

4.2.1 Precocity in Sävarån

Growth, recruitment and patterns of reproductive investment *can potentially* be the result of trade-offs (Stearns 1992). Trade-offs have been defined as "the linkage between traits that constrain the simultaneous evolution of two or more traits" (Stearns 1992). Resource allocations favouring one trait are carried out on the expense of other traits (Begon et al 2006). Trade-offs can be *physiological*, differences in energy allocations within individuals, *microevolutionary*, within populations coupled to genetic variation and *macroevolutionary*, variations in trade-off patterns between generas, families and so on (Stearns 1992).

Spawners in Sävarån were smaller [1], younger [2] and grew slower [3] than in Rickleån. The proportion of spawners in the smallest total length segment, 30-45 cm, was 42 % compared to 18 % in Rickleån. Also the smallest males had high gonad indexes [4], including a 20-cm male found in the stomach of another burbot. Moreover, the size group histograms and probability plots for individual size indicated that there were an under-representation of even smaller individuals in the sample. I failed to catch these on my gear. In all, the results indicated precocity (early maturity) in Sävarån. Life history trade-off theory predicts that precocity is favoured when the residual reproductive value (RRV) does not increase significantly by delaying reproduction. Precocity shortens generation length, and improves the opportunity for any individual to survive until reproduction. Hence, higher basic reproductive rate (R_0) is achieved. Precocity is favoured by selection when (Begon et al 2006):

a) **Habitats are size-neutral or even size-detrimental**

- *Mortality due to predation does not decrease with increased size, or is even higher in large individuals*. The preferred food size of the burbot is above one kilogram, age 5-9 years, average 7 years (Bengtsson 1973, author´s own data). In Sävarån, both recreational and commercial fishing were more intense than in Rickleån, and have been so during the last century. Hence, neither rapid growth nor large body size were beneficial in Sävarån [1, 3 and 5-11].

- *Competition is low, even small individuals will forage and reproduce*. This is true in burbots, with a low-competitive mating system. They spawn in bowls, all sizes, with females in the center and males circling around, releasing gonads simultaneously (Bengtsson 1973, Froese et al 2006, Jacobs et al 2006). Moreover, I found no correlations (Sävarån) or even indications of negative correlations (Rickleån), between total length and stomach indexes.

- *Growing big does not improve condition*. Large females in Sävarån did not have larger liver indexes [6] (but large males did). Also, the correlation between growth and liver indexes was weaker in Sävarån [7]. Larger males and females in Sävarån did not have higher K [10] and the correlation between growth and K was weaker in Sävarån [11].

b) **Fecundity is size-neutral.** Although total gonad weight naturally was higher in larger individuals, the gonad *indexes* did not differ between Rickleån and Sävarån, despite the

size differences [1]. Moreover, there were no correlation between size and gonad index in spawning males in Sävarån [4], but a positive correlation in both sexes in Rickleån.

c) **Residual Reproductive Value (RRV)** does not increase significantly when delaying reproduction. This can be the case when the

- *Costs of reproduction (CR)* are comparably low. Although immature burbots had faster growth and higher liver indexes, they were almost absent in Sävarån [5]. Despite condition benefits, costs of reproduction are evidently not high enough to favour a delayed reproduction in Sävarån.

- *Mortality caused by reproduction itself, is low*. Burbots are iteroparous with a non-competitive mating system. Spawning-related mortality has not been reported in this species. Precocity will not limit future spawning.

I found the presence of precocity among burbots in Sävarån confirmed.

4.2.2 …but different trade-offs in females!

In both rivers, spawning females were consequently older than males, and consequently, because of that, larger. They also had higher gonad indexes, developed gonads during a longer period, had higher liver indexes, higher stomach indexes, higher K and they descended river sooner after spawning. The life history strategy of females could be classified as semi-delayed. They foraged more intense, built larger livers and consequently, had better overall condition. This enabled higher fecundity. My assumption is a higher cost of reproduction in females was favoured by selection, because of the mating system.

a) Spawners formed a spinning globular mass with a few females in the center, a larger number of males swarming around, and released gametes collectively (Bengtsson 1973, Froese et al 2006, Jacobs et al 2006). This meant that the few females had access to an abundance of male gametes. A **higher fecundity** resulted in a correspondingly higher individual reproductive output for females.

b) Since burbots are **broadcast spawners**, it was possible that larger females also attracted more males, since a greater amount of roe made it more likely that a single male got the opportunity to reproduce. With other words, selection favoured females with large gonads, and males who selected to spawn with these females.

c) **Rapid descent after spawning**. The littoral in Gulf of Bothnia offered by far a more optimal foraging. By immediate descent, the females could soon compensate for their larger, compared with the males, investment in reproduction.

The differences between sexes are confirmed, the explanations are yet to be confirmed.

4.3 Abiotic/density-dependenent/parasitological factors and their effects

4.3.1 Recruitment

The population density was higher in Sävarån than in Rickleån [12]. Moreover, the respective population densities have been similar since the beginning of the 1990s.

a) **Episodical acidity** can be such a factor that limits recruitment (Kjellman 2003). Rickleån is not limed, and is episodically acidified, regularly reaching pH below 6.0 in spring. Sävarån was affected by acidification in the 1980s, but has been limed since 1991. Burbot eggs during incubation are able to withstand low pH levels but newly hatched larvae are very sensitive (Kjellman et al 1996, Kjellman 2003).

b) **High spring and summer temperatures** can enhance recruitment of young-of-the-year burbot (Hofmann et al 2003, Kjellman et al 2002). The Gulf of Bothnia outside the rivermouth of Sävarån is an archipelago with shallow, sheltered bays and islands, and may heat up more rapidly in the summer. Outside Rickleån, the islands are few, and the Rickleå bay is open and exposed. Littoral temperatures heat up slower in the summer. Consequently, cyprinids abound in Sävarån, but are sparse in Rickleån. This may affect the foraging rate and enhance recruitment in juvenile burbots in Sävarån.

4.3.2 Growth and longevity

Burbots grew faster in Rickleån than in Sävarån [3]. Also, they reached higher age. The oldest individuals caught were 12 years in Rickleån, but only 10 years in Sävarån. Moreover, 20 out of 216 aged burbots (9.3 %) in Rickleån were 9-12 years. In Sävarån, 14 out of 300 (4.7 %) were 9-12 years. Many factors may have contributed.

a) **"Rest years"** [5] and **delayed reproduction** [2] were factors that facilitated growth [5]. It may be appropriate to state that almost all of these immatures in Rickleån (39 out of 41) were caught in site Ri1, a pool near rivermouth, and that I did not sample near the rivermouth in Sävarån. Theoretically it may be possible that burbots in Sävarån exhibited a similar ascent behaviour, and that these grew faster.

b) **Low recruitment** in burbot has been shown to increase individual growth (Kjellman 2003, Pulliainen et al 1993).

c) **High summer temperatures** can reach critical levels for adult burbot (Hofmann et al 2002, Hardewig et al 2004) which may force adult burbot to evade areas with better foraging opportunities for colder and deeper, less profitable water areas. Stomach indexes plunged rapidly in late summer/early autumn. It proved that burbots, besides temperature stress, fed poorly in periods. This may have slowed down growth and shortened the lifespan of the largest burbots, even more in Sävarån.

d) **Liver parasites** were more common in Sävarån (69 %) than in Rickleån (54 %), also an indirect density-dependent effect. Although, liver parasites had no effects on neither growth, nor condition, in burbots.

I found the differences between Sävarån and Rickleån, in population density, growth and longevity, satisfactory explained, yet to be proved.

4.3.3 Why did anadromous burbots in Gulf of Bothnia grow faster than others?

Anadromous/brackish burbots in the Gulf of Bothnia area grew faster than most other compared populations worldwide. I concluded that three factors mattered.

a) **Summer temperature**. The Gulf of Bothnia, although affected by climate change, is a large water body, in northern Scandinavia. The water temperatures remained lower than in inland lakes and rivers, until the end of summer, and enabled the burbot to utilize the rich littoral zone for a longer period.

b) **Abundance of prey**. The littorals of Gulf of Bothnia is rich in preferred prey, for instance a variety of fish, malacostracans and amphipods.

c) **Salinity** in the Gulf of Bothnia and the main part of the Baltic Sea as a whole does not seem to be a limiting factor.

4.4 What happened with the large burbots in Sweden?

4.4.1 Has growth rate decreased over time?

There are, simply, two factors that enable large size, growth and/or longevity. **Growth (length-at-age)** in Rickleån in this study, seemed slower than in earlier studies (Bengtsson 1973), but similar to other populations in the area (Kjellman et al 1993; Pulliainen et al 1993). On the contrary, Sävarån indicated *increased* growth compared to earlier studies (Kjellman 1993). The growth factor could not alone explain the demise of large burbots.

4.4.2 Did they die earlier?

The other factor that enables large size, longevity, could be affected by a number of factors.

a) **Human harvest-related mortality on large individuals**. Burbots have been harvested for hundreds of years. The peak in the national registration of game fish burbot in Sweden, was in year 1992, when 36 burbots above 4.500 g were registered. The average in years 2000-2014 had plunged to 7.4 burbots. This despite the widely adopted practise of catch-and-release of large burbots. Moreover, the disappearance of large burbots was simultaneous in rivers like Rickleån, with low commercial and recreational harvest (Bengtsson 1973, Roos 2007, Boström 2007, Wahlström 2007, Andersson 2007). Until 1994, in Rickleån, I caught burbots (front page) between 75 - 81 cm every year. Between years 1994-2014, the largest was 69.5 cm.
The human harvest-related mortality could not explain why large burbots had vanished.

b) **Intra- or interspecific competition/predation**. There were no logical reasons to expect that larger and older burbots were targeted by non-human predators more frequently, or suffered more from intra- or interspecific competition. It is true that I found a negative correlation between size and stomach indexes in spawners. However, this was the period when burbots fed least, and concentrate on spawning. Neither competition, nor predation, could explain the disappearance of large burbots.

c) **Environmental degradation, as pollution, acidity and fertilizers**. Although this study did not investigate these matters in particular, I found no reasons to suspect that these factors had caused a more detrimental habitat for large burbots. General pH status had not changed since the 1990s (Rickleån), or even improved (the liming in Sävarån), since the beginning of 1990s. Neither dioxins nor heavy metal contents seemed to have increased. Agricultural practises or intensity had not increased, rather the contrary. <u>These factors could not explain the demise in large burbots.</u>

d) **The climate change**. Climate statistics proved that annual average temperatures (AAT, ^{o} C) in Sweden have increased the last decades. AAT (^{o} C) in the 1990s were significantly higher than in the 1960s and 1980s. AAT (^{o} C) years 2000-2009 were significantly higher than all other decades since 1960. This warmer climate could theoretically affect the lifespan of a cold-stenotherm species like burbot (Hofmann et al 2002, Hardewig et al 2004). The evidence is circumstancial. The increasing AAT (^{o} C) in the 1990s, coincided remarkably well with the sudden drop in the national burbot game fish registrations. It also coincided with my own observations in the low-harvest population, Rickleån. Climate change seemed to be the key. <u>A climatological threshold for burbots may have been exceeded, causing mortality.</u>

4.5 What's next?

4.5.1 Management recommendations

The climate can be done little about, at least in the short run. But burbot need more concern in management. This study proved that anadromous burbots have a very low impact on other, "more valuable" species. Feeding was mostly negligible, or absent, from ascent and until spawning. Liver tissues were used to develop gonads reserves. Consequently, stomach indexes were the lowest these months, and increased again in spring, well after descent. Occasionally, problems arose in rivers where there were massive stockings of smolt, and where burbots had adopted a forage ascent behaviour, like Luleälven (Lundquist 2007). But the main feeding phase in anadromous burbots took place in the brackish environs. The diet in my brackish data was dominated by benthic prey, like European eelpout <u>Zoarces viviparus</u> [L.] (18.5 % of stomachs), fourhorn sculpin <u>Triglopsis quadricornis</u> [L.] (18.5 %), polar sea sowbug <u>Saduria entomon</u> (29.6 %) and order Amhipoda (25.9 %). These are not species that humans value dearly. Contact with species of human interest, like herring <u>Clupea harengus</u> (L.), whitefish <u>Coregonus lavaretus</u> (L.) and smelt <u>Osmerus eperlanus</u> (L.), occurs from late summer and early autumn, as high littoral temperatures force burbots out to deeper areas. Still, stomach indexes plunged dramatically these months, proving poor feeding. Burbots does not seem to compete with humans on these resources.

Suggestions for legislative measures in management

a) Introduce a maximum catch-and-kill size, 60 cm, corresponding to an age of 8-9 years
b) Introduce the burbot on the Red-list for vulnerable species due to age-related mortality
c) Ban jerk-angling practises nationwide

The burbots have a value as game or food fish. Most important although, is that the burbot have a right to exist no matter its benefit, or nuisance, for us humans. They belong here.

4.5.2 Recommendation for further studies

a) A **true validation** of anadromous burbot otolith ageing is needed. Otoliths contained plenty of information. And riddles.

b) The different **trade-offs in males and females** need to be investigated thoroughly.

c) A **less selective river sampling**, including the smallest individuals, has to be made.

d) The **post-spawning development** of gonads and liver indexes in spawners needs to be confirmed, to secure that immatures and spent individuals are correctly identified.

e) **The diet, behaviour and movements in the brackish phase of anadromous burbots** should be studied thoroughly.

f) **The temperature-dependent effect on feeding, growth, condition and mortality**, of large burbots, should be studied in laboratory conditions.

Acknowledgements

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Appendix

Appendix 1. Harvest (Figure 5).

Year	Commercial inland harvest (mt)	Recreational inland harvest (mt)	Recreational users (x 1000)	Recreational efforts (days x 1000)
1973				25000
1990	2064			26000
1995	1927			31000
2000	1459	22490	2300	35000
2005	1418	20596	1800	29000

Appendix 2. Game fish registrations 1974-2014 (Figure 6).

Burbot Game Fish registrations 1974-2014						
	Decade					
Year	1970s	1980s	1990s	2000s	2010s	
0		10	8	3	15	
1		20	8	2	11	
2		8	36	3	3	
3		9	23	4	7	
4	3	10	15	1	6	
5	0	8	24	10		
6	0	11	24	12		
7	3	12	9	6		
8	1	12	6	15		
9	8	20	12	13		
Total	15,0	120,0	165,0	69,0	42,0	411,000
Average	2,5	12,0	16,5	6,9	8,4	
Variance	9,1	19,8	96,5	26,3	21,8	
Test period	70s vs. 80s	80s vs. 90s	90s vs. 00s	00s vs. 10s		
t-test	5,1	1,3	2,7	0,6		
Two-tailed P	0,0002	0,2	0,01	0,6		

Appendix 3. Pesola scale accuracy test.

Year	Mettler (g)	Pesola (g)	Diff (g)	% Dev	Year	Mettler (g)	Pesola (g)	Diff (g)	% Dev	Year	Mettler (g)	Pesola (g)	Diff (g)	% Dev
2006	39,2	40	-0,8	2,0	2007	1082,0	1085	-3,0	0,3	2008	13,0	15	-2,0	-13,4
2006	353,9	355	-1,1	0,3	2007	1464,5	1470	-5,5	0,4	2008	13,5	15	-1,6	-10,3
2006	439,7	440	-0,3	0,1	2007	2200,5	2205	-4,5	-0,2	2008	14,9	15	-0,1	-0,7
2006	767,1	770	-2,9	0,4	2008	3,2	3	0,2	6,3	2008	15,9	15	0,9	5,9
2006	1758,3	1765	-6,7	0,4	2008	5,7	5	0,7	14,6	2008	16,8	15	1,8	11,8
2006	2335,5	2335	0,5	0,02	2008	8,0	10	-2,0	-19,6	2008	35,1	35	0,1	0,2
2007	35,9	30	5,9	-16,4	2008	9,2	10	-0,8	-7,6	2008	52,6	55	-2,4	-4,4
2007	65,4	70	-4,6	7,0	2008	9,6	10	-0,4	-4,3	2008	53,6	55	-1,4	-2,6
2007	266,9	265	1,9	-0,7	2008	10,7	10	0,7	7,1	2008	55,0	55	0,0	-0,1
2007	491,8	490	1,8	-0,4	2008	11,6	10	1,6	16,3					
2007	932,2	935	-2,8	0,3	2008	12,6	15	-2,4	-16,1					
Correlation Coefficient 0,9999946														

Appendix 4. Pearson's r; otolith length (mm) versus total length (cm). First both rivers, then each river and both sexes compiled. Finally rivers and sexes treated separately (fig. 27).

Pearson's r: Otolith length (mm) vs. Total length (cm)	Sex	n	df	Pearson's r	t statistics Welch's app of T	2-tailed P
Both rivers	Both	516	514	0,86	37,7	< 0.001
Rickleån	Both	216	214	0,84	22,4	< 0.001
Sävarån	Both	300	298	0,86	29,5	< 0.001
Rickleån	Males	118	116	0,84	16,4	< 0.001
Sävarån	Males	146	144	0,84	19,0	< 0.001
Rickleån	Females	98	96	0,83	14,6	< 0.001
Sävarån	Females	154	152	0,87	22,3	< 0.001

Appendix 5. Pearson's r; ratio otolith width/length (mm) versus total length (cm), weight (g), and gonad, liver and Fulton's Condition indexes (all age-estimated burbots from both rivers).

Pearson's r: Quota otolith width/otolith length (mm) vs.	Sex	n	df	Pearson's r	t statistics Welch's app of T	2-tailed P
Total length (cm)	Both	516	514	0,27	6,3	< 0.001
Total weight (grams)	Both	516	514	0,26	6,1	< 0.001
Gonad index	Both	516	514	-0,01	0,2	0,8
Liver index	Both	271	269	0,16	2,7	0,007
Fulton's Condition index	Both	516	514	0,14	3,2	0,002

Appendix 6. Ratio otolith width/otolith length (mm) in Rickleån and Sävarån.

River	n	Mean	Variance	t statistics	2-tailed P
Rickleån	216	0,43	0,001	5,0	< 0,001
Sävarån	300	0,41	0,001		

Appendix 7. Age distribution in Rickleån and Sävarån. All burbots except immatures. For those caught Sep-Dec I used the estimated age at spawning e.g., age 7 yrs in September = age 8 yrs at spawning (fig. 28-29).

AGE AT SPAWNING	Sex	n	Min	Max	Mean	Median	Var	n	df	t stat	2-tailed p
Spawners (mature/spent)								Welch´s (unequal variances)			
Rickleån Sep 23-Feb 18	Both	175	3	12	6,8	7	2,3	473	471	2,6	0,01
Sävarån Dec 27-Mar 3	Both	298	3	10	6,4	6	1,8				
Both rivers combined,	Males	245	3	12	6,3	6	2,2	473	471	3,7	< 0.001
Sep 23-Mar 3	Females	228	4	11	6,8	7	1,7				
Rickleån Sep 23-Feb 18	Males	99	3	12	6,6	6	2,7	245	243	2,0	0,048
Sävarån Dec 27-Mar 3	Males	146	3	10	6,2	6	1,9				
Rickleån Sep 23-Feb 18	Females	76	4	11	7,1	7	1,6	228	226	2,2	0,03
Sävarån Dec 27-Mar 3	Females	152	4	10	6,7	7	1,7				

Appendix 8. Compilation of size parameters in Rickleån, Sävarån and Tavelån (fig. 30-31).

TERMS	COMPARISON OF SIZE											
Total length (cm)	Site	n♂	n♀	Min	Max	Mean	Median	Var	n	df	t	2-tailed P
All, full sample Sep 23-April 7	Rickleån	142	121	29	68,5	51,9	52,5	59,4	263	618	8,5	< 0,001
	Sävarån	202	155	31	69,5	46,7	46,50	53,1	357			
Mature only Sep 23-Feb 17	Rickleån	118	91	33,5	68,5	51,8	51,5	52,3	209	450	6,9	< 0,001
	Sävarån	100	143	31	69,5	47,0	47,0	55,9	243			
Mature only Jan 18-Feb 17	Rickleån	89	55	33,5	68,5	50,8	50,5	53,6	144	301	4,1	< 0,001
	Sävarån	71	88	31	69,5	47,2	47,0	59,0	159			
All, full sample Dec 27-Mar 10	Sävarån	202	155	31	69,5	46,7	46,50	53,1	357	377	2,4	0,02
	Tavelån	10	12	25,0	62,5	51,0	52,5	67,3	22			
Total weight (g)	Site	n♂	n♀	Min	Max	Mean	Median	Var	n	df	t	P
All, full sample Sep 23-April 7	Rickleån	142	121	135	2245	933	875	183634	263	618	9,7	< 0,001
	Sävarån	202	155	150	2285	625	555	110543	357			
Mature only Sep 23-Feb 17	Rickleån	118	91	215	2135	921	860	166005	209	450	7,0	< 0,001
	Sävarån	100	143	170	2285	668	615	123179	243			
Mature only Jan 18-Feb 17	Rickleån	89	55	215	2135	866	813	158867	144	301	4,1	< 0,001
	Sävarån	71	88	185	2285	683	615	139749	159			
All, full sample Dec 27-Mar 10	Sävarån	202	155	150	2285	625	555	110543	357	377	2,8	0,005
	Tavelån	10	12	100	1880	866	908	151889	22			

Appendix 9. TL (cm), males vs. females. **1st**, in all four anadromous/coastal populations (Rickleån, Sävarån, Tavelån and Västerviken), compiled. **2nd**, per population, all. **3rd**, only mature, non-spent individuals Dec 27th-Feb 17th, both with Rickleån and Rickleån compiled, and per river.

Total Length (cm), males versus females											
Location	Period	Sex	n	Min	Max	Mean	Median	Var	df	t	P
All four Full sample	Jul 25-Apr 20	Males	367	25,0	69,5	47,6	47,5	55,0	667	4,6	< 0,001
		Females	302	29,0	68,5	50,4	50,8	63,0			
Rickleån Full sample	Sep 23-Apr 7	Males	142	31,0	66,0	50,9	50,5	52,0	261	2,2	0,03
		Females	121	29,0	68,5	53,0	54,5	66,0			
Sävarån Full sample	Dec 27-Mar 10	Males	202	31,0	69,5	45,3	45,3	45,0	355	4	< 0,001
		Females	155	31,5	68,0	48,4	48,5	59,0			
Tavelån Full sample	Jan 10-Jan 31	Males	10	25,0	62,0	49,3	52,3	129,0	20	0,8	0,4
		Females	12	47,0	62,5	52,4	52,5	18,0			
Västerviken Full sample	Mar 15-Sep 19	Males	13	41,5	51,0	45,8	45,0	7,0	25	1,8	0,09
		Females	14	41,5	55,5	48,1	47,5	18,0			
Rickleån+ Sävarån Mature only	Dec 27-Feb 17	Males	200	31,0	69,5	47,5	47,5	53,0	405	2,8	0,006
		Females	207	31,5	68,5	49,6	50,0	60,0			
Rickleån Mature only	Dec 27-Feb 17	Males	100	33,5	66,0	49,7	50,0	48,0	162	2,5	0,01
		Females	64	38,0	68,5	52,6	53,8	52,0			
Sävarån Mature only	Dec 27-Feb 17	Males	100	31,0	69,5	45,3	45,5	49,0	241	3,1	0,002
		Females	143	31,5	65,5	48,2	48,5	57,0			

Appendix 10. Length-at-age; males vs. females; first both rivers compiled, then per river (fig. 32).

Length-at-age; full sample	Males				Females				t statistics		
Age	Mean	n	Variance	StD	Mean	n	Variance	StD	df	t	p
3	35,9	5	9,5	3,1	30,5	2	4,5	2,1	5	2,6	**0,046**
4	38,8	26	23,7	4,9	40,9	8	18,3	4,3	32	1,2	0,25
5	44,3	41	43,9	6,6	42,4	31	42,9	6,6	70	1,2	0,24
6	48,3	71	40,0	6,3	48,8	71	46,4	6,8	140	0,5	0,65
7	49,2	67	36,2	6,0	52,0	60	45,5	6,7	125	2,4	**0,02**
8	52,8	40	48,7	7,0	54,2	60	55,3	7,4	98	0,9	0,35
9	55,5	10	32,5	5,7	55,6	17	34,1	5,8	25	0,1	0,96
10	65,5	2	32,0	5,7	62,8	2	10,1	3,2	2	0,6	0,61
11	62,0	1			68,5	1					
12	62,5	1									
Total		264				252					

	RICKLEÅN								SÄVARÅN							
	Males			Females			Welch's			Males			Females			Welch's
Age	n	Mean	Var	n	Mean	Var	t stat	P	Age	n	Mean	Var	n	Mean	Var	t stat	P
3	1	40,0		2	30,5	4,5			3	4	34,9	5,7					
4	11	38,9	25,7	2	38,0	18,0	0,3	0,8	4	15	38,7	24,0	6	41,8	17,7	1,5	0,16
5	17	46,8	36,9	11	47,6	32,5	0,3	0,7	5	24	42,5	42,6	20	39,6	26,8	1,6	0,11
6	33	50,9	35,3	21	51,4	50,1	0,3	0,8	6	38	46,1	34,2	50	47,8	41,9	1,3	0,21
7	26	52,0	26,4	28	54,2	46,3	1,3	0,2	7	41	47,5	35,1	32	50,1	38,4	1,8	0,07
8	18	57,4	21,0	26	58,3	28,8	0,6	0,6	8	22	49,1	41,3	34	51,1	54,0	1,1	0,29
9	9	55,9	34,9	6	56,5	32,2	0,2	0,8	9	1	52,0		11	55,1	37,7		
10	1	61,5		1	65,0				10	1	69,5		1	60,5			
11	1	62,0		1	68,5				11								
12	1	62,5							12								
Tot	118			98					Tot	146			154				

Appendix 11. Average TL (cm) per year, Rickleån vs. Sävarån, and lowest/highest vs. total in Rickleån.

	Rickleån			Sävarån			Welch´s app			Welch´s app		
Year	n	TL (cm)	Var	n	TL (cm)	Var	df	t	P	df	t	P
2005	9	49,7	61,6									
2006	50	51,2	64,5	51	44,3	45,6	99	4,7	< 0,001		**Rickleån**	
2007	81	52,8	67,3	81	47,6	47,8	160	4,3	< 0,001		*2008 vs. Total*	
2008	56	53,3	59,3	112	47,3	51,0	166	4,9	< 0,001	317	1,3	0,2
2009	30	50,8	50,2	56	47,6	82,5	84	1,8	0,08		*2013 vs. Total*	
2013	26	49,7	51,9							287	1,3	0,2
2014	11	50,9	9,8	57	45,3	36,7	66	4,5	< 0,001			
Total	263	51,9	59,4	357	46,7	53,1	618	8,5	< 0,001			

Appendix 12. Large individuals ascend earlier. [1] TL (cm) data per month in Rickleån; [2] TL in Rickleån, Jan + Feb compiled vs., respectively, Mar + Apr, Sep + Oct and Nov + Dec. [3] TL in Rickleån, January vs., respectively, Mars, April, October, November and December (fig. 33.).

RICKLEÅN, TOTAL LENGTH (CM) PER MONTH														
Month	n	TL (cm)	Var	Months	n	TL (cm)	Var	df	Welch´s t	P	Month	df	Welch´s t	P
Total	263	51,9	59,4											
Jan	121	50,6	60,2	Jan + Feb	179	50,6	60,2				Jan			
Feb	58	50,7	61,2											
Mar	21	53,0	43,6	Mar + Apr	30	55,1	47,3	207	3,2	0,002	Mar	140	1,5	0,13
Apr	9	59,9	24,2								Apr	128	5,3	< 0,001
Sep	3	62,7	13,1	Sep + Oct	17	55,4	45,0	194	2,8	0,006				
Oct	14	53,9	38,6								Oct	133	1,8	0,07
Nov	16	55,6	36,7	Nov + Dec	37	53,7	50,9	214	2,4	0,019	Nov	135	3,0	0,003
Dec	21	52,3	59,1								Dec	140	0,9	0,35

Appendix 13: Length-at-age (cm), per river, all stadiums (mature/spent/immature) compiled.

LENGTH-AT-AGE, RICKLEÅN VS. SÄVARÅN (YEAR/ TOTAL LENGTH, CM)									
	Rickleån			Sävarån				t statistics	2-tailed P
Age	n	TL (cm)	Var	n	TL (cm)	Var	d(f)	Welch's app	
3	3	33,7	32,3	4	34,9	5,7	5	0,3	0,7
4	13	38,7	23,0	21	39,6	23,2	32	0,5	0,6
5	28	47,1	34,0	44	41,2	36,7	70	4,2	< 0,001
6	54	51,1	40,3	88	47,1	38,8	140	3,7	< 0,001
7	54	53,1	37,2	73	48,6	37,8	125	4,1	< 0,001
8	44	57,9	25,2	56	50,3	49,1	98	6,3	< 0,001
9	15	56,1	31,5	12	54,9	35,1	25	0,6	0,6
10	2	63,3	6,1	2	65,0	40,5	2	0,4	0,8
11	2	65,3	21,1						
12	1	62,5							
TOTAL	216	52,1	62,8	300	46,9	55,9	514	7,5	< 0,001

Appendix 14. Length-at-age (cm), immature vs. mature burbots, in Rickleån.

LENGTH-AT-AGE, IMMATURES VS. MATURES + SPENT (YEAR/ TOTAL LENGTH, CM)									
	Immatures			Matures + spent				t statistics	2-tailed P
Age	n	TL (cm)	Var	n	TL (cm)	Var	d(f)	Welch's app	
3	2	30,5	4,5	1	40,0				
4	3	37,2	56,1	10	39,2	17,1	11	0,5	0,7
5	5	52,3	6,3	23	46,0	33,2	26	3,8	< 0,001
6	14	57,0	20,3	40	49,0	31,2	52	5,3	< 0,001
7	9	56,7	14,1	45	52,4	39,2	52	2,7	0,009
8	7	60,9	29,6	37	57,4	23,2	42	1,6	0,1
9	1	53,5		14	56,3	33,4			
TOTAL	41	54,2	79,5	170	51,3	55,1	209	1,9	0,06

Appendix 15. Length-at-age (cm), per river and age group, only mature/spent compiled (fig. 34).

		Rickleån				Sävarån				t statistics		
Age	n	TL (cm)	Var	StD	n	TL (cm)	Var	StD	d(f)	t	P
3	1	40,0			4	34,9	5,7	2,4			
4	10	39,2	17,1	4,1	21	39,6	23,2	4,8	29	0,2	0,8
5	23	46,0	33,2	5,8	44	41,2	36,7	6,1	65	3,2	0,002
6	40	49,0	31,2	5,6	87	46,9	37,8	6,1	125	1,9	0,06
7	45	52,4	39,2	6,3	72	48,6	38,1	6,2	115	3,2	0,002
8	37	57,4	23,2	4,8	56	50,3	49,1	7,0	91	5,7	< 0.001
9	14	56,3	33,4	5,8	12	54,9	35,1	5,9	24	0,6	0,5
10	2	63,3	6,1	2,5	2	65,0	40,5	6,4	2	0,4	0,8
11	2	65,3	21,1	4,6							
12	1	62,5									
TOTAL	175	51,7	58,1	7,6	298	46,9	55,8	7,5	471	6,6	< 0.001

Appendix 16. Length-at-age in 25 alpine, boreal and coastal lakes, rivers and brackish marine areas and rivers, worldwide. Some locations have only one or a few data points (fig. 35).

Place, reference and year	n	0+	1	2	3	4	5	6	7	8	9	10	11	12	13
Lake Heming, Manitoba (Lawler 1963)	1441	9	15	25	28	32	37	40	43	47					
Lake Superior (Bailey 1972)	1285	14	25	31	34	38	41	43	49	51	56	59	64	71	
Bothnian Bay, Simo (Pulliainen et al 1993)	361			32	38	44	48	52	54	60	63				
Lake Kemijärvi (Pulliainen et al 1993)	116			28	35	41	44	48	52	55					
River Kitinen (Pulliainen et al 1993)	149				31	34	35	35							
River Kokemäenjoki (Kjellman et al 1993)	397				35	40	45	44	47	48	46				
River Kyrönjoki (Kjellman et al 1993)	572				31	35	41	43	45		61				
River Lappfjärds å (Kjellman et al 1993)	67				34	40	45	52	67						
River Rickleån (Bengtsson 1973)	244				36	45	50	54	59	62	65	66	74		
River Rickleån (Sandberg 2015)	216				34	39	47	51	53	58	56	63	65	63	
River Sävarån (Sandberg 2015)	301				35	40	41	47	49	50	55	65			
River Tavelån (Sandberg 2015)	22				31	42			54	53					
Lake Abborrtjärn (Sandberg 2015)	3				12				21						43
Lake Bjärten (Sandberg 2015)	3		12												
Lake Landösjön (Sandberg 2015)	8									45	47	46		50	
Lake Långviskasjön (Sandberg 2015)	1									37					
Lake Mjösjön (Sandberg 2015)	4		12	18											
Lake Mörtsjön (Sandberg 2015)	4			13	15			21							
Lake Stensvattnet (Sandberg 2015)	1				21										
Lake Stor-Holmsjön (Sandberg 2015)	1		9												
Lake Sunnansjö (Sandberg 2015)	4		13					46							
Lake Vångsjön (Sandberg 2015)	2			14		23									
River Kalixälven (Sandberg 2015)	1														59

Appendix 17. Organ indexes and K in anadromous/coastal burbot, No samples from May-June (fig. 36).

Indexes per month	Gonad			Liver			K			Stomach		
Month	n	Index	StD	n	Index	StD	n	Index	StD	n	Index	StD
Jul	3	0,06	0,05	3	0,40	0,08	3	0,68	0,05	3	0,42	0,07
Aug	1	0,05		1	0,38		1	0,66		1	0,38	
Sep	15	0,12	0,05	15	0,39	0,13	15	0,64	0,05	13	0,33	0,08
Oct	14	0,37	0,11	14	0,32	0,14	14	0,61	0,08			
Nov	16	0,67	0,21	16	0,36	0,10	16	0,64	0,09	9	0,37	0,08
Dec	47	0,79	0,21	38	0,32	0,09	47	0,64	0,07	9	0,42	0,10
Jan	336	0,79	0,30	135	0,23	0,09	342	0,60	0,06	49	0,37	0,09
Feb	187	0,35	0,41	168	0,18	0,10	187	0,54	0,07	95	0,33	0,08
Mar	27	0,07	0,13	11	0,50	0,22	27	0,64	0,09	2	0,52	0,07
Apr	18	0,03	0,02	18	0,57	0,21	18	0,72	0,09	9	0,59	0,25
TOTAL	664			419			670			190		

Appendix18. Pearson's r, *K* versus organ indexes, and organ indexes vs. each other, in all anadromous/brackish populations. All individuals, except in gonads, non-spent only.

Pearson's r; Condition/organ indexes							
All anadromous/brackish populations		Sex	n	df	Pearson's r	t stat	2-tailed P
Indexes/factor	Individuals					Welch's app of T	
Gonads vs liver	Mature/immature	Both	302	300	-0,39	7,4	< 0,001
K vs. liver	All	Both	419	417	0,68	19,1	< 0,001
K vs. stomach	All	Both	190	188	0,47	7,2	< 0,001
Liver vs. stomach	All	Both	190	188	0,34	4,9	< 0,001
Gonad vs. stomach	Mature Sep-spawn	Both	109	107	0,34	3,7	< 0,001

Appendix 19. Gonad index, Rickleån vs. Sävarån, mature, 1st Dec 27th-Feb 17th , 2nd Jan 18th-Feb 17th.

Gonad index	Site	n ♂	n ♀	Min	Max	Mean	Median	Var	n	df	t statistics	p
Mature only	Rickleån	100	64	0,034	0,171	0,079	0,074	0,001	164			
Dec 27-Feb 17	Sävarån	100	143	0,035	0,203	0,081	0,076	0,001	243	405	0,83	0,4
Mature only	Rickleån	89	55	0,034	0,171	0,080	0,076	0,001	144			
Jan 18-Feb 17	Sävarån	71	88	0,035	0,203	0,085	0,082	0,001	159	301	1,28	0,2

Appendix 20. Gonad index, Rickleån vs. Sävarån, mature, Dec 27th-Feb 17th , per sex and size class (fig. 37).

GONAD INDEX		Rickleån			Sävarån			t stat	2-tailed P
Size class (cm)	Sex	n	Mean	Var	n	Mean	Var	Welch's app	
30,5-40	Males	11	0,059	0,0004	25	0,064	0,0005	0,6	0,5
40,5-50	Males	40	0,062	0,0003	50	0,061	0,0002	0,3	0,8
50,5-60	Males	39	0,071	0,0005	24	0,063	0,0004	1,4	0,2
60,5-70	Males	10	0,081	0,0005	1	0,104			
TOTAL	Males	100	0,067	0,0004	100	0,063	0,0003	1,5	0,1
30,5-40	Females	4	0,082	0,0002	21	0,083	0,0004	0,2	0,9
40,5-50	Females	16	0,090	0,0006	67	0,094	0,0008	0,6	0,6
50,5-60	Females	36	0,099	0,0009	46	0,092	0,0006	1,1	0,3
60,5-70	Females	8	0,115	0,0004	9	0,133	0,0013	1,3	0,2
TOTAL	Females	64	0,098	0,0007	143	0,094	0,0008	0,8	0,4

Appendix 21. Gonad index males vs. females, both rivers; mature, Sep 23rd-Feb 17th, per size class (fig. 38).

GONAD INDEX		Males			Females			t stat	2-tailed P	M	F
Size class (cm)	River	n	Mean	Var	n	Mean	Var	Welch's app		StD	StD
30,5-40	Both	36	0,063	0,0005	26	0,083	0,0003	4,1	< 0.001	0,02	0,02
40,5-50	Both	95	0,060	0,0003	90	0,091	0,0008	8,8	< 0.001	0,02	0,03
50,5-60	Both	73	0,067	0,0005	93	0,091	0,0008	6,4	< 0.001	0,02	0,03
60,5-70	Both	14	0,076	0,0006	25	0,104	0,0018	2,5	0,02	0,03	0,04
TOTAL	Both	218	0,064	0,0004	234	0,092	0,0009	11,7	< 0.001	0,02	0,03

Appendix 22. Gonad index males vs. females, mature, Sep 23rd-Feb 17th, per size class and river.

GONAD INDEX		Males			Females			t stat	2-tailed P
Size class (cm)	River	n	Mean	Var	n	Mean	Var	Welch's app	
30,5-40	Rickleån	11	0,059	0,0004	5	0,083	0,0001	2,9	0,011
40,5-50	Rickleån	45	0,060	0,0003	23	0,081	0,0009	3,2	0,002
50,5-60	Rickleån	49	0,069	0,0005	47	0,091	0,0010	4,0	< 0,001
60,5-70	Rickleån	13	0,074	0,0006	16	0,088	0,0015	1,2	0,26
TOTAL	Rickleån	118	0,065	0,0005	91	0,087	0,0010	5,9	< 0,001
30,5-40	Sävarån	25	0,064	0,0005	21	0,083	0,0004	3,1	0,003
40,5-50	Sävarån	50	0,061	0,0002	67	0,094	0,0008	8,2	< 0,001
50,5-60	Sävarån	24	0,063	0,0004	46	0,092	0,0006	5,4	< 0,001
60,5-70	Sävarån	1	0,104		9	0,133	0,0013		
TOTAL	Sävarån	100	0,063	0,0003	143	0,094	0,0008	10,5	< 0,001

Appendix 23. Pearson´s Correlation, gonad index vs. TL (cm), mature, non-spent, Dec 27th-Feb 17th (fig. 39).

Pearson's r, gonad index vs. TL Unspent, mature Dec 27-Feb 17	Sex	n	df	Pearson's r	t stat	2-tailed P Welch's app of T
Both rivers combined	Both	407	405	0,28	5,8	< 0.001
Rickleån	Both	164	162	0,34	4,7	< 0.001
Sävarån	Both	243	241	0,27	4,3	< 0.001
Rickleån	Males	100	98	0,27	2,8	0,007
Sävarån	Males	100	98	0,08	0,8	0,4
Rickleån	Females	64	62	0,31	2,6	0,01
Sävarån	Females	143	141	0,25	3,1	0,002

Appendix 24. Gonad index per two-week intervals and per months, sexes separated (fig. 40).

GONAD INDEX PER TWO-WEEK INTERVALS						GONAD INDEX PER MONTH						
	Males			Females			Males			Females		
Period	n	Mean	StD	n	Mean	StD	Month	n	Mean	StD	n	Mean	StD
0917-0930				3	0,019	0,004	Sep				3	0,019	0,004
1001-1014	6	0,037	0,009	2	0,025	0,000							
1015-1028	5	0,041	0,014	1	0,048		Oct	11	0,039	0,011	3	0,033	0,013
1029-1112													
1113-1126	4	0,075	0,031	10	0,062	0,016	Nov	5	0,079	0,028	11	0,062	0,016
1127-1210	1	0,094		1	0,061								
1211-1224	2	0,072	0,001	10	0,089	0,015	Dec	15	0,076	0,020	31	0,084	0,017
1225-0107	19	0,078	0,021	24	0,079	0,018							
0108-0121	40	0,070	0,018	49	0,072	0,016	Jan	151	0,066	0,019	162	0,092	0,026
0122-0204	124	0,062	0,019	117	0,103	0,023							
0205-0218	116	0,020	0,019	34	0,071	0,064	Feb	141	0,024	0,022	42	0,077	0,061
0219-0304	8	0,011	0,008	3	0,007	0,005							
0305-0318	9	0,004	0,009	5	0,004	0,002	Mar	15	0,004	0,009	9	0,005	0,003
0319-0401	4	0,001	0,001	3	0,005	0,002							
0402-0415	4	0,001	0,001	4	0,004	0,002	Apr	4	0,001	0,001	5	0,004	0,003
TOTAL	342	0,045	0,030	266	0,082	0,039	TOTAL	342	0,045	0,030	266	0,082	0,039

Appendix 25. Liver index; Rickleån vs. Sävarån; mature, non-spent Dec 27th-Feb 17th.

LIVER INDEX Mature, non-spent	Sex	n	Min	Max	Mean	Median	Var	n	df	t stat	2-tailed p Welch´s (unequal variances)
Rickleån Dec 27-Feb 17	Both	69	0,07	0,41	0,20	0,19	0,006				
Sävarån Dec 27-Feb 17	Both	125	0,07	0,59	0,24	0,22	0,009	194	192	2,7	0,008
Both rivers combined, Dec 27-Feb 17	Males	98	0,07	0,53	0,20	0,19	0,007				
	Females	96	0,11	0,59	0,25	0,25	0,008	194	192	4,0	< 0,001
Rickleån Dec 27-Feb 17	Males	47	0,03	0,41	0,19	0,18	0,005				
Sävarån Dec 27-Feb 17	Males	51	0,07	0,53	0,21	0,20	0,008	98	96	1,7	0,1
Rickleån Dec 27-Feb 17	Females	22	0,13	0,36	0,24	0,23	0,006				
Sävarån Dec 27-Feb 17	Females	74	0,11	0,59	0,25	0,25	0,009	96	94	0,7	0,5

Appendix 26. Liver index, males vs. females. [1] Total sample [2] All individual, per month and per river. [3] spent, mature, immature separated, first with both rivers combined, then Rickleån and last Sävarån.

	LIVER INDEX	Males			Females			Total		t	2-tailed p
	Month, river (all individs)	n	Mean	Var	n	Mean	Var	n	df		Welch´s app
1	Sep 23-Apr 7, both	225	0,20	0,010	150	0,30	0,023	375	373	7,2	< 0,001
2	Jan, Rickleån	18	0,22	0,005	11	0,30	0,024	29	27	1,6	0,1
	Feb, Rickleån	33	0,16	0,004	19	0,28	0,033	52	50	2,7	0,008
	Mar, Rickleån	4	0,39	0,005	3	0,32	0,010	7	5	0,9	0,4
	Apr, Rickleån	4	0,52	0,031	5	0,68	0,027	9	7	1,4	0,2
	Sep, Rickleån				3	0,41	0,002	3			
	Oct, Rickleån	11	0,30	0,010	3	0,39	0,064	14	12	0,6	0,6
	Nov, Rickleån	5	0,31	0,007	11	0,38	0,011	16	14	1,4	0,2
	Dec, Rickleån	2	0,20	0,016	10	0,31	0,007	12	10	1,2	0,2
	TOTAL, Rickleån	**77**	**0,24**	**0,015**	**65**	**0,35**	**0,005**	**142**	**140**	**6,8**	**< 0,001**
	Jan, Sävarån	38	0,20	0,005	52	0,23	0,006	90	88	1,6	0,1
	Feb, Sävarån	101	0,15	0,004	15	0,23	0,020	116	114	2,1	0,04
	Mar, Sävarån				1	0,65		1			
	Dec, Sävarån	9	0,31	0,013	17	0,34	0,007	26	24	0,8	0,4
	TOTAL, Sävarån	**148**	**0,17**	**0,007**	**85**	**0,25**	**0,013**	**233**	**231**	**5,8**	**< 0,001**
	LIVER INDEX	Males			Females			Total		t	2-tailed p
	FEB, place, sample	n	Mean	Var	n	Mean	Var	n	df		Welch's app
3	Both rivers, spent	101	0,15	0,004	12	0,19	0,009	113	111	1,4	0,2
	Both rivers, mature	33	0,16	0,004	18	0,22	0,006	51	49	2,8	0,007
	Both rivers, immature				4	0,63	0,020	4			
	Rickleån, spent	4	0,15	0,003	4	0,18	0,001	8	6	0,9	0,4
	Rickleån, mature	29	0,17	0,005	12	0,22	0,004	41	39	2,6	0,01
	Rickleån, immature				3	0,66	0,025	3			
	Sävarån, spent	97	0,15	0,005	8	0,20	0,014	105	103	1,0	0,3
	Sävarån, mature	4	0,11	0,002	6	0,22	0,013	10	8	2,1	0,07
	Sävarån, immature				1	0,55		1			
	Sävarån, mature/immature	4	0,11	0,002	7	0,27	0,027	11	9	2,4	0,04

Appendix 27. Liver index; males vs. females; both rivers compiled (fig. 43).

Size group	Males				Females				t statistics		
	Mean	n	Var	StD	Mean	n	Var	StD	df	t	P
30,5-40	0,18	44	0,004	0,06	0,27	9	0,006	0,08	51	3,4	0.001
40,5-50	0,16	100	0,005	0,07	0,23	56	0,009	0,10	154	4,8	< 0.001
50,5-60	0,23	71	0,012	0,11	0,33	63	0,028	0,17	132	3,8	< 0.001
60,5-70	0,34	10	0,043	0,21	0,38	22	0,031	0,17	30	0,6	0.5
Total		225				150					

Appendix 28. Liver index, males vs. females, per size group, rivers separated.

LIVER INDEX		Males			Females			t stat	2-tailed P
Size class (cm)	River	n	Mean	Var	n	Mean	Var	Welch's app	
30,5-40	Rickleån	8	0,18	0,002	3	0,26	0,007	1,4	0,2
40,5-50	Rickleån	24	0,20	0,007	18	0,24	0,007	1,7	0,1
50,5-60	Rickleån	37	0,25	0,013	31	0,38	0,034	3,3	0,002
60,5-70	Rickleån	8	0,34	0,049	13	0,46	0,037	1,3	0,2
TOTAL	**Rickleån**	**77**	**0,24**	**0,015**	**65**	**0,35**	**0,031**	**4,4**	**< 0,001**
30,5-40	Sävarån	36	0,18	0,005	6	0,28	0,006	2,9	0,007
40,5-50	Sävarån	76	0,15	0,004	38	0,23	0,010	4,2	< 0,001
50,5-60	Sävarån	34	0,21	0,010	32	0,28	0,018	2,3	0,03
60,5-70	Sävarån	2	0,34	0,038	9	0,27	0,002	0,5	0,6
TOTAL	**Sävarån**	**148**	**0,17**	**0,007**	**85**	**0,25**	**0,013**	**5,8**	**< 0,001**

Appendix 29. Pearson's Correlation, liver index vs. TL (cm), both rivers, per river and sex (fig. 44).

PEARSON'S, LIVER INDEX VS. TL (CM)	Sex	n	df	Pearson's	t	2-tailed P
All year				r	Welch's app	
Both rivers combined	Both	375	373	0,46	9,9	< 0,001
Rickleån	Both	142	140	0,49	6,6	< 0,001
Sävarån	Both	233	231	0,33	5,3	< 0,001
Rickleån	Males	77	75	0,40	3,8	0,0003
Sävarån	Males	148	146	0,26	3,3	0,001
Rickleån	Females	65	63	0,52	4,8	< 0,001
Sävarån	Females	85	83	0,18	1,7	0,09

Appendix 30. Liver index; Rickleån vs. Sävarån; mature, non-spent; Dec 27th-Feb 17th ; per sex/size class (fig. 42).

Liver index; Rickleån vs. Sävarån; per sex and size group; only mature, non-spent; Dec 27-Feb 17												
Size		Rickleån				Sävarån				t statistics		
group	Sex	n	Mean	Var	StD	n	Mean	Var	StD	d(f)	t	P
30.5-40	Males	6	0,18	0,003	0,06	16	0,22	0,0022	0,047	20	1,5	0,2
40.5-50	Males	17	0,20	0,007	0,09	21	0,17	0,0035	0,059	36	1,1	0,3
50.5-60	Males	21	0,17	0,004	0,06	13	0,26	0,0141	0,119	32	2,5	0,02
60.5-70	Males	3	0,23	0,010	0,10	1	0,48					
Total	**Males**	**47**	**0,19**	**0,005**	**0,07**	**51**	**0,21**	**0,0082**	**0,091**	**96**	**1,7**	**0,1**
30.5-40	Females	2	0,26	0,013	0,11	5	0,30	0,0045	0,067	5	0,5	0,6
40.5-50	Females	8	0,23	0,010	0,10	33	0,24	0,0095	0,098	39	0,1	0,9
50.5-60	Females	10	0,23	0,004	0,07	27	0,26	0,0121	0,11	35	0,8	0,4
60.5-70	Females	2	0,29	0,0001	0,01	9	0,27	0,0017	0,042	9	1,2	0,3
Total	**Females**	**22**	**0,24**	**0,006**	**0,08**	**74**	**0,25**	**0,0093**	**0,096**	**94**	**0,7**	**0,5**

Appendix 31. Liver index in immature vs. mature individuals in Rickleån, December-February (n = 14-72).

LIVER INDEX	Rickleån immature Dec-Feb			Rickleån mature Dec-Feb			t stat	2-tailed P
Size class (cm)	n	Mean	Var	n	Mean	Var	Welch's app	
50,5-60	2	0,61	0,01	52	0,26	0,01	4,6	< 0,001
60,5-70	2	0,72	0,03	16	0,33	0,02	3,0	0,01
TOTAL	4	0,66	0,02	68	0,28	0,02	5,8	< 0,001

Appendix 32. Intact stomach index, all burbots, Sävarån versus Rickleån, per month and total.

INTACT STOMACH INDEX		Rickleån			Sävarån			Total		t statistics	2-tailed p
Month	Individuals	n	Mean	Var	n	Mean	Var	n	df	Welch's app of t	
January	All	11	0,41	0,008	38	0,36	0,007	49	47	1,7	0,11
February	All	27	0,33	0,01	68	0,33	0,005	95	93	0,4	0,68
September	All	1	0,36					1			
November	All	9	0,37	0,007				9			
December	All	9	0,42	0,01				9			
TOTAL	All	57	0,37	0,01	106	0,34	0,006	163	161	2,0	0,046

Appendix 33. Intact stomach index, males/females in Rickleån vs. males/females in Sävarån.

STOMACH INDEX		Rickleån			Sävarån			Total		t statistics	2-tailed p	R	S
Month	Individuals	n	Mean	Var	n	Mean	Var	n	df	Welch's app of t		StD	StD
All	Males	30	0,33	0,010	87	0,32	0,004	117	115	0,31	0,76	0,10	0,06
January	Males	6	0,37	0,007	20	0,32	0,003	26	24	1,44	0,16	0,08	0,06
February	Males	20	0,32	0,011	67	0,33	0,005	87	85	0,32	0,75	0,11	0,07
November	Males	3	0,34	0,017				3				0,13	
December	Males	1	0,32					1					
All	Females	27	0,41	0,006	19	0,40	0,009	46	44	0,38	0,71	0,08	0,09
January	Females	5	0,45	0,007	18	0,40	0,01	23	21	1,15	0,26	0,08	0,10
February	Females	7	0,39	0,003	1	0,41		8				0,05	
September	Females	1	0,36					1					
November	Females	6	0,38	0,003				6				0,06	
December	Females	8	0,43	0,01				8				0,10	
February	Males, mature	19	0,30	0,298	4	0,27	0,004	23	21	0,24	0,81	0,30	0,06
February	Males, spent	1	0,68		61	0,32	0,004	62					0,06

Appendix 34. Stomach index; males vs. females; both rivers compiled (fig. 46).

Stomach index per sex and size group											
Size	Males				Females				t statistics		
group	Mean	n	Var	StD	Mean	n	Var	StD	df	t	P
30,5-40	0,37	21	0,006	0,08	0,46	5	0,01	0,11	24	1,9	0,07
40,5-50	0,33	59	0,005	0,07	0,38	15	0,004	0,06	72	2,6	0,01
50,5-60	0,30	34	0,004	0,07	0,42	18	0,01	0,10	50	4,6	0.001
60,5-70	0,34	3	0,002	0,04	0,40	8	0,001	0,04	9	2,1	0,07
Total		117				46					

Appendix 35. **S**tomach index, males vs. females, per location and month. The two columns to the left, with italic letters, specify the total sample including those where stomachs were not weighted/indexed.

Males	*Females*	INTACT STOMACH			Males			Females			Total		t stat	P
n tot	*n tot*	Location	Month	Ind	n	Mean	Var	n	Mean	Var	n	df	Welch's	
345	*276*	**Rickle + Säv**	**All**	**All**	**117**	**0,33**	**0,006**	**46**	**0,40**	**0,007**	**163**	**161**	**5,6**	**< 0,001**
69	*52*	Rickleån	Jan	All	6	0,37	0,007	5	0,45	0,007	11	9	1,5	0,17
33	*25*	Rickleån	Feb	All	20	0,32	0,011	7	0,39	0,003	27	25	2,3	0,03
14	*7*	Rickleån	Mar	All	0			0						
4	*5*	Rickleån	Apr	All	0			0						
	3	Rickleån	Sep	All				1	0,36		1			
11	*3*	Rickleån	Oct	All	0			0			0			
5	*11*	Rickleån	Nov	All	3	0,34	0,017	6	0,38	0,003	9	7	0,5	0,62
6	*15*	Rickleån	Dec	All	1	0,32		8	0,43	0,010	9			
142	*121*	**Rickleån**	**All**	**All**	30	0,33	0,010	27	0,41	0,006	57	55	3,3	0,002
84	*115*	Sävarån	Jan	All	20	0,32	0,003	18	0,40	0,010	38	36	2,9	0,006
108	*21*	Sävarån	Feb	All	67	0,33	0,005	1	0,41		68			
2	*2*	Sävarån	Mar	All	0			0						
9	*17*	Sävarån	Dec	All	0			0						
203	*155*	**Sävarån**	**All**	**All**	**87**	**0,32**	**0,004**	**19**	**0,40**	**0,009**	**106**	**104**	**3,3**	**0,001**
10	*12*	Tavelån	Jan	All	0			0						
10	*12*	**Tavelån**	**All**	**All**	**0**			**0**						
2		Västerviken	Mar	All	2	0,52	0,005				2			
3	*6*	Västerviken	Apr	All	3	0,44	0,003	6	0,67	0,080	9	7	2,0	0,09
1	*2*	Västerviken	Jul	All	1	0,49		2	0,38	0,0001	3			
1		Västerviken	Aug	All	1	0,38					1			
6	*6*	Västerviken	Sep	All	6	0,33	0,008	6	0,33	0,007	12	10	0,1	0,95
13	*14*	**Västerviken**	**All**	**All**	**13**	**0,40**	**0,010**	**14**	**0,48**	**0,062**	**27**	**25**	**1,1**	**0,27**
368	*302*	**All**	**All**	**All**	130	0,33	0,006	60	0,42	0,02	190	188	4,6	< 0,001

Appendix 36. Pearson's r, total length (cm) vs. stomach index.

PEARSON´S RANK CORRELATION	Sex	n	df	Pearson's	t statistics	2-tailed P
INTACT STOMACH INDEX-TL (CM)				r	Welch's app of T	
Both rivers	Both	163	161	-0,003	0,03	0,98
Rickleån	Both	57	55	-0,29	2,3	0,03
Sävarån	Both	106	104	0,08	0,9	0,39
Rickleån	Males	30	28	-0,36	2,0	0,054
Sävarån	Males	87	85	-0,19	1,8	0,08
Rickleån	Females	27	25	-0,37	2,0	0,055
Sävarån	Females	19	17	0,28	1,2	0,25

Appendix 37. Percentage of caught individuals with empty stomachs, 0-15 g and 15-30 g stomach content, in the sample when stomachs were indexed, 2009-2014.

Years 2009, 2013-2014		Stomach content, % of caught individuals (bait excluded)			
Population	n	% empty	% 0-15 g	% 15-30 g	Total
Rickleån Sep 26th-Feb 14th	57	75,4%	21,1%	3,5%	100,0%
Sävarån Jan 31st-Feb 23rd	106	97,2%	1,9%	0,9%	100,0%
Rickleån Jan	11	72,7%	27,3%		100,0%
Rickleån Feb	27	81,5%	14,8%	3,7%	100,0%
Rickleån Sep	1		100,0%		100,0%
Rickleån Nov	9	77,8%	22,2%		100,0%
Rickleån Dec	9	66,7%	22,2%	11,1%	100,0%

Appendix 38. Prey, percentage (%) of occurrence in stomachs (fig. 48).

PREY FREQUENCY IN STOMACHS	Rickleån	Sävarån	Rickleån	Västerviken
	2005-2014	2006-2014	1969-1971	2014
Classification of prey	Sep23-Apr7	Dec27-Mar10	Jan-Dec	Mar15-Sep19
Percentage of stomachs containing:	n = 263	n = 357	n = 244	n = 27
Class Amphibia				
Common frog Rana temporaria	3,8%	1,7%	4,9%	
Class Actinopterygii				
Burbot Lota lota	0,4%	0,8%	1,2%	
Common dace Leuciscus leuciscus			0,4%	
European eelpout Zoarces viviparus				18,5%
Eurasian minnow Phoxinus phoxinus	0,4%	0,6%	5,3%	
Euroasian perch Perca fluviatilis	0,4%		2,9%	
Common sculpin Cottus gobio	3,8%	0,3%	11,9%	
Fourhorn sculpin Triglopsis quadricornis	0,8%			18,5%
"Fish", unidentified	12,2%	3,9%	54,5%	22,2%
Northern pike Esox lucius	1,1%		8,2%	
Smelt Osmerus eperlanus	0,4%			
Three-spined stickleback Gasterosteus aculeatus			0,4%	
Nine-spined stickleback Pungitius pungitius			1,2%	
Sticklebacks Gasterosteus spp	0,4%	0,3%		3,7%
Whitefish Coregonus lavaretus	0,4%			
Roe, burbot Lota lota	1,5%	0,6%		
Roe, family Salmonidae	8,0%	3,4%		
Roe, total	9,5%	3,9%	4,9%	
Class Cephalaspidomorphi				
European river lamprey Lampetra fluviatilis	5,3%	2,2%	11,1%	
Cl. Actinopterygii & cl. Cephalaspidomorphi, tot	**24,3%**	**7,0%**	**61,8%**	
Class Gastropoda and class Bivalvia	**3,0%**		**9,2%**	**3,7%**
Class Insecta	**9,9%**	**15,7%**	**57,0%**	
Subclass Hirudinea		**0,8%**	**4,9%**	
Class Malacostraca				
Aquatic sowbug Asellus aquaticus	2,3%	2,2%	21,3%	
Polar sea sowbug Saduria entomon				29,6%
European crayfish Astacus astacus	0,4%			
Order Amphipoda	1,5%	1,7%	0,8%	25,9%
Prey, any kind	**42%**	**27%**	**> 61,8%**	**74%**

Appendix 39. Percentage of empty stomachs, per sex, river and month, in total sample, all years (n = 620).

PERCENTAGE (%) OF EMPTY STOMACHS	Rickleån				Sävarån			
	n	Males	n	Females	n	Males	n	Females
January	69	69,6%	52	46,2%	84	69,0%	115	60,9%
February	33	66,7%	25	48,0%	108	90,7%	21	90,5%
March	14	57,1%	7	57,1%	1	100,0%	2	0,0%
April	4	50,0%	5	40,0%				
September			3	66,7%				
October	11	63,6%	3	0,0%				
November	5	20,0%	11	63,6%				
December	6	83,3%	15	53,3%	9	11,1%	17	70,6%
TOTAL	142	65,5%	121	48,8%	202	78,2%	155	65,2%

Appendix 40. *K* in Rickleån and Sävarån, [1] all individuals, per month. [2] mature, February.

	FULTON'S C.F.		Rickleån			Sävarån			Total		t statistics	2-tailed P
	Month	Sample	n	Mean	Var	n	Mean	Var	n	df	Welch's (unequal variances	
	Jan	All	121	0,62	0,004	199	0,59	0,003	320	318	5,0	< 0,001
	Feb	All	58	0,58	0,005	129	0,52	0,004	187	185	5,8	< 0,001
	Mar	All	21	0,63	0,003	3	0,59	0,006	24	22	0,8	0,44
	Apr	All	9	0,69	0,007				9			
1	Sep	All	3	0,61	0,002				3			
	Oct	All	14	0,61	0,006				14			
	Nov	All	16	0,64	0,007				16			
	Dec	All	21	0,64	0,004	26	0,64	0,005	47	45	0,3	0,76
	TOTAL	All	263	0,62	0,005	357	0,57	0,005	620	618	9,0	< 0,001
2	Feb	Mature	42	0,60	0,004	19	0,58	0,005	61	59	1,2	0,25

Appendix 41. Pearson's Correlation, *K* vs. TL, matures, first both rivers, and then sexes per river.

Pearson's, Fulton's CF vs TL (cm) Only matures Sep 23rd-Feb 17th	Sex	n	df	Pearson's r	t stat Welch's app of T	2-tailed P
Both rivers combined	Both	450	448	0,27	6,0	< 0,001
Rickleån	Both	209	207	0,31	4,6	< 0,001
Sävarån	Both	241	239	0,15	2,4	0,02
Rickleån	Males	118	116	0,22	2,4	0,02
Sävarån	Males	98	96	0,12	0,3	0,8
Rickleån	Females	91	89	0,33	3,3	0,002
Sävarån	Females	143	141	0,10	1,2	0,2

Appendix 42. Fulton's C.F., 10-cm-size intervals, both rivers, spent vs. matures, December-March.

Fulton's Condition Factor	Both, spent, Feb-Mar			Both, mature, Dec-Feb			t stat	2-tailed P
Size class (cm)	n	Mean	Var	n	Mean	Var		Welch's app
30,5-40	26	0,53	0,0033	62	0,59	0,0024	4,9	< 0,001
40,5-50	67	0,50	0,0021	175	0,59	0,0034	11,6	< 0,001
50,5-60	29	0,52	0,0032	150	0,62	0,0044	8,5	< 0,001
60,5-70	3	0,54	0,0059	32	0,65	0,0038	2,3	0,03
TOTAL	125	0,51	0,0028	419	0,60	0,004	16,0	< 0,001

Appendix 43. Fulton's C.F., 10-cm-size intervals, Rickleån immatures vs. matures, December-February.

Fulton's Condition Factor	Rickleån immature Dec-Feb			Rickleån mature Dec-Feb			t stat	2-tailed P
Size class (cm)	n	Mean	Var	n	Mean	Var		Welch's app
50,5-60	6	0,65	0,002	96	0,63	0,004	1,2	0,23
60,5-70	3	0,68	0,002	29	0,65	0,005	1,1	0,29
TOTAL	9	0,66	0,002	125	0,64	0,004	1,8	0,08

Appendix 44. K, males versus females, in all four populations, and in total.

Fulton´s Condition Factor			Males			Females			Total		t stat	P
Location	Month	Ind	n	Mean	Var	n	Mean	Var	n	df		Welch's
Rickleån + Sävarån	All	All	345	0,57	0,005	276	0,61	0,005	621	619	7,8	< 0,001
Rickleån	Jan	All	69	0,61	0,003	52	0,64	0,003	121	119	2,7	0,01
Rickleån	Feb	All	33	0,56	0,003	25	0,61	0,006	58	56	2,5	0,02
Rickleån	Mar	All	14	0,64	0,003	7	0,59	0,001	21	19	2,8	0,01
Rickleån	Apr	All	4	0,66	0,003	5	0,71	0,010	9	7	1,0	0,36
Rickleån	Sep	All				3	0,61	0,002	3			
Rickleån	Oct	All	11	0,60	0,003	3	0,65	0,019	14	12	0,7	0,49
Rickleån	Nov	All	5	0,66	0,011	11	0,63	0,006	16	14	0,7	0,52
Rickleån	Dec	All	6	0,65	0,003	15	0,64	0,004	21	19	0,3	0,80
Rickleån	All	All	142	0,61	0,004	121	0,63	0,005	263	261	3,0	0,003
Sävarån	Jan	All	84	0,57	0,002	115	0,60	0,004	199	197	4,1	< 0,001
Sävarån	Feb	All	108	0,52	0,003	21	0,55	0,009	129	127	1,8	0,07
Sävarån	Mar	All	2	0,53	0,002	2	0,63	0,0001	4	2	3,1	0,09
Sävarån	Dec	All	9	0,63	0,005	17	0,64	0,005	26	24	0,3	0,74
Sävarån	All	All	203	0,54	0,004	155	0,60	0,005	358	356	8,0	< 0,001
Tavelån	Jan	All	10	0,62	0,004	12	0,60	0,013	22	20	0,5	0,66
Tavelån	All	All	10	0,62	0,004	12	0,60	0,013	22	20	0,5	0,66
Västerviken	Mar	All	2	0,87	< 0,001				2			
Västerviken	Apr	All	3	0,78	0,012	6	0,73	0,005	9	7	0,7	0,53
Västerviken	Jul	All	1	0,73		2	0,65	< 0,001	3	1		
Västerviken	Aug	All	1	0,66					1			
Västerviken	Sep	All	6	0,66	0,004	6	0,63	0,001	12	10	1,1	0,29
Västerviken	All	All	13	0,72	0,010	14	0,68	0,005	27	25	1,5	0,16
All	All	All	368	0,58	0,006	302	0,62	0,006	670	668	6,8	< 0,001

Appendix 45. K, males vs. females, per size class and river.

Fulton's Condition		Males (spent truncated)			Females (spent truncated)			t stat	2-tailed P
Size class	River	n	Mean	Var	n	Mean	Var	Welch's app	
30,5-40	Rickleån	12	0,58	0,002	7	0,60	0,003	1,0	0,3
40,5-50	Rickleån	48	0,59	0,002	24	0,62	0,004	2,1	0,04
50,5-60	Rickleån	61	0,63	0,005	61	0,64	0,004	0,8	0,4
60,5-70	Rickleån	16	0,62	0,003	20	0,68	0,004	3,1	0,004
TOTAL	**Rickleån**	**137**	**0,61**	**0,004**	**113**	**0,64**	**0,004**	**3,7**	**< 0,001**
30,5-40	Sävarån	25	0,58	0,001	21	0,61	0,003	1,9	0,06
40,5-50	Sävarån	50	0,56	0,002	67	0,60	0,004	4,2	< 0,001
50,5-60	Sävarån	24	0,59	0,005	48	0,61	0,004	1,2	0,2
60,5-70	Sävarån	1	0,68		9	0,66	0,004		
TOTAL	**Sävarån**	**100**	**0,57**	**0,003**	**145**	**0,61**	**0,004**	**4,8**	**< 0,001**

Appendix 46. K, 10-cm-size intervals, per river and sex, mature December-February (fig. 49).

Fulton's Condition Factor		Rickleån mature Dec-Feb			Sävarån mature Dec-Feb			t stat	P
Size class (cm)	Sex	n	Mean	Var	n	Mean	Var	Welch's app	
30,5-40	Males	11	0,58	0,002	25	0,58	0,001	0,5	0,63
40,5-50	Males	40	0,58	0,002	50	0,56	0,002	2,7	0,01
50,5-60	Males	40	0,62	0,005	24	0,59	0,005	1,9	0,06
60,5-70	Males	11	0,60	0,002	1	0,68			
TOTAL	**Males**	**102**	**0,60**	**0,004**	**100**	**0,57**	**0,003**	**3,5**	**< 0,001**
30,5-40	Females	5	0,62	0,004	21	0,61	0,003	0,2	0,81
40,5-50	Females	18	0,63	0,004	67	0,60	0,004	2,0	0,048
50,5-60	Females	40	0,64	0,003	46	0,61	0,004	2,9	0,01
60,5-70	Females	11	0,68	0,004	9	0,66	0,004	0,6	0,57
TOTAL	**Females**	**74**	**0,64**	**0,003**	**143**	**0,61**	**0,004**	**4,3**	**< 0,001**

Appendix 47. CPUE per group (mature, spent, immature), per half-month-interval, in Rickleån and Sävarån, in years 2005-2014. CPUE was calculated through dividing total catch with total effort in angler*hours per interval; n $_{Individuals}$ = 612; n$_{Sampling occasions}$ = 86; n$_{anglers*hours}$ = 227.75 (fig. 51-52).

Population	n				% of total n			Effort		CPUE (n/effort)			
Rickleån	Mature	Spent	Immature	Total	Mature	Spent	Immature	n	(p*h)	Mature	Spent	Immature	Total
Sep 15-Sep 30	1	0	0	1	100,0%	0,0%	0,0%	3	4,50	0,22	0,00	0,00	**0,22**
Oct 1-Oct 15	8	0	0	8	100,0%	0,0%	0,0%	1	5,00	1,60	0,00	0,00	**1,60**
Oct 16-Oct 31	0	0	0	0	0,0%	0,0%	0,0%	1	6,00	0,00	0,00	0,00	**0,00**
Nov 16-Nov 30	16	0	0	16	100,0%	0,0%	0,0%	4	9,00	1,78	0,00	0,00	**1,78**
Dec 1-Dec 15	3	0	0	3	100,0%	0,0%	0,0%	2	9,50	0,32	0,00	0,00	**0,32**
Dec 16-Dec 31	17	0	1	18	94,4%	0,0%	5,6%	4	11,75	1,45	0,00	0,09	**1,53**
Jan 1-Jan 15	12	0	2	14	85,7%	0,0%	14,3%	8	16,50	0,73	0,00	0,12	**0,85**
Jan 16-Jan 31	102	0	5	107	95,3%	0,0%	4,7%	10	28,50	3,58	0,00	0,18	**3,75**
Feb 1-Feb 15	41	7	3	51	80,4%	13,7%	5,9%	12	34,75	1,18	0,20	0,09	**1,47**
Feb 16-Feb 28	1	5	1	7	14,3%	71,4%	14,3%	8	12,25	0,08	0,41	0,08	**0,57**
Mar 1-Mar 15	0	1	13	14	0,0%	7,1%	92,9%	4	14,00	0,00	0,07	0,93	**1,00**
Mar 16-Mar 31	0	0	7	7	0,0%	0,0%	100,0%	6	13,00	0,00	0,00	0,54	**0,54**
Apr 1-Apr 15	0	0	9	9	0,0%	0,0%	100,0%	4	6,25	0,00	0,00	1,44	**1,44**
TOTAL	**201**	**13**	**41**	**255**	**78,8%**	**5,1%**	**16,1%**	**67**	**171,00**	**1,18**	**0,08**	**0,24**	**1,49**
Sävarån	Mature	Spent	Immature	Total	Mature	Spent	Immature	n	(p*h)	Mature	Spent	Immature	Total
Dec 16-Dec 31	26	0	0	26	100,0%	0,0%	0,0%	1	4	6,50	0,00	0,00	**6,50**
Jan 1-Jan 15	58	0	0	58	100,0%	0,0%	0,0%	1	4	16,57	0,00	0,00	**16,57**
Jan 16-Jan 31	140	1	0	141	99,3%	0,7%	0,0%	6	23	6,22	0,04	0,00	**6,27**
Feb 1-Feb 15	19	104	1	124	15,3%	83,9%	0,8%	6	18	1,07	5,86	0,06	**6,99**
Feb 16-Feb 28	0	5	0	5	0,0%	100,0%	0,0%	2	2	0,00	2,50	0,00	**2,50**
Mar 1-Mar 15	0	2	1	3	0,0%	66,7%	33,3%	3	7	0,00	0,29	0,14	**0,43**
TOTAL	**243**	**112**	**2**	**357**	**68,1%**	**31,4%**	**0,6%**	**19**	**56,75**	**4,28**	**1,97**	**0,04**	**6,29**

Appendix 48. Mean CPUE/sampling occasion (other calculation than in tab. 55 and fig. 38) in Rickleån (n = 4-12). The period Jan 16-Jan 31 vs., respectively, Nov 16-Nov 30, Dec 16-Jan 15 and Feb 1-Feb 15.

Rickleån	Mean CPUE	Var	n			t	2-tailed P
Period	ind/p*hr		Individuals	Sampling occasions	Anglers*hrs	Welch's app	
Jan 16-Jan 31	3,76	6,34	107	10	28,50		
Nov 16-Nov 30	2,40	1,42	16	4	9,00	1,4	0,199
Dec 16-Jan 15	1,36	1,64	32	12	28,25	2,7	0,013
Feb 1-Feb 15	1,73	3,44	51	12	34,75	2,1	0,047

Appendix 49. Both rivers; number of individuals per reproductive stadium; Jan 27-Feb 25 (fig. 53).

Date	Both		
	Mature	Spent	Immature
01.27-01.31	82	1	0
02.01-02.05	30	0	3
02.06-02.10	13	10	0
02.11-02.15	17	101	1
02.16-02.20	1	4	0
02.21-02.25	0	6	1
	143	**122**	**5**

Appendix 50. Electro-fishing data (non-conclusive); six sites, six efforts, two per month (Aug-Oct), Rickleån, 1989-2003. Abundance calculated as number of individuals per 100 m^2 (Swedish Board of Fisheries 2009).

Date/Locality	Johanneslund	Fiskegränsen	Böle	Laxbacken	Gammströmmen	Nättingforsen	Average	Month
89.09.07	0,8	0	0	0,5	1,2	0,5		
94.09.13	1	0	0	0	2,4	4,1	0,2	**Aug**
96.08.07	0	0	0,5	0	0	0,5		
98.10.12	0	2,4	0,9	0	0	1,1	0,9	**Sept**
00.10.04	0	0	0	0	0	0		
03.08.21	0	0	0	0	1,1	0	0,4	**Oct**
Average	0,25	0,6	0,35	0	0,6	1,425		

Appendix 51. Pearson's Rank Correlation, CPUE (caught individuals/anglers*hours) vs. the four moon phases (New moon, 1st Quarter, Full moon, 2nd Quarter). Compiled, and per river. For correlation purposes, New Moon is numbered 1 (= small moon), 1st and 2nd Quarter is numbered 2 (= " half moon"), and full moon is numbered 3.

20010101-20140213	n	d(f)	Pearson's	t stat	2-tailed P	Mean CPUE per moon phase				
Populations			r			New Moon	1st Quarter	Full Moon	2nd Quarter	All
Both	116	114	0,04	0,5	0,6	1,9	3,5	2,5	2,9	2,7
Rickleån	97	95	-0,07	0,7	0,5	1,6	2,2	1,3	2,3	1,9
Sävarån	19	17	0,35	1,6	0,1	3,4	9,8	10,4	5,2	7,1

Appendix 52. Comparing moon phases with highest vs. lowest CPUE, both rivers compiled, and per river separately (which moon phase resulted in highest/lowest CPUE, varied between rivers).

Place, Moon phase	n	Mean	Variance	d(f)	t stat	2-tailed P
Both rivers, New Moon	24	1,9	3			
Both rivers 1st Quarter	29	3,5	22	51	1,6	0,11
Rickleån, Full Moon	26	1,3	6			
Rickleån, 2nd Quarter	27	2,3	6	51	1,5	0,14
Sävarån, New Moon	4	3,4	6,0			
Sävarån, Full Moon	4	10,4	60,7	6	1,7	0,13

Appendix 53. Presence of liver parasites or not, versus different indexes, in Rickleån and Sävarån.

River	Index	Parasites	n	%	Mean	Var	t stat	2-tailed P
Rickleån	Gonad	No	121	46%	0,062	0,001	0,67	0,50
		Yes	142	54%	0,059	0,001		
Sävarån	Gonad	No	109	31%	0,061	0,001	0,57	0,57
		Yes	248	69%	0,059	0,002		
Rickleån	Liver	No	56	39%	0,286	0,027	0,13	0,89
		Yes	86	61%	0,290	0,025		
Sävarån	Liver	No	57	24%	0,194	0,013	0,78	0,44
		Yes	176	76%	0,207	0,009		
Rickleån	Fulton's	No	121	46%	0,616	0,004	0,38	0,704
		Yes	142	54%	0,619	0,005		
Sävarån	Fulton's	No	109	31%	0,569	0,006	0,36	0,716
		Yes	248	69%	0,566	0,005		
Rickleån	Intact stomach	No	16	28%	0,394	0,007	1,38	0,172
		Yes	41	72%	0,357	0,010		
Sävarån	Intact stomach	No	26	25%	0,339	0,009	0,07	0,943
		Yes	80	75%	0,337	0,005		

Appendix 54. Annual Average Temperature (AAT, ^{o} C) in northern Sweden the last five decades, 1960-2008. Developed from Swedish Environmental Protection Agency 2009 and SMHI 2009.

	AAT (^{o} C)	Variance	Compared to (Student´s T, p =)				
YEAR			1960-1969	1970-1979	1980-1989	1990-1999	2000-2008
1960-1969	2,3	0,56	--------------	0,06	0,22	**0,0002**	**<0,0001**
1970-1979	3,05	0,80	0,06	--------------	0,44	0,06	**0,0008**
1980-1989	2,85	1,27	0,22	0,44	--------------	**0,04**	**0,0012**
1990-1999	3,73	0,38	**0,0002**	0,06	**0,04**	--------------	**0,02**
2000-2008	4,32	0,15	**<0,0001**	**0,0008**	**0,0012**	**0,02**	--------------

Appendix 55. Data set used in tab. 10.

Year x	AAT (^{o} C)	Aut year x until spawn year x+1	Factors, mean per period											
			TL (cm)		Gonad		Liver		In. stom		Em. stom		Fulton	
			n	mean	n	mean	n	mean	n	mean	n	mean	n	mean
2004	5,58	2005-2006	54	50,9	54	0,076	0		0		0		54	0,62
2005	5,94	2006-2007	42	52,7	42	0,089	1	0,21	0		0		42	0,63
2006	6,32	2007-2008	36	52,9	36	0,069	36	0,25	0		0		36	0,62
2007	6,18	2008-2009	30	52,7	30	0,066	30	0,27	8	0,35	8	0,35	30	0,62
2008	6,36	2009-2010	10	53,0	10	0,081	10	0,32	10	0,41	10	0,38	10	0,66
2009	5,56	2012-2013	17	47,5	17	0,083	17	0,21	17	0,39	17	0,35	17	0,60
2010	3,76	2013-2014	20	52,2	20	0,056	20	0,24	20	0,31	20	0,29	20	0,59
2011	6,28	**Total Rickleån**	**209**	**51,8**	**209**	**0,075**	**114**	**0,25**	**55**	**0,36**	**55**	**0,34**	**209**	**0,62**
2012	5,16	2005-2006	51	44,3	51	0,073	0		0		0		51	0,59
2013	5,74	2006-2007	70	46,7	70	0,076	3	0,25	0		0		70	0,57
2014	6,88	2007-2008	47	48,8	47	0,091	47	0,20	0		0		47	0,60
		2008-2009	71	47,8	71	0,086	71	0,27	38	0,36	38	0,35	71	0,61
		2013-2014	4	51,6	4	0,079	4	0,15	4	0,30	4	0,30	4	0,58
		Total Sävarån	**243**	**47,0**	**243**	**0,081**	**125**	**0,24**	**42**	**0,35**	**42**	**0,34**	**243**	**0,59**

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