

The Most Variable Vertebrate on Earth¹

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Abstract—In the search for the most variable non-human vertebrate on Earth, intraspecific variation of ten variable traits was compared among ten highly variable species. Mammals, birds and many reptiles, amphibians and fishes were excluded because most of the variation is among, and not within species. The focus was on northern fishes, where high intraspecific variation is well documented. The ten selected species were European whitefish *Coregonus lavaretus*, chinook salmon *Oncorhynchus tshawytscha*, sockeye salmon *O. nerka*, rainbow trout *O. mykiss*, atlantic salmon *Salmo salar*, brown trout *S. trutta*, arctic charr *Salvelinus alpinus*, brook charr *S. fontinalis*, dolly varden charr *S. malma* and threespine stickleback *Gasterosteus aculeatus*. Variation included not only size and phenotype, but also ecology, behaviour and life history. The traits were geographic range, migration, habitat, adult size, colour, body form, polymorphism, diet, reproduction and genetics. Arctic charr came on top in the final ranking, followed by dolly varden charr and rainbow trout. The two least variable were chinook salmon and threespine stickleback. It is proposed that arctic charr, which is also the northernmost fish on Earth, has evolved its unique variability in range, size, phenotype, ecology and life history by adapting to the extreme and highly unpredictable ecological conditions of arctic and other northern lakes for many glacial periods.

Keywords: intraspecific vertebrate variation, northern fishes, postglacial lakes

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FOREWORD

This contribution was given as the Keynote at the 7th International Charr Symposium in Yuzhno-Sakhalinsk, Russia in September 2012. It is written in the format used in the presentation, but without illustrations and with a reduced number of tables. The thoughts about this theme go back to unpublished invited talks given at previous charr symposia in Reykjavik, Iceland and Stirling, Scotland.

The Keynote was dedicated to Professor Ksenia Savvaitova at Moscow State University who died a short time before the symposium. Her extensive works on *Salvelinus* in Russia will always be remembered as central contributions to the science of systematics, ecology and evolution.

INTRODUCTION

In a recent review, I raised the question if arctic charr *Salvelinus alpinus* is the most variable of all vertebrates (Klemetsen, 2010). The invitation to give this keynote gave me an opportunity to go deeper into the matter in order to test if this is the case.

By variation, I think not only on size, colour and form but also on range, behaviour, ecology and life history. And, to be explicit, I look for variation within,

not among, species and exclude domestic vertebrates because their variation is the result of artificial selection.

My thesis is that you have to go north, to the fishes of postglacial lakes and rivers, and particularly the superfamily Salmonoidea, to look for candidates.

A WORD ABOUT MAN

Phenotypic variation in Man *Homo sapiens* is mainly restricted to skin colour and some morphological traits, and body size falls well within the ranges found in other mammals (McKellar & Hendry, 2009). Man is, however, the only cosmopolitan vertebrate, occupying all continents, archipelagos and climate zones and also the air and the seas. Dogs, cats, rats and other man-affiliated animals are also widely distributed, but no wild vertebrates are cosmopolites.

And Man has culture. It started 2.5 Myr ago when the Handy man *Homo habilis* started to use primitive tools (Meredith, 2011; Wilson, 2012). With time, the result is what we see today, with our technology, agriculture, science, art and music. The big debate about natural selection, sociobiology and the human condition (Wilson, 1975, 2012; Sterelny, 2007) set aside, you cannot ignore culture when you look at vertebrate variation. Without doubt, culture makes Man the most variable vertebrate on earth.

¹ The article is published in the original.

Is it game over then? No, Man and other vertebrates can not be compared because of culture. It all depends on our brain, as put so well by Greene (1960, cited from a 2004 edition, p. 116): “Evolution, as far as we can tell, has lodged itself finally in the brains of man. The ant, the fish, even the ape has gone as far as it can go, but in our brain evolution is moving—my God—at what a speed!” So, the comparison with Man is unfair and we must look for the most variable vertebrate on earth after ourselves.

THE APPROACH

Insects and vertebrates are the dominating animal phyla on earth today. There is a bewildering diversity of insects but also very high variability in vertebrates. With focus on variation within species, I consulted colleagues and searched literature and the net; aiming for a set of promising candidates and a set of traits where the variation was high and reasonably well documented.

Many taxa and many traits were screened before I decided to simplify and ended up by choosing 10 candidate species and 10 variable traits. This done, the variation for each trait was compared among the candidates, and each of them was allotted a score on a scale from 1–10, with 10 as the highest variation. This gave a range among the candidates for each trait and allowed a final ranking by summing up the scores from the 10 × 10 matrix of species and traits.

THE TRAITS

When thinking on variation in animals, the first that comes to mind is variation in size, colour and form. These three traits therefore came on the list at once. Geographical range was the next because of differences in distribution on continents, in oceans, and with altitude. Migration was included because it varies from strict residency to very long migrations. The important niche dimensions of habitat and diet were then added. Reproduction is also variable and was put on the list. As some species express distinct morphs related to life history or ecology while others do not, polymorphism was incorporated. Genetic variation was the final trait on the list.

Several other traits in ecology, physiology and behaviour are variable but were discarded either because they were found to vary less than those on the list above, or because it was difficult to document variation for all the candidates.

THE CANDIDATES

Endotherms, mammals and birds, show spectacular variation and adaptations, especially to terrestrial environments. Very much of the variation in range, colour and form, ecological niches and life histories is, however, among species. Importantly, their growth

patterns appear almost immutable and particular species of mammals and birds are notably constant with regard to final body size (Weatherley, 1972). It appears that endothermy constrains intraspecific variation, and highly variable species are not likely to be found among mammals and birds.

Ectotherms, reptiles, amphibians and fishes, also have high diversity but, again, very much of the variation is found at the interspecific level. Some groups are remarkably species-rich, like the well studied, about 360, anoles lizards (Losos, 2009). This is one of the best cases of adaptive radiation known, and it is strongly documented that all the sometimes very close species are still good species, but there is little intraspecific variation in ecology and phenotype. Similar adaptive radiations with many closely related species are found among amphibians, for instance in the about 175 colourful dendrobatid frogs (Wikipedia) of South America. The same is the case with many fish groups, not the least the cichlid family with its spectacular radiation of species, some of them with extremely narrow niches (Greenwood, 1981). The largest fish family, the cyprinids, also have many closely related species with little variation (Kottelat and Freyhof, 2007). I concluded that reptiles, amphibians and many fish groups do not have species with the high intraspecific variation I was looking for. I had to look elsewhere, and turned to northern fishes. Here, several highly variable species are well known and well studied.

In fish taxa of the northern hemisphere like sunfishes, whitefishes, sticklebacks, salmons, trouts and charrs, high phenotypic plasticity and ecologically driven evolution are well documented. Some species have wide geographic distributions and some populations perform long migrations. In contrast, other species like graylings (Thymallidae), pikes (Esocidae) and percids (Percidae) vary remarkably little despite having wide distributions (Kottelat & Freyhof, 2007). Most of the very variable species are freshwater resident or anadromous, but there are also marine species, like European herring *Clupea harengus* and Atlantic cod *Gadus morhua* that are widely distributed and have high interpopulation variation.

When picking the ten candidates, I tried to find species that showed high variation over as many of the traits as possible. Marine species and groups like sunfishes (Centrarchidae) were omitted because they were not found to vary enough over the set of traits, and the focus soon was on sticklebacks (Gasterosteidae), whitefishes (Coregonidae) and salmonids (Salmonidae). As it is one of the best studied of all fishes in terms of variation (Bell and Foster, 1994) the threespine stickleback *Gasterosteus aculeatus* was an obvious candidate. Likewise, the highly variable European whitefish *Coregonus lavaretus* (Østbye et al., 2006) was chosen among the coregonids. It was less easy among the salmonids as there are several highly variable species in all the three major genera, *Onc-*

rhyncus, *Salmo* and *Salvelinus*. I ended up with chinook salmon *Oncorhynchus tshawytscha*, sockeye salmon *Oncorhynchus nerka*, rainbow trout *Oncorhynchus mykiss*, Atlantic salmon *Salmo salar*, brown trout *Salmo trutta*, arctic charr *Salvelinus alpinus*, brook charr *Salvelinus fontinalis* and dolly varden charr *Salvelinus malma*.

A BRIEF FLASHBACK TO DROTTNINGHOLM

In Scandinavia and, indeed, in Europe, much of the modern post-war work on salmonoid variation was done at The Institute of Freshwater Research at Drottningholm, Sweden. It was fuelled for a large part by water power money but also, following a pre-war tradition, by an official will to support such work. The staff had several eminent biologists, among them well-known names like Gunnar Svärdson (still an icon in coregonid ecology and evolution) and Nils-Arvid Nilsson (who re-introduced competition theory to salmonid ecology). Here, I will go back to some of the work done by two heroes of mine, Torolf Lindström and Lennart Nyman.

Nyman was one of the first to point out the enormous phenotypic variation among and within charr populations in Scandinavia, and beyond. He was a pioneer in using and developing techniques for studying protein variation by electrophoresis. By screening a multitude of allozymes, he demonstrated the strong variation at the blood serum esterase locus in arctic charr. This allowed him to explore very many populations of charr and other northern fishes by combining genetic and ecological methods. He published widely, and his production deserves a proper review, but there is only room to touch on two of his influential papers here. The first (Nyman, 1972) presented esterase variation in 31 populations of arctic charr from Canada and Scandinavia. More than 3000 samples were analysed, an enormous effort in those days. Importantly, he demonstrated genetic differences between sympatric morphs of charr (or double charrs as he often called them) in five Swedish lakes and advised that the new tool should be used to aim a heavy effort at what he termed the 'char complex.' The second (Nyman et al., 1981) used material from a large number of populations to propose the hypothesis that there are three good species of charr in Scandinavia. This was heavily based on esterase variation but also on ecology and life histories. It was a bold but controversial contribution and it is fair to say that many workers in the field of salmonid evolution perhaps did not agree that this was right. In retrospect, I think that is beside the point. This was a stimulating paper because it created discussion that was based on two premises that were central at the time: Mayr's biological species concept and Svärdson's postglacial invasion theory. These two papers will always stand as important contributions from a creative and hard-working (and social!) biologist at Drottningholm.

Lindström worked in several fields of freshwater biology, including zooplankton, acid rain and fish. Sadly, some of his early but innovative contributions on variation in charr are almost forgotten, probably because they were mostly published as reports in Swedish. Working with colleague G. Andersson and with material from 1958 to 1981, he found that there were two morphs, one small and one large, of charr in the mountain lake (about 900 m elevation) Stora Rösjön (literally Big Charr Lake, there is a smaller one nearby) in Fulufjäll in south Sweden (Andersson et al., 1971; Lindström and Andersson, 1980; Lindström et al., 1982). In addition to size, there were differences in growth, colour, form, otolith shape, pyloric caeca and diet. Interestingly, 3400 small charr that were caught by beach seine and transferred to a lake without charr in 1964 developed the same differences in growth and size as in the donor lake. Svedäng (1990) then took fertilized eggs of the morphs and crosses between them to the lab and found that the differences in age and growth had a genetic basis. Stora Rösjön is not only interesting because it is a very early case of sympatric charr morphs where, moreover, life history differences were shown to have a genetic basis, but also because it is a very shallow lake. The maximum depth is only 4 m, so there is no profundal zone and practically no zooplankton (Hanson, 1976). It is, essentially, a 100 ha moss covered littoral zone. Two morphs of charr are nevertheless present. Double charrs are rarely found in lakes like this, where alternative pelagic and profundal niches are not present. I believe this is the first case that is described.

These pioneer studies from Drottningholm show how early the institute focussed on phenotypic, ecological and genetic variation in its scientific approach and provide a good starting point for the discussion below on variability in vertebrates.

SCORING, COMPARING AND RANGING

Variation was given as distribution on continents and in oceans for geographic range and as numbers for body weight and genetics. For the other traits, variation was sorted in two to several categories. Presence or absence of variation for a trait was first noted for each species. Presence was then quantified as barely present, present or strongly present, and given as (+), + and ++ in the tables. The scores were found by summing the plusses (with two (+) being equal to +). For brevity, the species are called by their shortest specifying vernacular name (for instance sockeye) or their last Latin name (without italics) in the text, for instance lavaretus for whitefish *Coregonus lavaretus*. Taxonomic order was used for the tables. The general information about the species was taken from Groot & Margolis (1991) for *Oncorhynchus*, Balon (1980) for *Salvelinus*, Elliott (1994) for *trutta*, Aass et al. (2011) for *salar*, Wootton (1984) and Bell and Foster (1995) for *aculeatus*, and from Wikipedia and FishBase without refer-

Table 1. Variation in geographic range

Species	Continent	Ocean	Altitude	Points
<i>C. lavaretus</i>	WPal	Atl (Arc)	1000	1
<i>O. tshawytscha</i>	WNeEPal	E&WPac	650	4
<i>O. nerka</i>	WNeEPal	E&WPac	1200	7
<i>O. mykiss</i>	WNeEPal	E&WPac	3000	7
<i>S. salar</i>	ENeWPal	Atl Arc	500	5
<i>S. trutta</i>	WPal	EAtl Arc	1600	3
<i>S. alpinus</i>	Hol	Atl (Pac) Arc	2800	10
<i>S. fontinalis</i>	ENe	WAtl Arc	1000	3
<i>S. malma</i>	EPalWNe	E&WPac Arc	1000	8
<i>G. aculeatus</i>	Hol	Atl Pac (Arc)	200	9

Presences of the species are given as Holarctic (Hol), East and West Palearctic (EPal, WPal), East and West Nearctic (ENe, WNe); Arctic, Atlantic and Pacific Oceans (Arc, Atl, Pac), and East and West sides of the Atlantic and Pacific Oceans (EAtl, WAtl, EPac, WPac). Notations in parentheses indicate weak presence. Maximum altitudes are given as m above sea level.

ring to the source every time. Other sources are specifically referred to.

GEOGRAPHIC RANGE

In Table 1, the distributions are given as Holarctic or as the east or west side of the Palearctic (Eurasian) and Nearctic (American) continents. Only natural distributions are used, not introductions by man. Then their distributions during anadromy in the Pacific, Atlantic or Arctic oceans are noted and the altitudinal ranges are given as the maximum elevation of occurrence.

Top scores were given to stickleback and arctic charr because they are the only ones with holarctic distributions and anadromy into all three oceans, but arc-

tic charr came first with 10 points because of the extreme range in altitude. Dolly varden came in third place as it occurs on both sides of the Pacific and also is a common anadromous fish in the Arctic Ocean. There was a draw for 7 points between sockeye and rainbow because of similar distributions on continents and in oceans, and not very different altitudes. Atlantic salmon has a parallel distribution on the Atlantic side and also migrates into the Arctic Ocean but was put behind due to a lower altitude range. Chinook came behind the other *Oncorhynchus* because of a lower altitude range. Brook charr and brown trout have matching ranges on their respective sides of the Atlantic and were given 3 points. The final place went to whitefish because of its restricted distribution in the west Palearctic and also because it is the least anadromous of the candidates.

MIGRATION

Only regular migrations related to ontogeny or life history were considered, not straying. Migration patterns were sorted in five categories: anadromous, river to lake or vice versa, lake to lake, lake resident and river resident. Rivers refer to all sizes of running waters.

Brown trout has the most variable migration patterns and was given a score of 10 (Table 2). Anadromy, migrations between rivers and lakes and residency in lakes and in rivers are all common. Rainbow trout is similar but came second because migrations between lakes and rivers are less strongly developed. Arctic charr is the only species where migration between lakes are found (Näslund, 1990) but anadromy is restricted to northern populations, therefore third place and 8 points. Malma is mainly a running water species but some lacustrine populations are found: 7 points. Migration patterns are also less variable in fontinalis, which is mainly resident in lakes and rivers

Table 2. Variation in migration patterns given as anadromous, between a river and a lake or vice versa, between two lakes, lake resident and river resident

Species	Anadromous	River-lake	Lake-lake	Lake res.	River res.	Points
<i>C. lavaretus</i>	(+)	+	-	++	+	3
<i>O. tshawytscha</i>	++	-	-	-	-	1
<i>O. nerka</i>	++	+	-	+	(+)	5
<i>O. mykiss</i>	++	+	-	++	++	9
<i>S. salar</i>	++	+	-	+	(+)	5
<i>S. trutta</i>	++	++	-	++	++	10
<i>S. alpinus</i>	+(+)	+	+	++	+	8
<i>S. fontinalis</i>	+	+	-	++	++	6
<i>S. malma</i>	++	+(+)	-	+	++	7
<i>G. aculeatus</i>	++	-	-	++	(+)	2

(+)—barely present, (+)—present, (++)—strongly present.

Table 3. Variation in habitat types given as sea, rivers, lake littoral, lake pelagic, lake profundal and as ontogenetic or seasonal habitat shifts in lakes

Species	Sea	River	Litt	Pel	Prof	Shifts	Points
<i>C. lavaretus</i>	(+)	+	++	++	+	+	8
<i>O. tshawytscha</i>	++	++	–	–	–	–	1
<i>O. nerka</i>	++	+	++	++	–	–	6
<i>O. mykiss</i>	++	+	++	(+)	–	–	4
<i>S. salar</i>	++	++	+	(+)	–	–	4
<i>S. trutta</i>	++	++	++	(+)	(+)	–	7
<i>S. alpinus</i>	+(+)	+	++	++	+	++	10
<i>S. fontinalis</i>	(+)	++	++	+	–	(+)	5
<i>S. malma</i>	++	++	+	+	(+)	(+)	9
<i>G. aculeatus</i>	++	(+)	++	(+)	–	–	2

Symbols as in Table 2.

but also has migratory patterns: 6 points. Sockeye and Atlantic salmon are quite similar, with strongly developed anadromous migrations but also some resident populations. Both were given 5 points. Lavaretus was just ahead of aculeatus because more patterns are present. The strongly anadromous chinook was the least variable.

HABITAT

The habitats were sorted as sea, rivers and lakes; and lakes were further divided into littoral, pelagic and profundal habitats. The final category was seasonal or ontogenetic shifts between lake habitats.

Here, alpinus was clearly number one (Table 3) because it uses all habitats including deep water and also often performs habitat shifts in lakes. Malma was similar but came second because habitat shifts are less common. Whitefish also uses all habitats, particularly in lakes, but came behind with 8 points because migration to the marine habitat is rare. Nerka and trutta were very close with trutta more common in rivers and nerka with kokanee, its resident form, more common in the pelagic zone. Trutta was ahead because piscivorous individuals are known to feed in the profundal habitat. Fontinalis is mainly a littoral or riverine fish and was next with 5 points. Although mykiss is more common in the littoral and salar more common in rivers, there was a draw between them at 4 points. Aculeatus is present at sea and in lake littoral zones and got 2 points. Again, chinook was last with its one-sided anadromous life history.

SIZE

Variation in size is given as body weights of sexually mature adults. Precocial males were omitted because I looked for variation among populations, not the strategy of one sex. Size ranges are given as the highest

weight divided by the lowest. Most of the maximum weights are taken from FishBase. Some low weights were estimated from recorded body lengths by assuming a condition factor of 1.0.

With the largest fish being more than 5000 times heavier than the smallest, arctic charr had the most variable body size of all (Table 4). The largest alpinus on record (15.9 kg) was an anadromous charr from the arctic islands of Novaja Zemlya, Russia (Yessipov, 1935, cited by: Johnson, 1980). The smallest are profundal charrs from Fjellfrøsvatn, Norway where mature fishes of both sexes weigh only 3–17 g (Klemetsen et al., 2003). Very small alpinus are also found in Sweden (Nyman, 1978), Iceland (Sandlund et al., 1992; Sigursteinsdottir and Kristjansson, 2005) and Greenland (Riget et al., 2000). Atlantic salmon was number two with a range of 2750 times. Only alpinus was more variable, so Fleming and Einum (2011) were right when claiming that the variability in size at maturity in salar is matched by few vertebrates. Populations of small-sized resident salmon are found on

Table 4. Variation in body size at maturity (range shows the highest weight divided by the lowest weight)

Species	Variation, g	Range	Points
<i>C. lavaretus</i>	20–10000	500×	5
<i>O. tshawytscha</i>	270–61400	230×	2
<i>O. nerka</i>	30–7710	260×	3
<i>O. mykiss</i>	20–24000	1200×	7
<i>S. salar</i>	17–46800	2750×	9
<i>S. trutta</i>	20–50000	2500×	8
<i>S. alpinus</i>	3–15900	5300×	10
<i>S. fontinalis</i>	27–9400	350×	4
<i>S. malma</i>	9–6700	750×	6
<i>G. aculeatus</i>	3–15	5×	1

both sides of the Atlantic, most of them on the west side (Aass et al., 2010). Sutterlin and MacLean (1984) reported mature females with 12 cm body lengths from Newfoundland. This corresponds to weights of about 17 g. Small fish (males 12 cm, females 14 cm) are also found in Norway, in the only river resident population of salmon in Europe (Berg and Gausen, 1988). Brown trout came very close with a range of 2500 times from the smallest (resident populations) to the largest (50 kg, Caspian Sea; Muus and Dahlström, 1978). Rainbows can be about as small as trutta but reach only half the maximum size and got 7 points. Malma can mature below ten grams, but do not get as large as alpinus and got 6 points. Whitefish varies between 20 g and 10 kg and came next with 5 points. Fontinalis and nerka have about the same minimum sizes but fontinalis grow larger. With a recorded maximum weight of 61.4 kg, chinook is by far biggest of the candidates. This salmon has two different anadromous strategies, termed ocean type and stream type by Healey (1991). Ocean type 'jacks' return to the rivers after a short migration to the sea, with sizes down to 30 cm. This corresponds to about 270 g, giving a size range of 230 times. This gave 2 points, and chinook came second to last. Stickleback was last with the largest weighing only 5 times more than the smallest.

COLOUR

Colour variation was studied through ontogeny and among populations for each species, and then compared. Variation in colour is difficult to compare objectively, but I did my best by consulting several sources, including the fabulous watercolour paintings by Prosek (1998).

Sockeye was found to be the clearly most variable through ontogeny. All the other salmonids also vary much through ontogeny, but not as much as sockeye. Sticklebacks vary somewhat because mature males get red bellies while whitefish hardly vary at all. Mykiss, alpinus and malma all have very high variation among populations. Nerka, salar, trutta and fontinalis also vary quite much while tshawytscha and aculeatus show little inter-population variation. Alpinus got 10 points because of the very high variation among populations. Mykiss and malma were close with 9 points. Then came nerka with 7 and salar, trutta and fontinalis with 6. The three last places with 3, 2 and 1 points went to chinook, stickleback and whitefish.

FORM

As with colour, I looked both for variation through ontogeny and variation among populations. The main characters were in body shape, fins, head and snout, eye size, teeth, gill-rakers and scales.

All three salmons have very strong ontogenetic changes in form. Trouts and charrs also vary through ontogeny while whitefish and stickleback vary little.

Arctic charr and whitefish have very high variability among populations, closely followed by dolly varden. The other species show less variation among populations. Again, alpinus came on top with 10 points because of very high variation among populations. Nerka was second because of its spectacular ontogenetic change of form and the different kokanee type. Salar, with its strong ontogenetic variation and many different freshwater populations followed next with 8 points. Then came malma with good variation both in ontogeny and among populations. In spite of little ontogenetic variation, whitefish was given 6 points because of the high morphological variation among populations. It was difficult to range chinook, rainbow and brook charr, and they tied for 5 points. Stickleback populations vary in body armour, but could not match any of the salmonoids.

POLYMORPHISM

Sympatric polymorphism is the ultimate expression of variability because it displays different intraspecific adaptive peaks in one locality. Here, I first looked for anadromous and resident forms of both sexes in the same system and then for cases with two or more sympatric forms in lakes.

All the ten species can have sympatric resident and anadromous forms. This is very common in nerka, mykiss, trutta and alpinus and is also found in salar, fontinalis and malma. It is rare in lavaretus, tshawytscha and aculeatus. Many cases of two sympatric lacustrine morphs are found in whitefish and arctic charr, usually as pelagic and littoral morphs and some of them are very different. It is frequent, but with differences less expressed, in brook charr (Bourke et al., 1997) and rare cases are also known in malma (Armstrong and Morrow, 1980; Markevich, 2012). The limnetic and benthic forms of sticklebacks in British Columbia are well studied and famous (Bell and Foster, 1994) but similar dimorphisms are, curiously enough, hardly found elsewhere in the circumpolar distribution of the species. Some cases of three or even four morphs are known in arctic charr (Klemetsen, 2010). Three morphs of whitefish are found in some Finnish and Norwegian lakes (Siwertsson et al., 2010) and one case is known in brown trout from Ireland (Ferguson and Taggart, 1991). The common occurrence of sympatric anadromous and resident forms and the many cases of two, three and four lake forms gave 10 points for alpinus. In trutta, sympatry between residency and anadromy is more or less the rule. Two lacustrine morphs, one of them piscivorous, do occur and there is also one lake with three morphs so it got 9 points. Lavaretus came third with 8 points because many cases of two and even three sympatric forms are well known. Fontinalis and malma both have anadromous and resident forms and lacustrine splits are also found in both, but fontinalis was given 7 and malma 6 since two lake forms seem to be more common in fon-

Table 5. Variation in diet given as the prey types of river drift, pleuston, plankton, littoral benthos (L benthos), profundal benthos (P benthos) and fish

Species	Drift	Pleuston	Plankton	L benthos	P benthos	Fish	Points
<i>C. lavaretus</i>	+	+(+)	++	++	+	(+)	4
<i>O. tshawytscha</i>	++	–	+	–	–	++	2
<i>O. nerka</i>	(+)	+	++	++	(+)	++	8
<i>O. mykiss</i>	++	+	(+)	++	(+)	++	8
<i>S. salar</i>	++	–	+	+	–	++	3
<i>S. trutta</i>	++	++	(+)	++	(+)	++	9
<i>S. alpinus</i>	+	++	++	++	+	+(+)	10
<i>S. fontinalis</i>	++	+	++	++	–	+	8
<i>S. malma</i>	++	+	+	++	(+)	+	8
<i>G. aculeatus</i>	–	(+)	++	++	–	–	1

Symbols as in Table 2.

tinalis. Nerka and mykiss do not have lake polymorphisms and got 5 points. As the dimorphism in aculeatus seems to be restricted to a few lakes, it came down on the list with 3 points. Neither of the two big salmons, salar and tshawytscha, have polymorphic lake forms but salar was ahead with 2 points because a few cases of resident populations along with anadromous forms are known (Berg and Gausen, 1988).

DIET

All the present species are predators but their diets vary much. In order to compare them, I grouped prey types in riverine drift, pleuston (surface food), plankton, littoral benthos, profundal benthos and fish.

10 points went to alpinus as a very broad generalist that regularly takes prey from all prey groups, including profundal benthos (Table 5). Trutta is also a generalist that can feed on all prey types apart from profundal benthos and was in second place with 9 points. Nerka, mykiss, fontinalis and malma also have varied diets, and came close behind, all with 8 points. Lavaretus rarely takes fish prey because of its small mouth and does not utilize drift much, and got 4 points. Salar and tshawytscha are strong on drift as parr and on fish later in life but do not eat much of the other prey types. Salar was put first of the two because some lake resident populations take plankton. Aculeatus is the least variable and got 1 point.

SPAWNING

Variation in time and place of spawning is important because it can lead to reproductive isolation. I grouped spawning time as spring, summer, autumn and winter, and spawning place in river, littoral and profundal habitats.

Most alpinus populations spawn in the autumn, but the species is also known to spawn in the winter

(Klemetsen et al., 1997), in the spring (Frost, 1965) and in the summer (Hesthagen et al., 1995). Moreover, it can spawn in rivers, in lake littorals and in deep water. It was the most variable of the candidates and was given 10 points. A draw for 9 points was set for lavaretus, nerka and mykiss. All are variable: lavaretus spawns in autumn and winter and in all habitats, nerka mostly in autumn and in all habitats, and mykiss in winter and spring and in rivers and lake littoral zones. Malma spawns in autumn and possibly in summer, and in rivers and lake littorals and got 6 points. Fontinalis and trutta mainly spawn in running water in the autumn but fontinalis also uses lake littorals while this is rare in trutta, so they got 5 and 4 points. The big salmons were again similar and were given 3 points. The spawning habits of aculeatus vary little and it came last with 1 point.

GENETICS

F_{st} is a useful measure of genetic differentiation when comparing populations. Here, I used variation in F_{st} from microsatellites (allozymes for malma and aculeatus) taken from Appendix 2 in Hendry and Stearns (2004) and, for aculeatus, from Buth and Hagelund (1994). Emphasis was put on the highest values but also on the range. Aculeatus varied most with a range of 0.034–0.651 (Table 6). The rest were scored after the values in the table but alpinus and fontinalis drew with 7 points because they were almost identical.

FINAL RANK

The summary of 10 variable traits for the 10 candidate species, and the final rank of scores are given in Table 7. Arctic charr was the winner with a score of 95 points. With scores above 70 points, dolly varden charr and rainbow trout were also highly variable but

Table 6. Genetic variation given as F_{st} values

Species	F_{st}	Points
<i>C. lavaretus</i>	0.088	2
<i>O. tshawytscha</i>	0.008–0.075	1
<i>O. nerka</i>	0.018–0.094	3
<i>O. mykiss</i>	0.007–0.440	8
<i>S. salar</i>	0.006–0.143	4
<i>S. trutta</i>	0.025–0.285	5
<i>S. alpinus</i>	0.039–0.370	7
<i>S. fontinalis</i>	0.33–0.370	7
<i>S. malma</i>	0.019–0.520	9
<i>G. aculeatus</i>	0.034–0.651	10

clearly behind arctic charr. Still variable, brown trout and sockeye salmon came a bit further down. Then followed brook charr, Atlantic salmon and whitefish. Finally, threespine stickleback took the second last place with 32 points and chinook salmon was last with 24 points.

After this exercise, I conclude that arctic charr is the most variable vertebrate on earth after Man. It has a wide circumpolar range and is found farther north than any other freshwater or anadromous fish but also in cool water at temperate latitudes. It migrates into the Arctic, Pacific and Atlantic oceans, has all kinds of migrations and habitat shifts within and between freshwater systems, and also displays residency to very restricted localities (Nyman, 1978; Sigursteinsdottir and Kristjansson, 2005). The vertical range is 3300 m from above 2800 m altitude in the Pyrenees (Machino, 1991) to 450 m depth in a lake in Norway (Søreide et al., 2006; Klemetsen, 2010). Its adult body size varies by more than 5000 times, far more than any other

species. All available niche dimensions (habitat, diet, time and place of spawning) in its range are used. This includes repeated use of the deep-water niche for the entire life cycle (Klemetsen, 2010). The phenotypic variation in colour and form is so large that it is impossible to show it here, but good examples are found in Kendall (1914), Nyman et al. (1981), Sandlund et al. (1992), Prosek (1998), Alexander and Adams (2000), Kottelat and Freyhof (2007) and Klemetsen (2010). The repeated occurrence of sympatric morphs up to an adaptive radiation of four morphs is matched by no other species. And, finally, it has a high genetic variation.

WHY SO VARIABLE?

The extreme variation of arctic charr has been on the agenda for a long time (see: Skulason and Smith, 1995; Snorrason and Skulason, 2004; Power et al., 2008; reviews by Jonsson B. and Jonsson N., 2001; Klemetsen et al., 2003 and Klemetsen, 2010) and it will, I think, still be on the agenda for a long time because it continues to stimulate new research. An extensive treatment is outside the scope of this keynote but I would like to offer a few brief comments to the question of why it is so variable.

—It is a tetraploid (like all salmonids) with high intrinsic potential for variation.

—Northern depauperate faunas offer high evolutionary opportunities because there are vacant niches.

—It is adapted to low, but still variable, temperatures and light conditions and has pushed extreme and unpredictable ecological limits for several glaciations. The relations to glaciations and seasonal ice were well treated by Power (2002) in the keynote to the fourth charr symposium.

—It is exposed to strong ecological selection forces and weak sexual selection forces. Sexual selection

Table 7. Summing up the scores for 10 variable traits on 10 species, and the final rank of the species

Rank	Species	Range	Migr	Hab	Size	Col	Form	Poly	Diet	Spawn	F_{st}	Points
1	Arctic charr <i>Salvelinus alpinus</i>	10	8	10	10	10	10	10	10	10	7	95
2	Dolly varden charr <i>Salvelinus malma</i>	8	7	9	6	9	7	6	8	6	9	75
3	Rainbow trout <i>Oncorhynchus mykiss</i>	7	9	4	7	9	5	5	8	9	8	71
4	Brown trout <i>Salmo trutta</i>	3	10	7	8	6	5	9	9	4	5	66
5	Sockeye salmon <i>Oncorhynchus nerka</i>	7	5	6	3	7	9	5	8	9	3	62
6	Brook charr <i>Salvelinus fontinalis</i>	3	6	5	4	6	5	7	8	5	7	56
7	Atlantic salmon <i>Salmo salar</i>	5	5	4	9	6	8	2	3	3	4	49
8	European whitefish <i>Coregonus lavaretus</i>	1	3	8	5	1	6	8	4	9	2	47
9	Threespine stickleback <i>Gasterosteus aculeatus</i>	9	2	2	1	2	1	3	1	1	10	32
10	Chinook salmon <i>Oncorhynchus tshawytscha</i>	4	1	1	2	3	5	1	2	3	1	24

tends to promote reproductive isolation and fast speciation while ecological selection is slower. This is a selection regime that promotes high intraspecific flexibility and phenotypic plasticity.

—Phenotypic plasticity sensu West-Eberhardt (1989, 2003, 2005) is in itself selected for. Pfenning et al. (2010) recently argued that phenotypic plasticity can play a large role in driving diversification and speciation. This is a crucial adaptation to the variable environments of the North.

—It is essentially a lake species. It is also found at sea and in running water, but the lake is its core evolutionary arena.

LAKES vs RIVERS

Lakes and rivers are integrated parts of freshwater ecosystems and therefore share traits that separate them from marine and terrestrial systems. But, although they share most of the chemical factors of fresh water, several physical and biological factors are not the same in lakes and rivers. Here, I will argue that these differences make lakes more important environments than rivers for ecologically driven evolution of the North.

Rivers and streams are in intimate contact with the landscape around because the contact zone (the banks) is extensive in relation to the volume of the water (Hynes, 1975). Their ecology is closely linked to the terrestrial environment (Allen, 1995). They are always shallow (the mighty Yenisei is not more than 24 m deep; Wikipedia) and their environment is strongly dominated by the one-way flow of water. There are of course differences but in general, running waters appear as relatively predictable environments with rather limited variation. Lakes are more self-sustained elements of the landscape with less influence from the surrounding land. Mainly formed by the Wisconsin/Weichsel glaciation, lakes are repeated millions of times in the northern hemisphere (the count for Norway alone is 429.834 lakes > 0.1 ha; Store Norske Leksikon, snl.no). Most of them are small but sizes can be hundreds of km². Physical properties (lake area, depth, shore development, wind exposure, ice cover, substrate, turbidity, retention times, temperature, light, and the sizes of littoral, pelagic and profundal zones) and chemical properties (oxygen, pH, nutrients) vary much among lakes. Consequently, biological communities also vary much. Except for the very small (that freeze solid during winter), all lakes can hold fish. This means that the northern landscapes have very many populations of arctic charr that live under highly variable and often unpredictable ecological conditions, both abiotic and biotic. At the same time, lakes have some characteristics that are repeated and to some extent are predictable, including seasonality in ice cover, light, temperature and production, and the presence of littoral, pelagic and profundal biological communities. Exactly this, that the arctic and

other northern lakes offer a combination of unpredictably variable and often extreme conditions, and at the same time a set of repeated and more predictable elements forms what I, with reference to the classic book by Hutchinson (1965), would call the ecological theatre of the lacustrine North where evolutionary plays continuously take place. I believe that pushing the very extreme limits of these unique conditions like no other fish over many glaciations and interglaciations (Power, 2002), often without competitors, has honed the arctic charr, the northernmost of all fishes, to be the most variable vertebrate on earth after Man, more flexible and variable than its close relatives.

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REFERENCES

- Aass, Ø., Einum, S., Klemetsen, A., and Skurdal, J., Eds., *Atlantic Salmon Ecology*, London: Wiley-Blackwell, 2011.
- Alexander, G.D. and Adams, C.E., The phenotypic diversity of Arctic Charr, *Salvelinus alpinus* (Salmonidae) in Scotland and Ireland, *Aqua, J. Ichtyol. Aquatic Biol.*, 2000, vol. 4, pp. 77–88.
- Allen, D.A., *Stream Ecology. Structure and Function of Running Waters*, London: Chapman & Hall, 1995.
- Andersson, G., Gustafson, K.J., and Lindström, T., Rödingen i Rösjöarna på Fulufjäll, *Inf. Sötvattenslab.*, 1971, vol. 1971, no. 8, pp. 1–9.
- Armstrong, R.H., and Morrow, J.E., The Dolly Varden Charr, *Salvelinus malma*, in *Charrs. Salmonid Fishes of the Genus Salvelinus*, Balon, E.K., Ed., The Hague: Junk Publishers, 1980.
- Balon, E.K., Ed., *Charrs. Salmonid Fishes of the Genus Salvelinus*, The Hague: Junk Publishers, 1980.
- Berg, O.K. and Gausen, D., Life history of a riverine, resident Atlantic salmon, *Salmo salar* L., *Fauna Norv. Ser. A*, 1988, vol. 9, pp. 63–68.
- Bell, M.A. and Foster, S.A., Eds., *The Evolutionary Biology of the Threespine Stickleback*, Oxford: Oxford University Press, 1994.
- Bourke, P., Magnan, P., and Rodriguez, M.A., Individual variations in habitat use and morphology in brook charr, *J. Fish Biol.*, 1997, vol. 51, pp. 783–794.
- Buth, G.B. and Hagelund, T.R., Allozyme Variation in the *Gasterosteus aculeatus* Complex, in *The Evolutionary Biology of the Threespine Stickleback*, Bell, M.A. and Foster, S.A., Eds., Oxford: Oxford University Press, 1994, pp. 61–84.
- Elliott, J.M., *Quantitative Ecology and the Brown Trout*, Oxford: Oxford University Press, 1994.
- Ferguson, A. and Taggart, J.B., Genetic differentiation among the sympatric brown trout (*Salmo trutta*) popula-

- tions of lough Melvin, Ireland, *Biol. J. Linn. Soc.*, 1991, vol. 43, pp. 221–237.
- Fleming, I.A. and Einum, S., Reproductive ecology: a tale of two sexes, in *Atlantic Salmon Ecology*, Aass, Ø., Einum, S., Klemetsen, A., and Skurdal, J., Eds., London: Wiley-Blackwell, 2011, pp. 33–65.
- Frost, W.E., Breeding habits of Windermere charr *Salvelinus Willughbii* (Günther), and their bearing on speciation of these fish, *Proc. Roy. Soc. Lond. (B)*, 1965, vol. 163, pp. 232–284.
- Greene, G., *A Burnt-out Case*, London: Vintage, 2004.
- Greenwood, P.H., *The Haplochromine Fishes of the East African Lakes*, Ithaca: Cornell University Press, 1981.
- Groot, C. and Margolis, L., Eds., *Pacific Salmon Life Histories*, Vancouver: UBC Press, 1991.
- Hanson, M., Biologin i en sur fjällsjö belyst av rödingens föda, *Inf. Sötvattenslab.*, 1976, vol. 1976, no. 5, pp. 1–13.
- Healey, M.C., Life history of chinook salmon (*Oncorhynchus tshawytscha*), in *Pacific Salmon Life Histories*, Groot, C. and Margolis, L., Eds., Vancouver: UBC press, 1991, pp. 311–394.
- Hendry, A.P. and Stearns, S.C., *Evolution Illuminated. Salmon and Their Relatives*, Oxford: Oxford University Press, 2004.
- Hesthagen, T., Hindar, K., Jonsson, B., and Ousdal, J.Ø., Effects of acidification on normal and dwarf Arctic Charr *Salvelinus alpinus* (L.) in a Norwegian Lake, *Biol. Conserv.*, 1995, vol. 74, pp. 115–123.
- Hynes, H.B.N., The stream and its valley, *Verh. Int. Ver. Limnol.*, 1975, vol. 19, pp. 1–15.
- Hurchinson, G.E., *The Ecological Theater and the Evolutionary Play*, New Haven: Yale University Press, 1965.
- Johnson, L., The Arctic Charr, *Salvelinus alpinus*, in *Charrs. Salmonid Fishes of the Genus Salvelinus*, Balon, E.K., Ed., The Hague: Junk Publishers, 1980, pp. 15–98.
- Jonsson, B. and Jonsson, N., Polymorphism and speciation in Arctic Charr, *J. Fish Biol.*, 2001, vol. 58, pp. 605–638.
- Kendall, W.C., The fishes of New England. The salmon family. Part 1—The trout or charrs, *Mem. Boston Soc. Nat. Hist.*, 1914, vol. 8, no. 1, pp. 1–103.
- Klemetsen, A., Amundsen, P.-A., Knudsen, R., and Hermansen, B., A profundal, Winter-spawning morph of Arctic Charr *Salvelinus alpinus* (L.) in Lake Fjellfrøvatn, Northern Norway, *Nord. J. Freshw. Res.*, 1997, vol. 73, pp. 13–23.
- Klemetsen, A., Amundsen, P.-A., Dempson, J.B., et al., Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic Charr *Salvelinus alpinus* (L.): a review of aspects of their life histories, *Ecol. Freshw. Fish*, 2003, vol. 12, pp. 1–59.
- Klemetsen, A., The charr problem revisited: exceptional phenotypic plasticity promotes ecological speciation in Postglacial Lakes, *Freshw. Rev.*, 2010, vol. 3, pp. 49–74.
- Kottelat, M. and Freyhof, J., *Handbook of European Freshwater Fishes*, Cornol: Publications Kottelat, 2007.
- Lindström, T. and Andersson, G., Otoliter av Fulufjäll-röding, *Inf. Sötvattenslab.*, 1980, vol. 1980, no. 7, pp. 1–9.
- Lindström, T., Dickson, W., Hanson, M., and Andersson, G., Dålig Kondisjon hos röding i et surt område—en effekt av næringsbrist eller fysiologisk stress?, *Inf. Sötvattenslab.*, 1982, vol. 1982, no. 5, pp. 1–23.
- Losos, J.B., *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*, Berkeley: University of California Press, 2009.
- Machino, Y., The Arctic Charr, *Salvelinus alpinus*, in France: present geographical distribution of original and transplanted populations, *Int. Soc. Arctic Charr Fanatics Inf. Ser.*, 1991, vol. 5, pp. 113–120.
- Markevich, G.N., Ecosystem of Kronotskoe Lake: the melting pot for microevolution process, in *7th International Charr Symposium Abstract Book*, Yuzhno-Sakhalinsk: Sakhalin Research Institute of Fisheries and Oceanography, 2012, pp. 1–13.
- McKellar, A.E. and Hendry, A.P., How humans differ from other animals in their level of morphological variation, *PLoS ONE*, 2009, vol. 4, pp. 1–9.
- Meredith, M., *Born in Africa. The Quest for the Origin of Human Life*, N.Y.: Public Affairs, 2011.
- Muus, B.J. and Dahlstrøm, P., *Europas Ferskvannsfisk*, Oslo: Gyldendal, 1978.
- Näslund, I., The development of regular seasonal habitat shifts in a Landlocked Arctic Charr, *Salvelinus alpinus* L., population, *J. Fish Biol.*, 1990, vol. 36, pp. 401–414.
- Nyman, L., A new approach to the taxonomy of the “*Salvelinus alpinus* species complex,” *Rep. Inst. Freshw. Res. Drottningholm*, 1972, vol. 52, pp. 103–131.
- Nyman, L., High, old and small: the dwarfs of ‘Chardom,’ *Int. Soc. Arctic Char Fanatics Inf. Ser.*, 1978, vol. 4, pp. 107–112.
- Nyman, L., Hammar, J., and Gydemo, R., The systematics and biology of landlocked arctic char from northern Europe, *Rep. Inst. Freshw. Res. Drottningholm*, 1981, vol. 59, pp. 128–141.
- Østbye, K., Amundsen, P.-A., Bernatchez, L., et al., Parallel evolution of ecomorphological traits in European Whitefish *Coregonus lavaretus* (L.) species complex during post-glacial times, *Mol. Ecol.*, 2006, vol. 15, pp. 3983–4001.
- Pfenning, D.W., Wund, M.A., Snell-Rood, E.C., et al., Phenotypic plasticity’s impacts on diversification and speciation, *Trends Ecol. Evol.*, vol. 25, pp. 459–467.
- Power, G., Charrs, glaciations and seasonal ice, *Env. Biol. Fishes*, 2002, vol. 64, pp. 17–35.
- Power, M., Reist, J.D., and Dempson, J.B., Fish in high-latitude Arctic Lakes, in *Polar Lakes and Rivers*, Vincent, W.F. and Laybourn-Parry, J., Eds., Oxford: Oxford University Press, 2008, pp. 249–267.
- Prosek, J., *Trout. An Illustrated History*, N.Y.: Alfred A. Knopp, 1998.
- Riget, F., Jeppesen, E., Lankildehus, F., et al., Landlocked Arctic Charr (*Salvelinus alpinus*) population structure and lake morphometry in Greenland—is there a connection?, *Polar Biol.*, 2000, vol. 23, pp. 550–558.
- Sandlund, O.T., Gunnarson, K., Jonasson, P.M., et al., The Arctic Charr *Salvelinus alpinus* in Thingvallavatn, *Oikos*, 1992, vol. 64, pp. 305–351.
- Sigursteinsdottir, R.J. and Kristjansson, B.K., Parallel evolution, not always so parallel: comparison of small benthic charr, *Salvelinus alpinus*, from Grimnes and Thingvallavatn, Iceland, *Env. Biol. Fishes*, 2005, vol. 74, pp. 239–244.
- Skulason, S. and Smith, T.B., Resource polymorphism in vertebrates, *Trends Ecol. Evol.*, 1995, vol. 10, pp. 366–370.

- Siwertsson, A., Knudsen, K., Kahilainen, K.K., et al., Sympatric diversification as influenced by ecological opportunity and historical contingency in a young lineage of whitefish, *Evol. Ecol. Res.*, 2010, vol. 12, pp. 929–947.
- Søreide, F., Dolmen, D., and Hindar, K., Den mystiske dypvannsfisken i Tinnsjøen, *Fauna*, 2006, vol. 59, pp. 122–129.
- Snorrason, S.S. and Skulason, S., Adaptive speciation in Northern Freshwater fishes, in *Adaptive Speciation*, Dieckmann, U., et al., Eds., Cambridge: Cambridge University Press, 2004, pp. 210–228.
- Sterelny, K., *Dawkins vs. Gould. Survival of the Fittest*, Cambridge: Icon Books, 2007.
- Sutterlin, A.M. and MacLean, D., Age at first maturity and the early expression of oocyte recruitment patterns in two forms of Atlantic Salmon (*Salmo salar*) and their hybrids, *Can. J. Fish. Aq. Sci.*, 1984, vol. 41, pp. 1139–1149.
- Svedäng, H., Genetic basis of life-history variation of dwarf and normal Arctic Charr, *Salvelinus alpinus* (L.), in Stora Rösjön, Central Sweden, *J. Fish Biol.*, 1990, vol. 36, pp. 917–932.
- Weatherley, A.H., *Growth and Ecology of Fish Populations*, London: Academic Press, 1972.
- West-Eberhardt, M.J., Phenotypic plasticity and the origin of diversity, *Ann. Rev. Ecol. Syst.*, 1989, vol. 20, pp. 249–278.
- West-Eberhardt, M.J., *Developmental Plasticity and Evolution*, Oxford: Oxford University Press, 2003.
- West-Eberhardt, M.J., Developmental plasticity and the origin of species differences, *Proc. Natl. Acad. Sci.*, 2005, vol. 102, pp. 6543–6549.
- Wilson, E.O., *Sociobiology: The New Synthesis*, Cambridge MA: Belknap Press, 1975.
- Wilson, E.O., *The Social Conquest of Earth*, N.Y.: Liveright Publishing, 2012.
- Wootton, R.J., *A Functional Biology of Sticklebacks*, London: Croom Helm., 1984.
- Yessipov, W.K., Data on the biology and fishery of the Novaja Zemlya Char (*Salvelinus alpinus*), *Tr. Arkt. Inst. Leningr.*, 1935, vol. 17, pp. 5–70 [in Russian].