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Comparison between the distributions of land-locked Atlantic salmon Salmo salar L. and three-spined stickleback Gasterosteus aculeatus L. in the river Namsen, Norway

OLE KRISTIAN BERG

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The land-locked salmon *Salmo salar L*. in the river Namsen is found up-stream to a waterfall situated 290 m above s.l. It is found both above and below the Trongfoss waterfall in the main river. The three-spined stickleback *Gasterosteus aculeatus* L. in the river Namsen is found as far up as about 130 m above s.l., below the Trongfoss waterfall, although in some of the tributaries it extends higher up than the land-locked salmon. An explanation of the differing distribution of the two species is that the salmon immigrated into the river before about 9500 B.P. (years before present), wheras the three-spined stickleback immigrated after 9500 B.P. but before 9100 B.P.

Ole Kristian Berg, Dept. of Zoology, University of Trondheim, N-7055 Dragvoll, Norway.

INTRODUCTION

Among the freshwater species of fish which immigrated into Norwegian rivers from the ocean after the end of the last ice age were the Atlantic salmon Salmo salar L. and the three-spined stickleback Gasterosteus aculeatus L. (Huitfeldt-Kaas 1918, Power et al. 1973). Atlantic salmon is found in hundreds of rivers along the coast of Norway, while land-locked populations of Atlantic salmon have only been recorded in the Lake Byglandsfjord and the River Otra (Dahl 1927, 1928), in the river Nidelva (Dahl 1929) and in the river Namsen (Berg 1953) (Fig. 1). The three-spined stickleback is found in most of the lakes and rivers along the coast of Norway (Huitfeldt-Kaas op.cit). The exact progress of the postglacial immigration of these fish species has not so far been known. The purpose of the present work was to map the distributions of the land-locked salmon and of the three-spined stickleback in the upper reaches of the river Namsen and eventually to determine the course of history of their immigration.

The natural distribution of the anadromous population of Atlantic salmon in river Namsen is up-river as far as the foot of the Fiskumfoss waterfall, 72 km from the rivermouth (Fig. 2). This stretch of the river has not been investigated. The land-locked salmon occurs above the Fiskumfoss waterfall. Because of the construc-

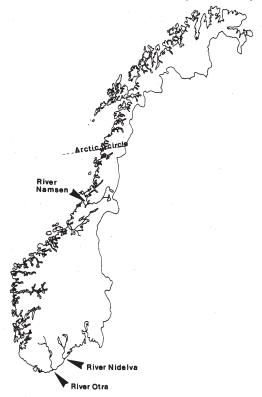


Fig. 1. Map of Norway showing the locations of the populations of land-locked Atlantic salmon.

tion of salmon-ladders, the anadromous population of salmon now has access to the foot of the Aunfoss waterfall, 8 km above Fiskumfoss. Brown trout *Salmo trutta* L. is widely spread in the area (Huitfeldt-Kaas op.cit.). Several larger and smaller tributary streams flow into the river Namsen within the area. The investigated streams within the area of distribution of the land-locked salmon are listed in Table 1.

METHODS

Brown trout and/or salmon were caught in the fast-flowing stretches above all the waterfalls with electrical fishing gear. In the rivers Lille Bjørhusdalselva and Store Bjørhusdalselva, however, the fishes were caught with small hooks baited with worms or flies. A catch of 20 brown trout and no land-locked salmon was taken to indicate an absence of land-locked salmon in that area. In the investigated areas where anadromous salmons were present, catch of maturing salmon female parr was taken as an evidence of the presence of land-locked salmon.

The distribution of the three-spined stickleback in river Namsen and its tributaries was found by electrical fishing in both calm and fastflowing stretches above all the waterfalls which could be difficult to surmount.

A total number of 62 sites were investigated, among these 32 sites were above the Trongfoss waterfall.

RESULTS

The distribution of the land-locked salmon and the three-spined stickleback in the river Namsen and its tributaries is shown in Table 1. In the main river the land-locked salmon is found both above and below the Trongfoss waterfall, 144 m above s.l. at the top, but below a waterfall situated at 290 m above s.l. In the tributaries it extends up to the first unsurmountable waterfall above river Namsen. It is absent from the river Tromselva, which falls directly into the river Namsen below the Trongfoss (Fig. 2).

Along the course of the main river there are no lakes into which the land-locked salmon can migrate, but in the tributaries two such lakes are present. Land-locked salmon were found in the outlets of both lakes, but not in the rivers flowing into these lakes. The three-spined stickleback was found to be present to an altitude of about 140 m above s.l. (Table 1) though only to below the Trongfoss waterfall in the river Namsen,

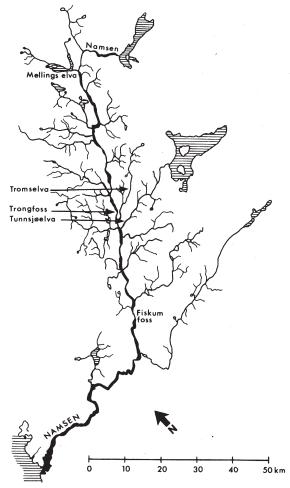


Fig. 2. The river Namsen with tributaries.

whereas in the tributary river Tromselva it extends above the earlier mentioned fall, which stops the further ascent of the land-locked salmon (Fig. 3).

DISCUSSION

Salmon were fished for in the fast-flowing stretches of the river. Several authors, e.g. Karlström (1977), have shown that salmon, when living sympatrically with brown trout, show a strong preference for fast-flowing stretches. The probability of catching salmon was tested by a comparison of the results of catches made with gill nets in slow-flowing stretches of the river Namsen. This method should be more favourable for catching brown trout than salmon. A

Table 1. The distribution of land-locked Atlantic salmon and three-spined stickleback in river Namsen and its tributaries. The distribution is given with UTM-references (e.g. Østbye 1971) of the highest registration of land-locked salmon and/or three-spined stickleback. Altitude of top of falls stopping further distribution is given in m. The investigated area is above the fall Fiskumfoss.

River name	UTM-reference				altitude	landlocked	threespined	remark
					m a.s.l.	salmon	stickleback	
Fiskumelva	33W	UM	795	622	80	×		
11	11	UM	806	675	140		×	
Nesåa	11	UM	849	620	100	, x		As Berg (1953)
'n	11	UM	887	603	130		×	
Fjerdingelva	**	UM.	885	708	130	×	×	
Vestre Folmerelva	**	UM	850	717	120	×	×	
Østre Folmerelva	**	UM	856	721	110	. x		
" "	"	UM	870	750	140		×	
Nesåa	**	UM	849	620	100	` x	×	As Berg (1953)
Fjerdingelva	11	UM	885	708	130	×	×	
Vestre Folmerelva	**	UM	850	717.	120			
Østre Folmerelva	11	UM	856	721	110	×	×	
Grøndalselva								Poisoned (mining)
Tunnsjøelva	***	VM	004	790	180	×	×	As Berg (1953)
Lindseta	11	UM	932	795	160	×	×	As Berg (1953)
Tromselva	11	UM	959	808	120	×		As Berg (1953)
H .	11	UM	996	823	140		×	As Berg (1953)
Trongfoss (Namsen)	11	UМ	979	833	144		×	
Lille Flåttådalselva	Ħ	UM	999	876	180	×		As Berg (1953)
Store Flåttådalselva	11	VM	003	912	220	×		
Brekkvasselva	11	VM	065	930	180	×		
Lille Bjørhusdalselva	11	٧N	023	048	300	×		As Berg (1953)
Store Bjørhusdalselva	11	٧N	065	065	240	×		
Frønningselva	11	VN	111	040	220	×		
Lille Sandåa	11	VN	140	006	220	, x		
Store Sandåa	. 11	VN	158	003	260	×		
Kjæråa	11	٧N	157	998	260	×		
Steinäa	11	٧N	195	115	245	· x		As Berg (1953)
Mellingselva	11	٧N	195	185	280	×		As Berg (1953)
Smalwasselva	. 11	VN	211	185	270	· x		As Berg (1953)
Lille Steinäa	**	VN	228	169	260	×		- · · · · · · · · · · · · · · · · · · ·
Namsen	н	VΝ	250	183	290	×		

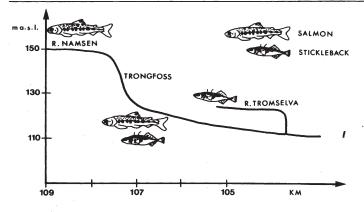


Fig. 3. Elevation of the river Namsen and the river Tromselva in the Trongfoss area. The distribution of land-locked salmon and three-spined stickleback is indicated.

total of 335 salmon and 344 trout were caught with the gill nets, which corresponds to a probability of 0,5 for catching salmon in comparison to trout.

The probability of catching salmon, in comparison to trout by both electro-fishing and by hook and line, is consequently presumed to be 0,5 when fishing in rapids. Assuming a binomial distribution, the probability, under the conditions described above, of catching 20 trout but no salmon approaches zero. Thus a catch of 20 trout and no land-locked salmon was taken to indicate an absence of land-locked salmon in that area. If the probability of catching salmon, compared to brown trout, is lowered to 0,25, then a catch of 20 trout and no salmon still yields a probability of less than 0,03 that the next fish caught will be a salmon. The method used therefore seems sensitive enough to provide a fairly accurate picture of the distribution of the land-locked salmon.

Three-spined stickleback was quickly located at all sites where it was present. This indicated that, where present, the species was easy to discover by the method chosen. The total number of investigated sites above the Trongfoss waterfall is 32. Three-spined stickleback is not found in any of these. The method used therefore seems sensitive enough to provide a picture of the main distribution of three-spined stickleback.

Land-locked salmon was found in the river Namsen both above and below the Trongfoss waterfall (144 m above s.l. at the top). This distribution can be explained if the salmon immigrated before the Trongfoss waterfall was formed. The Trongfoss waterfall is about 15 m and unsurmountable for salmon.

The so called 'marine limit' (i.e. the inland limit of marine influence following the isostatic depression of the land surface during the last ice age) in the Namsen area lies at 174 m above s.l. (Sollid 1976). Kjemperud (1981) has worked out a shore-line displacement curve for the nearby inner Trondheimsfjord area. In the present investigation area, the greater accumulation and the consequential slower melting of the ice should have led to a delay in the land rise of a maximum of 500 years compared to Kjemperud's data. The Trongfoss waterfall therefore became established about 9500 B.P. (years before present). Salmon therefore probably immigrated into the river before about 9500 B.P. at a time when the Trongfoss waterfall was still submerged.

Three-spined stickleback in the main river

was not found above the Trongfoss waterfall, but it was found about 140 m above s.l. in several tributaries. In most tributaries no falls are found immediately below the upper limit of distribution of three-spined stickleback. In the River Tromselva, however, three-spined stickleback is found above a fall situated 120 m above s.l. (at the top). This fall is unsurmountable for salmon and three-spined stickleback. The distribution of three-spined stickleback can be explained if it immigrated into the area after the Trongfoss became established, but before the waterfall in the Tromselva became established.

Applying the shore-line displacement curve from Kjemperud (1981), the waterfall in the river Tromselva became established about 9100 B.P. Three-spined stickle-back therefore probably immigrated into the river after about 9500, but before 9100 B.P., at a time when the waterfall in river Tromselva was still submerged.

No land-locked salmon has been recorded in the lakes of the investigated area (Bjarne Abrahamsen and Magnus Berg, pers.comm.). This is the only known population of land-locked Atlantic salmon that spends its entire life in running water. According to the classification of Rounsefell and Everhart (1953) it may therefore be called fluvial.

The distribution described by Berg (1953) still remains valid: «In all the side rivers and brooks the relict salmon usually will be found in the summer where it may come without hindrance of falls or lack of water». No populations of land-locked salmon exist which are isolated from the river Namsen. This indicates that the formation of isolated, land-locked populations of salmon either is difficult, or that they are vulnerable to extinction. Several such populations of the three-spined stickleback have been formed below the Trongfoss waterfall, and this species is also widely distributed in areas inhabited by salmon and/or brown trout. It is therefore unlikely that the three-spined stickleback has been exterminated from parts of its former area by competition from other fish species, such as salmon and brown trout.

There is no evidence that the species has been artificially spread by man in the investigated area. Huitfeldt-Kaas (op.cit.) has classified the three-spined stickleback as being a weaker stream-forcer than the salmon. Nevertheless this species is found quite far upstream in rapid-flowing tributaries like the river Tunnsjøelya.

In the river Otra the three-spined stickleback does not extend so far up as the land-locked At-

lantic salmon (Vold 1974). It is improbable that the three-spined stickleback should have been exterminated by competitors in the big lakes along this river system. This would seem to indicate a time progression of the immigration similar to that proposed for the river Namsen.

Power et al. (1973) stated that the char, rainbow smelt Osmerus mordax Mitch., three-spined stickleback and nine-spined stickleback Pungitius pungitius (L.) were the first immigrants into the Matamek River, Canada. The ouananiche (the Canadian land-locked Atlantic salmon), however, is not present in that river system. The lack of land-locked Atlantic salmon can therefore not be taken as evidence of a later time of immigration of salmon into a river system, since the formation of populations of landlocked salmon must be regarded as a selective process which succeeds only in some rivers. This is also the opinion of other authors, e.g. Behnke (1972) and Grimas et al. (1972). The river Namsen is one of the few European rivers which proffers suitable conditions for making a comparison of the time of immigration of the fish species in question in this part of Europe.

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