Distribution of non-native brook trout (*Salvelinus fontinalis*) across Norwegian waterbodies – is it an invasive species?

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Non-native brook trout (*Salvelinus fontinalis* MITCHILL, 1815) was introduced into Norway in 1883. However, it was not until the late 1970s that this acid-tolerant salmonid species was stocked into many acidified lakes that many populations became established. In 2004, all brook trout stocking in Norway ceased. In this study, we surveyed the distribution of brook trout in Norwegian water bodies. A totally of 202 self-sustaining populations were identified, mostly in unregulated lakes (n=101), streams (n=71) and also to some extent in reservoirs (n=25). Only four populations were found in inland rivers, and one population in a river with Atlantic salmon (*Salmo salar* L.). Localities with brook trout covered a wide range of altitudes and sizes. Analyses of time-series catches in sympatric populations of brown trout (*Salmo trutta* L.) and brook trout from 12 lakes (1997-2012) revealed a strong decline in brook trout stocks. A similar development in abundance has also emerged from other studies in recent years. Generally, lake-dwelling brook trout is regarded as a low-risk species with respect to invasiveness. However, brook trout/brown trout interactions may be habitat-specific, as brook trout may dominate in small and relatively cold streams.

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INTRODUCTION

Invasive species, i.e. non-native species that spread beyond the introduction site and become abundant and established (Rejmanek et al. 2002), are increasingly recognized as one of the main threats to biodiversity in fish communities at a gobal level (García-Berthou 2007; Trochine et al. 2017). Freshwater ecosystems are particularly affected by invasive fish species (Clavero & Garcia-Berthou 2006), which have become a growing source of concern worldwide for several decades (Kohler & Courtenay 1986; Sala et al. 2010; Gallardo & Aldridge 2015). The management of invasive species is therefore one of the major challenges that conservation biologists will face in the near future (Allendorf & Lundquist 2003).

Several large-scale intercontinental introductions of freshwater fishes have been carried out over the 19th century (Gozlan 2008; Clavero & Villero 2013; Gozlan et al. 2010). These have included three salmonid species; brook trout (*Salvelinus fontinalis* MITCHILL, 1815), rainbow trout (*Oncorhynchus mykiss* WALBAUM, 1792) and brown trout (*Salmo trutta* L., 1758) (MacCrimmon & Marshall 1968; MacCrimmon & Campbell 1969; MacCrimmonn 1971; Scott & Crossman 1973). Brook trout are native to northeastern North America (MacCrimmon & Campbell 1969; Scott & Crossman 1973). However, since the late 1800s, attempts have been made to establish brook trout all over the world, mainly due to its appeal as a sport fish.

Brook trout were successfully introduced into Norwegian waters in 1883 (Hesthagen & Kleiven 2013; Kleiven & Hesthagen 2013). However, subsequent releases of fry at 20-30 locations produced only one known self-sustaining population, in Overnbekken stream in Buskerud County (Eken 1988). In 1917 or 1918, another population of unknown origin was established from fry stocking in Øyfjell, Telemark County (Huitfeldt-Kaas 1924). In this area, brook trout were since translocated to several sites (Grande 1964; Hesthagen & Kleiven 2013). In the late 1970s, large-scale stocking of brook trout started in southern Norway. This mitigation measure was intended to compensate for the extensive damage to fish caused by acidification, as more than 9600 populations, mainly of brown trout, became extinct (Sevaldrud & Muniz 1980; Hesthagen et al. 1999). As brown trout in most cases was the only native fish species, large areas became completely devoid of fish. The reason for stocking brook trout was that it was recently recognized as an extremely acid-tolerant species (Dunson & Martin 1973; Trojnar 1977; Muniz & Leivestad 1979). At least 12 hatcheries in southern Norway have produced offspring (age 0+) of brook trout in recent decades (Hesthagen & Kleiven 2014). Most lakes were probably stocked with at least several hundred individuals. In regulated lakes, however, compensatory stockings were carried out by the power companies, and in most cases these amounted to between 1 000 and 10 000 individuals annually (Møkkelgjerd & Gunnerød 1985).

In 2004, the stocking of brook trout in Norwegian waters was stopped (Hesthagen & Sandlund 2007). The environmental authorities realized that introductions of this non-native species were at odds with the internationally adopted goal of conserving native biodiversity. Moreover, brown trout populations in previously acidified areas had recently started to recover (Hesthagen et al. 2011a, 2016). This is thanks to improved water quality through a substantial reduction in sulphates in precipitation (cf. Garmo et al. 2014). In addition, large scale liming campaigns have been carried out since the 1980s (Sandøy & Romundstad 1995).

When a non-native fish species is introduced into a body of water where it did not previously occur, there are several possible outcomes (Gozlan et al. 2010; Blackburn et al. 2011; Gallardo & Aldridge 2015). The negative ecological impacts vary highly depending on the species involved, community structure and abiotic environmental conditions (Savini et al. 2010; Henriksson 2016 a, b). For the majority of non-native species, no quantitative information is available regarding the consequences of such introductions (Simberloff et al. 2013). Brook trout is classified as a medium-risk species among non-native freshwater fish (Copp et al. 2009; Britton et al. 2010). Our article describes the distribution of brook trout in Norwegian water bodies. Furthermore, we studied their development in recent years in 12 lakes, based on time-series. The specific objective of the study is to assess whether brook trout is an invasive species.

METHODS

The distribution of brook trout in Norwegian water bodies was surveyed in 2012-2016 (Hesthagen & Kleiven 2013; Hesthagen & Sandlund 2016). Data was obtained via literature studies and interviews with fishermen, landowners, fishery organizations, and local and state environmental authorities. First, we grouped their occurrence at county level, and thereafter by individual watersheds. On both scales, possible occurrence of brook trout was identified, starting at the highest lake in each watershed. Downstream localities were then surveyed in order to establish the existence of brook trout. Their longevity is usually less than four years in Norwegian waters (Qvenild 1986; Sægrov et al. 2008). As stocking ceased in 2004, all populations that were identified in 2012 at the latest are considered self-sustaining.

Each stock was categorized according to the type of habitat it occupied; (i) unregulated lakes, (ii) regulated lakes [reservoirs for hydropower generation], (iii) first- and second-order inland streams, (iv) rivers with a maximum width of 4-5 m, and (v) rivers with anadromous salmonids. A stock of brook trout is defined as one that inhabits a single lake, river or stream. Any given lake is defined as containing only one stock, irrespective of whether spawning could occur in several tributary streams. Streams up- or downstream of lakes containing brook trout, or streams between two lakes with brook trout, are not regarded as separate stocks. Nor are stocks in tributaries or second-order inland rivers, if the first-order stream or river contains brook trout. However, stocks in tributaries to a river with Atlantic salmon (*Salmo salar* L.) are defined as reproductive units if that river does not host brook trout. We used different categories for lake size and altitude (both streams and lakes).

We analyzed the change in relative abundance of brook trout living in sympatry with brown trout from 11 un-limed lakes in upper stretches of the Tovdal watershed (170 to 218 m a.s.l.), Aust-Agder County, and from one limed lake in Otra watershed, Lake Dåsvatn at 190 m a.s.l., Vest-Agder County, based on catches between 1997 and 2012. Only these two species of fish are found in these 12 lakes. The lakes in Tovdal watershed were sampled only with gillnets with mesh sizes between 15-24 mm (knot to knot), from April to August every year. Sampling took place several times each month, using between 40 and 100 gillnets. Not all lakes were sampled every year in Tovdal watershed. In Lake Dåsvatn, sampling was mainly carried out with traps with mesh size of 10 mm, between mid-April and late November. Gillnets with 19.5 to 24 mm mesh sizes were also occasionally used. The total catch of brown trout and brook trout in lakes in the Tovdal and Otra watersheds were 334251 vs. 1634 and 45162 vs. 925 individuals, respectively.

These catch data from Lake Dåsvatn were analyzed using a mixed effect model with a logit link and binomially distributed residuals:

$$E[\mathrm{Logit}(y_j)] = b_0 + b_1(\mathrm{Year}_j - 1997) + c_j$$

where $E[\mathrm{Logit}(y_j)]$ is the expected proportion of brook trout in the catch (on logit scale) for each year j, b_0 is the intercept, b_1 the slope, and c a random factor distributed according to an AR(1) process to account for the non-independence among the data points.

For the Tovdal data, we used the same model, but with a random-regression component:

$$E[\mathrm{Logit}(y_{ij})] = b_0 + b_1(\mathrm{Year}_{ij} - 1997) + \beta_{0i} + \beta_{1i}(\mathrm{Year}_{ij} - 1997) + c_{ij}$$

where β_{0i} and β_{1i} are the random intercept and slope for each lake i. These random factors were assumed to be normally distributed with a mean of zero and a correlation between intercept and slope.

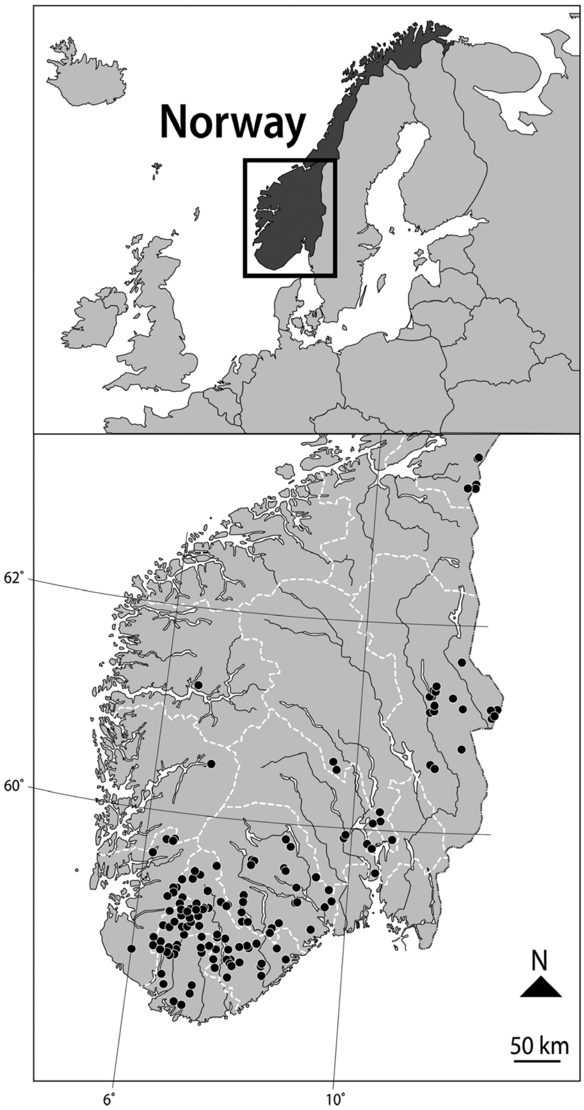

Figure 1. The distribution of brook trout in southern Norway mapped during the period 2012-2016.

RESULTS

A total of 202 self-sustaining populations of brook trout were recorded in southern Norway, mainly in the counties of Aust-Agder (n=62), Vest-Agder (n=49) and Telemark (n=38) (Figure 1). There are also some populations in southeastern Norway, in Hedmark county (n=22). The northernmost sites with brook trout are found in Trøndelag County (n=5), where they have dispersed from stocking sites in transborder watersheds in Sweden.

Most populations of brook trout were found in unregulated lakes (n=101) and streams (n=71), and to some extent also in reservoirs (n=25). Brook trout were found in only four inland rivers; Monn and Logna in Vest-Agder, and Tevla and Inna in Trøndelag. One population of brook trout was found in a river with Atlantic salmon; Sogndalselva in Vest-Agder.

Most of the lake-dwelling populations (n=126, 62.4 %) of brook trout were found in smaller lakes which covered areas of 0.010-0.099 km^2 (32.5 %) and 0.100-0.490 km^2 (29.4 %) (Figure 2A). A small proportion occupied lakes larger than 10 km^2 (4.8 %). Brook trout were found at a mean altitude (m a.s.l.) of 513±326 SD. They were most abundant in localities at 100-249 (27.7%) and 250-499 m a.s.l. (28.7 %) (Figure 2B). Furthermore, 9.9 % occurred above 1000 m a.s.l. (1014-1252 m a.s.l.).

There was a strong decline in the abundance of brook trout in both Lake Dåsvatn and in the 11 lakes in Tovdal watershed between 1997 and 2012 (Figure 3A, B). In Lake Dåsvatn, a total of 744 brook trout were caught during the first five years of the study, as opposed to seven specimens during the last five years. The proportion of brook trout in the total catch dropped from 19 % in 1997 to less than 0.1 % from 2007 and onwards. In the Tovdal watershed, a total of 894 brook trout were caught during the first five years of the study, as opposed to 92 individuals during the last five years. The average proportion of brook trout in the total catch across lakes was estimated to drop from 6.1% in 1997 to less than 0.1 from 2007 and onwards. There was some variation in this respect among the lakes in Tovdal (Figure 3B, Table 1). For one of the lake the estimated decline of brook trout was much smaller, ending up at an estimated proportion in the total catch in 2012 of 0.7% (Figure 3B, #4)

DISCUSSION

Brook trout have become well established in Norwegian waters following repeated stocking programs in a large number of lakes from the mid 1970s until the early 2000. Altogether 202 self-sustaining populations were recorded by an assessment in 2012-2016, most of them in the south of Norway. Inferences regarding distribution and habitat preference depend on sampling coverage. If sampling effort differs among habitats, it is impossible to investigate abundance patterns across habitats. Our data is based on literature studies and interviews with fishermen, landowners, fishery organizations, and local or state fish management authorities. Questionnaires and interviews have been used extensively to assess fish distribution and their status in Norwegian lakes (Sevaldrud & Muniz 1980; Hesthagen et al. 1993, 1999). Reliable data on fish in such localities can be obtained because (i) large areas belong to the state or rural communities, where all citizens can fish, as is also the case in many privately owned waters. (ii) there is a long tradition of, and keen interest in, exploiting inland fish stocks in Norway, that also includes fishing with gillnets. (iii) most of our lakes contain only a few fish species, usually only one or two (Tammi et al. 2003). (iv) brook trout is a relatively new fish species in Norwegian watersheds, and most people are aware of their appearance. (v) brook trout have become a popular sport fish. (vi) many landowners, fishery organizations, etc. have been involved in stocking of brook trout in recent years, and they have a keen interest in their fate. However, knowledge of populations in small lakes and streams may be under-represented, as such sites are less fully exploited or known by fishermen and landowners.

Brook trout do not seem to have been very successful in establishing self-sustaining populations in Norwegian waters.

Table 1. Parameter estimates for the logistic regression models for the changes in brook trout vs. brown trout in Lake Dåsvatn and in 11 lakes in Tovdal watershed. Intercept was estimated at year 1997. SD(int) and SD(slope) is the standard deviation of the intercepts and slopes among lakes, respectively, and and Cor(int, slope) is the correlation between the intercept and the slopes among lakes.

Model	Intercept	Slope	SD (int)	SD (slope)	Cor(int, slope)
Dåsvatn	-1.47±0.22	-0.54±0.04	-	-	-
Tovdal	-2.74±0.58	-0.46±0.11	1.08	0.27	-0.85

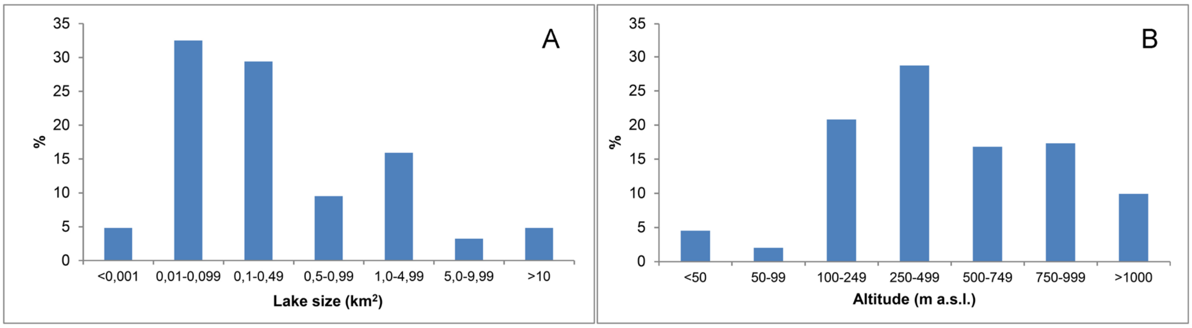

Figure 2. The occurrence of brook trout in Norwegian waters in relation to lake size (A) (n=126), and altitude (B) which includes both lotic and lentic habitat (n=202).

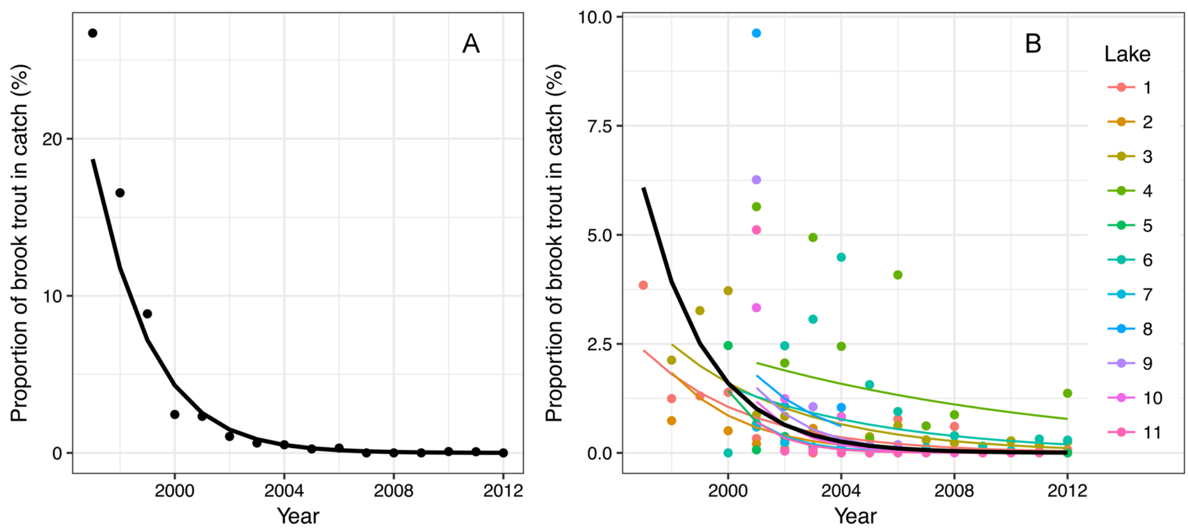

Figure 3. Changes in proportion of brook trout in reported catches from 1997 to 2012; A for Lake Dåsvatn and B for 11 different lakes in the Tovdal watershed. The black regression line shows the estimated line for Lake Dåsvatn and the average for all 11 lakes in the Tovdal watershed.

In Aust-Agder County, 292 stocking permits were issued from 1976 to 1990 (Kleiven 1995). Brook trout are also found downstream from their stocking sites, reflecting their capacity to disperse (cf. MacCrimmon & Campbell 1969; Scott & Crossman 1973). They therefore had access to a greater number of sites than those that were stocked directly. Brook trout seems to be able to establish self-sustaining populations in a wide range of habitats. The environmental conditions in most of the localities that were stocked with brook trout are generally regarded as suitable, as most of them are oligotrophic cold-water lakes (cf. MacCrimmon & Campbell 1969; Scott & Crossman 1973). Attempts to establish brook trout outside their native distribution area suggest that water temperature is the most important single factor that limits their geographic range (MacCrimmon & Campbell 1969). Furthermore, the lakes stocked hosted a simple fish community, and many of them were even completely devoid of fish after years of acidification. Species-poor ecosystems are usually more vulnerable to the arrival of new species than species-rich ecosystems (Carey & Wahl 2010).

The abundance of brook trout seems to have dropped greatly in lakes in recent years in waters that also contain brown trout. This was the case in the 11 lakes in the Tovdal watershed, and in Lake Dåsvatn in Otra watershed between 1997 and 2012. In the latter case, the proportion of brook trout fell from about 19 % in 1997 to near zero from 2007 to 2012. For lakes in the Tovdal watershed, the decline was not as strong as their abundance was already low in 1997, making up only about 4-6 % of the total catch. Other studies confirm the reduction in brook trout abundance during the same period. A study conducted in 1991 in Aust-Agder County documented natural recruitment among brook trout in 26 streams, most of which also contained brown trout (Kleiven 1995). In 2013, only 46% of these sites still had brook trout (Hesthagen & Kleiven 2013). In the River Litleåna, brown trout was originally the only fish species present, but they were nearly eradicated by acidification (Larsen et al. 2007). In 1994, the river was limed, and electrofishing surveys in 1995-2004 showed that brown trout had started to recover. At the same time, the density of brook trout started to decline, and by 2002 they had disappeared from the river.

Brook trout were found in only one river that contained Atlantic salmon, the unlimed River Songdalselva (Gabrielsen et al. 2010). However, their abundance is currently falling, a trend that seems to be occurring simultaneously with a growing salmon population. Previously, brook trout were regularly found in many salmon rivers in southern Norway (Hesthagen et al. 2011b). However, acidification eradicated or seriously reduced Atlantic salmon populations in these rivers. Liming was therefore carried out to restore Atlantic salmon, and this led to a significant increase in their abundance. In recent years, very few brook trout have been caught in these river systems, and they are found in only a few tributary streams.

It appears that the abundance of brook trout has fallen sharply in several areas during the past 20 years or so. This may be related to the fact that brown trout have recovered from acidification during the same period (Hesthagen et al. 2011a). In most cases, brown trout is the only fish species that lives in sympatry with brook trout in most of our inland waters. Several studies have suggested that brown trout are dominant over brook trout in streams in North America (Fausch & White 1981; Fausch 1988). In streams in the Canadian Rockies, the invasion of brook trout was negatively associated with co-occurring rainbow trout or brown trout, two other introduced species (Warnock & Rasmussen 2013). Brook trout appear to dominate communities over native bull trout (*Salvelinus confluentus* G. CUVIER, 1816) where thermal or habitat niche opportunities are provided for them, although other non-native species may restrict their invasion into bull trout streams. Brook trout densities in Swedish streams were also negatively affected by the presence of brown trout, but not *vice versa*, irrespective of stream size or watershed area (Öhlund et al. 2008). These authors suggest that brown trout performance is an important factor in structuring the outcome of Swedish brook trout introductions. However, the proportion of allopatric brook trout was greater in the smallest streams. They suggested that this is because brown trout are unable to sustain viable populations where brook trout are numerically dominant. This does not appear to be related to differences in access to such small streams, as brown trout are believed to have better swimming ability than brook trout (Peake et al. 1997). However, brook trout are also quite capable of invading steep stretches of streams, even those with gradients up to 31%, and they can ascend vertical waterfalls of at least 1.3 m (Björkelid 2003). Thus, in small streams, brook trout will sustain viable populations and are unlikely to be wiped out by brown trout due to interspecific competition.

However, on the basis of data from 193 boreal lakes in Sweden located at 68-455 m a.s.l. (Spens et al. 2007), brook trout may also have a long-term detrimental impact on brown trout. In fact, 65 (20%) of all brown trout populations studied became extinct. Brown trout in higher-altitude lakes, i.e. above 285 m, were more sensitive to the impact of brook trout. It was suggested that brook trout actively displace brown trout by competition, predation, spreading disease, or a combination of these (Spens et al. 2007). In Norwegian lakes, no lost population of brown trout due to brook trout introduction have been reported. This may be related to fish community and habitat type, as most Norwegian lakes contain only these two fish species, being oligotrophic, located at relatively high altitudes, and have suitable spawning streams for brown trout.

Brook trout may presently have some climate-related advantages in Norwegian waters, as about 27% of all populations were found at sites between 750 and 1252 m a.s.l. Most brook trout populations in Sweden inhabited small, cold streams (Öhlund et al. 2008). Such small streams may have groundwater upwelling areas, which are preferred by brook trout (Cunjak 1996). It has been suggested that brook trout have a competitive advantage in such cold habitats, in addition to their life history, with higher juvenile growth rates and earlier reproduction than brown trout (Öhlund et al. 2008). Such cold-water species may be vulnerable to the effects of warming temperatures caused by climate change (*cf.* Britton et al. 2010; Hulme 2017). In some streams in Nova Scotia, the population density of brook trout was strongly related to water temperature, as streams that had a summer water temperature of 19 ºC or more contained either few or no brook trout (MacMillan et al. 2008). In Rocky Mountain streams sites lacking brown trout but contained brook trout, tended to be small streams at the cold margin of between 19 and 22 ºC (Rahel & Nibbelink 1999). Within this thermal zone, brown trout were more likely to occur in large streams (> 4 m wetted width) than in small streams. Similarly, the structure of brook trout, rainbow trout and brown trout populations in streams in the Southern Appalachian Mountains was related to elevation (Flebbe 1994), as allopatric and sympatric brook trout were generally found at higher elevations than the two other salmonid species.

In Finland, brook trout are mostly established in tributary streams, where they may form dense populations that can be harmful to local brown trout populations (Korsu et al. 2007, Korsu & Huusko 2009). They found that propagule pressure in terms of the number of individuals released and introduction events leading to highly successful establishment of brook trout, came to about 8000 individuals. Furthermore, a quarter of the newly introduced fish rapidly located suitable habitat patches in terms of small tributaries during initial dispersal. However, the effect of brook trout on brown trout was habitat-specific, as brook trout excluded native brown trout only in small tributary streams (Korsu et al. 2007), while in larger streams brown trout were usually not affected.

The abundance of lake-dwelling brook trout has declined significantly in Norway in recent years. This development also seems to have occurred in rivers. No data exists to assess their status in streams. Based on results from other countries, brook trout may dominate and exclude brown trout in small cold-water streams. Nevertheless, brook trout seems to be a low-risk species as far as invasiveness in Norwegian water bodies is concerned.

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REFERENCES

Allendorf FW, Lundquist LL. 2003. Population biology, evolution and control and invasive species. Conservation Biology 17: 24-30. doi: 10.1046/j.1523-1739.2003.02365.x

Björkelid L. 2003. Invasiveness of brook charr (*Salvelinus fontinalis*) in small boreal headwater streams. Thesis at Institutionen för vattenbruk, Umeå. Sweden. 16 p.

Blackburn TM, Pysek P, Bacher S, Carlton JT, Duncan RP, Jarosik V, Wilson JRU, Richardson DM. 2011. A proposed unified framework for biological invasions. Trends Ecology and Evolution 26: 333-339. doi: 10.1016/j.tree.2011.03.023

Britton JR, Cucherousset J, Davies GD, Godard MJ, Copp GH. 2010. Non-native fishes and climate change: predicting species responses to warming temperatures in a temperate region. Freshwater Biology 55: 1130-1141. doi: 10.1111/j.1365-2427.2010.02396.x

Carey MP, Wahl DH. 2010. Native fish diversity alters the effects of an invasive species on food webs. Ecology 91: 2965-2974.

Clavero M, García-Berthou E. 2006. Homogenization dynamics and introduction routes of invasive freshwater fish in the Ibeian Peninsula. Ecological Applications 16: 2313-2324.t

Clavero M, Villero D. 2013. Historical ecology and invasion biology: long-term distribution changes of introduced freshwater species. BioScience 64: 145-153. doi: 10.1093/biosci/bit014

Copp GH, Vilizzi L, Mumford J, Fenwick GV, Godard MJ, Gozlan RE. 2009. Calibration of FISK, an invasive-ness screening tool for non-native fishes. Risk Analysis 29: 457-467.

Cunjak RA. 1996. Winter habitat of selected streams fishes and potential impacts from land-use activity. Canadian Journal of Fisheries and Aquatic Sciences 50: 575-585. doi: 10.1139/f95-275

Dunson WA, Martin RR. 1973. Survival of brook trout in a bog-derived acidity gradient. Ecology 54: 1370-1376. doi: 10.2307/1934201

Eken M. 1988. Bekkerøya i Overnbekken – Bestandsdynamikk og habitatbruk hos en selvreproduserende bestand i Modum. Thesis, Institutt for naturforvaltning, Norges Landbrukshøgskole. 55 p. (in Norwegian).

Fausch KD, White RJ. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for positions in a Michigan stream. Canadian Journal of Fisheries and Aquatic Sciences 38: 1220-1227. doi: 10.1139/f81-164

Fausch KD. 1988. Tests of competition between native and introduced salmonids in streams: what have we learned? Canadian Journal of Fisheries and Aquatic Sciences 45: 2238-2246. doi: 10.1139/f88-260

Flebbe PA. 1994. A regional view of the margin: salmonid abundance and distribution in the Southern Appalachian Mountains of North Carolina and Virginia. Transactions of the American Fisheries Society 123: 657-667. doi: 10.1577/1548-8659(1994)123<0657:ARVOTM>2.3.CO;2

Gabrielsen, S-E, Halvorsen GA, Barlaup BT, Skoglund H, Wiers T, Lehmann GB, Sandven OR, Kleiven E. 2010. Songdalselva i Vest-Agder – begynnende reetablering av laks etter redusert tilførsel av sur nedbør i Sør-Norge. Laboratoriet for ferskvannsøkologi og innlandsfiske, Bergen, Rapport Nr. 167. (in Norwegian).

Gallardo B, Aldridge DC. 2015. Is Great Britain heading for a Tonto-Caspian invasional meltdown? Journal of Applied Ecology 52: 41-49. doi: 10.1111/1365-2664.12348

García-Berthou E. 2007. The characteristcs of invasive fishes: what has been learned so far? Journal of Fish Biology 71 (Supplement D): 33-55. doi: 10.1111/j.1095-8649.2007.01668.x

Garmo ØA, Skjelkvåle BL, de Wit HA, Colombo L, Curtis C, Fölster J, Hoffmann A, Hruška J, Høgåsen T, Jeffries DS, Kelle WB, Krám P, Majer V, Monteith DT, Paterson AM, Rogora

M, Rzychon D, Steingruber S, Stoddard JL, Vuorenmaa J, Worsztynowicz A. 2014. Trends in surface water chemistry in acidified areas in Europe and North America from 1990 to 2008. Water, Air and Soil Pollution 225: 1-14. doi: 10.1007/s11270-014-1880-6

Gozlan RE. 2008. Introduction of non-native freshwater fish: is it bad? Fish and Fisheries 9: 106-115. doi: 10.1111/j.1467-2979.2007.00267.x

Gozlan RE, Brittion JR, Cowx IG, Copp GH. 2010. Current knowledge on non-native freshwater fish introductions. Journal of Fish Biology 76: 751-786. doi: 10.1111/j.1095-8649.2010.02566.x

Grande M. 1964. En undersøkelse av bekkerøya i Øyfjell i Telemark. Fauna 17:17-33. (in Norwegian with English summary).

Henriksson, A, Wardle JDA, Trygg J, Diehl S, Englund G. 2016a. Strong invaders are strong defenders – implications for the resistance of invaded species. Ecology Letters 19: 487-494. doi: 10.1111/ele.12586

Henriksson A, Yu J, Wardle DA, Trygg J, Englund G. 2016b. Weighted species richness outperforms species richness as predictor of biotic resistance. Ecology 97: 262-271. doi: 10.1890/15-0463.1

Hesthagen, T, Rosseland BO, Berger HM, Larsen BM. 1993. Fish community status in Norwegian lakes in relation to acidification: a comparison between interviews and actual catches by test-fishing. Nordic Journal of Freshwater Research 68: 34-41.

Hesthagen T, Sevaldrud IH, Berger HM. 1999. Assessment of damage to fish populations in Norwegian lakes due to acidification. AMBIO 28: 12-17.

Hesthagen T, Sandlund OT. 2007. Non-native freshwater fishes in Norway: history, consequences and perspectives. Journal of Fish Biology 71 (Supplement D): 173-183. doi: 10.1111/j.1095-8649.2007.01676.x

Hesthagen T, Fjellheim A, Schartau AK, Wright RF, Saksgård R, Rosseland BO. 2011a. Chemical and biological recovery of Lake Saudlandsvatn, a formerly highly acidified lake in southernmost Norway, in response to decreased acid deposition. Sciences of the Total Environment 409: 2908-2916. doi: 10.1016.j.scitotenv.2011.04.026

Hesthagen T, Larsen BM, Fiske P. 2011b. Liming restores Atlantic salmon populations in acidified Norwegian rivers. Canadian Journal of Fisheries and Aquatic Sciences 68: 224-231. doi: 10.1139/F10-133

Hesthagen T, Kleiven E. 2013. Forekomst av reproduserende bestander av bekkerøye (*Salvelinus fontinalis*) i Norge pr. 2013. Norwegian Institute for Nature Research, Report 900. 70 p. (in Norwegian). Available at www.nina.no

Hesthagen, T. & Kleiven, E. 2014. Bekkerøya - en fremmed fisk med godt fotfeste i norske vassdrag. pH-status 20 (nr.1-2014): 8-10. (in Norwegian).

Hesthagen T, Sandlund OT. 2016. Tiltaksrettet kartlegging og overvåking av fremmed ferskvannsfisk – en tilstandsvurdering av spredning pr. 2016. Norwegian Institute for Nature Research, Report 1302. 47 p. (in Norwegian). Available at www.nina.no

Hesthagen T, Fiske P, Saksgård R. 2016. Recovery of young brown trout (*Salmo trutta*) in acidified streams: what are the critical values for acid-neutralizing capacity? Atmospheric Environment 146: 226-244. doi: 10.1016/j.atmosenv.2016.07.010

Huitfeldt-Kaas H. 1924. Vellykket indførelse av bækkerøie. Norsk Jæger- og Fiskerforenings Tidsskrift 53: 401-403. (in Norwegian).

Hulme PE. 2017. Climate change and biogical invasions: evidence, expecttations, and rsposne options. Biological Reviews 92: 1297-1313. doi: 10.1111/brv.12282

Kleiven E. 1995. Enkelte erfaringar med bekkerøya. In Hogstad, O. & J. Skurdal (eds). Spredning av ferskvannsorganismer. Seminarreferat. DN-notat 1995-4: 189-194.(in Norwegian).

Kleiven E, Hesthagen T. 2013. Bekkerøye innført i 1883 med støtte frå «Finants-Departementet». Fauna 66: 34-37. (in Norwegian with English summary).

Kohler CC, Courtenay WR jr. 1986. Regulating introduced aquatic species: a review of past initiatives. Fisheries 11: 34-38. doi: 10.1577/1548-8446-11-2

Korsu K., Huusko A, Muotka T. 2007. Niche characteristics explain the reciprocal invasion success of stream salmonids in different continents. Proceedings of the National Academy of Sciences of the United States of America 104 (23): 9725-9729. doi: 10.1155/2012/813016

Korsu K, Huusko A. 2009. Propagule pressure and initial dispersal as determinants of establishment success of brook trout (*Salvelinus fontinalis* Mitchill 1814). Aquatic Invasions 4: 619-626. doi: 10.3391/ai.2009.4.4.8

Larsen BM, Sandlund OT, Berger HM, Hesthagen T. 2007. Invasives, introduction and acidification: the dynamics of a stressed river fish community. Water, Air, and Soil Pollution (Focus) 7: 285-291. doi: 10.1007/s11267-006-9073-y

MacCrimmon HR, Campbell SJ. 1969. World distribution of brook trout, *Salvelinus fontinalis*. Journal of Fisheries Research Board of Canada 26: 1699-1725. doi: 10.1139/f69-159

MacCrimmon HR, Marshall TL. 1968. World distribution of brown trout, *Salmo trutta*. Journal of Fisheries Research Board of Canada 25: 2527-2548. doi: 10.1139/f68-225

MacCrimmon HR. 1971. World distribution of rainbow trout, *Salmo gairdneri*. Journal of Fisheries Research Board of Canada 28: 663-704. doi: 10.1139/f71-098

MacMillan JL, Caissie D, Marshall TJ, Hinks L 2008. Population indices of brook trout (*Salvenlinus fontinalis*), Atlantic salmon (*Salmo salar*), and salmonid competitors in relation to summer water temperature and habitat parameters in 100 streams in Nova Scotia. Canadian Technical Report of Fisheries and Aquatic Sciences 2819. 34 p.

Muniz IP, Leivestad H. 1979. Langtidseksponering av fisk til surt vann. SNSF project Internal Report 44. 29 p. (in Norwegian).

Møkkelgjerd PI, Gunnerød TB. 1985. Utsetting av bekkerøye i regulerte vassdrag på Sørlandet. Rapport fra kontrollfiske I 1984. Direktoratet for vilt og ferskvannsfisk, Reguleringsundersøkelsene, Rapport nr. 10-1985. 53 p. (in Norwegian).

Peake S, McKinley RS, Scruton DA. 1997. Swimming performance of various freshwater Newfoundland salmonids relative to habitat selection and fishway design. Journal of Fish Biology 51: 710-723. doi: 10.1111/j.1095-8649.1997.tb01993.x

Qvenild T. 1986. Utsettinger av bekkerøye i Norge. Direktoratet for naturforvaltning. Rapport Fisk og fiskestell No 9. 41 p. (in Norwegian).

Rahel FJ, Nibbelink NP. 1999. Spatial patterns in relations among brown trout (*Salmo trutta*) distribution, summer air temperature, and stream size in Rocky Mountain streams. Canadian Journal of Fisheries and Aquatic Sciences 56: 43-51. doi: 10.1139/F99-210

Rejmánek M, Richardson DM, Barbour MG, Crawley MJ, Hrusa GF, Moyle PB, Randall JM, Simberloff D, Williamson M. 2002. Biological invasions: politics and the discontinuity of ecological terminology. Bulletin of the Ecological Society of America 83: 131-133.

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R., Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH. 2010. Biodiversity – global biodiversity scenarios for the year 2100. Science 287: 1770-1774. doi: 10.1126/science.287.5459.1770

Sandøy S, Romundstad AJ. 1995. Liming of acidified lakes and rivers in Norway. An attempt to preserve and restore biological diversity in the acidified regions. Water, Air and Soil Pollution 85: 997-1002.

Savini D, Occhipinti-Ambrogi A, Marchini A, Tricarico E, Gherardi F, Olenin S, Gollasch S. 2010. The top 27 animal alien species introduction into Europe for aquaculture and related activities. Journal of Applied Ichthyology 26 (Supplement s2): 1: 7. doi: 10.1111/j.1439-0426.2010.01503.x

Scott WB, Crossman EJ. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada. Bulletin 184. 966 p.

Sevaldrud, IH, Muniz IP. 1980. Sure vatn og innlandsfisket i Norge. Resultater fra intervjuundersøkelser 1974-1979. SNSF prosjektet , Internal Report 77/80. 95 p. (SNSF project, NISK, 1432 Ås, Norway (In Norwegian with English summary).

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J et al. 2013. Impacts of biological invasions; what's what and the way forward. Trends in Ecology and Evolution 28: 58-66. doi: 10.1016/j.tree.2012.07.013

Spens J, Alanärä AA, Eriksson L-O. 2007. Nonnative brook trout (*Salvelinus fontinalis*) and the demise of native brown trout (*Salmo trutta*) in northern boreal lakes: stealthy, long-term patterns? Canadian Journal of Fisheries and Aquatic Sciences 64: 654-654. doi: 10.1139/f07-040

Sægrov H, Hellen BA, Kålås S. 2008. Fiskeundersøkingar i Blåsjø i 2007. Rådgivende Biologer AS, Report 1104. 22 p. (in Norwegian).

Tammi J, Appelberg M, Hesthagen T, Beier U, Lappalainen A, Rask M. 2003. Fish status survey in Nordic lakes: effects of acidification, eutrophication and stocking activity on present fish species composition. AMBIO 32: 98-105.

Trojnar JR. 1977. Egg hatchability and tolerance of brook trout (*Salvelinus fontinalis*) fry at low pH. Journal of Fisheries Research Board of Canada 34: 574-579. doi: 10.1139/f77-092

Trochine,C. Brucet, S, Argillier C, Arranz I, Beklioglu M, Benejam L, Ferreira T, Hesthagen T, Holmgren K, Jeppesen E, Kelly F, Krause T. Rask M, Volta P, Winfield IJ, Mehner T. 2017. Catch-based local records of non-native fish occurrence and biomass in Western Palearctic lakes and reservoirs and their abiotic and biotic correlates. Ecosystems. doi: 10.1007/s10021-017-0156-6

Warnock WG, Rasmussen JB. 2013. Abiotic and biotic factors associated with brook trout invasiveness into bull streams of the Canadian Rockies. Canadian Journal of Fisheries and Aquatic Sciences 70: 905-914. doi: 10.1139/cjfas-2012-0387

Öhlund G, Nordwall F, Degerman E, Eriksson T. 2008. Life history and large-scale habitat use of brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) - implications for species replacement patterns. Canadian Journal of Fisheries and Aquatic Sciences 65: 633-644. doi: 10.1139/f08-003

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