Sum of freshwater habitat degradation as a major driver for collapsing seatrout (*Salmo trutta* L.) stocks in regions of Norway? – A case-study from Central Norway

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O.T. Sandlund er dessverre ikke blant oss lenger, og vi lyser fred over hans minne.

Sammendrag

Habitatdegradering av små vassdrag som drivkraft for kollaps i sjøørretbestander i Norge? – Eksempelstudie fra midt-norske sjøørretvassdrag. Bestander av sjøørret i Norge viser langvarig nedgang, og det observeres mer eller mindre sammenbrudd i bestander for noen kystområder og i regioner av landet. Økt dødelighet i marin fase av livssyklusen hos sjøørret har blitt fremhevet som hovedårsak til utviklingen. Årsakene til bestandsnedgangen synes imidlertid vesentlig mer sammensatt. Nedgangen kan ha startet for flere tiår siden, men manglende betsandsdata og endringsblindhet kan ha kamuflert utviklingen. En gradvis forringelse av sjøørretens produksjonsområder, spesielt etter andre verdenskrig og fram til i dag, har gitt et redusert produksjonspotensial i mange mindre vassdrag. Samlet sett kan kritiske grenser for å produsere levedyktige sjøørretbestander nå være nådd. Dette forsterkes av lavere sjøoverlevelse i tillegg. I denne studien foreslår vi enkle metoder for å kvantifisere endringer i areal og produksjonskapasitet for små sjøørretvassdrag ved å bruke Trondheim kommune, Midt-Norge, som en case-studie. Fra å ha en tilgjengelig vassdragslengde for sjøørreten på nesten 57 km i 37 bekker og små elver, med et vanndekt areal på mer enn 187 000 m², gjenstår kun 17 km og rundt 59 000 m² i dag. Dette gir et lengde- og arealtap på ca. 70%. Redusert vann- og habitatkvalitet i de gjenværende vassdragstrekningene fører til ytterligere tap, fra 70% til ca. 90%. Årsaken er gradvis økende samlet menneskelig belastning. Situasjonen synes lik for andre kystområder i regionen og i Norge fra midt-Norge og sørover. Vi konkluderer med at den gradvise, vedvarende nedgangen i gode gyte- og oppvekstområder for sjøørret i små vassdrag samlet sett kan bidra vesentlig i det observerte sammenbruddet av sjøørretbestander i noen regioner i Norge. En eventuell økt dødelighet i den marine fasen forsterker dette, og gir det observerte sammenbruddet hos enkelte sjøørretbestander i dag. Samtidig med fortsatt fokus på utfordringer med sjøoverlevelse, må det gjøres betydelig større restaureringsinnsats i norske vassdrag enn i dag for å snu utviklingen. Det er umiddelbart behov for omfattende, storskala restaureringer av små og store vassdrag, og vesentlig økt fokus på bedre forvaltning og vern av de få lite berørte og gjenværende sjøørretvassdragene. Vår tilnærming kan bidra til å etablere økt kunnskap om den faktiske referansetilstanden for små sjøørretvassdrag. Videre bidrar metodene til gode prioriteringer av restaureringstiltak for aktuelle vassdrag. Samlet sett vil dette være avgjørende for å snu den negative utviklingen sjøørretbestandene, både lokalt, regionalt og nasjonalt, og kan bidra til at sjøørreten igjen kan oppnå livskraftige bestandsnivåer.

Summary

Norwegian seatrout stocks are in a historical decline in some coastal regions. Increased mortality in the marine part of the life cycle is highlighted as the main driver in this development. However, the reasons for the general decline in stock are more complex, and could have started decades ago, along with an increase in impacts of freshwater habitats for small/medium-sized seatrout streams in Norway. A gradual degradation of sea trout stream habitats has decreased available seatrout streams and stream-quality. We may have reached critical limits for producing viable seatrout stocks as marine phase survival also decreases. In this study we propose simple methods to quantify the changes of anadromous area and production capacity in seatrout streams, using Trondheim municipality, Central Norway, as a case study. From a total anadromous stream length of almost 57 km in 37 small streams, with a wetted area of more than 187,000 m², only 17 km and about 59,000 m² remains, i.e., a total length and area loss of about 70%. Reduced production capacity in remaining areas leads to a further loss, from 70% to about 90%. The situation appears to be similar in other regions of Norway. We conclude that the sum of decline in good quality nursery streams contributes to the observed collapse of coastal seatrout stocks in some regions in Norway, and this happens regardless of increased mortality in the marine phase. The immediate need for large scale stream restoration of degraded streams is urgent, and increased focus on management and protection of the few remaining intact seatrout streams, is required. Our approach may help establishing the actual reference condition for seatrout streams, as well as assist in the prioritization of stream-candidates and successful restoration measures.

Introduction

Anadromous brown trout (sea migrating *Salmo trutta* L., hereafter seatrout) is mainly distributed around the North Atlantic Ocean. In many parts of the distribution area, populations are in serious decline [1–7], and in some cases even said to be collapsing [8–11]. Along the long and complex Norwegian coast (> 25,000 km, from 56 °N to 71 °N) there are thousands of coastal rivers and streams which historically harbored viable seatrout populations. In the central parts of Norway, including the inner Trondheimsfjord, which is the study area of this paper, seatrout populations are currently in serious decline [1, 12, 13,], with many local populations seemingly collapsing. This is supported by data from annual monitoring based on electrofishing surveys [eg. 14-19]. The exact reasons for the general decline of seatrout populations are poorly understood [12], but a complex set of multiple interacting manmade factors are probably in play; with sea phase mortality presently indicated to be the main driver [1]. Recent status assessments for Norwegian seatrout populations originating from larger rivers [1] concludes that 91% of the populations are negatively impacted by salmon lice, contributing 44 % of the presently observed population reduction due to human impacts induced. However, the sum of negative human impact of declining accessibility and quality of nursery habitats in river tributaries and coastal streams has not been analyzed or sum-evaluated.

Seatrout has a complex life cycle [20], relying on both freshwater and marine environments to maintain viable populations. The species is therefore susceptible to human impacts in both habitats. Spawning, egg incubation and juvenile life stages occur in freshwater, often in small and moderately sized streams [21, 22], while the subadult (postsmolt) and adult fish each year spend from a few weeks to several months feeding in the marine environment [23 and references therein]. Nursery streams may empty directly into the sea, or be tributaries to larger rivers dominated by Atlantic salmon (*Salmo salar* L.). The seatrout is iteroparous, with documented spawning up to twelve times [24]. Thus, even the smallest streams may be the origin of a high numbers of adult seatrout. Small tributaries often constitute a major proportion of overall river length [25]. The high number of small streams along the Norwegian coast form the production basis for the overall numbers of seatrout in coastal waters. However, these small and moderately sized streams are vulnerable to a plethora of human activities, while at the same time often being overlooked as important biotopes. As a consequence, over several decades, the production capacity of individual streams has been reduced or even completely destroyed, causing a gradual and "step by step" reduction in the production capacity in the freshwater habitat of seatrout. Numerous recent scientific surveys and monitoring studies indicate that this degradation of the small freshwater habitats continues and even increases [eg. 14, 19, 26). The cumulative effect on seatrout stocks at a local or regional scale has never been properly assessed. Even so, management institutions have recently concluded that anthropogenic degradation of the freshwater habitat and pollution is a "stabilized factor" for seatrout in Norway in general [13, 27].

There are two major issues concerning restoration of ecosystems [28]: insufficient information about the historical baselines (reference conditions) to guide restoration, and the divergence between the actual baselines and perceptions about historical conditions. These two conditions generate a phenomenon called "shifting baseline syndrome (SBS)" [29]. Developing SBS amongst relevant stakeholders might contribute to reduce the awareness of the gradual degradation of streams over decades, including the subsequent decline in sea-trout stocks. Thus, as the degradation of stream habitat has not been considered as a significant contributing factor in the decline of seatrout stocks, these habitats have generally been neglected by environmental authorities [26, 27, 30, 31]. On the other hand, restoration measures of nursery streams may often appear to be a relatively straightforward activity which may mobilize local communities and stakeholders [32]. Moreover, such measures are required in order to achieve environmental objectives and goals, e.g. "Good ecological status" [33], according to EU's Water Framework Directive (WFD) (in Norway: Vannforskriften, www.vannportalen.no/english).

The aim of this paper is to discuss and highlight the historical development of nursery streams for seatrout, using the municipality of Trondheim as a case study. The paper proposes a simplified approach to assess habitat degradation, highlighting the historical development and present status of available freshwater stream habitat for seatrout, based on more than 20 years of juvenile fish data, macroinvertebrate studies, water quality samples, aerial photos, and maps. Within the 37 streams that are identified as historically accessible seatrout streams in the Trondheim municipality, the loss of habitat (available stream length and area) and quality (production capacity) for seatrout in the streams are quantified. Further actions, expectations, and possibilities to restore streams are briefly discussed in a Norwegian context, using Trondheim municipality as an example.

Materials and Methods

2.1 Study area

Trondheim municipality* (pop. approx. 200,000 (2019)) borders the inner Trondheimsfjord and has a surface area of 342 km ^{2}, including areas of boreal forest (55 %), agricultural land (20 %) and urban and industrial areas (20 %; which

* Data refers to Trondheim municipality prior to the integration of Klæbu municipality in 2020

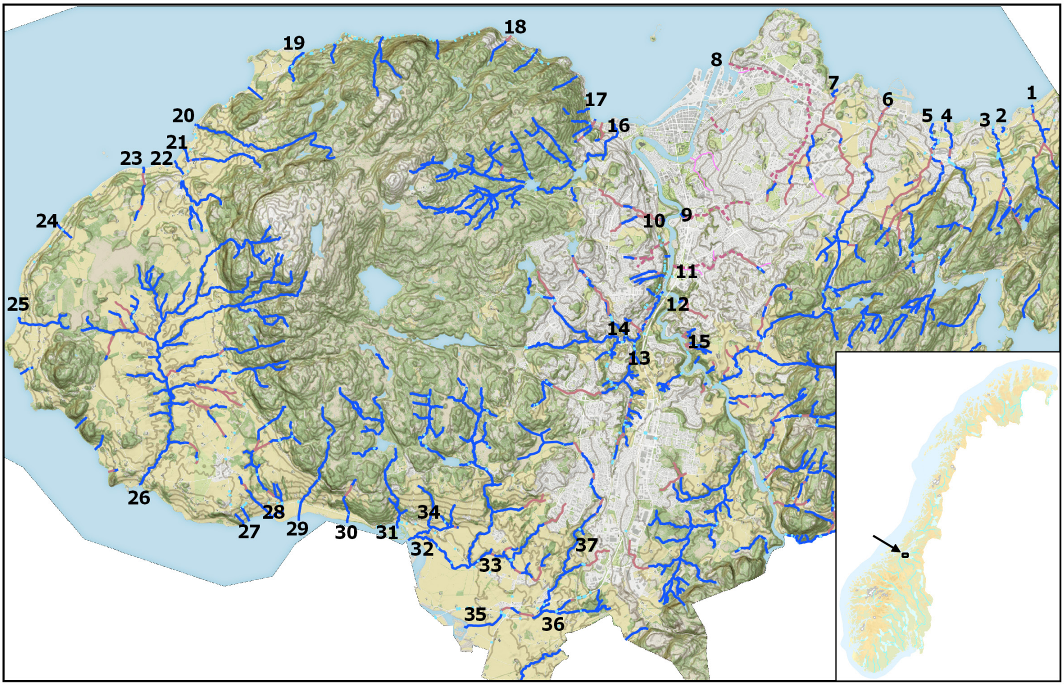

Figure 1. Study area and studied streams in Trondheim municipality. The names of the streams are given in table 3. Present status (both anadromous and stationary stretches): blue line - open streams, red line - closed streams.

constitutes the city of Trondheim (63° 26' N 10° 24' E), figure 1). Within Trondheim municipality as well as in the neighboring areas, there is a high number of small (1-3 meters stream width) and medium sized (3-8 meters stream width) streams, potentially harboring seatrout. Some of the streams drain directly into the Trondheimsfjord, while others are tributaries to the lower sections of the larger rivers Gaula and Nidelva, both of which currently have viable populations of Atlantic salmon as the dominating fish species [15, 17,33].

2.2 Methods

A number of technical reports from monitoring studies in the period 2006-2018 [35-38], utilizing electrofishing and other field methods, have identified streams within the municipality with variable status in terms of habitat for seatrout. The present anthropogenic impacts on stream ecology have also been well documented over the last 10 years from macroinvertebrate monitoring studies [39 and references therein]. Based on these monitoring surveys, five criteria are used to identify the potential seatrout streams in the municipality:

Sufficient continuous annual water runoff: catchment area ≥ 1km² and/or documented stable groundwater supply (observed during winter or dry periods in summer).

Stream width ≥ 1 m.

Gradient allowing the ascent of seatrout, i.e.: slope ≤ 25%, and natural waterfalls < 2 m with downstream pool depth / waterfall height ratio > 0.3 [40, 41].

Original stream habitat (observed, or assumed, if degraded) with suitable hydromorphological characteristics, providing seatrout spawning and nursery areas [42]

Discharge into the Trondheimsfjord, either directly or as tributaries below natural migration barriers in the large rivers Nidelva and Gaula.

Applying these criteria, 37 streams have been identified and selected for our case study. For these streams, we can assess and document the impact of human activities since the late 1930s,

*Table 1. Assessed production value expected total juvenile trout densities and fish community structure. *Additional consideration relates to an expected fish community structure in the smallest streams, or small tributaries to larger rivers with mainly spawning function (as described by [22, 43]).*

Production value	Expected total trout density / 100 m^2	Additional consideration*
1	≥ 200	YOY dominating
0,9-0,7	100-200	YOY dominating
0,6-0,4	100-50	YOY dominating
0,4-0,2	50-20	YOY dominating
0,1	<20	YOY not present = 0,05
0,05	<5	YOY not present = 0
0	1-0	YOY not present = 0

based on available digitalized historical aerial photos (www.norgeibilder.no; http://kart.finn.no), and historical information from locally published texts and oral or written information from local stakeholders. Of the 37 selected streams (figure 1), 29 have been surveyed and monitored by repeated field inspection and electrofishing over the last 20 years [35 and references therein]. Eight additional streams, which are no longer open or present as free running streams, were assessed implementing the above-mentioned criteria, as well as on-site observations combined with ancient maps ("Amtskart" from 1867 and earlier).

The present production capacity for seatrout in stream sections that are still accessible for the fish and open in the landscape, was assessed on a scale from zero (no fish production) to one (presumed natural production capacity) (table 1).

Based on existing monitoring data from electrofishing juvenile fish from these streams [35-38], as well as other seatrout streams in the region [31, 43], we defined an expected reference density of fish per 100 m^2, corresponding to the assessed production value in the streams (table 1). Ecological status classification from the period 2009-2018 based on macroinvertebrate samples [39 and references therein] were also used to evaluate present water and habitat quality.

2.3 Fish sampling

Annual juvenile salmonid monitoring surveys were performed by electrofishing (portable gear, TERIK model FA-3 and FA-4) during the period 2005-2017 [35-38], as part of environmental monitoring programmes. The annual surveys were conducted in August/September each year under similar conditions, i.e. low/medium water discharge and water temperatures between 8-16 °C. The multiple pass [44] as well as single pass method (using fixed catchability) have been applied to estimate fish density and population size [45, 46], with overfished area varying from approx. 30 m^2 up to more than 150 m^2, depending on stream size and fish abundance.

Results

Analysis of 37 streams within the Trondheim municipality demonstrated that the original stream stretches accessible for seatrout totalled nearly 57 km, with a watered area estimated at 187,163 m^2 (table 2). Streams located in the area east of the city centre, and tributaries to the river Gaula (nos. 1-8 and 26-37 in figure 1) accounted for most of the original stream length and area (approximately 40 and 35% respectively), while streams west of the city centre (nos. 16 – 25 in figure 1) originally had the lowest proportion of seatrout stretch and area.

The present stream length accessible for seatrout in the 37 streams is approximately 17 km, with a watered area of a little over 59,000 m^2 (figure 1, table 2). Thus, nearly 40 km, or more than 70%, of the original anadromous stream length have been lost or is presently inaccessible for seatrout. This corresponds to an area loss of

Table 2. Total length (meters) and area (square meters) for 37 seatrout streams in Trondheim; present situation compared with past (before WW2). Loss of length and area is indicated as a percentage. Stream number (Nos.) refers to figure 1.

		Length (m)			Area (m^2)		
Muncipality zone	**Nos.**	**Past**	**Present**	**% loss**	**Past**	**Present**	**% loss**
Streams east of city centre	1-8	23 990	2 702	88,7	70 120	9 235	86,8
Tributaries to Nidelva	9-15	8 162	4 410	46,0	28 330	14 800	47,8
Streams west of city centre	16-25	5 303	3 660	31,0	17 905	12 840	28,3
Tributaries to Gaula	26-37	19 453	6 493	66,6	70 808	23 178	67,3
Sum all streams/zones		**56 908**	**17 075**	**70,2**	**187 163**	**59 672**	**68,2**

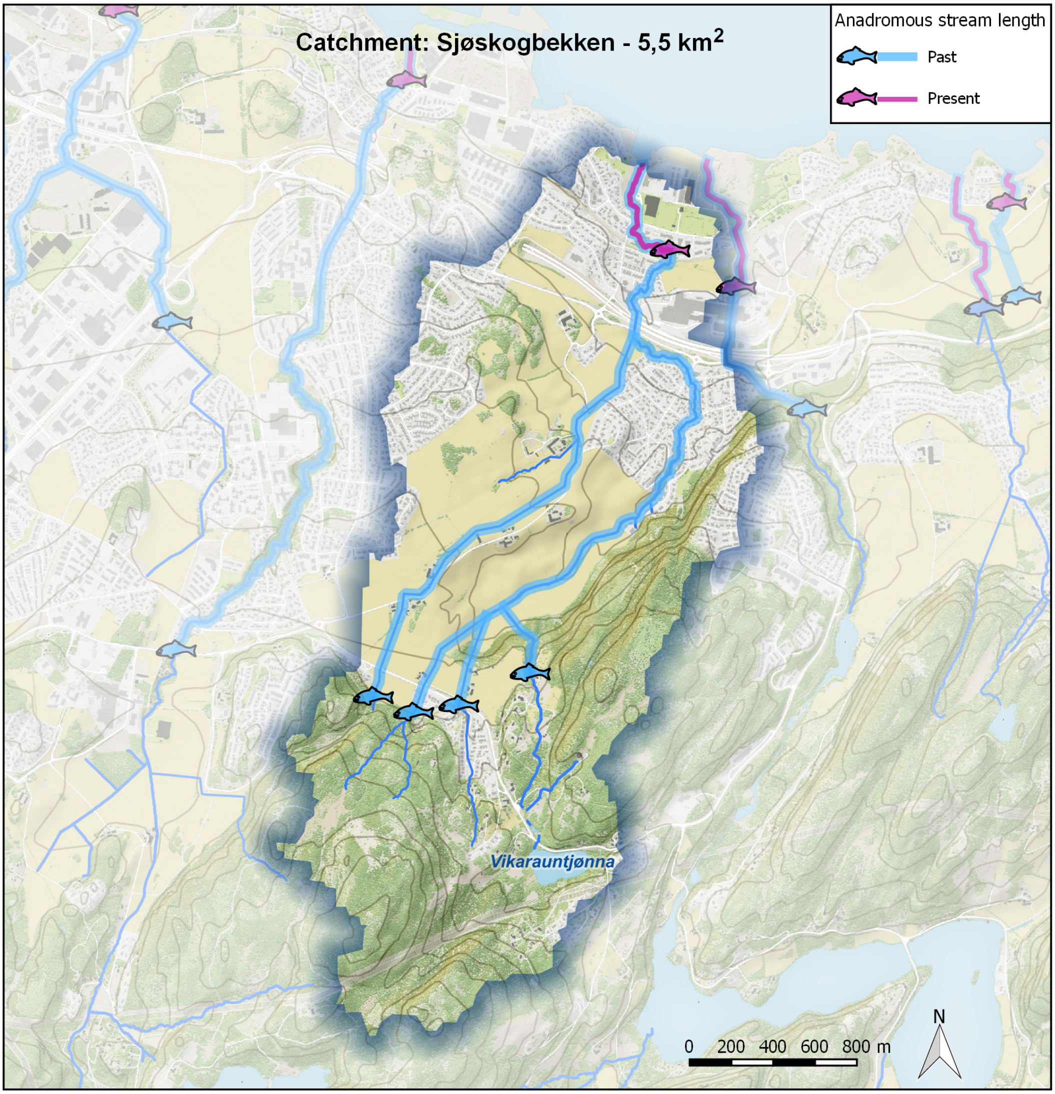

Figure 2. Example from a selected stream "Sjøskogbekken" (stream no. 5 in figure 1), located east of the city centre, in an area where the loss of anadromous stream length and habitat area is at its highest.

Table 3. Assessed present production capacity (PC) in available habitat/area. Density = Mean density/100 m^2 of trout (YOY/≥1+) in the period 2006-2017. Main impacts of the streams: 1= Stream closing, 2= Migration barrier/obstacle, 3= Catchment draining, 4=Pollution, 5= Streambed alteration.

No.	Name	Fish density	1	2	3	4	5	PC
1	Værebekken	4,3 /4,7 = 9,0	X	X	X			0***
2	Grytbakkbekken	No seatrout	X					0
3	Reppebekken	4,0 / 8,8 = 12,8		X	X			0.1
4	Vikelva	19,9-7,8 = 27,7	X	X		X	X	0.2
5	Sjøskogbekken	No seatrout	X	X	X	X	X	0
6	Grilstadbekken	0,7/2,0 = 2,7	X		X	X		0
7	Leangenbekken	No seatrout	X		X	X		0
8	Ladebekken	No seatrout	X		X	X		0
9	Nardobekken*	No seatrout	X		X	X		0
10	Sverresdalsbekken*	68,2 / 12,2	X		X	X	X	0.1**
11	Fredlybekken*	No seatrout	X		X	X		0
12	Leirelva*	89,5 / 20,9 = 110,4		X		X	X	0.7
13	Heimdalsbekken	4,8 / 12,2 = 17, 0		X		X	X	0.5
14	Uglabekken*	34,9/5,8 = 40,7				X	X	0.1
15	Hornebergsbekken	No seatrout				X	X	0
16	Ilabekken	31,2 / 30,8 =62,0					X	0.5
17	Killingdalsbekken	No seatrout	X			X	X	0
18	Trollabekken	No seatrout	X					0
19	Flakkbekken	15,3 / 3,5 = 18,8		X		X		0.1
20	Klefstadbekken	109,6 /52,5 = 162,1						0.9
21	Elsetbekken	11,6 /7,3 = 18,9	X			X	X	0.1
22	Ryebekken	8,2/3,5 = 11,7				X	X	0.1
23	Bjøra	0/0,7 = 0,7			X	X	X	0
24	Lausetbekken	No seatrout			X			0
25	Aunbekken	No seatrout			X			0
26	Ristelva	0/<10				X		0.05
27	Bråbekken*	No seatrout			X	X		0
28	Stordalsbekken*	0 / 0,6 = 0,6		X	X	X		0
29	Almlibekken*	No seatrout			X			0
30	Gravbekken*	0 / 5 = 5,0		X	X		X	0.05
31	Lauglobekken*	54,7/18,5 = 73, 2		X				0.3
32	Eggbekken*	23,0/ 10,1 = 33,1		X	X	X		0.3
33	Ustbekken	No seatrout		X	X	X		0
34	Buskleinbekken*	6,2/1,4 = 8,6		X	X	X		0.1
35	Søra *	No seatrout		X	X	X	X	0
36	Lersbekken *	No seatrout		X	X	X		0
37	Heggstadbekken*	No seatrout		X	X	X		0

* Tributary to large rivers (Gaula/Nidelva) ** data only from lower parts, no seatrout upstream *** resident brown trout only

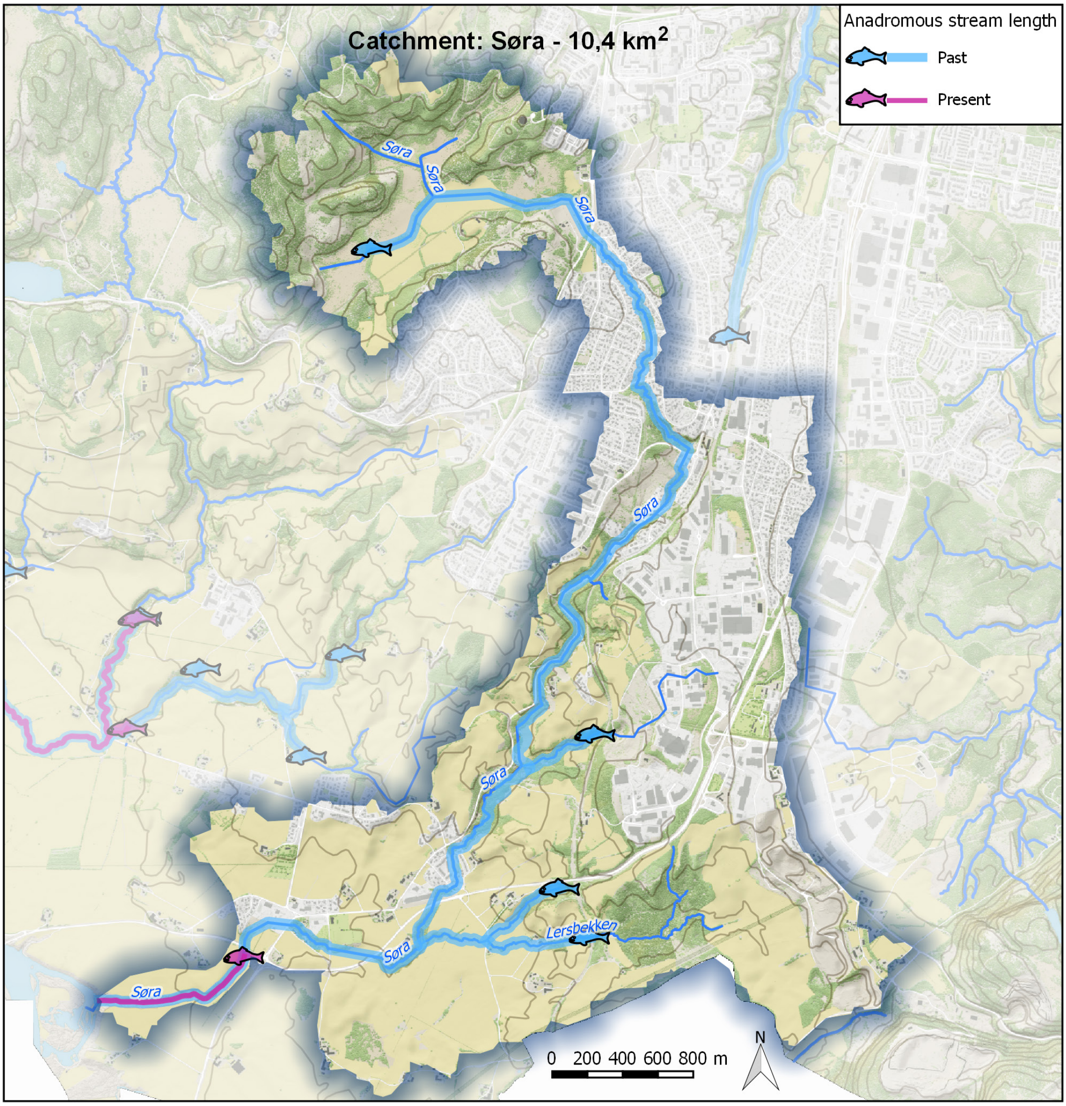

Figure 3. Example from a stream tributary to river Gaula, "Søra" (stream no. 35 in figure 1), representing a loss of approx.. 90 % anadromous stream length and habitat area.

Table 4. Original (past) and remaining (present) anadromous stream area in seatrout streams in Trondheim municipality, with present productive, good quality area adjusted by present assessed level of degraded habitat (PC, cf. table 3).

Muncipality zone	Past (m^2)	Present (m^2)	Adjusted (m^2)	Present area loss (%)
Streams east of city center	70 120	9 235	1 192	98
Tributaries to Nidelva	28 330	14 800	7 906	72
Streams west of city center	17 905	12 840	5 893	67
Tributaries to Gaula	70 808	23 178	4 169	94
Sum all zones	187 163	59 672	19 122	90

more than 27,000 m² or approx. 68%. The major reduction in stream length and area is in the streams east of the city centre, with a loss of almost 90%. (see table 2, and illustrated in a selected stream east of the city centre in figure 2 and a tributary stream to Gaula in figure 3). The least impacted streams (about 30% reduction) are located to the west of the city centre.

Using available information on water chemistry, hydromorphological conditions, macroinvertebrate diversity and abundance, as well as data on juvenile brown trout density, the production capacity in the remaining anadromous stretches of each stream were assessed and compared with the proposed "expected density values" (cf. table 1).

The main anthropogenic pressures causing reduced or lost production capacity are stream closing, migration barriers/obstacles, catchment draining, pollution and streambed alteration. To a varying degree, the stream habitats are affected by one or more of these factors, resulting in reduced stream conditions and fish production capacity (table 3). Low fish densities or absence of fish from suitable habitats may for example be due to manmade migration obstacles or barriers downstream. If fish have access to all the naturally available anadromous stretches of the stream, hydromorphological changes to the riverbed may have removed suitable spawning or nursery habitats, or pollution, nutrient enrichment and subsequent eutrophication/silting may have rendered the stream unsuitable for fish.

Adjusting the remaining accessible area of seatrout streams (approx. 60,000 m²) to these factors, by multiplying assessed present production capacity (PC, table 3) with remaining (present) area (table 4), shows that the present production capacity is further reduced, and corresponds to slightly above 19,000 m² of productive stream area. (table 4). Thus, combining the loss of accessible area (68 % loss, table 2) with the reduced production capacity of the remaining area, results in an overall loss of anadromous production capacity of approx. 90% in the 37 streams.

Discussion

We have quantified the present loss of freshwater habitat and production capacity for 37 streams in Trondheim municipality, which originally were harbouring viable seatrout stocks. Relative to the undisturbed condition of the streams, anadromous stream area and length has been reduced by approx. 70 %, and production capacity has been reduced by approx. 90%. The municipality of Trondheim is a suitable case study, due to access to digitalized historical maps, aerial photographs and GIS-based survey tools, combined with representative, good quality, biological data from a 20-year period from the streams. The present status of the 37 streams covers a gradient from nearly pristine to completely degraded. Today, only a very few streams in the municipality have a relatively intact access from sea, and a water and habitat quality sufficient to maintain viable seatrout populations.

Even the first human settlements with agriculture in this area, more than 1,000 YBP, would have impacted some of the streams. Still, the major human impacts have occurred during the last hundred years or so, with accelerating urbanization, infrastructure development and intensified agriculture. In particular, the changes have been significant during the period from 1945 (after World War II) until the late 1980s, as described by [30]. Old maps and other available documentation enable us to describe the situation around 1945, and the period from 1945 to 1990 may therefore serve to analyse changes in the streams and facilitate prioritization of restoration measures.

An important objective for the evaluation of each stream has been to determine the upstream distance that could historically be accessed by seatrout, and to estimate this area in terms of stream length (m) and wetted area (m²), compared to the present situation. This includes defining the point where the natural gradient (as verified on site or assessed from maps) would have formed a natural barrier to upstream migration from the sea or from the main rivers Nidelva or Gaula. The original hydromorphological properties (e.g., stream path and width) had also to be assessed. This map-based information was ground-truthed through in situ surveys, local information (written and oral) from landowners, and other relevant local historical information.

The streams identified as historically accessible seatrout streams constitute a minimum judging from ancient maps (e.g. "Amtskart" from 1867). Considering that the town was established approx. 1,000 years ago, there were originally even more potential seatrout streams, which have vanished due to urban development before the 1930s.

For the 37 streams in this study, an estimated 57 km of readily accessible and undisturbed seatrout stream length were available in the pristine situation, with an area of more than 187,000 m². Today, only 17 km of stream length is available for sea trout, constituting about 59,000 m² water covered habitat. Thus, there has been a reduction of nearly 70% in stream area available to migrating seatrout. Main pressures causing this loss are urbanization and intensified agriculture involving construction creating barriers to migration. The most dramatic reduction in stream length and area is in the streams east of the city centre, with a loss of almost 90%. Here the land use has been very extensive in recent decades, with few environmental limitations or restrictions [30]. Streams located to the west of the city have been subject to lower human impacts and consequently much lower loss (about 30% reduction in stream length and area). However, road crossings in this zone still constitute obstacles or barriers to fish migration, preventing optimal utilization of upstream spawning and nursery habitats [47, 26].

Production capacity of sea trout in the streams depends not only on available area, but also on present water and habitat quality. Annual monitoring studies [35,39] supports that today's water and habitat quality is severely reduced compared to the natural state in the remaining stream areas, affecting the productivity of the individual stream. However, the complexity of developing a quantitative and statistic model addressing this issue, is beyond the aim of our study, and should be a matter of further research and method development. Adjusting for these factors by expert evaluation indicates that the loss of production capacity increases from 70% to nearly 90%. This is due to a stream specific, mixed interaction of reduced water quality, obstacles to upstream migration, stream closures and a varying degree of hydromorphological modification of the stream course.

Originally, all seatrout streams situated in Trondheim municipality in this study had close to optimal conditions in terms of habitat and water quality, suitable for high natural production of seatrout [cf. 30 and references therein]. The juvenile brown trout density expected in pristine streams in central Norway is related to a nearly optimal climate for brown trout, suitable natural stream gradients and stable annual water discharge combined with groundwater supply, as well as relatively low proportion of fine sediments. Thus, "average", undisturbed seatrout streams in the region has highly suitable riverbed distribution for high seatrout production, consisting of riffles/runs covered with sufficient spawning substratum, pools and areas of coarser material, which provide shelter for older juveniles [52]. However, defining and estimating natural production capacity for seatrout in seatrout streams is challenging, since there are few data sets from pristine coastal streams and/or unaffected tributaries, and time series are more or less absent. In addition, there seems to be great variation under natural conditions, both in time and space [20]. It is known that small coastal streams can hold significant numbers of trout fry [43, 22]. In central Norway, a standard undisturbed or successfully restored seatrout stream may harbour trout densities of several hundred young of the year (YOY) per 100 m², as well as a varying number of older juveniles [48]. For instance, juvenile fish densities from five "average" seatrout stream-tributaries to River Verdalselva, considered to be in a nearly undisturbed state, were estimated at an average of 191 individuals (YOY and older juveniles) per 100 m² [31]. This density level is in the lower range of estimated average densities from a four-year monitoring study of a successfully restored seatrout stream in central Norway [48, 53], but appears to be representative for the natural state of average seatrout streams in the Trondheimsfjord area.

Our assessments of natural production capacity in this study are subject to expert judgement based on the estimated densities of juvenile trout per 100 m² from electrofishing surveys, supported by data on macroinvertebrates, water quality, analysis of aerial photos and maps, and visual inspection of substrate conditions. Data from similar streams in the region [31, 43, 48, 53], considered to be in a near natural condition or recently successfully restored streams are used as reference. Major factors for habitat quality are hydromorphological characteristics of the streambed, and whether the stream has a tributary status or flows directly into the sea. High densities of YOY is considered as the key indicator of intact ecological connectivity and good quality stream environment [49-51]. However, there is urgent need for further research and improved procedures to define the natural state, both concerning the natural range of juvenile seatrout densities, and natural variation both in time and space.

Our results and assessments suggest that the production capacity of the streams in Trondheim is currently critically low, suggesting that the limits for maintaining viable seatrout populations have been reached, or even exceeded. Other monitoring surveys suggest that this applies to the whole region of central Norway. [14] estimated a loss of productive area of 89,5 %, using a methodological approach similar to our study on stream tributaries to Gaula River. For tributaries to the river Verdalselva, [31] calculated a minimum specific area loss of 32% using a similar approach as in our study, rising to 80% when corrected for the degraded productivity in the remaining anadromous areas. Furthermore, ongoing, annual problem-mapping studies in tributaries to River Orkla indicate considerable habitat loss and quality degradation [19]. Numerous recent monitoring studies also highlights a considerable loss of anadromous area and quality in seatrout streams due to outdated dams [54], dams from the salmon-farming industry [55, 56] and multiple other human impacts (e.g. small-scale hydro-electric power stations).

Despite a ten-year period (since 2009) with strict regulations of recreational seatrout-fishing in rivers and harvest at sea in central Norway, we are observing a persistent "collapse" in sea trout stocks over the last decades [1]. Numerous contributing, interacting factors and pressures are identified, highlighting elevated sea lice (*Lepeophtheirus salmonis*) infestation levels from the fish farming (open-net pen-based aquaculture) industry as the main pressure causing sudden drops in populations the last decade. However, we demonstrate that the reduction and degradation of freshwater habitats could be a major contributing factor to declining seatrout stock. Thus, over several decades, freshwater habitat destruction and loss of available stream area had caused a major "undetected" decline in seatrout stocks, even before the increase in sea lice infection. Our study indicates that sea trout stocks in the region may already have been seriously decimated long before the recent impact of sea lice causing a "collapse". When fish stocks, such as coastal seatrout, are gradually reduced over many decades, camouflaged by natural stock fluctuations, the general stock decline is not easily detected. Being perceived as the poor relation of Atlantic salmon, with lack of historical data and available monitoring methods, together with lacking or insufficient catch statistics, has facilitated this phenomenon. Furthermore, a shifting baseline syndrome (SBS) amongst relevant stakeholders might also have contributed to cover up the degradation of streams as well as the subsequent detection of decline of seatrout populations. Most streams in our study area are subject to impacts which have been present for many decades, while some pressures have escalated during the recent years.

Conclusions and management implications

We conclude that reduced freshwater habitat is likely to have been a major stock-reducing factor for seatrout after WW2. This is combined with increased sea-phase mortality during the recent decade and has pushed natural regional seatrout stocks towards a collapse in many parts of coastal Norway. The degraded freshwater habitat, especially small rivers and streams must be acknowledged as an unstabilized driver. Our conclusions should also contribute to an increased awareness of stream management and conservation, and development of a more calibrated and correct baseline for natural seatrout stocks and stream production value. A comprehensive national effort is required to restore and regain lost anadromous habitat in streams, and to improve water and habitat quality. The main focus must be improvement of water quality in urban and agricultural areas, as well as reopening and restoration of closed streams. This includes measures directed at obstacle/barriers to migration, and improvement of spawning habitat quality. In accordance with the conclusions of [47], we propose culvert problem-mapping and subsequent culvert restoration efforts to re-establish connectivity with potential and previously accessible seatrout production area as the first step. Increased protection and consideration of streams in urban areas, including a variety of restoration efforts made during the last decades, have stopped the further degradation of a number of streams in Trondheim municipality [30]. Moreover, the present (2017) production capacity (90% loss) is probably somewhat better than the situation in the mid-1990s [30]. Several streams with previously extinct seatrout stocks, have recently achieved re-established seatrout production, with Leirelva (no. 12 in figure 1), Vikelva (no. 4) and Ilabekken (no. 16) serving as the most successful projects so far [57, 58, 60]. Our experience is that stream restoration is a long-term process, and it might take several years to re-establish and regain viable seatrout stocks. Ongoing restoration projects in Søra (no. 35 in figure 1; see also figure 3) and Sjøskogbekken (no. 5) are also expected to contribute to improvements during the next decade [59,60]. Further improvement of seatrout river and stream status in the municipality of Trondheim, as well as in the rest of Norway, will be crucial in order to reverse the negative trends and collapses in coastal seatrout stocks, parallel to solving issues relating to the marine life cycle stages.

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