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Lacustrine fish community turnover on a century time scale in south-eastern Norway

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Natural Resources Management
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Master thesis in Natural Resources Management (MSNARM)

Supervisor: Professor Anders G. Finstad, Department of Natural History

Co-Supervisor: PhD Candidate Sam Perrin, Department of Natural History

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Abstract

1. *Background.* Anthropogenic activity has contributed to significant changes in ecosystems over the last century. Freshwater ecosystems are particularly vulnerable to species turnover caused by anthropogenic activities. Several freshwater fish species are experiencing an increase in lake presence at rates previously not possible due to anthropogenic translocations. In order to target conservation and management efforts of freshwater ecosystems, identifying patterns in and causes of species turnover are vital. Yet, knowledge on species turnover and factors driving this is limited. Most studies are conducted on limited spatial and temporal scales. The main objective for this study was to identify changes in lacustrine fish communities on a century time scale in South-eastern Norway, and identify anthropogenic and natural factors that contribute to the observed changes.
2. *Methods.* The methodological approach for this study was to make use of historical and present large scale freshwater fish inventory data from south-eastern Norway. The combined dataset containing presence/absence data for individual lakes was combined with environmental variables to study changes in community composition, and, which natural and anthropogenic factors contribute to the observed changes.
3. *Results.* My findings suggest that the species richness increased over the last century. The increase in species richness was greatest in the densest human-populated areas of the study system. Temperate species had the greatest expansion in the last century. Lake area had a significant positive effect on species turnover, while lake elevation and shoreline complexity index (SCI) had a significant negative effect. Human footprint index (HFI) had no significant effect on species turnover.
4. *Conclusions.* My results indicate that both anthropogenic and natural factors contribute to the observed changes in community composition. There was a distinct spatial pattern in species turnover, correlating with the densest human-populated areas of the study system. HFI related parameters may therefore still be biologically significant for species turnover.

Sammendrag

1. *Bakgrunn.* Menneskelig aktiviteter har bidratt til store endringer i økosystemer det siste århundret. Ferskvannsøkosystemer er spesielt sårbare mot antropogene aktiviteter som forårsaker endringer i biodiversitet. På grunn av menneskelige utsetninger har mange ferskvannsfiskearter økt spredning i et stadig økende tempo. Med tanke på bevaring og forvaltning av ferskvannsøkosystemer og igangsetting av tiltak er det viktig å identifisere mønstrene for og årsakene til endringer i artsmangfoldet. Kunnskap om endringer i artsmangfold og faktorene som forårsaker dette er begrenset, siden vi mangler data på tilstrekkelige romlige og tidsmessige skalaer. Hovedmålet med dette studiet var å identifisere endringer i lakustrine (innsjøer) ferskvannsfisksamfunn på en hundreårs-skala i sørøst Norge, samt og undersøke hvilke antropogene og naturlige faktorer som bidrar til de observerte endringene.
2. *Metode.* Tilnærmingen til dette studiet var å kombinere historisk og nåværende stor-skala data på ferskvannsfisk samfunn fra innsjøer i sørøst Norge. Det sammensatte datasettet inneholdt tilstede/fravær-data på individuelt innsjø-nivå fra 1918 og 2019. Denne informasjonen ble kombinert med miljøvariabler for å identifisere antropogene og naturlige faktorer som bidro til de observerte endringene.
3. *Resultater.* Funnene mine antyder at artsrikdommen av ferskvannsfisk i innsjøer i sør-øst Norge har økt gjennom det siste århundret. Økningen i artsrikdommen var størst i de tettest befolkede områdene av studieområdet. Tempererte fiskearter opplevde de største endringene gjennom det siste århundret. Innsjøareal hadde en signifikant positiv effekt på endringene i biodiversitet. Mens innsjøens høyde over havet og strandlinje-kompleksitet (SCI) hadde en signifikant negativ effekt på endringene i biodiversitet. Menneskelig fotavtrykk indeks (HFI) hadde ingen effekt på endringene i biodiversitet.
4. *Konklusjon.* Resultatene mine tyder på at både antropogene og naturlige faktorer har bidratt til de observerbare endringene i ferskvannsfisk faunaen i sørøst Norge. Jeg fant også et romlig mønster for endringene i biodiversitet som tyder på størst forandring i de tettest befolkede områdene innenfor studieområdet.

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List of Abbreviations

HFI Human footprint index

SCI Shoreline complexity index

Key words: Freshwater fish, freshwater ecology, invasive species, species turnover, community ecology, temporal and spatial scale

1. Introduction

1.1 Background

Over the last century, human activity has contributed to significant changes in ecosystems worldwide (Butchart *et al.*, 2010). Changes in land- and sea use, direct exploitation of organisms, climate change, pollution and invasive species are all anthropogenic drivers of biodiversity turnover (Brondizio *et al.*, 2019). However, the factors responsible for the biodiversity turnover are not necessarily the same, or in the same order on regional or local levels (Sax and Gaines, 2003; Collen *et al.*, 2014). This uneven distribution of factors responsible for changes creates spatial differences in biodiversity turnover among landscapes, regions, ecosystems and habitats (Hooper *et al.*, 2005; Newbold *et al.*, 2015; Isbell *et al.*, 2018).

Introductions and extirpation of species often occur as a result of human drivers. This can lead to an increased species turnover and possible shifts in ecosystem functionality (Rahel, 2002; Sax and Gaines, 2003). The local community assembly in ecosystems is determined by several factors that can be viewed as a series of filters determining which species that can exist in an ecosystem (Poff, 1997). The filters can be divided into three groups. First, biogeographical filters that limit the dispersal and distribution of species that operate on a larger temporal and spatial scale. Second, physiological filters that limit the abiotic niche space due to e.g. temperature variation. Third, biological filters that limit the biotic niche space due to e.g. interspecific- and intraspecific competition (Tonn, 1990; Tonn *et al.*, 1990). If the conditions for one or more filter changes, or anthropogenic activity removes one or more filter, non-native species can expand their range to new ecosystems. When non-native species successfully spread and establish in new ecosystems, the whole ecosystem may experience fluctuations (Menge and Olson, 1990). This includes food web restructuring, and a switch from top-down to bottom-up control or *vice versa* (Cryer, Peirson and Townsend, 1986; Bergstrand, 1990).

Freshwater ecosystems are particularly vulnerable to species turnover caused by human translocation. Several freshwater fish species are currently expanding their range at levels previously not possible due to anthropogenic translocations (Carpio *et al.*, 2019). Additionally, warming temperatures in freshwater ecosystems can lead to cold-water species having their available habitat space restricted, as well as changed flow regimes, both of which can lead to local species extirpations (Meyer *et al.*, 1999; Hering *et al.*, 2010; Comte *et al.*, 2013; Schneider *et al.*, 2013). On a global scale, freshwater ecosystems are experiencing a much larger decline in native biodiversity than even the most degraded terrestrial ecosystems. A significant driver of this is the introduction of non-native species, leading to species turnover (Dudgeon *et al.*, 2006; Strayer and Dudgeon, 2010).

Identifying patterns in and causes of species turnover is vital for conservation and management of freshwater ecosystems (Harrison, Ross and Lawton, 1992; Darwall and Vié, 2005). Whilst they make up less than 1% of Earth's surface, freshwater ecosystems contribute a disproportionately large amount to Earth's species richness, holding roughly 40% of all described fish species (Dudgeon *et al.*, 2006). Introduction and extirpation of freshwater fish species often occur as a result of human drivers (Cambray, 2003; Gozlan *et al.*, 2010). Knowledge on species turnover and factors driving this is limited since we lack adequate time series on the necessary spatial and temporal scales (Vellend *et al.*, 2017; Cardinale *et al.*, 2018). At the same time, this is seen as vital knowledge in order to understand and mitigate threats to freshwater biodiversity and ecosystem services. Obtaining a large scale historical and present data set can improve our knowledge on the direct and indirect drivers leading to changes in community composition in freshwater ecosystems (Jackson, Peres-Neto and Olden, 2001).

Here I study species turnover on a century time scale for lacustrine freshwater fish communities in the densest human-populated area of Norway. I utilized a unique opportunity raised by lake freshwater fish species inventories collected at the onset of the 20th century, by matching it with a modern resurvey of the same species inventory collected in 2019.

South-eastern Norway's terrestrial landscape has a spatial heterogeneity with distinct regions. It ranges from coastal areas with deciduous forest, to alpine areas and remote coniferous forest (Čermák *et al.*, 2017). At the same time, it is the most urbanized area in Norway where the greatest anthropogenic changes have happened in the last century (Helle *et al.*, 2006). Both the abiotic and biotic frame has changed greatly on both temporal and spatial scales. This makes it a suitable system for studying how humans affect species turnover. The study system has experienced physical, chemical and biological changes during the last century that could have impacted freshwater fish communities (Hesthagen, Sevaldrud and Berger, 1999; Tammi *et al.*, 2003). Most of these anthropogenic changes involve factors, such as human translocation of native species, increased human population, acidification, introductions of non-native species, land use change, runoffs from the terrestrial landscape and damming (Rask, 2000). However, the interactions among these drivers and their spatial configurations are not fully understood (Carpenter, Stanley and Vander Zanden, 2011). Changes in freshwater fish communities may lead to unwanted consequences beyond just species conservation and changing community structure. These changes can affect trophic cascades, which in turn can affect essential services such as drinking water quality (Jeppesen *et al.*, 2000; Olden *et al.*, 2004).

1.2 Research objectives

Here I aim at identifying changes in lacustrine fish communities on a century time scale in south-eastern Norway, and which anthropogenic and natural factors contribute to the observed changes. This main objective will be answered by quantifying species turnover and spatial variation of such. I will quantify which factors that contribute to the species turnover by identifying regional differences, if any, and characteristics that lead to community composition changes.

2. Methods

The methodological approach was to combine historical large scale freshwater fish inventory data (Huitfeldt-Kaas, 1918) with a contemporary freshwater fish inventory survey. The geographical range of the contemporary survey was restricted to south-eastern Norway. I chose this region of Norway due to logistic and time limitations. The number of lakes within the different regions of Norway was a limiting factor on which the selection of this region was based. The data set containing occurrence status of freshwater fish species at individual lake level was combined with environmental variables to identify natural and anthropogenic factors influencing temporal changes in community composition.

2.1 Study system

The study system consisted of freshwater lakes in south-eastern Norway, located between 58.5 and 61.4 degrees latitude and 9.0 and 13.0 degrees longitude (figure 1). The lakes were found in 44 different water drainage basins, here defined as a region inside which all freshwater lakes drain to the same marine outlet.

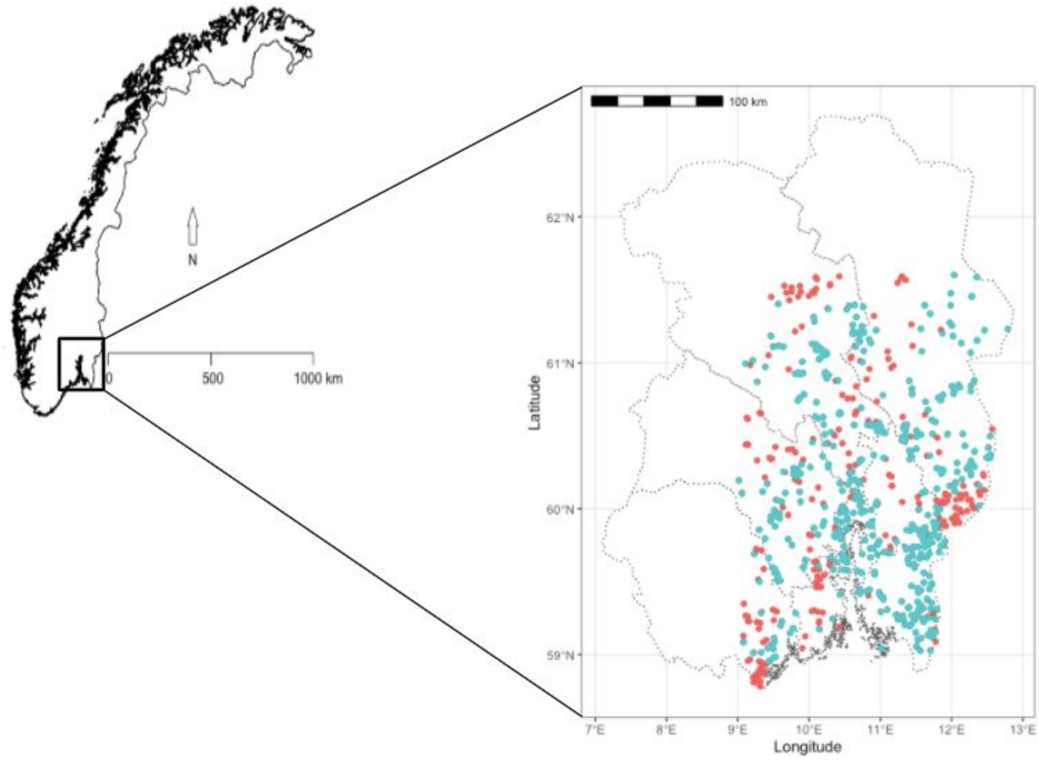

Figure 1. Maps showing the geographical extent of the study system. Western limit 9°E, eastern limit Norway-Sweden border, southern limit is the coastline and northern limit is 61.35°N. Blue circles indicate lakes surveyed both in 1918 and 2019. Red circles indicate lakes surveyed in 1918 but where information on fish species inventory was not obtainable in 2019.

South-eastern Norway's terrestrial landscape has profound spatial heterogeneity with regard to the landscape characteristics, ranging from coastal areas with deciduous forest to alpine areas and remote coniferous forest. The study system has several distinct mountainous and valley areas dividing the study system into discrete regions. These landscape formations were formed and created during the last glaciation, which abruptly divides the landscape into distinct water drainage basins.

Though the majority of Norwegian lakes are typically species-poor in regards to freshwater fish, lakes in south-eastern Norway generally have the highest species richness counts (Sandlund and Hesthagen, 2011). This is likely a product of colonisation from large freshwater bodies which were present after the last glacial maximum (Refseth *et al.*, 1998). As a result of these immigration pathways, many species not commonly found elsewhere in

Norway are present in Norway's south-east. The study system is also located in one of the most densely human-populated regions in Norway, with the population increasing drastically over the last century. Resulting in a relatively high level of anthropogenic disturbance (figure 2), compared to the rest of the country (Venter *et al.*, 2016).

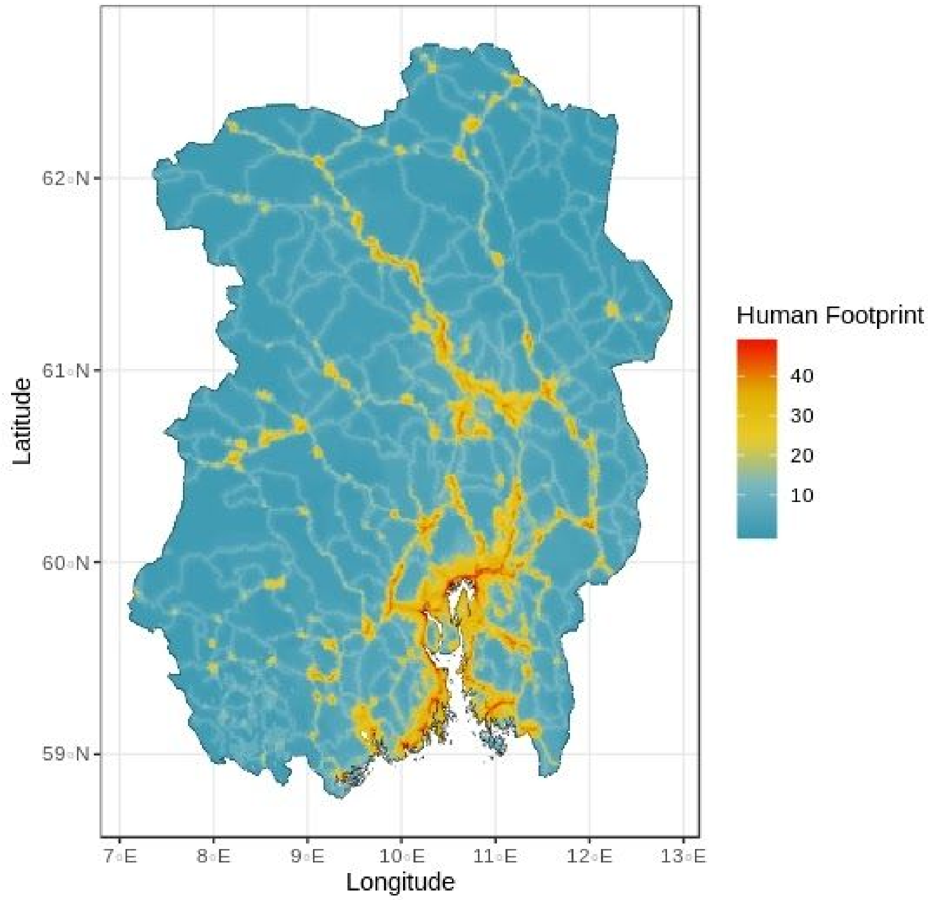

Figure 2. Heatmap showing levels of anthropogenic disturbance within the system. This is represented by the Human Footprint Index, an index which combines eight different human variables, including population density, nearby roads, crop land and built-up land.. Darker red color indicates a higher human footprint, which means that those areas have higher human presence and pressures.

2.2 Historical data collection

Historical data for the study system was obtained from Huitfeldt-Kaas' "Ferskvandsfiskenes utbredelse og indvandring i Norge : Med et tillæg om krebsen" (translation: The Range and Introduction of Freshwater Fish in Norway: With an Attachment on Crustaceans") (Huitfeldt-Kaas, 1918). The original individual lake inventory data was collected by

Huitfeldt-Kaas between 1902 and 1917. He mainly used questionnaires that were sent to local police stations and distributed to local fishermen. The fishermen were locals with good knowledge about freshwater fish species presence in their (former) administrative unit across Norway. The questionnaires consisted of questions about occurrence status for different fish species, with additional questions on establishment means for all species. Huitfeldt-Kaas also supplemented some information through personal travels. The survey information he received back consisted of individual lake fish inventories. The book consistently lists one species at a time. It then lists all municipalities within a county with one or more lakes where that species occurred. Lastly, all lakes within a municipality where that species occurred are listed. All information was later published.

The book by Huitfeldt-Kaas was transcribed and digitized between June 2018 and February 2019. The transcription process involved matching historical lake names with current lake names. Only historical lakes that could be matched with lakes present in The Norwegian Water Resources and Energy Directorate's lake database ("innsjødatabasen") were transcribed and digitized. For details on digitization and data quality checks see dataset metadata (Finstad and Poppe, 2019).

2.3 Present data collection

629 lakes from Huitfeldt-Kaas (1918) were included in the resurvey between June and December 2019 through an interview survey with informants consisting of local stakeholders and managers. In addition, information was gathered through searches in grey-literature and online sources. Details on the data-collections can be found in Poppe et al. (2020). In the following, I give a brief summary.

The informants were individuals primarily involved with volunteer work in local hunting- and fishing associations in one or more of the 103 municipalities that constituted the study system. All informants were first contacted by a standardized email. Informants were given a brief background for the purpose of the project and asked if they knew which freshwater fish species were present in a relevant subset of lakes previously surveyed by Huitfeldt-Kaas. 197 informants were contacted, of which 71 responded. 26 further informants were successfully contacted upon referral from the original 71. Of these 97, four were interviewed in person, and 20 gave information over the phone. From the 97 surveys, I was able to obtain presence/absence data for 453 lakes.

Information on fish inventory data through grey literature was obtained for 77 of the lakes within the study area. Reports, surveys and research from government bodies, independent research institutes and commons managing, and fishing licenses sales were included (see table S1).

2.4 Data analysis

The final data set consisted of 453 lakes where information on freshwater fish inventory existed both for the historical and contemporary dataset.

Due to species not being included in either historical or contemporary surveys, information on brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), goldfish (*Carassius auratus*), pumpkinseed (*Lepomis gibbosus*), gudgeon (*Gobio gobio*) and European flounder (*Platichthys flesus*) were excluded from the final dataset. Brown trout was absent from the historical dataset, and as such excluded. Brook trout was excluded since it is most commonly found in lotic ecosystems, and hence information on lake occurrence likely unreliable. The European flounder lives most of its life in marine ecosystems and migrate into lotic ecosystems. Newly arrived non-native species were also excluded from the study, due to their uncertain occurrence status in Norway. In addition, some species are unlikely to be correctly recognized by informants and hence treated as one species. This latter group included river (*Lampetra fluviatilis*) and brook lamprey (*Lampetra planeri*), and the two *Cottus* species (alpine and european bullhead).

To quantify the effect of local abiotic factors on overall species turnover, I created three different turnover metrics for each individual lake. These included i) number of species extinctions, ii) number of species introductions and iii) aggregated turnover (the sum of i and ii) for the period between the historical and contemporary data collection. These were then represented spatially through the use of hexagons with width of 4.75 kilometres showing average values for each metric for all lakes whose centroid was found in that hexagon. Similar studies have often used a proportional analysis to look at turnover as a percentage of the total species richness (Griffiths, 1997). However the low freshwater fish species richness in Norwegian lakes render such parameters uninformative in my study system.

I then obtained four variables describing environmental variables in order to identify potential drivers behind my turnover metrics (summarised in table 1). These were average lake elevation, lake area, shoreline complexity index (henceforth referred to as SCI) and Human Footprint Index (henceforth referred to as HFI). The SCI is the ratio between the shoreline length and the circumference of a circle of area equal to the lake. Lakes with a circular shape therefore have a smaller SCI value than those with a more complex shape (Wetzel, 2001). The HFI is a point score made up of eight combined human impact variables which approximate the level of human pressure on nature, assigned to cells measuring one square kilometer (Venter *et al.*, 2016). HFI was taken for the cells in and including a one kilometre buffer around the edge of the lake, as previous research has suggested that human activity in the immediate vicinity of freshwater sites is more likely to affect species introductions that activity up or downstream (Leu, Hanser and Knick, 2008; Chapman *et al.*, 2020). Lake surface temperature was initially included, however this was highly correlated with elevation and the decision was made to remove temperature, as elevation would likely act as an additional proxy for other factors influencing distribution, including downstream connectivity and water chemistry, which I did not have access to. As the distribution of lake area and shoreline complexity were right skewed, they were both log-transformed to improve convergence. All variables were scaled to a mean of zero and a standard distribution of one.

Table 1. Environmental covariates influencing likelihood of non-native species' establishment throughout Norwegian freshwater lakes. Table also includes their biological interpretation and their unit of measurement.

Name	**Description**	**Biological Interpretation**	**Units**
Area	Total surface area of lake	Larger lake has more available habitat space and niche breadth	Square kilometres
Human Footprint Index	Index comprising 10 different variables which calculates impact of human activity (Venter et al., 2016)	Higher HFI increases chances of local human introduction	Unitless scale from 1-50
Elevation	Average lake elevation above sea level	Proxy for accessibility, both for humans and fish, as well as for temperature	Meter above sea level
Shoreline complexity	Index describing complexity of lake edge. $SC = \frac{P}{2000\sqrt{\pi A}}$	Increased shape complexity has been suggested to increase species richness	Unitless

Whilst a spatial component may have been relevant, the manner of fish dispersal means that the most appropriate introduction of a spatial hierarchy would have been taking separate drainage basins. This proved unhelpful, as the majority of the 453 lakes were located within one drainage basin, resulting in too much spatial bias to justify the introduction of a spatial variable into the model.

I used a logistic regression with the model $Turnover \sim \sum_{i=1} x_i$, where x_i represents my four predictor variables. I fit the model with a Bayesian approach, utilising the greta package (Golding, 2019) in R (Version 3.5.2) (R core Team, 2019). Monte-Carlo Markov Chain (MCMC) sampling was done using 500 samples on four chains, giving a total of 2000 samples, with a burn-in of 500 samples on each chain. Parameter effects were considered to be significant if their 95% credible intervals did not intercept with zero.

The model criteria for my model assumptions were met. Meaning that there were no spatial autocorrelation patterns for the environmental covariates used in this analysis. The covariates showed low degree of collinearity ($r < 0.37$), except for temperature and elevation ($r = 0.95$). Temperature where accordingly removed as a covariate, as explained above.

Table 2. Freshwater fish species included in the study listed alphabetically according to their Norwegian vernacular name. English vernacular names are those most commonly used in English. Family is the family each species falls under. Scientific name is the species Latin name. Presence 1918/2019 is the number of lakes in which species were present in 1918 versus 2019. Establish means indicates if a species is native or introduced to Norway. Year of introduction is the year a species was first recorded in Norway if introduced. An Na for 'presence' indicates that the species either lives in lotic environments, or it has been introduced or gone extinct after 1918. Na for 'year of introduction' indicates that the species is native to Norway.

Norwegian vernacular name	English vernacular name	Family	Scientific name	Presence 1918/2019	Establish means	Year of introduction
Abbor	Perch	Percidae	*Perca fluviatilis*	342/406	Native	Na
Asp	Asp	Cyprinidae	*Aspius aspius*	1/3	Native	Na
Bekkeniøye	Brook lamprey	Petromyzontidae	*Lampetra planeri*	14/19	Native	Na
Bekkerøye	Brook trout	Salmonidae	*Salvelinus fontinalis*	Na/Na	Introduced	1883
Brasme	Common bream	Cyprinidae	*Abramis brama*	52/57	Native	Na
Dvergmalle	Brown bullhead	Ictaluridae	*Ameiurus nebulosus*	1/4	Introduced	1890
Elveniøye	River lamprey	Petromyzontidae	*Lampetra fluviatilis*	14/19	Native	Na
Flire	Silver bream	Cyprinidae	*Blicca bjoerkna*	19/25	Native	Na
Gjedde	Pike	Esocidae	*Esox lucius*	180/220	Native	Na
Gjørs	Zander	Percidae	*Sander lucioperca*	6/10	Native	Na
Gullbust	Common dace	Cyprinidae	*Leuciscus leuciscus*	5/13	Native	Na

Gullfisk	Goldfish	Cyprinidae	*Carassius auratus*	Na/Na	Introduced	ca. 1870
Harr	Grayling	Salmonidae	*Thymallus thymallus*	10/14	Native	Na
Hork	Ruffe	Percidae	*Gymnocephalus cernuus*	22/51	Native	Na
Hornulke	Fourhorn sculpin	Cottidae	*Myoxocephalus quadricornis*	2/2	Native	Na
Hvitfinnet Steinulke	European bullhead	Cottidae	*Cottus gobio*	9/10	Native	Na
Kanadarøye	Lake trout	Salmonidae	*Salvelinus namaycush*	0/3	Introduced	1971-1972
Karpe	Common carp	Cyprinidae	*Cyprinus carpio*	0/2	Introduced	1685
Karuss	Crucian carp	Cyprinidae	*Carassius carassius*	18/34	Introduced?	1500-1600
Krøkle	European smelt	Osmeridae	*Osmerus eperlanus*	30/42	Native	Na
Lagesild	Vendace	Salmonidae	*Coregonus albula*	19/18	Native	Na
Lake	Burbot	Lotidae	*Lota lota*	64/53	Native	Na
Laks	Atlantic salmon	Salmonidae	*Salmo salar*	6/6	Native	Na
Lakseabbor	Blackbass	Centrarchidae	*Micropterus salmoides*	1/0	Introduced (extinct)	1880-1890
Laue	common bleak	Cyprinidae	*Alburnus alburnus*	68/56	Native	Na
Mort	Roach	Cyprinidae	*Rutilus rutilus*	139/146	Native	Na
Nipigget stingsild	Ninespined stickleback	Gasterosteidae	*Pungitius pungitius*	4/8	Native	Na
Regnbueørret	Rainbow trout	Salmonidae	*Oncorhynchus mykiss*	0/2	Introduced	1902
Røye	Arctic Char	Salmonidae	*Salvelinus alpinus*	64/66	Native	Na
Sik	Whitefish	Salmonidae	*Coregonus lavaretus*	73/95	Native	Na
Stam	Chub	Cyprinidae	*Leuciscus cephalus*	4/5	Native	Na
Steinsmett	Alpine bullhead	Cottidae	*Cottus poecilopus*	9/10	Native	Na

Suter	Tench	Cyprinidae	*Tinca tinca*	0/20	Introduced	ca. 1800
Sørv	Common rudd	Cyprinidae	*Scardinius erythrophthalmus*	22/51	Native	Na
Trepigget stingsild	Three-spined stickleback	Gasterosteidae	*Gasterosteus aculeatus*	20/27	Native	Na
Vederbuk	Ide	Cyprinidae	*Leuciscus idus*	12/12	Native	Na
Ørekyte	Minnow	Cyprinidae	*Phoxinus phoxinus*	168/152	Native	Na
Ål	European eel	Anguillidae	*Anguilla anguilla*	94/50	Native	Na

3. Results

3.1 Species richness

Fish were recorded ‘present’ in all 453 lakes surveyed in both time periods. Median species richness increased from 3 (mean 4.01 ± 3.28 SD) in 1918 to 4 (mean 4.56 ±3.42 SD) in 2019. Temperate freshwater fish species, especially cyprinids, were the most common group of freshwater fish species observed over both sampling periods (see figure 3). Perch was the most common species observed both in 1918 and 2019, and perch occurred in more than half of the lakes in both time periods.

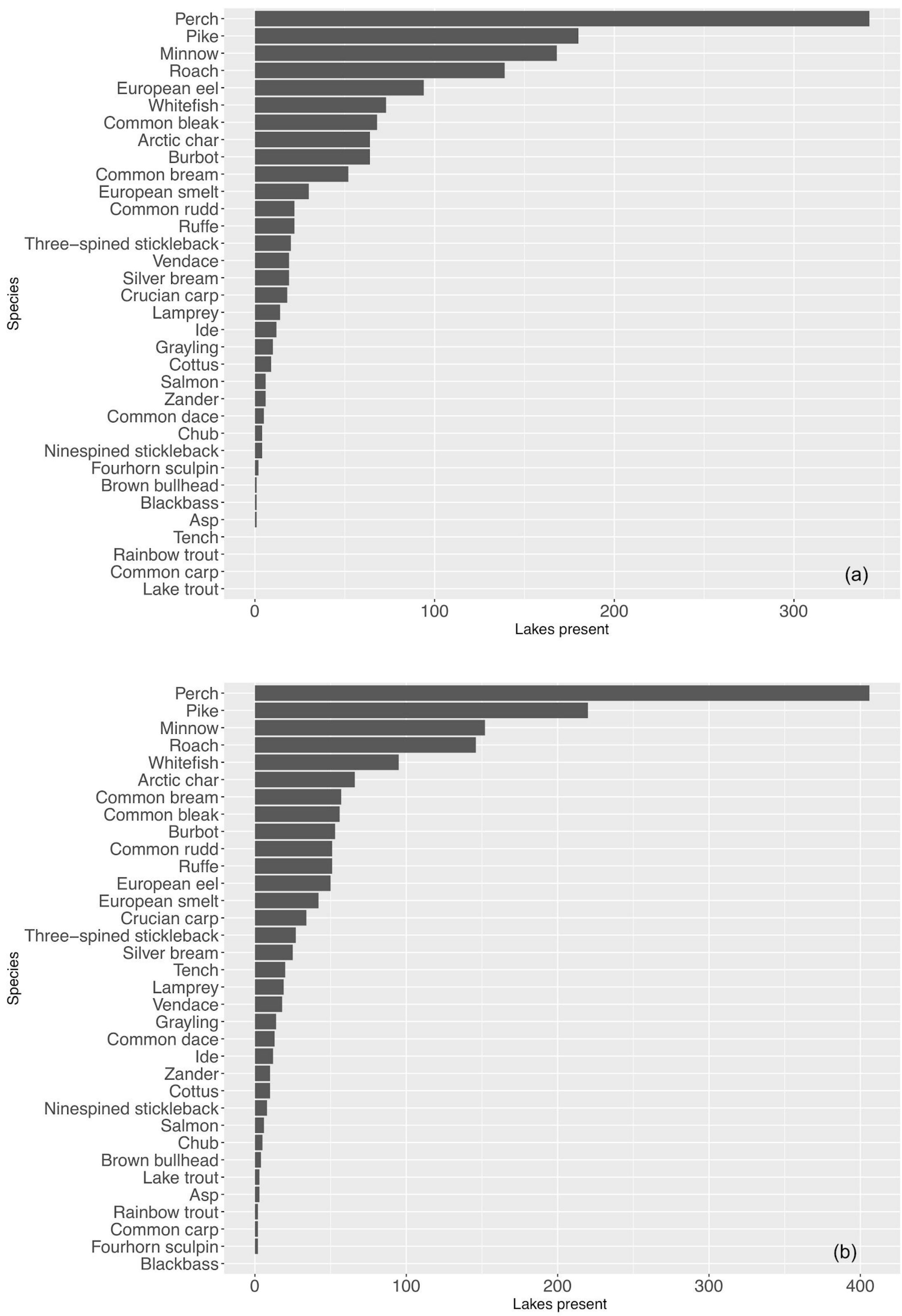

Figure 3. Bar charts showing the number of lakes each freshwater fish species was present in south-eastern Norway as observed in 1918 (a) and 2019 (b).

Species richness was highest in the south-eastern part of the region both in 1918 and 2019 (figure 4). This corresponds to a higher species richness around the most densely populated areas (see figure 2). This is illustrated in figure 4.

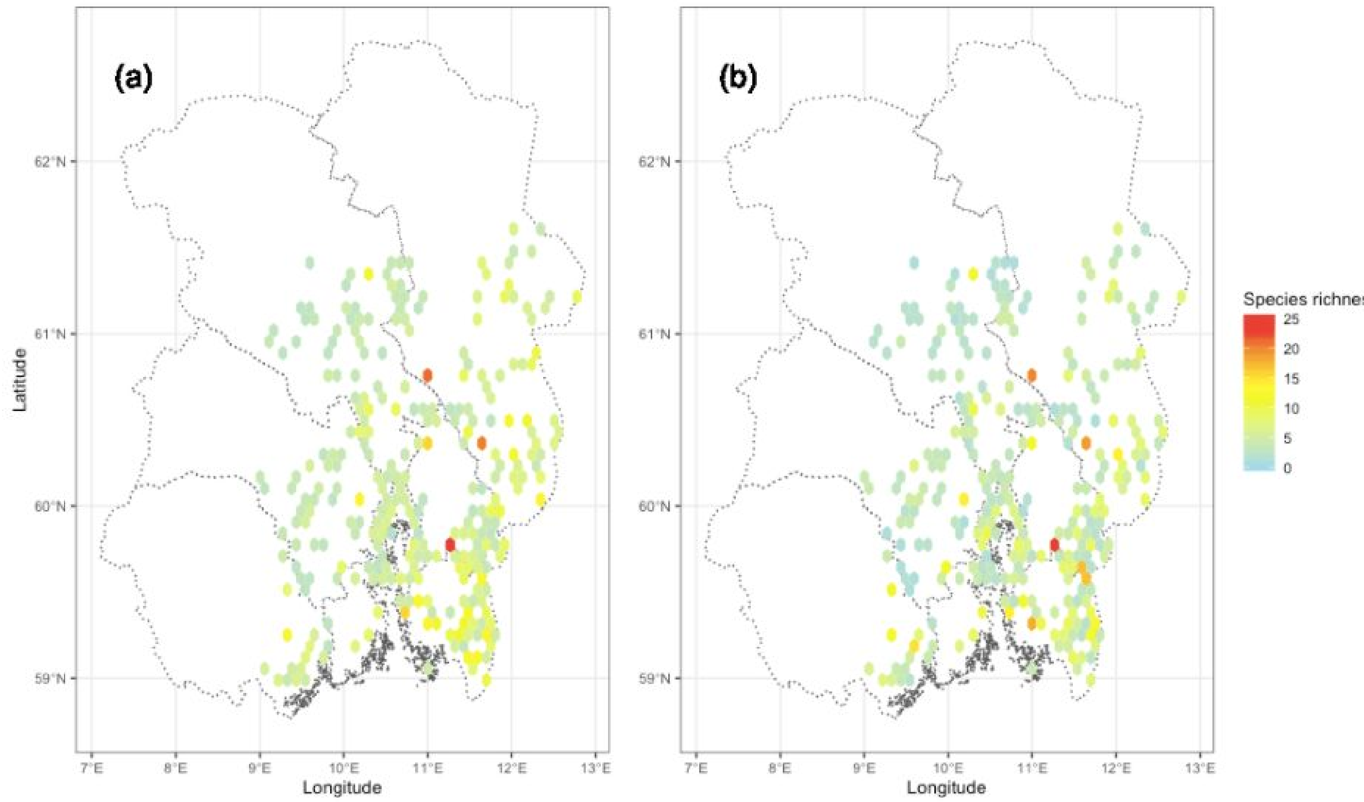

Figure 4. Heatmaps showing the freshwater fish species richness for individual lakes in south-eastern Norway as observed in a) 1918 and b) 2019.

The number of introductions for individual lakes ranged between 0 and 12 species. Median introductions for all lakes were 1, with mean 1.39 (± 1.57 SD). The number of introductions into individual lakes was greatest in the most densely populated areas, and in the south-eastern region. The number of extinctions for individual lakes ranged between 0 and 6 species. Median extinctions for all lakes were 1, with mean 0.84 (± 0.97 SD). The number of extinctions was low throughout the study system. Generally, lakes experiencing the highest number of extinctions were located in the south-eastern region and in the most densely human populated areas of the study system. There were also some spatial outliers for both introductions and extinctions (see figure 5a and 5b).

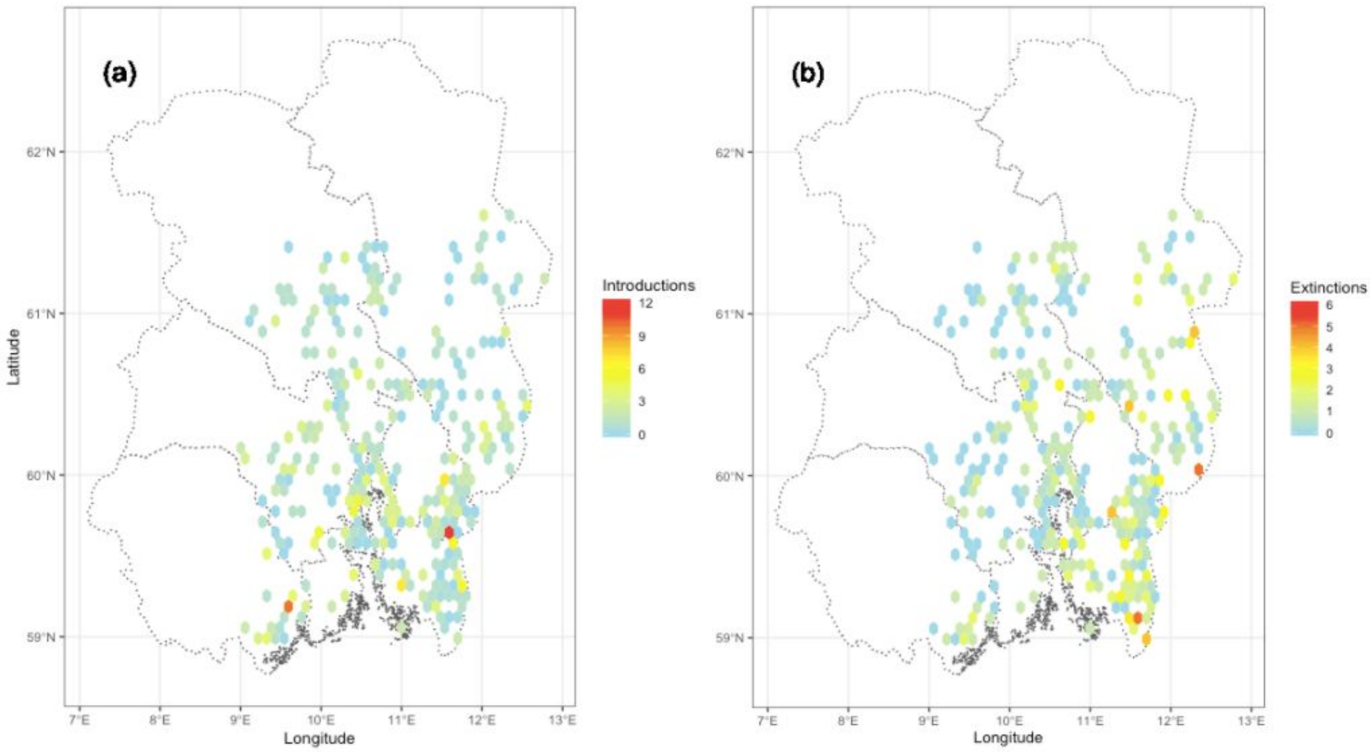

Figure 5. Heatmaps showing the number of a) introductions and b) extinctions of freshwater fish species at individual lake level in south-eastern Norway between 1918 and 2019.

Present individual lake species richness was still greatest along the south-eastern border of the study system, and in the densest human populated areas. Total species turnover, the number of introductions plus extinctions, ranged between 0 and 12 for individual lakes. Median total turnover for all lakes was 2, with mean 2.23 (± 1.76). As with both introductions and extinctions for individual lakes, the total species turnover was also greatest along the south-eastern border of our study system and in the most densely human populated areas (see figure 6).

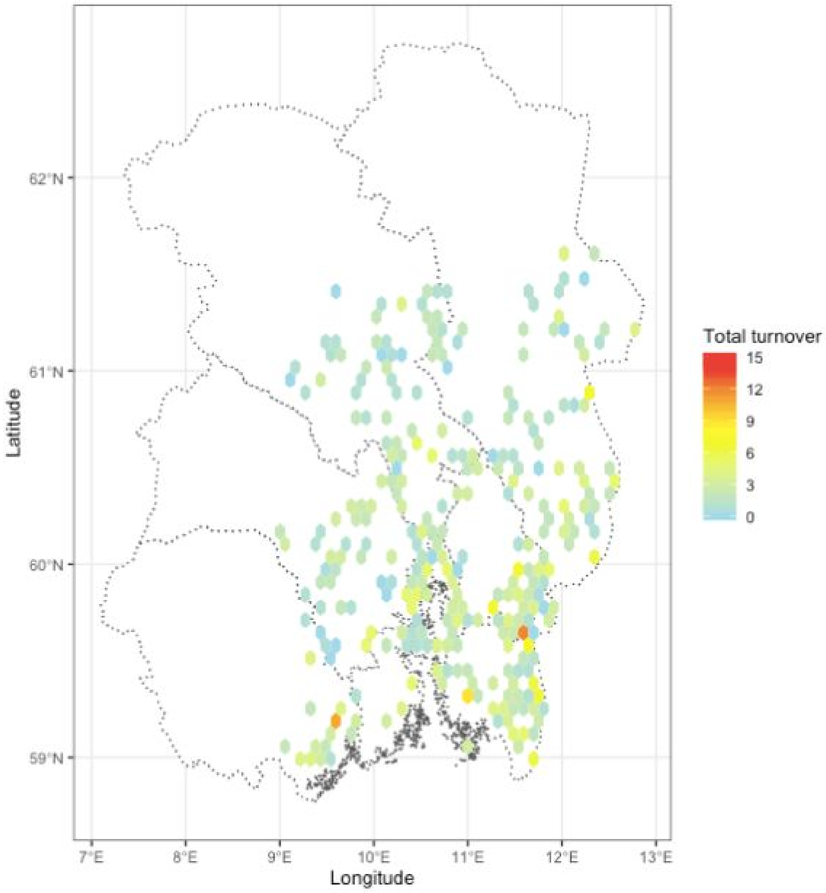

Figure 6. Heatmap showing the total species turnover for freshwater fish at individual lake level between 1918 and 2019 in south-eastern Norway.

Perch, pike and common rudd were the three species with the largest net introductions (introductions minus extinctions) to new lakes between 1918 and 2019. European eel, common bleak and minnow experienced the largest net extinctions in the same time period. While minnow was the species with the largest number of introductions, it also experienced the highest number of extinctions, making its net introduction total relatively low (figure 7a and b).

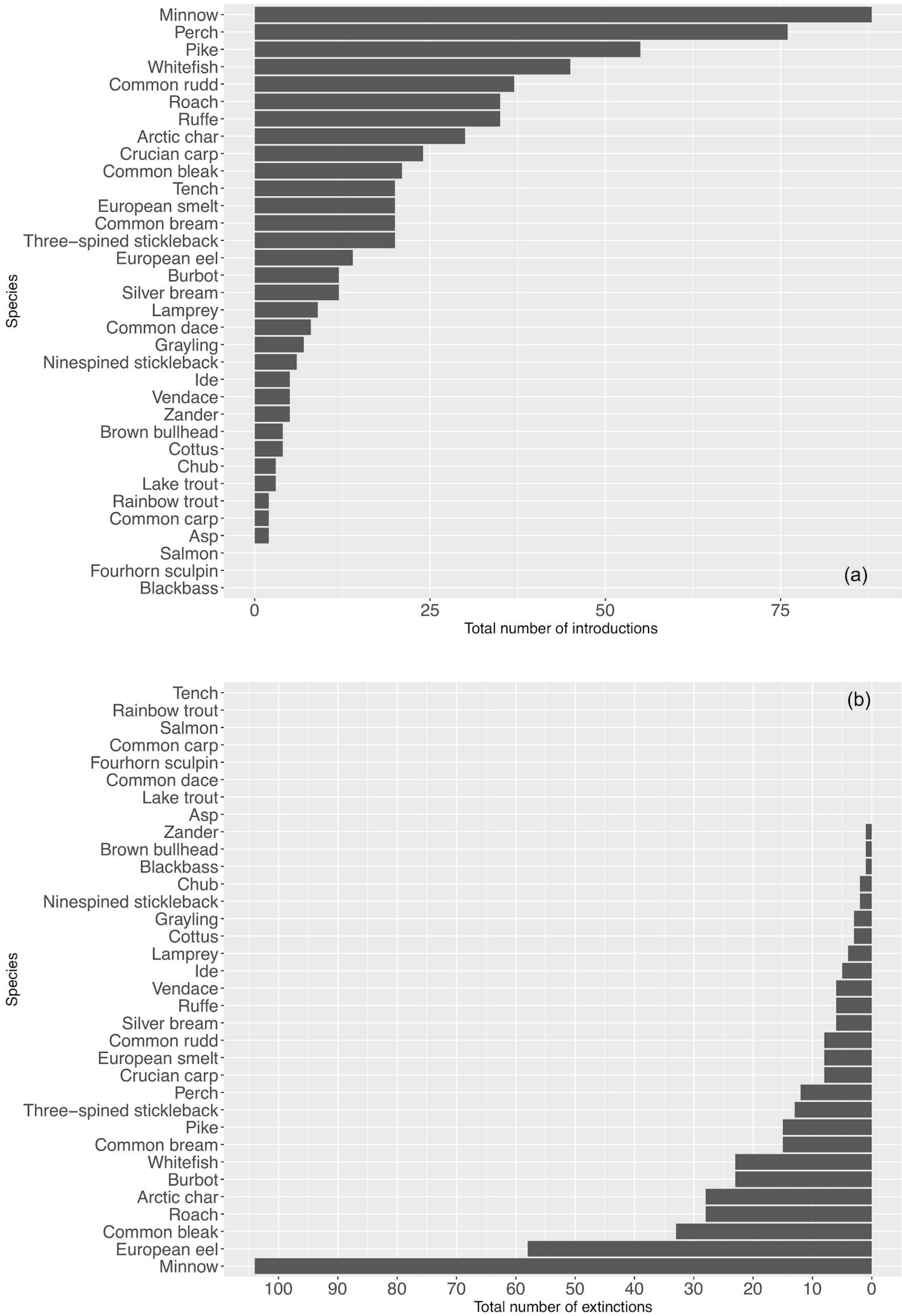

Figure 7. Bar charts showing the number of introduction events (a) and extinction events (b) for each freshwater fish species in south-eastern Norway between 1918 and 2019.

Perch was the species with the largest contribution to species turnover, with a net increase in presences of 64 lakes (76 introductions/12 extinctions), along with pike with a net increase in presences of 40 lakes (55/15), and common rudd with a net increase in presences of 29 lakes (37/8). European eel had the largest negative contribution to species turnover, with a net decrease in presences of 44 lakes (14/58), along with minnow with a net decrease in presences of 16 lakes (88/104), and common bleak with a net decrease in presences of 12 lakes (21/33), as shown in figure 8.

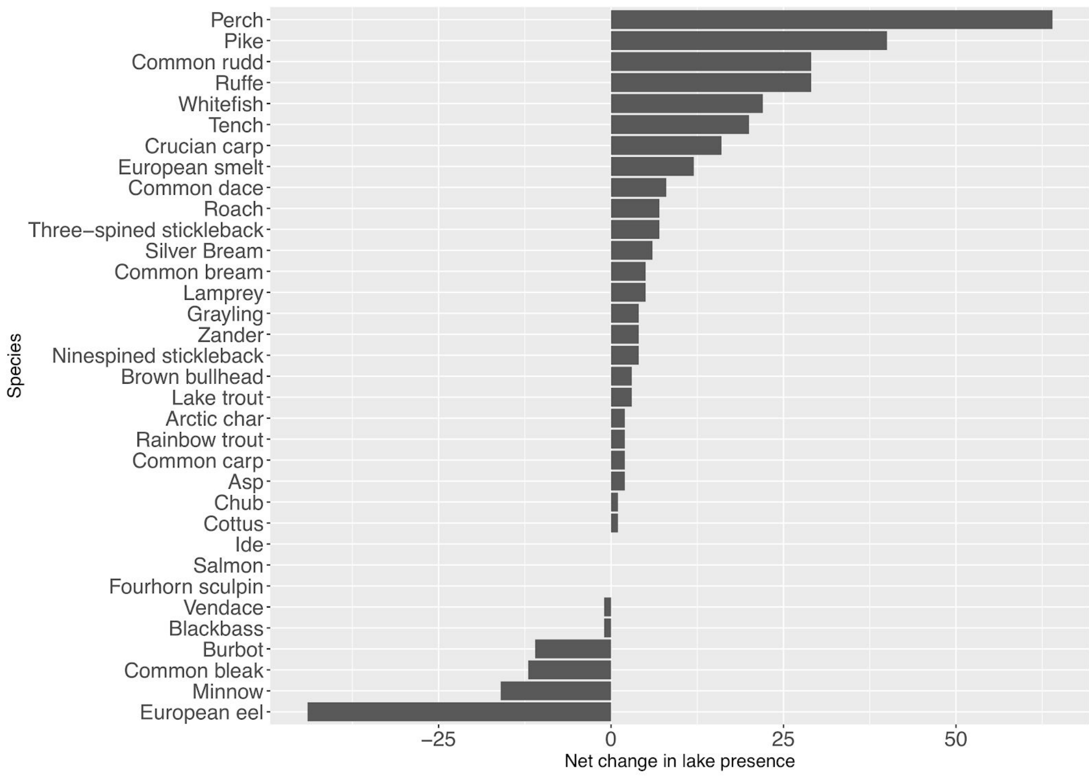

Figure 8. Bar chart showing the net change in lake presence for each freshwater fish species in south-eastern Norway between 1918 and 2019. Negative numbers indicate an overall decrease in lake presence for an individual species between 1918 and 2019.

3.2 Individual species range expansions and contractions

Both perch and pike were much more common and widespread than common rudd in 1918. Still, common rudd experienced the third largest net increase in occurrence from 1918 to 2019. Neither perch or pike showed any spatial patterns for either introductions or extinctions. Common rudd, on the other hand, has a spatial pattern for extinctions, where most of the extinctions are in the south-eastern part of the study system (see figure 9a-c).

As illustrated in figure 9d, extirpation of european eel was higher in the densest human-populated areas of the study system. Minnow was the species experiencing both the largest number of introductions and extinctions, according to my survey. Minnow showed no clear spatial trend for either introductions or extinctions within the study system (see figure 9e). Common bleak was the seventh most common species in 1918, where extirpation was highest and most common in the densest human-populated areas of the study system (see figure 9f).

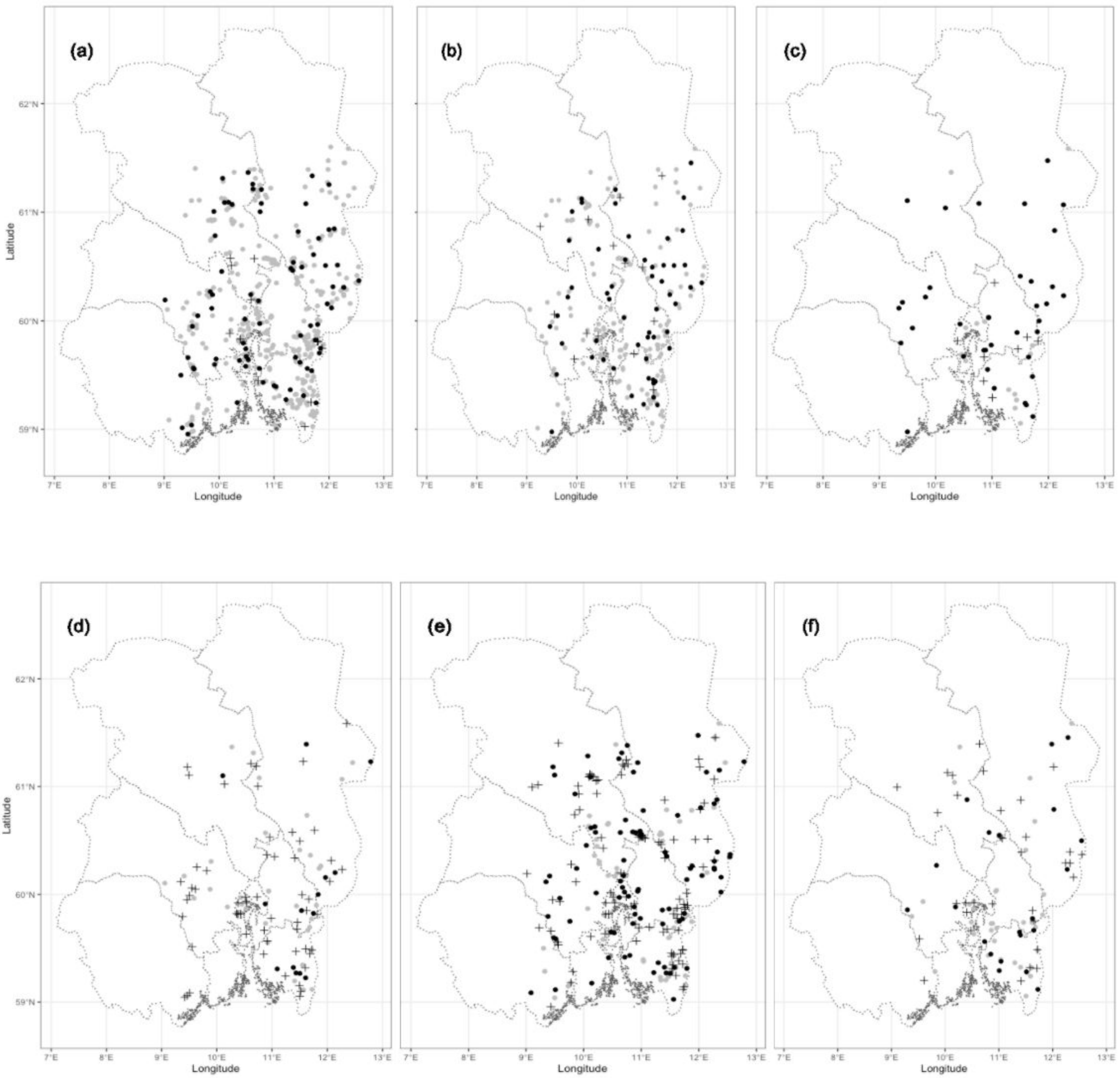

Figure 8. Maps showing the changes between 1918 and 2019 for the three freshwater fish species experiencing the largest net increase and decrease in lake presence in south-eastern Norway. Grey circles represent species presence in 1918 and 2019, black circles represent introductions between 1918 and 2019, cross represents species extinctions between 1918 and 2019. The three species experiencing the largest net increase are; a) perch, b) pike and c) common rudd. While the three species experiencing the largest net decrease are; d) european eel, e) minnow and f) common bleak.

3.3 Effect of anthropogenic and natural environmental covariates on species turnover

Lake area had a significant positive effect on aggregated species turnover, while lake elevation had a significant negative effect (figure 10). SCI also had a significant negative effect on turnover, though this was weaker than that of elevation. The Human Footprint Index (HFI) had no effect on turnover.

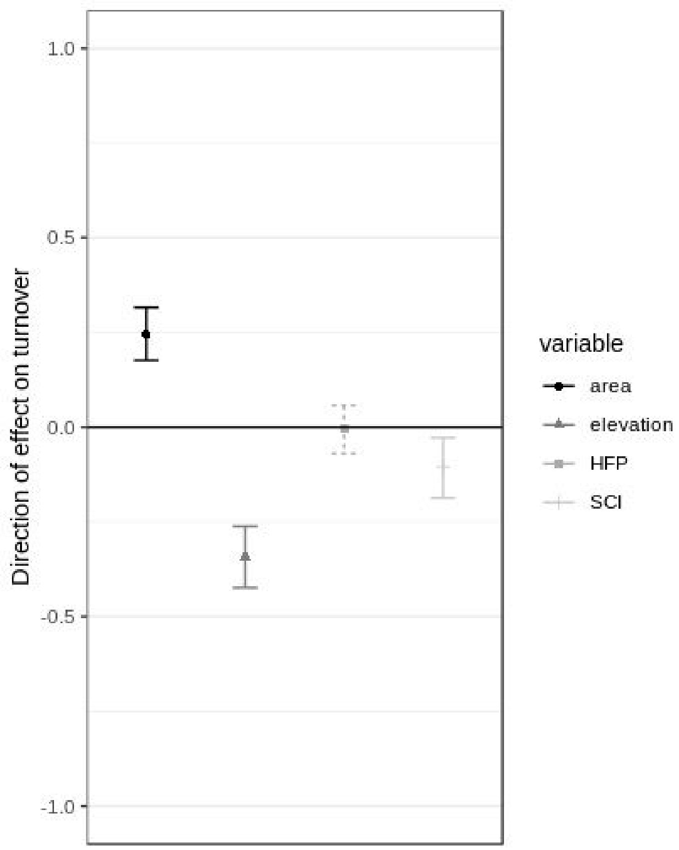

Figure 10. The effect of scaled environmental parameters had on aggregated extinctions and introductions. All 453 freshwater lakes were included for both 1918 and 2019. All 453 lakes are located in south-eastern Norway.

4. Discussion

Identification of both anthropogenic and natural drivers that lead to species turnover is vital in our efforts to understand how species distributions and community composition have changed and will change over the coming decades. Here, I analyse changes in community composition for lacustrine fish communities in south-eastern Norway on a century time scale. To my knowledge, this is the first time a historical data source of this scale has been combined with a modern resurvey. Creating a large scale data set with absence/presence observations on a temporal scale can educate managers on which species that are most likely to expand and contract their range in the future, and which environmental variables contribute to such change This type of study can therefore be a very useful tool.

4.1 Effect of anthropogenic and natural environmental covariates on species turnover

The total species turnover showed a high spatial correlation. The results indicate that the highest turnover has happened in the densest human-populated areas of the study system (figure 2 and 6). This was not reflected in the statistical modelling, where the HFI (human footprint index) was the only non-significant environmental variable according to my analysis.

HFI functions as a proxy for anthropogenic presence and activity. My analysis indicates that higher anthropogenic activity is likely to be a driving force for both introduction and extinction events. This has also previously been demonstrated by earlier studies (Kerr and Currie, 1995; Leprieur *et al.*, 2008; Villéger *et al.*, 2011). Since a high HFI value is a proxy for high anthropogenic presence and pressure, and is largest around the most densely human-populated areas, the observed species turnover is highly correlated with humans. This means that the largest turnover observed, is likely to have occurred in areas with high anthropogenic activity within the study system.

Lake area was the only environmental variable that had a significant positive effect on species turnover. Lakes with a larger area will generally be able to support a higher initial species richness for freshwater fish species. Which allows for a higher species turnover, since there is a larger species pool to take from (Minns, 1989; Amarasinghe and Welcomme, 2002).
Both SCI and lake elevation had a significant negative effect on species turnover, though SCI had a weaker negative effect than lake elevation. SCI and lake area are in many cases interlinked, meaning that larger lakes have a higher shoreline complexity (Kent and Wong, 1982). SCI describes the complexity of lake edges. In turn, a higher SCI value may lead to more niches and a higher proportion of available niche space for non-native species (Eadie and Keast, 1984). If this assumption is true, it means that lakes with a high SCI value most likely have a large lake area and thereby a greater initial species richness and are more prone to a higher species turnover.

Lake elevation had the largest negative effect on species turnover, meaning that lakes at higher elevations have a higher stability in species configurations, compared to lakes at lower elevations. Both historically and in present-day, mountainous lakes have fewer species (Tammi *et al.*, 2003). Even with the low species richness, which may indicate that there are more available niches to exploit, introductions of non-native fish species are low in these lakes. This is in large part due to the poor connectivity between species rich lakes at lower elevation and species poor lakes at higher elevation, and a low mean annual water temperature. Thus, these mountainous lakes are less suitable for temperate fish species. Combined, the connectivity and low mean annual water temperature makes it more difficult for temperate freshwater fish species to immigrate and establish in those lakes. Thus, they very often depend upon anthropogenic translocation to be able to reach high elevation lakes.

The anthropogenic and natural environmental variables included in the analysis of this project are all interconnected and affect species turnover, both positively and negatively. This interconnectedness between the variables is most likely the reason for why HFI showed no significant effect on species turnover. If one goes further back than 1918 and looks at historic settlement patterns and activity in south-eastern Norway, several findings suggest that all environmental variables included in my analysis are related. Historic settlement patterns and activity in south-eastern Norway have always been most prominent along the coastline (Boaz, 1997) and around the large lakes further inland (Bang-Andersen, 1996). Historical human activity has therefore been related to both large freshwater lakes and proximity to the coastline. Since lakes along the coastline are located at lower elevation, and lakes at lower elevation tend to have a larger area, both elevation and lake area may reduce the significance of human activity (HFI) when looking at species turnover. Because larger lakes most likely have a high HFI value means they have a higher probability for introduction and extinction events, and thereby species turnover. But, since larger lakes generally have a high SCI value, this probability may be zeroed out. This is because a high SCI value may lead to more available niche space, enabling niche segregation and therefore the persistence of native species after introduction of non-native species. Lake area, and thereby SCI and elevation, also follow some general trends. The elevation a lake is located at generally dictates the lake area. Lakes at higher elevations generally have a smaller area than lakes at lower elevations (Tammi *et al.*, 2003). As stated above, mountainous lakes usually have a low species richness, which may indicate that there are more available niches to exploit. But, since the connectivity between lakes at higher and lower elevation is poor, freshwater fish rely on humans to successfully immigrate to high elevation lakes. Historic human settlements have been concentrated at lower elevation areas and along the coastline, where fewer settlements means less human impact and thus a lower HFI value, ultimately leading to a smaller species turnover.

The HFI variable is therefore very much related to lake area and lake elevation, and SCI is linked to lake area. All three natural variables are connected to both historic and present human presence and pressure, which is probably why HFI was not significant, even though it is linked to anthropogenic activity and human presence.

Previous studies have shown that large lake area with high anthropogenic pressure can provide for coexistence between species (Hein, Öhlund and Englund, 2014). The species turnover patterns reported here are also consistent with similar studies (Leprieur *et al.*, 2009), meaning that human presence is the most important driver for introduction events of non-native species.

4.2 Species-specific contribution to turnover

The individual species contribution to turnover results align with other current research. Which also have found that perch, pike and many cyprinid species are those species experiencing the largest lake presence increase. Thereby expanding their range to previously inaccessible areas throughout Norway (Hesthagen and Sandlund, 2007). To my knowledge, no previous study has shown this trend to such an extent on a temporal scale.
Of the three species experiencing the largest increase in lake presence since 1918, perch experienced the largest net increase. Perch increase in lake presence shows little to no spatial pattern (figure 9a). Meaning its increase in lake presence was uniformly distributed throughout the study system. The same applies for pike. Both perch and pike are seen as the two most commonly translocated species in Norway. With historical sources stating that this began before 1918 (Huitfeldt-Kaas, 1918; Hesthagen and Sandlund, 2012).

In contrast to perch and pike, common rudd's increase in lake presence shows a larger degree of spatial pattern. Common rudd was not a widespread species in 1918, mainly confined to coastal lakes within the study system (Huitfeldt-Kaas, 1918). Since common rudd mainly depends on human translocation to successfully establish in new lakes, its success and thereby increase in lake presence is therefore likely only due to human translocation (Walseng, Hesthagen and Skjelbred, 2020). Common rudd is known to be used as live bait when fishing for both pike and european eel (Nilssen, 2009; Hesthagen and Sandlund, 2012). Common rudd's increase in lake presence in the study system is therefore most likely due to recreational fishers.

Of the three species experiencing the largest decrease in lake presence, european eel experienced the largest net decrease. Since the 1970s, european eel has experienced a decrease in populations, recruitment and geographical range (Bornarel *et al.*, 2018). It has been listed as a critical endangered species by the International Union for Conservation of Nature (IUCN) and included on their Red List of Threatened Species in 2008 (Jacoby and Gollock, 2013). The results showed a spatial extinction trend for european eel. Since it is a catadromous species, it migrates between its spawning grounds at sea and feeding grounds in coastal lakes, brackish water and coastal waters (van Ginneken and Maes, 2005). European eel was historically restricted to coastal and lower altitude lakes in the study system. Other studies have reported similar findings, that european eel is mainly restricted to lakes occurring at lower altitudes and mostly in lakes less than 87 kilometres from the coastline (Foldvik *et al.*, 2019). The decrease in european eel populations in south-eastern Norway is not fully understood, but factors that may contribute to the decline are direct exploitation, pollution, migration barriers, introduced species and parasites and other anthropogenic factors (Geeraerts and Belpaire, 2010; Durif, Gjøsaeter and Vøllestad, 2011; Larsen *et al.*, 2015).

Minnow was the third most common species in 1918 and 2019 according to my results. Minnow, which belongs to the cyprinids, originally had a limited presence in Norway at the beginning of the 20th century (Huitfeldt-Kaas, 1918). According to previous studies, minnow has increased its presence rapidly and it is now a common and widespread species in Norway (Hesthagen and Sandlund, 1997; Vøllestad *et al.*, 1999; Museth *et al.*, 2007). Minnow's increase in lake presence reported from other studies contradicts my finding. The analysis shows that minnow had both the highest number of extinctions and second largest net decrease in lake presence between 1918 and 2019. Minnow also had the highest number of introduction events, but still experienced the second largest net decrease in lake presence. There can be several explanations for this discrepancy between results, but two possible explanations stand out. First, informants contributing to the present survey for this project were unaware of minnow's presence. This could either be due to the taxonomic similarities between minnow and juvenile brown trout. Or simply that informants have not observed minnow in individual lakes, but it is still present. This leads to false negatives when information was systemized and recorded. Second, since this is a study spanning more than a century and minnow is very sensitive to changes in water chemistry and water quality (Larsen *et al.*, 2007), it is possible that minnow has been extirpated from lakes during the last century without being detected. This is due to the temporal scale other studies have used, which is either much shorter or non-existing.

4.3 Patterns in species richness

The increase in both median and mean species richness for freshwater fish species in the last century reported in this study aligns with findings from similar studies (Hesthagen and Sandlund, 2007). 25 of 34 species experienced a net increase in lake presence from 1918 to 2019. The largest increase in species richness happened in areas with the highest HFI values (figure 2). Colonisation of freshwater fish into Norway began in the south-east from large freshwater bodies, which were present after the last glacial maximum (Refseth *et al.*, 1998). Especially temperate species in Norway have a historical presence in the south-east and are not found elsewhere in Norway, where lakes further inland have a smaller proportion of temperate and less-mobile species. This indicates high congruence between colonization events and species richness patterns in Norwegian lakes at the beginning of the last century. This pattern in species richness is not as evident today as in 1918. While some regions have similar high species richness across study periods, my findings show that the overall species richness is more homogeneously distributed throughout the study system at present, especially in areas where human population-density has increased (figure 4). The increase in species richness can therefore be due to human population increase, which is one of the main causes for the increase in mean and median species richness across the study system.

From an ecological perspective, this increase in species richness may not necessarily emerge as a positive effect for native species. Lack of population data means it is currently not possible to assess whether species in individual lakes experience population decreases with increased species richness due to introduction of new species. However, other studies have shown that increased species richness and introduction of new (predatory) species can have negative consequences for native populations, especially salmonids (Spens, Englund and Lundqvist, 2007). At the same time, studies have shown a dependency between lake area and mean annual temperature: cold-water prey fish species and temperate predator fish species can coexist in small lakes if the mean annual temperature is low, but only to a certain threshold temperature (Öhlund, 2012). For lakes with a larger area, coexistence between prey and predatory species is more common. The most likely explanation for this coexistence is that larger lakes have both broader niche space and more available habitat to utilize, making them less affected by predation and thereby extinction (Hein, Öhlund and Englund, 2014).

The overall increase in median and mean species richness for freshwater fish species in lakes within my study system is most likely due to the increase in human presence and pressure. Areas have become more densely populated, which has led to higher anthropogenic activity in the last century, therefore contributing to increased species richness. My results also show that there was a larger increase in median and mean introductions than median and mean extinctions. The low initial species richness throughout the study system accounts for the observed increase in species richness, since individual lakes most likely have available niches to exploit for non-native species.

4.4 Methodological limitations

In order to replicate the original study design from 1918 (Huitfeldt-Kaas, 1918), as well as obtain a sufficient sample size (number of lakes), the contemporary dataset was also based upon interview surveys using informants. The limited time available for conducting the survey made it difficult to get more than one informant per lake. The same applies for lakes where information was collected from online grey literature.

Collecting information from multiple informants for the same lakes or combining the interview survey with actual test fishing for a subsample of the lakes could have allowed for the estimation of detection probabilities and the likelihood for false positives or negatives. Previous studies on freshwater fish community status in Norwegian lakes have found a general agreement between information received from interviews and survey test fishing using gillnets (Hesthagen *et al.*, 1993). However, species not commonly caught with gillnets were underrepresented in survey test fishing, while species having a lower commercial or recreation value were underrepresented in interviews. Species with a high commercial or recreational value were underrepresented in test fishing, but not in interviews (Tammi *et al.*, 2003). The current survey likely suffers from an underreporting of occurrences for species less associated with commercial or recreational use, introducing false negatives.

There can also be sources of error from the historical data set. Errors committed more than a century ago are not easy to spot. With that said, there were some obvious errors in the historical data set that need mentioning. First, for all water bodies characterized as a lacustrine environment by The Norwegian Water Resources and Energy Directorate, but actually being a part of a lotic system that was connected to the marine environment, the occurrence data recorded by Huitfeldt-Kaas was most likely inadequate. This suggests that he did not record species immigrating on a regular basis to this habitat from both upstream and downstream, thereby introducing false negatives from the beginning. Second, a small proportion of the lakes recorded by Huitfeldt-Kaas either had a species occurrence that were highly unlikely or that lakes had a species richness that were highly unlikely. Especially when looking at the geographical location and physical appearance for some of those lakes.

The methodological limitations mentioned above are likely to have implications for the results¸ but not to any degree that should alter the main conclusions. For example, the presence of species of low anthropogenic interest (e.g. minnows, which were comparably much less reported in the 2019 re-survey) are likely to be underreported, particularly so in lakes far away from human population centra (i.e. high altitude lakes). This bias towards false negatives reduces the actual aggregated species turnover, opposing the observed trend with decrease in turnover of high altitude populations.

5. Conclusions

This study demonstrates that both anthropogenic and natural factors have contributed to the observed changes in lacustrine fish communities in south-eastern Norway on a century time scale. While HFI was not significant, I have shown a plausible explanation for why HFI may still be biologically significant due to the connection between all variables included in the analysis. I found that the increase in human pressure and presence in the last century may have contributed to the observed increase in species richness and species turnover. All environmental variables are ultimately interconnected and related to each other, leading to the observed changes. I also found a spatial pattern in species turnover that correlates positively with the densest human-populated areas within the study system. This suggests that humans, specifically human translocation of freshwater fish species, play a key role for changes in freshwater fish communities. The densest human-populated areas are those where individual lakes have experienced the most introduction events, which increases the probability for successful establishment of non-native species. The species turnover and species-specific contribution to turnover found here also reveals a pattern where temperate species, especially the cyprinids, had the highest increase in lake presence. Species that experienced an increase in lake presence, which historically were confined to coastal areas, have expanded their geographical range and are now more widespread and further inland.

The methodological approach to this type of study and this study in particular have been proved to yield results. I conclude that relying on good historical data and a few key anthropogenic and natural environmental variables makes it possible to see trends that previously only had empirical evidence. A better understanding of the drivers leading to species turnover is therefore not only relevant for managers, but essential for closing the knowledge gap that exists today.

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8. Appendix

Table S1. Lakes where fish inventory data was collected from online grey literature. Online sources used collecting fish inventory are listed for each individual lake. Lakes are listed after the county and municipality they are located in. Lake ID references to The Norwegian Water Resources and Energy Directorate unique "Varnløpenummer" given to norwegian lakes. Accessed refers to the date I recorded the lakes utilizing the source given. Since first accessed, not all links work anymore. Østfold fylkeskommune no longer exists, and therefore their website is shut down. Other websites have either changed or shut down so information is no longer available.

County	Municipality	Lake name	Lake ID	Author	source	Accessed
Østfold	Aremark	Langetjernet	3445	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Aremark	Langtjernet	153142	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Aremark	Skinnarbutjernet	3437	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	14/08/2019
Østfold	Aremark	Kollerødtjernet	3490	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Hobøl	Bæretjernet	5782	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Hobøl	Bølertjernet	5778	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019

Østfold	Hvaler	Arekilen	153489	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	14/08/2019
Østfold	Marker	Huevannet	3364	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	14/08/2019
Østfold	Marker	Søndre Brutjern	3388	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Marker	Nordre Brutjern	3385	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Marker	Brokstjern	3381	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	14/08/2019
Østfold	Moss	Noretjernet	5820	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Rakkestad	Laksen	3469	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Rakkestad	Langtjernet	81257	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Rakkestad	Søndre og Nordre Honningen	3399	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019

Østfold	Rakkestad	Kjennertjernet	3436	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Rakkestad	Store Steinsvannet	3418	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Rakkestad	Rørvannet	3441	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Rakkestad	Øvre Sandvannet	3474	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Rakkestad	Nedre Sandvannet	3477	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Rakkestad	Ertevannet	134	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	04/09/2019
Østfold	Rakkestad	Stomperudtjernet	3446	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Rakkestad	Skjølja	3435	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Rakkestad	Kløsa	3448	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019

Østfold	Rakkestad	Store Krokvann	3411	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Rømskog	Gryttjenn	3257	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Rømskog	Vesle Risen	3292	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Trøgstad	Stiklatjern	3275	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Trøgstad	Kallaksjøen	3317	Fylkesmannen i Østfold-Miljøavdeling	https://www.fylkesmannen.no/globalassets/fm-oslo-og-viken/miljo-og-klima/rapporter/miljovernavdelingen-i-ostfolds-rapportserie-1985-2018/forvaltningsplaner/forvaltningsplan-for-hara-naturreservat.pdf	28/08/2019
Østfold	Trøgstad	Grefslisjøen	3336	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019

Østfold	Trøgstad	Hærsetsjøen	3326	Fylkesmannen i Østfold-Miljøavdeling	https://www.fylkesmannen.no/globalassets/fm-oslo-og-viken/miljo-og-klima/rapporter/miljovernavdelingen-i-ostfolds-rapportserie-1985-2018/forvaltningsplaner/forvaltningsplan-for-hara-naturreservat.pdf	28/08/2019
Østfold	Trøgstad	Måstadtjern	3281	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Østfold	Trøgstad	Damtjern	3342	Østfold fylkeskommune	https://www.ostfoldfk.no/natur-og-miljo/friluftsliv/jakt-og-fiske/fiske/	28/08/2019
Akershus	Asker	Nesøytjernet	5421	Fylkesmannen i Oslo og Akershus-Miljøavdeling	https://www.fylkesmannen.no/globalassets/fm-oslo-og-viken/miljo-og-klima/rapporter/miljovernavdelingen-i-oslo-og-akershus-rapporter/2016-forvaltningsplan-for-nesoytjern-naturreservat-asker-kommune-fmoa-rapport-3-2016pdf.pdf	04/09/2019
Akershus	Asker	Padderudvannet	5521	BioFokus	http://lager.biofokus.no/biofokus-rapport/biofokusrapport2012-25.pdf	29/08/2019
Akershus	Asker	Bondivannet	5509	BioFokus	http://lager.biofokus.no/sis-rapport/sistesjansenotat_2005-3.pdf	04/09/2019

Akershus	Asker	Semsvannet	5427	BioFokus and NINA	http://lager.biofokus.no/sis-rapport/sistesjansenotat_2005-3.pdf https://www.nina.no/archive/nina/PppBasePdf/oppdragsmelding/764.pdf	04/09/2019
Akershus	Asker	Finnsrudvannet	5497	BioFokus	http://lager.biofokus.no/biofokus-rapport/biofokusrapport2012-25.pdf	04/09/2019
Akershus	Asker	Gjellumvannet	2477	BioFokus	http://lager.biofokus.no/biofokus-rapport/biofokusrapport2012-25.pdf	04/09/2019
Akershus	Asker	Hogstadvannet	5491	BioFokus	http://lager.biofokus.no/biofokus-rapport/biofokusrapport2012-25.pdf	04/09/2019
Akershus	Eidsvoll	Utsjøen	4049	Eidsvoll Fiskesamvirke	https://www.eidsvoll.kommune.no/contentassets/fc7dbfc87a1342da871a5c93710237ea/brosjyre-om-fiske-i-eidsvoll.pdf	03/10/2019
Akershus	Enebakk	Mjær	292	Sportsfiske.nu	http://enebakk.fiskevatn.no/lake/details/575963	03/10/2019
Akershus	Oppegård	Gjersjøen	297	Erik Grimsøen	http://www.dybdekart.no/Map/View/87	03/10/2019
Buskerud	Ringerike	Øyangen	604	Øyangen Vel	https://oyangenvel.no/2013/04/11/fiskevannet-oyangen-regler-m-m/	25/09/2019
Buskerud	Ringerike	Samsjøen	562	Naturkompetanse AS	http://www.naturkompetanse.no/dok/2006-1_web.pdf	23/09/2019

Buskerud	Ringerike	Holsfjorden	522	Ringerikes sportsfiskere, Erik Grimsøen	http://ringerikessportsfiskere.no/wp-content/uploads/2018/03/Prospekt-ja-til-b%C3%A6rekraftig-%C3%B8rretstamme_TRYKK.pdf http://www.dybdekart.no/Map/View/9	25/09/2019
Buskerud	Øvre Eiker	Øksne	583	NINA	https://www.nina.no/archive/nina/PppBasePdf/oppdragsmelding/831.pdf	21/11/2019
Buskerud	Øvre Eiker	Eikeren	542	Eikeren Fiskevernforening	http://eikernfiskevern-forening.net/fiskeslag.html	25/09/2019
Hedmark	Grue	Skasen	124	Eivind Haugerud	https://nmbu.brage.unit.no/nmbu-xmlui/bitstream/handle/11250/186738/Masteroppgave%20-%20Skasen.pdf?sequence=1&isAllowed=y	01/10/2019
Hedmark	Hamar	Mjøsa	118	Vassdragforbundet	http://www.vassdragsforbundet.no/wp-content/uploads/2018/01/Fiskearter.pdf	24/09/2019
Hedmark	Ringsaker	Mjogsjøen	285	Åge Birkeland	https://docplayer.me/16212599-3-7-mesnavassdraget-3-7-1-vassdragsbeskrivelse.html	26/09/2019
Oppland	Gausdal	Veslesætervatnet	32811	Skeikampen	https://skeikampen.no/aktiviteter/sommer-host/fiske/veslesaetervatnet/	14/10/2019
Oppland	Gausdal	Raudsjøen	2499	Skeikampen	https://skeikampen.no/aktiviteter/sommer-host/fiske/rausjoen/	14/10/2019

Oppland	Gjøvik	Lauga	4434	Fiskeutvalget for utmarkslagene i Snertingdalen	https://ovresnertingdalgrunneierlag.no/wp-content/uploads/2017/09/DRIFTSPLAN-FOR-FISK.-snertingdal.pdf	14/10/2019
Oppland	Gjøvik	Lunken	4438	Fiskeutvalget for utmarkslagene i Snertingdalen	https://ovresnertingdalgrunneierlag.no/wp-content/uploads/2017/09/DRIFTSPLAN-FOR-FISK.-snertingdal.pdf	14/10/2019
Oppland	Gjøvik	Røstadvatnet	4442	Fiskeutvalget for utmarkslagene i Snertingdalen	https://ovresnertingdalgrunneierlag.no/wp-content/uploads/2017/09/DRIFTSPLAN-FOR-FISK.-snertingdal.pdf	14/10/2019
Oppland	Gjøvik	Bergevatnet	4447	Fiskeutvalget for utmarkslagene i Snertingdalen	https://ovresnertingdalgrunneierlag.no/wp-content/uploads/2017/09/DRIFTSPLAN-FOR-FISK.-snertingdal.pdf	14/10/2019
Oppland	Gjøvik	Skonnolstjernet	4455	Fiskeutvalget for utmarkslagene i Snertingdalen	https://ovresnertingdalgrunneierlag.no/wp-content/uploads/2017/09/DRIFTSPLAN-FOR-FISK.-snertingdal.pdf	14/10/2019
Oppland	Lunner	Mylla	117	Lunner Almenning	https://www.google.com/maps/d/viewer?mid=1oIVZx7GTMhckQGiNLp5AQxRoXEVahGBG&ll=60.25296713090313%2C10.68946905000007&z=11	25/09/2019

Oppland	Lunner	Svea	4927	Lunner Almenning	https://www.google.com/maps/d/viewer?mid=1oIVZx7GTMhckQGiNLp5AQxRoXEVahGBG&ll=60.25296713090313%2C10.68946905000007&z=11	25/09/2019
Oppland	Lunner	Skjerva	5910	Lunner Almenning	https://www.google.com/maps/d/viewer?mid=1oIVZx7GTMhckQGiNLp5AQxRoXEVahGBG&ll=60.25296713090313%2C10.68946905000007&z=11	25/09/2019
Oppland	Lunner	Grøa	186	Lunner Almenning	https://www.google.com/maps/d/viewer?mid=1oIVZx7GTMhckQGiNLp5AQxRoXEVahGBG&ll=60.25296713090313%2C10.68946905000007&z=11	24/09/2019
Oppland	Nord-Aurdal	Røssjøen	560	Etnedal Kommune	https://www.etnedal.kommune.no/_f/p1/i874a0263-a214-4d1b-8253-12d58fd8997a/temakart_fisk.pdf	14/10/2019
Oppland	Nord-Aurdal	Steinbui	33108	Etnedal Kommune	https://www.etnedal.kommune.no/_f/p1/i874a0263-a214-4d1b-8253-12d58fd8997a/temakart_fisk.pdf	14/10/2019
Oppland	Vestre Toten	Einavatnet	143	Dag Beito	http://www.dybdekart.no/Map/View/63	14/10/2019
Oppland	Østre Toten	Fiskelausen	4578	Totenviken JFF	https://www.inatur.no/fiske/57344cbbe4b09e73e4443626	14/10/2019

Telemark	Bamble	Rørholtfjorden	1242	Øverby Skog AS	http://webfileservice.nve.no/API/PublishedFiles/Download/201307574/1184756	14/10/2019
Telemark	Notodden	Heddalsvatnet	1	Skienselva grunneierlag	http://www.skienselva.no/index.php/om-vassdraget/fiskearter	14/10/2019
Telemark	Skien	Norsjø	6	Skienselva grunneierlag	http://www.skienselva.no/index.php/om-vassdraget/fiskearter	14/10/2019
Telemark	Skien	Børsesjø	6573	BioFokus	http://lager.biofokus.no/biofokus-rapport/biofokusrapport2008-13.pdf	18/10/2019
Telemark	Skien	Hjellevannet	6592	Skienselva grunneierlag	http://www.skienselva.no/index.php/om-vassdraget/fiskearter	18/10/2019
Vestfold	Horten	Borrevannet	312	Visit Vestfold	https://www.visitvestfold.com/no/Horten/Aktiviteter/?TLp=1248447&Borrevannet	14/10/2019
Vestfold	Sande	Blindevatnet	5771	Svelvikportalen	https://svelvikportalen.no/leve-og-bo-kategori/fiske/	18/10/2019
Vestfold	Sande	Røysjø	5706	Svelvikportalen	https://svelvikportalen.no/leve-og-bo-kategori/fiske/	18/10/2019
Vestfold	Svelvik	Ebbestadvannet	5738	Svelvikportalen	https://svelvikportalen.no/leve-og-bo-kategori/fiske/	18/10/2019
Vestfold	Sandefjord	Goksjø	378	Goksjø grunneierlag	http://www.goksjo.no/	25/09/2019
Vestfold	Sandefjord	Akersvannet	314	Akersvannet grunneierlag	http://akersvannet.no/?page_id=147	25/09/2019