# A paradoxical bias in knowledge about Norwegian freshwater fishes: research efforts during 1980-2020

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Norwegian freshwater systems are in general species poor. That is particularly the case for the freshwater fishes. Only 32 species are considered native, whereas an additional 12 species are non-native. Some of the non-native species are also considered to be invasive and have negative ecosystem effects. Freshwater fishes are exposed to numerous stressors through their life cycle, many of which are of anthropogenic origin. In order to manage and conserve the diversity of fish there is a need for basic knowledge and understanding. Here I make an effort to review the published research on all Norwegian freshwater fish species during the 1980-2020 period, based on a standardized search on the Web of Science. Over 2000 relevant articles were retrieved and evaluated following the search. The research activity has been highly biased, with most research activity directed at a few species of high economic and societal value. Most work was directed at Atlantic salmon *Salmo salar* and brown trout *S. trutta*, and in general towards species within the salmonid family. Extremely little attention was directed at species such as the lampreys (four species) and sculpins (three species). Also, many species that has been listed on the Norwegian Red List during various time periods has not been given any particular attention. This lack of attention was also evident for most of the non-native species. The strong bias in research activity and lack of attention given to many species will clearly lead to difficulties in making appropriate management decisions. This is unfortunate, in particular in a time when climate change may lead to numerous ecosystem level changes

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## INTRODUCTION

Scandinavian freshwater ecosystems are in general species poor, in particular when it comes to freshwater fish. In Norway only 32 species are registered as native (Hesthagen and Sandlund 1996), whereas an additional 12 species are classified as non-native and for some as invasive (Hesthagen and Sandlund 2007, Jonsson and Jonsson 2016, Artsdatabanken 2018, Sandvik *et al.* 2019).

Freshwater ecosystems are exposed to a large range of anthropogenic stressors, worldwide (Dudgeon *et al.* 2006, Darwall *et al.* 2018, Reid *et al.* 2019). Water is diverted to a wide range of usages, waterways are fragmented by dams and other physical structures (Belletti *et al.* 2020), and terrestrial infrastructures and usages leads to pollution of various kinds. This leads to loss of connectivity and also extensive loss of suitable habitat (Parasiewicz *et al.* 2022). In addition, global climate changes may lead to changes in water temperature, stability and quality (Markovic *et al.* 2017, Pilla *et al.* 2020, Hébert *et al.* 2021, Woolway *et al.* 2021) and ice phenology (Sharma and Magnuson 2014, Sharma *et al.* 2019, L'Abée-Lund *et al.* 2021). Further, introduction of non-native and invasive species may challenge native fauna (Rahel 2002, Cucherousset and Olden 2011). Anadromous fish, such as Atlantic salmon *Salmo salar* Linnaeus 1758, are also exposed to numerous challenges associated with the coastal and marine environments (Forseth et al. 2017). In total, freshwater fish are really exposed to many challenges, putting stress on the management systems at different levels. In order to properly manage different fish species detailed biological knowledge is clearly needed.

Biological knowledge can be acquired in various ways. Here, I focus on knowledge acquired by using scientific methods and published in peer-reviewed outlets. This is only one particular type of knowledge, and much information is also available in so-called grey literature. Many such reports are not easily available or searchable using standard search engines. Thus, information contained in many such reports do not properly take part in the build-up of a common and global knowledge base. Other types of knowledge, such as what many call traditional knowledge (Gómez-Baggethun 2013), is important in many ways but requires particular types of investigations to be merged with the scientific knowledge base.

Here, I use published information in peer-review journals to ask the question if we really have the necessary knowledge to manage our freshwater fishes in a sustainable way. As a freshwater ecologist, it has for a long time been my impression that we have limited knowledge about many, maybe most, of the freshwater fishes in Norway. I also ask the question to what degree our knowledge is biased. This type of question is asked by others also, and a recent study found a vast knowledge gap regarding endangered fishes on a global scale (Guy *et al.* 2021). I here show that the situation in Norway is just as bad.

## The freshwater fishes in Norway

In this paper I define freshwater fish to only include fishes that spawn in freshwater. This means that catadromous species like the European eel *Anguilla anguilla* (Linnaeus, 1758) and the plaice *Platichthys flesus* (Linnaeus, 1758) are not included. The Norwegian mainland is species poor when it comes to native freshwater fishes. Svalbard is even more species poor, usually assumed to contain only one species – the Arctic char *Salvelinus alpinus* (Linnaeus, 1758). However, recently also the threespine stickleback *Gasterosteus aculeatus* (Linnaeus, 1758) have been observed in freshwater there (Svenning *et al.* 2015). In addition to the native species a variety of non-native species has been introduced to Norway by humans. When classifying a species as non-native I follow Artsdatabanken.no. For a brief summary of all registered species that are assumed to be reproducing in Norwegian waters today see Table 1.

The first extensive description of the distribution of the freshwater fish species dates back to early 1900s, when Hartvig Huitfeldt-Kaas published his famous book with the title “Ferskvandsfiskenes utbredelse og indvandring i Norge, med et tillæg om krebsen” (Huitfeldt-Kaas 1918). Before that Robert Collett had published a book on the fishes (Collett 1875), but his information on the distribution of the freshwater fish was rather limited. Huitfeldt-Kaas also produced hypotheses about how the various freshwater fishes had invaded the country after the last glaciation. His hypotheses have mainly stood the test of time.

A total of 32 species of freshwater fish can be classified as native to Norway. When I present the list of species, I follow the most updated systematics presented by Eschmeyer’s Catalog of Fishes (Fricke *et al.* 2021). This is an extensive web-based resource that is updated monthly. The phylogeny of the rayfinned fishes has changed dramatically during the last decades (Dornburg and Near 2021), and I here use what is the most updated systematics. This differs from that used in most other on Norwegian fishes (Pethon 2019) and also by the Norwegian Biodiversity Information Centre (Artsdatabanken in Norwegian; see https://www.biodiversity.no/). The main difference for Norwegian freshwater fish is that species that were classically grouped into the cyprinid family (Cyprinidae) now are grouped into four families (Cyprinidae, Leuciscidae, Gobionide and Tincidae). The species are, on the other hand, the same.

Some fish species have a very limited distribution in Norway, whereas others are widely distributed. The species are also to different degrees exposed to human encroachments such as habitat changes, pollution, and harvesting. The Norwegian Red List for Species, presented by the Norwegian Biodiversity Information Center, is prepared in accordance with the criteria used by IUCN (The International Union for Conservation of Nature). The freshwater fishes have been evaluated in 2006, 2010, 2015 and 2021. Several species have been listed, but listing has varied through time (for various reasons and using various criteria) (Table 1). In 2006, a total of six species was listed. The number of listed species was reduced to two in 2010 (arctic lamprey *Lethenteron camtschaticum* (Tilesius, 1811) and fourhorn sculpin *Myoxocephalus quadricornis* (Linnaeus, 1758)) and 2015 (arctic lamprey and sea lamprey *Petromyzon marinus* (Linnaeus, 1758)). In 2021, the Atlantic salmon was added to the list together with the two lamprey species. The only species that has been listed throughout the period is the arctic lamprey, but the listing has varied from vulnerable (VU), near threatened (NT), to data deficient (DD).

In addition to the 32 species that are native to Norway, a total of 12 species are classified as non-native (Table 1) (Sandvik *et al.* 2019). These species have been introduced to Norway either intentionally or non-intentionally, and are expected to pose very different threats to the local biodiversity. The expected threats are evaluated by the Norwegian Biodiversity Information Centre. Only 11 of the 12 non-native species are classified as invasive (Table 1), as the chum salmon *Oncorhynchus keta* (Walbaum, 1792) is assumed to not be reproducing in Norway. In 2015, the non-native and potentially invasive fishes were classified based on the ecological effect the species were assumed to have (Artsdatabanken 2018). The ecological risk is classified as either no risk, low risk, relatively high risk, high risk, or very high risk (Sandvik *et al.* 2017). One species is classified as having no risk (chum salmon), six species as low risk, whereas five species are classified as having high ecological risk (Table 1) (Artsdatabanken 2018). Further, some species that are native to Norway have also been translocated extensively outside its native area. This has happened for many centuries, and in particular the brown trout *Salmo trutta* Linnaeus, 1758 have been extensively transported and stocked (Huitfeldt-Kaas 1918). The Norwegian Biodiversity Information Center has also evaluated the ecological risk of such translocations. In their 2018 report they classify in total six species that are called regionally foreign. Two of these species are classified as having low risk, one as having high risk, and three as having very high ecological risk (Table 1).

# MATERIAL AND METHODS

I used the Clarivate Web of Science to search for relevant publications selecting the “All databases” option. Further, I formulated a search query of the form: (“species name”) AND (Norway OR Norge) in the “all fields” search widow. The species name was first the valid formal Latin name, then I used searches with synonyms and also common names (in English). I constrained the search to only include articles published between 1980-2020. By including the (Norway OR Norge) clause in the search, papers that do not have information on either the species or the country in the title, abstract or key words will be missed. This will introduce some bias, but I assume that that the papers found will give a realistic picture of the overall publication process.

The publications that were returned for each individual search was individually investigated for relevance. This was particularly important for a few species that returned high number of hits, many of which were not relevant to my aim. For example, the search may return publications only mentioning the search topic (the species) in a comparison with another species, but not bringing anything new to the literature. I also excluded publications that were mainly focused on toxicology, physiology and aquaculture. The reason for this is that my focus was on wild populations. I also excluded publications that were not performed in Norway, or where no authors with a Norwegian address was listed in the author list. To evaluate the various publications, I regularly had to read the abstract, if the title did not give enough information. In some cases, the complete publication had to be investigated. The searches sometimes returned reference to conference proceedings; these were included if the papers

Table 1. Summary of all known freshwater fishes in Norway, organized by family. Number of articles retrieved by a Web of Science search for the time period 1980-2020 is given (see main text for description of search algorithms for the global and the Norwegian search). The state indicates if the species is native (N) or non-native (I). Potential listing on the various versions of the Norwegian Red List for species is also given (NT Near threatened; VU vulnerable; DD data deficient; EN endangered), together with the classification of the nationally or regionally non-native fishes and their potential ecological impact (LR low risk; HR high risk; VHR very high risk; no risk).

| Species number and name | | No. articles | | State | Norwegian Red List | | | | Non-native | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Global | Norway | | 2021 | 2015 | 2010 | 2006 | National | Regional |
| Petromyzontidae | | | | | | | | | | |
| *1 Petromyzon marinus* | sea lamprey | 2866 | 0 | N | NT | NT | | | | |
| *2 Lampetra fluviatilis* | river lamprey | 1117 | 1 | N | | | | | | |
| 3 Lampetra planeri | brook lamprey | 391 | 1 | N | | | | | | |
| *4 Lethenteron camtschaticum* | arctic lamprey | 102 | 0 | N | VU | NT | DD | DD | | |
| Cyprinidae | | | | | | | | | | |
| *5 Carassius carassius* | crucian carp | 1650 | 16 | N | | | | | | LR |
| *6 Carassius auratus* | goldfish | 10105 | 3 | I | | | | | HR | |
| *7 Cyprinus carpio* | carp | 18770 | 7 | I | | | | | HR | |
| Leuciscidae | | | | | | | | | | |
| *8 Rutilus rutilus* | roach | 4633 | 43 | N | | | | | | HR |
| *9 Leuciscus leuciscus* | common dace | 508 | 1 | N | | | | | | |
| *10 Leuciscus cephalus* | chub | 1229 | 2 | N | | | | | | |
| *11 Leuciscus idus* | ide | 500 | 3 | N | | | | | | |
| *12 Phoxinus phoxinus* | Eurasian minnow | 1085 | 28 | N | | | | | | VHR |
| *13 Scardinius erythrophthalmus* | rudd | 781 | 4 | N | | | | | | VHR |
| *14 Aspius aspius* | asp | 261 | 2 | N | | | | VU | | |
| *15 Alburnus alburnus* | bleak | 874 | 7 | N | | | | | | |
| *16 Blicca bjoerkna* | silver bream | 474 | 4 | N | | | | NT | | |
| *17 Abramis brama* | bream | 2544 | 11 | N | | | | | | |
| *18 Leucaspius delineatus* | sunbleak | 234 | 2 | I | | | | | LR | |
| Gobionidae | | | | | | | | | | |
| 19 Gobio gobio | gudgeon | 690 | 2 | I | | | | | LR | |
| Tincidae | | | | | | | | | | |
| *20 Tinca tinca* | tench | 1496 | 3 | I | | | | | HR | |
| *Ictaluridae* | | | | | | | | | | |
| 21 Ameiurus nebulosus | brown bullhead | 486 | 2 | I | | | | | LR | |
| Esocidae | | | | | | | | | | |
| *22 Esox lucius* | pike | 4174 | 30 | N | | | | | | VHR |
| Osmeridae | | | | | | | | | | |
| *23 Osmerus eperlanus* | smelt | 571 | 22 | N | | | | | | |
| Salmonidae | | | | | | | | | | |
| *24 Salmo salar* | Atlantic salmon | 21717 | 610 | N | NT | | | | | |
| *25 Salmo trutta* | brown trout | 10133 | 528 | N | | | | | | |
| 26 Oncorhynchus mykiss | rainbow trout | 35910 | 15 | I | | | | | HR | |
| *26 Oncorhynchus gorbuscha* | pink salmon | 2001 | 8 | I | | | | | HR | |
| *27 Oncorhynchus keta* | chum salmon | 2890 | 1 | I | | | | | No Risk | |
| *28 Salvelinus alpinus* | Arctic char | 3761 | 318 | N | | | | | | |
| *29 Salvelinus fontinalis* | brook trout/brook char | 4231 | 8 | I | | | | | LR | |
| *30 Salvelinus namaycush* | lake trout | 2317 | 2 | I | | | | | LR | |

Table 1. Continued.

| Species number and name | | No. articles | | | Norwegian Red List | | | | Non-native | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Global | Norway | State | 2021 | 2015 | 2010 | 2006 | National | Regional |
| *31 Coregonus lavaretus* | whitefish | 1571 | 95 | N | | | | | | |
| *32 Coregonus albula* | vendace | 877 | 49 | N | | | | | | LR |
| *33 Thymallus thymallus* | grayling | 921 | 37 | N | | | | | | |
| Lotidae | | | | | | | | | | |
| *34 Lota lota* | burbot | 1112 | 17 | N | | | | | | |
| Gastrosteidae | | | | | | | | | | |
| *35 Gasterosteus aculeatus* | three-spined stickleback | 5144 | 49 | N | | | | | | |
| *36 Pungitius pungitius* | nine-spined stickleback | 610 | 5 | N | | | | | | |
| Cottidae | | | | | | | | | | |
| *37 Cottus gobio* | bullhead | 673 | 2 | N | | | | NT | | |
| *38 Cottus poecilopus* | alpine bullhead | 119 | 16 | N | | | | | | |
| *39 Myoxocephalus quadricornis* | fourhorn sculpin | 90 | 0 | N | | | DD | VU | | |
| Percidae | | | | | | | | | | |
| *41 Perca fluviatilis* | Eurasian perch | 5066 | 55 | N | | | | | | |
| *42 Sander lucioperca* | pikeperch | 1093 | 4 | N | | | | EN | | |
| *43 Gymnocephalus cernuus* | ruffe | 809 | 5 | N | | | | | | |
| Centrarchidae | | | | | | | | | | |
| *44 Lepomis gibbosus* | pumpkinseed | 1219 | 2 | I | | | | | LR | |

were reasonably easy to access. Various types of institutional reports (non-refereed publications) were excluded. In total, this search with the associated evaluation and exclusion process, will not pick up all relevant publications. But I assume that the publications that ended up in the final list give a representative picture of the research activity that has gone on in Norway during the selected time period. The approach I used here is very similar to that used in a recent review of management of regulated rivers with Atlantic salmon *Salmo salar* Linnaeus, 1758 (Watz *et al.* 2022).

To have a global comparison I also completed a similar search, excluding the local search clause, and excluding the detailed evaluation of the papers. This global search was mainly to investigate the relative research activity focused on the different species. This will indicate if the species bias is the same globally as I expect to find for Norwegian research.

The same article may turn up in several different searches, as a given publication may report research on several species. This publication will then be listed several times in the full list of publications. I find this unproblematic, since in this analysis I am interested in the level of research activity directed at the various species. A total of 2020 articles are included in the database after exclusion of publications that were outside the scope (as explained above). There was very large variation in the number of publications found for the various species. For some of the most studied species I further investigated the temporal variation in publication rate, and to what degree the research focus had changed over the decades.

## RESULTS AND DISCUSSION

A total of 2020 articles were registered following the search. On average, 49 ± 3 SE (range 12-94) articles were published each year, and there was a significant tendency that number of publications published each year increased with time (Figure 1).

Clearly, there was large variation in the number of articles published about the different species. The plot shown in Figure 2 indicates that there are a few species with high publication intensity, whereas several others have very few or no articles. The number of articles per species varied from zero to 610, with a high mean of 46 and a low median of five. This indicates an extreme bias.

I will treat each fish family in some detail below, but the first observation to make is that species belonging to the salmonid family is strongly overrepresented, whereas many families are highly underrepresented (Figure 3, 4). The heatmap in figure 4 clearly show

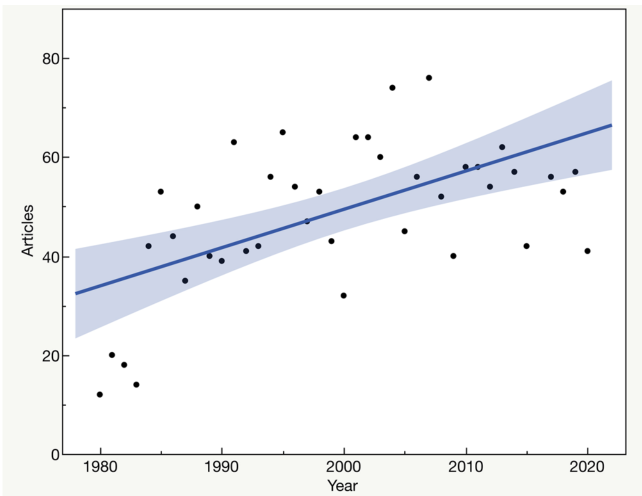


Figure 1. Annual number of articles produced on Norwegian freshwater fish during 1980-2020. Regression line with confidence band is added (slope ± SE: 0.77 ± 0.18 year$^{-1}$; $r^2$ = 0.32, P < 0.001).

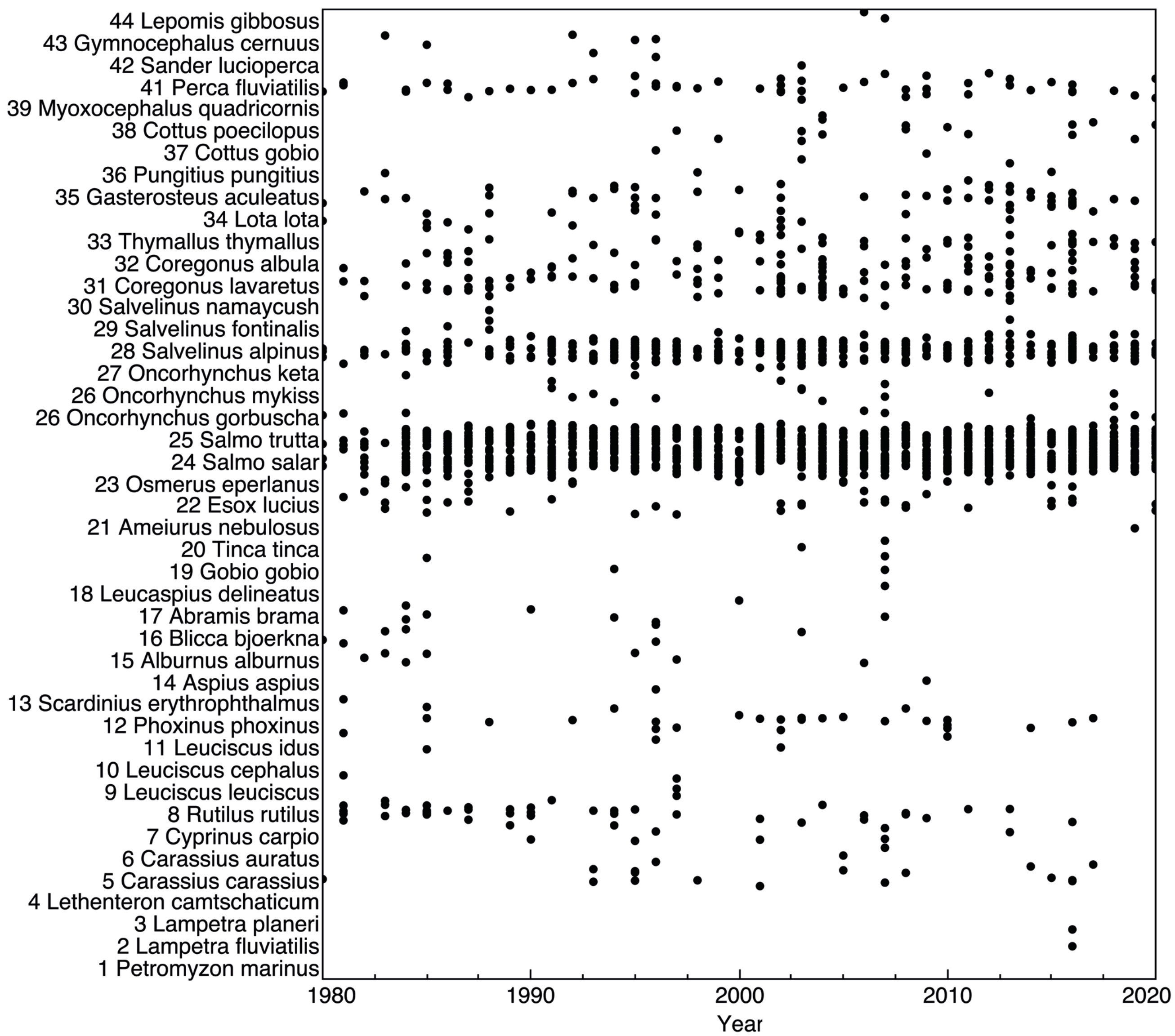


Figure 2. Plot showing the publication time of all articles produced for Norwegian freshwater fishes during 1980-2020. The species are numbered following Table 1.

the preponderance of published work on salmonids throughout the whole period, but also that the families Percidae, Leuciscidae and Gasterosteidae seems to be reasonable well covered. However, as I will show later this is probably not completely representative. The lamprey family (Petromyzontidae), with its four species, is very much underrepresented. The same is the non-native Ictaluridae, Gobionidae and Centrarchidae. On average, only 5 ± 2 articles were found for the non-native species (covering the total time period). This is an order of magnitude smaller that for the native species (61 ± 26).

There was a significant positive correlation between the publication rate for different species at the Norwegian and the global scale ($R^2$ = 0.241, P = 0.001). The relationship var not very strong, however it did indicate that the bias found at the Norwegian scale is to large degree also present globally.

I will now in some detail comment on the publication activity for the different species, mentioning them in the systematic order given in Table 1 (organized per family). While describing the publication activity I will give examples and try to evaluate the publication effort and type that has been performed during the 1980-2020 time period. The full list of retrieved publications is freely available (https://doi.org/10.5061/dryad.31zcrjdq6).

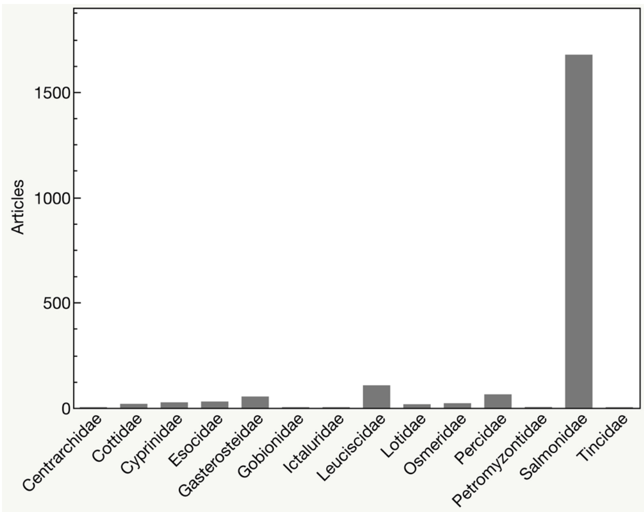


Figure 3. Bar-graph showing the total number of articles published on Norwegian freshwater fishes during 1980-2020, sorted by family.

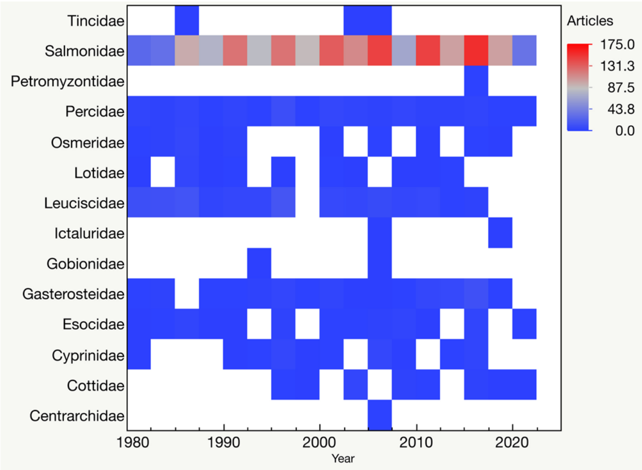


Figure 4. Heatmap showing the temporal variation in total number of articles published during 1980-2020 on Norwegian freshwater fishes, sorted by family.

## Petromyzontidae

A total of four lamprey species has been registered in Norwegian freshwaters. Two of these species (sea lamprey, arctic lamprey) have regularly been listed on the Norwegian Red List for Species (see Table 1). Both are still listed in 2021, with the sea lamprey listed as near threatened (NT) and the arctic lamprey as vulnerable (VU). However, only one article has been registered in the Web of Science during the 1980-2020 time period. This paper reports on lamprey as food for pike *Esox Lucius* Linnaeus, 1758, and it is unclear if it relates to brook lamprey *Lampetra planeri* (Bloch, 1784) or river lamprey *L. fluviatilis* (Linnaeus, 1758) (Sandlund *et al.* 2016b). What else is known about these species is usually published in Norwegian-language technical reports. Information on the distribution of two of the species (sea lamprey and brook lamprey) have recently been summarized in a Norwegian popular science journal (Hesthagen *et al.* 2020, Hesthagen *et al.* 2021a). In total, however, there is a complete lack of basic biological knowledge about these four species in Norwegian lakes, rivers and streams.

## Cyprinidae, Leuciscidae, Gobionidae and Tincidae

These four families were earlier considered to belong to one single family – Cyprinidae. I therefore, for simplicity, treat them together here. A total of 16 species belong to these families, whereof five species are introduced and non-native (Table 1). On average only three papers were published for each of the non-native species, compared with on average 11 articles for the native species. However, the number of articles published for the native species was very biased, with most articles being published for only four species (roach *Rutilus rutilus* (Linnaeus, 1758), Eurasian minnow *Phoxinus phoxinus* (Linnaeus, 1758), bream *Abramis brama* (Linnaeus, 1758), crucian carp *Carassius Carassius* (Linnaeus, 1758)).

Both the roach and the minnow are classified as regionally non-native species and suggested to have a high to very high ecological risk to the local ecosystem. However, few of the articles on the roach were relevant in order to evaluate the effect of translocations, but were rather classical ecological studies (L'Abée-Lund and Vøllestad 1985, Vøllestad and L'Abée-Lund 1987, L'Abee-Lund and Vøllestad 1989). Further, most of these studies was published during the period 1980-1995. This was a time when biomanipulation of freshwater ecosystems in order to increase water quality was popular (Carpenter and Kitchell 1992, DeMelo *et al.* 1992); this was evidently the focus for some of the studies (Brabrand *et al.* 1990, Faafeng *et al.* 1990, Brabrand and Faafeng 1993). During recent years, most of the retrieved studies actually did not focus on the roach, but information on the roach was rather a by-product of the main topic of the study. The listing of roach as a species with potentially high ecological impact when translocated to new locations has seemingly not led to more studies. However, in 2021 a new study trying to forecast the distribution of roach was published (Perrin *et al.* 2021). This study also discussed several other species that are considered as regionally invasive.

The Eurasian minnow has been studied in different contexts. Most studies are set in an ecosystem context, with focus on predator-prey relationships (Borgstrøm *et al.* 1985, L'Abée-Lund *et al.* 1996) and parasite-host dynamic (Museth 2001, Pettersen *et al.* 2016, Borgstrøm *et al.* 2017). It has been a clear focus on the interaction between the minnow and the native fish fauna, in particular interactions with the brown trout (Lien 1981, Museth *et al.* 2007). During recent years there has been an intensive action by various management authorities to reduce the spread of the minnow to new locations (Museth *et al.* 2007), but it has only to limited degree led to increased and relevant research activity on the species.

The crucian carp is also classified as regionally non-native, but it is assumed to have only low ecological effects in the new environment. Most of the reported studies are focused on the particular physiology of the crucian carp (Sollid *et al.* 2005), in particular its ability to survive long periods without oxygen (Poléo 1993). This ability also makes the species very tolerant to high concentrations of labile aluminium at low pH (Poléo *et al.* 2017). Also, the fact that the crucian carp develop different body shapes in the presence or absence of gape-limited predators has attracted some attention (Poléo *et al.* 1995). However, no studies up to 2020 focused on the crucian carp as a regionally invasive species with potential negative effects. Such studies seem to appear more recently (de Meo *et al.* 2022).

A total of 11 articles were found to report data on the bream – indicating at least some interest in this species. Almost 50% of these articles are from the National History Museum at the University of Oslo, and focus on distribution, feeding and parasites (Brabrand 1984, Brabrand *et al.* 1994, Sterud and Appleby 1996). The bream is an important component of many large lakes in the south-east part of Norway. It is therefore strange that so little attention has been diverted to learn more about its ecology, and potential interactions with other species.

The rudd *Scardinius erythrophthalmus* (Linnaeus, 1758) is classified as a regionally non-native species with a potential for very high ecological effects. However, in total only four articles have been published on this species. None of these studies focused on ecosystem effects or on potential interactions with native species. However, the potential future establishment of this species was evaluated in a 2021 study (Perrin *et al.* 2021).

The five non-native species in these families are classified as having variable ecological risks (Table 1). Three species were classified as having high ecological risk following translocation, and the other two were assumed to have limited ecological risk. However, only a very limited number of papers (varying from 2-7) was published for each of the species. For the carp *Cyprinus carpio* Linnaeus, 1758 a total of seven papers were registered. Most of these papers were notes of the present and historical distribution of carp (Kålås and Johansen 1995, Kleiven 2013), but there was no paper on its ecology and interaction with other species. For the tench *Tinca tinca* (Linnaeus, 1758), one paper on age and growth was found (L'Abée-Lund 1985). For the three other species (sunbleak *Leucaspius delineates* (Heckel, 1843), gudgeon *Gobio gobio* (Linnaeus, 1758), goldfish *Carassius auratus* (Linnaeus, 1758)), no study on ecology was found. In total, for most of the species that was classified as either non-native and invasive at the national scale or at the regional scale very limited ecological information has been gathered during the period 1980-2020.

Two species were classified on the Norwegian Red List during 2006 (Table 1), but not on the later iterations of the list. Thus, I would assume that some ecological information had been gathered to facilitate this new evaluation. The silver bream *Blicca bjoerkna* (Linnaeus, 1758) was classified as NT in 2006. However, only four papers focusing on this species were found – the newest from 1996. This paper was on parasites (Appleby and Sterud 1996). The asp *Aspius aspius* (Linnaeus, 1758) was classified as VU in 2006. Only two papers were found for this species, one on a potential observation in a new location (Spikkeland and Basnes 2009), and one on parasites (Sterud and Appleby 1996). Thus, basically no relevant information has been published formally either before or after the Red list listing.

For the remaining species in these four families very little published information could be found. In total, the information available is very biased towards a few species. Even the non-native species with suggested high ecological risks (impacts) have not been studied to any extent. This is, of course, unfortunate.

## Ictaluridae

The brown bullhead *Ameiurus nebulosus* (Le Sueur, 1819) is a non-native species with a limited distribution in Norway. The only published information is actually on its national distribution (Hesthagen and Sandlund 2007, Hesthagen and Brabrand 2018). The brown bullhead has a very constricted distribution, and it does not seem to have expanded much since the early 1900s (Huitfeldt-Kaas 1918). However, some expansion has happened – mainly locally. The brown bullhead has been categorized as an non-native species with a limited potential for negative ecological effects (Forsgren *et al.* 2018). In spite of it being a non-native species in Norway there is no information on its ecology in Norwegian lakes and thus also no studies that can document how and to what degree it influences other fish species or other organisms.

## Esocidae

The pike is a common species both in south-eastern and northern Norway. As a top predator it usually attracts attention, but still only 30 articles were found based on the standard search. If I included articles by Norwegian researchers working on pike in other countries the numbers would have been much higher (for example see Haugen *et al.* 2006, Carlson *et al.* 2007, Edeline *et al.* 2007, Haugen *et al.* 2007).

The ecology of the pike is well known (Skov and Nilsson 2018). In Norway, studies have to some degree focused on pike diet and thus its ecosystem effect as an apex predator (Vøllestad *et al.* 1986, Sandlund *et al.* 2016b). Some papers also investigate the ecological effects of various management actions, such as the effect of size-selective harvesting (Sharma and Borgstrøm 2008a). Such selective harvesting may also have unexpected effects on the accumulation of pollutants such as methyl-mercury (Sharma *et al.* 2008). As a top predator such pollutants may be up-concentrated in large and old individuals (Frøslie *et al.* 1985, Sharma *et al.* 2009, Olk *et al.* 2016), potentially posing a risk to human health. In total, even if the number of published papers is relatively small, the level of ecological knowledge on the pike is in general good.

The pike has repeatedly been translocated outside of its native area, and is classified as a regionally non-native species with a potentially very strong ecological effect (Table 1) (Byström *et al.* 2007, Hesthagen *et al.* 2015, Dunker *et al.* 2018, Jalbert *et al.* 2021, Perrin *et al.* 2021). Our knowledge about the ecological effects of new introductions seems adequate, but still some main understanding of their population dynamics is missing for Norwegian conditions. In particular, more knowledge about the effects of pike introduction into species poor and cold environments is needed. Clearly, also a better understanding of the invasion dynamics, such as dispersal dynamics and the drivers on long-distance translocations is needed.

## Osmeridae

The smelt *Osmerus eperlanus* (Linnaeus, 1758) is an important component of the food web in many lakes in south-east Norway. Several of the 22 studies that was retrieved by the search in some way evaluated the smelt in an ecosystem context, either as food for other fish (Garnås 1983, Sandlund *et al.* 2005, Eloranta *et al.* 2019) or as a predator on zooplankton (Sandlund *et al.* 1987, Hessen *et al.* 1988). As it is prey for economically important species such as brown trout there has also been some interest in how smelt accumulate pollutants (Frøslie *et al.* 1985, Skurdal *et al.* 1985).

There are also some studies on the present-day distribution of smelt, discussing either the presence of new locations following translocations (Hagenlund *et al.* 2015) or the potential rediscovery of populations in locations where it was considered extinct (Kleiven 2000). This small-sized species is usually easy to see during the spawning season, or as food items in the stomach of predatory fish. However, as the species is small-sized, it can be overlooked when density is low or if fishing effort is limited.

The smelt is a very important player in the local food web, both as food for various predatory fishes and as an efficient zooplankton feeder. Thus, the smelt can be called a keystone species (Lammens *et al.* 1990, Sandlund *et al.* 2005), in the same way as the close relative the capelin *Mallotus villosus* (Müller, 1776) is a keystone species in the arctic marine environment (Hjermann *et al.* 2010). Given this, it should be important to know the dynamics of the smelt populations to better predict transfer of energy through the lake food web. However, such studies could not be found.

## Salmonidae

A total of 11 species belonging to the Salmonidae family are registered in Norway. Of these, five species are non-native. As shown in Figure 3 this family in strongly over-represented when it comes to research effort as determined by number of publications. For most of the native species, I found a relatively high number of publications with Atlantic salmon on top, followed by the brown trout and the Arctic char (Figure 5).

The non-native species are on average little studied, listing between one and 15 publications per species during the whole period (Figure 5) The chum salmon is probably not established with reproducing populations in Norway, whereas the pink salmon *Oncorhynchus gorbuscha* (Walbaum, 1792) has appeared in large numbers during even years lately (Mo *et al.* 2018, Sandlund *et al.* 2019). Management authorities has initiated large efforts to keep the pink salmon invasion at bay, and this might lead to more publications on this species in the years to come. For example, interesting questions arise on how energy in transferred from the marine environment to the freshwater and terrestrial environments as large numbers of carcasses of pink salmon decomposes (pink salmon are semelparous) (Dunlop *et al.* 2021a, Dunlop *et al.* 2021b). Studies in order to understand the population dynamics of this species is underway (Paulsen *et al.* 2022). It is more worrying that there is so little information on species such as the rainbow trout *O. mykiss* (Walbaum, 1792), lake trout *Salvelinus*

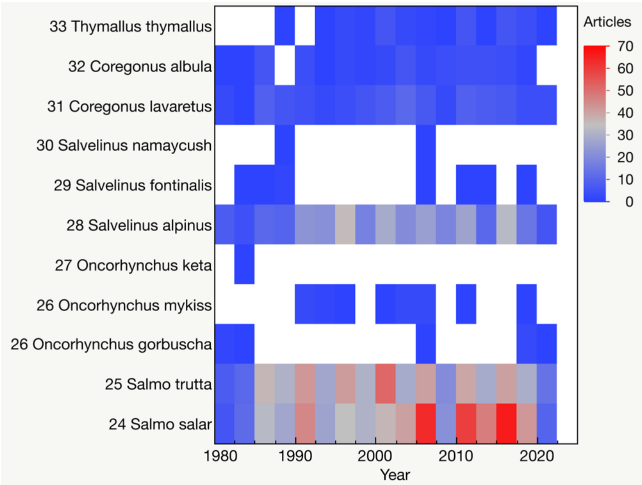


Figure 5. Heatmap showing the temporal variation in total number of articles published during 1980-2020 on different species of salmonid fish.

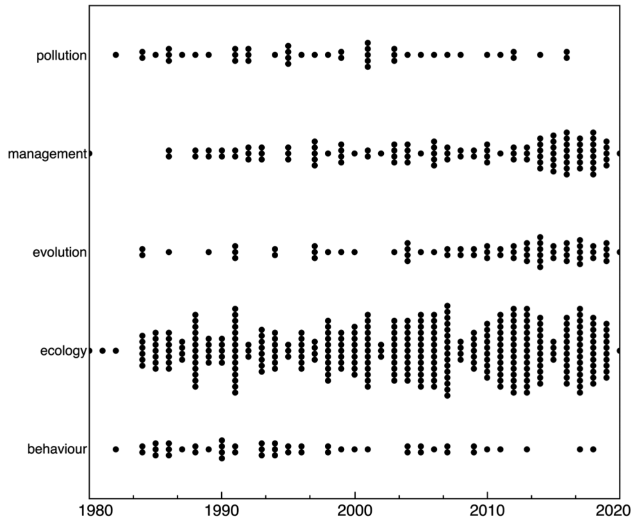


Figure 6. Temporal variation in number of articles on *Atlantic salmon* published in different categories during 1980-2020.

*namaycush* (Walbaum, 1792) and brook char *S. fontinalis* (Mitchell, 1815) (but see Hesthagen *et al.* 2018). These species have been present in Norwegian freshwaters for decades, but still very little is published on their biology and potential interaction with other species. The rainbow trout is classified as having a high ecological risk, whereas both the lake trout and the brook char has low risk. In total, it is worrying that the ecology of these three species basically in unknown in Norwegian freshwater systems.

Six salmonid species are categorized as native to Norway. The two species belonging to the *Salmo* genus, Atlantic salmon and brown trout, are extensively studied both in Norway and globally (Table 1). For both species I retrieved more the 500 publications for the 1980-2020 time period. Further, the Arctic char was treated in 320 publications, whitefish *Coregonus lavaretus* (Linnaeus, 1758) in 98 publications and the vendace *C. albula* (Linnaeus, 1758) in 50 publications. The grayling *Thymallus thymallus* (Linnaeus, 1758) is the least studied of these species, with only 37 publications listed. These six species, however, deserve separate chapters.

## Atlantic salmon *Salmo salar* Linnaeus, 1758.

The Atlantic salmon is the species which has received by far the most attention by fish biologist in Norway. Also, the publication rate (number of published articles per year) has increased significantly (number or articles per year; linear regression, $R^2 = 0.396$, slope = 0.37 ± 0.07, $P < 0.001$). This interest has also manifested itself globally by the publication of several books (Aas *et al.* 2011, Jonsson and Jonsson 2011). The large interest in Atlantic salmon is due to many factors, both economic, societal and political. Without going into detail here, there are large conflicts about how to manage and conserve the wild populations in the face of numerous challenges (Forseth *et al.* 2017). A major factor leading to conflicts is the interaction between the Atlantic salmon farming industry and the local wild populations (Liu *et al.* 2011). This has led to the build-up of large conservation plans with associated programs for collecting relevant data. Further, specific fjords and rivers are set aside where fish farming and other encroachments should not be allowed (Vøllestad *et al.* 2014, Vøllestad *et al.* 2018). All in all, this long-term interest and level of conflict has led to the production of a large number of articles on the Atlantic salmon – and as shown earlier, the numbers are increasing.

I tried to classify the articles into different topics – ending with classifying them as either mainly focussing on behaviour, ecology, evolution including genetics, management, or on the effect of pollution (Figure 6). It was not easy to do this classification, as many publications are at the interface between topics. However, the exercise probably gives an indication of temporal changes in scientific focus.

Throughout the 40 years covered by this summary a large proportion of the published papers could be classified as mainly ecological. Without going into details, it was clear that early in the period focus was on the freshwater part of the life cycle – studying topics such as growth, survival and habitat use of juveniles (Jensen and Johnsen 1985, Berg and Gausen 1988, Heggberget 1988, Heggenes *et al.* 1991). More recently there has been more focus on the marine phase – mainly by the inclusion of modern methods like telemetry (Haraldstad *et al.* 2017, Halttunen *et al.* 2018), electronic tags of different kinds (Hedger *et al.* 2017, Strøm *et al.* 2017, Strøm *et al.* 2020), and different types of state-of-the-art modelling (Vøllestad *et al.* 2009, Otero *et al.* 2011, Castellani *et al.* 2018). It is also evident that focus has changed from local-scale studies in individual rivers to more regional and global scales. Local scale studies also tend to become more long-term and focussing on mechanisms. These changes in publication pattern to a large degree follow general trends in many ecological fields, where focus has changed from descriptive small-scale studies to studies focussing on hypothesis testing and synthesizing data over larger temporal and spatial scales.

Behaviour was a topic of interest in particular in the 1980-2000 time period. These studies were focussed on two particular types of behaviours: migration mainly in freshwater (rivers and lakes), and spawning behaviour. The study of downstream migration of smolt has always been interesting, often set in a phenological context (Hansen *et al.* 1984, Jonsson and Ruud-Hansen 1985, Hvidsten *et al.* 1995). Also the upstream migratory behaviour of adult fish have been studied (Heggberget *et al.* 1993, Lennox *et al.* 2018). More recently, studies on the swimming behaviour of post-smolts through fjords and older salmon at sea also have been published (Økland *et al.* 2006, Manel-La *et al.* 2009). These studies have been facilitated by the development and use of acoustic telemetry, pop-up satellite tags and data storage tags. Several such studies have appeared recently (Strøm *et al.* 2020, Rikardsen *et al.* 2021), and more is expected following larger research programs that have been initiated. More classical behavioural studies were uncommon.

Evolutionary questions have been studied throughout the period, but in particular during later years. In this context I include studies on population genetics. During the early period some studies focusing on genetic structure (Vuorinen and Berg 1989, Skaala *et al.* 1998) and its relation to aquaculture (Hindar and Balstad 1994, Garant *et al.* 2003) was published, however usually with limited scopes and limited sets of genetic markers. This was probably due to lack of proper and economically available methods. Recent developments in methods and collaborations have led to many studies on both the general genetic structure of the Atlantic salmon (Vähä *et al.* 2017, Wennevik *et al.* 2019), and the level of interaction with aquaculture (Glover *et al.* 2013, Zhang *et al.* 2013, Glover *et al.* 2018). Many studies in the last category are here classified as focused on management (see below). Numerous studies from the river Tana (Teno) were not retrieved in the search because it did not fit the search criteria, or because they were published after 2020. Also, the publication of the annotated full genome of the Atlantic salmon was not picked up by the search (Lien *et al.* 2016). However, these publications are important in an international context, as they either produce high-quality results or may help develop major tools for a diverse set of later studies (Ayllon *et al.* 2015, Barson *et al.* 2015, Czorlich *et al.* 2018). These last studies are trying to understand major evolutionary questions, rather than more local scale questions of applied importance. Overall, also in the published studies that were retrieved by the search such a change from local to global scale questions is evident. Also, studies of more functional character have appeared, such as on the genetic resistance to sea lice (often called salmon lice) *Lepeophtheirus salmonis* (Krøyer, 1837) infections (Kolstad *et al.* 2005), the genetic consequences of inbreeding (Roberge *et al.* 2008), and regulation of growth (Besnier *et al.* 2020).

Research focusing on issues related to management has increased in number with time – this is to a large degree related to the increased conflict between wild salmon interests (conservation and recreational fisheries) and the Atlantic salmon farming industry (Forseth *et al.* 2013, Forseth *et al.* 2017). In the earlier part of the time period, management-related research was usually on the effect of hydropower development (Brooks *et al.* 1989, Raddum and Fjellheim 1995, Saltveit *et al.* 2001), managing of the commercial and recreational fishery (Jensen *et al.* 1999, L'Abée-Lund and Aspås 1999, Thorstad *et al.* 2007), or the handling of local and regional infestations of the ectoparasite *Gyrodactylus salaris* Malmberg, 1957 (Johnsen and Jensen 1991, Pettersen *et al.* 2013, Sandodden *et al.* 2018). These types of studies have continued to be important throughout the period investigated. However, in the recent decades focus has also been centred on the interaction between wild populations and the salmon farming industry. The two main topics are the effect of escapement of farmed fish into rivers (Skilbrei *et al.* 2015, Diserud *et al.* 2019), and the effect of sea lice on wild fish (Torrissen *et al.* 2013, Kristoffersen *et al.* 2018). Even if management-oriented studies are published at a reasonably high pace, most of the ongoing research is still published in the grey literature and not picked up in my search.

The final topic that I grouped the papers into was pollution – or rather the effect of pollution. The popularity of such studies seems to have decreased with time, or the pollution problems are becoming less important. In the 1980s acidification was a problem in freshwaters, also in Atlantic salmon rivers (Skogheim *et al.* 1984, Rosseland *et al.* 2001, Hesthagen and Larsen 2003, Hesthagen *et al.* 2011b). The problem has to a large degree been mitigated, either due to reduction in emissions of acidifying compounds or due to local mitigating actions (liming) (Sandøy and Langåker 2001). There was also a small burst in publications on the distribution and effect of radiocaesium following the Chernobyl accident (Forseth *et al.* 1998), but the focus was rarely on Atlantic salmon.

Overall, the publication rate on the Atlantic salmon has been high and is still increasing. Still, the wild populations overall are not doing well. This led to listing of the Atlantic salmon as being near threatened (NT) on the 2021-version of the Norwegian red list (Hesthagen *et al.* 2021d). On previous versions of the red list the Atlantic salmon was not listed. So, despite extensive efforts by numerous management authorities and organizations, and extensive research activity, the situation is not becoming better. And this is the situation for the species where most basic ecological information is available for any Norwegian freshwater fish, and where most research activity and funding has been directed.

## Brown trout *Salmo trutta* Linnaeus, 1758

The brown trout (hereafter trout) is the most widely distributed freshwater fish in Norway (Huitfeldt-Kaas 1918). It is very popular for sports fishing, and was historically extensively used for household fishing. Numerous books have been written about it, both nationally (Qvenild 1994, Nilssen 2017) and internationally (Elliott 1994, Jonsson and Jonsson 2011, Lobón-Cerviá and Sanz 2018). This large interest has also led to extensive research efforts in Norway during the 40-year time period checked here (Table 1).

A total of 528 publications was retrieved by the search, leading to more than 12 publications per year during the 40-year period. There was a weak increase in the number of publications per year during the period (linear regression, $R^2 = 0.152$; slope $0.16 \pm 0.06$, $P = 0.012$). Over 50% of the retrieved publications could be classified as focusing on ecology, and ecological studies have been published with more or less the same frequency throughout the time period (Figure 7). Studies on behaviour have, on the other hand, been relatively few, and most of these studies were on migration and movement.

Evolutionary studies were rare in comparison to the ecologically focused studies. Almost all of the studies that could be classified as evolutionary were focused on population genetics of some kind. Over time these studies use different methods, most were analysing variation in allozymes and microsatellites (Skaala and Jørstad 1987, Skaala and Solberg 1997, Sønstebø *et al.* 2007, Serbezov *et al.* 2012b, Vøllestad *et al.* 2012). Most studies were at relatively small geographic scales (within river systems) and focus on classical fixation index estimations ($F_{ST}$), and thus gene flow and level of differentiation on putatively neutral makers. These studies can to some degree be put into a conservation genetics context. Some studies also estimated

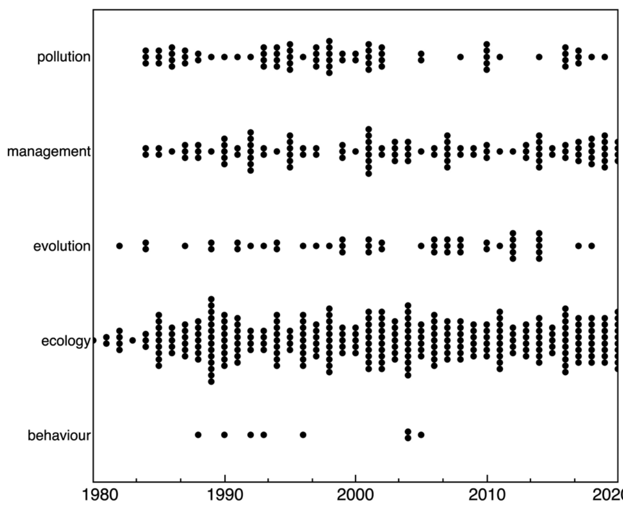


Figure 7. Temporal variation in number of articles on brown trout published in different categories during 1980-2020.

directly relevant parameters such as the effective population size (Serbezov *et al.* 2012a, b) or more directly assess the effects of for example habitat fragmentation (Junge *et al.* 2014) or introgression from stocked fish (Sønstebø *et al.* 2008). The limited scale of many of these studies, as also was common in northern Europe in general (Vøllestad 2018), contrasts the current trend for the study of Atlantic salmon, and limits the understanding of the genetic structure of the trout at the national scale. This is unfortunate, as it makes it difficult to take part in the ongoing and heated discussion on the phylogenetics of the trout (Bernatchez 2001, Kottelat and Freyhof 2007, Sanz 2018, Guinand *et al.* 2021). It is also unfortunate that more modern genetic methods have not been used to any degree.

A limited number of studies have also taken a more quantitative or life history approach. Such studies are clearly useful for understanding how trout may respond to various selective forces (Haugen *et al.* 2008, Robertsen *et al.* 2011). It may also help in understanding to what degree genetic architecture and phenotypic plasticity determine life history decisions (resident vs migratory) (Jonsson 1982, Jonsson *et al.* 1994). The trout is often highly migratory, and it is important as an anadromous species along the coast. However, very few studies address questions related to variation in level of anadromy. Even the few studies that were classified as behavioural did rarely include the marine phase of life (but see later in relation to management).

Trout are found in all kinds of freshwaters throughout Norway. And over time it has been exposed to numerous pollutants, with variable effects on individuals and populations. In the early part of the investigated period the effect of acid rain and subsequent acidification of surface waters were studies by many. The studies focused on individual level effects (Rosseland and Skogheim 1984, Rosseland *et al.* 1986, Muniz *et al.* 1987), population level effects (Hesthagen 1986, Muniz 1991, Bulger *et al.* 1993, Barlaup and Åtland 1996), and mitigation measures (Rosseland and Hindar 1988, Traaen *et al.* 1997, Hindar and Wright 2005). Studies of acidification has become rare during the last years. There are two additional topic that have been investigated by Norwegian researchers – the effect of the Chernobyl accident, and heavy metal pollution. The trout is the freshwater fish that was most studied in order to understand the dynamics of radioactive caesium in the environment (Ugedal *et al.* 1997, Forseth *et al.* 1998, Jonsson *et al.* 1999, Braaten *et al.* 2019). Such studies were limited in time. However, studies on the importance of mercury in fish and in the environment as such is still ongoing (Skurdal *et al.* 1985, Amundsen *et al.* 1997, Olsvik *et al.* 2001, Thomas *et al.* 2016). In total 75 of the articles that were retrieved from the search could be classified as focusing on pollution issues.

As a widely distributed and sought-after species, there was a large number of studies with a management perspective. More than 110 such studies were retrieved by the query. In particular, numerous studies have investigated the various effects of hydropower development. Such development, with the building of dams and changing of water flow will impact on connectivity, habitat quality and habitat availability. This is an ongoing issue for study, and will probably be so given the recent incentives to develop more so-called green energy (Aass *et al.* 1989, Heggenes and Saltveit 1996, Halleraker *et al.* 2003, van Leeuwen *et al.* 2016). Recently there has been some more interest in evaluation of the efficiency of fishways and how to facilitate safe two-way migration past dams and weirs (Fjeldstad *et al.* 2012, Fjeldstad *et al.* 2018, Holter *et al.* 2020).

Throughout the period there has been strong interest in stocking of trout, and numerous studies have focused on the stocking method (Fjellheim *et al.* 1995, Hesthagen *et al.* 1995, Finstad and Jonsson 2001, Solås *et al.* 2019). Stocking and translocation have been common for a long time (Huitfeldt-Kaas 1918, Nilssen 2017), but rarely has management goals been formulated and even more rarely have it been tested if the goals have been met (Vøllestad and Hesthagen 2001). Stocking has been used for different reasons, but most often to increase the potential yield in recreational inland fisheries. Such stocking is being discontinued, and studies on the potential population level effects of stopping stocking should be done (Nater *et al.* 2022). One effect of stocking that should be evaluated further is the effect of introgression of stocked, non-native trout into wild populations (Wollebæk *et al.* 2010). The genetic effect on native gene pools by the use of non-native stocked fish has been intensively discussed internationally (Ryman 1981, Ryman and Utter 1987, Ryman and Laikre 1991, Araki *et al.* 2007).

A recent problem for trout is the interaction with the aquaculture industry. The main problem is the interaction between anadromous trout and the sea lice (Vollset *et al.* 2017, Vollset *et al.* 2018, Serra-Llinares *et al.* 2020). Overall, this interaction between sea trout and the Atlantic salmon farming industry has also led to some more studies on the marine phase of the life cycle of the trout. However, were little if any information is published on the harvesting of sea trout at sea. Almost all studies on management-related issues are from fresh water.

Overall, the brown trout has been extensively studied – with a variety of topics being handled. The biology of trout is thus in general well understood. However, the marine (coastal) part of the life cycle is less well understood (Thorstad *et al.* 2016, L'Abee-Lund and Vøllestad 2018). Fortunately, this seems to be changing (Davidsen *et al.* 2014, Jensen *et al.* 2014, Flaten *et al.* 2016, Eldøy *et al.* 2021).

## Arctic char *Salvelinus alpinus* (Linnaeus, 1758)

A total of 318 articles presenting relevant data on Arctic char (char hereafter) were retrieved. The char is distributed throughout most of the country, with anadromous populations in the northern parts. It is also the only freshwater species that has populations on Svalbard and Bjørnøya (Bear Island) (Gulseth and Nilssen 2001, Bytingsvik *et al.* 2015). Other species have been recorded from freshwater at Svalbard (Svenning *et al.* 2015), but it seems that only the char has well-established populations.

The char exhibits extreme variability in life history, behaviour and demography (Klemetsen 2010). This variability has by some been called the "char problem" (Nordeng 1983). Numerous articles describe phenotypic and life history variation in the char, many focusing on the existence of alternative morphs or ecotypes within watercourses. The number of morphs within a system may vary from one (called "normal" char) to the newly discovered four-morph system in Tinnsjøen (Østbye *et al.* 2020). The system in Tinnsjøen is kind of similar to the well-studied char-system in the Icelandic lake Thingvallavatn (Sandlund *et al.* 1992). In some river systems in the north, the char can be classified into three different morphs (one anadromous, and two resident morphs) (Nordeng 1983). Some sympatric morphs may be part of the same population, whereas other morphs are more or less reproductively isolated (Hindar and Jonsson 1993, Præbel *et al.* 2016). This leads to a classic discussion about the importance of genetic differentiation and phenotypic plasticity (Nyman 1972, Hindar *et al.* 1986, Whiteley *et al.* 2019). For example, some researchers have classified selected populations from Norwegian lakes as separate species (Kottelat and Freyhof 2007). Understanding the structuring of char seems particularly difficult. But it is also a common topic of discussion regarding other species that have invaded lakes and rivers post-glacially (Bernatchez 2004). It is at times difficult to detect the existence of sympatric populations, and potentially also species, as it may require more sensitive genetic methods than has been in use until recently (Jorde *et al.* 2018). Clearly, the systematics of the Arctic char is not fully resolved.

On average, eight articles focusing on the char were published per year during the 40-year period. It was a tendency that number of published papers increased through the period ($R^2 = 0.115$, slope estimate $0.13 \pm 0.05$ $y^{-1}$, $P = 0.014$), but the among-year variation was large. Most of the retrieved articles could be classified as ecological (76.8 %), whereas behaviour was investigated to a very limited degree (1.9 %). The ecological studies had a wide range of contexts, but many were focusing on the position of the char in the ecosystem. Many have studied the diet of the char, usually in lakes (Dervo *et al.* 1991, Dahl-Hansen *et al.* 1994, Gregersen *et al.* 2006, Amundsen *et al.* 2008). In that context, numerous studies have also investigated the transmission of various parasites (Knudsen and Klemetsen 1994, Knudsen 1995, Amundsen *et al.* 2003b, Siwertsson *et al.* 2016). A particular observation is that most of these studies are from North-Norway.

The char is considered to be a very efficient zooplankton predator, and several studies consider the interaction between char and other fish species. In particular, the relationship between char and trout (Saksgård and Hesthagen 2004, Persson *et al.* 2007, Hesthagen *et al.* 2011a, Guenard *et al.* 2012, Persson *et al.* 2013) has had particular interest. The char have high growth efficiency relative to the trout, but still seem to be out-competed by the trout - in particular in relatively warm and productive lakes (Finstad *et al.* 2011). Modelling exercises from Sweden indicates that increasing temperatures and interaction with trout may lead to an extensive population loss (Hein *et al.* 2012). Similar predictions have been made from other locations in Europe (Kelly *et al.* 2020). No such studies are available from Norway yet. The char may also be at peril due to the increasing distribution of the pike (Hein *et al.* 2012).

Overall, the feeding biology of the char is well understood as also seems the case with variation in life history (Nordeng 1983, Vøllestad and L'Abée-Lund 1994). Also the anadromous part of the life cycle of char has been investigated – focus has been both on why some individuals or populations are migratory (Finstad and Hein 2012), and the migration process itself (Berg and Berg 1989, Finstad and Heggberget 1995). Even if the ecology of the char is relatively well understood, the drivers of the extensive phenotypic variation are still in need of understanding. In order to acquire such understanding evolutionary questions has to be asked.

In total only 29 papers with an evolutionary focus were found by the search. Some small-scale population genetic studies were found (Hindar *et al.* 1986, Westgaard *et al.* 2004, Wollebæk *et al.* 2011, Præbel *et al.* 2016, Østbye *et al.* 2020). However, the number of studies were very small relative to the large phenotypic variability that can be found. More classic evolutionary studies focussed on various aspects of sexual selection (Skarstein and Folstad 1996, Skarstein *et al.* 2005, Egeland *et al.* 2015), and also some more functional genetics studies were found (Eliassen *et al.* 1998, Lysfjord and Staurnes 1998).

A relatively limited number of papers (n = 15) handled the effects of pollution. As expected, some papers focused on the effect of acidification of surface waters (Andersen *et al.* 1984, Hesthagen and Sandlund 1995), while some also followed the effects of the Chernobyl accident (Forseth *et al.* 1998, Jonsson *et al.* 1999). Otherwise, few if any studies focused on other kinds of pollutants and their effect on individuals or populations. Thus, even if the number of papers published on the char is relatively large (n = 318), the number of studies with a direct management application is limited. There are some studies focussing on the effect of harvesting (or different ways of harvesting) (Langeland 1986, Finstad *et al.* 2000, Smalås *et al.* 2020), and there are some studies focusing of the potential for the char to be a temporary host for parasites such as *Gyrodactylus salaris* (Bakke *et al.* 1996, Robertsen *et al.* 2007, Winger *et al.* 2008b). Recently, there has also been some studies on the effect of sea lice infections of sea-run char (Bjørn *et al.* 2001, Bjørn and Finstad 2002). However, the number of such studies are small relatively to those published on Atlantic salmon and sea trout. Overall, even if the ecology of char is well-understood, there clearly is a wide range of topics that needs better understanding. The important drivers of phenotypic variability are not understood, as well as the importance of genetic differentiation and level of response to natural selection (potentially leading to local adaptation).

## Whitefish *Coregonus lavaretus* (Linnaeus, 1758)

The whitefish is one of the most phenotypically variable freshwater fishes, in Norway and globally. This has led to large controversy regarding number and naming of species (Kottelat and Freyhof 2007). For example, in Sweden different authors have suggested the presence of many different species (see summary by Svärdson 1998). Gunnar Svärdson published during several decades numerous papers in a series he called "the coregonid problem". And clearly the taxonomy and systematics is still a mess. Today, the SLU Swedish Species Information Center recognizes one species of whitefish, *Coregonus maraena* (Bloch, 1779), with four taxa that are classified as morphotypes. In Norway, the Norwegian Biodiversity Information Centre recognized only one species, *C. lavaretus*. Also, in Finland the whitefish is classified as *C. lavaretus* by the Finnish Biodiversity Info Facility. Clearly, this is a situation that should be sorted out – as the whitefish clearly has a continuous distribution in Scandinavia.

One reason for the taxonomic confusion is the large phenotypic variability and also flexibility in use of spawning and feeding habitat. In Norway this has led to the presence of numerous reproductively isolated sympatric populations in many lakes. Many studies have focused on trying to describe this variability, using both classic ecological and population genetic methods (Østbye *et al.* 2005, Østbye *et al.* 2006, Siwertsson *et al.* 2013, Bitz-Thorsen *et al.* 2020). Most of these studies are from North-Norway or from the lake Femunden in mid-Norway. Clearly, there is still a need for more studies, from different geographic regions, in order to understand the origin and drivers of the genetic and phenotypic variation in sympatric whitefish populations. More extensive genomic tools are probably needed, such as full-genome sequencing using next-generation sequencing tools. An example of this is the detailed studies of a whitefish radiation in alpine European lakes (Vonlanthen *et al.* 2012, Frei *et al.* 2022). However, also here it can be discussed if the taxa studied are species, or populations of the same species.

One interesting topic that has been studied recently is on how various whitefish morphs/phenotypes are differentially impacted by the invasion of other species. In particular the effect of the invasion of vendace *C. albula* to Pasvik has led to the dramatic reduction in the abundance of the small-sized plankton-feeding morph (Bøhn *et al.* 2004, Bøhn *et al.* 2008). Clearly, the existence of different morphs of whitefish in a lake is contingent on ecological opportunity driven by habitat availability and presence of competitors and predators. Whitefish may have a very diverse ecological niche, and may therefore also impact on other freshwater species. This potential interactions with other species have also been investigated to some degree, in particular the interaction with Arctic char has received some interest (Amundsen *et al.* 2010, Eloranta *et al.* 2011, Sandlund *et al.* 2016a).

The whitefish has been repeatedly translocated in Norway, and it is unclear what is a naturally recruited population or what is due to human translocation (Sandlund *et al.* 2013b, c). It would be interesting to use modern genetic methods to try to investigate this. This should be possible as more and more high quality genomes are published, also for various *Coregonus* species (Merot *et al.* 2022).

On average, more than two papers focusing on whitefish biology has been published per year, and the publication rate has been stable throughout the time period investigated (slope estimate 0.03±0.02 year$^{-1}$). Overall, the biology should be well understood, but given the phenotypic and genetic diversity present a full understanding is eluding us. In a biodiversity context, a complete understanding as well as a Scandinavian agreement on the taxonomic status of the different populations/morphs is needed.

## Vendace *Coregonus albula* (Linnaeus, 1758)

Vendace was investigated in a total of 49 papers over the 40-year time period investigate. On average a little over one paper has been published per year, and there was no temporal trend in the publication rate (slope estimate 0.02 ± 0.02 year$^{-1}$). The vendace has a limited distribution in Norway, with its main distribution along the border to Sweden in the south-eastern part of the country. Previous stocking efforts have, however, also led to the species being distributed outside its natural distribution area (Sandlund *et al.* 2013b).

The introduction of the vendace to the Pasvik river system in North-Norway has raised particular interest (Amundsen *et al.* 1999). The focus has been on how the introduction of this efficient zooplankton predator has led to changes in the ecosystem, and in particular how it has impacted the dynamics of the polymorphic whitefish (Bøhn and Amundsen 2001, Bøhn *et al.* 2008). Almost half of the publications on vendace were on various topics related to the invasion into the Pasvik system. All of these papers are from the 1990s onwards. This means that almost all articles on the vendace during the last 20 years are from the Pasvik system, and mainly focussing on the ecosystem effects of the invasion of vendace into this river system. Based on these observations the vendace is classified as a regionally invasive species with low risk (Artsdatabanken 2018).

Clearly, a lot has been learnt on the trophic ecology of the vendace, and how this species interacts with different parts of the food web in arctic systems. But the strong geographic bias also indicates that little effort has been invested into understanding the ecological function of vendace in more southern and biologically complex systems. Even in the lake Mjøsa, where there earlier was a famous fishery for vendace (or lågåsild as it is locally known) (Huitfeldt-Kaas 1917, Aass 1972), very little recent work has been published (Næsje *et al.* 1986, Næsje *et al.* 1991, Gregersen *et al.* 2011). This is unfortunate, as this and other comparable lakes have experienced large environmental changes during the last decades (Moe *et al.* 2022).

## Grayling *Thymallus thymallus* (Linnaeus, 1758)

The grayling is distributed in the south-eastern and the far northern part of Norway, and is usually considered to be a purely river-living species (Huitfeldt-Kaas 1918). However, it is also found in numerous lakes, including the largest Norwegian lake – Mjøsa (Huitfeldt-Kaas 1917). Phylogeographic studies have shown that two different evolutionary lineages have immigrated into Norway following deglaciation (Koskinen *et al.* 2000), however this has not been followed up by more detailed studies.

A total of 37 articles were retrieved by the literature search, most of which (almost all) were based on studies from the Glomma river-system in the south-eastern part of Norway. Glomma is the largest river in Norway, splitting into two main upstream branches; Glomma and Gudbrandsdalslågen. In the upper part of Gudbrandsdalslågen the introduced grayling has been intensively studied during over 30 years. Most of these studies are initiated from the University of Oslo (Vøllestad and Primmer 2019). These studies originally focussed on classical ecological topics (Haugen and Rygg 1996b, Haugen 2000a), but later focussed on evolutionary processes including population genetics (Barson *et al.* 2006, Junge *et al.* 2011) and adaptation to differential temperatures (Haugen 2000a, b, Kavanagh *et al.* 2010, Mäkinen *et al.* 2016). Lately it has led to genomic studies of different types (Papakostas *et al.* 2010, Papakostas *et al.* 2014, Mäkinen *et al.* 2018). For example, the annotated genome of grayling was published recently (Varadharajan *et al.* 2018, Sävilammi *et al.* 2019), facilitating even more detailed evolutionary studies. Most of these studies are based on grayling in the upper reaches and high-altitude systems. Further downstream in the two rivers and the lake Mjøsa detailed studies with applied focus on the population structure, dispersal, and the effect of lack of connectivity has been performed (Linløkken 1993, Kristiansen and Døving 1996, Heggenes *et al.* 2006, van Leeuwen *et al.* 2016, van Leeuwen *et al.* 2018, Holter *et al.* 2020). All these studies have increased our understanding of grayling life history. However, there is still only limited knowledge about feeding (Haugen and Rygg 1996a, Amundsen *et al.* 2010) and parasitism (Mo *et al.* 1998, Ieshko *et al.* 2001), etc. The grayling is host to the monogenean parasite *Gyrodactylus thymalli* Zitnan, 1960, and this parasite is of great interest as it is very similar to the pathogenic *G. salaris* (Fromm *et al.* 2014, Mieszkowska *et al.* 2018). Some work has been done on the biology of *G. thymalli* (Pettersen *et al.* 2015, Pettersen *et al.* 2021), but clearly more work should be done.

The biology of the grayling is relatively well known, but the information is geographically biased towards one particular river system. And there are no studies focusing on population dynamics or on how grayling populations might vary over time.

## Lotidae

The family Lotidae have earlier been classified as a sub-family under the Gadidae. The family contains only five species in total and one species, the burbot *Lota lota* (Linnaeus, 1758), is found in freshwater in Norway. The burbot is mainly distributed in southeast and north in Norway, but with a few populations in mid-Norway (Huitfeldt-Kaas 1918, Hesthagen *et al.* 2021c).

Only 17 articles were retrieved by the search, indicating that very little research has focussed on the burbot. In many of the articles the burbot was not the primary species of interest, rather if was a minor part of investigations of the food web (Amundsen *et al.* 2003a, Sandlund *et al.* 2013a). Very few studies focussed on the biology of the burbot (Sandlund *et al.* 1985, Vøllestad 1992). On the other side, some articles have studied the effects of pollution (Frøslie *et al.* 1985, Mariussen *et al.* 2008, Berg *et al.* 2013). However, these studies are mainly from lake Mjøsa.

In total, the knowledge about the biology of burbot in Norway is very limited. There are no studies available on the reproduction, migration, spawning behaviour or population dynamics of the species. This is unfortunate, as the burbot may be an important part of the benthic ecosystem in many lakes and large rivers. It is also an important predator.

## Gasterosteidae

Two species of stickelbacks are native in Norwegian freshwater. Both species can also be found in both brackish and marine waters. In particular the three-spined stickleback *Gasterosteus aculeatus* Linnaeus, 1758 in common throughout coastal waters as well as marine waters along the Norwegian coast (Huitfeldt-Kaas 1918, Klepaker 1996). The nine-spined stickleback *Pungitius pungitius* (Linnaeus, 1758) has a more limited distribution. Sticklebacks are intensively studies globally, in particular the three-spined stickleback is used as a model species in a wide range of research fields (Östlund-Nilsson *et al.* 2007, Wootton 2009). The nine-spined stickleback has gotten less interest. This is also clear in Norway, where only five articles were retrieved by the search. Only one of the studies focussed on the nine-spined stickleback in some detail (Klepaker *et al.* 2013). Two studies focussed on parasites, but mainly in the three-spined stickleback (Rødland 1983, Soleng and Bakke 1998). Overall, we know almost nothing about the biology of the nine-spined stickleback in Norwegian ecosystems. This is in stark contrast to the three-spined stickleback, where we retrieved 49 articles by the search.

Many of the studies on three-spined stickleback focussed on the phenotypic variation observed in lateral bony plates – a trait that is extensively studied in this species. These studies concerned the large-scale (Klepaker 1995, 1996, Voje *et al.* 2013) and small-scale distribution (Le Rouzic *et al.* 2011, Østbye *et al.* 2016, Østbye *et al.* 2018) of the plate morphs among and within ecosystems, and how it differs depending on various selective processes (Myhre and Klepaker 2009, Bjærke *et al.* 2010, Mazzarella *et al.* 2015). These studies also included the use of modern genetic/genomic methods (Taugbøl *et al.* 2014, Mazzarella *et al.* 2016). Also, the other main anti-predator defence system – the dorsal and pelvic spines – have been studied (Klepaker *et al.* 2012, Klepaker *et al.* 2013). These studies in general are set in an evolutionary context.

The three-spined stickleback is an important prey fish for many freshwater fishes, and several studies have investigated such predator-prey relationships (Jakobsen *et al.* 1988, L'Abée-Lund *et al.* 1992, Amundsen 1994). In an ecosystem context, distribution, transmission and importance of various parasites has also been studied in some detail (Amundsen *et al.* 2013, Braicovich *et al.* 2016, Kuhn *et al.* 2016). This has also been studied in the context of sexual selection and spawning behaviour (Folstad *et al.* 1994). In addition to this parasite focus, several studies have used three-spined stickleback to study toxic effects of various compounds (Wibe *et al.* 2002, Knag and Taugbøl 2013).

Even if the tree-spined stickleback has been studied in some detail, little is known about its population dynamics and ecosystem effects. This is unfortunate, in particular based on reports from the brackish Baltic Sea where changes in the stickleback density have had strong effects on numerous other species (Bergström *et al.* 2015, Byström *et al.* 2015, Eklöf *et al.* 2020). This lack of basic biological information is shared by many other small-sized fish species – both in freshwater and in the sea.

## Cottidae

In total three species of sculpins are found in Norwegian freshwaters (Table 1). Only the alpine bullhead *Cottus poecilopus Haeckel, 1835* is distributed over a larger geographic area. The other species, bullhead *C. gobio* Linnaeus, 1758 and fourhorn sculpin have very limited natural distribution.

I found no publication on the fourhorn sculpin during the time period investigated. This species is only observed in two large lakes, Mjøsa and Store Le, but there is almost no information about population size or biology. The species has also been listed on the Norwegian Red List both in 2010 (VU) and 2015 (DD). However, it was removed from the list in 2021 (Hesthagen *et al.* 2021b). Even if no articles were recovered by the formal search, there are a few Norwegian reports available.

The bullhead is also a species with very limited distribution in Norway. However, it has relatively recently been found in new locations and may be spreading (Frilund *et al.* 2009). The limited natural distribution led to a listing as Near Threatened on the 2006 Red List; it was subsequently removed from the list. There is, however, almost no knowledge about this species in Norway.

The biology of the alpine bullhead, on the other hand, has been studied to some degree. In particular it has been studied how it might interact with sympatric species such as trout (Holmen *et al.* 2003, Hesthagen *et al.* 2004, Hesthagen *et al.* 2011a) and Atlantic salmon (Gabler and Amundsen 1999, Gabler and Amundsen 2010, Sanchez-Hernandez *et al.* 2016). The studies of the interaction with Atlantic salmon were initiated because the alpine bullhead had invaded a salmon river (River Tana/Teno with tributaries), producing a need to know more about how bullhead and other species may engage in competitive interactions. Following this, there has also been some studies on how the alpine bullhead may be a vector for important parasites such as *Gyrodactylus salaris* (Winger *et al.* 2008a, Bakke *et al.* 2019).

In general, there is very little knowledge about population biology (dynamics, structure) and ecology of the three sculpin species under Norwegian conditions. This lack of knowledge is shared with a number of other small-sized species with little economic interest.

## Percidae

Three species of percids are found in Norway, but only the Eurasian perch *Perca fluviatilis* Linnaeus, 1758 is common over large areas. The perch is common both in North-Norway and in the south-eastern part of the country and is considered as one of the most common freshwater fishes in the country (Huitfeldt-Kaas 1918). Being common, and also of interest for recreational fishers, there has been considerable interest in this species by researchers. In total 55 articles were retrieved by the search, indicating that more the one article has been published per year in the period investigated.

The perch is a cold-water adapted fish that spawn early in spring. Being cold-adapted the perch was one of the first non-anadromous freshwater species that invaded Norway after the last glaciation. It is also one of the few Norwegian freshwater fish species where the immigration routes and phylogeography has been investigated in some detail (Refseth *et al.* 1998, Nesbø *et al.* 1999). These studies indicated that perch in southeast Norway probably belong to two different evolutionary lineages that penetrated into Norway via either a southern route (along the coast in the cold meltwater) or from the east through the Baltic Sea and through the large Swedish watercourses. If was postulated that these immigration routes probably have been used by other freshwater fishes also. Unfortunately, this has not been followed up using more up-to-date genetic methods.

Many studies on the perch have otherwise focussed on general population ecology (Heibo and Vøllestad 2002, Heibo *et al.* 2005, Linløkken and Haugen 2006), including studies of food webs (Amundsen *et al.* 2003a, Sharma and Borgstrøm 2008b, Linløkken and Hesthagen 2011). In relation to these food-web related studies there has been numerous studies on the accumulation of various pollutants (mercury, DDT, PCB, etc) (Frøslie *et al.* 1985, Brevik *et al.* 1996, Amundsen *et al.* 1997, Okelsrud *et al.* 2016).

The perch is distribution in areas that was heavily impacted by acidification. Thus, several studies focussed on the effects and potential recovery following the reduction in acidification (Hesthagen *et al.* 1993, Øxnevad *et al.* 1995, Saksgård and Hesthagen 1995, Østbye *et al.* 1997, Poléo *et al.* 1997). Clearly, the various studies that has been performed on perch has produced a general understanding of the ecology of this species. The perch also seems very resilient towards various ecological stressors. However, as evidenced by what is happening in the Baltic Sea where perch and pike has been reduced drastically during recent years (Bergström *et al.* 2015, Eklöf *et al.* 2020), we need to keep an eye also on this species.

The two other percid species (ruffe *Gymnocephalus cernuus* (Linnaeus, 1758) and pikeperch *Sander lucioperca* (Linnaeus, 1758)) have a very limited distribution in the south-eastern part of Norway, and only a very few studies were found focussing on these species (Table 1). Actually, the retrieved studies only rarely focussed on the ecology of these two species (Brabrand 1983, Vøllestad 1985, Kålås 1995, Hesthagen *et al.* 2012), and they were mostly published in Norwegian. This lack of focussed studies on these species are unfortunate, as they tend to be important parts of the food-web in lakes where they occur (Brabrand and Faafeng 1993).

### Centrarchidae

Fish belonging to the family Centrarchidae is native to North America, and thus the species found in Norway (pumpkinseed *Lepomis gibbosus* (Linnaeus, 1758)) is a recent introduction (Sterud and Jørgensen 2006). The species has a very limited distribution, and is expected to have a limited ecological impact (Hesthagen and Sandlund 2007). However, there is basically no available knowledge about its ecology and potential interaction with other parts of the local food webs.

## CONCLUDING REMARKS

In this paper I have tried to critically evaluate the research that has been performed on Norwegian freshwater fishes during 1980-2020. By using a rather simple search query in the Web of Science I retrieved over 2000 published articles, indicating a relatively high publication rate in general. These articles are not all the articles that have been produced in the time period, but my assumption is that they give a good and representative picture about the research that has been performed. What the results show is that Norwegian research on the freshwater fishes is strongly biased towards a very few species. It is also evident that very little research effort is directed towards the species that have been listed on the Norwegian Red List, and also towards the 12 species that are considered as non-native.

It is understandable that much research effort should be directed towards species of economic interest, and also towards species that are widely distributed in the country. However, it is not to be expected and very unfortunate that almost no research activity has been directed towards a large number of species that either are rare (sometimes even red-listed), are newly invaded fish (based on human transport) to the country or to new regions, or may potentially have important functions in the ecosystem. This very biased knowledge base clearly will challenge our ability to properly manage and conserve fish diversity in Norwegian freshwater systems. This bias towards production of knowledge on a biased list of species is also evident on a global scale (Guy *et al.* 2021). This is particularly problematic given the climatic vulnerability of the world's freshwater fishes (Comte and Olden 2017, Staudinger *et al.* 2021) and the potential ecological impacts invasive non-native fishes may have (Cucherousset and Olden 2011). Why this bias in research focus has developed is not part of this study, but should clearly be a topic of further enquiry. What is evident, however, is that research effort is a direct result of the availability of funds and the geographic distribution of researches with particular interests. The development of a knowledge base at the national level should not be dependent on the interests of individual researches and their efforts, but rather the result of long-term planning and investment by relevant authorities and institutions. The summary of research effort provided in Table 1 may indicate to funding institution where research efforts needs to be directed, and my evaluation of the previous research activity may give an indication as to what kind of knowledge is most urgently needed.

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