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Environmental drivers of food webs in charr and trout-dominated cold-water lakes

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Abstract

Cold-water lakes situated in high latitudes and altitudes have pivotal socio-ecological importance both globally and locally. However, they are increasingly threatened by multiple anthropogenic stressors, such as climate change, hydropower and invasive species. The development of efficient management strategies is therefore urgently needed and requires a comprehensive understanding of the factors influencing the biodiversity and ecological processes of these ecosystems. We provide a holistic knowledge base for informed future research and management by addressing the interplay between local and global environmental drivers of food webs in Arctic charr (*Salvelinus alpinus*, Salmonidae) and brown trout (*Salmo trutta*, Salmonidae) dominated cold-water lakes in Fennoscandia. The trophic niche and population dynamics of these generalist top consumers provide extensive insights into the effects of natural and anthropogenic drivers on food webs in intensively studied Fennoscandian cold-water lakes, covering marked biogeographical gradients in abiotic and biotic conditions. Drawing on a synthesis of existing literature, our focus is on three pivotal drivers: (1) lake location and connectivity, (2) lake area and morphometry and (3) fish community composition. These drivers significantly influence the complexity and the origin and flow of energy in lake food webs, and ultimately the size structure of the charr and trout populations. Furthermore, we highlight ongoing environmental changes in Fennoscandian cold-water lakes caused by hydropower and invasive species. Finally, we identify crucial knowledge gaps and propose management actions for improving the future state of Fennoscandian cold-water lake ecosystems and their charr and trout populations.

KEYWORDS
Arctic, food-chain length, population size-structure, subarctic, trophic ecology, trophic niche

1 | INTRODUCTION

Northern lakes are socio-ecologically important ecosystems that are increasingly subjected to multiple anthropogenic stressors including climate change, invasive species and hydropower (Heino et al., 2009, 2020, 2021; Rolls et al., 2017). Most of the recent environmental changes seen in northern freshwater ecosystems have been driven by anthropogenic stressors and the magnitude of local and global stressors acting on these habitats has drastically increased in recent decades (Heino et al., 2009; Lento et al., 2019). What makes northern lakes especially vulnerable to environmental change are their relatively simple communities controlled by cold-adapted, generalist top predators, namely salmonid fishes (Christoffersen et al., 2018). Moreover, the changes that are occurring in northern lake ecosystems affect the socio-economical and physical well-being of local communities (Lento et al., 2019), making it important to increase our knowledge of the structure and function of these ecosystems to better understand their potential responses to anthropogenic stressors (Harvey et al., 2017). Improved understanding will help in developing urgently needed management and monitoring actions and may additionally benefit the sustainable development of local ecosystem services (Heino et al., 2020; Lento et al., 2019).

To comprehensively understand how anthropogenic stressors affect northern lakes, it is important to expand our knowledge on how the landscape, that is, the catchment area, geographical location of the lake, connected rivers and streams, and the lake-specific environmental conditions affect the lake ecosystem (Heino et al., 2021; Soininen et al., 2015). Food web studies provide a useful framework for this as they integrate the fluxes of energy and nutrients through the biotic community (Alp & Cucherousset, 2022; Thompson et al., 2012). The structure (e.g., species diversity, number of nodes and links) and function (e.g., energy flow in the ecosystem) of northern lake food webs are determined by multiple drivers, such as lake area, the fish community assemblage and lake productivity (Amundsen et al., 2010; Eloranta, Kahilainen, et al., 2015; Karlsson et al., 2009; Laske et al., 2019). Although many of these drivers are well studied, we lack a comprehensive synthesis of their effects on food webs that could serve as a guideline for policymakers and stakeholders, reveal fundamental knowledge gaps and provide suggestions for future research and management.

Here, we provide a synthesis of the main environmental drivers of food webs in northern and high-altitude lakes (hereafter cold-water lakes) in Fennoscandia, defined as mainland Norway, Sweden and Finland. By focusing on lakes in Fennoscandia, representing a wide range of latitudinal and altitudinal environmental variation, we provide a simple framework for disentangling large ecological questions in an approachable setting. Additionally, as these lakes have been extensively studied over many decades, they provide a useful basis for a comprehensive synthesis. Although our focus is on Fennoscandian cold-water lakes corresponding patterns can be expected to be found in other regions with similar environmental conditions but different species compositions, such as the subarctic

and Arctic regions of North America, and high-altitude lakes of central and southern Europe (Hershey et al., 1999; Laske et al., 2019).

We focus on lakes dominated by Arctic charr (*Salvelinus alpinus*, Salmonidae; hereafter charr) and brown trout (*Salmo trutta*, Salmonidae; hereafter trout). Charr and trout are considered of high socio-economic importance, particularly in remote Arctic regions where they provide highly nutritious food and numerous cultural values for indigenous people (Roux et al., 2011). In Fennoscandia, charr and trout are among the most valued fishes for recreational and commercial fishing, with fish tourism creating jobs and income for numerous business sectors (accommodation, restaurants, fishing guide, nature tourism) (Liu et al., 2019). Both species are highly adapted to cold and oligotrophic environments, making them particularly vulnerable to environmental changes, such as climate change-induced warming (Jeppesen et al., 2010; Klemetsen et al., 2003). In the subarctic and Arctic regions of Fennoscandia, the higher trophic levels of food webs are often dominated by these two generalist top consumers (Bartley et al., 2019; Karlsson & Byström, 2005; Klemetsen et al., 2003; Sánchez-Hernández et al., 2017; Vander Zanden & Vadeboncoeur, 2002). Hence, the ecosystem services provided by charr and trout are not restricted to only human welfare as these generalist keystone species play critical roles in the structuring and function of the freshwater ecosystems they inhabit (McMeans et al., 2016). Moreover, charr and trout are of particular concern in the management and conservation of Fennoscandian

cold-water lakes as their adaptive foraging increases food web stability and their behavioural responses can act as first warning signals of major ecosystem disturbances (Bartley et al., 2019).

Our review is structured in three parts. Firstly, we describe the process and results of the systematic literature search in the Methods section. During the process of literature search, we have defined three key environmental drivers that affect cold-water lake food webs (location and connectivity, lake area and morphometry, and fish community composition), further defined in the next chapter and in Table 1. We have also defined three key food web properties that depict the changes in the ecosystem structure and function, following the influence of the environmental drivers (food web complexity, origin and flow of energy in food webs, and size structure of charr and trout populations; Figure 1). Each food web property is defined at the beginning of the corresponding chapter and in Table 1. Secondly, we review each food web property and discuss how it is affected by each of the environmental drivers, as depicted in Figure 1. Finally, we provide a short synthesis of local stressors and future directions of cold-water lake food webs and propose some future management and monitoring actions as well as key areas for further research.

2 | METHODS

We conducted a systematic literature search following standard procedures (see e.g., Foo et al., 2021), with the process summarised in Figure 1. Firstly, we conducted a scoping literature search using online databases including Web of Science (WOS), Scopus, Aquatic Sciences and Fisheries Abstracts (ASFA) and Google Scholar. Based on the scoping search and multiple iterations of the search string we formatted the final search string and conducted the final literature search in three different databases (WOS, ASFA and Scopus). The search was limited to topic fields (i.e., title, abstract and keywords) and peer-reviewed scientific publications. Each publication had to include at least one word from each of the following categories:

1. *System type*: lake OR freshwater
2. *Region*: Arctic OR subarctic OR high-latitude OR high-altitude
3. *Food web terms*: "food web*" OR "foodweb" OR "food-web" OR "energy mobilisation" OR "energy transfer" OR "food chain" OR "trophic level" OR "trophic position" OR "trophic niche" OR "trophic interaction*" OR "trophic dynamic*"

TABLE 1 Definitions of food web properties and environmental drivers.

	Definition
Food web property	
Food web complexity	Food web complexity includes both structural and functional dimensions. Structurally, complexity increases with the increasing number of nodes (representing species and morphs) and links (depicting interactions within and between species, primarily predation). Functionally, broader niche widths at both the individual and population levels for charr and trout indicate more complex food webs
Origin and flow of energy in food webs	Origin refers to the source of carbon utilised in a food web. This source can be categorised as pelagic (derived from phytoplankton), benthic (produced by littoral benthic algae) or allochthonous (originating from outside the lake, such as terrestrial organic matter). Flow of energy refers to how these various energy sources are utilised by different consumers, here focusing on charr and trout. This relationship can be examined through stable isotope analysis, which assesses whether the carbon within the consumer tissue originates from a pelagic source (indicated by low δ^{13}C values) or a benthic source (indicated by high δ^{13}C values)
Size structure of charr and trout populations	Population size structure refers to the number of individuals in different size classes (body size) of charr and trout populations. Different size structures include for example populations consisting of equal numbers of small, intermediate and large individuals, populations consisting of predominantly small individuals (dwarfed population) or populations consisting of many small and large individuals and only few of intermediate size (bimodal population). Body size significantly influences the diet of individuals through factors like gape-width limitation and predation risk, making it a crucial factor to consider when studying food webs.
Environmental driver	
Location and connectivity	Location and connectivity refer to the latitude and altitude of the lake, along with the associated catchment characteristics. This includes considerations of whether the lake is situated in mountainous or northern regions, often characterized by sparse vegetation and colder climates, or in more southern or lower latitude areas, indicative of richer vegetation and warmer climates in the catchment. Connectivity refers to the surface water connectivity of the lake, that is, how well the lake is connected to other water bodies by free-flowing streams and rivers
Lake area and morphometry	Lake area and morphometry encompass the surface area and depth of the lake, as well as the morphological characteristics of its basin. This includes considerations of whether the lake features a uniform depth across its basin or if it comprises shallow and deep areas, influencing the proportion of littoral, pelagic and profundal habitats
Fish community composition	Refers to both the fish community assemblage (what fish species and morphs of species are present in the lake) and how these species interact (competition and predation) within and between populations
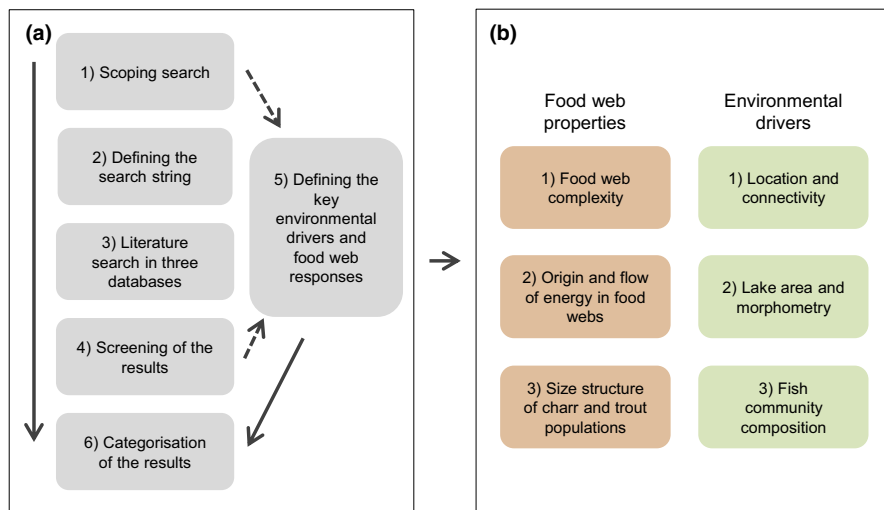
FIGURE 1 (a) A flowchart illustrating the systematic literature search process, with dashed lines representing how the results of the scoping search (2) and the screened results of the literature search (4) were used to define the environmental drivers and responses (5). Solid lines represent the flow of the literature review process. (b) The food web properties and environmental drivers used in the structuring of this paper. For each food web property, the effect of each individual driver was synthesised and discussed separately.

4. *Target species*: "arctic char*" OR "salvelinus alpinus" OR "salmo trutta" OR "brown trout"

The literature search was conducted on 13 March 2024. After removing the duplicates, we had 207 results. We then screened the papers based on title, abstract and if needed (for example to define the geographical area of the study), the full text. Included papers needed to meet the following criteria: (1) paper focuses on Fennoscandian lakes with charr and/or trout; (2) paper focuses on food webs or trophic dynamics; (3) paper focuses on the open-water season, as most of the research has been conducted during that period; and (4) paper does not focus on anadromous charr and/or trout populations. Anadromous populations were excluded as their population dynamics and potential impacts on food webs are typically associated with complex cross-ecosystem processes (marine versus freshwater) that are hard to generalise for resident charr and trout populations and the food webs that support them (Klobucar & Budy, 2020; Laske et al., 2019). After screening, 42 papers remained. A list of these publications can be found in Table S1. It is important to note that while the results provide a robust representation of the current literature, they may still not encompass all published studies on the topic to date. Furthermore, we have expanded the scope of references in this paper beyond the findings of our literature search to include widely cited papers dealing with Arctic or high-latitude systems that address broader ecological principles or that focus on comparable geographical regions outside Fennoscandia. This approach highlights both the distinctions and parallels evident in cold-water lake food webs across Arctic and subarctic regions, while also emphasising the unique characteristics of Fennoscandian lake ecosystems.

We identified three key environmental drivers and three food web properties that were used in structuring this paper (Figure 1). The drivers and properties describe the effects of abiotic and biotic factors on the structure and function of food webs in cold-water lakes in Fennoscandia. To define the drivers and properties, we used the listing of topics from the final search results coupled with a word cloud analysis of the scoping search results to identify drivers and properties that appear frequently in the abstracts of the papers. Similar drivers and properties were pooled together (e.g., latitude and altitude of the lake = location) and the most commonly occurring three were chosen as the key drivers and properties (Figure 1).

The three environmental driver groups were: (1) the location and degree of surface-water connectivity among lakes; (2) the area and morphometry of lakes; and (3) fish community composition in the lakes, encompassing the assemblage and trophic interactions within and between coexisting fish species (defined in Table 1). Correspondingly, the three food web and ecosystem level properties were (1) complexity of the food web; (2) origin and flow of energy within the food webs and (3) the size structure of charr and trout populations (further defined in coming chapters and Table 1).

To estimate the relative prevalence of each driver and food web property in the current literature, we manually categorized the literature search results (42 papers) into their respective environmental driver and food web property groups (Table S1). We allowed each paper to be linked with as many groups as applicable—meaning one paper could be associated with one, two or all three environmental driver and food web property groups (Figure 1). Based on the categorisation of the results, fish community composition was studied the most (31 publications), lake area and morphometry the second most (13 publications), and location and connectivity of the lakes the least (8 publications). Regarding the food web properties, food web complexity, and origin and flow of energy in food webs were studied the most (34 and 32 publications, respectively), and the size structure of charr and trout populations the least (15 publications). In the following sections, we synthesise the main relationships among the environmental drivers and food web properties, with key findings summarised in Table 2 and Figure 2.
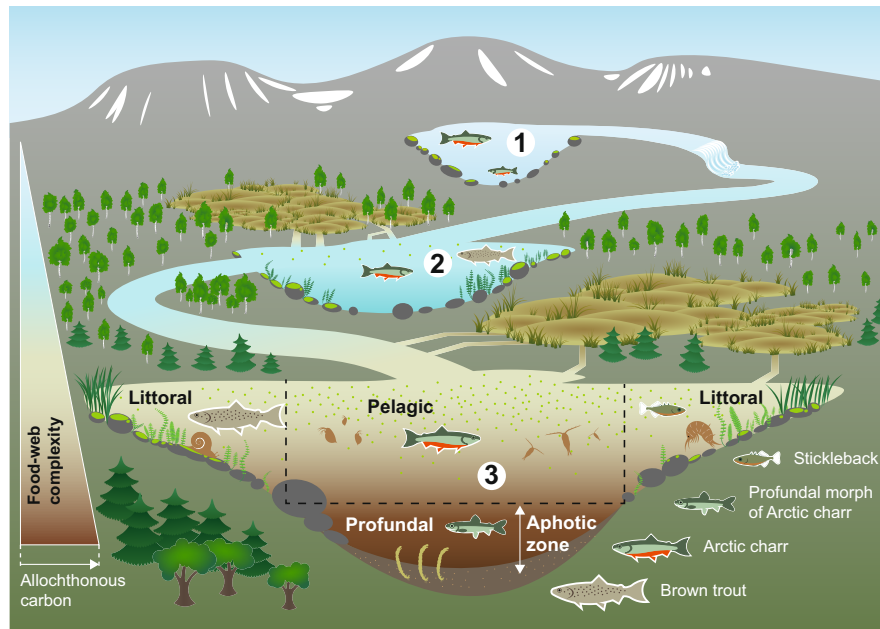
3 | FOOD WEB COMPLEXITY

Food web complexity is an important factor to consider when studying cold-water lakes. It can refer to the topological structure of food

FIGURE 2 A schematic illustration of the main environmental drivers affecting charr and trout populations and food webs in cold-water lakes. (1) Lakes that are situated at high altitudes and/or are isolated typically have simple food webs due to species-poor communities (often only charr or trout) and limited availability of pelagic and terrestrial carbon and nutrient sources. High intraspecific competition can lead to niche expansion of charr and trout populations. Charr may also shift to cannibalism, which increases food web complexity. (2) Littoral benthic production usually dominates the primary and secondary production in clear and oligotrophic cold-water lakes. Hence, in allopatric lakes, charr and trout populations typically rely heavily on benthic food resources. In contrast, the sympatric populations of charr and trout often segregate to pelagic/profundal and littoral benthic trophic niches, respectively, to reduce resource competition. (3) Larger and deeper lakes at lower altitudes have a higher diversity of food resources, habitats and species, leading to more complex food webs and longer food chains. With increasing lake area, charr shifts to pelagic resources. Larger lakes may also facilitate the development of ecologically distinct morphs of the same species, such as profundal small benthivorous and/or large piscivorous morphs of charr. Figure by Mãris Grunskis.

webs (i.e., number of nodes and links) or to the processes that shape the variation in diets of individuals and populations (i.e., variation in the trophic niche) (Amundsen et al., 2009; Dunne et al., 2002). Understanding the complexity of food webs provides important insights on trophic interactions within the ecosystem and can reveal how landscape properties may, for example, impact community's ability to withstand and adapt to environmental change (Mougi & Kondoh, 2016). Here, we define food web complexity as the number of nodes (species and morphs) and interactions (within and between species competition and predation) in a food web. In other words, more complex food webs have more nodes and more interactions. In addition, we further examine complexity by considering the variation in individual and population level niche width of charr and trout, and what affects the size of it, with wider niche width reflecting a more complex food web.

3.1 | Location and connectivity

Across the Arctic region, including Fennoscandia, the post-glacial immigration history of species largely determines the diversity and abundance of freshwater fish species and thus the food web complexity of cold-water lakes (Hershey et al., 1999; Tammi et al., 2003). In Fennoscandia, following the last ice age, two main routes dominated

the immigration of fish species: (1) the eastern and southern routes where immigrants entered through the Ancylus Lake (the freshwater phase of the current Baltic Sea) and (2) the western route where immigrants entered from the North Atlantic Ocean. Accordingly, the western immigrants were confined to a few species that could tolerate colder saline water, that is, predominantly salmonids and three-spined stickleback (*Gasterosteus aculeatus*, Gasterosteidae). Immigrants using the Ancylus route were more diverse and included warm-water-adapted species, such as cyprinids that entered from the south, and cold-water-adapted species, such as coregonids, perch (*Perca fluviatilis*, Percidae) and pike (*Esox lucius*, Esocidae) that entered from the east (Tammi et al., 2003). The central Scandinavian Mountain range constituted an effective dispersal barrier that kept the two fish assemblages mostly separate.

Fennoscandia covers a wide geographical area and encompasses a large variation in climatic conditions and vegetation (Moen, 1999). This makes the climate-related geographical factors (mainly latitude and altitude) important for determining the distribution of fish species. Warm-water-adapted species are mostly confined to the lowland and southern areas, and cold-water-adapted species to higher altitudes and latitudes (Klemetsen et al., 2003; Power et al., 2008; Tammi et al., 2003). Accordingly, we presently find three types of fish communities in Fennoscandian lakes: (1) species-poor systems dominated by the cold-water-adapted charr and/or trout located to

the north and west, and in mountainous areas, (2) semi-diverse systems dominated by cold-water-adapted species like coregonids, pike and perch, primarily located to the east, and (3) species-rich systems with a high diversity of fish species, such as pike, perch and cyprinids, mostly confined to the larger lakes of southern Finland and Sweden (Figure 3).

On a regional scale, the geomorphology of the immediate lake landscape plays an important role in determining the distribution of fish species (Figure 2). In North American high-latitude lakes, the positive relationship between increasing surface-water connectivity and fish species richness has been associated with increasing food web complexity, illustrating how landscape properties may indirectly control lake trophic structure via fish species distribution (Hershey et al., 1999; Laske et al., 2019). Similar geomorphic drivers are also important in Fennoscandian lakes, where the number of fish species has been shown to decrease with altitude, often related to decreasing lake connectivity (Tammi et al., 2003; Figure 3). However, it should be noted that the existing fish diversity results from a combination of drivers such as lake temperature and area and the migration history of resident fish species (Hesthagen & Sandlund, 2007; Klemetsen et al., 2003; Tammi et al., 2003).

3.2 | Lake area and morphometry

Besides location in the landscape, lake area and morphometry are essential drivers of food web complexity (Figure 2; Table 2). Across the Arctic regions, in larger and deeper lakes, the number of available habitats and resources typically increases, which can support higher fish diversity and biomass (Cordero & Jackson, 2021; Eloranta, Kahilainen, et al., 2015; Nolby et al., 2015). Accordingly,

ecosystem size has been shown to affect food chain length. For example, in some Fennoscandian lakes the trophic position of charr has been observed to be higher in large lakes with multiple fish species as compared to small lakes dominated by charr (Eloranta, Kahilainen, et al., 2015). Increasing lake area and habitat heterogeneity are often related to a wider variety of available resources that can broaden the trophic niche of charr (Eloranta, Kahilainen, et al., 2015). For example, in lakes with deep profundal habitats, charr may switch to less preferred profundal food resources to avoid competition and predators, leading to a broader diet for the population and thus increased overall food web complexity (Knudsen, Amundsen, et al., 2016; Sandlund et al., 2016; Smalås et al., 2013). Such plasticity among individuals (i.e., resource polymorphism) is most common under intense intraspecific competition, low species diversity and in the presence of many diverse resources that can support individual-level variation in diet (Jonsson & Jonsson, 2001; Skúlason et al., 2019). Resource diversity typically increases with lake surface area (Cordero & Jackson, 2021; Nolby et al., 2015) and charr polymorphisms have been mostly documented in large and deep lakes in Fennoscandia (Knudsen et al., 2007, 2019; Knudsen, Amundsen, et al., 2016; Moccetti et al., 2019; Simonsen et al., 2017). However, in similar regions across the Arctic, including Ellesmere Island, Greenland, Iceland, Northern Québec and Alaska, resource polymorphisms among charr and trout populations have been documented in both deep and shallow cold-water lakes (Doenz et al., 2019; Guiguer et al., 2002; Jónsson & Skúlason, 2000; Power et al., 2009; Woods et al., 2013). This illustrates both the importance of other aspects of lake morphometry (i.e., depth) and the difficulty of establishing clear links between lake area and the degree of resource polymorphism, particularly as the latter is also affected by competition and predation, including cannibalism (Andersson et al., 2007; Hammar, 2000).
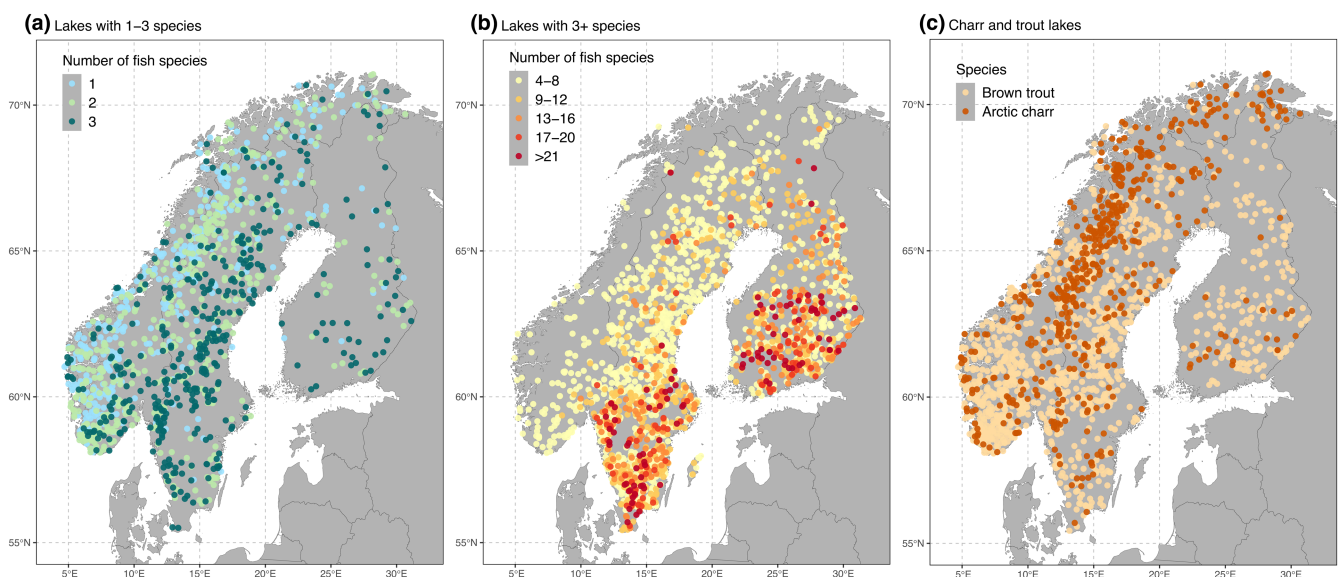
FIGURE 3 Maps of freshwater fish species richness in Fennoscandian (mainland Norway, Sweden and Finland) lakes hosting (a) one to three fish species, (b) over three fish species and (c) charr or trout populations. Data from Henriksen et al. (1998).

3.3 | Fish community composition

As illustrated above and in Figure 2 and Table 2, fish species diversity and the trophic interactions within and between species are key drivers of food web complexity in cold-water lakes. Traditionally, high interspecific competition for shared resources has been argued to restrict the niche width of coexisting species (Roughgarden, 1974). Accordingly, interspecific competition between charr and trout has often been documented to lead to niche compression for both species, as the more flexible and generalist charr shifts to use pelagic and/or profundal resources such as zooplankton and chironomid larvae (Eloranta et al., 2011; Eloranta, Knudsen, & Amundsen, 2013; Jensen et al., 2017; Sandlund et al., 2016), while the more aggressive and competitively superior trout dominates the preferred littoral benthic habitat and food resources (Klemetsen et al., 2003; Nilsson, 1963, 1967; Prati et al., 2021; Sánchez-Hernández & Amundsen, 2015). Unlike charr, trout has been shown to remain within a relatively stable trophic niche in subarctic Lake Takvatn (Norway), regardless of the long-term fluctuations in charr and trout densities and the apparent intensity of intra- and interspecific interactions (Prati et al., 2021). In contrast to interspecific competition, high intraspecific competition has often been documented to lead to individual-level diet variation, which can increase the population-level niche width of charr (e.g., Amundsen, 1995; Prati et al., 2021).

In general, predatory interactions commonly affect the resource use of both prey and predator species as increasing predation risk often causes prey to use refuge habitats and, consequently, a more specialised diet (Werner et al., 1983; Werner & Gilliam, 1984). Both charr and trout are well-documented predators, known to prey on smaller members of their own species, and on various other fish species including three-spined sticklebacks, whitefish, vendace (*Coregonus albula*, Salmonidae), smelt (*Osmerus eperlanus*, Osmeridae) and bullhead (*Cottus* sp., Cottidae) (Eloranta, Kahilainen, et al., 2015; Eloranta & Jones, 2022; Finstad et al., 2001; Hammar et al., 2018; Kahilainen et al., 2019; Sánchez-Hernández & Amundsen, 2015; Sánchez-Hernández et al., 2017; Thomas et al., 2017). These predatory interactions can have various effects on the trophic niche of charr and trout, and typically the effects change with increasing body size (Eloranta et al., 2010; Hammar et al., 2018; L'Abée-Lund et al., 1992; Sánchez-Hernández et al., 2017, 2022). Ontogenetic niche shifts (i.e., changes in the trophic niche with increasing body size) can expand the niche width and degree of omnivory in charr and trout, resulting in more complex lake food webs (Sánchez-Hernández et al., 2019). Such niche shifts are typically more common in lakes with multiple fish species where small-sized prey fish can facilitate the shift to piscivory for large charr and trout, resulting in increased food-chain length, population-level niche width and overall food web complexity (Amundsen, 1994; Eloranta et al., 2019; Eloranta, Kahilainen, et al., 2015; Kahilainen et al., 2019; L'Abée-Lund et al., 1992).

Overall, the effects of fish community composition on ontogenetic niche shifts and trophic interactions between charr and trout significantly influence the complexity of food webs in cold-water lakes. Interspecific competition typically narrows population-level niches, while intraspecific competition tends to broaden them. Predatory interactions further shape resource use and trophic niches. However, future studies might consider potential drivers of intraspecific and individual-level niche variation among charr and trout to address knowledge gaps focusing on the complexity of food webs.

4 | ORIGIN AND FLOW OF ENERGY IN FOOD WEBS

A holistic view of lake food webs requires knowledge about the origin and flow of energy from basal resources to top consumers. Here, we refer to origin as the basal source of carbon incorporated in the food web, that is, how much of the carbon is pelagic (produced by phytoplankton), littoral benthic (produced by littoral benthic algae; hereafter benthic) or allochthonous (from outside the lake, e.g., terrestrial). The flow of energy refers to how these different energy sources subsequently are utilised by charr and trout. In past decades, stable isotope analyses have become a widely used method for studying the proportion of benthic versus pelagic carbon in the long-term diet of fish, including charr and trout (e.g., Eloranta et al., 2011; Eloranta, Knudsen, & Amundsen, 2013; Eloranta, Nieminen, & Kahilainen, 2015; Karlsson & Byström, 2005). The stable isotopes of carbon (represented as δ^{13}C values) in fish muscle tissue reflect the long-term assimilated diet of fish, with lower δ^{13}C values typically indicating a more pelagic diet and higher values a more benthic diet (Layman et al., 2012). Consequently, this methodology serves as a valuable and commonly used tool for determining the source and flow of energy in lake food webs.

Understanding energy flows can help us to better predict how cold-water lake food webs and ecosystems respond to regional and global changes for example in climate and land use (e.g., Keva et al., 2021). The landscape and within-lake properties determine the abiotic (e.g., water quality, temperature and habitat availability) and biotic (e.g., community composition) conditions of lakes and the consequent contribution of pelagic and benthic production to overall lake primary production (Vadeboncoeur & Steinman, 2002; Puts et al., 2022; Figure 2; Table 2). In Fennoscandia and other similar regions across the Arctic, generalist top consumers such as charr and trout play an important role in the coupling of benthic and pelagic habitats and food web compartments through their flexible foraging (Eloranta, Knudsen, & Amundsen, 2013; Schindler & Scheuerell, 2002; Vander Zanden & Vadeboncoeur, 2002). Moreover, the productivity and flow of benthic and pelagic energy sources determine the growth and biomass of large-growing top consumers, with high benthic production in clear-water lakes typically supporting higher fish growth and biomass (e.g., Karlsson et al., 2009; van Dorst et al., 2019) and the associated ecosystem services such as fishing (Holmlund & Hammer, 1999). Here, we synthesize how both landscape and within-lake properties can affect the origin and flow of energy in cold-water lake food webs, with a

special focus on understanding the balance between benthic and pelagic energy pathways supporting the generalist top consumers of interest, that is, charr and trout.

4.1 | Location and connectivity

Location in the landscape is a key environmental driver influencing the origin and flow of energy in lake food webs. At high latitudes and altitudes, the energy supply of lake consumers is predominantly autochthonous as the cold climate, scarce terrestrial vegetation, permafrost and short open-water season result in a low input of terrestrial-derived carbon and nutrients (Lyons & Finlay, 2008; Figure 2). However, charr and especially trout can also utilise terrestrial-derived carbon for example, by feeding on terrestrial invertebrates on the water surface and occasionally also on small rodents (Eloranta & Jones, 2022; Milardi, Käkelä, et al., 2016; Milardi, Thomas, & Kahilainen, 2016). In clear and oligotrophic lakes, the large proportion of illuminated bottom areas supports the high growth of photosynthetic benthic algae (Björk-Ramberg & Ånell, 1985; Karlsson et al., 2009; Karlsson & Byström, 2005; Vadeboncoeur & Steinman, 2002; Figure 2). Low nutrient concentrations in the water column also limit the growth of pelagic phytoplankton, which increases the benthic proportion of lake gross primary production (GPP) (Karlsson et al., 2009; Vadeboncoeur & Steinman, 2002). At both lower latitudes and altitudes, temperature, catchment vegetation and total lake GPP typically increase, shifting lake communities towards dominance of pelagic production (Hayden et al., 2019; Keva et al., 2021). Overall, location significantly influences cold-water lake basal energy sources, with consumers in high-latitude and high-altitude lakes predominantly relying on benthic primary production.

Recent studies of GPP in shallow northern Swedish lakes have demonstrated how catchment characteristics can have interactive effects on total GPP and the relative share of benthic versus pelagic primary production (Puts et al., 2022). Increasing terrestrial vegetation and warmer climates at lower latitudes and altitudes often lead to the increased runoff of dissolved organic carbon (DOC) into lakes, which can either support or reduce total GPP. In highly oligotrophic cold-water lakes, moderate increases in DOC can lead to increased GPP, whereas in more nutrient-rich subarctic and boreal lakes, high DOC concentrations can decrease GPP due to a reduction in light availability that limits the growth of benthic algae and phytoplankton (Seekell et al., 2015; Puts et al., 2022). The importance of benthic versus pelagic GPP is in turn mainly influenced by the relative size of the littoral benthic zone, which is determined by the interactive effects of the light attenuation coefficient (the rate at which light decreases in intensity as it travels through water) and lake bathymetry (Puts et al., 2022). Consequently, in a study of nutrient-poor Swedish lakes, fish were found to mainly use benthic food resources and to have higher population biomass with increasing light availability in the benthic areas, rather than with increasing pelagic nutrient concentrations (Karlsson et al., 2009). This highlights how catchment characteristics significantly influence the balance between pelagic

and benthic primary production in cold-water lakes. Forested landscapes typically increase DOC concentrations in lakes and thereby reduce light availability for benthic primary production, shifting food webs towards higher pelagic reliance. Thus, it is important to define thresholds for DOC increases in cold-water lakes, as moderate increases can enhance the overall lake productivity, whereas larger increases can lead to reduced lake GPP, with the magnitude of responses depending on lake bathymetry.

4.2 | Lake area and morphometry

Lake area and depth are two of the main drivers influencing the origin and flow of energy in cold-water lakes (Figure 2; Table 2). Small and/or shallow lakes naturally have relatively large littoral areas that support higher rates of benthic production as compared to large and deep lakes that tend to have relatively high pelagic production (Karlsson & Byström, 2005; Puts et al., 2022). Consequently, charr and trout typically rely more on benthic invertebrates in small and shallow lakes and shift towards higher pelagic reliance in larger and deeper lakes (Eloranta, Kahilainen, et al., 2015). In some large Fennoscandian lakes, the presence of small planktivorous prey fish can facilitate an ontogenetic niche shift to piscivory and thereby increase the pelagic resource use of charr and trout (Eloranta et al., 2019; Eloranta, Kahilainen, et al., 2015; Kahilainen et al., 2019; Kahilainen & Lehtonen, 2003). Similarly, some large and deep Fennoscandian lakes host large-sized planktivorous invertebrates, such as opossum shrimp (*Mysis relicta*, Mysidae), that can support increased pelagic resource use by charr (Gregersen et al., 2006; Knudsen et al., 2019). Besides littoral benthic and pelagic habitats, the aphotic profundal zone can also serve as an important additional habitat for salmonid fish species, offering thermal refugia and a relatively vacant niche (Eloranta et al., 2011; Knudsen, Amundsen, et al., 2016). However, the research to date conducted in Fennoscandian cold-water lakes has mainly focused on the source and flow of energy in the pelagic and littoral benthic niches, leaving the role of profundal resources as an important topic for future research. For example, how does the utilisation of profundal resources by charr and trout vary along large biogeographical gradients (e.g., ecosystem size, climate, productivity and connectivity)? Such understanding would help in developing a more holistic understanding of habitat coupling and the population and community dynamics of charr and trout in cold-water lakes.

4.3 | Fish community composition

Fish community composition is another critical factor influencing the origin and flow of energy in cold-water lake food webs (Figure 2; Table 2). Sympatric populations of charr and trout often segregate into pelagic/profundal and littoral benthic trophic niches, respectively (Paterson et al., 2019), which can in turn reduce coupling between the benthic and pelagic habitats and food web compartments

(Eloranta, Knudsen, & Amundsen, 2013). In lakes with abundant charr, whitefish and grayling (*Thymallus thymallus*, Salmonidae), charr often utilise profundal benthic habitats and small prey fish, while the more zooplanktivorous whitefish utilises the pelagic resources and grayling feeds on littoral benthic invertebrates (Amundsen et al., 2010; Eloranta et al., 2011). A restricted pelagic or profundal trophic niche for charr can also be found in the large and deep lakes of southern Norway where the species coexists with abundant trout, whitefish, perch and/or roach (*Rutilus rutilus*, Cyprinidae) (Sandlund et al., 2016). In addition to effects on benthic and pelagic energy flow, potential negative interactions with coexisting fishes can reduce the overall biomass of charr and trout (e.g., Eloranta et al., 2016) and thus ecosystem services associated with, for example, fishing (Holmlund & Hammer, 1999). What remains to be studied is how benthic and pelagic energy pathways to top consumers are modified by the fish community composition along large biogeographical gradients. Such large-scale patterns in the origin and flow of energy may, in turn, influence the resource availability for different fish life stages and the size structure of charr and trout populations as addressed in the following section.

5 | SIZE STRUCTURE OF CHARR AND TROUT POPULATIONS

Population size structure refers to the number of individuals within different size classes of the population. The diets of charr and trout are highly influenced by individual body size, making the size structure of charr and trout populations an important ecosystem property to consider when studying food webs. For example, predation risk and gape-width limitation decline with increasing body size, allowing fish to expand their diet (Sánchez-Hernández et al., 2019; Werner & Gilliam, 1984). Thus, understanding the various mechanisms responsible for determining the individual body size of charr and trout, such as ontogenetic niche shifts, is vitally important for the development of holistic understanding of cold-water lake food webs. Consequently, we here disentangle how the size structure of charr and trout populations is related to lake environmental drivers.

5.1 | Location and connectivity

In Fennoscandia, bimodal size distributions (populations that host many small and large individuals, and only few of intermediate size) are frequently observed in charr and sometimes in trout populations (Borgstrøm et al., 2015; Byström, 2006; Finstad et al., 2006). While this bimodality to some extent may be an artefact of sampling procedures (Finstad et al., 2003, 2006), several functional mechanisms promoting it have been proposed. In northern lakes across the Arctic, including Fennoscandia, seasonal variation in the food supply is typically higher compared to southern regions, with prey availability generally diminishing during the winter months (Eloranta, Mariash, et al., 2013; Griffiths, 1994).

Such seasonal variation in food availability can influence population size bimodality, because the limited prey availability can constrain the growth of smaller individuals, whereas larger individuals can have sufficient food supply throughout the winter (Griffiths, 1994). Similarly, in Finnish Lake Saanajärvi, large-sized (>200 mm) charr was shown to maintain seasonally more stable feeding habits, as compared to smaller conspecifics (Eloranta, Mariash, et al., 2013). Low prey availability can also increase cannibalism (Byström, 2006), which has been proposed as one of the main mechanisms promoting size bimodality in charr across the Arctic (Griffiths, 1994; Johnson, 1980), including lake Øvre Skarddørsjø in Norway (Finstad et al., 2001), and various lakes in Svalbard (Hammar, 2000; Svenning & Borgstrøm, 1995), Greenland (Doenz et al., 2019; Sparholt, 1985), and Bear Island (Klemetsen et al., 1985). Alternatively, a study focusing on several salmonid lakes in Northern Quebec proposed that bimodality in salmonid populations arose from the interaction of growth and mortality dynamics, where juveniles express high growth and high mortality, with both becoming more stable with age (Power, 1978).

Recently, several studies of Fennoscandian lakes have concluded that the relationship between the location of the lake (influencing temperature and productivity) and the body size of salmonids, including charr and trout, can often be non-linear (Hayden et al., 2017; Linløkken, 2021). Although small increases in lake temperature and productivity can support charr and trout growth, the mean body size of fish typically decreases in the considerably warmer and more productive lakes found in the southern areas of Fennoscandia (Hayden et al., 2017; Linløkken, 2021). This is likely a consequence of higher pelagic productivity shifting fish community composition towards smaller and more pelagic species (Jeppesen et al., 2010). In lakes with temperatures below the optimal range for maximum growth, elevated water temperatures can enhance the somatic growth of charr, which, in turn, may lead to an overall increase in population biomass (Smalås et al., 2020). However, more substantial temperature rises often result in an increased abundance of warm-water-adapted species exhibiting smaller body sizes, given that the species already exist within the lake or in connected waterbodies (Hayden et al., 2017; Jeppesen et al., 2010). Hence, lake location and connectivity, via their strong control on temperature and productivity, emerge as important but complex drivers of charr and trout population size structure.

5.2 | Lake area and morphometry

Lake area and morphometry are important drivers of population size structure, as the habitat preferences of charr and trout change depending on their body size (Knudsen et al., 2006; Sánchez-Hernández et al., 2022). Fish may shift from a littoral nursery habitat to the open-water pelagic habitat with increasing body size, as larger body size decreases predation risk (Sánchez-Hernández et al., 2019). In large and deep lakes, charr and trout populations often consist of both large and small individuals as the variable habitats of large

lakes facilitate individual differences in growth and life-history trajectories (Knudsen et al., 2007; Knudsen, Amundsen, et al., 2016; Moccetti et al., 2019; Smalås et al., 2013). The relative proportion of benthic versus pelagic productivity has also been shown to influence the biomass and size structure of charr and trout populations in Fennoscandian lakes (Finstad et al., 2014; Hayden et al., 2017; Norman et al., 2022). For example, in a recent study of northern Swedish lakes, high benthic primary production generally supported higher biomass and body size of charr and trout feeding on large benthic macroinvertebrates (Norman et al., 2022). Thus, the influence of lake area and morphometry on the population size structure of charr and trout appears to be highly variable and dependent on other environmental drivers. This highlights the significance of understanding how population size structure can be modified by multiple interactive environmental drivers.

5.3 | Fish community composition

Competition is assumed to be one of the main drivers of charr and trout population size structure in Fennoscandian cold-water lakes, as it can change the among-individual feeding and growth patterns (Nilsson, 1963, 1967; Norman et al., 2022). Consequently, lake fish community composition can shape the size structure of charr and trout populations by promoting different types of competitive interactions (Byström et al., 2007; Eloranta, Kahilainen, et al., 2015; Sánchez-Hernández, 2020; Sánchez-Hernández et al., 2017; Sánchez-Hernández & Amundsen, 2015). Both intra- and interspecific competition promote ontogenetic niche shifts of charr and trout, which can shift the diet of charr and trout for example from zooplankton to benthic macroinvertebrates, and finally to piscivory (Klemetsen et al., 2002; Nilsson, 1967; Norman et al., 2022; Sánchez-Hernández et al., 2019, 2022). These shifts in diet can facilitate higher somatic growth and the occurrence of large individuals within charr and trout populations (Norman et al., 2022; Sánchez-Hernández et al., 2019).

In lakes with no other fish species (allopatric lakes), charr may shift to cannibalism with increasing body size which often results in a bimodal population size structure, as observed in cold-water lakes of Fennoscandia (Amundsen, 1994; Byström, 2006; Knudsen, Gjelland, et al., 2016). Since charr is typically the weaker competitor compared to trout (Eloranta, Knudsen, & Amundsen, 2013; Klemetsen et al., 2003; Paterson et al., 2019; Prati et al., 2021; Figure 2), it may profit from the relaxed competition and acquire a larger body size by being able to feed on large and energy-rich prey such as littoral amphipods in allopatric lakes (Eloranta et al., 2010; Eloranta, Mariash, et al., 2013; Nilsson, 1963, 1967).

Trophic relationships between charr and trout commonly also involve intraguild predation (i.e., mixed competition–predation interactions), where small charr and trout compete for shared resources and large trout feed on small charr (Persson et al., 2013; Sánchez-Hernández et al., 2017, 2022). However, the presence of small-sized prey fish such as three-spined stickleback has been shown to promote trout ontogenetic niche shifts more commonly than the presence of larger, mixed competitor-prey species such as charr (Sánchez-Hernández et al., 2017). Therefore, the size structure of charr and trout populations may largely depend on the fish community configuration, with multi-species fish communities hosting small-sized prey fish and typically supporting larger body sizes and associated higher trophic positions of charr and trout (Eloranta, Kahilainen, et al., 2015; Sánchez-Hernández et al., 2017).

6 | STRESSORS AND MANAGEMENT OF COLD-WATER LAKES

Our synthesis provides a holistic framework for studying cold-water lake food webs by focusing on local and global drivers and considering lakes as integral parts of the connected aquatic and terrestrial ecosystems. Such approach that departs from a narrow, single-lake perspective is a pivotal requirement for advancing the future research and management of cold-water lakes (Heino et al., 2020) and will help identify environmental constraints and develop effective, sustainable solutions for tackling challenges associated with environmental change and the loss of biodiversity in cold-water lake ecosystems.

The food web properties discussed above are intricately connected with numerous ecosystem services that hold significant ecological, cultural and socio-economic importance for local communities. Schirpke et al. (2021) identified ecosystem services relevant to mountain lakes in the European Alps, many of which are also applicable to Fennoscandian cold-water lakes. The ecosystem services of Fennoscandian cold-water lakes are diverse and include the utilisation of lake water for energy production, drinking water sources and the provision of recreational opportunities such as fishing, boating, lakeside hiking and skiing which support local tourism and the economy. In addition, lakes have an aesthetic value and educational significance and are culturally important for indigenous Sámi communities (Fontana et al., 2023; Nuttall, 2007; Schirpke et al., 2021). Charr and trout, as keystone species, also offer numerous other ecosystem services beyond recreational, economic and cultural values. Their generalist feeding behaviour, for example, enhances food web stability, and their responses in resource use serve as early indicators of significant ecosystem disturbances (Bartley et al., 2019; McMeans et al., 2016).

All these ecosystem services are directly and/or indirectly linked to the food web properties of cold-water lakes. For instance, the complexity of food webs, including the presence of different species, and the size structure of charr and trout populations can profoundly influence the recreational value of lakes, particularly for fishing activities. Additionally, the browning of lakes, that is, the increasing water colour of lakes due to increased terrestrial input of DOC can alter the energy flow within food webs but also diminish the aesthetic appeal of lakes (Hayden et al., 2019; Seekell et al., 2015). Thus, changes in food web properties caused by anthropogenic stressors
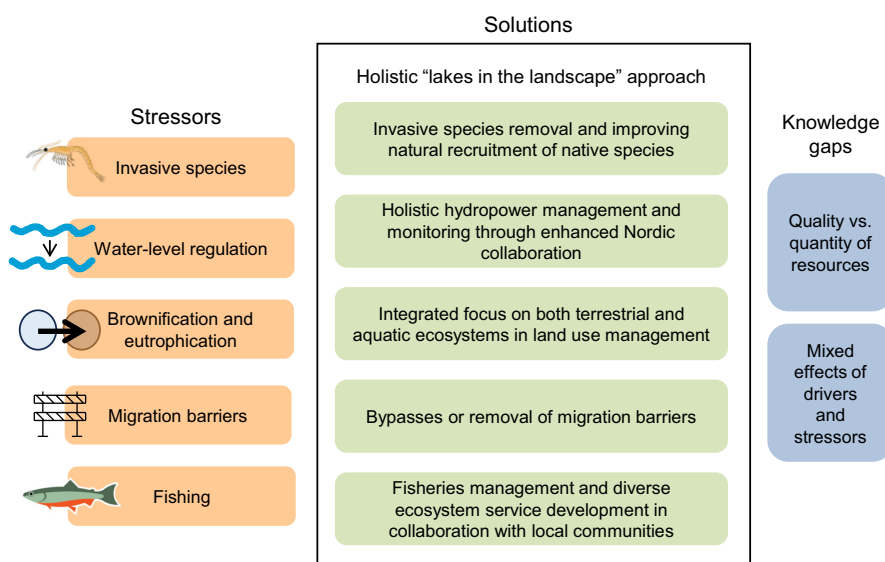
can have far-reaching implications for the sustainability of local ecosystem services (Ebner et al., 2022). Here, we illustrate the impacts of two prevalent regional stressors, hydropower and invasive species, on the food web properties discussed above as well as on the ecosystem services provided by cold-water lakes and propose potential mitigation strategies and highlight key areas for further research (Figure 4).

Hydropower and its associated water-level regulation have been among the biggest and most consistent anthropogenic stressors affecting Fennoscandian cold-water lakes over the past decades (Hirsch et al., 2017). In Norway alone, over 1000 lakes have been transformed into hydropower reservoirs, with some annual regulation amplitudes (difference between the lake minimum and maximum water level) reaching over 100 m (Alfredsen et al., 2022; Hirsch et al., 2017; NVE, 2022). The resulting variation in water levels has been shown to result in erosion of the littoral zone, reduced water clarity and reduced connectivity of the lakes (Hirsch et al., 2017; Milbrink et al., 2011), all of which negatively impact lake ecosystem services by reducing their aesthetic value and the size and quality of fish stocks (e.g., Ebner et al., 2022).

In regulated lakes, charr and trout typically have lower condition and abundance, as the availability of spawning sites and benthic food resources decrease, leading to increased pelagic resource use and competition within and among fish species (Eloranta et al., 2017; Eloranta, Kahilainen, et al., 2015; Milbrink et al., 2011). In a Norwegian hydropower reservoir, water level regulation was shown to negatively affect the condition and growth of trout by decreasing the abundance of energetically profitable, large-sized Arctic tadpole shrimp (*Lepidurus arcticus*, Triopsidae) (Lakka et al., 2020). This suggests that both the food quantity and quality can influence the abundance and body size (and thus the population size structure) of charr and trout, thereby affecting linked ecosystem services such as fishing. Consequently, the significance of resource quality versus quantity is a crucial question for future research. Some potential mitigation solutions for hydropower impacts include habitat restoration (e.g., barrier removals or bypasses, restoration of spawning habitats) and enhanced long-term monitoring of the reservoirs that focuses on the entire river–lake continuum and the surrounding landscape.

Another common anthropogenic stressor that has influenced cold-water lake food webs over the past decades is invasive species (Amundsen et al., 2013; Byström et al., 2007; Eloranta et al., 2019; Eloranta, Nieminen, & Kahilainen, 2015; Museth et al., 2002). Introductions of fish and invertebrate species are common in Fennoscandian lakes and hydropower reservoirs, and often aim to increase food availability and growth of salmonids (Eloranta et al., 2019; Hirsch et al., 2017; Museth et al., 2002). In addition, warm-water-adapted species may also naturally spread towards higher latitudes and altitudes with the warming and eutrophication of lakes (Jeppesen et al., 2010; Rolls et al., 2017). Invasive species may significantly alter lake food webs, ecosystem status and ecosystem services such as the abundance and growth of socio-economically important native salmonids (Eloranta et al., 2019). For example, in Lake Tunhovdfjord (Norway), the food-chain length increased following species introductions, as the introduced charr and European minnow (*Phoxinus phoxinus*, Leuciscidae) facilitated a shift to piscivory for the resident trout population, thus altering both the population size-structure and the food web complexity (L'Abée-Lund et al., 2002). In some large Fennoscandian hydropower reservoirs, introductions of alternative pelagic prey, such as opossum shrimps (mysids), have induced marked changes in the diet of charr and reduced dietary segregation between sympatric charr morphs (Gregersen et al., 2006; Knudsen et al., 2019). Future areas of research and potential mitigation solutions for tackling the impacts of invasive species include studying the specific effects these species have on local ecosystems, removal of invasive species and improving the recruitment of native charr and trout populations through restoration of spawning sites and habitats (Figure 4).

Solutions

Holistic "lakes in the landscape" approach

- Invasive species removal and improving natural recruitment of native species
- Holistic hydropower management and monitoring through enhanced Nordic collaboration
- Integrated focus on both terrestrial and aquatic ecosystems in land use management
- Bypasses or removal of migration barriers
- Fisheries management and diverse ecosystem service development in collaboration with local communities

Stressors
- Invasive species
- Water-level regulation
- Brownification and eutrophication
- Migration barriers
- Fishing

Knowledge gaps
- Quality vs. quantity of resources
- Mixed effects of drivers and stressors

FIGURE 4 A conceptual figure of key anthropogenic stressors acting on Fennoscandian cold-water lake ecosystems, their corresponding potential mitigation solutions and related knowledge gaps that require future research.

So far most of the research on charr and trout populations and food webs in cold-water lakes has focused on one or two anthropogenic stressors at a time. However, lake fish populations and food webs are typically subject to multiple natural environmental drivers and anthropogenic stressors. The interactive effects of multiple drivers and stressors on food webs should be explicitly addressed in future research (Lin et al., 2021). For example, how do the effects of hydropower and invasive species differ in lakes that vary in size, regulation amplitude or location? Such research could help us better develop targeted management and conservation actions and aid in estimating the resilience that different types of cold-water lakes have against environmental stressors.

The impacts of regional stressors depend on the natural characteristics of the lakes, which in turn are influenced by global stressors such as climate change (e.g., Heino et al., 2009). Climate change can lead to an increased abundance of warm-water-adapted species, brownification of lakes, and increased water temperatures and productivity (Arranz et al., 2016; Finstad et al., 2017; Hayden et al., 2019; Jeppesen et al., 2010; Rolls et al., 2017; Figure 4). Such changes will almost certainly have negative impacts on ecosystem services related to recreation, the maintenance of fish populations and the aesthetic value of lakes (Ebner et al., 2022; Fontana et al., 2023). Small and isolated cold water lakes are likely most vulnerable to global anthropogenic stressors as they show rapid responses to climate-related hydrological changes and have low habitat heterogeneity, meaning native biota have restricted access to alternative habitats. On the other hand, many large lakes in Fennoscandia are subject to multiple local stressors, such as hydropower operations, species introductions and intensive fishing, which can all have cascading impacts on the native charr and trout populations and lake food webs (e.g., Thomas et al., 2016; Amundsen et al., 2019; Eloranta et al., 2019; Figure 4). Thus, future research and management actions should identify the most vulnerable and ecologically important ecosystems that are critical for supporting the natural functioning and high biodiversity of cold-water lakes (Heino et al., 2020; Helland et al., 2019). Additionally, we must recognize the ecosystem services that cold-water lakes provide and more actively involve local communities, including indigenous people, in the research, decision-making, and conservation efforts (Knopp et al., 2022).

In summary, having a holistic understanding of food webs in Fennoscandian cold-water lakes is not as straightforward as their seemingly simple structures suggest. The food webs are influenced by multiple environmental drivers and stressors, the cumulative effects of which remain largely understudied and unknown. A holistic approach that views lake food webs as an integral part of their surrounding ecosystems and acknowledges their associated ecosystem services will be crucial in future studies and management of cold-water lakes. We believe our synthesis will help in this by (1) providing an overview of existing knowledge and knowledge gaps critical for understanding the characteristics and drivers of food webs and charr and trout populations in Fennoscandian lakes and other similar regions and (2) stimulating future research critical for linking how anthropogenic stressors impact vital ecosystem services in Fennoscandian cold-water lakes.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

This study does not include new empirical data that could be shared in public archives.

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SUPPORTING INFORMATION

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