



# A systematic review of the trophic ecology of eight ecologically and culturally important fish species in the North American Arctic

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## Abstract

Rapid climate change occurring in the Arctic may affect the diet of ecologically and culturally important northern fish species. Here, a systematic literature review was completed for eight fish species found across the North American Arctic, with a focus on Inuit Nunangat, to identify major prey items, summarize feeding strategies, and highlight data gaps. Arctic Char (*Salvelinus alpinus*), Dolly Varden Char (*Salvelinus malma*), Lake Trout (*Salvelinus namaycush*), Bull Trout (*Salvelinus confluentus*), Inconnu (*Stenodus leucichthys*), Lake Whitefish (*Coregonus clupeaformis*), Broad Whitefish (*Coregonus nasus*), and Burbot (*Lota lota*), were selected as species of interest due to their ecological and cultural importance. The 74 studies reviewed indicate that these species are generalist feeders that demonstrate wide dietary niches, as well as the tendency to avoid agonistic interactions by partitioning resources when they co-occur with an overlapping species. Across coastal, lacustrine, and riverine systems, the most commonly consumed prey items are insects (Diptera spp.), as well as benthic forage fishes such as sculpins (Family: Cottidae). Insects are major prey items in riverine systems, where diets appear to be more generalized, compared to lakes. Anadromous species in coastal waters most commonly feed on various crustaceans and forage fishes. Benthic forage fishes, insects, zooplankton, and mollusks are widely consumed prey items in Arctic lakes. Burbot, Inconnu, and resident Dolly Varden had the most specialized feeding strategies, due in part to their habitat requirements and morphology, while Lake Trout and resident Arctic Char often form multiple ecotypes in lakes, some with different feeding behaviors. Knowledge gaps regarding northern fish trophic ecology are highlighted, and in particular include riverine systems and winter foraging behavior. This review is intended to inform predictions regarding the impacts of climate change on fish trophic ecology and to guide future research.

**Keywords** Arctic · Freshwater · Trophic ecology · Anadromous · Stomach content · Stable isotopes

## Introduction

Climate change is predicted to affect trophic dynamics of fishes and influence geographic range shifts (Brandt et al. 2002; Jackson and Mandrak 2002; Chu et al. 2005), with outcomes anticipated to be particularly acute for the Arctic (Prowse et al. 2006; Hayden et al. 2015; Jansen et al. 2020; IPCC 2022). As temperatures continue to rise, for instance, anadromous life histories may become less common, potentially increasing competition in freshwater (Reist

et al. 2006b). The increased productivity of warmer waters may result in longer growing seasons (Reist et al. 2006a) but may also increase metabolism and therefore energy intake, potentially exacerbating current food limitations (McDonald et al. 1996). Environmental change and any resulting shifts in energy intake may also influence fish growth (Huang et al. 2021). Northward range shifts of sub-Arctic species can also impact the diet of Arctic fishes, as has already occurred with a shift to Capelin (*Mallotus villosus*) and Pacific Sandlance (*Ammodytes hexapterus*), from Arctic Cod (*Boreogadus saida*) and crustaceans as prey for Arctic Char (*Salvelinus alpinus*) in some parts of the species' range (Falardeau et al. 2017; Yurkowski et al. 2018; Ulrich and Tallman 2021a). Range-expanding species may also benefit native species by providing an alternate source of nutrients in typically oligotrophic Arctic systems, as may occur with the continued expansion of Pacific salmon into the Canadian Arctic

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(Dunmall et al. 2013). These range-expanding fish may also, however, compete with Arctic fishes for food, as demonstrated with a high level of diet overlap between increasingly common Capelin and endemic Arctic Cod (McNicholl et al. 2016), and there is potential for trophic interactions between Arctic Char and Atlantic Salmon (*Salmo salar*) in the fresh water (Bilous and Dunmall 2020). The predicted northward expansion of sub-Arctic cyprinids, such as Lake Chub (*Couesius plumbeus*), may also result in competition with native planktivores, such as ciscoes (*Coregonus* spp.), and result in a shift in the prey of top predators (Reist et al. 2006a). Changes in species composition due to northward range expansions may be balanced, however, by potential losses of temperature-sensitive northern fishes, with implications cascading through the trophic web (Reist et al. 2006b). The predicted and apparent impacts of climate change on the trophic ecology of Arctic fishes are indeed complex, with reverberations extending across ecosystems (Reist et al. 2006a) and influencing the food security of northern communities (Lynch et al. 2016; Loring et al. 2019).

The feeding ecology of northern fishes is shaped by their environment, making them adapted to harsh Arctic conditions and, at the same time, particularly vulnerable to warming temperatures (Power et al. 2008; Reist et al. 2006a). Many species in Arctic waters display generalist feeding strategies, allowing them to exploit temporal variance in prey availability, as well as resources from multiple habitat types and trophic levels (Laske et al. 2018). This adaptation also minimizes agonistic interactions with other species, which conserves energy (Power et al. 2008). Generalist feeding strategies are often further coupled with migratory and facultative life history strategies, such as seasonal migrations for feeding or the presence of resident and anadromous forms, that allow selection of optimal feeding environments and food resources (Power et al. 2008). As such, most northern aquatic food chains are short, and end with one to three generalist terminal predator species. These predators often partition prey both within (e.g., specialized ecotypes), or between species when they occupy a similar trophic level (Power et al. 2008; Guzzo et al. 2016).

Arctic Char, Dolly Varden Char (*Salvelinus malma*), Lake Trout (*Salvelinus namaycush*), Bull Trout (*Salvelinus confluentus*), Broad Whitefish (*Coregonus nasus*), Lake Whitefish (*Coregonus clupeaformis*), Inconnu (*Stenodus leucichthys*), and Burbot (*Lota lota*) are ecologically and culturally important fishes in Arctic freshwater or coastal systems. These species are harvested for subsistence among many Indigenous communities and are identified as important species by northern stakeholders throughout the Canadian Arctic (Stewart et al. 2009; McNicholl et al. 2020). In addition to the importance of these species for the food security and nutrition of northern Indigenous communities, fishing is also an important part of Indigenous ways of life, helping

to strengthen community networks, facilitates the transmission of knowledge, and preserve cultural traditions (Proverbs et al. 2020; Galappaththi et al. 2022). The western Arctic populations of Bull Trout and Dolly Varden Char (hereafter: “Dolly Varden”) are also categorized as Special Concern species under the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (COSEWIC 2011, 2013). Additionally, some species, such as Arctic Char, are commercially fished (Galappaththi et al. 2022). Finally, these fishes serve as an important energetic link as a mid-trophic species among coastal ecosystems and as upper trophic predators in freshwater ecosystems.

In order to inform predictions regarding the effects of climate change on culturally and ecologically important fishes in the North American Arctic, a comprehensive overview of available information is required. This was done using a systematic literature review and focusing on eight key Arctic fish species occurring in riverine, lacustrine, and coastal habitats across Inuit Nunangat (traditional Inuit homelands consisting of Nunavut, the Inuvialuit Settlement Region, Nunavik, and Nunatsiavut), while also considering information gathered in the rest of the North American Arctic (the Yukon, Alaska, and the remainder of the Northwest Territories). Our objectives here are to summarize the diet information and feeding strategies of fish species with varying life-history types (resident or anadromous, where applicable) by geographic region, and highlight data gaps related to trophic ecology for these Arctic fishes. This review focuses on the North American Arctic because it was conceptualized around fish species relevant in Inuit Nunangat, and is intended to be most applicable to that region, while also including information on fish species that may become more relevant in Inuit Nunangat as thermal barriers are lowered by climate change. While focused here on the North American Arctic, these results will aid predictions regarding the impacts of climate change on northern fishes more broadly and guide future research that will, together, inform resulting management decisions and improve our understanding regarding the effects of climate change on Arctic aquatic ecosystems.

## Methods

A systematic literature review was conducted to gain a thorough appraisal of diet information on eight selected fish species (Arctic Char, Dolly Varden, Lake Trout, Bull Trout, Inconnu, Lake Whitefish, Broad Whitefish, and Burbot) throughout Inuit Nunangat, as well as the rest of the North American Arctic. The geographic scope of this review was restricted to studies conducted in the Yukon, Northwest Territories (NWT), Nunavut, Nunavik, Nunatsiavut, and Alaska, which encompasses the entirety of the selected

species' geographic distributions in the North American Arctic. While the eight species selected were chosen primarily due to their relevance in Inuit Nunangat, the large spatial scale of this study was required in order to compile a sizeable base of information for these species, given that there is limited knowledge of their feeding ecology in northern ecosystems. Studies investigating the diets of both freshwater populations, as well as those that make marine migrations to feed, were included. To maintain consistency with the language used in the majority of studies on fish that make marine feeding migrations, the term “anadromous” was used, rather than more specific terms such as “diadromous” and “amphidromous.”

Web of Science and the Canadian Department of Fisheries and Oceans (DFO) internal catalogue were chosen as the main literature sources to use a publicly available search engine, provide a broader temporal coverage, and to search technical reports that are not published as scientific journal articles. The search string terms (Appendix 1) were the same for both searches in Web of Science and within the DFO catalogue, but the syntax was modified by removing the Web of Science-specific field tags for the DFO catalogue search. The search results were imported into an Excel (2016) spreadsheet in CSV (comma separated value) format and arranged into a database that contained title, authors, journal, abstract, and DOI.

Papers were subjected to an initial screening of titles and abstracts, followed by full-text screening. Initially, only titles and abstracts of the papers were screened according to the exclusion criteria (Appendix 2) to eliminate papers that did not discuss the target species, were not found within the geographic range, and/or did not have diet information obtained through stable isotope, stomach content, and/or fatty acid analyses. Stomach contents were searched for in order to meet the objective of determining specific prey items, while stable isotope and fatty acid analyses were searched for to give insight into trophic levels and broader patterns of resource use. After screening of abstracts and titles, remaining papers were then subjected to full text screening. First, papers were assessed if they contained feeding data, which was done by examining the methods and results sections, followed by a CTRL + F word search for the terms “diet,” “forag\*,” and “feed,” in case diet information was available elsewhere in the paper.

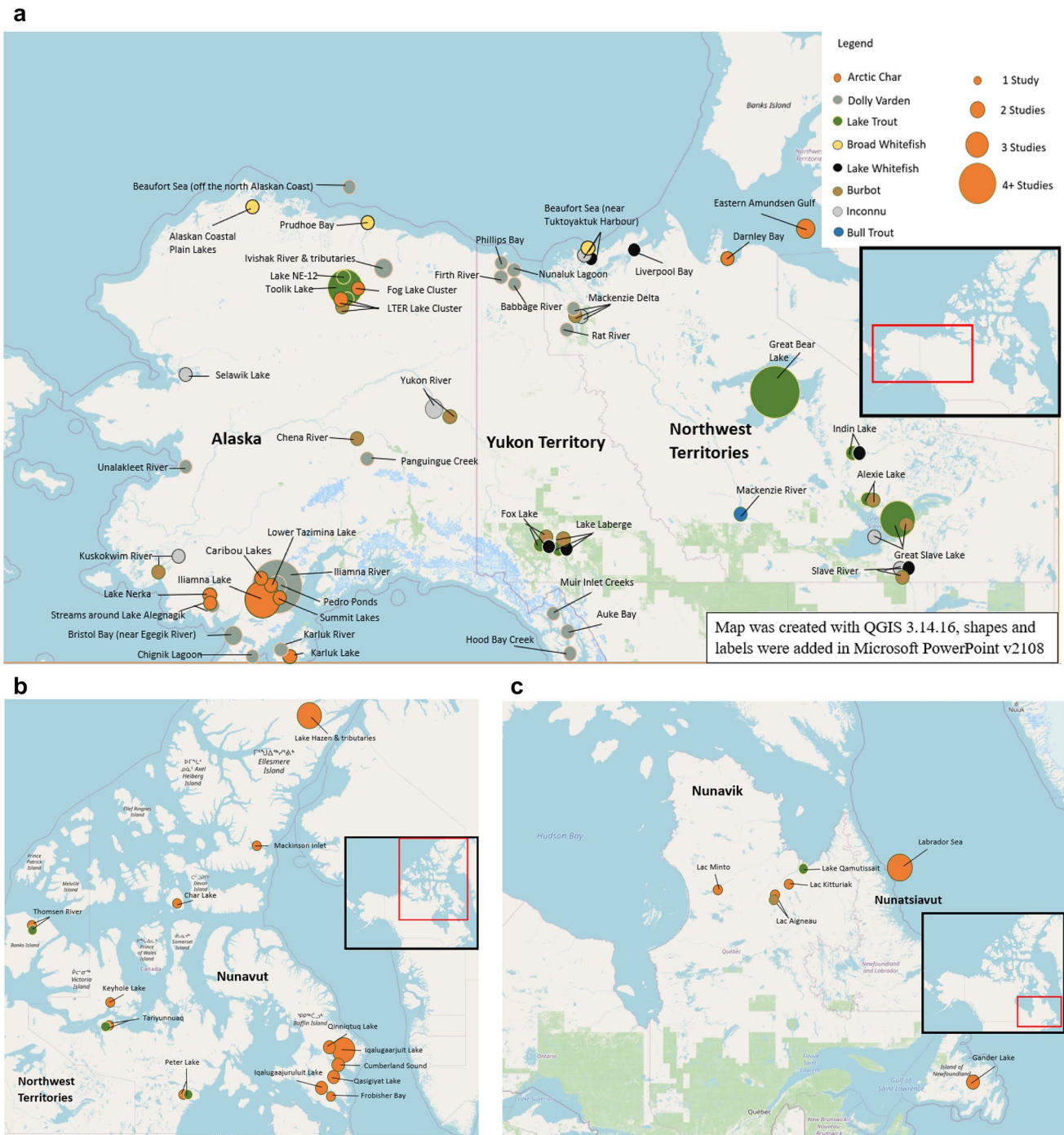
Following screening, the included papers were coded according to a list of questions (Appendix 3) into a database that collated the relevant information contained in the papers. The coding questions were developed to record the requisite data for each species of interest, establish regional and temporal trends in feeding, as well as list diet items from stomach contents to the lowest taxonomic level (i.e., order for invertebrates, species for fishes).

The information about diet and feeding strategies (defined for the purposes of this study as the degree of generalism or specialization in the types of prey consumed, as well as factors that affect feeding behavior such as habitat use, daily or seasonal migrations, and interactions with other species) was summarized by species and region. The range of prey items was assessed, which allowed for primary prey items to be identified, as well as variations resulting from habitat type or region. If applicable, interactions with other species were summarized to provide context for the feeding strategies displayed by the focal species, especially in cases where they interacted with one another. Tables 1–10 (available as supplementary files) were constructed to give a more thorough list of recorded prey items, while also highlighting knowledge gaps by showing where diet information has been collected in each species' range (denoted by a “1”—present or “0”—absent, respectively). Regions outside of a species' range were denoted with “N/A,” the ranges being verified in Lindsey (1962), Scott and Crossman (1973), Wilson and Hebert (1996), Sawatzky et al. (2007), Stapanian et al. (2010), Mee et al. (2015), and Taylor (2016).

## Results

### Search string and coding

The search string on Web of Science returned 323 papers and the search of the DFO catalogue returned 42, for a total of 365. Of these, 291 were excluded due to not meeting the various inclusion criteria (Appendix 2), leaving 74 inclusions to be coded. Of the included publications, 11 were DFO reports, the rest being academic journal articles, and spanned from 1955 to 2022. Studies were mapped to demonstrate their geographical distribution and the number of studies done per system, with Alaska, Nunavut, and the NWT hosting the majority (Fig. 1). Studies were largely performed in the open-water season from late spring to early fall (Fig. 2). Arctic Char was the most frequently studied species ( $n = 34$ ), followed by Lake Trout and Dolly Varden ( $n = 20$  and 17, respectively, Fig. 3). Analyses of stomach contents was the most common method used ( $n = 63$ ), followed by stable isotope analyses ( $n = 26$ ) and fatty acid analyses ( $n = 3$ ). The results are summarized by species, and within each species, with the information grouped by life history (i.e., resident or anadromous) if applicable, and throughout the region of known distribution (i.e., Northwest Territories, Yukon, Nunavut, Alaska, Nunavik, and Nunatsiavut) (Online Resource 1, Tables 1–10).



**Fig. 1 a.** Map showing the distribution and frequency of diet studies per-species in Alaska, the Yukon and the mainland NWT. **b.** Map showing the distribution and frequency of diet studies per-species in

Nunavut and Banks Island, NWT. **c.** Map showing the distribution and frequency of diet studies per-species in Nunavik and Nunatsiavut

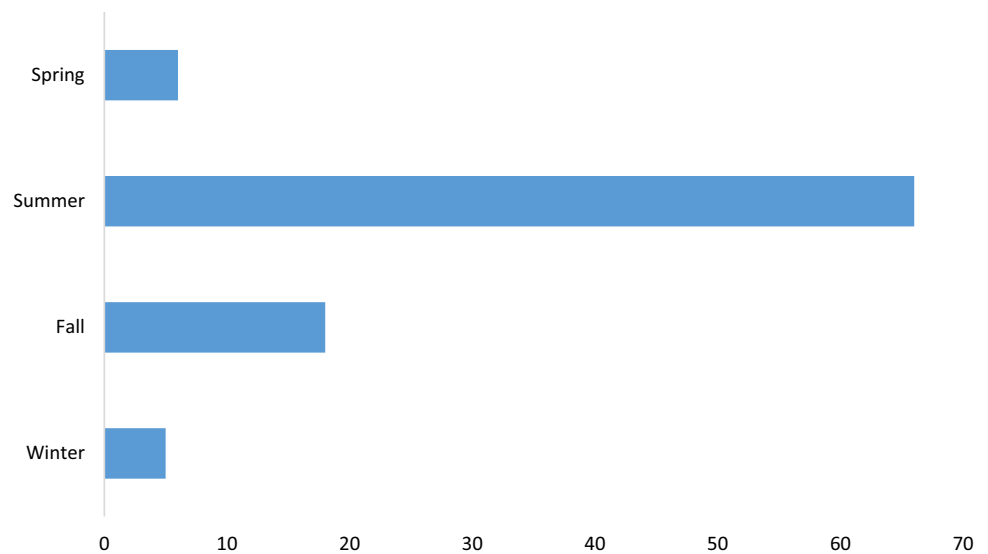
**Arctic Char**

**Anadromous form**

Anadromous Arctic Char feed heavily on marine

crustaceans and fishes, as well as mollusks and other invertebrates in some cases (Online Resource 1, Table 1). Anadromous individuals in the NWT feed extensively on forage fishes such as sandlance (*Ammodytes* spp.) and Capelin (Harwood et al. 2015; Harwood and Babaluk

**Fig. 2** Studies performed by season. Some studies included more than one season. Seasons were defined as summer (June–August), Fall (September–October), Winter (November–February), and Spring (March–May)



2014). This is a shift away from diet data collected in the region during the late 1970's, which saw Arctic Char diets mainly consist of Arctic Cod, mysids, and amphipods (Harwood et al. 2015). It is not known if these differences result from shifts in prey availability, predator preferences, temporal variation, or some combination thereof. Similarly, prior to 2005, most Arctic Char in Nunavut primarily fed on amphipods and mysids, which composed of up to ~80% of prey biomass, with other prey, such as Arctic Cod and sculpins (Family: Cottidae) making up the remainder (Ulrich and Tallman 2021a). After 2005, Capelin began to make up 65–75% of Arctic Char diets, while previous prey items were consumed in far lower numbers, or not at all (Yurkowski et al. 2018; Ulrich and Tallman 2021a). A similar increase in Capelin as prey, however, has not occurred across all of Nunavut. In Frobisher Bay for instance, amphipods and mysids made up nearly 95% of prey biomass consumed by Arctic Char as recently as 2009 (Spares et al. 2012) (Online Resource 1, Table 1). Individuals in Tariyunnuaq in the Kitikmeot region of Nunavut also feed on Capelin, as well as Pacific Herring (*Clupea pallasii*) and zooplankton but the dominant prey species is unknown (Swanson et al. 2011). Anadromous individuals in the northern areas of the archipelago consume mostly crustaceans, but information in these regions is sparse (Peet 1979). Arctic Char are opportunistic feeders in the marine environment, and their diets will likely shift in response to climate-driven changes to the marine Arctic food web. Falardeau et al. (2022) observed changes in the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures of individuals in the Kitikmeot Sea, Nunavut, which potentially reflect climate-driven diet shifts. Explanations for this shift could be a result the expansions in the distribution of boreal prey species, increased pelagic offshore foraging to escape warming nearshore waters, or an increase of pelagic prey

availability due to earlier sea ice breakup and melting (Falardeau et al. 2022).

Anadromous Arctic Char in Nunatsiavut, off the north coast of Labrador, are largely piscivorous but also feed on crustaceans, depending on the population, and individual size (Cote et al. 2021). Long-term data collected in this region suggests that fishes such as Capelin and various Sculpins make up ~72% of prey biomass for Arctic Char, averaged across years and individual populations (Dempson et al. 2002, 2008). Amphipods, mysids, and other invertebrates are also preyed upon, but only make up the majority of diets in individuals smaller than 300 mm fork length (FL) (Dempson et al. 2002).

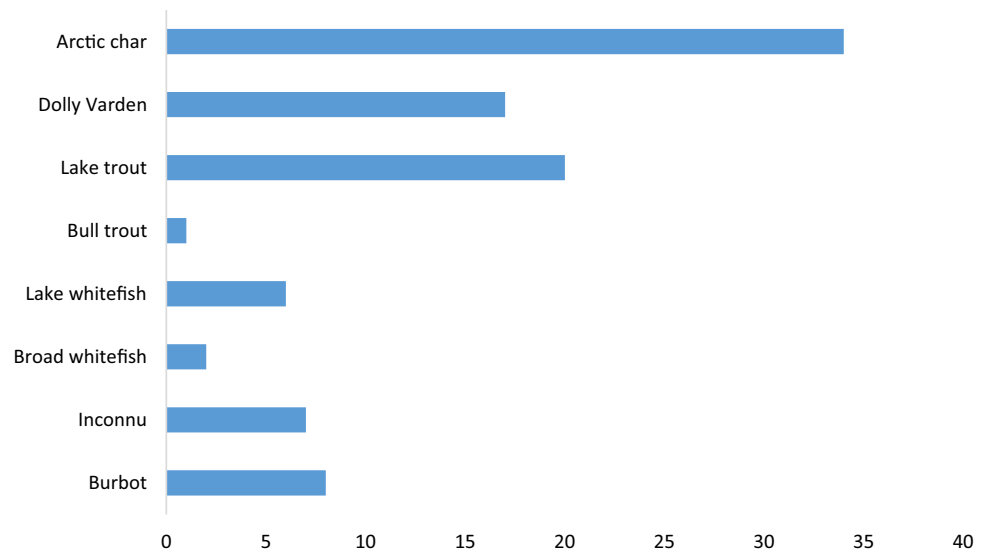
### Resident form

Resident Arctic Char are primarily lacustrine generalist predators but, unlike their anadromous form, they feed in freshwater exclusively and tend to be smaller and less piscivorous. When another top predator is present (e.g., Lake Trout), resident Arctic Char forego piscivory entirely and prey more heavily on invertebrates (Fraser and Power 1989; Klobucar and Budy 2020). Such invertebrates include insects (especially chironomids and other aquatic emergents), zooplankton, and gastropods (Fraser and Power 1989; Kidd et al. 1998).

Data on resident Arctic Char in the NWT are limited to summer foraging. Individuals are noted to prey on a variety of invertebrates in the Thomsen River on Banks Island, with 65% of prey items being stoneflies, craneflies, or chironomids (Stephenson 2010) (Online Resource 1, Table 2). Overall, there is limited information on the diet of resident Arctic Char in the NWT.

Resident Arctic Char in Nunavut most frequently consume insects, zooplankton, and crustaceans (Gallagher and

**Fig. 3** Number of available diet studies published per species in the North American Arctic. Numbers include anadromous and freshwater resident forms of all applicable species



Dick 2011, 2010; Curtis et al. 1995) (Online Resource 1, Table 3). Larger individuals (> 350 mm FL) feed on small fishes (including cannibalism), except when co-occurring with Lake Trout (Kidd et al. 1998; Young et al. 2021; Vanriël and Johnson 1995). During the winter, feeding becomes less frequent but piscivorous individuals often become more cannibalistic during the winter, with smaller Arctic Char being eaten by up to 33% of large-form individuals, even in cases where they had not been cannibals during the summer (Gallagher and Dick 2010; Young et al. 2021; Young and Tallman 2021). In high-Arctic lakes such as Lake Hazen and Char Lake, which do not feature a forage fish species, cannibalism becomes the only form of piscivory (Hobson and Welch 1995; Guiguer et al. 2002; Gallagher et al. 2009; Sinnatamby et al. 2012).

Resident Arctic Char in Nunavik and Nunatsiavut (particularly Gander Lake) show similar diet proclivities, with larger individuals being more piscivorous, feeding on smaller Arctic Char, Threespine Stickleback (*Gasterosteus aculeatus*), and Ninespine Stickleback (*Pungitius pungitius*), among other species (O'Connell and Dempson 2002; Power et al. 2005) (Online Resource 1, Table 2). Smaller individuals feed more on invertebrates, such as chironomids and other aquatic and emergent insects (Online Resource 1, Table 2). Resident Arctic Char in southwest Alaska are more frequently piscivorous, perhaps due to a greater diversity of forage fishes being present in these lower-latitude systems (Woods et al. 2013; Fournier and Schindler 2021). Feeding on salmon eggs and juveniles by Arctic Char occasionally occurs in these areas but to a lesser extent than do Dolly Varden, which may feed extensively on salmon eggs and juveniles found in the streams of this region. Arctic Char tend to occupy lakes and are therefore restricted to preying on Sockeye Salmon (*Oncorhynchus nerka*) populations which have

runs connected to such lakes (Morton 1982; Stewart et al. 2009; Dennert et al. 2016; Fournier and Schindler 2021). Arctic Char in this region have also been recorded to consume small mammals such as shrews (Woods et al. 2013).

At the species level, resident Arctic Char are generalists but in many lakes they diverge into 2–4 distinct morphs or ecotypes which can be segregated on the basis of habitat use and feeding strategies (Reist et al. 1995; Power et al. 2005, 2008). Arctic Char become piscivorous between 200 and 350 mm FL, although this can be affected by the presence of other large piscivores such as Lake Trout which will often exclude even large Arctic Char from piscivory (Fraser and Power 1989; Klobucar and Budy 2020). Outside of this scenario, large Arctic Char can form a piscivorous ecotype, often cannibalizing smaller individuals, especially in high-latitude systems with no other fish species available. Additionally, in some cases a large planktivore ecotype will also arise, as well as small and large benthivorous ecotypes (Power et al. 2008).

## Dolly Varden

### Anadromous form

Anadromous Dolly Varden feed primarily in coastal areas, where they consume fishes and crustaceans, feeding less frequently as they overwinter in freshwater (Online Resource 1, Table 3) (Stewart et al. 2009). Available information indicates anadromous Dolly Varden are heavily piscivorous at larger sizes (400 mm FL) (Stewart et al. 2009). Smaller individuals will primarily prey upon crustaceans such as mysids and amphipods, as well as chironomids in areas with a strong freshwater influence. In the Beaufort Sea, Dolly Varden often feed on sympagic (i.e., those which spent at least part

of their life cycles in, or on, the sea ice) amphipods, and follow sea ice movements to do so, indicating their feeding habitat use is influenced by sea ice position and condition (Gallagher et al. 2021). Large, piscivorous individuals in the Beaufort Sea feed on a variety of fishes such as Fourhorn Sculpin (*Myoxocephalus quadricornis*), small whitefishes (*Coregonus* spp.), and others (Stewart et al. 2009) (Online Resource 1, Table 3). Large anadromous Dolly Varden in western Alaska feed primarily on marine fishes, such as Pacific Sandlance and Capelin, while smaller individuals feed on crustaceans, especially amphipods and malacostracans (Narver and Dahlberg 1965; Hart et al. 2015). When returning to freshwater in the fall, anadromous Dolly Varden feed infrequently until the spring migration, although various insects may be consumed during this time (Stewart et al. 2009). An exception occurs in southwestern Alaska, where some anadromous Dolly Varden make shorter coastal migrations and time their return to freshwater in the early fall to coincide with Pacific salmon runs (Sergeant et al. 2014). This allows these individuals to gorge themselves on lipid-rich salmon eggs to sustain themselves during spawning and overwintering (Sergeant et al. 2015). Salmon smolts are occasionally consumed during the winter as well (Hart et al. 2015).

### Resident form

Resident Dolly Varden are primarily insectivorous and almost exclusively inhabit rivers and streams in Alaska and the Canadian Arctic. Chironomids are an important prey item, alongside other emergent insects, making up 75% or more of prey items consumed by resident Dolly Varden in many cases (Milner 1994; Parker and Huryn 2006; Stewart et al. 2009) (Online Resource 1, Table 4). Terrestrial insects and aquatic beetles are also occasionally eaten, with terrestrial insects becoming more prevalent as prey items later in the year (Stewart et al. 2009; Wipfli 1997). Resident Dolly Varden in the Babbage and Firth rivers in the Yukon occasionally eat amphipods and oligochaetes, which is not commonly recorded elsewhere (Stewart et al. 2009). Some large individuals will feed on small fishes, such as Arctic Grayling (*Thymallus arcticus*), as well as fish eggs, but this is not common compared to feeding on insects (Stewart et al. 2009). An exception to this is in western Alaska (e.g., Unalakleet, Chena, Iliamna, and upper Yukon rivers), where Dolly Varden ranges overlap with spawning Pacific salmon, and eggs and out-migrating juveniles, as well as scavenged flesh and dipteran larvae from dead adults make up the majority of diets while available (Armstrong 1970; Denton et al. 2009, 2010; Jaecks and Quinn 2014; Schoen et al. 2021). Resident individuals in an Alaskan stream feed less during winter, though they still feed on larval dipterans and stoneflies (Huryn and Benstead 2019).

Resident Dolly Varden are riverine insect specialists, with other types of invertebrates and small fishes only consumed incidentally (and only by large individuals in the case of the latter) and there appear to be no instances of resident Dolly Varden shifting their primary prey away from insects (Stewart et al. 2009). This feeding strategy is possibly shaped by morphology, given that resident Dolly Varden have smaller gapes than similarly sized Bull Trout and Arctic Char, which would necessitate feeding on smaller prey, even for larger individuals (Stewart et al. 2007). The feeding habitat use of Dolly Varden while drift foraging can be shaped by dominance hierarchies among individuals (Cullen and Grossman 2019). Larger dominant individuals occupy upstream positions in streams which allows for the first opportunity to consume drifting prey and consequently, higher foraging rates (Cullen and Grossman 2019).

### Lake Trout

In Great Bear Lake, NWT, Lake Trout are noted to differentiate among habitat use and diet, forming several distinct morphs or ecotypes (Blackie et al. 2003). These include a more generalist ecotype and more specialized ecotypes that feed on more specific prey or at specific lake areas, although fatty acid analysis indicates that there is significant diet variation within the morphs (Chavarie et al. 2016). The generalist morph feeds on crustaceans as well as Round Whitefish (*Prosopium cylindraceum*), Slimy Sculpin (*Cottus cognatus*), adult caddisflies, ants (Formicidae spp.), and small amounts of other insects (Chavarie et al. 2016). The specialized benthic morph feed heavily on ants, as well as bivalves and mysids, but fewer fish compared to other morphs (Chavarie et al. 2016, 2021). The generalist pelagic morph feed on pelagic forage fishes (presumably *Coregonus* spp.), as well as crustaceans and terrestrial ants (Chavarie et al. 2016). The fourth morph, a pelagic piscivore, feeds on coregonids and small Northern Pike (*Esox lucius*) but also occasionally switches to Trichoptera spp. and cannibalism of the benthic morph (Chavarie et al. 2016). Each of these morphs feeds on terrestrial insects to some degree, demonstrating that, despite being more specialized ecotypes, they are still opportunistic.

In Great Slave Lake, NWT, Lake Trout exist in three different morphs but their preferred feeding habitat appears to be more related to size rather than morph (Zimmerman et al. 2009). There are shallow and deep-water piscivorous morphs, and a zooplanktivorous morph, but all three tend to forage benthically, and shift to pelagic feeding at approximately 430 mm standard length (Zimmerman et al. 2009). Smaller individuals of piscivorous morphs prey on sculpins during their benthic phase, but switch to coregonids as they grow larger and shift to pelagic feeding (Zimmerman et al. 2009). All morphs in Great Slave Lake also

consume terrestrial insects opportunistically (13% occurrence averaged across morphs) (Moshenko and Gilman 1983; Zimmerman et al. 2009). Diets of Lake Trout in Great Slave Lake change throughout the year in accordance to thermal conditions (MacKenzie et al. 2022). Early in the season, foraging for terrestrial insects and littoral fishes in shallow water is more common, but Lake Trout become barricaded from nearshore prey later in the summer when the lake's upper layer reaches 15 °C (MacKenzie et al. 2022).

In smaller lakes in the NWT, Nunavut, and the Yukon, Lake Trout will feed on zooplankton, insects and fishes such as stickleback, Slimy Sculpin, and others (Kidd 1996; Kidd et al. 1998; Hulsman et al. 2016) (Online Resource 1, Table 5). The ability of Lake Trout to resource partition is displayed in Alexie Lake, NWT, where Lake Trout, Burbot, and Northern Pike all inhabit similar trophic levels, but feed in different areas of the lake, according to stable isotope data (Guzzo et al. 2016). The diet of Lake Trout in the Thomsen River, NWT appears to be very generalized, likely due to the homogenous nature of a riverine system and contain an array of insects and fishes (Stephenson 2010). On rare occasions, Lake Trout are known to consume small mammals, as lemmings (*Lemmini* spp.) were found in several Lake Trout stomachs in the Thomsen River (Stephenson 2010).

Nunavut also features rare examples of anadromous Lake Trout populations that migrate to the sound of Tariyunnaq, Nunavut, for summer feeding (Swanson et al. 2011). During these migrations to coastal areas, Lake Trout feed on Pacific Herring, Capelin, and marine crustaceans (Swanson et al. 2011). Anadromous populations of Lake Trout are present in Husky Lakes, NWT (Kissinger et al. 2016), but there is little detailed information published about their diets.

Lake Trout in Alaska and in Nunavik are also generalist predators. Most Alaskan systems featuring Lake Trout are similar to Toolik Lake, which are relatively shallow and lack pelagic prey (MacDonald and Hershey 1992). This leads larger Lake Trout to feed on benthic fishes and mollusks, while smaller individuals feed on zooplankton closer to shore (McDonald and Hershey 1992; Merrick et al. 1992; McDonald et al. 1996; Keyse et al. 2007). In Nunavik, Quebec, larger individuals (> 600 mm FL) prey heavily on other fishes and occasional crustaceans (branchiopods) (Benoit and Power 1983; Murdoch et al. 2013) (Online Resource 1, Table 5). Mid-size individuals (300–600 mm FL) are generalist foragers (stickleback, small Burbot, and juvenile salmonids) but also feed heavily on insects (craneflies and chironomids; Benoit and Power 1983). The smallest size class of Lake Trout in these Nunavik lakes (< 300 mm FL) feed mostly on dipterans (Benoit and Power 1983).

## Bull Trout

The diet and feeding habits of Bull Trout in the Mackenzie River drainage are poorly understood, especially outside of summer. Juvenile Bull Trout feed on a broad array of adult and larval insects (Stewart et al. 2007) (Online Resource 1, Table 6). As Bull Trout grow larger, they become more piscivorous, with the shift in prey occurring when the individual is between 100 and 200 mm FL, and many individuals in lakes become exclusively piscivorous as adults (Stewart et al. 2007). In the NWT and Yukon, Slimy Sculpin, Arctic Grayling, Longnose Sucker (*Catostomus catostomus*), and juvenile or small Bull Trout are the preferred prey species. If available, large adults will also eat small or young birds, amphibians, snakes, and small mammals such as shrews and mice (Stewart et al. 2007). It is unknown if this species shifts its diet to avoid interspecific competition after it has reached typical piscivory sizes or if it exhibits prey preferences once it reaches such a size (Stewart et al. 2007).

## Inconnu

Inconnu are a large, primarily piscivorous freshwater coregonid that are found in both resident and anadromous forms (Tallman and Howland 2017); however, diet data on Inconnu are sparse. Inconnu in both rivers and lakes feed almost entirely on a diverse range of fishes, while invertebrates tend to only be consumed by some juveniles (Fuller 1955; Little et al. 1998; Gallagher and Dick 2015; Stuby et al. 2018). An exception to this has been recorded in Selawik Lake, Alaska, where very large individuals feed on mysids, alongside fishes (Alt 1965). Additionally, Inconnu in the Upper Yukon and Chena rivers feed heavily on juvenile Chinook Salmon (*Oncorhynchus tshawytscha*) when they are present. (Online Resource 1, Table 7). Anadromous individuals in the nearshore Beaufort Sea similarly feed primarily on fish, though some mysids are also consumed (32% by number of prey items consumed) (Lacho 1991).

Inconnu are comparatively specialized to other large predators because of their heavy reliance on piscivory, even in smaller individuals, in their relatively narrow habitat range (shallow, silty areas of lakes; large rivers, and brackish areas) (Fuller 1955; Smith and Sutton 2015). The linkage of individual size to level of piscivory is difficult to establish in Inconnu because small individuals occasionally eat invertebrates, but even smaller individuals have been discovered feeding on fish (Fuller 1955; Alt 1965). Thus, more work is needed to contextualize the prey preferences of Inconnu.

## Lake Whitefish

Lake Whitefish is a benthic and occasionally pelagic, mid-trophic level coregonid species, primarily found in lacustrine



environments and is a generalist benthic predator of aquatic invertebrates (Jessop et al. 1993). A distinct pelagic zooplanktivore ecotype forms in some instances (Bernatchez et al. 1996). It is limited by its small, subterminal mouth which is adapted for benthivory, though instances of piscivory have been recorded outside the Arctic (Pothoven and Madenjian 2013). The species is primarily freshwater but anadromous populations exist in the Mackenzie River Delta and in Alaska (Sawatzky et al. 2007). Benthic prey such as mollusks, aquatic insects, and crustaceans make up the majority of Lake Whitefish diets (Jessop et al. 1993; Kidd et al. 1996; Little et al. 1998; Mackenzie et al. 2022). In some systems, such as the Slave River, the relative importance of different prey items shifts throughout the year – ostracods make up over half of the diet during the spring, while corixids make up 68% of diets by the fall (Little et al. 1998). Lake Whitefish have a lower salinity tolerance than other coregonids, meaning that anadromous feeding is not especially common, individuals that do migrate to coastal areas to feed remain in nearshore areas (Sawatzky et al. 2007). These anadromous Lake Whitefish in Tuktoyaktuk Harbour and Liverpool Bay, NWT feed primarily on crustaceans and other invertebrates (Lacho 1991; Bond and Erickson 1993) (Online Resource 1, Table 8).

### Broad Whitefish

Broad Whitefish are primarily an anadromous coregonid species that are generalist benthic foragers found throughout the coastal Beaufort Sea and Mackenzie River Delta; however, a lacustrine form also exists (Sawatzky et al. 2007). Anadromous Broad Whitefish found in the marine environment near Tuktoyaktuk, Northwest Territories, were found to feed heavily on copepods (98% by number), as well as some nematodes and Diptera larvae (Lacho 1991) (Online Resource 1, Table 9). Anadromous Broad Whitefish in Prudhoe Bay, Alaska feature a more varied diet, also feeding on copepods, but with other crustaceans and chironomids being present as well (Fechhelm et al. 1995). An exception in Broad Whitefish diets occurs in the Arctic Coastal Plain of Alaska, where adult dipterans made up 35% of the diets of several individuals (Laske et al. 2018). In comparison to Least Cisco (*Coregonus sardinella*) and Dolly Varden, Broad Whitefish occupy a lower trophic level which limits them to feeding on small mollusks and other invertebrates (Kline et al. 1998).

### Burbot

Burbot are specialized piscivores that primarily inhabit benthic areas, often emerging at night to feed in littoral zones. In the NWT, adult Burbot in the Mackenzie Delta are exclusively piscivorous during the winter, feeding largely

on juvenile Burbot and Northern Pike, as well as Ninespine Stickleback, among others (Gallagher and Dick 2015) (Online Resource 1, Table 10). Juveniles are also piscivorous, being highly cannibalistic, and eating young Northern Pike and Ninespine Stickleback (Gallagher and Dick 2015). To a lesser extent, juveniles also consume invertebrates (Online Resource 1, Table 10). This combination of invertebrates and small fishes has also been recorded in juveniles in the Slave River system (Little et al. 1998). Burbot piscivory increases with size, between 100 and 460 mm FL, reinforced by the  $\delta^{15}\text{N}$  differences between adults and juveniles (Gallagher and Dick 2015). Young Burbot that prey on fish appear to grow faster, which may explain the prevalence of cannibalism, as rapid growth would enable juveniles to grow to where they are at less risk of predation (Gallagher and Dick 2015). Winter cannibalism may also be favored by sexually mature individuals, as the energy gained would be beneficial for spawning (Gallagher and Dick 2015). Cannibalism among Burbot appears to be more prevalent in the Mackenzie River Delta than throughout most of its North American range (Gallagher and Dick 2015). In Great Slave Lake, Burbot feed on juvenile coregonids, as well as forage fishes such as Ninespine Stickleback, Trout-Perch, and various minnows (MacKenzie et al. 2022). In the Yukon, Burbot are similarly piscivorous, with individuals in Fox and Laberge lakes consuming Slimy Sculpin and various coregonids (Kidd 1996). In Alaska, Burbot in the Chena and Upper Yukon rivers feed on coregonids as well as juvenile Chinook Salmon when available, while in the Kuskokwim River, individuals consume various forage fishes (Rausch and Adams 2000; Schoen et al. 2021) (Online Resource 1, Table 10). Burbot in Nunavik consume littoral forage fishes, presumably during nightly feeding migrations (Power et al. 2009).

Burbot are the most specialized among the species reviewed. These fish are almost solely piscivorous as adults, typically feeding on littoral and some benthic fishes after reaching 460 mm total length at the latest (Power et al. 2009; Gallagher and Dick 2015; Guzzo et al. 2016). The feeding strategies of Burbot are further specialized by its photophobic and crepuscular nature, they remain at the benthos in cooler waters and protected from sunlight during the days of the open water season until nightfall, when they migrate to littoral zones to forage (Cott et al. 2015; Guzzo et al. 2016). Burbot also prefer low-complexity and soft substrates at the bottom of these lake slopes that it can burrow in during the day, which further shapes its hunting behavior (Cott et al. 2015).

### Knowledge gaps

While consolidating available information, this review also highlighted a number of knowledge gaps relating to the

diets and feeding strategies of Arctic fishes. For instance, basic year-round diet information is still needed for many Arctic species across all life-stages, especially given that current information is primarily focused on the open-water season (Fig. 2). This is particularly apparent for Inconnu, Broad Whitefish, Lake Whitefish, and Bull Trout, which lack even basic diet data for much of their Arctic ranges (Online Resource 1, Tables 1–10). Assessing ontogenetic diet shifts is important across species as several fishes (e.g., Arctic Char, Bull Trout, Burbot) feature significant diet shifts after reaching a certain size, but it is unknown if such shifts occur in Inconnu, for example. As well, the available information focuses on lacustrine and coastal ecosystems, highlighting the need for an expansion of information about the diets of fishes in riverine habitats in the Arctic.

The limited number of fish diet studies in the Arctic leads to several geographic knowledge gaps. For instance, studies in the NWT tend to be focused on the northern Great Lakes and the Mackenzie Delta, while the majority of smaller lakes and the rest of the Mackenzie River upstream of the delta remain unstudied (Fig. 1a). The Yukon features a severe lack of diet studies, with key species such as Burbot, Inconnu, Lake Trout, Lake Whitefish, and Bull Trout having virtually no available diet information in the territory (Fig. 1a). Additionally, there were no studies found in this review for Nunavut that consider species other than Arctic Char and Lake Trout (Fig. 1b). The logistics of performing diet studies in remote northern areas are a limiting factor, which highlights the need to focus research efforts on constructing a baseline for each species across seasons and habitat types, to reduce redundant efforts. When comparing the diet studies reviewed here, it is apparent that variation in overall diets and feeding strategies within and among regions is low, with the biggest factor in differences between regions being latitude and its limitation on prey diversity. Therefore, studies conducted in one region are likely to be applicable to fish diets in other regions, provided the type of environment is broadly similar (i.e., data collected on a lacustrine population is unlikely to be relevant to riverine individuals of the same species). Research efforts should therefore be focused on assessing fish diets and feeding strategies on species and environments where information is sparse, extremely dated, or subject to rapid current changes, given the more extensive body of literature on the most well-studied species (i.e., lacustrine Arctic Char; Lake Trout in the northern Great Lakes and smaller Arctic lakes; resident Dolly Varden).

## Discussion

This review gives a thorough appraisal of the diet and feeding behaviors of eight ecologically and culturally important mid- to upper-trophic fish species throughout the Canadian

Arctic and Alaska. The species included in this review largely display generalist feeding strategies, though within-species specialization did occur in several instances (e.g., Power et al. 2005; Zimmerman et al. 2009). Diet generalization is regarded as an adaptation common in northern fishes as it both reduces costly agonistic interaction with other species and allows for rapid exploitation of varied prey (Power et al. 2008; Ulrich and Tallman 2021a). The majority of fish dietary research in the region is focused on lake-resident or anadromous species during the summer. Therefore, several data gaps were identified, the most prominent being the need for information about winter feeding across species and ecosystems, as well as a lack of information available for riverine species. While some species such as Lake Trout and Arctic Char are well-studied, available information for other species is either dated (e.g., Inconnu) or limited (e.g., Lake Whitefish and Bull Trout). Diet studies on Broad Whitefish are also few in number, although two studies were recently published (Leppi et al. 2022; Stanek et al. 2022). Brewster et al. (2016) also contains information about diets and trophic niches in Dolly Varden, Broad Whitefish, Lake Whitefish, Burbot, and Inconnu, although the information was not included here as the study was not detected during keyword searches in Web of Science. There is also very little diet information available in the Yukon for the species considered, aside from Dolly Varden. Assessing the diets of fishes that are predicted to expand into the Arctic with continued warming is also important to better predict the resulting interactions with native fishes in Arctic habitats (e.g., McNicholl et al. 2016; Harris et al. 2022). Documentation of Indigenous knowledge of fish diets, as well as parameters related to diet (e.g., flesh color and condition), is needed and would expand upon and provide additional context to current understandings (e.g., Zerehi 2016; Cott et al. 2018).

In anadromous species, crustaceans (especially copepods, amphipods, and mysids) are the most widely consumed type of prey during marine feeding migrations. This is likely due to their presence in high density patches in marine environments and ideal for northern anadromous fishes looking to maximize food intake during their short feeding periods (Ulrich and Tallman 2021a). Crustaceans make up a portion, and in many cases the majority, of diets for Arctic Char, Broad Whitefish, Lake Whitefish, Dolly Varden, and Inconnu during their marine feeding migrations. Larger individuals of these species also eat an array of fishes, most of which are benthic-dwelling coastal species such as sandlances, blennies, pricklebacks, and sculpins. The recent increase in Capelin in the diet of some Arctic Char populations appears to be an exception to this tendency (Dempson et al. 2008; Ulrich and Tallman 2021a). This is possibly a result of Capelin aggregating in large spawning shoals when Arctic Char begin their feeding migrations (Ulrich and Tallman 2021a).

Changes in sea ice breakup timing, movements, and melt onset may have impacts on the diets and feeding strategies of Arctic Char and Dolly Varden (Harris et al. 2022). In the Beaufort Sea, predation of crustaceans by these species is connected to sea ice conditions, because both species prey on sympagic crustacean species (Gallagher et al. 2021; Falardeau et al. 2022). In the Kitikmeot Sea, changes in  $\delta^{13}\text{C}$  values in Arctic Char reflect a shift toward a higher level of pelagic prey being consumed, compared to sympagic or benthic prey sources. A potential mechanism for this shift is earlier sea ice breakups and melt onset, which results in a phytoplankton bloom and in turn, a greater abundance of pelagic crustaceans present when Arctic Char arrive at sea to feed (Falardeau et al. 2022). This pattern has been observed in other Arctic predators, such as Belugas (*Delphinapterus leucas*) (Brown et al. 2017). Additionally, the shift toward more  $\delta^{13}\text{C}$ -poor prey could be explained by the warming of nearshore coastal waters, which necessitates individuals moving to cooler, offshore areas, where pelagic prey lower in carbon enrichment (Falardeau et al. 2022). Conversely,  $\delta^{15}\text{N}$  signatures have increased over time, indicating that Arctic Char occupy higher trophic levels in the Kitikmeot Sea than in the past. Falardeau et al. (2022) suggest this may be due to the increased distribution of boreal prey species (i.e., Capelin and Pacific Sandlance) into Arctic waters. Boreal species have higher trophic levels and pelagic  $\delta^{13}\text{C}$  signatures, which may explain the isotopic shift seen in Arctic Char, although further research is needed to fully understand this pattern (Falardeau et al. 2022). While Arctic Char is an adaptable feeder that can react to shifts in the food web, the species has a narrow thermal range, and the physiological consequences of warming waters will likely restrict the species' adaptability (Gilbert and Tierney 2018).

In riverine environments, diet overlap seems to be more extensive and resource partitioning is less common, possibly due to the more confined nature of such systems, or because resources may be partitioned by territorial behavior over prime feeding areas rather than species feeding on different prey items (Hearn 1987; Arostegui and Quinn 2018). In the Thomsen River, NWT, Lake Trout and resident Arctic Char share a large number of invertebrate prey sources, with chironomids and arachnids being the only ones exclusive to Arctic Char (Stephenson 2010). In Iliamna Lake, Alaska and its surrounding streams, Arctic Char exclude Rainbow Trout (*Oncorhynchus mykiss*) from piscivory and from feeding on benthic invertebrates alongside forage fishes; the Rainbow Trout are limited to insects (Arostegui and Quinn 2018). Conversely, in the tributaries of the same system, stream-resident Dolly Varden have significant diet overlap with stream-resident Rainbow Trout, indicating that these environments are less conducive to resource partitioning (Arostegui and Quinn 2018). Insects appear to be the most important group of prey for most fish in riverine systems,

especially chironomids, trichopterans, and plecopterans, as well as other emergent and aquatic insects. Even high-level predators, such as Lake Trout and Inconnu, appear to feed upon insects more commonly when in rivers (Alt 1965; Stephenson 2010).

Lakes demonstrate clearer patterns of diet resource use and partitioning. Benthic fishes such as sculpins and sticklebacks are important prey for most piscivores, as many higher latitude Arctic lakes lack pelagic forage fishes (McDonald and Hershey 1992). Littoral foraging on prey fishes is relatively uncommon among the species considered here, limited mostly to Burbot in accordance to their nightly migrations to such areas to feed (Power et al. 2009; Guzzo et al. 2016). Inconnu also appear to specialize in piscivory in shallower waters in Great Slave Lake, although it is not known if they are specifically targeting littoral species (Fuller 1955). The importance of benthic feeding in many of these lakes is reinforced by the prevalence of mollusks (gastropods and bivalves) in the diets of Lake Whitefish, Arctic Char, and Lake Trout, with the latter two species forming benthivore-specialist ecotypes in some cases (Power et al. 2008; Chavarie et al. 2016). Zooplankton is also an important food source, especially for Arctic Char and small Lake Trout, the former of whom form a zooplanktivorous ecotype to avoid competition with piscivorous conspecifics or Lake Trout, while the latter are sometimes restricted to nearshore planktivory by larger individuals (Merrick et al. 1992; Kidd et al. 1998; Power et al. 2008).

Differences in prey items across the ranges in each species appears to be governed mostly by latitude, as food chains in the higher Arctic are simpler and less diverse (Power et al. 2008). Beyond the differences in prey diversity inherent to latitude, overall diet preferences and feeding strategies do not vary markedly within, and across, regions. Piscivorous resident Arctic Char feed on a more diverse array of fishes in western Alaska, Nunatsiavut, and Nunavik than in the High Arctic, due to the larger variety of different forage fishes at lower latitudes (O'Connell and Dempson 2002; Power et al. 2009; Dennert et al. 2016). There is a greater array of invertebrates eaten by Arctic Char in these regions as well, such as leeches, hemipterans, Odonata spp., Ephemoptera spp., and various Gastropods (O'Connell and Dempson 2002; Power et al. 2009; Woods et al. 2013; Dennert et al. 2016). Arctic Char in places such as northern Nunavut have simpler diets, relying heavily on emergent insects and bivalves, with piscivory restricted only to the large piscivore ecotype which preys on smaller Arctic Char and the few available forage fishes such as sticklebacks (Guiger et al. 2002; Gallagher and Dick 2011; Ulrich and Tallman 2021b). Lake Trout also show some differences in their diets across their range due to changes in environment. The Lake Trout of large, deep lakes, such as Great Slave Lake and Great Bear

Lake, feature a greater emphasis for some individuals on pelagic feeding upon various fishes such as ciscoes and whitefishes, as well as various crustaceans (Zimmerman et al. 2009; Chavarie et al. 2016), but at higher latitudes in smaller and shallower lakes, Lake Trout instead feed very generally on mollusks, oligochaetes, and benthic fishes (McDonald and Hershey 1992; Keyse et al. 2007; Stephenson 2010).

Continued understanding of trophic ecology and interactions of Arctic fishes for food resources will assist predictions of how native fish populations may respond to a rapidly changing Arctic (Niemi et al. 2019), or potential outcomes resulting from climate-driven distributional shifts to the north (Dunmall et al. 2013; Bilous and Dunmall 2020). Future research that addresses these gaps will contribute toward a robust baseline of diet information for northern fishes and improve understanding regarding Arctic fishes and the potential effects of climate change on Arctic ecosystems.

## Appendices

### Appendix 1: Search strings

The following search strings were used to conduct the literature searches on Web of Science and the DFO catalogue. The search terms are identical and modified only to reflect differences in the syntax requirements of each search engine.

Web of Science search string:

(TS=(canad\* OR alask\* OR newfoundlan\* OR quebec OR labrador\* OR yukon OR northwest OR nunavut)) AND (TS=("arctic char\*" OR "dolly varden" OR "inconnu" OR "sheefish" OR "burbot" OR "lake trout" OR "lake char\*" OR "lake whitefish" OR "broad whitefish" OR "bull trout" OR "bull char\*")) AND (TS=(diet\* OR feed\* OR "stable isotop\*" OR "fatty acid" OR stomach OR prey OR food OR web OR trophic\* OR niche)) NOT TS=(mercury OR contamin\* OR pollution)

DFO collection search string:

(canad\* OR alask\* OR newfoundlan\* OR quebec OR labrador\* OR yukon OR northwest OR nunavut) AND ("lake trout" OR "lake char\*" OR "arctic char\*" OR "inconnu" OR "sheefish" OR "dolly varden" OR "lake whitefish" OR "broad whitefish" OR "bull trout" OR "bull char\*" OR "burbot") AND (diet OR feed\* OR stomach OR "stable isotop\*" OR "fatty acid\*" OR food OR web OR trophic\* OR niche) NOT (pollution OR contamin\* OR mercury)

### Appendix 2: Exclusion criteria

Bases on which papers were included or excluded in the sample

Dimension	Inclusion	Exclusion
Geographic scope	Inuit Nunangat and the rest of Arctic Canada and Alaska	BC, Alberta, Saskatchewan, Manitoba, Ontario, Quebec outside of Nunavik, lower 49 US states, the rest of the world
Language	English and French	Non-English and non-French
Focus	Diet/Trophic ecology	Anything else
Publication type	Case studies, research articles, technical reports (DFO), manuscript reports (DFO), and research documents (DFO)	Models, predictions
Temporal scope	Current and past	Future projections
Species	Dolly Varden, Arctic Char, inconnu, broad whitefish, lake whitefish, bull trout, lake trout, burbot	Any other fish species, unless the focal species was a prey species for one of the 8 studied species, and included relevant feeding data in the paper

### Appendix 3: Coding questions

Questions designed for extracting diet information from each paper in a standardized manner and how that information was coded into the database

#	Column item	Description	Coding
A	Included/excluded	Is it included or excluded from analysis?	1 = Included; 0 = Excluded
0.1	Document Type	What kind of document is it?	J = Journal Article D = DFO report
0.2	Geographic focus	What state/province/territory does the study take place in?	Name(s)
0.3	Study area(s)	Name the bodies of water under study	Name(s)
0.4	Timeframe	When was the data collected?	Most specific dates available

#	Column item	Description	Coding
0.5	Season(s)	What season(s) did the study occur in (Summer: Jun-Aug, Fall: Sept-Oct, Winter: Nov-Feb, Spring: Mar-May)	Sp = Spring, S = Summer, F = Fall, W = Winter
1.1	Species studied	Common names of species studied, alphabetically	Name(s)
1.1.2	Habitat type	Were specimens collected in still, coastal or flowing water systems?	F = Fluvial, L = Lacustrine, A = Anadromous
1.2	Diet sampling method	What diet sampling technique(s) are used?	Mark "X" if applicable
1.2.1	Stomach contents	Were stomach contents analyzed?	"X"
1.2.2	Stable isotopes	Were stable isotopes analyzed?	"X"
1.2.2.1	Flesh type	Where was the flesh for SI analysis taken from?	List location(s)
1.2.3	Fatty acids	Were fatty acids analyzed?	"X"
1.3	General diet characteristics	What broad groups of prey were consumed?	Mark "X" if applicable
1.3.1	Fish	Were fish consumed?	"X"
1.3.2	Insects	Were insects or insect larva consumed?	"X"
1.3.3	Worms	Annelids, platyhelminthes, nematodes etc	"X"
1.3.4	Crustaceans	Amphipods, copepods etc	"X"
1.3.5	Molluscs	Gastropods, bivalves etc	"X"
1.3.6	Fish eggs	Eggs of other fish	"X"
1.3.7	Plankton		"X"
1.3.8	Other	Other prey items: mammals, lizards, amphibians etc	"X"
1.3.9	Please specify	List the additional prey items	List

#	Column item	Description	Coding
1.4	Specific diet components	List the specific prey items to order for invertebrates, species for fishes	List
1.5	Competition/overlap with other species	If the paper describes how species react to competitors, describe here	Describe

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## Declarations

**Conflict of interest** The authors declare no conflicts of interest.

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