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RESEARCH ARTICLE

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Climate tracking by freshwater fishes suggests that fish diversity in temperate lakes may be increasingly threatened by climate warming

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Abstract

Aim: Many freshwater fishes are migrating poleward to more thermally suitable habitats in response to warming climates. In this study, we aimed to identify which freshwater fishes are most sensitive to climatic changes and asked: (i) how fast are lakes warming? (ii) how fast are fishes moving? and (iii) are freshwater fishes tracking climate?

Location: Ontario, Canada.

Methods: We assembled a database containing time series data on climate and species occurrence data from 10,732 lakes between 1986 and 2017. We calculated the rate of lake warming and climate velocity for these lakes. Climate velocities were compared with biotic velocities, specifically the rate at which the northernmost extent of each species shifted north.

Results: Lakes in Ontario warmed by 0.2°C decade^{-1} on average, at a climate velocity of 9.4 km decade^{-1} between 1986 and 2017. In response, some freshwater fishes have shifted their northern range boundaries with considerable interspecific variation ranging from species moving southwards at a rate of −58.9 km decade^{-1} to species ranges moving northwards at a rate of 83.6 km decade^{-1} over the same time period. More freshwater fish species are moving into northern lakes in Ontario than those being lost. Generally, predators are moving their range edges northwards, whereas prey fishes are being lost from northern lakes.

Main Conclusions: The concurrent loss of cooler refugia, combined with antagonistic competitive and predatory interactions with the range expanding species, has resulted in many commercially important predators moving their range edges northwards, whereas prey species have contracted their northern range edge boundaries. Trophic partitioning of range shifts highlights a previously undocumented observation of the loss of freshwater fishes from lower trophic levels in response to climate-driven migrations.

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KEYWORDS
biotic velocity, climate change, climate velocity, freshwater fish, range edge shifts

1 | INTRODUCTION

Terrestrial and aquatic species are migrating into new regions, tracking shifts in their climatic niches (climate tracking) in response to global warming (Pecl et al., 2017; Pinsky et al., 2013; Lenoir et al., 2020). Habitat changes (Buisson et al., 2008; Burrows et al., 2011), combined with novel species interactions, may restructure and reshuffle communities (Alexander et al., 2015; Erős et al., 2020; Urban, 2020), favouring the spread of nonindigenous species but displacing or extirpating native species (Conti et al., 2015). A consistent pattern of poleward climate tracking by marine and terrestrial species has been observed, albeit at species-specific rates (Hiddink et al., 2012; Pinsky et al., 2013). Freshwater fish in rivers may also be tracking climates poleward (Comte & Grenouillet, 2013, 2015). However, comparatively few studies have examined whether freshwater fish in North American lakes are similarly shifting their ranges to the north in response to recent climate changes (i.e. Alofs et al., 2014; Heino et al., 2009; Lynch et al., 2016).

Lakes have warmed rapidly in recent decades (O'Reilly et al., 2015; Schneider & Hook, 2010). Between 1985 and 2009, global lake summer surface temperatures warmed by 0.34°C per decade on average, with seasonally ice-covered lakes warming twice as fast as the global average (O'Reilly et al., 2015). Shorter seasonal ice cover (Sharma et al., 2021) is contributing to earlier and modified stratification regimes (Austin & Colman, 2007; Woolway & Maberly, 2020; Woolway & Merchant, 2019). Warmer water temperatures have altered thermal habitats (Kraemer et al., 2021; Woolway & Maberly, 2020). With recent increases in suitable thermal habitats in northern lakes (Sharma et al., 2007), freshwater fishes may be shifting their ranges poleward (Van Zuiden et al., 2016), either to escape unsuitable oxythermal habitats in southern lakes (Herb et al., 2014) or to invade newly productive northern lakes (Campana et al., 2020; Guzzo & Blanchfield, 2017). The direction and magnitude of these shifts may vary among species (Alofs et al., 2014; Comte et al., 2013, 2014), and it is not yet clear whether there is a consistent pattern of poleward shifts in freshwater species ranges.

Abiotic constraints, including temperatures, are crucial to demarcating fundamental climate niche limits to range expansions by ectothermic freshwater fish populations (Comte et al., 2013; Comte & Olden, 2017; Magnuson et al., 1979). Breeding populations cannot establish beyond these limits as fish reproductive processes, growth and mortality rates are sensitive to thermal changes (Buckley et al., 2012; Guzzo et al., 2017). Additionally, biotic constraints such as trophic position and interspecific interactions may play an important role in species range shifts (Comte et al., 2014; Ockendon et al., 2014), particularly predation (Alofs & Jackson, 2014). For example, northward range expansions of predator fishes may limit similar northward expansions of smaller-bodied prey fish (Biswas et al., 2017). Moreover, the resulting novel interactions and voracious predation may extirpate native fishes from northern lakes (Cazelles et al., 2019; Staudinger et al., 2021; Van Zuiden et al., 2016). Other factors to dispersal success include life histories, diets and body traits (Angert et al., 2011; Mims et al., 2010; Whitney et al., 2017), with generalist, longer-living and larger-bodied species more likely to expand ranges (Alofs et al., 2014; Comte & Olden, 2018). Stochastic events and commercial importance have also significantly increased the likelihood of dispersal by the human-facilitated release of many popular sportfish (Dextrase & Mandrak, 2006; Drake et al., 2010; Sharma, Vander Zanden, et al., 2011). Differential responses among species suggest grave implications for the future of freshwater fish biodiversity in northern lakes (Alofs et al., 2014; Comte et al., 2013; Comte & Olden, 2017).

Lakes in Ontario, Canada, sit at the forefront of climate change in North America, with rapidly warming lakes that may provide early warning for unprecedented freshwater fish assemblage changes further north (Campana et al., 2020; Cazelles et al., 2019; Poesch et al., 2016). Reduced thermal habitat availability and increased competition and predation pressures from range expanding warmwater fish species, such as smallmouth bass (*Micropterus dolomieu*), may lead to reduced abundance, fecundity, size and extirpations of commercially and ecologically important cold and coolwater freshwater fish, including salmon, trout, perch and minnows (Sharma, Herborg, et al., 2009; Van Zuiden et al., 2016; Van Zuiden & Sharma, 2016). In this study, we sought to identify patterns of range edge shifts among predator and prey freshwater fishes from warm, cool and coldwater thermal guilds, most vulnerable to climate change (Hiddink et al., 2015). We quantified how fast lakes are warming, how fast fish are moving, and whether the northern range edge shifts of freshwater fishes are tracking the climate in Ontario lakes for a diverse assemblage of fish species. More specifically, we asked (1) What are the trends in summer water temperature for lakes in Ontario between 1986–2017; (2) At what speed are lake temperatures changing (i.e. their climate velocity)?; (3) What are the rates of range edge shifts (biotic velocity) for fishes of differing thermal guilds and trophic status; and (4) Are freshwater fishes tracking climate in Ontario lakes?

2 | METHODS

2.1 | Data acquisition

We acquired data on fish communities and lake geomorphometric characteristics for 10,732 lakes across Ontario, Canada from the Ontario Ministry of Natural Resources. Data were collected over two surveys: Aquatic Habitat Inventory that sampled 9878 lakes

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between 1957 and 1986 (historical), and the Broad-scale Monitoring Programme that sampled 854 lakes between 2007 and 2017 (contemporary) (Dodge et al., 1985; Sandstrom et al., 2010). Some lakes were resampled repeatedly because of the new sampling methodology of the contemporary survey (Sandstrom et al., 2010). Therefore, to maintain uniformity in sampling efforts across surveys (Whittier & Kincaid, 1999), we used geophysical properties such as geographic coordinates, surface area (ha) and depth (m), to identify and retain only the latest unique lake entries within each dataset. For these analyses, we used 9878 lakes from the historical dataset and 854 lakes from the contemporary dataset.

2.2 | Water temperatures

Water temperatures from 1986 to 2017 were downloaded from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA5 reanalysis product. Surface water temperature of lakes was simulated within ERA5 (Hersbach et al., 2020) via the Freshwater Lake model, FLake (Mironov, 2008; Mironov et al., 2010), which is implemented within the Hydrology Tiled ECMWF Scheme for Surface Exchanges over Land (Balsamo et al., 2012; Dutra et al., 2010) of the ECMWF Integrated Forecasting System. The water temperature model is one of the most widely used lake models and has been tested extensively in past studies (Le Moigne et al., 2016; Woolway & Merchant, 2019). Lake temperatures in ERA5 are simulated at a 0.1° by 0.1° longitude-latitude grid resolution, based on the mean depth and surface area of all known lakes within a given 0.1° grid. The lake temperature simulations therefore represent a "typical lake" for each grid (hereafter simply referred to as "lake"), notably simulating the average lake thermal environment in that location using the grid cell's climate forcing. The surface water temperature model in the Integrated Forecasting System is supported by two climatological fields: (i) an inland water mask, provided by the US Department of Agriculture—Global Land Cover Characteristics Data (Loveland et al., 2000), at a nominal resolution of 1 km, which provides the fractions of each surface grid occupied by surface water; and (ii) depth, which is specified according to Kourzeneva, 2010, and combined with a 1 arc-min global bathymetry dataset. All data from January 1986 to December 2017, inclusive, were accessed and analysed at an hourly resolution. Hourly lake water temperatures were predicted in part using hourly air temperatures within the FLake model. Seasonal averages (Jun–Aug), which were used in all velocity calculations (see below), were calculated from the hourly data.

2.3 | Fish community composition

Fish community data consisted of species occurrence (presence/absence) for up to 131 taxa (106 species; 25 genera). Historical surveys utilized large gillnets and trap nets to sample species occurrences. However, Bowlby and Green (1987) showed that the historical sampling could have been biased towards larger fish species. Therefore, to reduce the potential under-sampling of smaller-bodied fishes, small-meshed equipment was additionally used during the contemporary surveys (Sandstrom et al., 2010). We excluded genera-specific information and occurrence data on rare species. Rare species were defined as any species that occurred in <5% of lakes within both time periods sampled (Alofs et al., 2014). More specifically, fishes found in less than 494 lakes of the 9878 lakes sampled during the historical survey and 43 of 854 lakes sampled during the contemporary survey were excluded, leaving 30 species for consideration (Table 1). This focal grouping represents 19% of the 155 freshwater fish species in Ontario including 4 species from each of the Centrarchidae, Percidae and Salmonidae families, 5 Cyprinids, 7 Leuciscids and 1 Ictalurid (Eakins, 2021).

Each species in our focal group was assigned a thermal guild as defined by Magnuson et al., 1979, based on a preferred temperature range; cold: >15°C (7 species), cool: 15–25°C (14 species) and warm: <25°C (9 species). Preferred temperature values were extracted from Hasnain et al., 2010, with seven missing values supplemented by the mean of preferred thermal ranges from the Ontario Freshwater Fishes Life History Database (v5.11; Eakins, 2021). Where classifications conflicted, we retained the Ontario Freshwater Fishes Life History Database designation except when a colder guild was indicated. We also classified species by an aggregated trophic level based on feeding guild and lifestyle according to FishBase (Froese & Pauly, 2021), to quantify patterns in trophic levels and inter-trophic interactions on freshwater fish dispersal and range shifts (Whitney et al., 2017). A species was classified as prey fish if herbivorous or planktivorous and prey to higher trophic adult fish. Intermediate predators were typically omnivores, invertivores or carnivores that consumed prey fish but were themselves prey even as adults. Predators fed on prey fish and/or intermediate predators but were not prey to other freshwater fish as adults. Each trophic class was assigned an ordinal value from 1 to 3; 1 = prey fish; 2 = intermediate predator; 3 = predator for a pre-experimental Kendall's Tau correlation between trophic level and maximum body length values extracted from FishBase (Froese & Pauly, 2021). A positive correlation was identified between trophic level and maximum body length (Kendall's Tau; $p = 5.78\,E^{-05}$; $\tau = 0.59$).

2.4 | Data analysis

2.4.1 | Water temperature trends and climate velocity

Climate velocities (km year^{-1}) were calculated from the ERA5 lake temperature simulations by dividing long-term temperature trends (°C decade^{-1}) by the spatial temperature gradient (°C km^{-1}). Long-term trends of each grid cell were calculated as the slope of a linear trend model, and the spatial gradients were calculated using a 3 × 3 grid cell neighbourhood. Ultimately, the spatial temperature gradient was calculated as the vector sum of the north–south and east–west temperature gradients for each grid. Specifically, the spatial

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TABLE 1 Ontario freshwater fish species list with thermal guild (coldwater, coolwater and warmwater) and trophic level (intermediate predator, predator and preyfish).

Common name	Scientific name	Thermal guild	Trophic level	Distance moved north (km)	Biotic velocity (km decade^{-1})	*p*-value	Standard deviation
Rock Bass	*Ambloplites rupestris*	Warmwater	Intermediate Predator	155.7	50.2	<0.001	25.2
Brown Bullhead	*Ameiurus nebulosus*	Warmwater	Intermediate Predator	92.2	29.7	<0.001	13.4
Longnose Sucker	*Catostomus catostomus*	Coldwater	Preyfish	259.1	83.6	<0.001	30.4
White Sucker	*Catostomus commersonii*	Coolwater	Preyfish	24.2	7.8	<0.001	19.7
Northern Redbelly Dace	*Chrosomus eos*	Coolwater	Preyfish	−95.7	−30.9	<0.001	19.9
Cisco	*Coregonus artedi*	Coldwater	Intermediate Predator	80.0	25.8	<0.001	14.6
Lake Whitefish	*Coregonus clupeaformis*	Coldwater	Intermediate Predator	63.6	20.5	<0.001	18.3
Brook Stickleback	*Culaea inconstans*	Coolwater	Preyfish	−126.5	−40.8	<0.001	21.6
Northern Pike	*Esox lucius*	Coolwater	Predator	21.7	7.0	<0.001	19.5
Johnny Darter	*Etheostoma nigrum*	Coolwater	Preyfish	−139.1	−44.9	<0.001	14.9
Pumpkinseed	*Lepomis gibbosus*	Warmwater	Preyfish	223.4	72.1	<0.001	27.6
Burbot	*Lota Lota*	Coldwater	Intermediate Predator	53.1	17.1	<0.001	15.4
Common Shiner	*Luxilus cornutus*	Coolwater	Intermediate Predator	160.4	51.7	<0.001	23.1
Allegheny Pearl Dace	*Margariscus margarita*	Coolwater	Intermediate Predator	15.5	5.0	<0.001	17.7
Smallmouth Bass	*Micropterus dolomieu*	Warmwater	Predator	217.9	70.3	<0.001	27.0
Largemouth Bass	*Micropterus salmoides*	Warmwater	Predator	125.5	40.5	<0.001	31.3
Golden Shiner	*Notemigonus crysoleucas*	Coolwater	Preyfish	−10.0	−3.2	<0.001	26.8
Blacknose Shiner	*Notropis heterolepis*	Coolwater	Preyfish	−64.2	−20.7	<0.001	11.9
Spottail Shiner	*Notropis hudsonius*	Coolwater	Preyfish	36.0	11.6	<0.001	16.9
Mimic Shiner	*Notropis volucellus*	Warmwater	Preyfish	−29.1	−9.4	<0.001	14.5
Yellow Perch	*Perca flavescens*	Coolwater	Intermediate Predator	37.9	12.2	<0.001	18.5
Common Logperch	*Percina caprodes*	Warmwater	Preyfish	87.3	28.1	<0.001	23.7
Trout-Perch	*Percopsis omiscomaycus*	Coldwater	Intermediate Predator	180.6	58.3	<0.001	23.5
Bluntnose Minnow	*Pimephales notatus*	Warmwater	Preyfish	−19.6	−6.3	<0.001	40.2
Fathead Minnow	*Pimephales promelas*	Warmwater	Preyfish	−182.6	−58.9	<0.001	26.0
Ninespine stickleback	*Pungitius pungitius*	Coolwater	Preyfish	−31.0	−10.0	<0.001	22.3
Brook Trout	*Salvelinus fontinalis*	Coldwater	Predator	−63.7	−20.6	<0.001	16.1
Lake Trout	*Salvelinus namaycush*	Coldwater	Predator	49.7	16.0	<0.001	12.5
Walleye	*Sander vitreus*	Coolwater	Intermediate Predator	38.7	12.5	<0.001	16.5
Creek Chub	*Semotilus atromaculatus*	Coolwater	Intermediate Predator	79.3	25.6	<0.001	12.2

Note: Median distance moved north is the change in median latitude calculated from the top 3% northernmost occurrences between historical and contemporary time frames. Median biotic velocity is the change in median distance moved north over the time between the latest recorded occurrences in the historical survey and contemporary survey.

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temperature gradient for a focal cell was calculated as the difference in temperature for each northern and southern pair divided by the distance between them (Burrows et al., 2011). For these calculations (temperature trend, spatial gradient and climate velocity) we used the R package "Vocc" (García Molinos et al., 2019; R Development Core Team, 2021). Climate velocities and warming rates were then converted to decadal scales (i.e. km year^{-1} ≥ km decade^{-1}; °C year^{-1} ≥ °C decade^{-1}) and basic statistics calculated (i.e. mean, median max, min) to investigate potential geographic trends in lake thermal habitat changes. Geographic visualizations and map analyses were generated via ArcMap 10. 8.1 (Esri Inc., 2020), with Ontario geographical map data derived from boundary files provided by Statistics Canada (Statistics Canada, 2017).

2.4.2 | Biotic velocities

To determine how fish species' ranges have shifted in response to recent climatic shifts, we quantified the direction and magnitude of shifts in northern range boundaries for each species and calculated their biotic velocities (i.e. leading edge velocity) using the equation below. We note that these range edges are quantified solely within the province of Ontario, where some of the warmwater fishes captured in this study are at their far most northern range. However, there are populations of coolwater and coldwater fishes further northeast and northwest of the province of Ontario. Northern range boundaries were used solely as they were analogous to the leading edge of a climate-sensitive region and most sensitive for identifying climate-vulnerable species (Hampe & Petit, 2005). We defined the northern range boundary as the top 5% of northernmost lakes occupied by each fish during historical and contemporary time periods. This follows the definition of a northern range boundary as outlined by Alofs et al. (2014) by using a top percentile of a species' lake occurrence data accounts for uneven sampling between time periods and fish species (Button et al., 2013; Shapiro et al., 1968). A 5% threshold was chosen to reduce undue influences of geographic outliers on the representative subset representing the northern boundary range (Nenzén & Araújo, 2011; Quinn et al., 1996). However, owing to the sample size imbalances in species occurrence data between the historical (9878 lakes) and contemporary (854 lakes) surveys, we approximated the position of the northern range boundary in each time period using the median latitude because the ranges of the latitudinal subsets defining each species' northern range boundaries were nonparametric, skewing towards higher latitudes and multiple outliers. We used a bootstrapping approach to sample 400 lakes with replacement from both the historical and contemporary datasets to further minimize the bias estimation of the northern range edge position owing to the higher sampling density in the historical period, which led to a higher probability of detecting species at any given latitude. We calculated the northern range edge positions for focal species from both historical and contemporary datasets. We repeated the calculation 10,000 times to develop a distribution of the estimated range edge positions for each species in each time period (i.e. Zhou et al., 2021). We used 111 as the multiplier to convert latitudinal degrees to kilometres, as is standard in temperate latitudinal zones. We then calculated the rate and direction at which the position of each fish species' northern range boundary shifted from 1986 to 2017 using the formula below:

$$Biotic\ Velocity = \frac{(Median\ Latitude_{Contemporary} - Median\ Latitude_{Historical} \times 111)}{\Delta Time}$$

$$\Delta\ Time = Final\ Year_{Contemporary} - Final\ Year_{Historical}$$

To test whether the magnitude and direction (i.e. positive = northward vs negative = southward) of range edge shifts in the northern range boundary were significantly different between historical and contemporary time periods, we conducted parametric one-tailed paired *t*-tests of significance for each species' biotic velocity. If the standard deviation of the biotic velocity was higher than the biotic velocity, we designated the change as "no change," even if it was a statistically significant different range edge shift (Fredston-Hermann et al., 2020; La Sorte & Jetz, 2012; Maggini et al., 2011). We also compared the absolute magnitude of biotic velocities between northern range boundary expanding and contracting species using a one-tailed *t*-test. Next, we compared average range edge shifts between fish of different thermal guilds (coldwater, cool water and warm water) and aggregated trophic levels (prey fish, intermediate predator and predator) using a Kruskal–Wallis test with post-hoc Mann–Whitney pairwise tests to identify whether there were significant differences in range edge shifts between fish of differing thermal guilds and trophic levels. Lastly, we compared the calculated biotic velocities of each fish species to the median climate velocity to identify which of our focal species were tracking the climate velocity. Successful climate tracking species were defined as having biotic velocities equal to or greater than the calculated climate velocity, while species shifting north at rates slower than the climate velocity were climate laggers (Devictor et al., 2008; Lenoir et al., 2020; Loarie et al., 2009).

3 | RESULTS

3.1 | How fast are lakes warming?

Lakes in Ontario warmed 0.2°C decade^{-1} on average between 1986 and 2017 (Figure 1a). Summer water temperatures increased most rapidly in the northeast of the province, just north of Sudbury, Ontario at rates averaging 0.4°C decade^{-1}. By contrast, the slowest

FIGURE 1 (a) Summer water temperature warming rates (°C decade^{-1}) between 1956–2017 across Ontario, Canada. Darker coloured dots indicate lakes with faster rates of warming. (b) Climate velocities (km decade^{-1}) over 1956–2017 for lakes across Ontario, Canada. Darker coloured dots indicate lakes with faster rates of climate change.

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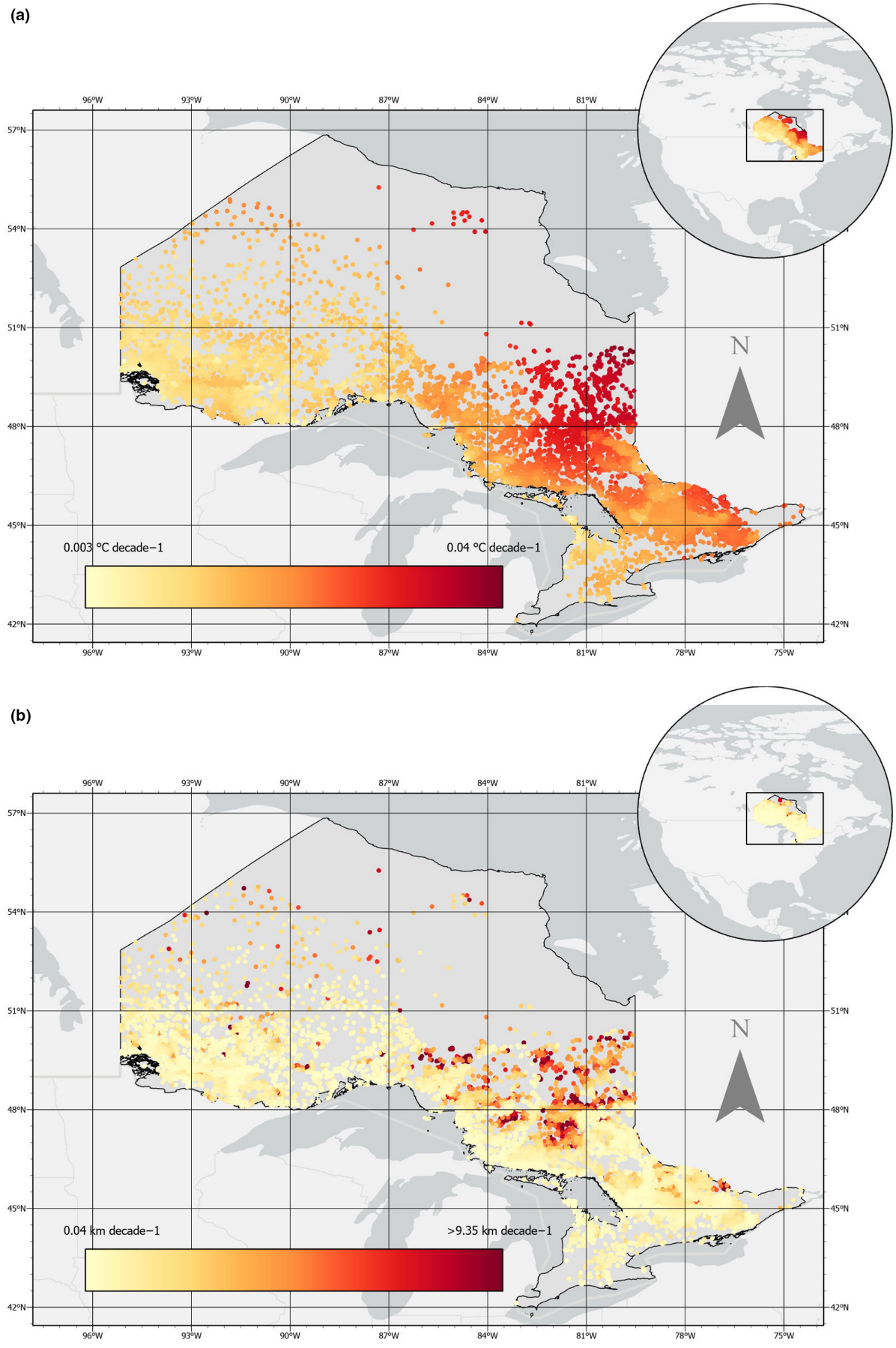

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warming lakes were in the west, close to the border with Manitoba at 0.03°C decade^{-1}. Mean and median climate velocities across Ontario between 1986 and 2017 were 24.5 and 9.4 km decade^{-1}, respectively (Figure 1b). The highest climate velocities were in lakes found at higher latitudinal lakes, in particular lakes around Sudbury, Ontario where climate velocities exceeded 907 km decade^{-1}. Generally, lakes with the slowest climate velocities of 0.4 km decade^{-1} were found in the south but were also interspersed throughout the province.

3.2 | How fast are fish moving?

Between 1986 and 2017, on average, fish in Ontario have expanded their northern range boundaries by 0.37° or ~41 km at a rate of 13.3 km decade^{-1}, with more fish species expanding into lakes they previously did not inhabit, than were lost from northern lakes (Figure S1). Fourteen fishes expanded their northern range boundaries; shifting 42.1 km decade^{-1} northwards on average. Conversely, six fishes contracted their northern range boundaries by 36.1 km decade^{-1} (Table 1). Range contracting species were defined as those which were present in lakes within their northern boundary range during the historical period but absent from the latitudinal region defined by the northern range boundary of the contemporary period. Ten fishes were defined as not shifting their ranges northwards or southwards.

Generally, warm water fishes of mixed to higher trophic status expanded their range northwards, whereas cold and cool water prey fish predominantly experienced range contractions in Ontario (Figure 2a–f). Those species whose ranges are contracting southward are significantly faster than those expanding ranges northward ($t = 3.71$; $p = 6.6E\text{-}04$). Despite great variation in range edge shifts, there were no statistically significant differences in range edge shifts between fishes from thermal guilds or trophic status ($F = 0.68$; $p = 0.64$). A variety of freshwater fishes from all thermal guilds and trophic status moved their northern range edge northwards. For example, the top three fastest range expanding fishes included the longnose sucker (*Catostomus catostomus*; 83.5 km decade^{-1}), a coldwater preyfish, the pumpkinseed (*Lepomis gibbosus*; 72.1 km decade^{-1}), a warmwater preyfish and the smallmouth bass (*Micropterus dolomieu*; 70.3 km decade^{-1}), a warmwater predator. Whereas fishes moving south from their northward range edge were almost entirely preyfish, except for the brook trout, a coldwater predator (−20.6 km decade^{-1}) (Figure 2). The fish being lost the most rapidly from northern lakes was the fathead minnow (Pimephales promelas; −58.9 km decade^{-1}). There was no significant difference in the rates at that species moved northwards or were lost from northern lakes ($t = 0.88$; $p = 0.19$). However, there were statistically significant differences in range edge shifts between fishes from different thermal guilds or trophic status. For example, coolwater fishes (pKruskal–Wallis = 0.06; pMann–Whitney pairwise = 0.04) and preyfish (pKruskal–Wallis = 0.03; pMann–Whitney pairwise = ~0.01) were most likely to be losing habitat in northern lakes by 1.2 and 1.6 km decade^{-1}, respectively, on average (Figure 3a,b). By comparison, cold and warm water fishes both moved their northern range edge boundaries by 28.7 and 24.0 km decade^{-1}, respectively, whereas predators and intermediate predators expanded by 22.6 and 28.06 km decade^{-1} (Figure 3a,b).

3.3 | Are freshwater fishes tracking climate?

The median climate velocity was 9.4 km decade^{-1} for 10,732 lakes in Ontario between 1986 and 2017. Seventeen of our focal freshwater fishes were identified as exceeding recent climate changes with calculated biotic velocities exceeding 9.4 km decade^{-1}. Each thermal guild and trophic status was represented by at least three climate tracking fish species. For example, warm water fishes exceeding the climate velocity included the brown bullhead, rock bass, largemouth bass, smallmouth bass, common logperch and pumpkinseed. Cool water fishes included the yellow perch, walleye, creek chub, common shiner and spottail shiner, while coldwater fishes consisted of the burbot, lake whitefish, cisco, trout-perch, lake trout and longnose sucker. Preyfish with biotic velocities exceeding the climate velocity included the spottail shiner, common logperch, pumpkinseed and longnose sucker. Intermediate predator species included the yellow perch, walleye, burbot, lake whitefish, creek chub, cisco, brown bullhead, rock bass, common shiner and trout-perch, while predator fishes consisted of lake trout, largemouth bass and smallmouth bass. On average, these fishes moved their range northwards at biotic velocities ranging from 11.6 to 83.6 km decade^{-1} (Table 1).

Thirteen out of our 30 focal species were found to be lagging behind the calculated climate velocity. However, three of these species continued to expand their northern range boundaries but at rates slower than the climate velocity, ranging from 5 to 7.8 km decade^{-1}. All trophic guilds were represented by at least one of these 3 species; however, this grouping consisted only of coolwater species. The fastest was the white sucker (*Catostomus commersonii*; Leuciscidae, cool water; preyfish; Distance moved north: 24.2 km; Biotic velocity: 7.8 km decade^{-1}; Table 1).

The remaining 10 focal species with biotic velocities that lagged behind the climate velocity lost their northern lake habitats, albeit at rates slower than range expanding species, at biotic velocities ranging from 3.2 to 58.9 km decade^{-1} (Table 1). All northern range edge contracting species were lower trophic preyfish, with the exception of brook trout. Range contracting species included 6 cool

FIGURE 2 Comparison of individual mean biotic velocities with standard deviations along thermal and trophic guilds compared with the climate velocity. (a) Coldwater fishes, (b) coolwater fishes, (c) warmwater fishes; (d) predators; (e) intermediate predators; (f) preyfish. Species with biotic velocities found to be statistically significant have a black outline. The purple line represents the median climate velocity of Ontario lakes at ~9.4 km decade^{-1}.

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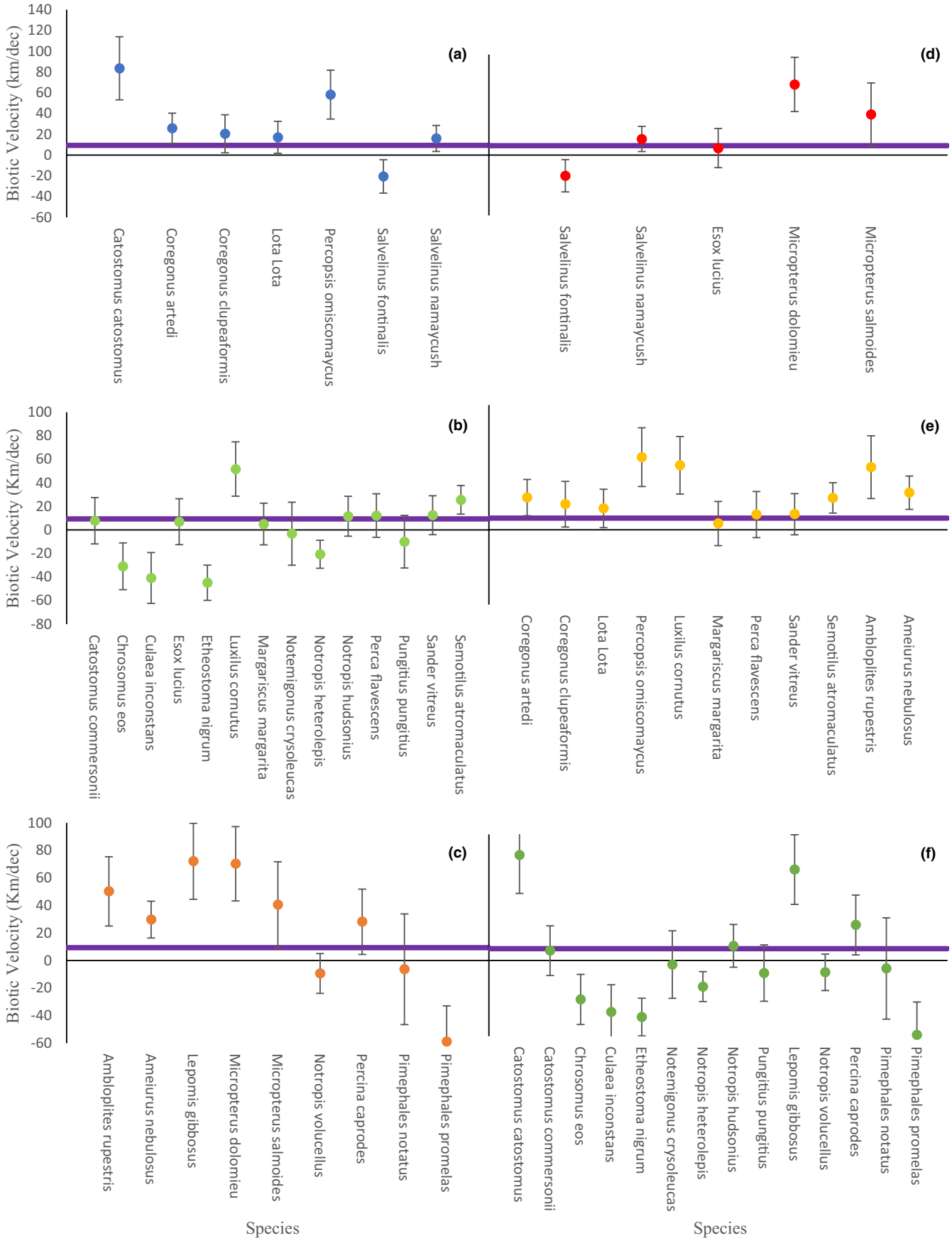

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water fishes: the johnny darter, brook stickleback, northern redbelly dace, blacknose shiner, ninespine stickleback and golden shiner, as well as 3 warm water species: the fathead minnow, mimic shiner and blunthead minnow. Only one coldwater fish experienced the loss of habitat in northern lakes, the brook trout, at 20.6 km decade^{-1}.

4 | DISCUSSION

As lakes across Ontario continue to warm in response to recent climatic warming, climate niches are shifting north and northeast (Figure 1). In response, some freshwater fishes are shifting the northern boundaries of their ranges with the direction and rate varying considerably between our focal species, ranging from losing their northernmost lake habitats at rates as fast as 58.9 km decade^{-1} to expanding or moving their ranges northwards up to rates of 83.6 km decade^{-1} over the past 31 years. Our results are congruent with projections based on climate interactions (Campana et al., 2020; Minns & Moore, 1995) and freshwater fish responses to similar climate changes in French rivers (Comte & Grenouillet, 2013), with more species expanding into previously uninhabited lakes in Ontario, than those losing northern lake habitats. Though fish of all thermal guilds among our focal species group expanded or contracted ranges, in general, warm water fishes were the fastest at expanding into new northern lakes, whereas coldwater and cool water species, in particular, prey fish were rapidly lost from their historic northern range edges. Fourteen of our focal set of freshwater fish species were tracking the northward shift of their climate niches. The fastest climate tracking fish tended to be warmwater sportfish predators, who may be most likely to escape climate debt extinction and colonize previously uninhabited lakes across northern Ontario, whereas preyfish may be facing potentially historic population declines.

4.1 | How fast are lakes warming?

Across the studied lakes, surface water temperature trends were suggested to be increasing at an average rate of 0.2°C decade^{-1} between 1986 and 2017. This rate of change in surface water temperature contributed to the average climate velocity rate of 24.5 km decade^{-1} (median = 9.4 km decade^{-1}) in the studied region. Our analysis also suggested that the greatest climate velocities are calculated at higher latitudes, which, in some extreme cases, could exceed 907 km decade^{-1}. The lowest climate velocities of 0.4 km decade^{-1} are calculated in southern regions. In brief, higher climate velocities are expected in regions with high surface temperature trends and low spatial temperature gradients (e.g. due to low gradients in elevation). Regarding the influence of surface temperature trends, it is not unexpected that higher latitude regions experience the greatest change. This agrees with previous studies (O'Reilly et al., 2015; Schneider & Hook, 2010; Woolway & Merchant, 2019) and largely reflects the amplified increase in air temperature at high latitudes. Both the trend and velocity of climate change at the lake surface follow closely those projected in air temperature (Woolway & Maberly, 2020). This follows our expectation, given that air temperature is one of the dominant drivers of lake surface water temperature. However, other atmospheric drivers can also influence lake surface temperatures, including wind speed (Woolway & Merchant, 2019) and solar radiation (Schmid & Koster, 2016), among others (Edinger et al., 1968). It is also important to appreciate the thermal lag between air and water (Toffolon et al., 2020) and can lead to a weaker relationship between air and water temperature at seasonal timescales. These factors, as well as the influence of lake morphometry (Kraemer et al., 2021) and the presence of winter ice cover (Austin & Colman, 2007), account for some of the variability in the air-water temperature relationships.

4.2 | How fast are fish moving?

Recent climate warming may be driving range edge shifts for freshwater fishes. We found that on average, species are moving into new northern lakes at faster rates (42.1 km decade^{-1}) than species have been lost (36.1 km decade^{-1}) from lakes at the northernmost extent of their historical ranges. Preyfish were predominately being lost from northern lakes, including coolwater preyfish species, such as various shiners (blacknose, mimic, golden etc.), but also the fathead minnow, a warmwater preyfish, which lost northern lake habitats at the fastest rate among range contracting species at 59.5 km decade^{-1}. By comparison, range expanding species were primarily composed of cool and warm water species, with the fastest among them almost entirely warmwater predators. Most of these fishes were also popular sport or game fish, including smallmouth bass and yellow perch, but also include preyfish like pumpkinseed and longnose sucker (Kerr et al., 2011; Poesch et al., 2016).

Despite the inherent fragmented "island-like" nature of their habitats preventing passive dispersal (Hodgson et al., 2012; Tonn & Magnuson, 1982), freshwater fishes in lakes are responding to the direct and indirect effects of climate changes in Ontario, in much more apparent ways than freshwater fish in interconnected river habitats and some terrestrial organisms, moving between 3.2–83.6 km decade^{-1}. For example, marine species have shifted their global leading edges at rates ranging between 1.4 and 60.2 km decade^{-1} (Cheung et al., 2009; Lenoir et al., 2020), whereas terrestrial species have shifted their global ranges by 6.1 km decade^{-1} (Parmesan & Yohe, 2003). In Ontario, Alofs et al. (2014) reported range shifts of 12. 9–17.5 km decade^{-1} for warm and cool water sportfish. The fastest northbound sportfish/predator in our focal group, the smallmouth bass shifted northern range boundaries by 70.3 km decade^{-1}. Furthermore, our results concur with other range edge shifts and projections of habitat loss calculated in the past decade. For example, Alofs et al. (2014) also reported contractions in ranges for preyfish like northern redbelly dace (*C. eos*), blacknose shiner (*N. heterolepis*), bluntnose minnow (*P. notatus*) and golden shiner (*N. crysoleucas*). Our updated and expanded study showed that these species are expanding their northern range boundaries at rates ranging

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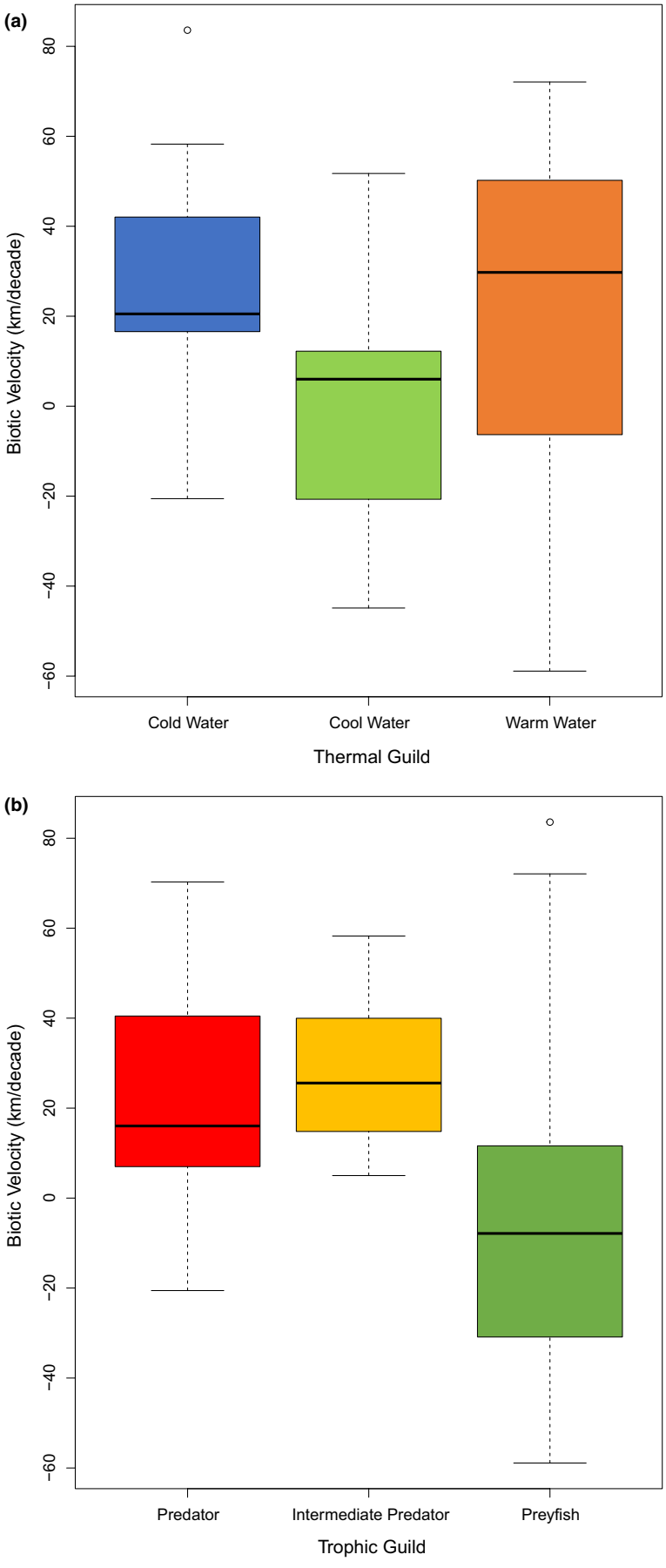

FIGURE 3 Comparison of biotic velocities across fish of different guilds. (a) Thermal guilds. (b) Trophic classes. Guilds or classes found to be relatively significantly different are denoted by an asterisk. The black line indicates the median, while hollowed circles represent outliers, and error bars show the maximum and minimum values without outliers.

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from 3.2 to 30.9 km decade^{-1}. Alofs et al. (2014) also reported similar expansions of brown bullhead, largemouth bass, rock bass, smallmouth bass and pumpkinseed, which we report as expanding into new lakes at rates of 29.7–72.1 km decade^{-1}. Similarly, Edwards et al. (2016), reported northward movement of lake whitefish and walleye, as these fishes escaped warming habitats in central and southern Ontario, at rates of 20.5 and 12.5 km decade^{-1}, respectively.

We found a high degree of variation in species range shifts even among fishes of similar thermal guilds and trophic classes, with no significant differences in biotic velocities between species from different thermal guilds or trophic classes. Similarly, Comte and Grenouillet (2013) reported a high degree of variation between a similarly sized grouping of freshwater fish species in riverine habitats across France but found stream fish to be moving slower at rates of 13.7 m decade^{-1} and 0.6 km decade^{-1} towards higher elevations and upstream, respectively. Whereas cool water and warm water predators were expanding their range northwards, preyfish of many thermal guilds lost northern lake habitats. As lakes across Ontario continue to warm, coldwater (11–15C ± 4C) and cool water (15–25C ± 4C) refugia are being replaced with warm water habitats. Therefore, coldwater and cool water species may contract their ranges as they are stressed by the loss of suitable thermal refugia and heightened predation from warm water species (Poesch et al., 2016; Shuter et al., 2012). By contrast, warm water species such as smallmouth bass may be able to expand and establish themselves more rapidly in a climate-warmed region more suitable to their temperature preferences (Sharma et al., 2007; Sharma, Vander Zanden, et al., 2011; Van Zuiden et al., 2016).

Generally, we found that prey fish were losing northern habitats and not tracking climate, regardless of whether they belonged to the warm water, cool water or coldwater thermal guilds. Alofs et al. (2014), also observed a similar potential divide between baitfish (prey fish and intermediate predators) and sportfish (predators and intermediate predators) in the direction and magnitude of range changes. Trophic classification is another measure of dispersal ability, positively correlating to life histories and physiological traits such as total length, fecundity and longevity (Alofs et al., 2014; Comte et al., 2014; Whitney et al., 2017). For example, fish with specialized diets such as herbivorous prey fish are less likely to shift ranges northward, compared with intermediate predators and predators, which have broader diets (Ontario Freshwater Fishes Life History Database; v5.11; Eakins, 2021; Whitney et al., 2017). In addition, smaller fish tend to have a lower capacity to disperse, whereas intermediate and apex predators tend to be larger and are better able to swim to new sites (Alofs et al., 2014; Perry et al., 2005). Moreover, the range expansion of warm water predators and subsequent biotic interactions between freshwater fish of differing trophic classes can also impact fish diversity (Conti et al., 2015; Erős et al., 2020). For example, the northwards expansion of smallmouth bass has consistently been linked in the literature to decreased abundances and extirpations of cold and cool water intermediate predators such as rainbow smelt (*Osmerus mordax*), cisco (*Coregonus artedi*) (Sharma, Vander Zanden, et al., 2011), walleye (*Sander vitreus*) (Van Zuiden et al., 2016; Van Zuiden & Sharma, 2016; Vander Zanden et al., 2004) and prey fish, including northern redbelly dace, finescale dace, fathead minnow and pearl dace (Jackson & Mandrak, 2002). Lost recruitment because of competition or predation may result in reduced abundances of cold and cool water prey fish and intermediate predators, delaying their ability to expand or even drive range contractions via extirpations (Burgess et al., 2017; Vadas, 1990). Notably, the few preyfish that moved their range edges northwards are all commercially important, including the pumpkinseed, longnose sucker and white sucker (Kerr et al., 2011; Poesch et al., 2016), or important baitfish like the spottail shiner (Smith & Kramer, 1964), which highlights the importance of human-mediated dispersal in freshwater fishes (Sharma, Legendre, et al., 2011).

4.3 | Are freshwater fishes tracking climate?

Some freshwater fish have adapted to recent climatic changes by shifting their current ranges to track the poleward movements and stay within their preferred thermal niches, with differential biotic velocities among our focal species implying differential degrees of vulnerability to climate-driven extinctions (Pinsky et al., 2013; Whitney et al., 2017). However, only those freshwater fishes that can disperse at rates equal to or exceeding the rate of climate change in Ontario (9.4 km decade^{-1}) will be able to stay within their climate niches (Lenoir et al., 2020; Loarie et al., 2009) and escape the risk of climate-driven extirpations (Hiddink et al., 2015; Loarie et al., 2009; Zhu et al., 2012), We identified three types of climate tracking: (1) range contracting species that were unable to track recent climate shifts, had negative biotic velocities and were losing lake habitats at the northernmost extent of their range in Ontario; (2) climate lagging species with positive biotic velocities slower than the climate velocity; (3) and climate trackers migrating into northern lakes at rates that kept up with or exceeded the shifts in their climatic niches. Our analysis revealed that some freshwater fish, in particular, prey fishes in Ontario may not be successfully tracking the northward shift of their climate niches. We found that more than half of our focal species were moving their northern range boundaries at rates sufficient to keep up with the changing climate. Another three species (allegheny pearl dace, northern pike and white sucker) were also expanding into northern lakes but at rates ranging from 5.0 to 7.8 km decade^{-1}, well below the calculated climate velocity of 9.4 km decade^{-1}. All three climate lagging fishes were coolwater species that may be accruing "climatic debt," potentially putting them at risk of extirpation (Hiddink et al., 2015).

Ten fishes, composed of range contracting prey fish and one predator are likely already accruing extinction debt. This failure to track the climate, resulting in colonization lag, will be compounded by and may even be a direct result of the invasion of northward tracking predator species such as the smallmouth and largemouth bass (i.e., Alofs & Jackson, 2015; Sharma et al., 2007; Van Zuiden et al., 2016), wherein increased co-occurrence decreased the abundances or even extirpated cold and cool water competitors and prey (Hansen et al., 2017; Jackson & Mandrak, 2002; Sharma, Vander Zanden, et al., 2011; Tonn & Magnuson, 1982; Van Zuiden & Sharma, 2016;

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Vander Zanden et al., 2004; Whittier & Kincaid, 1999). These 10 species may be the most climate-vulnerable fishes of Ontario and include commercially or ecologically important species, such as brook trout (*Salvelinus fontinalis*) (Haxton et al., 2020; Lynch et al., 2016). Their range contractions may be an early indication of population declines (Opdam & Wascher, 2004).

4.4 | Conclusions and implications

Our analysis covered a broad geographic territory constituting 1.076 million km^2 encompassing numerous lake habitats currently at the forefront of climate change (Woolway & Maberly, 2020). To our knowledge, we provide the first comprehensive analysis of range edge shifts for a wide variety of Ontarian freshwater fish taxa, covering 30 species from 11 families, some of which have never been examined before in the context of lake habitats and lake fish communities. Our results suggest that many more species beyond those included in this study may also be responding to recent climate changes and correspondingly could be at risk. Despite this large grouping of species, it still does not represent most of the freshwater fishes of Ontario, which number over 155 species across 29 families (Eakins, 2021; Froese & Pauly, 2021). Continued sampling efforts and monitoring of freshwater fishes, many of which are already highly climate-vulnerable, are required to continue to understand the impacts of climate change on Ontarian freshwater fish biodiversity. In particular, we highlight the importance of studying prey or forage fishes to elucidate a more complete picture of the impacts of climate change on lake fish communities (Biswas et al., 2017).

Due to a paucity of sampling data, climate-driven shifts of freshwater fish distributions in Ontario remain comparatively understudied (Alofs et al., 2014; Heino et al., 2009; Staudinger et al., 2021). Although climate velocity as a benchmark for climate vulnerability has been extensively used to analyse range shifts for a variety of marine and terrestrial species within a continuous environment for dispersal (Burrows et al., 2011; Pinsky et al., 2013), its usage has not yet been evaluated for species in inherently fragmented habitats such as lakes where passive dispersal may be much more difficult (Hodgson et al., 2012; Tonn & Magnuson, 1982). Furthermore, while climate velocity represents an upper bound for a species' migration without consideration for thermal plasticity, biotic velocity represents an actuated lower bound for a species' climate-driven migration (Carroll et al., 2015). The approach we used in this study could be added to the conservation and management toolbox to quantify large-scale changes in species range shifts for both native and non-native freshwater fishes. Multiple approaches to quantify latitudinal and longitudinal changes in species ranges across marine and terrestrial habitats have been developed (i.e. Lenoir et al., 2020; Loehle, 2020), yet significantly less work has been done in Canadian freshwater lakes. Comparisons of these approaches, development of new techniques and additional metrics for understanding range changes, in conjunction with biotic and climatic velocities, may be helpful for quantifying the exposure of freshwater fish in lentic habitats to the effects of climate change (Carroll et al., 2015).

Future work in range edge shifts should consider geographical nuances and non-north–south movements that could have altered or restricted calculated range edge shifts (Loehle, 2020). Significantly more research is necessary to compare and contrast range boundary definitions (i.e. centroid, leading and trailing edges) for effectiveness in evaluating freshwater fish range changes in the "island" like nature of lake ecosystems (Strayer & Dudgeon, 2010). Indeed, populations at the "core" or nearer to the centroid of the range, may respond differently compared with populations at the leading and trailing edges of a species range shifts (Brown et al., 1996; Whitney et al., 2017). Furthermore, without evaluating species richness and population density to truly assess "declines," broad isotherm definitions for range contractions may not be able to account for microrefugia where a species could persist despite its range contracting (Lenoir et al., 2013; Ralston et al., 2017). Lastly, directly accounting for environmental (e.g. altered precipitation, lake elevation, pH, stratification, lake depth) and biotic mechanisms for the interspecific variation in range shifts, may be helpful in demonstrating causal relationships (Alofs & Jackson, 2014; Ockendon et al., 2014).

Our study does not provide evidence that all freshwater fishes are moving polewards in Ontario lakes in response to warming climates. Rather, we found that predators are generally shifting their ranges northward into previously thermally unsuitable northern lakes and tracking climate well before others and prey fish, are either losing northern habitats or lagging significantly behind the climate velocity. The implications of these findings are important to the conservation and management of the highly valued freshwater fishery in Ontario lakes. For example, smallmouth bass, a warmwater non-native fish, is rapidly moving northwards both naturally in response to warmer climates and intentionally spread by humans to establish bass fisheries for anglers (Sharma, Vander Zanden, et al., 2011). The continued northward range expansion of smallmouth bass is wreaking havoc on native fish biodiversity in Ontario lakes by stifling populations of native predators, such as walleye and lake trout (Hansen et al., 2017; Sharma, Jackson, et al., 2009; Van Zuiden & Sharma, 2016; Vander Zanden et al., 2004), and also decimating native prey populations (Jackson & Mandrak, 2002; MacRae & Jackson, 2001; Sharma, Herborg, et al., 2009). We found that four common forage fishes (fathead minnow, Johnny darter, brook stickleback and northern redbelly dace) are being rapidly lost from northern lakes, which will only be exacerbated further by ongoing climate warming and the concomitant spread of non-native warmwater predators (Alofs et al., 2014; Van Zuiden et al., 2016; Van Zuiden & Sharma, 2016). Despite the widespread documented impacts on native fisheries, smallmouth bass continues to be intentionally introduced into aquatic systems in order to establish this prized fishery. Focused management strategies on halting the intentional introduction of smallmouth bass will be required to conserve ecologically and economically important native fisheries.

Our study highlights that cold and cool water prey fish across Ontario may be in danger of declining populations and local

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extirpations, with widespread consequences on the food web of Ontario lakes (Jackson & Mandrak, 2002). Native forage fish communities are threatened by a combination of no longer inhabiting ideal thermal habitats and increased co-occurrence with non-native warm water predators, which will be further exacerbated as the climate continues to warm. Commercially significant, especially predatory warm water fishes are shifting ranges at rates orders of magnitude above the calculated climate velocity to escape climate debt extinction and colonize previously uninhabited lakes across northern Ontario. This selective colonization is liable to disrupt many native fish assemblages in lakes across northern Ontario, potentially jeopardizing local fisheries and native fish biodiversity.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The lake water temperature data that support the findings of this study are openly available in the Climate Data Store at https://doi.org/10.24381/cds.adbb2d47. Unfortunately, the fish occurrence data that support the findings of this study are only available from the Ontario Ministry of Natural Resources and Forestry. Restrictions apply to the availability of these data, which were used under licence for this study. Data are available from the authors with the permission of the Ontario Ministry of Natural Resources and Forestry. For publication: doi:10.5063/F1VM49Q2.

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BIOSKETCH

A common research interest between all members of our team is to understand the impacts of climate change on lakes, including lake ice, water temperatures, thermal stratification, water quality and fish communities at broad spatial and temporal scales. More details on the research program in the laboratory of Sapna Sharma can be found at: https://sharmalab.wordpress.com.

Author contributions: T. Wu and S. Sharma led the project; T. Wu, M.A. Imrit, Z. Movahedinia, J. Kong, and R.I. Woolway compiled and analyzed data. T. Wu developed figures and tables. T. Wu led the writing of the manuscript and R.I. Woolway and S. Sharma contributed text. All coauthors revised the manuscript.

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