

Home range size of freshwater fishes: a meta-analysis through a new lens

Johnathan Lemay

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Signed by the final examining committee:

_____	Chair/Examiner
Dr. Grant E. Brown	
_____	External Examiner
Dr. Emma Despland	
_____	Examiner
Dr. Ian Ferguson	
_____	Co-Supervisor
Dr. James W. A. Grant	
_____	Co-Supervisor
Dr. Dylan J. Fraser	

Approved by

Dr. Robert B. Weladji, Graduate Program Director

_____, 2024

Dr. Pascale Sicotte, Dean of Arts and Science

ABSTRACT

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Johnathan Lemay

Measuring the home range size of freshwater fishes provides crucial information on community structure, population dynamics, and conservation management. Earlier studies have shown that home range size increases with fish size, water body size, and trophic level, and that lake fishes have larger home ranges than stream fishes. However, in previous studies, there were sometimes conflicting findings, a lack of a standardized methodological approach, and some key variables that may influence home range were not considered. Using a systematic quantitative review of 272 studies, we revisited previous meta-analyses and evaluated the home range estimates in both lentic and lotic environments to verify whether home range: 1) increases with fish length, water body size, latitude, and study duration; 2) is influenced by trophic guild and data collection method; 3) decreases with the presence of dams; and 4) varies across fish family. Our results indicated that home range size was 4 times larger in lake than stream fishes and increased with fish length. However, home range size of lake fishes was mainly influenced by lake surface area and latitudinal gradient, not fish length. In streams, fish length, stream width, data collection method, and study duration all significantly influenced home range size. We also found significant fish family variation across lakes and streams when using the most robust available data from three families. These results demonstrate that the home range size of freshwater fishes was explained by different predictors in both lentic and lotic environments.

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Contribution of Authors

Johnathan Lemay¹, Sozos Michaelides¹, Dylan J. Fraser¹, James W. A. Grant¹

¹Department of Biology, Concordia University, 7141 Sherbrooke St. West, Montreal (QC) H4B 1R6

Study concept: JL, JG

Acquisition of data: JL, SM

Analysis and interpretation of data: JL, SM, DF, JG

Drafting of manuscript: JL

Critical revision: JL, SM, DF, JG

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Introduction

First introduced in mammals, the concept of home range size was originally described as an area that an animal learns and routinely uses for its “normal activities of food gathering, mating, and caring for the young” with “normal activities” referring to the repeated use of an area required by an animal to fulfill all its dietary and reproductive needs (Burt, 1940, 1943). Since this original definition, the concept has been updated for most animals with the primary focus of quantifying the space most frequently used by an animal for most of its life, excluding movement related to exploration, dispersal, and migration (Gerking 1953, 1959; Baguette et al., 2014). However, some animals like planktonic invertebrates do not have a home range since they move without a fixed reference point in space (Wilson, 1975), while other animals can have multiple home ranges. For instance, some bird species have breeding and wintering home ranges, separated by migratory paths (Rühmann et al., 2019). These migratory paths are more closely linked to dispersal patterns than the home range concept. While distinct from the concept of dispersal, both home range size and dispersal distance are linked by the movement ecology of a species. For example, home range size increases with maximum dispersal distance in mammals (Bowman et al., 2002), and home range size has been linked to the stationary component of movement in stream fishes (Radinger & Wolter, 2014). Hence, home range size can predict patterns of dispersal, which are crucial for meta-population dynamics, gene flow and the rescue effect (Hastings & Harrison, 1994; Hanski, 1998; Eriksson et al., 2014).

Extensive research has documented the factors influencing an animal’s home range size with many studies indicating that home range increases primarily with body size in mammals (McNab, 1963; Harestad & Bunnell, 1979; Janis & Wilhelm, 1993; Jetz et al., 2004; Ofstad et al., 2016), birds (Schoener, 1968), reptiles (Turner et al., 1969), and fishes (Minns, 1995;

Woolnough et al., 2009; Nash et al., 2015; Barry et al., 2016; Slavík & Horký, 2019). An animal's dietary requirements can also affect its home range size. For instance, carnivorous animals have a larger home range than herbivores because less energy is available at higher trophic levels, larger animals require more energy, and the increased energy requirements associated with hunting for their prey (McNab, 1963; Harestad & Bunnell, 1979; Nash et al., 2015; Tamburello et al., 2015; Viana et al., 2018). Similarly, home range size tends to increase in less productive ecosystems found at higher latitudes (Harestad & Bunnell, 1979; Lindstedt et al., 1986; Nilsen et al., 2005) and during adult life stages because of an increase in body size and trophic level (Cederlund & Sand, 1994; Slavík et al., 2007; Izzo et al., 2022). However, home range size will still vary seasonally due to resource availability and reproductive requirements (Kaus et al., 2016; Viana et al., 2018; Pennock et al., 2020). Therefore, understanding the factors affecting an animal's home range size can provide important information on community structure (Buchmann et al., 2011), population dynamics (Chu et al., 2006; Wang & Grimm, 2007) and density (McNab, 1963; Šálek et al., 2015; Efford et al., 2016), predator-prey interactions (Hobart et al., 2019; Beardsell et al., 2023), and even parasite exposure levels (Bordes et al., 2009; Aalvik et al., 2015). From a conservation perspective, the home range concept can also inform on the management of protected areas, especially in marine and freshwater ecosystems, since larger protected areas are required for animals with larger home ranges (Kramer & Chapman, 1999; Di Franco et al., 2018; Acreman et al., 2020; Zolderdo et al., 2019, 2024).

Freshwater ecosystems are some of the most negatively impacted habitats across the globe. Specifically, freshwater populations have declined by an average of 83% between 1970 and 2018 with freshwater migratory fishes experiencing an average decline of 76% from 1970 to

2016 (WWF, 2022). Anthropogenic pressures such as habitat loss and fragmentation have been driving much of this decline, with climate change set to amplify these negative trends even further (Collen et al., 2014; Best, 2019; Barbarossa et al., 2020; Crozier et al., 2021; WWF, 2022; IPCC, 2023). For example, in fishes, artificial structures such as dams and weirs negatively impact freshwater habitats by restricting fish movement and migration patterns (Morita & Yamamoto, 2002; Fuller et al., 2015; van Puijenbroek et al., 2019). Today, approximately half of all river systems across the globe are affected by dams resulting in over 10,000 lotic fish species facing a decline in habitat connectivity (Liermann et al., 2012; Barbarossa et al., 2020). With freshwater habitat fragmentation estimated to increase 12% by 2030 due to the construction of new dams (Grill et al., 2015; Best, 2019) and average global surface temperature predicted to exceed the 1.5°C target warming before 2040 (Diffenbaugh & Barnes, 2023; IPCC, 2023), the combination of these two events will lead to an ever-growing pressure on freshwater fishes. Therefore, there is an urgent need to enhance freshwater habitat conservation efforts, particularly for fishes. A key pre-requisite to predicting the ecology of freshwater fishes is to quantify their home range size.

The home range size of freshwater fishes has been well documented since Gerking (1953, 1959) first introduced the concept to the fish literature (Miller, 1957; Gunning & Shoop, 1963; Cadwallader, 1976; Bachman, 1984; Guy et al., 1994; Colyer et al., 2005; Walsh et al., 2012; Davidsen et al., 2020), including three meta-analyses (Minns, 1995; Woolnough et al., 2009; Burbank et al., 2023). In a pioneering study, Minns (1995) showed that the home range size of freshwater fishes increased with body size and was 19.6 to 23 times larger in lakes than streams, likely due to lakes being less productive than streams (Randall et al., 1995; see Table 1). However, the author found no support for two expected results: home range size will increase

with increasing latitude and trophic level. Furthermore, Minns (1995) hypothesized that home range size would be affected by fish family and data collection method (telemetry versus mark-recapture) but found no support for either (Table 1).

In the second meta-analysis, Woolnough et al. (2009) criticized Minns (1995) for not properly describing his method of calculating home range size and for including territory size and movement-based data in his home range data set. Given these limitations, the authors excluded all but thirteen data points (i.e., 72% of the original data set) from Minns (1995) in their larger data set (Table 1). Most importantly, they showed that water body size is a better predictor of home range size than body size (Woolnough et al., 2009). They also argued for the use of linear home ranges for streams and areal home ranges for lakes, but these different units precluded comparisons of home range size in the two water body types. However, the different data sets used in the two meta-analyses beg the question of whether Woolnough et al.'s (2009) novel conclusions about water body size are related to including water body size as a new variable in their analysis or using a primarily new data set.

In the third meta-analysis, Burbank et al. (2023) confirm that water body size and fish length are the primary predictors of home range size in both lakes and streams with fish length being more important in streams. Furthermore, they revisited two predictions from Minns (1995) showing for the first time that latitude may influence home range size, possibly due to confounding geographical factors, and that piscivores have larger home ranges than benthivores in both lotic and lentic environments (Burbank et al., 2023). However, their study had two key limitations. First, they added only 20 new telemetry studies to the data sets of the two previous meta-analyses and provided very little information on how home range estimates were extracted from the literature. Second, water body size in streams was defined as the length of stream

accessible to the fish, but no description was provided on how this was quantified. In addition, stream length may not be an appropriate measurement of water body size because fish with large home ranges will automatically have a larger length of stream that is accessible for movement. Instead, stream width provides a more objective measurement of water body size for streams (Radinger & Wolter, 2014).

Although fish body size, water body size, trophic guild, and latitude have been shown to influence home range size, inconsistencies in the methodology have reduced the replicability of the three previous meta-analyses, especially when disagreements still remain on how best to measure and calculate the home range size of freshwater fishes (Anderson, 1982; Hodder et al., 2007; Rogers & White, 2007; Martin et al., 2009). Despite the abundant recent literature about fish movement from telemetry studies, few new studies have been included since 2008 in any of the existing meta-analyses. Likewise, crucial variables that were overlooked in previous analyses, such as study duration and stream width, which are significant predictors of fish dispersal distance (Radinger & Wolter, 2014), require further attention.

Therefore, using an expanded global data set, we revisited past work to bridge the gap between previous meta-analyses using a standardized approach of evaluating the home range size of freshwater fishes. We also investigated whether additional variables that were previously overlooked can better predict home range size. Specifically, we tested the predictions that home range: 1) increases with fish length; 2) increases with stream width and lake surface area; 3) is larger for piscivores than omnivores; 4) increases with distance from the equator; 5) increases with study duration; 6) is greater in telemetry compared to mark–recapture studies; and 7) decreases with the presence of dams. In addition, we ask whether home range size varies among fish family in both lakes and streams, as suggested by Minns (1995).

Materials & Methods

Literature search & article screening

Home range data on freshwater fishes were collected from peer-reviewed literature using a combination of four different methods: 1) the ISI Web of Science search engine, 2) studies previously cited by three meta-analyses (i.e., Minns, 1995; Woolnough et al., 2009; and Burbank et al., 2023), 3) studies that cited Minns (1995) according to Google Scholar, and 4) additional papers found in Google Scholar (see Figure S1, Appendix B). Using these four methods, we reviewed a total of 1,064 studies published until September 2023. A primary literature search was conducted using the ISI Web of Science with the following key terms: (“home range*”) AND (stream* OR lake* OR pond* OR river*) AND (fish* OR salmo* OR trout OR charr OR cyprinid* OR centrarchid* OR cottid* OR fundulid* OR percid* OR anguillid* OR catostomid* OR percid* OR ictalurid* OR rivulid* OR sciaenid* OR esocid* OR moronid* OR sturgeon* OR sparid* OR percichthyid* OR alestid* OR tigerfish*). We then reviewed each paper’s abstract for at least one of the following terms: home range, movement, activity range/core, spatial core/area, or minimum activity. We subsequently removed studies relating to mammals, marine species, and theoretical papers. A final round of vetting was conducted to include studies only if: i) authors presented home range size in areal (m²) or linear units (m) (e.g., not in angles nor movement percentages) for wild freshwater fishes in streams and/or lakes (i.e., excluding: homing, translocations, and territoriality studies primarily related to spawning behaviour); ii) raw data were available for calculation when home range size estimates were not summarized; iii) home range size data were provided for a period of > 1 day; iv) captured fish were released at or near their original location within 72 hours; and v) water bodies were not experimentally

modified (e.g., modifying stream discharge with dams, adding woody debris, modifying the fish habitat quality, etc.), except when studies provided home range data for the system before manipulation (i.e., control group) or if there was no significant influence on the home range value after manipulation occurred. From an initial search of 600 papers, a total of 159 articles were selected after two rounds of screening, not including articles presented in Minns (1995), Woolnough et al. (2009), and Burbank et al. (2023). From the three meta-analyses, a total of 92 out of 115 articles met the vetting criteria mentioned above, while 17 articles were included that cited Minns (1995). An additional 4 articles that did not cite Minns (1995) but provided home range-related data were extracted from Google scholar. In total, 272 articles (including 16 published in symposia and 1 government report) were selected using four literature extraction methods, including 180 studies that were not presented in previous meta-analyses.

Data extraction procedures

Data were either extracted directly from papers or estimated from external sources (see Table 2). Home range (areal and linear) data were extracted using: 1) raw data for individual fish presented in tables or supplementary materials; 2) data that were summarized by biological (i.e., age/sex/length), temporal (i.e., monthly/seasonal/annual), or spatial (i.e., sampling site) categories in tables or figures; or 3) data reported as means, medians, or, rarely as, the maximum home range size of a population in the text, which was used only when no other information was presented. Using these three extraction methods, home range size was calculated as a median or mean value, with maximum values only being used in rare circumstances. The median home range size was calculated from raw data when $n \geq 5$, whereas the mean home range was calculated when $n < 5$ or when home range size was reported as the mean of a category (e.g., mean home range size of males and females). If only one home range metric (i.e., either areal or

linear) was provided, the other was calculated using the corresponding water body width (see below). For papers that only reported home range data in figures, the mean or median values were extracted using an online tool known as WebPlotDigitizer version 4.7 (Rohatgi, 2024). Given the diversity of methods used to calculate home range size (Anderson, 1982; Rogers & White, 2007), we categorized them as: longitudinal displacement; minimum convex polygon (MCP); kernel density estimator; mixed methods (i.e., when more than one method was used by authors); and other less commonly used methods (i.e., grid-cell, cluster analysis, and lattice and univariate probability estimators). When multiple home range calculation methods were presented within a study, we selected the method that was either highlighted in the abstract or the method the authors believed most accurate. If the authors did not identify a preferred method, we used the 90-95% kernel density estimator for areal and linear home range size (see Worton, 1995; Seaman & Powell, 1996; Vokoun, 2003; Tripp et al., 2019).

Fish size (mean length (mm) and weight (g)) data were extracted using the same three methods applied to home range size (see above). We used fish length data in whatever form provided by authors (e.g. fork, standard, or total), but prioritized fork length, followed by standard length, and then total length when available. When fish length was not reported, we used the common length reported by FishBase (Froese & Pauly, 2024). In rare circumstances, we used the minimum fish length or weight value (e.g., greater than 115 mm) when it was the only reported metric. However, when only fish weight was reported, we calculated fish length using a length-weight calculator in FishBase and rounded to the nearest millimeter (Froese & Pauly, 2024). For almost half of the data set, fish weights were calculated using the length-weight calculator from FishBase. In rare instances when no weight data were available for a species, we used data from the genus or family. Fish age was rarely reported in home range studies, so we

incorporated it as a categorical variable (i.e., adult, juvenile, or mixed). When data were deficient, the FishBase species summary description and/or length at maturity or maximum length was used as an indication of whether the target fish species was a juvenile or an adult.

Two categories of trophic guild were used: piscivores and omnivores. Omnivores are fish species that primarily eat invertebrates (i.e., aquatic insects, crustaceans, and occasionally aquatic plants, phytoplankton, and zooplankton) whereas piscivores primarily eat fish. We prioritized data presented by authors using the appropriate age class of each species since diet varies with age (Elliott, 1967; Tallman & Gee, 1982; Soriguer et al., 2000; Trested et al., 2011). If data were missing, the diet and food items category of FishBase was used for each species or genus. However, when authors did not provide data for salmonid species, those less than and greater than 310 mm in length were categorized as omnivores and piscivores, respectively (Keeley & Grant, 2001).

Study duration was quantified using the mean number of days that fish were tracked; otherwise we used the total number of days of the study. The former provides a more accurate estimate of the number of observations for each fish compared to the latter. To account for sampling interval across studies, we used the time interval between each sampling event (e.g., sampling occurred once a week) or as a mean value per season/tracking period (e.g., fish were tracked 4 times per month during the spring and 8 times during the summer months). All data were converted into days between samples.

Water body information was evaluated using a combination of author-provided information and Google Earth (Google Earth Pro, version 7.3.6.9796). For instance, to determine the water body type (i.e., stream/lake) of a study, we first used the author's description and/or the study map of the system, which was sufficient in most cases. If study systems were affected by

dams or weirs, we used Google Earth satellite imagery to classify them as a lake or stream. Since satellite images vary in resolution and temporal frequency, we selected images based on resolution, study sampling date, and study location. When determining water body size, we used mean stream width (m) and lake surface area (m²) provided by the author. If water body size was not provided, it was calculated using Google Earth with the most recent and high-resolution satellite images available. If only linear home range size was provided, the areal home range was calculated by multiplying the linear unit by the corresponding water body width. Likewise, when only an areal home range value was provided, the areal unit was divided by the water body width to obtain the linear home range. We recognize the bias introduced by these methods and only use these estimates in specific circumstances (see below).

Since artificial barriers are ubiquitous in freshwater ecosystems, we also evaluated the degree of anthropogenic disturbance in each study. Water bodies were categorized for habitat type as being either natural (i.e., no major artificial barriers and/or structures influencing fish habitat quality and migration), semi-natural (i.e., major artificial barriers and/or structures influencing fish habitat quality and migration), or artificial (i.e., man-made lake or artificially channelized/linearized stream; not present naturally). If this information was not provided by authors, we used Google Earth satellite images and supporting documents from other studies to validate the habitat type. Lastly, latitudinal data were usually provided by the author, otherwise we used Google Earth satellite images.

Sub-data set criteria

To compare within and between streams and lakes, we divided our data set into three sub-data sets using only author-provided estimates: 1) areal home range size in lakes (n = 71); 2)

linear home range size in streams ($n = 262$); and 3) areal home range sizes in both lakes ($n = 71$) and streams ($n = 64$), respectively. These three distinct data sets were chosen because home range size in lakes and streams are generally reported in areal and linear units, respectively (Woolnough et al., 2009; Burbank 2023). Hence, any comparisons within lakes or streams used areal and linear estimates, respectively, while areal estimates were used to compare between lakes and streams. These data sets avoided the biases introduced by manually calculating home range estimates using stream or lake widths. Manually calculated home range estimates in lakes and streams were only used when comparing with author-provided estimates to measure errors associated with using both data source types in the same analysis (see Appendix A).

Statistical analysis

To address our research questions, we used a combination of different statistical analyses: ordinary least squares (OLS) regressions, analysis of covariance (ANCOVA), and generalized linear mixed models (GLMM). Specifically, when testing bivariate relationships like the home range—fish length and home range—water body size relationships in lakes and streams, we used an OLS regression analysis. When evaluating the bivariate relationships across water body type, fish family and data source type (i.e., author-provided or manually calculated home range estimates), we used an ANCOVA to test for differences in slope or adjusted means across the categorical variables. GLMMs were used to select the best predictors of home range size in lake and stream fishes.

The stream data set demonstrated slightly heteroscedastic residuals when assessing the home range—fish length and home range—water body size relationships, which would have required a weighted least squares (WLS) regression instead of an OLS regression analysis

(Carroll, 1982; Müller & Stadtmüller, 1987). However, because the OLS and WLS regressions were nearly identical for stream fishes, we only used the OLS regression. For the home range—fish length relationship across water body type and fish family in streams and the home range—water body size relationship across fish family in lakes, we used ANCOVAs to compare regression slopes and group means. We also used ANCOVAs to compare regression slopes between manually calculated and author-provided home range values for the home range—fish length relationship. Each of these statistical analyses were tested for normality and homoscedasticity assumptions using residual plots and formal statistical tests such as the Shapiro–Wilk normality test and the studentized Breusch–Pagan test (Shapiro & Wilk, 1965; Breusch & Pagan, 1979). All figures were subsequently plotted using the ggplot2 package in R (version 3.3.3; Wickham, 2016).

To evaluate the effect size of predictor variables on areal home range size in lakes (data set 1) and linear home range size in streams (data set 2), two separate GLMM models were conducted with a gamma distribution to evaluate the right-skewed data distribution and a log-link function to log-transform home range estimates using the glmmTMB package (Brooks, 2017). Fixed effects for each model included: the absolute value of latitude, log₁₀-transformed continuous variables (i.e., fish length (mm), lake surface area (m²; data set 1), stream width (m; data set 2), and study duration (days)), and categorical variables (i.e., trophic guild, habitat type, data collection method, and home range calculation method). Fish age and sampling interval were excluded from these models because they provided similar information as fish length and study duration, respectively, which may inflate model selection values, while fish weight was excluded due to multicollinearity restrictions with fish length (see below). To account for fish family variation using the three most abundant families in lakes (data set 3) and streams (data set

4), we also ran two separate GLMM models with a gamma distribution and log-link function. The continuous variables included: the absolute value of latitude, \log_{10} -transformed fish length, lake surface area (m^2 ; data set 3), stream width (m; data set 4), and study duration (days), while fish family, trophic guild, data collection method (data set 4), home range calculation method, and habitat type were categorical variables. Similarly, fish age, fish weight, and sampling interval were excluded from these models. The only random effect that was included in all models was study ID to account for study variation. To test the models above, we performed a stepwise model selection procedure starting with the random effect (study ID) until all variables of interest were included. A weighting factor using \log_{10} -transformed fish sample size for each study was also included in the GLMMs to account for sample size variation; the logarithmic transformation was required to correct the models since fish sample size varied from 1 to 3286. To compare models, we used Akaike's information criterion (AICc), where the model with the lowest AICc value was selected. If models were within 2 AICc from each other, we took the model with the simplest structure and the lowest Bayesian information criterion (BIC). Once the best model was selected, we tested for homoscedasticity, normality, model dispersion, model convergence, and outlier assumptions using the DHARMA package (Hartig, 2022). We also ran a multicollinearity performance test using the variance inflation factor (VIF) to test for collinearity among predictors, with a cutoff set at ≥ 3 (Zuur et al., 2010). All analyses were conducted in R statistical software version 4.3.3 (R Core Team, 2024).

Results

Data summary

A total of 393 home range size estimates (79 in lakes and 314 in streams) were extracted from 272 articles published in 1947-2023. Of these 272 articles, 180 (260 home range estimates) were not included in past meta-analyses, including 83% of which were published since 2000. The 272 articles were from 33 countries across 6 continents, but most were found in North America (63%) and Europe (21%; Figure 1). In total, we described the home range size of 148 species from 36 families with 18 and 33 families present in lakes and streams, respectively. The three most common families were Centrarchidae, Salmonidae, and Percidae in lakes and Salmonidae, Cyprinidae, and Centrarchidae in streams. Trophic guild varied across water body type with omnivores being predominate in streams (70%) and piscivores in lakes (66%; see Table 3). In streams, the most common home range calculation methods were longitudinal displacement (73%), kernel density estimator (13%), and minimum convex polygon (MCP; 9%), with telemetry (67%) and mark–recapture (33%) being the primary data collection methods. In lakes, MCP (48%), kernel density estimator (30%), and longitudinal displacement (10%) were the most common calculation methods with telemetry (90%) and mark–recapture (10%) being the primary data collection methods.

Predictors of home range size

As expected, home range size increased with fish length in both lakes (OLS regression, $\text{adj. } R^2 = 0.28, p < 0.0001, n = 71$; Figure 2A) and streams (OLS regression, $\text{adj. } R^2 = 0.55, p < 0.0001, n = 258$; Figure 2B). However, fish length explained much less of the variation in the home range size of fishes in lakes compared to streams. In addition, areal and linear home range

size increased strongly with water body size in both lakes and streams, respectively (OLS regression, $\text{adj. } R^2 = 0.61, p < 0.0001, n = 71$; Figure 3A; OLS regression, $\text{adj. } R^2 = 0.56, p < 0.0001, n = 261$; Figure 3B). To compare home range size in lakes and streams, we plotted home range area versus fish length (Figure 4). The slopes did not differ between lakes and streams (ANCOVA, $F_{1,131} = 1.217, p = 0.272$), but home range area was four times larger in lakes than in streams (ANCOVA, $F_{1,132} = 7.639, p < 0.01$).

When evaluating all variables of interest, the best model predicting home range area in lakes included lake surface area and latitude (GLMM, $\text{AICc} = 2156.03, p < 0.01$; Table 4), indicating that home range size increased in larger lakes and at higher latitudes (model estimates: 1.93 (\log_{10} lake surface area) and 0.05 (absolute value of latitude)). To illustrate the positive effect of latitude on home range area, we plotted the residuals of the home range area—lake surface area relationship against latitude (Figure 5). The second-best model, which was within 2 AICc units, included fish length. Therefore, we cannot rule out the effect of fish length, but we can rule out the predicted effects of trophic guild, study duration, data collection method, home range calculation method, and habitat type.

In streams, the best model predicting linear home range included fish length, stream width, data collection method (i.e., telemetry versus mark–recapture), and study duration (GLMM, $\text{AICc} = 5145.08, p < 0.001$; Table 5). Specifically, linear home range increased with fish length, stream width, and study duration, while linear home range was greater for studies using telemetry compared to mark–recapture sampling techniques (model estimates: 2.19 (\log_{10} fish length); 1.47 (\log_{10} stream width); 1.25 (data collection method); and 0.68 (\log_{10} study duration)). To illustrate the effect of study duration and data collection method, see Figure 6. The second-best model included trophic guild as an additional variable but had an AICc value just

slightly greater than 2 units. To illustrate the possible effect of trophic guild on linear home range, we plotted the residuals of the linear home range—stream width relationship against trophic guild (Figure 7). Hence, we likely cannot rule out the effect of trophic guild, but we can rule out latitude, home range calculation method, and habitat type.

Fish family (taxonomy) variation

Using the three most abundant fish families (Figure S2, Appendix B), the best model to predict home range area for lake fishes included lake surface area and family (GLMM, AICc = 1302.65, $p < 0.01$; Table 6) with salmonids and percids having larger home ranges than centrarchids with increasing lake surface area (ANCOVA, $F_{2,38} = 8.776$, $p < 0.001$; Figure 8). In streams, using the three most abundant families (Figure S3, Appendix B), the best model to predict linear home range in streams included fish length and stream width (GLMM, AICc = 2560.09, $p < 0.0001$; Table 7). We cannot rule out the effect of fish family since the second-best model was within 0.12 AICc and included family. To illustrate the variation among families, we plotted the linear home range versus fish length for the most abundant families in streams. Salmonids had significantly smaller linear home ranges compared to centrarchids and cyprinids, with cyprinids having the largest home ranges (ANCOVA, $F_{2,134} = 8.752$, $p < 0.001$; Figure 9). Overall, the home range size of fishes varied with family in both lakes and streams.

Discussion

Using a standardized methodology and a large global data set, we found that the home range size of freshwater fishes was best explained by different predictors in lakes versus streams. While some of our findings corroborated earlier studies, others were new. As predicted, home range area was positively correlated with fish length, was larger in lake than stream fishes (Minns, 1995), and water body size was an important predictor of areal and linear home range size in lakes and streams, respectively (Woolnough et al., 2009; Burbank et al., 2023). However, fish length explained more variation in the home range size of stream than lake fishes, as suggested by Burbank et al. (2023). Our new findings showed that: areal home range was 4 times larger in lakes than streams; water body size explained most of the variation in lakes followed by latitudinal gradient; and, fish length, stream width, data collection method, and study duration were all significant predictors of linear home range in streams. In addition, using a reduced data set with the three most abundant families, home range size varied among families; salmonids had significantly larger areal home ranges than centrarchids in lakes and significantly smaller linear home ranges than centrarchids in streams, respectively. Finally, unlike Burbank et al. (2023), we found that latitude was only an important predictor of home range size in lakes and trophic guild was possibly important, but only in streams.

Assessing predictors of home range size

Fish length was an important predictor of home range size, especially in streams. The positive relationship observed between fish length and home range size was likely more important in stream than lake fishes because swimming ability increases with body size, allowing larger fishes to travel greater distances and exhibit larger home ranges (Wolter & Arlinghaus,

2003; Jones et al., 2020). As suggested by Burbank et al. (2023), this allometric effect is more important in stream environments, where fish must swim against a directional current to navigate their home range. Like previous meta-analyses, water body size was also a significant predictor of both areal and linear home range size because water body size sets an upper limit to the total space used by an individual fish (Woolnough et al., 2009; Burbank et al., 2023). Larger lakes and wider streams may also provide a more spatially heterogeneous environment, so that fish are required to move over larger areas in search for food and shelter, and to meet reproductive requirements (Imhof et al., 1996). Here, we found that lake surface area was the main predictor of areal home range size, while stream width was the second most important predictor of linear home range size.

The larger home ranges in lakes compared to streams may be related to differences in food availability. On average, streams are more productive than lakes (Randall et al., 1995), leading to smaller home ranges in streams than lakes. Furthermore, most stream fishes in our data set were omnivores, feeding primarily on invertebrates in the benthos or stream drift. Invertebrate production in streams tend to increase with current velocity in a spatially predictable way, thereby reducing mobility and energy expenditure in stream fishes (Fausch, 1984; Piccolo et al., 2014). In contrast, most fishes in our lake data set were piscivorous, feeding on shoaling fish that have unpredictable spatial distributions (Benson & Magnuson, 1992.). Thus, fishes tend to be less mobile when feeding on spatially predictable prey (Grand & Grant, 1994a, 1994b), which might explain why home ranges were smaller in streams than in lakes. Overall, unlike Burbank et al. (2023), we found that fish length was the most important predictor of linear home range size, followed by stream width, and both water body size and fish length differed in importance between lake and stream fishes.

Linear home range size in streams was larger for studies using telemetry rather than mark-recapture sampling techniques likely due to differences in sampling interval and sample size. In telemetry studies, fish can be tracked multiple times a day with long detection ranges, while in mark-recapture studies, sampling intervals tend to occur weekly or monthly, resulting in fewer data points per home range estimate (McMichael et al., 2010; Crossin et al., 2017). With fewer data points, mark-recapture studies are more likely to underestimate home range size compared to telemetry studies because home range size tends to increase with the number of fish detections, especially when using the minimum convex polygon (MCP) method (Schoener, 1981; Rogers & White, 2007). Furthermore, since telemetry was the main sampling technique in our data set, sample size may also explain the difference in home range estimates between telemetry and mark-recapture studies. These findings highlight the need to account for data collection method to reduce the variation in home range estimates introduced by differing sampling techniques.

In addition to fish length, stream width, and data collection method, study duration was positively correlated with linear home range size in stream fishes. Similarly, Radinger & Wolter (2014) showed that study duration explained approximately 20% of dispersal distance variation in stream fishes. Here, study duration likely had two effects on home range size: the sample size effect noted above and the dynamic nature of aquatic environments over time. Specifically, a small home range may be sufficient for a short period of time, but a larger home range is required to deal with environmental heterogeneity over time. We also noted an interaction between study duration and data collection method on the measured home range size; telemetry studies produced larger home range estimates than mark-recapture studies with increasing study

duration. In contrast, study duration was not an important predictor of areal home range size in lakes, perhaps due to the smaller sample size for lake fishes.

As a proxy of productivity, latitudinal gradient indirectly provides insight on energy availability – more productive lakes are found near the equator and fishes exhibit smaller home ranges (Harestad & Bunnell, 1979; Lewis, 1996). The lack of a latitudinal effect in streams may be related to primary production playing a less important role in the productivity of streams compared to lakes (Rosenfeld et al., 2024). In both lake and stream fishes, habitat type and home range calculation method were not significant predictors of home range size. However, trophic guild appeared to have a weak effect on home range size in streams, but not in lakes. Burbank et al. (2023) showed that piscivorous fishes exhibit larger home ranges than benthivores in both lakes and streams, but this difference was only observed in a simple boxplot comparison and trophic guild was not included in the best model mixed effect models for either lake or stream fishes. Therefore, trophic guild may not be a strong predictor of the home range size of freshwater fishes, but it cannot be ruled out in stream fishes.

Differences between fish family (taxonomy)

With a larger data set, we revisited whether home range size varies with fish family, as proposed by Minns (1995). In our analyses, the three most abundant fish families had significantly different home range sizes in both streams and lakes. Salmonids exhibited the smallest home range size in streams and the largest home range size in lakes, while centrarchids had the smallest home ranges in lakes and significantly larger home ranges than salmonids in streams. The difference in home range size between lakes and streams may be related to the different feeding strategies exhibited by salmonids and centrarchids. For instance, most salmonid

species are drift-feeders in streams, but are piscivores in lakes (Elliott, 1967; Brandt, 1986; Piccolo et al., 2014). The encounter rate with potential prey increases with mobility for piscivorous fishes in lakes, but not for drift-feeding fishes in streams (Grant & Noakes, 1987; Beauchamp et al., 1999). Hence, different feeding strategies may account for the relatively small and large home ranges observed for salmonid fishes in streams and lakes, respectively, when compared to centrarchids. However, further research is needed in lake fishes, especially for large ambush predators, to increase statistical power.

Research gaps and recommendations for home range studies

Based on our extensive review of the literature, we propose some recommendations to guide and help standardize methods for future home range studies. First, when selecting a home range calculation method, use a method that incorporates 90-95% of the space used by all individuals throughout the study period, not just the core area (50%); the latter is a subset of the home range size and is more susceptible to seasonal variations (Vokoun, 2003; Lapointe et al., 2013). For calculation purposes, we recommend the 90-95% kernel density estimator method because it omits long-range exploratory movements of short duration and favours continuous sampling intervals (Vokoun, 2003). As an alternative, the MCP method can also be used to calculate the areal home range estimates in both streams and lakes, but this method has important limitations (see Schoener, 1981; Rogers & White, 2007). However, one standardized home range calculation method will not be applicable for all studies, so calculation method should be included as a variable in future syntheses.

Second, it is also important to indicate any possible biases associated with calculating home range estimates. For instance, measuring the home range size of sexually mature fishes

during the spawning season can misrepresent annual home range estimates because sexually mature fishes migrate long distances during reproductive seasons (Neely et al., 2009; Lapointe et al., 2013; Izzo et al., 2022). To account for this bias, we recommend presenting spawning and non-spawning home range estimates as two separate data sets. Third, when reporting study duration data, authors should present the mean tracking period or recapture rate of all individuals in the study instead of the start and end date of the data collection period to more accurately represent study duration. Ideally, the tracking period of individually tagged fish or the number of recaptures per fish in a telemetry and mark-recapture study, respectively, should be presented. Lastly, although more variables were included here than in prior studies, additional variables that may be important in predicting the home range size of freshwater fishes were omitted due to data deficiencies. For instance, slope, discharge, and water temperature, have been shown to affect the home range size of fishes in small streams (Slavík et al., 2005; Slavík et al., 2007). Since these three variables are rarely provided by authors, future studies may need to collect these data from external sources to investigate their potential influence in the home range size of stream fishes. Overall, by implementing all these recommendations, freshwater fish studies will more accurately present home range estimates and help reduce ambiguity across the literature.

Conservation implications

The home range size concept has important implications for the conservation of freshwater biodiversity, primarily for evaluating anthropogenic impacts and establishing protected areas. An animal's home range size can be extrapolated to calculate the space required to support a minimum viable population (Larson et al., 2009). For instance, fishes with smaller home ranges will require a smaller area to sustain a population; thus, reducing exposures to anthropogenic disturbances. However, fishes with larger home ranges are more likely to encounter artificial

structures (e.g., dams and weirs) or anthropogenically altered habitats, such as oil spills and industrial effluents, than less mobile individuals (Bower et al., 2015). Since the construction of artificial structures are continually increasing around the globe, mobile fishes are more likely to face ever-growing pressures than sedentary fishes (Grill et al., 2015; Best, 2019). To minimize these anthropogenic impacts, there is a need to establish more protected areas.

Freshwater protected areas (FPAs) are often used to mitigate anthropogenic impacts. Specifically, protected areas are naturalized reserves designed to provide species with a pristine habitat without anthropogenic disturbances (Crivelli, 2002). However, determining the size, shape, and level of habitat connectivity of FPAs can be challenging due to the heterogeneous life-history requirements of freshwater species, especially migratory fishes (Bower et al., 2015; Acreman et al., 2020). One way to establish FPAs for fishes is to use their home range size. For instance, conservation managers can use the largest home range size exhibited by freshwater fish species in a particular ecosystem to determine the minimum FPA size required to adequately protect the entire community. By using the largest home range size, fishes that are most susceptible to anthropogenic pressures and/or that migrate long distances will benefit from larger protected areas (Bower et al., 2015). Other methods of establishing FPAs include using the home range size of the most vulnerable fish species and applying a multiplication factor (e.g., two or three times the home range size) to set the minimum FPA size, as shown by Kramer & Chapman (1999) in coral fishes, or combining freshwater habitats with existing terrestrial protected areas that contain fragmented freshwater habitats (Abell et al., 2007; Acreman et al., 2020). In combination with our new synthesis, these three methods will not only benefit the most vulnerable species and increase the size of existing protected areas, but also help establish more FPAs of varying shapes and improve habitat connectivity.

Conclusion

Using the largest global home range data set of freshwater fishes, we have demonstrated that the space used by stream and lake fishes can depend on more variables than previously thought with each variable differing in predictive power between lake and stream fishes (Minns, 1995; Woolnough et al., 2009; Burbank et al., 2023). In streams, both fish length and stream width were the most important predictors of linear home range in streams, followed by data collection method and study duration, while in lakes, surface area and latitude were the main predictors of home range area. We also showed that the home range size of lake fishes were 4 times larger than stream fishes since lakes are less productive than streams; thus, indicating that lake fishes require larger protected areas than stream fishes. Furthermore, linear and areal home range size was shown to vary with fish family where salmonids exhibited the smallest home range size in streams and the largest in lakes, while centrarchids illustrated the opposite relationships. Although, trophic guild provides insight on an animal's energy requirements (McNab, 1963; Harestad & Bunnell, 1979; Nash et al., 2015; Tamburello et al., 2015), trophic guild was not a significant predictor of home range size. Lastly, we highlighted several recommendations for future studies to incorporate, including: (i) a standardized methodology of collecting, calculating, and reporting home range estimates; (ii) stream-specific productivity and morphological variables to better predict the home range size of stream fishes; and (iii) more research in lake fishes. Each of these recommendations will help improve the home range literature of freshwater fishes and enable conservation managers to establish more freshwater protected areas.

Tables and Figures

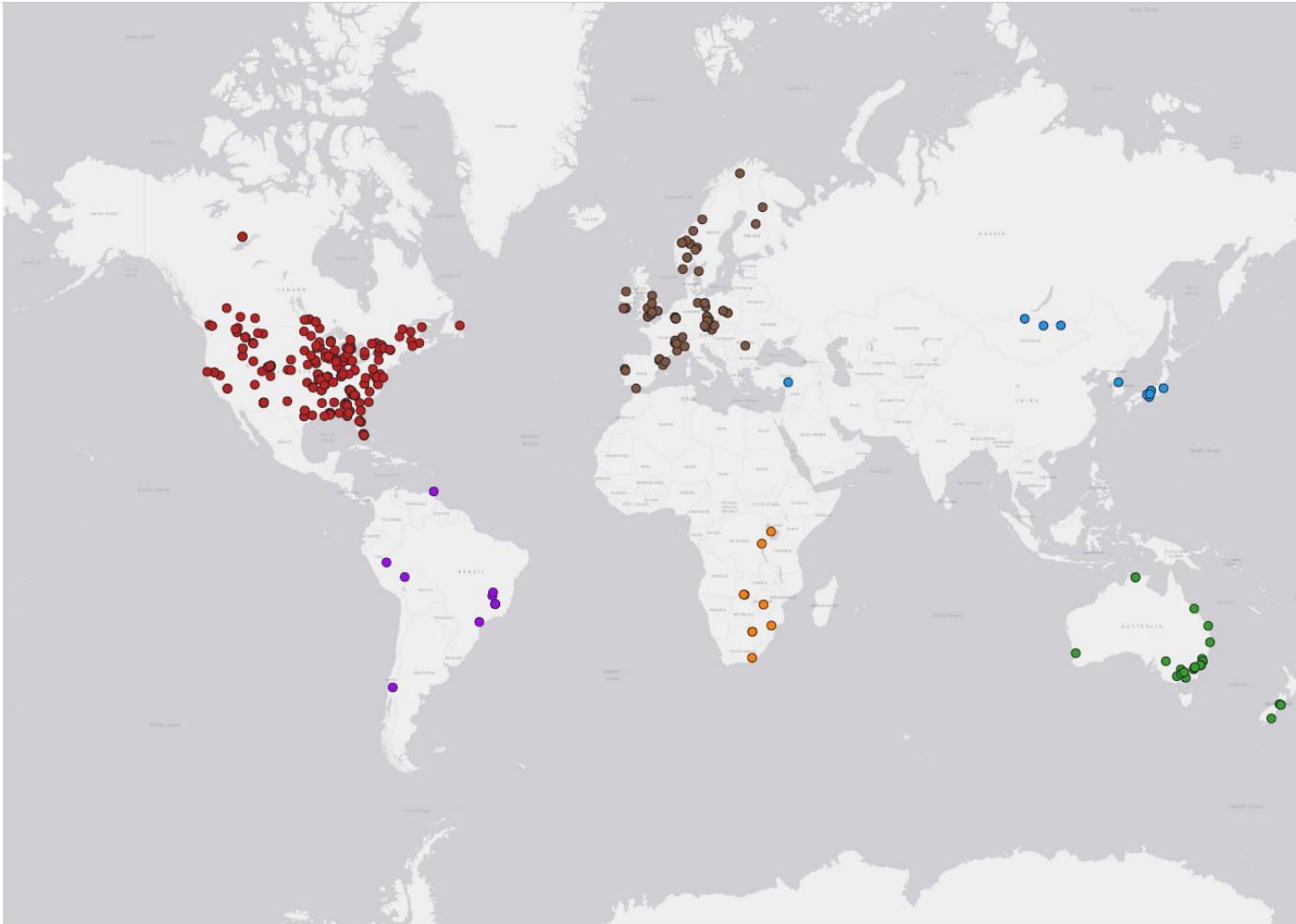


Figure 1. Distribution of home range size estimates across six continents: North America ($n = 249$), Europe ($n = 81$), Oceania ($n = 31$), Asia ($n = 13$), South America ($n = 10$), and Africa ($n = 9$).

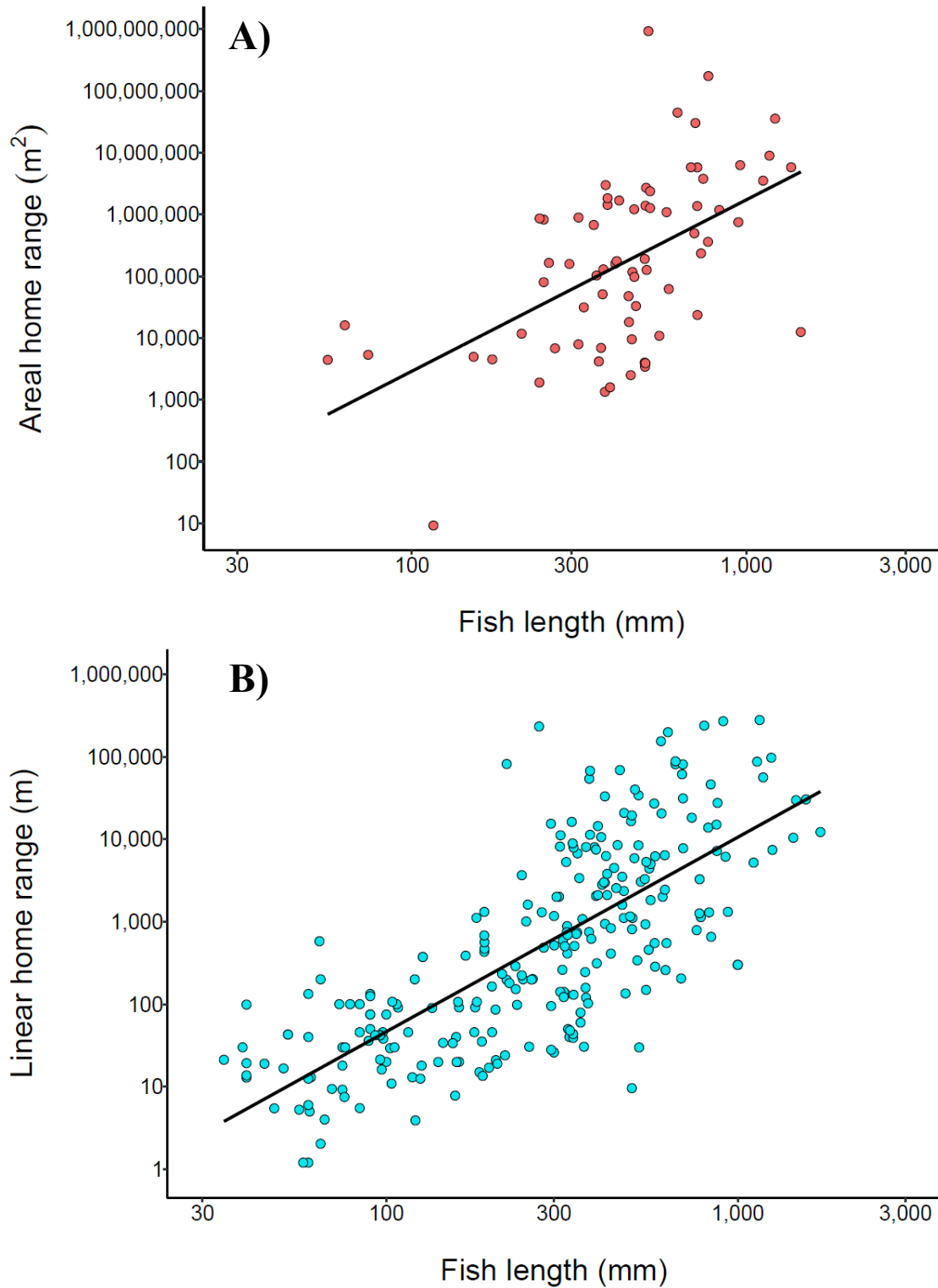


Figure 2. Regressions of home range size versus fish length: (A) areal home range of lake fishes (least squares regression: \log_{10} areal home range = $-2.08 + 2.77 \cdot (\log_{10}$ fish length)) and (B) linear home range of stream fishes (\log_{10} linear home range = $-3.04 + 2.36 \cdot (\log_{10}$ fish length)).

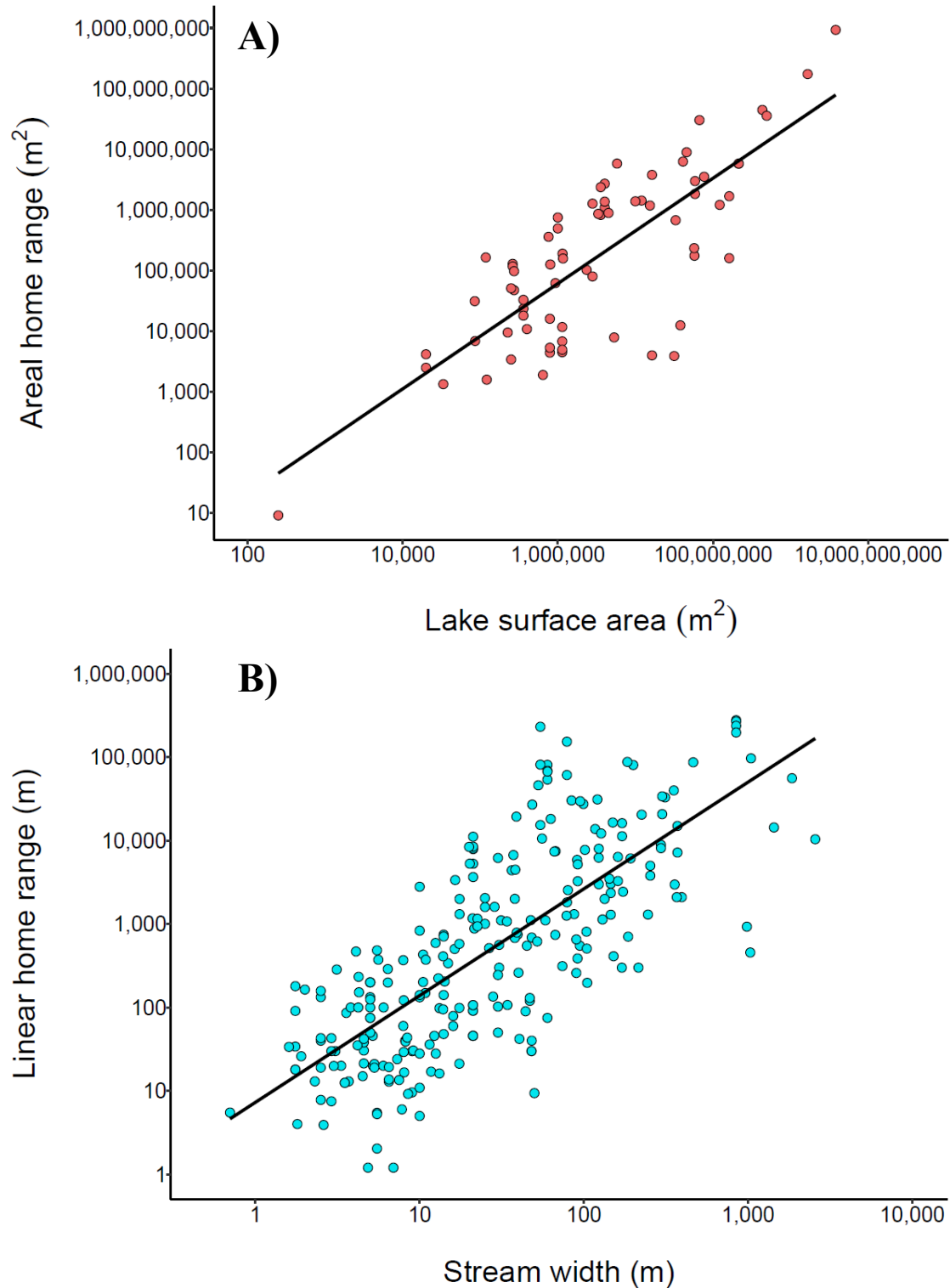


Figure 3. Regressions of home range size versus water body size: **(A)** areal home range of lake fishes versus lake surface area (least squares regression: $\log_{10} \text{ areal home range} = -0.43 + 0.87 \cdot (\log_{10} \text{ lake surface area})$) and **(B)** linear home range of stream fishes versus stream width ($\log_{10} \text{ linear home range} = 0.86 + 1.28 \cdot (\log_{10} \text{ stream width})$).

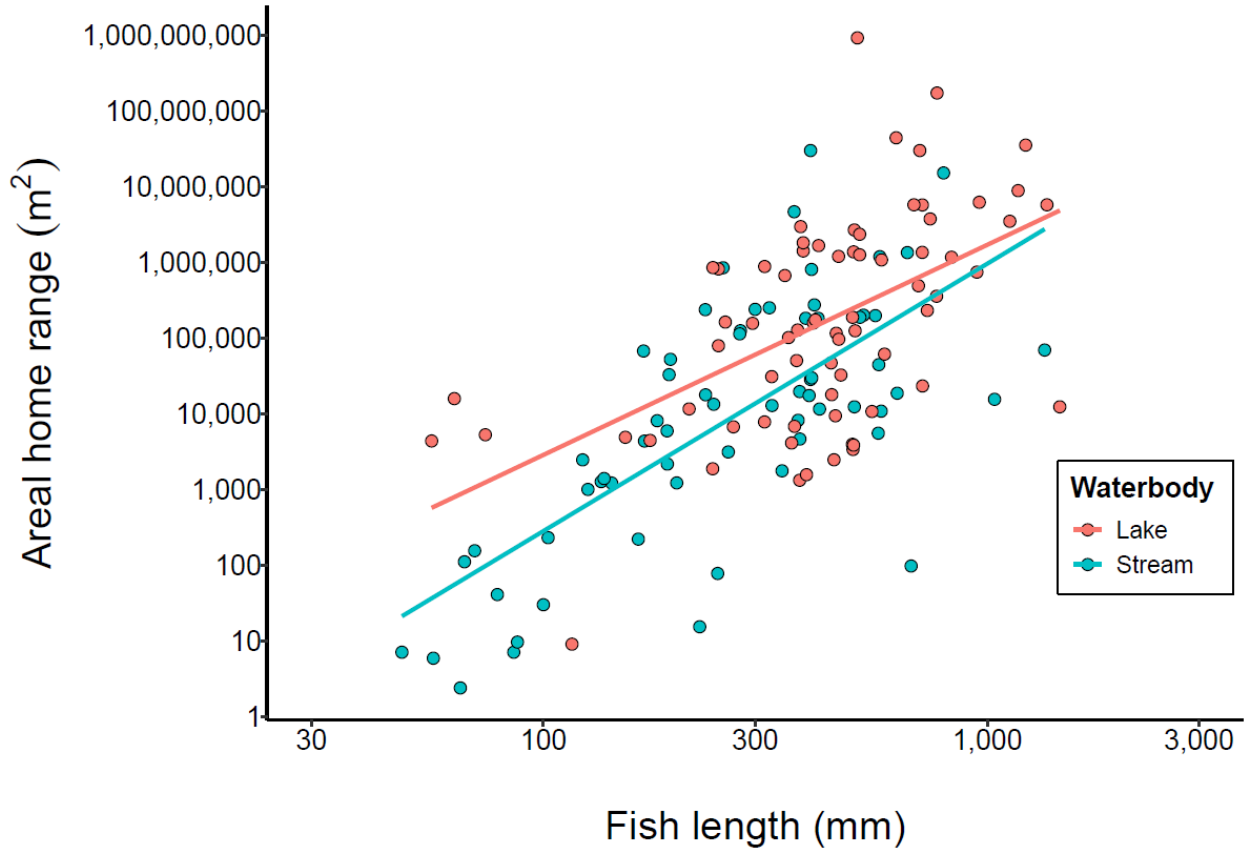


Figure 4. Home range area and fish length relationship across lakes and streams (adj. $R^2 = 0.49$; $n = 135$). The ANCOVA regression model was: \log_{10} areal home range = $-3.19 + 3.19 \cdot (\log_{10}$ fish length) $- 0.60 \cdot (\text{water body type})$ where water body type is 0 for lakes and 1 for streams. Note: the lines are least squares regressions.

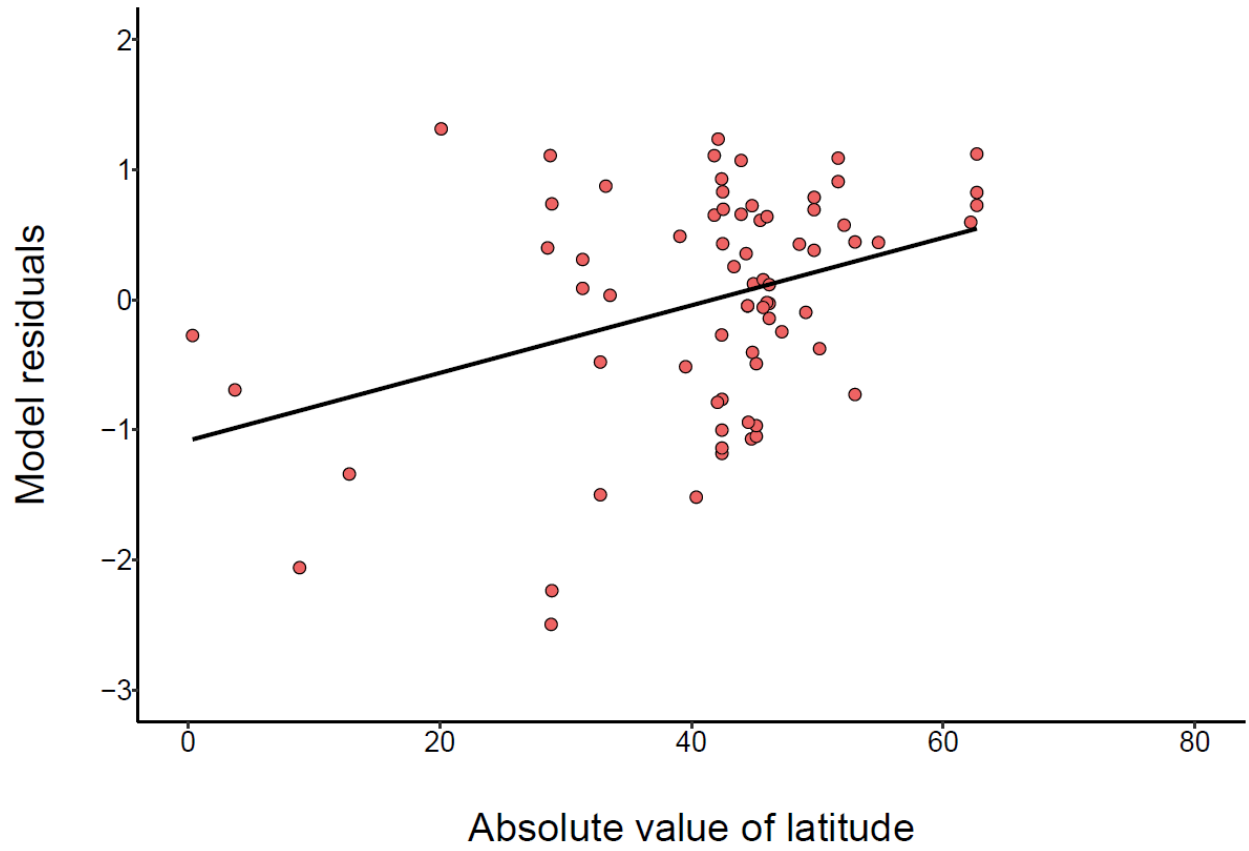


Figure 5. Least squares regression of home range area versus lake surface area residuals plotted against the absolute value of latitude.

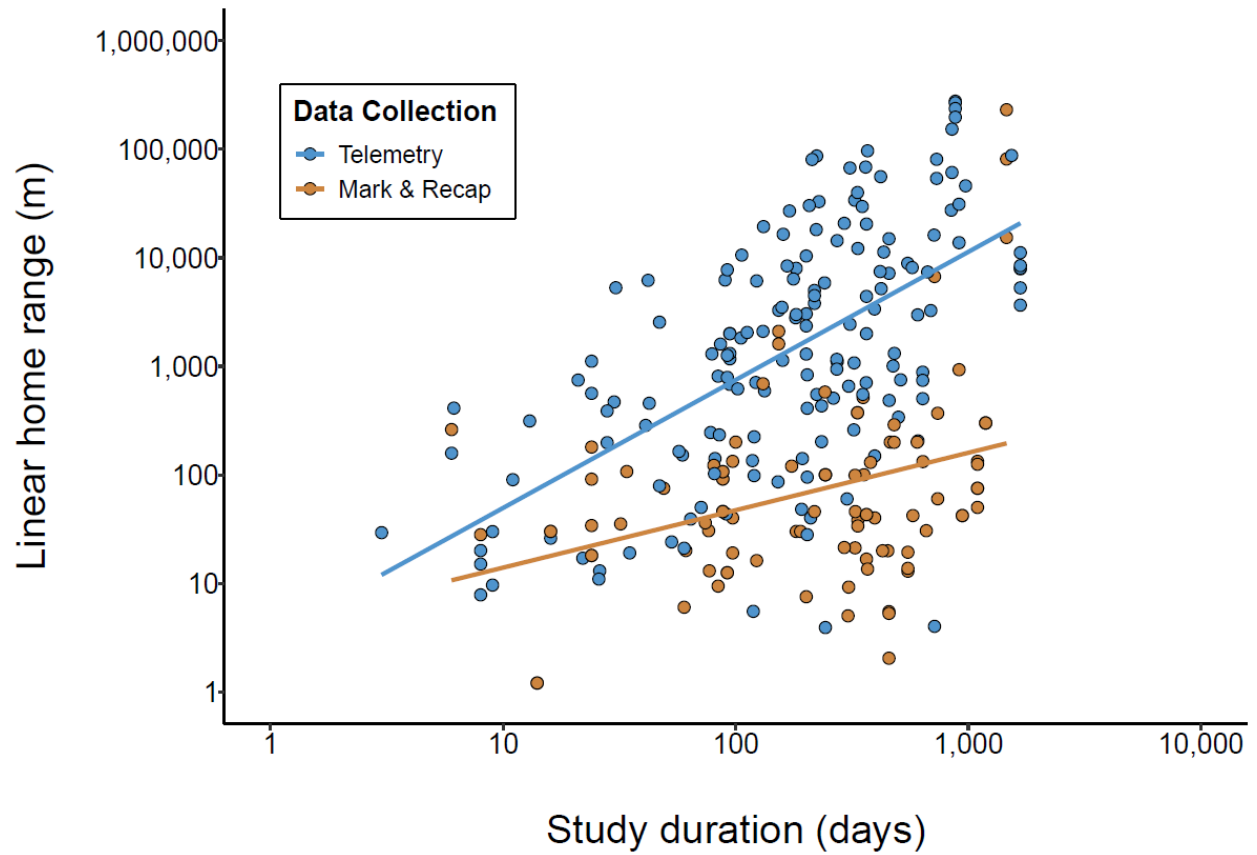


Figure 6. Least squares regressions of linear home range size versus study duration for two data collection methods.

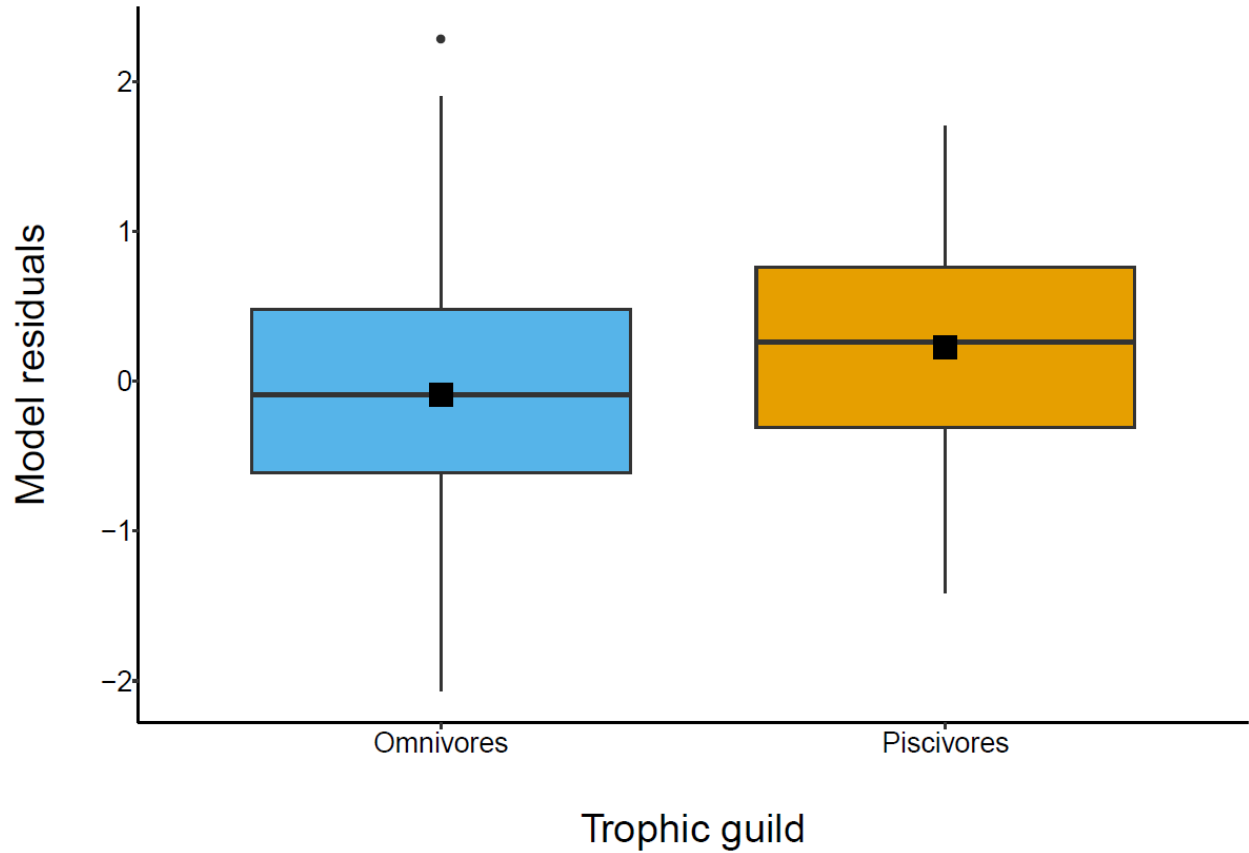


Figure 7. Boxplot of linear home range versus stream width residuals plotted against trophic guild. Boxplot shows the median value (midline) and interquartile range (whiskers) while squares represent the mean value.

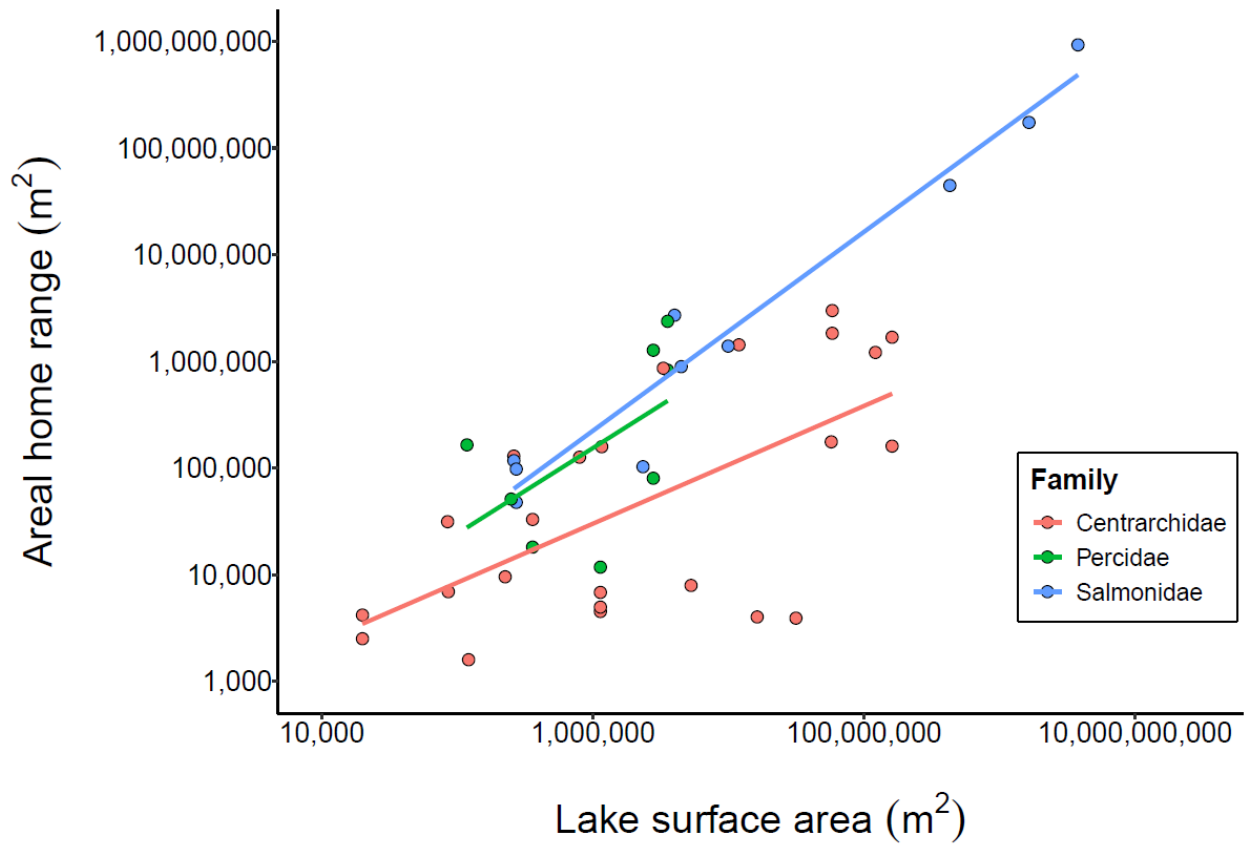


Figure 8. Least squares regressions of areal home range size versus lake surface area for the three most abundant families in lakes (ANCOVA, adj. $R^2 = 0.66$; $n = 42$).

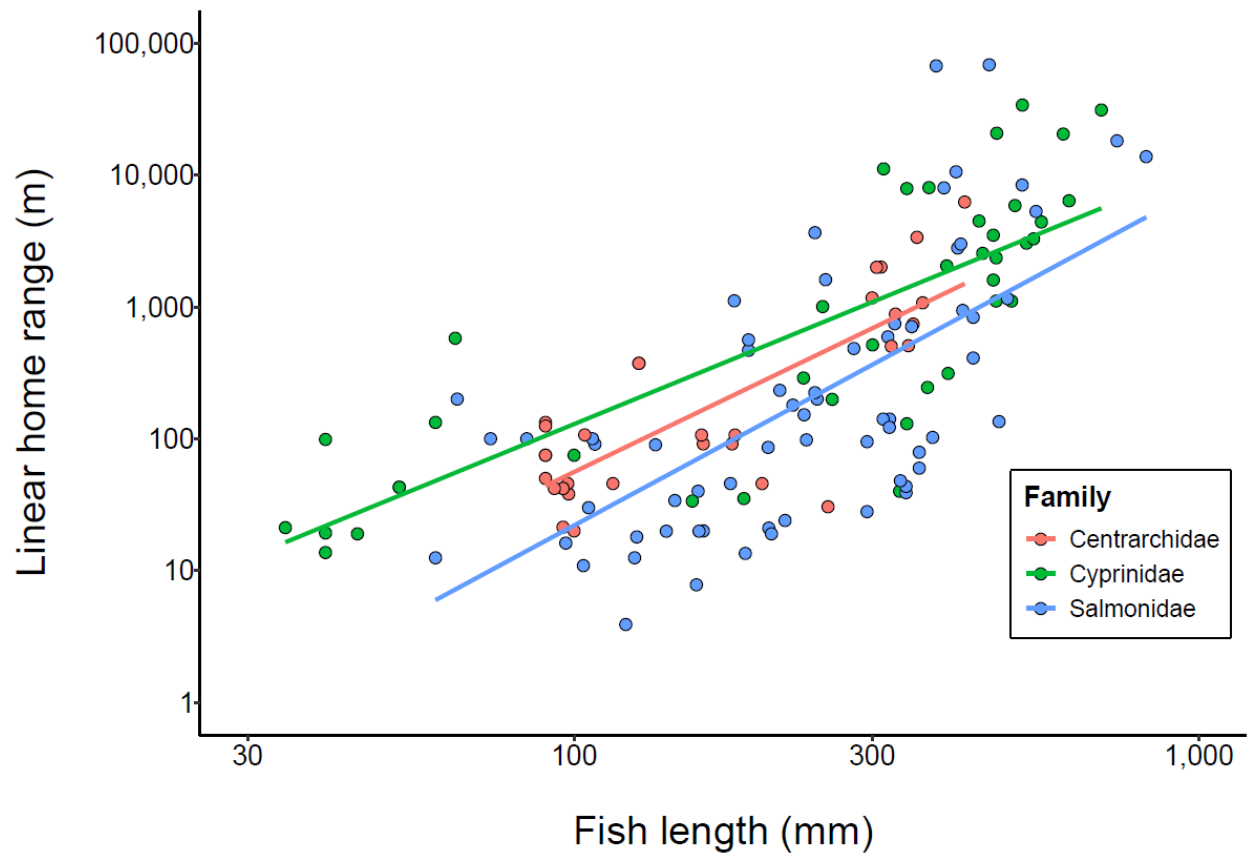


Figure 9. Least squares regressions of linear home range size versus fish length for the three most abundant families in streams (ANCOVA, adj. $R^2 = 0.54$; $n = 138$).

Table 1. Summary of meta-analyses on home range size in freshwater fishes. The sample size (n) refers to the number of articles used in each meta-analysis, while (+) indicates a positive relationship with home range size.

Study	n	Main results	First to:	Limitations
Minns (1995)	32	Body size: (+) Home range of lake fishes 20x > stream fishes Not significant: latitude, fish family, diet, and data collection method.	Demonstrate that home range size increases with body size and is greater in lakes than streams	Small sample size and lacked a comprehensive method of extracting home range estimates.
Woolnough et al. (2009)	71	Body size: (+) Water body size: (+)	Include water body size and differentiate between linear & areal home range size.	Excluded most articles used by Minns (1995).
Burbank et al. (2023)	73	Body size & water body size: (+) Piscivores > benthivores & planktivores	Demonstrate effects of diet and possibly latitude.	Only added 20 new articles compared to previous meta-analyses and briefly described methodology.
This Study	272	Body size & water body size: (+) Home range of lake fishes 4x > stream fishes Significant: Latitude, study duration, data collection method, and fish family.	Demonstrate positive effects of latitude, study duration, data collection method, and fish family. First study since Minns (1995) to differentiate between home range size of lake and stream fishes using an updated data set.	84% of articles were conducted in North America and Europe, which limits the global perspective of the data set.

Table 2. Summary of variables extracted from each study or estimated for use in the meta-analysis.

Variables	Description
Species	Common & scientific name provided by authors and validated with FishBase.
Family	Provided by authors and validated with FishBase.
Latitude/Longitude	Provided by authors or manually acquired using Google Earth.
Region	Province, state, or official region recognized by each country.
Country	Provided by authors.
Water body name	Provided by authors.
Data collection method	Telemetry or mark–recapture.
Habitat type ¹	Natural, semi-natural, or artificial. Described by authors and/or validated with Google Earth.
Fish age	Adult, juvenile, or mixed. Provided by authors or acquired from FishBase.
Home range size	Linear (m) and/or areal (m ²). Areal presented by Minns (1995) or areal and linear presented by Woolnough et al. (2009), individual authors or calculated by JL.
Home range calculation method	Provided by authors and classified as: longitudinal displacement, minimum convex polygon, kernel density estimator, mixed methods (when more than one method was used by authors), and other methods (i.e., grid-cell, cluster analysis, and lattice and univariate probability estimators).
Sample size	Total number of fish used to calculate the home range size in the study. Provided by authors.

Fish length	Mean fish length (mm) of all individuals included in the study. Provided by authors or acquired from FishBase.
Fish weight	Mean fish weight (g) of all individuals included in the study. Provided by authors or acquired from FishBase.
Water body type	Stream or lake. Provided by authors and/or validated on Google Earth.
Stream width	Provided by authors and/or validated on Google Earth (m).
Lake surface area	Provided by authors and/or validated on Google Earth (m ²).
Stream length	Length of stream (m) included in the study. Provided by authors and/or validated on Google Earth.
Sampling interval	Number of days between each sampling event. Provided by authors or calculated manually using raw data.
Study duration	Mean or total duration (days) for which fish were observed. Provided by authors or calculated manually using raw data.
Spawning season	Yes or no. Whether spawning fish were included in home range estimates.
Trophic guild	Piscivores or omnivores. Provided by authors or acquired from FishBase.

¹ Level of anthropogenic disturbances: Natural (no major artificial barriers), semi-natural (major artificial barriers), artificial (man-made lake or stream)

Table 3. Summary of mean (minimum and maximum) continuous variables and trophic guild percentages for both lakes and streams using the complete data set (n = 393).

Variable	Lakes	Streams
Areal home range (m ²)	16,200,451 (9.20—927,127,500)	4,364,340 (2.43—235,466,000)
Linear home range (m)		9,666 (0.44—278,000)
Fish length (mm)	488 (50.00—1457)	369 (34.50—1,719)
Fish weight (g)	2,396 (2.00—30,472)	1,525 (1.00—33,553)
Water body area (m ²) or length (m)	101,007,622 m ² (250.00—3,809,857,343)	181 m (0.70—20,000)
Trophic guild	Omnivore: 34% Piscivore: 66%	Omnivore: 70% Piscivore: 30%
Latitude (absolute value)	41.41 (0.36—62.68)	40.65 (10.63—69.69)
Study duration (days)	222 (3—1,079)	331 (3—1,675)

Table 4. Results of generalized linear mixed models (GLMM) evaluating the relationship between areal home range size (HR_Area) and predictors in lakes (i.e., Study = study ID, SA = lake surface area, Lat = latitude, FishL = fish length, Trophic = trophic guild, Duration = study duration, Data_Collection = data collection method, HR_Method = home range calculation method, and Habitat = habitat type). Bold indicates the best model selected.

Models	AICc	Log-Link	ΔAICc	BIC
HR_Area ~ log10(SA) + abs(Lat) + (1 Study)	2156.03	-1072.56	0.00	2166.42
HR_Area ~ log10(SA) + abs(Lat) + log10(FishL) + (1 Study)	2157.37	-1072.03	1.34	2169.64
HR_Area ~ log10(SA) + abs(Lat) + log10(FishL) + Trophic + (1 Study)	2159.83	-1072.03	3.80	2173.89
HR_Area ~ log10(SA) + (1 Study)	2159.93	-1075.66	3.90	2168.37
HR_Area ~ log10(SA) + abs(Lat) + log10(FishL) + Trophic + log10(Duration) + (1 Study)	2161.47	-1071.58	5.44	2177.25
HR_Area ~ log10(SA) + abs(Lat) + log10(FishL) + Trophic + log10(Duration) + Data_Collection + (1 Study)	2163.45	-1071.25	7.42	2180.87
HR_Area ~ log10(SA) + abs(Lat) + log10(FishL) + Trophic + log10(Duration) + Data_Collection + HR_Method + (1 Study)	2168.13	-1069.37	12.10	2189.90
HR_Area ~ log10(SA) + abs(Lat) + log10(FishL) + Trophic + log10(Duration) + Data_Collection + HR_Method + Habitat + (1 Study)	2172.12	-1068.31	16.09	2196.30
HR_Area ~ (1 Study)	2221.61	-1107.63	65.58	2228.04

Table 5. Results of generalized linear mixed models (GLMM) evaluating the relationship between linear home range size (HR_Linear) and predictors in streams (i.e., Study = study ID, FishL = fish length, SW = stream width, Duration = study duration, Data_Collection = data collection method, Trophic = trophic guild, Lat = latitude, HR_Method = home range calculation method, and Habitat = habitat type). Bold indicates the best model selected.

Models	AICc	Log-Link	ΔAICc	BIC
HR_Linear ~ log10(FishL) + log10(SW) + log10(Duration) + Data_Collection + (1 Study)	5145.08	-2565.31	0.00	5169.29
HR_Linear ~ log10(FishL) + log10(SW) + log10(Duration) + Data_Collection + Trophic + (1 Study)	5147.21	-2565.31	2.13	5174.82
HR_Linear ~ log10(FishL) + log10(SW) + log10(Duration) + Data_Collection + Trophic + abs(Lat) + (1 Study)	5148.82	-2565.04	3.74	5179.80
HR_Linear ~ log10(FishL) + log10(SW) + log10(Duration) + Data_Collection + Trophic + abs(Lat) + HR_Method + Habitat + (1 Study)	5149.73	-2559.98	4.65	5197.31
HR_Linear ~ log10(FishL) + log10(SW) + log10(Duration) + Data_Collection + Trophic + abs(Lat) + HR_Method + (1 Study)	5150.46	-2562.58	5.38	5191.46
HR_Linear ~ log10(FishL) + log10(SW) + log10(Duration) + (1 Study)	5163.30	-2575.48	18.22	5184.11
HR_Linear ~ log10(FishL) + log10(SW) + (1 Study)	5164.05	-2576.90	18.97	5181.43
HR_Linear ~ log10(FishL) + (1 Study)	5237.56	-2614.70	92.48	5251.52
HR_Linear ~ (1 Study)	5375.01	-2684.46	229.93	5385.52

Table 6. Results of generalized linear mixed models (GLMM) evaluating the relationship between areal home range size (HR_Area) and predictors in lakes using only the three most abundant families (i.e., Study = study ID, SA = lake surface area, Family = fish family, FishL = fish length, Trophic = trophic guild, Lat = latitude, Duration = study duration, HR_Method = home range calculation method, and Habitat = habitat type). Data collection method was excluded because only telemetry studies were present in the three most abundant families in lakes. Bold indicates the best model selected.

Models	AICc	Log-Link	Δ AICc	BIC
HR_Area ~ log10(SA) + Family + (1 Study)	1302.65	-644.13	0.00	1310.68
HR_Area ~ log10(SA) + Family + log10(FishL) + (1 Study)	1305.26	-643.98	2.61	1314.12
HR_Area ~ log10(SA) + (1 Study)	1305.84	-648.38	3.19	1311.71
HR_Area ~ log10(SA) + Family + log10(FishL) + Trophic + (1 Study)	1308.13	-643.88	5.48	1317.67
HR_Area ~ log10(SA) + Family + log10(FishL) + Trophic + abs(Lat) + (1 Study)	1309.64	-643.01	6.99	1319.66
HR_Area ~ log10(SA) + Family + log10(FishL) + Trophic + abs(Lat) + log10(Duration) + (1 Study)	1312.52	-642.71	9.87	1322.80
HR_Area ~ log10(SA) + Family + log10(FishL) + Trophic + abs(Lat) + log10(Duration) + HR_Method + (1 Study)	1319.45	-642.34	16.80	1329.54
HR_Area ~ log10(SA) + Family + log10(FishL) + Trophic + abs(Lat) + log10(Duration) + HR_Method + Habitat + (1 Study)	1327.58	-642.01	24.93	1336.35
HR_Area ~ (1 Study)	1336.31	-664.84	33.66	1340.89

Table 7. Results of generalized linear mixed models (GLMM) evaluating the relationship between linear home range size (HR_Linear) and predictors in streams using only the three most abundant families (i.e., Study = study ID, FishL = fish length, SW = stream width, Family = fish family, Trophic = trophic guild, Lat = latitude, Duration = study duration, Data_Collection = data collection method, HR_Method = home range calculation method, and Habitat = habitat type). Bold indicates the best model selected.

Models	AICc	Log-Link	ΔAICc	BIC
HR_Linear ~ log10(FishL) + log10(SW) + (1 Study)	2560.09	-1274.81	0.00	2574.15
HR_Linear ~ log10(FishL) + log10(SW) + Family + (1 Study)	2560.21	-1272.67	0.12	2579.67
HR_Linear ~ log10(FishL) + log10(SW) + Family + Trophic + (1 Study)	2562.05	-1272.45	1.96	2584.15
HR_Linear ~ log10(FishL) + log10(SW) + Family + Trophic + abs(Lat) + log10(Duration) + Data_Collection + (1 Study)	2563.16	-1269.51	3.07	2592.97
HR_Linear ~ log10(FishL) + log10(SW) + Family + Trophic + abs(Lat) + (1 Study)	2564.08	-1272.32	3.99	2588.78
HR_Linear ~ log10(FishL) + log10(SW) + Family + Trophic + abs(Lat) + log10(Duration) + (1 Study)	2565.74	-1271.98	5.65	2593.02
HR_Linear ~ log10(FishL) + log10(SW) + Family + Trophic + abs(Lat) + log10(Duration) + Data_Collection + HR_Method + (1 Study)	2566.92	-1268.96	6.83	2601.69
HR_Linear ~ log10(FishL) + log10(SW) + Family + Trophic + abs(Lat) + log10(Duration) + Data_Collection + HR_Method + Habitat + (1 Study)	2570.06	-1268.01	9.97	2609.60
HR_Linear ~ log10(FishL) + (1 Study)	2610.07	-1300.88	49.98	2621.42
HR_Linear ~ (1 Study)	2655.02	-1324.42	94.93	2663.58

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Appendix A: Measuring Biases in the Data set

We assume that multiplying lake home range length by lake width will overestimate areal home range estimates because fish will rarely include the entire lake in their home range, while dividing stream home range area by stream width will underestimate linear home range estimates. In lakes, 90% of studies measured home range size in areal units, so we converted the linear home ranges from the other studies into areal units. Contrary to our expectation, there was no significant difference between author-provided and manually calculated areal home range estimates in lakes (ANCOVA, $F_{1,76} = 0.089$, $p = 0.766$; Figure S1, Appendix A), and the slopes did not differ between data sources (ANCOVA, $F_{1,75} = 0.018$, $p = 0.894$). For streams, 84% of studies presented home range size in linear units. As expected, we found a significant difference between author-provided and manually calculated linear home ranges with the latter underestimating home range size (ANCOVA, $F_{1,305} = 20.47$, $p < 0.0001$; Figure S2, Appendix A), and the slopes did not differ between data sources (ANCOVA, $F_{1,304} = 0.148$, $p = 0.700$). However, this analysis includes 13 stream studies that provided both linear and areal home range estimates without converting units (e.g., using longitudinal displacement and MCP for linear and areal home range, respectively). When comparing these 13 studies using author-provided and manually calculated home ranges, we found no significant difference for both areal (ANCOVA, $F_{1,23} = 0.167$, $p = 0.687$; Figure S3A, Appendix A) and linear home range estimates (ANCOVA, $F_{1,23} = 0.543$, $p = 0.468$; Figure S3B, Appendix A). The slopes also did not differ between author-provided and manually calculated home ranges for both areal (ANCOVA, $F_{1,22} = 0.001$, $p = 0.970$) and linear home range estimates (ANCOVA, $F_{1,22} = 0.005$, $p = 0.947$). Hence, home range estimate biases were only found when dividing home range area by stream width for linear home range estimates in streams, likely due to sample size.

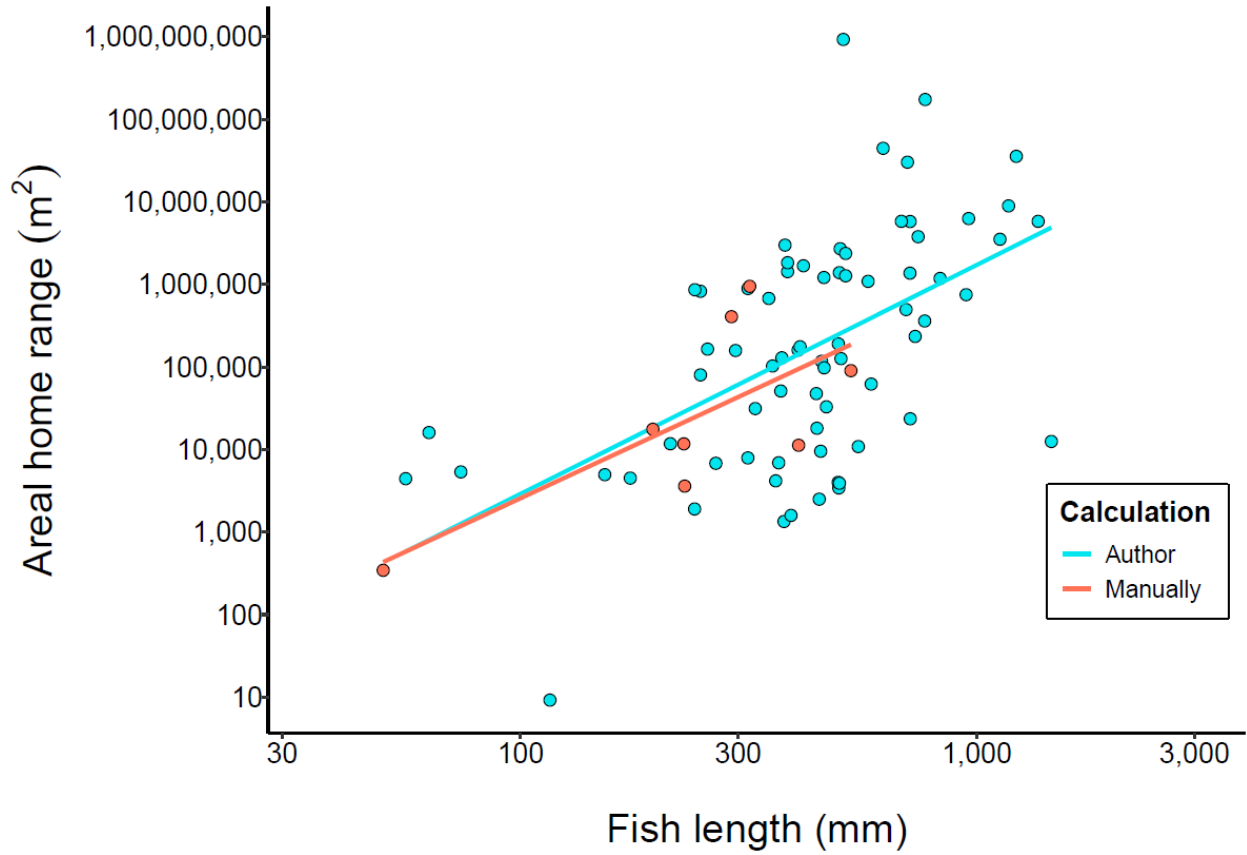


Figure S1. Illustrating a nonsignificant difference between author-provided and manually calculated areal home range estimates using the home range—fish length relationship in lakes (adj. $R^2 = 0.31$, $p < 0.0001$, $n = 79$).

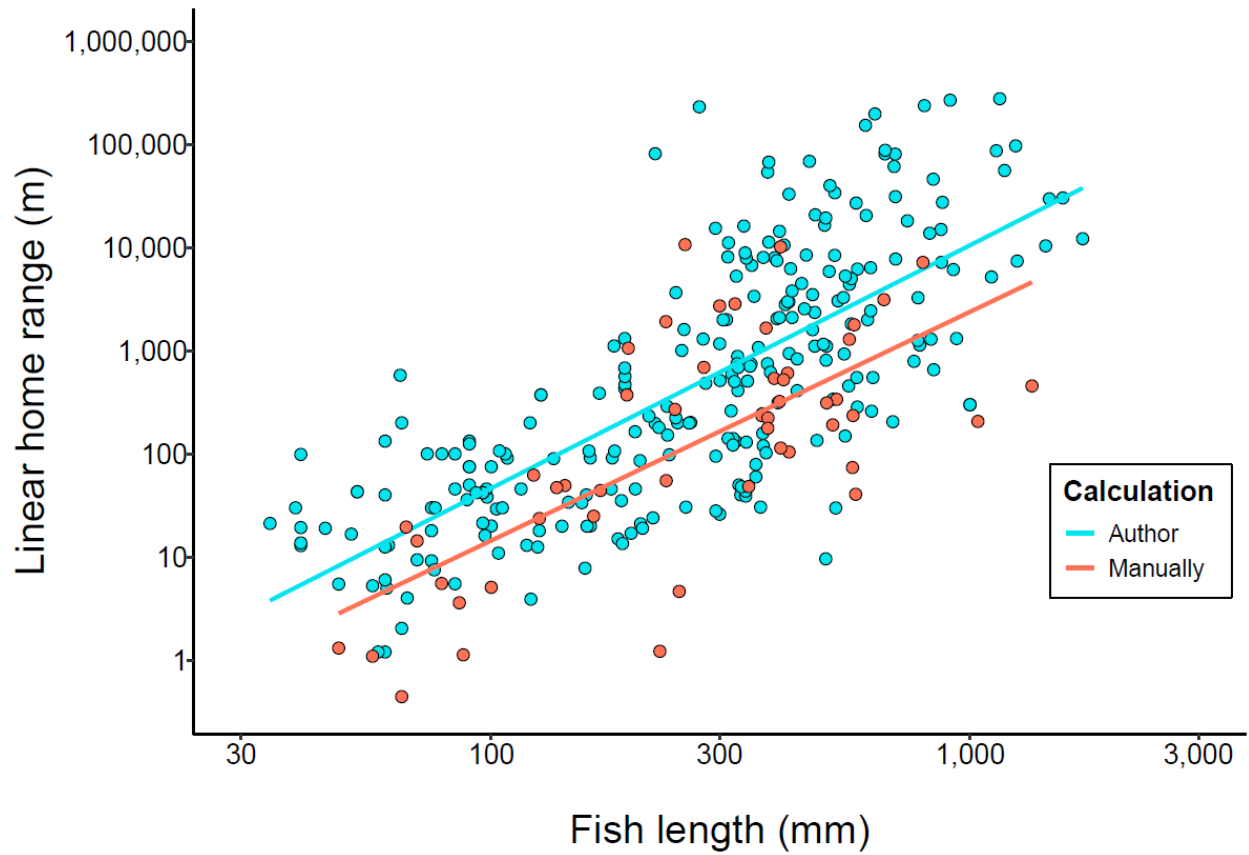


Figure S2. Illustrating a significant difference between author-provided and manually calculated linear home range estimates using the home range—fish length relationship in streams (adj. $R^2 = 0.55$, $p < 0.0001$, $n = 308$).

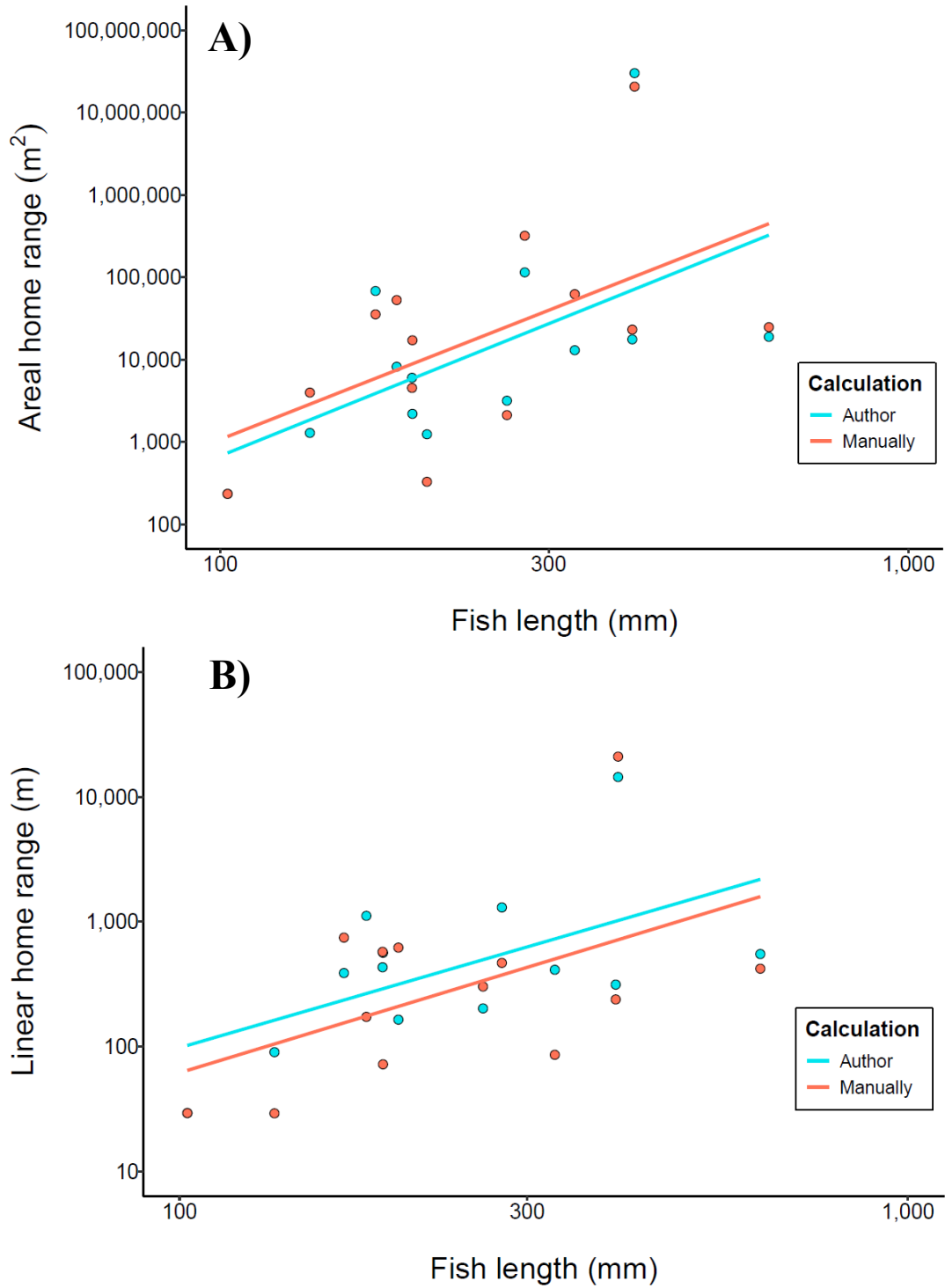


Figure S3. Illustrating a nonsignificant difference between author-provided and manually calculated (A) areal and (B) linear home range estimates using the home range—fish length relationship in streams for studies that provided both areal and linear values ((A): $\text{adj. } R^2 = 0.26$, $p < 0.0001$, $n = 26$; (B): $\text{adj. } R^2 = 0.24$, $p < 0.0001$, $n = 26$).

Appendix B: Supplementary Materials

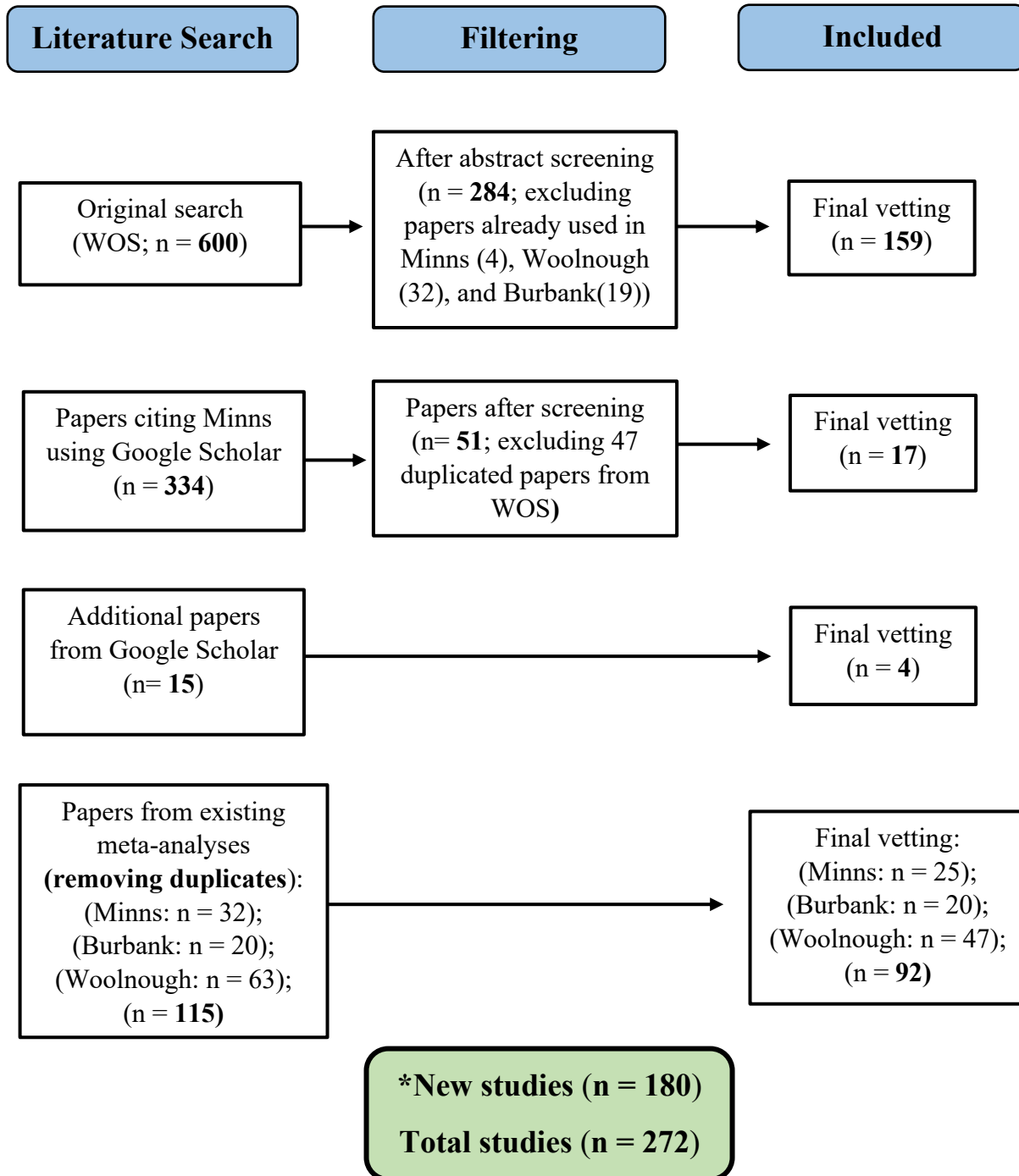


Figure S1. Flow chart of literature extraction procedure. *New studies refer to studies that were not included in previous meta-analyses.

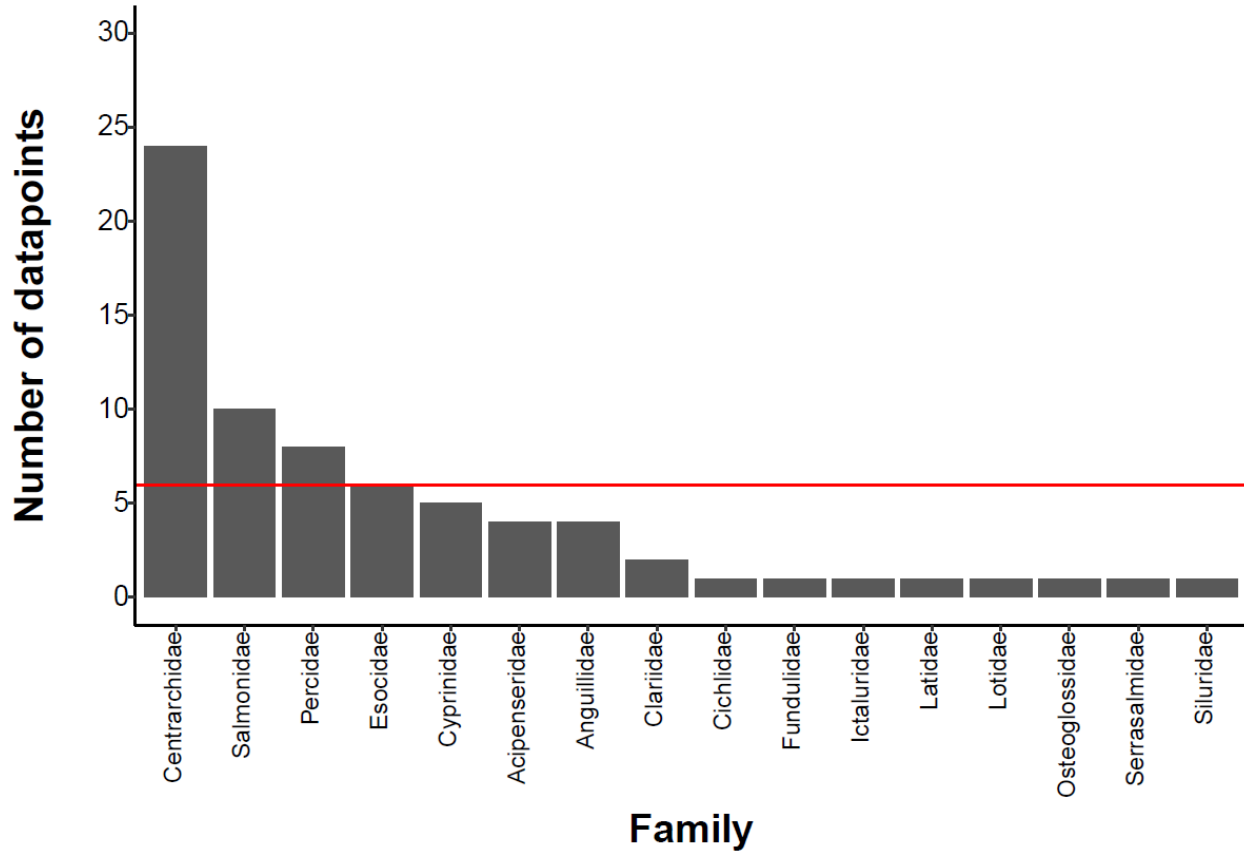


Figure S2. Number of author-provided data points for each family represented in lakes with the red horizontal line highlighting the three most abundant families.

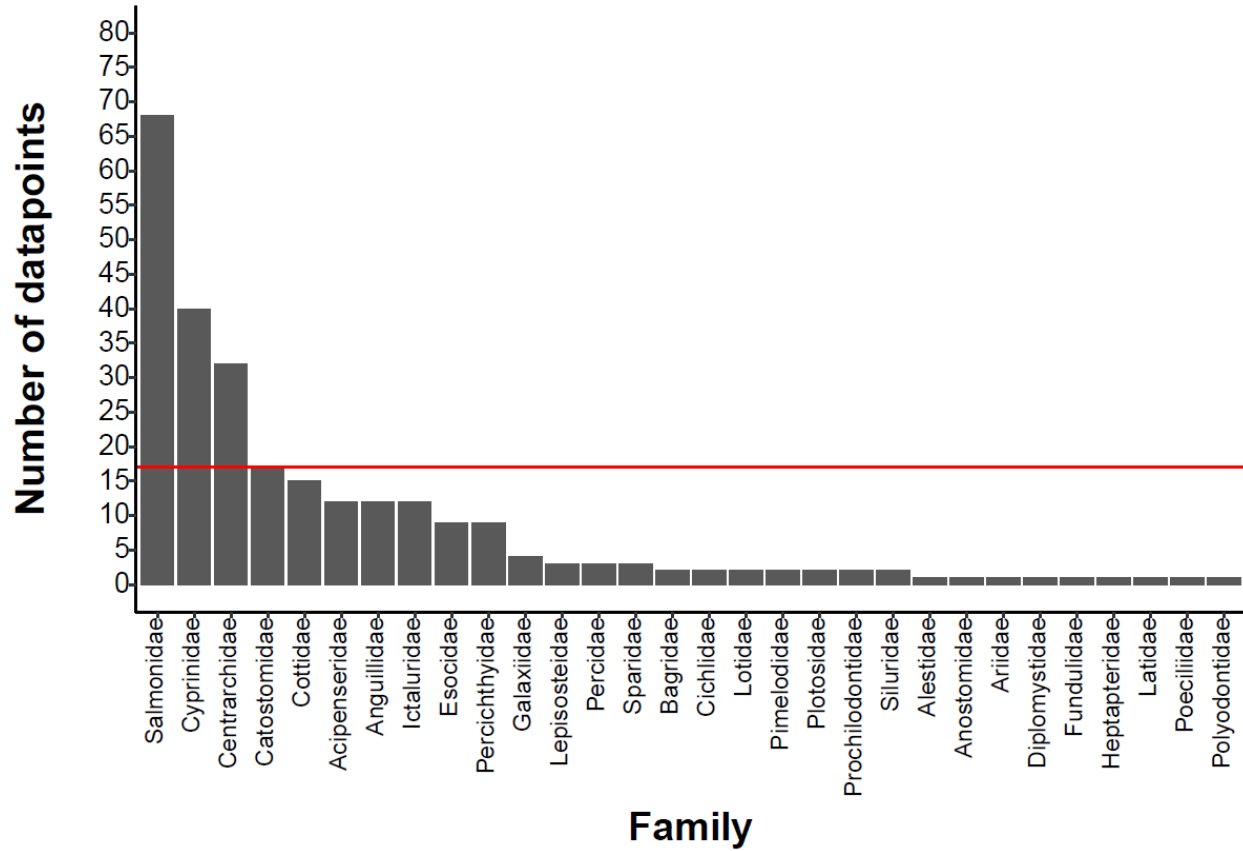


Figure S3. Number of author-provided data points for each family represented in streams with the red horizontal line highlighting the three most abundant families.