ORIGINAL ARTICLE

Synchrony in whitefish stock dynamics: disentangling the effects of local drivers and climate

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ABSTRACT

Synchronic variations in abundance in populations of the same species are common phenomena encountered in various environments, including lakes, and different taxa of freshwater fishes. This phenomenon can be caused by similar environmental conditions across physically separated populations. In the context of the ongoing climate change, it is essential to test this hypothesis, identify the factors driving the synchrony and elucidate the mechanisms, in the attempt to improve fisheries management. This study investigates synchronic variations in European whitefish (*Coregonus* spp.) populations in five peri-alpine lakes. The hypothesis suggests that shared biotic or abiotic factors contribute to similar trends in whitefish landings. Environmental and seasonal variables impacting the early life stages of the species were analyzed, and the Euclidean distances between the multivariate time series were calculated to identify similarities or dissimilarities in lake environmental parameters. We found that regional winter and spring temperatures were consistent across the lakes, but these factors did not fully account for variations in landings statistics. Wind intensity, water level and zooplankton abundance showed lake-specific patterns that could better explain local conditions and dynamics. Linear models did not reveal a coherent correlation with a common environmental variable across all lakes. However, distinct relationships were found in four of the lakes, with local factors significantly contributing to abundance variations. The spring abundance of *Daphnia* spp., a primary food source for whitefish larvae, was the main factor correlated with fish landing trends in Lake Geneva and Lake Bourget. Higher availability of *Daphnia* spp. may decrease intraspecific competition and density-dependent mortality. In Lake Neuchâtel, winter water temperature was negatively correlated with fish abundance proxies, suggesting that warmer winters may compromise reproduction success. Lake Annecy saw an increase in whitefish landings following a substantial reduction in fishing efforts during the late 2000s. A significant negative correlation was found between whitefish landings and fishing efforts. No relationship was found for Lake Aiguebelette, maybe due to a lack of zooplankton data. In conclusion, the observed synchrony in the European whitefish population is likely driven by a combination of interacting environmental and anthropogenic factors rather than a single common variable. Further research and a more detailed dataset are needed to better understand these complex relationships.

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Key words: *Coregonus* spp.; multivariate time series; dissimilarity; regional-scale factors; temperature; zooplankton.

Citation: Bourinet F, Anneville O, Drouineau H, *et al.* Synchrony in whitefish stock dynamics: disentangling the effects of local drivers and climate. *J. Limnol. 2023;82:2134.*

Edited by: Diego Fontaneto, *National Research Council, Water Research Institute (CNR-IRSA), Verbania Pallanza, Italy.*

Contributions: all the authors made a substantive intellectual contribution, performed part of the experiments. All the authors read and approved the final version of the manuscript and agreed to be accountable for all aspects of the work.

Conflict of interest: the authors declare that they have no competing interests, and all authors confirm accuracy.

Received: 15 March 2023.
Accepted: 17 May 2023.

J. Limnol., 2023; 82:2134
DOI: 10.4081/jlimnol.2023.2134

INTRODUCTION

Synchrony between distant populations of the same species can be explained by three phenomena: i) dispersion of individuals and exchange between populations; ii) regionally synchronized biotic factors such as common predators, preys, or competitors; and iii) abiotic factors, such as temperature or meteorological events (Zischke *et al.*, 2017). Spatial synchrony in the dynamics of geographically isolated populations has often been associated with the covariation of environmental parameters (Liebhold *et al.*, 2004; Vendrametto Granzotti *et al.*, 2022), known as the Moran effect (Moran, 1953; Hansen *et al.*, 2020). Large-scale climatic features, such as the North Atlantic Oscillation (Hurrell *et al.*, 2003; Dokulil *et al.*, 2006), influence regional meteorological conditions (Andrade *et al.*, 2012; Steirou *et al.*, 2017), which are correlated to a variety of ecological processes across taxa (Lynam *et al.*, 2004; Faillettaz *et al.*, 2019). Furthermore, global change is modifying environmental conditions similarly among some ecosystems (IPCC, 2022), driving synchronous or asynchronous changes in population dynamics (Hernvann and Gascuel, 2020).

The Moran effect often influences fish population dynamics in inland waters (Cattanéo *et al.*, 2003; Dembkowski *et al.*, 2016; Honsey *et al.*, 2016). The embryonic, larval and juvenile developmental stages are especially sensitive to environmental conditions (Miller *et al.*, 1988; Cury and Roy, 1989). Therefore, small changes in these parameters can induce strong mortality or conversely, improve reproduction and recruitment rates (Houde, 1987), indirectly impacting population structure, abundance of different size classes, and ultimately fish landings. Traditional stock assessment methods in fisheries science postulate that biomass fluctuations are mainly triggered by variations in fishing efforts (Tanaka, 2019). However, the importance of considering the effects of the environment in these methods has been emphasized (Maunder and Watters, 2003; Tanaka, 2019). This is particularly critical in the context of climate change since water warming has caused stock collapses (Drinkwater, 2005; Hernvann and Gascuel, 2020; ICES, 2022) and threatens many other fish populations (Arnason, 2006; Hauge *et al.*, 2009).

Spatial synchrony in partially or completely separated lacustrine populations has been studied in several fish species (Phelps *et al.*, 2008; Dembkowski *et al.*, 2016; Bunnell *et al.*, 2017). Nearby populations of large lakes often endure impacts from shared stressors. Global warming is affecting lakes across the globe (Woolway *et al.*, 2020), with observed impacts on the physical and chemical lacustrine environment, including water temperature (Kraemer *et al.*, 2021), mixing regime (Woolway and Merchant, 2019), and oxygen concentration (Jane *et al.*, 2021). Lakes appear to be warming at higher rates than marine systems and the atmosphere, though a high response variability has been observed (O'Reilly *et al.*, 2015). Studies have shown regional patterns of warming trend (Schneider and Hook, 2010; Woolway *et al.*, 2017; Desgué-Itier *et al.*, 2023), suggesting that similar trajectories of population dynamics between nearby lakes can be hypothesized. Eutrophication has also impacted many lacustrine aquatic ecosystems in different regions worldwide (Tilman *et al.*, 2001; Bhagowati and Ahamad, 2019) due to anthropogenic phosphorus inputs that decrease dissolved oxygen concentrations. Recently, re-oligotrophication processes have occurred in some of the world's large lakes (Jenny *et al.*, 2020) induced by reductions in agricultural inputs and improvements in sewage treatment plants (Jeppesen *et al.*, 2005; Schindler *et al.*, 2016; Sabel *et al.*, 2020). Due to regional or national policies, different lakes could follow similar eutrophication and re-oligotrophication trajectories, inducing synchronous environmental responses (Özkan *et al.*, 2016). At a regional scale, both global warming and eutrophication or re-oligotrophication processes could lead to synchronic trajectories of environmental factors among nearby lakes.

European whitefish (*Coregonus* spp.) are stenothermic fish species of high socio-economic value in numerous lakes (Anneville *et al.*, 2015). Multiple biotic and abiotic factors have been identified as impacting the reproduction and recruitment efficiency of coregonid species across lakes and regions worldwide. Examples include ice breakup timing (Nyberg *et al.*, 2001; Lynch *et al.*, 2015), water temperature (Mehner *et al.*, 2011; Stewart *et al.*, 2021), dissolved oxygen concentration (Eckmann, 2013), and food availability (Hoyle *et al.*, 2011; Zischke *et al.*, 2017). The sensitivity of coregonid to environmental conditions leads to interannual variations in fish landing among different fisheries (Kangur *et al.*, 2020; Sarvala *et al.*, 2020; Rook *et al.*, 2021). Synchrony in whitefish abundance has been reported between nearby stocks in North America (Bunnell *et al.*, 2010; Myers *et al.*, 2015) and Scandinavia (Marjomäki *et al.*, 2004).

In five deep peri-alpine lakes, where pelagic ecomorph European whitefish represent a major part of fish landings, fishery managers and fishermen observed similar trends in catch fluctuations for four lakes, with a period of catch increase followed by sharp drops over the last two decades. Landings depend both on population abundance and fishing intensity. As such, we explored whether the observed synchrony in landings can originate from similar trends in fishing efforts or whether they were more likely related to similar variations due to regional-scale forcings. Given their geographical proximity, we suspected common environmental forcings may have synchronized abundance, i.e., a Moran effect, and subsequently synchronized landings. In this context, we searched for similarity and dissimilarity patterns between critical environmental variables affecting the growth and survival of the first life stages, which are the most sensitive to the environment. These variables include water temperature variables covering the development of eggs, larvae, and early juveniles, which are key parameters for survival rates; zooplankton abundance variables, which are the main prey for each early stage; water level and wind intensity variables during egg development, both suspected to emerge or move the eggs out of the spawning ground. We used the R package "*distantia*" to calculate Euclidean distances between the ecological multivariate time series of each lake to compare the five lake environments between 2000 and 2020. The fishing effort, which reflects the intensity of the fishing activity on the whitefish populations, was also included to check for inter-lake similarities. Finally, we looked for linear relationships between proxies of European whitefish abundance based on fisheries statistics and the environmental variables, the fishing effort and the stocking intensity.

METHODS

Study sites and focus species

The study focuses on five nearby but isolated lakes: Lake Geneva, Lake Neuchâtel, Lake Bourget, Lake Annecy, and Lake Aiguebelette (Fig. 1). As deep peri-alpine lakes, they exhibit significant temperature and oxygen stratifications for most of the year and have been undergoing re-oligotrophication process since the 1980s (Jacquet *et al.*, 2014, 2022; Tran-Khac *et al.*, 2021; Frossard *et al.*, 2022). The term "European whitefish" includes many species from the genus *Coregonus* found across the European continent, showing a high genetic diversity with various species and ecomorphs sometimes living in sympatry (Douglas and Brunner, 2002; Selz *et al.*, 2020; De-Kayne *et al.*, 2022; Selz and Seehausen, 2023). Based on genetic studies, Bernatchez and Dodson (1994) indicated that populations in the alpine region should be considered as one species, *Coregonus lavaretus*, which was also referred to as the *Coregonus lavaretus* species complex (Østbye *et al.*, 2005). The five studied lakes harbor one common pelagic ecomorph of European whitefish, fished with similar fishing gear (large drift-net targeting the thermocline). Lake Neuchâtel is also home to a benthic ecomorph that is captured using different gears and exhibits different ecological behaviors, thus considered a distinct stock. The fishing statistics described below for each lake refer only to the pelagic ecomorph which exhibits similar life history traits, ecological behavior, diet, and seasonality among the five lakes (Vonlanthen *et al.*, 2012). Later on, "European whitefish" refers specifically to this ecomorph. The main ecological and whitefish fishery characteristics of these lakes in the last two decades are summarized in Tab. 1 (Lang, 1984; Rimet *et al.*, 2020).

Defining environmental variables

Environmental parameters that could directly impact the abundance of European whitefish stocks were selected based on their predicted effect on the early life stages of the target populations (eggs, larvae, and early juvenile stages).

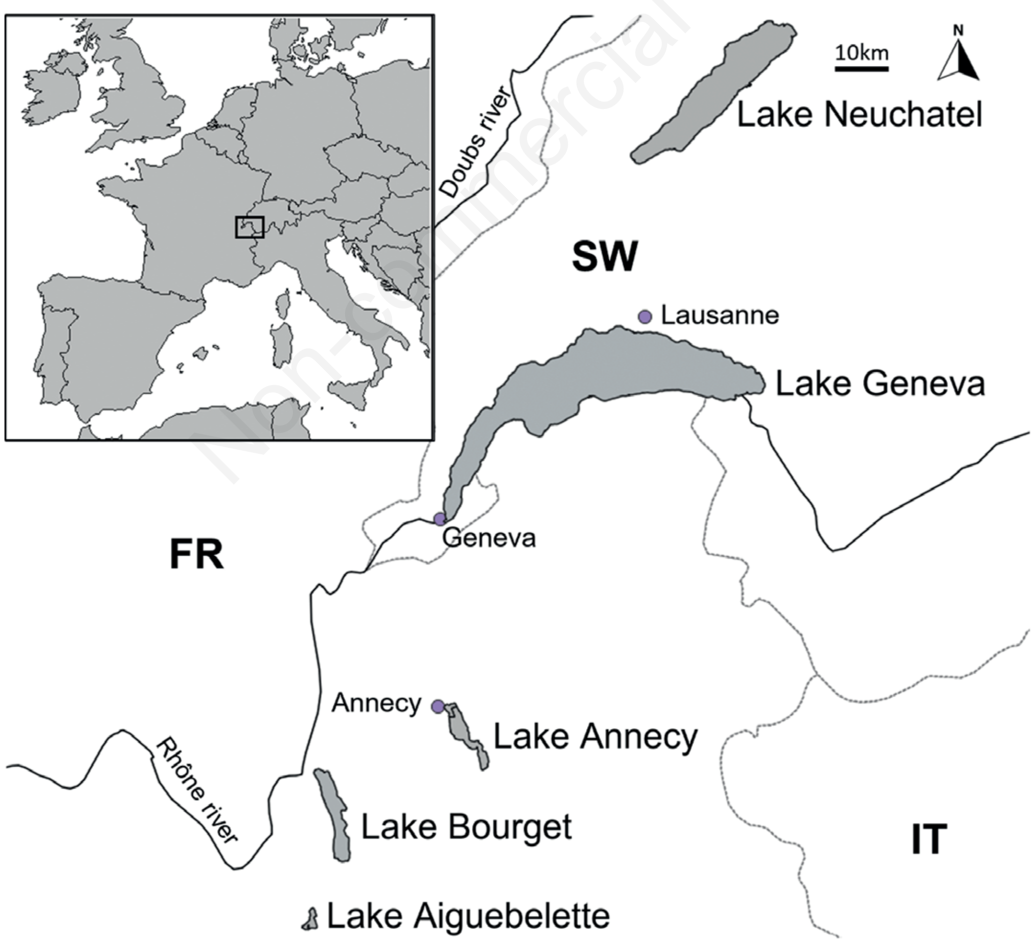

Fig. 1. Location of the five studied lakes. FR = France; SW = Switzerland; IT = Italy. Cities with over 100,000 inhabitants are represented with purple circles.

These parameters included temperature, zooplankton abundance, water level, and wind as identified by Straile *et al.* (2007) and Myers *et al.* (2015) and are detailed in Tab. 2. The data used in this study were collected from ongoing long-term monitoring programs for the five lakes, covering the longest available common period from 2000 to 2020 (Tab. 2). Approximately 4% of the collected data were missing during the studied period. Temperature and zooplankton data were collected once or twice per month, depending on the season and weather conditions, at the deepest point of each lake, following the usual monitoring protocols for deep lakes (Pourriot and Meybeck, 1995; Jacquet *et al.*, 2014). Zooplankton was collected in the first 50 m of the water column from the surface at the same coordinates as the temperature. However, zooplankton data were not available for Lake Aiguebelette as this variable was not monitored over the study period. The water level was recorded daily, while daily mean wind speed was obtained from the closest automatic meteorological station for each lake.

Water temperature is a known factor affecting the growth and survival rates of all life stages of European whitefish. Each life stage, from the egg to the juvenile, has an optimum temperature value and a tolerance temperature range for the development (Eckmann and Pusch, 1989; Stewart *et al.*, 2021). Warmer water temperatures within the species' tolerance range can increase growth and survival rates (Perrier *et al.*, 2012; Anneville *et al.*, 2017). While warmer water temperatures can reduce oxygen rates, the studied peri-alpine lakes maintain high oxygen levels throughout the year, and therefore there was no suspected direct impact of this parameter on the early life stages of whitefish. Three temperature variables were selected to characterize environmental conditions during different early stages of development: average winter surface temperature for eggs (0-5 m; December to February), average spring surface temperature for larvae (0-5 m; March to May), and average summer surface temperature for juveniles (0-10 m; June to August) (Fig. 2; Tab. 2).

High prey abundance is expected to enhance the survival rates of whitefish larvae and juveniles (Hoyle *et al.*, 2011; Pothoven, 2020) due to lower intra- and interspecific competition and growth rate increases (Eckmann, 2013). Eutrophication and re-oligotrophication processes have altered the composition and abundance of phytoplankton and zooplankton in most peri-alpine lakes, which may impact European whitefish populations at all life stages through bottom-up relationships (Matsuzaki *et al.*, 2018). Based on the known diets of European whitefish throughout ontogenesis (Pomeroy, 1991; Anneville *et al.*, 2007; Anneville and Hamelet, 2019), three seasonal variables for zooplankton were defined, overlapping temporally with coregonid larvae, spring juveniles, and summer juveniles in the lakes studied (Tab. 2). These variables are the mean abundance of small copepods (Calanid and *Cyclops* species, all stages except nauplii) from February to April, the mean abundance of *Daphnia* species from April to June, and the mean abundance of carnivorous Cladocera (*Bythotrephes* and *Leptodora* species) from August to October (Fig. 2; Tab. 2).

Intense wind events that create waves and currents can transport eggs outside the spawning grounds, where they may no longer find optimal conditions (Ventling-Schwank and Livingstone, 1994; Roseman *et al.*, 2001). Sediment can be remobilized and deposited over the eggs, reducing the oxygen rate available for the eggs. Negative effects of wind and waves have been reported on the larvae of various fish species including European whitefish (Ward *et al.*, 2004; Claramunt *et al.*, 2010; Myers *et al.*, 2015). Early lar-

Tab. 1. Main physical, trophic, and fishery characteristics of the five studied lakes.

	Lake Geneva	Lake Neuchâtel	Lake Bourget	Lake Annecy	Lake Aiguebelette
Surface (km²)	581.3	218.3	44.5	27.6	5.5
Maximum depth (m)	309	152	147	82	71
Altitude (m)	372	429	232	447	390
Range of total phosphorus concentration between 2000 and 2020 ($\mu g.L^{-1}$)	21.50; 41.20	6.29; 14.60	7.99; 31.11	5.25; 9.30	5.91; 20.66
Current trophic status	Mesotrophic	Oligotrophic	Oligomesotrophic	Oligotrophic	Oligotrophic
Professional whitefish fishery activities	Yes	Yes	Yes	Yes	No
Recreational whitefish fishery activities and relative importance of this fishery compared to professional fisheries (expressed as the mean percentage of recreational fisheries landings compared to total landings between 2000 and 2020)	Yes (1%)	Yes (7%)	Yes (7%)	Yes (41%)	Yes (100%)
Total annual landings ranges	82.0; 761.0*	16.5; 160.0*	6.2; 78.4*	5.3; 17.4*	5171; 14731#
Range of annual stocking in equivalent of million yolk-stage fry between 2000 and 2020.	7; 85	14; 90	0; 19	0	Uncertain

**Tons of fish landed in professional fisheries between 2000 and 2020; #individuals landed by recreational fishermen between 2000 and 2020.*

vae of the studied ecomorph may be affected as they are found close to the shore during the first days of their development (Anneville *et al.*, 2007). A wind variable was defined as the number of days where the daily mean wind velocity was greater than 5 $m.s^{-1}$ over a period from December 15th (previous year) to February 15th, covering the period from the start of reproduction (approximately mid-December) to approximately 15 days after most larvae hatched (Goulon *et al.*, 2021). This wind speed threshold value was defined based on the values of previous studies on the impact of extreme winds (Ventling-Schwank and Livingstone, 1994; Roseman *et al.*, 2001). Furthermore, this value was used in Soulignac *et al.* (2018) as the limit value above which surface thermal stratification could not occur, implying high surface water currents and extreme wind events for Lake Geneva.

The studied whitefish ecomorph spawning in winter on shallow gravel beds near the shoreline, their eggs could be exposed if there is a drop in the water level. Therefore, a variable was defined as the difference between the water level on December 15th of the previous year, when spawning begins, and the minimum water level over a 2-month period until February 15th (Fig. 2; Tab. 2).

Fishery and management data

Data on annual landings of whitefish, stocking (Tab. 1; *Appendix A*) and fishing efforts (Fig. 2) were obtained from the fisheries management organizations of each lake. For Lake Aiguebelette, the data was retrieved from the local recreational fishermen association (AAPPMA Aiguebelette); for the French territory of Lake Geneva, Lake

Tab. 2. Defined variables. Period: period covered by the environmental variable (DEC, December; JAN, January; FEB, February; MAR, March; APR, April; MAY, May; JUN, June; JUL, July; AUG, August; SEP, September; OCT, October). Life-cycle stages detail the corresponding stages that are expected to be affected during this period. Expected effect details whether the impact of increasing values from this variable is expected to be positive [+; positive correlation between this variable and the abundance of European whitefish (*Coregonus* spp.)] or negative (-; negative correlation). It reflects the current state of scientific knowledge for each variable, according to previous studies and experts. Abbreviation shows the name used in the figures (Win, winter; Spr, spring; Sum, summer). Source details the origin from which the data used to build these variables were collected.

Variables	Period	Life-cycle stages	Expected effect on the affected stages	Unit	Abbreviation	Source
Surface (0-5 m) temperature	DEC/JAN/FEB	Eggs	-	°C	Win. Temp.	Observatory on LAkes https://siola.inrae.fr/ (Rimet *et al.*, 2020), Neuchâtel Canton water services
Surface (0-5 m) temperature	MAR/APR/MAY	Larvae	+	°C	Spr. Temp.	
Surface (0-10 m) temperature	JUN/JUL/AUG	Juvenile	-	°C	Sum. Temp.	
Small copepods abundance	FEB/MAR/APR	Larvae	+	$ind.m^{-3}$	Copepods	Observatory on LAkes https://siola.inrae.fr/ (Rimet *et al.*, 2020), Bern Canton water services
Daphnia abundance	APR/MAY/JUN	Larvae and early-juvenile	+	$ind.m^{-3}$	Daphnia	
Large Cladocera abundance	AUG/SEP/OCT	Juvenile	+	$ind.m^{-3}$	Large Cladocera	
Number of strong wind day	15th of DEC to 15th of FEB	Eggs and early larvae	-		Wind Intensity	Météo France, Portail de données pour l'enseignement et la recherche (IDAWEB)
Negative water level range	15th of DEC to 15th of FEB	Eggs and early larvae	+	m	Water Level	Electricité De France (EDF), Direction Départementale des Territoires (DDT) Haute Savoie, Annecy City, Comité Intercommunautaire pour Assainissement du Lac du Bourget (CISALB), Office Fédéral de l'Environnement (OFEV)

Bourget, and Lake Annecy, it was obtained from the Haute-Savoie and Savoie Direction Départementale du Territoire (DDT) and from each respective fisheries services of the Swiss cantons (Genève, Vaud, Neuchâtel, and Fribourg) bordering the Lakes Geneva and Neuchâtel. The stocking data were expressed as equivalent yolk-stage fry (Tab. 1; *Appendix A*; Gerdeaux, 2004). In Lake Annecy, whitefish stocking has not been practiced since the end of the 1990s. For Lake Aiguebelette, stocking data was unreliable due to interannual variations of life stages at which they were stocked and unreported sharing information between the lakes stocked with the Lake Aiguebelette hatchery.

To assess the temporal fluctuation of whitefish abundance, two complementary fishery indicators were used. The first proxy was based on the total annual landings declared by fishermen (Ctot) (Fig. 3a). However, since both fishing effort and stock abundance can affect total landings, the second indicator was based on the Catch Per Unit of Effort (CPUE) (Fig. 3b), which is obtained by dividing the annual landings by the annual fishing effort. The CPUE is considered a better proxy for fish abundance in fisheries sciences (Ricker, 1940). Both indicator trends were compared and confirmed using data from selected dependable fishermen. The accuracy and reliability of the fishing effort variable varied depending on the nature of the available data for each lake. For instance, the number of drifting nets was the most accurate measure of fishing effort for Lake Geneva, Annecy, and Bourget (Fig. 2). The number of angling sessions was used for Lake Aiguebelette, and the number of fishing days with whitefish landings was used for Lake Neuchâtel (Fig. 2).

We postulate that environmental conditions mainly affect the early life stages of whitefish. To obtain whitefish abundance proxies that match the environmental conditions experienced by the caught fish at age 0+, we rescheduled the Ctot and CPUE series with appropriate time lags for each lake (Anneville *et al.*, 2009). The time lag was determined based on the age-structured annual landings data

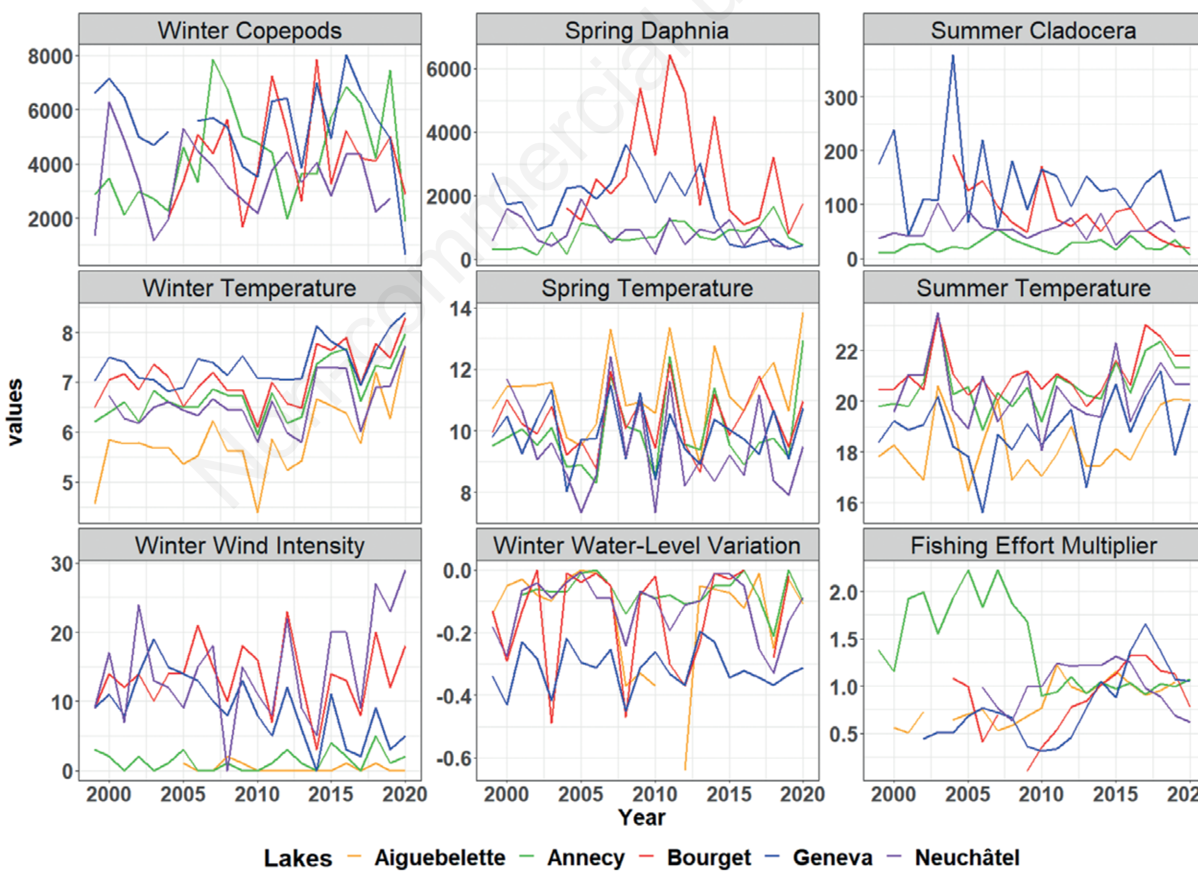

Fig. 2. Environmental variables and fishing effort for the five lakes. Units: number of individuals/m3 for zooplankton abundance variables (winter copepods, spring *Daphnia*, and summer cladocera); °C for the temperature variables (winter, spring and summer temperature); number of days > 5 $m.s^{-1}$ for the wind intensity (winter wind Intensity); m for the water level range (winter water level variation); fishing effort multiplier corresponds to the ratio between fishing effort and the average fishing effort between 2010-2020. This unit was chosen to have a common reference period across lakes.

(*Appendix B*; Goulon and Guillard, 2020, 2022; Nusslé, 2021; Jacquet *et al.*, 2022). In Lake Annecy, whitefish landings were dominated by the 4-year-old cohort in Lake Annecy within the studied time interval. Therefore, a time lag of four years was applied to the fish abundance proxies for Lake Annecy. In the other lakes, landings were dominated by 3-year-old cohorts, and thus three years of lag were applied to the proxies.

Synchrony analysis

To first explore the abundance synchrony between European whitefish stocks, we began to visually examine a fisheries time-series plot (Fig. 3). We then quantified the synchrony of the time series of the two fish abundance proxies using the non-parametric Kendall's coefficient of concordance (W) (Legendre, 2005; Gouhier and Guichard, 2014). W ranges between 0 (no concordance) and 1 (perfect concordance).

Similarity analysis

The R package *distantia* (Benito and Birks, 2020) was used to explore similarities and dissimilarities among lakes characterized by the set of eight environmental variables and the fishing effort time series (Tab. 2; Fig. 2). The package computes a measure of dissimilarity Ψ (eq. 1) between datasets (in our study, each lake is considered as a multivariate dataset composed of the different environmental time series) as the pairwise Euclidean distance between each pair of multivariate ecological time series (i.e. here, each pair of lake). The distance between two lakes l_1 and l_2 is denoted $AB_{between}(l_1,l_2)$ (eq. 2) and is the sum of the distance between each environmental variable for each year:

$$\Psi = \frac{AB_{between} - AB_{within}}{AB_{within}} \quad \text{(eq. 1)}$$

$$AB_{between}(l1,l2) = \sqrt{\sum_{i=1}^{i=Y}\sum_{j=1}^{j=J}(X_{l1,j}(y) - X_{l2,,j}(y))^2} \quad \text{(eq. 2)}$$

where $X_{l1,j}(y)$ is the value of one of the J environmental variables *j* (e.g., winter temperature, spring temperature, *etc.*) measured at lake l_l in year *y*.

Note that in the original *distantia* method, $AB_{between}$ is standardized by a metric AB_{within} that aims to normalize $AB_{between}$ in cases where the datasets have different number of years. However, since our datasets have the exact same years, and AB_{within} tends to overdrive the dissimilarity values for variables that show high interannual variations, we used only the $AB_{between}$ values to measure distances between lakes. We examined the inter-lake Euclidean distances between each lake pair using adjacency networks and then identified the variables that contributed the most to these distance values. It was done by calculating the drop in distance values between two lakes when removing a variable from the dataset: an important drop in the distance when removing a variable means that it greatly contributes to the multivariate distance between the two lakes, indicating different temporal trends for this variable between these two lakes. The package uses restricted permutation tests to estimate the significance of distance values and calculates the probability of randomly obtaining a distance value lower than or equal to the one first calculated. Throughout this analysis, we used a 5 % level of significance.

This approach requires that each dataset has the same set of variables to measure $AB_{between}$. However, there was no zooplankton monitoring data for Lake Aiguebelette. Thus, two different runs were carried out: [5lakes_noZOO], which includes the five studied lakes

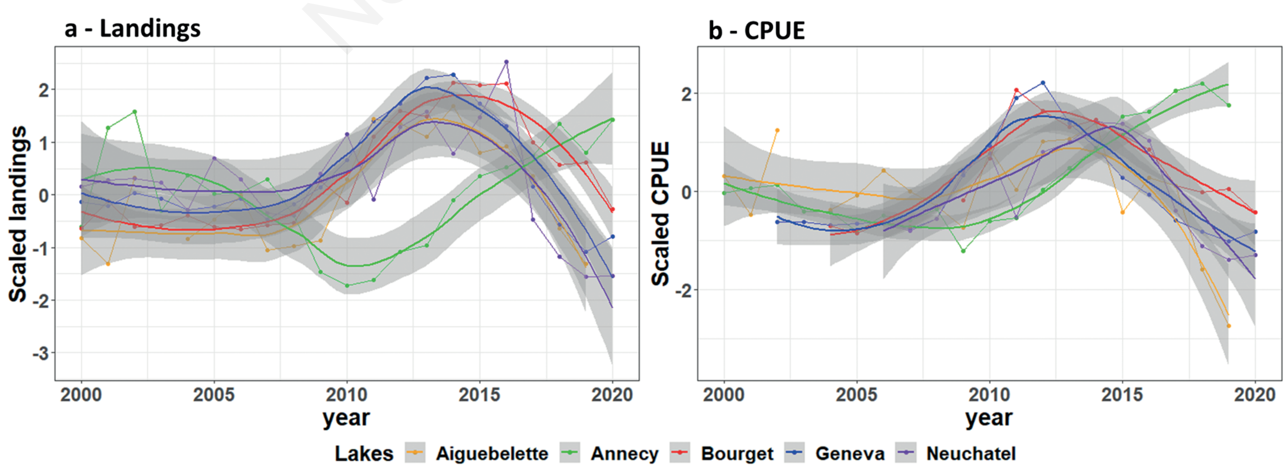

Fig. 3. Scaled fish landings (a) and CPUE (b) series for the five studied lakes. Points represent the observed data, thick lines represent smoothed trends (local polynomial regression method), and grey areas are 95% confidence intervals (CI). Data with different units and scales are scaled (subtracting the mean and dividing by the standard deviation) to facilitate comparisons.

and only six variables, i.e., without the three variables of zooplankton abundance, and [4lakes_withZOO], which includes all nine variables in four lakes, i.e. without Lake Aiguebelette. Moreover, two different scaling methods were adopted to compare both the absolute values and trends of each variable across lakes. The INTER approach scaled the values of the variables on the overall dataset, standardizing each variable by subtracting the mean over all lakes and dividing by the standard deviation over all lakes. This way, the absolute values of each lake's variables are compared to the global mean of these variables across all lakes, highlighting extremely high or low values with a high dissimilarity. The INTRA approach scaled each lake dataset separately, standardizing each variable of each lake centered around its own mean and scaled with its own standard deviation. This way, the temporal trends are compared to the global trends across all lakes, highlighting lakes with trends as opposed to the global trend with high dissimilarity. Therefore, two lakes with similar temporal trends in environmental conditions (e.g., temperature) but with different mean values (e.g., one warm and one cold lake) will have a large distance with INTER scaling but a small distance with INTRA scaling. Due to missing values, the *distantia* analysis was applied to 13 years for the [5lakes_noZOO] run and 14 years for the [4lakes_withZOO] run. The stocking variable was not considered in the *distantia* analysis as it was missing in Lake Annecy, unreliable in Lake Aiguebelette and managed independently in the three other lakes, which implies a high expected distance contribution of this variable, due to local policy. The *distantia* analysis focused on similarities between environmental and fishing variables, looking to identify variables with synchronous fluctuations or similar absolute values to identify variables that could present regional similarities and explain a Moran effect.

Linking fisheries data and environmental variables

Linear models were used to explore the relationships between proxies of whitefish abundance and environmental variables. Each lake was analyzed separately by fitting models with Ctot and CPUE as response variables and the eight environmental factors (Tab. 2) as explanatory variables. In addition, fishing effort and stocking were included as explanatory variables; however, the former was only added when modeling total landings since it is already included in the CPUE calculation. All models with one variable at a time were tested, and in the case of multiple significant variables, additive effects were tested. The models were compared based on several criteria, including R^2 (proportion of the response variable that is explained by the explanatory variable), BIC (Bayesian Information Criterion, used for model selection based on the maximum of likelihood, the number of parameters, and the number of data), F value (taken from the F-test, which tests the null hypothesis that the coefficients are null), and residual analysis. Only the best model for each lake and response variable was retained, based on cross-comparing the R^2 value, BIC value (to avoid model over-parametrization), residual analysis, and p-values. Models that presented ecological inconsistencies, i.e., incoherent relationships based on the ecology of the whitefish, were rejected.

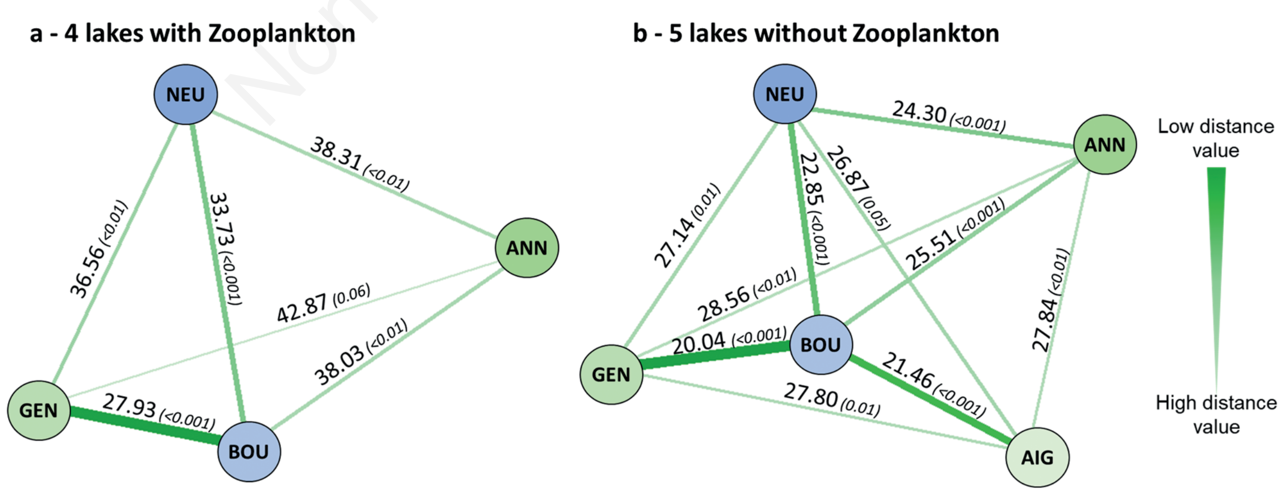

Fig. 4. Adjacency networks illustrating the total multivariate distance between the five lakes with the INTRA scaling method for (a) four lakes with the zooplankton abundance variables and (b) five lakes without the zooplankton abundance variables. GEN = Lake Geneva, NEU = Lake Neuchâtel, BOU = Lake Bourget, ANN = Lake Annecy, AIG = Lake Aiguebelette. Line thickness and color intensity both quantify multivariate similarity in temporal fluctuations; multivariate distance values are reported above lines; in parentheses: probability of randomly obtaining an equal or lower distance value.

RESULTS

Qualitatively, clear synchrony of fluctuations in fish abundance proxies was observed for four of the studied lakes (Lake Geneva, Lake Neuchâtel, Lake Bourget, and Lake Aiguebelette) (Fig. 3a). Kendall's W for the four Ctot time series was moderate and significant (0.52; $p<0.0001$). In these lakes, Ctot and CPUE began to increase in 2008-2009, peaked in 2014-2016, and then rapidly and steadily decreased. In Lake Annecy, Ctot and CPUE initially decreased until 2010 and then steadily increased. However, adding the Lake Annecy time series decreased Kendall's W value to 0.33 ($p=0.002$).

The *distantia* analysis used the INTRA scaling method to compare trends between lakes and the INTER scaling method to compare values between lakes. Since both methods produced similar results, only the INTRA scaling outputs are presented (Figs. 4 and 5). Outputs from the INTER scaling method are reported in *Appendix C*. However, it is important to note that the INTER scaling method showed Lake Neuchâtel to be closer to the other lakes (Fig. C1), implying similar ranges of environmental values but dissimilar trends over time. Moreover, adding zooplankton variables changed the distance pattern, indicating that inter-lake distances based on absolute values differed between zooplankton and other variables (Fig. C1). With the INTRA scaling method, similar distance patterns were observed between Lakes Geneva, Bourget, Annecy, and Neuchâtel in both runs (Fig. 4), suggesting that adding zooplankton variables did not greatly affect the multivariate distance between these lakes. Looking at pairwise distance among lakes, Lake Geneva and Lake Bourget had the smallest distance, indicating that these two lakes display very similar environmental trends.

The contribution of each environmental variable to the multivariate distance between two lakes is evaluated by measuring the drop in distance values between two lakes when removing the variable from the dataset (Fig. 5). Results are consistent between the two scaling methods, with few differences observed with the INTER scaling method (Fig. C2). Wind intensity plays a greater role in distances between lakes with the INTER scaling method, indicating similar trends but dissimilar ranges of values. However, zooplankton variables have a higher impact on the multivariate distance in most pairwise comparisons when using the INTRA scaling method than with the INTER scaling method (Fig. 5a). Results obtained with the INTRA scaling method suggest that zooplankton abundance greatly contributes to dissimilarity in temporal fluctuations among lakes. Spring and winter surface temperature have a lower impact on the multivariate distance value using both scaling methods in most pairwise comparisons, except for the winter temperature between Lake Geneva and Lake Aiguebelette with the INTER scaling method (Fig. C2), indicating that these two lakes are respectively the hottest and coldest in winter among the studied lakes. However, the INTRA scaling results suggest that these variables greatly contribute to the similarity in temporal fluctuations among lakes.

Winter wind intensity, water level, and fishing effort showed more heterogeneous participation between lake pairs. Although larger contributions to multivariate similarities were observed in some pairwise comparisons, there was no clear pattern at a broader scale. Fishing effort was the variable that contributed the most to the multi-

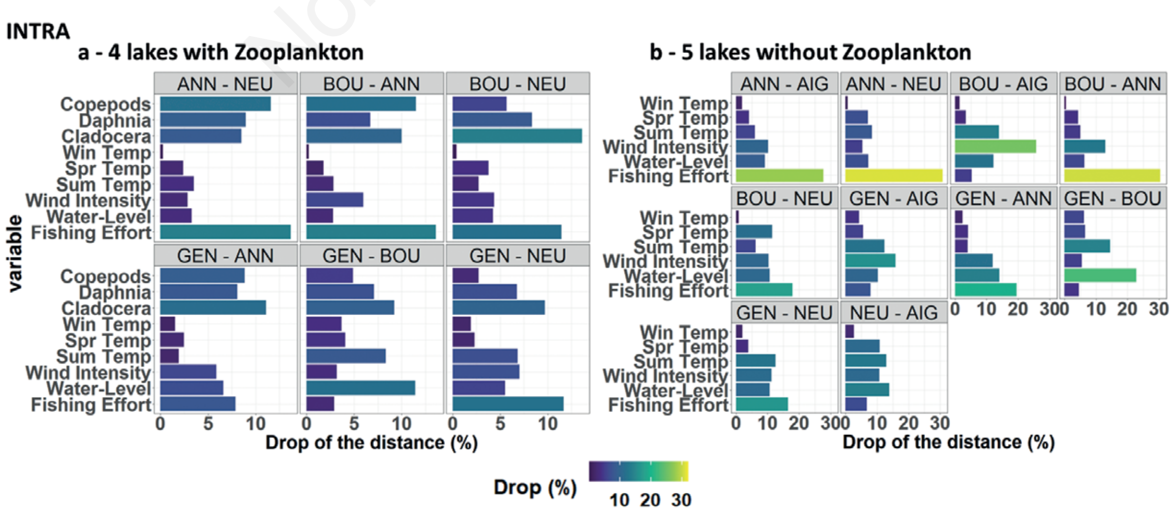

Fig. 5. Pairwise drops of distance values when a variable is removed from the dataset with the INTRA scaling method for (a) four lakes with the zooplankton abundance variables and (b) five lakes without the zooplankton abundance variables. The higher the percentage drop, the higher the contribution of that variable to the multivariate distance value.

variate distance between several pairs, especially those including Lake Annecy. The fishing effort of Lake Annecy was distant from the fishing effort series of the other lakes, suggesting opposing trends and values between Lake Annecy and the four other lakes. These analyses showed that spring and winter surface temperatures might trigger regional synchrony among the studied lakes, while other variables appeared more lake-specific and asynchronous at the regional scale.

Linear models were used to explore the relationship between fish abundance proxies based on Ctot and CPUE and explanatory variables in each lake, including the eight environmental variables and fishing effort. The best models explaining the temporal fluctuations in whitefish abundance proxies had a single explanatory variable (Tab. 3) and were selected based on the highest R^2 values, lowest p-values and BIC ranking (*Appendix D*). Similar significant models were obtained using both fish abundance proxies for Lakes Geneva, Neuchâtel and Bourget, which had the same selected variable, similar statistical values, and identical direction of the relationships (Tab. 3). For Lakes Bourget and Geneva, the best explanatory variable was spring *Daphnia* abundance, which was positively correlated with fish abundance proxies (Fig. 6). Lake Neuchâtel fish abundance proxies were negatively correlated with winter surface temperature (Fig. 6). For Lake Annecy, no significant model could be fitted between CPUE and environmental variables, while Ctot was negatively correlated with fishing effort (Fig. 6). For Lake Aiguebelette, no statistically significant model could be fitted. Other variables were not statistically significant for any lake, except for fishing effort in Lake Geneva, which was negatively correlated with Ctot, but with a lower R^2 and a higher p-value than the model with *Daphnia* abundance (*Appendix D*, Tab. D2). The model testing possible additive effects of *Daphnia* and fishing effort in Lake Geneva did not explain much more variance than the simpler models (*Appendix D*, Tab. D2) and was therefore rejected to avoid overfitting. One statistically significant but ecologically inconsistent model was rejected for Lake Aiguebelette, with water level as the explanatory variable showing a positive correlation, which does not seem consistent with the ecology of the species.

DISCUSSION

Climate change is affecting lakes worldwide and is significantly impacting abiotic parameters (Woolway and Merchant, 2019; Jane *et al.*, 2021; Kraemer *et al.*, 2021), which in turn directly or indirectly affect fish recruitment success and stock abundances (Brunel and Boucher, 2007; Dippold *et al.*, 2020; Wootton *et al.*, 2021). Lake fish species, unlike marine species, are particularly vulnerable to the effects of climate change as they cannot shift their distribution poleward (Shoji *et al.*, 2011). Fish recruitment is a stochastic process with high interannual variability (Houde, 2016) and is sensitive to a wide range of interacting factors (Planque and Buffaz, 2008; Sandström *et al.*, 2014). Thus, identifying and separating the variables that drive recruitment success is challenging (Planque and Buffaz, 2008).

We explored the relationship between whitefish fishery statistics in several nearby lakes, which were used as proxies for fish abundance, and multiple potential driving factors, to expand and enhance our understanding of likely common or similar recruitment drivers. Fishery landings revealed comparable trends among four neighboring lakes, indicating a synchrony of abundance between them. This type of synchrony among different coregonid stocks has been investigated in other regions and explained by large-scale climatic factors (Bunnell *et al.*, 2010). Temperature is the most frequently cited factor to explain regional-scale synchrony (Marjomäki *et al.*, 2004; Bunnell *et al.*, 2010;

Tab. 3. Statistics of the best models obtained for each lake with either total landings (Ctot) or CPUE as response variables. Correlation indicates the sign of the correlation: ↗ means a positive correlation, ↘ means a negative correlation. Significance indicates the statistical significance of the linear regression coefficient.

Lake	Model	Correlation	Coefficient	adj_R²	Significance	p-value
Geneva	Ctot ~ Daphnia	↗	1.6×10^{2}	0.49	**	<0.01
Geneva	CPUE ~ Daphnia	↗	7×10^{-3}	0.51	***	<0.01
Neuchâtel	Ctot ~ Temp. Win.	↘	-5.4×10^{4}	0.39	**	<0.01
Neuchâtel	CPUE ~ Temp. Win.	↘	-1.3×10^{1}	0.29	*	0.03
Bourget	Ctot ~ Daphnia	↗	1.0×10^{1}	0.49	**	<0.01
Bourget	CPUE ~ Daphnia	↗	2×10^{-3}	0.35	*	0.03
Annecy	Ctot ~ Fishing effort	↘	-5.5	0.32	*	0.02
Annecy	CPUE ~ Temp. Win.		3.7	0.07	NS	0.32
Aiguebelette	Ctot ~ Temp. Win.		-1.8×10^{3}	0.13	NS	0.24
Aiguebelette	CPUE ~ Temp. Win.		-1.8×10^{-1}	0.10	NS	0.21

****p<0.001; **p< 0.01; *p<0.05; NS, p>0.05.*

Myers *et al.*, 2015) since it is typically synchronized on a very large scale and can impact whitefish development and survival at all stages. Myers *et al.* (2015) also demonstrated that the maximum wind speed during larval emergence was a synchronized variable with probable impacts on larval survival rates. These three studies identified synchrony among whitefish populations that were separated by 100 km to 600 km.

The five peri-alpine lakes examined in our study are situated within a perimeter of 170 km, which falls within the range of observed spatial synchrony for whitefish. Despite specific conditions that could have caused a distinct trend in Lake Annecy, it was assumed that the synchrony of landings observed in four lakes could result from similar changes in environmental conditions among the lakes. The *distantia* analysis confirmed regional similarities in both values and trends for winter and spring temperatures, which are consistent with the lakes' geographical proximity (Desgué-Itier *et al.*, 2023). Therefore, between-lake synchrony was observed for both seasonal temperature variables and whitefish landings, which could align with the Moran effect theory. However, winter temperature was identified as the best explanatory variable for the variations in whitefish abundance proxies in only one lake, whereas plankton abundance seemed to be another significant recruitment driver, despite displaying different trends among the lakes.

We first examined the relationships between whitefish abundance proxies and environmental variables using Generalized Additive Models (GAMs), suspecting complex relationships. However, only linear relationships were found to be statistically significant, possibly due to the relatively small dataset. Therefore, we switched to linear models. The relationships were not consistent across all lakes. For Lakes Geneva and Bourget, the recent decline in landings could be attributed to lower *Daphnia* abundances in spring, which may be limiting the production capacity of total larvae and early juveniles. This food resource has already been identified as a potentially important driver of European whitefish abundance in Lake Geneva (Anneville *et al.*, 2017). Lake Geneva and Lake Bourget exhibited similar smoothed trends of spring *Daphnia* abundance over the period. There was a peak around 2010 (Fig. 2) that corresponds to the high whitefish landings, followed by a substantial decrease.

Years with high *Daphnia* concentrations in spring (>2000 ind.m^{-3}) may significantly impact the growth and survival of whitefish larvae in Lake Geneva and Lake Bourget. Conversely, Lake Annecy and Lake Neuchâtel had relatively low and stable *Daphnia* abundance over the period (863 ± 455 ind.m^{-3} for Lake Neuchâtel; 756 ± 377 ind.m^{-3} for Lake Annecy), which could be compensated by other food sources such as small copepods and *Bosminidae* (Ponton and Müller, 1989; Anneville *et al.*, 2007). This hy-

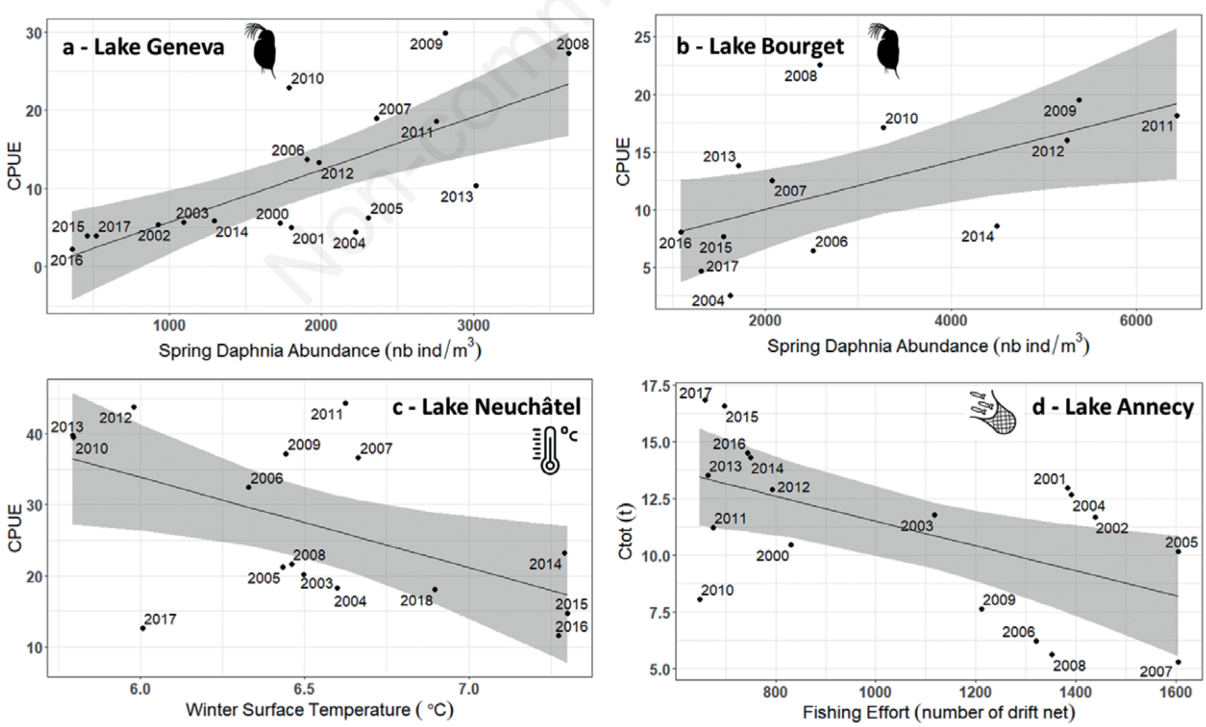

Fig. 6. Significant relationships obtained with the selected linear models between environmental variables and CPUE of Lake Geneva (a), Lake Bourget (b), Lake Neuchâtel (c) and Ctot of Lake Annecy (d). Points represent the observed values; lines represent the modeled trend; grey areas represent the 95% CI.

pothesis could not be verified for Lake Aiguebelette, as zooplankton was not monitored. Developing a regular monitoring program similar to those of the other four lakes to extend the dataset and strengthen future inter-lake comparisons would be highly valuable.

Zooplankton abundance was based on long-term surveys conducted only twice a month, so rapid variations in abundance may have been missed. Additionally, differences in zooplankton size or quality were not considered, despite their importance in diets (Hayden *et al.*, 2022; Hinchliffe *et al.*, 2023). *Daphnia* abundance is influenced by a complex combination of biotic and abiotic factors. Lake Bourget exhibited similar trends to Lake Geneva for these two processes; both lakes are still undergoing re-oligotrophication, which is known to have important consequences for the complex plankton assemblages and food-web interactions (Nõges *et al.*, 2018; Anneville *et al.*, 2019). This process could cause phytoplankton and zooplankton synchrony (Özkan *et al.*, 2016). The recent decline in *Daphnia* abundance in both lakes could be linked to changes in the phytoplankton community structure, lower specific prey abundance or reduced quality (bottom-up effect) (Lorenz *et al.*, 2019), or top-down control by planktivorous fish species, especially whitefish (Anneville *et al.*, 2019; Rasconi *et al.*, 2020), which displayed particularly synchronized high landings for these two lakes in the 2010s.

Winter water temperature also directly impacts egg development and survival (Brooke, 1975; Cingi *et al.*, 2010). The five lakes studied have shown exceptionally high winter temperatures since 2014 compared to the rest of the time-series (Fig. 2). The influence of water temperature on egg and embryo development has been extensively studied in laboratories, demonstrating a direct relationship with survival rate, with lower survival occurring at extremely low and high water temperatures (Luczynski, 1985). High water temperature reduces survival rates through lower egg and embryo sizes (Brooke, 1975; Viljanen and Koho, 1991; Wilkońska, 1992), higher rates of abnormally developed embryos (Brooke, 1975; Cingi *et al.*, 2010), and higher rates of unfertilized eggs (Cingi *et al.*, 2010). Rising temperatures are also directly linked to lower oxygen concentration, leading to death by asphyxiation in the worst cases (Viljanen and Koho, 1991). In Lake Neuchâtel, winter temperatures above 6.9°C were recorded for six out of seven years between 2014 and 2020, which was unprecedented before 2014. High winter surface temperatures appear to negatively impact the whitefish abundance proxies in Lake Neuchâtel, potentially due to lower egg survival rates. However, no significant effects of this variable were observed in other lakes, despite Lake Neuchâtel being colder in winter than Lake Geneva, Lake Bourget, and Lake Annecy. Stewart *et al.* (2021) demonstrated a negative correlation between water temperature and egg survival, with varying sensitivities to high temperatures among multiple coregonid species from different lakes and continents. Physically separated populations can exhibit different optimum and tolerance limits for water temperature in response to local conditions as an adaptative measure (De-Kayne *et al.*, 2022). Populations from Lake Geneva, Lake Bourget, Lake Annecy, and Lake Aiguebelette may not have yet reached their threshold values for winter temperature, which could affect egg development. It would be relevant to conduct similar experiments to those carried out by Stewart *et al.* (2021) with fish from the studied lake to confirm this hypothesis.

The *distantia* analysis revealed that *Daphnia* abundance was not the most synchronized environmental factor among these lakes. Since water temperature is a critical driver of *Daphnia* population dynamics (Moore *et al.*, 1996; Giebelhausen and Lampert, 2001; Heugens *et al.*, 2006), the direct influence of spring *Daphnia* abundance may be an indirect response to the synchronized increase in temperature. Although fluctuations in *Daphnia* abundance do not explain the variation in Lake Neuchâtel's abundance proxies, it is still linked to winter temperature. In general, for Lakes Neuchâtel, Bourget, and Geneva, this suggests that synchronized changes in both winter and spring temperatures may explain the synchrony in landings. This could occur either through a direct improvement in the survival of younger life stages in winter or an indirect increase in *Daphnia* abundance resulting in better growth and survival of juveniles in spring. Water temperature during egg development serves as a trigger for hatching (Stewart *et al.*, 2021). Consequently, higher water temperatures result in earlier hatching dates (Eckmann, 1987). *Daphnia* phenology is also directly linked to temperature (Straile *et al.*, 2012). However, mismatch may arise, leading to high mortality due to a lack of food during the early development of whitefish larvae (Patrick *et al.*, 2013; Pothoven, 2020). Given the challenge of studying the temperature-sensitive phenology of multiple fish and zooplankton species (Wojtal-Frankiewicz, 2012), this hypothesis is still a subject of debate (Viljanen and Koho, 1991; Straile *et al.*, 2007).

Stocking intensity was considered a potential explanatory variable in the modeling analysis but did not demonstrate significance for any lake. During the eutrophic period, whitefish stocking offset the natural recruitment deficit and contributed significantly to the adult biomass (Champigneulle and Cachera, 2008). As the re-oligotrophication process progressed, which corresponded to improved environmental conditions, this contribution decreased, thus creating more favorable conditions for spawning and egg-to-larvae development (Müller, 1992; Gerdeaux, 2004; Anneville *et al.*, 2009). The precise role of stocking in landings was not assessed in the studied lakes except in Lake Bourget (Champigneulle and Cachera, 2008), where it did not exceed 15% of the landings. Future studies requiring marking of hatchery fish with fluorescent dyes (Eckmann, 2003) will address stocking efficiency, which is believed to be lake-specific as recent studies in other European lakes have sometimes reported high contributions of whitefish stocking even after re-oligotrophication (Eckmann *et al.*, 2007; Wanke *et al.*, 2016; Wedekind *et al.*, 2022).

Fishery statistics were obtained from professional fisheries in all lakes except in Lake Aiguebelette, where they came from recreational fishing. Consistent CPUE series between professional and recreational fisheries were reported in Lake Annecy (Gerdeaux and Janjua, 2009) and Lake Bourget (unpublished data), indicating that data from both sources may be used in line with the observed synchronized landings between Lake Aiguebelette and the other three lakes. Fishing effort was not significant in all models except for those of Lake Annecy and Lake Geneva. In Lake Annecy, significant variations in fishing efforts during the survey appeared to be the primary factor contributing to the different trends, which was the only significant relationship found for this lake. The negative correlation between total landings and the fishing effort variable suggests high sensitivity towards fishing effort for this whitefish population. This situation may have masked the effects of local environmental conditions on recruitment success. The gradual decline in fishing efforts starting in 2007 due to the retirement of fishermen followed by new fishing regulations in 2011 has led to a gradual and later increase in abundance (Goulon and Guillard, 2022). This landings trend reflects a typical response of an overexploited stock: increasing landings when fishing effort decreases (Rosenberg, 2003). The slower increase in annual landings during the most recent years may indicate that the European whitefish population of Lake Annecy is still reaching equilibrium and will likely exhibit more sensitivity towards environmental conditions affecting recruitment in other lakes in the near future (e.g., winter surface water temperature and spring *Daphnia* abundance). A negative relationship was also observed between whitefish landings in Lake Geneva and fishing effort. Although considered less reliable than the one with *Daphnia* abundance, this relationship confirms the likely major effect of fishing effort on whitefish abundance in the studied lakes.

CONCLUSIONS AND PERSPECTIVES

This study aimed to investigate the influence of the most likely explanatory variables for European whitefish population abundances and recruitment success proxies, as well as the apparent synchrony among four lakes. This synchrony in landing time series cannot be attributed to a single common variable, as multiple interacting drivers are likely at play. Fishing effort is probably one of the primary drivers of population abundance for all lakes, as it is for most fished stocks globally (Jackson *et al.*, 2001; McCauley *et al.*, 2015). While we elucidated the sensitivity of Lake Geneva and Lake Bourget's whitefish stocks to spring *Daphnia* abundance and Lake Neuchâtel's stock to winter temperature, more complex combinations may exist, including fishing effort and indirect effects of other environmental factors.

The European whitefish stocks in the five studied lakes support substantial fishery activities. However, the status of these stocks has not been evaluated, and the regulations on fisheries are based on limited information. Our study highlighted the role of both environmental variations and fishing efforts in whitefish abundance fluctuations. It is imperative to develop models to disentangle the effects of fishing harvest and environmental pressure on recruitment to gain a better understanding of past abundance fluctuations and make useful predictions for the future fisheries management.

ACKNOWLEDGMENTS

This research was carried out as part of a PhD funded by the ANRT (Association Nationale de la Recherche et de la Technologie), three Swiss cantons (the Geneva Canton, the Vaud Canton, the Valais Canton), the OFEV (Office Fédéral de l'Environnement), and the DDT (Direction Départementale des Territoires) of Savoie and Haute-Savoie. The authors acknowledge all the organizations who gave access to the data and people who contributed to the collection and analysis of these data. Special thanks to Alice Theurel and Lilia Guillet, who markedly took part in data collection and the first explanatory approach of this study.

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Online supplementary material:

Appendix A. Stocking data.

Appendix B. Age-structured fisheries data.

Appendix C. Outputs from the INTER transformation of the distantia analysis.

Appendix D. Linear model selection.