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Impact of fishing activities on the population dynamics of European whitefish in four peri-alpine lakes

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Abstract – Inland fisheries play a crucial role in socio-economic activities and food production. However, these fisheries are often less intensively monitored and studied than marine fisheries. In the past two decades, important fluctuations in European whitefish (*Coregonus lavaretus*) landings have been observed in four peri-alpine lakes in France and Switzerland. To better gauge the impact of fishing removal, a multi-lakes Delay-Difference model was developed and adapted to these fisheries. A hierarchical state-space Bayesian framework was used to integrate stochasticity for each process and incorporate diverse data. The model gave estimates of time series for biomass, recruitment, stage-structured landings, and fishing mortality, as well as estimates of natural mortality rate, Brody growth coefficient and mean recruitment productivity. Differences in the estimates of variables predicted by the model were observed among lakes. Negative impacts of exploitation have been highlighted for Lakes Geneva, Bourget, and Annecy. Low levels of biomass under high fishing mortality rates were observed, while landings tended to increase under lower mortality rates. Lakes Geneva and Bourget outputs suggest stocks were impacted by fishing activities and that fishing effort reduction could ultimately increase yields. Lake Annecy abundance and landings trends increased after 2010, suggesting management strategies that focused on effort reduction were successful. Lake Neuchâtel stock abundance was low after 2017 and probably more fragile due to low biomass levels and recruitment. The observed changes in European whitefish biomass cannot be attributed solely to fishing, suggesting that environmental factors may also influence recruitment success alongside the impacts of fishing pressure.

Keywords: Delay-difference model / stock assessment / inland fisheries / European whitefish / state-space Bayesian framework

1 Introduction

Inland fisheries have often been overlooked by policy-makers and researchers with large landings from the marine environment absorbing the most attention. However, inland fish catches still represent a globally important, albeit unevenly distributed resource (Lynch *et al.*, 2016; Funge-Smith and Bennett, 2019). They are locally and internationally of great socioeconomic importance, contributing to human consumption and food security (Welcomme *et al.*, 2010; Lynch *et al.*, 2016).

As with all fish stocks, the exploitation of freshwater species raises questions about the sustainability of fisheries and

the impacts on the fish populations. While complete extirpation of fish populations due to fishing pressure alone is scarce, overfishing can lead to the collapse of fish stocks, where fish populations become so depleted that it undermines their sustainability (Jackson *et al.*, 2001; Mullan *et al.*, 2005). Fish population dynamics are influenced by various factors, both environmental and anthropogenic. However, fishing pressure has been widely recognized as the primary driver explaining abundance fluctuations in many fish stocks (e.g., Alcala and Russ, 1990; Kleisner *et al.*, 2013; Lyach, 2020).

Studying and quantifying the relationship between fishing effort, fish abundance and productivity has been a key focus of fisheries science and management over the past decades. These efforts have been aimed at ensuring the sustainable management of fishing activity and the health of fish populations (Hilborn and Walters, 1992). Various stock assessment

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methods have been developed to quantitatively estimate variations in fish abundance under different fisheries management scenarios (Hilborn and Walters, 1992). First developed for marine fisheries, these methods were then adapted for inland fisheries and tailored to various fisheries and ecological contexts, including invasive species, stock enhancement, habitat degradation and others (Berger *et al.*, 2012; Munyandorero, 2012; Alves *et al.*, 2013; Pitcher, 2015; Lorenzen *et al.*, 2016).

Except for a few fisheries in Europe or in the North American Great Lakes, inland fisheries are usually less intensively monitored than marine fisheries (Pitcher, 2015). Inland fisheries scientists frequently face data-poor situations, where adequate time series of catch-at-age, fishing effort, abundance indices, and accurate estimations of critical life-history traits are missing or only partially available. Diverse methods have been developed to work on population and fishery dynamics in a data-poor context (*e.g.*, Pilling *et al.*, 2008; Fitzgerald *et al.*, 2018), including methods based on catch data and life-history traits (Chrysafi and Kuparinen, 2016), the analysis of simple indicators from Catch Per Unit of Effort (CPUE) of both commercial and recreational fisheries statistics (Gerdeaux and Janjua, 2009), population or biomass models (Fisch *et al.*, 2019), management experiments (Lorenzen *et al.*, 2016), or simply expert knowledge (Stokes *et al.*, 2021).

Whitefish, salmonid species belonging to the genus *Coregonus*, are cold water stenothermic fish representing major resources for inland fisheries in Europe and North America (Fera *et al.*, 2015; Winfield and Gerdeaux, 2015). In peri-alpine lakes, whitefish often constitute a substantial part of the annual landings for both commercial and recreational fishermen (41% of the total Swiss landings in 2020 [OFEV, 2021], > 40% of the French landings in lakes Geneva, Annecy and Bourget [Haute Savoie and Savoie Direction Départementale du Territoire]). However, these species exhibit large stock fluctuations over time, partly because of their high sensitivity to both environmental conditions (Straile *et al.*, 2007; Myers *et al.*, 2015) and fishing pressure (Lukin *et al.*, 2006; Anneville *et al.*, 2015; Rook *et al.*, 2022). Moreover, whitefish are especially sensitive to climate change because of their ecology and physiology (Roberts *et al.*, 2024). These variations highlight the need for a better understanding of the factors influencing recruitment and abundance to better quantify the current whitefish stock biomass, predict future fluctuations, and ensure sustainable fisheries management.

Various stock assessment methods have been applied to whitefish fisheries, mostly in the North American Great Lakes (Cox and Kitchell, 2004; Harford *et al.*, 2006, 2007). These vast lakes contain multiple water units and, consequently, distinct whitefish stocks managed with separate Total Allowable Catches (TAC). Stock assessments and whitefish population dynamics studies in European lakes are scarcer and have to adapt to heterogeneous data coming from various sources (Bartley *et al.*, 2015; Vehanen *et al.*, 2020; Stokes *et al.*, 2021). They often rely on trend analyses of indicators derived from basic fisheries statistics (Anneville *et al.*, 2009; Gerdeaux and Janjua, 2009), scientific surveys with gillnets, or hydroacoustic abundance estimations (Jurvelius *et al.*, 2006; Harrison *et al.*, 2010).

Similar trends in whitefish landings have been observed over the last two decades in three geographically proximate peri-alpine lakes (Bourinet *et al.*, 2023): Lake Geneva, Lake Neuchâtel, and Lake Bourget, while a contrasting trend was observed in a fourth nearby lake (Lake Annecy). These interannual variations in landings raise questions for both scientists and managers about the key determinants of the population dynamics of these whitefish stocks. Previous research has already described the sensitivity of these four lakes to various environmental or anthropogenic factors (Bourinet *et al.*, 2023), taking into account environmental variables, fishing effort and stocking intensity as explanatory variables. However, recent knowledge of the fishery characteristics and their interactions with whitefish populations is lacking. Indeed, the last stock assessment and population dynamics study took place at the end of the previous century and was conducted only at Lake Annecy (Caranhac, 1999).

We aimed to further explore the impact of whitefish harvest on some key processes of population dynamics in the four peri-alpine lakes over the last two decades, with a particular focus on the similarities and differences among lakes. We hypothesized that the large interannual variations in fishing efforts may conceal periods of strong fishing exploitation. To make the best use of the heterogeneous available data, we developed an inter-lake Delay-Difference stock assessment model within a hierarchical state-space framework (Meyer and Millar, 1999). It estimated the time series of the main population dynamics variables, including annual recruitment, spawner biomass, fishing mortality, and exploitation rates. With important fluctuations in productivity and fishing efforts in these lakes, negative impacts from exploitation may have occurred and could still be a problem. This multi-lake model allowed us to assess the status of past and current exploitation and whether these fisheries could benefit from fishing mortality reductions in the future.

2 Materials and methods

2.1 Studied lakes and fisheries

Lakes Geneva, Neuchâtel, Bourget, and Annecy are neighboring deep peri-alpine lakes situated in France and Switzerland (Fig. 1; Tab. 1). Each lake supports both commercial and recreational fisheries targeting a common large pelagic ecomorph of European whitefish that (1) lives in the pelagic zone below the thermocline, (2) feeds mainly on zooplankton and (3) spawns in winter near the shore. European whitefish refers to the species from the genus *Coregonus* living in the European lakes. This genus is known for its high genetic diversity and numerous species encountered in the peri-alpine lakes (De-Kayne *et al.*, 2022). Within this study the ecomorph is represented by two whitefish species: *Coregonus lavaretus* in Lake Bourget and Lake Annecy; and *Coregonus palea* in Lake Geneva and Lake Neuchâtel (Bernatchez and Dodson, 1994; Østbye *et al.*, 2005; Vonlanthen *et al.*, 2012; Alexander and Seehausen, 2021; Bourinet *et al.*, 2023).

These fisheries are characterized by similar fishing gears, seasonality and regulations. Fishermen deploy large drifting gillnets at appropriate depths according to the season, usually targeting age-3 to age-5 whitefish, corresponding to the age of

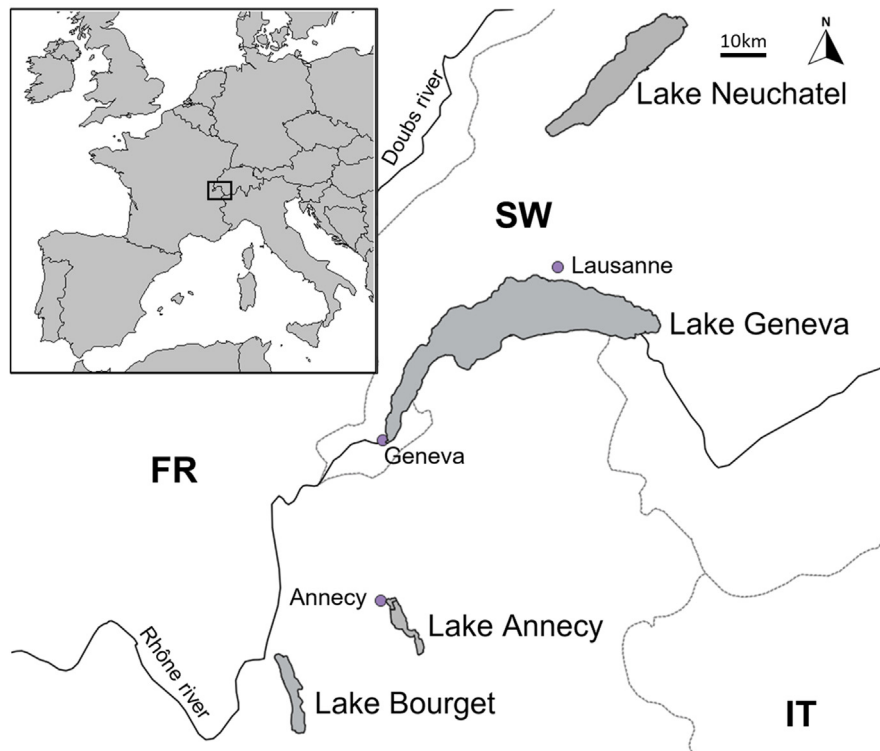


Fig. 1. Location of the four studied lakes. FR = France; SW = Switzerland; IT = Italy. Purple circles represent cities with over 100,000 inhabitants. Adapted from [Bourinet *et al.* \(2023\)](#).

Table 1. Main physical, trophic, and fishery characteristics of the four studied lakes between 2000 and 2020.

	Lake geneva	Lake neuchâtel	Lake bourget	Lake annecy
Surface (km ²)	581.3	218.3	44.5	27.6
Maximum depth (m)	309	152	147	82
Current trophic status	Meso-trophic ¹	Oligo-trophic ²	Oligo-mesotro-phic ³	Oligotr o-phic ⁴
Relative part of commercial fishery landings compared to total landings (expressed as the mean percentage of commercial fisheries landings over total landings)	99%	93%	93%	59%
Total annual landings ranges (t)	82.0; 761.0	16.5; 160.0	6.2; 78.4	5.3; 17.4
Number of commercial fishermen licenses in 2020	138	31	10	2
Fishing effort ranges, measured as the annual number of drifting nets*	10254; 54201	1109; 2381	399; 5700	648; 1605

¹Tran-Khac *et al.* (2021).

²OFEV (2016).

³Jacquet *et al.* (2022).

⁴Frossard *et al.* (2022).

*Except for Lake Neuchâtel, for which the fishing effort is measured as the number of fishing days targeting whitefish.

sexual maturity. Fishing season goes from January to October. Mesh sizes are defined by the local fisheries managers of each lake to target age-3 fish (age-4 fish for Lake Annecy). The total landings are dominated by commercial fishermen, although in Lake Annecy, recreational fisheries also significantly contribute to the annual landings ([Tab. 1](#)).

Over the period from 2000 to 2020, landings in these lakes have varied significantly, with a ratio between the minimum

and the maximum values ranging from 3.3 to 12.6 according to the lake ([Tab. 1](#)). The fishing effort, measured as the annual total number of drifting nets deployed on Lake Geneva, Lake Bourget, and Lake Annecy, or the number of whitefish fishing days on Lake Neuchâtel, varied with a ratio between the minimum and the maximum values ranging from 2.1 to 14.3. Fisheries statistics were then gathered from the local fisheries management organization of each lake to whom commercial

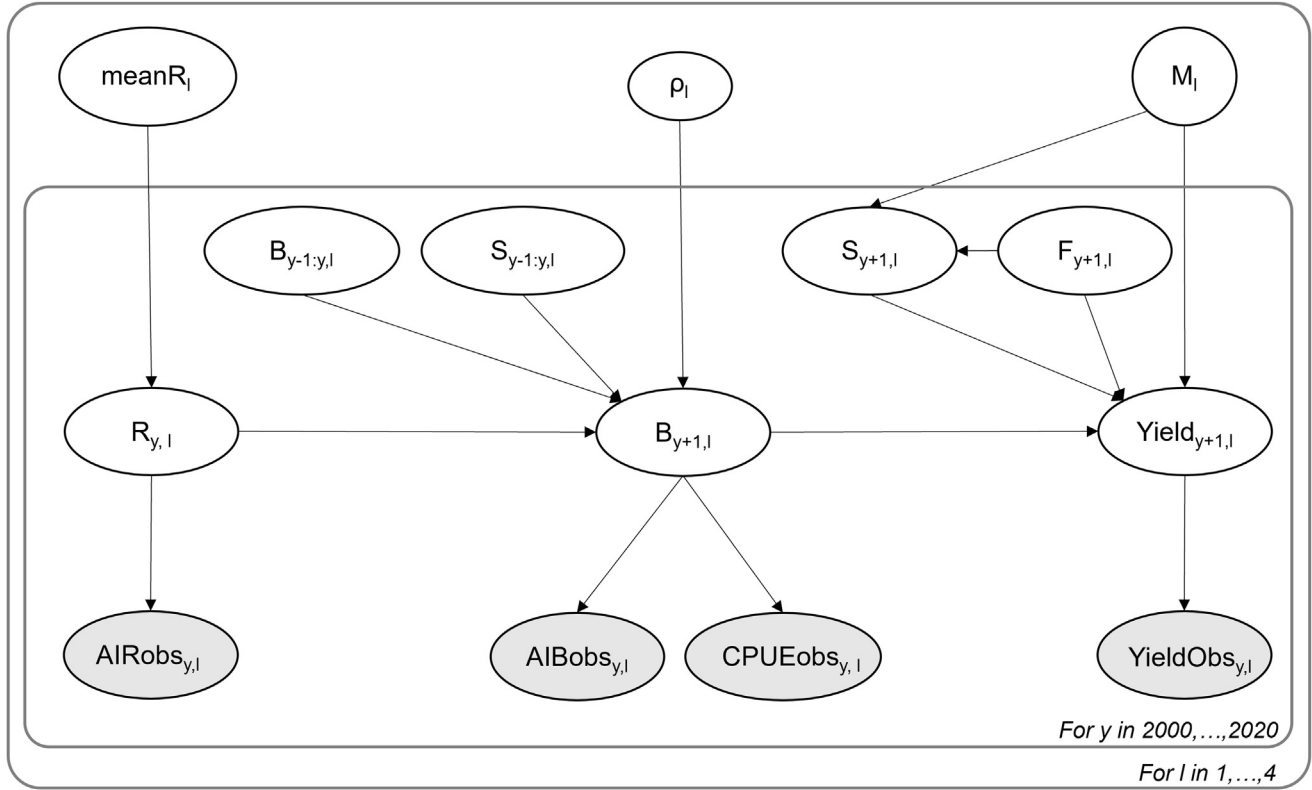


Fig. 2. Directed Acyclic Graph (DAG) of the adapted Delay-Difference Model. Observed data are represented in grey ellipses and unknown data in white ellipses. Arrows represent the causal relationship between two variables. Frames represent the repetition of structure over to lakes (l) or years (y). Parameters and variables are fully described in the text.

fishermen report their daily performance: from the Haute-Savoie and Savoie Direction Départementale du Territoire for the French territory and from each respective fishery service of the Swiss cantons (Genève, Vaud, Fribourg and Neuchâtel). These fisheries have been supplemented by traditional stocking activities, with contemporary stocking occurring on all lakes except Lake Annecy (Bourinet *et al.*, 2023).

2.2 Adapting a delay-difference model to the multi-peri-alpine lakes context

2.2.1 State model

A Delay-Difference model (Deriso, 1980; Schnute, 1985, 1987) was used to assess the effect of the fisheries in the four studied lakes (Fig. 2). Delay-Difference models can be seen as an intermediary that bridges the gap between simpler surplus production models or other data-limited models and the more complex, fully age-structured models that require complete and detailed age-structure of the landings (Hilborn and Walters, 1992). While not based on full age-structured dynamics and contrary to the surplus production model, the Delay-Difference model explicitly accounts for growth, recruitment, and natural mortality, three key processes of fish population productivity. Despite extensive monitoring of peri-alpine whitefish fisheries for years, data remain incomplete for the use of a fully age-structured model for the period between

2000 and 2020 (Appendix A). As such, the use of a Delay-Difference model within a hierarchical state-space Bayesian framework (Meyer and Millar, 1999) was considered the most suitable approach (Fig. 2). This choice facilitated the integration and enhancement of diverse incomplete data sources, accounting for the heterogeneous availability of information across various lakes while addressing the inherent stochasticity arising from both process and observation errors (Meyer and Millar, 1999; Parent and Rivot, 2012).

The Delay-Difference model is a stage-structured model, dividing the populations into recruits and post-recruits (*i.e.*, the first cohort fully exploited and the older cohorts, respectively). In our case study, recruits correspond to the age-3 group, except in Lake Annecy, which is composed of the age-4 group (Goulon and Guillard, 2022). The age structures of the annual landings were determined from scale readings of annual landing samples spread over the fishing season (Appendix B) (Bourinet *et al.*, 2023). The biomass equation used is adapted from the Deriso-Schnute Delay-Difference model (Deriso, 1980; Schnute, 1985, 1987) (Eq. (1)), starting from a von Bertalanffy weight model (Meyer and Millar, 1999), with p being the Brody growth coefficient:

$$B_{l,y+1} = Surv_{l,y} B_{l,y} + \rho_l Surv_{l,y} B_{l,y} - \rho_l Surv_{l,y} Surv_{l,y-1} B_{l,y-1} - \rho_l Surv_{l,y} Wrecr_l R_{l,y} + Wpost_l R_{l,y+1} \quad (1)$$

Table 2. Definition of the prior of the model parameters. MVNormal corresponds to the multivariate normal distribution, $\mathcal{U}$ to the uniform distribution, Γ to the gamma distribution, $\mathcal{N}$ to the normal distribution, and Beta to the Beta distribution.

Parameter	Distribution	Range
FL_Prior	MVNormal($\mu_p, \sigma_{p,p}$)	
M_l	$\exp(\text{FL_Prior [1]})$	
ρ_l	$\exp(-\exp(\text{FL_Prior [2]}))$	
$\text{tau}R_l$	$1/\exp(\text{FL_Prior [3]}^2)$	
$\text{mean}R_l$	$\mathcal{U}(2,1000)$	
$\text{tau}Alhydro$	$\Gamma(0.01,0.01)$	$\text{tau}Alhydro > 4$
$\text{tau}CPUE_l$	$\Gamma(0.01,0.01)$	$\text{tau}CPUE_l > 1$
$\text{tau}Yield_l$	$\Gamma(0.01,0.01)$	$\text{tau}Yield_l > 1$
$\text{tau}F_l$	$\Gamma(0.01,0.01)$	$\text{tau}F_l > 1$
$\text{catchability}CPUE_l$	$\mathcal{N}(1,10)$	$1.9 > \text{catchability}CPUE_l > 0.1$
$\text{catchability}Alhydro_l$	$\mathcal{N}(1,1)$	$1.5 > \text{catchability}Alhydro_l > 0.5$
initDensity_l	$\mathcal{U}(1,1000)$	
$\text{fact_ini_Biomass}_l$	$\mathcal{U}(0.80,1.2)$	
$B_{l,1}$	$\text{initDensity}_l \times \text{Surface}_l$	
$B_{l,2}$	$B_{l,1} \times \text{fact_ini_Biomass}_l$	
$\text{fact_ini_Recruitment}_{l,1}$	Beta(1,1)	
$\text{fact_ini_Recruitment}_{l,2:3}$	$\mathcal{U}(0.25,4)$	
$\text{Recruitment}_{l,1}$	$B_{l,1} \times \text{fact_ini_Recruitment}_{l,1}/W_{\text{post}l}$	
$\text{Recruitment}_{l,2:3}$	$\text{Recruitment}_{l,1:2} \times \text{fact_ini_Recruitment}_{l,2:3}$	
$F_{l,1}$	$\mathcal{U}(0, 1)$	

With p corresponding to the indices of the parameters which prior are taken from the Fishlife R package: M, K from von Bertalanffy model (for the growth parameters ρ), $\ln_margsd$ as the log of the standard deviation of the recruitment.

$$Surv_{l,y} = e^{-M_l + F_{l,y}}, \quad (2)$$

$$R_{l,y} \sim \log N\left(\text{mean}R_l, \frac{1}{\text{tau}R_l}\right). \quad (3)$$

where l is the lake and y corresponds to the year. $B_{l,y}$ is the biomass for a lake in a given year, and $Surv_{l,y}$ the survival rate, calculated from the annual natural mortality rates (M) (Tab. 2) and the annual fishing mortality rates (F) (Eq. (2)). The same F was assumed for both stages. The size selectivity of these gillnet fisheries is adapted on each lake to target the recruitment stage and the first age class of the post-recruitment stage. The Brody growth coefficient (ρ) represented the only growth parameters in this simplified set of equations. W_{recr} and W_{post} correspond to the mean weight of a fish from the recruitment stage and the post-recruitment stage, respectively (Appendix B). They were calculated on each lake based on the length-at-age data converted to weight-at-age through a length-weight relationship (Appendix B). As the length-weight relationships were found to be similar between lakes, the same length-weight relationship was used.

The annual recruitment $R_{l,y}$, corresponding to the abundance (in numbers) of the first cohort entering the fishery, follows a log-normal distribution (Eq. (3)) around a mean recruitment productivity value $\text{mean}R_l$, defined for each lake and expressed as a number of individuals per hectare. The studied ecomorph exhibits the same reproductive ecology, spawning in December on shallow gravel beds close to the shore. Thus, the mean recruitment is assumed to be relative to the surface area of the lakes. $\text{tau}R_l$ is the precision parameter of the log-normal distribution, integrating the stochasticity for the recruitment process (Tab. 2). A non-informative prior was assigned for $\text{mean}R_l$ (Tab. 2), as no recent information on the recruitment productivity was available for any of the lakes.

The yields were calculated for three stages s (Eq. (4)): the yield from the recruitment stage, the yield from the post-recruitment stage, and the total yield corresponding to the sum of the two previous partial yields.

$$Yield_{l,y,s} = B_{l,y,s} \times (1 - Surv_{l,y}) \times \frac{F_{l,y}}{M_l + F_{l,y}}, \quad (4)$$

where $B_{l,y,s}$ is the biomass of the respective stage s :

$$B_{l,y,1} = R_{l,y} W_{\text{recr}l}, \quad (5)$$

$$B_{l,y,2} = B_{l,y,3} - B_{l,y,1}, \quad (6)$$

$$B_{l,y,3} = B_{l,y}. \quad (7)$$

Values for parameters used in the main calculations were assigned from independent prior probability distributions. The Fishlife R package (Thorson *et al.*, 2017) was employed to generate suitable priors for life-history parameters based on life-history invariants. This package has compiled life-history traits for 32, 000 fish species and applied a multivariate model to predict distribution and standard deviation of several life-history traits of any fish species, including growth and mortality. It incorporated the taxonomy of the fish species, here the *Coregonus lavaretus*, to calculate priors for natural mortality M_l and the Brody growth coefficient ρ_l (Tab. 2).

The Fishlife package was also utilized to define the prior on τRi (Tab. 2). For other precision parameters (τ) used in the model to account for stochasticity in each process, a non-informative prior definition was applied based on an inverse-gamma distribution (Tab. 2).

Because of the iterative process in equation (1), there was a need to initialize the first two timesteps of biomass and the first three time-steps of recruitment, using a non-informative prior proportional to each lake surface (Tab. 2). The initial recruitment was forced to be inferior to the initial biomass.

The annual fishing mortality was defined using a random-walk process, as interannual variations are supposed to be low compared to the trends and shifts over the studied period. Thus, the first time-step of F was initiated using a non-informative prior (Tab. 2).

2.2.2 Observation model

The model was fitted on all available fishery-dependent and fishery-independent data. Total landings were almost always available for each lake and year. Staged-landings, corresponding to the respective landings from each stage, were scattered depending on the lakes (Appendix A). Staged landings were calculated from the respective proportion weighted by the respective mean weight of the fish from the recruitment stage (W_{recr}) and from the post-recruitment stage (W_{post}), respectively. To take into account stochasticity around the observation process, observed total and staged landings ($YieldObs_{l,y,s}$) were defined through a log-normal distribution (Eq. (8)).

$$YieldObs_{l,y,s} \sim \log N \left(\log(Yield_{l,y,s}) - \frac{0.5}{\tau Yield_l}, \frac{1}{\tau Yield_l} \right) \quad (8)$$

CPUE was used as an index of abundance (Ricker, 1940). While the use of CPUE in fishery modeling has been frequently debated (Richards and Schnute, 1986; Maunder *et al.*, 2006; Campbell, 2015), it is commonly utilized in studies where fishery-independent abundance estimates are missing (Gerdeaux and Janjua, 2009; Campbell, 2015; Lappalainen *et al.*, 2020). Moreover, no significant changes that could modify the catchability (q) of the fishery had occurred in the studied period (*e.g.*, same boats, technology and gears were used). Some years were missing for fishing effort at the beginning of the time series (*e.g.*, up to eight years for Lake Neuchâtel; Appendix A). CPUE was calculated only from commercial fishery statistics. While the recreational fishery can represent up to 60% of annual landings in Lake Annecy, the commercial CPUE was considered more reliable and accurate (Gerdeaux and Janjua, 2009). Still, recreational and commercial CPUE presented similar trends between 2000 and 2020. CPUE was assumed to be proportional to the true biomass (Ricker, 1940), and CPUE scaled to the mean CPUE followed a log-normal distribution (Eq. (9)).

$$\frac{CPUEobs_{l,y}}{CPUEobs_l} \sim \log N \left(\log \left(\frac{B_{l,y}}{B_l} \right) - \frac{0.5}{\tau CPUE_l}, \frac{1}{\tau CPUE_l} \right) \quad (9)$$

where $CPUEobs_{l,y}$ represents the observed CPUE values for lake l and year y , $CPUEobs_l$ represents the mean of $CPUEobs_{l,y}$ over the time period; $\tau CPUE_l$ is the precision parameter of these log-normal distributions, its prior is defined in Table 2; $qCPUE_l$ is the proportionality factor linking observed and estimated CPUE, assumed constant over the period and defined in Table 2. CPUE values were standardized by their mean ($CPUEobs_l$) to facilitate interpretation of abundance trends with consistent scales between lakes.

Abundance index (AI) values for both the recruits stage and the total biomass on each lake were extracted from hydroacoustic surveys, with surveys spanning one to nine years (Appendix A). The echosounders used were SIMRAD (Simrad Kongsberg Maritime AS, Horten, Norway) EY500, EK60 and EK80, using 70 or 120 kHz frequencies: previous analyses showed that results are independent of the equipment and from the two frequencies (Draštík *et al.*, 2017; Mouget *et al.*, 2019; Rautureau *et al.*, 2022). The same method (*i.e.*, sampling strategy, threshold, filtering, analysis software) was deployed on each lake to estimate fish abundance per hectare during the end of summer according to European standards (CEN, 2014) and described in previous publications (Guillard *et al.*, 2006; Girard *et al.*, 2020). In peri-alpine lakes when the thermocline is well established, the fish community is distributed above or below the thermocline: deeper and cooler habitats support salmonids and coregonids (Mehner and Schulz, 2002; Winfield *et al.*, 2008), while the upper pelagic area supports percidae and cyprinidae (Imbrock *et al.*, 1996; Guillard *et al.*, 2006; Deceliere-Vergès and Guillard, 2008; Probst *et al.*, 2009). So, fish detected under the thermocline in open water at the end of summer were assumed to be European whitefish, as Arctic charr (*Salvelinus alpinus*) is scarce and mainly found close to the bottom (Lemaire *et al.*, 2020). AI values from hydroacoustic surveys, expressed in biomass per hectare, were assumed to be proportional to the respective biomass reduced by the surface of the lake (Eqs. (10) and (11)).

$$AI Robs_{l,y-1} \sim \log N$$

$$\left(\log \left(\frac{R_{l,y} * qAlhydro_l}{Surface_l * \exp(-M_l) - \frac{0.5}{\tau Alhydro_l}} \right), \frac{1}{\tau Alhydro_l} \right) \quad (10)$$

$$AIBobs_{l,y} \sim \log N \left(\log \left(\frac{B_{l,y} * qAlhydro_l}{Surface_l - \frac{0.5}{\tau Alhydro_l}} \right), \frac{1}{\tau Alhydro_l} \right) \quad (11)$$

where $AIRobs_{l,y}$ and $AIBobs_{l,y}$ indicate the AI in $kg\ ha^{-1}$ taken from hydroacoustic data for the recruitment stage and total biomass, respectively; $qAlhydro_l$ represents the proportionality factor linking the observed values to the estimated values, common for both recruitment stage and total biomass, but lake dependent (Tab. 2); $Surface_l$ is the surface area of each lake; M_l is the annual natural mortality rate (Tab. 2); $\tau Alhydro_l$ is the precision parameter of these lognormal distributions, common across all lakes (Tab. 2).

2.2.3 Bayesian inference

The model was run in the JAGS software using Markov Chain Monte Carlo (MCMC) sampling. For the modeling process, the runjags (Denwood, 2016), rjags (Plummer, 2023) and coda (Plummer *et al.*, 2006) R packages were used. Three chains with different initial values were run in parallel with an adaptation phase of 50,000 iterations, a burn-in phase of 20,000 iterations and sampling one out of ten of the 10,000 following iterations. The convergence of the MCMC process was assessed using the potential scale reduction factors (Gelman and Rubin, 1992). The fitting of the model's estimates to the observation data was also evaluated by ensuring that all observations were encompassed within the 95% Credibility Interval (CI). The code were run using the R software (R Core Team, 2023) and the figures were generated using the ggplot2 package (Wickham, 2016).

2.3 Metrics for stock assessment status

The assessment of the past and present status of the four stocks involved the use of various metrics.

2.3.1 Exploitation rate (E)

The first indicator employed was the comparison of annual fishing mortality rates to annual natural mortality, with the former ideally not exceeding the latter (Gulland, 1970; Bousseba *et al.*, 2021). Thus, the ratio of the exploitation rate (Eq. (12)) should not exceed 0.5, representing roughly the MSY target (Pauly, 1985; Bousseba *et al.*, 2021).

$$E_{l,y} = \frac{F_{l,y}}{M_l + F_{l,y}}. \quad (12)$$

The fishing mortality rate was used as a proxy for exploitation intensity. Given the assumption of constant natural mortality rates over the study period, variations in fishing mortality served as direct indicators of total mortality, survival rates, and exploitation rates as estimated by the model.

2.3.2 Stage structure

The stage structure of the landings provides informative insights. Well-managed fisheries often target older and larger fish (Griffiths *et al.*, 2023), and a higher proportion of post-recruitment fish in landings indicates the presence of older fish in the population. These older individuals are better spawners, contributing to higher egg production and larger larvae (Berkeley *et al.*, 2004; Birkeland and Dayton, 2005).

2.3.3 Remaining biomass $B/B_{f=0}$

Another diagnostic was to compare biomass estimates from the complete model (B) with those in a scenario assuming no fishing exploitation between 2000 and 2020 ($B_{f=0}$). Taking the outputs estimated by the model for parameters and latent variables time series, the biomass time series can be calculated under a no-fishing scenario by replacing the fishing mortality time series with zero. The ratio of annual biomass estimated by the complete model divided by the annual biomass estimated

under this hypothetical no-fishing scenario ($B/B_{f=0}$) is equivalent to a measure regularly used in fishery management: the Spawning Potential Ratio (SPR) (Goodyear *et al.*, 1993; Slipke *et al.*, 2002; Walters and Martell, 2004; Hordyk *et al.*, 2015).

3 Results

The model exhibited good convergence, with potential scale reduction factors from Gelman and Rubin's convergence diagnostic all below 1.043. Most of the observed values fall inside of the CI range, and the posterior distribution confirms a good fit of the model (Figs. 3 and 5). However, differences in trends between observed CPUE and AI from hydroacoustic seem to cause residual patterns. Moreover, high interannual variations in landings can be hard to match for the model, as is the case for staged landings at Lakes Neuchâtel and Bourget.

On Lake Geneva, a sudden increase in total biomass was noted in 2009 (Fig. 3a), corresponding to a high recruitment that year (Fig. 3b). Lake Bourget displays a similar biomass trend (Fig. 3a) but is associated with strong recruitment after 2009 (Fig. 3b). The biomass in Lake Annecy increased after 2010, as indicated by observed CPUE. This increase did not appear to correspond to substantially greater numbers of recruits (Fig. 3b). Lake Neuchâtel's total biomass was rather stable but decreased abruptly at the end of the time series, reaching very low levels by 2017 (Fig. 3a), which is concurrent with a decline in mean recruitment after a prolonged period of strong interannual variations (Fig. 3b).

The annual values of fishing mortality rates exhibit a large CI around the median of the estimates. The trends of fishing mortality presented in Figure 3c as the annual fishing mortality estimates, divided by the mean of the respective simulation, are more accurate with a narrower CI. Fishing mortality rates on Lake Annecy continuously decreased over the period, experiencing a significant drop around 2010. Annual fishing mortality rates are the smallest on this lake, with an average median posterior estimate of 0.19 year^{-1} . On Lake Neuchâtel, fishing mortality steadily decreased with an average median posterior estimate of 0.28 year^{-1} . More variability is observed for Lake Geneva and Lake Bourget, with high fishing mortality rates on both lakes in the most recent years, surpassing the natural mortality rates (Tab. 3). Lake Geneva reached 0.81 year^{-1} in 2017, and Lake Bourget 0.55 year^{-1} at the end of the time series.

All four lakes exhibited an initial decrease of the remaining biomass ratio $B/B_{f=0}$ between 2000 and 2006 (Fig. 4). This finding supports the basic notion that fishing removal directly reduces the biomass of whitefish. Subsequently, two distinct trends emerge among the four lakes. In the cases of lakes Geneva and Bourget, the increase in the ratio $B/B_{f=0}$ corresponds to the increase in total biomass previously observed in 2009 (Fig. 3). Afterwards, both lakes experienced a steady decrease in this ratio until the end of the studied period, although Lake Geneva showed an increase in 2020. The Lake Bourget ratio dropped to 0.44, and the Lake Geneva ratio reached its lowest value of 0.23 in 2019. Conversely, for Lake Neuchâtel and Lake Annecy, a stable trend appears, with the ratio $B/B_{f=0}$ fluctuating around 0.75.

Comparing the mean recruitment over the period relative to the surface area of each lake provides insights into their overall

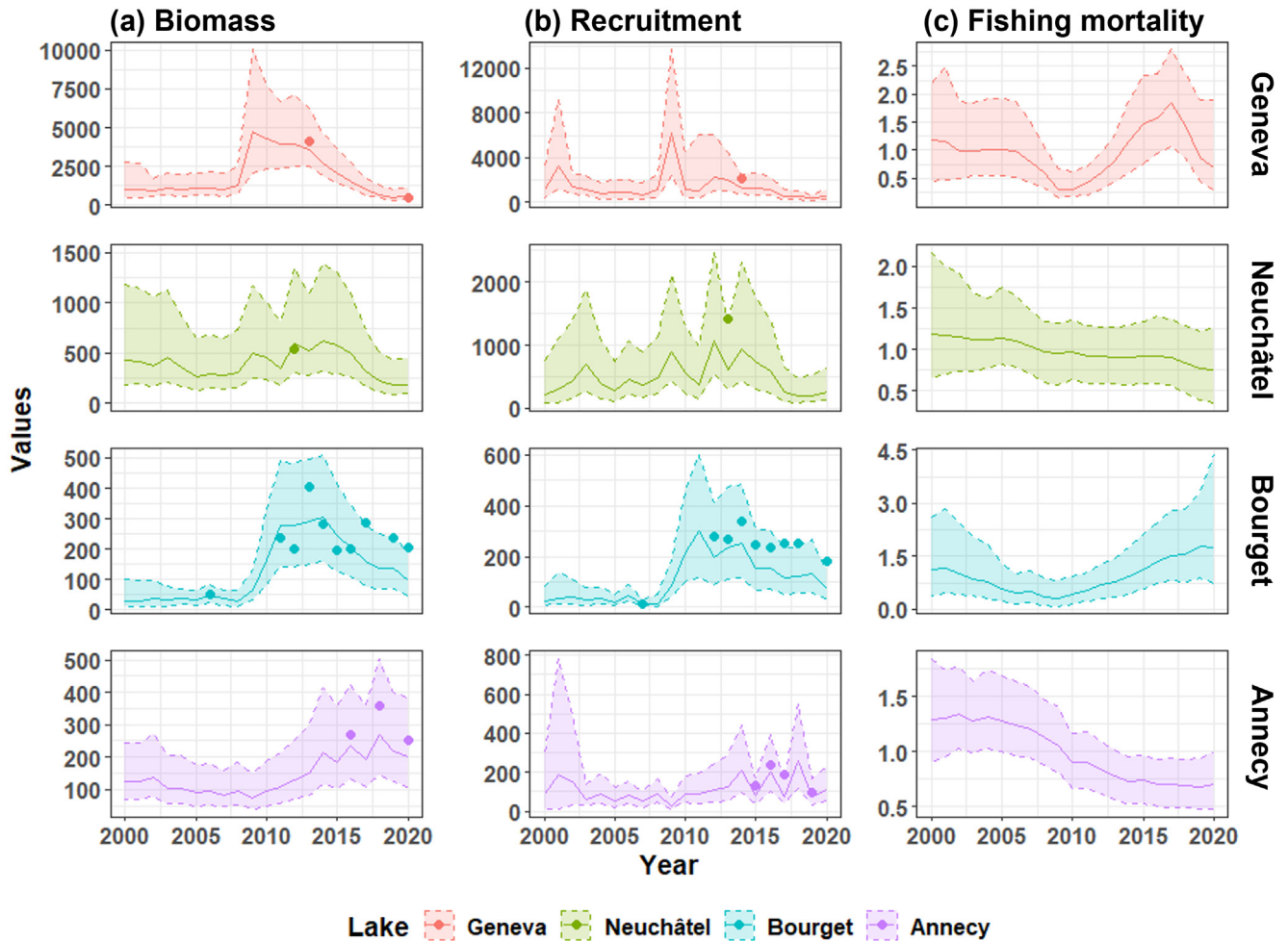


Fig. 3. Estimated outputs from the model for (a) total biomass (tons), (b) recruitment (in number of 1000 individuals) and (c) trends in fishing mortality (corresponding to the ratio of the annual F over the mean F from the period). Lines represent the median of posterior estimates, while the shaded areas denote the 95% CI (Credibility Interval). The dots represent observed values after conversion using the model parameter outputs; for both the biomass and recruitment plots, these correspond to the AI (Abundance Index) obtained from the hydroacoustic data.

Table 3. Posterior statistics of the three parameters.

Parameter	Lake	Median posterior estimate	Standard deviation posterior estimate
Brody growth coefficient (ρ)	Geneva	0.754	0.021
	Neuchâtel	0.743	0.021
	Bourget	0.742	0.021
	Annecy	0.760	0.020
Natural mortality rates (year^{-1})	Geneva	0.400	0.072
	Neuchâtel	0.625	0.092
	Bourget	0.479	0.069
	Annecy	0.351	0.047
Mean Recruitment productivity (ind/ha)	Geneva	17.3	5.41
	Neuchâtel	11.3	4.60
	Bourget	17.9	6.34
	Annecy	23.9	8.00

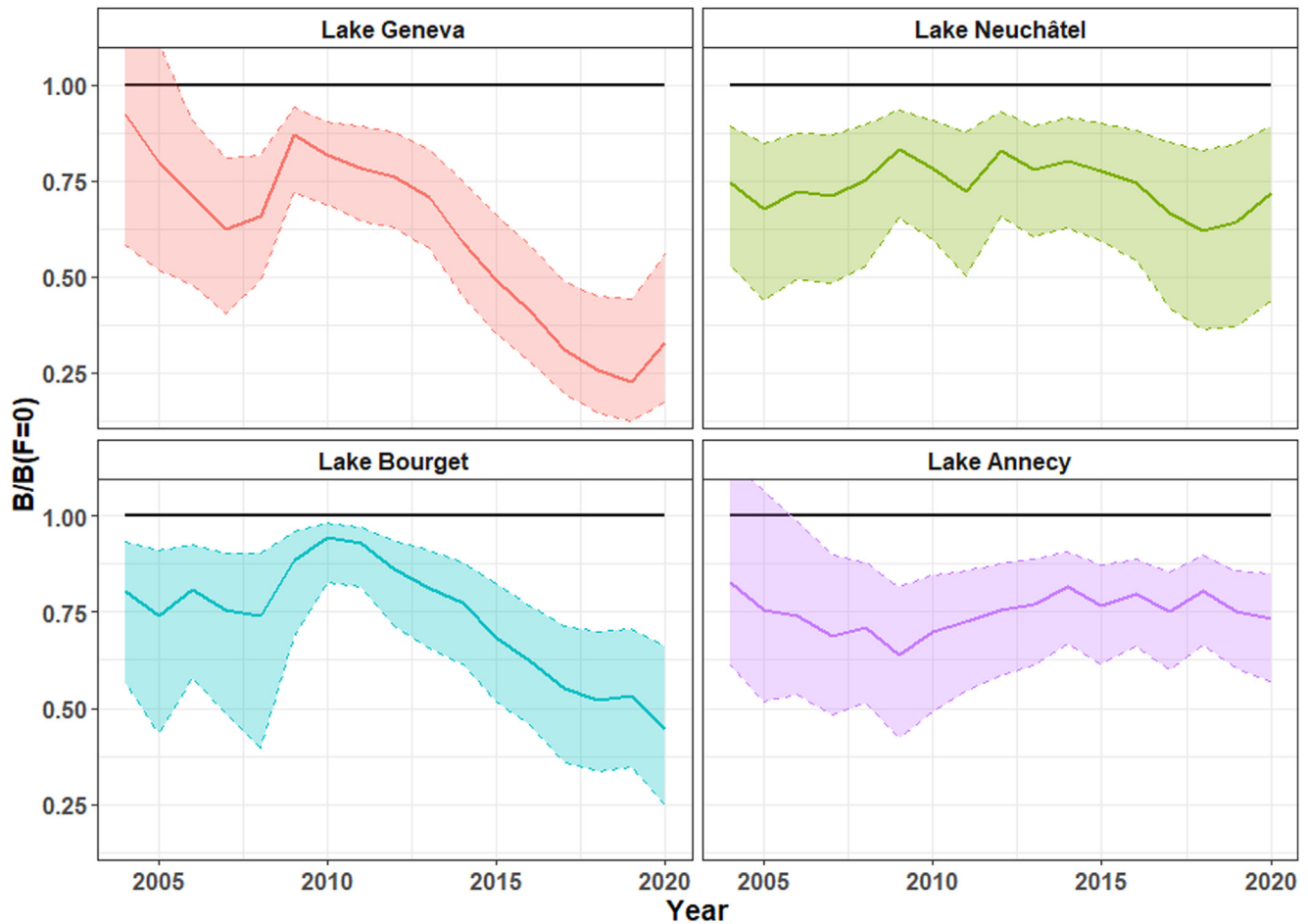


Fig. 4. Ratio of the biomass estimated by the model (B), divided by the biomass estimated under a no-fishing scenario ($B_{F=0}$). Lines represent the median of posterior $B/B_{F=0}$ estimates; the shaded areas denote the 95% CI (credibility interval).

productivity between 2000 and 2020 (Tab. 3). Lake Annecy emerges as the most productive of the four lakes, with Lake Neuchâtel being the least productive. Lake Geneva and Bourget exhibited similar intermediate values.

Both natural mortality rates and the mean recruitment productivity exhibited different posterior distributions between lakes (Tab. 3). Lake Annecy was the most productive lake for recruitment and displayed the lowest natural mortality rate. Conversely, Lake Neuchâtel had the highest natural mortality rates and the lowest recruitment productivity. Lake Geneva and Lake Bourget had similar outputs for both parameters. For natural mortality rates and the mean recruitment productivity, the posteriors standard deviations were lower than the prior ones, and their mean values were distinct between lakes, indicating that the priors were effectively updated by the information in the data. In contrast, the posterior distributions for the Brody growth coefficient ρ were similar across lakes and not markedly different from the prior distribution (Tab. 3).

The estimates for total landings fit well with the observed landings (Fig. 5). For lakes Geneva, Neuchâtel and Annecy, recruitment landings displayed important interannual variations (Fig. 5a), probably reflecting interannual recruitment variations. Post-recruitment landings were more stable on these lakes (Fig. 5b), with trends very similar to the ones for

total landings on Lake Geneva and Lake Annecy (Fig. 5c). High interannual variations for observed values between post-recruitment and recruitment on Lake Neuchâtel were hard to match for the model, with some observed annual data out of the CI range (Fig. 5). Lake Bourget exhibited the same pattern for both staged landings and thus for total landings (Fig. 5), with first a stable low landings period, then a sudden increase in 2009 and then a steady slow decrease.

4 Discussion

Whitefish fisheries across the world have experienced significant landings fluctuations, influenced by both interannual environmental changes (Kangur *et al.*, 2020; Bogdanov *et al.*, 2021) and variations in stock productivity due to modifications in ecosystem functioning (Rook *et al.*, 2022) or fishery overexploitation (Sarvala *et al.*, 2020). Bourinet *et al.* (2023) identified links between whitefish abundance and environmental variables in Lakes Geneva, Neuchâtel and Bourget, revealing inter-lake differences. Conversely, Lake Annecy demonstrated a negative relationship with fishing intensity. The authors pointed out the need for a more detailed analysis of the relationship between whitefish population dynamics and fishing activity. The application of a multi-lake Bayesian Delay-Difference model provided detailed metrics

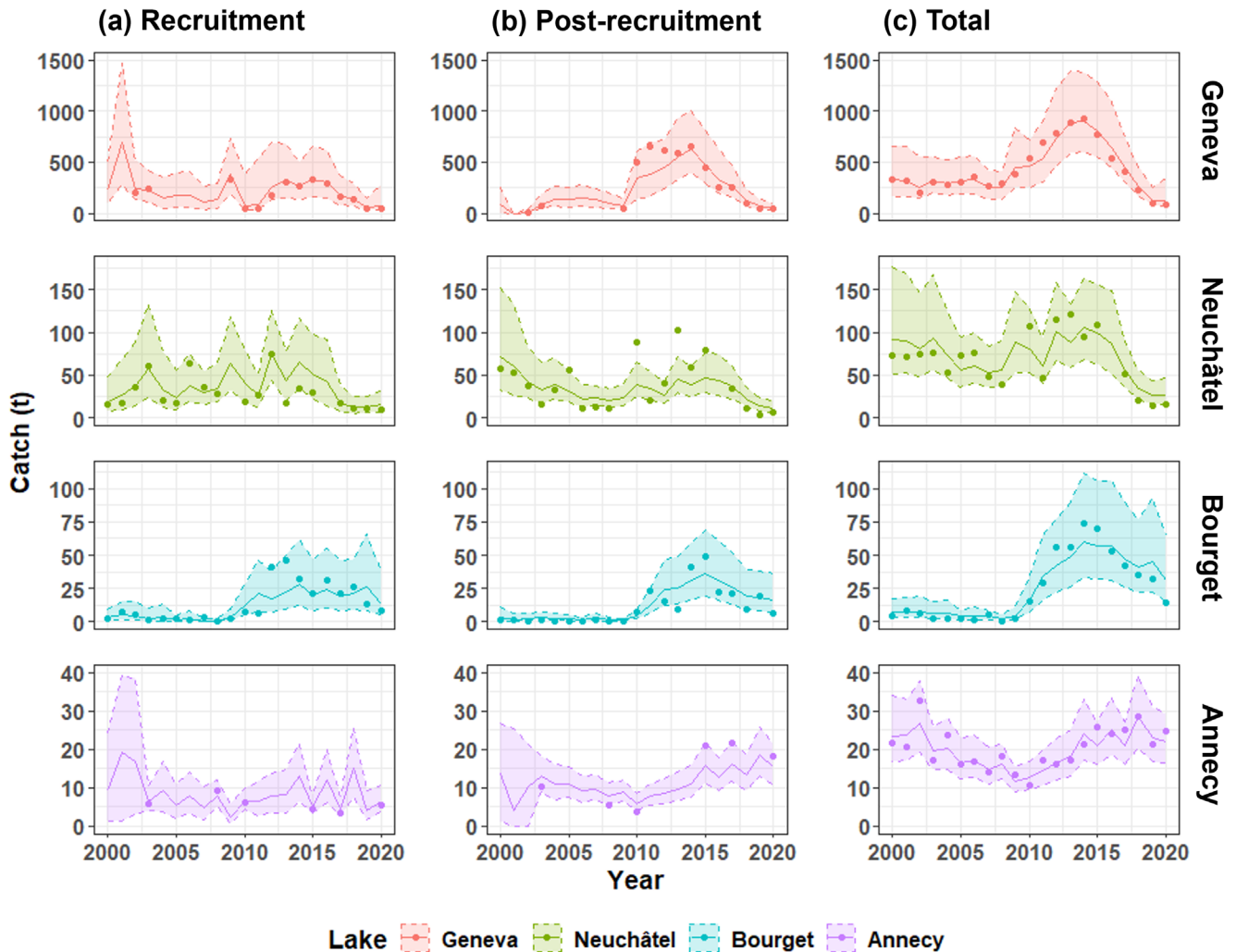


Fig. 5. Estimated outputs in tons (t) of (a) recruitment landings, (b) post-recruitment landings and (c) total landings. Lines represent the median of posterior landings estimates; the shaded areas denote the 95% CI (credibility interval); the dots are the observed values of landings.

related to population dynamics in each lake. It leveraged diverse data sources despite some gaps in the fisheries data.

4.1 Comparison of population dynamics between lakes

Significant synchronicity in both total landings and CPUE was described in these lakes over the 2000–2020 period by Bourinet *et al.* (2023). The period from 2013 to 2020 was marked by a continuous decrease in whitefish biomass in Lake Geneva, Neuchâtel, and Bourget. No common environmental driver could explain this abundance synchrony. Similarly, the present work did not reveal any similar population dynamics variable which could account for this synchrony. The estimated biomass and landings are consistent with these observations, but the time series of recruitment, fishing mortality rates and stage-structured landings were dissimilar between lakes. The parameters of the model do not show inter-lake similarities, except for the Brody growth coefficient (ρ) that exhibits close posterior distributions among lakes, similar to the prior definition. As determined from

the Fishlife package, considering the life-history traits of *Coregonus lavaretus*, the Brody growth coefficient might be close to the actual value, given all the studied lakes harbor a common ecomorph. However, it seems more plausible that the model did not use ρ for biomass estimates, with no significant deviation from the prior distribution. Variations in biomass estimates were most probably driven by annual survival rates instead (Eq. (1)). It might be because the growth differences are already incorporated through the mean weight of the two stages. It could also be due to the informative prior definition, already close to the actual values.

Interestingly, all four lakes exhibited distinct values of recruitment, landing structure, fishing mortality dynamics, and other parameters. The natural mortality rates aligned with values reported in other studies on the same species, ranging between 0.2 and 0.5 depending on the local context and the species (Auvinen, 1987; Linløkken, 1995; Vainikka *et al.*, 2017). As anticipated for the lake with the highest age at maturity and the slowest growth (Pauly, 1980; Beauchamp *et al.*, 2004; Gislason *et al.*, 2010; Swain, 2011), Lake Annecy exhibited the lowest mortality rates. In contrast, Lake

Neuchâtel had higher natural mortality rates, potentially due to its whitefish population having a shorter lifespan (Beverton and Holt, 1959; Hewitt and Hoenig, 2005). This could also be influenced by greater predation, considering the large colonies of cormorants (*Phalacrocorax carbo*) in Lake Neuchâtel (Keller and Müller, 2012). For modeling purposes, we had to constrain natural mortality rates to be constant over time, a common assumption in fisheries stock assessment models (Lorenzen *et al.*, 2016). However, it is recognized as not always accurate, and its variability should not be overlooked (Vetter, 1988).

4.2 Indicators of fishing pressure impact

The adapted model used in this study represents an innovative approach, providing insights into the effects of fisheries on European whitefish stocks. Such valuable information complements the qualitative analyses of landings and fishermen's feedback currently used to manage the fisheries. A negative impact of fishing exploitation was observed in three out of four lakes over the period 2000–2020, based on three complementary indicators. Higher fishing mortality rates correspond to elevated total mortality and exploitation rates, underscoring the significant impact on whitefish stocks (Rochet and Trenkel, 2003; Keskar *et al.*, 2017). The low contribution of older fish (assessed through post-recruitment) in total landings reveals a low proportion of post-recruitment in the total biomass, as the model assumed equal F for both stages. This may rather reflect unstable fisheries sensitive to the high instability of recruitment abundance (Griffiths *et al.*, 2023). High exploitation impact is also revealed with low remaining biomass ratio $B/B_{F=0}$, indicating that the biomass estimated by the model is low compared to the hypothetical situation of a no-fishing scenario. This ratio is equivalent to the SPR frequently used in fisheries science, for which different thresholds have been debated with different reference points (Clark, 2002; Legault and Brooks, 2013; Larijani *et al.*, 2024). As it depends on the management goal and of the species, we did not pick a specific limit, but opted for working qualitatively with this indicator.

Fisheries strategies vary based on the lake and population dynamics. The increase in total landings on Lake Geneva and Lake Annecy seems to be mainly supported by an increase in post-recruitment landings and lower fishing mortality rates. These observations suggest that efforts should be made to protect the recruitment stage to increase survival rates. Multi-cohort populations, coupled with the conservation of older fish, are known to enhance population stability. Older fish typically possess better spawning capacities, resulting in higher quality and quantity of larvae (Scott *et al.*, 2006; Hixon *et al.*, 2014). The presence of several cohorts and old fish in a population not only contributes to population growth but also increases resilience and resistance to natural and anthropic stressors (Hsieh *et al.*, 2010; Charbonneau *et al.*, 2022). Lower fishing mortality rates thus play a crucial role in this dynamic by directly enhancing the survival rates of recruits, leading to a higher abundance of post-recruitment stages in subsequent years (Charbonneau *et al.*, 2022).

4.3 Fishing pressure impact and status of the fisheries

For Lake Annecy, past overexploitation has already been discussed in Bourinet *et al.* (2023). Significant regulation changes occurred in 2011, including reduced daily retention limits for the recreational fishery, a halving of the number of commercial fishermen between 2007 and 2010, and a reduction of the nets' mesh size (Goulon and Guillard, 2022). This management resulted in a substantial overall reduction in fishing efforts. A subsequent steady increase was observed in both biomass and landings, suggesting that the stock was overexploited before 2011 (Rosenberg, 2003). The ratio $B/B_{F=0}$ was stable after 2010 at a high value. The Lake Annecy whitefish fishery appeared to be in good status at the end of the time series. Because fishing mortality rates were well below natural mortality rates, there was high productivity relative to its small surface area, and only a small fraction of the biomass was missing compared to the no-fishing simulation. This high productivity is particularly noteworthy considering the lake's oligotrophic nature, where conventional wisdom might anticipate lower whitefish productivity due to bottom-up control (Downing *et al.*, 1990; Müller *et al.*, 2007). Lake Annecy is known as an oligotrophic lake with good trophic efficiency and notable high productivity, as reported in two Ecopath models (Janjua and Gerdeaux, 2009; Lemaire *et al.*, 2020). It is interesting to highlight that our biomass estimates are consistent with the ones obtained through these models, which ranged between 74 t and 143 t.

On Lake Geneva, the reduction in fishing mortality estimated after 2006 was followed by an increase in both biomass and total landings, driven by increased post-recruitment biomass and landings. It shows the negative impact of exploitation at the beginning of the study period, followed by a rapid recovery. At the same time, an increase in the $B/B_{F=0}$ ratio was observed. Such an increase cannot be solely attributed to variations in exploitation. It seems closely tied to abundant annual recruitment. Thus, one or several environmental factors seem to be the most plausible drivers of high recruitment. This sudden increase in biomass starting in 2009 corresponds to the integration of the abundant 2006 cohort into the stock that year (Anneville *et al.*, 2017). The subsequent high abundance of whitefish with a gradual decrease in the following years appears to be driven by the survival of the 2006 cohort, as total mortality rates were low for this cohort. Low $B/B_{F=0}$ ratio values on Lake Geneva after 2013 might suggest major impacts from fishing exploitation on fish biomass, removing a large part of the potential stock abundance. The three recent consecutive years of decreasing fishing mortality up to 2020 may be the consequence of a reduced fishing effort after several years of decreasing landings or an effect of the recent fishery regulation changes (Goulon *et al.*, 2023). These hypotheses could explain the sudden increase in the ratio $B/B_{F=0}$ in 2020.

Lake Bourget's whitefish population showed low recruitment before 2009; then, it suddenly increased to a higher level. This sudden shift suggests an important change in ecosystem functioning. Lake Bourget experienced intense eutrophication and re-oligotrophication processes over the last decades, with

total phosphorus concentrations dropping constantly since 1980 and going below the $10 \mu\text{g L}^{-1}$ threshold around 2010 (Eckmann *et al.*, 2007a; Jacquet *et al.*, 2014a). This total phosphorus concentration decrease drove changes in phytoplankton and zooplankton composition and abundance (Jacquet *et al.*, 2014b; Moiron *et al.*, 2021). This shift may have impacted whitefish population dynamics through a bottom-up effect (Müller *et al.*, 2007), explaining upward whitefish trends after 2009. This hypothesis is also supported by the increase in $B/B_{F=0}$ in 2009: as the only difference between B and $B_{F=0}$ is the absence of fishing removal in the latter, an increase of this ratio implies an environmental influence. It could be induced by the high spring daphnia abundance observed in these years (Perga and Lainé, 2010; Jacquet *et al.*, 2023), as a positive relationship was found in Bourinet *et al.* (2023). Still, important changes in management tactics also occurred in 2008 and 2009 and the ensuing changes to fishing effort cannot be ignored (Jacquet *et al.*, 2022). Starting in 2017, the biomass estimated by the model significantly deviated from the observed hydroacoustic AI, which displayed a more stable trend. During recent years, the catch for commercial fishermen has decreased. A sudden shift in the growth of European whitefish has been observed (Jacquet *et al.*, 2023), with age-3+ whitefish still below the minimum required size for commercial fishermen. Thus, the overall biomass remains high, with a substantial number of small fish not integrated into the fishery. Our model did not account for variations in growth, and such sudden shifts are likely challenging to model.

In Lake Neuchâtel, after a continuous decrease in fishing mortality rates, there was an acceleration in the last three years, along with a drop in biomass, recruitment and landings. The decrease in the fishing mortality rates resulted from a decrease in fishing effort, as the fishery became unprofitable with critically low total whitefish biomass levels. However, the ratio $B/B_{F=0}$ remained stable, with only a slight increase. This means that, without any fishing removal, the abundance would have followed the same declining trend, according to other model outputs. This is particularly evident in the recruitment time series, reflecting the interannual variability of reproduction success. One or several environmental parameters have likely reached threshold values, hindering successful egg deposition, development, or larvae survival. Winter water temperature has been identified as negatively correlated with whitefish abundance on Lake Neuchâtel (Bourinet *et al.*, 2023). The mean winter water temperatures exhibited a sudden increase in 2014, with all subsequent values (except 2017) surpassing the maximum recorded temperature between 2000 and 2013. Despite Lake Neuchâtel being the coldest of the four studied lakes, the local population of pelagic European whitefish might be facing excessively high winter temperatures, restricting reproduction success (Brooke, 1975; Cingi *et al.*, 2010; Stewart *et al.*, 2021). This lake is also managed with high stocking intensity, releasing millions of just-hatched larvae each spring. However, it does not seem to offset the natural reproduction failure, suggesting that other environmental parameters affecting post-hatch stages may also be at play. It is worth noting that Lake Neuchâtel has the least accurate and the most limited data among the four lakes studied. The fishing effort is recorded as the number of whitefish fishing days, whereas the other lakes have a more accurate measure of the

annual number of drifting nets deployed. Furthermore, Lake Neuchâtel lacks more annual data, displaying the shortest CPUE time series and only one hydroacoustic observation. While the hierarchical framework helps transfer information from data-rich to data-poor lakes, Lake Neuchâtel remains more susceptible to bias than the others. It highlights the importance of ensuring accurate long-term monitoring of fisheries statistics and scientific surveys, as the invaluable hydroacoustic data provide a comparable AI between lakes and across time. The method applied to the four lakes was the same, with a common error process and similar stochasticity. These data ensure the absolute productivity comparisons between the lakes. Consequently, instituting an annual survey encompassing all four lakes would be highly beneficial for enhancing the accuracy and completeness of the data. Such a comprehensive survey could further refine our understanding of the population dynamics and productivity variations across the peri-alpine lakes.

To conclude, fishing exploitation has been shown as a crucial driver of European whitefish population dynamics in peri-alpine lakes, with periods of negative impacts on population abundance over the last two decades. However, it is essential to also acknowledge the significant influence of environmental factors, both direct and indirect (Lynch *et al.*, 2015; Myers *et al.*, 2015; Zischke *et al.*, 2017; Stewart *et al.*, 2021). In a study by Bourinet *et al.* (2023), direct sensitivity to spring daphnia abundance in Lake Geneva and Lake Bourget, as well as winter surface temperature in Lake Neuchâtel, was highlighted. However, the environmental impact on these populations is likely a complex interplay of multiple factors, including environmental and anthropic variables along with fishing exploitation (Pepin, 2016; Bai *et al.*, 2022). The model could benefit from integrating these factors. Recruitment could be delineated by a Stock-Recruitment Relationship (SRR) that accounts for the influence of selected environmental variables (Chen and Irvine, 2001; Heikinheimo *et al.*, 2014; Bai *et al.*, 2022). In addition, it would be relevant to incorporate stocking effects into the SRR, given its historical significance as a management measure in three of the four lakes, Lake Annecy being the only lake without whitefish stocking since 2000. Although the inclusion of a stocking parameter in a SRR has not been extensively studied, some insights have been gleaned over the last few decades through peri-alpine lake-specific, *ad hoc* studies (Eckmann *et al.*, 2007b; Champigneulle and Cachera, 2008; Wedekind *et al.*, 2022; Baer *et al.*, 2023). This expanded model would offer a more comprehensive understanding of the interplay between environmental factors, stocking practices, fishing exploitation and European whitefish population dynamics. It could assist peri-alpine lake whitefish fishery managers by testing fishing scenarios and making short-term predictions of recruitment and abundance.

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Appendix A: Available observed data

Table A1 displays the number of annual data available for our study and used as observed data in the model.

Appendix B: Length-weight relationships (LWR) and data

We used available individual length and weight data on Lake Annecy and Lake Bourget from standardized scientific sampling surveys (Tab. B1) EN 14757 (Appelberg, 2000). This type of data allows information on fish below the legal catch size. On Lake Annecy, data were completed with data collected from professional fishermen as part of the fisheries monitoring program. We added data from another lake, Lake Aiguebelette, a smaller peri-alpine lake situated a few kilometers away from Lake Bourget, where the same type of data was available on *Coregonus lavaretus*. Furthermore, on Lake Annecy, the database was completed with data collected from professional fishermen as part of the fisheries monitoring program. Data required were not available for Lake Geneva and Lake Neuchâtel. The three length-weight relationships (LWR) showed very close parameter values (intercept and slope of the equation value) (Fig. B1 and Tab. B1). These relationships were also compared to the 11 relationships gathered on the Fishbase website (Froese and Pauly, 2024), with similar parameter values between this study and the value estimated as reliable on Fishbase. So, we decided to use only one length-weight relationship for all studied lakes, assuming that the relationships for these lakes are similar (Fig. B1). We picked the relationship derived from Lake Annecy data, as it was the most complete dataset.

On each lake, length-at-age was determined from scale reading and back-calculation data. The scales used in this study came from the COLISA collection (DOI: <https://doi.org/10.15454/D3ODJM>) collected as part of the monitoring of landings by professional fishermen in Lake Geneva, with one sample taken each month. In the case of Lake Annecy, the scales came from monitoring of landings by professional fishermen, carried out directly by scientists or by fishermen as part of participatory science approaches. On Lake Neuchâtel, scales were collected monthly for growth monitoring by scientists. The data range is 2002–2020 for Lake Geneva, 2001–2020 for Lake Neuchâtel, 1989–2020 for Lake Bourget, and 2003–2020 for Lake Annecy. The steps for determining ages are detailed in Hamelet *et al.* (2022).

We pulled all data covering the studied period to get an average length of the age dataset. Then, it was converted in weight-at-age through the length-weight relationship. This way, we could calculate directly the weight of the two stages:

Table A1. Number of annual observed data used in the model, covering the period between 2000 and 2020.

	Lake geneva	Lake neuchâtel	Lake bourget	Lake Annecy
Catch Per Unit of Effort (CPUE)	19	15	16	21
Total landings	21	19	21	21
Stage-structured landings	14	19	21	6
Hydroacoustic Campaigns used to calculate Abundance Indices	2	1	10	3

Table B1. Length-weight relationship for *Coregonus lavaretus* collected during gillnetting standardized surveys and with additional data from fisheries for Lake Annecy, based on the equation $\log(W) = \log(a) + b \log(L)$ (a : intercept and b : slope of the equation). Sample size (N); length (L) in mm; weight (W) in g; minimum (min) and maximum (max) of L & W ; Standard error (SE); coefficient of determination (r^2), p is the significance of regression (p) with p significant at <0.05 .

Species/Lake	Coregonus lavaretus	Coregonus lavaretus	Coregonus lavaretus
	Lake aiguebelette	Lake bourget	Lake annecy
Data collection dates	2009, 2014, 2020	2010–2022	2000–2021
N	240	449	4767
$L_{\min-\max}$ (mm)	104–437	101–471	67–570
$W_{\min-\max}$ (g)	6.0–900.0	6.6–816.2	2.8–1850.0
a	3.26	3.14	3.15
b	0.003	0.004	0.004
$SE(a)$	0.02	0.02	0.01
$SE(b)$	0.06	0.04	0.02
r^2	0.99	0.99	0.98
p	$p < 0.001$	$p < 0.001$	$p < 0.001$

W_{recr} for the mean weight of the recruitment stage, and W_{post} for the mean weight of the post-recruitment stage (Tab. B2).

Appendix C Fitting of biomass trends estimates with CPUE time series

The CPUE (Catch Per Unit of Effort) scaled by the mean CPUE was supposed to be proportional to the total biomass trend, *i.e.*, the total biomass scaled by the mean of the total biomass. The fit of the biomass estimate trends is presented in Figure C1.

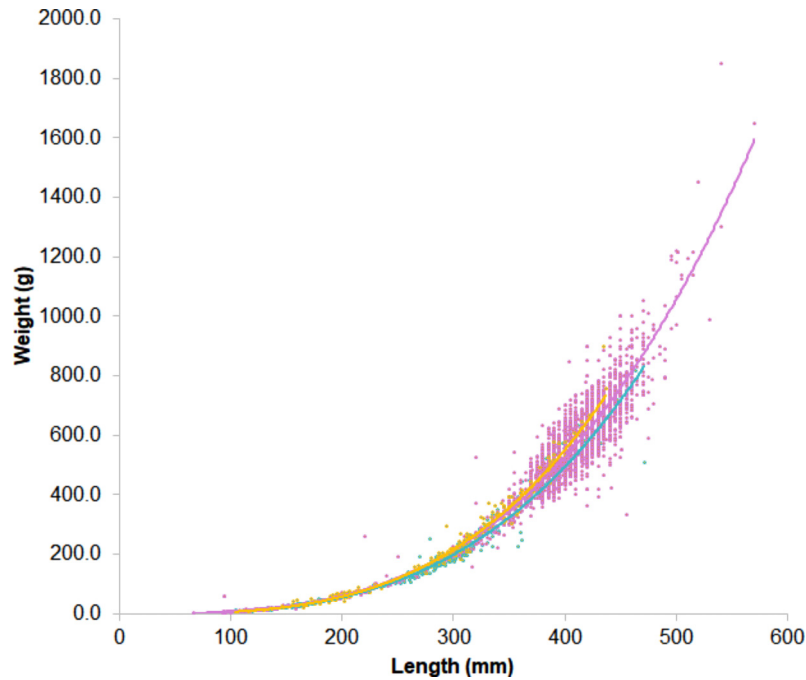


Fig. B1. Length-weight relationship fitted on each lake dataset. Dots are observed values; lines are the statistically fitted relationship. Yellow = Lake Aiguebelette; Blue = Lake Bourget; Purple = Lake Annecy.

Table B2. Mean weight at recruitment (W_{recr}) and post-recruitment (W_{post}) stages in grammes for the four studied lakes.

Lake	W_{recr}	W_{post}
Geneva	510.4	644.5
Neuchâtel	343.8	403.7
Bourget	439.9	561.5
Annecy	474.3	539.9

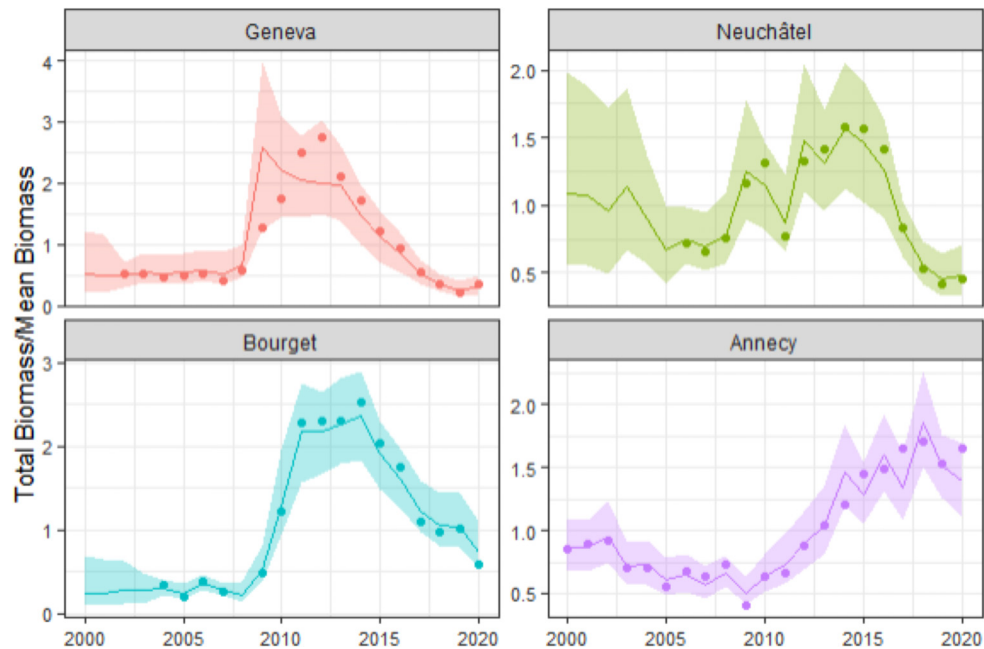


Fig. C1. Estimated outputs from the model for the total biomass scaled to the mean total biomass. Lines represent the median of posterior estimates, while the shaded areas denote the 95% CI (Credibility Interval). The dots represent observed values of CPUE scaled to the mean CPUE.