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New insights into the collapse of Upper Lake Constance whitefish (*Coregonus wartmanni*) and the impact of commercial fisheries management

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Abstract

The whitefish *Coregonus wartmanni* is the key fishery resource in Upper Lake Constance (ULC), one of Central Europe's largest lakes. A significant stock decline resulted in the closure of the commercial whitefish fishery in 2024. Reasons for the decline have been contested, with suggestions ranging from environmental changes to overfishing. As in many inland fisheries, management in ULC previously lacked standardized protocols for stock assessment, and relied instead on technical measures like regulating mesh size and net numbers. To assess stock dynamics and estimate biomass and fishing mortality over the past 25 years (1997–2022), a surplus production model was applied using scientific gillnet surveys and commercial catch data. The results confirm that the whitefish stock is at a historically low level. Apparently, in 2012, when the stock already showed signs of overfishing, invasion of the pelagial by non-native stickleback (*Gasterosteus aculeatus*) triggered an ecosystem shift. Additional factors including oligotrophication, other invasive species and climate change also impact stock development, suggesting that reduced fishing pressure alone may not be enough to ensure short-term stock recovery.

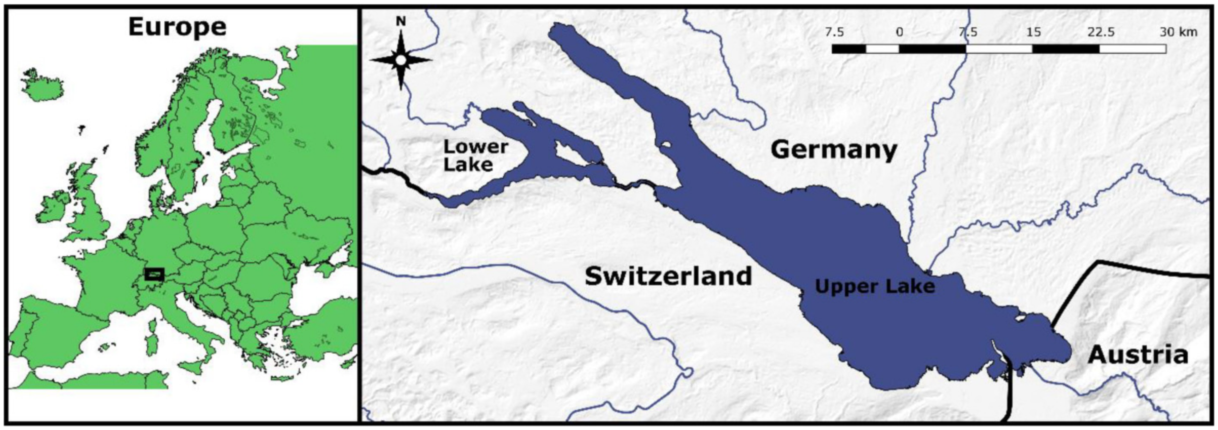
Key words: assessment tool, inland fisheries, SPiCT, surplus production model, stock recovery

Introduction

Inland freshwater fisheries have significant socio-economic importance for their respective regions (Song et al. 2018). Despite the capacity for stock data collection and analysis and the relative ease of monitoring closed lake systems compared to oceans, inland fishery managers often lack the assessment tools routinely available to their marine counterparts. As a result, most freshwater fisheries are managed without routine formal stock assessment, even where long time series data are available (Lorenzen et al. 2016). However, there is potential to rectify this by adapting and applying methods frequently used in the management of marine fisheries to freshwater stocks (Pitcher 2015; Lorenzen et al. 2016).

One case that would be suitable for this approach due to its long history of data collection is that of the pelagic whitefish (*Coregonus wartmanni*) fishery of Europe's second largest pre-alpine water body, Upper Lake Constance (ULC) (Fig. 1). The ULC commercial fishery was until recently one of the most important inland fisheries in Europe (Baer et al. 2017). In the years after the Second World War, hundreds of tons of pelagic whitefish were caught annually by more than 200 commercial fishermen and sold profitably on the regional market. The fishery provided an outstandingly tasty and ecologically sustainable product that was central to tourism in a region hosting about 35 million guest nights per year. However, in 2024 the fishery had to be closed following a stock collapse and this local product has been replaced by mostly oversea imports whose ecological footprints are enlarged by transport and freezing (Tyedmers 2004). Even with long time series of data pertaining to catch and effort and additional gillnet surveys carried out by the fisheries and independently, the causes of the collapse of the stock were initially unclear and highly contested. A stock assessment model capable of estimating current and future stock scenarios for whitefish in ULC is thus highly desirable. That no such model has previously been adopted is somewhat surprising given the sound database and the exceptionally long history of fisheries regulation, dating back as far as 1350, when rules were first instigated to manage competition (Zeheter 2015). In more recent decades regulations for the whitefish fisheries have been amended nearly every year including changes in mesh size and number of allowed nets (Baer et al. 2017). Only one consistent but controversial rule has been applied, that is still popular in parts of the scientific community today (Roberts et al. 2024): legal landing

Fig. 1. Map of Lake Constance.



size must ensure at least one successful spawning during the individual's life.

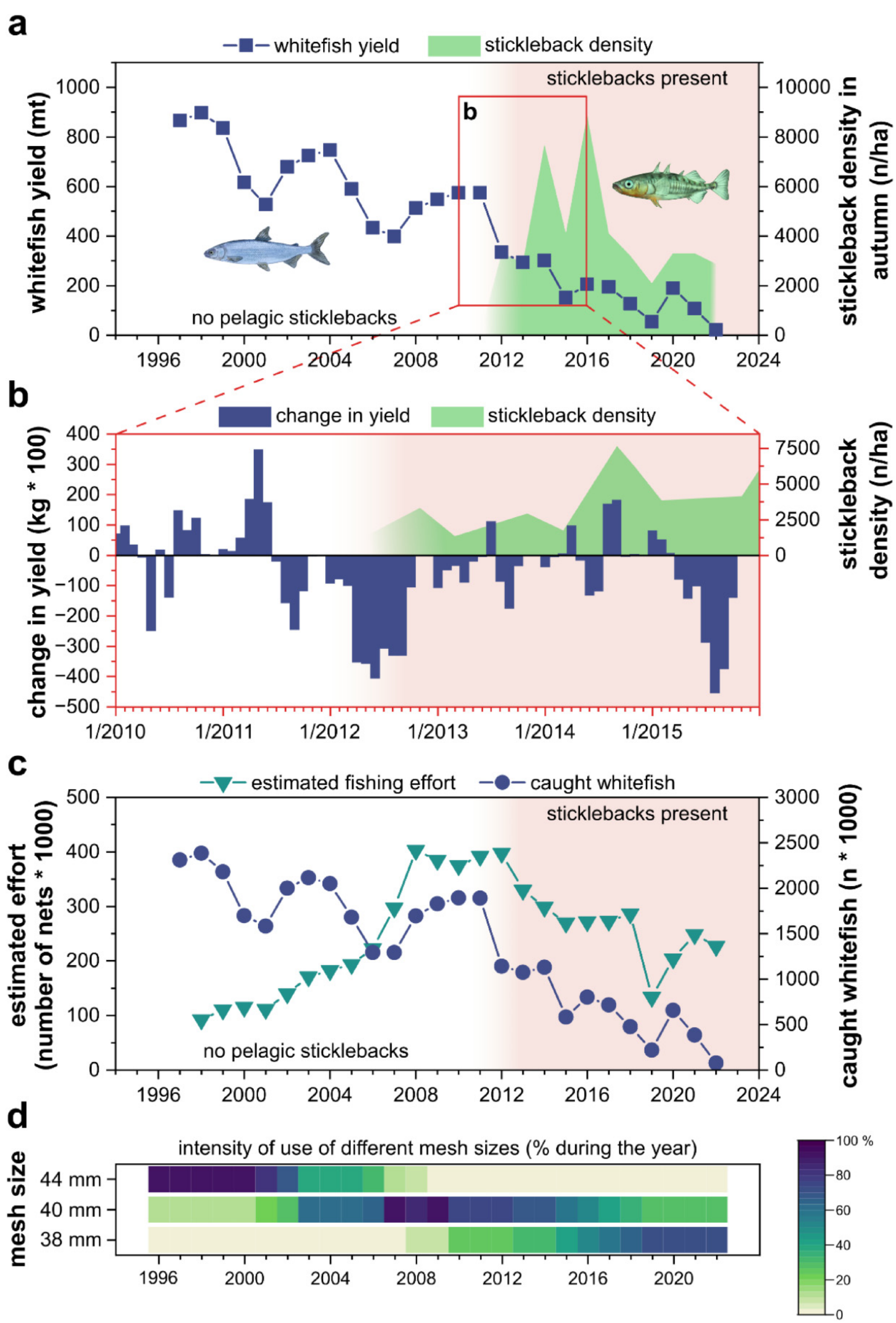
ULC has undergone pronounced shifts in trophic status during the last 100 years (Stich and Brinker 2010) with the productivity of fish stocks and fishery yields changing accordingly (DeWeber et al. 2022). At the beginning of the 21st century, following internationally coordinated measures to reduce nutrient inputs, the lake was restored to an oligotrophic state. Declining whitefish catches (Figs. 2*a* and 2*b*) prompted subsequent adjustments to management measures to sustain the viability of a small fishery. The legal mesh size for catching whitefish was gradually reduced from 44 to 38 mm (Fig. 2*d*). These smaller mesh sizes caught whitefish more effectively (DeWeber et al. 2021), amounting to an increase in fishing intensity (Fig. 2*c*), and the number of individuals continued to decrease (Fig. 2*a*). The increased exploitation of stock brought about by these technical measures coincided with an invasion of stickleback to the pelagic zone of ULC (see below). Instead of anticipated long-term yields of whitefish of around 300 tonnes a year, equivalent to that realized during previous oligotrophic times (1910–1955) (Baer et al. 2017), commercial catches declined by more than 50% (Fig. 2*a*), reaching an unprecedented low of 10 tonnes in 2023 (Baer et al. 2024). Furthermore, from 2013 onwards catch data show a massive reduction in year-class strength of young whitefish and a distinct depression of growth (Rösch et al. 2018). As an emergency measure, in 2023 the decision was made to close the commercial whitefish fisheries for 3 years (2024—2026).

Quantitative knowledge of past whitefish stock dynamics might have helped the fisheries adapt more effectively to those changes, but the need for detailed stock models was perhaps less apparent in the past. The lake fisheries had already endured for more than a century and so the assumption that existing management was sufficient is understandable (Baer et al. 2017). Furthermore, past experience suggested that both fecundity and resilience of the whitefish could be relied upon, as during the 1960s and 1970s when technical measures including a partial closure of the fishery for some months resulted in rapid stabilization of the population (Nümann 1972). However, recent decades have seen the emergence of novel stressors, which require more careful and informed fisheries management. Of these stressors, the most important for Lake Constance are invasive species and climate change (DeWeber et al. 2022).

The decreases in whitefish population in ULC coincided with a habitat shift and explosion of the population of nonendemic three-spined stickleback (*Gasterosteus aculeatus* L.), which took place from autumn 2012 (Eckmann and Engesser 2019). A lake-wide survey in September 2014 revealed that 96% of all individuals in the pelagic fish community were sticklebacks, accounting for 28% of total fish biomass (Alexander et al. 2016). Surveys with pelagic trawls between 2017 and 2019 identified densities exceeding 10 000 individuals/ha (Gugele et al. 2020). Stomach content and isotope analysis showed that stickleback and whitefish have a significant prey overlap, while stickleback additionally feed on whitefish eggs and larvae (Roch et al. 2018; Ros et al. 2019; Baer et al. 2021; Gugele et al. 2023). Interspecific competition for food thus leads to reduced whitefish growth and survival, while predation by sticklebacks on whitefish larvae and eggs hampers recruitment (DeWeber et al. 2022; Gugele et al. 2023).

Sticklebacks were detected for the first time in the lake in the 1950s, but were associated exclusively to the littoral zone until 2012 (Roch et al. 2018). An important factor in the sudden and explosively successful move to the pelagic zone may be the descent of this population from a marine lineage (Hudson et al. 2021). This heritage imparts a limited ability to desaturate and elongate fatty acids (Ishikawa et al. 2019) and a need to feed on essential fatty acid (EFA)-rich prey to avoid malnutrition. It appears such prey are not sufficiently available in the littoral of Lake Constance where sticklebacks exhibit a clear deficit in EFAs. Meanwhile, in the pelagial they can forage on EFA-rich prey, i.e., copepods, and show a well-balanced EFA profile (Baer et al. 2024). An obvious question arises as to why under these circumstances it took them 60 years to enter the pelagic zone, but a possible explanation would be the changing density of interspecific competition (Baer et al. 2024) from the zooplanktivorous pelagic whitefish, the original keystone species in ULC (Ogorelec et al. 2022). Coincidentally in 2012, the whitefish yield reduced by more than 50% (Fig. 2*a*) and decreased even further in the

Fig. 2. (*a*) Dynamics in whitefish yield and density of pelagic sticklebacks between 1997 and 2022, (*b*) the monthly changes in yield and stickleback density in the years shortly before and after the stickleback invasion, (*c*) the estimated fishing effort and the number of caught whitefish by commercial fisheries, and (*d*) the changes in the legal mesh sizes between 1997 and 2022.



following years (Fig. 2*b*). Thus, from 2012 on, sticklebacks may have been presented with an "underpopulated" habitat (Baer et al. 2024), which they were then able to exploit. However, factors contributing to the low density of whitefish in the pelagic zone in 2012, and thus to the opportunity for stickleback niche expansion, have remained unclear.

To test the hypothesis that a combination of overexploitation and environmental changes were the causes of the whitefish stock decline, we applied a surplus production model taking into account both fishery-dependent and fishery-independent data sources. We aimed to reconstruct the pattern of stock decline and to understand the effect the commercial fishery played. Furthermore, we aimed to gain a perspective on the potential for stock recovery.

Materials and methods

Study area and fisheries management

Lake Constance is one of the largest lakes in Central Europe and bordered by Austria, Germany, and Switzerland (47°38′N; 9°22′E). The total surface area of 536 km^2 is divided between the large (472 km^2), deep (>250 m) Upper Lake (ULC) and the smaller (63 km^2), shallower Lower Lake Constance. This paper deals solely with the warm, monomictic, oligotrophic ULC.

The fish community of ULC comprises a minimum of 30 species (Eckmann and Rösch 1998) of which about 10 are targeted by professional fishermen (Rösch 2014). Among these, whitefish (*Coregonus* spp.) is the most economically important. Whitefish have been caught with floating, mostly free-drifting pelagic gill nets since 1957, when specialist whitefish seine nets were banned. Further details of the whitefish fishery are given in Baer et al. (2017). Since 1893, ULC fisheries have been managed by a political decision-making body, the*International Lake Constance Fishery Commission* (in German: Internationale Bevollmächtigtenkonferenz für die Bodenseefischerei, IBKF, www.ibkf.org), whose board meets at least once a year and also serves as a regional fisheries management organisation (see Løbach et al. 2020).The IBKF has the authority to establish legally binding conservation and management measures based on the best available scientific evidence. The board is advised by a group of local fisheries experts who base their advice on the latest monitoring data and take into account the stakeholder opinions of professional fishers and recreational anglers (numbering around 13 000) to review and adjust harvest regulations such as minimum-landing sizes, seasonal closures, mesh sizes, and other measures that control fishing effort. Monitoring data are generated by a variety of fishery administrators and local research stations in each country.

Input data for modelling

The current study takes into account data from 1997 onwards, when the phosphorus level fell below 20 μg/L^{-1} and subsequently plateaued at 7–8 μg/L^{-1} after 2005 (Supplement 1). Commercial catches were reported monthly for all fishers and were summed up to quarterly catches.

The estimated effort (EE) from all fishers was first calculated for a given year y, month m, and mesh size j as:

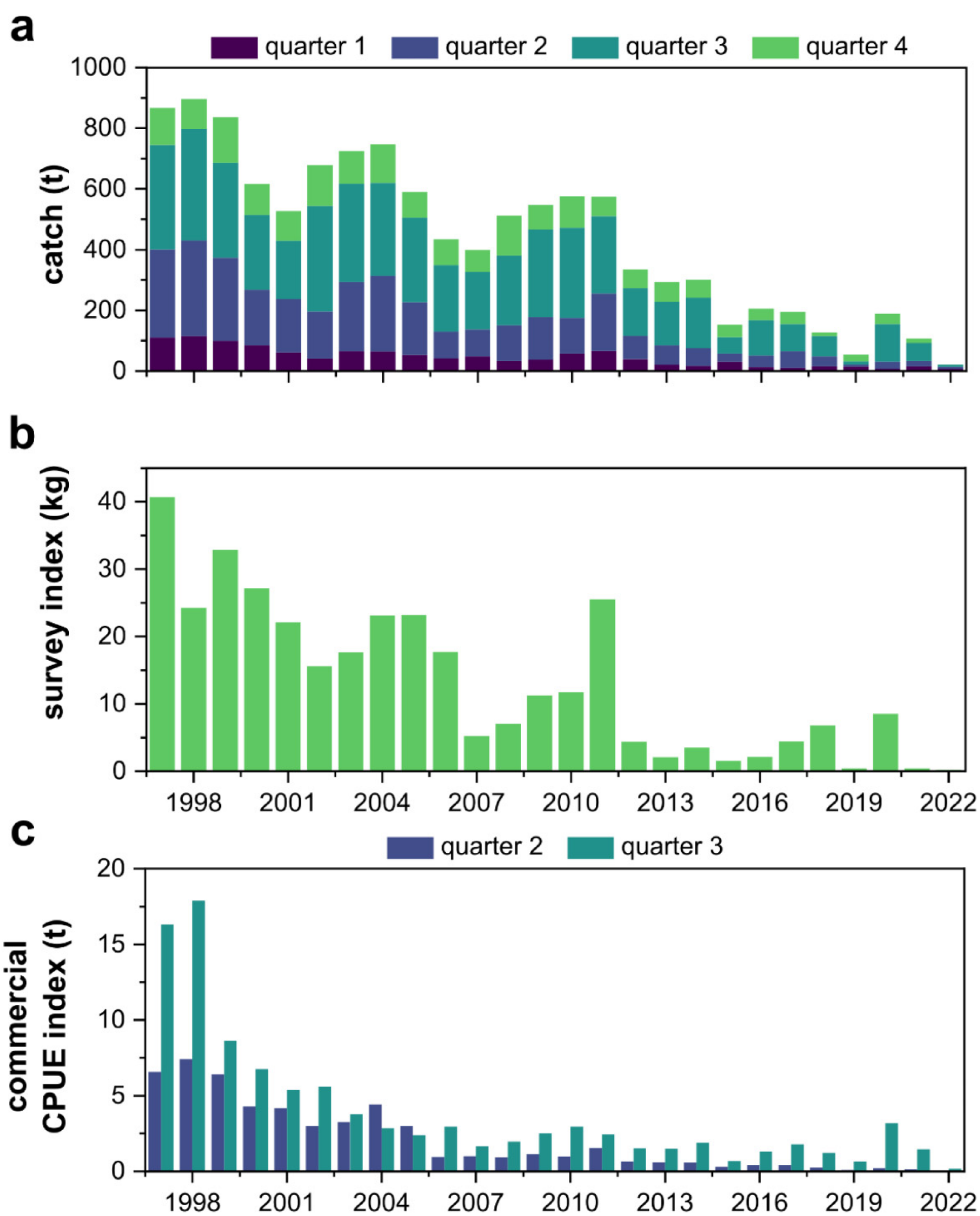
$$\mathrm{EE}_{ymj} = \mathrm{Permits}_y * \mathrm{Nets}_{ymj} * \mathrm{Days}_{ym} * \pi_{ym} \tag{1}$$

where Permits is the total number of fishery permits, Nets is the number of nets allowed of mesh size j, Days is the number of days open for fishing, and π is the proportion of active fishers in a given year y and month m. Actual effort was then assessed by multiplying EE by an expert assessment of the number of active fishers in a given year and month. The proportion of active fishers was estimated for each year y and month m using data available from Switzerland and Baden-Württemberg, Germany. Fishers in Switzerland have been required to report daily catches and nets used since 1995 and fishery observers in Baden-Württemberg, Germany have often recorded the monthly proportion of active fishers since 1990 (for more details see Supplement 2). Similar data on actual effort were not available in Bavaria, Germany, or Austria. Due to the fact that all fishermen have to use the same nets and are allowed to fish anywhere in the lake, it can be assumed that the data from Switzerland and Baden-Württemberg are representative for the whole lake. Therefore, we used these data to interpolate the overall effort. Commercial fishermen were allowed to fish with 44 mm mesh during the whole study period (1997–2022). The number of permitted nets with smaller mesh sizes (40 and 38 mm) was increased over time (Fig. 2*d*). To take this increasing efficiency into account, the monitoring data were used to calculate how many more whitefish the 38 and 40 mm mesh sizes catch relative to 44 mm nets (and 38 mm nets compared to 40 mm nets). These correction factors were multiplied by the effort of the three net types per month and summed up to obtain values for quarterly and annual EE (Fig. 2*c*). In the following, only the adjusted effort data accounting for the reduction in mesh size were used.

Between 1997 and 2022, more than 80% of catches were taken during spring and summer (quarter 2: April–June and quarter 3: July–September) (Fig. 3*a*). Thus, only these quarters were incorporated into the model. Quarters 4 and 1 (October–March) were excluded, because during autumn and winter certain closed seasons are implemented, less efficient anchored gillnets are used, and the catch of whitefish spawners is only used for captive breeding and stocking purposes (Baer et al. 2023). To calculate the commercial catch per unit effort (CPUE), quarterly catches for quarters 2 and 3 were divided by the relevant quarterly effort (Fig. 3*c*).

Scientific monitoring using gillnets has been conducted for almost 100 years to support the ecosystem of Lake Constance and the management of its fish community (see DeWeber et al. (2021) for further details). Surveying took place between April and September, using multi-mesh gillnets with mesh sizes between 17 and 50 mm, though only 40 and 44 mm mesh nets (the sizes routinely deployed by the commercial fishery) were used consistently throughout the entire time series. Thus, we used these sizes to calculate a survey index. Additionally, we selected July–September as the months, which typically yield the highest whitefish catches in the survey nets. The gillnet area was standardized to 1000 m^2. As not all individuals were weighted, annual individual measurements of length and weight were used to calculate mean weight per length class caught in a certain year. The total catch biomass of the standardized gillnet haul, representing the biomass survey index when aggregated (Fig. 3*b*), was calculated by multiplying the number of individuals by the weighted mean weight, adjusted for the length distribution.

Fig. 3. Quarterly catches (*a*), survey index (*b*), and commercial catch per unit effort (CPUE) (*c*) between 1997 and 2022 for Lake Constance whitefish.



Surplus production model SPiCT

We fit the Stochastic surplus Production model in Continuous Time (SPiCT) (Pedersen and Berg 2017) to the Lake Constance whitefish data using the R-package "spict" and the associated manual (both available at https://github.com/DTUAqua/spict). Catch data in weight depict the most important input to the SPiCT model and are available both annually and quarterly.

In SPiCT, it is necessary to complement catch data with a minimum of one independent biomass index. To this end we applied data from the scientific gillnet surveys (given here as calculated biomass index) and commercial CPUE data simultaneously. The gillnet survey was modified as explained above to incorporate the dynamics of the exploited part of the stock, as recommended by Pedersen and Berg (2017).

While it is possible to run SPiCT with quarterly catch data, this requires seasonal models for fishing mortality and consideration of seasonal surplus production (Mildenberger et al. 2020). Thus, to simplify the model and because the seasonal fishing pattern changed over time (Fig. 3*a*), we considered only yearly aggregated commercial catches and omitted dynamic seasonal elements.

The CPUE time series are assumed to be proportionate to exploitable stock biomass at a specific time-point in SPiCT. As described in the previous section, catchability and effort of commercial catches are low in quarters 1 and 4 and the CPUE time series of these quarters is not considered proportionate to the exploitable stock biomass. Consequently, quarters 1 and 4 were excluded from the CPUE time series. As we use an annual time step in the model that does not consider seasonal dynamics, we do not expect any potential loss of information. Thus, the timing of the commercial CPUE in quarter 2 was set to year +0.375 and in quarter 3 to time +0.625. The gillnet survey in July, August, and September was set to year +0.75.

The fishing process including changes in efficiency resulting from, for example, changes in mesh size (Fig. 2*d*) was modelled as an unknown stochastic process and thus does not require a standardization (Fitzgerald et al. 2018). As the intrinsic growth rate *r* was often unrealistically high for this stock, the prior for log(*r*) was set to log(0.4) with a standard deviation of 0.4 in the baseline scenario (fit 1). Fishbase classifies this species as having medium resilience (https://www.fishbase.se/summary/Coregonus-wartmanni.html, last accessed on 8 April 2025). This can be translated into an *r*-prior between 0.2 and 0.8 (Froese et al. 2017), which corresponds to the chosen prior for log(*r*). Further, the shape parameter of the production curve *n* was fixed to 2, imposing a symmetric Schaefer model (Schaefer 1991) in the baseline scenario. Although phosphorous levels in Lake Constance have been influencing stock productivity in the past, they were stable in the chosen study period. We thus did not consider time-varying productivity in the model. These prior specifications were based on expert opinion and are a fair reflection of available knowledge of the system.

Next to our baseline scenario (fit 1), we tested four additional sensitivity runs to evaluate the effect of prior assumptions (Kokkalis et al. 2024) as specified below:

- Fit 2: Including spin-up phase; in this sensitivity run, we added a spin-up phase of 10 years meaning that the model started 10 years earlier than the data. This ensures that the first biomass state after the spin-up is not substantially larger than the carrying capacity K.
- Fit 3: Fixing skewness of the production curve; this sensitivity run tests the effect of fixing the production curve almost to a Fox model (Fox 1970) that describes an asymmetrical production curve with the Maximum Sustainable Yield (MSY) at 37% of the carrying capacity (Kokkalis et al. 2024). The log(*n*) parameter was fixed to log(1.1) and the *r* prior was adjusted accordingly, as suggested in Kokkalis et al. (2024).
- Fit 4: Increasing the coefficient of variation (CV) of low CPUE observations; as the residuals from fit 1 increase in magnitude over time as the stock size decreases. Rather than assuming a constant standard deviation for the observation error on the CPUE indices on log scale (i.e., constant CV), in this fit the observation error on log-scale is assumed to be proportional to 1/year$^{0.1}$, where *y* is the observation (on natural scale) in a given year. This scales the standard deviations for the log indices from around 0.8 times average for the earliest years to around to 1.3 times average in the last year.
- Fit 5: Shortening of the time series; as both catches and density of whitefish in the surveys decrease over time, fit 5 tests the effect of the time series starting in 2001. This sensitivity run aims to test how the model reacts to a shorter time series.

The script and input data are available at https://github.com/StefanieHaase/whitefish_assessment.

Results

According to the SPiCT modelling, whitefish biomass in ULC declined continuously since 1997 to a historically low level in 2022, independent of the five sensitivity runs (Fig. 4). Sensitivity runs 1 and 4 showed the same trajectory of biomass over time. A shortening of the time series (fit 5) led to a higher relative biomass (B/B_{MSY}) compared to fit 1, while including a spin-up phase (fit 2) or fixing the skewness of the production curve (fit 3) resulted in a lower relative biomass (Fig. 4). By including the spin-up phase, fit 2 avoided values for B/B_{MSY} exceeding the carrying capacity by four times at the beginning of the time series, and thus this was chosen as the more realistic and preferred fit. The time when the relative biomass B/B_{MSY} is below 1, and thus "overexploited" according to Food and Agriculture Organization (FAO) definitions (Cadima 2003), differs between the five sensitivity runs. However, in the latest this threshold was reached in any scenario was 2014 (fit 5), and in most scenarios it occurred sooner (Fig. 4). Although the point values of biomass are estimated with substantial uncertainties (for fit 2 see Supplement 3, Fig. 1), the downward trend in biomass is consistent.

The trend in relative fishing mortality (F/F_{MSY}) was also similar among the sensitivity runs (Fig. 4). Fishing mortality was higher than the limit reference point F_{MSY} ($F/F_{\mathrm{MSY}} > 1$; Cadima 2003) in all scenarios from the beginning of the 2000s and increased further up until 2010 (Fig. 4). Again, the estimated point values for relative fishing mortality carry substantial uncertainty (Supplement 3), but the trend is consistent in all five scenarios with an increase from 2000 until 2010, stabilising at an elevated level from 2011 to 2022 (Fig. 4).

The biomass target reference point B_{MSY} ranges between 687 *t* (fit 5) and 2165 *t* (fit 2) depending on the sensitivity run (Table 1). The fishing mortality limit reference point F_{MSY} is predicted at between 0.10 (fit 5) and 0.20 (fit 3; Table 1). The asymmetric confidence intervals of both parameters are rather wide, highlighting the uncertainty of the point estimates.

Without any fishing activity, the models predict that stock recovery to levels above B_{MSY} would take between 9 (fit 3) and 15 (fit 1, 4, and 5) years on average, assuming constant conditions with no change compared to the actual status (e.g., no change in stickleback density).

A Kobe-plot (Supplement 3, Fig. 3) depicts relative fishing mortality (F/F_{MSY}) over relative biomass (B/B_{MSY}) over time as estimated in the run with a spin-up phase (fit 2), which was considered as the final run. In the first years of the time series (1997–2005) whitefish stocks were not overfished, but signs of overfishing begin to be apparent in the years 2006–2014 and from 2008 fm/F_{MSY} values (mean and 95% confidence intervals) for fit 2 significantly exceed 1, pointing to overexploitation (Supplement 3, Fig. 1). Since 2015, B/B_{MSY} is significantly different from 1 (mean and 95% confidence intervals, see Supplement 3, Fig. 1) again indicating an overfished stock. If we use our baseline scenario (fit 1) to depict relative fishing mortality and relative biomass with confidence intervals,

Fig. 4. Relative biomass and relative fishing mortality between 1997 and 2022 in Upper Lake Constance, according to five different sensitivity runs (fit 1–fit 5) as estimated with the Surplus production model SPiCT. Dashed lines represent the area which, if undercut (B/B_{MSY}) or exceeded (F/F_{MSY}), indicates an overexploited stock or overexploitation of the stock, respectively.

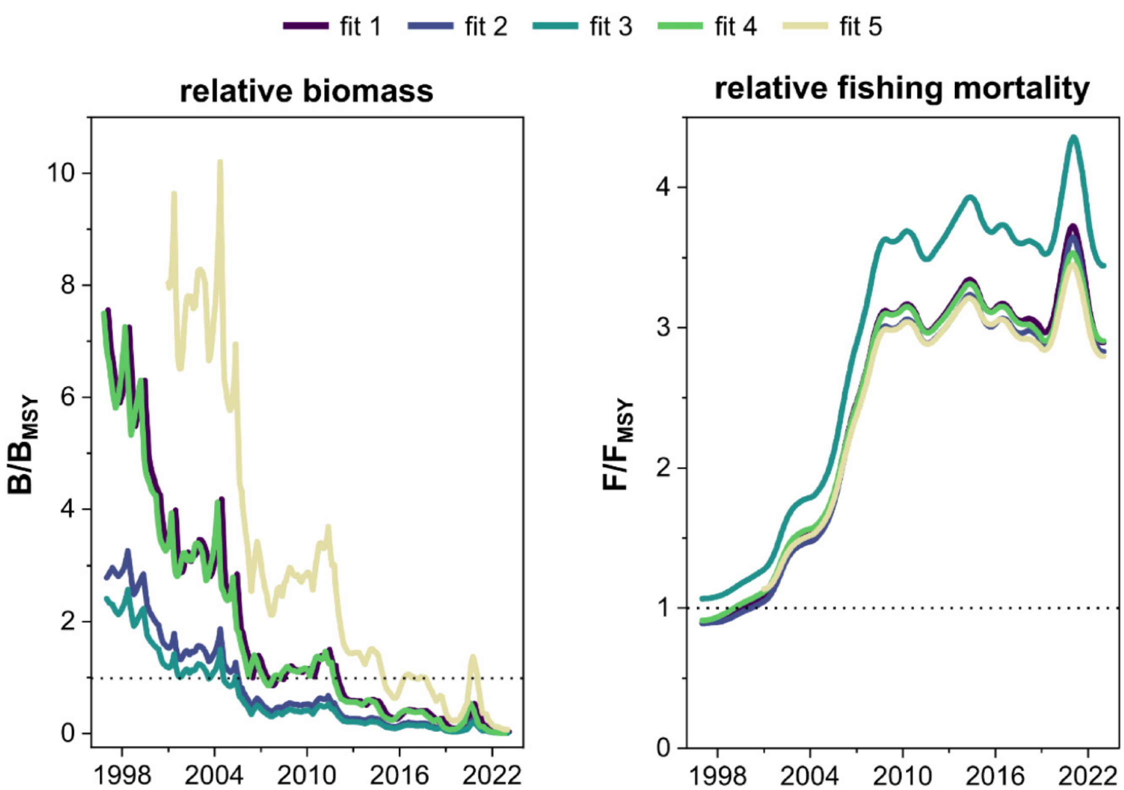


Table 1. Stochastic parameter estimates and corresponding confidence intervals (95% CI) for the five sensitivity runs.

Sensitivity run	Mean biomass (*t*) providing MSY (B_{MSY})	CIs of B_{MSY}	Mean fishing mortality per year providing MSY (F_{MSY})	CIs of F_{MSY}
Fit 1	1234	377–4042	0.13	0.03–0.64
Fit 2	2165	523–8958	0.17	0.04–0.79
Fit 3	1940	159–2365	0.20	0.09–0.47
Fit 4	1215	376–3927	0.13	0.03–0.64
Fit 5	687	99–4757	0.10	0.01–0.75

the period were overfishing took place but the stock was not yet overfished was longer (2009–2019) (Supplement 3, Fig. 2). The first year with signs of overexploitation was 2012 (Supplement 3, Fig. 3) and it became significant in 2019 (Supplement 3, Fig. 2).

Discussion

As with many other commercially used inland fisheries (Fitzgerald et al. 2018), a formal stock assessment process for whitefish in ULC was lacking. To overcome this shortcoming, we adapted a surplus production model frequently applied to marine fish stocks (Pedersen and Berg 2017; Kokkalis et al. 2024). A limitation of this approach is that the model assumes fishing mortality as the main driver. Given that whitefish stocks are influenced by several other environmental stressors, this results in uncertainties in estimates for biomass and fishing mortality, and rather wide confidence intervals for point estimates. However, by applying a series of different sensitivity runs, we successfully obtained significant trends and consistent results, offering new insights to inform future management. We found that (i) the whitefish stock appears to have been overfished since around 2006 and that (ii) current levels of severe depletion take many years to reverse, even with a moratorium on fishing.

According to the model output and available input data, the whitefish stock of Lake Constance shows clear signs of overexploitation in the recent past. First of all, the biomass index resulting from fishery-independent gillnet survey data has declined since 2000, indicating a reduction in adult whitefish biomass. At the same time, commercial catches also decreased though this was partially offset by changing fishery management regulations, including an increase in the number of nets permitted and a reduction in mesh size (IBKF 2003). These led to short-term increases in commercial catches but only up until 2004 (Fig. 2). Although these regulations did not directly lead to an overfished stock during that period, overexploitation was already taking place as noticeable in all sensitivity runs ($F > F_{MSY}$ but $B > B_{MSY}$; Fig. 4; Supplement 3, Figs. 2 and 3). Further changes in regulation from 2007 (the authorisation of smaller mesh sizes and more months in which they could be used; IBKF 2007) led to further increases in fishing effort and more short-term increases in commercial yield until 2011. Thus, the greatest fishing effort of the entire time series was realised between 2008 and 2012, when the standing stock was already rather small as indicated by a low survey index. This pattern in fishing mortality was confirmed in all sensitivity runs (Fig. 4). This resulted in a standing biomass below biomass reference points since at least 2012 in sensitivity runs 1–4 (2015 in sensitivity run 5) and a threshold was crossed into overexploitation (Cadima 2003). Only one season later, sticklebacks started to dominate the pelagial in ULC (Eckmann and Engesser 2019). The multiple sensitivity runs show that the modelled stock dynamics are insensitive to parameter choices and only result in different timings when the stock reached the overfished state. Model fit 2 including a 10-year spin-up phase to avoid overshooting carrying capacity aligns well with historical management practices and observed patterns in stickleback invasion.

At the beginning of the 21st century, more than a decade before the strong increase in stickleback biomass, other forces were already impacting negatively on whitefish stock dynamics. These included an ongoing decline in phosphorus concentration, which began impacting the whitefish fisheries around 2005 (Müller et al. 2007), and climate change effects (Stich and Brinker 2010; DeWeber et al. 2022). The impacts of these factors are unpredictable, as reflected in the large confidence interval of the model, but along with repeated increases in fishery effort the result was that fishing mortality exceeded sustainable levels ($F/F_{MSY} > 1$; Cadima 2003). This resulted in a stock that showed first signs of an overexploited stock in 2006 which became significant in 2015. The general stock depletion was accompanied by significantly impaired growth (Kugler 2022) (Supplement 2) with strong negative implications for whitefish fecundity as numbers of eggs correlates positively with spawner weight (Rösch 1987). This is empirically evidenced by a strong decline in observed egg density on the lake bottom following spawning since the beginning of the 21th century (ISF 2021) (Supplement 2). In short, the model indicates whitefish recruitment has been disrupted for more than two decades. Mitigation measures, including intensive stocking with whitefish larvae, have failed (Baer et al. 2023), and the drastic declines recorded in catch and biomass index in 2012 point to an extremely low overall density of whitefish.

This interplay of a changed ecological framework combined with more intensive fishing is thought to have led to a regime shift giving sticklebacks the opportunity to replace whitefish as the dominant fish species of the pelagial in ULC. This is not the first example of extreme increase in stickleback population in the near absence of regular keystone species. In the Baltic Sea in the late 20th and early 21st century, anthropogenic disruption of the food web could lead to an extreme stock increase of sticklebacks (Bergström et al. 2015; Byström et al. 2015) with similarly severe ecological and economic consequences (Eklöf et al. 2020; Olin et al. 2024). However, the change was particularly swift in ULC, within sticklebacks achieving abrupt and lasting domination in the space of one season in 2012 (Eckmann and Engesser 2019). The density of whitefish subsequently underwent a sustained and relentless decline (Rösch et al. 2018) to an unprecedented low in 2023 (Kugler 2022). Our results suggest that the dramatic decrease in whitefish stock since 2012 is unlikely to be solely a consequence of high fishing pressure, but the result of interlinked processes connected to the niche expansion of the sticklebacks: including sticklebacks predation on whitefish larvae and eggs (Baer et al. 2021; Gugele et al. 2023), and competition for food between sticklebacks and whitefish (Ogorelec et al. 2022).

Most stock assessment models, including the surplus production model SPiCT, assume that environmental conditions and management are stable (Pedersen and Berg 2017). As discussed extensively in the literature, in ULC neither environmental conditions nor whitefish fishing pattern have been constant. Nutrient load and thermal conditions have varied in the long-term (Nümann 1972; Eckmann et al. 1988; Stich and Brinker 2010; DeWeber et al. 2022). To avoid including shifts in the trophic status of the lake, we decided to shorten the time series and only used model input data starting in 1997. During this time span, phosphorus values only decreased slightly before reaching stable values (Supplement 2). Still, the analyses and conclusions outlined above are to be treated with some caution, as emphasised statistically in the rather wide confidence intervals for point estimates. These wide confidence intervals underlines that the whitefish stock dynamics are not only driven by fishing mortality but other factors, including changes in natural mortality. Further, they can be explained the limited contrast in the survey and catch input data that almost only declined in the observed period (Fig. 3). Nevertheless, the available time series of fisheries-dependent and -independent data are suitable as a basis for an informed management. The independent sensitivity runs consistently indicate severe overfishing and stock levels at a historical low. Furthermore, the stock exhibits typical signs of overexploitation, e.g., impaired recruitment and decreased growth (Murawski 2000; Ben-Hasan et al. 2021). Even allowing for the uncertainty acknowledged above, in combination with expert information the present assessment provides an urgent new perspective for fishery management. In general, the consequences of an overly conservative management approach are much less severe for fish stocks than those of overly optimistic approaches, justifying in the view of these authors, a more cautious management approach. There is little evidence that continued management based on the simple rule of allowing fish to spawn at least once in a lifetime will be sufficient to ensure a sustainable harvest in the long-term.

Following the whitefish stock collapse, in 2023 all countries around ULC implemented a total ban on whitefish fisheries for 3 years (2024–2026). The present analysis suggests that not only is the stock unlikely to recover in this time frame but that even if no whitefish are fished and all other conditions, including phosphorus level and water temperature, remain stable it may take 15 years for the stock to recover above B_{MSY}. However, this timescale might be significantly shortened with a combined suite of mitigations including reducing the stickleback population with a targeted fishery (Ojaveer 1999) and stocking whitefish larvae large enough to exceed stickleback gape limitations (Ros et al. 2019). Early results suggest that it could be possible to control stickleback population by trawling (Gugele et al. 2020). A significant decrease in the stock size of sticklebacks would directly reduce both the rate of predation on whitefish eggs and larvae, and competition for food. However, the effects of both options (trawling sticklebacks and stocking larger whitefish) on the recovery of the whitefish stock are unknown and thus it is also unclear if and how these measures might reduce the timescale of recovery. The impact of these and other developments can only be detected by regular monitoring and assessment of stock dynamics, which will also provide the basis of a sustainable management in the future.

Conclusion

The surplus production model applied in this study successfully reconstructed trends in biomass and fishing mortality of whitefish in ULC. Uncertainty in point estimates and reference points was addressed through a range of sensitivity runs. The analyses confirm historically low levels for the pelagic whitefish stock and suggest that overfishing since the beginning of the time series coincided with a regime shift allowing non-native sticklebacks to replace native whitefish as the dominant species in the pelagic zone. The stock assessment model estimates an average rebuilding time of 15 years for whitefish stock to recover above B_{MSY}, assuming constant conditions. Additional knowledge further suggests that other factors apart from fisheries may be casting both positive and negative influence on stock development, and thereby acting to reduce or extend the time until recovery. Thus, a reduction in fishing pressure alone might not lead to a recovery of the ULC whitefish stock in the short- and medium-term and further management actions should be considered.

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The data and code underlying this article are available at https://github.com/StefanieHaase/whitefish_assessment (https://doi.org/10.5281/zenodo.15681220).

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Competing interests

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2024-0370.

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