



Long-term changes in littoral fish community structure and resilience of total catch to re-oligotrophication in a large, peri-alpine European lake

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Funding information

European Regional Development Fund: Interreg V-A-Germany-Austria-Switzerland-Liechtenstein (Alpenrhein-Bodensee-Hochrhein 2014-2020), Grant/Award Number: ABH060; Deutsche Forschungsgemeinschaft, Grant/Award Number: 298726046/GRK8872

Abstract

1. The littoral zone of lakes is used as spawning, shelter, or feeding habitat for many fish species and hence is of key importance for overall lake functioning. Despite this, hardly any studies exist examining the long-term dynamics and response of the littoral fish community, composed mostly of juvenile fish, to environmental change. Here, we study the response of total catch per unit effort (CPUE) and individual species CPUE of such a community to 17 years of oligotrophication and examine whether the species responses can be characterised as synchronous or asynchronous.
2. We analyse a data set of beach seine catches carried out during morning and twilight, late spring and late summer at three sites in large and deep Lake Constance from 1997 to 2014. Generalised additive mixed models were used to explore changes in CPUE of the overall community and of the most frequently occurring species, and Kendall's *W* test was applied to examine whether the dynamics of fish species were synchronous or asynchronous.
3. Species-specific and total CPUE strongly differed between morning and twilight and between spring and summer indicating an important role of behavioural and life cycle adaptations of species for CPUE. In addition, also the CPUE of some species seeking shelter behind larger stones was lower at sites without these.
4. Total CPUE did not decline suggesting the overall abundance of littoral fish was resilient to declining nutrients. In contrast, fish community composition changed strongly during the study period due to increases in some species (dace, loach, perch) and decreases in others (bream, burbot, chub, ruffe), indicating response diversity of fish to oligotrophication. The type of community dynamics was scale-dependent, whereby significantly synchronous dynamics according to Kendall's *W* were observed when taking seasonal variability into account. In contrast, significantly asynchronous species dynamics were observed when only

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the low-frequency variability of species dynamics was considered separately for spring and summer time series.

5. Resilience of littoral fish total CPUE to oligotrophication might have important consequences for ecosystem dynamics and ecosystem services beyond the littoral zone. As small fish often impose strong predation pressure on zooplankton, their resilience might sustain a high top-down control on zooplankton resulting in a further reduction of zooplankton biomass. This could contribute to delayed food web responses and reduced growth of fish with oligotrophication.

KEYWORDS

compensatory dynamics, juvenile fish, Lake Constance, response diversity, synchrony

1 | INTRODUCTION

In many lakes in Europe and Northern America, the ban of phosphorus in detergents and massive investment in lake restoration create cultural re-oligotrophication (Jeppesen et al., 2005). While the effects of re-oligotrophication on pelagic dynamics and organisms are regularly investigated (Gerdeaux, Anneville, & Hefti, 2006; Jeppesen, Jensen, Søndergaard, Lauridsen, & Landkildehus, 2000), long-term studies of littoral organisms are rare (but see Clady, 1976; Gopalan, Culver, Wu, & Trauben, 1998). However, the littoral zone is a highly productive and heterogeneous habitat that provides many resources for fish. For example, the shallow littoral is used as a refuge from predation (Fischer & Eckmann, 1997b; Hall & Werner, 1977), as a habitat for spawning (Balon, 1975; Probst, Stoll, Peters, Fischer, & Eckmann, 2009) and as a nursery habitat for juvenile fish (Allen, 1982; Lewin, Mehner, Ritterbusch, & Brämick, 2014). Consequently, the fish community in the littoral is highly diverse (Brosse, Grossman, & Lek, 2007; Fischer & Eckmann, 1997b), but also highly dynamic (Fischer & Eckmann, 1997a) as these resources are used by some species only temporally, for example for a specific time of the year and/or a specific time during ontogenetic growth (Werner & Gilliam, 1984) as a result of ontogenetic habitat shifts (Hofmann & Fischer, 2001). Furthermore, species-specific daytime activity patterns will cause communities to differ also between day and night samples (Pierce et al., 2004).

Despite its diversity and importance, we are not aware of any long-term study (but see Brosse et al., 2007 for within-season studies) focussing on the abundance and biomass dynamics of the juvenile and small fish community in the shallow littoral zone. Hence, our study fills an important gap as knowledge of the dynamics of this community is essential for the understanding of fish recruitment and overall community dynamics (Keast & Harker, 1977; Northcote, 1988; Werner et al., 1977).

Besides re-oligotrophication, fish communities are affected by many other environmental stressors such as acidification, over-fishing, eutrophication, and global warming (Albaret & Laë, 2003; Jacobson, Hansen, Bethke, & Cross, 2017; Jeppesen et al., 2010; Le Quesne & Pinnegar, 2012). The capacity of communities to withstand

these environmental changes, i.e. their resilience, has been suggested to be related to the response diversity of species (Elmqvist et al., 2003; Mori, Furukawa, & Sasaki, 2013): high response diversity might result in asynchronous, compensatory dynamics, which in turn may increase community resilience. Accordingly, resilient community abundances or biomasses are expected to be associated with changes in the dominance structure of the community, i.e. asynchronous or compensatory dynamics (e.g. Gifford, Collie, & Steele, 2009), whereas changes in overall community abundances or biomasses are associated with synchronous changes of species abundances (Pedersen et al., 2017). Likewise, changes in the degree of synchrony of species within a reef fish community are associated with changes in the stability of total fish abundances (Viviani et al., 2019).

Here, we use a unique dataset to analyse spatio-temporal variability in the abundance and biomass catch per unit effort (CPUE) of the juvenile fish community in the littoral zone of Lake Constance. Using a 17-year long data set covering a period in which total phosphorus concentrations declined from mesotrophic to oligotrophic conditions, we test the hypothesis that total CPUE declined due to decreasing productivity, i.e. total CPUE will not show resilience to declining nutrients. Likewise, we expect that the CPUE of most frequent species also decreases, i.e. species show synchronous dynamics in response to oligotrophication.

2 | METHODS

2.1 | Study site and sampling

Lake Constance is a large and deep peri-alpine lake situated at the northern edge of the European Alps, bordering Germany, Switzerland, and Austria (47°N, 09°E). Its littoral zone covers about 10% of the entire lake with a water depth of about 5 m during high water conditions in summer. The trophic status of the lake has changed twice in the past century, with total phosphorus concentrations increasing from <10 µg/L in the 1950s to almost 90 µg/L in the late 1970s, followed by a return to oligotrophic conditions of <10 µg/L by the beginning of the 21st century with

concomitant changes in phytoplankton (Jochimsen, Kümmerlin, & Straile, 2013), zooplankton (Straile, 2015) as well as fisheries catches (Baer, Eckmann, Rösch, & Arlinghaus, 2017). During the study period (1997–2013) total phosphorus concentrations declined from 18 to 6–7 $\mu\text{g/L}$.

Fish were sampled at three sites (Birnaue, Fels, and Langenargen) located 7–29 km apart (Figure S1). The sites differed in several habitat characteristics such as the extension of the littoral zone (from c. 50 m in Fels, towards c. 250 m (Birnaue) and 500 m at Langenargen), substrate characteristics (from sandy sediment with some gravel and pebbles in Langenargen, to gravel and pebbles in Birnaue, and large stones and boulders in Fels), and wind exposure (increasing from Fels, towards Birnaue and Langenargen). For a more detailed description of sampling sites, see Reyjol, Fischer, Lek, Rösch, and Eckmann (2005) in which the three sites Birnaue, Fels, and Langenargen were named North I, South I, and North II, respectively.

Standardised sampling was carried out with beach seines (length 16 m, height 2 m, mesh size 4 mm [bar mesh]) hauled from 1 m water depth to the shoreline. Each sampling event consisted of one seine hauled at three non-overlapping but neighbouring sites. For all analyses, the three successive hauls were averaged to one sampling event. All caught individuals were immediately killed with 2-phenoxyethanol solution or clove oil and stored on ice. In the laboratory, all fish were identified to species level (when in doubt, the pharyngeal teeth of cyprinids were dissected out to verify the identification), counted, and weighed.

Sampling was done monthly from 1997 to 2013 at all three sites—both in the morning and at twilight. For the present study, only spring (May and June) and summer (August and September) samples are considered as sampling in the other months was less regular (Table S1). During these 4 months, a total of 938 beach seines were hauled.

2.2 | Statistical analysis

Catch per unit effort was analysed in term of numbers (CPUE_N) and biomasses (CPUE_B). However, as the results were similar, we report only results for CPUE_B if they differ from CPUE_N results and provide more details about CPUE_B results in the Supporting Information. Prior to statistical analyses, all data were \log_{10} -transformed (Ives, 2015) with zero replacements, corresponding to 50% of minimum detection limits, i.e. 0.5 for CPUE_N and 0.04 for CPUE_B . In addition, we calculated the geometric mean across replicates, which was used as our unit of observations ($n = 320$) in the statistical analyses.

For statistical analysis involving individual species, 11 species with a relative frequency exceeding 10% were included (Figure 1). These 11 species comprised, on average, $98.4 \pm 5.6\%$ of the total CPUE_N of each sample.

Principal component analysis (PCA) was used to visualise the co-variability between species and to identify the spatio-temporal scales (i.e. time of day, season, site, and long-term) separating species occurrences. For PCA, \log -transformed data of species were

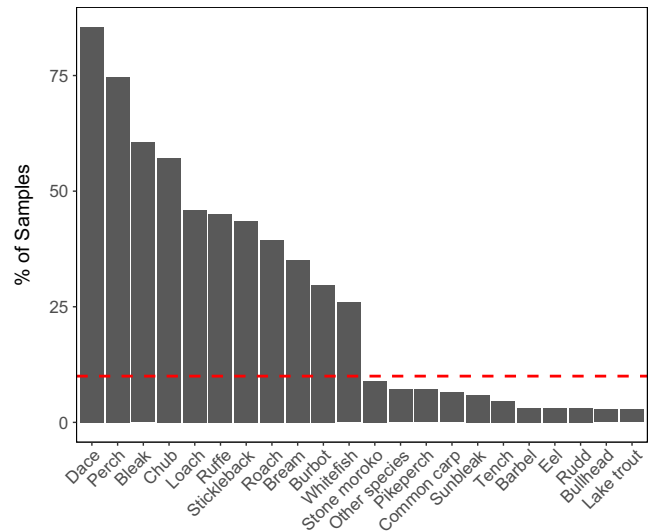


FIGURE 1 Relative occurrence of all 29 species caught in the morning and twilight samples taken at three different sites (Birnaue, Fels, and Langenargen) in spring (May and June) and summer (August and September) months from 1997 to 2013. The spatio-temporal variability of species with relative frequencies exceeding 10% (red, dashed line) was analysed in this manuscript. Other species include: European bitterling (*Rhodeus amarus*, Cyprinidae), Crucian carp (*Carassius carassius*, Cyprinidae), common nase (*Chondrostoma nasus*, Cyprinidae), catfish (*Silurus glanis*, Siluridae), grayling (*Thymallus thymallus*, Salmonidae), gudgeon (*Gobio gobio*, Cyprinidae), pike (*Esox Lucius*, Esocidae), and Prussian carp (*Carassius gibelio*, Cyprinidae) [Colour figure can be viewed at wileyonlinelibrary.com]

centred and standardised. Although a broken-stick model identified four significant principle components, only the first two are shown as only these could be clearly related to spatio-temporal scales.

We used generalised additive mixed models (GAMMs) to study the temporal dynamics of CPUE as GAMMs allow analysis of nonlinear relationships and include auto-correlated errors. GAMMs were established for total CPUE (in the following total CPUE models), for the fish community, consisting of the 11 most frequent species (community models), and for each of the 11 species separately (species CPUE models). All GAMMs included a smooth function of date, an autocorrelated error structure, allowing for non-evenly spaced data (corCAR1), and various combinations of the covariates season, time of day, and site. In addition, the smooth function of date (in the following: $s(\text{date})$) was allowed to vary between the covariates in the total CPUE and community models, i.e. we included smooth factor interactions in the models. To avoid overly complex models, the dimension of the basis of the smooth factor was set to $k = 6$. Unfortunately, during sampling, environmental variables were measured irregularly (i.e. water temperature) or not at all (e.g. nutrient concentrations). Hence, we only analysed the role of covariates and long-term dynamics, but did not include environmental variables in our models. We used the Akaike information criterion (AIC) to compare the different models, and only the five best models (i.e. the models with the lowest AIC) are shown. For each set of GAMMs, analysis of variance (ANOVA) of the best models was performed

to analyse the effects of covariates, $s(\text{date})$, and smooth factor interactions.

Community synchrony was analysed using Kendall's coefficient of concordance (short: Kendall's W ; Legendre, 2005), a non-parametric statistic measuring the concordance between ranked variables, i.e. CPUEs for individual species. Kendall's W is calculated as.

$$W = 12 \frac{\sum R_i^2 - \frac{(\sum R_i)^2}{T}}{N^2 (T^3 - T) - N \sum \tau} \quad (1)$$

where R_i is the ranked time series of species i , N is the number of species, T is the number of time steps, and $\sum \tau$ is a correction for ties such that: $\sum_{i=1}^j (t_i^3 - t_i) 0$. Here, t_i is the number of tied ranks in each group i of j groups of ties (Zar, 1999).

Kendall's W is bound between 0 and 1, and we test its significance using a randomisation procedure that displaces each time series randomly thereby preserving the temporal autocorrelation structure within each time series and generating correct type I errors despite autocorrelation (Gouhier & Guichard, 2014). We consider community dynamics as synchronous if Kendall's W is larger than the 97.5% percentile and as asynchronous if it is smaller than the 2.5% percentile of Kendall's W calculated from randomised time series. Identification of asynchronous dynamics additionally requires negative mean Spearman correlation coefficients between the time series of species (Gouhier & Guichard, 2014).

Before synchrony analyses, CPUE time series were averaged across time of day and site. To investigate the time-scale dependence of Kendall's W , we first computed this metric separately for spring and summer values, but also for time series combining spring and summer data. Secondly, besides for the actual data we also computed Kendall's W for the fitted and residual values of the most supported GAMM. We assume that the smooth term of the GAMM ($s(\text{date})$) extracts the long-term variability, i.e. low-frequency variability of the data, whereas the residuals of the GAMM include high-frequency variability, for example, due to short-term weather variability before each sampling. In the following, we use the terms entire frequency (EF) variability, low-frequency (LF) and high-frequency (HF) variability to refer to the results of Kendall's W calculated based on data, GAMM fits and GAMM residuals, respectively. All calculations were conducted using R (R Core Team, 2018) using the packages *mgcv* (Wood, 2017) and *synchrony* (Gouhier & Guichard, 2014).

3 | RESULTS

Spring and summer catches yielded in total 154,730 fish, which were mainly small and/or juvenile (95% of fish < 9.63 cm). Median CPUE_N was 207 fish and 90% of all samples yielded a CPUE_N between 13 and 1,729 fish. In total 29 different species were caught with dace (*Leuciscus leuciscus*, Cyprinidae) as the most persistent species (caught in 85.49% of all samples, Figure 1). Eurasian perch (*Perca fluviatilis*, Percidae, hereafter referred to as perch), bleak (*Alburnus alburnus*, Cyprinidae), and chub (*Squalius cephalus*, Cyprinidae)

were caught in >50% of all samples, and 6 species—stone loach (*Barbatulus barbatulus*, Nemacheilidae, hereafter referred to as loach), ruffe (*Gymnocephalus cernua*, Percidae), three-spined stickleback (*Gasterosteus aculeatus*, Gasterosteidae, hereafter referred to as stickleback), roach (*Rutilus rutilus*, Cyprinidae), bream (*Abramis brama*, Cyprinidae), burbot (*Lota lota*, Lotidae), and whitefish (*Coregonus* spp., Salmonidae)—were caught in >25% of all samples, all other species being caught in <10% of all samples (Figure 1).

3.1 | Total CPUE analysis

At all sites, total CPUE_N was higher in summer than spring (Figure 2), and twilight catches were higher than morning catches in spring, but not so in summer. The catches at site *Fels* were lower than the catches at the other two sites (Figure 2). Accordingly, the model with the lowest AIC (Table 1) included the covariates site, time of day, season, the interaction between time of day and season, and $s(\text{date})$. However, CPUE_N did not show a temporal trend (Figure 2) and $s(\text{date})$ did not contribute significantly to the model (Table 1). The best model for total CPUE_B included the same covariates and interactions, but biomass increased significantly during the study period ($p = 0.001$; Table S5 and Figure S4).

3.2 | Community CPUE analysis

Principal component analysis ordination of the 11 most frequent species also revealed the importance of season and time of day for catch variability (Figure 3). The first axis (27.2% explained variability) separated species mainly caught in spring (i.e. whitefish and sticklebacks) from species mainly caught in summer (i.e. bleak, bream, chub, dace, perch, and roach). On the second axis (16.1% explained variability), species predominantly caught in the twilight samples (i.e. burbot, loach, and ruffe) were separated from the other species.

The best two community models suggest that species differ significantly in their spatio-temporal distribution patterns (Table 2). The highest ranked model included all higher order interactions of covariates with the exception of the fourfold interaction between site, season, time of day, and species, whereas the second ranked model additionally excludes the three-way interactions between site, time of day, and season. However, both models—as all the top-ranked models—include the smooth factor interaction between species and $s(\text{date})$, indicating that species clearly differ in their long-term dynamics. The best model revealed significant relationships for the covariates season and species as well as for the interaction between all covariates, except for the three-way interactions between site, time of day, and season (Table 2). With the exception of chub ($p = 0.077$), whitefish ($p = 0.474$), and loach ($p = 0.169$), all species showed significant long-term variability (Table 2 and Figure 4). Catches of bream ($p = 0.002$), burbot ($p < 0.001$), and ruffe ($p < 0.001$) significantly decreased, whereas that of perch ($p < 0.001$) significantly increased during the study period. Other species showed non-monotonic

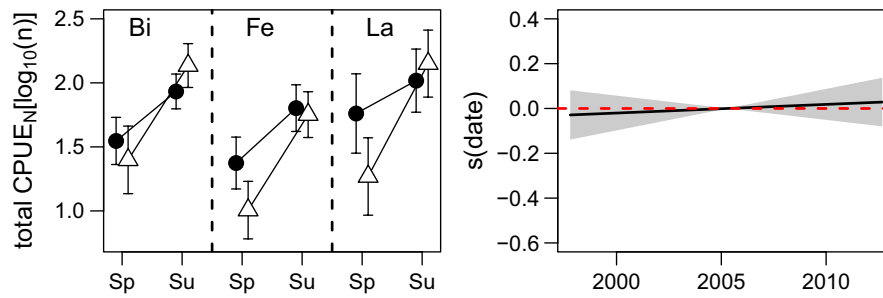


FIGURE 2 Left panel: Total catch per unit effort ($\log_{10}(\text{CPUE}_N) \pm$ standard error) separated by time of day (white triangle = morning; black circle = twilight), season (Sp = spring; Su = summer), and site (Bi = Birnau, Fe = Fels, La = Langenargen). Right panel: Smooth function (mean \pm 1 SE) of the total CPUE_N development according to the best fit model (m34 in Table 1). No significant long-term patterns are evident ($p = 0.599$) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Generalised additive mixed models with various combinations and interactions between covariates (time of day, season, and site) and the smooth function of time (with or without interaction) were calculated for the abundance data of the total catch per unit effort (CPUE_N: total CPUE_N models). The best five models are listed, starting with the model with the highest weight and therefore the best fit for the data according to the Akaike information criterion (AIC). dAIC indicates the differences between the AIC of the different models and the best model. Analysis of variance (ANOVA) values are only shown for the model with the best fit

Total CPUE _N models	df	dAIC	Weight
m34 = site + time of day*season + s(date)	10	0.0	0.696
m33 = site + time of day*season + s(date, by = season)	12	4.0	0.096
m24 = site*time of day + time of day*season + s(date, by = time of day)	14	5.0	0.058
m20 = site*time of day + time of day*season + s(date, by = season)	14	5.0	0.058
m28 = site*time of day + time of day*season + s(date, by = site)	16	7.5	0.016

ANOVA (m34)			
Parameter	df	F	p-value
Site	2	8.96	<0.001
Time of day	1	8.601	<0.001
Season	1	69.469	<0.001
Time of day:Season	1	11.531	0.001
s(Date)	1	0.751	0.599

Significant values are found for site ($p < 0.001$), time of day ($p < 0.001$), season ($p < 0.001$), and time of day:season ($p = 0.001$).

dynamics with, for instance, maximum catches of bleak ($p < 0.001$), dace ($p < 0.001$), and roach ($p = 0.014$) between 2005 and 2010, and sticklebacks ($p < 0.001$) with minimum catches around 2006 (Table 2 and Figure 4). For most of the species, temporal patterns resulted from the dynamics in one season, i.e. the one in which they were most abundant (Table S4 and Figure S3a,b). The temporal dynamics of species in the community models for CPUE_B resembled those for CPUE_N (Table S6 and Figure S6), except for dace, which significantly increased in biomass over time ($p < 0.001$; Table S6 and Figure S6), and perch, which experienced an initial decrease in biomass but increased after 2001 (Table S6 and Figure S6).

Species CPUE models (Figure 5 and Table S2) revealed that six species (bleak, bream, chub, perch, roach [$p < 0.001$], and dace [$p = 0.019$]) had higher numbers in the summer catches, while whitefish ($p < 0.001$) was only abundant in spring. Whitefish ($p = 0.001$) also showed significantly lower numbers at Langenargen compared with

the other sites, whereas ruffe ($p = 0.018$) was most abundant at this site. Between sites, seasonal differences in CPUE were found for bleak, chub, and roach (significant season and site interaction: $p = 0.002$, $p < 0.001$, $p = 0.017$, respectively). Whitefish ($p = 0.019$) was significantly more abundant in the morning, while perch, ruffe, and stickleback ($p < 0.001$, $p = 0.002$, $p < 0.001$, respectively) demonstrated significantly higher numbers at twilight. The seasonal increase in CPUE differed between morning and twilight samples for bleak, burbot, dace, loach, and perch (significant interaction between time of day and season: $p < 0.001$, $p < 0.001$, $p = 0.002$, $p = 0.001$, $p < 0.001$, respectively). Differences between twilight and morning samples were more pronounced at Birnau compared with the two other sites for loach and stickleback (significant time of day and site interaction, $p = 0.002$ and $p = 0.02$, respectively). The interaction of all three variables was significant for burbot and ruffe ($p < 0.001$ and $p = 0.034$). Burbot was most abundant in the twilight summer

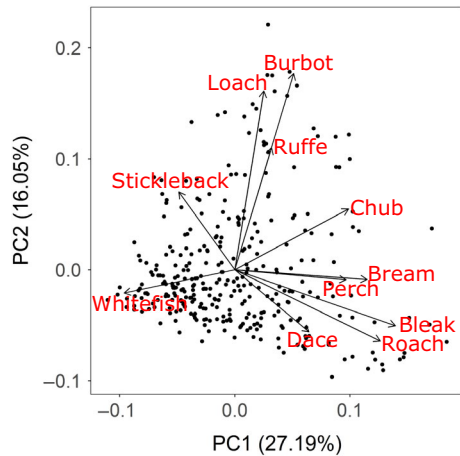


FIGURE 3 Principal component (PC) analysis of catch per unit effort of the 11 most frequent species. PC1 axis (27.19% explained variability) separates species mainly caught in spring (i.e. whitefish and sticklebacks) versus summer (e.g. bleak), while species are grouped by morning (e.g. dace) and twilight (i.e. burbot, loach, and ruffe) activity on the PC2-axis (16.05% explained variability) [Colour figure can be viewed at wileyonlinelibrary.com]

catches with the highest numbers at Birnau, followed by Fels and Langenargen. Ruffe, too, was most abundant in the twilight catches, showing higher numbers in summer at Birnau and Fels, while it was more abundant in spring at Langenargen.

3.3 | Synchrony analysis

Kendall's W indicates significant synchrony for the entire, low-, and high-frequency variability of time series including spring and summer data, as well as for the high-frequency variability of the spring-time series (Figure 6). In contrast, Kendall's W was smaller than expected by chance for low-frequency spring and summer data, which in combination with a negative mean Spearman correlation coefficient suggests asynchrony.

4 | DISCUSSION

Our study revealed large diel and seasonal differences, as well as long-term changes of the fish community, but notably no decline in total CPUE in the littoral zone of Lake Constance. Hence, we found no support for our first hypothesis, but evidence for resilience of the total CPUE of the littoral fish community in response to oligotrophication.

4.1 | Total CPUE resilience is unlikely the result of low power to detect changes

The lack of response of total CPUE might, in principle, also have methodological reasons: Firstly, total phosphorus concentrations in Lake Constance started to decline in the early 1980s, while responses of the pelagic food web were observed with some delay,

for instance, phytoplankton biomass dropped in the late 1980s/early 1990s (Jochimsen et al., 2013), zooplankton biomass around the mid- 1990s (Straile, 2015), and whitefish yield at the end of the 1990s (Baer et al., 2017). Thus, pelagic responses to nutrient decline were observed already before the start of our beach seine monitoring, and we cannot fully exclude the possibility that we missed a first initial response of total CPUE to oligotrophication. However, major changes in fish catches were also observed during our study period, for example for whitefish and perch (Baer et al., 2017), and we consider it unlikely that the failure to detect any oligotrophication response of total CPUE can be attributed to its occurrence before our study period. Secondly, problems with detecting environmental change effects on CPUE data have been termed *notorious* due to high inter-annual variability of fish recruitment and abundance (Rose, 2000) and the rather high variability (low precision) of CPUE estimates due to the small area of the beach seine relative to the scarce and patchy distribution of fish and their movement patterns (Bayley & Herendeen, 2004; Leslie & Timmins, 1992). High sampling variability might therefore potentially mask long-term trends of CPUE. However, in contrast to total CPUE, we detected clear trends at the species level, making it also unlikely that the failure to support our first hypothesis was due to large sampling variability.

4.2 | Ecological causes for total CPUE dynamics and resilience

Several ecological processes possibly contributed to the resilience of total CPUE to oligotrophication: littoral productivity might not—less strongly—have declined relative to pelagic productivity due to the release of phosphorus from littoral sediments (Güde, Seidel, Teiber, & Weyhmüller, 2000), allochthonous input of organic C from the shore region (Güde & Straile, 2016), and/or improved light conditions for benthic producers due to the decline of phytoplankton (Vadeboncoeur, Vander Zanden, & Lodge, 2002). In addition, food availability for fish in the littoral might have increased during the study period because of the invasion of the mysid *Limnomysis benedeni*, which inhabits the littoral but feeds on plankton thereby channelling pelagic food resources to the littoral (Rothhaupt, Hanselmann, & Yohannes, 2014). Furthermore, the decline of piscivorous perch with oligotrophication as evidenced from fishermen catches (Eckmann, Gerster, & Kraemer, 2006) might have released juvenile fish from predation pressure.

In addition to oligotrophication, we cannot exclude that also climate warming might have contributed to the observed changes in community composition. Water temperatures in Lake Constance increased during the study period and thus may have impacted cold-water species negatively (Jeppesen et al., 2012). For the two cold-water species (i.e. whitefish and burbot; Hofmann & Fischer, 2004; Jeppesen et al., 2012) in our dataset, we could either not detect any long-term change (whitefish) or observed a decrease (burbot). However, as oligotrophication and warming occurred concomitantly, it is difficult to disentangle the effects of both factors based on the data of juvenile fish CPUE.

TABLE 2 Generalised additive mixed models with various combinations and interactions between covariates (time of day, season, site, and species) and the smooth function of time (with or without interaction) were calculated for the abundance data of the community consisting of the 11 most frequent species (community models). The best five models are listed, starting with the model with the highest weight and therefore the best fit for the data according to the Akaike information criterion (AIC). dAIC indicates the difference in AIC between the different models and the best model. ANOVA values are only shown for the model with the best fit

Community models	df	dAIC	Weight
m19 = site*time of day*season + species*time of day*site + species*time of day*season + species*season*site + s(date, by = species)	136	0.0	0.505
m20 = species*time of day*site + species*time of day*season + species*season*site + s(date, by = species)	134	0.1	0.485
m18 = site*time of day*season*species + s(date, by = species)	156	7.9	0.009
m21 = site*time of day*season + species*time of day*season + species*season*site + s(date, by = species)	116	29.5	<0.001
m23 = site*time of day*season + species*time of day*site + species*time of day*site + s(date, by = species)	116	68.5	<0.001

ANOVA (m19)			
Parameter	df	F	p-value
Site	2	1.392	0.249
Time of day	1	3.316	0.069
Season	1	138.67	<0.001
Species	10	17.561	<0.001
Site: Time of day	2	8.992	<0.001
Site:Season	2	12.461	<0.001
Time of day:Season	1	14.485	<0.001
Time of day:Species	10	8.55	<0.001
Site:Species	20	2.739	<0.001
Season:Species	10	24.485	<0.001
Site: Time of day:Season	2	1.976	0.139
Site: Time of day:Species	20	3.399	<0.001
Time of day:Season:Species	10	14.435	<0.001
Site:Season:Species	20	5.337	<0.001
s(Date):Bleak	3.789	20.391	<0.001
s(Date):Bream	1	9.79	0.002
s(Date):Burbot	1	13.078	<0.001
s(Date):Chub	1	3.139	0.077
s(Date):Dace	2.310	10.434	<0.001
s(Date):Whitefish	1	0.513	0.474
s(Date):Loach	1	1.891	0.169
s(Date):Perch	1	25.603	<0.001
s(Date):Roach	2.173	4.525	0.014
s(Date):Ruffe	1	97.595	<0.001
s(Date):Stickleback	4.387	9.672	<0.001

Significant values are found for season ($p < 0.001$), species ($p < 0.001$), site:time of day ($p < 0.001$), site:season ($p < 0.001$), time of day:season ($p < 0.001$), time of day:species ($p < 0.001$), site:species ($p < 0.001$), season:species ($p < 0.001$), site:time of day:species ($p < 0.001$), time of day:season:species ($p < 0.001$), and site:season:species ($p < 0.001$), as well as for bleak ($p < 0.001$), bream ($p = 0.002$), burbot ($p < 0.001$), dace ($p < 0.001$), perch ($p < 0.001$), roach ($p = 0.014$), ruffe ($p < 0.001$), and stickleback ($p < 0.001$).

While we are unsure about the relative importance of these changes for CPUE, there is evidence that fish species showed response diversity (sensu Elmqvist et al., 2003) to environmental

change, i.e. the CPUE of three species (dace, loach, and perch) increased, while the CPUE of four other species (bream, burbot, chub, and ruffe) decreased significantly during the study period.

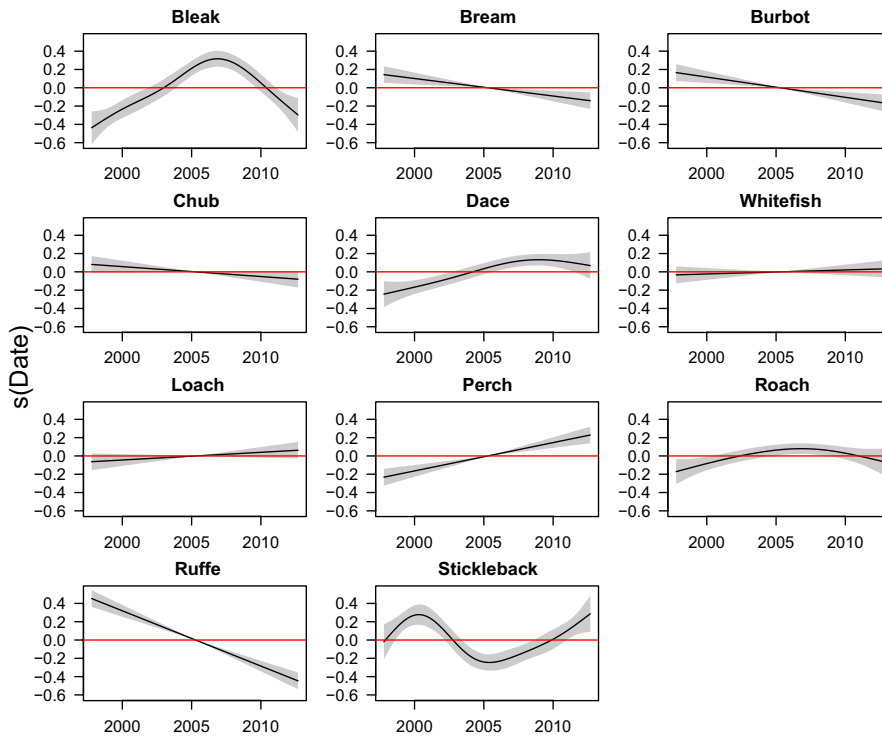


FIGURE 4 Smooth functions (mean \pm 1 SE) of the catch per unit effort development of the 11 most frequent species according to the best fit GAMM (m19 in Table 2). Absence of a temporal pattern is rejected for bleak at $p < 0.001$, bream: $p = 0.002$, burbot: $p < 0.001$, chub: $p = 0.077$, dace: $p < 0.001$, whitefish: $p = 0.474$, loach: $p = 0.169$, perch: $p < 0.001$, roach: $p = 0.014$, ruffe: $p < 0.001$, and stickleback: $p < 0.001$ [Colour figure can be viewed at wileyonlinelibrary.com]

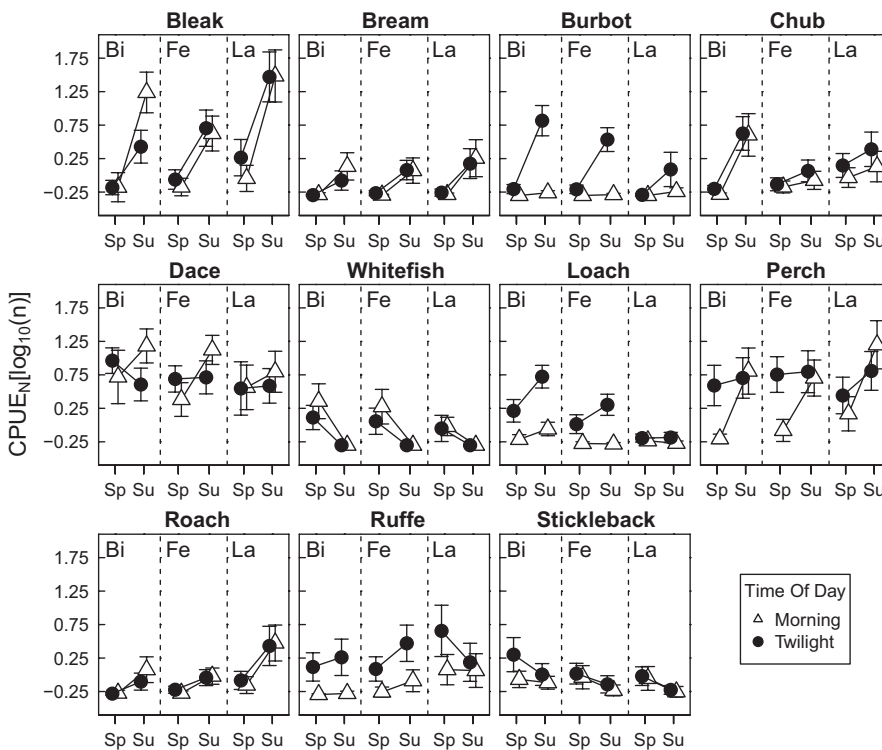


FIGURE 5 Spatio-temporal variability of fish species catch per unit effort ($CPUE_N$; mean \pm 1 SE of \log_{10} -transformed data). $CPUE_N$ at the three sites *Birnau* (Bi), *Fels* (Fe), and *Langenargen* (La) during spring (Sp) and summer (Su) and in the morning (open triangle) versus twilight (filled circle) samples

4.3 | Differences in CPUE between species

Spatio-temporal variability of species CPUE was strongly determined by the behaviour and life history of species. Behavioural adaptations determined diel differences in catches and partly the differences between sites. Predominantly nocturnal species such as burbot, loach,

and ruffe (Ryder & Pesendorfer, 1992; Schleuter & Eckmann, 2008; Welton, Mill, & Pygott, 1991) were mostly caught in the twilight samples. During the day, juvenile burbot and loach hide between stones and gravel (Fischer & Eckmann, 1997b), suggesting that these species should be mostly caught at sites that providing such shelter. This is also supported by our data as these species were most often caught at the

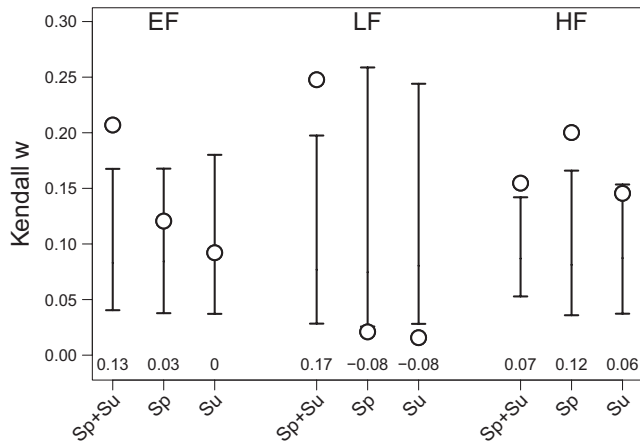


FIGURE 6 Community synchrony (Kendall's W) of the 11 most frequent fish species calculated for observed catch per unit effort (entire frequency, EF; low-frequency, LF; and high-frequency, HF), catch per unit effort for time series consisting of both spring and summer (Sp + Su) samples, as well as of spring (Sp) and summer (Su) samples separately. Vertical lines comprise 95% of the distribution of W calculated from randomised time series. Numbers below vertical lines indicate the mean Spearman rank correlation coefficient

two stony sites Birnau and Fels and less frequently at Langenargen, which is characterised by fine sediment. The latter habitat type is preferred by bream, perch and roach (Fischer & Eckmann, 1997b a; Reyjol et al., 2005) and at least for roach our data showed higher numbers at this site. CPUE was also strongly determined by the life histories of species, i.e. their spawning phenologies and ontogenetic habitat shifts. Higher catches in late summer than late spring are probably due to the fact that juvenile fish of several species spawn between late spring and early summer (i.e. bleak, loach, perch, roach, ruffe, bream, and chub (Berg, 1993). In contrast, the absence of whitefish in the late summer samples results from a habitat shift of juvenile whitefish from the littoral to the pelagic zone in summer (Eckmann & Rösch, 1998).

4.4 | Community synchrony and compensatory dynamics

The type of community dynamics observed was scale-dependent. Time series combining spring and summer data include seasonal, short-term, and multiannual variability, whereas only short-term and/or multiannual variability of time series is considered when spring and summer CPUE is analysed separately. Generally, synchronous dynamics were observed when the seasonal variability was taken into account. This suggests synchrony between species because for most species, CPUE was higher in summer than in spring. In contrast, when considering spring and summer time series separately, low frequency, i.e. multiannual, variability was significantly asynchronous, whereas high-frequency variability tended to be synchronous. Such time-scale dependent variability in community dynamics has been observed also in plankton systems (e.g. Keitt & Fischer, 2006; Vasseur & Gaedke, 2007). For example, in an acidified

basin of Little Rock Lake (Wisconsin, USA) synchronous dynamics were observed between two *Daphnia* species at the seasonal scale, whereas compensatory dynamics were observed at multiannual time scales presumably due to different sensitivities of the two species to acidification (Keitt & Fischer, 2006). Likewise, in our study, significant asynchronous dynamics were only observed for the juvenile fish community when spring and summer were considered separately, but only at the low-frequency time scale. Presumably, the rather high variability of CPUE estimates (see above) resulted in a low power to detect asynchronous dynamics when considering the entire variability or when considering only high-frequency variability. Interestingly, significant synchronous dynamics were also observed for high-frequency data in spring suggesting that small-scale variability influenced the CPUE of various species in a similar way. However, in response to oligotrophication, i.e. at the low-frequency multiannual scale, we did not find evidence for synchronous dynamics, which contrasts our second hypothesis. Rather, Kendall's W for low-frequency multiannual variability indicates asynchronous, i.e. compensatory, dynamics of species. For example, the decline of ruffe might have contributed to the observed increase in perch catches. Both species compete, at least partially, for food resources, and competition due to large ruffe populations is thought to affect perch populations negatively (Eckmann et al., 2006). Hence, a decline of ruffe might have released perch from competition, which may have at least contributed to the compensatory increase in perch CPUE. However, the increase of juvenile perch might also be due to reduced top-down control due to a decline of piscivorous and cannibalistic larger perch with oligotrophication. Eckmann et al. (2006) report that larger perch in Lake Constance feed almost exclusively on juvenile perch. Hence, if the perch catch of fishermen is a good proxy for the abundance of cannibalistic perch, mostly juvenile perch, but not juvenile ruffe, might have benefitted from the decline of older perch.

Our results concur with those of other studies showing that fish communities can exhibit compensatory dynamics in response to environmental change (Gifford et al., 2009) and show increasingly asynchronous dynamics after disturbance (Viviani et al., 2019). However, with increasing disturbance, the capacity for compensatory dynamics will decline, which might result in synchronous population reductions and hence decreased total abundances. For example, over-fishing resulted in a synchronous collapse of the groundfish community in the Northwest Atlantic (Pedersen et al., 2017), and there was no potential for compensation in a fish community in a lake undergoing acidification (Vinebrooke et al., 2003). In Lake Constance, phytoplankton exhibited compensatory dynamics during a period when total phosphorus concentrations varied between 35 and 90 $\mu\text{g/L}$, but synchronous dynamics when a longer time period was considered where total phosphorous concentrations ranged between 7 and 90 $\mu\text{g/L}$ (Jochimsen et al., 2013). Hence, we cannot exclude the possibility that an earlier start of our study, and thus a larger environmental gradient, would have resulted in different conclusions with respect to the type of community dynamics observed.

We are not aware of the existence of other investigations with explicit focus on the type of community dynamics in lakes undergoing oligotrophication, but the decline in total CPUE observed in several lakes (Gerdeaux et al., 2006; Jeppesen, Jensen, & Søndergaard, 2002) suggest that compensation—if any—was not strong enough to sustain resilience of CPUE. However, when comparing the results of our study with those of other studies analysing effects of trophic status or oligotrophication on fish communities, it is important to note that this study specifically considers the small fish (mainly juveniles) community in the littoral zone of a large lake changing from mesotrophic to oligotrophic conditions. Hence, comparisons with studies analysing whole-lake fish communities (Jeppesen et al., 2005; Ludsins, Kershner, Blocksom, Knight, & Stein, 2001; Persson, Diehl, Johansson, Andersson, & Hamrin, 1991) or responses of fish communities to changes from eutrophic to mesotrophic conditions (Jeppesen et al., 2000) or with studies analysing the non-standardised catches of fishermen (Gerdeaux et al., 2006; Massol, David, Gerdeaux, & Jarne, 2007) should be done with caution as these are targeted towards the entire fish community, including the larger fish. Partially, species-specific responses do match with predictions derived from studies comparing lakes with different trophic status or during oligotrophication, which suggest absolute and/or relative declines of, for instance, bream, roach, and ruffe CPUE (Jeppesen et al., 2012; Mehner, Diekmann, Brämick, & Lemcke, 2005), and absolute or relative increases in perch (Jeppesen et al., 2005) with oligotrophication.

4.5 | Consequences for ecosystem dynamics

The temporal dynamics of fishermen catches in Lake Constance did not correspond with the dynamics of littoral CPUE. The fishermen catches of the two locally most valued fish species, perch and whitefish, strongly declined during the study period, and the average catches during the last 5 years of our study period (2009–2013) were 48 and 60% of the catches during the first 5 years of our study period for perch and whitefish, respectively (Baer et al., 2017). In contrast, we found either no change (whitefish) or even an increase (perch) in juvenile CPUE of these species in the littoral. This discrepancy suggests that recruitment of these two fishes was not hampered by oligotrophication, but that processes affecting these species after their juvenile stage, i.e. slow growth and increased mortality, might be responsible for the decline in fishermen catches. Conclusions drawn about the type of community dynamics in lake systems might, therefore, differ whether the juvenile community or the large fishes typically targeted by fishermen are considered. While the latter might be important regarding ecosystem services for humans, the type of dynamics of the juvenile fish community might be of considerable importance for ecosystem dynamics as the smallest size group of fish (1+ in spring and 0+ in summer/autumn) often dominate predation pressure on lower trophic levels, and strong recruitment might reduce the growth of juvenile and older fish

(Hamrin & Persson, 1986; Townsend, 1989). Hence, despite declines in fishermen catches, compensatory dynamics of juvenile fish, i.e. compensatory dynamics of recruitment, might at least for a certain period sustain a high predation pressure on littoral zooplankton and meiobenthos, thereby influencing ecosystem dynamics and enhancing competition between fish species for food. Likewise, resilience of the juvenile fish community and prolonged predation pressure on e.g. zooplankton might be also an important factor contributing to delayed food web responses to oligotrophication and hysteresis in respect to nutrient dynamics. Clearly, more studies on the juvenile fish community in lakes undergoing oligotrophication are needed to test whether resilience of juvenile fish is a general phenomenon and to fully understand its implications for food web structure.

5 | CONCLUSION

Our study revealed large spatio-temporal variability of the juvenile fish community in the littoral zone of a large lake. CPUE was strongly influenced by behavioural and life cycle adaptations of the species. In addition, we observed large changes in community composition in which significant declines of some species (bream, burbot, chub, and ruffe) were compensated by increases of others (dace, loach, and perch) during a shift from mesotrophic to oligotrophic conditions. This might suggest that the overall predation pressure of juvenile fish on littoral zooplankton and macrozoobenthos did not change strongly during the study period. The type of community dynamics observed was scale-dependent with synchronous dynamics resulting from the seasonal increase in the CPUE of most species and compensatory dynamics resulting from low-frequency multi-annual variability. The observed changes in the littoral zone of juveniles of commercially important species (perch, whitefish) did not match with the dynamics of those species in fishermen catches. This suggests that processes resulting in a decline in fishermen catches operate mostly after the juvenile stage. Total CPUE was remarkably stable, suggesting resilience of total juvenile fish abundance in the littoral zone to the shift from mesotrophic to oligotrophic conditions, possibly due to species-specific increases in feeding conditions and compensatory dynamics.

ACKNOWLEDGEMENTS

We thank Philipp Fischer, all students and technical assistants involved in the intensive field work, as well as Myriam Schmid and Pia Mahler, who identified and counted the individuals. Comments by Jelena Pantel, Eva Lievens, and several anonymous reviewers greatly enhanced the content of the manuscript. This work was supported by the European Regional Development Fund: Interreg V-A-Germany-Austria-Switzerland-Liechtenstein (Alpenrhein-Bodensee-Hochrhein 2014–2020) under grant no. ABH060 ("SeeWandel: Life in Lake Constance – the past, present and future") and the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – 298726046/GRK8872.

DATA AVAILABILITY STATEMENT

Data are available from the Fisheries Research Station Baden-Württemberg (poststelle-ffs@lazbw.bwl.de).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Sabel M, Eckmann R, Jeppesen E, Rösch R, Straile D. Long-term changes in littoral fish community structure and resilience of total catch to re-oligotrophication in a large, peri-alpine European lake. *Freshwater Biology*. 2020;65:1325–1336. <https://doi.org/10.1111/fwb.13501>