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Changes in the fish species composition of all Austrian lakes >50 ha during the last 150 years

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Abstract The fish communities of all Austrian natural lakes ($n = 43$) larger than 50 ha in surface area were assessed and the historical fish communities in *c*. 1850 were reconstructed. During the last 150 years, the fish communities of Austrian lakes have altered: in 49% of lakes at least one indigenous fish species, usually sensitive or small-bodied taxa, is now missing. Conversely, in all but one of the 43 lakes the number of fish species has increased. In particular, certain fish species of interest to angling and commercial fisheries now occur in more lakes. Generalised linear models were used to identify variables that would explain the loss of fish species using categories of lake use (ranking score). The category *human population density* around the lakes seemed to be one of the main causes for the loss of fish species.

KEYWORDS: fish communities, human impact, indigenous fish species, loss of fish species, Water Framework Directive.

Introduction

In recent years, increased interest in aquatic ecosystem health has created a need for approaches to assess aquatic ecosystem condition. The European Union Water Framework Directive (EU-WFD) uses the biological elements phytoplankton, macrophytes, benthic invertebrate fauna and fish to assess the status of lakes (EU 2000). To determine ecological condition, knowledge about the near natural state of ecosystems, i.e. before human degradation, is important. Unfortunately, lakes with undisturbed, natural fish communities, which can be used as reference, are not available in Austria; anthropogenic impacts over the past 100 years have affected European freshwater ecosystems and cultural eutrophication has caused changes in fish communities. For instance, most Austrian lakes have undergone cultural eutrophication and more recent re-oligotrophication (Gassner, Jagsch, Zick, Bruschek & Frey 2002). The modification of lake in- and outflows represents another important stressor for aquatic organisms. Many of the Austrian lakes are affected by hydroelectric power plants and exhibit water level fluctuations between 1 m and approximately 15 m.

For centuries most Austrian lakes have been managed for commercial fisheries and angling. Consequently, changes in composition or abundance of fish assemblages not only result from degradation of the environment, but also through fisheries management. Annual stocking programmes and overfishing often resulted in a deterioration of the fish communities. One of the major impacts on aquatic ecosystems is suggested to originate from fish stock enhancement practices

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(Cowx 1998), particularly species from North America favoured by anglers. To date, 27 species have been intentionally or accidentally introduced in Austria (Mikschi 2002). Not all of them are able to reproduce successfully, but many have established in Austrian lakes.

Generally there is an enormous scientific deficit concerning knowledge of fish communities in Austrian lakes. There are valid fish species lists for only two of the nine Austrian provinces: Lower Austria (Kummer 1999) and Carinthia (Honsig-Erlenburg & Petutschnig 2002). However, the fish species of particular lakes (e.g. Lake Constance: Fischer & Eckmann 1997) have been studied and there are several studies on the ecology, biology and management of specific fish species like coregonids *Coregonus* sp. (e.g. Wanzenböck & Jagsch 1998; Wanzenböck, Gassner, Hassan, Lahnsteiner & Hauseder 2002; Gassner, Hassan & Wanzenböck 2004; Lahnsteiner & Wanzenböck 2004) or perch, *Perca fluviatilis* L., but a complete list of fish species for all Austrian lakes is not available.

Unfortunately, no undisturbed large lakes with native fish communities are available in Austria, thus the native fish communities can only be characterised using historical information. Steedman, Whillans, Behm, Bray, Cullis, Holland, Stoddart & White (1996) and Kelso, Steedman & Stoddart (1996) showed that historical information was helpful for the reconstruction of original conditions in the Great Lakes region of North America.

The aim of this study was to assess the present fish communities of all natural Austrian lakes > 50 ha, and to reconstruct the original native fish communities of these lakes, before intensive human interference. These reconstructed historic fish assemblages provide an essential basis for the implementation of the EU-WFD, and knowledge about the historical fish communities is very useful for fisheries management in the future, especially for stocking programmes. The relationship between the loss of fish species and various categories of human impact were also examined.

Materials and methods

Data collection

The native fish species composition of all Austrian natural lakes ($n = 43$) larger than 50 ha in surface area was reconstructed using various historical documents and historical harvest records. Historical data on fish communities were collected from Austrian archives, libraries, an inquiry to fisheries managers and the internet (FishBase; homepages of museums). Further, the fish collection of the Natural History Museum in Vienna was searched for deposits of fish species from Austrian lakes.

A total of 1161 historical quotations about fishes in Austrian lakes was analysed. The references ranged from monthly historical papers, to books and hand-written documents. In addition, there were 172 historical museum specimens (21 species) verified for 22 different lakes. Most of the historical fish references dated from 1850 to 1900, nevertheless the oldest documents used in this study dated back to the 15th century. For each lake all data collected were summarised as a preliminary fish species list and the native fish communities were reconstructed using six specific criteria (Table 1).

The nomenclature of the Austrian freshwater fishes used in the past was quite different from the current nomenclature according to Spindler (1997). For this reason, historical data were checked for synonyms explained in, for example Fitzinger (1832); Heckel (1854); Heckel & Kner (1858); Henschel (1890) and Kottelat (1997), and they were fitted to the current nomenclature of the Austrian fresh water fishes according to Spindler (1997). Coregonid fishes were named as *Coregonus* sp. for simplification. The results of the reconstruction were expressed as lists of native fish species in *c*. 1850 for each of the large Austrian lakes.

Table 1. Criteria list for the reconstruction of the native fish species lists (based on the preliminary species lists) in the Austrian lakes

No.	Definition
1.	Alien species were excluded from the preliminary lists of native fish species [i.e. species introduced from abroad, e.g. pumpkinseed, *Lepomis gibbosus* (L.)]
2.	Translocated fish species were excluded [i.e. species native to another Austrian region, but untypical for the location, e.g. European eel, *Anguilla anguilla* (L.), or pikeperch, *Sander lucioperca* (L.), in the Salzkammergut lakes]
3.	In the historical literature running waters fish species, such as brown trout, *Salmo trutta* f. *fario* L., grayling, *Thymallus thymallus* (L.), barbel, *Barbus barbus* (L.), spirlin, *Alburnoides bipunctatus* (Bloch), dace, *Leuciscus leuciscus* (L.), ide, *Leuciscus idus* (L.) and nase, *Chondrostoma nasus* (L.) were often described as inhabiting standing waters. Nevertheless these fish species inhabit lakes only for a short period of time and do not live there over their whole life cycle. Thus they were not considered in the present study
4.	Sometimes there was confusions of names; incorrectly named fish species were excluded
5.	A lack of available data resulted in exclusion from the preliminary list of native fish species
6.	In a few unclear cases, the decision about native presence/absence of a fish species was done by expert opinion

The current fish species composition was compiled using an inquiry to the fisheries management committee of the particular lakes and, if available, using recent fishing surveys (e.g. Gassner & Wanzenböck 1999). The questions to the fisheries management committees of the Austrian lakes were: 'What are the contemporary fish species in your lake?'; 'What are the native fish species in your lake?' and 'Is there some recent or historical literature available about your lake?' All but one questionnaire was returned and they contained useful data that could be analysed. The construction procedure of the current fish species lists was similar to the historical fish species lists except point 1 (alien species) and 2 (translocated species) (Table 1). Although an inquiry is recognised as not being an error-free method to assess the current fish assemblages, it provides a first insight to the status of the fish species assemblages in Austria.

Statistical analysis

The goal of the statistical analysis of the data was to understand the relationship between a target variable and the predicting variables. However, because of the categorical or binomial variables, a classical least squares regression approach would not be appropriate because nonlinear relationships and heteroscedasticity would result in a poor model fit. Therefore a more flexible class of models, namely generalised linear models (GLMs), was used (McCulloch & Searle 2001; Simonoff 2003). GLMs allow a unified treatment of statistical methodology for several important classes of models. The binomial model for binomial target variables and the Poisson model for categorical target variables were considered. The analysis was done with the statistics software package R (available at http://cran.R-project.org) following the details of Venables & Ripley (1999). To keep the models simple, only main effects models were considered. For the model selection, a stepwise procedure was used where the value of the Akaike Information Criterion (AIC) was minimised. The AIC (Akaike 1974) is a number associated with each model, it is most commonly used for model selection. A measure for the model fit was the residual deviance which measures the discrepancy between observed and fitted values. This measure is approximately chi-squared distributed (with the corresponding residual degrees of freedom), and a chi-squared *P*-value can be computed. If this chi-squared *P*-value is $< 5\%$, the model fit can be considered to be poor.

Chovanec, Fink, Gruber, Jagsch, Nagy, Weber & Wimmer (2002) summarised data about the use of Austrian lakes and their catchment areas. Based on this information, it was hypothesised that different human activities would impair the fish species assemblages of the lakes, and thus nine predicting variables were defined. Indicators for human stressors were the intensity of tourism, fishery and water removal, and the variables human population density and the amount of soil sealing in the catchment area. In lakes with high values for these typical human stressors more species should be missing than in lakes with, for example, greater areas for agriculture or forest and bushes in their catchments. Furthermore, it was hypothesised that membership of one of the four lake types in Austria based on fish community structure as defined by Gassner, Wanzenböck, Zick, Tischler & Lahnsteiner (2005) would have an impact on the fish assemblages, since each type is managed in completely different ways concerning fisheries, use for leisure activities and hydroelectric power generation. Lake trophy was also selected as a defining variable because this may influence the survival of sensitive, oxygen demanding species. For the calculation of the GLMs, five different target variables were defined relating to missing fish species, varying from binominal data (yes/no) to species categories. It was hypothesised that human stressors (predicting variables) accounted for the loss of fish species. With reference to so-called sentinel species of the fish based Austrian lake types, minnow is missing in some Minnow Lakes. As there were no other sentinel species missing, only the variable of 'is minnow missing' was used for the GLM analyses.

To analyse the impact of intensity of human activity on the fish species inhabiting lakes, the data of Chovanec *et al.* (2002) were adapted and pooled into categories. Afterwards, the different categories of lake use (ranking score, Table 2) were tested for their contribution to the loss of fish species (Table 3). All 43 lakes were used in the analyses, with the exception of 'number of missing species' from which Neusiedlersee was excluded because the extreme value of eight missing species severely affected the model fit.

Results

The present fish communities of the Austrian natural lakes were fundamentally different than the situation approximately 150 years before present. Forty-three fish species (native, translocated and alien species) were recorded as inhabiting the Austrian lakes at present, compared with only 33 fish species historically (three of them are now missing; Fig. 1). Nine of the 13 newly recorded fish species are alien species: North American lake trout, *Salvelinus namaycush* (Walbaum), grass

Table 2. Lake use variables (and categories) used for prediction in the generalised linear models

Category	Definition
1.*	Tourism (=bathing, diving, excursion boating, individual boating, winter sports)
2.*	Fishery (=commercial fishing, angle fishing, fish farming)
3.*	Water removal (=hydroelectric power plants, irrigation, industrial water, fire-water, other water removals)
4.*	Human population density (=settlements, traffic) in the catchment area
5.	Trophy = oligotroph, oligo-mesotroph, meso-eutroph
6.	Fish based lake type = Arctic Char Lake, Minnow Lake, Bleak Lake, Pikeperch Lake (Gassner *et al.* 2005)
7.	Soil sealing = km^2 covered with buildings in the catchment area
8.	Agricultural area = km^2 farm land in the catchment area
9.	Forest and bushes = km^2 in the catchment area

*The category consists of several subcategories, for each subcategory ranking scores for the degree of utilisation from 0 (none) to 3 (intensive) were used. The sums of the subcategories were used for calculations.

Table 3. Lack of fish species variables (and categories) used as target in the generalised linear models

Category	Definition
1.	Are there any fish species missing: yes/no
2.	Number of missing fish species
3.	Category of missing fish species: no species missing = 0; 1–2 species missing = 1; 3–5 species missing = 2; > 5 species missing = 3
4.	Are there any small-bodied taxa missing: yes/no (i.e. minnow, *Phoxinus phoxinus*, bullhead, *Cottus gobius*, stone loach, *Barbatula barbatula*)
5.	Is minnow missing (type specific fish species for Austrian lakes, Gassner *et al.* 2005): yes/no

carp, *Ctenopharyngodon idella* Val., stone moroko, *Pseudorasbora parva* Temminck & Schlegel, threespine stickleback, *Gasterosteus aculeatus* L., largemouth bass, *Micropterus salmoides* (Lacepède), bighead carp, *Hypophthalmichthys nobilis* (Val.), silver carp, *Hypophthalmichthys molitrix* (Val.), pumpkinseed, *Lepomis gibbosus* (L.) and brown bullhead, *Ictalurus nebulosus* (Le Sueur). For example, pumpkinseed and grass carp were documented in nine (21%) and silver carp in seven (16%) of the 43 lakes. In addition to the alien fish species, four translocated fish species, prussian carp, *Carassius gibelio* (Bloch), tubenose goby, *Proterorhinus marmoratus* (Pallas), starlet, *Acipenser ruthenus* L. and ziege, *Pelecus cultratus* (L.), were newly documented in Austrian lakes. In all but one of the 43 lakes, the number of fish species increased (mean: 4.95 added species; min = 0, max = 13). Fish species of interest to angling and commercial fisheries, e.g. European eel, *Anguilla anguilla* (L.), pikeperch, *Sander lucioperca* (L.), common carp, *Cyprinus carpio* L., catfish, *Silurus glanis* L., whitefish, *Coregonus* sp. and tench, *Tinca tinca* (L.), showed a large increase. Historically, eel inhabited only one lake (2%), but this species is now found in 25 lakes (58%). Pikeperch extended its occurrence from three lakes (7%) to 24 lakes (56%). Some non-commercially-exploited fish species, like rudd, *Scardinius erythrophthalmus* (L.), crucian carp, *Carassius carassius* (L.), ruffe, *Gymnocephalus cernuus* (L.) and perch, *P. fluviatilis* L., also extended their distribution enormously. Most species were added in the lowland lakes, and generally the number of species decreased with increasing altitude (Fig. 2). Large lakes as well as small lakes gained new species (Fig. 3).

Conversely, in 21 of the 43 large Austrian lakes some native fish species were missing. Small-bodied taxa, such as minnow, *Phoxinus phoxinus* (L.), bullhead, *Cottus gobio* L., or stone loach, *Barbatula barbatula* (L.), could no longer be found in many lakes. Minnow was missing in seven, bullhead in six and stone loach in five Austrian lakes. Furthermore, sensitive species like Arctic charr, *Salvelinus alpinus* (L.), burbot, *Lota lota* (L.), European lake trout, *Salmo trutta* f. *lacustris* L. and pearlfish, *Rutilus frisii meidingeri* (Heckel), often disappeared. In Neusiedlersee, three native species mudminnow, *Umbra krameri* Walbaum, spined loach, *Cobitis taenia* L., blue bream, *Abramis ballerus* (L.), which originally occurred in this lake only, are now missing. In some lakes even hardy species like pike, *Esox lucius* L., (Haldensee), bream, *Abramis brama* (L.) (Fuschlsee, Haldensee, Vilsalpsee) or white bream, *Abramis bjoerkna* (L.) (Klopeinersee) were missing.

Statistical analysis

For the target variable *fish species are missing*, the model was built with the variables *tourism*, *fishery*, *human population density*, *trophy*, *lake type*, *soil sealing* and *agricultural area* (Table 4). The variables *fishery* and *agricultural area* had significant influence to the target variable *fish species are missing* ($P = 0.05$), whereas the *soil sealing* was significant only at $P = 0.1$. The *number of missing species* was significantly related with the *human population density* around the lake ($P = 0.001$), although the model fit was rather poor (chi-squared *P*-value: 5.73%). The model fit was better for the *category of missing species*, where the categories *fishery* and *lake type* were determining. The *missing*

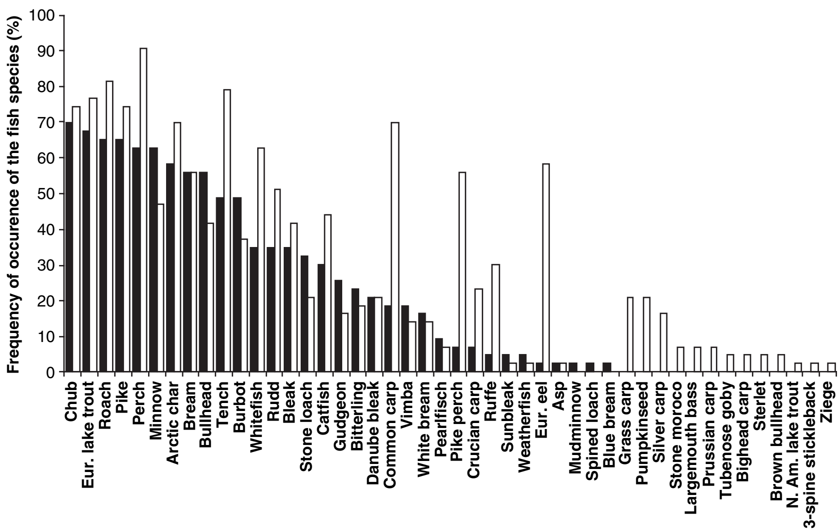

Figure 1. Frequency of occurrence of fish species in all natural Austrian lakes > 50 ha. ■ Reconstructed occurrence, □ current occurrence.

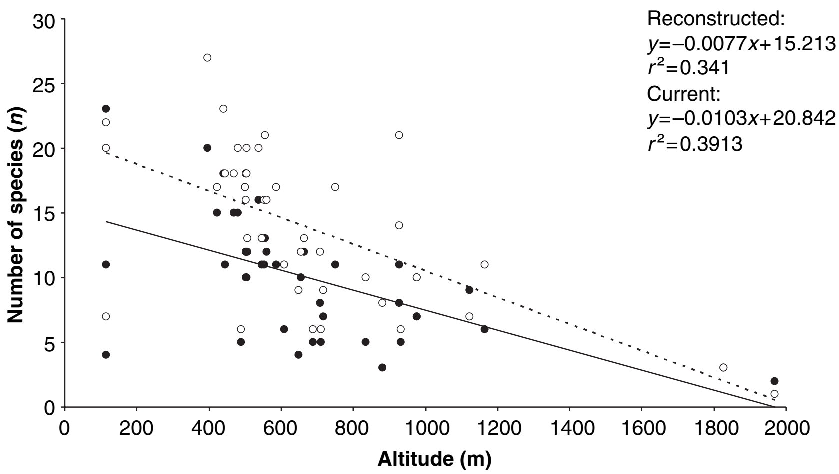

Figure 2. Altitude and number of fish species in natural Austrian lakes > 50 ha. ● Reconstructed number of species, ○ current number of species.

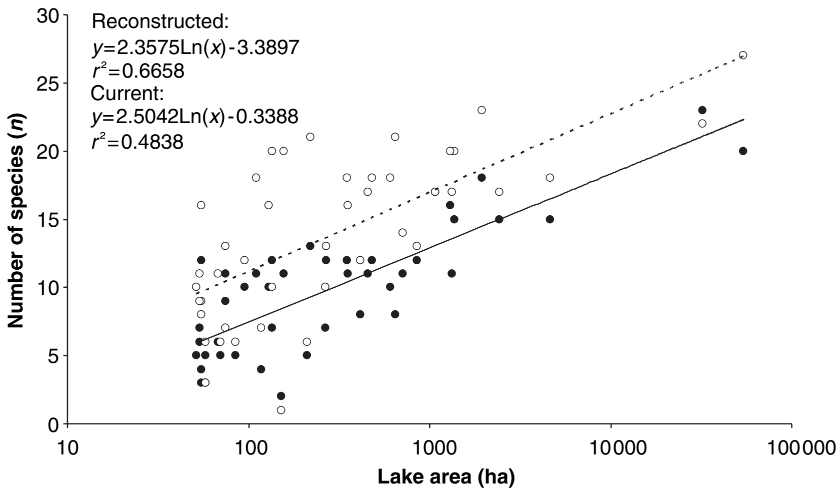

Figure 3. Lake area and number of fish species in natural Austrian lakes > 50 ha. ● Reconstructed number of species, ○ current number of species.

Table 4. Results of the generalised linear model (GLM) analysis. Each column in the box corresponds to a particular GLM. The predicting variables are arranged vertically and the target variables horizontally

	Fish species are missing (yes/no)	Number of missing species‡	Category of missing species	Small-bodied taxa are missing (yes/no)	Minnow is missing (yes/no)
Tourism	yes				*
Fishery	*		†		*
Water removal					*
Human population density	yes	***		†	*
Trophy	yes				
Lake type	yes		†		
Soil sealing	†			*	†
Agricultural area	*			yes	†
Forest and bushes					†
GLM model	Binomial	Poisson	Poisson	Binomial	Binomial
Residual deviance	44.6	55	37.8	48.7	16
Residual degrees of freedom	35	40	40	39	35
Chi-squared *P*-value	12.85%	5.73%	57.16%	13.66%	99.76%

Empty cell, variable was not selected for the model; yes, variable was selected for the model.
*Significance at level 0.05, **significance at level 0.01, ***significance at level 0.001.
†Significance at level 0.1.
‡Neusiedlersee excluded.

small-bodied taxa seemed to be influenced by *soil sealing* ($P = 0.05$). The target variable *minnow is missing* was connected with most of the tested variables.

Discussion

The species composition of fish communities is an important quality element of the EU-WFD. The objective of the EU-WFD is to prevent the further deterioration of the condition of water bodies, and that all more or less strongly impaired and disturbed water bodies achieve 'good' status by the year 2015. One of the basic components of an assessment of changes in species communities is definition of reference status, which is based on anthropogenically least-disturbed or near natural ecological conditions. Unfortunately, nearly all of the lakes in the alpine and prealpine regions of central Europe are changed by human activities. Thus, it is necessary to use historical data sets for the lake-specific reconstruction of the native fish species for all Austrian lakes > 50 ha. Historical records on fisheries in Austrian lakes date back to the 15th century. Many of these old records were hand-written and therefore very difficult and time consuming to evaluate. Furthermore, in these hand-written documents, it was the commercially important species that were mainly documented. Commercially unimportant species, such as minnow, bullhead and stone loach, were often imprecisely documented (Gassner *et al.* 2005). In many cases different cyprinid species were regularly summarised in a group called "Weißfische" and juveniles of various species were called "Sängel" (Freudlsperger 1936). Sometimes these facts made it very difficult to identify specific fish species. However, the huge amount of data and the reconstruction procedure gave some confidence in the historical fish species lists. Nevertheless, the application of historical data for the reconstruction of native fish species lists always includes an undefined uncertainty, which is based on the different quality and quantity of historical data. Conversely, if historical data are used carefully they will give very important, and often the only, information about the native fish species composition of lakes (Steedman *et al.* 1996). During the last century the fish communities of the Austrian natural lakes have been fundamentally altered. Human-induced environmental changes in surface waters have led to a loss of indigenous fish species. In 49% of the lakes at least one native fish species was missing. On the other hand, certain fish species of interest to commercial fisheries and angling increased enormously.

On a worldwide scale, the main cause of freshwater fish species decline is various forms of habitat alteration (Harrison & Stiassny 1999). For instance, human-induced nutrient input caused fundamental changes in lake chemistry leading to dissolved oxygen depletion. Evants, Nicholls, Allen & McMurtry (1996) showed that oxygen depletion and associated loss of cold-water habitat severely affected some fish species in Lake Simcoe, where the end-of-summer hypolimnetic dissolved oxygen conditions shifted from sublethal to incipient lethal for North American lake trout, *S. namaycush*, and possibly for lake whitefish, *Coregonus clupeaformis* (Mitchill), and lake herring, *Coregonus sardinella* Val. In Austria, hypolimnetic oxygen depletion during the 1970s and 1980s led to the extinction of Arctic char in lakes Irrsee and Mondsee (Jagsch 1987) and to a dramatic break down of the *Coregonus* population in the Trumer Lakes (Moog & Jagsch 1980).

In Austria, 28% of the natural lakes are affected by hydroelectric power plants (Chovanec *et al*. 2002), e.g. Achensee undergoes water level fluctuations of 11 m every year. In such circumstances, juvenile fishes are impaired by the loss of habitat because of massive shoreline degradation. Other impacts of hydraulic engineering result from the establishment of migration barriers that interrupt the river continuum causing breakdown of lake trout population in many lakes. Since 1950 the loss of spawning migrations has nearly led to the extinction of this fish species in Lake Constance (Ruhlé 1996) and in other lakes.

Since 1950, lakes have been used for recreational activities. The impact of tourism could be an important stressor, especially for sensitive and small-bodied taxa. Fishes may be severely disturbed by recreational activities, such as permanent bathing, boating, diving, skating or curling and even loose their habitats or spawning areas.

Strong impacts on aquatic ecosystems were also caused by fisheries management. Fish populations tend to be heavily influenced by direct manipulation of the assemblage through overfishing, removal of unwanted species or addition of desirable species (Cowx 2002). The fish species–lake area relationship deteriorated as a result of the introduction of new fish species ($r^2_{\text{reconstructed}} = 0.67/r^2_{\text{current}} = 0.48$). Introduced species may affect indigenous species by competing for resources, preying on native fauna, transferring pathogens, significantly altering habitat or by genetic deterioration through hybridisation (Cowx 1998). An example of favouring a commercially interesting fish species is the European eel. In Austria, the eel occurred only in Lake Constance (Rhine drainage system), but the species has been introduced into 24 other lakes (Danube drainage system). The presence of this predator could be a serious problem for small-bodied taxa.

Mehner, Diekmann, Brämick & Lemcke (2005) showed that fish community composition in German lakes was mainly determined by abiotic factors, whereas the impact of anthropogenic alterations of shore structure and human-use intensity of lakes were of minor importance. Nevertheless the *number of missing species* was significantly connected to the *human population density* around the lake. Increased population densities lead to increased human pressure via, e.g. commercial utilisation or recreational activities, that affect the fish communities.

Minnow is a sentinal fish species in Austrian lakes (Gassner *et al*. 2005), consequently, it is important to determine which factors caused the loss of this small-bodied species. The relation with *tourism* and *water removal* seems reasonable, as minnows prefer mainly shallow habitats that are severely influenced by recreational activities and water level fluctuations. *Fishery* may also have an impact, mainly due to species introduction (e.g. European eel as a predator), but generally it is very hard to detect the main stressors for fish species and which human activities or which combination of factors finally lead to species extinction. Although much information about the use of Austrian lakes was available (Chovanec *et al*. 2002), it was not yet possible to identify precisely the main stressors to fish communities using GLM. Nevertheless, there are correlations between the lack of species and human impacts. It is very difficult to interpret the responses of a fish community to a variety of stressors. Kelso *et al*. (1996) assumed, it may be possible to relate unequivocally the effect of a change in a single factor (e.g. temperature) on the well-being of a single fish, but it is another matter to interpret the complex responses of fish communities to a suite of stressors. In many cases pollution, habitat modification and fisheries management, e.g. introduction of alien or translocated species or overfishing, appear to have worked either simultaneously or sequentially to induce the eventual extinction of fish species (Harrison & Stiassny 1999; Cowx 2002), and this may also be true in Austria.

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