

SeeWandel

Life in Lake Constance – the past, present
and future

SeeWandel closing event

13/14 June 2023

Konzil Konstanz, Germany

www.seewandel.org



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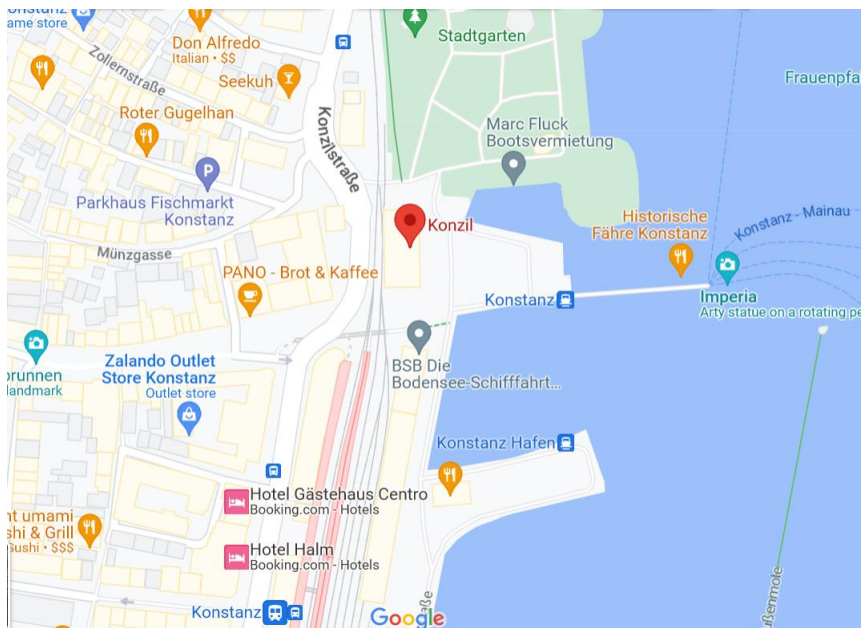
Venue

Konzil Konstanz



Hafenstraße 2, 78462 Konstanz, Germany

www.konzil-konstanz.de



Please note, that there is no on-site parking.

Information

WLAN: Konzil-event

Password: YhZG75i44BGzLhBv

Contact phone number: +41 79 524 5451

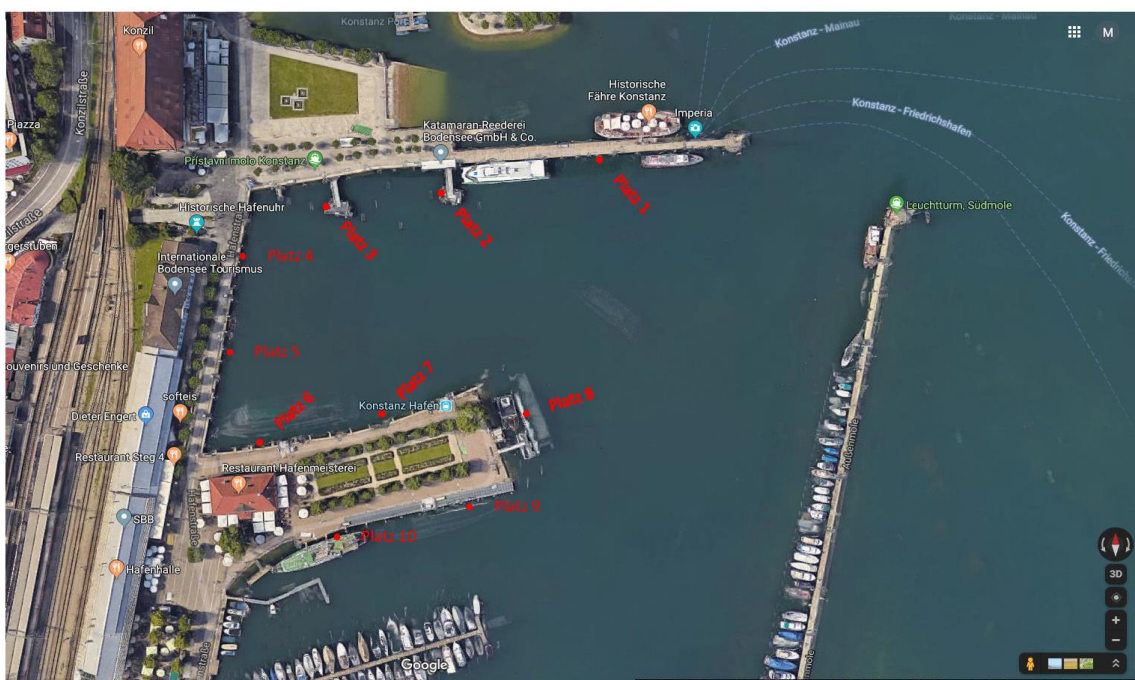
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Boat trip with MS Radolfzell: social event & dinner

For those who have registered

Boarding 17:45, departure 18:00, mooring 4 or 5 ("Platz" 4 or 5)





Life in Lake Constance – the past, present and future

Programme
&
Abstracts oral and poster presentations

SeeWandel closing event
SeeWandel Scientific Symposium

13 June 2023
Konzil Konstanz, Germany

www.seewandel.org

Programme

Tuesday 13 June 2023

| | | |
|-------|-------|--|
| 08:00 | 09:00 | Registration, <i>Entrance hall</i> & Welcome coffee |
| 09:00 | 09:05 | Welcome (PD Dr. Piet Spaak, Eawag) |
| 09:05 | 10:00 | Plenary lecture "Quagga mussel in the Great Lakes: What have we learned in 35 years of invasion" (Prof. Dr. Alexander Y. Karatayev / Dr. Lyubov E. Burlakova, Great Lakes Center, SUNY Buffalo State University) |
| 10:00 | 10:30 | Coffee break |
| 10:30 | 10:45 | "Tracking natural and anthropogenic biodiversity changes in and around Lake Constance from the Late Pleistocene to the 21 st century" (Prof. Dr. Laura S. Epp, Limnological Institute, University of Konstanz) |
| 10:45 | 11:00 | "The establishment of <i>Planktothrix rubescens</i> as an hypolimnetic cyanobacterium in changing deep peri-alpine lakes" (Prof. Dr. Bastiaan W. Ibelings, University of Geneva) |
| 11:00 | 11:15 | "A century of changes for the Blauefelchen fishery – how did we get here and what can we learn?" (Dr. J. Tyrell DeWeber, LAZBW Fisheries Research Station Baden-Württemberg) |
| 11:15 | 11:30 | Poster flash presentations |
| 11:30 | 12:00 | Poster presentation |
| 12:00 | 13:30 | Buffet lunch |
| 13:30 | 13:50 | SeeWandel synthesis: neozoa & climate change (PD Dr. Piet Spaak, Eawag) |
| 13:50 | 14:10 | SeeWandel synthesis: littoral zone (Prof. Dr. Klaus Schmieder, University of Hohenheim) |
| 14:10 | 14:30 | SeeWandel synthesis: pelagic zone (Prof. Dr. Markus Möst, Research Department for Limnology, Mondsee, University of Innsbruck) |
| 14:30 | 14:50 | SeeWandel synthesis: fishes (PD Dr. Piet Spaak, Eawag) |
| 14:50 | 15:10 | SeeWandel synthesis "Habitat shifts exceed community and genetic change in Lake Constance" (Dr. Benjamin Kraemer, University of Konstanz) |
| 15:10 | 15:45 | Coffee break |
| 15:45 | 16:30 | Plenary lecture "The Local and Global Importance of Pond Ecosystems" (Prof. Dr. Meredith Holgerson, Cornell University) |
| 16:30 | 16:45 | Conclusion (PD Dr. Piet Spaak, Eawag) |
| 17:45 | | Boarding |
| 18:00 | | Aperitif on the boat Social event & Dinner on the boat |

Abstracts Plenary Lectures

Quagga mussel in the Great Lakes: What have we learned in 35 years of invasion

Prof. Dr. Alexander Y. Karatayev & Dr. Lyubov E. Burlakova

Great Lakes Center, SUNY Buffalo State University, USA

We summarized over 35 years of research on zebra and quagga mussels in the Laurentian Great Lakes. Invasion dynamics, growth, and reproduction of dreissenids in the Great Lakes are governed by lake morphometry. In shallow polymictic lakes, lakes basins, and embayments quagga mussels became dominant 4 – 12 years after coexistence but did not fully replace zebra mussels and sometimes we recorded the reverse process. In contrast, in deep stratified lakes quagga mussels became dominant faster at greater depths, form much higher density, and drive zebra mussels to virtual extirpation. At <30 m mussels overshot their carrying capacity and declined within 13 – 15 years after first detection. At 30 – 90 m their densities increased more slowly and declined to a lesser extent, while at >90 m populations continue to increase even after 35 years of invasion. After the proliferation of quagga mussels, benthic wet biomass (including molluscs shells) increased about two orders of magnitude and currently exceeds zooplankton biomass >40-fold. Strong benthic/pelagic coupling redirects food and energy from the water column to the bottom causing an increase in Secchi depth, decline in phosphorus, chlorophyll, phytoplankton and zooplankton biomass. The abundance of commercially important fishes declined as a result of the dramatic decrease in their main food deep water amphipods *Diporeia*, which has been outcompeted by exotic mussels. However, the introduction of round goby into the Great Lakes in the 1990s provided an important link between dreissenids and commercially and recreationally valuable fish species, increasing their productivity. In addition, we will present data on the often-overlooked ecosystem services provided by exotic ecosystem engineering dreissenids including water filtration, their use for the assessment and biomonitoring of contaminants and pathogens, and provisioning services. There are currently 143 species recorded as dreissenid predators in Europe and North America, including 39 species of birds and 77 species of fish. Other natural enemies of *Dreissena* include parasites (86 species and higher taxa, with commensals) and competitors (14 species). A cumulative effect of a growing suite of enemies, however, may have a constant, but overall limited, role in suppressing *Dreissena* densities – one far from any likelihood of population eradication.

The Local and Global Importance of Pond Ecosystems

Prof. Dr. Meredith Holgerson

Department of Ecology & Evolutionary Biology, Cornell University, USA

Most of the world's lakes are small enough to be considered ponds: over 95% of lakes are estimated to be less than 0.1 km² (10 ha) in size. Yet, most research overlooks these small waterbodies; paradigms for lake ecosystem ecology largely come from larger, deeper temperate lakes. How can studying ponds inform broader limnological patterns? Is anything that we learn from ponds relevant for larger lakes, such as Lake Constance? In this presentation, I'll describe our lab's research on pond ecosystems, including greenhouse gas emissions, carbon sequestration, and how plants and animals mediate aquatic carbon cycles. Ultimately, the study of pond ecosystems broadens our view of limnology and informs our understanding of larger lake dynamics, including how littoral habitats operate and how changes in mixing regimes may regulate ecosystem functions.

Abstracts Oral Presentations

Tracking natural and anthropogenic biodiversity changes in and around Lake Constance from the Late Pleistocene to the 21st century

Laura S. Epp¹, Yi Wang¹, Anna Chagas¹, Rebecca Kühner¹, Lisa Gutbrod¹, Anan Ibrahim^{1,2}, Martin Wessels³, Elena Marinova⁴

¹Limnological Institute, University of Konstanz, Konstanz, Germany; ²Department of Paleobiotechnology, Leibniz Institute for Natural Product Research and Infection Biology, Jena, Germany; ³Institute for Lake Research (ISF) of the Landesanstalt fuer Umwelt Baden-Wuerttemberg (LUBW), Langenargen, Germany; ⁴State Office for the Preservation of Monuments, Hemmenhofen, Germany

Lake Constance has recently experienced and is experiencing well-documented biodiversity changes due to anthropogenic environmental changes, such as eutrophication, temperature increase and the spread of invasive alien species (IAS). The shores of Lake Constance have, however, been settled for millennia, and humans have putatively been a driving force for biodiversity change on very long timescales. While changes preceding the 20th century are not well documented, they can be elucidated by investigating lake sediment cores. Traditional paleolimnology and paleoecology relies on the analysis of visible remains, and is thus limited in taxonomic breadth. An alternative source of data to analyse biodiversity history is ancient environmental DNA, which is highly local in deposition and can reconstruct past biota at a high taxonomic resolution.

We are analysing records from Upper and Lower Lake Constance, spanning a time from the Late Pleistocene to the present, covering organisms from across the tree of life in the aquatic and near-shore terrestrial environments. We see distinct changes related both to natural environmental changes, such as the start of the Holocene, and to increased anthropogenic impact at different periods across the millenia, and the past century. Combining these datasets, we can understand when humans started influencing the biota of the lake, and how the current and recent historical perturbations compare to earlier turnovers.

The establishment of *Planktothrix rubescens* as an hypolimnetic cyanobacterium in changing deep peri-alpine lakes

Ena Lucia Suarez¹, Lukas De Ventura², Arno Stöckli², Césa Ordóñez¹, Mridul K. Thomas¹, Daniel F. McGinnis¹, Bastiaan W. Ibelings¹

¹University of Geneva, Switzerland; ²Departement Bau, Verkehr und Umwelt, Kanton Aargau, Switzerland

Toxic cyanobacteria such as *Planktothrix rubescens* came to dominate temperate lakes in the mid-to-late 20th century, as a result of eutrophication. Even after decades of re-oligotrophication, where phosphorus levels were reduced by 1 - 2 orders of magnitude, *P. rubescens* remains present in different lakes. In this study we examine the persistence and changes of *P. rubescens* deep chlorophyll maximum (DCM) in Lake Hallwil (Switzerland) over 35 years of steadily decreasing phosphorous concentrations. Although lake transparency increased and the euphotic layer deepened during this period, the *P. rubescens*

population maximum moved even deeper. It is now found ca. 7.7 m deeper than its shallowest position in the 2000s, and this depth no longer coincides with the depth of maximal water column stability. *P. rubescens*' neutral buoyancy has now driven it beneath the stable metalimnion into the hypolimnion, where buoyancy regulation is restricted due to reduced metabolic activity at low light and low temperature. If *P. rubescens* DCM continues to deepen each year, it will eventually reach a region of lower stability in the hypolimnion where turbulent conditions are strong enough to dissolve the DCM. We also explore the mechanisms that ensure *P. rubescens* ongoing presence in peri-alpine lakes despite strong re-oligotrophication and ongoing climate change. We find that *P. rubescens* in the lake is mainly sustained by growth during fully mixed conditions in winter, not during stratification in summer. This may contradict another commonly made prediction that periods of longer stratification will promote future blooms of this cyanobacterium.

A century of changes for the Blaufelchen fishery – how did we get here and what can we learn?

J. Tyrell DeWeber, Jan Baer, Alexander Brinker

Fisheries Research Station Baden-Wuerttemberg (FFS) of the Landwirtschaftliches Zentrum fuer Rinderhaltung, Grünlandwirtschaft, Milchwirtschaft, Wild und Fischerei Baden-Wuerttemberg (LAZBW), Langenargen, Germany

The Blaufelchen *Coregonus wartmanni* was historically the most culturally and economically important species for the fishery Lake Constance fishery, but dramatic ecosystem changes have upended this status. We investigate how nutrient dynamics, invasive species, fishery harvest, and water temperature changes have affected growth, population dynamics, and fisheries harvest from 1925 – 2020. Blaufelchen growth increased strongly with phosphorous from the 1950s to the 1970s before decreasing to pre-eutrophication levels by 2010. Following the pelagic zone invasion by three-spined stickleback *Gasterosteus aculeatus* in 2012, growth and body condition sunk to historic lows. The growth and body condition changes have greatly altered population dynamics and the Blaufelchen fishery. Relatively fat fish were harvested at a smaller length and younger age, for example, which resulted in recruitment overfishing in the 1960s. The most recent dip in body condition reduced the probability of catching fish of harvestable length, which fish first reach at a later age due to slower growth. Thin and short spawning females also produce fewer eggs, which results in lower expected recruitment. The combination of lower productivity, stickleback invasion, and warming temperatures have drastically reduced fishery yields to historic lows and pushed many fishers beyond the brink of economic subsistence. By accounting for these various changes, it is possible to understand how Blaufelchen could respond to ecosystem and fishery changes (e.g., changing mesh sizes or fishing pressure) through a scenario approach. These results can help sustainably manage the fishery and prepare for any other surprising changes in the near future.

SeeWandel synthesis: neozoa & climate change

presented by Piet Spaak

Department of Aquatic Ecology, Swiss Federal Institute of Aquatic Science and Technology (Eawag), Duebendorf, Switzerland

In addition to eutrophication and climate change, especially the invasion of non-native plant and animal species are endangering natural biodiversity, also in Lake Constance. This leads to changes in the food web and affect ecosystem functioning. Specifically the three-spined stickleback (*Gasterosteus aculeatus*) and Quagga mussel (*Dreissena bugensis*) are major invaders in Lake Constance. But many other species invaded the lake, especially in the littoral, there we studied the impact of trophic change and non-native species on near-shore (i.e. littoral) communities. Using a long-term dataset (1997 to 2015) the response of the littoral macroinvertebrate and fish communities of Lake Constance to declined nutrient concentrations and the introduction of non-native species was studied in Project L9: "Resilience of the littoral community of Lake Constance: effects of neozoa, trophic- and climate change".

The three-spined stickleback and Quagga mussel populations have exploded in the last years, with sticklebacks becoming the most abundant pelagic fish species of the lake. The Quagga mussel is able to settle in all water-depths, which causes problems with water intake pipes and other structures. Furthermore, the Quagga mussel is an important competitor for zooplankton-species feeding on phytoplankton. In the SeeWandel Projects L10 "Competition between filter feeders in Lake Constance" and L13 "Ecology and diversity of stickleback in Lake Constance", on both invasive species genetic studies were done. Also experiments were carried out to understand better why these species are so successful. Our genetic data shows that both invasive species differ in their genetic structure throughout Switzerland, however within Lake Constance no population structure was found within the Quagga mussels. We also show that quagga mussels are spreading fast, even to the deepest parts of the lake. Neozoa seem to have long-term consequences for the lake Constance ecosystem.

SeeWandel synthesis: littoral zone

presented by Klaus Schmieder

Institute of Landscape and Plant Ecology, University of Hohenheim, Stuttgart, Germany

The comparison of recent surveys in the investigated areas of the littoral zone with other surveys shows a marked increase of total vegetated area compared to bare sediment surfaces in the last decades. Furthermore, the macrophyte beds extended towards deeper areas. On the other hand, a substantial change in the species composition took place since the 1990ies, with a loss of tall growing macrophytes, in particular broadleaved species to the benefit of *Chara* beds due to oligotrophication. Re-oligotrophication, since the 1970ies zebra mussel and in the last decade quagga invasion contributed to higher water transparency and may have promoted increase of macrophyte covered area and its expansion to deeper water. On the other hand, dense charophyte beds limit the potential habitat of quagga in the littoral zone. Instead, they increase

the spawning habitat suitability for stickleback in the littoral zone. As well, shells of dead quagga are used to cover stickleback nests. Stickleback population depends on availability of breeding habitats. Total CPUE numbers and biomass of littoral fish did not decline 1997-2014, however community composition changed strongly. An increase of dace, loach and perch, whereas a decrease of bream, burbot, chub and ruffe took place. This might be related to climate change, since coldwater fish species like burbot and whitefish decreased. On the other hand food availability increased markedly due to *Limnomysis benedeni* invasion in 2009.

SeeWandel synthesis: pelagic zone

presented by Markus Möst

Research Department for Limnology, Mondsee, University of Innsbruck, Innsbruck, Austria

In this presentation, we will present the results of the SeeWandel Thematic Working Group “Pelagic Zone” (SeeWandel sub-projects P5, P6, P7, P8, [P3]). As one of four thematic working groups within the SeeWandel project, this working group “Pelagic Zone” unites projects that study the consequences of environmental change on multiple organisms inhabiting the open, free water column – the pelagic zone. We will report environmental conditions favouring the occurrence of potentially toxic blooms of *Planktothrix rubescens* and present predicted scenarios for Lake Constance. Moreover, we will show how planktonic communities are spatially distributed in Lake Constance and how they react to stressors. On the one hand, we will present paleolimnological reconstructions that highlight patterns of resilience and phenotypic change. On the other hand, we show genomic data for the *Daphnia* community in Lake Constance that show a very detailed picture of evolutionary change during the course of trophic changes in lake. We also treat the recent appearance of *D. cucullata* in the lake and discuss potential explanations for this surprising invasion. Finally, we will summarize and discuss our findings on the consequences of trophic and climate on the plankton communities in the pelagic zone and identify future research questions.

SeeWandel synthesis: fishes

presented by Piet Spaak

Department of Aquatic Ecology, Swiss Federal Institute of Aquatic Science and Technology (Eawag), Duebendorf, Switzerland

The massive increase of the non-native three-spined stickleback (*Gasterosteus aculeatus*) in Lake Constance, is thought to have strong negative effects on the native fish community as well as local fisheries. After more than 50 years of inconspicuous existence, sticklebacks now represent more than 80% of the fish individuals in Upper Lake Constance (96% in open water), the habitat of the originally dominant whitefish. The invasive stickleback is potential a direct competitor for food, particularly for whitefish. Therefore several projects in SeeWandel investigated several aspects of the Stickleback invasion, as well as

the whitefish in the lake, this with the goal to get a better understanding about stickleback – white fish interactions.

In project P1: “The stickleback in Upper Lake Constance” the autecology of the stickleback was studied. In project P2: “Bioenergetic modelling of fishing strategies on the fish communities of Upper Lake Constance” the focus was on modelling energy flow in food webs with emphasis on whitefish and sticklebacks, to investigate the effects and outcome of different fishery management practices. Project P3: “Effects of re-oligotrophication, climate change and invasive species on fish-zooplankton interactions and the population dynamics of whitefish” concentrated on food and diet of both whitefish and sticklebacks, where Project P4: “Reconstruction of the genome of the extinct Lake Constance whitefish and characterisation of the genetic bases of habitat adaptation to the profundal zone” was solely on whitefish, investigating the genetic make-up of the different species. Finally in project L12: “Development and application of methods for the assessment of fish communities in large and deep lakes” we quantified the fish diversity of the lake and compared it to the results of 2014 (Projet Lac).

In my presentation, I will summarize and synthesize the variety of research done on fish related themes within SeeWandel. I will focus especially on the stickleback – whitefish interaction and possible consequences for Ecosystem services of Lake Constance.

SeeWandel synthesis: Habitat shifts exceed community and genetic change in Lake Constance

presented by Benjamin Kraemer

Limnological Institute, University of Konstanz, Konstanz, Germany

Habitat shifts play a crucial role in shaping biotic change across a range of scales from genes to communities. But the shortage of consistent metrics of change limits our ability to compare shifts in habitat to biotic shifts across this range of scales. Here we expand on a metric of change called non-overlap which we use to quantify and compare change in habitats, communities, and allele frequencies over 6 decades in Lake Constance. Community and genetic non-overlap were consistently lower than habitat non-overlap by 25 to 86 % suggesting that the lake community is resistant to such environmental changes. However, lower biotic non-overlap could also arise from time lags or dispersal limitations which will eventually bring biotic non-overlap in step with habitat non-overlap over longer timescales. The broader application of the non-overlap metric used here could improve our understanding of how different axes of biodiversity track temporal and spatial habitat differences in the environment.

Abstracts Poster Presentations

Reconstructing population size, timing and mode of quagga mussel invasion using sedimentary DNA

Rebecca Dorendorf¹, Silvan Roszbacher², Piet Spaak², Laura S. Epp¹

¹Limnological Institute, University of Konstanz, Konstanz, Germany; ²Department of Aquatic Ecology, Swiss Federal Institute of Aquatic Science and Technology (Eawag), Duebendorf, Switzerland

The invasion of non-native species is considered one of the most significant threats to biodiversity and ecosystem stability worldwide. *Dreissena rostriformis*, commonly known as quagga mussel, is one such invasive species that has recently gained attention in freshwater ecosystems. We use environmental DNA (eDNA) from sediments (sedDNA) to assess the population sizes and distribution of quagga mussels, as well as perspective investigate the timing and mode of quagga mussel populations appearance and migrations between water bodies of the northern perialpine region. In our preliminary work for the development of a sedDNA quantification approach for quagga mussels in Lake Constance, we designed a probe for ddPCR assay to quantify the target DNA of quagga mussels. For the quantification, we use surface sediment collected during the quagga monitoring campaign of the SeeWandel project, performed by the Swiss Federal Institute of Aquatic Science and Technology (Eawag) in October 2022. Ponar grab samples were taken at 54 sites spanning the entire lake. Quantitative data obtained at the Eawag through Ponar samples and the Benthic Imaging System are compared to quagga DNA quantities measured by ddPCR. From a previous study, we have indications that dreissenid mussels can be detected in sediment and that genetic findings are in temporal agreement or even precede initial detections. This sedDNA-based reaction can thus potentially deliver a sensitive and efficient additional approach for early detection of quagga mussels and can be used to track the establishment of dreissenid mussels through time across sediment cores of multiple lakes in the area.

Phytoplankton community composition in Lake Constance changes seasonally and interannually along a tradeoff between phosphate affinity and light affinity

Anton Pranger¹, Sebastian Diehl², Dietmar Straile¹, Frank Peeters¹

¹Limnological Institute, University of Konstanz, Konstanz, Germany; ²Department of Ecology and Environmental Science, Umeå University, Sweden

The combination of traits of an organism determines the environment in which it is most competitive. Environmental change therefore affects the competitive ability of the organisms in a community and thus leads to selection and community change. Earlier work has shown that in large pre-alpine Lake Constance, trophic change was associated with considerable changes in phytoplankton community composition. These changes in composition resulted in substantial changes community mean phosphate affinity, light affinity and these traits were strongly anti-correlated. Here we present seasonal dynamics

of community mean phosphate affinity and light affinity and we explore how these traits are affected by dynamics in phosphate concentrations, light availability and community composition.

The metabolic temperature dependence of littoral and profundal *Dreissena bugensis* morphotypes in Lake Constance

Lisa Klingele, Frank Peeters, Anton Pranger

Limnological Institute, University of Konstanz, Konstanz, Germany

The quagga mussel (*Dreissena bugensis*) is a bivalve that has invaded many freshwater ecosystems in Europe and North America. In Lake Constance, it has quickly replaced the invasive zebra mussel (*Dreissena polymorpha*) within two years after it was first detected. The quagga mussel can establish itself at much greater depths than the zebra mussel and is therefore an important player in both the epilimnetic and hypolimnetic zone. The different temperature regimes of these two zones are likely to affect considerably the development, physiology and importantly, the energetics of the mussels. We therefore measured respiration rates of individuals collected from the littoral zone (10m) and from the pelagic zone (100m), and we investigate their relationships with temperature and the mass, morphology, and origin of the mussel. Respiration rates increased with increasing temperature and shell size and differed between mussels that were collected at different water depth. The latter suggests that Quaggas adapt to the conditions in different water depth.

Sampling emissions in Lake Geneva

Maria Almada

University of Geneva, Switzerland

While it is well established that citizen science is an emerging and promising tool for the study of environmental sciences, so far there has been little interest in knowing how this branch of science is environmentally, socially and economically performing compared to more classic academic studies. Through a Life Cycle Assessment (LCA), our study compared the carbon emissions of two sampling campaigns in Lake Geneva, Switzerland. While the first campaign ("Quagga") was done through purely academic means, the second ("Co-Fish") was part of a co-created citizen science project, built together with fishers of the lake. Both campaigns used a noticeable amount of CO₂ at 7500Kg for Co-Fish and 12000 for Quagga. The largest emitter was the sampling of the Quagga campaign at an estimated 9000 kg of CO₂. The manufacturing of the Co-Fish equipment resulted in a considerable volume of emissions. Co-creating the Co-Fish campaign was expensive and time consuming. Nevertheless, the Quagga campaign had a high level of cost-free advantages. Fishers' time constraints, local boat production and boat daily use, gave an ultimate advantage to Co-Fish on emissions saving. The well-established university setup was a great advantage on the preparation of the campaign. Academic science can learn of the viability of small boats used in citizen science sampling as an example of sustainable vehicle. On the other hand, homemade material was very carbon

intensive and less accurate than the university device. In both campaigns cooperation was the key to lower campaign emissions.

Recovery of cladoceran communities from eutrophication in three basins of Lake Constance differing in morphology

Marjahn Yucada Baluda, Simone Wengrat Ribeiro, Dietmar Straile

Limnological Institute, University of Konstanz, Konstanz, Germany

Cladocerans are known to respond strongly and rapidly to environmental changes such as eutrophication and climate variability. As cladoceran remains are furthermore well preserved in lake sediments, cladocerans are an ideal group to study the resilience of lake ecosystems. Here we investigate cladoceran dynamics during approximately the last 100 years in three basins of Lake Constance, which went a similar history of trophic changes and warming, but differ in morphology: the large Upper Lake Constance ($z_{\max} = 250$ m), and Zellersee ($z_{\max} = 22$ m) and Gnadensee ($z_{\max} = 19$ m), the two basins in Lower Lake Constance. In all three basins, eutrophication resulted in phosphorus concentrations around $100 \mu\text{g/L}$ in the 1970s, with subsequent declines due to the establishment of sewage plants towards $<10 \mu\text{g/L}$ in Upper Lake Constance, and $<20 \mu\text{g/L}$ in the other two basins. The three basins exhibited comparable patterns in the relative abundances of *Bosmina* and *Daphnia*, which mirrored the alterations in total phosphorus levels. Conversely, there were significant dissimilarities in the dynamics of traits, indicating divergent paths of the food web among the basins over the past century.

Influence of sticklebacks on whitefish

Sarah M. Gugele, Alexander Brinker

Fisheries Research Station Baden-Wuerttemberg (FFS) of the Landwirtschaftliches Zentrum fuer Rinderhaltung, Grünlandwirtschaft, Milchwirtschaft, Wild und Fischerei Baden-Wuerttemberg (LAZBW), Langenargen, Germany

Since 2012, a massive invasion of the three-spined stickleback *Gasterosteus aculeatus* has taken place into the pelagic area of Lake Constance. This species, which had previously been restricted to the littoral zone, is now by number the dominant pelagic fish and the former dominant whitefish *Coregonus wartmanni* has suffered severe reductions in growth and recruitment. Food competition with sticklebacks seems to be one main reason for decreased growth. Furthermore, sticklebacks uses the eggs and the whitefish larvae (up to a size of 35 mm total length) as a food source, further decreasing cohort sizes of whitefish. In addition, it is suspected that climate change, predation by cormorants, and the impact of other invasive species hamper growth and recruitment of whitefish. Different immediate fisheries management options with the potential to increase the whitefish stock and to reduce the predation pressure on their food sources exist: stickleback stock reduction (e.g. by trawling with marine equipment, however, pilot studies pending), stocking of whitefish larvae in sizes above 35 mm length (exceeding sticklebacks gape size), conservation of big, old, fat, and fecund female whitefish (to increase size and

quality of the eggs to booster natural recruitment and breeding success in the hatcheries).

Turning summer into winter

J. Tyrell DeWeber, Alexander Brinker

Fisheries Research Station Baden-Wuerttemberg (FFS) of the Landwirtschaftliches Zentrum fuer Rinderhaltung, Grünlandwirtschaft, Milchwirtschaft, Wild und Fischerei Baden-Wuerttemberg (LAZBW), Langenargen, Germany

Understanding the mechanisms driving growth responses to environmental change is important for interpreting past dynamics and sustainably managing ecosystems. We use integrated bioenergetics and growth modelling to understand how nutrient dynamics, species invasions and changing temperatures have altered growth of the keystone pelagic whitefish *Coregonus wartmanni* in Lake Constance, Germany from 1925 to 2020. Growth variation was modelled by allowing covariates to alter temperature-dependent consumption, while size-specific metabolism varied only with temperature. Consumption and growth increased strongly to a maximum with phosphorous, and this effect was stronger when intraspecific competition (measured as whitefish biomass) was low. Increasing whitefish biomass reduced growth under mesotrophic conditions, but had no effect under oligotrophic conditions. In contrast, increasing competition with invasive three-spined stickleback *Gasterosteus aculeatus* was predicted to reduce growth even under oligotrophic conditions. The invasion has effectively turned summer into winter for whitefish, with older fish ceasing to grow and younger fish losing up to 10 % of their body weight during the normal growing season in subsequent years. Warming is predicted to further reduce whitefish growth due to competition with invasive stickleback, which would further alter zooplankton food availability and reduce already low fishery yields. These results demonstrate the importance of considering biotic interactions and synergistic effects in global change studies, as well as the value of mechanistic based models for understanding effects. Similar growth responses to ecosystem change are likely within and across ecosystems, and bioenergetic models can help understand effects to support informed ecosystem management.

Stickleback, whitefish and zooplankton interactions

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The aim of this project was to provide an improved understanding of the interactions between whitefish, zooplankton and sticklebacks, which expanded their habitat from the littoral to the pelagic zone in Lake Constance. Laboratory experiments revealed that sticklebacks had comparable or even larger feeding rates on various zooplankton species compared to similar sized whitefish. Analyses of stomach contents of whitefish and sticklebacks also show that both

species – the former more efficiently – selected large zooplankton species when available. A mesocosm experiment showed that sticklebacks and whitefish suppress large daphnids, whereas in mesocosms without fish large daphnids increased in abundance and suppressed small ones. Finally, analyses of zooplankton long-term data showed that after the habitat expansion of sticklebacks, small zooplankton species, including the newly arrived *Daphnia cucullata*, increased in biomass at the expense of large zooplankton.

Genomic consequences of eutrophication-induced speciation reversal

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Anthropogenic environmental change is causing the loss of biodiversity at an unprecedented rate. When reproductive isolation between species is contingent on features of the environment, environmental change can weaken reproductive isolation and result in extinction through hybridization, a process called speciation reversal. In Lake Constance, a deep-water whitefish species went extinct through speciation reversal during the period of anthropogenic eutrophication mid last century. Using historical and contemporary samples, we sequenced genomes of all species of the Lake Constance whitefish radiation from before and after the eutrophication period. We show that despite the extinction of the deep-water species, fractions of its genome including regions shaped by positive selection and thus potentially adaptive in deep water, persist within surviving species as consequence of introgression. Thus, introgression of old variants derived from extinct species can improve the ecological resilience of ecosystems. Given the prevalence of environmental change, studying the genomic consequences of speciation reversal provides fundamental insights into the evolution of biodiversity, especially its dynamics under environmental change, and informs biodiversity conservation.

P5: *Daphnia* resilience

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Hybridization is recognized as an important evolutionary process that can facilitate speciation and rapid adaptation to rapidly changing environments. However, a hybridization event may have various outcomes and selection against hybrids may eradicate the traces of hybridization and contribute to the maintenance of stable species boundaries. At the other extreme, species boundaries may completely collapse upon secondary contact. Factors affecting the outcome and dynamics of hybridization include spatial heterogeneity and – often underappreciated – features of species' life cycles, such as cyclical parthenogenesis or propagule banks. Here, we focus on the importance of these

factors in hybridizing water fleas in the *Daphnia longispina* species complex. We make use of whole-genome time series obtained from *Daphnia* resting eggs deposited in lake sediments to investigate changes in species composition over time and reconstruct recent cases of interspecific hybridization following anthropogenic habitat disturbance through cultural eutrophication in Lake Constance. Despite periods of extensive hybridization during ecological transitions, the parental species still exist as distinct units alongside hybrid lineages. However, the recent populations in Lake Constance are genetically distinct from the historic population that was native to Lake Constance before eutrophication. Here, we discuss the possible mechanisms reducing the impact of hybridization events on species boundaries and preventing introgression and highlight the role and interaction of life cycle features and spatio-temporal ecological heterogeneity in maintaining species boundaries in this hybridizing species complex.

Reasons for the growth of *Planktothrix rubescens* in Lake Zurich and Lake Constance – long term data, experimental approaches and genetic analyses

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The long-term dataset for Lake Zurich provides strong evidence, that changes in the mixis regime due to warming is coupled to an increasing importance of the filamentous cyanobacterium *Planktothrix rubescens*. Meanwhile, it is the dominant primary producer in the lake. *P. rubescens* is generally considered toxic for animals and humans, by storing cyclic heptapeptides (microcystins - MCs). The 'surprising' mass development of *P. rubescens* in Lake Constance in the year 2016, was leading to the following research questions:

- Which physico-chemical parameters (reference state) in deep temperate lakes can promote a successful establishment of *P. rubescens*?
- How well do the *P. rubescens* related data collected for Lake Constance correspond with the defined reference state?
- Can we predict/estimate how *P. rubescens* will develop in Lake Constance in the coming years / decades?

For the year 2016, extremely weak water turnover occurred in both lakes, with positive effects on *P. rubescens*. However, in principle *P. rubescens* seems to be strongly limited by phosphorus in Lake Constance. High frequency monitoring data in Lake Zurich showed the importance of a synchrony between metalimnion and ideal light climate for the growth of *P. rubescens*. Two gas vesicle genotypes could be described for Lake Constance. The majority of analysed *Planktothrix* filaments were tested positive for the MCs gen cluster, i.e., filaments are potentially toxic. Three areas in Lake Constance (Überlinger See, Bregenzer Bucht and Untersee) seem to be more susceptible to *P. rubescens* blooms. We defined a reference status for the establishment of *P. rubescens* in a lake and provide a comparison with Lake Constance. The consequences for lake management are: ozonation of raw water is required for drinking water supply; during mass developments in summer swimming restrictions are needed. Finally,

we give a workflow to recognize *P. rubescens* blooms in time and to set measures to inform the public.

Distribution of planktic communities in Upper Lake Constance

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Monitoring is most important for the detection of environmental changes in lakes and it provides the basis for an effective water management. To better understand the distribution and dynamics of plankton in lakes, the spatial distribution of plankton in Lake Constance was intensively studied from 2019 to 2020. As part of these studies a biomolecular method was tested and further developed. The aim is to use this method to supplement the joint monitoring of the countries bordering Lake Constance.

P8: A paleo-limnological view on Lake Constance resilience

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We analyzed diatoms and cladoceran remains in sediment cores from Upper Lake Constance to study the trajectories, their reversibility and resilience to decades of eutrophication and subsequent oligotrophication. Diatom trajectories suggest three important messages: 1) the community dynamics were characterized by a period of slow eutrophication (1920s-1950s), a short period of rapid eutrophication (1960s), 25 years of community stasis, and subsequent oligotrophication. 2) 2010 community state was similar to the community state of the 1950s, thus, diatoms showed a high degree of reversibility, and 3) the trajectories in response to changes in total phosphorus during winter mixis were clock-wise hysteretic. Fluxes of three cladoceran taxa (*Daphnia* spp., *Bythotrephes longimanus* and *Leptodora kindtii*), but not of *Bosmina* spp. were similar to diatom community trajectories suggesting that dynamics of *Daphnia* and invertebrate predators were primarily bottom-up controlled during the last century.

Resilience of littoral food webs

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In contrast to long-term changes in the pelagic zone, long-term changes in the littoral of Lake Constance were rarely studied. We used time series of the littoral fish community and of macroinvertebrate stable isotope signatures to study resilience of the littoral food web to roughly two decades of oligotrophication (late 1990s to mid/late 2010). The study of the (mostly juvenile) littoral fish community revealed resilience of total fish abundance (catch per unit effort),

but strong changes in community composition: perch and dace increased during the study period, whereas burbot and ruffe decreased. Stable isotope signatures differed between macroinvertebrates during the study period, but we found no evidence that signatures of invertebrate species responded differently to environmental change. However, reoligotrophication seems to have resulted in a minor shift in isotopic signals toward higher $\delta^{13}\text{C}$ in spring and lower $\delta^{15}\text{N}$ values in spring and autumn. This suggests only minor shifts in carbon and nitrogen fluxes during the late phase of oligotrophication.

L10: Quagga mussel in Lake Constance: past, present and future

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The quagga mussel (*Dreissena bugensis*) was first detected in Lake Constance in 2016 and has since spread throughout the entire near shore areas as well as in deeper areas of the lake. Compared to the zebra mussel (*Dreissena polymorpha*), which has been recorded since the 1960s, the quagga mussel can also colonize deeper habitats and occurs in much higher numbers. Both mussel species can attach themselves to a wide variety of substrates and structures in the water (e.g. stone, wood, anchor chains, jetties, pipes), which further promotes their high densities and enables them to occupy previously empty niches.

The aim of project L10 “Competition between filter feeders in Lake Constance” was to investigate the invasion potential and possible consequences of the quagga mussels on the ecosystem. We studied the detailed distribution, spread and potential colonisation pathways of quagga mussel in various lakes with a special focus in Lake Constance, we investigated which factors affect in which depth/environment dreissenid larvae settle how fast and we investigated if quagga mussels are genetically adapted or have adjusted filtration rates as a response to living in deep-water.

Our data show that quagga mussels colonize the whole depth range of the investigated lakes, but settlement starts in the littoral zone of a lake, i.e. the entire littoral zone of Lake Constance was colonised within 2 years after the first detection. We also found little evidence for local adaptation, which suggests that quagga mussels are highly plastic to be able to adjust to different environments. Results from the population genetics study suggests that the most likely dispersal pathway into Swiss lakes was by independent introductions into Lake Geneva, Lake Neuchâtel and Lake Constance from already differentiated source populations.

L11: Resilience of submerged macrophytes in the littoral zone

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The submersed vegetation of Lake Constance has undergone massive changes in recent decades as a result of nutrient fluctuations. Submersed plant stands offer a variety of habitat structures, which take on important functions such as food, protection and growth refuge for fish and invertebrates in the littoral zone. The survey of the submersed macrophytes therefore provides valuable information on the state of the ecosystem. Lake-wide submersed macrophyte surveys were conducted in 1967, 1978 and 1993. In the SeeWandel sub-project L11, further extensive surveys were carried out in two study areas. The area covered by submersed macrophytes and thus their primary production in the littoral of Lake Constance have increased significantly over the past decades. The spatial heterogeneity of aquatic plant vegetation has also increased during this time period. Above all, the stonewort algae have spread steadily over the past few decades, while the high-growing pondweeds in the Untersee have drastically decreased. This could affect habitat quality for macroinvertebrates and fish.

Fish routine monitoring of Lake Constance

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The Water Framework Directive (2000/60/EC) requires member states to achieve Good Ecological Status (GES) of their surface waters by 2027. Good Ecological Status is determined by assessing various measurable components within a water body: including its fish community. The multi-mesh gillnet sampling design DIN 14757 was designed to fulfil the requirements of GES fish community monitoring by assessing both abundance and biomass of fish species. However, obtaining reliable data in large lakes will be challenging due to the high number of nets needed to satisfy DIN 14757 sampling design requirements. This study aimed to establish an alternative, reliable and feasible routine monitoring design for Lake Constance, which could then be possibly be applied in other large lakes.

In 2019, a survey of the whole-lake fish community in Lake Constance was conducted using multi-mesh gillnets, vertical nets and electrofishing. Alongside standard CEN nets, we used modified (MOD) nets, which lack the smallest and largest mesh sizes (5 mm and 55 mm). In addition, mesh size areas vary within MOD nets. The areas of small mesh segments were reduced compared to the standard CEN nets, while the areas of large segments were increased in order to reduce catch per net and thereby fish mortality.

The results showed that MOD nets achieved a 48% reduction in fishing mortality (compared to standard CEN nets) and required 38% less effort for working steps directly affected by fish abundance, while still maintaining a similar catch composition when compared to standard CEN nets. However, in large lakes

electrofishing is also required to accurately record littoral fish species biomass and abundance.

Ecology and Diversity of Stickleback in Lake Constance

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The stickleback population in Lake Constance is interesting from both a local and global perspective. Locally, the population is relatively young (e.g. only present in past 150 years), and is closely related to stickleback originating from a catchment of the Baltic Sea in Poland. Recently, the population has increased in abundance and it is widely distributed in the lake, including the open-water region. Globally, the stickleback population is interesting because there are few large lakes in the world with stickleback that are as big as those in Lake Constance. Here, we report on the likely origins of stickleback in Lake Constance, the traits that underlie their foraging performance, and how well they perform in different environmental conditions (i.e. low and high productivity). We conclude that understanding the origin and diversity of stickleback in Lake Constance can better inform decisions about how to manage the population and the entire ecosystem.