

Focus



Piet Spaak, biologist,
is head of the Aquatic
Ecology department.
Co-author: Pascal
Vonlanthen

How aquatic ecosystems are altered by nutrients

The reduction of phosphorus loads in Swiss lakes is a positive outcome of water pollution control efforts. But now, in order to increase fish yields on Lake Brienz and other waterbodies, members of the fishing community have called for phosphorus elimination to be reduced at local wastewater treatment plants. However, increases in phosphorus inputs to nutrient-poor lakes can lead to the extinction or merging of species, producing irreversible changes in aquatic ecosystems.

The past few decades have seen a marked decrease in eutrophication of Swiss lakes, thanks to the construction of wastewater treatment plants (WWTPs), a ban on phosphates in detergents (enacted in 1985) and additional phosphorus precipitation at WWTPs. As a result, water quality has improved substantially and habitats and species compositions have returned to a more natural state. But the subject of phosphorus inputs has recently been raised once again, in particular because some people believe that a lack of this nutrient is partly to blame for declining yields of fish from certain lakes. Accordingly, it has been proposed in two parliamentary motions (tabled in the National Council and the Council of States) that inputs of phosphorus to Lake Brienz should

be increased as part of a pilot project. The supporters of this plan argue that fish yields would then rise as a result of higher primary production (algal growth) [1]. Similar ideas are under consideration for Lake Lucerne and other waterbodies.

Displacement and merging of species. In the absence of nutrients, surface waters would be inhospitable to any form of life. To be able to exist in a lake, organisms require a certain minimum level of nutrients, which enter waters via natural processes of erosion and decomposition. Nutrient availability also determines how many organisms an ecosystem can support – i.e. how productive it is. Growth is generally limited by the least abundant nutrient. In our latitudes, the limiting nutrient for algal growth is almost always phosphorus. Algae, the main primary producers, represent a vital source of food for other aquatic organisms within the lake food web. A certain amount of phosphorus and other nutrients is thus indispensable for a functioning freshwater ecosystem. Just how much is required varies from one lake to another, depending for example on the catchment. The availability of nutrients also influences species composition.

After the Second World War, as the use of phosphate detergents and fertilizers rose sharply, many Swiss lakes were exposed to unnaturally high inputs of phosphorus from municipal wastewater and agricultural run-off. This led to the proliferation of algae (algal blooms) and, consequently, to oxygen depletion and fish kills. Today, the nutrient content of various lakes has returned to pre-pollution levels (Fig. 1).

As well as adversely affecting chemical water quality, the eutrophication of lakes altered aquatic ecosystems. In some respects, these changes are still apparent today. For example, in a number of studies, Eawag reconstructed how the composition of water flea (*Daphnia*) species changed as a result of eutrophication. These zooplanktonic crustaceans feed on algae and are an important source of food for fish. For many whitefish, for example, they are the primary food source.

With the aid of genetic analyses of resting eggs retrieved from the sediments of lakes exposed to various degrees of pollution, we found that, prior to anthropogenic nutrient inputs,

As part of "Projet Lac", researchers investigated biodiversity in Lake Brienz. The survey revealed the presence of small whitefish species adapted to deep-water nutrient conditions.



Stefan Kubi

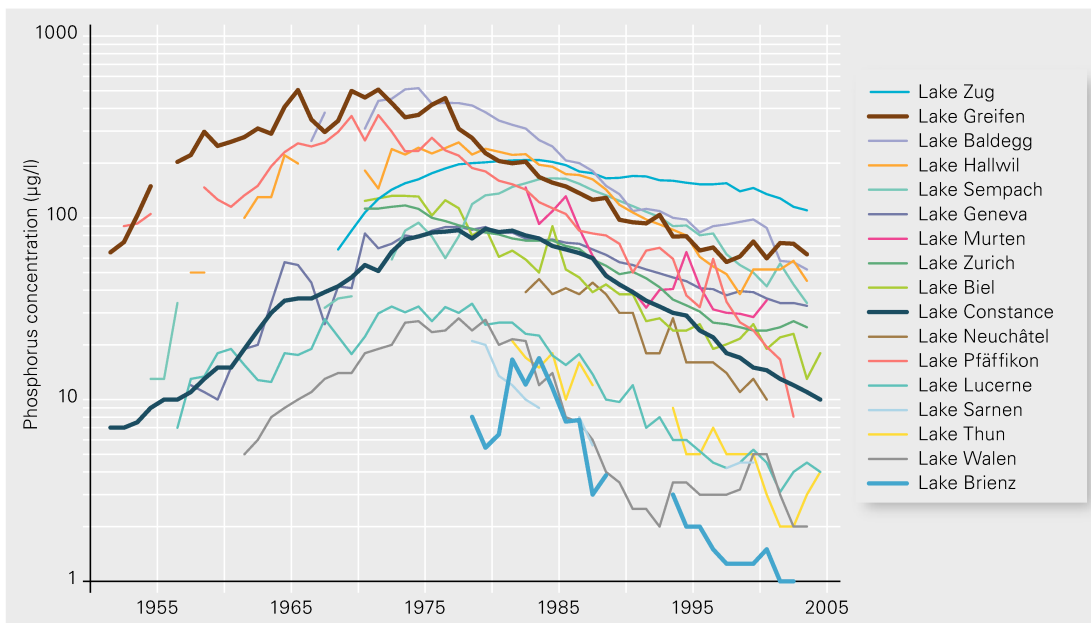
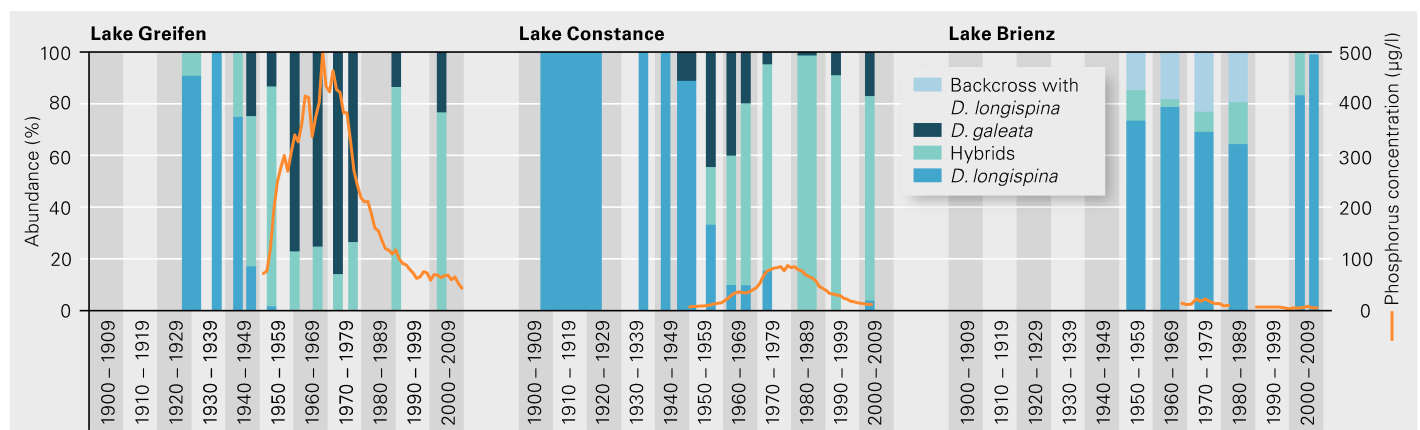


Fig. 1: Phosphorus concentrations in Swiss lakes declined as a result of water pollution control measures.

D. longispina had been the predominant water flea species in all the Swiss lakes studied [2, 3]. During the period of eutrophication, the invasive species *D. galeata* became established in many lakes – including Lakes Constance and Greifen – and displaced *D. longispina*. In some cases, these two species also merged, forming hybrids (Fig. 2). Today, as a result, *D. galeata* and the hybrid form are the only *Daphnia* species occurring in many lakes, even where the nutrient status has returned to normal. In waterbodies such as Lake Brienz, which naturally contain very little phosphorus and were less exposed to nutrient inputs, populations of *D. longispina* have tended to survive. Here, however, backcrossing has occurred between the hybrids and *D. longispina*. Current *D. longispina* individuals therefore also contain genetic material from *D. galeata* – in many lakes, the species *D. longispina* no longer exists in its original genetic form. In other words, changes of this kind may be permanent and irreversible.

Loss of ecological niches. Recently, we also experimentally demonstrated the mechanisms underlying changes in species composition. In the laboratory, we compared the fitness of clones of the two *Daphnia* species from various lakes reared under nutrient-poor and nutrient-rich conditions [4]. While *D. longispina* fared better with a sparse food supply typical of oligotrophic lakes, *D. galeata* performed better with eutrophic food. This also explains why *D. longispina* was not displaced from all Swiss lakes: in sediments from the small number of lakes minimally affected by eutrophication, we found only a few or no resting stages of *D. galeata*. This means that this species almost never occurred in Switzerland's cleanest lake – Lake Brienz – although it is found in neighbouring Lake Thun. In fact, the studies indicate that no permanent *Daphnia* populations existed in Lake Brienz before 1950. A population of *D. longispina* only became established with the onset of (relatively low) phosphorus inputs.

Fig. 2: *Daphnia* species composition was altered as phosphorus concentrations changed.





Eawag

A sediment core is retrieved from Lake Greifen: resting eggs recovered from sediments can be used to reconstruct how *Daphnia* species composition changed over time as a function of phosphorus concentrations.

As Eawag scientists have shown, the disappearance and merging of species induced by eutrophication is not confined to water fleas but can also be observed in fish. Recently, for example, Pascal Vonlanthen and Ole Seehausen of the Fish Ecology & Evolution department, together with colleagues from the University of Bern, demonstrated that – over a period of just a few decades – eutrophication has led to a 38 per cent reduction in the number of endemic whitefish species in Swiss lakes [5]. In the lakes studied, the higher the maximum phosphorus concentrations recorded, the greater the loss of species (Fig. 3a).

In seven lakes (Lakes Geneva, Murten, Sempach, Baldeg, Hallwil, Greifen and Pfäffikon), the original whitefish populations are now extinct and have been replaced by hatchery stocks. Only in deep perialpine lakes less exposed to nutrient inputs (Lakes Thun, Brienz and Lucerne) have the historical species been able to survive. In both Lake Walen and Lake Zurich, two of three historical whitefish species have survived, and four of five historical species are still found in Lake Constance. As the study also points out, there are at least 25 lakes in the European Alps which harbour one or more endemic whitefish species – i. e. species found exclusively in the lake in question.

In addition to species loss, the decline in whitefish diversity is also due to the hybridization of formerly distinct species. As

a result of massive phosphorus inputs between 1950 and 1990, the bottom and deep waters of many lakes became severely oxygen-depleted. Specialists which had evolved since the last ice age (around 15,000 years ago) and were adapted to feeding and spawning in deep waters were thus deprived of their ecological niches. (Deep, oligotrophic lakes in particular appear to be unique reservoirs of biodiversity, where new species can evolve.) With the loss of these niches, the whitefish moved to shallower waters, where they interbred with related species. As a result, they lost their genetic and functional distinctiveness within a few generations – a process known as “speciation reversal”. In lakes with higher phosphorus concentrations, genetic differentiation among the surviving populations is now also lower than in oligotrophic lakes (Fig. 3b). Specializations to particular spawning times or types of feeding have thus also been lost, and phenotypic variation has declined.

Back to the “good” old days? The studies on water fleas and whitefish provide striking illustrations of how even slight nutrient enrichment can adversely affect the natural condition of lakes – with changes in species composition, losses of genetic differentiation and, possibly, extinctions. They also demonstrate that such alterations may be irreversible: the endemic whitefish

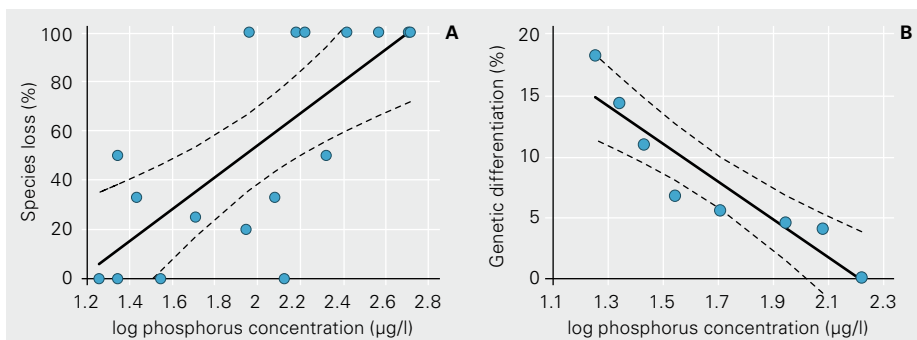


Fig. 3: In whitefish, higher phosphorus concentrations led to a greater loss of species (A) and to less genetic differentiation among different populations (B).

species which have disappeared or the original *D. longispina* cannot be recovered even in those lakes where nutrient levels have returned to normal.

Over the past three decades, as a result of the measures mentioned above, phosphorus loads have declined again in most Swiss lakes. In the cleanest – or most oligotrophic – waters, such as Lakes Brienz, Walen or Lucerne, phosphorus concentrations are now less than five micrograms per litre (see Fig. 1). From a water protection perspective, this represents a major success, but one which is now being called into question as the fishing lobby calls for nutrient elimination practices to be reconsidered.

The proponents of this idea have suggested, for example, that a phosphate limit of two to five micrograms per litre should be introduced for Lake Brienz, which corresponds to the conditions prevailing in the 1970s. In their view, this measure should once again permit “ecologically desirable plant and fish growth”. According to commercial fishery statistics for Lake Brienz, while the annual whitefish yield averaged almost 15 kilograms per hectare during the period of increased nutrient inputs, it is now less than 1 kilogram [6]. The supporters of the parliamentary motions attribute this decline to a lack of nutrients in the lake. With the aim of achieving a renewed increase in algal production and hence fish yields, they are calling for WWTPs in the Lake Brienz catchment to reduce or even completely abandon phosphate precipitation. An increase in nutrient inputs would also be designed to prevent collapses of *Daphnia* populations, which have occurred regularly since 1999, thereby safeguarding the main food source for whitefish.

While *Daphnia* represented the primary food source for whitefish over the last 30 years, we did not observe any resting eggs in lake sediments from before 1950. The absence of water fleas is also mentioned in earlier studies of Lake Brienz plankton [7]. This suggests that the endemic whitefish species most likely managed without *Daphnia* as a constant food source. The recurrence of temporary declines in *Daphnia* populations should therefore be seen as a return to a natural state, rather than as a threat to whitefish.

Lower yields, but more endemic species. In the autumn of 2011, a systematic survey of fish species carried out as part of the Eawag/Bern Natural History Museum “Projet Lac” revealed that naturally spawning whitefish populations live in the depths of

Lake Brienz. The low fish yields recorded by professional fishermen are thus not indicative of a general scarcity of fish in the lake. In fact, according to the Canton Bern Fishery Inspectorate, fishing effort has declined continuously since the end of the 1970s to just a fifth of the former level. The non-normalized commercial fish yield statistics thus give a distorted picture.

In the light of the above, the proposed phosphorus management measures would appear to be redundant. In addition, artificial nutrient enrichment of a natural lake would effectively reduce it to the status of a fish farm, which does not accord with the principles of sustainable use of natural resources. Switzerland has a number of highly productive, nutrient-rich lakes; the few naturally oligotrophic waters – and their unique biodiversity – should, however, be preserved, especially in view of the possible ecological consequences of eutrophication, based on the experience of the past 80 years. ○ ○ ○

- [1] Phosphatmanagement Brienzersee: 11.4091 Motion von Ständerat Werner Luginbühl, 11.4158 Motion von Nationalrat Erich von Siebenthal.
- [2] Brede N., Sandrock C., Straile D., Jankowski, T., Spaak, P., Streit B., Schwenk K. (2009): The impact of human-made ecological changes on the genetic architecture of *Daphnia* species. Proceedings of the National Academy of Sciences of the United States of America 106, 4758–4763.
- [3] Rellstab C., Keller B., Girardclos S., Anselmetti F., Spaak, P. (2011): Anthropogenic eutrophication shapes the past and present taxonomic composition of hybridizing *Daphnia* in unproductive lakes. Limnology and Oceanography 56, 292–302.
- [4] Spaak P., Fox J.A., Hairston Jr. N.G. (2012): Modes and mechanisms of a *Daphnia* invasion. Proceedings of the Royal Society Biological Sciences Series B, published online.
- [5] Vonlanthen P., Bittner D., Hudson A.G., Young K., Müller R., Lundsgaard-Hansen B., Roy D., Di Piazza S., Largiadier C.R., Seehausen O. (2012): Eutrophication causes speciation reversal in whitefish adaptive radiations. Nature 482, 357–362.
- [6] Eawag (2012): Fakten zum Phosphor im Brienzersee, www.eawag.ch/phosphor_brienzersee
- [7] Flück H. (1926): Beiträge zur Kenntnis des Phytoplanktons des Brienzersees. Dissertation ETH Zürich.