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zebra mussel

Effect of eutrophication on species composition and growth of freshwater mussels *(Mollusca, Unionidae)* in Lake Hallwil (Aargau, Switzerland)

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ABSTRACT

Species composition, relative abundance and life history of unionid mussels are compared between 1982–86 and 1915–19 in Lake Hallwil and the outflowing brook. The recent samples of unionid mussels were collected by divers, whereas the older ones were from a shell collection. The motivation for the comparison was that the trophic degree of the lake has changed since the beginning of the century from mesotrophic to highly eutrophic. The effects of this increased trophic degree of the lake on the life cycle of unionid mussels is discussed. Predictions are made about species composition and life history in the context of the ongoing lake restoration by the authorities.

1. Introduction

Consequences of the eutrophication process on unionid mussels

The rehabilitation of a lake is in general easily measurable by tracking nutrient cycles [34, 36]. However, freshwater communities respond in a more complex way than water chemistry. The freshwater communities change during the transition of a lake from a lower trophic to a higher trophic degree [37]. The species composition, the spatio-temporal distribution and the life history of species differ between polluted and unpolluted sites or change over time with the trophic degree of the drainage system. The responses to such temporal eutrophication processes are well documented for some taxonomic groups, e. g. algae and water plants [19], freshwater fishes [13, 14, 21, 29, 28] and oligochaetes [20, 26], but not for unionid mussels. The great variability in shell forms is one reason for the lack of detailed studies on the effects of eutrophication on unionids. This variability lead early workers to describe hundreds of species. Eventually, only a few highly variable species were recognized [16, 30, 31], but the reluctance to use unionid mussels in ecological projects seems to persist.

Much of the shell variability of unionid mussels is determined by the environment,

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e. g. shell form and color are sensitive to current, water chemistry and trophic degree, as the taxonomic studies revealed [15, 25]. In contrast to the extensive data on shell morphology, variation in life history patterns in unionids remains undescribed. In this paper, I report the impact of the temporal eutrophication process on species composition, relative abundance and life history of unionid mussels in Lake Hallwil. I discuss possible consequences of the eutrophication process on the unionid life cycle. I promote their use as sensitive indicators of biological relevant processes acting on freshwater communities.

The eutrophication process at the study site

Lake Hallwil is situated in the Swiss midland and was formed after the last ice age, some 10,000 years ago [10]. The surface area is 10.29 km^2, the maximum depth 48.0 m and the average depth 28.6 m [23]. Because the lake is sheltered between two hill chains, the influence of wind is low and the water column therefore rarely circulates [4]. The lake is slowly disappearing, observed on a geological time scale [10]. During the natural aging process, the lake changed from an alpine lake with glacial, cold water to a lowland lake with much warmer water.

As are many other lakes in Switzerland [34], Lake Hallwil is today highly eutrophic [23] and the history of the pollution process is well documented, allowing the comparison of unionid populations exposed to different levels of lake eutrophication. The eutrophy is caused by recent cultural changes, mainly trough fertilization by agriculture and trough sewage from housing development, but is not related to the natural aging process of the lake [23]. The declining yield of whitefish indicated early in the century that the ecosystem changed slowly towards a eutrophic stage. The catch of the fishermen steadily declined from 3600 kg (1914) to 900 kg (1919) [7]. The authorities (Baudepartement Kanton Aargau) tried without success to reverse the eutrophication process during its early stages by technical rehabilitation [7, 4, 23, 24]. Sewage disposal plants were built (1961 to 1964) and a system for hypolymnetic aeration and destratification was installed (since 1985, project "Tanytarsus").

Sediment cores from the lake reveal the history of the eutrophication process over a longer time span [38]. The lake was only slightly polluted by sewage during the last century, but since 1898 the blue-green alga *Oscillatoria rubescens* has appeared sporadically. Phytoplanktonic production increased over the period from 1900 to 1962, indicated by the strong increase of carotenoids in the corresponding sediment layers. In the late 1970's, the phytoplanktonic production was stabilized on a high level and has slightly decreased ever since [5]. The oxygen profile in the water column also shows that the water quality has declined since the beginning of the century [4, 7, 18].

Biology of unionid mussels

The reproductive cycle of unionid mussels is highly specialized and therefore susceptible to changes of habitat and freshwater communities [15, 31, 37]. The Swiss unionid mussels of the genus *Unio* are gonochoristic and the species of the genus *Anodonta* are gonochoristic or hermaphroditic [37]. The mussels live several years (*Unio tumidus:* 11 years, *U. pictorum:* 15 years, *A. cygnea:* 9 years [27]). Reproduction starts after two or three years of age, long before the shell is fully grown [35]. The male releases sperm in the water column. The eggs are fertilized within the female, who broods them in the gill sacs for several weeks. Hatched larvae are released in slime clusters which float. This, together with small hooks on the fringe of the shells, allows the larvae to attach themselves to gills and skin of the fish [37]. The parasitic phase is mandatory for the successful development of the larvae [11, 12]. After the metamorphosis, the mussel fall off the host fish [16, 25, 37]. The main dispersal phase occurs during the larval stage of the mussels when their larvae are carried by the fish host. In comparison, the dispersal of the adult mussels by creeping on the sediment is much lower.

In the temperate climate, unionid mussels do not grow throughout the year. Instead, shell growth stops during the winter season when the water temperature is low and when the mussels remain mostly buried [27]. Dark rings appear on the surface of the shells as a consequence of this halt in growth. They are formed by the overlapping of the old shell layers with a the newly formed layers of periostracum when shell growth resumes in spring [22, 17]. Negus [27] named them winter rings and demonstrated their use for age determination and growth rate estimation. When the shell reaches its final size, shell weight increases because additional layers are formed on the inside of the shell [22].

2. Material and methods

Collection of unionids 1982–86

During 1982, 1983 and finally 1986, twenty SCUBA divers collected freshwater mussels at 23 sites in Lake Hallwil (Tab. 1) [2]. A diving site was investigated by two or more divers from the depth of 10 m up to the surface for a period of one hour. The divers counted the number of winter rings on the shell and measured the size of living mussels under water. All living mussels were counted and only empty shells were collected. In 1986, living mussels from Mosen were collected (Tab. 1, no. 20) and the growth rate of these shells was measured in order to compare them with the collected shells. Additionally, I tried to reproduce Schnitter's method by searching for mussels (without diving) along the waterline and in shallow areas of the lake.

The search for mussels by SCUBA diving poses some difficulties and leads to varying search efficiency for the individual divers, because *Unio tumidus* is mostly totally buried and is easily overlooked. The inhalant and exhalant craters are usually the only visible signs that a mussel is buried [25]. In contrast to *U. tumidus*, *Anodonta cygnea* is often only partly buried. But the exposed shell surface of this species is covered with green algae or the Zebra mussel (*Dreissena polymorpha*), making it equally difficult to spot underwater. Other obstacles are the muddy water and the thick plant coverage. The most successful way to find living mussels is to collect them under the numerous boathouses along the beach (Tennwil, Beinwil), where shade reduced

Table 1. Collected sites 1982 to 1986, sorted by date. Two types of shells were distinguished: soft shells (group A) and hard shells (group B, see text). Living mussels were measured and released (except sample no. 20).

sample*				species					
	diving group**			*Unio tumidus*			*Anodonta cygnea*		
		date	site	soft	hard	living	soft	hard	living
1	3	14. 3. 82	Aabach lake outlet	7	1	·	22	·	·
16	5	14. 3. 82	Seengen Brestenberg	2	·	2	9	1	12
4	4	15. 3. 82	Birrwil	16	·	·	11	·	·
2	1	15. 3. 82	Birrwil upstream side	92	2	·	13	·	·
10	1	16. 3. 82	Birrwil	21	1	·	12	1	·
3	2	19. 4. 82	Mosen Wald	30	3	·	21	1	·
17	2	19. 4. 82	Mosen Wald	15	·	·	12	·	·
9	1	21. 4. 82	Seerose	9	·	·	4	·	·
6	4	22. 4. 82	Delphin	27	·	·	·	·	·
12	2	25. 4. 82	Seerose	40	·	·	2	·	·
14	1	9. 5. 82	Birrwil downstream side	22	2	·	·	·	·
7	5	23. 5. 82	Tennwil	20	·	4	2	4	·
11	4	29. 5. 82	Beinwil	45	1	·	2	·	·
15	4	30. 5. 82	Beinwil	33	·	·	6	·	·
8	5	6. 6. 82	Hallwil castle – lake	10	2	7	3	1	1
13	6	1. 7. 82	Aabach lake outlet – Seengen	3	1	3	6	2	12
18	1	3. 7. 82	Alliswil	36	·	·	5	1	6
5	2	4. 7. 82	Aesch	17	·	·	10	·	·
21	6	27. 8. 82	Delphin	–	–	1	–	–	·
22	6	10. 6. 83	Seengen	–	–	4	–	–	·
20	6	16. 7. 86	Mosen forest	–	–	26	–	–	·
$\sum = 687$				445	13	47	140	11	31

* sample no. 19 not used
** the names of the divers are listed in [2]
– only living mussels collected

plant and algal growth. A second place where they are easily found is under steps in the lake slope (Mosen, Beinwil). There, the mussels cannot move uphill when they try to migrate to shallow areas during their yearly vertical migration [8]. Even with these numerous difficulties, diving is still the best collection method for unionid mussels and cannot be replaced by any other method, such as dredging.

The shell collection from 1982–86 is stored in the Mollusc Collection of the Zoological Museum in Zurich, under the numbers 129,460 to 129,500; some shells are in the author's collection. The taxonomic status of the species in the genus *Anodonta* is not resolved [3]. Two morphs and intermediate forms were found in Lake Hallwil (*A. cygnea (L.) syn. A. cygnaea* and *A. piscinalis Nils.* [9, 16]). I use the name *A. cygnea* without distinguishing between the two forms.

The Schnitter Collection from 1915–19

Between 1915 and 1919, unionid mussels were collected in the lakes and rivers in northern Switzerland by Schnitter [31] for an extensive biometrical and biogeographic study of the Swiss unionids. Schnitter gave an account of collection methods and collections sites in great detail. He also collected in Lake Hallwil and the outflowing brook (Aabach) and received some shells from Handschin (Tab. 2). Schnitter described high densities of freshwater mussels in the lake outlet and around Hallwil castle. In the lake itself, he collected mussels along the water line and in shallow areas. The shell collection is today situated at the Natural History Museum in Basel.

Table 2. Collection from Lake Hallwil and outflowing brook from 1915–19, as listed by Schnitter [31].

sample	date	species site	**Unio tumidus**	**U. crassus**	**A. cygnea**
F64	13. 8. 1915	Dampfschifflände Beinwil	·	·	43
F128*	9. 9. 1919	Meisterschwanden	24	6	·
F62, 59	12. 8. 1915	Aabach downstream from Hallwil castle	·	240	32
F63	12. 8. 1915	around Hallwil castle	·	53	90
$\sum = 488$			24	299	165

* collected by Ed. Handschin [31], 27 shells were found in Schnitter's collection, see Table 3.

Shell analysis

Because many shells of the 1982–86 collection were corroded, they had to be transported in lake water and later stored in phenoxetol (2% solution, NIPA Laboratories Ltd., Great Britain). Without this treatment, the shells cracked and fell apart. The weight and the length of each shell were measured. Shells selected for the comparison of growth patterns were prepared as follows: The shell ligament was cut with a sharp knife and the shells were stored twelve hours each in alcohol (100%), in alcohol/xylene (1:1) and finally in an acrylum/xylene-mixture (1:1, Acrylglasur 40x-Glanz, Lascaux Farbenfabrik, Brüttisellen, Switzerland). On the fourth day, they were dried at room temperature. This procedure hardened the shells and prevented the drying shells from cracking and the periostracum from peeling off from the hypostracum. The general shell appearance was not changed by this procedure.

The growth rate of the shells was estimated by measuring the size of the winter rings using a sliding caliper. The size of the ring was plotted against the rank number of the ring. The slope of the curve was used as growth rate estimate. Similar winter rings are present on shell and ligament (Fig. 1), but because of their smaller size the interpretation of the ligament rings is more difficult. A comparison of both ring patterns gave consistent results. The age estimation by this method is obviously only possible until the growth of the shell ceases. Thereafter, the internal structure of the shell has to be analyzed [17, 22].

The shell structure of the soft and hard shell types from *Unio tumidus* (see results) was compared with cross-sections of two shells. A strip (10 mm thick) was cut from the umbo to the lip of the shell. This strip was fixed on an aluminium block by hot glue and then cut in a Leitz Saw Microtome 1600. In the first step, a clean surface was cut by cutting off a slice of the strip. A cover slip was then glued onto the dried surface by instant glue. In the second step, a small cross-section (80 µm) with the coverslip on top were cut off from the strip. After drying, the coverslip was then glued on a glass mount by instant glue. The structure of the shell was inspected and photographed in a microscope, under polarized light and phase contrast.

The growth rate was initially estimated from winter ring data by an asymptotic regression of the form $l(r) = ß_0 + ß_1 (1-e^{-ß_2 r})$ [32], where l = length of the winter ring, r = number of winter rings on shells from different sites and $ß_{0,1,2}$ = parameters of the model. This type of regression was satisfactory only for some of the shells. In order to compare the groups, linear regression was used and these parameters were compared pairwise between groups by the Scheffé-test [32]. The values were used without transformation.

3. Results

Species and their relative abundance in the lake 1982 to 1986

The divers found many empty shells and only a few living mussels of the two species *Unio tumidus Retz.* and *Anodonta cygnea (L.)*. Only one shell from *U. crassus (Phil.)* was found in Beinwil, but the small shells of this species are easily overlooked by divers. In Table 1 the shells and mussels are listed by site and date. The divers found many more empty shells (n = 609) than living mussels (n = 78) due to the fact that shells decay slowly and are accumulated in shell beds over the years where persistent populations of unionids are present.

Two shell types could be distinguished in the samples (group A and B). Many shells were soft and characterized by a periostracum that could be peeled off easily and required preparation, as described in the previous chapter. The hypostracum was white and its shell layers could be carved by a fingernail. Hard shells were often present in the same samples as the soft shells. They were not corroded in contrast to the soft shells. The hypostracum was ivory-colored and hard, sometimes covered with algae. This hard shells were similar in appearance to living mussels and their growth rate was similar (see below).

The absolute age of the two types of shells seems to be very different. Because shells corrode slowly, I conclude that the soft shells are much older hard shells, possibly by hundreds of years, while the hard shells may have been only a few years old. Figure 1 shows these two types of shells. Figures 1.A and 1.C show a typical soft shell (group A), Figure 1.B and 1.D a typical hard shell (group B). Isotopic analysis may yield better estimates of their age but was not used.

Soft shells were found everywhere in the lake, with more *Unio tumidus* shells (n = 445) than *Anodonta cygnea* shells (n = 140). These numbers may not be related to the abundance of the mussels in the lake, because the valves of *A. cygnea* are much more fragile and lighter than those of *U. tumidus*. Therefore, they often drift downhill, as I observed in Lake Zurich. Living mussels and hard shells from *U. tumidus* were found at 13 out of 18 sites, from *A. cygnea* at 8 of 18 sites. The greatest number of mussels was collected at Mosen (sites 3, 17, 20) and between Seengen and the Hallwil castle (sites 1, 8, 13, 16, 22). These are mostly shallow areas in the lake which are easily reached by divers and which are additionally in the region of the lake where the greatest mussel density can be expected [25]. The sides of the lake are less suitable as habitat for the mussels because the steep shoreline profile provides little of the shallow areas which suit them best (from 10 m deep up to the water line).

Growth pattern: relation between length and weight of the shells

The shell weight of *Unio tumidus* and *Anodonta cygnea* is strongly influenced by the local environment [31]. I found differences in both species between the samples listed in Table 1 (ANOVA, $p < 0.001$). In addition to this effect, collecting efficiency for small shells is lower and this will also bias the data [8]. As a consequence of sampling error and low numbers per site, I could not compare the shells between sites, and the analysis of group A and group B was done only on the pooled samples.

To compare the growth pattern between shell types, a linear regression model ($\ln(w) = m \ln(l) + c$, w = weight, l = length) was used on the logarithmic values of shell

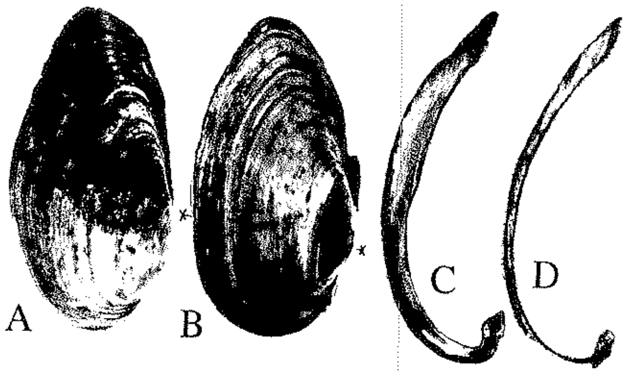

Figure 1. Comparison of the shell types of *Unio tumidus*. Figure 1.A – "soft" shell, group A, sample 3. Figure 1.B – "hard" shell, group B, sample 3. Figure 1.C – "soft", l = 44.4 mm, sample 2. Figure 1.D – "hard", l = 40.2 mm, sample 3.

The distance between winter rings in Figure 1.A is smaller than in Figure 1.B. This indicates, that the growth rate of the soft shell was much slower than of the hard shell. Figure 1.C and 1.D show sections through shells from the umbo (bottom) to the periphery (top). The periostracum is situated on the left. The line (x-x) indicates the alignment of the cross-cutting. The "soft" shell has additional layers over the hypostracum, formed after growth ceased. This layers are missing in the "hard" shell. Dark areas on the outside of the crosscuttings indicate that the crystalline structure of the layers was destroyed by corrosion.

weight and shell length for both species [32]. This regression showed that the increase of weight with length in *Anodonta cygnea* is less than in *Unio tumidus* ($m_{Ac} = 2.70 \pm 0.10$, $m_{Ut} = 3.18 \pm 0.07$, $r^2_{Ac} = 0.850$, $r^2_{Ut} = 0.839$). The difference between shell types A and B within species is not significant in *A. cygnea* ($n_{hard} = 7$, $n_{soft} = 141$, $c_{hard} = -10.62 \pm 2.54$, $c_{soft} = -9.80 \pm 0.45$, $m_{hard} = 2.87 \pm 0.54$, $m_{soft} = 2.68 \pm 0.01$) but is significant in *U. tumidus* ($n_{hard} = 13$, $n_{soft} = 442$, $c_{hard} = -7.42 \pm 1.52$, $c_{soft} = -10.63 \pm 0.27$, $m_{hard} = 2.24 \pm 0.35$, $m_{soft} = 3.24 \pm 0.06$). This indicates that the growth pattern between the soft and hard shell types is different in *U. tumidus* but not in *A. cygnea*.

Life history of U. tumidus

If the hard and the soft shells (Fig. 1, group A vs. group B) are from mussel populations of the same species but from different times, then this leads to the interpretation that the life history of *Unio tumidus* has changed over time. To confirm this, I compared the growth rates between shell types A and B, with mussels of Schnitter's collection and living *U. tumidus* (Fig. 2).

In general, soft shells have more winter rings than hard shells (Fig. 1), confirming that soft shells grew slower than hard shells. Because the absolute age of the various shells was not known, I compared these two groups of shells with mussels of Schnitter's collection which were collected alive in 1919 and mussels I collected alive in 1986. Table 3 contains the classification of those groups and Figure 2 shows the individual growth curves for these groups. Table 4 contains the pairwise comparisons of regression slopes between the shell types by the Scheffé-test. This test corrects for the type I error that several comparisons were made [32].

Table 3. *Unio tumidus* shells used for the comparison of growth rates in Figure 2.

group	year	no. of sites	no. of shells	origin
A	1982/83	8	13	soft shell type, shells collected, Tab. 1, samples 1 to 19 and 21, 22.
B	1982/83	8	13	hard shell type, shells collected, Tab. 1, samples 1 to 19 and 21, 22.
C	1919	1	27	living mussels collected, Tab. 2, sample F128.
D	1986	1	24	living mussels collected, Tab. 1, sample 20.

Table 4. Pairwise comparisons (top) of the regression slopes m (bottom) between shell groups of *Unio tumidus* by Scheffé's F-test [32]. * = m significantly different. $P < 0.01$; m in [mm/ring], $\bar{x} \pm$ s.e.

	group			
	pooled shells from different sites 1982/83		living mussels	
group	A (soft)	B (hard)	C (F128, 1919)	D (site 20, 1986)
B	8.108*	.		
C	0.014	9.506*	.	
D	7.305*	0.302	9.211*	
slope				
m	9.6 ± 0.8	16.0 ± 0.9	9.9 ± 0.3	14.9 ± 1.0

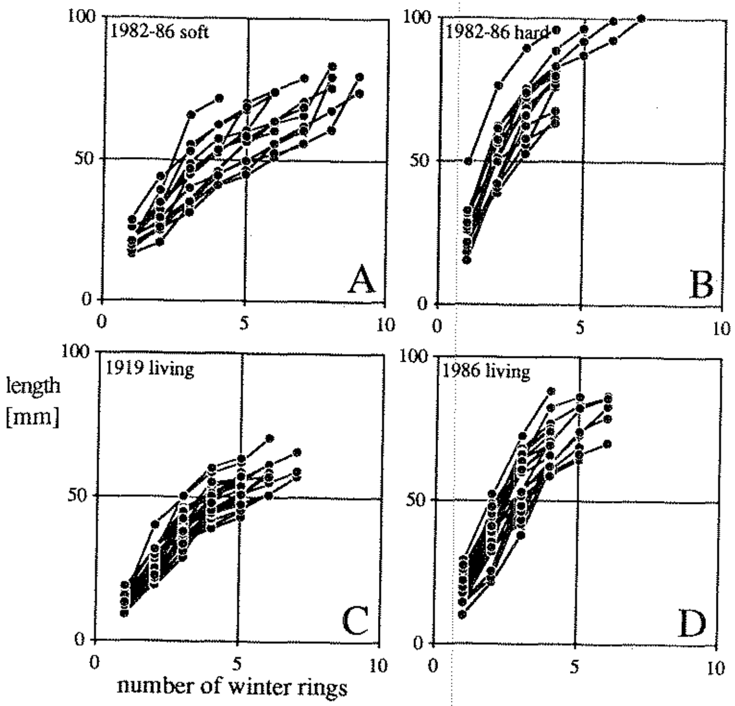

Figure 2. Individual growth curves of *Unio tumidus*. Figure 2.A – Shells collected 1982–86, "soft" type, several samples, n = 15. Figure 2.B – Shells collected 1982–86, "hard" type, several samples, n = 13. Figure 2.C – Living mussels collected 1919, Meisterschwanden, n = 27. Figure 2.D – Shells from living mussels collected 1986, Mosen, n = 24. The size of the winter ring is plotted against the age estimate. A line connects the measurements of a single shell. The highest point gives the final size of the shell and the slope estimates the growth rate. The growth pattern of A is equivalent to that of C. The pattern of B is equivalent to that of D (Tab. 3).

The diagrams in Figure 2 can be split into two pairs as is confirmed by the Scheffé-test. The first pair is the slow growing shells in group A (soft shells) and C (Schnitter collection), the second pair, the rapidly growing shells in group B (hard shells) and D (living mussels in the lake). This can be interpreted as follows: First, the divers collected old soft shells which represent mussels of the type that Handschin found in

1919, whereas the new hard shells represent mussels of recent populations in the lake. Second, mussels in 1982–86 grew faster than the older ones in 1919. Although the mussels in Figure 2.A and 2.B are from different sites in the lake, whereas the ones in Figure 2.C and 2.D are sampled from one population each, the differences between contemporary populations in the lake are much smaller than between temporally separated populations (1915–19 to 1982–86) and therefore the pooling of the samples did not cripple the analysis.

Did the life span of *Unio tumidus* also change? The cross-sections (Fig. 1) show that the soft shell is thicker than the hard shell. Additionally, the soft shell has layers on the inside of the shell which are usually formed after the mussel reached its final size [17, 22]; thus the mussel lived for some time thereafter. In contrast, the hard shell is thinner and does not show the additional layers on the hypostracum. Therefore, these mussels with hard shells died before the shell was fully completed. The difference in thickness was consistent between the two types. The final conclusion from the winter ring analysis and the sections is that mussels from older populations in the mesotrophic lake grew more slowly and died older than mussels in the highly eutrophic Lake Hallwil today.

4. Discussion

The influence of eutrophication on unionid mussels was described by Agrell [1]. He found that the abundance of *Anodonta cygnea* and *Unio pictorum* was higher and *U. tumidus* lower in lakes with increased trophic degree. In addition, he found that the shell weight in *U. tumidus* decreased with increased trophic degree between localities. I found the same results in Lake Hallwil, but here trophic degree increased over time. Agrell's conclusions are from a comparison of contemporary populations in different lakes and rivers of different trophic degrees, and he collected only from 1 m depth to the water surface. This sampling method can bias the results because the species differ in their depth distribution [25].

Only two of the three species that Schnitter [31] found in the lake are still present today: *Unio tumidus* and *Anodonta cygnea;* whereas *U. crassus* is absent. *U. crassus* is present mostly in oxygen rich, cold water, mainly brooks and rivers [31, 16]. That it can survive in eutrophic water is shown by populations I found in the upper part of Lake Zurich. The mussels there are of the same size (between 50 and 71 mm, 60.55 ± 1.01 mm, n = 60) as the ones Schnitter described (61 mm). The difference between this part of Lake Zurich and Lake Hallwil is that the lake bed is covered with stones and the oxygen supply seems to be better in Lake Zurich than in Lake Hallwil. Surprisingly, *U. pictorum* could not be found in Lake Hallwil during the investigation. This species is present in the river Aare [3] and could be dispersed by fish. The brook from the lake outlet flows into the Aare, but the absence of *U. pictorum* suggests that fish do not migrate upstream from the river Aare into Lake Hallwil. I expect that *U. pictorum* will eventually be found in Lake Hallwil, due to the general expansion of this species [3, 6].

Handschin was able to collect *Unio tumidus* and *Anodonta cygnea* in 1919 on a walk along the beach in Meisterschwanden [31]. I was unable to collect mussels at any site in Lake Hallwil by this method, indicating a lower abundance of mussels in Lake Hallwil today. In the Aabach brook where Schnitter found thick layers of mussels, the densities in 1982–86 were much lower than during Schnitter's visit in 1915. In spite of the fact that Handschin and Schnitter collected by other methods, I can conclude that the overall abundance of unionid mussels are lower today than in 1915–19. They collected more mussels with less effort, indicating clearly the trend of declining abundance of unionid mussels in Lake Hallwil.

Several factors may explain this trend. First, there is the strong dependence of unionid mussel on fish as hosts for larval development and dispersal. When the species composition of the fish community changes, the probability of infection of fish by glochidiae can change also, due to differences in infection rates of different fish species [11]. In Lake Hallwil whitefish declined while perch, burbot and pike increased [7]. Additionally, the spatial distribution of fish within the lake changed. In an oligotrophic lake, fish feed primarily on benthic and allochtonous material, whereas in a eutrophic lake they feed more in the pelagic zone on plankton [7, 28]. A second reason could be that sediment in the eutrophic lake is different (e. g. oxygen is often absent). This could decrease the survival of the freshly settled mussels. Adult mussels can use the increased nutrient content of the water and the sediment under eutrophic conditions, as the increased growth rate shows, but reproductive success, in terms of offspring produced, is unknown and is very difficult to measure. Third, the adult mussels are influenced by the invading zebra mussel *Dreissena polymorpha*, a species that attaches to hard substrata and often covers the shell of unionids. *Unio tumidus* is not very susceptible to this because it is mostly buried, but *Anodonta cygnea* is often only partly buried and might have suffered more from the invasion of *D. polymorpha* in Lake Hallwil during the 1970's. All these factors could contribute to the overall decline of the unionid mussels in Lake Hallwil.

In addition to this change in species composition and density, the analysis of the growth rate by winter rings and the comparison of the life span by cross-sections leads to the conclusion that the life history of *Unio tumidus* changed with the increase of the trophic degree of the lake. In the highly eutrophic lake the mussels grew more quickly and died earlier than in the mesotrophic lake. This points to the interpretation that the eutrophication of the lake had counteracting effects on the life cycle of *U. tumidus*. The increased food supply seems to allow a greater growth rate and should allow the mussels to breed more offspring. But this advantage does not seem to increase the mussel abundance within the lake, presumably because the mortality rate of larvae and smaller size classes of mussels may have increased as well.

The life history of *U. tumidus* may change again if the technical measures towards lake rehabilitation taken by the authorities is successful. *U. tumidus* mussels will presumably grow more slowly and live longer than today. It also seems possible that *U. crassus* could return, if fish were able to migrate between different lakes and rivers and import the glochidia from areas where *U. crassus* is still present.

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