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PRIMARY RESEARCH PAPER

Spatial distribution and age structure of the freshwater unionid mussels *Anodonta anatina* and *Unio tumidus*: implications for environmental monitoring

Jonsson Annie · Bertilsson Ann · Rydgård Mats

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Abstract Surveys of unionid populations have been incorporated into the Swedish national environmental monitoring program. Nevertheless there is still lack of knowledge of important aspects of the biology of many unionid species. There may also be differences between species. This work compares the spatial distribution of two unionid species, *Anodonta anatina* and *Unio tumidus*, at four sites in Sweden. Samples were taken at transects along the shoreline at different water depths on the surface bed and in the sediments. Individual mussel ages were determined. Our results indicated that younger mussel individuals do not show differences in horizontal spatial distribution compared to older mussel individuals. However, they showed a preference to be burrowed in the sediment compared to older individuals that were predominantly found at the sediment surface. We also found a large difference in burrowing frequency between species with a higher frequency of burrowed adult individuals of *A. anatina* than *U. tumidus*. This result may be due to the timing of our field survey that coincided with the period of glochidia release for *U. tumidus*. We can conclude that a monitoring program for freshwater mussel populations needs to be carefully planned in time.

Keywords Unionid mussels · Age structure · Spatial distribution · Burrowing behaviour · Environmental monitoring

Introduction

In unpolluted water, the sedentary unionid mussel species live a relatively long life. Depending on which species, individual mussels can reach ages of 10 to far over 100 years old (Aldridge, 1999; Hastie et al., 2000a, b). They are dependent on unpolluted water for this long lifespan due to their need to filter large quantities of water for food intake, and an adult *Anodonta anatina* may filter between 15 and 45 l/day (Strayer, 2008). Thus, it has been proposed that the presence of unionids indicates good water quality and environmental managers have been encouraged to use them as biological indicators (Grabarkiewicz & Davis, 2008). Moreover, large adult freshwater mussels are comparably easy to survey due to their large size and sedentary nature. Part of the extraordinary life cycle of unionids involves parasitic larvae (glochidia) on a host fish. Hence, the presence of reproducing mussel populations is indicative of a good status of the host fish populations (Watters, 1996). From 2010, surveys

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J. Annie (✉) · B. Ann
Systems Biology Research Centre, Skövde University,
P.O. Box 408, 7, 541 28 Skövde, Sweden
e-mail: annie.jonsson@his.se

R. Mats
Water Protection Department, County Administrative
Board of Västra Götaland, 542 85 Mariestad, Sweden

of unionids have been incorporated into the Swedish national environmental monitoring program.

Besides being a good biological indicator, unionids are seen as ecosystems engineers due to their influence on the river or sea bed structure by creating new habitats for many other organisms. Aldridge et al. (2007) showed in their study a positive correlation between high densities of freshwater mussels and diversity of other invertebrate taxa. In addition, the mussels can have a large effect on the water quality by their capacity to filter up to 45 l of water per day. When this effect is multiplied over dense beds, they are able to significantly decrease phytoplankton biomass and remove phosphorus which in turn leads to improved water clarity (Vaughn & Hakenkamp, 2001). Despite their potential usefulness in environmental monitoring, there is still a lack of knowledge of important aspects of the biology and ecology of many unionid species. There is also a tendency to treat the group of unionid mussel as homogenous, that is, as one species. This is an issue where we should be careful since there could be large differences in reproduction biology and habitat preferences. This study is an attempt to increase our knowledge about spatial distribution of the two most common unionid species in Sweden, *Anodonta anatina*, Linnaeus, 1758, (duck mussel) and *Unio tumidus*, Philipsson, 1788, (swollen river mussel).

In 2007 and 2008, we surveyed 33 mussel localities in the region of Västra Götaland (Fig. 1), Sweden (Gustavsson, 2007; Ingvarsson et al., 2009) to assess the ecological status of the Unionid populations in this region. We found that within 67 populations of the species *Anodonta anatina* (duck mussel), *Anodonta cygnea*, Linnaeus, 1758, (swan mussel), *Unio tumidus* (swollen river mussel) and *Pseudoanodonta complanata,* Rossmaessler, 1835 (depressed river mussel), only one third seemed to show a satisfactory recruitment status, according to the threshold value of 10% of the individuals being less than 50 mm in length

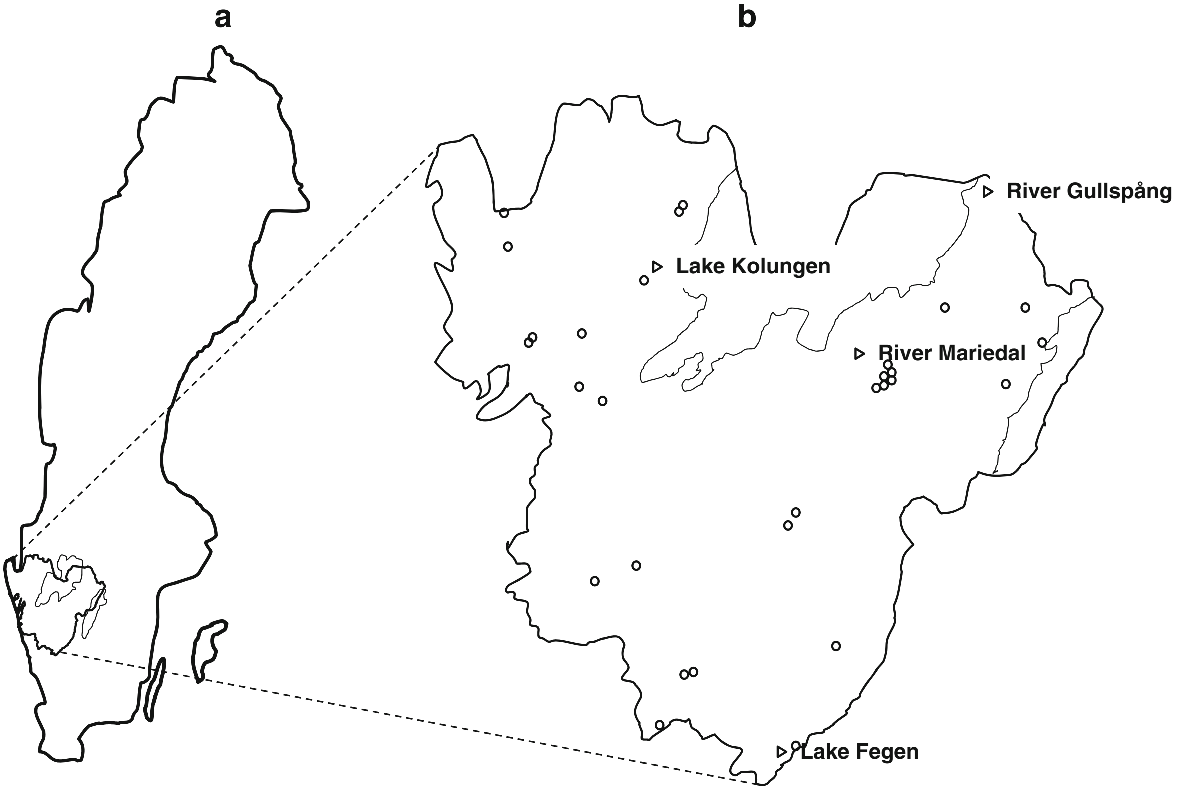

Fig. 1 **a** Map of Sweden with Västra Götaland region and the two largest lakes marked. **b** Map of Västra Götaland region with the 33 mussel sites surveyed, 2007 and 2008 marked with *circles*, including the four sites resurveyed in present study, 2009 marked with *triangles* and titled

(Wiberg-Larsen & Larsen, 2006). We focused our search for unionids on the surface of the river or lake bed, and supplemented this by completing a number of sediment samples to include burrowed individuals. Results indicated that younger mussels are found borrowed deeper in the sediment in a higher frequency than older individuals which tend to be found on the bed surface. Since we were uncertain whether there was any size bias (the probability of finding large mussels easier than small) in our study we carried out more comprehensive surveys at 4 of the 33 original localities, which we will report on here. We concentrated on the two most common species in these waters, *A. anatina* and *U. tumidus* and focused on studying whether younger mussel individuals have a different spatial distribution, both horizontally and vertically, compared to adults.

Burrowing behaviour in unionid mussels differ between species and have been shown to depend on various factors. Watters et al., (2001) performed studies of eight freshwater mussel species in outdoor enclosures, and found vertical migration patterns related to spring spawning and autumn season. One group of species surfaced in spring and remained there until August and another group of species surfaced at spring, reburied again, but surfaced a second time and remained there until August. Lewis & Riebel (1984) compared the burrowing rates of three species between different substrates, sand, clay, mud and gravel. Sand seemed to be the easiest substrate to burrow in, but there were also differences in burrowing rates between species. Balfour & Smock (1995) studied the species *Elliptio complanata*, Lightfoot, 1786, and found that all young mussels were burrowed into the sediment, whereas older individuals occurred both at bed surface and within the sediment surface, depending on time of year. Allen & Vaughn (2009) observed burrowing behaviour of different mussel species in experimentally manipulated communities. They found that burrowing behaviour differed depending on community structure.

Based on the life history of unionids, juveniles and adults are also expected to have different spatial horizontal distributions. Firstly, referred to the hypothesis that predominately young fish host juvenile mussels, it could be predicted that younger mussels will occur in shallower water because the fish hosts of the mussels mostly occur in shallow water. Secondly, juvenile mussels may have other habitat preferences than adults, as is indicated by Hastie et al. (2000a, b). They investigated spatial distribution of adult and juveniles of the mussel species *Margaritifera margaritifera* in correlation to a number of physical parameters. They concluded that adults and juveniles generally had the same preferences. However, juveniles were never found in silty or muddy conditions, which adults could tolerate. Thus, our hypothesis is that we will not find adults and juvenile mussels occurring simultaneously in the same spots. Thirdly, adults may be more aggregated than juveniles since adults probably aggregate for reproductive purposes (Amyot & Downing, 1998; Watters et al., 2001). Some evidence of differences in spatial distribution of juvenile and adult freshwater mussels can be found in the literature. A Norwegian study in the early 1960s (Ökland, 1963) shows a tendency of juveniles to inhabit shallower water than larger individuals of *A. anatina*. Similar evidence can be found in a Finnish study by Haukioja & Hakala (1974). They could show that small individuals of the four freshwater unionid mussel species *A. anatina*, *U. tumidus*, *P. complanata* and *Unio pictorum*, Linnaeus, 1758, (painter's mussel) had a tendency to occur in shallower water and the larger individuals in deeper water. Müller & Patzner (1996) examined individual growth and age structure for the species *A. cygnea* in Austria at different water depths. They found juveniles at all depths; however, there was a larger percentage of juveniles in shallow waters (defined as 1–2 m). They could also see a higher growth rate of individuals in shallower than deeper water (0–4 m vs 6–7 m). In addition to differences in mussel distribution with respect to water depth, Neves & Widlak (1987) showed that density among juvenile mussels was higher behind large stones and in faster water flows but they also concluded that older juveniles (ages 2–3 years) inhabited the same habitats as adults. From these studies, we conclude that knowledge about spatial distribution (vertical and horizontal) of juvenile and adult mussels in specific species is still uncertain. Thus, we have in this study explicitly analysed four questions:

- Are younger individuals found more frequently in shallow waters, less than 1-m depth?
- Are younger individuals more frequently burrowed in the sediments?
- Are younger and older individuals spatially separated from each other or do they mix together?

- Are older individuals more aggregated than younger ones?

We discuss the implications of our results in the light of mussel population surveys and environmental monitoring.

Methods

Anodonta anatina and *Unio tumidus*

A. anatina is the most pervasive unionid species in Sweden (von Proschwitz et al., 2006). It is found in all kinds of water with the exception of the very nutrient poor. Substrates can vary from coarse grained to fine grained. The reproductive season (occurrence of mature eggs found) in *Anodonta* species lasts from August to October and glochidia release occurs from February (sometimes from November) to April (Nagel, 1985; Aldridge, 1999; Blâzek & Gelnar, 2006; Wengström, 2010). *U. tumidus* has a more restricted distribution, but is still quite common in Sweden, found in both lakes and low flowing rivers (von Proschwitz et al., 2006). The preferred substrate is a finely grained clay material. The reproductive season of *Unio* species lasts from May to June/July and glochidia release occurs from June to July/August (Nagel, 1985; Aldridge, 1999; Blâzek & Gelnar, 2006; Wengström, 2010).

Study sites

Four sites (from previous 33 inventoried localities) were included in the field study; two lakes, Fegen and Kolungen and two rivers, Gullspång and Mariedal (Fig. 1). These were chosen to include sites that previously had shown signs of high as well as low recruitment for the two species *A. anatina* and *U. tumidus*. Lake Fegen is an oligotrophic lake with clear water. The substrate at this site was predominantly composed of fine-grained sediments and shore vegetation from the riparian deciduous forest. Lake Kolungen is an eutrophic lake with turbid water and fine-grained clay sediment. The riparian vegetation is grazed meadow. The River Gullspång is 60–70-m wide with a large section of fast running water. The annual average discharge is 61.9 m^2/s. The water is clear and the riparian vegetation grazed meadow and deciduous forest. The substrate at the site is dominated by boulders with sand and gravel. The River Mariedal is much smaller, about 4–8-m wide. The water is clear and slow running, the average annual discharge is 0.38 m^2/s, with riparian vegetation consisting of meadow and deciduous forest. The predominant substrate is coarse grained sediments.

Sampling and analyses

The field survey was performed during July to August 2009. At each locality, transects were laid every second metre along a section of 100-m perpendicular to the shoreline (except at Lake Kolungen, where the section was halved to 50 m, due to the high abundance of mussel individuals). Along each transect, 3 squares with an area of 1 m^2 each were laid out in the appropriate depths 0.2, 0.6 and 1.0 m, respectively, and surveyed using a water scope or free diving where the water was too deep (e.g. $\geq$1 m) or very muddy. All mussel individuals at the bed surface were collected, measured and then released.

When the surface was freed from visible mussel individuals, sediment samples were taken with a specially constructed sediment sampler which sampled a volume of 2.5 l (10 × 12.5 × 20 cm, surface area of 0.025 m^2). Sediment samples were sieved (mesh size of 1 mm^2) to locate any small mussels in the sediment. On harder beds or between stones where it was impossible to use the sediment sampler, samples of an area of 0.025 m^2 were taken using a spade. All mussel individuals were measured by length to the nearest mm, and age was estimated in the field by counting the number of external annual winter rings (Wiberg-Larsen & Larsen, 2006; Haag & Commens-Carson, 2008). Owing to the lack of more specific data for our Swedish populations, we defined juveniles as 5 years or younger, according to a Danish study by Wiberg-Larsen & Larsen (2006), where the unionid species *Unio crassus*, Philipson, 1788, was considered to mature at an age between 4 and 6 years.

In figures and analyses, data on mussel abundances were normalised to individuals/m^2. Local mussel density is calculated for each sampled square. Regression tree analysis was used to sort out the importance of different explanatory factors (site, water depth, burrowed or not and local mussel density) for variation in mussel age in general. Differences in age and distribution of juveniles between localities, bottom surface and sediment and depths were analysed by Fisher's exact test, Student's *t* test, one-way ANOVA and G-test of independence. Morisita's index of dispersion was calculated as a measure of aggregation. A positive value indicates that individuals are aggregated. The significance of aggregation was tested by Chi square analysis. Regression tree analysis was performed in Matlab and the other statistical analyses in Excel.

Results

In total, 1197 individuals were found at the four localities (Table 1). About 80% of these were found in Lake Kolungen. *A. anatina* was represented by 351 individuals (37 juveniles) and was found in all four sites, *U. tumidus* was represented by 846 individuals (15 juveniles), and found in two of the sites, River Gullspång and Lake Kolungen. Figure 2 shows the age distribution of the two species at the four sites. Lake Fegen (Fig. 2a) and River Gullspång (Fig. 2c and e) populations had proportionally more individuals of younger ages and significantly lower mean ages (ANOVA, $P < 0.001$) compared to River Mariedal (Fig. 2b) and Lake Kolungen (Fig. 2d, f). There was a large difference in burrowing frequency between the two species. Overall, 61% of *A. anatina* individuals were found burrowed in the sediment, compared to 24% of *U. tumidus.* Juveniles were significantly more frequently burrowed in the bottom sediments (Fisher's exact test, $P < 0.001$). Of all *A. anatina* and *U. tumidus* mussel juvenile individuals (5 years and less), 92 and 91%, respectively, were burrowed compared to adults with 44 and 16% burrowing frequency, respectively (Fig. 3a). This indicates that *A. anatina* has a significant higher burrowing frequency than *U. tumidus* among adults (Fisher's exact test, $P < 0.001$). Complementary calculations of the mean age between sediment dwellers and surface inhabitants show that sediment dwellers differed significantly from surface inhabitants, for *A. anatina* (Fig. 3b) 6.2 years in sediments compared to 8.6 years on surface and for *U. tumidus* (Fig. 3c) 7.9 years in sediments compared to 9.2 years on surface (Student's *t* test, $P < 0.001$). Additionally, we also found that *A. anatina* had a higher borrowing frequency in running waters, 77% of all individuals were burrowed in the rivers compared to 44% in the lakes (Fisher's exact test, $P < 0.001$). The species *U. tumidus* was not found in running waters since the individuals of *U. tumidus* in River Gullspång inhabited more or less stagnant water located in a small bay. In River Gullspång, 22% of all individuals of *U. tumidus* were burrowed compared to 24% in Lake Kolungen.

The distribution of juveniles and adults at different water depths showed significant differences (G-test of independence, $P < 0.001$). The general trend was a preference for the depth of 0.6 m for juveniles and adults in both species (Fig. 4a, b). There was no significance of a higher frequency of juveniles at the most shallow water depth 0.2 m. The mean age at the deepest depth of 1.0 m was significantly higher than the mean age at 0.2 and 0.6 m for both species (Student's *t* test, $P < 0.001$). But, there was no significant difference between 0.2 and 0.6 m (Fig. 4c, d).

The order of importance of factors influencing differences in age distribution was examined with regression tree analysis (Fig. 5). For *A. anodonta*, the most important predictor for age distribution is site, followed by the factors burrowed and depth ruled by the site (Fig. 5a). Two sites have lower mean age,

Table 1 Number of adult and juvenile individuals per square metre of A. *anatina* and U. *tumidus* as well as mean age sampled at 2 lakes and 2 river sites. In total, 1197 individuals were measured

	Anodonta anatina			*Unio tumidus*		
	No. of adults	No. of juveniles	Mean age	No. of adults	No. of juveniles	Mean age
Lake Fegen	35	6	6.2	–	–	–
Lake Kolungen	191	8	9.4	761	12	9.5
River Gullspång	55	23	7.2	70	3	8.2
River Mariedal	33	–	9.7	–	–	–

Data on mussel abundances were normalised to individuals/m^2

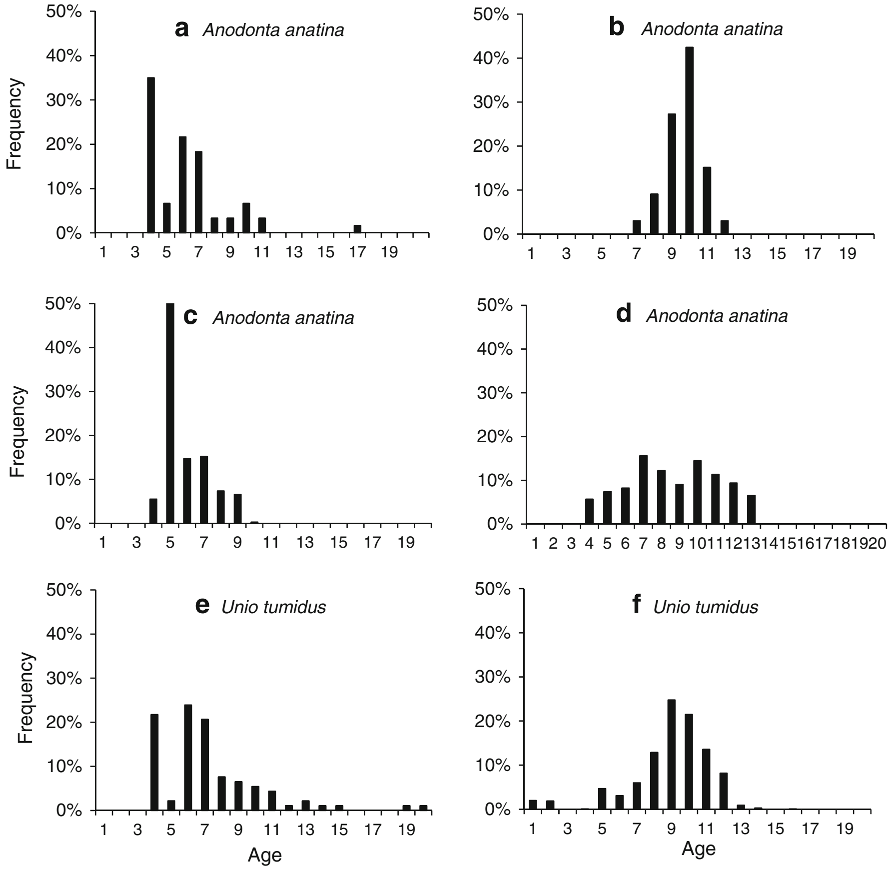

Fig. 2 Age structure of the six surveyed mussel populations of the two species *Anodonta anatina* (two first rows; **a–d**) and Unio tumidus (last row; **e–f**) at the four sites Lake Fegen (**a**), River Gullspång (**c**, **e**), River Mariedal (**b**) and Lake Kolungen (**d**, **f**). Data on mussel abundances were normalised to individuals/m^2

Lake Fegen and River Gullspång, as we also have seen in the frequency distribution of ages (Fig. 3a, c). At these two sites the next split is explained by the factor burrowed or not. Mussels that are found burrowed within the sediment have a lower mean age than mussels on the surface bed. At the two sites with few young mussels, Lake Kolungen and River Mariedal, water depth explains the next split with younger mussels at the more shallow depths 0.2 and 0.6 metre. For *U. tumidus* (Fig. 5b) the first split is explained by the factor burrowed or not. As with *A. anatina* mussels that are found burrowed within the sediment have a lower mean age than mussels on the surface bed. The second split is explained by local density for burrowed individuals with a lower mean age at lower densities (below 37 individuals in a spot), and on depth for individuals on the surface bed with younger individuals at lower depths (0.2 and 0.6 m).

We did not find a clear pattern of spatial separation between adults and juveniles. Among the samples containing mussel individuals, 48% of sample squares with *A. anatina* showed cohabitation with adults and juveniles and 67% with *U. tumidus*. Calculations of Morisita's index of dispersion (*id*) show significantly (Chi square, $P > 0.001$) that adult and juvenile mussels aggregated on the bottom surface (*A. anatina*: adults $id = 3$, juveniles $id = 2$ and *U. tumidus*: juveniles $id = 35$ and adults $id = 4$). The Morisitas index for sediment dwelling individuals could not be calculated due to the low number of individuals.

Discussion

To evaluate the status of a mussel population, it is crucial to include indicators for successful reproduction. However, as demonstrated by many reports, this is a problematic task due to the difficulty of finding juveniles. This was also true in our study. Disregarding the possibility that the population is declining with the poor recruitment, rareness of juveniles in field studies have been discussed and are thought to be

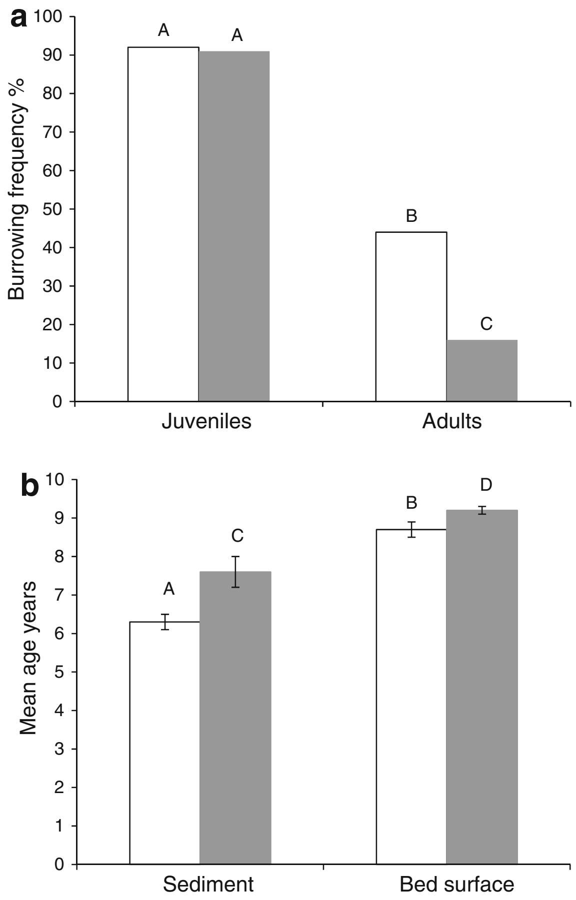

Fig. 3 **a** Burrowing frequency of juvenile and adults of the two species *Anodonta anatina* (*white*) and *Unio tumidus* (*grey*). The frequency of burrowing juveniles is significantly higher than adults (Fisher's exact test, $P < 0.001$). Also, note that *A. anatina* have a significant higher burrowing frequency than *U. tumidus* among adults (Fisher's exact test, $P < 0.001$). **b** Mean age of individuals in sediment and on bed surface of the two species *Anodonta anatina* (*white*) and *Unio tumidus* (*grey*) with 95% confidence interval added. Mean age of sediment dwellers is significantly lower than surface bed inhabitants for both species (Student's test, $P < 0.001$). Capital letters above bars indicate where there are significant differences and not. Data on mussel abundances were normalised to individuals/m^2

caused by irregularities in reproduction and uniqueness of juvenile habitat (Payne & Miller, 1989, 2000; Hastie et al., 2000a, b; Aldridge et al., 2007). Our results, however, do not lend support to the suggestions that younger mussel individuals occupy different habitats than older individuals. Younger individuals, however, showed a preference to be burrowed in the sediment and there was a slight indication that younger mussels do not reach as deep as older ones by the result of a higher mean age at the depth of 1 m. This finding is in accordance with the research in western Virginia by Neves and Widlak (1987) that concluded that older juveniles of age 2 and 3 years occupy similar habitats as adults. However, for newly released, age zero unionids, they found a higher abundance behind boulders in riffles compared to other sites. This result in combination with our finding of lower mean age at depth below 1 m can support the hypothesis that movement pattern or preferred habitats of host fish influences the distribution of the youngest mussel individuals.

Burrowing behaviour in unionid mussels differs between species and has also been shown to depend on different factors such as substrate, season, reproductive cycle, parasitism and flow regime (Lewis & Riebel, 1984; Balfour & Smock, 1995; Amyot & Downing, 1997; Di Maio & Corkum, 1997a, b; Watters et al., 2001; Taskinen & Saarinen, 2006; Allen & Vaughn, 2009). The reason why mussels burrow themselves in the sediment may be multiple. Burrowing can protect the individuals from predators or parasites. Interstitial feeding may supply the mussel with more or essential nutrients. Moreover, burrowing may be a way of anchoring in running water. Juvenile mussels are smaller and more fragile. Thus, they may be of greater benefit when burrowing since they have no need to appear on the surface bed for reproduction or glochidia release business as adults do (Amyot & Downing, 1998; Bauer, 2001; Wächtler et al., 2001). Our finding of a higher frequency of older mussels on the river and lake bed surface is in accordance with the findings of Schwalb & Pusch (2007). They noticed that more individuals of *Unio tumidus* were found on the bed surface during reproductive period in early summer than in late summer and suggested that reproduction activity may influence burrowing behaviour. In contrast, a study by Negishi & Kayaba (2010) showed that juvenile individuals of the unionid species *Pronodularia japanensis*, Lea, 1859, are more frequently found on the surface than adults during growth season. These contradictory results point out the importance of being aware of potential differences between species or habitats. Besides differences in burrowing behaviour between young and old mussels in our study, we found a large difference in burrowing frequency between species with a higher frequency of burrowed adult individuals of *A. anatina* than *U. tumidus*. This result may be due to the timing of our field survey that

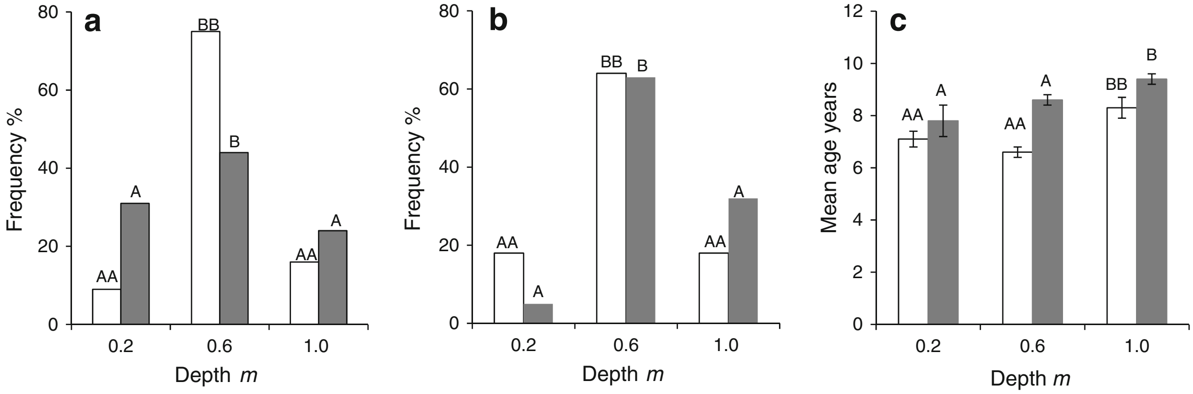

Fig. 4 Frequency of juveniles (*white*) and adults (*grey*), respectively, at different water depths of *Anodonta anatina* (**a**), *Unio tumidus* (**b**). A significant preference for the depth of 0.6 m in both species, adults and juveniles equally, can be shown (G-test of independence, $P < 0.001$). Capital letters above bars where there are significant differences and not, for juveniles (*double letter*) and adults (*single letter*), respectively. Mean age at different depths (**c**) of the two species *Anodonta anatina* (*white*) and *Unio tumidus* (*grey*) with 95% confidence interval added. Mean age in 1.0-m depth is significantly higher than at 0.2 m and 0.6 m for both species (ANOVA, Tukey–Kramer minimum significant difference). Capital letters above bars indicate where there are significant differences and not. Data on mussel abundances were normalised to individuals/m^2

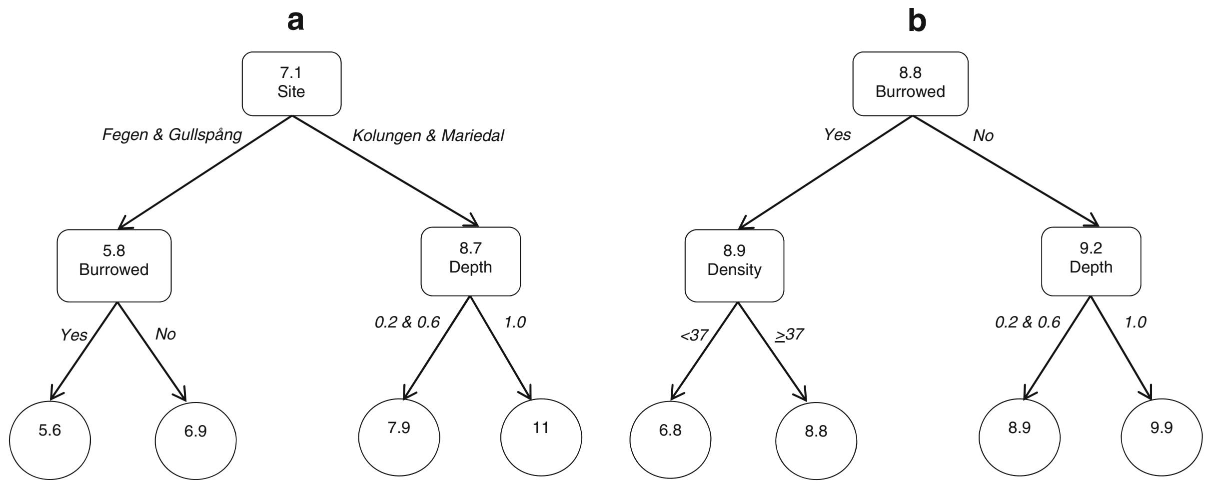

Fig. 5 Regression tree showing the three most important predictor variables explaining variation in mussel age for (**a**). *Anodonta anatina* and (**b**). *Unio tumidus*. The following five explanation factors were included in the analysis: site, water depth, (m), vertical distribution, that is, burrowed yes or no and local mussel density (individual/m^2 in each sampled square) for differences in the response variable age. Mean age is given in the figure by the numbers denoted before split and at the end leaves. Data on mussel abundances were normalised to individuals/m^2

coincided with the period of glochidia release for *U. tumidus*, June to July, but not for *A. anodonta*, February to April, (Nagel, 1985; Aldridge, 1999; Blâzek & Gelnar, 2006; Wengström, 2010). Since the glochidia need a host fish, it is important for the glochidia releasing mussel to appear on surface. *Unio tumidus* releases glochidia on mucus threads (Aldridge & McIvor, 2002). Some of the mussel species do also have different display behaviour to attract host fishes, and for certain species even including modification of the mantle as a host attracting lure (Bernard et al., 2012).

Due to the differences in burrowing behaviour between younger and older mussel individuals and between species, a monitoring program for freshwater mussels needs to be carefully planned. A survey on river and lake bed surfaces without sediment sampling would give very different results depending on in which season the survey is done and which species are included. Time of the year may also be very important since the density of adult mussels on the bed surface is likely to vary greatly between seasons during a year. A survey such as ours, carried out in July which only focused on the surface would have favoured higher density values of *U. tumidus* before *A. anatina* since a higher frequency of adult *A. anatina* are likely to be burrowed into the sediment compared to adult *U. tumidus*. Assuming a constant fraction of individuals on the bed surface and using percentage of juveniles to estimate recruitment in the population will also lead to an unreasonably high recruitment value for *A. anatina*. Burrowing behaviour may also vary by some factors for example flow velocity in rivers (Schwalb & Pusch 2007) as indicated by our results with a higher frequency of *A. anatina* burrowed in the rivers where water flows compared to the lakes. The burrowing behaviour can act as an anchor to the substrate to avoid excessive drag at high or increased flows (Di Maio & Corkum, 1995, 1997a, b). Burrowing may also increase survival during low velocity with a high risk of desiccation. Drought due to low velocity may cause severe reduction in mussel population densities (Haag & Warren, 2008).

From our results, we can conclude that adult mussel individuals from two different species have altered their burrowing behaviour, probably due to differences in the timing of their lifecycle stages. Juveniles, however, had a high and similar burrowing frequency in both species. To be able to compare abundances or recruitment between localities or years, it seems that sediment sampling is necessary to achieve reliable measurements. These results are likely transferable to other more rare species, in similar habitats, that, to a higher extent are endangered. Therefore, correct calculation of abundance and recruitment are especially important for these species. However, sediment sampling is time consuming and may damage the sediment environment. Finding efficient sampling designs such as suggested by Smith et al. (2001) is consequently very important. They used a statistical sampling technique called double sampling design. Finally, it is important to remember that burrowing behaviour is population or site specific, i.e. you need knowledge of local conditions. Since juveniles may be very sparse in abundance or very difficult to find, an alternative to sediment sampling would be to measure the age or size structure of the population as a historical measure of changes in population recruitment status where it might be possible to discover for example a trend of decrease of younger age classes.

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