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The rediscovery of Spengler's freshwater pearlmussel *Pseudunio auricularius* (Spengler, 1793) (Bivalvia, Unionoidea, Margaritiferidae) in two river systems in France, with an analysis of some factors causing its decline

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Pseudunio auricularius (Spengler, 1793) was rediscovered in two river systems in France. The populations are described regarding size, size-range of the animals, length-distribution, age and sexual maturity. At both sites the population consisted of only adult animals. The oldest animal seen was about 43 years old. The animals become mature at an age of about 18 to 22 years having a length of about10 cm. *P. auricularius* can stand rather high degrees of eutrophication as an adult. Some remarks are made on biology and shell characters, especially of the umbo. Literature and data on host fishes are presented. The author doubts whether the sturgeon was the only host fish. Some factors responsible for decline and extinction, viz. eutrophication, dredging and draining, are discussed. The author suggests that juveniles after the stage of glochidiosis may be found between *Fraxinus* and *Alnus* roots.

Key words: *Pseudunio auricularius*, Unionoidea, ecology, extinction, decline, France.

1. INTRODUCTION

The oldest and probably most threatened group of freshwater mussels (*Unionoidea*) in Europe is the family of Margaritiferidae. Most information is available from studies on *Margaritifera margaritifera* (L., 1758), which is widely distributed. Only scant information is available for the second species *Pseudunio auricularius* (Spengler, 1793). In 1985 Altaba rediscovered a population in the Ebro-basin in Spain (Altaba, 1990: 274). In 1998 Araujo & Ramos began to study the biology of this species in the Ebro-basin (Araujo & Ramos, 1998a: 129, b: 1553). The last population in the Iberian peninsula was mentioned by Azpeitia (1933: 443), also in the Ebro-basin, but it is not completely certain whether these animals have been collected recently (Ramos, pers. comm., 2003). In 1989 Nesemann & Nagel reported a very fresh complete bivalve of a relatively small animal of 10.1 cm from the Indre, a tributary of the Loire, collected near Huismes in 1985. Perhaps the last documented find of a living animal before this date in France is from 1952 which was collected in or near a small tributary of the Loire between Blois and Tours (Moolenbeek, 2000: 132) together with two other unionoids: *Unio crassus* (Retzius, 1788) and *Potomida littoralis* (Lamarck, 1801). On the basis of the find in the Indre (1985) together with my experience with *Pseudunio* spec. in Morocco, I decided to look for populations in the Loire system in France. In 1998 I rediscovered a small population of approximately 200 only adult individuals in the Vienne, another affluent of the Loire system. For reasons to be explained further on I also looked for populations in other river systems and in 2001 I found a population of again only old individuals in the Charente. This population consists of at least 5000 individuals with some relatively small animals of 7 cm. Cochet (1999: 29) published the find of freshly dead animals in 1997 in the Loire system. Araujo & Ramos (2000: 49) published a critical revision of the distribution of what they called: *Margaritifera auricularia* (Spengler, 1782) in Europe and Morocco based on museum specimens. They showed that *P. auricularius* was living in The Netherlands, Germany, France, Spain, northern Italy and Morocco (Pallary, 1918). They overlooked a 5750-year-old valve of *P. auricularius* in Belgium (Gittenberger et al., 1998: 171) and shells found in pleistoceen deposits in eastern England (Preece, 1988: 50). At the moment living populations of *Pseudunio* spec. are known in France, Spain and Morocco (Nienhuis, 2001: 50). This publication describes the populations in the Loire and Charente systems and two extinct populations in the Garonne and the Isle, a tributary of the Dordogne.

2. MATERIAL AND METHODS

With the help of the publication by Nesemann & Nagel (1989:1), who found a freshly dead, complete specimen in the Indre (SMF 307624), I started from 1997 onward to look for traces in this river, however, without any results. Why I did not find any animals in the Indre is still unclear. The method used to find mussels was to walk along the riverside especially after the water level of the river had fallen and to snorkel at sites where freshly empty, complete specimens of other unionoids were generally found. This method was also used in the Vienne. In that river *Pseudunio auricularius* shells were collected until 2002 between 2 km upstream of l'Ile Bouchard to 6 km downstream of Chinon. One population suitable for research was found in this area of the Vienne. With the information from Araujo & Ramos (2000: 49) I began to search the Charente. In this case no unionoids were found along the river. The method used to look for unionoids in general was based on the experience that these are certainly more common upstream of towns than downstream, that pollution of the water can be detected by smelling and that a deceptively beautiful slightly bluish colour of the water is an unfavourable sign. The occurrence of one species of Unionoidea is always a very good indication of the occurrence of other species, although it became clear for reasons to be explained further on that the Charente population was highly atypical. By snorkelling in the water with a visibility of 1 m to less than 15 cm the big *Pseudunio* shells could be collected by sight or in the blind. Beautifully preserved empty, complete specimens are a good indication of living individuals. In situ dead animals are an indicator of no value for living animals. However, with these experiences in mind, it took several weeks to find this population of living animals in the lower part of the Charente.

The reader has to keep in mind that in situations of very scant information together with the need for protection in the near future, data in combination with reasonable presumptions are the best tools to tempt other scientists into doing further research on this almost extinct species. The author has taken every effort though, to present his article in such a way that data and presumptions can be separated by the reader. It must be stressed that plasticity within one species (Hochwald, 2001: 127) can be very high so even the data about one species have to be handled with care in other situations.

3. RECENTLY DISCOVERED POPULATIONS OF *PSEUDUNIO AURICULARIUS*

3.1 The sites

3.1.1 The Vienne site

Near the site where the population occurs, the river is in summer 110 m wide and up to 6 m deep. At the surface the current is approximately 2.5 km /hour and 1.2 km/hour near the bottom. The bottom is covered with fine yellow sand with coarse gravel of up to approximately 4 cm in diameter and some calcareous boulders of up to 25 kg, partly covered with the red freshwater alga *Hildenbrandia rivularis* (Liebm.) J. Agardh. The most common unionoid mollusc living there is *Potomida littoralis*. Furthermore *Unio mancus* (Lamarck, 1819) (see: Nagel & Badino, 2001: 71) and the rarer *Unio crassus* (Retzius, 1788) and *Anodonta anatina* (L., 1758) are present. The other large molluscs that can be found are the bivalves *Corbicula fluminea* (Müller, 1774), *Sphaerium rivicola* (Lamarck, 1818), and the prosobranch molluscs *Viviparus viviparus* (L., 1758) and *Theodoxus fluviatilis* (L., 1758). When some *P. auricularius* were discovered, the size of the population area was determined by snorkelling for several days, looking carefully where animals could be found. The population began at 4 m from the riverside in summer and proved to be a strip of 70 x 12 m parallel to the riverside. The depth was between 60 and 200 cm.

3.1.2 The Charente site

Near the site where the population occurs, the river is in summer about 40 m wide and 7 m deep. On either side the river slopes to a depth of 7 m across a distance of 15 m, thus leaving an almost flat area of 10 m wide and 7 m deep. In the middle of the river the current at the surface is approximately 1.2 km/hour and 0.8 km/hour at the bottom. The slopes of the river are clayish or covered with fine calcareous gravel (4 mm in diameter). Boulders of calcareous rock of up to 100 kg covered with mats of the green alga *Rhizoclonium* spec. are present. The flat bottom is also covered with this fine gravel and also there boulders of up to 100 kg are present. Further large amounts of shells of the unionoids *Potomida littoralis, Unio mancus, Anodonta anatina, Pseudanodonta* spec. and some *Anodonta cygnea* (L., 1758) can be observed together with a second unidentified *Unio* species. Visibility up to 4 m deep was about 90 cm. At this depth there was a temperature discontinuity. Below this visibility was reduced to 60 cm. Therefore, at the site of the population observation could be done by sight. The other large molluscs present were *Corbicula fluminea* and a few *Theodoxus fluviatilis*. Dead *Viviparus viviparus* could be observed in large amounts. The population of *Pseudunio auricularius* lives only in the bottom at a depth of 7 m with a few exceptions up to 4 m deep on the slopes. The length of the river section where the population lives was not investigated.

3.1.3 The Garonne site

In the Garonne near la Reole a small in situ population of empty, complete specimens was discovered 0-50 cm above the summer water level. This case will be discussed in Chapter 8.

3.1.4 The Isle site

In the Isle, a tributary of the Dordogne, near St. Seurin sur l'Isle two old valves were collected. This case will be discussed in Chapter 8 as well.

3.2 The populations

3.2.1 The Vienne population

To get a rough estimate of the population size, the site was visited 12 times from 1998 to 2000 and 8 times in 2001 and 2002. During each visit an area of 4 m² was searched for mussels using a quadrant made of rope of 2 x 2 m which was fixed on the bottom of the river and marked with a buoy. By snorkelling several times to the quadrant all living mussels could be observed. Inside 20 randomly chosen quadrants 19 living mussels and 54 empty, complete specimens could be seen and their lengths measured. Because in 2001 and 2002 all empty, complete specimens had been removed from the population site this means that under normal circumstances 20/12 x 54 empty, complete specimens could be observed, which makes a total of 90 empty, complete specimens. Because the site itself covered an area of 840 m² this means that the population consisted of roughly 200 animals. It must be stressed however that this number is only a rough estimate because the animals were sometimes found in small groups and because they tended to occur more frequently at a depth of 1.5 m. All living animals had a length of between 11 and 16 cm.

3.2.2 The Charente population

In 2001 and 2002 I visited the site 10 times in summer. Because most animals lived in a 10 m wide area in the middle of the river at a depth of 7 m, only that area was searched for *Pseudunio auricularis* by snorkelling. The same method with a 2 x 2 m quadrant and a buoy was used. As during each visit two quadrants were searched, also in this case an area of 80 m² was observed. In these 80 m² 42 living animals were found and 51 empty, complete specimens. Also here the animals sometimes lived in small groups of 2-3 individuals, but they were equally distributed over the 7 m deep area.

Again the length of all animals was measured. All living animals measured between 10 and 15 cm with two small ones between 7 and 8 cm. Because the 7 m deep area is 10 m wide and because roughly one animal was collected in each 2 m², this means that in a 1m stretch of the river 5 individuals are living. However, the length of the river section where the population lives was not measured. For reasons of protection I cannot give exact information about the site of the population and about my theoretical calculations concerning the entire river section where the population lives. Suffice it to say that this stretch is at least 1 km long, which means that if the density remains the same the population counts at least 5000 animals.

3.3 The size range of the animals

Because visibility on both sites ranged from rather to very good, the animals could easily be detected on sight. With a few exceptions all animals were more than 10 cm long (fig. 1). The question arose whether other techniques could be used to find smaller individuals. Four techniques were used.

A. Bottom material was collected at the site to a depth of 10 cm and sieved on a 3 mm screen. At both sites this technique yielded no evidence of dead or living juvenile animals.

B. Because juveniles of unionoids can live separate from adults (unpublished data on *Anodonta anatina* from The Netherlands, 1975, and *Unio crassus* from Poland, 1991), bottom material to 10 cm deep was collected in areas where the current velocity was less and juveniles have a smaller chance to be washed away. At both sites this technique yielded no dead or living animals.

C. The last two techniques could only be used at the Vienne site. In this area the nutria [*Myocastor coypus* (Molina, 1782)] of South American origin is a very common mammal. This animal can be easily detected by its footprints, droppings, the entrance to its deep holes and by sight because they are less shy and bigger than the muskrat [*Ondatra zibethicus* (L., 1758)], which is also much less common in the area. The nutria used to be common at the Charente site (pers. comm. by villagers, 2001) but is very rare today. Although there is a lot of information about unionoids being part of the diet of the muskrat (Bauer, 2001: 160; Zahner-Meike & Hanson, 2001: 163), less is known about the nutria eating these mussels. (Niewold & Lammertsma, 2000: 60; Hendrix, 1986: 8). However, in September 1998 large amounts of unionoid mussels of the size between 3 and 6 cm, eaten by the nutria, were collected just near the *Pseudunio auricularius* site. These unionoids belonged to the species *Unio crassus*, *U. mancus* and *Potomida littoralis*. Shells of *Pseudunio auricularius* eaten by the nutria were not observed.

D. The fourth technique used at the Vienne site was to look for young dying animals in June 1999 when the river began to fall rapidly. In this way large amounts of *Unio crassus*, *U. mancus* and *Potomida littoralis* measuring between 3.0 and 1.5 cm could be collected. Also in this case no juvenile *Pseudunio auricularius* could be found. The negative results of all four techniques suggest that it is almost certain that *P. auricularius* of less than 10 cm are extremely rare or absent at both sites.

3.4 Size-frequency distribution of the shells

In fig. 1 the size-frequency distribution of *Pseudunio auricularius* in the Vienne and Charente is given. As can be seen the size-frequency distribution of the living animals is different from that of the empty, complete specimens. In the Vienne living and dead individuals together measured between 11.3 and 15.6 cm with one dead animal of 7.9 cm. In the Charente shell length varied between 10.0 and 14.4 cm with two living animals between 7 and 8 cm and one dead individual of 7.2 cm. As has been stated before, all empty, complete specimens were removed in 2001 and 2002 from the Vienne site, which means that about 90 empty, complete specimens could have been obtained if the site had not been disturbed. Therefore the live–dead ratio was 19-90 for the Vienne site and 42-51 for the Charente site, which suggests that mortality in the Vienne was much higher than in the Charente. This high mortality rate will continue because many *P. auricularus* in the Vienne are at their maximum length, which means that they are at the end of their lifespan. Looking at the size-frequency distribution of the Charente site it seems as if many animals begin to die before they have reached their maximum length.

3.5 Age and sexual maturity of *P. auricularius*

In order to understand population dynamics it is very important to have information about the age of the animals. It is clear that in both populations results of reproduction are not seen any longer. So if the situation does not change, these populations will vanish in the near future. For reasons of protection therefore the question arises how soon this will happen. It is also clear that if it is possible to know at what time reproduction results became unsuccessful, more reasonable hypotheses can be made about the factors responsible for this crisis in reproduction results. Age determination was done by counting the rings on the periostracum and by taking into account information about the much better known *Margaritifera margaritifera*. Whether this information about *M. margaritife-*

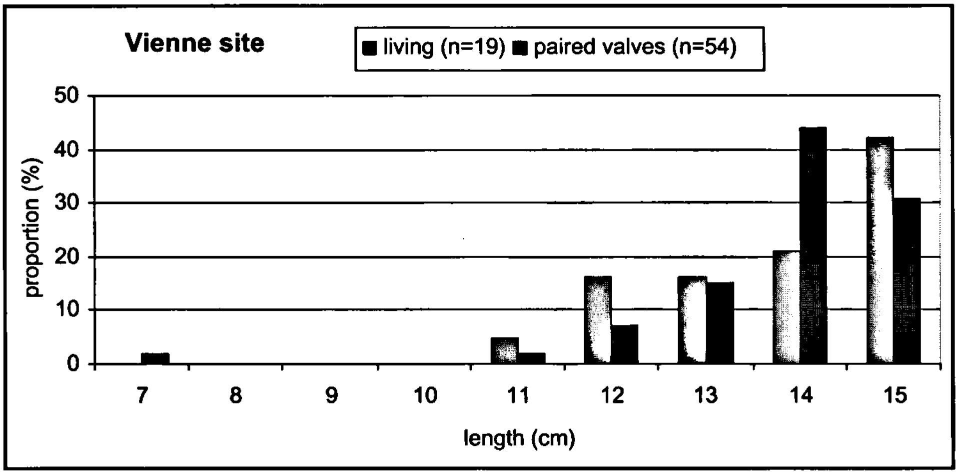

Fig. 1. Size frequency distribution of *Pseudunio auricularis* at the Vienne site (see chapter 3.4). Size 7 = 7.00 7.99 cm, etc.

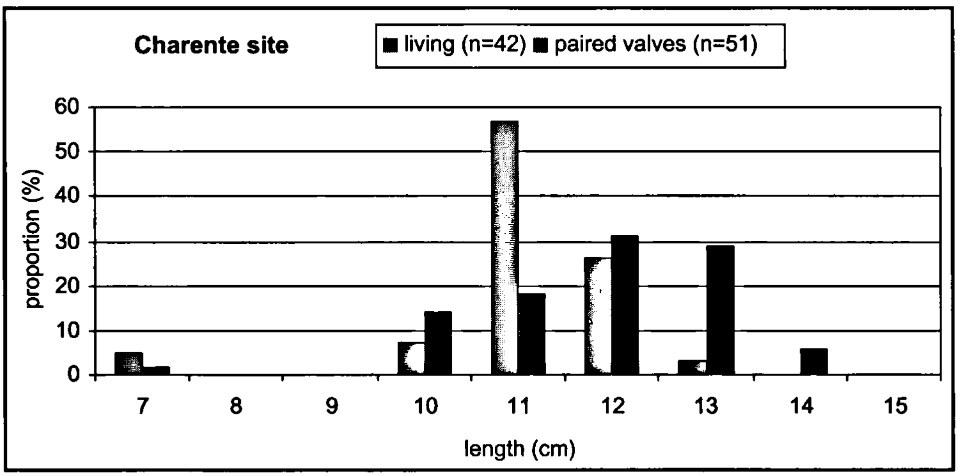

Fig. 2. Size frequency distribution of *Pseudunio auricularis* at the Charente site (see chapter 3.4). Size 7 = 7.00 7.99 cm, etc.

ra can be used for *Pseudunio auricularius* is unknown and only future research will prove if I was right in doing so. The shells of the population of the Vienne all show corroded umbones and age rings are extremely difficult to see. Therefore I concentrated on the Charente population where even the largest animals have an uncorroded umbo, rings can be seen much more easily and more material was available. The first ring to be seen appears when the animals are between 1.0 and 1.4 cm (20 specimens) long. This small

Fig. 3. *Pseudunio auricularis*, Vienne site, 2001; shell length 15.0 cm. Above, right valve interior; below, left valve (same specimen), exterior. Shell with corroded umbo. Photographs by J. Goud, Leiden.

cap has a yellow-brownish colour with mostly rugae. The second ring appears when the animals are between 1.7 and 2.1 cm. The area between these rings is brownish. After this second ring the periostracum is black (see Chapter 5 for further information). Then after 13-17 rings (20 specimens) at a length of between 9.4 and 10.5 cm the rings rather abruptly begin to grow closer together in all animals so that counting rings becomes difficult. Although I took great pains to establish the number of these rings I decided to publish only part of my results because I do not feel very confident about this simple technique (for more refined techniques, see: Baer, 1995: 74; Mutvei & Westermark, 2001: 368). The only results I wish to give in this chapter is that the largest animal collected in the

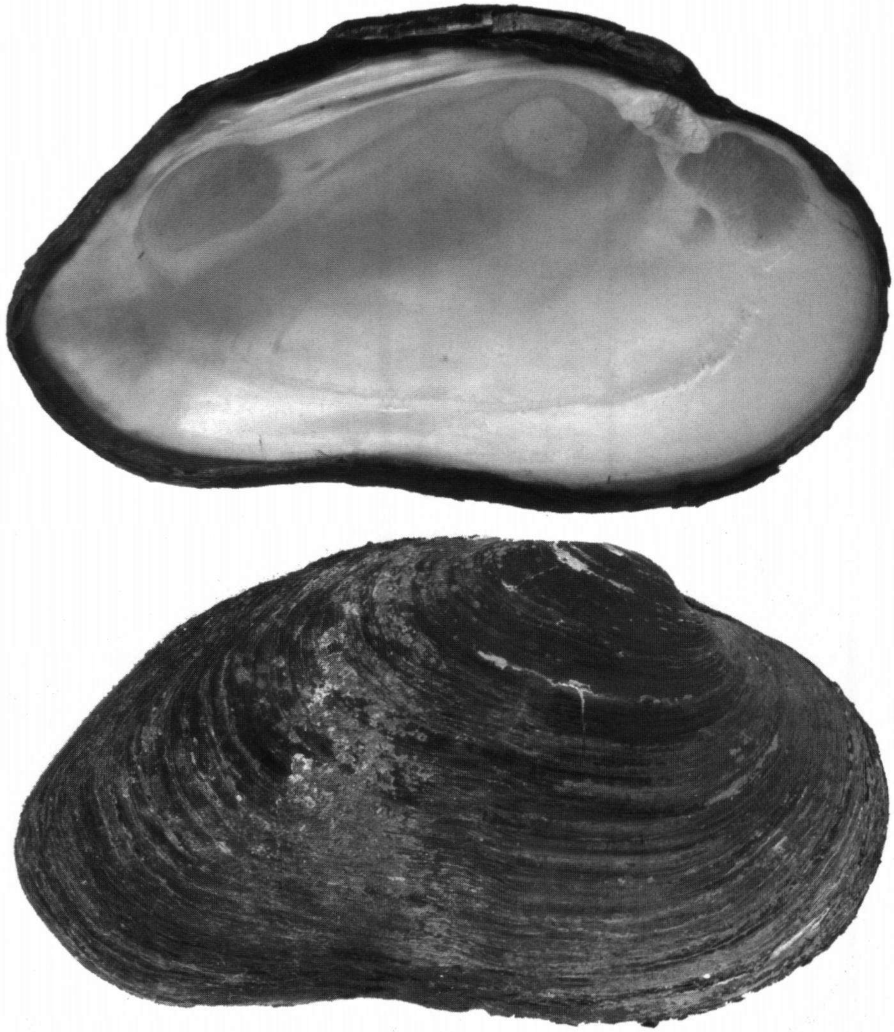

Fig. 4. *Pseudunio auricularis*, Charente site, 2002; shell length 12.0 cm. Above, left valve interior; below, right valve (same specimen), exterior. Shell with intact umbo. Photographs by J. Goud, Leiden.

Charente had a presumed age of 43 years. Moreover, most animals in the Charente with a length of 11.0-12.0 cm had an age of about 29 years. At the moment also Ramos (pers. comm., 2003) believes that the maximum age for 17 cm long animals of the Ebro basin is 60 years. Therefore the ages of animals found in the Charente and the Ebro are comparable. The information about *M. margaritifera* used in order to understand age in *P. auricularius* is based on the following. In August the glochidia of *M. margaritifera* begin their life on the host fish, the best-known host fish being the brown trout *Salmo trutta* (L.,

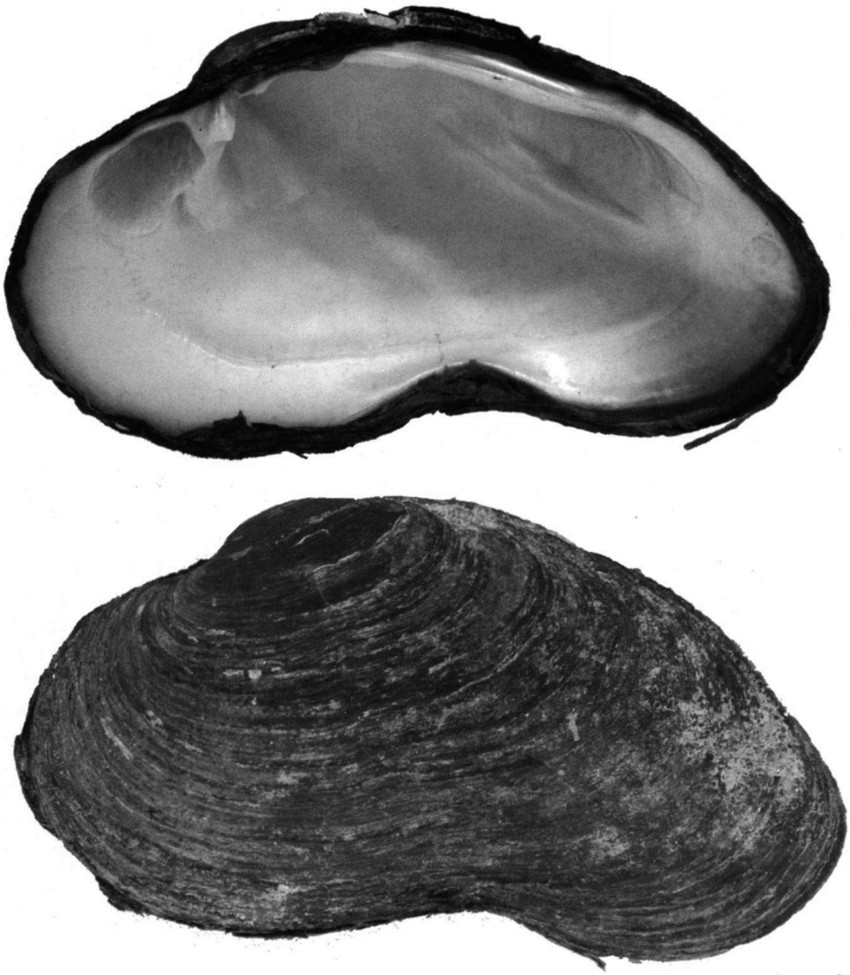

Fig. 5. *Pseudunio auricularis*, Charente site, 2002; shell length 11.2 cm. Above, right valve interior; below, left valve (same specimen), exterior. Shell with intact umbo and strongly incurved ventral side with periostrcum slightly growing inside. Photographs by J. Goud, Leiden.

1758). In June of the following year they end their parasitical life in the gills of the fish and drop to the bottom of the river. There they settle in the substrate and for 5 years they live underneath the surface feeding on detritus. After this they are about 2.5 cm long and their life at the surface of the substrate begins (Bischoff et al., 1986: 12; Hruška, 1999: 73). Ellis (1978: 20) described the colour of very young shells as being light yellowish brown streaked with green rays. *M. margaritifera* is normally unisexual and reaches sexual maturity at the age of 15-20 years. Then the growth of the shell decreases more or less abruptly (Mutvei & Westermark, 2001: 368). Because the yellow brownish cap of 1.0-1.4 cm together with the brown area measuring 1.7-2.1 cm is so different in colour from the black periostracum of the other parts of the shell, I assume for the time being that these are also the lengths to which *P. auricularius* juveniles will grow in the substrate. Assuming for the time being as well that the number of years *P. auricularius* lives in the substrate is comparable to the number of years of *M. margaritifera* living in the substrate, this means that 5 years have to be added to the number of rings counted in order to determine the age of the animal. The abrupt decrease in growth of *P. auricularius* after 13-17 rings (n=20) very much resembles the decrease seen in *M. margaritifera* when they reach sexual maturity at the age of 15-20 years. Therefore it is expected that *P. auricularius* reaches sexual maturity at an age of between 18 and 22 years at a length of 9.4-10.5 cm. These facts strongly suggest that reaching sexual maturity is more closely related to length than to age.

4. THE BIOLOGY OF *PSEUDUNIO AURICULARIUS*

All observations were made between June and September during snorkelling. Because visibility was reasonable to good, at both sites the animals could be observed rather easily. The Vienne site showed a density of one animal/4m^2; at the Charente site this density was twice as high. Mostly the animals were isolated specimens but sometimes 2-3 individuals formed a small group. All the animals I observed stood in an almost vertical position. In comparison with all other European unionoids this position seems unique. Also Arauja & Ramos (2001: 144) and Falkner (1990: 254) have made remarks on this phenomenon. Very remarkable as well is that of more than 90% of the animals the ventral side points upstream. Also the dead and in situ animals showed this. It can also be observed in *Margaritifera margaritifera* (Baer, 1995: 25). Further, the part of *Pseudunio auricularius* protruding from the substrate is 1/2 which is considerable compared to other unionoids. Digging traces were never observed. However, Altaba (1997: 141) showed a photograph of a moving animal. After a publication in a regional newspaper '*La Nouvelle République*' (Anonymus, 2001) on *P. auricularius*, villagers started to kill animals looking for pearls or keep animals in aquaria. In the latter artificial situation the animals also showed the ability to move.

5. SHELL CHARACTERS AND SYSTEMATICS

The author has a long experience with *Pseudunio* spec. in Morocco (Nienhuis, 2001: 50), and is planning to publish an article on the shell morphology of *Pseudunio* spec. in Morocco, France and Spain in the near future. Therefore only some preliminary notes are given here on the morphology of the adult shells. With few exceptions all *P. auricularius* of the Vienne site measured between 11.2 and 15.6 cm, the heaviest complete specimen weighing 300 grams. At the Charente site they measured between 10.0 and 14.4 cm, the heaviest complete specimen weighing 250 grams. All the Charente shells have an uncorroded umbo and show rather clear growth rings. A phenomenon never seen in the Vienne material but on several occasions seen in the Charente material is a strongly incurved ventral side. In these cases even the periostracum sometimes grows inwards. Finding *Potomida littoralis* at the same site, showing in a very few cases the same phenomenon, makes it likely that this strongly incurved ventral side must be considered a response to the environment. Moreover the *Potomida littoralis* of the Vienne site never shows

Fig. 6. *Pseudunio auricularis*, Charente site, 2002; shell length 12.1 cm. Umbo with very pronounced rugae. At a shell length of 1.24 cm the first age ring is visible and at 2.10 cm the second one. In this exceptional case the corrugate plication can be seen very clearly between the first and the second age ring. Photograph by J. Goud, Leiden.

this incurvation. Because most museum specimens of *P. auricularius* show a corroded umbo, that part of the shell is described in some detail here. This description can also be used while looking for juvenile animals in suitable biotopes (see Chapter 8). Most unionoids and also *P. auricularius* show a great variability within one population as to form, strength and number of rugae. As in all unionoids, the rugae in the left and those in the right valve of the same animal are not symmetrical but alternate. Apart from this, the strength of the rugae on the left and right valves can be different. As has been described before, the first ring appears between a length of 1.0 and 1.4 cm (a ring sometimes observed at a length of some mm is not described here). This cap is of a yellow brownish colour. The second ring appears at a length of 1.7-2.2 cm. The area between these rings is brown. The umbo is here defined as that part of the shell which has a length between 1.7.and 2.2 cm. After this second ring the colour of the periostracum is almost black. In prime condition the cap shows 50-70 very fine concentric striae almost at equal distances which are seen most clearly on the distal-rostral side of the small cap. Between the first and second rings 30-40 fine striae can sometimes be observed as well at almost equal distances. Also in this case they are most clearly seen at the distal-rostral side of the

Fig. 7. *Pseudunio auricularis*, Charente site, 2002; shell length 10.9 cm. Umbo with slightly corroded rugae. At a shell length of 1.01 cm the first age ring is visible and at 1.70 cm the second one. In this case, which is the normal condition, corrugate plication can only be seen faintly. Photograph by J. Goud, Leiden.

umbo. Rugae are not always present but mostly 7-12 rugae can be observed on the cap and also sometimes in the area between the two rings. On the rostral side these rugae are concentric like the striae. On the ventral side they show an incurvation and on the distal side they curve outwards. On this side they can fade away but sometimes this part is most pronounced. Especially when the rugae are not seen between the first and second rings, superimposed over the fine striae 7-12 concentric rings can be observed. Especially in cases where the rugae are pronounced between the first and second rings, but also sometimes a little further, there is the presence of a sculpture described by Johnson (1983: 301) as corrugate plication. In his reasoned classification of the Margaritiferidae, Smith (2001: 42) mentioned three genera: *Pseudunio, Margaritifera* and *Margaritinopsis*. *Pseudunio* is characterized by this corrugate plication. So according to Smith the correct name for Spengler's freshwater pearlmussel should be *Pseudunio (Pseudunio) auricularius* (Spengler, 1793). It should be noted that because of the corroded shells of the Vienne site, this plication is not seen in this population and that only a part of the Charente material shows this feature.

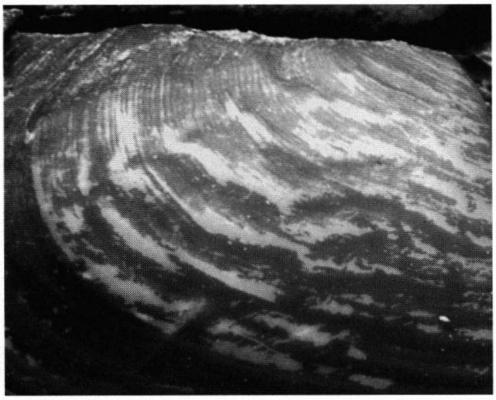

Fig. 8. *Pseudunio auricularis*, Charente site, 2002; shell length 10.9 cm (same specimen as in fig. 7). At a shell length of 1.01 cm the first age ring is visible and very fine striae can be seen especially on the distal-rostra part of the umbo. Photograph by J. Goud, Leiden.

6. THE RELATION BETWEEN THE STURGEON *ACIPENSER STUREO* (L., 1758) AND *PSEUDUNIO AURICULARIUS*

6.1 How the sturgeon initially became the accepted host fish for glochidia of *Pseudunio auricularius*

Preece (1988: 50) described finding shells of *Pseudunio auricularius* in Pleistocene deposits in eastern England together with remains of the sturgeon. With this small article the myth of the sturgeon being the host fish for *P. auricularius* began. After discovering a population of *P. auricularius* in the Rio Ebro basin in 1985, Altaba (1990: 274) put forward four interesting arguments for the sturgeon as the main host fish.

(A) The area of distribution of *P. auricularius* falls within the range of the sturgeon. (B) Its feeding and spawning habits could allow infection by the glochidia. (C) The sturgeon is an anadromous fish, so a high gene-flow between populations of *P. auricularius* in different river systems is possible with the result that these different populations show similar traits. (D) The populations of both species dwindled considerably in the last century.

Araujo & Ramos (1998: 129) described the existence of an interesting theory (without giving a source or sources) about the relation between *P. auricularius* and the sturgeon. On the basis of this theory laboratory experiments were done (Araujo & Ramos, 2001: 147) showing that: (A) glochidia are released only once a year during February and March with a peak in mid-March, and (B) these glochidia can infect exotic sturgeon and pass through the metamorphosis in the gills of those fishes. By means of electrofishing in the Ebro basin they also proved that during the glochidial release period none of the autochthonous or exotic fish species showed symptoms of infection although other unionoids did infect these fishes. It seems a good argument that the sturgeon, which had not been observed for a long time in the Ebro basin, must be the host fish. However, because glochidiosis in fish gills is normally low (Bruenderman & Neves, 1993: 83), the question arises whether they examined enough fishes.

6.2 The sturgeon may not have been the or the only host fish in France and Spain

In cases of scant information also scientists, especially in western countries (or more accurately, in those cultures where there is a belief in only one God) show a strong tendency to think in terms of a single cause. However, most unionoids can infect many host fish species (Bauer, 2001: 246) and even *Margaritifera margaritifera* living in very specific habitats show glochidiosis on more species of host fish (Bauer, 2001: 246). This must be good news to biologists interested in the protection of *Pseudunio auricularius* because a complicated reintroduction of the sturgeon may not be necessary when glochidiosis is also possible on other fishes. Two arguments are given here why it is highly uncertain that the sturgeon is the only host fish. (A) Ladiges & Vogt (1965: 60) described that the arrival of the sturgeon in the river begins in April and May, with June and July as the spawning time. Cemagref (1994: 9) described the arrival in March and April with May and June for spawning. Therefore, infection during spawning is not possible and only infection during swimming upstream is possible taking into account that the peak of release of the glochidia is in mid-March. (B) The oldest *P. auricularius* I saw in the Charente were about 43 years old, some juvenile animals of 7-8 cm even having an age of less than 18 years. Old professional fishermen near the mouth of the Charente (2001) told me that the sturgeon would arrive every year at the mouth of the Charente until the end of the 1950s. At that time they were rather common but within a few years they stopped appearing in spring. These fishermen blamed this rather abrupt decrease on the introduction of nets made of nylon. Before this they used nets made of cotton which were much weaker and would break more easily, thus letting the sturgeons through. This means that the last glochidiosis took place about 20 years after the sturgeon disappeared. At the end of the 19th century the sturgeon was already very rarely observed in the Loire (Janvier, Paris, pers. comm. 2003). So also in the case of the Vienne site the sturgeon could not have been the host fish assuming that *P. auricularius* cannot reach the age of 100 years at all. At the moment also Ramos (pers. comm. 2003) believes that the maximum age of *P. auricularius* is 60 years. Because most animals they observed were between 13 and 18 cm with some individuals measuring up to 10 cm, these smaller animals must be much younger. At the Charente site animals between 9.4 and 10.5 cm are between 18 and 22 years old. Because the sturgeon was last observed at the mouth of the Rio Ebro in 1950 (Cemagref, 1994: 3), also here there is a time gap of 30 years. These arguments and data show that correlation between the decline of *P. auricularius* and the sturgeon is highly questionable.

7. BIO-INDICATORS AND WATER QUALITY

In order to obtain information about eutrophication in the two river systems, bio-indicators were used (see table 1). The bio-indicators used were benthic algae, unionoids in general, juvenile unionoids, the other four large molluscs present and fishes sensitive to eutrophication. In the Vienne the beautiful red alga *Hildenbrandia rivularis* (Liebm.) J. Agardh (Rhodophytae) can be observed everywhere as crusts on the rocks. This alga is sensitive to eutrophication. In the Charente on the other hand, the green alga *Rhizoclonium* spec. (det. G.M. Lokhorst, 2003) can be seen as mats on the boulders. This alga can live in very eutrophied waters (Simons et al., 1999: 97). As some unionoids are rather sensitive to eutrophication, especially stenoucious species like *Unio crassus*, and as eutrophication has a dramatic effect on juvenile mussels (Patzner & Müller, 2001: 328), these groups were treated separately as indicators for eutrophication. Apart from *Pseudunio auricularius* the other unionoids or their shells in the two rivers belonged to the same species. Only *Pseudanodonta* spec. showed two different formae and although I took great pains also to find remnants of *U. crassus* in the Charente, I did not succeed. Apart

	Vienne site			Charente site		
	P	NP	OP	P	NP	OP
Algae						
Hildenbrandia rivularis	+		?		+	?
Rhizoclonium spec.		+	?	+		?
Mollusca						
Pseudunio auricularius	+		+	+		+
Unio crassus	+		+		+	—
Unio mancus	+		+		+	+
Anodonta anatina	+		+		+	+
Pseudanodonta spec.	+		+		+	+
Potomida littoralis	+		+		+	+
Pseudunio auricularius juv.		+	+		+	+
Unio crassus juv.	+		+		+	—
Unio mancus juv.	+		+		+	+
Anodonta anatina juv.	+		+		+	+
Pseudanodonta spec. juv.	+		+		+	+
Potomida littoralis juv.	+		+		+	+
Corbicula fluminea	+		intr.	+		intr.
Sphaerium rivicola	+		?		+	?
Viviparus viviparus	+		+		+	+
Theodoxus fluviatilis	+		?	+		+
Pisces						
Alosa fallax	+ R		+		+	?
Alosa alosa	+ R		+		+	?
Gobio gobio	+ VR		+		+	?
Barbus barbus	+ D		+		+	+

Table 1. Bio-indicators and water-quality. P, present alive till 2002; NP, not recorded alive between 1998 and 2002; OP, once present, but not seen alive for several years. For the fishes the information on earlier occurrences is based on conversations with villagers; for the mollusks it is based on personal observations of empty shells at or in the vicinity of the sites. Old empty shells show no longer yellow and/or green colours of the periostracum but only shades of brown. In the case of *Pseudunio* or *Potomida*, the ligament shows no elasticity any more. On the basis of personal experience, the author expects that these animals died at least 10-20 years ago. D = decreasing, R = rare, VR = very rare, + = yes, — = no, ? = no information available.

from these unionoids four large molluscs were found. In France *Corbicula fluminea* can stand almost anything provided sufficient oxygen is present and also *Theodoxus fluviatilis* given sufficient oxygen, is not very sensitive to eutrophication (pers. obs., 1998-2002). The bivalve *Spaerium rivicola* and the prosobranch *Viviparus viviparus* are in France rather sensitive to eutrophication (pers. obs., 1998-2002). A list of fishes in lowland rivers sensitive to eutrophication is added (Muus & Dahlstrøm, 1968). The fishes seen were: twaite shad *Alosa fallax* (Lacépède, 1803), allice shad *Alosa alosa* (L., 1758), barbel *Barbus barbus* (L., 1758) and gudgeon *Gobio gobio* (L., 1758). With this information it is easy to see in table 1 that the Vienne is a beautiful, comparatively clean river whereas the Charente is polluted. Apart from juvenile *P. auricularius* all unionoids and their juveniles are present. All the other four molluscs are present as well as the four fish species sensitive to eutrophication, although most are becoming rare or are decreasing. Looking at the Charente we see that all other unionoids have disappeared except for *P. auricularius*. The alga *Rhizoclonium* spec., a good indicator for eutrophication, is present. Fishes sensitive to eutrophication are absent and also the large molluscs *S. rivicola* and *V. viviparus* are not recently present. This means that although in both rivers adult *P. auricularius* can be observed, the degree of eutrophication and, as a result, also the accompanying flora and fauna are completely different.

8. THE FACTORS RESPONSIBLE FOR THE DECLINE OF THE *PSEUDUNIO AURICULARIUS* POPULATIONS

Before discussing in more detail the populations of the Vienne and Charente, I wish to give some data on the extinct populations of the Garonne and Isle sites because the factors causing extinction in these cases are so obvious.

8.1 Extinction by dredging: the Garonne site

During the years between 1975 and 1995 large amounts of sand for the construction of houses were dredged from the river. Thus the summer level of the river dropped by about one metre. This dredging also resulted in the bottom profile of the river becoming levelled out. This led to a considerably increased current velocity (pers. comm. of villagers, 2002). During snorkelling in the extremely clear water of this river the beautiful red-purple coverings of the red alga *H. rivularis* on boulders and stones could be observed everywhere together with the minnow *Phoxinus phoxinus* (Linné, 1758), a fish very sensitive to pollution. However, the velocity of the current was so high that no unionoid could possibly live there any longer. Only *Corbicula fluminea* rolling like little balls on the bottom of the river could be seen on several occasions. The typical corrosion of all their shells showed that this animal could survive in this situation for at least some time. In an area of $2m^2$ a small group of *P. auricularius* could be observed 0 -50 cm above the surface of the water, two of which were rather small animals measuring between 7 and 9 cm. These remnants of a, compared to the populations of the Vienne and the Charente, very sound population disappeared as a result of the dropping of the summer level by about one metre after dredging.

8.2 Extinction by draining: the Isle site

"Le chômage du fleuve", "the strike of the river", is a technique commonly used in rivers in France where dams are present. In the Isle near St. Seurin sur l'Isle many dams have been built in the river. Every few years for reasons of inspection or repairs, sections of the river between dams are completely drained, inevitably resulting in the death of all unionoids and therefore also of *Pseudunio auricularius* in these parts of the river.

8.3 Decline by eutrophication: the Charente site

Also because it is possible to determine the age of this population, its decline is easier

	Vienne site	Charente site
Estimated population size	200	> 5000
Paired valves/living animals	90/19	51/42
Size range (generally)	12 - 16 cm	11 - 13 cm
% with maximum size	high	lower
Maximum age	?	> 43 years
% sexually mature animals	?	> 90%
Other unionoids	present	not present
Eutrophication	low	high
Dredging	yes	no
Crisis in the population	?	c. 30 years ago

Table 2 (see chapter 8). The factors responsible for the decline of the *P. auricularius* populations. Data concerning the two *Pseudunio* populations of the Vienne and Charente sites.

to understand than the decline of the Vienne population (see table 2). What is surprising is the absence of any living unionoids except *Pseudunio auricularius*. As can be seen in fig. 1 nearly all animals are larger than 11 cm, which means that nearly all are older than about 30 years. So 30 years ago a crisis must have occurred in the population which has continued until now. Because especially juvenile unionoids are sensitive to eutrophication (Patzner & Müller, 2001: 333), it seems that 30 years ago all unionoid species stopped producing juveniles. As *P. auricularius* has a maximum age of more than 30 years, this species can still be found alive whereas the other species reaching a maximum age of less than 30 years are found only as empty shells. Approximately 30 years ago (pers. comm. of villagers, 2001) the farmers in the country changed from cattle-breeding to growing crops, especially maize and grapes. Because arable farming causes much more pollution than cattle breeding, it is likely that the crisis in the population of *P. auricularia* is connected with this change in the 1970s. As can be seen in table 1 many species of fish are not present, so it is very well possible that eutrophication also killed all kinds of host fish.

8.4 Decline by dredging; the Fraxinus-alnus roots hypothesis: the Vienne site

The Vienne is a river with less eutrophication and more kinds of fish than the Charente. If the sturgeon is at least not the only host fish, this means that it is very well possible that other kinds of host fish are still present. However, also in this case the *Pseudunio auricularius* population is in a very bad condition because no juveniles can be found any longer. Because the nutria is a predator of unionoid mussels of between 3 and 6 cm, this means that given this mammal had been living there for a longer time, predation on small *P. auricularius* in the past cannot be excluded. After a publication in a regional newspaper (Anonymus, 2001) animals were killed and collected. Therefore all information about the sites of populations has to be presented with great discretion. Because juvenile animals of all other unionoids were found but no juveniles of *P. auricularius* and because it is likely that the sturgeon was at least not the only host fish, we have to look at stages of the life cycle after glochidiosis that are different for *P. auricularius*. The only hypothesis the author can present is related to the following facts. For centuries sand had already been dug by hand when in the 1920s the use of dredgers was introduced, a practice which was only discontinued in the 1990s. The result was that the summer level of the river fell by 30-40 cm, the current velocity increased somewhat and that tree roots, especially those of the ash tree, *Fraxinus* spec., but also of the alder, *Alnus* spec., growing near the water, became exposed (F. de I., pers. comm., 2003). Having a long experience with snorkelling the author has on several occasions observed that the optimum of adult unionoids, at least in running water, can be different from the optimum of juveniles (unpublished data on *Anodonta anatina* from the Netherlands, 1975, and *Unio crassus* from Poland, 1991). Juveniles prefer biotopes where the velocity of the current is lower. Because *P. auricularius* grows more slowly (If my extrapolation of the data of *M. margaritifera* to *P. auricularius* is correct this means 17-22 mm for 5-6 years-old animals) than all the other unionoids present in the river, it is very important that especially this unionoid should have been able to live in almost undisturbed circumstances for many years. The author suggests that the soil between the *Fraxinus* and *Alnus* roots was an ideal habitat for these juveniles but that this was destroyed by dredging. It is hoped that this hypothesis can be tested in future research in Europe at population sites which have not been mentioned so far.

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