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Notes on reproduction, growth and habitat of *Microcondylaea bonellii* (Mollusca: Bivalvia: Unionidae) in the Torrente Versa (Italy)

Karl-Otto Nagel [1], Lucio Castagnolo [2], Elisa Cencetti [2] & Guiseppe A. Moro [3]

[1] Dr.-Gremmelsbacher-Straße 6, 79199 Kirchzarten, Germany
[2] Università di Siena, Dip. Scienze Ambientali "G. Sarfatti", Via P.A. Mattioli 4, 53100 Siena, Italy
[3] Via Nardini 18, 33100 Udine, Italy

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> Abstract

Microcondylaea bonellii is a freshwater mussel with a restricted distribution area that faces a serious decline. Presently, little is known about its biology and ecology. Data on reproduction, growth and habitat of a population living in a stream in north-eastern Italy were collected in the years 1990–2003. The species is a short-time breeder with eggs and larvae present in its marsupia from April to June; it is capable of consecutive brooding. It releases infectious larvae in the form of conglutinates, i.e. distinct worm-like objects with glochidia embedded in a filamentous matrix. The host fish range is supposedly narrow but direct observations are lacking. The preferred bottom substratum are stable banks of fine to coarse-grained sand, eventually overgrown by higher water plants. The growth pattern of the study population appears to be unchanged for over a century. Identification of host fishes and preservation of favourable substratum conditions are the main factors for the conservation of the species.

> Kurzfassung

Notizen zu Reproduktion, Wachstum und zum Habitat von *Microcondylaea bonellii* (Mollusca: Bivalvia: Unionidae) im Torrente Versa (Italien). – *Microcondylaea bonellii* ist eine Süßwassermuschel mit einem beschränkten Verbreitungsgebiet, deren Bestand stark zurückgeht. Gegenwärtig ist nur wenig über ihre Biologie und Ökologie bekannt. Im Zeitraum 1990–2003 wurden Informationen über Fortpflanzung, Wachstum und Habitat einer Population in einem Bach in Nordost-Italien gesammelt. Die Art ist ein Kurzzeitbrüter, deren Eier und Larven von April bis Juni in den Brutkiemen vorhanden sind. Bei einzelnen Tieren wurde Mehrfachträchtigkeit beobachtet. Infektiöse Larven werden in Paketen in Form einzelner, wurmförmiger Objekte („Conglutinates"), in denen die Glochidien in einer filamentösen Matrix eingebettet sind, entlassen. Das Wirtsfischspektrum ist vermutlich eingeschränkt, doch fehlen noch direkte Beobachtungen. Das bevorzugte Bodensubstrat sind stabile Sandbänke mit feiner bis grober Körnung, die gelegentlich von höheren Wasserpflanzen bedeckt sein können. Das Wachstumsmuster der untersuchten Population scheint seit etwa einhundert Jahren unverändert zu sein. Wesentliche Faktoren für die Bewahrung der Art sind die Identifikation ihrer Wirtsfische und der Erhalt günstiger Substratbedingungen.

> Key words

Microcondylaea bonellii, Unionidae, Bivalvia, reproduction, glochidium, conglutinate, growth, habitat, conservation, north-eastern Italy.

Introduction

Microcondylaea bonellii A. Férussac, 1827 (= *M. compressa* Menke, 1828) has a restricted distribution area in northern and eastern tributaries of the Adriatic Sea, from the Po Basin down to northern Greece (Modell 1951; Jaeckel et al. 1957). Until the beginning of the last century it was quite abundant in several localities of northern Italy (Alzona 1971, and references therein; Castagnolo & Nagel 1994; Bodon et al. 2005). More recently, relatively few extant populations have been recorded in northern Italy (Nagel & Hoffmeister 1986, Cencetti & Castagnolo 1997, Bodon et al. 2005), Slovenia (Fischer & Reischütz

1999, Bössneck 2002, Reischütz & Reischütz 2002), and Albania and Montenegro (Dhora et al. 2001). The drastic decline of this species is probably due to human impact, among which habitat destruction and water pollution are the most important factors. To effectively protect this species, it is essential that we know more about the general biology and ecology of *M. bonellii*. Our knowledge of the reproductive biology and habitat requirements of this species is disappointingly fragmentary. Some early studies on shell morphology and general anatomy exist (von Vest 1866, Haas 1924) as well as field observations on habitat and growth (Gallenstein 1894). Recent publications have focused on detailed descriptions on anatomy (stomach and siphonal papillae: Nagel 1999, glochidium larva: Cencetti 1994) and allozyme variability (Nagel & Badino 2001).

Haas (1969) placed *Microcondylaea bonellii* in the family Unionidae. Nagel (1988) confirmed this classification on the basis of anatomical characters of the stomach and the gills. More precisely, the species belongs to the Ambleminae with *Potomida littoralis* as the only other European species of the subfamily. However, some anatomical features suggest that it is only distantly related to the other European unionids. For example, the siphonal papillae surrounding the inhalant opening are of a unique type (arboriform, Nagel 1999: Fig. 2b) and a comparison of 15 characters of the stomach floor demonstrated a low level of overall similarity with other genera (Nagel 1988, Nagel et al. 1998: Figs. 1 and 2). Preliminary results from DNA analysis confirm the species' isolated position among European Unionidae (Araujo, pers. comm.). Interesting is that Modell (1951) considered the species to be of Asiatic origin and that its most closely related species occur in the Middle East.

In this article we present results from field and laboratory studies about reproductive biology and habitat preference of *M. bonellii*. Our aim is to contribute to a better understanding of the species' requirements for effective protection.

Material and methods

Study area

Observations on living animals in their natural habitat were made in the Torrente Versa (locality: Capriva del Friuli, province of Gorizia, Italy). The Torrente Versa is a right-hand tributary of the Isonzo (Soca) river in the flysch hills of eastern Friaul.

Histology

A minimum of 10 animals was collected monthly between June 1991 and September 1992 with additional samples taken in 1994 (March, May, August, November and December). Gonadal tissue was fixed in Bouin-Hollande and stained with hematoxiline-eosine.

Laboratory observations

Twenty animals were collected live on April 4, 1991. They were kept in aquaria at Turin for two months and then brought back to the Torrente Versa. They were fed by adding small amounts of food for aquarium fish every three to five days. About half of the water in the aquaria was replaced every week.

Field observations

Detailed field observations were made on April 4, 1991, and May 13, 2003. In 1991, a stretch of the Torrente Versa with shallow water (length 50 m, channel width 5 m and maximum depth 0.6 m, approximately) was searched for all unionids in order to determine their distribution in the habitat. On May 13, 2003, mussel density was estimated in a pool section of the stream (approximately 5 by 3 m) that was accessible for direct observation due to an extremely low water level.

Growth studies

On June 11, 1991, 54 animals (total length: 36.0–82.5 mm) were sampled in the Torrente Versa. Their total length was measured to the nearest 0.1 mm using a slide-gauge. The typical precision of these measurements is ±0.5 mm (Nagel 1991). All specimens were numbered individually with white varnish colour and released into their habitat in their original locations. On September 8, 1992, they were searched for again. Six specimens were found and measured. The individual growth records were used in a Walford plot. The parameters of the linear regression line were compared (Sachs 1997: 555) to previous results in which the raw data were lengths of consecutive growth lines ("winter rings") on the outer surface of empty shells collected in the same locality in 1984 (Nagel & Hoffmeister 1986 and references therein). Von Bertalanffy growth curves were constructed from Walford plots. However, statistical tests of the underlying linear regression model are only an approximation due to the

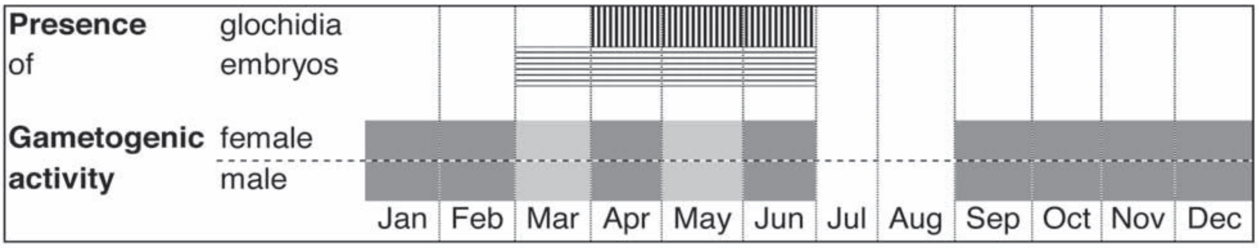

Fig. 1. Reproductive cycle. Colour symbols for gametogenic activity: dark, intense; light, weak.

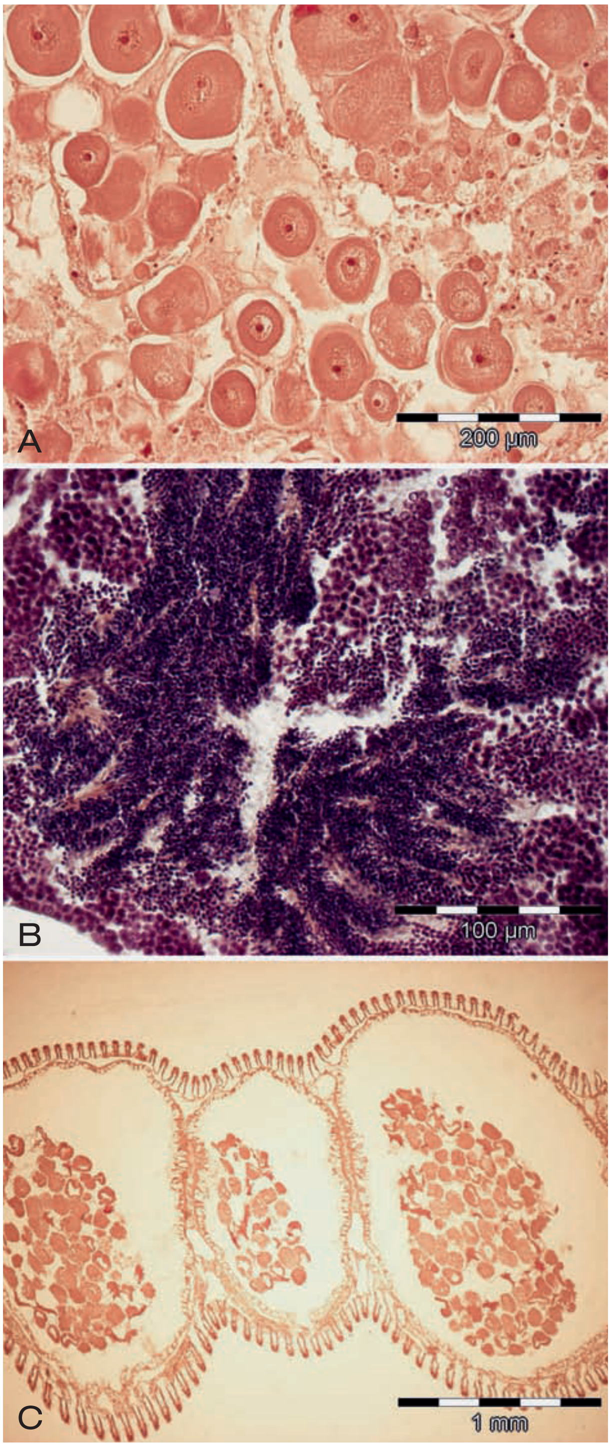

Fig. 2. Histology of reproductive organs. **A.** Female gonad with oocytes. **B**. Male gonad with sperm cells and spermatocytes. **C**. Marsupium filled with glochdia. Scale bars: A=200 µm; B=100 µm; C=1 mm.

lack of a distribution theory for stochastic differences equations (DRYGAS, pers. comm.).

Results

Reproductive cycle

M. bonellii uses both outer and inner demibranches as marsupia. All four demibranchs were filled up to the anterior and posterior ends, leaving no conspicuous non-marsupial portions at their terminal ends. In histological sections the individual gonads were either male or female and there was no hint of the occurrence of hermaphrodites. In both female and male gonads all types of gametocytes were found at the same time.

The annual cycle of gonadal activity shows an active phase of about 10 months followed by a resting phase of about two months (Fig. 1).

September, October: Follicles of female gonads are full of various stages of oogenesis (mature eggs together with premature oogenic cells), acini of male gonads filled with various stages of spermtogenesis, which progressively maturate towards the inside (the first fully developed spermatozoa visible).

November, December, January: Male and female gonads are full of mature sexual products with earlier stages still present (Figs. 2A, B).

February: Early stages of spermatogenesis (spermatogonia and spermatocytes) have mainly disappeared.

March: The gonads of both sexes are full with ripe gametes, in two animals developing eggs were already found in the marsupial gills (Fig. 2C).

April: Condition of gonads as in March, first mature glochidia were being expelled.

May, June: Mature eggs are less numerous in the follicles, again marsupia filled with developing eggs and glochidia.

July, August: Both female and male gonads have small, empty and nearly collapsed germinal follicles without any mature sexual products. No larvae were observed in the marsupia (CENCETTI 1994).

Field observations

On May 13, 2003 in two mussel beds in the Torrente Versa (Fig. 3A) where *M. bonellii* was present in high density whitish masses were observed on the stream bottom. Water temperature was unusually high with 18.3°C at 7.00 a.m. The masses proved to be identical with the conglutinates already observed in the laboratory. They contained mostly mature glochidia. These conglutinates were either trouser-shaped or consisted a simple cylindrical structure. There were no signs that the animals had moved about before expelling the packets. Most of the objects were lying on the bottom immediately near the individuals that had expelled them although the deposition could not be directly observed. Some of those conglutinates were flowing and gently swaying with the water current. They were obviously fixed by thread-like extensions to the mussels or to some object on the stream bottom.

Laboratory observations

In 1991, six gravid females were among the animals kept alive for two months in the laboratory. After ca. one week masses of marsupial content were found both on and buried into the sandy bottom of the aquarium. At least two animals had deposited their marsupial masses into the substratum (sand) immediately near them. It was apparent that individual adult mussels can bury themselves totally into the sand and thus disappearing from the surface without even showing the siphonal openings.

The marsupial masses form characteristic objects that take the form of a "pair of trousers". They probably are the content of two neighbouring water tubes that are separated by an incomplete septum. Hereafter they are called conglutinates for reasons given in the discussion. However, the paired objects separate into single cylinders after some hours or a few days (Fig. 3B). It seems that the two parts are only loosely held together by filaments. This corresponds to observations in the field in which the majority of conglutinates lying on the stream bottom were single cylinders.

The conglutinates contained eggs or larvae, but the conglutinates of a single female were apparently in the same stage of development. Thus the maturing of the larvae appears to be synchronous. Four females that were collected on June 11, 1991 all expelled mature glochidia two days later. The glochidia were still embedded in the matrix of the marsupial masses (Fig. 3C). On another occasion (26.–30.4.2001) it was observed that single free infectious larvae appeared 3 days after conglutinates had been expelled.

The conglutinates are formed and held together by filaments that originate in the egg membrane, which continues to surround the developing glochidium until it breaks free. The filaments envelop the eggs or larvae and seem to create a fibre in the centre of the conglutinate.

Fig. 3. Conglutinates. **A**. View of stream bottom with conglutinates dispersed around siphonal openings of deeply buried *M. bonellii*. **B**. Conglutinates in the laboratory on glass dish. **C**. Broken conglutinate containing ripe glochidia. Scale bars: B=2 mm; C=100 µm.

One animal collected in the Torrente Versa was found gravid on April 6, 1991. Since then it was

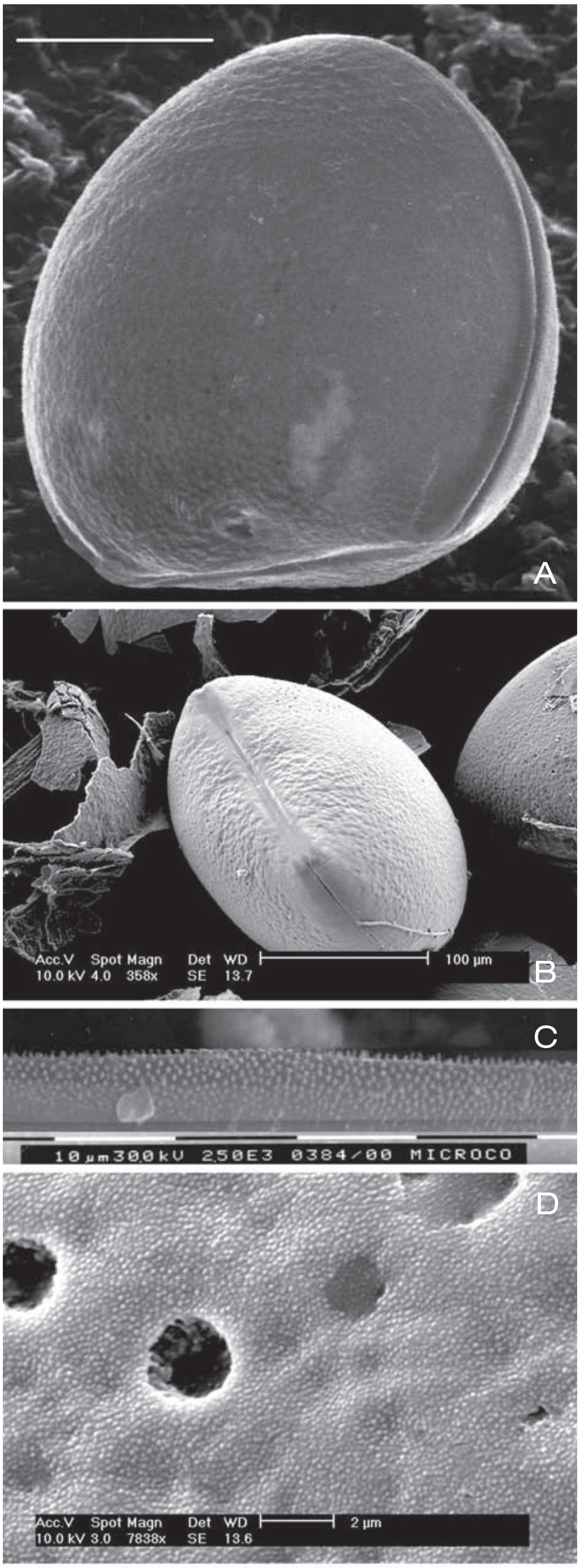

Fig. 4. Details of glochidium shell morphology at SEM. **A**. Lateral view. **B**. Dorsal view. **C**. Ventral margin with denticles. **D.** Outer surface of valve with shell pores and surface microsculpture. Scale bars: A, B=100 µm; C=10 µm; D=2 µm.

held separately in a glass cup in an aquarium where 6 *U. pictorum mancus* were kept in the same way. It expelled its larvae and was recorded as non-gravid (i.e. without thickened outer marsupial gills) on May 15. On June 10, marsupial masses containing eggs were found buried in the sand immediately near the animal.

The glochidium

The glochidium is subspherical, hookless (without a prominent hook at the apices of the larval shell), but the lower margin is covered with numerous little spines for at least 1/3 of its length, beginning at the apex of the lower rim. The surface of the periostracum lacks any sculpture and appears to be smooth (Figs. 4A–D). Like all other glochidia of European Unionidae, *M. bonellii* has 4 ciliated sense cells on either side of the body. The glochidium is provided with a larval filament.

The dimensions of the glochidium are:

- **mean length:** 146 µm (range 132–154, SD 4.81, n=17)
- **mean height:** 140 µm (range 130–153, s.d. 6.49, n=16)
- **width of one shell valve:** range 57–64 µm (n=3) (Cencetti 1994, Nagel et al. 1998, Nagel 1999)

Habitat choice and population density in the Torrente Versa

On April 4, 1991, a stretch of the Torrente Versa with shallow water (maximum depth 0.6 m) was searched for all unionids in order to determine their distribution in the habitat. Two other Unionidae co-occur with *M. bonellii*: *Unio pictorum pictorum* Linnaeus, 1758 (sensu Nagel et al., 1998; Nagel & Badino, 2001), as well as an *Anodonta* species that has not yet been identified (Nagel et al. 1996). *M. bonellii* preferred sections with a distinctive flow, but higher densities were also observed in pools and among the roots of *Schoenoplectus lacustris*, the latter growing on shallow banks of the channel (Fig. 5).

In a main flow section 25 animals per square meter were observed on the bottom surface. In this section *U. pictorum* was rare and the animals were found at the margins of the main channel. *M. bonellii* and *U. pictorum* co-occurred in weakly flowing water without any obvious spatial separation. *U. pictorum* were found to a greater extent in stagnant waters than *M. bonellii*. Searching by hand we uncovered 16 *M. bonellii*, 19 *U. pictorum*, and 4 *Anodonta* per square meter in the stagnant water habitat.

On May 13, 2003, the mussel density could be estimated in a river section by direct observation since the water level was extremely low. About 20 ani-

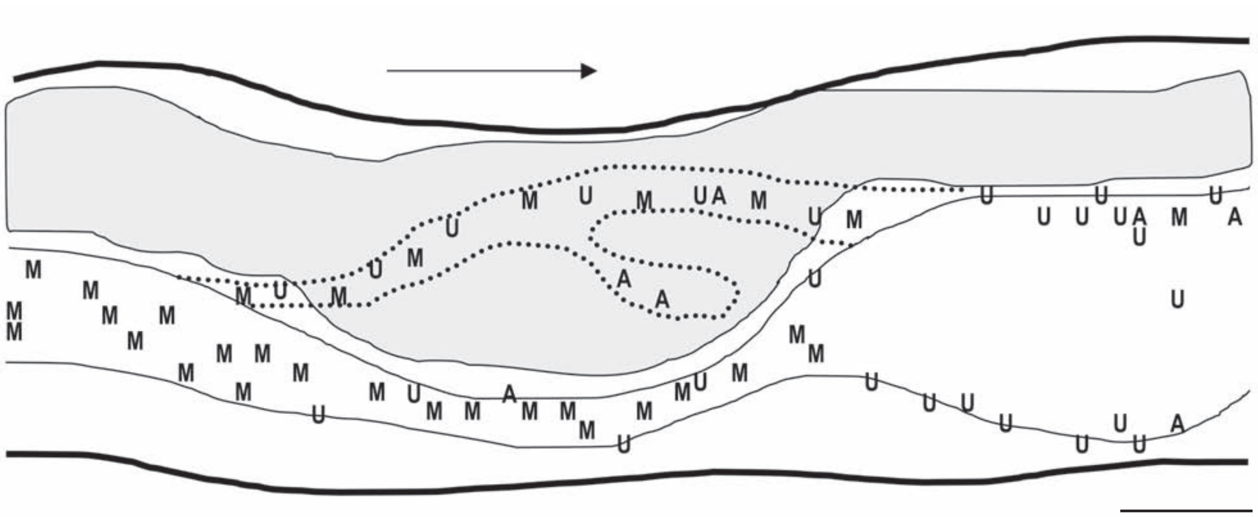

Fig. 5. Distribution scheme of unionid species in a stretch of the Torrente Versa. Symbols: M, *M. bonellii*; U, *Unio pictorum pictorum*; A, *Anodonta* sp.; thick line, water line; thin line, main channel; broken line, side channel; shaded area, *Schoenoplectus* stand; arrow, flow direction. Scale bar: 1 m.

mals per square meter were observed in a pool of the stream.

CENCETTI (1994) reported the following population densities on a surface of 7 m^2 without providing details on the type of habitat: *Microcondylaea bonelli* 16.3 m^{-2}, *Unio pictorum* 19.7 m^{-2} and *Anodonta* sp. 3.9 m^{-2}.

Growth

Length increments observed in the field varied from 0.9 to 9.7 mm with a mean value of 3.7 mm in 454 days. The smallest individual (total length 47.1 mm) grew the fastest, while the largest individual (82.5 mm) decreased in length. All other mussels showed length increments between 2.9 and 4.2 mm.

The slopes of the two Walford plots (Fig. 6) do not differ significantly (p>0.2). The parameter values of the resulting von Bertalanffy growth curves [$L(t)=L(\infty) * (1–e^{-(k*t)})$] are $L(\infty)$=99 mm, k=0.24 for the 1984 data and $L(\infty)$=75 mm, k=0.34 for data from field growth records in the years 1991 and 1992, respectively.

Discussion

Precise and comprehensive information on the breeding cycles and reproductive behaviour of Unionoidea species is scarce (HEARD 1998). Only with a combination of individual records from both field and laboratory observations on complete year-cycle studies is it possible to obtain a picture of individual reproductive behaviour, which may be more complicated than the reproductive behaviour of the population. From the present results it appears that *M. bonellii* is a short-time breeder capable of consecutive brooding. It carries eggs and larvae in spring/early summer in its marsupia for several weeks. GALLENSTEIN (1894: 38) was the first to report that all four gills carry eggs or larvae. Consecutive reproduction, i.e. the ability to produce more than one brood in an annual breeding cycle, has been observed in other European Unionidae: *Unio* species (HOCHWALD 2001; and references therein) and *Potomida littoralis* (NAGEL 2004). However, consecutive reproduction seems to be rather widespread among the Unionidae (HEARD 1998). Anyway, it is remarkable that a female was able to produce a second brood in the absence of males. We are aware of only one other observation of this kind in *Unio crassus* (ENGEL 1990: 65) with up to three broods produced while kept in isolation. Whether the animals are able to store sperm or whether they are cryptic hermaphrodites is not known. More detailed studies are needed to answer these questions.

Our observations lead us to suppose that the common method of discharge in *M. bonellii* is to release ripe, infectious glochida in the form of cylindrical masses. In *Unio pictorum* and *U. tumidus* the release of compact masses of eggs or developing larvae was also observed. Since infectious glochidia were never found in their discharges it was interpreted to be a reaction to stress due to unfavourable conditions in captivity (ALDRIDGE & MCIVOR 2003). All observations of the masses released by *M. bonellii* were also made under stress conditions (laboratory keeping, extremely low discharge and high water temperatures of the Torrente Versa on May 13, 2003). In some cases, however, the discharge was formed by masses of infectious glochidia that were still held together in a filamentous matrix. It thus seems plausible that this is the usual manner in which the species releases ripe larvae under natural conditions. If this is true, the masses

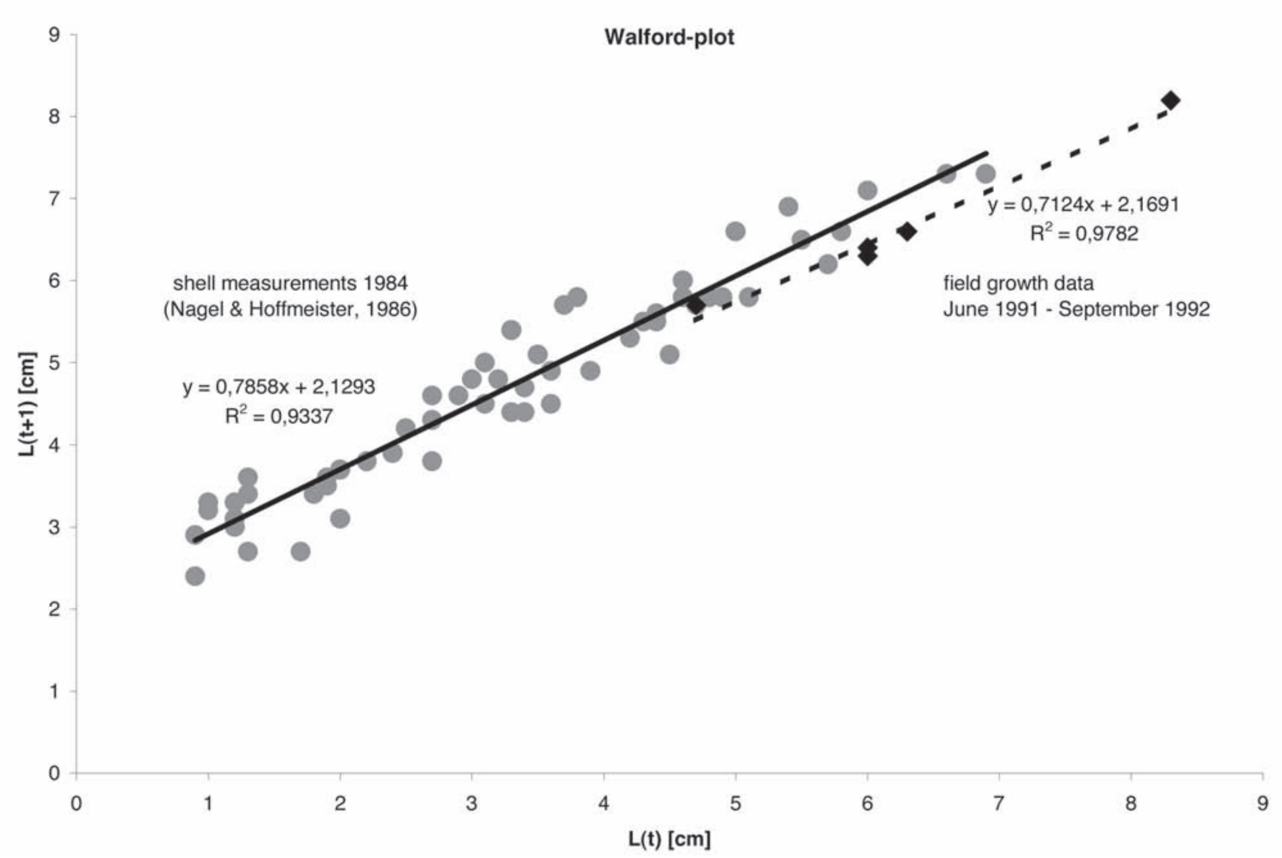

Fig. 6. Walford plots from two data sets taken in the same area. Dots, solid line: lengths at consecutive winter rings from shell measurements (Nagel & Hoffmeister 1986). Squares, broken line: field growth data (June 1991–September 1992).

of *M. bonellii* would correspond to the conglutinates previously described for a number of North American species (Lefevre & Curtis 1910, Watters 2001, Strayer et al. 2004). This is the first account of conglutinates in any European unionid species. The conglutinates mimic prey for fish (worms, maggots, fish fry) and thus attract possible host fishes. By eating or attacking conglutinate the fish becomes infected with glochidia. This strategy increases the chance and the number of glochidia which can come into contact with suitable host fish. The conglutinates of *M. bonellii* resemble dipteran larvae or worms and they may serve as prey-mimic to attract fish, as well. Direct observations are lacking although fish were frequently found near the mussels. According to Pizzul et al. (2006) the following fish species occur in the stream section inhabited by *M. bonellii*: *Alburnus alborella* (Bonaparte, 1841), *Barbus plebejus* Bonaparte, 1839, *Chondrostoma nasus* (Linnaeus, 1758), *Cobitis taenia* Linnaeus, 1758, *Esox lucius* Linnaeus, 1758, *Lepomis gibbosus* (Linnaeus, 1758), *Leuciscus cephalus* (Linnaeus, 1758), *Padogobius bonelli* (Bonaparte, 1846), *Pseudorasbora parva* (Temminck & Schlegel, 1846), *Rutilus aula* (Bonaparte, 1841), *Scardinius erythrophthalmus* (Linnaeus, 1758).

As yet, the identity of the host fishes remains unknown. From the presence of conglutinates one may assume a rather narrow host fish range (Strayer et al. 2004). Preliminary laboratory infections and field inspections to determine possible host fishes have so far been unsuccessful (Nagel, Moro, unpublished).

The glochidium of *M. bonellii* is of the lampsiline type (Nagel 1999, and references therein) and has all characteristics of an unionid glochidium including the larval thread. Bauer (1994) reports that the length of the larvae in 13 mostly North American species of Ambleminae ranges between 0.078 to 0.29 mm. The glochidium of *M. bonellii* therefore is among the smaller ones known for that subfamily. This suggests that the larvae are predominantly gill parasites.

Most records of *M. bonellii* were taken from running waters. Already Gallenstein (1894) gave a description of the preferred flow and substratum characteristics which fits well with the present findings. Accordingly, the preferred bottom substratum is fine to coarse-grained sand lying in stable banks and eventually overgrown by higher water plants. Furthermore Gallenstein (1894: 40) mentions that the mussels live in holes of loess banks. We could not confirm this in our study but there is no reason to doubt his observation. Whether these particular habitats are colonised by chance or whether the animals actively search for them remains unclear. *M. bonellii* anchors itself firmly into the bottom substratum with its foot which is longer than that of *Unio pictorum* (original identification: *Unio requienii*) or *Anodonta* sp. (original identification: *A. cygnea*). It poses considerably more resistance to being taken out than the two other co-occurring species. According to GALLENSTEIN (1894: 47) this force can be up to 1.5 kp.

Apparently, the growth pattern of *M. bonellii* in the Torrente Versa has not altered between 1984 and 1992. Furthermore, the differences in theoretical maximum shell lengths (99 vs. 75 mm) rather reflect the natural local variability of growth than profound changes in growing conditions over the years. The maximum shell lengths recorded in the study area of the Torrente Versa (1984: 77 mm, 1991: 82.5 mm) fall within the range given by GALLENSTEIN (1894: 40; 98 mm in the upper part, 82 mm in the middle part and ca. 70 mm in the lower part of the stream), to which the theoretical maximum values fit quite well. These data, too, do not indicate any dramatic change in growth conditions over a span of one hundred years.

The present findings offer some clues for a conservation strategy for the species. In the period of glochidium release any disturbance to the fish fauna should be minimised in order to allow a maximum number of larvae to complete metamorphosis. For more specific measures it is necessary to identify the natural host fishes of *M. bonellii*. There are reasons to assume that the host fish range is rather small and therefore host fish availability may be a critical factor for a population to survive. Since the species seems to be strictly dioecious the local population density should be high in order to ensure successful fertilisation of eggs (HOCHWALD 2001). Although *M. bonellii* is able to live on a variety of bottom substrates stable deposits of gravel and sand seem to be most suitable. Management works in streams and channels inhabited by this and other unionid species should be carried out in a way to preserve such habitats including sections in which the stream bottom is covered by higher water plants.

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