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Diurnal activity, mating behaviour and structure of the egg envelopes in four species of Danubian gudgeons (Cyprinidae)*

Diurnale Aktivität, Paarungsverhalten und Struktur der Eihüllen von vier Donau-Gründlingen (Cyprinidae)*

Rüdiger Bless[1] & Rüdiger Riehl[2]

[1]An der evangelischen Kirche 19, D- 53340 Meckenheim, Germany; bless.r@t-online.de
[2]Institut für Zoomorphologie, Zellbiologie und Parasitologie der Heinrich-Heine-Universität Düsseldorf, Universitätsstraße 1, D-40225 Düsseldorf, Germany; riehl@uniduesseldorf.de

Summary: Adults of the Danubian gudgeons *Gobio gobio*, *Romanogobio kessleri*, *Romanogobio uranoscopus* and *Romanogobio vladykovi* are largely nocturnal. *Romanogobio kessleri*, however, the most pelagic species, is active also during daytime. In the laboratory under simulated natural conditions gudgeons began to spawn at a temperature of 12 °C. Spawning takes place close to the water surface and is similar in all species. The female rotates at an angle of approximately 90°; then the male winds around her genital region. In this position eggs and sperm were simultaneously released into the open water. The four species examined are multiple and pelagic spawners with no specific preference of any substratum type. Depending on the species the spherical or oval eggs (*R. uranoscopus*) are provided with attaching villi of different lengths, which obviously enhance adhesiveness. Length of attaching villi does not correlate with the current velocities the fish spawn. Eggs have micropyles with a large pit and a short canal.

Key words: circadian and seasonal activity patterns, reproduction, eggs, attaching villi, micropyle

Zusammenfassung: Die Donau-Gründlinge *Gobio gobio*, *Romanogobio kessleri*, *Romanogobio uranoscopus* und *Romanogobio vladykovi* sind, mit Ausnahme des überwiegend pelagischen *R. kessleri*, der auch während der Tagesphase aktiv ist, als Adulte überwiegend nachtaktiv. Die Tiere beginnen unter simulierten natürlichen Bedingungen im Labor bei etwa 12 °C nahe der Wasseroberfläche abzulaichen. Der Laichakt ist bei allen Arten ähnlich. Dazu drehen sich die Weibchen in einem Winkel von 90° auf die Seite und werden dann von den Männchen wie mit einem Gürtel umschlungen. In dieser Position werden Sperma und Eier gleichzeitig in das freie Wasser abgegeben. Alle vier Arten sind multiple, pelagische Laicher, die kein besonderes Laichsubstrat zu bevorzugen scheinen. Die abgelegten Eier der vier Arten sind rund bis oval (*R. uranoscopus*) und besitzen, je nach Art, unterschiedlich lange Zotten, die offenbar das Haften am Substrat ermöglichen. Die Länge dieser Zotten ist nicht eindeutig mit den Strömungsgeschwindigkeiten, bei denen die Tiere laichen, in Zusammenhang zu bringen. Alle vier Arten haben Mikropylen mit einer großen Grube und einem kurzen Kanal.

Schlüsselwörter: Circadiane und saisonale Aktivitätsmuster, Reproduktion, Eier, Haftzotten, Mikropyle

1. Introduction

Most members of the gudgeon genera *Gobio* and *Romanogobio* are ground dwelling cyprinid fishes with an inferior mouth and a pair of maxillary barbels. Probably because of their small body size and low economic importance, considerable gaps in the knowledge of their life histories exist. In addition, some of the European species are endangered and others are limited in the range of their distribution.

Romanogobio kessleri (Dybowski, 1862) and *Romanogobio uranoscopus* (Agassiz, 1828) are concentrated in the Danube area in a comparative-

*Dedicated to our friend Tony Lelek †, Frankfurt ly small zone, are severely endangered and are extinct in parts of their range in Europe (Bless 1997, Kottelat & Freyhof 2007). *Romanogobio vladykovi* (Fang, 1943) is confined to the Danube drainage (Naseka 2001, Naseka & Freyhof 2004) and G*obio gobio* (Linnaeus, 1758) is present throughout nearly the whole of Europe. These four species live sympatric in parts of the Middle Danube and their tributaries (e.g. Wanzenböck et al. 1989). Among them *Gobio gobio* is the species with the broadest ecological amplitude (Banarescu 1953, 1964, Banarescu et al.1999a, Wanzenböck et al. 1998).

Data on the reproduction of these species are only fragmentary or lack completely. The objectives of the present contribution are to broaden knowledge of life history parameters namely of reproduction in the four gudgeons mentioned.

2. Material and methods

Specimens of *Romanogobio vladykovi* were caught in the River Drau (Austria), *Gobio gobio* in River Isar (Germany), *Romanogobio kessleri* in the River Dniester (Ukraine) and *Romanogobio uranoscopus* in River Riul Doamnei (Romania).

Breeding experiments were carried out between January 1995 and December 1999 at the limnological laboratory of the Federal Agency for Nature Conservation in Bonn. In three aquaria (1.44 m long, 0.35 m wide, 0.3 m deep) and a tank (4.0 m long, 0.5 m wide, 0.3 m deep) day length, light intensity above water surface, water temperature and current velocity were adjusted weekly to simulate conditions of the natural habitats.

All aquaria were closed systems, driven by adjustable circulation pumps. Water was withdrawn at floor level in one corner and returned to the basins after passing filters in the diagonally opposite corner, thus creating a circular flow. The oxygen content of the water was kept at ± 100 % saturation. Weekly 20 % of the water in all systems was replaced by fresh water from aerated tanks. Available substrates in the aquaria and the tank were sand, fine gravel, coarse gravel, cobble and rocks (± 1.6-8, 20-30, 60-80, ± 150 mm diameter). The different substrata were exposed in open containers, which were brought into the aquaria. Stream velocities above the substrata range from "non measurable" to 1.2 ms^{-1}. Stream velocity was measured 1 cm above the surface of the exposed substrata by a flow meter (TAD-W25, Höntsch).

Under these conditions gonadal maturation was achieved without any application of hormonal substances. Activity was recorded by means of a ultrared sensitive video camera (Monicor TVCCD-250). During the night the aquaria were illuminated with dimmed red light reaching 4 lux near the water surface. The camera was connected to a time-lapse device and records were taken throughout the whole year, i.e. from January to December.

During the spawning period all substrates were controlled daily and site of spawning events, position of deposited eggs in the interstices, date, temperature, stream velocity and substrate type were recorded. Arrows in figs. 5-8 indicate every week with at least one spawning event.

Sixteen 1 min-sequences per h were recorded and examined in one 24 h period every week of the respective research year. Definition of activity was: n_x specimen moving freely in the water column at one time randomly selected during the 1 min-sequences. Due to the large quantity of sequences, we were able to document spawning events for all species. The videotapes were analysed picture by picture.

Deposited eggs were fixed in 2.5% glutaraldehyde in Veronal acetate buffer (pH 7.3) for some days. The samples were washed in the same buffer solution, dehydrated in a graded acetone series, critical point dried with liquid CO_2 in a Balzers critical point dryer, and mounted on brass stubs either complete or fractured. All mounts were coated with gold, observed, and photographed using a Leitz AMR 1000 scanning electron microscope at an accelerating voltage of 30 kV.

3. Results

3.1. Circadian activity

The circadian cycles of the specimens showed a tendency for nocturnal activity (figs. 1-4).

Fig. 1: Circadian activity of *Romanogobio vladykovi*, n = 3, Σ n: active fishes in 16 samples per h during a 24 h-cycle once a week (week 38 in 1996 to week 37 in 1997) in total; dark: shortest night of the year, light: longest night of the year.

Abb.1: Circadiane Aktivität von *Romanogobio vladykovi*, n = 3, Σ n: aktive Fische in 16 Stichproben per h während eines 24 h-Zyklus einmal pro Woche (Woche 38, 1996 bis Woche 37, 1997) akkumuliert; dunkel: kürzeste Nacht des Jahres, hell: längste Nacht des Jahres.

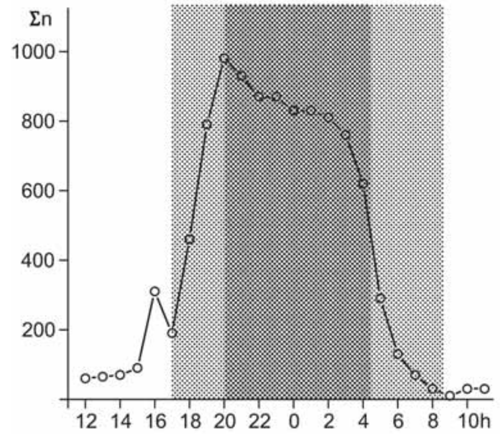


Fig. 2: Circadian activity of *Gobi gobo,* n = 7, Σ n: active fishes in 16 samples per h during a 24 h- cycle once a week in 1995 (week 1-52) in total; dark: shortest night of the year, light: longest night of the year.

Abb. 2: Circadiane Aktivität von *Gobio gobio*, n =7, Σ n: aktive Fische in 16 Stichproben per h während eines 24 h-Zyklus einmal pro Woche 1995 (Woche 1-52) akkumuliert; dunkel: kürzeste Nacht des Jahres, hell: längste Nacht des Jahres.

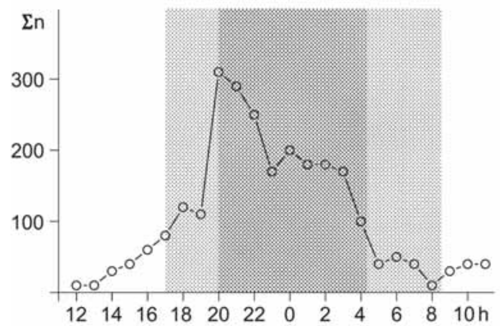


Fig. 3: Circadian activity of *Romanogobio kessleri,* n = 3, Σ n: active fishes in 16 samples per h during a 24 h-cycle once a week in 1997 (week 1-52) in total; dark: shortest night of the year, light: longest night of the year.

Abb. 3: Circadiane Aktivität von *Romanogobio kessleri*, n = 3, Σ n: aktive Fische in 16 Stichproben per h während eines 24 h-Zyklus einmal pro Woche 1997 (Woche 1-52) akkumuliert; dunkel: kürzeste Nacht des Jahres, hell: längste Nacht des Jahres.

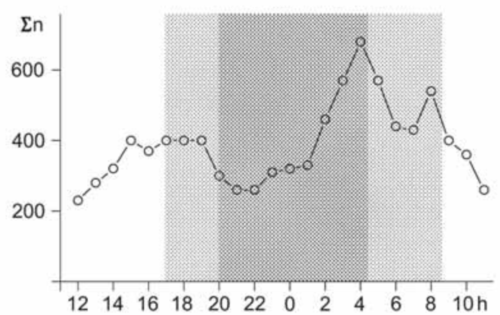
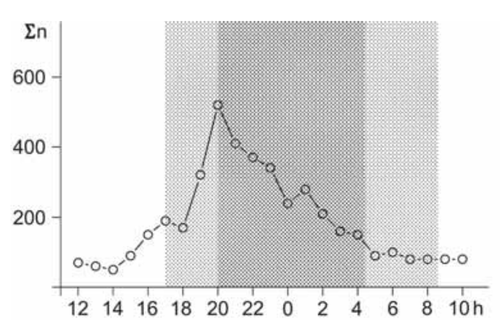


Fig. 4: Circadian activity of *Romanogobio uranoscopus*, n = 10, Σ n: active fishes in 16 samples per h during a 24 h-cycle once a week in 1996 (week 10-36) in total; dark: shortest night of the year, light: longest night of the year.

Abb. 4: Circadiane Aktivität von *Romanogobio uranoscopus*, n =10, Σ n: aktive Fische in 16 Stichproben per h während eines 24 h-Zyklus einmal pro Woche 1996 (Woche 10-36) akkumuliert; dunkel: kürzeste Nacht des Jahres, hell: längste Nacht des Jahres.



Three species revealed peak activities just after the start of the dark phase, *Romanogobio kessleri*, the most pelagic species, swam in the water column also during the light phase (fig. 3).

3.2. Spawning period

Romanogobio vladykovi started spawning during April (week 17) in 1997, when water temperature reached 12 °C for the first time. The spawning period lasted 10 weeks. Seven spawning phases with five females revealed that at least one female spawned more than once. Therefore *R. vladykovi* has to be considered as a multiple spawner (fig. 5).

Spawning of *Gobio gobio* started in May (week 18) at 12 °C in 1995 and lasted to the end of 1998. There was a correlation between the beginning of the reproductive phase, the water temperature and increasing day length. An extremely long spawning period of 25 weeks could be observed during an experiment in 1996 running permanently with 16 °C water temperature. Here multiple spawning was observed (fig. 6).

Spawning of *Romanogobio kessleri* started during April (week 17) in 1997 at a water temperature of 12 °C. Also *R. kessleri* is a multiple spawner (fig. 7).

Spawning of *Romanogobio uranoscopus* started during May (week 19) in 1996 and ended in August (week 33) (fig. 8). A prolonged warm temperature cycle (12 °C) extended the reproductive phase. In this period more spawning events were recorded than females were present, which shows that also this species is a multiple spawner.

3.3. Mating and spawning behaviour

Mating and spawning is similar in all species: A male which encounters a ripe female follows her; both mates swim to the surface with their bodies parallel to each other. *Romanogobio uranoscopus* and *Romanogobio kessleri* rapidly moved into the zone of the strongest current, which was on average (n= 10) 1.1 ± 0.12 ms^{-1} (*R. uranoscopus*) and 0.51 ± 0.16 ms^{-1} (*R. kessleri*). Spawning of *Romanogobio vladykovi* and *Gobio gobio* took place in sites where current velocity was below 0.1 ms^{-1}. Close to the water surface mates swam in a loop wrapped by the male like a belt. The genital openings remained close to each other while about 50 eggs and sperms were released simultaneously. This occurred very rapidly.

Spawning took place mostly in the second half of the night and during the early morning. The fertilized eggs drifted in the free-flowing water for 29 s at most (fig. 9). The eggs are very adhesive and adhered to all substrates provided. We observed 52 spawning events of *R. uranoscopus*, 22 of *G. gobio*, 7 of *R. vladykovi* and 4 of *R. kessleri* between 1993 and 1999, in no case specimens preferred a given substrate.

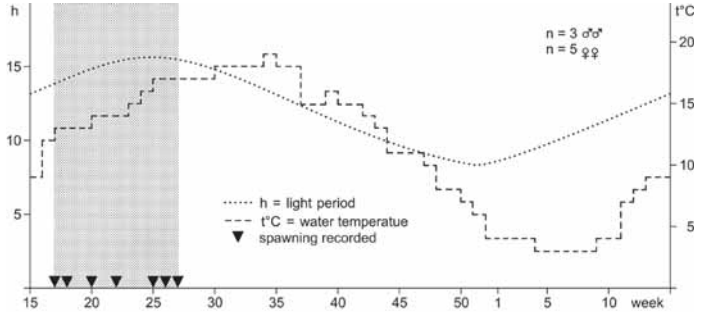
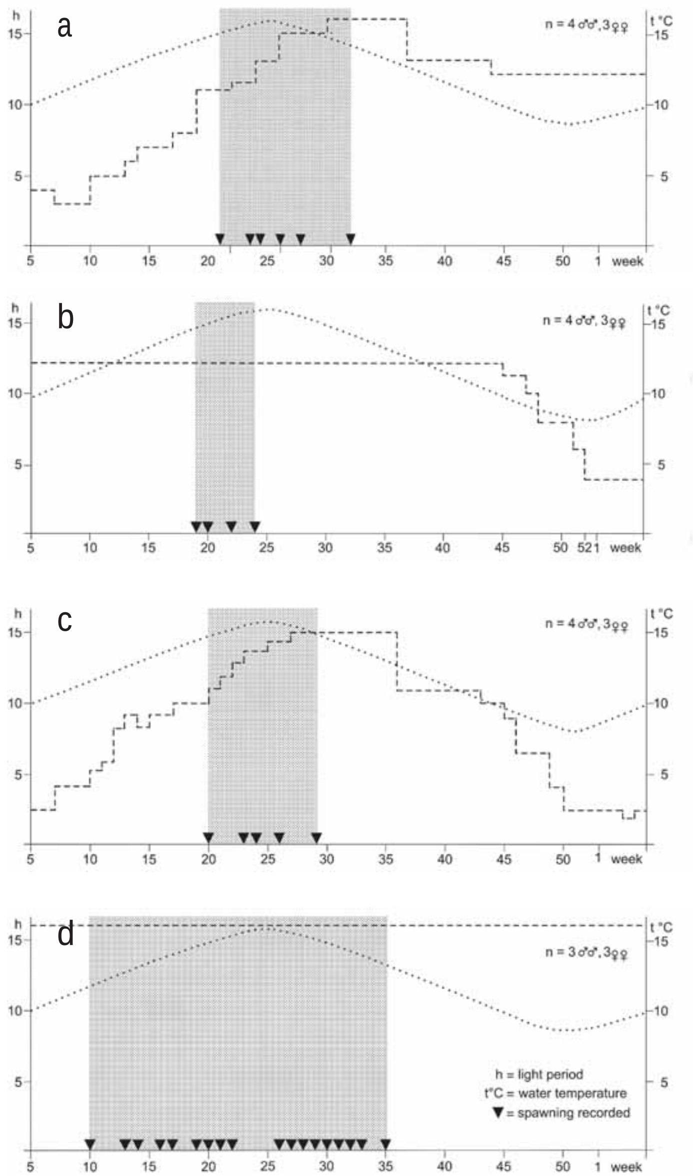


Fig. 5: Spawning period of *Romanogobio vladykovi* under laboratory conditions; simulated natural t°C-cycle in 1999.

Abb. 5: Laichperiode von *Romanogobio vladykovi* unter Laborbedingungen; simulierter natürlicher t°C-Zyklus 1999.



Figs. 6a-d: Spawning periods of *Gobio gobio* under laboratory conditions; different t°C-cycles.

Abb. 6a-d: Laichperioden von *Gobio gobio* unter Laborbedingungen; unterschiedliche t°C-Zyklen.

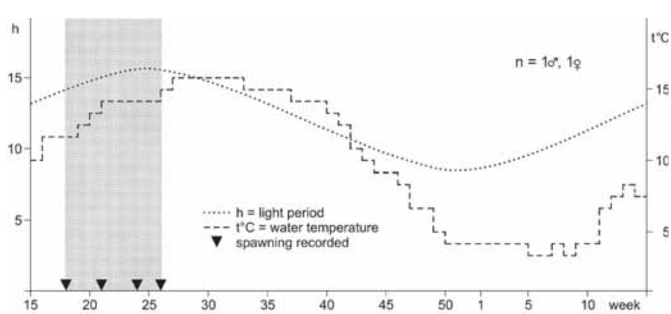


Fig. 7: Spawning period of *Romanogobio kessleri* under laboratory conditions; simulated natural t°C-cycle in 1999.

Abb. 7: Laichperiode von *Romanogobio kessleri* unter Laborbedingungen; simulierter natürlicher t°C-Zyklus.

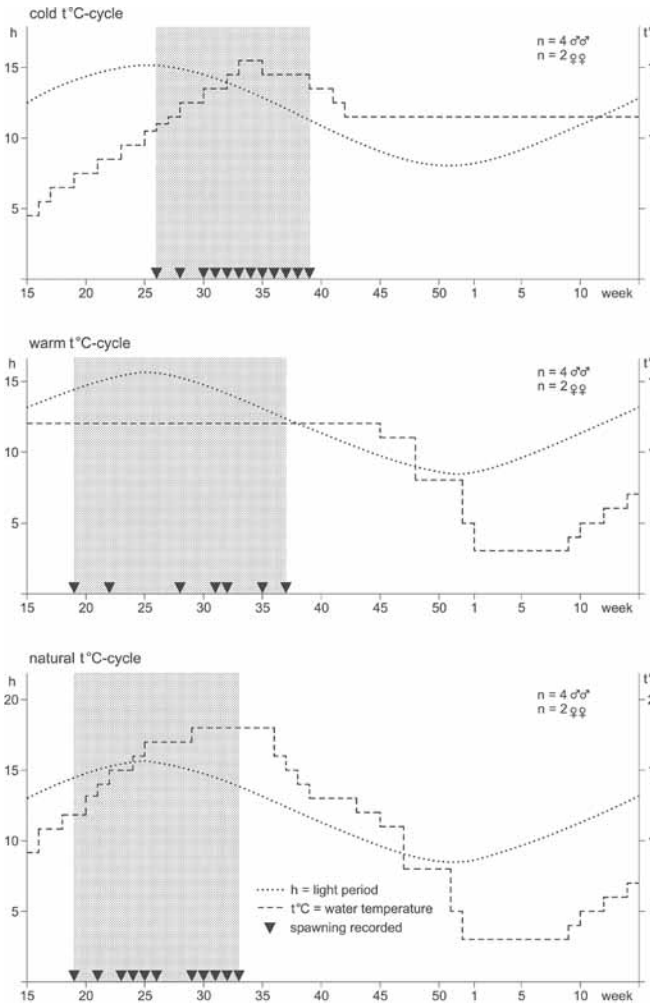
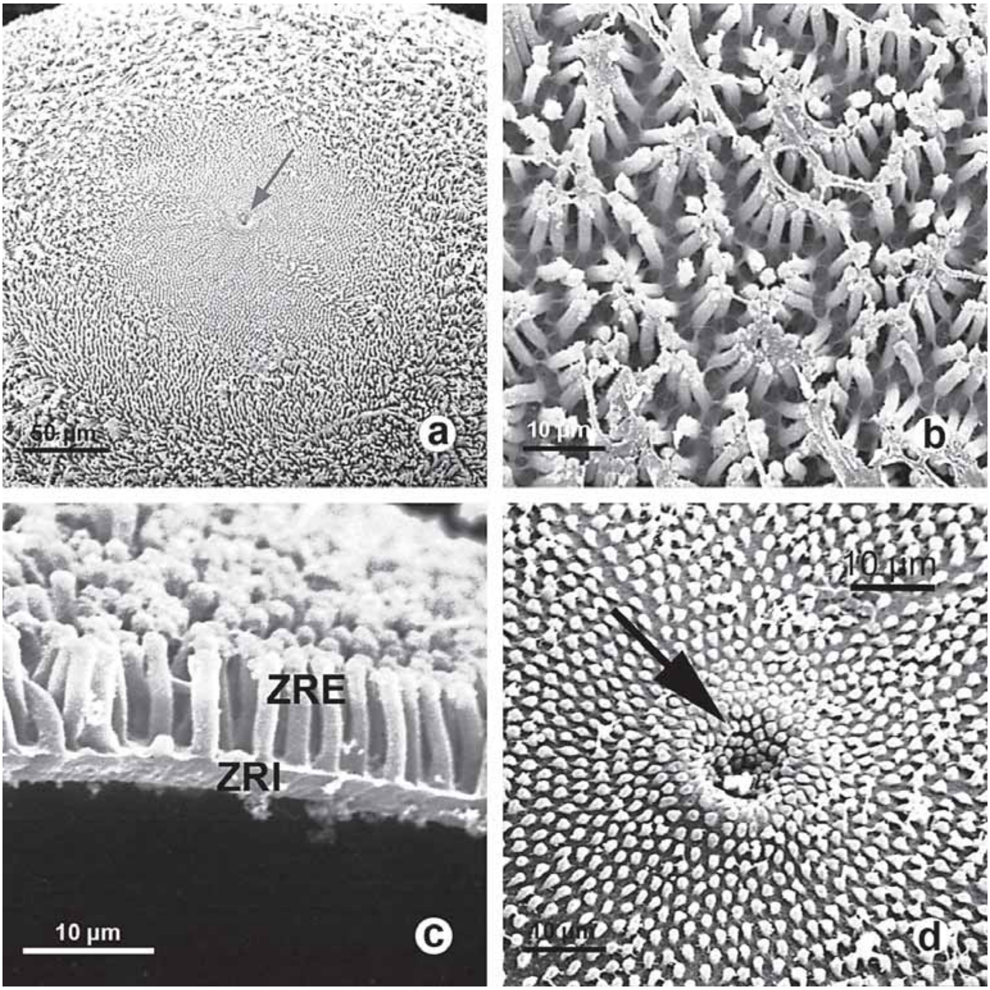


Fig. 8: Spawning periods of *Romanogobio uranoscopus* under laboratory conditions; different t°C-cycles.
Abb. 8: Laichperioden von *Romanogobio uranoscopus* unter Laborbedingungen; unterschiedliche t°C-Zyklen.

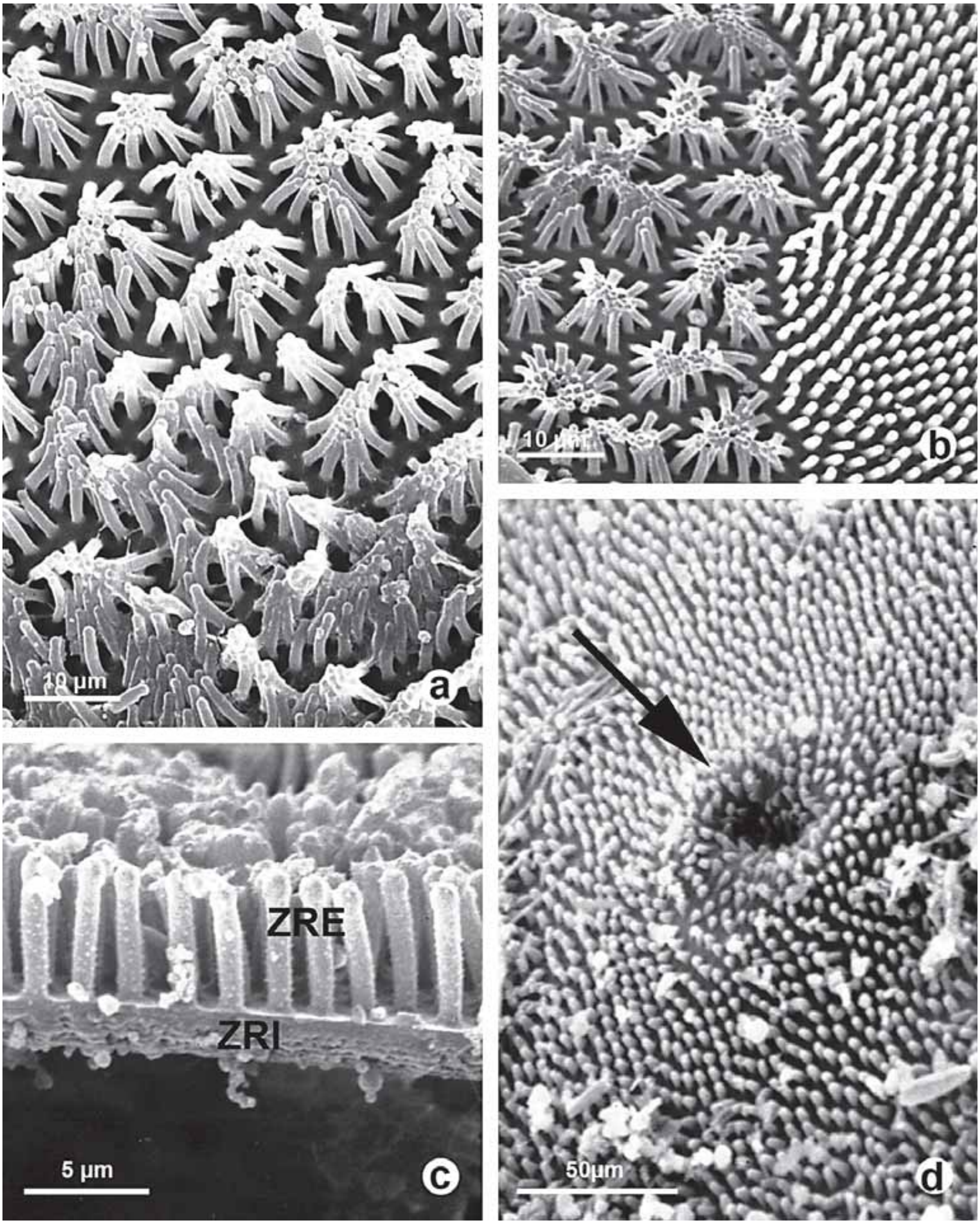
Fig. 9: *Romanogobio uranoscopus*, spawning in the free flowing water close to the surface.
Abb. 9: *Romanogobio uranoscopus* beim Ablaichen in der fließenden Welle nahe der Oberfläche.



Figs. 10 a-d: Deposited eggs of *Romanogobio vladykovi*. **a** Egg surface, around the micropyle (arrow) the attaching villa are shortened; **b** attaching villa form rosettes; **c** fracture of the zone radiate; **d** micropyle (arrow). ZRE = zona radiata externa = attaching villi, ZRI = zona radiata interna.
Abb. 10 a-d: Abgelegte Eier von *Romanogobio vladykovi*. **a** Eioberfläche mit Haftzotten, die im Bereich der Mikropyle (Pfeil) kürzer sind; **b** Rosettenartig angeordnete Haftzotten; **c** Bruchkante der Zona radiata; **d** Mikropyle mit tiefer Grube. ZRE = Zona radiata externa = Haftzotten, ZRI = Zona radiata interna.

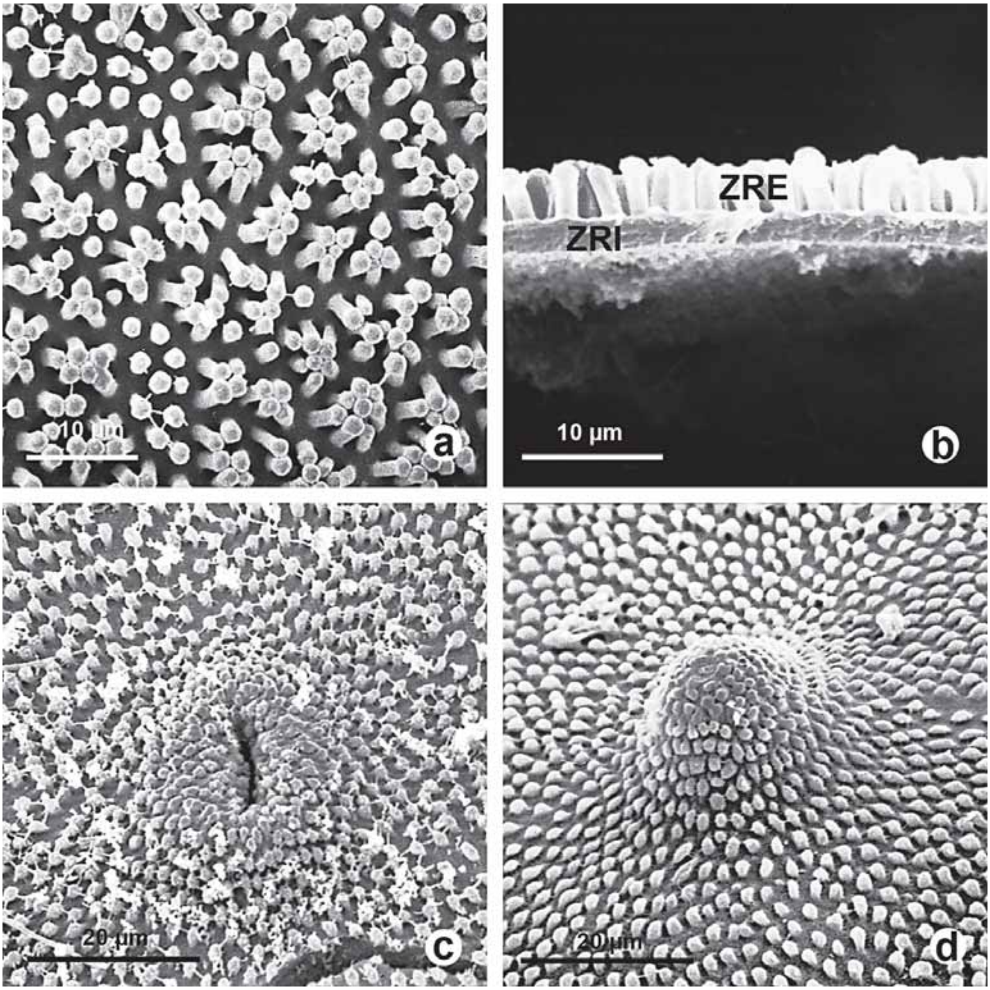
3.4. Eggs

Romanogobio vladykovi: The spheric eggs (diameter approximately 1.5 mm) are opaque and greyish-white; oil-droplets are lacking. Their surface is covered by numerous long attaching villi (14 µm on average), which prevent the view on pores very probably present (fig. 10 a). Occasionally attaching villi form rosettes (fig. 10 b). The egg envelope (= zona radiata or zona pellucida) measures about 4.0 µm in thickness (fig. 10 c). The micropyle consists of a large pit (diameter approximately 20 µm) and a short canal with an aperture of approximately 3,7 µm in diameter (fig. 10d). The micropyle is surrounded by a circular area (diameter approximately 235 µm) of shortened villi (fig. 10 d).



Figs. 11 a-d: Deposited eggs of *Gobio gobio*. **a** The attaching villi are relatively short; **b** attaching villi and villi forming rosettes; **c** fracture of the zona radiata. The apical ends of the attaching villi are thickened; **d** micropyle (arrow). ZRE = zona radiata externa = attaching villi, ZRI = zona radiata interna.

Abb. 11 a-d: Abgelegte Eier von *Gobio gobio.* **a** Haftzotten; **b** Haftzotten und Zotten, die Rosetten bilden; **c** Bruch durch die Zona radiata. Die Enden der Haftzotten sind verdickt, **d** Mikropyle (Pfeil). ZRE = Zona radiata externa = Haftzotten, ZRI = Zona radiata interna.

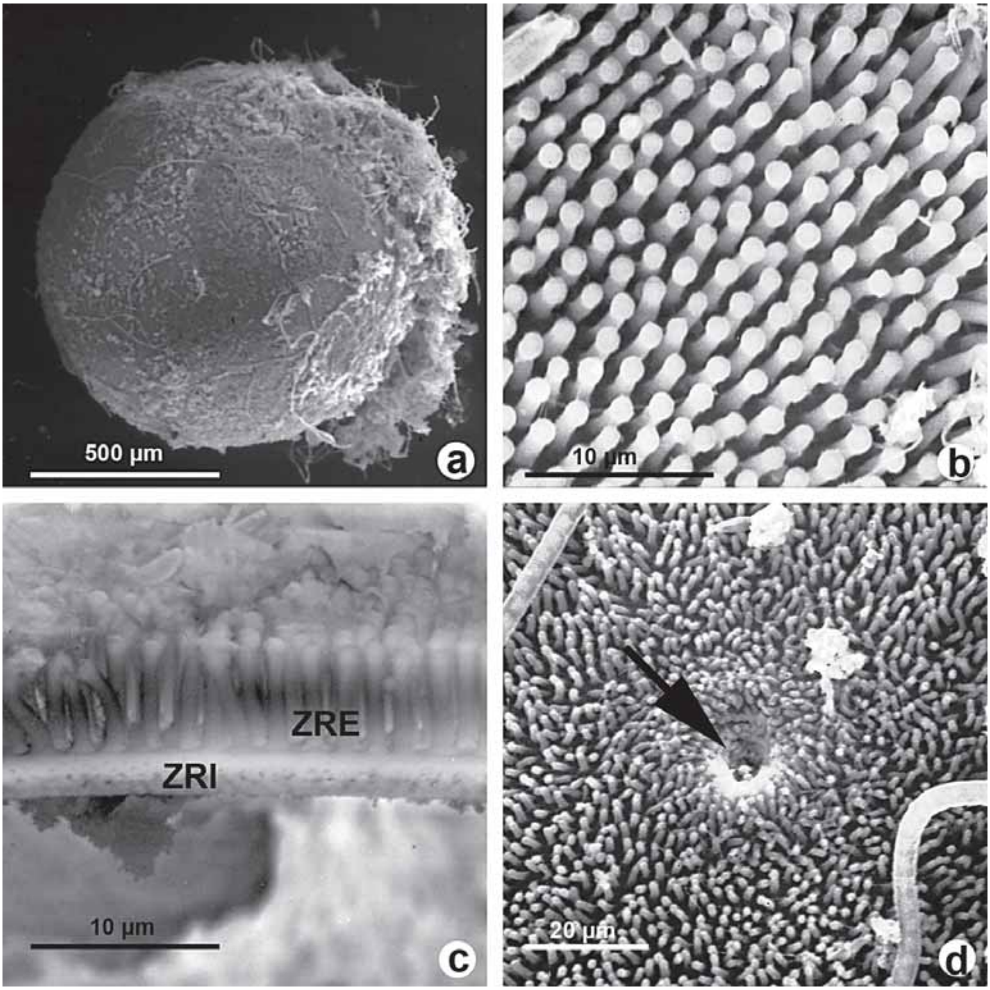


Figs. 12 a-d: Deposited eggs of *Romanogobio kessleri*. **a** Short attaching villa and villa arranged in rosettes; **b** fracture of the zone radiate; **c** micropyle; **d** closed micropyle. ZRE = zona radiata externa = attaching villi, ZRI = zona radiata interna.

Abb. 12 a -d: Abgelegte Eier von *Romanogobio kessleri*. **a** verkürzte Haftzotten und rosettenartig angeordnete Zotten; **b** Bruch durch die Zona radiata; **c** Mikropyle; **d** verschlossene Mikropyle. ZRE = Zona radiata externa = Haftzotten, ZRI = Zona radiata interna.

Gobio gobio: The spheric eggs (diameter 0.4-1.3 mm, in some cases even 1.6 mm) are yellow-orange; oil-droplets are missing. Attaching villi (fig. 11a) measure 8.3-9.6 µm in length and are thickened apically (fig. 11c). Occasionally rosettes are found adjacent to areas with freestanding villi (fig. 11a, b). The zona radiata is 3.2 µm thick (fig 11c). The micropyle pit measures 50-60 µm, the aperture of the canal 3-3.5 µm in diameter. In the specimen examined a plug of cytoplasm clogged the micropyle.

Romanogobio kessleri: The spheric eggs (diameter approximately 1.2-1.5 mm) are whitish; oil-droplets are lacking. Attaching villi measured 3.8-5.8 µm in length (fig. 12a, b). Rosettes were small and formed by only a few villi (fig. 12b). The zona radiata is approximately 3.8 µm thick (fig. 12b). The pit of the micropyle has a diameter of approximately 28 µm, the central



Figs. 13 a-d: Deposited eggs of *Romanogobio uranoscopus*. **a** The surface is covered by debris, due to its stickiness; **b** thickened ends of the attaching villi; **c** fracture of the zona radiata; **d** micropyle (arrow). ZRE = zona radiata externa = attaching villi, ZRI = zona radiata interna.

Abb. 13 a-d: Abgelegte Eier von *Romanogobio uranoscopus*. **a** Die klebrige Eioberfläche ist mit Detritus bedeckt; **b** verdickte Enden der Haftzotten; **c** Bruch durch die Zona radiata; **d** Mikropyle (Pfeil). ZRE = Zona radiata externa = Haftzotten, ZRI = Zona radiata interna.

aperture of the canal 3.45 µm (fig. 12c). In the eggs studied the micropyle was closed (fig. 12d).

Romanogobio uranoscopus: The spheric to oval eggs are whitish to light yellow (fig. 13a), have a diameter of 1.5-2 mm; oil droplets are lacking. Apically thickened attaching villi measure 10.8-12.2 µm in length (fig. 13b). The zona radiata is 3-3.5 µm thick (fig. 13c). The surface of the eggs was coated with detritus (fig. 13a). The micropyle pit has a diameter of approximately 20 µm, the central pore of approximately 4 µm (fig. 13d).

4. Discussion

Our findings broaden knowledge of Danubian gudgeons with regard to diurnal and seasonal activities, spawning sites and spawning modes as well as egg surface structures.

HOLCÍK et al. (1998) considered gudgeons as psammophilic open substratum spawners (see BALON 1964, 1975, 1981). The psammophilic character of *Gobio gobio*, however, was already questioned by PONCIN et al. (1997). We did not find signs of psammophily in the four gudgeon species examined herein.

The beginning of the reproductive phase was clearly correlated with rising temperatures and a prolonged photoperiod. Water temperatures of about 12 °C seem to be a stimulus threshold to produce ripe gametes. Mating and spawning of *Gobio gobio* have been incompletely described by PONCIN et al. (1997), and of *Romanogobio uranoscopus* more detailed by BANARESCU et al. (1999b). Males of *R. uranoscopus* spend many hours in the night at the bottom of the spawning site. If two males encounter each other, they swim rapidly to the surface head to head keeping the bodies parallel to each other. Then they dive straight down to the bottom where they continue chasing each other. After a male has encountered a female, it follows her and both swim head to head at the surface with their bodies parallel to each other, moving rapidly into the zone of the strongest current. The males swim a loop, then the female rotates at an angle of approximately 90° and the male winds around her genital region like a belt. In this moment about 50 eggs and sperm are simultaneously released. This action takes place very rapidly and lasts only a split second. Therefore we saw this action only by analysing the videotapes picture by picture. Spawning may take place in a similar manner in all gudgeons as suggested by our observations.

Our findings also suggest that the four species might be classified as pelagic spawners, which do not perfer a specific substratum. Further, they are multiple spawners mainly active during dark hours. Compared to the other gudgeons *Romanogobio kessleri* is the most pelagic species and active also during daytime throughout most of the year.

Species obviously prefer different water velocities during the spawning season. *Romanogobio vladykovi* and *Gobio gobio* spawned in waters without significant current, whereas *R. kessleri* and especially *R. uranoscopus* spawned in current waters. Deposited eggs of all four species are firmly attached to the substratum and attaching villi may enhance adhesiveness. Such attaching devices consist largely of mucosubstances as previously described in *G. gobio* (RIEHL 1977, 1978).

The attaching villi of the eggs of *R. vladykovi*, which spawns in calm waters, are very long. Relatively long villi were also found on the egg surface of *Gobio gobio*, whereas in *R. kessleri*, which spawns in waters with a measurable current (compared to the spawning sites of *R. vladykovi* and *G. gobio*), they are short. Long attaching villi may allow the egg to move also in relatively stagnant waters, thus probably enhancing the oxygen supply of the developing embryo. However, this does not explain the long attaching villi of eggs in *R. vladykovi*. We have no idea how to interpret the rosettes of attaching villi found in three species (see above), but exclude fixation artefacts.

All species have large micropyles of type 1 according to RIEHL (1991), which is often present in pelagic spawners. Obviously this type facilitates insemination by concentrating the spermatozoa within this depression. The reduction of the villi inside the pit may assist this process. Clogging of the micropyle as seen in *R. kessleri* and *R. uranoscopus* may be the consequence of successful insemination, but has not proved in detail in the present study.

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