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## Life Cycles and Ecological Interactions of Freshwater Sponges (Porifera, Spongillidae) in the River Rhine in Germany

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With 5 Figures and 3 Tables

Key words: Spongillidae, river Rhine, ecology, life cycles, reproduction, faunal list

### Abstract

In the years 1993–1995 the species composition and ecological interactions of freshwater sponges (Porifera, Spongillidae) were investigated in the river Rhine between Karlsruhe and Bonn (Germany).

The species *Trochospongilla horrida*, *Ephydatia fluviatilis*, *Spongilla lacustris*, *Ephydatia muelleri*, *Eunapius fragilis* and *Eunapius carteri* were found. *E. muelleri*, *T. horrida*, *S. lacustris* and *Eun. fragilis* were only found in habitats which remained flooded year-round, whereas *E. fluviatilis* occurred in similar habitats, but its abundance remained high at places which dried out regularly.

Colonies of *E. fluviatilis* were found throughout the year, colonies of *E. muelleri*, *T. horrida*, *S. lacustris* and *Eun. fragilis* were only present during the warm season, in the cold season only gemmules of the latter species were found.

The dispersal of *E. fluviatilis* within the habitat was mainly ensured by sexually produced larvae; the role of asexually produced gemmules was negligible. *Eun. fragilis* was also dispersed via larvae, it ensured its overwintering through production of abundant gemmules. In *E. muelleri*, *T. horrida* and *S. lacustris* sexually produced larvae were not observed.

Beside having no free moving larvae, the gemmules of *T. horrida* were tightly fixed to the substrate, so the distribution ability of this species was restricted.

In the case of *E. muelleri* and *S. lacustris* some gemmules became free and were dispersed within the habitat. Other gemmules rested in the dead body of their mothersponges and ensured the recolonization of the same place in following suitable seasons.

*Ephydatia muelleri* produced many gemmules, using almost its whole tissue for gemmulation before desintegrating.

Freshwater sponges in general interact with a number of animals from other phyla, nevertheless these associations were less frequent as reported in the literature at other places.

### Introduction

The Rhine was subject to major changes since the first corrections undertaken by TULLA 1840–1880. Today the Rhine gains its enormous economic value as the most important water way in central Europe and is almost entirely changed and influenced by an enormous human impact, pristine areas are only rarely found.

At the beginning of the 20th century LAUTERBORN could distinguish 83 macrobenthic animals within the Rhine (TITTIZER et al. 1990). The number of macrozoobenthic species decreased to 12 species in the 70's (CONRATH et al. 1977) due to an extremely high level of pollution. Since that time great efforts to purify the water were undertaken and the number of macrobenthic animals rose again steadily (SCHÖLL et al. 1995). The species numbers even exceed LAUTERBORNS numbers, but the species-composition changed considerably due to the heavy changes in the river (TITTIZER et al. 1990). In recent years ongoing invasions of formerly foreign species (Neozoa: KINZELBACH 1995) took place, these neozoans influenced the biocoenosis heavily.

The following five species of freshwater sponges from the river Rhine were originally known: *Spongilla lacustris* (LINNAEUS 1758) (in LAUTERBORN 1905, 1907, 1910), *Ephydatia fluviatilis* (LINNAEUS 1758) (in LAUTERBORN 1908), *Ephydatia muelleri* (LIEBERKÜHN 1855) (in LAUTERBORN 1905) and *Trochospongilla horrida* WELTNER 1893 (in LAUTERBORN 1905).

In the 70's only *Ephydatia fluviatilis* was found (CONRATH et al. 1977), since the 80's the other formerly known species reappeared.

Most publications on the life cycles of freshwater sponges (e.g. GILBERT et al. 1975; FROST et al. 1982; COURRÈGES & FELL 1989; BISBEE 1992) deal with single life cycle events like formation of larvae or gemmulation and often include only a single species. A limited number of papers deals with associations of several species and their colonization strategies and spatial competition (e.g. WILLIAMSON & WILLIAMSON 1979; MUKAI 1989; PRONZATO & MANCONI 1991).

MANN et al. (1972) state, that the productivity of filter feeders is extremely high within man-influenced waters in general. Results of FRANZ (1992) indicate the high suitability of the Rhine as habitat for sessile filter feeders. Indeed, the feeding type of filter feeders is very wide spread in the Rhine and not only restricted to sessile animals like sponges, in particular many insects gain their nutrition from filter feeding.

The knowledge about freshwater sponges in the Rhine is still rather fragmentary, despite that in the past repeatedly high abundance of single species attracted attention (SCHÖN 1957; BARTL 1984; GUGEL 2000).

The present investigation deals with the actual species composition of freshwater sponges occurring in the river Rhine between Karlsruhe and Bonn (Germany), their interac-

tion with the benthozoocenosis and their ecological adaptations especially in connection with changing water levels and their life cycles.

All freshwater sponge species included in this study belong to the family Spongillidae, which is traditionally placed within the Haplosclerida (Porifera, Demospongiae, Ceractinomorpha).

## Material and Methods

### 1. Study area

The investigations took place at the Rhine (Germany), the exact locations are given in Fig. 1. The dates of the collections are summarized in Table 1.

Under usual conditions these parts of the Rhine show high water levels in winter (December–February). In spring (March–May) the water levels sink, but retain rather high. In late summer and early autumn (August/September) the water levels tend to sink considerably (Fig. 2). The daily water level at the station Worms is shown in Fig. 2. Water levels from stations all along the river Rhine were made available by the Management of Water and Shipping/South (Wasser- und Schifffahrtsdirektion Süd) via telephone service.

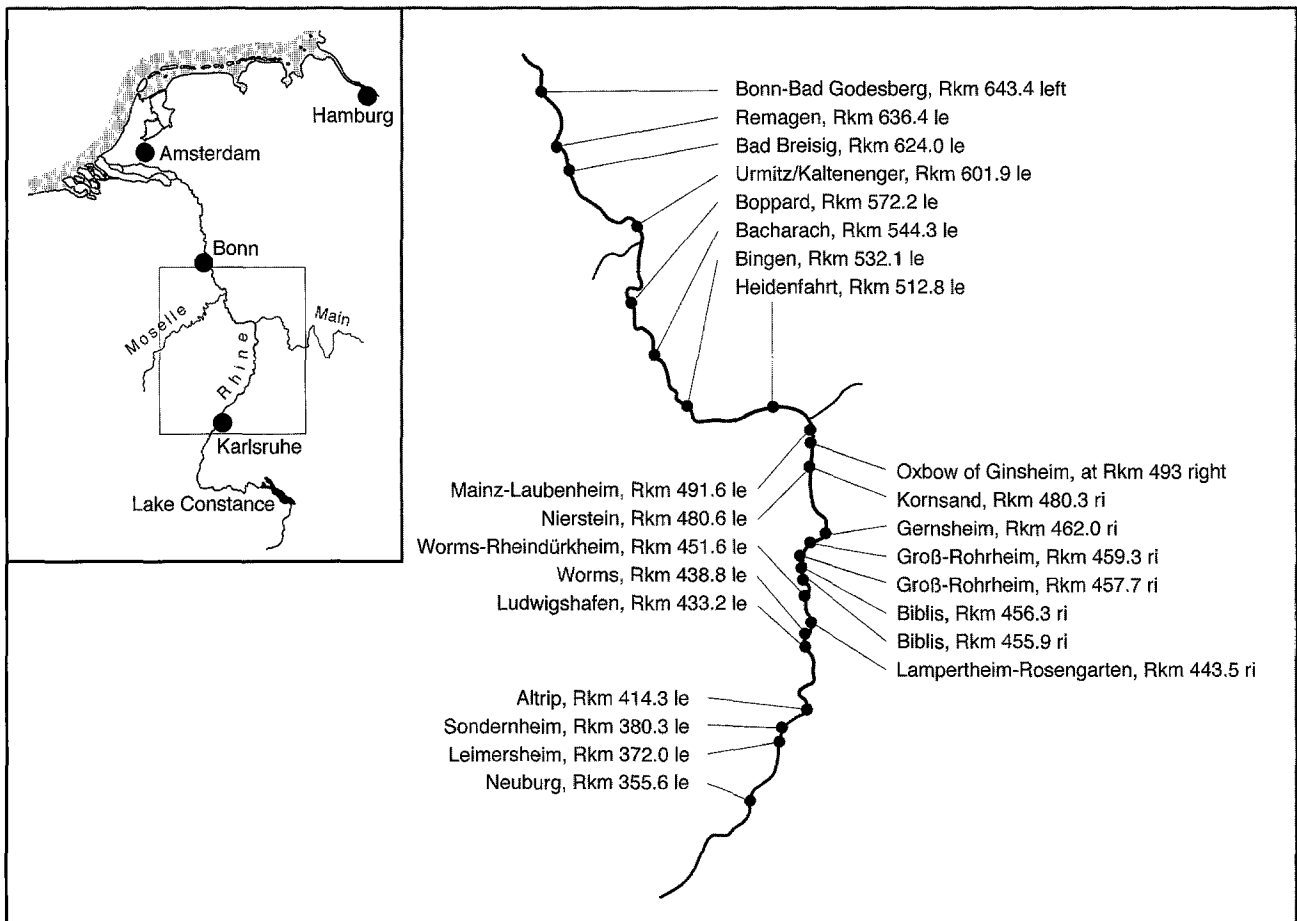


Fig. 1. The collecting sites; Rkm = Rhine-kilometer (River-kilometers).

**Table 1.** Collecting sites and dates, Rkm = Rhine-kilometer (River-kilometers).

Locality	22./23.1.1993	08./11.5.1993	24./26.8.1993 <sup>4</sup>	7./8.9.1993 <sup>4</sup>	25./26.9.1993	6./7.11.1993	22.2.1994	11.5.1994 <sup>5</sup>	8.6.1994 <sup>5</sup>	30.6.1994 <sup>5</sup>	15./26.7.1994	10./11.8.1994	14./15.10.1995	15.3.1995	3.8.1995	8.10.1995	12./14.10.1995
Neuburg, Rkm 355.6	×	×										×					×
Leimersheim, Rkm 372	×	×															×
Sondernheim, Rkm 380.3	×	×															×
Altrip, Rkm 414.3	×	×															×
Ludwigshafen <sup>1</sup> , Rkm 433.2	×	×															×
Lampertheim-Rosengarten, Rkm 443.5					×		×										×
Worms, Rkm 438.8				×													×
Worms-Rheindürkheim, Rkm 451.6	×	×			×												×
Biblis, nuclear power plant <sup>2</sup> , Rkm 455.9																	×
Biblis, downstream n.p.pl., Rkm 456.3																	×
Gross-Rohrheim, Rkm 457.7																	×
Gross-Rohrheim, Rkm 459.3					×												×
Gernsheim, Rkm 462					×												×
Kornsand, Rkm 480.3					×												×
Nierstein, Rkm 480.6		×			×												×
Mainz-Laubenheim, Rkm 491.6	×	×			×												×
Oxbow of Ginsheim <sup>3</sup> , at Rkm 493																	×
Mainz, Rkm 510																	×
Heidenfahrt, Rkm 512.8																	×
Bingen, Rkm 532.1	×	×															×
Bacharach, Rkm 544.3	×	×															×
Boppard, Rkm 572.2	×	×															×
Urmitz/Kaltenenger, Rkm 601.9	×	×															×
Bad Breisig, Rkm 624	×	×															×
Remagen, Rkm 636.4																	×
Bonn-Bad Godesberg, Rkm 643.4																	×

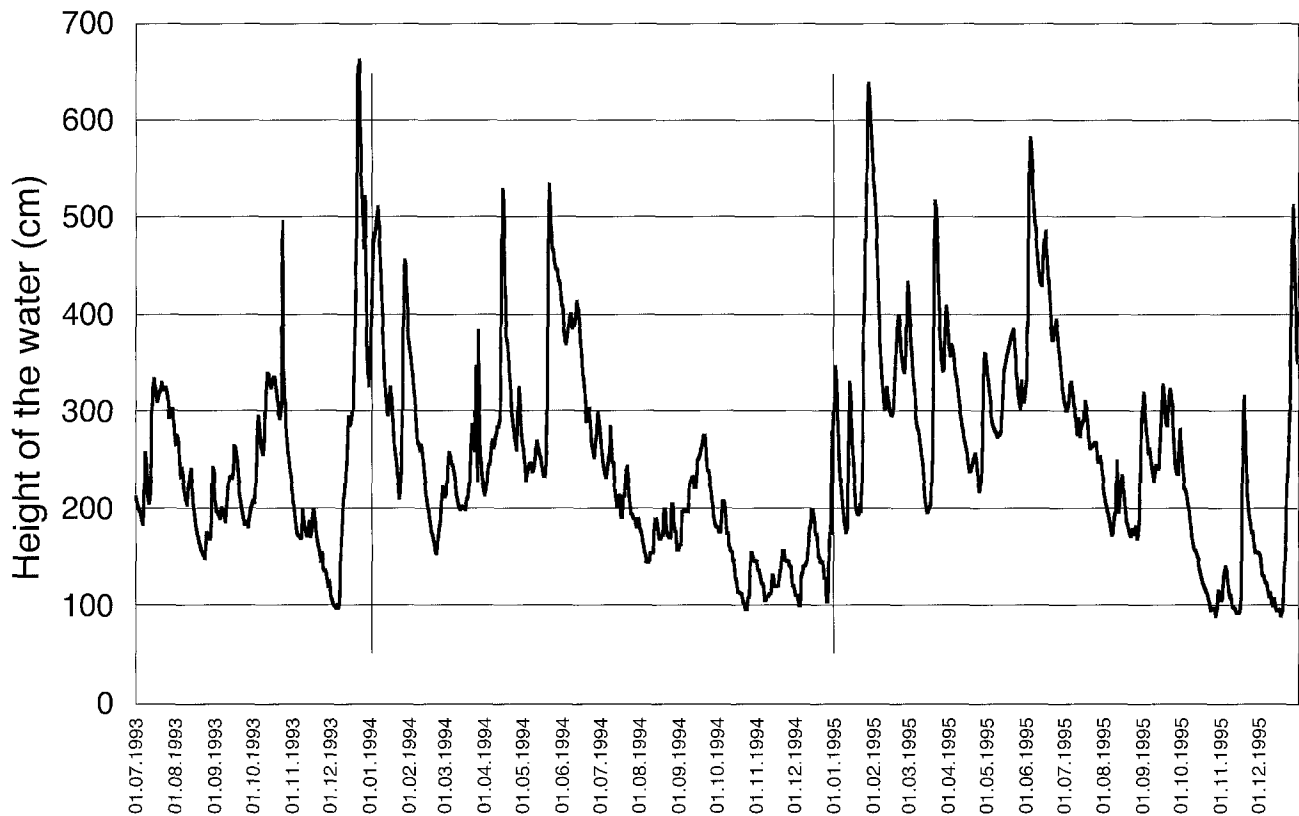
<sup>1)</sup> Near the facilities of the BASF AG.

<sup>2)</sup> Outflow of the cooling water circuit of the power plant, the temperature is here up to 10 °C higher than in the surrounding river.

<sup>3)</sup> Slightly polluted stagnant water.

<sup>4)</sup> The collection was conducted with a grab on board of the research ship "Argus".

<sup>5)</sup> Collections taken by J. WITTMANN.



**Fig. 2.** The niveau of daily water levels at Worms from July 1993–December 1995, the vertical lines indicate the turn of the years (the scale is a relative one without a defined zero point), the data originate from the Management of Water and Shipping/South (Wasser- und Schifffahrtsdirektion Süd).

**Table 2.** Physical-chemical data from the Rhine in Mainz from 1993–1995, in each case the mean values for days from March till October are given (the period, in which active colonies of most sponge-species were found), if outside this period different values appeared, the range for the whole year is given in brackets; the data originate from the station of water examination of the Rhine from the Landesamt für Wasserwirtschaft in Rheinland-Pfalz, the measurements were taken daily in Mainz.

Parameter	1993	1994	1995
Temperature (°C)	6.6–24.1 (3.4–24.1)	9.0–27.1 (5.5–27.1)	5.2–25.2 (4.9–25.2)
O <sub>2</sub> (mg l <sup>-1</sup> )	6.1–11.6 (6.1–12.0)	6.0–10.6 (6.0–11.7)	6.6–11.4 (6.6–11.8)
pH	7.7–8.4	7.6–8.1	7.7–8.2
Electrolytic conductivity (µS cm <sup>-1</sup> at a reference-temperature of 20 °C)	360–1070	383–811 (333–917)	355–889 (351–889)
Chlorid (mg l <sup>-1</sup> )	32–239 (31–239)	29–152	31–196
Calcium (mg l <sup>-1</sup> )	58–82	59–67 (59–71)	58–70 (58–79)
Magnesium (mg l <sup>-1</sup> )	8.4–11.0	8.8–9.7 (8.8–10.0)	8.3–10.0 (8.3–11.0)

Physical-chemical properties are given in Table 2. The data were taken daily and originate from the station for water examination of the river Rhine from the Landesamt für Wasserwirtschaft in Rheinland-Pfalz. The water-temperature is rarely lowered below 5 °C (Table 2), a closed ice sheet is an extremely rare event.

In the investigated area of the river Rhine the substrate consists entirely of rocks placed along the banks to protect them from water movements; wood is rarely found. Aquatic macrophytes are almost non-existent in the investigated area, only once a small *E. fluviatilis* was found epizootic on *Fontinalis* sp. (Bryophyta, Fontinalaceae).

## 2. Collection

Collections were made from the banks, by wading and removing the substrate by hand, except on the dates indicated in Table 1, when collections were made with a grab from the research ship “Argus” of the federal state Hesse. On the whole 120 collections on 17 collection trips were taken between 22.01.1993 and 14.10.1995 (Table 1). The collection trips took place regardless of the season.

The sponges were removed from the substrate with a knife and preserved in 70% ethanol.

The individual sponges on approximately 1.3 m<sup>2</sup> (5 rocks about 40 × 15 × 15 cm, randomly chosen in an area of about 10 m<sup>2</sup>) of substrate at each collecting site were counted and the number of individual sponges per m<sup>2</sup> available substrate was calculated (see Figs. 3, 5). Only active colonies were considered. In Figs. 3–5 data from all collections were summarized.

After the removal of the sponges, the remaining organisms crawling or growing on the substrate were removed (with a brush), collected (with a sieve) and preserved in 70% ethanol. The macrobenthic organisms were determined.

The organisms collected during this study were deposited in the Museum of Natural History in Mainz.

Those animals, which were attached to sponges or were collected crawling on or in them were defined as sponge-associated.

At each collection water-depth was recorded. For each site, the period of flooding before collection was calculated. [Example: At 03.08.1995 the water level in Worms was 180 cm, the collection in Lampertheim took place at a depth of 20 cm, therefore at a level-height of 160 cm. In the beginning of January 1995 the level was below 160 cm, afterwards the level was above 160 cm till August (see Fig. 2). The collection site was permanently flooded seven months before the collection.].

### 3. Preparation

From each individual sponge one microscope slide was prepared. The preparation followed ARNDT (1928), and the determination was conducted according to ARNDT (1926, 1928) and PENNEY & RACEK (1968).

The slides prepared during this study were deposited in the Senckenberg Museum of Frankfurt (SMF).

## Results

### 1. Descriptions of Rhine-populations of the six species

The species *Trochospongilla horrida* WELTNER 1893; *Ephydatia fluviatilis* (LINNAEUS 1758); *Spongilla lacustris* (LINNAEUS 1758); *Ephydatia muelleri* (LIEBERKÜHN 1855); *Eunapius fragilis* (LEIDY 1851) and *Eunapius carteri* (BOWERBANK 1863) were found, they are ordered from abundant to rare.

#### • *Trochospongilla horrida* WELTNER 1893

Description: Thin crusts (never thicker than 5 mm), color in life whitish to light grayish-brown, surface velvet-like, no outgrowths, larger colonies (diameter >0.2 m<sup>2</sup>) with irregular outline.

Skeletal architecture: Rather irregular reticulation of spicules, megascleres occurring within the pinacodermal layer.

Gemmules: 600–800 µm in diameter, laid down as a pavement-layer-like crust (single layered) adhering to the substrate at the base of the sponge body, surrounded by a common “layer of small boxes” (SALLER 1990b), with lots of megascleres embedded in it.

Spiculation:

Megascleres: Straight till (rarely) slightly curved, strongly spined acanthoxea; dimensions: 160–290 µm, average 220 µm (n = 1950 spicules in 39 colonies) long, about 12–15 µm wide, fusiform; according to SALLER (1990a) three types of megascleres occur in *T. horrida*, which are slightly different concerning their dimensions: pinacodermal megascleres, choanosomal megascleres and gemmular megascleres (in the present study no distinction was made between the three types, probably mainly choanosomal megascleres were measured).

No microscleres.

Gemmuloscleres: Birotulates with entire margins of the rotules, arranged in one layer within the „layer of vacuoles“ (WEISSENFELS 1989) of the gemmules, the rotules regularly overlapping.

#### • *Ephydatia fluviatilis* (LINNAEUS 1758)

Description: Irregular crusts, with a thickness of up to 2 cm.

Skeletal architecture: Tracts consisting of 2–3 parallel megascleres, connected via single megascleres resulting in a rather regular reticulation, no pinacodermal spicules.

Gemmules: Globular, pale yellow, built and laid singly within the basal tissue of the mothersponge, diameter: about 300–400 µm.

Spiculation:

Megascleres: Smooth, straight till slightly curved oxea, rarely slightly spined; dimensions: 194–425 µm, average 305 µm (n = 3900 spicules in 78 colonies) long, about 13–19 µm wide, fusiform.

No microscleres.

Gemmuloscleres: Birotulates, sometimes 1–2 strong spines on the trunk, trunk about 22–25 µm long, the rotules incised at the margins, diameter of the rotules about 15 µm, the birotulates arranged as a single, very regular layer within the “layer of vacuoles” of the gemmules, neighbouring rotules rarely overlapping.

#### • *Spongilla lacustris* (LINNAEUS 1758)

Description: Usually irregular crusts, rarely arborescent growth form.

Skeleton architecture: Tracts consisting of 3–5 parallel scleres, connected by tracts consisting of fewer megascleres. Microscleres within the pinacoderm.

Gemmules: Globular, perfectly round or slightly oval, usually orange, few gemmuloscleres within the pneumatic layer, micropyle not elevated, diameter about 500–700 µm.

Spiculation:

Megascleres: Straight till slightly curved, smooth oxea; dimensions: 190–365 µm, average 283 µm (n = 1700 spicules in 34 colonies) long, about 13–17.5 µm wide, fusiform.

Microscleres: Acanthoxea, slightly curved, always at least some microscleres within the pinacoderm, mostly very abundant within the parenchym; dimensions: about 65–80 µm long, width about 4.5 µm.

Gemmuloscleres: Slightly to strongly bent acanthoxea or acanthostrongyls, spination more crude than the spination of the microscleres; dimensions: about 70–100  $\mu\text{m}$  long, width about 5.5  $\mu\text{m}$ , arranged tangentially within or upon the pneumatic layer.

- *Ephydatia muelleri* (LIEBERKÜHN 1855)

Description: Cushionshaped crusts, a thickness of up to 4 cm.

Skeletal architecture: Tracts of about 5 parallel megascleres, connecting tracts similar to the main tracts, resulting reticulation very regular, single megascleres irregularly between the tracts, no pinacodermal spicules.

Gemmules: Globular, pale yellow, built singly within the mothersponge, diameter 400–500  $\mu\text{m}$ , the sponge uses often its whole tissue for the production of gemmules.

Spiculation:

Megascleres: Slightly spined acanthoxea, certain degree of variation in the spination, the tips of the spicules always smooth, megascleres which seem to be wholly smooth occur, a SEM examination often reveals in these cases a very slight spination; dimensions: 165–306  $\mu\text{m}$ , average 241  $\mu\text{m}$  ( $n = 900$  spicules in 18 colonies) long, width about 13–15.5  $\mu\text{m}$ , fusiform.

No microscleres.

Gemmuloscleres: Birotulates similar to those of *E. fluviatilis*, though smaller dimensions, diameter of the rotules about 18  $\mu\text{m}$ , trunks with a length of about 10–15  $\mu\text{m}$ , the rotules deeper incised than those of *E. fluviatilis*, trunks only rarely spined, the birotulates are arranged in up to three layers within the “layer of vacuoles” of the gemmules, rotules overlap rarely.

- *Eunapius fragilis* (LEIDY 1851)

Description: Low crusts, thickness of about 0.5–1 cm.

Skeletal architecture: Rather irregular reticulation of single megascleres, tracts occur rarely, no pinacodermal spicules.

Gemmules: Globular, usually orange-brown, diameter of about 300–400  $\mu\text{m}$  + a common pneumatic layer of about 50–100  $\mu\text{m}$ ; the gemmules tightly fixed to the substrate and laid as a pavement-layer-like crust, the very abundant gemmuloscleres tangentially upon and inside the pneumatic layer.

Spiculation:

Megascleres: Smooth, straight to slightly curved oxea, dimensions: 155–290  $\mu\text{m}$ , average 225  $\mu\text{m}$  ( $n = 1050$  spicules in 21 colonies) long, width about 12–15  $\mu\text{m}$ , fusiform.

No microscleres.

Gemmuloscleres: Mostly straight, seldom slightly curved acanthostrongyles till acanthoxea (similar to those of *S. lacustris*, but never strongly bent): About 80–110  $\mu\text{m}$  long, width about 5.5  $\mu\text{m}$ .

- *Eunapius carteri* (BOWERBANK 1863)

Description: Thin, circular crust (about 4 cm in diameter), one central oscule, only slightly elevated, color whitish.

Skeleton architecture: Vertical tracts of 2–4 parallel spicules, interconnected by irregular single megascleres or loose tracts.

Gemmules: Globular, brown, with a 40–60  $\mu\text{m}$  thick layer of regularly arranged airchambers, gemmuloscleres lying in this layer, micropyle a tubular process through this layer, not elevated above it, diameter about 320–450  $\mu\text{m}$ , gemmules forming a pavement layer.

Spiculation:

Megascleres: Straight till slightly curved, smooth oxea; dimensions: 265–350  $\mu\text{m}$ , average 307  $\mu\text{m}$  ( $n = 50$  spicules in one colony) long, width about 14–18  $\mu\text{m}$ , fusiform.

No microscleres.

Gemmuloscleres: Mostly straight, smooth oxea, dimensions about 150–220  $\mu\text{m}$  long, width about 6  $\mu\text{m}$ , resembling the megascleres, arranged tangentially upon the airchambers.

Found only once the 06.11.1993 within the outflow of the cooling water circuit of the nuclear power plant in Biblis (GUGEL 1995).

## 2. Substrate

As a rule, the larger rocks (immovable by average currents) were more likely to be colonized with sponges. Smaller rocks (often moved by average currents) were rarely settled by sponges or other sessile organisms. These preliminary data agree with those of RÜTZLER (1965) on colonization by marine sponges in the Mediterranean Sea.

## 3. Seasonal development

A generalized model of a life cycle of a freshwater sponge in the Rhine is as follows: In March–April young sponges hatched from their overwintering gemmules. The sponges grew until midsummer (July–August), sexually produced larvae might occur from May to July. Asexual gemmules were produced year-round, but more regularly towards autumn. In September–October the colonies declined and desintegrated, thus producing overwintering units (gemmules). Fig. 3 shows the seasonal development.

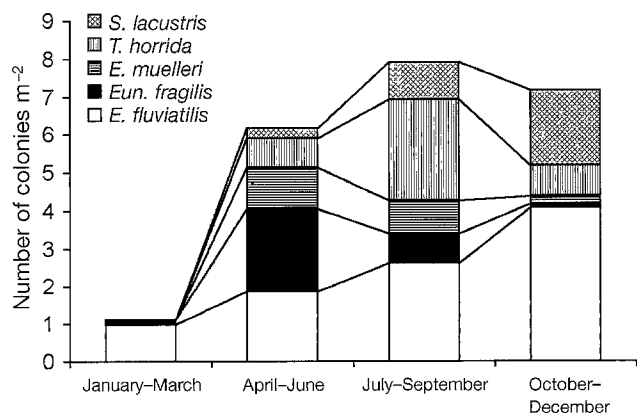


Fig. 3. Seasonal appearance of the Spongillidae in the investigated area.

## 4. Preferred flooding regimes

The species-assemblage was clearly different at deeper sites, which were not affected by changing water levels and remained flooded during the whole active phase of freshwater sponges, compared with higher places which were flooded only a few weeks before collection (only flooded during high tides and dried out regularly).

Sites flooded more than six months before collection were thought to be not affected by the changing water levels, those flooded only nine weeks before collection were thought to be flooded only at high tides (Fig. 4).

*E. fluviatilis* was the only species occurring regularly at sites flooded only nine weeks before collecting. At places flooded more than six months before collecting *E. fluviatilis* had the same absolute abundance in colony-counts, but the colonies grew much larger. The species *T. horrida*, *S. lacustris*, *Eun. fragilis* and *E. muelleri* only occurred at these deeper places in considerable numbers. Sponge colonies were generally very small at places flooded only nine weeks before collection. The majority had a diameter of less than 1 cm.

## 5. Sponge-associated animals

Since the correct identification of some sponge-associated animals needs the involvement of experienced specialists and these animals were not collected systematically, the results can only be preliminary. In this section no distinction between results and discussion is made, the results are discussed immediately.

The animals found regularly attached to or crawling on or in sponges belong to the ecological categories:

- Space competitors;
- Obligatory predators or parasites of sponges;
- Commensals, which inhabit sponges accidental without injuring them;
- Potential predators or parasites, only accidental inhabiting sponges.

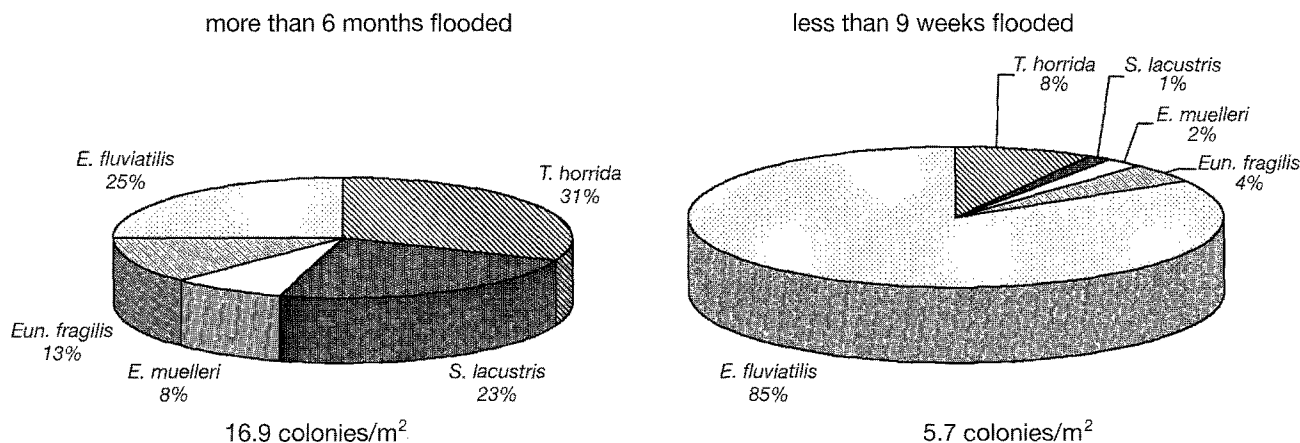
## 5.1. Space competitors

Space competitors for sponges are other sessile (in the Rhine: Bryozoa, Hydrozoa, Kamptozoa) and hemisessile (mostly filterfeeding insects and crustaceans) invertebrates. Since the early 90's the pontocaspian amphipod *Corophium curvispinum* SARS 1895 invaded the Rhine-system and became the dominant benthic animal. Its housing-tubes covered in summer as a layer of several centimeters all available substrates (see WITTMANN 1994). The abundance of *C. curvispinum* built a major threat to all sessile or hemisessile animals (SCHÖLL et al. 1995). The only organisms, that competed successfully with *C. curvispinum* were the Spongillidae, the most successful competitor was *T. horrida*. The ecological preferences of *C. curvispinum* and most Spongillidae differed slightly: Whereas freshwater sponges settled preferable underneath the rocks, *C. curvispinum* settled on top of the rocks. In the investigated area *C. curvispinum* was by far the most important space competitor.

Bryozoa used to be a major component of the potamo-coenosis (FRANZ 1992), recently they only occurred rarely. The species *Plumatella repens* (LINNAEUS 1758), *P. emarginata* ALLMANN 1844, *Fredericella sultana* (BLUMENBACH 1779) and *Paludicella articulata* (EHRENBERG 1833) were obtained in low abundance, the latter species regularly overgrown by sponges. Single floatoblasts from *Cristatella mucedo* CUVIER 1798 were found in November 1993 (Biblis, downstream the nuclear power plant) and from *Lophopus cristallinus* (PALLAS 1766) in November 1993 (oxbow of Ginsheim).

The only place, where some bryozoans were considerable space competitors, was within the outflow of the cooling water circuit of the nuclear power plant of Biblis. At this site the abundance of both *C. curvispinum* and Spongillidae was considerably lowered, the most abundant benthic animal was *F. sultana*, *P. emarginata* too was obtained there in considerable numbers.

Often both Spongillidae and Bryozoa remain healthy when growing tightly adjoined to each other (GUGEL 1996b).



**Fig. 4.** Species-assemblages at places with different times of flooding before collection, the numbers are calculated for 1 m<sup>2</sup>, 26 collections took place at sites more than 6 months before collection flooded, 28 collections took place at sites flooded less than 9 weeks before collections.

Nevertheless sponges often overgrow bryozoans and kill them.

The only sessile hydrozoan in the Rhine-system is *Cordylophora caspia* LANKASTER 1880 (Hydrozoa, Clavidae), this species occurred regularly, but only in low densities, so it was not an important space competitor.

Another sessile invertebrate occurred mainly within the outflow of the cooling-water circuit of the nuclear power plant of Biblis: *Urnatella gracilis* LEIDY, 1851 (Kamptozoa, Barentsiidae). Outside the cooling water outflow the species was never observed, so it was too rare to be important as space competitor.

Hemisessile larvae of insects were too rare to be considered as important space competitors, in former years they were much more abundant. Sometimes housing-tubes of *Hydropsyche* spp. (especially *H. contubernalis* McLACHLAN, 1865, Trichoptera) attached to sponges were observed. Tubes of Chironomidae, especially *Rheotanytarsus* spp., which used to be a major component of the potamocoenosis in former years, nearly disappeared.

Another sessile invertebrate, which declined considerably in recent years, was the clam *Dreissena polymorpha* (PALLAS, 1771). The few *D. polymorpha*, which were observed, were sometimes overgrown by Spongillidae, especially from *T. horrida*.

## 5.2. Obligatory predators or parasites of sponges

Only a few number of organisms prey or parasite obligatory on sponges. Their actual occurrence in the investigated area is reviewed.

Well known as parasites of sponges are larvae of *Sisyra* spp. (Insecta, Planipennia, Sisyridae) (WESENBERG-LUND 1939; WEISSMAIR 1994). During the present investigation only in five cases sponges infested with single specimens of *Sisyra* spp. were obtained.

The insects (as genus, the species could not be distinguished) were not restricted to certain sponge species: *E. fluviatilis* and *S. lacustris* both served as hosts on two occasions each, *T. horrida* was infested one time. Responsible for the low densities of *Sisyra* seemed to be the ecological requirements of the adult insects: According to WEISSMAIR & WARNINGER (1994) they need well-structured habitats, rich in woods. Such habitats occur only rarely along the Rhine.

A few times larvae of the genus *Ceraclea* (Insecta, Trichoptera, Leptoceridae) were found living on sponges: *Ceraclea* spp. were found on three occasions living on *E. fluviatilis*, one time lots of empty puparia were found inside this species (in October 1995 in Worms). The species *C. alboguttata* (HAGEN 1860) was found one time on *T. horrida*.

In a few cases specimens of *Ceraclea* were found independent of sponges, but always sponge-spicules were interwoven in their cases, in one occasion substituted by floatoblasts of *Plumatella emarginata*.

Larvae of *Ceraclea* spp. were long known as inhabitants and predators of freshwater sponges (WUNDSCH 1943; RESH

1976a), some species even show adaptations in their life cycles to their sponge hosts (RESH 1976a, 1976b).

Larvae of Chironomidae (Insecta, Diptera) are often found on and inside sponge-colonies, some of these species are thought to be obligatory sponge inhabitants and predators (e.g. WUNDSCH 1943; RESH 1976a). Among these is *Xenochironomus xenolabis* KIEFFER 1921 (WUNDSCH 1943; RESH 1976a). In the present investigation specimens of *X. xenolabis* were found only three times, sponge-spicules were never found in their intestine.

Mites of the genus *Unionicola* (Acari, Hydrachnellae, Unionicolidae) are often cited as "parasites" of sponges, but it seems questionable, if this is real "parasitism" (GUGEL 1996a). The life of the adults is planktonic, this explains their rarity in running water, indeed during the present investigation *Unionicola* species were never found. Nevertheless, SCHÖLL et al. (1995) cited *Unionicola crassipes* MÜLLER 1776 from the middle Rhine. In stagnant waters sponges infested with the mites were regularly found (GUGEL 1996a, 1996b).

## 5.3. Commensals, which inhabit sponges accidental

In this category animals are listed, which inhabited regularly but accidental sponges, without obvious signs of injury of the hosts.

Larvae of *Hydropsyche* sp. and *Ecnomus tenellus* (RAMBRUR 1842) (Insecta, Trichoptera) both occurred in considerable numbers on sponges, their abundance on sponges was much higher compared with their occurrence independent from sponges. According to WUNDSCH (1943) both taxa are occasional sponge-consumers, it remains unknown, whether they consumed sponges in the present investigation.

Not confirmed are the results of ARNDT (1933) and MARTYNOW (1924), who stated that the first developmental steps of *C. curvispinum* regularly take place within sponges. This amphipod was indeed frequently found on sponges, but never inside them. The high numbers of *C. curvispinum* on sponges seemed to be due to its high overall frequencies.

Other Amphipoda occurring occasionally on sponges were *Gammarus tigrinus* SEXTON 1939 and *Chaetogammarus ischnus* (STEBBING 1906) (Crustacea, Amphipoda, Gammariidae). Their occurrence on sponges seemed truly to be accidental.

The species *Prostoma graecense* BÖHMIG 1892 (Nemertea, Tetrastemmatidae) was found in three cases on sponges. The species was probably searching for sponge-associated animals it preys on, it did not consume sponges themselves.

KAHL & KONOPACKA (1981) reported a rich association of Oligochaeta living on *S. lacustris* from Poland. Within the Rhine Oligochaeta other than *Stylaria lacustris* (LINNAEUS 1767) (see below) could only rarely be found. The species occurring together with sponges were *Nais breitschei* MICHAELSEN 1899 and *Nais* sp. In each case single specimens without obvious host-specificity were found.



Less conspicuous were specimens of the Nematoda, that occurred sometimes on sponges.

Occasional specimens of juvenile *Dugesia tigrina* (GIRARD, 1850) (Turbellaria, Tricladida) and larvae of *Caenis luctuosa* (BURMEISTER 1893) (Insecta, Ephemeroptera) were obtained from sponges, their occurrence probably was accidental.

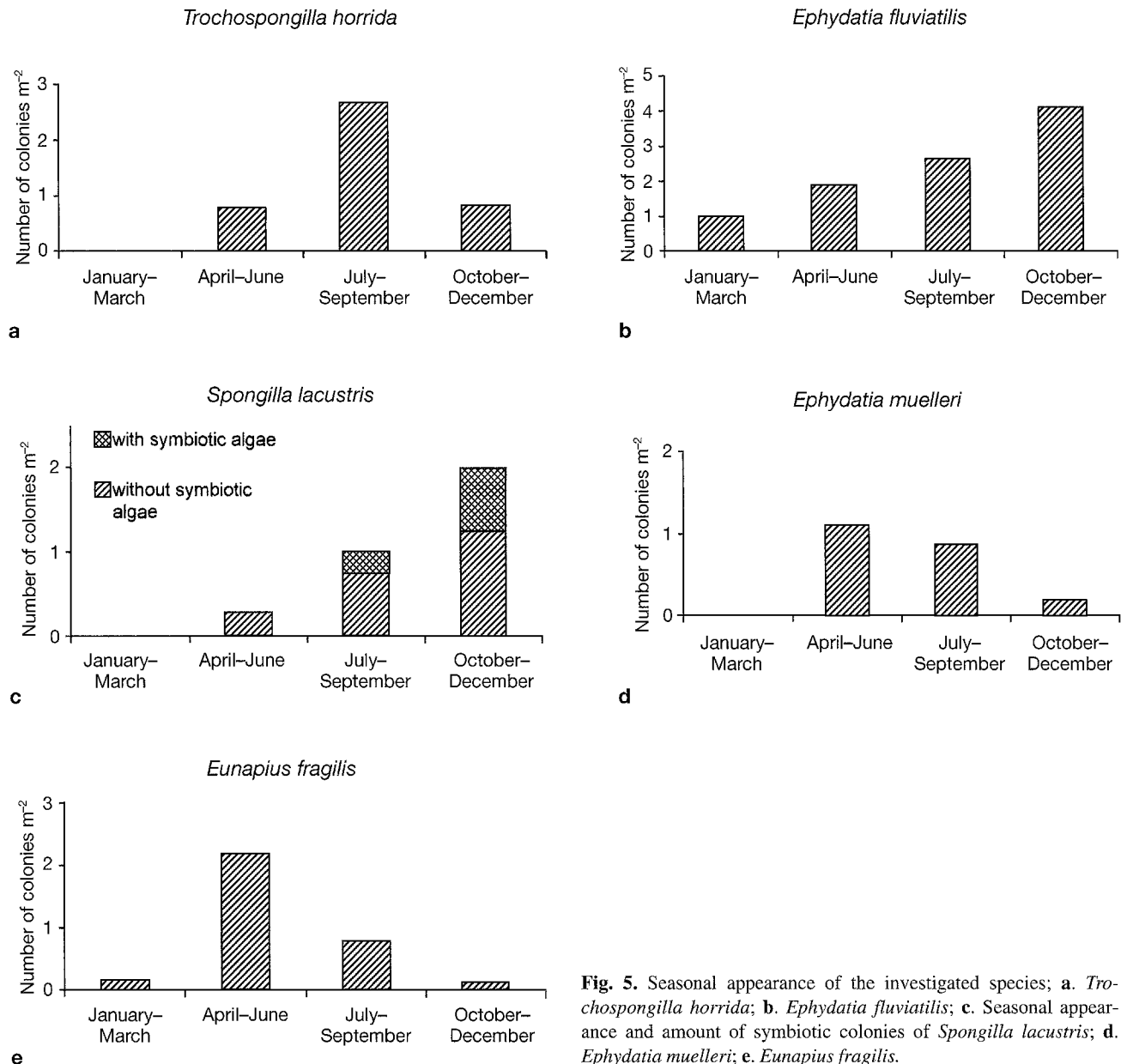
#### 5.4. Potential predators or parasites inhabiting sponges accidental

Here species are listed, which inhabit sponges accidental but injured them.

One of the major taxa occurring on sponges were free-living members of the Chironomidae. It remained unclear, whether they consumed sponges or not, maybe they should be assigned to category 5.3.

12 specimens of Chironomidae could not be determined on a species or genus-level. Of the determined species *X. xenolabis* (see above) *Glyptopendipes* sp. and members of the Tanypodinae could be observed as inhabitants of *E. fluviatilis*, all the taxa were reported by WUNDSCH (1943) and WESSENBERG-LUND (1939) as occasional but not obligatory sponge predators. Only in the case of *Glyptopendipes* sp. rarely sponge-spicules were found within the gut.

*Styaria lacustris* (Oligochaeta, Naidiae) seemed to be an occasional sponge-consumer since it was abundant but not restricted to sponges and in one case spicules (probably of *E. fluviatilis*) were found in the gut of a specimen. KILIAN (1964) was the first to mention a possible damage of some Oligochaeta on their sponge-hosts, especially *Styaria lacustris* (= *Nais probiscoidea*) and *Aelosoma* sp.



**Fig. 5.** Seasonal appearance of the investigated species; **a.** *Trochospongilla horrida*; **b.** *Ephydatia fluviatilis*; **c.** Seasonal appearance and amount of symbiotic colonies of *Spongilla lacustris*; **d.** *Ephydatia muelleri*; **e.** *Eunapius fragilis*.

In the outflow of an eutrophic pond near Darmstadt (the "Steinbrücker Teich") high numbers of *Nais simplex* PIQUET 1906 were observed in August 1994 consuming and mining in *S. lacustris* (unpublished results), within the Rhine the species never occurred on or in sponges during the present investigation.

## 6. Autecology of the species

### • *Trochospongilla horrida*

*T. horrida* began hatching from gemmules in spring (early April). The highest abundance was reached in summer (August, Fig. 5a), in both numbers and size of colonies. In autumn (September/October) the colonies always disintegrated and left the gemmule crusts tightly adhered on the substrate. As in *Eun. fragilis* the gemmules remain fixed at their place of production, they cannot be dispersed within the river. Gemmulation started in early summer (June/July). Especially in summer *T. horrida* was a successful space-competitor against the otherwise dominating neozoan crustacean *C. curvispinum*. When growing, small colonies tended to fuse with other colonies of the same species, thus forming large colonies, when fully grown. Neither larvae nor colonies containing symbiotic algae were observed. The species was mainly distributed in permanently flooded habitats (Fig. 4).

### • *Ephydatia fluviatilis*

Colonies of *E. fluviatilis* were regularly seen alive in winter (December–February), in contrast to the other species. The overwintering colonies were small crusts only 1.5 cm diameter, in which no canal systems were visible. They probably survived in a reduced state, as suggested by ARNDT (1928) and WEISSENFELS (1989). In early spring (April) their abundance was only slightly increased in comparison with winter (Fig. 5b), probably due to hatching of gemmules (see below), whereas the number of colonies dramatically increased during June–July (Fig. 5b) at which time a large-scale production of larvae took place (June), and in July these larvae had settled and built new colonies. The gemmulation process was irregular throughout the whole year and a considerable number of colonies was always devoid of gemmules. When gemmules were present their number was reduced: In colonies of 5 cm diameter not more than 10 gemmules were found. During fragmentation of the sponges few gemmules were freed from the mother-sponges and hatched in spring. The highest number of colonies was found during October–December. As in the case of *S. lacustris*, the large colonies present in autumn fragmented into several smaller colonies, many of which died towards winter (December–February); the overwintering colonies were also small.

In May/June about 25% of colonies produced larvae. This seemed to be the most important event in the life cycle of *E. fluviatilis*, as in July many very small colonies were seen

in close proximity to each other, a phenomenon quoted as „Sprühinfektion“ (spray infection) by STEUSLOFF (1938). As already indicated *E. fluviatilis* was the only species which occurred in higher numbers at places flooded only a few weeks prior to collection (Fig. 4). This was probably due to the more active dispersal of the larvae compared to gemmules. Symbiotic colonies were never found.

### • *Spongilla lacustris*

In winter (December–February) only gemmules were found. The first young sponges hatched from gemmules at spring (beginning of April), the number of colonies then rose steadily until October (Fig. 5c). The high numbers of colonies reported during the period from October–December were mainly due to these colonies being present at the beginning of October, whereas by the end of October their numbers had declined rapidly. Furthermore, the larger colonies observed in October fragmented in several smaller colonies before dying, so that counts of number of colonies rose before they dropped and disappeared completely in December–March.

Gemmules generally appeared from August on, but their appearance seemed to be less dependent of season and more dependent on colony-size. This is also true for other species (see RASMONT 1962, 1963; SIMPSON 1980). Colonies of *S. lacustris* larger than 3 cm in diameter always contained at least some gemmules; smaller colonies were mostly gemmule-free, at whatever time of the year they were encountered. Gemmules were built singly within the tissue of the mother-sponge, always within the basal parts of the colonies. The gemmulation process was more regular towards the end of the life span of the intact colonies. There were often dense, single-layered carpets of gemmules, resting where they were built. The whole sponges disintegrated after death, but sheltered parts of the skeleton still remained intact so that gemmules resting in these patches of still intact skeleton were bound together and weakly fixed to the substrate. Green gemmules due to an infestation with unicellular symbiotic algae and a gemmule-polymorphism as described by GILBERT & SIMPSON (1976) and BRØNDSTED & BRØNDSTED (1953) were not observed in this study. Within Rhine sponges larvae were not observed. This was very intriguing because in other habitats larvae-containing colonies of *S. lacustris* were regularly found (e.g. within the outflow of the "Steinbrücker Teich" near Darmstadt, Germany, nearly 50% of the colonies in July 1994 contained larvae, unpublished results).

In early autumn about 30% of the colonies were bright green due to the presence of symbiotic algae (Fig. 5c). Only during this part of the year were water levels low enough to provide the preferred habitats of *S. lacustris* (in slightly deeper, permanently flooded water, Fig. 4) with sufficient light for a successful photosynthesis of symbionts.

### • *Ephydatia muelleri*

The first colonies of *E. muelleri* appeared in spring (at the beginning of April), and soon after hatching the species was

**Table 3.** Life cycle data and ecological strategies of the five sympatric sponge species.

	<i>E. fluviatilis</i>	<i>S. lacustris</i>	<i>E. muelleri</i>	<i>Eun. fragilis</i>	<i>T. horrida</i>
Time of greatest abundance	October (autumn)	October (autumn)	June (early summer)	May/June (early summer)	August/September (late summer)
Overwintering units	whole colony	weakly fixed free gemmules	fixed free gemmules	attached gemmule crusts	attached gemmule crusts
Distribution units	larvae	drifting gemmules	drifting gemmules	larvae	?
Colonisation of newly established habitats	through active swimming larvae	not observed	not observed	not observed	not observed

found in high numbers. During summer (July/August) their abundance peaked. After completing gemmulation the colonies died, usually from the beginning of August to October (Fig. 5d). Active colonies of the species were not observed during winter (November–March), only dead colonies with gemmules. *E. muelleri* often used its entire tissue for gemmule-production, whereas its skeleton remained intact for a considerable period of time after the death of the mother-sponge. Large numbers of gemmules were fixed by the skeleton to the place of production. In this way a successful recolonization of the same place was ensured in the following year. In addition, when single gemmules became free and were not anymore fixed to the substrate, they could be distributed by the current within the habitat, providing an effective mechanism for dispersal and recolonization of adjacent habitats. Sexually produced larvae were not observed in this species, and only a single symbiotic colony was found (from 10.08.1994 in Sondernheim), close to symbiotic colonies of *S. lacustris*. *E. muelleri* is mainly distributed in deeper waters, below the levels affected during river-level fluctuations (Fig. 4).

• *Eunapius fragilis*

Colonies of *Eun. fragilis* usually disintegrated in summer (July–September). In winter (December–February) intact colonies were rarely found (Fig. 5e). The first sponges hatched from gemmules in spring (April). Immediately after hatching the highest numbers of *Eun. fragilis* colonies appeared (Fig. 5e). The species completed up to summer (July) its gemmulation process, after which the first colonies began to disintegrate. Gemmules were laid down like a pavement-like gemmule crust, tightly fixed to the substrate. The unmovable gemmules could not contribute to the dispersal within the habitat, but in May/June 1994 free movable larvae were found in about 10% of the colonies. Colonies containing symbiotic algae could never be found within the Rhine, probably due to a preferred distribution in permanently flooded deeper habitats where light regimes may be insufficient for photosynthesis (Fig. 4).

• *Eunapius carteri*

This species was encountered in the Rhine for the first time in central Europe (GUGEL 1995). It was found on 06.11.1993 within the cooling-water outflow of the nuclear power plant in Biblis. A detailed description and discussion about its dispersal are given in GUGEL (1995).

Data about time of greatest abundance, overwintering units, distribution units and the ability to colonize newly established habitats are summarized for the different species in Table 3.

## Discussion

### 1. Synecological aspects

Compared with the findings of WUNDSCH (1943), MATTESON & JACOBI (1980) or KONOPACKA & SICINSKI (1985) the number of sponge-associated animals was both in numbers of species and individuals low. The relationship between sponges and their inhabitants in the Rhine was never as intimate as the relationship of sponge associated invertebrates and *Lubomirskia baikalensis* (PALLAS 1772) (Porifera, Lubomirskiidae) in Lake Baikal, Russia reported by KAMALTYNOV et al. (1993).

Making the resources of the seston available for the rest of the benthic community seems to be one of the major ecological roles of sponges (GILI & COMA 1998, for marine systems). It is important to note that most of the resources will only be available after the death of the sponges.

Sponges play a significant role as competitors for space vs. other sessile or hemisessile animals. Especially in times of mass-occurrences of sponge-species these are effective competitors against their rivals.

Sponges were the only successful competitors against the otherwise the Rhine-benthos dominating *C. curvispinum*.

### 2. Demecological aspects

It seems remarkable, that five species of freshwater sponges coexist in the same habitat. Many of the above mentioned dif-

ferent strategies and life cycles help the species to avoid competition or enhance their competitive abilities. It is concluded that mainly competition for space takes place. Competitive interactions among sponges are regularly observed in the field. As shown above, the species have in different times of the year their highest abundance (Table 3, Fig. 5), or have different colonization abilities (Table 3) to avoid competition. Many details in the life histories can be interpreted as methods to enhance the competitive abilities, so is during the highest abundance of *S. lacustris* the proportion of colonies with symbiotic algae considerable (Fig. 5c). These symbionts strongly enhance the growth of their host (FROST & WILLIAMSON 1980). In *T. horrida* regularly smaller colonies fuse to form larger ones. NEUBERT & EPPLER (1991) discussed whether the competitive ability of this species is reduced and therefore it is quite rare. In the present case it was the most abundant sponge at all, and it proved to be very competitive, as well among sponges as in competition with other organisms.

The means to enhance the competitive abilities often play a more obvious role in competition with other animals.

As long as the sponge colonies stay small, the species usually try to avoid competition, in contrast large colonies can often be seen overgrowing other sponges or competing organisms from other phyla.

### 3. Autecological aspects

The species reacted different to different flooding regimes. In *E. fluviatilis* free moving larvae were the main distribution units, in the other species their role was taken by passively moving gemmules (with the exception of *Eun. fragilis*, but here by far fewer larvae than in *E. fluviatilis* were produced, whereas in *E. fluviatilis* the larvae occurred each year, the larvae of *Eun. fragilis* only occurred in 1994, Table 3). This explained the different colonization abilities and was the reason why *E. fluviatilis* in contrast to all other species could colonize successfully high regions not all the time flooded.

It was concluded, that the different times of flooding before the collections was the main factor responsible for different depth preferences of sponge species. Other factors show no depth dependent variations in the river environment. Nutrition should be evenly distributed within the waterbody, due to turbulent currents. Light can only penetrate about 0.75 m due to high turbidity.

It was also concluded, that sponges could not survive being dried out for more than one day (it is not possible to transfer living freshwater sponges from one body of water to another without keeping them submersed all the time, unpublished data). Indeed the main reason why higher places were only scarcely settled, was the fact that these places regularly dried out.

Different flooding regimes affected the whole river at different depths where the collections took place.

It became clear that a vertical zonation occurred at all collection sites, a horizontal zonation (differences between collection sites) did not occur, the species assemblages were the same at all sites (concerning sponges and other macrobenthic animals as well).

Freshwater sponges often display a considerable plasticity in their ecological strategies (PRONZATO & MANCONI 1994a), their life cycles are often adapted to the special requirements of their habitats, e.g. *E. fluviatilis* in temperate regions usually is active during summer and inactive during winter. In hot, arid regions it is active during winter and inactive during summer (HARSHA et al. 1983; CORRIERO et al. 1994). This shows, that the life cycle is very adaptable to specific climatic conditions (PRONZATO & MANCONI 1994b). According to PRONZATO et al. (1993) the life cycle of *E. fluviatilis* seems to be controlled by exogenous factors in regions with strongly oscillating environmental conditions. In more stable habitats endogenous control seems to dominate.

For several species data presented in the literature differ from those presented here. So reported BISBEE (1992) for *S. lacustris* in North Carolina, USA the presence of active colonies year-round. He observed gemmulation in late spring/early summer. Sexual reproduction occurred in April and some sponges disappeared during summer.

According to CHEATHUM & HARRIS (1953) both *Eun. fragilis* and *T. horrida* were active year-round in Texas, USA. PRONZATO & MANCONI (1995) counted in Sardinia up to 324 gemmules/cm<sup>2</sup> tissue of *E. fluviatilis*.

So for almost all species different results under different environmental conditions should be expected.

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