Fugitive Species of Coleoptera Colonize the Water's Edge of Alpine Rivers

Vagabundierende Käferarten besiedeln den Ufersaum alpiner Flüsse

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Summary: Beetle assemblages which colonize the water's edge of both an alpine river and a brook were investigated from May to July, 2012. At the brook, discharge took place only after heavy or long-lasting rain. It is assumed that the change between terrestrial and aquatic phases has a dramatic effect on beetle assemblages in the brook, whereas the flow pulses of the river with their moderate expansion-contraction pulses have no influence. This assumption has proved to be true for assemblages living at the brook, but assemblages colonizing the water's edge of the river also changed considerably in terms of their α -diversity and density. Droughts (at the brook) and flow pulses (at the river) acted similarly: they pauperized species assemblages. Critical components of streamflow regimes such as water level, magnitude of discharge, frequency of flow events and the rate of change of discharge from one condition to another may modify escape and re-establishment of beetle assemblages. Resilience as calculated for the river sites was high in June and low in July. Throughout the sampling period, the α -diversity continuously increased with the number of individuals collected, with the sample area studied and with time. Many transitory species staying at the water's edge for a limited time may help explain this observation.

Key words: Flow pulses, drought, resilience, α -diversity, dispersion

Zusammenfassung: Es wurden Käfergemeinschaften untersucht, die sowohl den Ufersaum eines Flusses besiedeln als auch die angrenzenden Flächen eines Baches, bei dem es nur nach heftigen oder lang andauernden Regenfällen zu einem Abfluss kam. Am Bach sollte es zwischen den terrestrischen und aquatischen Phasen zu erheblichen Änderungen in der Artenvielfalt (a-Diversität) und Besiedlungsdichte kommen, geringe Schwankungen mit nur geringen Expansions- und Kontraktionsphasen der Wasseroberfläche am Flussufer sollten diese beiden Kenngrößen der Käfergemeinschaften nicht beeinflussen. Die Veränderungen in den Lebensgemeinschaften am Bach entsprachen den Erwartungen, aber auch am Fluss veränderten sich α-Diversität und Besiedlungsdichte deutlich: Trockenphasen am Bach und Wasserstandsschwankungen am Fluss führten zu einer Verarmung der Käfergemeinschaften. Eigenschaften der Wasserdynamik, wie Höhenlage des Ufersaums, Menge der Abflussrate, Häufigkeit der Flutereignisse und Geschwindigkeitsänderungen in der Abflussrate von einem Zustand in einen anderen, dürften das Fluchtverhalten und die Wiederbesiedlung modifizieren. Die Resilienz war hoch, wenn die Flutereignisse im Juni auftraten, sie war gering, wenn die Flutereignisse im Juli stattfanden. Im Laufe der Untersuchungsperiode stieg die Artenvielfalt ständig an und zwar mit der Anzahl der erfassten Individuen, der Ausdehnung der Untersuchungsfläche und der Zeitspanne der Untersuchung. Mehrere durchziehende Arten, die sich nur für einen kurzen Zeitraum im Uferbereich aufhielten, geben eine mögliche Erklärung.

Schlüsselwörter: Flut, Trockenheit, Resilienz, Artenvielfalt, Dispersion

1. Introduction

River-floodplain ecosystems reflect perturbations caused by fluvial dynamics. These perturbations are seen as the major driving force in creating a diversity of geomorphological structures as well as rich biodiversity and bioproduction. Fundamental models on river-floodplain dynamics are summarized in the flood pulse concept (JUNK et al. 1989; TOCKNER et al. 2000). This has stimulated several scientists to investigate the ecological effects of perturbation and biophysical interactions (LAKE 2000; NAIMAN et al. 2000; BOULTEN 2003).

A further issue in river-floodplain ecology is the trophic linkage across the aquaticterrestrial interface. Many carnivorous arthropods colonize the riparian zone and even survive in habitats of low productivity such as gravel banks. These gravel banks receive input from adjacent water bodies; the terrestrial predators survive because of the input of aquatic insects (HERING & PLACHTER 1997; PAETZHOLD & TOCKNER 2005; PAETZHOLD et al. 2005).

Studies on the distribution patterns of terrestrial arthropods living adjacent to rivers have mainly focused on rare and extreme flood events (HERING et al. 2004; ILG et al. 2008). When observed over short time periods and at low discharge rates when rivers flow well below the bankfull stage, moderate expansion-contraction events will occur. Even at these moderate expansion-contraction events, streamflow can be considered to be a "master variable", differing in terms of magnitude of discharge, frequency, duration, its predictability and rate of change (POFF et al. 1997; NAIMAN et al. 2000).

In this study I present the distribution pattern of beetle assemblages living at the water's edge of a brook and a river. In the brook, long, dry phases are interrupted by high discharge rates caused by melting snow and heavy or long-lasting precipitation. In the river, varying discharge rates resulted in higher and lower water levels. I hypothesize that beetle assemblages establishing themselves along the brook will change dramatically between terrestrial and aquatic phases, whereas beetle assemblages at the river's edge when the water level changes moderately well below bankfull will be stable.

2. Material and methods

2.1. Site description

One study site was on the River Melezza, which is situated in Ticino (Switzerland). The river Melezza flows from the Italian border to the River Maggia and further to the Lago Maggiore (Fig. 1a). The selected beetle sampling site on the River Melezza is situated at Terre di Pedemonte and stretches over a length of 100 m. Riverine sediments vary between boulders, gravel beds and sandy shores (Fig. 1b, 1c).

The other study site was a tributary of the River Melezza situated below the Val Comora o di Golino. It is a brook exhibiting discharge rates only after snow melt and heavy or long-lasting rain. The brook's bank

Fig. 1: a View of the River Melezza and the Terre di Pedemonte from the passenger bridge at Tenja/Losone. **b** Boulders are the preferable microhabitat for the rove beetle *Paederus rubrothoraci-cus*. **c** Gravel beds are colonized mainly by tiny rove beetles (*Thinobius crinifer, Hydrosmecta* spp) and scavenger water beetles (*Laccobius alternus*). **d** Shady spots at the brook's edge are dominated by rove beetles of the genus *Aloconota*

Abb. 1: a Blick zum Fluss Melezza und dem Terre di Pedemonte von der Fußgängerbrücke bei Tenja/Losone. **b** Felsen bilden den bevorzugten Lebensraum für den Kurzflügler *Paederus rubrotho-racicus*. **c** Schotterflächen werden bevorzugt von kleinen Kurzflüglern (T*hinobius crinifer, Hydrosmecta* spp) und Wassserkäfern (*Laccobius alternus*) besiedelt. **d** Schattige Flächen am Bachufer werden von Kurzflüglern aus der Gattung *Aloconota* dominiert.



varies in terms of sediment size and sorting vegetation cover and shading (Fig. 1d). The section from which beetles were sampled stretches over 150 m and is situated 200-300 m away from the site at the river Melezza. Both sites are situated at an elevation of 250 m a.s.l.

2.2. Trapping method and sampling

Beetles were trapped by flooding the water's edge and sweeping the floating beetles from water surface with a net. The method is described in detail by Köhler (1996).

A single flooded area covered 0.2 m², with a length of 1.0 m and a width of 0.2 m. Eight replicates were flooded on a single date, including sunny and shady sites as well as the whole range of sediment characteristics. This means that the number of microhabitats sampled on a single day was constant and did not increase during the study. Sampling took place during the time interval from May 28th until July 17th and included collections on seven dates along the brook and on 15 dates along the river (see Appendix, Table 1, Table 2). Beetles were swept from the water's surface in the morning at relatively low temperatures and at sites at which the water flow was moderate, minimizing the number of escaping beetles. During dry phases of the brook, beetles were collected by hand sampling from areas of adequate size.

The systematics and nomenclature of the beetles followed FREUDE et al. (1964-1994), FREUDE et al. (2004-2012) and KÖHLER & KLAUSNITZER (1998).

2.3. Environmental variable

The discharge rate and the water level changed throughout the study; the two factors are correlated. Only water levels are presented in this study (Fig. 2). The water level never reached bankfull (i. e. 4.70 m above 198 m a.s.l.) situation. The data come from a water station situated 5 km downwards and 50 m below the sampling area (www.hydrodaten.



Fig. 2: Changes in the elevation of water level of the River Melezza (cm above 198 m a.s.l.) during the sampling period from May 28th until July 17th. Flow pulses are well below bankfull (i.e. 4.70 m above 198 m a.s.l.) and are marked by arrows.

Abb. 2: Veränderungen in der Höhe des Wasserspiegels der Melezza (cm über 198 m.ü. M.) während des Untersuchungszeitraums vom 28. Mai bis zum 17. Juli. Erhöhte Wasserstände erreichen nicht die oberste Uferlinie von 4,70 m über 198 m. ü. M. und sind durch Pfeile markiert.

admin.ch/2368). Thus, the water level gives compositi

only approximate information for the local situation.

2.5. Data analysis

Most of the data obtained were not normally distributed. Therefore, data for α -diversity and density of a single data set are represented as median and range. The non-parametric Mann-Whitney U-test was used for pair-wise comparison of data sets.

The SØRENSEN-index C was used to measure β -diversity. C = 2j/ (a + b), for which j is the number of taxa found in both assemblages, a is the number of taxa found in assemblage a, and b is the number of taxa found in assemblage b. Samplings taken from June 4th, June 11/14th, June 17/18th, until June 20/23th at brook- and river sites were compared. β -diversity measures ranges from 0 (indicating that no taxa are common between assemblages) to 1, with identical taxa

composition. Species turnover rates between pre and post flow events and even between successive samplings were calculated by one minus SØRENSEN-index C.

3. Results

3.1. The brook: Val Comora o di Golino

Only single beetles occurred in the range of the water's former edge during dry phases (App. Tab. 1). Some of them were newly hatched adults of ripicolous species, others were hygrohilic and characterized moist sites of the forest floor. A higher number of species was collected at times of varying discharge rates along the water's edge. Only four species were common immediately after rain showers when the brook reached its maximum water level as well as during the following days when water level contracted: Two species are the congeneric but differently sized rove beetles *Aloconota debilicornis* and



Fig. 3: Species richness (α -diversity) (median and range, n = 8) of beetles colonizing the water edge of the River Melezza from May 28th until July 17th. Asterisks indicate significant differences of α -diversity before and after flow pulses (*: p < 0.05, **: p < 0.01, ***: p < 0.001). Flow pulses are indicated by arrows, the increase in water level by numbers (cm) in the boxes.

Abb. 3: Artenvielfalt (α -Diversität) (Median und Spannweite, n = 8) der Käfer, die den Uferbereich der Melezza vom 28. Mai bis zum 17. Juli besiedelten. Sterne kennzeichnen signifikante Unterschiede vor und nach den erhöhten Wasserständen (*: p < 0,05, **: p < 0,01, ***: p < 0,001). Erhöhte Wasserstände sind durch Pfeile markiert, der Wasserastieg durch Zahlen (cm) in den Kästchen.



Fig. 4: Density (median and range, n = 8) of beetles colonizing the water edge of the River Melezza from May 28th until July 17th. Asterisks indicate significant differences before and after flow pulses (*: p < 0.05, **: p < 0.01, ***: p < 0.001). Flow pulses are indicated by arrows, the increase in water level by numbers (cm) in boxes.

Abb. 4: Besiedlungsdichte (Median und Spannweite, n =8) der Käfer, die den Uferbereich der Melezza vom 28. Mai bis zum 17. Juli besiedelten. Sterne kennzeichnen signifikante Unterschiede vor und nach den erhöhten Wasserständen (*: p < 0.05, **: p < 0.01, ***: p < 0.001). Erhöhte Wasserstände sind durch Pfeile markiert, der Wasseranstieg durch Zahlen (cm) in den Kästchen.



Fig. 5: Turnover rates (numbers in boxes) at the water's edge of the River Melezza as influenced by flow pulses and – when no flow pulse occurred – between subsequent samplings. Studies were carried out from May 28th until July 17th. Flow pulses are indicated by arrows.

Abb. 5: Arten-Austauschraten (Zahlen in Kästchen) im Uferbereich der Melezza unter dem Einfluss erhöhter Wasserstände und – wenn keine sichtbaren Schwankungen des Wasserstands erfolgten – bei aufeinanderfolgenden Aufsammlungen. Die Untersuchungen erfolgten vom 28. Mai bis zum 17. Juli. Erhöhte Wasserstände sind durch Pfeile markiert.



Fig. 6: a More species of beetles appear at the water's edge as more individuals are collected. Flow pulses are indicated by arrows. **b** Number of species increases with an increasing number of small collection areas. Flow pulses are indicated by arrows. **c** The species-area relationship fits almost a straight line in log-log space. Flow pulses are indicated by arrows. **d** Species richness (α-diversity) increases with time. Flow pulses are indicated by arrows.

Abb. 6: **a** Die Anzahl der Käfer-Arten steigt mit der Anzahl der Individuen, die im Uferbereich gesammelt wurden. Erhöhte Wasserstände sind durch Pfeile markiert. **b** Die Anzahl der Käferarten steigt mit der Zunahme an kleinen Flächen. Wasserhöchststände sind durch Pfeile markiert. **c** Die Arten-Flächen-Beziehung steigt bei logarithmischer Darstellung nahezu linear an. Wasserhöchststände sind durch Pfeile markiert. **d** Die Artenvielfalt (α -Diversität) steigt mit der Zeit. Wasserhöchststände sind durch Pfeile markiert.

A. cambrica; the others are the click beetle *Zorochrus minimus* and the ground beetle *Lionychus quadrillum*. The rove beetles both followed the contracting water levels. Their size ratio, as measured between the outer parts of the mandibles at their base (n=10), was calculated as 1.3. This is the critical value proposed by HUTCHINSON (1959) for two species of the same trophic level to be able to coexist when different in size only. The click beetle and the ground beetle preferred thin mats of crushed organic detritus which had accumulated in pits of the brook. The click beetles mainly colonized moist sandy substrates underneath the mats or spaces

between the organic material, whereas the ground beetles mainly patrolled the surface of the organic mats in sunny patches.

3.2. The river: Melezza at Terre di Pedemonte

The river's edge was colonized by higher numbers of species and individuals per m² than the brook's edge across a wide range of habitat types (App. Tab. 2). However, similar to the results obtained for the brook, both factors of beetle assemblages (number of species and individuals) varied considerably for the river between successive sampling



Fig. 7: Similarity (measured using the species-index of Sørensen) between samplings taken at 1) June 4th at the brook and the river, 2) June 11th at the brook and the river, 3) June 13th at the brook and June 14th at the river, 4) June 17th at the brook and June 18th at the river, 5) June 20th at the brook and June 23rd at the river. For further information, see Appendix, table 1 and table 2.

Fig. 7: Ähnlichkeitsdiagramm nach dem Arten-Index von Sørensen zwischen den Aufsammlungen, die an folgenden Terminen durchgeführt wurden: 1) 4. Juni an Bach und Fluss, 2) 11. Juni an Bach und Fluss, 3) 13. Juni am Bach, 14. Juni am Fluss, 4) 17. Juni am Bach, 18. Juni am Fluss, 5) 20. Juni am Bach, 23. Juni am Fluss. Weitere Informationen im Anhang Tabelle 1 und Tabelle 2.

dates. Significant effects were observed for each of the four flow pulses which occurred (Fig. 3, 4). Critical components of streamflow regimes such as the magnitude of discharge, the frequency of flow events, the volume of the rising and falling discharge and the rate of change may modify only the strength under which species assemblages change.

Turnover rate of species assemblages between flow pulses was low in June but high in July (Fig. 5). High values were also obtained for successive samplings without any influence of a flow pulse when taken later than July 15th. The one exception calculated for data taken at the beginning of July (Fig. 5) was obtained when the time interval between successive samplings was short (= 1d).

Species numbers grew steadily with the number of individuals collected (Fig. 6a). An increase in species numbers also depended on the area sampled (Fig. 6b). A species-area curve tended to fit a straight line in log-log space (Fig. 6c). The number of species also increased steadily as data accumulated over the sampling time (Fig. 6d).

3.3. Comparison between brook- and river sites

Beetle assemblages were compared at the species level using the SØRENSEN-index C

(Fig. 7). The assemblages from the brook and the river were separated, although the distance between the two collection sites was only 200 - 300 m. At the brook, the assemblage which deviated most strongly from all others was the one sampled on June 4th, after a long dry period. At the river, the assemblage recorded at the maximum discharge rate was the least similar to all the other assemblages.

4. Discussion

4.1. Distribution

The microhabitat choice of many species inhabiting the aquatic-terrestrial interface can be remarkably stable (ANDERSEN 1969). Beetles can be sensitive to physical factors - such as sediment size and sorting, temperature, humidity and inundation - and to biotic factors such as the degree of vegetation cover and to the quality of aquatic food (ANDERSEN 1969; ANDERSEN 1985; EYRE et al. 2001, BROSE 2003). After flow events when water level drops, most species will rapidly re-establish their specific microspatial distribution pattern (BATES et al. 2007). Riverine sediments with a greater diversity of microhabitats support more species-rich assemblages (SADLER et al. 2004). In this study, beetle species sampled from the edge of the river are adapted to different microhabitat types present in sunny areas without vegetation cover but characterized by alterations in sediment size and sorting. In contrast, beetles occurring at the edge of the brook mostly preferred shady sites with dense vegetation cover; only a few species colonized sunny sites (for example Lionychus quadrillum).

The study sites of the river are exposed to the south and the sun; the brook is mostly situated in shaded areas of a forest. Differences in the degree of vegetation and the amount of direct sunlight are seen to be the main factors which explain the dissimilarity found between brook and river sites.

4.2. Segregation

The distribution pattern of species is not only caused by spatial segregation but probably also by competition between sympatric species. The existence of competition can be explained by spatial segregation of species. And indeed, there is little evidence to suggest that competition results in a distribution pattern of beetles colonizing exposed riverine sediments (BATES et al. 2007). However, avoidance of competition can be assumed when sympatric species are specialized to different food items. According to HUTCHIN-SON (1959), two species of the same trophic level will coexist in an assemblage only when the size ratio of these species exceeds the critical value of 1.28. STRONG et al. (1979) and SIMBERLOFF & BOECKLEN (1981) produced rigorous, testable hypotheses about the size structure of species assemblages. In ground beetle assemblages, Pterostichus spp. living in stable habitats over a long time interval had a size structure consistent with competition theory (BRANDL & TOPP 1985). ANDERSEN (1988) suspects that also species packing of ground beetles (Bembidion spp.) living on riverine sediments is partly governed by size ratios.

The size difference between the two staphylinids *Aloconota debilicornis* and *A. cambrica* means they feed most efficiently on food items of different sizes. Both species preferably feed on midge larvae that remain at the receding water line.

Litter mats accumulate in pits when the brook dries out. Beneath these mats, midge larvae can find appropriate habitats for survival even when water recedes. However, they have to pass two more barriers prior to leaving their developmental site as adults. Two predators that can feed on midges (*Zorochrus minimus* and *Lionychius quadrillum*) colonized the litter mats in high numbers. *Z. minimus* preferred the lower vertical layers above the sediment and those between the crushed litter. In contrast, *L. quadrillum* patrolled the surface of the litter mats to catch their prey.

4.3. Disappearence

My assumption that flow pulses of the river with their moderate expansion-contraction pulses will have no influence on pauperization of beetle assemblages results from observations made at seashores. At the seashore, many beetles continuously colonize the water line during the warm season. The α -diversity and density of beetles increase between successive tides when the water level rises moderately during spring tides. Beetles dwelling in the lower littoral zone move ahead of rising water levels in order to avoid immersion, accumulating in the upper littoral. When tides are extremely high, *a*-diversity and density increase further, mainly because of a passive dispersion of individuals arriving from distant habitats (Palmén 1944; Topp 1988).

Some beetles living at the seashore evolved different adaptation mechanisms to survive flooding. These survival mechanisms have a great deal in common and are successful when they help to keep beetles away from turbulent waters (TOPP 1975; TOPP & RING 1988a, b). Disastrous storm events mainly occur in spring and autumn before beetles reach the littoral zone and after they have left it.

In contrast to the conditions at the seashore, flow events at alpine rivers are less predictable. Moreover, disastrous flood events at alpine rivers usually occur during the warm season when beetles have left their hibernation sites and have already colonized the water's edge. Consequently, the evolution of avoidance mechanisms should be the best fit for beetles colonizing such unstable environment.

Even when the water level rose moderately, most beetles seemed to have already left the water's edge by flying a good distance away. Searching for beetles on the surface of the littoral fringe during maximum discharge rates, I only found a few individuals of *Paederidus rubrothoracicus* running on rocks about 2 m above the water level.

4.4. Resilience

Turnover rates calculated between flow events at the beginning of June were low and resembled data calculated for ground-living beetle assemblages colonizing floodplain hardwood forests before and after flood events (TOPP 2012). In respect to ground beetle assemblages (Carabidae) colonizing floodplain grasslands, similarly low turnover rates were obtained in subsequent years when no disturbances by floods occurred (ILG et al. 2008). In contrast, turnover rates calculated between flow events at the beginning of July were high and were in the range of data found for ground beetle assemblages in floodplain grasslands before and after an extreme flood (ILG et al. 2008).

Some data evident in this study may help explain the difference in turnover rates. Firstly, when comparing all calculations of turnover rates (even those when flow pulses are absent), one will find low values until June 15^{th} (n = 4) and high values after June 15^{th} (n = 7), with one exception when samplings were taken daily, independent of flow events.

Secondly, increased turnover rates coincided with the emergence of adults of new generations (pale and not sclerotisized individuals of several species were found). It is well known that beetles disperse during the first days of their adult lives. Ripicolous beetles may disperse along the water's edge, but also hygrophilic and not exclusively ripicolous beetles will use the water's edge like a stepping stone.

4.5. Numerical response

ROSENZWEIG (1995) asked the question: What could account for larger mainland areas having more species? His answer was based on good explanations from the literature: Larger areas have more individuals; larger areas have more habitats.

In this study species richness (α -diversity) increased with the number of individuals sampled, the time interval of sampling, and the area sampled. However, the number of habitats did not give an explanation: The number of microhabitats was the same for each of the 15 samplings taken at the river's edge. It can be assumed that species richness increases because a substantial proportion of the beetles belong to transitory species that dwell at the water's edge, remain there for a certain time and then leave it again thereafter.

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Appendix

Tab. 1: Species assemblages collected on different dates at the water's edge of a brook at the base of Val Comora o di Golino. Maximum water levels are marked with M in bold. Lowest water levels at which the brook dried out are marked with d in italics. The numbers refer to the sum of individuals per species collected at eight sample areas of 1 m length and 0.20 m width.

Tab. 1: Käfer-Artengemeinschaften, die an verschiedenen Tagen im Uferbereich eines Baches unterhalb des Val Comora o di Golino eingesammelt wurden. Wasserhöchststände sind durch ein M (fett) markiert, Niedrigstände mit Trockenphasen des Baches sind durch d (kursiv) gekennzeichnet. Die Zahlen geben die Summe der Individuen an, die in acht Parallelproben von jeweils 1 m Länge und 0,20 m Breite eingesammelt wurden.

		М		d	М		d
	04.06.	11.06.	13.06.	17.06.	23.06.	24.06.	05.07.
Astop							
Carabidae							
Perilettus aerolatus			1	1			
Elaphropus sexstriatus			1				
Paratachys hisulcatus		1	1				
Bembidion lambros					1		
Bembidion veniculatum		3	1		1		2
Bembidion varicolor		1	1				20
Bembidion femoratum		-	1		1		
Bembidian decarum		1	-		-		
Bembidion testaceum		-		1			
Limodromus assimilis				-			1
Paranchus albithes							1
Lionychus auadrillum			1	12			
Dytiscidae			1				
Lybius fuliginosus						1	
Staphylinidae						-	
Euconnus wetterhali			1				
Paederus fuscites			1				
Scopaeus sulcicollis		2	1				
Philonthus mannerheimi		-	1			1	
Gvrohvtnus angustatus	1					-	
Tachyporus abdominalis				1			
Tachvusa constricta				-	1		
Ischnopoda balteata				1	-		
Ischnopoda umbratica				-	1		
Gnypeta carbonaria				1	-		
Hydrosmecta longula				-	1		
Hydrosmecta cf. fravilis		1			1	1	
Hydrosmecta spec.			1				
Aloconota debilicornis		23	34	6	15	10	
Aloconota cambrica		32	8	2	7	1	1
Aloconota sulcifrons		4	-	_		-	-
Amischa analis	1						
Atheta hyprotopora	-	2	1	1			
Drusilla canaliculata	1				1		
Ocalea concolor	1				-		
Bythinus reichenbachi		1					
Elateridae		-					
Zorochrus minimus	11	4	9	67	11	17	
Drvopidae							
Drvpos luridus					1		
Drvops nitidulus					1		
Cybocephalidae							
Cybocephalns festivus			1				
Nitidulidae							
Stelidota geminata					3		
Corylophidae							
Sericoderus lateralis			1				
Cuculionidae							
Dorytomns occalescens			1				

Tab. 2 : Species assemblage with an M in bold. The nu Tab. 2 : Käfer-Artengemei M. angegeben. Wasserhöch Länge und 0,20 m Breite e	s collected mbers ref nschaften, nststände ingesamm	d on diffe er to the , die an ve sind durc nelt wurd	rent dates sum of ir srschieder h ein M (en.	s at the ed ndividuals nen Tager [fett) marl	ge of the per spec i im Ufer siert. Die	river Me ies at eigl bereich d Zahlen g	lezza. Th ht sample ler Melez; geben die	e elevation areas of 2a eingesa Summe e	n of wate 1 m leng ummelt w der Indiv	er line is ir gth and 0. 7. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1.	ndicated. 20 m wid ie Höhe e die in ac	Maximur ith. des Wasse ht Paralle	n water le erspiegels Iproben v	vels are n ist in 198 von jewei	aarked 8 m. ü. ls 1 m
date	28.05	M 04.06.	05.06.	M 09.06.	11.06	14.06.	18.06.	20.06.	30.06.	M 02.07.	04.07.	05.07.	M 06.07.	13.07.	17.07
m.a.198m s.l.	2.02	3.45	2.46	3.68	2.46	2.16	1.99	1.95	1.86	2.02	1.90	1.88	2.32	1.95	1.92
Carabidae															
Clivina collaris	ı	ı	ı	ı	I	I	-	I	I	I	I	I	ı	I	I
Perileptus aerolatus	0	I	4	I	Ŋ	8	6	4	З	I	I	-	I	З	3
Paratachys micros	ı	ı	·	ı	ı	I	12	ı	1	ı	, - 1	I	ı		ı
Elaphropus sexstriatus	I	I	÷4	I	I	I	-	I	~ 1	I					
Bembidion punctulatum	I	I	I	I	ŝ	0	I	ı	ı	I	I	~ -	1	1	فسعا
Bembidion varicolor	·	ı	Ļ	ı	,	,	ı	•	ı	Ļ	I	I	ı	~~	I
Bembidion conforme	I	ı	·	2	ı	I	ı	1	r	I		~ - 1	ı		I
Bembidion ascendens	I	-	ı	ı	I	I	I	ı	I	-	0	I	I	I	I
Bembidion decorum	ı	2	ł	ı	1	I	I	0	0	I	I	0	ı	I	-
Bembidion tetracolum	I	I	I	I	I	I	I	1		I	1	0	I	I	I
Bembidion tibiale	\$	i	I		ſ	t	ſ	I	t	I	I	1	ı	ᢆᠵ᠆ᠬ	1
Paranchus albipes	ı	ī	ı	ı	ı	ı	ı	ı	ı	·	ı		ı	ı	ı
Chlaenius vestitus	I	I	I	I	I	I	1	I	I	I	I	I	I	I	I
Lionychus quadrillum	ſ	ţ	ŧ	ŧ	ı	t	t	t	t	I	-	L	ſ	ł	1
Haliplidae Haliplus lineatocollis	1	,	٠	۲	ſ		,	I	T	I	÷	I	I	I	I

Tab. 2: Fortsetzung. Tab. 2: Continued.		Σ		Σ						Σ				Z	×
date	28.05	04.06.	05.06.	09.06.	11.06	14.06.	18.06.	20.06.	30.06.	02.07.	04.(.7.	07. 05.07.)7. 05.07. 06.07 .	07. 05.07. 06.07 . 13.07
m.a.198m s.l.	2.02	3.45	2.46	3.68	2.46	2.16	1.99	1.95	1.86	2.02	1.90		1.88	1.88 2.32	1.88 2.32 1.95
Dytiscidae Bidescus															
minutissimus	12	I	6	1	4	48	23	56	16	I	26		6	- 6	9 - 5
Oreodytes															
septentrionis	4	0	5	14	ŝ	9	0	3	6	ŝ	7		13	13 -	13 - 1
Hydraenidae															
Hydraena testacea	ı	I	ı	ı	ı	1	ı		7	ı	4		2	2 -	2
Hydraena lapidicola	I	1	I	ı	ı	ı	ı	I	ı	ı	I		ı	1	, ,
Hydraena subimpressa	I	I	ı	ı	ı	ı	ı	ı	ı	ī	Ţ		ī	ı ı	
Ochthebius exsculptus	I		1	ı	I	I	0	7	0	ı	7		9	0	9
Ochthebius gibbosus	Ŋ	I	I	I	4	11	Ļ	16	I	I	4		0		2 - 1
Limnebius crinifer	I	I	I.	I	I	ı	1		-	I	I		ı.	ı ı	1
Hydrophilidae															
Anacaena lutescens	,	,	·	ı	ı	,	,	ı		I	I		ī	I	1
Anacaena lohsei	I	I	I	I	I	I	I	I	ı	I	ļ		T	I	1
Laccobius striatulus	0	I	0	I	3	4	16	Ŋ	10	4	9		0	2 -	2
Laccobius minutus	ı	ı	ı	ı	I	ı	I	I	З	I	I		ı	ı	1 1 1
Laccobius alternus	8	ł	15	~~	18	36	10	14	10	4	9		4	4	4
Laccobius obscuratus	1	1	ł	۲	8	ł	۲	ł		5	0		2		
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m.a.198m s.l.	2.02	3.45	2.46	3.68	2.46	2.16	1.99	1.95	1.86	2.02	1.90	1.88	2.32	1.95	1.92
Chaetarthria seminulum	~	I	~ `	I	I	I	5	0	\tilde{c}	4	7	~ `	I	I	I
Staphylinidae Bledius subterraneus	1	I	1	1	0	1	~ 1	I	2	ŝ	I	I	ı	÷	
Bledius opacus	,	ł	ı	ı	ł	·	ſ	1	1	6	Ţ	Ţ	, -	I	ı
Thinobius crinifer		I	ı	ı	I	3	I	ı	5	2	6	7	I	0	I
Carpelimus punctatellus	I	ī	ı	ī	ı	ī	I	T	1	ī	ı	ı	ī	ı	ı
Stenus comma	I	ı	1	I	ı	ì	ì	1	ı	ı	ı	ı	ī	1	
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Lathrobium elongatum	ι	I	ı	T	ı	I	-	1	ţ	I	I	t	I	I	I
Thinodromus arcuatus	₹1	I	I	1	T	I	I	I	I	I	I	I	I	I	ı
Thinodromus dilatatus	I	ı	I	1	ı	ı	ц			ı	ı	ı	ı	I	ī
Thinodromus hirticollis	ı	ı	ı	ı	ı	1	ì	3	3	ı	ı	1	1	ì	4
Platystethus capito	I	ı	ı	ī	ı	ι	ı	ι	Ļ	ī	ı	ı	t	ι	ı
Platystethus alutaceus	I	I	ı	ı	ı	I	I	I	1	ī	ı	ı	ī	I	ī
Pseudobium gridelli	1	1	3	ı	Ţ	-	ş	1	ſ	ı	ſ	ſ	I	ł	ł
Paederidus															
rubrothoracicus		10	4	16	10	2	0	8	4	0	9	0	4	3	Ļ
Scopaeus gracilis	I	I	Ţ	I	ı	ī		ī	I	I	I	1	I	I	ı

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	2.02	3.45	2.46	3.68	2.46	2.16	1.99	1.95	1.86	2.02	1.90	1.88	2.32	1.95	1.92
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Helodidae Hydrocyphon deflexicollis	ı	ı	ı	ı	ł	I	I	I	I	ı	4	4		I	I
Coccinellidae Thea vigintiduopunctata Propylaea quatuordecimpunctata	1 1	1 1	1 1) 1	y 1	y 1	1 1	1 1	Ţ Ţ	1 1	1 1) 1	1 1) I	1 1

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