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Habitat Use and Distribution of *Oligoneuriella rhenana* (Ephemeroptera: Oligoneuriidae) in the Neckar River Drainage, South-West Germany

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With 2 figures and 1 table

Summary

Between 1991 and 1998 we obtained data on the occurrence and density of larvae of the mayfly *Oligoneuriella rhenana* (Imhoff 1852) from 78 locations on the Neckar River and its tributaries in the southwestern part of the drainage basin (south-west Germany). *Oligoneuriella rhenana* was present at 35 sites, covering more than 200 continuous stream kilometres on the Nagold, Enz, and Neckar rivers. Densities ranged from 1–464 larvae/m² between sites and, largely independent of site location, density correlated positively with the extent of fast (>0.8 m/s) flowing riffle sections and the presence of large (>20 cm diameter) rocks with bottom surfaces at least partially exposed to the current. Both the occurrence and the density distribution of *O. rhenana* was consistent with the idea that the lower Nagold River represents a refugial habitat from which first the Enz River and then the Neckar River have been recolonized.

Keywords: *Oligoneuriella rhenana;* larvae; abundance; distribution; streams; habitat use; south-west Germany.

Zusammenfassung

Zwischen 1991 und 1998 wurden Daten zum Vorkommen und zu Larvendichten der Eintagsfliege *Oligoneuriella rhenana* (Imhoff 1852) von 78 Probenahmestellen am Neckar und seinen Nebenflüssen im südwestlichen Einzugsgebiet erhoben. *Oligoneuriella rhenana* konnte an 35 Stellen nachgewiesen werden, wobei unter anderem 200 zusammenhängende Flusskilometer an der Nagold, der Enz, und dem Neckar besiedelt sind. Larvaldichten an den jeweiligen Probenahmestellen betrugen zwischen 1–464 Individuen/m². Weitgehend unabhängig von der Lage des Untersuchungspunktes korrelierte die Bestandsdichte positiv mit dem Anteil schnell (>0,8 m/s) fließender ‚riffle'-Abschnitte und dem Vorhandensein größerer (>20 cm Durchmesser) Steine, deren Unterseiten wenigstens teilweise der freien Strömung ausgesetzt waren. Sowohl das Vorkommen als auch die larvale Dichteverbreitung von *O. rhenana* stimmen mit der Hypothese überein, daß die untere Nagold ein Refugialhabitat darstellt, von dem aus zunächst die Enz und dann auch der Neckar wiederbesiedelt wurden.

Contents

1. Introduction

Until the middle of this century, the mayfly *Oligoneuriella rhenana* inhabited most large central European rivers (for distribution map see JANSEN, in press). During the summer months, its fast growing larvae dominated the benthic biomass of the potamal and hyporithral river sections (e.g. RUSSEV & VIDINOVA 1994), and mass swarming of subimagos and imagos was frequently reported (IMHOFF 1852; STEINMANN 1919; SCHOENEMUND 1930). With the increase in pollution and the reduction in the morphological diversity of many streams, *O. rhenana* largely disappeared, and by the 1980s, this mayfly was considered extinct in most of its characteristic central European habitats (Rhine: CONRATH et alii 1977; CASPERS 1980a,b; TITTIZER et alii 1991; SCHÖLL et alii 1995; Mosel: MAUCH 1963; Elbe: SCHÖLL et alii 1997; northern Baden-Württemberg: BUCK 1978; area of the DDR: KLAUSNITZER et alii 1982). Only a few small, remnant populations were reported from the Werra (ALBRECHT, 1954), Kyll and Sauer (MAUCH 1963), Fulda (ZWICK 1969; MARTEN 1986), Argen (MALZACHER 1973), Alz and Isar (BURMEISTER 1985), Rot (GRIMM 1988), Naab (BURMEISTER 1989), and Singine (HEFTI & TOMKA 1991) rivers. Most of these findings were from hyporithral or epipotamal habitats upstream of known sources of pollution or from tributaries of the larger rivers. Thus, the recent distribution of *O. rhenana* and the timing of local extinctions in relation to structural and limnochemical alterations of larval habitats suggests that this species has survived in upstream refugia, but at the cost of relatively low population densities because of suboptimal habitat conditions. Water quality in many rivers has recently improved compared to worst-case conditions during the mid 1970s (LfU 1992), and there have been efforts to improve stream morphometry, particularly to enhance longitudinal connectivity. As a possible consequence of these improvements in habitat quality *O. rhenana* may be recolonizing its former (optimal) potamal habitats. In fact, *O. rhenana* has recently expanded its distribution in German rivers (JANSEN, in press) and this species has been reported from the Elbe River for the first time in over 100 years (SCHÖLL et alii 1997). To test the recolonization hypothesis, and to identify possible refugial habitat(s), we surveyed almost 80 locations in the Neckar River drainage for the occurrence and the abundance of larvae of *O. rhenana.* Furthermore, we measured several habitat descriptors at each sampling site to evaluate habitat use of *O. rhenana* on a small spatial scale.

2. Material and methods

Between the summers of 1991 and 1998 we sampled 51 sites in the Neckar River drainage, focusing on rivers with occurrences of larvae of *O. rhenana,* and locations that would provide insight into possible dispersal routes. Some sites were visited in more than one year. Since in all cases, except site 42 on the Würm River, the absence or presence scores, and the observed larval densities were identical between years within the categories set for this study, only the results from the first sample have been presented. To increase the chances of finding larvae, we preselected locations based on our knowledge of preferred larval habitats of *O. rhenana.* At most sites, we inspected between 20–40 rocks of ≥10 cm diameter individually for the presence and number of larvae (hand sampling), and took 3–4 kick-samples with a pond net (500-µm mesh). We also examined macrophytes for attached larvae of *O. rhenana.* Densities of larvae were calculated as the average/m² of rock surface area (length × width), except for a few sites where larval abundances were measured as total counts for a 30 minute sampling period. This method took into account that larvae were almost exclusively found on the underside of rocks, that only at a few sites with dense populations of *O. rhenana* did we find larvae on floating strands of *Ranunculus fluitans,* and that kick-sampling in small gravel substrate did not yield more than 5 % of the individuals found at any site. To evaluate abiotic habitat conditions at each site, we estimated the relative contribution of different fractions (sand, gravel, rocks 5–10 cm, 10–20 cm, >20 cm diameter) to the bottom substrate. We measured minimum and maximum river width, and took 10–25 measurements of water depth and water velocity (at half the measured depth) with a model MiniAir2 (Fa. Schiltknecht, Switzerland) current meter near rocks sampled for larvae. We also measured water temperature and electrical conductance with a model LF 92 meter (Fa. WTW, Weilheim). To at least partially overcome the difficulties of mid stream sampling in larger river, for the Neckar River, we obtained data from 28 sites taken in June 1995 during routine benthos sampling with a bottom dredge (0.5 m wide, 0.2 m high opening, 0.3 mm screen) pulled over a distance of approximately 20–50 m from aboard the research vessel 'Max Honsell' (H. Vobis, Landesanstalt für Umweltschutz, Baden-Württemberg, pers. comm.).

3. Distribution and larval densities of *Oligoneuriella rhenana*

Larvae of *O. rhenana* were obtained at 35 of the 79 sites sampled (Fig. 1, not all sites with zero catches shown). However, mean larval densities differed considerably between locations, ranging from less than 1 to 464 animals/m² (Table 1). There was a clear pattern in the occurrence of *O. rhenana* in the Neckar River drainage, which was further accentuated when larval densities were also considered. The most upstream location where larvae were found in the drainage system was at Hirsau on the Nagold River (site 22; Fig. 1, Table 1). Over the next approximately 18 river kilometres (including sites 23–25), of which more than half were impounded sections above weirs, densities in the Nagold River remained very low and no larvae were found at site 24. After two further weirs south of site 26, densities of *O. rhenana* increased rapidly to over 460 larvae/m² at site 27, the maximum level observed at any site. Larval densities in the Nagold River gradually decreased over the next 10 km until the confluence with the Enz River to 69 individuals/m² at site 30 within the city limits of Pforzheim. This decrease in density was associated with an increasing level of channelization and the absence of fast (>0.8 m/s) flowing riffle sections downstream of site 28.

Despite considerable sampling effort at a number of suitable sites (i.e. many rocks of 15–30 cm diameter; fast, turbulent current) in 1996, we were unable to find any larvae of *O. rhenana* at the most downstream 5 km of the Würm River (only site 42 shown in Fig. 1). However, larvae were found in the Würm River in 1998 at 11 sites within an approximately 13 km long section upstream of and including site 42 (Tab. 1). Within this river section, larval densities were highest at the central sites (35–39) and strongly decreased both upstream and downstream.

No larvae were found in the Enz River and its tributaries upstream of the confluence with the Nagold River (sites 1–4, 15, 16). Downstream of this location, larvae were found at all 10 sites (5–14) sampled in the Enz River, although densities dif-

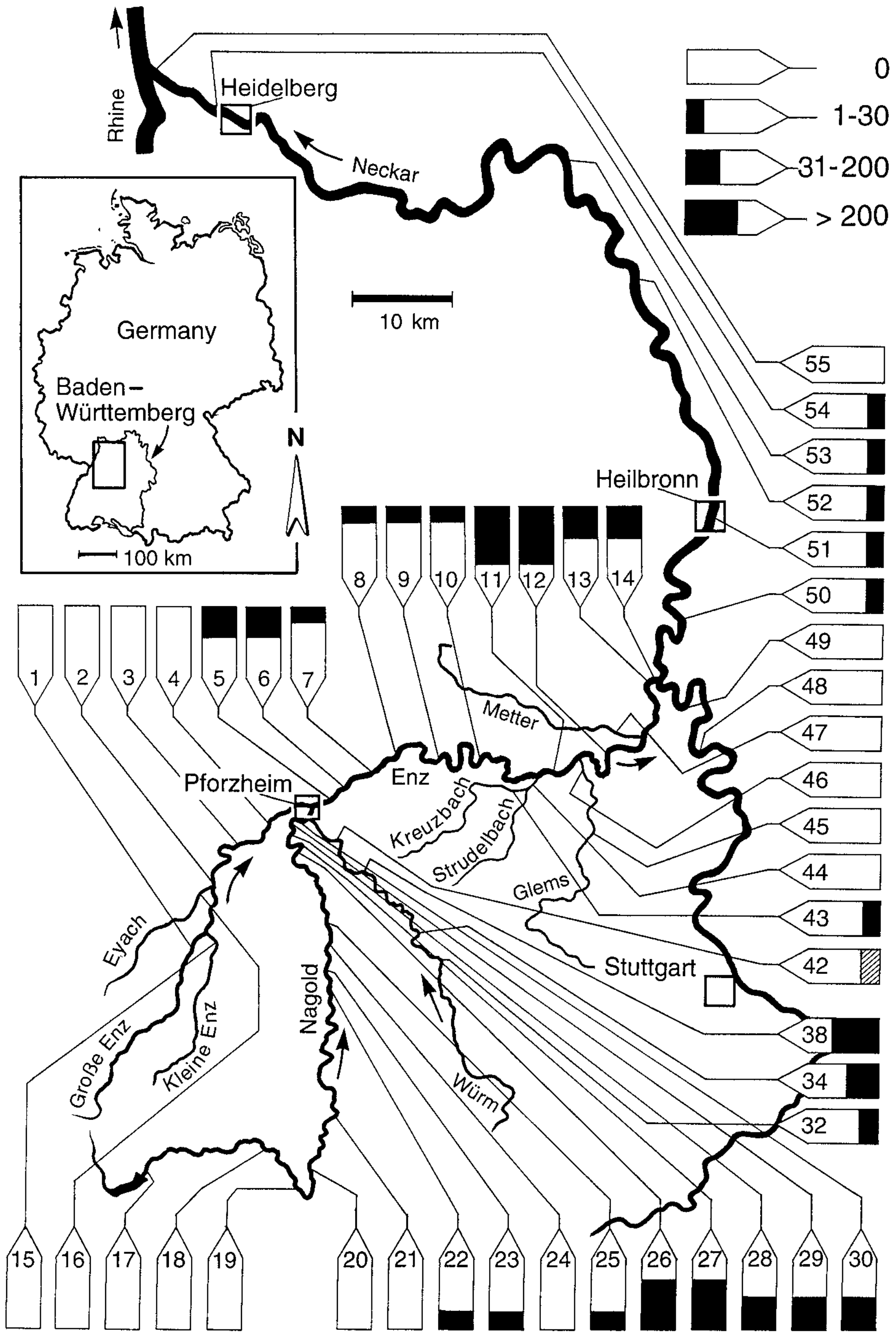

Fig.1 Densities (four groups) of larvae of *Oligoneuriella rhenana* in the south-west part of the Neckar River drainage. Some sampling sites with zero captures of *O. rhenana* are not shown. The striped pattern at site *42* indicates that larvae were found in 1998 but not in 1996 (see Tab. 1).

Tab. 1. Larval densities of *Oligoneuriella rhenana* and physical characteristics [water temperature *(Temp)*, conductivity *(Cond)*, river width *(Width)*, Water depth *(Depth)*, contribution of rocks larger 0.2 m diameter to the sediment *(Rocks)*, and current speed *(Current)*] at 55 sites in the Neckar River drainage. Under location, the nearest town is given: *E* = east of; *N* = north of; *NE* = north east of, *NW* = north west of, *W* = west of, *S* = south of, *SW* = south west of. Values for river width, water depth and current speed represent ranges observed at each site. Densities of *O. rhenana* are expressed as numbers of larvae for 1 m^2 of rock surface except for sites denoted by [a], for which the total number of larvae found within a 30 min sampling period is given. [b] representative for most other sites in the impounded section of the Neckar River and for which specific data are not available. [c] low flow channel near an hydroelectric power plant. "–" missing data.

River, location	**Site**	**Date**	**Density** (n/m^2)	**Temp** (°C)	**Cond** (µS/cm)	**Width** (m)	**Depth** (m)	**Rocks** (%)	**Current** (m/s)
Große Enz, N Bad									
Wildbach	1	Aug 04, 96	0	12.3	68	6–8	0.4–0.9	35	0,4–1.8
Enz, NE Höfen	2	Aug 04, 96	0	13.9	88	8–12	0.3–0.8	15	0.6–1.4
NO Neuenburg	3	Aug 04, 96	0	14.4	102	10–15	0.2–0.7	25	0.4–1.3
SW Brotzingen	4	Aug 04, 96	0	14,8	89	14–16	0.2–0.8	10	0.4–1.2
Pforzheim	5	Aug 06, 96	73	18.3	390	30–35	0.3–1.2	15	0.2–1.1
Eutingen	6	July 07, 95	184	17.1	398	25–28	0.2–1.1	20	0.2–1.2
Niefern	7	Aug 01, 91	5[a]	17.5	640	25–40	0.3–0.5	10	0.2–0.5
Enzberg	8	Aug 01, 91	3[a]	17.6	680	18–25	0.3–0.5	20	0.2–0.5
Lomersheim	9	Aug 06, 96	27	16.7	408	18–22	0.2–0.6	20	0.2–0.5
Roßwag	10	Aug 01, 91	5[a]	17.7	490	12–25	0.3–0.5	5	0.2–0.5
Oberriexingen	11	June 13, 95	314	16.4	508	12–14[c]	0.2–0.8	20	0.3–1.0
Untermberg	12	Aug 02, 96	348	–	–	10–20[c]	0.1–0.5	40	0.2–0.9
Besigheim	13	Aug 06, 96	79	16.9	650	35–40[c]	0.1–0.3	40	0.2–0.8
N Besigheim	14	Aug 06, 96	55	16.9	640	25–30	0.2–1.1	50	0.2–1.5
Eyach, NW Höfen	15	Aug 04, 96	0	12.7	49	4–6	0.2–0.4	15	0.2–1.1
Kleine Enz, S Calmbach	16	Aug 04, 96	0	12.1	81	4–7	0.2–0.7	20	0.3–1.2
Nagold, NE reservoir	17	Aug 16, 96	0	12.2	103	3	0.2–0.5	80	0.2–1.2
NW Ebenhausen	18	Aug 16, 96	0	12.8	162	8–10	0.1–0.5	30	0.1–1.5
W Nagold	19	Aug 16, 96	0	13.4	183	14–16	0.2–0.4	20	0.2–1.3
SW Emmingen	20	Aug 04, 96	0	13.5	210	12–14	0.2–0.8	15	0.2–1.2
S Wildberg	21	Aug 04, 96	0	13.9	265	5–7[c]	0.2–0.5	10	0.3–0.5
Hirsau	22	Aug 04, 96	1	15.9	392	10–12	0.4–1.1	5	0.4–1.2
Ernstmühl	23	Aug 04, 96	18	16.8	411	15–18	0.3–0.9	10	0.4–0.9
Bad Liebenzell	24	Aug 04, 96	0	16.4	423	16–20	0.4–1.3	5	0.3–1.0
S Monbachtal	25	Aug 04, 96	7	15.7	402	19–21	0.4–1.0	15	0.4–1.6
N Unterreichenbach	26	Aug 08, 96	375	16.5	408	20–23	0.2–0.6	10	0.3–1.1
S Dillweißenstein	27	Aug 04, 96	464	17.3	394	23–30	0.2–0.8	20	0.3–1.3
SW Dillweißenstein	28	Aug 08, 96	190	17.2	397	24–31	0.3–1.0	5	0.2–0.8
Dillweißenstein	29	Aug 08, 96	124	17.6	387	22–23	0.3–0.9	5	0.3–0.9
NE Dillweißenstein	30	Aug 08, 96	69	18.1	399	20–21	0.3–0.7	10	0.2–0.9
Würm, NW Merklingen	31	July 25, 98	0	16.5	788	6–7	0.2–0.3	10	0.3–0.6
N Hausen	32	July 25, 98	1	17.0	864	8–10	0.2–0.3	20	0.6–1.1
S Mühlhausen	33	July 25, 98	18	18.1	1092	7–10	0.2–0.4	20	0.5–0.9
Mühlhausen	34	July 25, 98	125	18.0	976	8–11	0.2–0.4	20	0.4–1.0
S Tiefenbronn	35	July 25, 98	148	17.9	956	8–12	0.2–0.5	15	0.3–0.9
N Steinegg	36	July 25, 98	309	18.0	941	7–9	0.1–0.4	20	0.5–0.9
NW Tiefenbronn	37	July 25, 98	135	18.7	1049	6–8	0.2–0.5	5	0.2–0.5
E Hohenwart	38	July 25, 98	320	17.8	1004	7–11	0.1–0.4	25	0.2–1.0
S Würm	39	July 25, 98	200	17.8	1001	8–9	0.2–0.4	15	0.3–0.8
S Würm	40	July 25. 98	31	18.2	1004	9–11	0.2–0.5	20	0.2–0.8
E Würm	41	July 25, 98	35	17.9	1023	8–10	0.2–0.5	5	0.3–0.7
Würm	42	Aug 06, 96	0	16.1	839	7–9	0.3–0.7	30	0.3–1.0
		July 25, 98	3	17.9	1024	7–9	0.3–0.7	30	0.2–1.0
Kreuzbach, Aurich	43	July 19, 93	4[a]	16.2	–	2–5	0.1–0.3	15	0.2–0.4
Strudelbach,									
Enz-Weihingen	44	July 19, 93	0	18.7	–	1–2	0.1–0.3	0	0.2–0.4
Glems, Schwieberdingen	45	May 23, 95	0	13.5	1086	7–9	0.2–0.8	5	0.2–0.9
Unterriexingen	46	May 22, 95	0	13.3	855	9–10	0.1–0.5	10	0.4–0.9
Metter, Bietigheim	47	Aug 06, 96	0	14.4	1152	5–7	0.1–0.4	15	0.2–0.4
Neckar, Freiberg	48	Aug 07, 96	0	–	–	6–15	0.1–0.3	20	0.1–0.4
Hessigheim	49	June 22, 95	0[a]	–	–	–	–	–	–
Lauffen	50	June 21, 95	5[a]	–	–	–	–	–	–
Horkheim	51	June 20, 95	1[a]	16.4	555	80	2.7	10	0.2
Neckarzimmern	52	June 13, 95	2[a]	–	–	–	–	–	–
Hirschhorn[b]	53	June 08, 95	1[a]	19.6	855	100	3.2	15	0.3
Wieblingen	54	June 07, 95	1[a]	–	–	–	–	–	–
Mannheim	55	June 07, 95	0[a]	–	–	–	–	–	–

fered considerably (Fig. 1). However, densities only approached those found in the Nagold River at sites 11 and 12 (Tab. 1). The sensity differences observed in the Enz River showed no obvious relationship to the presence and spatial sequence of the relatively few weirs and impounded sections, but seemed to be dependent on the structural and hydrodynamic conditions at each site. Again, sites with fast flowing, turbulent water and large rocks in the sediment (sites 6, 11, 12) yielded the highest larval densities (Table 1). Of the four tributaries of the lower Enz River (sites 32–36), we only found a few larvae of *O. rhenana* in a section of the 'Kreuzbach' (site 43) almost adjacent to the Enz River (Fig. 1).

In the Neckar River downstream of the confluence with the Enz River, five of the 17 sites sampled with the bottom dredge yielded between 1 and 5 larvae (sites 50–55). *Oligoneuriella rhenana* was not captured at the two most downstream sites on the Neckar River (only site 55 shown in Fig. 1) approximately 3 and 11 km upstream of the confluence with the Rhine River. No *O. rhenana* were also found at the 12 sites on the Neckar River upstream from where the Enz enters, and which were sampled by dredge (only site 49 shown in Fig. 1) or by hand collecting (site 48). The most upstream site sampled on the Neckar River was located at the southern edge of the city of Stuttgart.

Densities of *O. rhenana* were predictably associated with specific structural and hydrodynamic conditions, largely independent of site location within the drainage system. Densities were highest in fast flowing (>0.8 m/s), turbulent riffle sections. Larval densities were 5–20 % of those in adjacent riffles in stream sections with current speeds of <0.4 m/s, which at the Nagold and Enz rivers were commonly associated with either water depth of more than 0.5 m in unregulated runs or shallow shoreline habitats. One notable exception was site 12, where densities of >300 larvae/m² were found in a shallow (0.2–0.3 m), slow-flowing (0.2 m/s) area downstream of a weir. However, under more normal water levels, current at this site is quite turbulent (JANSEN, pers. observ.). Similar to all other locations, larvae at site 12 were mainly associated with larger (>20 cm-diameter) rocks, whose bottom surfaces were not completely embedded into a small grained sediment, and partially protruded into the water column. Almost all larvae were found on the undersides of such larger rocks at the low-density (<80 larvae/m²) sites, whereas at the high-density (>300 larvae/m²) sites 5–20 % of all larvae were also found on smaller rocks or in kick-samples from mineral substrates measuring 2–5 cm. No larvae were obtained from sandy sediments, filamentous algae, water mosses, and macrophytes other than *Ranunculus fluitans.*

Although there was no obvious relationship between larval densities and water temperature or conductivity, no larvae of *O. rhenana* were found at any site with a temperature below 15 °C and a conductivity below 390 µS/cm (Fig. 2). This pattern was particularly striking for the two sets of sites along the Nagold and Enz rivers (Tab. 1, Fig. 2).

4. Discussion

The habitat preferences of *O. rhenana* observed in our study and previously described in JANSEN et alii (1997) are consistent with findings from other hyporithral and epipotamal habitats. Larvae of *O. rhenana* predominantly occur on the under-

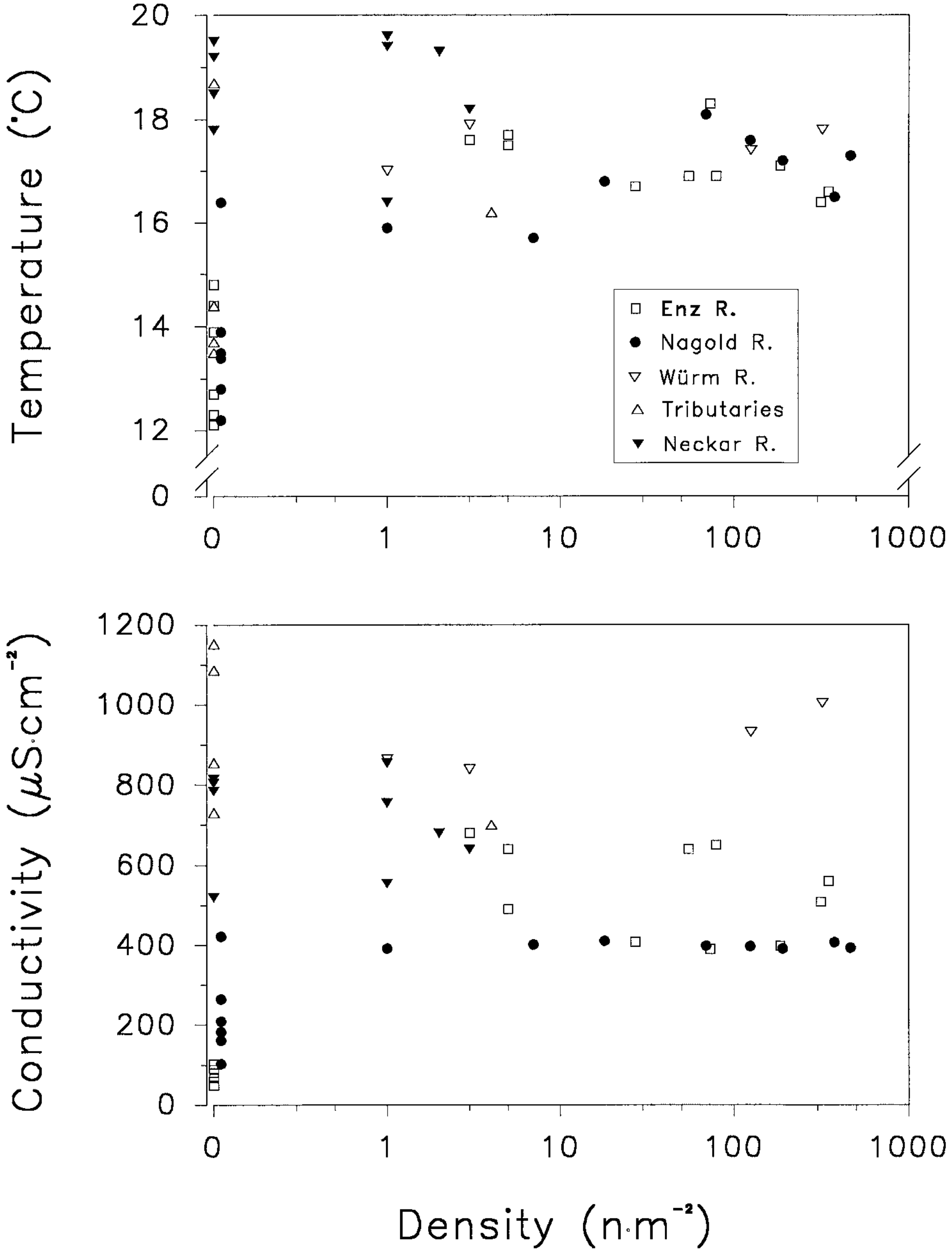

Fig. 2 Density (logarithmic scale) of larvae of *Oligoneuriella rhenana* in relation to water temperature *(above)* and conductivity *(below)* for 51 sites on the Enz, Nagold, Würm, and Neckar rivers and four tributaries of the lower Enz River. Densities of 0 for the Nagold River have been set at 0.1 to avoid complete overlap with other values.

side of loosely packed large rocks in fast flowing, well oxygenated river sections (STEINMMAN 1919; PINET 1962; BAUERNFEIND 1990; RUSSEV & VIDINOVA 1994; ELPERS & TOMKA 1995; WIESER 1996). Only very rarely has this species been found on macrophytes (*Ranunculus* spec., ALBRECHT 1954) or on drifting wood (RUSSEV & VIDINOVA 1994).

The complete absence of larvae in the two branches of the upper Enz River and the Eyach tributary suggest that, apart from sediment structure and current conditions, water temperature and water chemistry might also determine habitat suitability for *O. rhenana.* Daytime temperature fluctuations in the Enz and Nagold can be as high as 2.4 °C (JANSEN, unpubl. data). Therefore, the single measurements from this study, which on a given day were taken over a 10-hour period, are only an approximate indicator of summer water temperatures in these two rivers. Nevertheless, they correctly reflect that average temperatures in August in the upper Enz (sites 1–4, 15, 16) are at least 2.5 °C lower than in the Enz downstream of Pforzheim (LfU Baden-Württemberg, unpubl. data), and that maximal values rarely exceed 16 °C. Furthermore, conductivity in the lower Enz is at least three times higher than in the upper Enz. Although not as pronounced as in the Enz, the water chemistry and larval distributions of *O. rhenana* in the Nagold and Würm rivers also support the idea that, at least in the Neckar River drainage, *O. rhenana* requires water temperatures of approximately 17 °C and ion concentrations equivalent to a conductivity of 400 µS/cm or higher for complete larval development. This approximate temperature threshold has been confirmed by results from other biogeographical regions. Among some larger creeks in Kärnten (Austria), only those with temperatures close to 16 °C were inhabited by larvae of *O. rhenana,* whereas those with maxima of 14 °C and less were not (WIESER 1996).

The recent pattern of occurrence of *O. rhenana* in the southwestern part of the Neckar River drainage indicates that this mayfly is distributed almost continuously over more than 200 kilometres between site 22 on the Nagold River and site 54 on the Neckar River. Based on the mainly individual finds of larvae in the dredge samples, it is difficult to ascertain if the lack of larvae over the most downstream 11 km of the Neckar River is real or just a chance event. The absence of *O. rhenana* in the Neckar River very close to the Rhine River is however consistent with the fact that despite recent intense sampling efforts, the so-called 'Rheinmücke' (STEINMANN 1919) ist still missing from one of its classical former habitats (SCHÖLL et alii 1995; IKSR 1996).

Density estimates obtained from the Nagold and Enz rivers cannot be directly compared with those from the Neckar River because of the differences in sampling technique. Nevertheless, the mainly individual finds from the Neckar River suggest that densities of *O. rhenana* are very low, and that this species has just recently (re)established a population in this river. No published accounts of *O. rhenana* from the Neckar River exist, and this species was not found with the beginning of routine sampling for water quality assessment in the early 1950s (H. BUCK, Murr a. d. Murr, pers. comm.). However, the historic occurrence of this mayfly in the Neckar River (i.e. before the conversion of the river into a shipping canal and the dramatic increases in pollution) is almost certain (JANSEN, in press). It is surprising that this species has been found in the Neckar River at all, considering that the middle and lower Neckar River are characterized by an almost continuous sequence of impoundments, and that the resulting abiotic conditions, particularly the very slow water current, do not match the habitat requirements of *O. rhenana.* Similar impounded conditions may also explain the absence of *O. rhenana* from the most downstream 5 km of the Würm River. In addition, the water quality (measured as biodegradable organic load) of the Würm River, and particularly the downstream section, was among the worst of all sites sampled by hand (German Water Quality Class 2–3, LfU 1992). Although the high densities of larvae found at similarly polluted sites upstream on the Würm River (site 38) and on the Nagold River (sites 26 and 27) indicate that *O. rhenana* is probably more tolerant to organic pollution than is suggested by the low saprobic index of this species (e.g. MOOG et alii 1997), the levels in the lower Würm River may not have been tolerated by the larvae. It is also possible that the high organic load contributes indirectly to the absence or low abundance of *O. rhenana* by stimulating a massive growth of filamentous algae. Such growth (in which we never found larvae), was particularly obvious at site 42 and further downstream on the Würm River, where the algae completely covered most of the rocks in the sediment (JANSEN, pers. observ.).

Oligoneuriella rhenana is known from the Kocher River, which enters the Neckar River 8 km north of Heilbronn, and was not sampled by us. Larvae were abundant in epipotamal reaches of the Kocher in 1953, upstream of the first sewage treatment plants, but disappeared around 1957 (BUCK 1978 and pers. comm.). MALZACHER's (1985) state-wide survey of Ephemeroptera in Baden-Württemberg between 1985 and 1986 referred to these earlier reports of *O. rhenana* in the Kocher River, but he was unable to find them again (P. MALZACHER, Ludwigsburg, pers. comm.).

The high density of *O. rhenana* at site 27, which persists over an almost 5-km long section of the lower Nagold River (estimated population size of more than 11.5 million larvae, JANSEN et alii 1997) has probably persisted for a long time. More than 65 years ago LAUTERBORN (published in EIDEL 1933) found larvae of *O. rhenana* in the Nagold River close to the present site 30, from where BUCK (pers. comm.) and MALZACHER (1985) also collected larvae in the early 1970s and mid 1980s, respectively. Densities of *O. rhenana* in 1985 (approximately 100 larvae/m^2, MALZACHER 1985) were similar to the 70 animals/m^2 found in 1996 at site 30, which is 200 m further upstream. The data by MALZACHER (1985), who was unable to find *O. rhenana* at Unterreichenbach (2 km south of site 26), and thus in between the two impounded river sections separating the present sites 26 and 25, also confirm the dramatic upstream decrease in larval densities over this approximately 7 km long section of the Nagold River.

Oligoneuriella rhenana disappeared from the Enz River in the late 1970s (A. ALF, Ministry of the Environment, Baden-Württemberg, pers. comm.). The first recent larval find from August 1988 comes from a location close to our present site 14 (ALBRECHT, unpubl. data) which is located approximately 60 km downstream from the confluence with the Nagold River. Thus, several lines of evidence support the theory that the lower Nagold River, particularly between sites 26 and 27, represents a major refugial habitat from which the recolonization into the Neckar River started. This process presumably coincided with the first pronounced improvements to water quality of the Enz River in the late 1980s (LfU 1992). However, the existence of small remnant populations in the Enz River could have served as additional stepping stones and thus may have accelerated the downstream colonization of *O. rhenana.*

The status of *O. rhenana* in the Würm River is difficult to interpret. In contrast to the Nagold River, no historical data exist. Because of the documented negative impact of impoundments on the distribution of *O. rhenana* (also see JANSEN et alii, in press) it can be assumed, that before the construction of the three weirs on the lower Würm River this stream and the lower Nagold River formed the habitat for one continuous refugial population of this mayfly. Although female *O. rhenana* have been found to lay their eggs into water buckets almost 2.5 km away and approximately 89 m higher than the nearest location on the Würm River (JANSEN, in press), considering the steep and relatively high (150–200 m above valley bottom) mountains that separate the two rivers, it is likely that the present population of *O. rhenana* in the Würm River no longer interbreeds with that of the Nagold River, and represents a disjunct population.

In summary, the few larvae of *O. rhenana* found in the lower Neckar River in this study, the recent absence of *O. rhenana* from all major tributaries downstream of the confluence with the Enz River (U. BRAUKMANN, Landesanstalt für Umweltschutz, Baden-Württemberg, pers. comm.) and from the Neckar River upstream of this location (e.g. GRIMM 1989), the low abundance and isolated occurrence of *O. rhenana* in the Kocher River, and the density distribution of *O. rhenana* with the south-western part of the drainage system suggests that the recolonization of the Neckar River occurred and likely still proceeds via the Nagold and Enz Rivers.

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