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The importance of abiotic and biotic factors for the structure of odonate communities of ponds (Insecta: Odonata)*

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1. Introduction

Many ecological studies of odonates consist mainly of semi-quantitative species lists (e. g. RUDOLPH 1979). Precise studies on the diversity and population sizes of odonate communities which could allow for a quantitative assessment of the importance of certain abiotic and biotic factors for species composition and abundance are scarce (e. g. THOMES 1987).

Ponds can be regarded as habitat islands for freshwater insects in an ocean of inhospitable environment. The theory of island biogeography, as developed by MAC ARTHUR & WILSON (1967), can be transferred from real ocean islands to virtual islands of habitats (DIAMOND & MAY 1981). According to MADER (1981), area-size and degree of isolation, are the most important parameters of community composition in continental habitat islands such as ponds.

Many ponds, and consequently many dragonfly habitats, have been destroyed in the process of intensification of agricultural practices in Central Europe since the 1950s. Most of the remaining ponds do not have a buffer zone against agricultural activities. Therefore, applications of fertilizers cause high nutrient loads of ponds situated in fields. Although dragonflies have been recommended as indicators of the disturbance of freshwater habitats by eutrophication (e. g. SCHMIDT 1983), there is a lack of quantitative research on the effects of a high nutrient load on odonate communities of ponds.

According to TISCHLER (1984), the diversity of species of a habitat increases with its resource richness and heterogeneity. The species capacity of a habitat depends on its diversity of niches which in turn is influenced by the density of suitable structures per unit area (HEYDEMANN 1981). The validity of these fundamental statements has never been investigated quantitatively for odonate communities of ponds.

The habitat heterogeneity of a pond can be quantified by mapping its vegetation cover. Helophytes, hydrophytes, low pioneer plants and open water surface form a mosaic of structures which dragonflies require as resources for emergence and oviposition. The diversity of odonate communities should be high at ponds with a high diversity of structures which are vital resources for dragonflies. Moreover, a particular odonate species should be most abundant at ponds where its specific resources predominate.

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The importance of the ecofactors area-size, degree of isolation, chemical load (eutrophication) and habitat heterogeneity for the structure of odonate communities of ponds, is tested in this paper. It is, of course, impossible to quantify all ecofactors relevant to dragonflies within a single study. Therefore, those ecofactors were chosen which were most likely to affect odonate communities of ponds. An analysis of present nature conservation practices has shown that they are often based on unproven assumptions (BRÖRING & WIEGLEB 1990). Therefore, conclusions for conservation strategies for natural and man-made ponds form the final part of this paper.

2. Study sites and methods

2.1. Study sites

Field work was carried out between April 1986 and October 1987 at twelve ponds in Schleswig-Holstein in northern Germany (Table 1).

Table 1. Names, co-ordinates and sizes of the studied ponds.

No.	Name of Pond	Co-ordinates		Size
1.	Steffen, Landgraben-Muxall	10°15'00"E	54°20'49"N	133 m^2
2.	Kieckbusch, Muxall	10°16'05"E	54°21'05"N	315 m^2
3.	Wiesenteich Kasseteich	10°16'12"E	54°20'55"N	40400 m^2
4.	Hälter 2, Kasseteich	10°16'02"E	54°20'54"N	212 m^2
5.	Hagener Ziegelei	10°16'37"E	54°20'59"N	261 m^2
6.	Schulteich, Probsteierhagen	10°17'30"E	54°21'39"N	1222 m^2
7.	Bornbrook (northern part)	10°15'55"E	54°22'11"N	5460 m^2
8.	Krützfeldt 1, Schrevendorf	10°16'07"E	54°22'15"N	144 m^2
9.	Krützfeldt 2, Schrevendorf	10°16'08"E	54°22'21"N	212 m^2
10.	Steffen-Stamer 1, Röbsdorf	10°15'23"E	54°22'35"N	440 m^2
11.	Steffen-Stamer 2, Röbsdorf	10°15'19"E	54°22'42"N	148 m^2
12.	Lilienthal, Freienfelde	10°16'07"E	54°22'50"N	332 m^2

Ponds 3 and 7 are fish-ponds, pond 4 is a storage pond for carp from the neighbouring pond 3. The other nine ponds are situated in fields and/or pastures; some of them are quite new, man-made ponds, some are old marl-pits. Ponds of different size, age and vegetation cover were chosen to allow a comparison of odonate communities of ponds with differing characteristics.

2.2. Methods

An examination of the importance of certain ecofactors for odonate communities requires that suitable parameters for both, the odonate communities and the ecofactors, are found.

Parameters for the odonate communities of ponds:

Semi-quantitative odonatological habitat-inventarizations (SCHMIDT 1985), do not allow an assessment of ecofactors by regression analyses. Instead, the following quantitative method was developed.

For each of the twelve studied ponds, a sampling site with a size of 40 m^2 was chosen. For most ponds a sector of pond edge was selected, 10 m long and 4 m wide, half of it water, half of it bank, and with a composition of vegetation representative of the pond. For the larger pond 3 it was necessary to proceed in a different way because of the considerable differences in the vegetation cover of certain sections of this pond. Two quadrats from each of the following five dominant vegetation types, each 2 m square, were selected (nomenclature follows RUNGE 1980 and WILMANNS 1984): Schoenoplectetum lacustris, Typhetum angustifoliae, *Alisma plantago-aquatica*-community, Caricetum elatae and Equisetetum fluviatilis. Sampling sites were selected during preliminary studies in 1986, and all quantitative data were collected in 1987.

During the entire flight period of the dragonflies (May—October) all sampling sites were inspected at least once a pentad. All adult dragonflies were counted and observations of emergence and oviposition were recorded. Counts were conducted during the main hours of flight activities (10 a. m. until 4 p. m.) if possible under conditions with the highest concentration of odonates (DREYER 1984, SCHMIDT 1985). In addition to the counts of adult dragonflies, larvae and exuviae were collected to ascertain which dragonfly species were breeding in a pond.

The results of the counts of all pentads were summed up for each pond. If a sampling site had been inspected more than once a pentad, only the count with the highest number of individuals was used. The sums were used to calculate the relative abundance, p_i, of each dragonfly species for each pond and used to calculate Shannon diversity index, H_s, and evenness, E, for each dragonfly community (SOUTHWOOD 1978, MÜHLENBERG 1989). In addition, the Vajnstein index of species similarity, K_v, of the odonate communities of ponds 1—2 and 4—12, in comparison to the odonate community of pond 3, the largest pond, was calculated (TISCHLER 1984, MÜHLENBERG 1989).

Capture-recapture experiments were conducted to investigate population densities of several zygopteran species. In July and August 1987, a total of 4146 dragonflies was captured at ponds 9 (2760 individuals) and 11 (1386 individuals) and marked with a day code using a waterproof pen. Ponds 9 and 11 were used because they had sufficient numbers of odonates and their topography allowed capturing them. The capture-recapture data were analysed using the Petersen estimate and the Manly-Parr method (BEGON 1979).

Parameters for ecofactors of ponds:

Size of ponds: Maps at a scale of 1:200 were drawn of all ponds after the dimensions of the ponds in the 1:5000 topographical maps and in aerial photographs had been checked with a 30 m measuring tape. Area-size and circumference of the ponds were determined from the 1:200 maps with a digitizer.

Chemical load of ponds: Water samples of the ponds were taken in May and August 1987. The samples were taken at a depth of 40 cm, 1 m from the water's edge in areas where dragonfly larvae had been observed. The concentration of phosphate, nitrate, nitrite and ammonium was determined photometrically in the laboratory of Professor K. Böttger, limnological study group of the University of Kiel.

Habitat heterogeneity of ponds: The following four types of plant structures were distinguished:

- horizontal plant structures: hydrophytes with floating leaves such as *Potamogeton natans* and Lemnaceae
- vertical plant structures: helophytes (marsh or reed plants) such as *Schoenoplectus lacustris* and *Sparganium erectum*
- low pioneer plants on temporarily flooded mud areas such as *Ranunculus sceleratus* and *Ranunculus repens*

– willow bushes close to the water's edge, e. g. *Salix caprea* and *Salix cinerea*

The plant structures were mapped using the 1:200 maps of the ponds (see above), and area-size and circumference were determined with a digitizer. This could not be done for pond 3 because of its large size.

3. Odonate communities of the studied ponds

A total of 23 odonate species was observed at the twelve ponds studied. Their status at the ponds is given in Table 2. Fifteen species were found breeding in at least one study site. *Lestes sponsa* was the only species breeding in all ponds.

Table 2. Status of the odonate species of the studied ponds.

■ breeding species (larvae, exuviae and/or freshly emerged adult dragonflies observed)

○ possibly breeding species (copulation and/or oviposition observed)

\+ visitor (no reproductive activities observed)

– species not observed

Species	Number of Pond 1	2	3	4	5	6	7	8	9	10	11	12
Calopteryx splendens	–	–	–	–	–	–	–	–	+	–	–	–
Lestes viridis	–	–	+	+	–	–	–	–	+	+	–	–
Lestes sponsa	■	■	■	■	■	■	■	■	■	■	■	■
Lestes dryas	+	+	+	–	–	+	–	–	■	–	■	■
Pyrrhosoma nymphula	–	–	+	+	–	–	–	–	–	+	–	–
Ischnura elegans	■	+	■	■	■	■	+	■	■	■	■	■
Coenagrion puella	■	+	+	+	+	■	o	■	■	■	■	■
Coenagrion pulchellum	o	■	■	o	■	■	+	+	■	■	■	■
Coenagrion lunulatum	–	–	–	–	–	–	–	–	–	–	–	+
Enallagma cyathigerum	–	–	–	–	+	–	–	–	–	–	–	–
Erythromma najas	–	–	■	o	+	–	–	–	–	–	–	–
Brachytron pratense	–	–	■	o	–	–	–	–	–	–	–	–
Aeshna cyanea	–	+	+	+	–	■	+	+	■	o	■	–
Aeshna grandis	–	–	+	o	–	o	+	o	■	o	■	■
Aeshna mixta	–	+	■	+	+	–	+	+	■	o	+	+
Anaciaeschna isosceles	–	–	+	–	–	–	–	–	–	–	–	–
Somatochlora metallica	+	–	+	+	–	–	–	–	–	–	–	–
Libellula depressa	–	–	–	–	–	–	–	■	■	–	+	–
Libellula quadrimaculata	–	–	■	o	–	–	–	–	–	–	–	–
Orthetrum cancellatum	–	–	+	–	–	–	+	–	–	–	–	–
Sympetrum sanguineum	o	+	■	o	–	–	o	+	■	+	■	■
Sympetrum flaveolum	–	+	■	–	–	–	–	+	■	o	+	–
Sympetrum vulgatum	o	+	■	o	–	–	–	+	■	–	–	■
S (number of species)	8	10	19	15	7	7	9	11	14	11	11	10

Relative abundance of all species, Shannon diversity indices and evenness-values are given in Table 3. The diversity indices and evenness-values of ponds 1–6 and 8–12 are fairly similar (H_s 1.4–1.8; E 0.6–0.8). Both parameters are distinctly lower for pond 7 (H_s = 0.860; E = 0.391). Only *L. sponsa* was found breeding at pond 7 and the p_i-value of *L. sponsa* at this pond is the highest of all recorded relative abundances.

The highest number of dragonfly species and the highest Shannon diversity index of all ponds was found for pond 3, by far the largest study site. For a comparison of the odonate community of this pond with the communities of the other ponds, Vajnstein indices of species similarity are given in Table 3. The similarity is highest between pond 3 and the neighbouring pond 4 (50.7 %). The second largest similarity value is between ponds 3 and 5 (35.5 %), all other values are lower (c. 20–30 %).

Table 3. Parameters of the odonate communities of the studied ponds.
Relative abundance (p_i) or the odonate species observed at the ponds; Shannon diversity index (H_s) and evenness (E) of the odonate communities of the ponds; Vajnstein index of species similarity (K_y) of the odonate communities of ponds 1–2 and 4–12 in comparison to the odonate community of pond 3.
* = species observed in 1986 only. N = total numbers of individuals counted in 1987.

	Number of Pond											
Species	1	2	3	4	5	6	7	8	9	10	11	12
Calopteryx splendens	–	–	–	–	–	–	–	–	0.001	–	–	–
Lestes viridis	–	–	0.002	0.004	–	–	–	–	0.001	0.006	–	–
Lestes sponsa	0.460	0.487	0.319	0.508	0.264	0.377	0.773	0.363	0.511	0.272	0.307	0.347
Lestes dryas	0.020	0.025	0.002	–	–	0.016	–	–	0.065	–	0.025	0.042
Pyrrhosoma nymphula	–	–	*	*	–	–	–	–	–	0.006	–	–
Ischnura elegans	0.140	0.034	0.109	0.198	0.352	0.123	0.023	0.073	0.094	0.278	0.094	0.023
Coenagrion puella	0.160	0.067	0.005	0.012	0.154	0.352	0.133	0.435	0.160	0.283	0.433	0.292
Coenagrion pulchellum	0.050	0.210	0.353	0.073	0.187	0.098	0.008	0.024	0.046	0.078	0.072	0.218
Coenagrion lunulatum	–	–	–	–	–	–	–	–	–	–	–	0.005
Enallagma cyathigerum	–	–	–	–	0.011	–	–	–	–	–	–	–
Erythromma najas	–	–	0.008	*	0.011	–	–	–	–	–	–	–
Brachytron pratense	–	–	0.026	0.008	–	–	–	–	–	–	–	–
Aeshna cyanea	–	0.017	0.003	0.004	–	0.025	0.008	0.008	0.022	0.017	0.006	–
Aeshna grandis	–	–	0.005	0.016	–	0.008	0.008	0.040	0.022	0.017	0.031	0.023
Aeshna mixta	–	0.008	0.037	0.024	0.022	–	0.016	0.008	0.010	0.022	0.003	0.005
Anaciaeschna isosceles	–	–	0.003	–	–	–	–	–	–	–	–	–
Somatochlora metallica	*	–	0.002	0.004	–	–	–	–	–	–	–	–
Libellula depressa	–	–	–	–	–	–	–	0.016	0.009	–	0.003	–
Libellula quadrimaculata	–	–	0.034	0.016	–	–	–	–	–	–	–	–
Orthetrum cancellatum	–	–	*	–	–	–	0.008	–	–	–	–	–
Sympetrum sanguineum	0.090	0.076	0.040	0.073	–	–	0.023	0.016	0.028	0.011	0.022	0.032
Sympetrum flaveolum	–	0.017	0.018	–	–	–	–	0.008	0.009	0.011	0.003	–
Sympetrum vulgatum	0.080	0.059	0.037	0.060	–	–	–	0.008	0.022	–	–	0.014
N	100	119	626	248	91	122	128	124	689	180	319	216
H_s (diversity index)	1.572	1.606	1.781	1.596	1.504	1.419	0.860	1.429	1.675	1.645	1.511	1.584
E (evenness)	0.808	0.697	0.629	0.622	0.773	0.729	0.391	0.596	0.635	0.686	0.630	0.688
K_v (species similarity) [%]	23.7	35.5	–	50.7	17.8	19.9	19.1	23.4	31.1	30.0	25.8	28.0

4. Effects of abiotic and biotic factors on the odonate fauna

4.1. Effects of pond size on the number of odonate species

Studies comparing the number of species, S, on islands (oceanic and habitat islands) of different area, A, led to the development of the empirical equations $S = c \cdot A^z$ and $S = a + b \cdot \log A$ (MAC ARTHUR & WILSON 1967, DIAMOND & MAY 1981). Proportionality constant c depends on taxon, biogeographic region and population density, parameter z changes little among taxa, most values of z cluster in the range 0.20–0.35 (MAC ARTHUR & WILSON 1967).

Species-area relationships for the odonate communities studied were examined using both equations. Total numbers of species are given in Table 2, pond sizes in Tables 1 and 4. Both calculated correlation coefficients, r, do not deviate significantly from r = 0 ($r = 0.33$ for $S = c \cdot A^z$; $r = 0.42$ for $S = a + b \cdot \log A$; $P > 0.05$ in both cases).

The species-area relations of the ponds studied did not conform to that predicted by the equations. While the largest pond, No. 3, had the highest number of dragonfly species, the second largest pond, No. 7, had only a small number of species. Consequently, other factors must be responsible for the different numbers of dragonfly species of the ponds.

4.2. Effects of isolation on the composition of odonate species

According to MADER (1981), the degree of isolation is the second important parameter for community composition in continental habitat islands. The empirical rule from the theory of island biogeography is a decrease of the number of species, S, with increasing distance from the colonization source, D (DIAMOND & MAY 1981).

In the present study, pond 3, the largest pond with the highest number of dragonfly species and the highest diversity index, was considered as possible colonization source for the smaller ponds, most of which were situated in fields and/or pastures.

To examine the influence of an increasing distance from pond 3 on the composition of odonate species, a linear regression analysis was carried out. An increasing distance, D, from pond 3 (given in Table 4) had no significant effect on species similarity, K_v. The negative correlation coefficient of $r = -0.34$ ($P > 0.05$) was only a result of the high species similarity between the neighbouring ponds 3 and 4.

Table 4. Ecofactor-parameters of the studied ponds.
Size of pond; distance of ponds 1–2 and 4–12 to pond 3; chemical load (at sampling dates in May and August 1987); supply of plant structures (oviposition sites). – Due to limited laboratory facilities only samples of eleven ponds could be analysed. Pond 4 was omitted because of its close distance to pond 3.

	Number of pond											
Parameter	1	2	3	4	5	6	7	8	9	10	11	12
A (size of pond) [m²]	133	315	40400	212	261	1222	5460	144	212	440	148	332
D (distance to pond 3) [km]	1.10	0.12	-	0.01	0.38	1.79	2.15	2.26	2.44	3.01	3.21	3.35
Date of first sampling	4.5.	4.5.	4.5.	-	4.5.	11.5.	11.5.	11.5.	11.5.	11.5.	11.5.	4.5.
total P [µg/l]	227	270	87	-	140	79	320	740	130	760	159	69
PO_4-P (inorg.) [µg/l]	40	55	13	-	20	25	164	47	0	219	0	22
NO_3-N [mg/l]	0.4	0.0	0.6	-	0.0	1.6	0.55	0.5	0.75	0.5	7.5	16.0
NO_2-N [µg/l]	0	0	0	-	0	69	73	5	9	9	500	98
NH_4-N [µg/l]	185	25	20	-	40	310	110	70	50	2	3800	145
Date of second sampling	17.8.	17.8.	17.8.	-	17.8.	17.8.	17.8.	10.8.	10.8.	10.8.	10.8.	10.8.
total P [µg/l]	370	340	75	-	310	79	600	450	76	750	560	510
PO_4-P (inorg.) [µg/l]	224	207	20	-	18	0	410	290	26	650	154	380
NO_3-N [mg/l]	0.6	0.3	0.2	-	0.5	7.4	0.5	0.7	0.5	0.3	0.3	0.2
NO_2-N [µg/l]	0	0	0	-	7	150	38	0	0	0	0	0
NH_4-N [µg/l]	0	355	0	-	395	630	320	0	0	110	185	235
Circumference of plant structures [m]	120.6	209.0	-	168.1	170.2	276.1	691.4	140.8	241.9	200.9	145.7	207.4
Circumference of structures / Size of pond [m/m²]	0.90	0.66	-	0.79	0.65	0.23	0.13	0.98	1.14	0.46	0.98	0.62
Ratio of the areas of horizontal and vertical structures	0.096	0.436	-	0.790	1.001	4.295	0.553	0.659	0.247	4.339	5.760	3.796
Ratio of the circumferences of horizontal and vertical structures	0.283	0.483	-	0.549	1.259	1.017	0.492	0.934	0.215	0.636	0.573	0.563
Mean of area-ratio and circumference-ratio	0.189	0.460	-	0.670	1.130	2.656	0.522	0.796	0.231	2.487	3.167	2.179

4.3. Effects of chemical load on the diversity of odonate species

Odonates have been recommended as indicators of the disturbance of freshwater habitats by eutrophication (SCHMIDT 1983). However, the precise tolerance limits of water-chemical parameters in dragonfly larvae are poorly known (RUDOLPH 1979).

For that reason, a direct assessment of the concentrations of phosphate, nitrate, nitrite and ammonium in the water samples, as given in Table 4, would have been of little use. Instead, an index of the chemical load of a pond was calculated. For all measured water-chemical parameters, the ponds were ranked in order of concentration of parameters. The ranked positions of each pond for all parameters were added and taken as an index of the chemical load of that pond.

A Spearman's rank correlation with these indices and the Shannon diversity indices reveals a highly significant negative effect of the chemical load of a pond on the diversity of odonates ($r_s = -0.78$, $P < 0.005$). The higher the chemical load of a pond, the less diverse is its odonate community.

4.4. Effects of habitat heterogeneity on the diversity of odonate species

Odonates require certain habitat structures for emergence and oviposition. Most species select a vertical plant stem as emergence site (GERKEN 1984). Differences between species are much more pronounced when oviposition sites are considered (SCHMIDT 1965, 1975b). For that reason, oviposition sites are more suitable for quantification and assessment of habitat heterogeneity.

Three distinct modes of oviposition can be recognized (DREYER 1986, MILLER 1987, ASKEW 1988). In half of the 80 Central European odonate species (zygopteran and most aeshnid species), the females lay eggs into living or dead plant tissue (endophytic oviposition). Females of other anisopteran species place their eggs on the surface of plants (epiphytic oviposition), oviposit into mud or scatter eggs into the water (exophytic oviposition).

A close relationship between a dragonfly species and a certain plant species, as described for *Aeshna viridis* and its preference for *Stratiotes aloides* as oviposition site (MÜNCHBERG 1956, SCHMIDT 1975a), is obviously exceptional. Most dragonfly species deposit their eggs into several plant species (SCHMIDT 1983, DREYER 1986, ASKEW 1988).

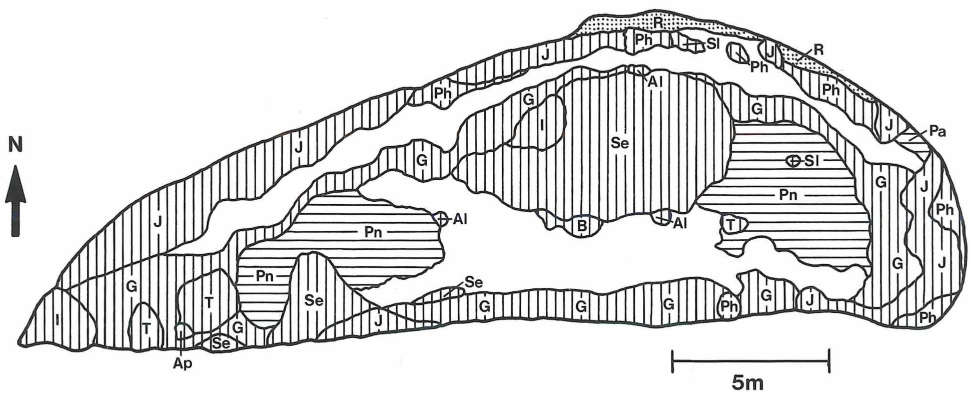

Figure 1. Vegetation map of pond 9.
This pond had a diverse mosaic of helophytes and hydrophytes with vertical plant structures as the predominating type of oviposition site resource for odonates. The odonate community of this pond had the highest diversity of all ponds where the diversity of plant structures could be quantified. The dominant odonate species was *Lestes sponsa*.

blank – open water surface
horizontal lines – horizontal plant structures
vertical lines – vertical plant structures
dots – low pioneer plants on temporarily flooded mud areas

Al	*Alisma lanceolatum*	Ph	*Phalaris arundinacea*
Ap	*Alisma plantago-aquatica*	Pn	*Potamogeton natans* (with *Lemna minor* and *Hottonia palustris*)
B	*Butomus umbellatus*	R	*Ranunculus repens*
G	*Glyceria fluitans*	Se	*Sparganium erectum*
I	*Iris pseudacorus*	Sl	*Schoenoplectus lacustris*
J	*Juncus effusus* (with *Juncus articulatus*)	T	*Typha latifolia*
Pa	*Polygonum amphibium*		

Among helophytes and hydrophytes, guilds of species with a similar plant architecture (e. g. floating leaves, reeds) can be distinguished. Some odonatologists have suggested that plant architecture and physical structure of the plant rather than the species of plant are important for dragonflies as a cue for habitat selection (PAULSON 1983, SCHMIDT 1983).

Lestes sponsa and *Lestes dryas* oviposit in vertical plant structures, *Coenagrion puella* and *Coenagrion pulchellum* in horizontal plant structures. The species of *Aeshna* and *Brachytron pratense* oviposit in half-decomposed rushes and sedges as well as damp mosses at the foot of willow bushes close to the water's edge. The species of *Libellula* and *Sympetrum* scatter eggs into the water or on temporarily flooded areas with low pioneer plants (accounts from DREYER 1986, BELLMANN 1987, ASKEW 1988).

The types of plant structures which were mapped to quantify the habitat heterogeneity of the ponds were chosen after the oviposition site preferences mentioned above: horizontal plant structures, vertical plant structures, low pioneer plants on temporarily flooded mud areas and willow bushes close to the water's edge. The results of the mapping are given in Table 4, two examples for the maps of vegetation/plant structures are given in Fig. 1–2.

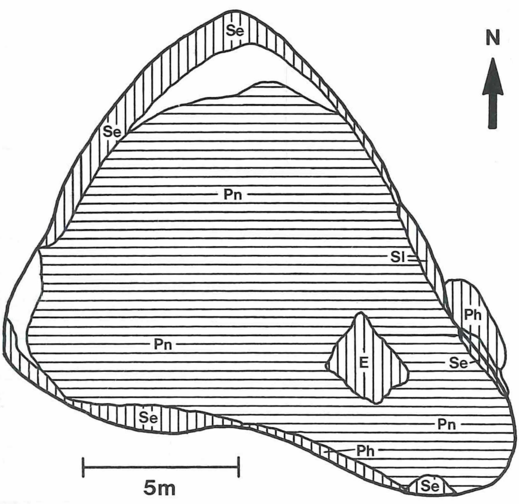

Figure 2. Vegetation map of pond 11.
This pond had a simple mosaic of helophytes and hydrophytes with horizontal plant structures as the predominating type of oviposition site resource for odonates. The odonate community of this pond was less diverse than the community of pond 9. The dominant odonate species was *Coenagrion puella*.
blank – open water surface
horizontal lines – horizontal plant structures
vertical lines – vertical plant structures

E	*Equisetum fluviatile*
Ph	*Phalaris arundinacea*
Pn	*Potamogeton natans* (with *Spirodela polyrhiza* and *Lemna mino*)
Se	*Sparganium erectum* (with *Glyceria fluitans*)
Sl	*Schoenoplectus lacustris*

The quotient of the circumference of all mapped plant structures and the size of a pond was taken as an index of the habitat heterogeneity of that pond.

A linear regression analysis with these indices and the Shannon diversity indices reveals a significant positive effect of the habitat heterogeneity of a pond on the diversity of odonates ($y = 1.19 + 0.43\,x$, $r = 0.61$, $r^2 = 0.38$, $P < 0.05$). The more heterogeneous the mosaic of plant structures which odonates require as resources for oviposition (and emergence) the more diverse is the odonate community of a pond.

The highest habitat heterogeneity was found for pond 9. The diversity index of the odonate community of this pond is the highest of the eleven ponds where the habitat heterogeneity could be quantified. Only pond 3 has a higher diversity index. Because of its large size, the supply of oviposition resources of this pond could not be quantified and is difficult to compare with the supply of the smaller ponds.

A regression analysis with the habitat heterogeneity indices and the evenness-values does not reveal a significant relation ($r = 0.27$, $P > 0.05$).

4.5. Effects of oviposition site abundance on the population density of odonate species

The vertical oviposition sites of *Lestes sponsa* and *L. dryas* and the horizontal oviposition sites of *Coenagrion puella* and *C. pulchellum* could be mapped and quantified most accurately. For that reason, and considering the abundance of these four species (the sum of their relative abundances at the twelve studied ponds ranged between 0.59 and 0.91, see Table 3) the impact of the supply of their oviposition sites on the abundance of the *Lestes* and *Coenagrion* species was analysed more detailed.

For each pond a quotient of the relative abundance, p_i, of the two common species of *Lestes* and of *Coenagrion* was formed and termed *C./L.*-ratio:

$$C./L.\text{-ratio} = \frac{{}^{p}C.\ puella + {}^{p}C.\ pulchellum}{{}^{p}L.\ sponsa + {}^{p}L.\ dryas}$$

To examine the effects of the abundance of horizontal and vertical structures on the population of the odonate species which require these structures as resources for oviposition, Spearman's rank correlation coefficients were calculated for three ratios of the plant structures:

(a) x = ratio of the areas of horizontal and vertical structures, y = *C./L.*-ratio
$r_s = 0.74$, $P < 0.01$
(b) x = ratio of the circumferences of horizontal and vertical structures, y = *C./L.*-ratio
$r_s = 0.59$, $P < 0.03$
(c) x = mean of area- and circumference-ratio, y = *C./L.*-ratio
$r_s = 0.75$, $P < 0.005$

Thus, the abundance of certain plant structures has a significant effect on the population densities of those odonate species which require these structures as resources for oviposition.

Horizontal plant structures are usually situated in the centre of a pond and due to their circular form they have a comparatively small circumference for a quite large area. Compared with this, vertical plant structures, situated close to the water's edge, have a comparatively large circumference for a quite small area. Therefore, the means of area- and circumference-ratio, correlation (c), might be the best way for an assessment of the oviposition site resources. These means revealed the most significant correlation ($r_s = 0.75$, $P < 0.005$).

As further support, the results of the capture-recapture experiments at ponds 9 and 11 were examined. The two ponds had a very different vegetation cover (Fig. 1–2). Pond 9 had a diverse mosaic of helophytes and hydrophytes with vertical plant structures as the predominating type of oviposition site resource. Pond 11 had a less diverse vegetation cover with predominating horizontal structures.

The capture-recapture data allowed only a calculation of the abundances of male *Coenagrion puella* and male *Lestes sponsa*. Means of the abundance of males of both species were calculated for their main flight periods (early July and mid August, resp.). A connection of the abundance of the two species at the two ponds with the supply of plant structures for oviposition was tested with a 2×2 chi-square contingency analysis, for both the results of the Petersen estimate and the Manly-Parr method (Table 5). This analysis shows that a particular odonate species is most abundant at ponds where its specific resources for oviposition predominate ($P < 0.001$ for both methods).

Table 5. 2×2 chi-square contingency analysis for the connection of the abundance of male *Lestes sponsa* and male *Coenagrion puella* with the supply of plant structures for oviposition (from capture-recapture data of ponds 9 and 11).

(a) results of the Petersen estimate:

	pond 9: vertical structures predominate	pond 11: horizontal structures predominate
mean male abundance of *L. sponsa*:	760	78
mean male abundance of *C. puella*:	222	819

$chi^2 = 895.4$, df = 1, $P < 0.001$

(b) results of the Manly-Parr method:

	pond 9: vertical structures predominate	pond 11: horizontal structures predominate
mean male abundance of *L. sponsa*:	631	67
mean male abundance of *C. puella*:	181	696

$chi^2 = 757.4$, df = 1, $P < 0.001$

5. Discussion

Odonate communities of the studied ponds

The observed 23 species of Odonata, 15 of which were found breeding in at least one study site, are a representative spectrum of odonate species of ponds in North-Central Europe (FISCHER 1984). *Lestes sponsa* was the only species breeding in all ponds. This species is known to survive even in intensively used fish-ponds which are drained regularly (BELLMANN 1987).

Only three species could have been expected to be more common and breeding in one of the studied ponds: *Lestes viridis, Pyrrhosoma nymphula* and *Enallagma cyathigerum.* According to DREYER (1978, 1984), *Lestes viridis* requires some high trees close to ponds as mating sites in addition to the availability of suitable oviposition sites. This requisite was missing at all study sites. The rarity of the other two species mentioned cannot be explained.

Most dragonfly species at ponds are considered as eurytopic (WILDERMUTH & SCHIESS 1983). Only two of the species which were found breeding in one of the ponds are considered as endangered, and are included in the German Red Data Book: *Lestes dryas* and *Brachytron pratense* (CLAUSNITZER et al. 1984). Of these two species, *Brachytron pratense* was only found breeding in the large pond 3. Thus, *Lestes dryas* was the only stenotopic species found breeding in the smaller ponds.

Influence of pond size and degree of isolation

Neither an effect of the pond size on the number of odonate species nor an effect of the degree of isolation on the composition of odonate species could be proved.

The difficulty in documenting a species-area relation for a taxon at/in ponds was also shown by KONOLD & WOLF (1987) who studied the effect of pond size on the number of helophytes and hydrophytes. Despite their comparatively large sample size of 62 ponds they only found a correlation coefficient of $r = 0.64$ with $P < 0.1$.

DIDION & HANDKE (1989) recorded the odonate fauna of 130 ponds and did not find a significantly higher number of species at larger ponds. They suppose that any possible positive effect of an increase in pond size on the number of dragonfly species may be lost due to the intensity of the utilization of large ponds. Thus, the influence of pond size may be confounded by other factors such as differences in vegetation cover which were one of the criteria of study site choice.

Although the distance from possible colonization sources must have some influence on the composition of odonates of isolated ponds, obtaining empirical proof is difficult. This is particularly so when all dragonfly species are considered jointly without regard for the differences in vagility and territoriality among species (cf., e. g., BANKS & THOMPSON 1985a, b, KAISER 1985, POETHKE 1988).

Influence of chemical load of the ponds

The chemical load of the studied ponds (concentrations of phosphate, nitrate, nitrite and ammonium) had a highly significant negative effect on the diversity of odonates ($r_s = -0.78$, $P < 0.005$). This result is difficult to interpret as many eurytopic odonate species seem to be quite tolerant of different water qualities and limits of their tolerance are not known precisely (RUDOLPH 1979, WELLINGHORST & MEYER 1982).

According to ASKEW (1988), *Lestes dryas,* the only stenotopic species found breeding in the smaller ponds, is declining in parts of northern Europe where heavy applications of fertilizers are causing eutrophication of standing water on arable land.

Phytosociological studies suggest that physico-chemical parameters have a strong influence on the plant succession of ponds (MIERWALD 1988). Thus, a high chemical load could have an indirect effect on the odonates of a pond by promoting certain habitat structures exclusively (e. g. "one species type of vegetation", see MIERWALD 1988), simplifying the mosaic of plant structures and thereby causing a less diverse odonate community. A further negative effect of a high chemical load might be a reduction of the food resources for dragonfly larvae.

Influence of habitat heterogeneity

The heterogeneity of plant structures had a significant effect on the diversity of the odonate community of a pond ($r = 0.61$, $P < 0.05$). The ratio of the abundance of *Coenagrion* and *Lestes* species was highly significantly correlated with the supply of their oviposition sites, i. e. horizontal and vertical plant structures ($r_s = 0.75$, $P < 0.005$).

Habitat heterogeneity, quantified as the diversity of plant structures, is, therefore, most essential to the understanding of the odonate community structures of ponds.

Ponds with a diverse odonate community accomodate several anisopteran species (Table 3). Anisopterans usually occur in lower abundances than zygopterans. Therefore, the evenness-values, which measure the uniformity of the abundance of species, are low for ponds with a diverse odonate community. For that reason, evenness-values were not positively correlated with habitat heterogeneity.

A connection between the composition of plant structures and the odonate community of a habitat has likewise been proposed for other types of habitat. THOMES (1987) showed that the abundance of several odonate species at a lowland stream was correlated with the area covered by emersed or submersed vegetation and by the extent of shade caused by alder trees. For true rheophile species the substrate required by the larvae was of further importance (THOMES 1987). DREYER (1988) argues that the low number of tyrphobiont dragonflies is due to a lack of three-dimensional plant structures in *Sphagnum*-bogs.

Some oviposition sites are difficult to quantify, e. g. half-decomposed rushes required by species of *Aeshna*. A higher level of significance may have resulted for the correlation analysis referring to the whole odonate community if it had been feasible to quantify all types of oviposition sites with equal precision.

Dragonflies do not only require plant structures as oviposition sites. Plant structures also serve as sites for emergence, mating and perching. Nonetheless, it is only when oviposition sites are considered, that pronounced differences between species are evident (VAN NOORDWIJK 1978, MILLER 1987, LENZ 1988).

On the other hand, the use of plant structures for the understanding of the habitat selection of odonates should not promote the idea of dragonfly associations similar to the plant associations of the phytosociological classification system. Such a system of dragonfly associations (coenoses), proposed by JACOB (1969), contains many inconsistencies (SCHMIDT 1982). Instead, SCHMIDT (1982) suggests an autecological approach.

Congeneric species with similar oviposition site requirements should show mechanisms to avoid interspecific competition. However, it has been difficult to document such mechanisms, particularly with closely related sibling species, such as *Lestes sponsa* and *L. dryas* or *Coenagrion puella* and *C. pulchellum* (VAN NOORDWIJK 1978, SCHMIDT 1983). There is a lack of research on the mechanisms permitting the coexistence of ecologically similar odonate species. The majority of more recent papers deal with the genus *Sympetrum* (e. g. MICHIELS & DHONDT 1987, REHFELDT & HADRYS 1988, WATANABE & TAGUCHI 1988, KÖNIG 1990), so more research on other taxa might be rewarding.

Conclusions for conservation strategies for ponds

As already mentioned, only two endangered species were found breeding in one of the studied ponds, and only one of these, *Lestes dryas*, was found breeding in the smaller ponds. Certainly, the protection of the main habitats (e. g. clean streams, bogs) of the most endangered dragonfly species is of more immediate importance for the conservation of a diverse odonate fauna than the protection of ponds (WILDERMUTH & SCHIESS 1983, CLAUSNITZER et al. 1984).

But the number of ponds has been declining dramatically in Central Europe. If this process is continuing, eurytopic dragonfly species of today will be rare and endangered in future. Hence, it is necessary to develop conservation strategies for the fauna of ponds.

According to MADER (1983), continental habitat islands show high amplitudes of environmental parameters and a low stability of resources. At small ponds, the mosaic of plant structures changes quickly and usually the predictability of their succession is limited (MIERWALD 1988).

The odonate community of a pond changes with the supply of plant structures. Pioneer species which prefer open water are followed by early colonizers which prefer combinations of open water and plant structures, and these are followed by late colonizers which prefer dense reed or large areas of floating leaves. A high habitat heterogeneity and a diverse odonate community is only a temporary stage in the succession of a pond.

For this reason, a great number of ponds of different stages of succession is essential for the long-term survival of dragonflies and other animals and plants of ponds. WILDERMUTH SCHIESS (1983) have suggested the conservation of a diversity of succession stages by regenerating early stages in a rotation model.

The study presented in this paper has shown that a particular odonate species attains its highest abundance at ponds where its specific resources for oviposition predominate. Ponds with these high abundance populations can serve as colonization sources and are of special importance for the survival of the concerned species. This should be taken into consideration before regeneration measures are carried out.

6. Abstract

The influence of several abiotic and biotic factors on odonate communities was studied at twelve ponds in Schleswig-Holstein, northern Germany. Neither an influence of the pond size nor of the degree of isolation (distance to a possible colonization source) could be found. A highly significant negative correlation was found between the chemical load (eutrophication) of a pond and the diversity (Shannon index) of its odonate community ($r_s = -0.78$, $P < 0.005$). Habitat heterogeneity, quantified by mapping several types of plant structures which odonates require as resources for oviposition, was positively correlated with the diversity of odonates ($r = 0.61$, $P < 0.05$). The horizontal oviposition sites (e. g. floating leaves) of *Coenagrion puella* and *C. pulchellum* and the vertical oviposition sites (e. g. reed plants) of *Lestes sponsa* and *L. dryas* could be mapped and quantified most accurately. The population density of these species was highly significantly correlated with the supply of their resources for oviposition ($r_s = 0.75$, $P < 0.005$). The importance of habitat heterogeneity to the understanding of odonate community structures of ponds and conclusions for conservation strategies for ponds are discussed.

7. Zusammenfassung

Der Einfluß mehrerer abiotischer und biotischer Faktoren auf die Zusammensetzung der Libellenfauna wurde an zwölf Teichen in Schleswig-Holstein untersucht. Weder ein Einfluß der Teichgröße noch des Isolationsgrades (Entfernung zu einem möglichen Besiedlungsursprung) konnte nachgewiesen werden. Ein deutlich signifikanter negativer Zusammenhang wurde zwischen der Wasserbelastung (Eutrophierung) eines Teiches und der Diversität (Shannon-Index) seiner Libellenfauna nachgewiesen ($r_s = -0{,}78$; $P < 0{,}005$). Die Strukturvielfalt eines Teiches, quantifiziert durch Vermessung von Pflanzenstrukturen, die

Libellen als Eiablage-Ressourcen benötigen, ist positiv mit der Libellendiversität verknüpft ($r = 0{,}61$; $P < 0{,}05$). Die horizontalen Eiablagestrukturen (z. B. Schwimmblattvegetation) von *Coenagrion puella* und *C. pulchellum* und die vertikalen Eiablagestrukturen (z. B. Röhricht) von *Lestes sponsa* und *L. dryas* konnten am genauesten vermessen werden. Die Populationsdichte dieser Arten korrelierte deutlich signifikant mit dem Angebot an ihren Eiablage-Ressourcen ($r_s = 0{,}75$; $P < 0{,}005$). Die Bedeutung der Strukturvielfalt für das Verständnis der Zusammensetzung von Libellen-Gemeinschaften an Teichen sowie Folgerungen für die Naturschutzpraxis an Kleingewässern werden diskutiert.

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