

Odonate assemblages of running waters in the Upper Guinean forest

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With 2 figures and 3 tables

Abstract: In order to describe the assemblages of adult Odonata of running waters in the Upper Guinean forest, 36 sites in Liberia and Ghana were analysed using Non-metric Multidimensional Scaling. Five groups were identified, which correspond with different assemblages in the sequence of habitats from small streams to large rivers. Taxonomically related species demonstrate distinct ecological segregation within this gradient, occupying different sections of running waters, or different microhabitats therein. The balance of sun and shade, resulting from a varying degree of habitat openness, is thought to be an important factor in habitat selection, but it is difficult to distinguish from other factors associated with stream size. Anthropogenic opening of stream habitat (e.g. by deforestation or damming) can downscale the present fauna, i.e. result in the invasion of species of downstream habitats (more open) and the disappearance of upstream (dense forest) species.

Key words: Odonata, West Africa, Upper Guinea, Ghana, Liberia, forest, running waters, assemblages, habitats, indicators.

Introduction

Odonata (dragonflies and damselflies) are among the most promising insects to serve as an indicator group, for instance of species richness or habitat health (BROWN 1991, SUTTON & COLLINS 1991). Their amphibious habits make them useful indicators above and below the water surface: The larvae are critical in regard to aquatic habitat morphology, such as bottom substrate and water clarity, while adult habitat selection is strongly dependent on structural characteristics, like shading and vegetation structure (BUCHWALD 1992, CORBET 1999, KINVIG & SAMWAYS 2000, SCHRIDDE & SUHLING 1994, STEYTLER & SAMWAYS 1995). Because of their sensitivity to physical habitat quality, odonates

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show strong responses to habitat change, such as deforestation and increased erosion (e.g. CLARK & SAMWAYS 1996, RITH-NAJARIAN 1998, SAHLÉN 1999, SAMWAYS & STEYTLER 1996, STEWART & SAMWAYS 1998), and they are therefore suitable to evaluate landscape degradation (CARLE 1979, MOORE 1984, SAHLÉN & EKESTUBBE 2001, SCHMIDT 1985, WATSON et al. 1982). Human disturbance of watersheds, with the consequent loss of soil and water-sources, is a problem world-wide, especially in the tropics. In order to use Odonata as monitors of degradation, conservation and restoration of watersheds, baseline knowledge of assemblages and habitat preferences of species is required (CORBET 1993). Describing odonate occurrence in running waters of successive size seems an obvious first step. In the tropics, this has been addressed in Côte d'Ivoire (LEGRAND & COUTURIER 1985), Liberia (LEMPERT 1988), Malaysia (BISHOP 1973, FURTADO 1969), Nepal (MAHATO & EDDS 1993), South Africa (CLARK & SAMWAYS 1996), Sri Lanka (STARMÜHLNER 1984) and Surinam (WASSCHER 1993).

Numerous interrelated variables determine the characteristics of the habitats from source to mouth (VANNOTE et al. 1980), also in tropical running waters (e.g. BISHOP 1973, DUDGEON 1992). Shadiness, coarseness of detritus and grain size of the bottom substrate become greater towards the source. Water-course size, temperature, frequency of still-water sections and riverside pools, as well as concentrations of silt, nutrients and pollutants, increase towards the mouth. The highest occurrence of aquatic and riparian macrophytes, as well as rapids, is in the middle reaches of the courses. Odonate species select specifically for distinct manifestations of such factors, and therefore a strong turnover of odonate species and assemblages is expected as one goes downstream. Similar changes may also be expected as human disturbance increases. Deforestation and damming, for instance, will result in a more open character of running water sites. Associated changes may be a decrease of flow velocity and permanence of water, and an increase of silt load. This may result in a habitat shift and the accompanying change of the odonate assemblage. A dammed forest stream, for instance, could result in a sunny, slow-flowing stretch of water with species typical of a small river. A river that has been cleared of forest, resulting in increased erosion and an irregular discharge of water, may lead to a fauna of temporary pools.

Because adult Odonata select for specific habitat characteristics, we expect that they can be used to describe the assemblages that occur in running water habitats of various sizes and degrees of human disturbance. This paper aims to provide such a description for running waters in the Upper Guinean forest, based on studies by LEGRAND & COUTURIER (1985) and LEMPERT (1988), augmented with data from Ghana (DIJKSTRA & OLSVIK, unpubl.). Furthermore, we attempt to give a preliminary assessment of the ecological backgrounds and the regional potential of Odonata as environmental sentinels.

Methods

Odonata were recorded at 22 Ghanaian and 14 Liberian sites. Most records are based on collected adults, augmented with a few sight records and finds of larvae or exuviae. Each site concerned a fairly uniform section of a running water. All sites were in lowland forest, ranging from dry semi-deciduous to wet evergreen forest and from primary to severely degraded vegetation. This encompasses a broad spectrum of habitats from gallery forest in the relatively dry hills of Ghana's Volta Region to the rainforests of Western Ghana and Eastern Liberia. Details per site are provided in Table 1.

Species were scored per site in a presence-absence matrix. Species were given value 0 (absent), 1 (present but considered stray, e.g. single records of species normally occurring at high densities, or showing no reproductive behaviour) or 2 (present and believed to reproduce there, e.g. based on behaviour and abundance). The matrix was analysed with Non-metric Multidimensional Scaling (NMS), using PC-ORD (McCune & Mefford 1999). NMS is an ordination method that is suitable for heterogeneous data, e.g. on arbitrary or discontinuous scales. The analysis is based on ranked distances and is therefore well-suited for data-sets with numerous zero values, like presence-absence matrices (Beals 1984, Clarke 1993). Only the 66 species found at three or more sites were included.

NMS axes, along which both sites and species can be plotted (Fig. 1), were interpreted using site characteristics, the preliminary site classification of Lempert (1988) and species information of Legrand & Couturier (1985). Accordingly, five groups of sites were recognised (Fig. 1, Tables 1, 2). For each group indicator values for species were calculated with the method of Dufrene & Legendre (1997) (Table 3). This method combines the concentration of records of a species in a particular group (the percentage of all occurrences of the species that is confined to sites in the group) with their abundance there (the percentage of sites in the group where the species occurs): 100 represents the maximal indicative value, i.e. the species is restricted to that group and found at all sites therein. The significance of the highest indicator value was established with a Monte Carlo test (1000 runs).

Results

NMS resulted in three axes (79.1% of variation explained, the first axis accounting for 52.4%, the second for 13.9% and the third for 12.8%). The first axis (the horizontal axis in Fig. 1) was correlated strongest with mean breadth of watercourse, openness and human disturbance (correlation coefficients -0.514 , -0.837 and -0.433 , respectively). The second axis (the vertical axis in Fig. 1) was correlated strongest with country (0.525). The third axis was not correlated strongly with any site characteristic. The five groups identified are described below, details per species are given in Table 3. Fig. 2 shows the relation between the assemblage occurring at a site and the breadth of the watercourse and degree of human disturbance there. Sites with strong disturbance had narrower watercourses than sites with no or slight disturbance that had similar odonate assemblages.

Table 1. Basic data for 36 study sites. Abbreviations and definitions – stream breadth: estimate in metres, openness: degree of sun and shade (closed sites are shaded, save some sunspots, open sites always have at least one bank in the sun, patchy sites are intermediate), human disturbance: degree of anthropogenic alteration (sites classified as having no disturbance may have human presence, but vegetation and streambed are intact, strongly disturbed sites have either vegetation or streambed severely altered, or both, slightly disturbed sites are intermediate), L 1988: preliminary site classification of LEMPert (1988) (US: upper, MS: middle and LS: lower course of streams, SR: small and LR: large rivers), source: origin of records and source of further details (D: DIJKSTRA & OLsvik, unpubl., L: LEMPert 1988 and O: O'NEILL & PAULSON 2001), days: number of days in the course of which the site was sampled, odonate assemblage: group to which site belongs (see Tables 2 and 3).

name	country	stream breadth	open- ness	human disturbance	L 1988	source	days	odonate assemblage
Afegame 1	Ghana	2–4	patchy	none		D	2	large streams
Afegame 2	Ghana	3–5	open	slight		D	1	large streams
Amedzofe 1	Ghana	0–1	closed	slight		D	1	interm. streams
Amedzofe 2	Ghana	0–1	closed	slight		D	2	interm. streams
Ankasa 1	Ghana	3–7	patchy	none		D	5	small rivers
Ankasa 2	Ghana	3–7	open	slight		D	5	small rivers
Ankasa 3	Ghana	2	closed	none		D	5	large streams
Ankasa 4	Ghana	0–1	closed	none		D	5	interm. streams
Ankasa 5	Ghana	2–5	patchy	slight		D	2	small rivers
Ankasa 6	Ghana	3–5	closed	none		D	2	large streams
Ankasa 7	Ghana	0–1	closed	none		D	2	interm. streams
Antwikwaa 1	Ghana	2–4	patchy	none		D	1	large streams
Antwikwaa 2	Ghana	1–2	open	strong		D	1	small rivers
Asiakwa 1	Ghana	0.5	closed	slight		D	1	small streams
Asiakwa 2	Ghana	2–4	patchy	slight		D	1	large streams
Brimsu	Ghana	5	open	strong		D	1	large rivers
Bunso	Ghana	8–10	open	slight		D	1	small rivers
Kakum 1	Ghana	0.5–1	closed	none		O	1	small streams
Kakum 2	Ghana	1	closed	none		O	1	interm. streams
Kintampo	Ghana	3–5	patchy	none		D	1	large streams
Liati Wote	Ghana	2	closed	none		D	1	large streams
Odome	Ghana	1–2	open	strong		D	1	large streams
Bentley's Goldmine	Liberia	0–1.5	closed	none	US	L	3	small streams
Cavalla 1	Liberia	2–4	closed	none	MS	L	2	interm. streams
Cavalla 2	Liberia	2–5	closed	none	LS	L	3	interm. streams
Cavalla 3	Liberia	70	open	none	LR	L	7	large rivers
Dugbi River	Liberia	3–4	open	strong		L	4	large rivers
Gwen	Liberia	3–5	open	strong		L	1	small rivers
Jalay Town 1	Liberia	0.8–2.5	closed	slight	US	L	25	small streams
Jalay Town 2	Liberia	3–6	patchy	slight		L	7	large streams
Juarzon	Liberia	1–3	patchy	strong		L	5	large streams
Mofe Creek	Liberia	8–15	patchy	slight	SR	L	5	small rivers
Ni Dwe	Liberia	8–15	patchy	slight	SR	L	10	small rivers
Sinoe River	Liberia	60	open	none	LR	L	18	large rivers
Zwedru 1	Liberia	0.7–2.5	closed	none	MS	L	23	small streams
Zwedru 2	Liberia	1.2–4	closed	none	LS	L	21	interm. streams

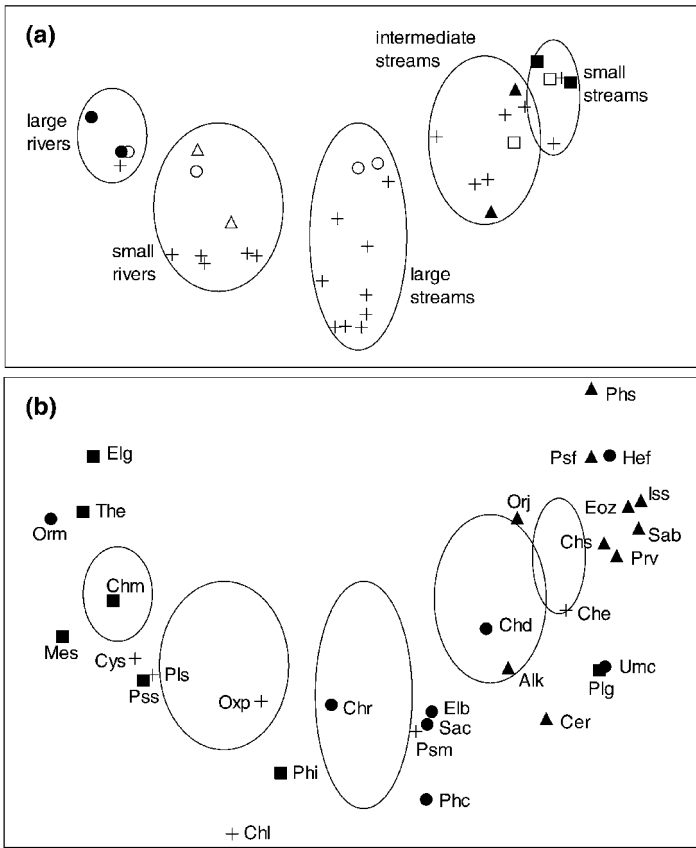


Fig. 1. Scatter plot of the sites (a) and a selection of species (b) along the same two NMS axes. The horizontal axis accounts for 52.4% of variation, the vertical for 13.9%. Site groups are indicated in (a), their contours are superimposed in (b). Symbols in (a) represent sites in Ghana (crosses) and in Liberia (other symbols) according to the preliminary site classification of LEMPERT (1988): upper (filled squares), middle (open squares) and lower course of streams (filled triangles), small (open triangles) and large rivers (filled circles) and additional sites (open circles). Symbols in (b) represent species discussed by LEGRAND & COUTURIER (1985) as inhabiting upper (triangles), middle (circles) or lower reaches (squares) of running waters (see Table 3) and additional species found at a minimum of ten sites (crosses). Abbreviations – Alk: *Allorhizucha klingi*, Cer: *Ceriagrion rubellocerinum*, Chd: *Chlorocypha dispar*, Che: *Chlorocnemis elongata*, Chl: *Chlorocypha luminosa*, Chm: *Chlorocypha pyriformosa*, Chr: *Chlorocypha radix*, Chs: *Chlorocypha selysi*, Cys: *Cyanothemis simpsoni*, Elb: *Elatoneura balli*, Elg: *Elatoneura girardi*, Eoz: *Eothenis zygoptera*, Hef: *Heliaeschna fuliginosa*, Iss: *Isomecocyphus subnodalis*, Mes: *Mesocnemis singularis*, Orj: *Orthetrum julia*, Orm: *Orthetrum microstigma*, Oxp: *Oxythemis phoenicosceles*, Phc: *Phaon camerunensis*, Phi: *Phaon iridipennis*, Phs: *Phyllomacromia sophia*, Plg: *Platycnemis guttifer*, Pls: *Platycnemis sikassoensis*, Prv: *Prodasineura villiersi*, Pst: *Pseudagrion flavipes*, Psm: *Pseudagrion melanicterum*, Pss: *Pseudagrion sjoestedti*, Sab: *Sapho bicolor*, Sac: *Sapho ciliata*, The: *Thermochoria equivocata* and Umc: *Umma cincta*.

Table 2. Basic data for the five site groups.

	streams			rivers		total
	small	intermed.	large	small	large	
number of sites Ghana	2	5	9	5	1	22
number of sites Liberia	3	3	2	3	3	14
total number of species	44	44	62	47	49	115
mean number of species	20.6	12.9	13.6	14.8	22.5	15.7
per site (and range)	(11–34)	(5–26)	(7–23)	(4–25)	(7–37)	(4–37)

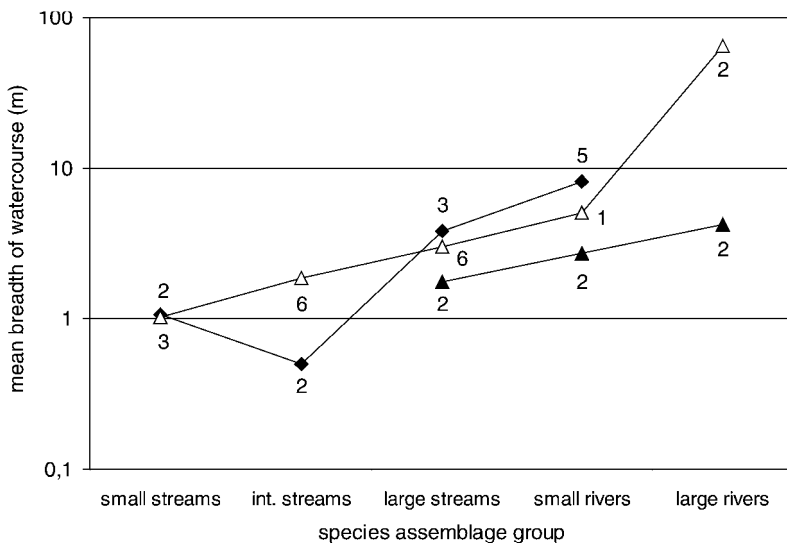


Fig. 2. The relationship between watercourse breadth at a site (on a logarithmic scale), the group to which the species assemblage there belongs and the degree of human disturbance: Sites have no (open triangle), slight (filled diamond) or strong (filled triangle) disturbance. Each point represents the average breadth of waters with a certain combination of assemblage and disturbance (sample size indicated for each point).

Small streams

Tiny forest runnels in dense vegetation. Sun only reached the water in a few sunspots. The streams were rarely wider than 2 metres, shallow and heavily loaded with detritus. The most characteristic species were *Sapho bicolor*, *Chlorocypha selysi*, *Pseudagrion flavipes*, *Chlorocnemis elongata*, *Chlorocnemis flavipennis*, *Isomecoccnemis subnodalis*, *Prodasineura villiersi*, *Heliaeschna fuliginosa*, *Eothemis zygoptera*, *Notiothemis robertsi* and *Porpax bipunctus*. Other species were *Diastomma gamblesi*, *Phyllomacromia sophia*, *Allorrhizucha klingi*, *Orthetrum julia* and *Trithemis africana*.

Intermediate streams

Very similar to the former group, but the streams were generally broader, with sandy banks and the vegetation was more open, although sun was still limited. Many small stream species were still present here (e.g. *Chlorocypha selysi*, *Prodasineura villiersi*, *Allorrhizucha klingi* and *Orthetrum julia*), while large stream species also became frequent (e.g. *Sapho ciliata*, *Chlorocypha radix*, *Pseudagrion melanicterum* and *Elatoneura balli*). *Umma cincta* and *Chlorocypha dispar* occurred maximally in this group.

Large streams

The streams in this group were still more open and broader, with many sunny patches. This also included streams in hilly terrain with many rocks and boulders. The species of small and intermediate streams had largely dropped out here (except *Allorrhizucha klingi* and *Chlorocypha dispar*) and the fauna was dominated by species like *Sapho ciliata*, *Chlorocypha luminosa*, *Chlorocypha radix*, *Elatoneura balli* and *Pseudagrion melanicterum*. Species of torrents and riffles (*Zygonyx chrysobaphes* and *Zygonyx natalensis*) peaked here and a few species more typical of rivers appeared (e.g. *Eleuthemis* sp.).

Small rivers

Because of their size, rivers were much more open than streams. There were extensive sunny tracts with branches overhanging the water. Locally aquatic and marshy riparian vegetation developed. The most characteristic species of these assemblages were *Cyanothemis simpsoni* and *Oxythemis phoenicosceles*. Other typical species were *Chlorocypha radix*, *Gomphidia gamblesi*, *Pseudagrion glaucoideum*, *Allorrhizucha campioni*, *Eleuthemis* sp. and *Sympetrum navasi*. Typical large river species that became frequent here were *Pseudagrion sjoestedti* and *Platycnemis sikassoensis*.

Large rivers

The rivers where these assemblages occur were still more open. The riverbed was wide and flat, allowing the persistence of pools after high water periods. Typical river species were *Chlorocypha pyriformosa*, *Pseudagrion camerunense*, *Pseudagrion sjoestedti*, *Pseudagrion sublacteum*, *Mesocnemis singularis*, *Platycnemis sikassoensis*, *Elatoneura girardi*, *Eleuthemis buettikoferi*, *Olpogastra lugubris*, *Trithemis aconita* and *Trithemis grouti*. Most distinctive for these habitats were not only the river species, but also those of stagnant, often temporary, waters. Examples were *Bradinopyga strachani*, *Palpopleura lucia*, *Pantala flavescens*, *Tholymis tillarga* and *Trithemis arteriosa*.

Table 3. Indicator values of species per site group. Only species found at a minimum of three sites are shown, as well as two-site species also listed by LEGRAND & COUTURIER (1985). For several taxonomically unresolved genera (indicated with *) data are also given, showing that several ecologically different species are concerned. Within families (and smaller taxonomic units in Libellulidae) species have been sorted in order of group affinity. Abbreviations – L&C 1985: categories identified by LEGRAND & COUTURIER (1985) (U: upper, M: middle and L: lower reaches), openness: average openness of inhabited sites (1: closed, 2: patchy, 3: open), n: number of sites where species encountered, p: significance of highest site value. Taxonomy follows TSUDA (2000) with changes in DIJKSTRA (2002, in press).

taxonomic unit	genus or species	L & C 1985	streams			rivers		open- ness	n	p
			small	inter.	large	small	large			
Calopterygidae	<i>Sapho bicolor</i>	U	73	10				1.00	8	0.001
	<i>Umma cincta</i>	M	15	23	3			1.13	8	0.188
	<i>Sapho ciliata</i>	M	11	21	25	15		1.62	23	0.359
	<i>Phaon camerunensis</i>	M		5	2	5		1.67	3	1.000
	<i>Phaon iridipennis</i>	L	2	6	22	6	23	2.05	18	0.407
Chlorocyphidae	<i>Chlorocypha selysi</i>	U	58	23				1.09	11	0.001
	<i>Chlorocypha dispar</i>	M	9	23	18	1		1.50	14	0.318
	<i>Chlorocypha curta</i>				36			2.25	4	0.025
	<i>Chlorocypha radix</i>	M		13	15	20	3	1.94	16	0.471
	<i>Chlorocypha luminosa</i>				23	19	5	2.00	11	0.230
	<i>Chlorocypha pyriformosa</i>	L		1		19	43	2.47	8	0.010
Coenagrionidae	<i>Pseudagrion flavipes</i>	U	38	7	1			1.17	6	0.026
	<i>Ceragrion rubellocerinum</i>	U	25	7	3	2		1.43	8	0.152
	<i>Pseudagrion epiphonematicum</i>		26	7	8			1.43	8	0.118
	<i>Pseudagrion melanicterum</i>		6	21	25	9	2	1.91	22	0.324
	' <i>Pseudagrion</i> ' <i>malagasoides</i>			5	2	5		1.67	3	1.000
	' <i>Pseudagrion</i> ' <i>cyathiforme</i>				8	14		2.00	4	0.299
	<i>Pseudagrion basicornu</i>				2	18		2.00	3	0.183
	<i>Pseudagrion glaucoideum</i>					38		2.67	3	0.049
	<i>Pseudagrion sjoestedti</i>	L			5	24	34	2.73	11	0.043
	<i>Pseudagrion sublacteum</i>	L					50	3.00	2	0.011
	<i>Pseudagrion camerunense</i>					100	3.00	4	0.001	
Platycnemididae	<i>Platycnemis guttifera</i>	L	6	20		2		1.40	5	0.312
	<i>Platycnemis sikassoensis</i>			1	4	22	32	2.33	12	0.062
	<i>Mesocnemis singularis</i>	L				13	50	2.83	6	0.007
Protoneuridae	<i>Isomecrocnemis subnodalis</i>	U	89	1				1.00	6	0.001
	<i>Chlorocnemis flavipennis</i>		54	5	2			1.07	8	0.001
	<i>Chlorocnemis elongata</i>		61	9	5			1.36	11	0.001
	<i>Prodasineura villiersi</i>	U	54	31				1.00	12	0.003
	<i>Elattonaura balli</i>	M	6	12	32	12		1.65	19	0.126
	<i>Elattonaura girardi</i>	L			3	7	28	2.36	6	0.091
Aeshnidae	<i>Heliaeschna fuliginosa</i>	M	42	7				1.00	5	0.018
Gomphidae	<i>Diastatomma gamblesi</i>		26	3	1			1.25	4	0.131
	<i>Lestinigomphus</i> *		18	2	1		7	–	5	–
	<i>Phyllogomphus</i> *		4		1	15		7	–	6
	<i>Paragomphus</i> *		10	1	4	1	34	–	10	–
	<i>Gomphidia gamblesi</i>				4	27	7	2.29	7	0.083

Table 3. Continued.

taxonomic unit	genus or species	L & C 1985	streams			rivers		open- ness	n	p	
			small	inter.	large	small	large				
Corduliidae	<i>Phyllomacromia sophia</i>	U	30	3				1.00	3	0.069	
	<i>Neophya rutherfordi</i>		26		1	3		1.50	4	0.157	
Tetrathemistinae	<i>Eothemis zygoptera</i>	U	61	6				1.00	6	0.001	
	<i>Notiothemis robertsi</i>		54	12				1.00	7	0.003	
	<i>Allorrhizucha klingi</i>	U	29	18	19	1		1.41	17	0.093	
	<i>Allorrhizucha campioni</i>						23	10	2.50	4	0.190
<i>Eleuthemis</i>	<i>Eleuthemis</i> sp.				15	29		2.13	8	0.082	
	<i>Eleuthemis buettikoferi</i>				1	12	46	2.86	7	0.013	
<i>Orthetrum</i>	<i>Orthetrum julia</i>	U	24	26	2	1		1.36	11	0.179	
	<i>Orthetrum stemmale</i>			3	3			13	2.00	3	0.478
	<i>Orthetrum microstigma</i>	M						75	3.00	3	0.001
<i>Trithemis</i>	<i>Trithemis africana</i>		25	10				1.00	4	0.160	
	<i>Trithemis basitincta</i>		3	2	1	2	9	1.67	5	0.790	
	<i>Trithemis grouti</i>				1	6	52	2.67	6	0.011	
	<i>Trithemis aconita</i>					6	56	3.00	5	0.004	
	<i>Trithemis arteriosa</i>				1		92	3.00	5	0.001	
<i>Zygonyx</i>	<i>Zygonyx natalensis</i>				27			1.67	3	0.101	
	<i>Zygonyx chrysobaphes</i>				27	3		1.80	5	0.103	
	<i>Zygonyx torridus</i>				8		14	2.67	3	0.303	
	<i>Zygonyx flavicosta</i>				1	11	11	2.25	4	0.659	
remaining	<i>Porpax bipunctus</i>	U	40					1.00	2	0.021	
Libellulidae	<i>Hadrothemis coacta</i>		33	2				1.00	3	0.070	
	<i>Hadrothemis versuta</i>		21	12				1.00	4	0.175	
	<i>Lokia incongruens</i>		7	12	2			1.50	4	0.470	
	<i>Chalcostephia flavifrons</i>			3	36			1.83	6	0.041	
	<i>Oxythemis phoenicosceles</i>		1		5	41	5	2.14	11	0.011	
	<i>Cyanothemis simpsoni</i>				2	49	16	2.45	11	0.011	
	<i>Sympetrum navasi</i>					23	10	2.50	4	0.183	
	<i>Thermochoria equivocata</i>	L				13	13	2.33	3	0.514	
	<i>Palpopleura lucia</i>		2	2	1			31	2.11	5	0.070
	<i>Olpogastra lugubris</i>				1	19	42	2.50	8	0.010	
	<i>Tholymis tillarga</i>		2	1				59	2.33	6	0.001
	<i>Bradinopyga strachani</i>				1			67	2.75	4	0.002
	<i>Pantala flavescens</i>							75	3.00	3	0.001

Discussion

The high explanatory value of the first NMS axis and its strong correlation with stream size demonstrate a strong pattern of odonate species associations along Upper Guinean running waters. Although assemblages probably change continuously from source to mouth, it is possible to distinguish five groups of sites, corresponding with the habitat turnover along running waters. The distinction between the assemblages of small and intermediate streams is relatively minor, but has been maintained to demonstrate the faunal transition towards large streams. LEMPERT (1988) even defined three types within the two

(Fig. 1 a), but his intermediate category overlaps with his upper and lower categories (also when Liberian data are analysed separately).

Differences within Upper Guinea

Part of the variation between sites may be explained as regional differences between Liberia and Ghana. The data were lumped because both countries possess an essentially similar, Upper Guinean, fauna. Because the axis correlated with country explains only 13.9 % of variation in our presence-absence matrix, this effect appears of relatively minor importance. When data from both countries were analysed separately, similar results were obtained. The Liberian sites were spread more evenly along the habitat gradient, including the more typical small stream and large river sites (Table 2). Large stream sites are relatively abundant in the Ghanaian data. Additionally, the Liberian sites were studied more intensively (Table 1). This may explain the absence of rarer small stream species in the Ghanaian data (e.g. *Phyllomacromia sophia* and *Porpax bipunctus*). The total number of species recorded is highest in the large stream group, which has the greatest number of sites (Table 2). The highest average score per site is reached in the small stream and large river groups, where there is a higher proportion of Liberian sites. It is thus impossible to say anything about the variation of species diversity along the gradient. Besides this heterogeneity in the data, there may also be actual geographical variations in species ecology within Upper Guinea, but more data are required for that assessment.

Our results largely agree with the findings of LEGRAND & COUTURIER (1985) in Tai Forest, Côte d'Ivoire (Fig. 1 b). These authors classified species according to their occurrence in the upper, middle and lower reaches of running waters (Table 3). All species of the upper reach ("partie haute") are typical of small streams in this study. The single exception is *Gynacantha bullata*, which was not included in this study for paucity of data. LEGRAND & COUTURIER (1985) suggest that this species may only use the vegetation here to rest. Their middle reach ("partie moyenne") includes intermediate and large stream species (e.g. *Sapho ciliata* and *Umma cincta*). Unlike our results, *Heliaeschna fuliginosa* and *Orthetrum microstigma* are also listed in this category. The authors mention that both prefer standing water, the former shaded, the latter sunny. Interestingly, *Phaon camerunensis* is also given for this habitat, which agrees with our assessment, based on limited data. Finally, river species are listed for the lower reach ("partie basse"). The only discrepancy with the present data is shown by *Platynemis guttifera*. Our records are from smaller streams, with one exception from a small river. A possible explanation might be the occurrence of two similar, ecologically segregated species, as the taxonomy of this genus in Africa is unresolved.

Ecological segregation

Table 3 reveals some sister-species pairs that are clearly separated along the stream-size gradient. The pairs *Chlorocypha dispar* > *C. pyriformosa* and *Allorrhizucha klingi* > *A. campioni* both involve near-identical species of which the first is a species of streams, the second of rivers. *Eleuthemis* sp. was recognised by LEMPERT (1988) as a distinct colour-form of *Eleuthemis buettikoferi*. It is possibly a valid species, and is treated as such in our analysis. It inhabits more strongly shaded habitats, and as a result, relatively smaller running waters. Other examples of source-to-mouth succession in related species are in the genus *Sapho* (*S. bicolor* > *S. ciliata*), protoneurids related to *Prodasineura* (*P. villiersi* > *Elatoneura balli* > *E. girardi*) and lindeniine gomphids (*Diastatomma gamblesi* > *Gomphidia gamblesi*). Gradual replacement occurs in the genus *Chlorocypha*, of which rarely more than two species are found together (at only 19% of the sites). The species succeed each other from the source downwards as follows: *selysi* > *dispar* > [*radix* > ? *luminosa*] > *pyriformosa*. Where forest cover of streams is largely absent *curta* appears. The data of *radix* and *luminosa* are somewhat inconclusive, as they appeared largely to occur together in Ghana, but not in Liberia where *radix* most frequently co-occurred with *dispar*. Ecological segregation at a higher taxonomic level occurs in *Pseudagrion* (two species marked by quotes in Table 3 are atypical and must be relegated to other genera). The species of streams (*epiphonematicum*, *flavipes* and *melanicterum*) belong to group A of PINHEY (1964), whilst those of rivers (all others listed) belong to group B.

Table 3 also demonstrates groups of related species that are restricted to a small section of the gradient. The libellulid subfamily Tetrathemistinae is concentrated in the smaller streams, including the widespread *Allorrhizucha klingi*, *Eothemis zygoptera* and *Notiothemis robertsi*, as well as *Malgassophlebia bispina* and *Micromacromia camerunica* in Liberia. The genera differ in the oviposition substrate: *Allorrhizucha* and *Micromacromia* deposit the eggs in shallow water, *Eothemis* on the stream bank, *Notiothemis* on emergent roots and twigs, and *Malgassophlebia* on leaves overhanging the water (CLAUSNITZER & LEMPERT 1998, LEMPERT 1988). The protoneurids related to *Chlorocnemis* (*C. elongata*, *C. flavipennis* and *Isomecognemis subnodalis*) are also confined to smaller streams. The adults are partially segregated in time of day, the first being most active in the morning, the second in the afternoon and the third especially around midday (LEMPERT 1988). The genus *Mesocnemis* was found only along rivers. The widespread *Mesocnemis singularis* preferably perches on exposed, sunny rocks in the current. The Liberian *Mesocnemis tisi* confines itself to banks shaded by overhanging trees. The first is entirely covered with reflecting pruinescence, which the second largely lacks (LEMPERT 1992). Four species of *Zygonyx* occur on the larger running waters and all of

them can coexist on a single stream. They require sections of fast flowing water as larval habitat. The species differ in the required type of rapids: *natalensis* prefers waterfalls, *chrysobaphes* calmer riffles and *flavicosta* more or less intermediate rapids (GAMBLES 1963, own observations).

Habitat selection

Describing how species are distributed along the gradient does not explain why they are distributed this way, i.e. how habitat selection determines distribution. Because the ecology of most species is unknown, the step from how to why is difficult to take. Nonetheless, some preliminary explanations are possible. The preferred perches of *Mesocnemis singularis* (see above) can only be found in rivers. The rapids for *Zygonyx* species are similarly absent in smaller streams. The larvae of *Neophya rutherfordi* and *Phyllomacromia sophia* are so-called sedentary sprawlers (see CORBET 1999) living amongst coarse detritus, which they find in the form of leaf-litter in the smallest streams. Some species bask avidly and also need a specifically structured habitat: *Cyanothemis simpsoni*, for instance, requires sunny perches overhanging the water for territorial males and surfaces of dammed flotsam for oviposition. *Oxythemis phoenicosceles* prefers sunny, slow-moving or standing corners of waters (often with aquatic plants or a marshy border) overhung by or adjacent to tall, leafy perches. As a consequence both species are found mainly along open watercourses where riverside vegetation and a diversely structured streambed provide such microhabitats.

To the human observer, the shifting balance of sun and shade forms one of the most obvious habitat changes in the described gradient (as expressed in some of the foregoing examples). This coincides with the marked faunal break that occurs between streams and rivers. Our openness data (Table 3) give indications of the preferences of species within assemblages, as well as of species without resolved assemblage associations. *Umma cincta* and *Prodasineura villiersi* are both frequent in intermediate stream assemblages, but only when the habitats are well shaded. Among typical large stream species *Elattonneura balli* (and to a lesser degree *Sapho ciliata*) searches out the more shady places, while *Pseudagrion melanicterum* favours the sunnier reaches. *Trithemis basitincta* is found as a rare element throughout the running water gradient, but all its sites have shadiness in common. It is noteworthy that CLARK & SAMWAYS (1996) regard *Phaon iridipennis*, *Pseudagrion sjoestedti* and *Trithemis aconita* as characteristic of heavily shaded parts of the Sabie River in South Africa, while they were found at the more open sites in our study. This can be explained as a difference between rivers in forest (our study) and savannah (Sabie): In the strongly sunned savannah these species can perhaps only cope under very shady (i.e. forest-like) conditions.

Based on the above observations and the data in Table 3, species can be roughly classified into four ecological types:

1. Species of closed courses. These are strongly dependent on forest cover and are therefore largely restricted to smaller streams. Examples: *Umma cincta*, *Chlorocypha selysi*, *Chlorocnemis elongata*, *Prodasineura villiersi* and *Allorrhizucha klingi*.
2. Species of patchy courses. These require forest cover, but also plenty of sunny patches, and are thus found predominantly in larger streams and small rivers. Examples: *Sapho ciliata*, *Chlorocypha radix*, *Pseudagrion melanicterum* and *Elattonneura balli*.
3. Species of open courses. Running water specialists of well-sunned waters, generally rivers. Examples: *Pseudagrion sjoestedti*, *Platycnemis sikassoensis*, *Cyanothemis simpsoni* and *Oxythemis phoenicosceles*.
4. Species of standing water. These are indicative of (usually temporary) pools in the streambed. Examples: *Bradinygya strachani*, *Palpopleura lucia*, *Pantala flavescens* and *Trithemis arteriosa*.

Effects of human disturbance

Human disturbance of running waters will lead to a more open character of these sites. Such a habitat shift may see an accompanying change of the odonate assemblage. Our data suggest that human disturbance can indeed 'down-scale' a site (Fig. 2). Disturbed sites have a fauna indicative of comparatively larger undisturbed waters, suggesting an upstream shift of species. A similar observation is described by WASSCHER (1993), who found species typical of sites downstream where a black-water creek passed through a forest clearing in Surinam. This author stresses the importance of sun and shade in the habitat selection of tropical stream Odonata. Research in temperate regions has shown a decrease of odonate diversity in cleared or disturbed forest (RITH-NAJARIAN 1998, SAHLÉN 1999). Our data are insufficient to draw parallels for a tropical situation. Observations from Liberia, where streams in primary and younger secondary forests could be directly compared, suggest that the age of the forest bordering running water sites is of little influence for the odonate assemblage there, as long as the required cover is present (LEMPERT 1988).

Concluding remarks

Although the decrease of shading is an obvious change for adult Odonata as one goes downstream, it is hard to distinguish from other factors that gradually change along a water's course, such as morphology and substrate. Interactions between species, by predation and competition, further complicate the com-

position of species assemblages (SUHLING 2001). Detailed sampling and ecological studies of the species concerned, especially of the larvae, are needed to determine the precise influence of these factors. A possible way to identify habitats of particular scientific (and conservation) interest, is to see where species with restricted geographical ranges occur. 30 % of the analysed species occur no further east than Nigeria. They are not concentrated in a particular section of the stream-size gradient, but are distributed evenly along it. Thus no such 'priority section' can be identified.

That running water Odonata are strongly selective of their habitat is expressed by the marked succession of species described, including clear segregation of closely related species. The existence of such patterns is essential if Odonata are to be used successfully as indicators of running water conditions.

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