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Dragonfly assemblages in arid tropical environments: a case study from western Namibia

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Abstract. Dragonflies have been proposed as indicators for the ecosystem health of freshwater wetlands. For their useful functioning as indicators it is, however, necessary to identify species compositions in specific habitats and species-habitat associations, particularly in the tropics, where such knowledge is still weak. We examined the dragonfly species composition of 133 localities in the arid environment of western Namibia. An analysis of nestedness indicated that distinct, and predictable patterns of species associations can be expected. Discriminant analyses revealed that most of the nine habitat types separated by structural and hydrological parameters are well discriminated by their dragonfly assemblages. Spring brooks in particular host a specific assemblage, which is threatened due to the habitat restriction of several species, as well as by recent habitat loss and degradation. Using a hierarchical method of several criteria we demonstrated the selection of a set of potential indicator species from the species set, most of these being useful indicators for spring brook assemblages. The conservation status of certain habitats and species is discussed. We propose that dragonflies will have a high indicator potential for threatened freshwater wetlands in such areas and may also serve as an indication of the sustainable use of water resources including evaluating measures to rehabilitate environments.

Introduction

One of the challenges for the future lies in protecting the ecological integrity and biodiversity of freshwater aquatic systems, particularly in the tropics. Anthropogenic habitat alterations may cause significant changes in freshwater biodiversity (Ward 1998). These environments are essential resources for development (Ward 1998; Crisman et al. 2003) and face ever-increasing pressure especially in arid countries where freshwater is disproportionately important to humans and other species (Barnard and Shikongo 2000; Day 2003). Gaining knowledge about tropical freshwater communities and of potential indicators of freshwater ecosystem health is therefore crucial.

When compared to the attributes desired for indicators (cf. McGeoch 1998; McGeoch and Chown 1998; Simberloff 1998) dragonflies are among the most

promising animals to serve as an indicator group, e.g. for species richness and ecosystem health of freshwater wetlands (Brown 1991; Sahlén and Ekestubbe 2001; Clausnitzer and Jödicke 2004). However, in order to use dragonflies as indicators, basic knowledge of assemblages and habitat preferences of species is required (Corbet 1993). There are several recent approaches to assess and compare dragonfly communities and species richness in relation to habitat in the tropics (Cleary et al. 2004) and particularly in Africa (Samways and Steyler 1996; Clausnitzer 2003; Dijkstra and Lempert 2003). However, the general knowledge of habitat associations of African Odonata is still scarce and requires further research action (e.g., Suhling et al. 2003, 2004a; Clausnitzer 2004a,b; Dijkstra and Vick 2004).

Our first aim was to assess dragonfly communities on a large scale in Namibia. If the dragonfly species composition differed significantly between various types freshwater habitats, i.e. the species composition is nested, then it would indicate that the dragonfly community is not randomly organised. Distinct and predictable patterns of occurrence might be expected with a high level of nestedness. Distinct types of habitats may likewise have a nested species composition, hosting certain species assemblages. Our second goal was to identify species that might be indicative of different assemblages. We suggest a set of five criteria, including frequency, habitat specificity and criteria derived from the statistical analyses we applied to select such species. In our context the presence of particular species in distinct habitats would indicate the completeness of the typical community expected at such sites (cf. Sahlén and Ekestubbe 2001). Such indicator species might then be used to identify threatened environments and monitor the impact of human activities on the aquatic biodiversity of Namibia.

Materials and methods

Study area

Namibia is the most arid country of the Afrotropical region, i.e. south of the Sahara. The only perennial rivers occur along the northern and southern borders of the country. Natural permanent surface water in the interior parts of Namibia only occurs at widely separated springs around mountains and in ephemeral river courses (Breen 1991). Water is therefore one of the most relevant, and limited, resources in Namibia (Heyns et al. 1998; Christelis and Struckmeyer 2001). Development and changes in human lifestyle during the 20th century have affected the way in which water is managed (Stern and Lau 1990; Seely 1998). Large impoundments have been built to ensure reliable water supply for industrial development, urban centres and irrigated agriculture, which altered flood regimes and destroyed perennial wetlands in ephemeral rivers. Large-scale extraction of groundwater to provide water for smaller urban centres, mining and intensive livestock agriculture has caused to a fall in water tables, a loss of spring

habitats (Jacobsen et al. 1995; Seely 1998), and changes in vegetation structure through die-back of large trees and other vegetation tapping the aquifers. Some large-scale water transfer schemes have been established, channelling or piping water over long distances to major urban and industrial centres to meet the increasing demand for water. These schemes are likely to become more extensive due to the planned development of dams on the perennial rivers along both the northern and southern borders in order to meet projected requirements of the 21st century.

Our study was conducted in western Namibia approximately between 17° and 25° S and 13° and 18° E (Figure 1), an area characterised by arid climate and therefore mainly by savannah, karoo and desert biomes (Mendelsohn et al. 2002). We restricted our study mainly to the western ephemeral river catchments that originate in the central Namibian highlands and flow into the Atlantic Ocean (cf. Jacobsen et al. 1995). Additionally, we selected sites in areas adjacent to the watershed to consider habitats that were otherwise underrepresented in the study, i.e. large impoundments and spring brooks.

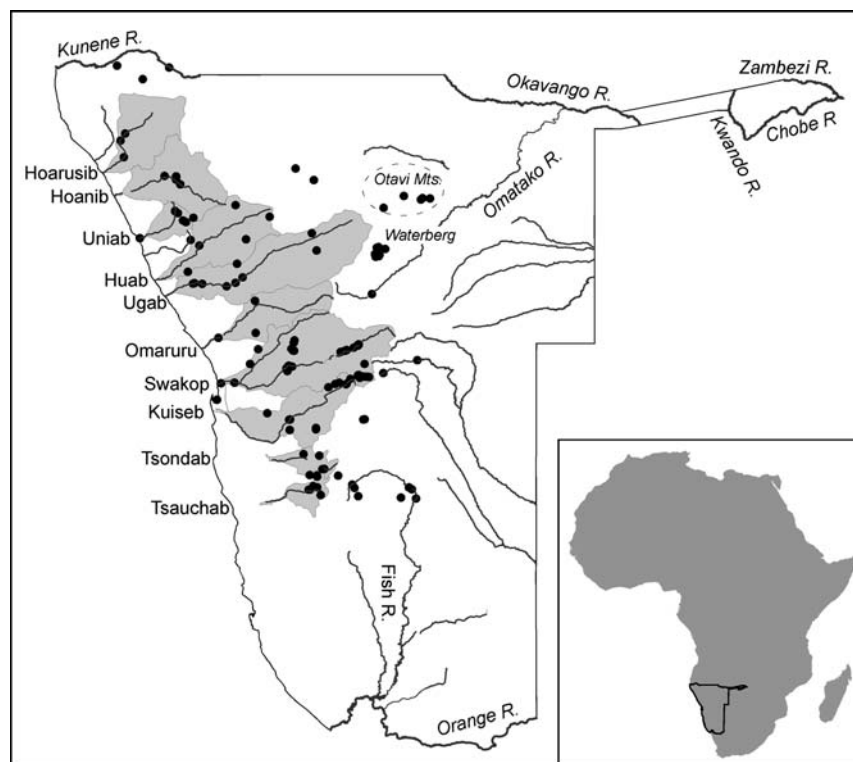


Figure 1. Map of Namibia showing the distribution of the sample sites and the western ephemeral river catchments and the Fish River catchment. Note that some few sites do not belong to the western catchments.

These sites were mainly in the Kunene River catchment, in the Otavi Mountains, at the Waterberg and in the upper Fish River catchment.

In terms of altitude the study area is broadly declining from about 2000 m a.s.l. in central Namibia down to sea level, with the study sites ranging from 29 to 1786 m a.s.l. The average annual rainfall in the area is varying from about 550 mm in the Otavi Mountains to less than 50 mm at the coast. The average maximum temperatures during the hottest month increase from 20 °C at the coast to about 30–34 °C in central Namibia and are higher than 36 °C in the southern part of the study area. The average minimum of the coldest month ranges between 10 °C at the coast and 4 °C inland, with about 1–10 days of frost per year. All climate and geographical data are from the Atlas of Namibia (Mendelsohn et al. 2002).

Recording of dragonflies and habitats

Between January 2001 and May 2004 we recorded dragonflies at 133 localities (Figure 1 and Appendix) that represented all major types of freshwater habitats in the study area, from ephemeral rain pools and artificial water holes to large impoundments and perennial spring brooks. At all localities dragonflies were recorded by identifying adults *in vivo* if possible. Difficult taxa, e.g. the genera *Pseudagrion* and *Orthetrum*, were collected using an insect net and identified to species using a microscope and the illustrated key to Namibian dragonflies (Martens and Suhling unpublished manuscript). Additionally, at all sites we searched for odonate exuviae and/or larvae, which were preserved and, if possible, identified to species using the illustrated key to the larvae of Namibian dragonflies (Suhling et al. unpublished manuscript) and Samways and Wilmot (2003). Because only about 50% of the larvae of the Namibian dragonflies are described, full species lists per locality based on larvae were not feasible. We are aware that species lists of adults will also include non-breeding vagrants in the data set (Sahlén 1999). However, with these exceptions the occurrence of adults may generally be interpreted as active selection for a certain type of habitat.

Different types of habitats were examined at different frequencies. Whereas temporary rain pools, which may only exist for a few weeks, were recorded once, perennial and longer lasting temporary waters were visited more frequently, i.e. up to 10 times (cf. Appendix), as the species assemblage may change during the ongoing season due to phenological differences. Especially on localities that were only investigated on one or two occasions, the phenology of certain species may have caused an under-estimation of the true species numbers, which may have influenced our analysis. However, re-examinations at more than 40 localities in 2004 corroborated our results concerning the species assemblages (Suhling unpublished data). From all records we produced a presence/absence matrix for the species at all localities. The entry for a species at a given locality was 1 if either an adult or a larva/

exuvia was recorded at least once, and it was 0 for a given locality if a species was never encountered. For analysis (below) the localities were sorted into nine functional types of habitats. These are:

(1) *Wetlands below dams* (Number of localities $n = 9$): Leakage at most of the large impoundments (see 9) results in small perennial running waters and wetlands immediately below the dams. Some of these are similar to spring brooks with respect to their wetland habitat structures. All sites were well vegetated by various submerged plants and reeds.

(2) *Spring brooks* ($n = 12$): Small perennial running waters fed by strong springs, which run for stretches of up to 2 km before they vanish into the ground or evaporate. Many streams consisted of linked pools and included small waterfalls and rapids. All spring brooks sustain trees in their surroundings. However, some sites were completely shaded, e.g. at Zebra River, whereas others were widely exposed to the sun, e.g. Ongongo Fall. All sites contained semiaquatic vegetation, i.e. reeds (*Phragmites* sp. *Typha latifolia* and Cyperaceae), submerged vegetation (*Chara* sp., *Potamogeton* spp.) and/or mosses.

(3) *Degraded spring brooks* ($n = 10$): Here we grouped former spring brooks that have been extensively altered by humans. Most sites have been changed into perennial spring-fed ponds by the construction of dams just below the spring, e.g. in the Otavi Mountains and at Klein Barmen. Others have become degraded due to water extraction reducing the length of perennial section (Otjisingombe) and subjected to heavy cattle grazing. All have in common that the normal structure of a spring brook has been lost.

(4) *Spring pools* ($n = 10$): Perennial springs with weak discharge or in depressions may form pools or small chains of pools. Most of these are densely vegetated by rushes; even those that are subjected to heavy grazing by cattle or game. All of them are widely exposed to the sun.

(5) *Ephemeral river sections* ($n = 34$): Wetlands – some being perennial – along the courses of the large ephemeral rivers result from the resurgence of underground water due to geology or topography (Jacobsen et al. 1995). Unlike the other habitat types, these wetlands may be subjected to extensive disturbance or even complete alteration due to strong floods. Consequently, vegetation and bottom substrate, which mainly consists of sand, may be washed away. We were able to register a rapid succession after such an event in the Ugab River, with the vegetation recovering within a few months. The vegetation consisted mainly of reeds and the shorelines were covered with fast growing shrubs. The water had appreciable levels of dissolved salts resulting in high conductivity of 2–8 mS/cm, with a peak value of 42 mS/cm (Swakop River near Swakopmund).

(6) *Temporary waters* ($n = 23$): This category includes ponds as well as small springs that contain water only after heavy rains and may persist for some months during and shortly after the rainy season. Most sites contain no vegetation or only some scattered terrestrial plants. One site, however, contained some rushes.

(7) *Artificial waters* ($n = 14$): Man-made waters including water holes for cattle and game, fish ponds and even some swimming pools. A common feature of most artificial sites are that they are concrete constructions and extremely poor in wetland structures. However, in large parts of the study area they represent the only permanent freshwater habitats during the dry season.

(8) *Farm dams* ($n = 12$): Small earth dams in drainage gullies and smaller ephemeral rivers may form larger ponds that – after being filled – may persist for several months. Because the ponds are in riverbeds they are affected by mechanical stress (see type 4) so that aquatic vegetation is very sparse, if not absent altogether. Also the shores are often free of vegetation due to grazing cattle and the varying water levels.

(9) *Lakes* ($n = 8$): Large impoundments forming perennial lakes. All these impoundments were created in larger ephemeral rivers for water supply to towns. Due to the variability of annual rainfall, evaporation and the use of water the water level may vary by several meters between years and even seasons. Most lakes therefore contained very little aquatic vegetation, of which the most common were *Potamogeton* spp.

One locality, an artificial canal with high current velocity, did not fit to any of these categories and was therefore omitted in the analyses of assemblage patterns and of habitat specificity of the species, but was used in the nestedness analysis of all localities (see below).

Analysis of nestedness

The use of nestedness as a tool for analysing species composition in fragmented habitats is controversial (e.g., Simberloff and Martin 1991; Wright and Reeves 1992; Atmar and Patterson 1993; Lomolino 1996; Worthen 1996). Several different methods are in use, among them the Nestedness Temperature Calculator, NTC (Atmar and Patterson 1995), which is available on the World Wide Web. Fischer and Lindenmayer (2002) noted that this method has been used indiscriminately. They showed that even randomly generated data sets may indicate significant nesting if all species is treated as equally common. Bearing this in mind we decided to use two methods to corroborate whether our species assemblages were nested, *viz.* the NTC and the Standardised Nestedness Score (C) described by Wright and Reeves (1992).

First we included all species and localities in a presence–absence matrix and analysed the nestedness of species in the study area. Second we analysed the nestedness of each habitat type (see above) separately. Contrary to Sahlén and Ekestubbe (2001), we included all species in the matrix, also the obligate migrants. Migrating species have a more random occurrence and will elevate the temperature in the NTC (Atmar and Patterson 1993) and hence lower the C -score. But since the ecology of all species in the area is not known, we cannot exclude known migrants while other unknown migrants may be hiding in the rest of the species pool. The size, shape and fill of the matrix will also affect the

temperature in the NTC (Atmar and Patterson 1995). A rectangular matrix as well as an empty one (more zeros than ones) will result in a lower temperature than a square one or one, which contains more ones than zeroes. This may cause a non-nested composition to be classified as a nested one, hence our use of the *C*-score. In order to be able to compare the methods we used the same packing of the matrix for *C* as when calculating matrix temperature in NTC. As we use the *C*-score to verify the statistics of the NTC, the *z*-score statistics (Wright and Reeves 1992) or *Q*-value (cf. also McCulloch 1985) was not calculated. Considering that the *C*-score varies between 0 and 1 and there is no consensus on how low score a nested community may have still being nested, we decided to compare our *C*-scores with those presented in other analyses of odonate communities.

Analysis of assemblage patterns

We performed a discriminant function analysis using SPSS 11.0 to determine if the nine types of habitats we distinguished (see above) were, indeed, separate with regard to the odonate assemblages of the localities. Given a set of independent variables, discriminant analysis attempts to find linear combinations of those variables (discriminant functions) that best separate the groups of cases (here types of habitats). A matrix of presence/absence data as used in the nestedness analysis of species served as independent variables in the analysis. In addition, the procedure produces Eigenvalues, which provide information about the relative efficacy of each discriminant function, and Wilks' lambda values as measures of how well each function separates cases into groups. Wilks' lambda is equal to the proportion of the total variance in the discriminant scores not explained by differences among the groups, i.e. smaller values indicate greater discriminatory ability of the function. By associated chi-square statistics we tested the hypothesis that the means of the functions listed are equal across groups. Canonical correlations indicate which variables (species) correlate best with the respective functions. Finally, the analysis provides classification results, i.e. how well the distinguished types of habitats are predicted by the assemblage structure.

Selection of indicative species

For the selection of indicative species we used a set of five criteria in a stepwise order. We decided that species had to match all five criteria to serve as potential indicators for the health of dragonfly assemblages of certain habitats. (1) We analysed the habitat specificity of the species by comparing the number of sites to the habitat (see above) at each site. We assumed that generalist species and migrants were found in most, if not all, of the nine types of habitat, while habitat specialist species were expected in maximally one-third (i.e. 1–3) of the habitat types. (2) We selected species from the group of

'moderately common' species to compare to general species richness according to Sahlén and Ekestubbe (2001). As moderately common we counted those that were recorded at $<20\%$ and $\geq 3\%$ of all localities surveyed. (3) As a second criterion of habitat specificity we used univariate ANOVAs analyses on the equality of the distribution of each species, which is used as test of the potential of each independent variable in the discriminant analysis. A species was only selected when its distribution was significantly different from random. (4) We assumed that a potential indicator should not be too rare in its specific habitat type. We therefore accepted only species that occurred at least at 25% of the localities of a particular habitat. (5) We selected species, of which the distribution were correlated with one of the significant discriminant functions according to the canonical correlation analyses derived from the discriminant analysis.

Results

Nestedness

The matrix (59 species, 133 localities; fill 13.3%) was nested in the NTC giving a temperature of 4.38 °, which was significantly different from the temperature generated by 1000 Monte-Carlo simulations of random distributions ($49.6 \pm 1.6^\circ\text{sd}$; $p < 0.001$). The *C*-score for the matrix was 0.351. All of the nine separate habitats were also nested using both methods, with *C*-scores ranging from 0.388 and 0.389 in spring brooks and artificial waters to 0.676 and 0.895 in wetlands/lakes and spring pools respectively (Table 1). All of the individual habitats had higher *C*-scores than the total species pool in the region. All temperatures but one derived from the NTC were higher than that of the total species pool, the lowest temperature (3.01 °) in temporary waters and the highest (28.38 °) in degraded spring brooks (Table 1).

Assemblage composition and diversity

Discriminant analyses used eight discriminant functions of which the first four functions were significant. The first function (Eigenvalue = 45.44, Wilks' lambda = 0.00004, $\chi^2 = 1009.709$, $df = 416$, $p < 0.001$) explained 78.4% of the variance. Function 2 (Eigenvalue = 5.17, Wilks' lambda = 0.002, $\chi^2 = 623.97$, $df = 357$, $p < 0.001$) explained 8.9%, function 3 (Eigenvalue = 2.73, Wilks' lambda = 0.012, $\chi^2 = 441.08$, $df = 300$, $p < 0.001$) explained 4.7%, and function 4 (Eigenvalue = 1.99, Wilks' lambda = 0.046, $\chi^2 = 300.87$, $df = 300$, $p = 0.004$) explained 3.44%. The first two functions together explained in total 87.3% of the variance.

In total, 81.1% of all habitats were correctly classified according to their odonate assemblage structures. But, the classification results varied between the habitats (Table 2), from about 50% (spring pools) to 100% (spring

Table 1. Comparison of the nestedness values (temperatures and C-scores) and species diversity (total number species and median, minimum, and maximum number of species per type of habitat) of the nine habitat types.

	Wetlands /lakes	Spring brooks	Degraded spring brooks	Spring pools	Ephem. R. sections	Temp. waters	Artificial waters	Farm dams	Lakes
Replicates	9	12	10	10	34	23	14	12	8
Nestedness	9.21***	23.85***	28.38***	17.93**	11.82***	3.01***	19.22***	25.56***	18.44***
temperatures (°)									
C-scores	0.676	0.388	0.638	0.895	0.605	0.430	0.389	0.469	0.500
Total species	40	41	26	14	24	27	19	21	24
Median	13	13	9	6	8	2	2	7	12
Min. species #	6	4	4	1	1	1	1	3	3
Max. species #	35	26	17	9	15	23	10	12	17

** p < 0.01, *** p < 0.001.

Table 2. Classification results of a discriminant analysis showing groups predicted from the dragonfly assemblage pattern (presence/absence data of species) in relation to the original habitat type groups according to the classification given in the methods (n = original numbers of habitats included).

Original group	n	Group predicted									% Correctly classified
		1	2	3	4	5	6	7	8	9	
(1) Wetlands below lakes	9	8	-	-	-	-	1	-	-	-	88.9
(2) Spring brooks	12	-	12	-	-	-	-	-	-	-	100.0
(3) Degraded spring brooks	10	-	-	8	-	1	-	-	1	-	80.0
(4) Spring pools	10	-	-	-	5	3	2	-	-	-	50.0
(5) Ephemeral river sections	34	-	-	-	1	25	7	-	1	-	73.5
(6) Temporary waters	23	-	-	-	-	2	21	2	1	-	91.3
(7) Artificial waters	14	-	-	-	-	2	-	11	1	-	78.6
(8) Farm dams	12	-	-	-	-	2	1	-	9	-	75.0
(9) Lakes	8	-	-	-	-	-	-	-	-	8	100.0

Bold are the numbers of localities correctly classified.

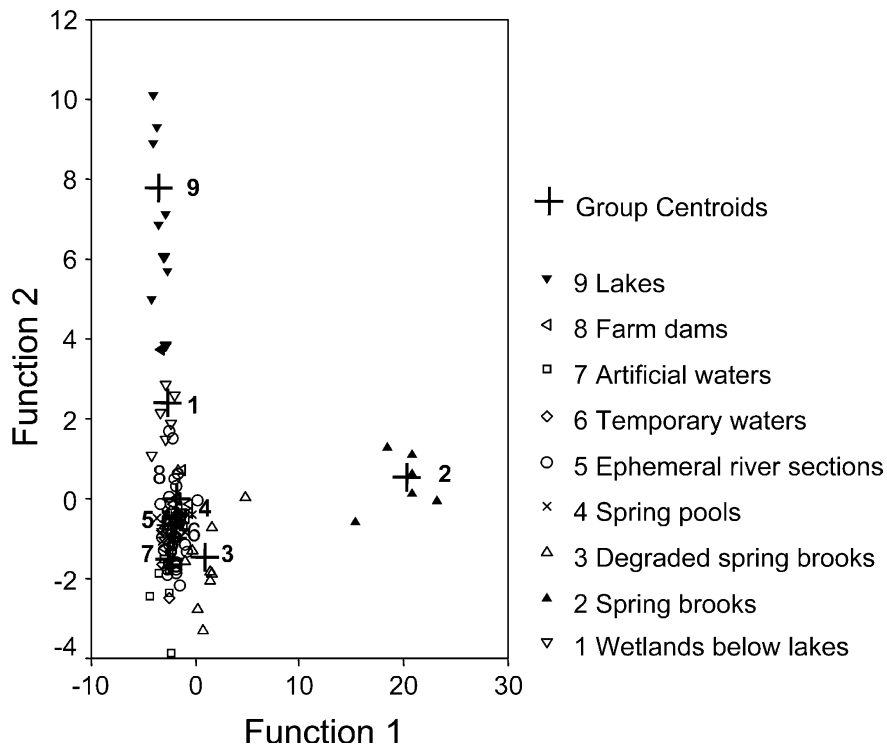


Figure 2. Diagram showing the sorting of examined localities according to the first two Canonical Discriminance Functions. The symbols depict the different habitat types and the group centroids.

brooks, lakes). The habitat types do, however, seem to be sufficiently discriminated. Particularly the habitat types lakes and spring brooks were clearly separated (Figure 2). Species correlated (canonical correlation) with the first discriminant function mainly occurred in perennial spring brooks, while species correlated to the second function were mainly recorded from lakes. The nine habitat types differed widely in species richness (Table 1). The highest total species numbers were noted from wetlands below lakes and spring brooks, whereas the lowest numbers were noted from spring pools (Table 1). The median number of species per habitat followed a similar pattern. Degraded spring brooks had much lower species numbers than natural spring brooks. The variation between minimum and maximum species numbers was high in all kinds of habitats, suggesting a relative high heterogeneity. This is also indicated by the high, although significant, nestedness temperatures and low *C*-scores (Table 1).

Selected indicator species and their habitats

Twenty-five species were present in more than four (> 50%) of all types of habitats and most species of this group were also present in more than 20% of all localities examined. Although *F*-tests (Table 3) indicated significant differences in the distribution of a number of these species, all appeared not to be very specific at least in the selection of adult habitats. Additionally, 22 species were recorded at less than four localities so that no useful information about their habitats and assemblage associations could be derived.

Of the remaining 12 species two showed no significant difference in distribution (Table 3), which suggests low habitat specificity. Hence, according to our criteria, 10 species remain, which may be useful indicators for the health of their assemblages. Canonical correlations indicate that the proportions of *Crocothemis sanguinolenta* (correlation 0.20), *Anax speratus* (0.17), *Orthetrum julia* (0.12), *Pseudagrion kersteni* (0.12), *Trithemis stictica* (0.12), all showing particularly high specificity to spring brooks, correlated best with discriminant function 1. Species that correlate best with function 2 were *Ceratogomphus pictus* (0.51) and *Ictinogomphus ferox* (0.35), both mainly recorded in lakes. Whereas function 3 was represented by *Azuragrion nigradorsum* (0.42) and *Agriocnemis exilis* (0.20), *Palpopleura jucunda* (0.10) represented function 4.

Discussion

The species assemblages in our study are nested, which means that distinct, and predictable, patterns of species associations can be expected. Discriminant analyses revealed that most out of nine habitat types separated by structural and hydrological parameters are well discriminated by their dragonfly assemblages, particularly spring brooks and large impoundments (lakes).

Table 3. Distribution of species recorded.

Species	Total		Habitat type									Function				
	n	M	1	2	3	4	5	6	7	8	9	8	9	2	1	4
			0.89	1.00	0.80	0.60	0.79	0.52	0.93	0.75	0.75					
<i>Tritheimis kirbyi ardens</i> (Gerstäcker, 1891)	102	9	0.89	1.00	0.80	0.60	0.79	0.52	0.93	0.75	0.75	*				
<i>Crocothemis erythraea</i> (Brullé, 1832)	86	9	1.00	0.92	0.90	0.80	0.65	0.30	0.36	0.67	0.88	*				
<i>Orithetrum chryso stigma</i> (Burmeister, 1839)	85	9	1.00	0.92	0.90	0.80	0.76	0.22	0.43	0.50	0.50	*				
<i>Pantala flavescens</i> (Fabricius, 1798)	85	9	0.78	0.58	0.50	0.80	0.62	0.61	0.57	0.92	0.38	*				
<i>Anax imperator</i> Leach, 1815	78	9	1.00	0.67	0.70	0.60	0.59	0.30	0.36	0.83	0.75	*				
<i>Sympetrum fonscolombii</i> (Selys, 1840)	63	9	1.00	0.25	0.20	0.10	0.53	0.43	0.36	0.83	0.63	*				
<i>Ischnura senegalensis</i> (Rambur, 1842)	58	9	0.78	0.50	0.60	0.50	0.56	0.13	0.07	0.25	0.88	*				
<i>Paragomphus genei</i> (Selys, 1841)	55	9	0.56	0.58	0.40	0.20	0.68	0.17	0.29	0.17	0.38	*				
<i>Tritheimis annulata</i> (Palisot de Beauvois, 1807)	40	9	0.56	0.25	0.50	0.10	0.21	0.17	0.21	0.42	0.75	*				2
<i>Orithetrum trinacria</i> (Selys, 1841)	40	8	0.56	0.08	0.60	–	0.24	0.13	0.14	0.58	0.88	*				
<i>Pseudagrion massaicum</i> Sjöstedt, 1909	35	9	0.44	0.50	0.30	0.10	0.32	0.04	0.14	0.17	0.63	*				
<i>Diplacodes lefebvrei</i> (Rambur, 1842)	33	9	0.56	0.42	0.30	0.20	0.32	0.09	0.07	0.25	0.13	*				4
<i>Tritheimis arteriosa</i> (Burmeister, 1839)	30	8	0.56	0.83	0.40	0.20	–	0.04	0.29	0.08	0.25	*				
<i>Lestes pallidus</i> Rambur, 1842	27	8	0.22	0.17	0.20	–	0.15	0.39	0.07	0.33	0.25	*				
<i>Africallagma glaucum</i> (Burmeister, 1839)	17	5	0.67	0.33	0.00	–	0.12	0.09	–	0.08	–	*				4
<i>Brachythemis leucosticta</i> (Burmeister, 1839)	14	6	0.22	–	0.10	–	0.06	0.04	–	0.08	0.88	*				2
<i>Zygonyx torridus</i> (Kirby, 1899)	14	4	0.22	0.50	–	–	0.15	0.04	–	–	–	*				
<i>Ceragrion glabrum</i> (Burmeister, 1839)	12	5	0.33	0.17	0.50	0.10	0.03	–	–	–	–	*				3
<i>Diplacodes luminans</i> (Karsch, 1893)	10	7	0.22	0.17	0.20	–	0.03	0.04	0.07	0.08	–	*				
<i>Tramea basilaris</i> (Palisot de Beauvois, 1807)	10	6	0.11	0.08	0.30	–	–	0.04	0.14	0.08	–	*				
<i>Pseudagrion salisburyense</i> Ris, 1921	10	4	0.11	0.50	–	–	0.03	–	–	–	0.25	*				2
<i>Orithetrum julia falsum</i> Longfield, 1955	10	2	–	0.58	0.20	–	–	–	–	0.08	–	*				1
<i>Anax ephippiger</i> (Burmeister, 1839)	9	6	0.11	0.17	–	–	0.06	0.04	0.14	–	0.13	*				
<i>Ictinogomphus ferox</i> (Rambur, 1842)	8	3	0.22	–	0.10	–	–	–	–	–	0.63	*				2
<i>Ceratogomphus pictus</i> Selys, 1854	8	2	0.22	–	–	–	–	–	–	–	0.75	*				2
<i>Crocothemis sanguinolenta</i> (Burmeister, 1839)	8	1	–	0.67	–	–	–	–	–	–	–	*				1
<i>Orithetrum brachiale</i> (Palisot de Beauvois, 1817)	7	4	0.22	–	–	–	0.03	–	–	–	–	*				4
<i>Pseudagrion sublacteum</i> (Karsch, 1893)	7	4	0.22	0.17	–	–	0.06	0.04	–	–	–	*				4

Community nestedness

Wright and Reeves (1992) considered an average score of 0.58 might be regarded as typical for terrestrial habitat systems, while for freshwater systems no such value is available. The value in this study is low (0.351), thus indicating a more loosely ordered species composition. This is comparable to other heterogeneous habitats, e.g. the least nested habitat in Sahlén and Ekkestubbe (2001; data re-analysed by GS) has a *C*-score of 0.358 but a *C*-score from a North American river surveyed by Worthen (2003) was only 0.250. Although this river had the 'least nested' species assemblage, many sites within this locality were pristine (Worthen 2003) and the odonate species belonged to several ecological groups. Thus, a low *C*-score does not necessarily indicate a degraded species assembly, but rather a more varied one. The species composition in our study area is probably varied, including species with many different ecological preferences.

Dragonfly assemblages and diversity

Although the different habitat types were generally well discriminated by their dragonfly assemblages, ephemeral river sections, temporary waters, and farm dams, all suffering high degrees of abiotic disturbance, i.e. drying out and/or flash floods, displayed very similar assemblages. This fit well with the general theory that communities of habitats subjected to harsh conditions are mostly affected by abiotic factors and are mainly colonised by generalist species (cf. Menge and Sutherland 1976; Peckarsky 1983). In fact the great majority of the recorded species are widespread in the study area and colonise all habitat types (cf. Table 3). Due to rapid development (cf. Johansson and Suhling 2004; Suhling et al. 2005b) and high dispersal ability these species are able to cope with such adverse habitat conditions. Hosting only generalist species, farm dams in Namibia do therefore not play an important role as potential refugia for dragonflies, unlike in South Africa (Samways 1989). Artificial waters like water holes and spring pools belong to this group, the former probably due to their poor habitat structures (see Materials and methods). All spring pools we examined were highly disturbed by grazing cattle or game.

Very well defined by their dragonfly assemblages, by contrast, are lakes and spring brooks, and, to a minor extent also wetlands below lakes and degraded spring brooks. Lakes and particularly wetlands below lakes have high species diversity and contribute highly to the regional γ -diversity. For instance, they add species like *Ceratogomphus pictus*, *Ictinogomphus ferox* and *Trithemis donaldsoni* to the fauna of our study area, which otherwise only occur along the large rivers (Martens et al. 2003). The wetlands below lakes also provide suitable habitats for a number of species that depend on well-vegetated perennial wetlands, such as *Urothemis edwardsi* and *Hemistigma albipunctum*. Although these habitats are in many ways similar to spring brooks, obviously

no species specialised to such spring brooks was able to use them as replacement habitats. Despite contributing to γ -diversity and hosting a specific assemblage lakes and wetlands below lakes are artificial and are not in need of special conservation measures.

Spring brooks, on the other hand, hold a very diverse and unique assemblage containing a number of species that were exclusively or almost exclusively recorded here in the entire Namibia (cf. Martens et al. 2003), including *Pseudagrion kersteni*, *Aeshna minuscula*, *Anax speratus*, *Crocothemis sanguinolenta*, *Orthetrum julia* and *Trithemis stictica*. Except for *A. minuscula*, which is mainly restricted to South Africa (Samways 1999), most are widespread in tropical Africa, some of them being common in certain regions, e.g. in Kenya (V. Clausnitzer personal communication). However, in Namibia all these species are rare, most probably due to habitat restrictions (cf. Suhling et al. 2003, 2005).

Threats and conservation of spring assemblages

Most perennial springs in the interior of Namibia occur in the mountain ranges of Damaraland and Kaokofeld, the Otavi Mts., the Waterberg and the Naukluft and Tsaris Mts. To our knowledge natural undisturbed spring brooks currently only remain in remote or protected areas of the Kaokofeld/Damaraland and the Naukluft and Tsaris regions. Historical distribution data (up to the 1990s, cf. Martens et al. 2003) demonstrated that *P. kersteni*, *C. sanguinolenta*, and *O. julia* occurred until fairly recently at springs in the Waterberg and the Otavi Mts. During our own fieldwork we only recorded *O. julia*. Overextraction of the aquifer in the region is a probable major cause as we have personally observed that some of the spring brooks that were still flowing strongly during the drought years of the early 1980s and 1990s have completely dried up. Today, even large springs, such as the one in Grootfontein in the Otavi Mts. (meaning ‘big spring’), which contained *P. kersteni*, are completely dry in most years. In other cases the springs were capped so that only the strongly shaded spring itself remained, where *O. julia* as a shade tolerant species can exist. Sadly, many of these springs occurred in proclaimed conservation areas, indicating that the conservation ethic often does not extend to include natural water bodies. All still existing spring brooks in the Otavi Mts. were degraded due to the construction of dams at the spring outflow and, consequently, typical spring brook species were absent while the generalists were still present.

Potential indicators

Indicators should demonstrate the health of communities in selected habitats (McGeoch 1998; Simberloff 1998). In our study we aimed to identify species

that would reflect the completeness or conservation status of their respective communities. We identified species (Table 4), which are mainly associated with two distinct habitat types (cf. Figure 2). Two lake species, *C. pictus* and *I. ferox*, appear to be good indicators for healthy lake assemblages. However, these lakes are impoundments created during the 20th century and hence are not original to the region (see above). Indicators are therefore not necessarily needed. *Azuragrion nigradorsum* occurs in natural and particularly degraded spring brooks and may mainly need perennial waters with vegetation. It is probably less sensitive to destruction of the original spring structure. The same may apply to *Agriocnemis exilis* and *Palpopleura jucunda*.

The majority of potential indicator species occurs exclusively in spring brooks (cf. Table 3), which are natural habitats in Namibia and host a number of unique assemblages and endemic species in various taxonomic groups. The potential value of reliable indicators to determine the conservation status of freshwater habitat refugia in arid areas is therefore highly relevant. Indicators should be sensitive enough to indicate the particular vulnerability and early recognition of habitat decline. Thus, the most sensitive indicators will be the first to show the effects of habitat deterioration. Indicators serve as a kind of trip-wire to show that habitat destruction has occurred, or are in the process of occurring. As we demonstrated above at least some of the selected species, viz. *P. kersteni*, *C. sanguinolenta*, *O. julia*, severely suffered from habitat destruction. Hence, at least these species are proven indicators according to the sensitivity standard. *Anax speratus* and *Trithemis stictica* should also meet the requirements due to their habitat restriction, although historical records to confirm local extinctions do not exist. These five species appear to be good indicators for the health of spring brook ecosystems. We suggest, however, that at least two species should be recorded at a given locality to assume good health of the assemblage, as the presence of one species may be accidental. If at least two species are around, the probability of good conditions is indeed favourable.

Hence, we suggest indicators for at least perennial spring brooks, which are under severe pressure in Namibia. We cannot comment on potential indicators for the health of the large perennial river systems, as we did not deal with the more humid northern parts of the country, where a bigger species pool occurs.

Table 4. Overview of the species finally proposed as indicators of the health of freshwater assemblages in central Namibia.

Indicator species	Type of habitat/assemblage
<i>Anax speratus</i>	Spring brooks
<i>Crocothemis sanguinolenta</i>	Spring brooks
<i>Orthetrum julia falsum</i>	Spring brooks
<i>Pseudagrion kersteni</i>	Spring brooks
<i>Trithemis stictica</i>	Spring brooks
<i>Ictinogomphus ferox</i>	Lakes
<i>Ceratogomphus pictus</i>	Lakes

The types of assemblages to which the species belong are indicated.

However, several rare species of dragonflies are present in that region, which depend on certain habitat conditions, such as undisturbed riverine forests and swamps (Suhling et al. 2004a). We therefore assume that dragonflies will have a high indicator potential for most kinds of freshwater wetlands in the entire area and may also serve as an indication of the sustainable use of water resources including evaluating measures to rehabilitate environments.

Namibia generally recognises that wetlands provide essential ecological services and cannot be allowed to degrade to such an extent that costly measures have to be taken to rehabilitate or even re-establish wetland processes. Though Namibia has recognised a decline in some species associated with freshwater ecosystems (cf. Bethune 1998; Curtis et al. 1998) the decline of such habitats has largely passed unnoticed. The establishment of an Index of Biological Integrity for wetlands and the implementation of regulations for the protection of wetlands have been identified as critical issues for management. If such an Index is to be introduced to evaluate the status, and possible vulnerability, of wetlands, then the identification of likely indicators is essential. We believe that our results indicate that odonates are at least sensitive indicators for natural spring brooks assemblages and because monitoring is repeatable and simple (i.e. without complex apparatus or training) they form a valuable tool for evaluating ecosystem integrity.

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Appendix

Table listing the localities surveyed. Presented are the geographical coordinates, the altitude, the river catchment to which they belong, their habitat type and the total number of surveys per locality. Table 1.

Locality	Degree S	Degree E	Altitude (m a.s.l.)	River catchment	Habitat type	No. of surveys
Fish R. Hardap	24.498	17.863	1132	Fish	Wetland below lake	3
Oanob River	23.297	17.054	1520	Fish	Wetland below lake	4
Kamanjab R.	19.624	14.838	1250	Huab	Wetland below lake	4
River at C28/Farm	22.692	16.548	1662	Kuiseb	Wetland below lake	3
Omdel River	21.900	14.544	150	Omaruru	Wetland below lake	2

Appendix. Continued.

Locality	Degree S	Degree E	Altitude (m a.s.l.)	River catchment	Habitat type	No. of surveys
Augeigas River	22.539	16.956	1626	Swakop	Wetland below lake	6
Gross Barmen 3	22.116	16.735	1238	Swakop	Wetland below lake	4
Koch River	22.549	16.938	1711	Swakop	Wetland below lake	4
S. Von Bach River	22.016	16.953	1333	Swakop	Wetland below lake	10
Ongongo Fall	19.140	13.820	730	Hoanib	Spring brook	4
Baynes River	17.231	12.805	969	Kunene	Spring brook	1
Spring Swartbooisdrif	17.263	13.700	778	Kunene	Spring brook	2
Tsams Ost	24.254	16.110	1439	Tsams R.	Spring brook	2
Gororosib River	24.280	16.237	1452	Tsauchab	Spring brook	4
Naukluft River	24.263	16.230	1482	Tsauchab	Spring brook	8
Tsauchab River 2	24.503	16.115	1100	Tsauchab	Spring brook	3
Zebra River Spring	24.598	16.300	1510	Tsauchab	Spring brook	3
Köcherbaumschlucht	24.153	16.327	1215	Tsondab	Spring brook	2
Noab Fountain	23.922	16.275	1396	Tsondab	Spring brook	2
Aub Gorge	19.727	13.800	992	Uniab	Spring brook	3
Palmwag	19.887	13.937	925	Uniab	Spring brook	8
Sesfontein	19.123	13.620	614	Hoanib	Degraded spring brook	1
Warmquelle	19.185	13.817	648	Hoanib	Degraded spring brook	2
Fransfontein	20.209	15.018	1137	Huab	Degraded spring brook	2
Didimala	19.527	18.019	1533	Omatako	Degraded spring brook	1
Lone Star	19.509	18.175	1423	Omatako	Degraded spring brook	2
Otjiosongombe Spring	20.474	17.276	1533	Omatako	Degraded spring brook	3
Waterberg Spring	20.510	17.243	1524	Omatako	Degraded spring brook	2
Klein Barmen	22.141	16.641	1209	Swakop	Degraded spring brook	2
Neuras	24.463	16.238	1198	Tsauchab	Degraded spring brook	3
Otavifontein Dam	19.670	17.378	1462	Ugab	Degraded spring brook	2
Okondeka Etosha	18.995	15.868	1110	Cuvelai	Spring pool	1
Ongongo	19.131	13.821	760	Hoanib	Spring pool	2
Ongongo	19.131	13.819	732	Hoanib	Spring pool	2
Ongongo	19.133	13.817	729	Hoanib	Spring pool	2
Gai-As	20.767	14.020	581	Huab	Spring pool	2
Weener Farm Spring	23.446	16.218	1042	Kuiseb	Spring pool	1
Otjisandjima Spring	17.462	13.246	1130	Omatako	Spring pool	2
Mariabronn	19.503	18.047	1486	Omatako	Spring pool	3
Awaxas Spring	19.761	13.849	964	Uniab	Spring pool	3
Bergsig	20.221	14.068	1026	Uniab	Spring pool	6
Fish R. Gamis	24.264	16.598	1329	Fish	Ephemeral R. section	2
Fish R. Kabib	24.617	16.943	1417	Fish	Ephemeral R. section	2
Fish R. Trib. Farm Lever	24.641	17.676	1400	Fish	Ephemeral R. section	2
Fish R. Usib	24.475	16.879	1351	Fish	Ephemeral R. section	2
Fish R. Mariental	24.656	17.935	1100	Fish	Ephemeral R. section	3
Khovarib Gorge	19.267	13.891	732	Hoanib	Ephemeral R. section	3
Hoarusib River	18.801	12.922	278	Hoarusib	Ephemeral R. section	1
Hoarusib River 2	18.516	12.866	279	Hoarusib	Ephemeral R. section	1
Hoarusib River 3	18.395	12.945	541	Hoarusib	Ephemeral R. section	1
Huab River	20.316	14.217	474	Huab	Ephemeral R. section	4
Gaub R., Weener Farm	23.470	16.218	1000	Kuiseb	Ephemeral R. section	3
Gaub River, Pass	23.483	15.767	752	Kuiseb	Ephemeral R. section	5

Appendix. Continued.

Locality	Degree S	Degree E	Altitude (m a.s.l.)	River catchment	Habitat type	No. of surveys
Kuiseb R. Friedenau	22.697	16.735	1621	Kuiseb	Ephemeral R. section	3
Kuiseb R. side canyon	23.305	15.758	750	Kuiseb	Ephemeral R. section	2
Kuiseb River Bridge	23.300	15.774	740	Kuiseb	Ephemeral R. section	3
River at C28	22.670	16.617	1680	Kuiseb	Ephemeral R. section	2
Pool at Neudam	22.504	17.373	1783	Nossob	Ephemeral R. section	2
Augeigas River	22.585	16.972	1630	Swakop	Ephemeral R. section	3
Kloake	22.564	17.023	1642	Swakop	Ephemeral R. section	4
River at B 1	22.347	17.051	1471	Swakop	Ephemeral R. section	2
Stengel River	22.546	16.938	1700	Swakop	Ephemeral R. section	5
Swakop Groß Barmen	22.122	16.711	1232	Swakop	Ephemeral R. section	2
Swakop on B1	22.034	16.936	1331	Swakop	Ephemeral R. section	3
Swakop R. Mouth	22.679	14.589	48	Swakop	Ephemeral R. section	7
Tsauchab River	24.504	16.093	1085	Tsauchab	Ephemeral R. section	5
River at C 35	20.629	14.865	911	Ugab	Ephemeral R. section	2
Ugab at Bridge C 35	20.862	14.959	618	Ugab	Ephemeral R. section	8
Ugab at Sorris Sorris	20.956	14.838	551	Ugab	Ephemeral R. section	8
Ugab Brandberg West	20.970	14.108	227	Ugab	Ephemeral R. section	8
Ugab Rest Camp	21.016	14.685	471	Ugab	Ephemeral R. section	8
Ugab Rhino Camp	20.961	14.135	254	Ugab	Ephemeral R. section	8
Uniab Delta	20.190	13.197	57	Ugab	Ephemeral R. section	8
Aub River	19.723	13.801	998	Uniab	Ephemeral R. section	3
Uniab Spring	19.915	13.988	1002	Uniab	Ephemeral R. section	8
Rainpools in Etosha	19.193	16.182	1130	Cuvelai	Temporary pond	1
Fish R.: Pond at C 4	24.418	16.841	1351	Fish	Temporary pond	2
Pond at D1998	23.194	15.383	900	Kuiseb	Temporary pond	1
Pond at C28	22.747	16.431	1786	Kuiseb	Temporary pond	2
Rainpool at C 28	22.604	16.809	1688	Kuiseb	Temporary pond	1
Rainpool at C36	21.266	15.173	986	Omaruru	Temporary pond	1
Spitzkoppe	21.815	15.184	1122	Omaruru	Temporary pond	2
Waterberg Pool 2	20.483	17.235	1686	Omatako	Temporary pond	2
Waterberg Pool 3	20.462	17.231	1613	Omatako	Temporary pond	2
Waterberg Pool 4	20.353	17.262	1687	Omatako	Temporary pond	2
Waterberg Pool 5	20.344	17.294	1686	Omatako	Temporary pond	2
Waterberg Pool 6	20.375	17.406	1701	Omatako	Temporary pond	2
Gross Barmen 2	22.069	16.865	1238	Swakop	Temporary pond	3
Karibib Pond	21.942	15.849	1199	Swakop	Temporary pond	3
Leopard Quelle	22.398	15.734	781	Swakop	Temporary pond	2
Pool near Stengel Dam	22.540	16.939	1691	Swakop	Temporary pond	1
Python Valley	22.436	15.728	780	Swakop	Temporary pond	2
Rainpool at B2	22.095	15.227	1077	Swakop	Temporary pond	1
Sand Pit at B1	22.028	16.931	1329	Swakop	Temporary pond	5
Tsaobis Kudu Ponds	22.379	15.749	740	Swakop	Temporary pond	*
Bergplaas	20.401	16.229	1325	Ugab	Temporary pond	1
Rainpool on C40	19.823	15.423	1291	Ugab	Temporary pond	1
Pool E Brandberg West	20.974	14.267	320	Uniab	Temporary pond	1
Birds Paradise	22.962	14.520	29	Kuiseb	Artificial waters	3
Ghaub Farm	19.466	17.726	1550	Omatako	Artificial waters	1
Goanikontes Oasis	22.669	14.820	176	Swakop	Artificial waters	7
Pool de la Bat Camp	20.509	17.243	1524	Swakop	Artificial waters	4
Puccinis	22.569	17.077	1668	Swakop	Artificial waters	4

Appendix. Continued.

Locality	Degree S	Degree E	Altitude (m a.s.l.)	River catchment	Habitat type	No. of surveys
Tsaobis waterhole 1	22.426	15.709	740	Swakop	Artificial waters	4
Tsaobis waterhole 2	22.470	15.728	714	Swakop	Artificial waters	4
Tsaobis waterhole 3	22.381	15.763	749	Swakop	Artificial waters	6
Tsaobis waterhole 4	22.393	15.809	732	Swakop	Artificial waters	6
Zoopark ponds	22.567	17.086	1700	Swakop	Artificial waters	5
Buellspport	24.149	16.362	1417	Tsauchab	Artificial waters	3
Urikos	24.444	16.171	1172	Tsauchab	Artificial waters	2
Solitaire	23.894	16.005	1105	Tsondab	Artificial waters	4
Outjo Fountain	20.105	16.148	1319	Ugab	Artificial waters	2
Kamanjab Dam	19.624	14.838	1250	Huab	Farm dam	4
Friedenau Dam	22.686	16.745	1670	Kuiseb	Farm dam	2
Gaub River Dams	23.479	15.769	749	Kuiseb	Farm dam	3
Otjosongombe Dam	20.478	17.308	1444	Omatako	Farm dam	2
Arandis	22.347	15.087	751	Swakop	Farm dam	6
Dam at C 32	21.983	15.838	1222	Swakop	Farm dam	3
Habib Dam	22.118	15.824	1241	Swakop	Farm dam	3
Habib Dam 2	22.088	15.796	1292	Swakop	Farm dam	3
Habis Dam 3	22.121	15.843	1240	Swakop	Farm dam	2
Koch Dam	22.550	16.938	1714	Swakop	Farm dam	4
Stengel Dam	22.547	16.938	1715	Swakop	Farm dam	5
Grootberg Pass	19.840	14.115	1411	Uniab	Farm dam	4
Hardap Dam	24.465	17.813	1129	Fish	Lake	4
Oanob Dam	23.301	17.031	1550	Fish	Lake	3
Otjivero Dam	22.283	17.957	1700	Nossob	Lake	3
Omatako Dam	21.149	17.178	1368	Omatako	Lake	2
Augeigas Dam	22.538	16.953	1689	Swakop	Lake	3
Avis Dam	22.572	17.129	1738	Swakop	Lake	3
Gross Barmen Dam	22.109	16.745	1239	Swakop	Lake	3
S. Von Bach Dam	22.012	16.950	1377	Swakop	Lake	10
Canal at Otjosongombe	20.500	17.293	1433	Omatako	Canal	4

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