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Species richness and conservation of Namibian freshwater macro-invertebrates, fish and amphibians

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Namibia is an arid country but has a diverse array of wetland habitats ranging from ephemeral water bodies and rain-pools, artesian springs supporting small perennial pools and streams, to the large perennial rivers of the north-east with their associated floodplains. These rivers drain wetter areas north of Namibia and contribute many tropical species to Namibia's wetlands. There are 778 described species of macro-invertebrates representing eight phyla with 81 endemics. Many invertebrates still have to be identified or described but presently the greatest endemism occurs among the Ostracoda (18 species), Coleoptera (17), Diptera (14), Anostraca (six) and Amphipoda (five species). In total, Namibia has 50 species of frog with three endemics. No caecilians or salamanders occur in Namibia. There are 114 species of freshwater fish with five endemics. Most Namibian wetlands occur outside protected areas. Over-exploitation of wetland resources and flow regulation are currently major threats, but new environmental legislation being formulated is based on the goal of sustainable use.

Keywords: Namibian wetlands; invertebrates; fish; amphibians; conservation.

Introduction

As a newly independent country, Namibia is concerned about the conservation of its biological diversity and a policy guideline to this effect is entrenched in the National Constitution. In accordance with the Convention on Biological Diversity, a national assessment of the current state of knowledge of biodiversity and conservation issues is currently nearing completion in Namibia.

In 1971 wetlands became the first, and so far, the only type of ecosystem to have their own international convention: the Convention on Wetlands of International Importance (Breen, 1991; Davis, 1994). The importance of wetlands is magnified in a country such as Namibia, which is generally arid with little surface water. Rainfall is variable, sporadic and often localized, ranging from less than 10 mm year^{-1} in the west to more than 600 mm year^{-1} in the northeast. Potential evaporation rates are high, ranging from 2600 mm year^{-1} to 3800 mm year^{-1} (Crerar and Church, 1988). In other words, evaporation is many times that of rainfall in all areas, so that rivers, lakes and other wetlands are few and most are ephemeral. These factors make Namibia's wetlands both valuable and vulnerable

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ecosystems. The use of wetland resources by a rapidly growing human population and anthropogenic changes to wetlands from water withdrawal, river flow regulation, siltation and other factors, increasingly threaten the survival of the wetland plants and animals that provide many of those resources in Namibia.

The western and southern third of the country is classed as arid, receiving rainfall of less than 150 mm year^{-1} (Fig. 1) (Lancaster *et al.*, 1984; Ward, 1992). This encompasses the Namib Desert, which extends from southern Angola along the coast of Namibia to just south of the South Africa–Namibia border and inland to about the 100 mm isohyet. Surface water in this region, west of the 150 mm isohyet, occurs mainly as ephemeral pans, or pools in granite outcrops or ephemeral river courses. Pans are shallow depressions, periodically containing water from local rainfall or discharge from endoreic rivers, that naturally dry out through evaporation. The biota of ephemeral waters are adapted to long periods of dormancy during dry phases and to rapid life cycles during the brief wet phases (e.g. Channing, 1976). Small permanent springs also support plants and animals adapted to less arid conditions than prevail in the surrounding area. The westward flowing ephemeral rivers that drain much of Namibia act as linear oases which link the wetlands of the arid coastal plain with those of the more mesic inland plateau. They support plants and animals in the Namib Desert that are typically found only in the wetter eastern regions (Jacobson *et al.*, 1995) and provide resources for local arid-adapted plains species during unfavourable rainfall periods (Loutit, 1991).

Most of Namibia is considered semi-arid and receives rainfall of between 150–600 mm year^{-1} (Ward, 1992). Surface water here (between the 150 and 600 mm isohyets, Fig. 1) occurs mainly as a result of impounding ephemeral river flow, but permanent springs, sometimes with small streams, are found in the Brandberg, Waterberg, Naukluft and Karas mountains. Numerous ephemeral pans occur in the north and northeast of this section of the country.

Northeastern Namibia has perennial rivers with seasonal floodplains and marshes which support a greater species richness than the rest of the country (Schlettwein *et al.*, 1991). None of these rivers has its headwaters in Namibia. As most of their water derives from upper catchments in Angola and Zambia, much of the aquatic fauna is characteristic of more mesic habitats than the arid zones of inland Namibia (Griffin and Channing, 1991). This area and the dolomite sinkholes and water-filled caves of the 'Karstveld' to the southeast of Etosha Pan receive rainfall of between 600 and 700 mm year^{-1}.

This paper is one of a series on the biodiversity and conservation of the natural environment in Namibia. It consolidates and updates previously published material on the species richness of Namibian aquatic macro-invertebrates, fish and amphibians, and presents this information by wetland type.

Species richness and endemism

Biodiversity can be addressed at various levels, the most fundamental of which is species richness. Table 1 gives the currently known species richness for each of the wetlands or wetland types, together with the probable number of endemics. These data are presented by order for invertebrates, and by family for fish and amphibians in Tables 2, 3 and 4 respectively. Table 4 also divides the families by wetland type. Endemic species, in this paper, are species that only occur in Namibia unless stated otherwise. The data for each group have been compiled from the literature, from recently identified material and from

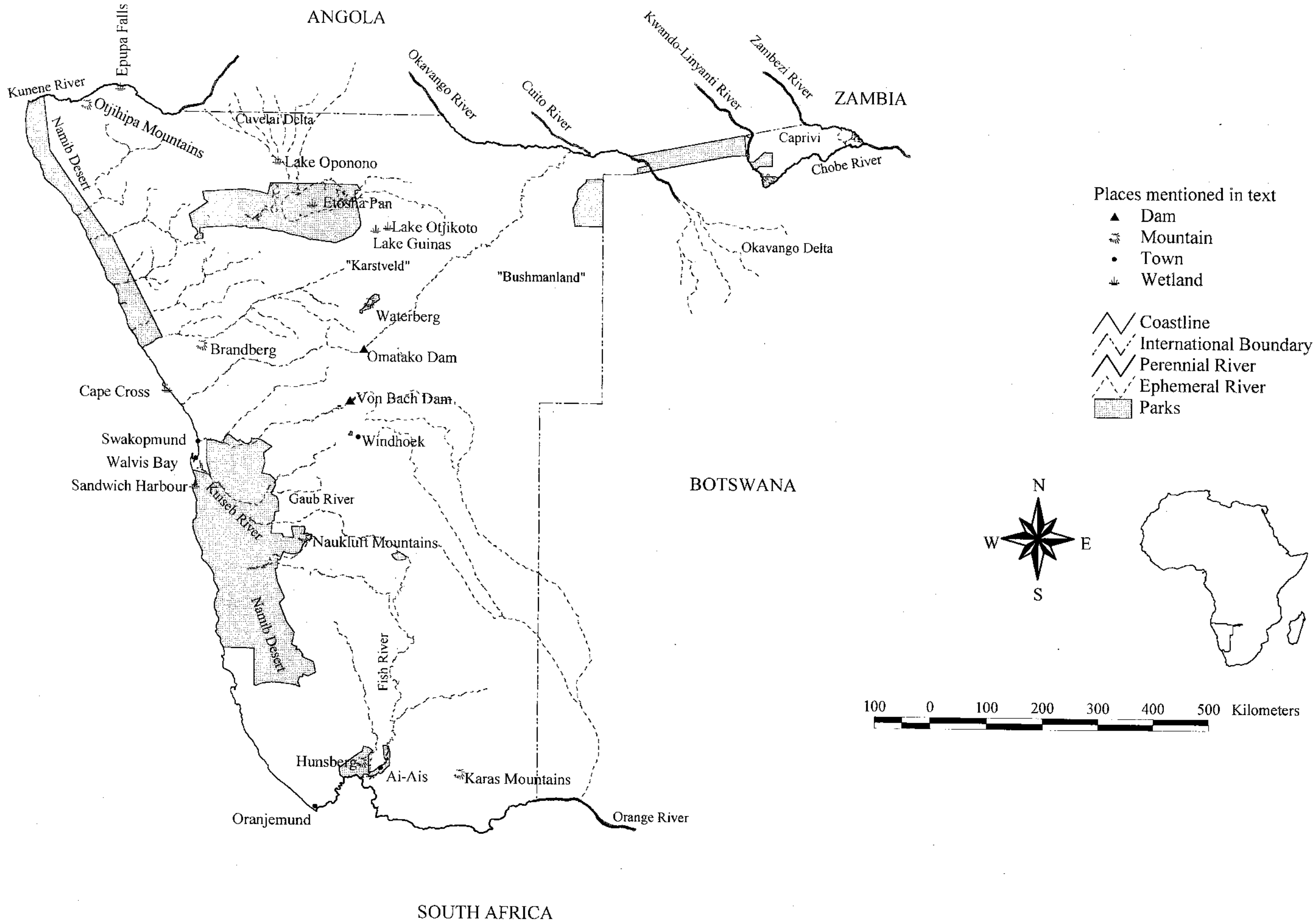

Figure 1. Map of Namibia showing the wetlands mentioned in the text as well as the major rivers and state dams.

Table 1. The species richness (S) and number of endemics (E) of major wetlands and wetland types in Namibia

Wetland or wetland type	Molluscs		Crustaceans		Insects		Other inverts[a]		Amphibians		Fish		Total species	Total endemics
	S	E	S	E	S	E	S	E	S	E	S	E		
Kunene River	15	0	9	0	105	4	1	0	11	2	65	5	206	11
Okavango River	27	0	6	0	203	?	10	0	30	0	79	0	355	0
Caprivi Rivers	28	0	24	1	254	?	22	1	38	1	82	1	448	4
Lower Orange and Fish Rivers	10	0	17	3	88	?	8	1	10	0	14	2	147	6
Ephemeral rivers	2	0	34	4	90	?	4	0	8	4	6	0	144	8
Dams	4	0	17	0	45	0	5	0	20	4	11	0	102	4
Etosha and the Cuvelai pans	11	0	60	16	72	4	7	0	15	0	49	0	214	20
Other pans[b]	5	0	30	8	54	0	3	0	0	0	4	0	96	8
Springs and seeps	3	0	20	3	127	2	8	0	7	1	0	0	165	6
Karst systems	3	0	12	8	60	1	5	0	5	0	7	2	92	11

[a]Refers to freshwater macro-invertebrates other than molluscs, crustaceans and insects.
[b]Refers to all pans not in the Cuvelai drainage.

continuing work on the biology and distribution of wetland fauna in Namibia. The number of aquatic invertebrate species is incomplete as many of those collected have not yet been identified to species. Study of the taxonomy and distribution of known and new species of invertebrates is ongoing, thus we refer only generally to taxon richness in this group. Similarly, because the fauna of neighbouring countries is poorly known, some species currently regarded as endemic may prove to be more widely distributed.

The fish are the best known of these three faunal groups in Namibia (Skelton *et al.*, 1985; van der Waal, 1991a,b; Hay, 1993; Skelton, 1993), but even in this group there have been some recent new records and the collection of unknown species, especially from the Kunene River (C.J. Hay, unpubl. data). Presently there is a total of 114 species of fish present in Namibia but only five are endemic.

Three new species of frog, a group previously thought to be relatively well known, have been discovered in the last 5 years (Channing, 1991; Griffin and Channing, 1991; Channing and Griffin, 1993; Branch and Braack, 1995; Griffin, 1995; Channing and Bogart, 1996). Three of the approximately 50 Namibian amphibian species are considered endemic. Table 5 shows the richness of Namibian amphibia compared to southern African and global amphibian taxa.

The freshwater macro-invertebrates of Namibia were reviewed by Curtis (1991). The best studied group is the Gastropoda, with a total of 26 species but no endemics in Namibia (Brown *et al.*, 1992; Brown, 1994). The largest group is the aquatic Coleoptera, of which some families have been well studied (references in Curtis, 1991) with recent work by Biström (1995), Hebauer (1995) and Uhlig and Jaeger (1995). A possible 17 species of aquatic Coleoptera are endemic to Namibia from a total of 200 identified species. Presently, 29 endemic species of freshwater Crustacea are thought to occur, with the Ostracoda (Martens, 1988, 1989, 1990) and Anostraca (Hamer and Brendonck, 1993, 1995; Hamer and Appleton, 1996) predominating.

Perennial rivers

Namibia's five perennial rivers occur on the borders of the country and are shared with neighbouring states (Fig. 1). Many species of fish and invertebrates are endemic to sections of one or more of the river systems, rather than exclusively to Namibia, and these are not included in the list of endemics. For instance, the snail *Bellamya monardi* is endemic to the Okavango and Kunene Rivers, while *Pila occidentalis* is endemic to the northern rivers and pans of Namibia (Brown, 1994). The common freshwater mussel *Coelatura kunenensis* is known from the Kunene and Okavango Rivers as well as the Etosha/Cuvelai system, while the larger, less common *Aspatharia pfeifferiana* is known only from the Kunene, Okavango and upper Zambezi Rivers (Appleton, 1996). Several new species of insects have been collected recently in relatively undisturbed river margin vegetation, but have not been found where the vegetation has been partially destroyed (E. Marais, pers. comm.).

The richness of Namibian frogs is greatest along the perennial rivers, because these faunas include riverine and wetland species plus species of more arid areas with broad regional distributions. Namibian endemic frogs, however, are characterized as being arid-adapted and are not generally associated with perennial river systems (M. Griffin, unpubl. data). The one endemic frog in the Caprivi, the Mpacha grass frog *Ptychadena mpacha*, is dependent on perennial waters and will probably prove to have a wider distribution within the marshy habitat of the Caprivi region.

Table 2. The numbers of families and species of freshwater macro-invertebrates with numbers of potential endemics recorded from Namibian wetlands (updated from Curtis, 1991)

Phylum	Class	Sub-Class	Order	Families	Species	Endemics	Reference
Porifera				2	3	0	Curtis (1991)
Cnidaria				2	2	0	Curtis (1991)
Platyhelminthes				6	9	0	Curtis (1991)
Ectoprocta				2	5	0	Curtis (1991)
Nematoda				6	10	1	Curtis (1991)
Annelida							
	Oligochaeta			5	13	1	Curtis (1991), Palmer (1997)
	Hirudinea			3	16	3	Curtis (1991), Palmer (1997)
Mollusca							
	Gastropoda			9	26	0	Brown (1994)
	Bivalvia			5	13	0	Appleton (1996), Curtis (1991)
Arthropoda							
	Crustacea						
		Ostracoda		3	52	18	Curtis (1991), K. Martens (*in litt.*)
		Copepoda		2	19	1	Curtis (1991). N.A. Rayner (*in litt.*)
		Branchiopoda					
			Anostraca	3	19	6	Hamer *et al.* (1993, 1995, 1996)
			Cladocera	5	19	1	Curtis (1991), N.A. Rayner (*in litt.*)
			Notostraca	1	2	0	Curtis (1991)
			Conchostraca	6	15	3	Curtis (1991)
		Malacostraca					
			Amphipoda	2	6	6	Griffiths (1989, 1991a,b)
			Isopoda	1	4	4	Kensley (1995)
			Decopoda	3	6	0	Curtis (1991)
	Insecta						
			Ephemeroptera	6	19	0	Curtis (1991), Palmer (1997)
			Plecoptera	1	2	1	Curtis (1991)
			Trichoptera	6	35	3	E. Marais (pers. comm.)

Table 2. (*Continued*)

Phylum	Class	Sub-Class	Order	Families	Species	Endemics	Reference
			Odonata	10	77	0	NIC, Curtis (1991)
			Diptera	13	179	14	NIC, Curtis (1991)
			Neuroptera	1	1	1	Curtis (1991)
			Coleoptera	10	200	17	[a]
			Hemiptera	12	45	3	Curtis (1991)
			Orthoptera	2	7	0	Gunther (1995)
Totals				127	804	83	

[a] Perkins and Balfour-Browne (1994), Hebauer (1995), Biström (1995), Uhlig and Jaegar (1995).
NIC = National Insect Collection.

Table 3. Families of freshwater fish found in Namibia with the current numbers of species and endemics (Skelton *et al.*, 1995; van de Waal, 1991a,b; Hay, 1993; Skelton, 1993)

Family	Species	Endemics
Mormyridae	6	
Kneriidae	3	
Characidae	4	
Hepestidae	1	
Distichodontidae	3	
Cyprinidae	34	
Claroteidae	1	
Amphiliidae	3	
Austaglanididae	1	
Schilbeidae	1	
Clariidae	8	2
Mochokidae	9	
Cyprinodontidae	7	1
Aplocheilidae	1	1
Poeciliidae	2	
Centrachidae	1	
Cichlidae	26	1
Anabantidae	2	
Mastacembelidae	2	
Total	115	5

Kunene River. The 340 km of the lower Kunene River bordering Namibia has a steep gradient and narrow gorge with no floodplains or associated standing water. The river flows swiftly with little submerged or emergent vegetation (van Zyl, 1991). It has a low richness of macro-invertebrates and frogs compared with the northeastern rivers (Table 1), perhaps because it has been less extensively sampled. Within the lower phyla only one leech has been recorded (Oosthuizen and Curtis, 1990) and the crustacean fauna is poorly represented. The freshwater shrimp *Macrobrachium vollenhoveni* reaches its southern limit in the Kunene (Kensley, 1970), as does the freshwater oyster *Etheria elliptica* (Appleton, 1996). Both of these edible species are found nowhere else in Namibia.

The Kunene River has 65 fish species, of which at least five are thought to be endemic (C. Hay, unpubl. data). Fifty-nine of the Kunene species also occur in the Okavango River, suggesting previous links between the two catchments (Skelton *et al.*, 1985). Of the five endemics, *Schwetzochromis machadoi* and *Thoracochromis buysi* are common species, *Thoracochromis albolabris* and *Sargochromis coulteri* are commonly encountered, but *Chetia welwitchi* is known only from museum specimens and has not been collected in recent surveys. Also, little is known of two other species, *Kneria maydelli* and *Clariallabes* sp, the latter of which is so far undescribed (P.H. Skelton, pers. comm.).

Although the upper Kunene River drains areas with a rich frog fauna in the central highlands of Angola, the Namibian portion of the river apparently contains no downstream elements of this fauna (M. Griffin, unpubl. data).

Table 4. Watershed and regional distribution of Namibian frogs (figures include those species known and expected to occur)

Area/biotope	Pipidae	Bufonidae	Microhylidae	Ranidae	Rhacophoridae	Hemisotidae	Hyperoliidae	Total
East Caprivi wetlands	2	6	2	18	1	1	4	34
West Caprivi wetlands	2	5	2	11	1	0	4	25
Okavango River system	2	5	2	13	1	0	5	28
Kunene River system	1	5	1	6	0	0	2	15
Ephemeral west flowing rivers	1	6	1	4	0	0	0	12
Cuvelai and Etosha system	1	5	2	6	0	0	1	15
Kavango,Bushmanland and Hereroland	1	5	2	10	0	0	3	21
Karstveld	1	2	2	4	0	0	1	10
Impoundments	1	6	2	8	0	0	2	19
Springs and Seeps	1	6	2	13	0	0	2	24
Orange River system	1	4	1	5	0	0	0	11
Fish River system	1	0	1	3	0	0	0	5
Southern third of country temporary wetlands	1	2	1	4	0	0	0	8
Ephemeral east flowing rivers	1	0	0	3	0	0	0	4

Table 5. Species richness of Namibian amphibians compared to southern African and global amphibian totals

Taxa	Namibia	Southern Africa	Global
Orders	1	1	3
Families	7	9	41
Genera	17	31+	428+
Species	50+	140+	4522+

Kwando-Linyanti and Zambezi-Chobe Rivers (Caprivi wetlands). The Kwando-Linyanti and Zambezi-Chobe systems have gentle gradients in Namibia, with extensive seasonal floodplains, backwaters and seasonal and permanent swamps. In Table 1, the three river systems are considered together because, in times of exceptional flooding, the systems are inter-linked and much of the eastern Caprivi area becomes one large floodplain. Table 6 shows the lengths of these and other perennial rivers in Namibia. The Caprivi wetlands have the highest overall species richness of Namibian wetland systems (Table 1). Endemism is low, however, because the Namibian sections of these rivers are but a small part of these large systems.

The largest number of species of lower phyla has been collected here, including the rare freshwater jellyfish, *Limnocnida tanganjicae* (Seaman *et al*., 1977; Curtis, pers. obs.) and the freshwater sponge, *Potamophloios hispida* (National Museum of Namibia collection). Fourteen species of Annelida have been recorded (Oosthuizen and Curtis, 1990; Curtis, 1991). The greatest variety of Mollusca occurs in the Caprivi, with 16 snail, one limpet and ten mussel species. The tiny snail *Lobogenes michaelis* has only been recorded in Namibia from the Kwando River (Brown *et al*., 1992). Crustacean richness is higher than in the other perennial rivers. The Coleoptera have 140 species, representing 55% of the insect species of these river systems. The second highest richness of Odonata and Diptera species in Namibia occurs here (Table 2).

Eighty-two fish species occur in the Namibian part of this river complex (van der Waal and Skelton, 1984; Bethune and Roberts, 1991; C.J. Hay unpubl. data). Thirty-eight species of frogs are known or are expected to occur in the Caprivi wetlands (Griffin, 1995a) representing three quarters of all known Namibian frog species. This fauna is characterised by a large number of highly water dependent species, e.g. the genus *Ptychadena* and the Hyperoliidae, taxa with otherwise very limited distributions in the arid regions of Namibia.

Table 6. Lengths of permanent rivers in Namibia and the approximate lengths officially protected in reserves

River	Length in Namibia (km)	Approximate length protected (km)	Protected (%)
Kunene	340	40	12
Okavango	470	15	3
Kwando-Chobe	484	85	18
Zambezi	152	0	0
Orange	620	80	13
Totals	2076	220	

Okavango River. The 470 km of the Okavango River in Namibia (Table 6) also has a high species richness, partly due to its varied habitats, with rapids, backwaters and floodplains (Bethune, 1991). The mollusc fauna is similar to that of the Caprivi wetlands (Brown *et al.*, 1992), but the insect fauna differs, with around 40 species recorded only from the Okavango. This river has the highest odonate and dipteran species richness of any wetland habitat in Namibia. Very few Crustacea have been recorded.

The Okavango River holds 79 fish species, none of which is endemic (Hay *et al.*, 1996). Two species, the catfish *Clariallabes platyprosopos* and the spiny eel *Aethiomastacembalus vanderwaali*, are listed as red data species (Skelton, 1987). Although they occur in both the Okavango and Zambezi Rivers, they have distributions restricted to rapids which are uncommon habitats of these rivers in Namibia. The frog fauna is very similar to that of the Caprivi wetlands but with fewer (about 30) species.

Orange River. The 620 km of the Orange River on the southern border of Namibia has a low gradient with tree-lined banks and few submerged aquatic macrophytes. Except for the vicinity of the mouth, the lower Orange River has no seasonal floodplains or backwaters. Regulation of the river flow this century has changed the Orange from a seasonal to a perennial river, and this is reflected in its low invertebrate richness (Palmer, 1997) (Table 1). Of the ten mollusc species found, *Physa acuta* and *Lynaea columella* are aliens introduced into Africa from North America (Brown, 1980).

One of the 14 fish species is endemic to the lower Orange River, and four to the Orange River system (Hay, 1993). Two of these species, *Barbus hospes* and *Austroglanis sclateri*, are listed as rare in the red data book (Skelton, 1987). Although *B. hospes* is common in the lower Fish River (Hay, 1991), its restricted distribution makes it vulnerable to manipulation of the system, such as from impoundments. The Fish River is a tributary of the Orange River sustained by permanent springs and seepage water from the Hardap Dam. This dam retains any annual floodwater from the upper catchment except during exceptional floods. The Fish River contributes a number of species to the richness of the Orange River system, including three endemic Crustacea (Barnard, 1929; Martens, 1984).

The amphibian fauna is as depauperate as that of the Kunene River, by contrast to the species-rich Caprivi fauna. Most species here are range extensions of the Namaqualand fauna, which includes arid-adapted species of otherwise wetland-dependent genera, e.g. *Strongylopus*, or are wetland dependent species from upstream in South Africa. No Namibian endemic amphibians are associated with this system.

Ephemeral rivers

All of central Namibia's rivers are ephemeral. They have periodic surface flow, following local rains, of a few days or weeks, sometimes not for several years in succession. The sandy river courses contain alluvial aquifers that provide perennial groundwater to riparian vegetation, people, livestock and wildlife. At some places groundwater seeps provide surface water pools and streams; at others the water table is shallow enough to be reached by digging. Oryx and elephants are adept at this and the holes they dig are used by a myriad of other creatures as water sources (Jacobson *et al.*, 1995).

The greater invertebrate richness in ephemeral rivers compared with the now perennial Orange River (Palmer, 1997) (Table 1) is probably due to greater habitat variety (permanent pools and streams of varying depth and vegetation cover, rainwater pools, floodwater pools and marshy areas) of ephemeral rivers which the Orange River has lost since river regulation. The fauna of these localized habitats comprises some taxa typical of ephemeral habitats such as Crustacea, as well as lotic elements brought downstream during floods. Insects predominate in the permanent streams and pools, with Coleoptera making up 39% of the insect fauna. Ostracoda comprise 30% of the Crustacea species here, but only four species are endemic. Day (1990) separates the species richness of ephemeral river invertebrates by micro-habitat, and found higher richness present in permanent lakelets and streams than in ephemeral rainwater pools. The greater variety of invertebrate fauna in rainpools in ephemeral rivers than in similar rainpools on open plains (see below) may reflect the greater predictability of rain inland on the headwaters of these rivers. Rainpools in rivers tend to be longer lasting and become colonized by insects.

The ephemeral rivers contain no fish species capable of surviving dry periods as eggs, such as the endemic *Nothobranchius* sp of Caprivi. However, where the topography provides deep rock pools, as in the Gaub and Kuiseb canyons, some vertebrates survive the periods between flood events (Seely and Griffin, 1986). Fish species introduced to the dams on these rivers are occasionally found in such pools after floods (see Impoundments or Dams). The status of *Barbus breviceps*, an indigenous fish species found in isolated pools in the Otjihipa mountains near the Kunene River, is still under investigation. Although the introduced platanna *Xenopus laevis* depends on permanent water and is found in these isolated habitats, the indigenous frogs are essentially opportunistic users of these ephemeral river pools.

Karst sinkholes and subterranean lakes

To the southeast and east of Etosha Pan, underground aquifers exist in extensive dolomite and limestone formations known as the 'Karstveld' (Fig. 1). Karst features are caves, subterranean lakes, and water filled sinkholes which formed after the roofs of caves collapsed. The karst systems, especially those to the west, have yet to be fully explored (Irish, 1991). The habitats have a low species richness but a high level of endemism, even between water bodies, among their crustacean (six Amphipoda: Griffiths, 1989, 1991a,b, and four Isopoda: Kensley, 1995) and fish faunas (Skelton, 1990). There are no amphibians endemic to the karst lakes, but they are used opportunistically by amphibians such as *Kassina senegalensis*, *Tomoptera* spp and *Bufo* spp (Marais, 1990).

Pans

Throughout Namibia shallow depressions or pans fill up periodically with rainwater. This form of ephemeral wetland is characteristic of arid lands where evaporation is higher than rainfall (Williams, 1985). Some form large or extensive wetlands when inundated. Pans in the higher rainfall regions fill seasonally, but in the arid west and south they may remain dry for many years. The more regularly inundated pans and those which retain water for longer periods tend to have a greater biodiversity (Allan *et al.*, 1995).

The fauna of pans is typical of ephemeral waters, with species adapted to withstand long dry periods and to respond rapidly to rainfall (Channing, 1976; Williams, 1985; Kok, 1987; Hamer and Appleton, 1991a,b). The Crustacea predominate because of their short life cycles and desiccation-resistant eggs. Many can hatch, grow and produce eggs within 24 hours (Allan *et al.*, 1995). Some frogs can complete the necessary cycle in 22 days (Channing, 1976). These wetlands have the highest crustacean richness in Namibia and a high level of endemism, especially among the Ostracoda (Martens, 1988, 1989, 1990) and to a lesser extent the Anostraca (Hamer and Brendonck, 1993, 1995; Hamer and Appleton, 1996). The overall taxon richness of Crustacea found in Namibian pans is greater than that in pans of the Orange Free State in South Africa, where no ostracods and fewer species of other groups are found (Seaman and Kok, 1987). The overall richness of lower phyla is low. In the north and northeast, species of molluscs such as *Pila occidentalis* and various bulinids occur which are capable of aestivation from one wet season to the next. In the south the only mollusc species capable of surviving very long dry periods is the tiny *Bulinus reticulatus* (Curtis, 1991). The insects are represented by species capable of flying into newly inundated areas.

In general, fish are absent or rare in seasonal pans. One endemic fish, *Nothobranchius* sp, a red data fish yet to be described, has desiccation-resistant eggs with arrested development. It occurs in a few ephemeral rainpools in Caprivi (van der Waal and Skelton, 1984).

Approximately a third of Namibia's amphibian fauna uses pans opportunistically. This fauna tends to be arid-adapted with broad sub-regional distributions. Several of Namibia's endemic frogs use pans for breeding (M. Griffin, unpubl. data).

The largest pan system is the Etosha-Cuvelai drainage, which extends from southern Angola southeastward to the Etosha Pan (Fig. 1). Oshanas, linearly-linked shallows pans in the lower part of the Cuvelai drainage, fill with local rainwater and sometimes floodwater from the perennial Cuvelai headwaters in Angola. Periodically during exceptional floods, once in 7–10 years, this water reaches the Etosha Pan. The oshanas of the Etosha-Cuvelai system differ from other pans in that during floods, fish move southwards with the water from Angola (van der Waal, 1991b). When this happens the aquatic invertebrates of ephemeral lentic waters are suddenly subjected to conditions and predators of lotic systems.

The greatest richness of Ostracoda (50% of the 60 species of Crustacea) has been recorded from the Cuvelai system, partly as a result of extensive sampling over the years (Sars, 1927; Martens, 1984, 1988). The 16 endemic crustacea in Table 1 are all Ostracods. The numbers of insect species here are low and dominated by the Coleoptera (38% of species). The mollusc fauna found in the oshanas of the Cuvelai system has a higher richness than other pans because of species associated with the more permanent water to the north. In addition, some invertebrate species have been translocated to the Cuvelai drainage with the interbasin transfer of water from the Kunene River (Curtis, 1995).

Seventeen fish species have been recorded in the northern part of the Cuvelai River, seven in Lake Oponono, a large oshana to the north of Etosha, and five in the Etosha Pan. Forty-six fish species from the nearby but separate Kunene River have been inadvertently introduced to the Cuvelai drainage system since 1972, via pipes, a dam, and canals that supply northern Namibia with water. Some of these have invaded the oshana system, with unknown implications for the local fauna (van der Waal, 1991b). Angolan species of amphibia do not, by contrast, appear to move southwards with floods. No records of Angolan amphibia in the lower reaches of the Cuvelai have been confirmed. Several species of sand frogs, *Tomopterna* spp, use this system extensively, as does the African bullfrog *Pyxicephalus adsperus*, which provides a seasonally important food source for rural people.

Springs and seeps

Despite Namibia's aridity, numerous springs of various kinds are found throughout the country in differing climatic and geological situations. Many are associated with ephemeral rivers but some, not found in riverbeds, support deep pools and small streams while others merely form small shallow pools or damp patches. The invertebrate species richness of springs and seeps is the highest of all the systems except the perennial river wetlands. The more water-dependent insects predominate, particularly the Coleoptera and Diptera.

Kneria maydelli and *Barbus breviceps* are the only species of fish found in spring pools, but the biology and status of these species need further study. Although springs are used for opportunistic breeding by local amphibians, most of the frog species inhabiting them are adapted to ephemeral conditions. The water dependent *Rana fuscigula* occurs as a disjunct population in the Naukluft Mountains, where tadpoles of this species occasionally exhibit neoteny in this isolated stream habitat (M. Griffin and A. Channing, unpubl. data).

Small mineral springs which seep from faults in gypsous crusts are common in several deserts (Day and Seely, 1988). In the Namib Desert, a fault line running along much of the coast provides a series of springs, one of which was studied extensively by Day and Seely (1988). Due to the intense solar radiation, water evaporates rapidly and $CaCO_3$ precipitates from the water resulting in a calcium enriched NaCl brine. Only one of the 31 taxa occurring in these gypsous springs is a crustacean, the ostracod *Sarscypridopsis ochracea* (Day, 1990). A third of these taxa appear to be restricted to this type of habitat, while just less than a third also occur in freshwater springs. Five beetle species occur in gypsous springs as well as ephemeral waters, reflecting their ability to withstand not only high salinity but also desiccation (Day, 1990). Although several species of frogs occur in the vicinity of these springs, the springs are not used as breeding sites.

Impoundments or dams

Namibia is one of few countries in the world where impoundments are built on ephemeral rivers. Twelve large state dams and innumerable farm dams hold water for varying lengths of time. All have widely fluctuating water levels, consequently have very little marginal or submerged vegetation, and offer little habitat variety. The number of macro-invertebrate species is low and no endemics are associated with these waterbodies (Table 1). In a study on the zooplankton diversity in three Namibian impoundments, ten crustacean species (seven cladocerans and three copepods) and one rotifer were identified (Rayner *et al.*, 1995). Of these, only the cladocera *Ophryoxis* sp in Omatako Dam appears to be a new species and the first record of this genus in southern Africa. An uncommon invertebrate found in a few dams is an unidentified species of freshwater bryozoan capable of withstanding desiccation (B.A. Curtis, unpubl. data). The snail *Bulinus tropicus*, which is intermediate host for the livestock parasitic stomach fluke *Calicophoron microbothrium*, is widespread throughout Namibia as a result of these artificial waterbodies (Curtis, 1990).

Five cyprinid fish, including the alien *Cyprius carpio*, four cichlids, a clariid, and the alien centrachid *Micropterus salmoides*, have been introduced to state and farm dams (Hay, 1993). Occasionally these introduced species are found in downstream pools in the ephemeral rivers after floods. The common platanna occurs in artificial impoundments and nearly all permanent water bodies in Namibia, but few other amphibians have exploited this unfamiliar habitat.

Conservation status of Namibian wetlands

The Convention on Wetlands of International Importance encourages contracting parties to promulgate wetland reserves (Davis, 1994). Namibia became a contracting party in

December 1995 and initially designated four wetlands to the list, totalling 6296 km^2. Etosha Pan is the only Ramsar site that is not a coastal wetland; the other three are the Walvis Bay wetlands, Sandwich Harbour and the Orange River mouth. The last is a transboundary site shared with South Africa. A further eight wetlands, of which five are inland systems, and three of Namibia's offshore islands have been identified as possible candidates for the Ramsar list. These are the Kunene River mouth, Cape Cross lagoons, Swakopmund saltworks, lakes Guinas and Otjikoto, the 'Bushmanland' pans, the lower Okavango river, the wetlands of the East Caprivi, and the offshore islands of Ichaboe, Possession and Mercury. Of the listed wetlands, currently only Sandwich Harbour and Etosha Pan are protected in reserves (see Barnard *et al.*, this issue).

Sections of the perennial Okavango River, Kwando River and Linyanti River wetlands are included in parks, as are the Naukluft Mountain wetlands (Table 6). All the protected sections of perennial rivers in Namibia extend only to the centre of the main channel since they are either Namibian border rivers or form the protected area boundary. The 80 km of the Orange River under formal protection (Ai-Ais/Hunsberg Reserve Complex) is in fact poorly safeguarded and is being continually degraded by human activities.

Unfortunately, most other Namibian wetlands are not formally protected. Because of this they are open to over-exploitation and inadvertent destruction. No species of aquatic invertebrate, fish or frog is protected in Namibia. Although most wetlands are not in protected areas there is scattered legislation theoretically controlling many human activities that can lead to wetland degradation, such as pollution, removal of riparian forest, introduction of alien species and abstraction of water (Glazewski and Kangueehi, 1997). A new freshwater fisheries act aims to control fish exploitation, prevent the introduction or transfer of alien fish, and protect vulnerable species and habitats of special ecological significance (MFMR, 1995).

Threats to Namibian wetlands

Approximately 60% of the Namibian population lives around or near major wetlands (National Planning Commission, 1993). Overuse of natural wetland resources and agricultural land has led to severe deforestation (Kojwang and Erkkilä, 1996), overgrazing (Bester, 1996) and over-fishing (van der Waal, 1991a; Hay *et al.*, 1996) in many areas.

National campaigns to combat human and stock disease vectors and agricultural pests using pesticides, including DDT, appear to have had a negative impact on the aquatic invertebrate fauna of Namibia's northern wetlands, particularly the Kwando River. Although no local data are available, the same can be expected of indigenous frogs and bats, groups also known to be sensitive to environmental poisons.

The efforts to supply Namibia's major urban centres with water and electricity are further threats to Namibia's wetlands. Boreholes and dams can no longer satisfy the nation's water demand, necessitating new water transfer schemes. Most notable of these is the Eastern National Water Carrier which, when complete, will transfer water from the Okavango River via pipelines and open canals some 700 km to Von Bach Dam, the main supply dam for Windhoek (Bethune and Chivell, 1985; Ravenscroft, 1985). On the Kunene River, a planned hydroelectric scheme at Epupa Falls requires the building of a large dam which will inundate some 90 km of river and riverine forest and cover 295 km^2. This project and a 6 m^3/s water abstraction scheme at Calueque will both have serious consequences on the downstream ecological functioning of this river (Simmons *et al.*, 1993;

Bethune, 1995). New large-scale groundwater abstraction schemes are also planned for the Karstveld area. These will have implications for the wetland biota in this region.

Human interference poses a threat to three IUCN red data freshwater fishes endemic to Namibia. *Clarias cavernicola* (cave catfish), *Tilapia guinasana* (Otjikoto tilapia) and *Nothobranchius* sp (Caprivi killifish) are threatened with extinction because each occurs in a single or very few water bodies which are highly vulnerable to human impact. The three red data fish species occurring in the lower Orange River are also of conservation concern.

Namibian endemic frogs are for the most part safe from human impacts. Most are highly adapted for opportunistic and irregular breeding (Channing, 1976), and occur in habitats not particularly under direct human threat. Namibia's most threatened frog, the desert rain frog *Breviceps marops*, is one of several Namibian species that are not wetlands dependent. The tadpole stages in these species are completed within the eggs which are laid in moist ground. The threat to *B. marops* is from the destruction of habitat (coastal hummocks) during diamond extraction processes (Griffin, 1995b).

Sustainable use of natural resources is a guiding principal included in Namibia's constitution, and a policy requiring environmental assessment of developments is in place (Tarr, 1996). Water is considered a major wetland resource but is also fundamental to the habitat. The consultative process needed to decide the desired future state of particular wetlands or wetland resources, which is a first step to determine their environmental water requirements, needs to be formalized in Namibia if sustainable use is to work.

Conclusion

Despite its aridity, Namibia has a diverse array of wetland habitats which support a variety of aquatic fauna. The high rainfall of the northeast, together with rivers draining well-watered upland regions, increases Namibia's wetland biotic diversity significantly and links the country faunistically to the more mesic tropical systems to the north. The unusual formations of the karst system, as well as the ephemeral pans and numerous artesian springs, provide a variety of isolated habitats which has led to extensive speciation among certain groups, particularly the Crustacea.

Namibian wetlands are all threatened by the impact of man's activities, but particularly those in the north, around which more than 60% of the country's human population is centred. All conservation legislation is currently being reviewed in a process designed to consolidate and improve it (Glazewski and Kangueehi, 1997). There is need for an inventory of all Namibian wetlands and their associated fauna and flora so that those of special scientific interest can be included in this legislation. To achieve sustainable use of wetland resources in Namibia, the methodologies developed in other countries to determine wetland water requirements need to be applied in Namibia. These measures will not address the present lack of law enforcement and further efforts need to be made to improve education and create incentives for community based wetland conservation, so as to increase awareness of the values of Namibian wetlands.

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