# Environmental Correlates of Aquatic Faunal Distribution in the Namib Desert

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The very limited literature on the limnology of the Namib Desert is reviewed. The major habitat types are described: permanent systems include two relatively large lakelets, a number of freshwater springs that form shallow trickles or pools, and a series of brackish to hypersaline mineral springs on gypsous crusts; ephemeral systems include rainpools that form in endorheic basins, pools left in river-beds after they have stopped running, and the rivers themselves, which contain water for very short periods.

A checklist of the aquatic fauna is provided. Analyses of the entries in the list show that ephemeral waters are dominated by crustaceans and permanent waters by insects, especially immature forms. The number of taxa is greatest for permanent lakelets and streams and least for endorheic rainpools and gypsous springs. The number of taxa does not correlate with salinity for any of the habitat types nor with depth of water in any except the gypsous springs. The major determinant of faunal richness is isolation, the number of taxa showing strongly significant negative correlations with distance from a given pond to another of the same kind, or another of any kind, for all types except the gypsous springs.

## INTRODUCTION

The characteristics of athalassic (non-marine) surface waters in any region depend primarily on the geology of their catchments and on the climate. In arid areas, by far the more significant of these two is the climate, to the extent that one might expect deserts to have no surface waters at all except for ephemeral pools that form, or rivers that run, for a brief period after rain. This is far from the truth, although the most obvious waterbodies in deserts are certainly temporary.

The Namib Desert is no exception. Climatic conditions are severe, to the extent that evaporation rates may reach 4000 mm $y^{-1}$ (Lancaster, Lancaster and Seely, 1984, give a mean pan evaporation rate of 3168 mm $y^{-1}$ for the central Namib). Rainfall is spatially erratic and highly unpredictable from year to year, while the mean annual rainfall over most of the Namib is considerably less than 100 mm $y^{-1}$ (Lancaster *et al.*, 1984). Winds are high. Thus it is not surprising that, as in deserts everywhere, although surface waters do exist in the Namib, they are small, scattered, and often ephemeral.

Despite their small sizes and scattered distribution, the inland waters of the Namib are chemically very diverse, resulting in a variety of permanent or semi-permanent pools and springs with a more diverse aquatic fauna than may otherwise be expected in the region. Because the rate of evaporation exceeds rainfall, permanent waterbodies cannot form unless they are fed from underground sources. Thus all the surface waters in the Namib can be divided into ephemeral ones that form as a result of rainfall, and semi-permanent or permanent ones fed by groundwater.

This paper briefly reviews the literature pertinent to Namib limnology, documents what is known of the distribution and the physical and biotic features of the major types of surface waterbody in the Namib Desert and examines some of the determinants of species richness in the aquatic fauna. The area under discussion is limited to that from the Munutum River in the north (Fig. 1) to Lüderitz (27° N, 15° E) in the south and extends inland to about the 100 mm isohyet because, although the Namib Desert extends well into Angola, no limnological information is available on that region. Further, with the exception of ephemeral pools forming after rain at Sossusvlei and in a few small depressions near Lüderitz, there are virtually no athalassic surface waters (i.e., those not influenced by the sea) in the dune field south of the Kuiseb River.

Largely for logistic reasons, including the unpredictability of rainfall, the Namib Desert is remarkably poorly known limnologically so that the literature on the topic is very limited. A few papers provide some limnologically pertinent information on climate (Lancaster *et al.*, 1984), historical climatology (Seely and Sandelowsky, 1974; Sandelowsky, 1983) and geology and soils (Martin, 1965; Scholz, 1972) or a combination of these topics (Logan, 1960; Goudie, 1972). Some aspects of the distribution of surface and subsurface waters are mentioned in, for example, Hellwig (1988).

Somewhat more published information is available on the chemistry of surface waters on the gravel plains of the central Namib (Kok and Grobbelaar, 1985), on gypsous crusts (Martin, 1963; Watson, 1979), on hot springs (Gevers, Hart and Martin, 1963), on waterholes in the Kuiseb River canyon (Kok and Grobbelaar, 1980), and on Kuiseb River water (Grobbelaar and Seely, 1980). Some aspects of the limnology of Sossusvlei, a large ephemeral interdune lake, are described

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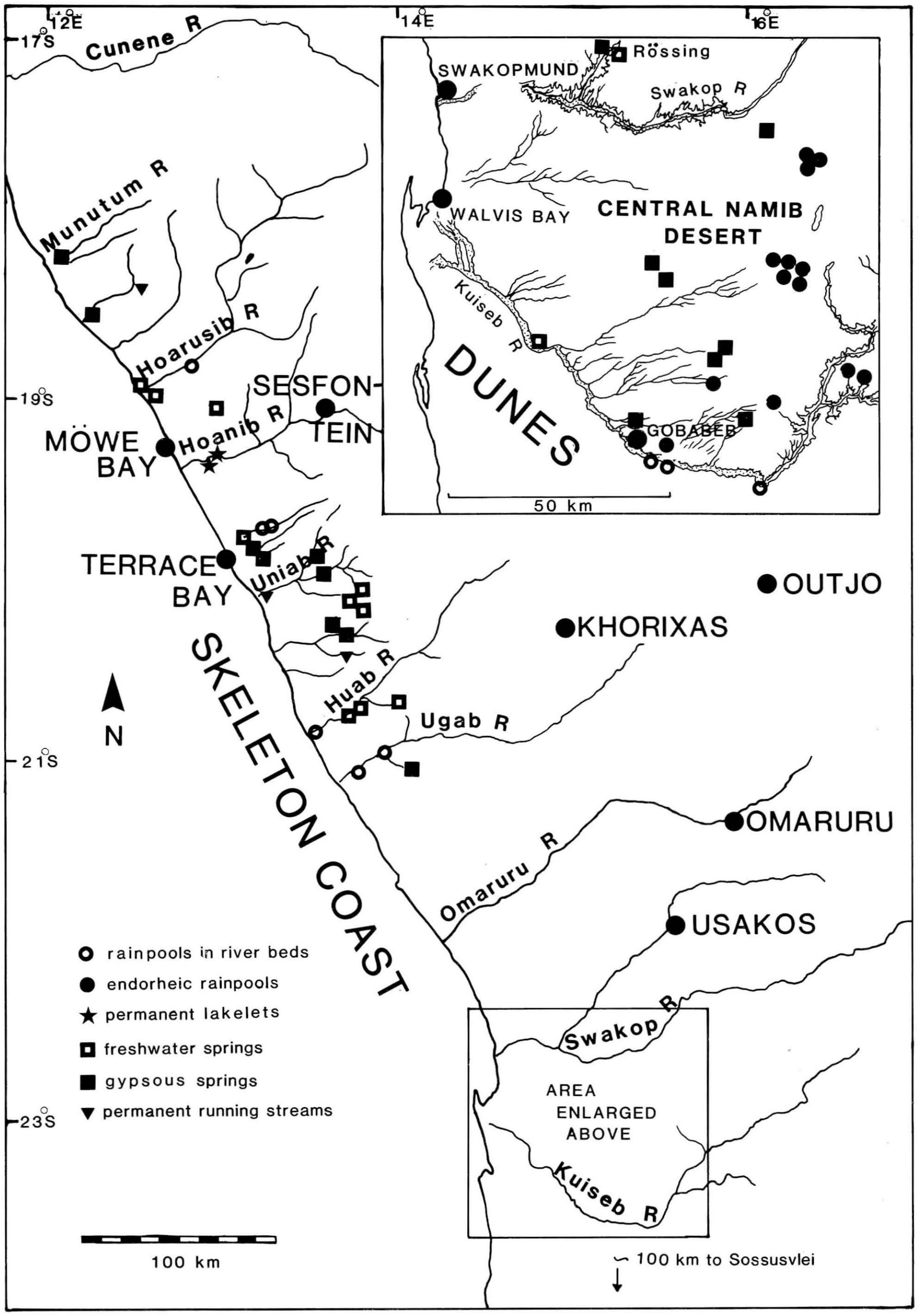

**Fig. 1**

Map of the northern and (inset) central Namib Desert showing the positions of the waterbodies referred to in the text. Each symbol may refer to more than one site.

by Grobbelaar (1976) and of Hosabes, a hypersaline spring, by Day and Seely (1988). A number of features of the Kuiseb River are described in the report edited by Huntley (1985) and by Stengel (1964), who also examines the Swakop River.

With the exception of several articles on frogs, including those by Channing (1976) and Jurgens (1985), it appears that nothing has been published on the biology of the Namib aquatic biota, although a number of systematic papers (see references in Table 1) deal either exclusively with, or include information on, Namib forms. The paper on the flamingoes of Etosha Pan (Berry, 1971) and that on the diatoms of thermal springs near Windhoek (Schoeman and Archibald 1988), for example, contain some information on taxa that probably also occur in the Namib itself.

## MAJOR TYPES OF AQUATIC ECOSYSTEM

In most climatic zones, surface waters are conveniently divided into standing (lentic) and running (lotic) systems. In deserts, though, a more appropriate and fundamental division is between permanent and semi-permanent, and temporary (ephemeral) waters, a division that is also reflected in the major elements of the biota. Below is a classification and brief description of the major types of aquatic habitats in the Namib. The localities of those known to the author are indicated in Fig. 1 and Table 1.

### Permanent and semi-permanent waterbodies

Such systems are fed by groundwater springs. Their surface areas and fluctuations in depth are thus determined by the relationship between the rate of flow of spring water (they are often recharged by subsurface flow from rain that has fallen many kilometres inland), the rate of evaporation, and the occasional influx of rainwater.

Although no systems in the Namib fit the definition of a true lake (a waterbody too deep for rooted plants to grow on the bottom), at least two lakelets (Ausis and 'The Oasis', both in the region of Möwe Bay) cover several hundreds of square metres, reach a depth of a metre or more, and appear to be permanent. They can be classified as *permanent endorheic* (closed-basin) *lakelets* (PL in Table 1).

On some geological formations, the water in smaller permanent springs remains fresh, or nearly so. On others, usually on gypsous crusts, evaporation from the surface, together with precipitation of $CaCO_3$, results in brackish to highly saline surface waters.

*Freshwater springs* (FS in Table 1) are found in dry river-beds or on the open plains and vary from small trickles to standing pools up to a metre or so deep. Most are permanent. In a few places (near the mouth of the Uniab River and at Wolfwasser, for instance) enough groundwater escapes to produce very fresh, fast-running, *permanent streams* (St in Table 1).

The small, highly mineral *springs on gypsous crusts* (GS in Table 1) are common in several deserts, where they seep from faults, extend for a few tens or hundreds of metres, and then disappear. A fault-line running along much of the coast of the Namib provides a series of these springs, one of which has been described in detail by Day and Seely (1988). It appears that the groundwater supplying the springs is fresh, or nearly so, but owing to the intense solar radiation and the hygroscopic gypsous soils, the water evaporates until enough $CaCO_3$ precipitates for the water to become a slightly calcium-enriched NaCl brine. One of these systems in the central Namib is unique in possessing the only known athalassic species of the protozoan group Foraminifera (Brain and Adams, 1984).

### Ephemeral waters

Ephemeral waters include rivers that run for short periods after rain has fallen high in their catchments, the pools that they leave behind as they cease to flow, and pools that form in depressions after rain.

The borders of that part of the Namib under discussion are more or less coincident with the Orange River in the south and the Cunene River in the north, the only permanent rivers in the region. Nothing has been published on the Cunene, while Cambray, Davies and Ashton (1986), Agnew (1986) and Skelton (1986) address various aspects of the limnology of the Orange River.

One of the characteristic features of the Namib north of about 22° S (roughly Walvis Bay) is a series of dry river-beds running perpendicular to the coast. They act more as canals than as rivers in the usual limnological sense, in that they carry water infrequently and do not develop a lotic biota. Their waters are allogenic (derived from elsewhere, being precipitated in the more mesic uplands and channeled towards the sea *via* the rivers) and in many cases little or no water actually reaches the sea, except during periods of unusually heavy rain. The more northerly rivers run to the sea almost every year, while those in the south are less predictable. Of all of the rivers, the Kuiseb, which divides the dune fields of the southern Namib from the gravel plains of the north, is the best known. The upstream damming of both the Kuiseb and the Swakop Rivers, and extraction of water from below the bed of the Kuiseb (Huntley 1985), has resulted in these rivers flowing for shorter distances and for shorter periods, and consequently in less frequent and less intense flooding in recent years. Nonetheless, when flood-waters recede, *pools* of very fresh water are left in the *river-beds* (RR in Table 1). In deep canyons, these may persist for months.

Although surface flow is seasonal and ephemeral, the river-beds act as permanent courses for subsurface water. Where this water is close beneath the surface of the river-bed, the rivers form longitudinal oases supporting a variety of plants (often including large trees) and their associated fauna, while larger mammals are able to excavate waterholes in the river-beds.

After rain, water will also collect in *rainpools in endorheic basins* (RE in Table 1), which may be depressions in rocky outcrops or on any other sealed surfaces such as clay or salt pans. Depending on the intensity and duration of rainfall, the pools may persist for as little as a day or two, or for as long as several weeks or, exceptionally, months. Although the water in most pools remains fresh to brackish, in some it may become very saline.

## THE AQUATIC FAUNA OF THE NAMIB

Table 1 is a preliminary list of the taxa known so far from athalassic waters of the Namib. It has been compiled from the available literature on the taxonomy and distribution of the aquatic fauna of the Namib Desert, together with records from my personal collections and hatching experiments on dried mud, and from the State Museum, Windhoek. As is frequently the case in Africa, the taxonomy of most groups is poorly known, so that many of the taxa are incompletely or tentatively identified. For this reason, the term 'species diversity' has been avoided in the following discussion, where 'richness' refers merely to the number of taxa. Further, the apparent distribution of the various taxa must reflect collecting bias, in that most samples were obtained from the central Namib and the

**Table 1**

A preliminary checklist of the aquatic metazoan animals known from athalassic surface waters in the Namib. RR = rainpools in river-beds; RE = endorheic rainpools; PL = permanent lakelets; FS = permanent freshwater springs; St = permanent streams; GS = springs on gypsous beds. 'Sp. indet.' refers to species considered to be new by the authorities who have examined them.

| | RR | RE | PL | FS | St | GS |
|---|---|---|---|---|---|---|
| COELENTERATA[13] | | | | | | |
| *Hydra sp.* | + | – | – | – | – | – |
| **PLATYHELMINTHES**[13] | | | | | | |
| Turbellaria | + | + | – | – | – | – |
| **NEMATODA**[13] | – | + | – | – | – | – |
| **ROTIFERA** | | | | | | |
| *Brachionus calyciflorus dorcas*[12] | – | – | + | – | – | – |
| Others[13] | + | + | – | – | – | – |
| **ANNELIDA** | | | | | | |
| OLIGOCHAETA[13] | – | – | – | – | + | – |
| HIRUDINEA | | | | | | |
| *Limnatis* sp. indet.[12] | – | – | – | + | – | – |
| **ARACHNIDA** | | | | | | |
| HYDRACARINA[13] | | | | | | |
| Sp. A | – | – | – | + | – | + |
| Sp. B | – | – | – | + | – | + |
| Sp. C | + | – | – | + | – | + |
| Sp. D | – | – | – | + | – | – |
| Sp. E | + | – | – | – | – | – |
| Sp. F | – | – | – | – | + | – |
| ARANEIDA[12] | | | | | | |
| *Pardosa* sp. | – | – | – | – | – | + |
| *Theridion* sp. | – | – | – | – | – | + |
| **CRUSTACEA** | | | | | | |
| NOTOSTRACA[1,2,13] | | | | | | |
| *Triops granarius* | – | + | – | – | – | – |
| CONCHOSTRACA[13] | | | | | | |
| *Caenestheriella* cf. *australis* | + | – | – | – | – | – |
| *Eocyzicus* sp. | + | + | – | – | – | – |
| *Eulimnadia* cf. *africana* | – | + | – | – | – | – |
| *Leptestheriella* cf. *inermis* | + | + | – | – | – | – |
| *Leptestheria* cf. *rubidgei* | – | + | – | – | – | – |
| *L.* cf. *striatoconcha* | – | + | – | – | – | – |
| ANOSTRACA[12] | | | | | | |
| *Branchipodopsis* cf. *kaokoensis* | – | + | – | – | – | – |
| *B. tridens* | + | + | – | – | – | – |
| *Branchipodopsis* sp. indet. | – | + | – | – | – | – |
| *Streptocephalus cafer* | – | + | – | – | – | – |
| *S. ovamboensis* | – | + | – | – | – | – |
| *Streptocephalus* sp. indet. | + | + | – | – | – | – |
| CLADOCERA | | | | | | |
| *Alona karua*[12] | – | + | – | – | – | – |
| *Alona* sp. (*rectangula* group)[12] | + | + | – | – | – | – |
| *Ctenodaphnia cornuta rigaudi*[12] | – | – | + | – | – | – |
| *C. dubia*[12] | + | – | – | – | – | – |
| *Ctenodaphnia* sp.[7] | – | + | – | – | – | – |
| *Daphnia* sp.[7] | – | + | – | – | – | – |
| *Macrothrix* cf. *gouldi*[12] | + | + | – | – | – | – |
| *M. triserialis*[12] | + | – | – | – | – | – |
| *Moina belli*[12] | + | + | – | – | – | – |
| *M. dubia*[7] | – | + | – | – | – | – |
| *M.* cf. *hartwigi*[12] | + | – | – | – | – | – |
| *M.* cf. *micrura*[12] | + | + | – | – | – | – |
| *M.* cf. *reticulata*[12] | + | – | – | – | – | – |
| *Oxyurella singalensis*[12] | – | – | – | – | + | – |
| COPEPODA | | | | | | |
| *Eucyclops (Afrocyclops) gibsoni*[12] | + | – | – | – | + | – |
| *Mesocyclops major*[12] | – | – | + | – | – | – |
| *M. (Thermocyclops) oblongatus*[12] | + | – | + | – | – | – |
| *Metadiaptomus meridianus*[7] | – | + | – | – | – | – |
| *Microcyclops inopinatus*[12] | – | + | – | – | – | – |
| OSTRACODA[3,12] | | | | | | |
| *Amphibolocypris* sp. indet | – | + | – | – | – | – |
| *Apatelecypris schultzei* | + | + | – | + | + | – |
| *Eucypris* cf. *trigona* | – | + | – | – | – | – |
| *Heterocypris* cf. *congenera* | + | + | – | – | – | – |
| *H.* cf. *giesbrechti* | – | + | – | – | – | – |
| *Isocypris perangusta* | – | + | – | – | – | – |
| *Plesiocypridopsis inaequivalva* | – | + | – | – | – | – |
| *Plesiocypridopsis* sp. indet. | – | + | – | – | – | – |
| *Potamocypris mastigophora* | – | + | – | – | – | – |
| *Sarscypridopsis ?glabrata* | ? | – | – | – | – | – |
| *S. ochracea* | – | – | – | + | – | + |
| *S. cf. pygmaea* | – | + | – | – | – | – |
| *Sclerocypris coomansi* | – | + | – | – | – | – |
| *S. dayae* | + | – | + | – | – | – |
| *S. dedeckkeri* | – | + | – | – | – | – |
| *Strandesia* cf. *vinciguerrae* | + | – | – | – | – | – |
| **INSECTA** | | | | | | |
| EPHEMEROPTERA[13] | | | | | | |
| Baetidae | | | | | | |
| *Cloeon* sp. | + | + | – | – | – | – |
| Other | + | – | – | + | + | – |
| ODONATA | | | | | | |
| Libellulidae | | | | | | |
| *?Crocothemis* sp. (nymph)[13] | – | – | – | + | – | – |
| *?Nannothemis* sp. (nymph)[13] | + | + | – | – | – | – |
| *?Paltothemis* sp. (nymph)[13] | + | + | – | – | – | – |
| *Pantala flavescens* (adult)[5] | ? | | | | | |
| *Trithemis kirbyi ardens* (adult)[5] | ? | | | | | |
| Gomphidae | | | | | | |
| *Paragomphus genei*[12] | ? | | | | | |
| *Paragomphus* sp. (nymph)[13] | + | – | – | + | + | – |
| Coenagrionidae | | | | | | |
| *Enallagma* sp. (nymph)[13] | + | – | – | + | – | – |
| *Enallagma glaucum* (adult)[4,5] | ? | | | | | |
| *Ischnura senegalensis* (adult)[5] | ? | | | | | |
| *Ischnura* sp. (nymphs)[12] | ? | | | | | |
| HEMIPTERA | | | | | | |
| Notonectidae[6,13] | | | | | | |
| *Anisops sardea* | + | – | + | + | + | – |
| Gerridae[13] | | | | | | |
| *Limnogonus* sp. | – | – | – | + | – | – |
| Hebridae[13] | | | | | | |
| Sp. A | – | – | – | + | – | – |
| Naucoridae[13] | | | | | | |
| *?Pelocoris* sp. | + | – | – | + | + | – |
| Saldidae[13] | | | | | | |
| Sp. A | – | – | – | – | – | + |
| Corixidae | | | | | | |
| *Sigara* cf. *contortuplicata*[6,13] | + | + | + | + | + | – |
| *Sigara* sp.[13] | + | + | + | + | – | – |
| COLEOPTERA | | | | | | |
| Gyrinidae | | | | | | |
| *Dineutus subspinosus*[9] | – | – | – | + | – | – |
| *Dineutus* sp.[13] | + | – | – | – | + | – |
| Hydrophilidae | | | | | | |
| *Berosus* sp. A[13] | – | – | – | + | – | – |
| *Berosus* sp. B[13] | – | – | – | + | – | – |
| *Berosus* sp. C[13] | + | – | – | + | + | – |
| *Caelostoma rufitarse*[12] | + | – | – | + | + | + |
| *Helochares (Helochares)* sp.[12] | – | – | – | + | – | – |
| *Helochares (Hydrobaticus)* sp.[12] | – | – | – | + | – | – |
| *Tropisternus* sp.[13] | + | – | – | + | – | – |
| Dytiscidae | | | | | | |
| *Cybister tripunctatus africanus*[12] | + | – | – | – | – | + |
| *Eretes stictus*[13] | + | + | – | + | – | + |
| *Graphoderus* sp.[12] | – | – | – | + | – | – |
| *Herophydrus* sp.[12] | + | – | – | + | + | – |
| *Hydroglyphus infirmus*[12] | – | – | – | + | – | – |
| *H. lineolatus*[12] | + | – | – | + | – | + |
| *H. zanzibarensis*[12] | – | – | – | + | – | – |
| *Hydroglyphus* sp. A.[12] | – | – | + | – | – | – |
| *Hyphydrus signatus*[12] | – | – | – | – | + | – |
| *Laccophilus simplicistriatus*[10] | – | + | – | – | – | – |
| *Yolina brincki*[12] | – | – | – | + | – | – |
| Hydraenidae[13] | | | | | | |
| *Ochthebius* sp. A | + | – | – | + | + | + |

Table 1 (continued)

| | RR | RE | PL | FS | St | GS |
|---|---|---|---|---|---|---|
| *Ochthebius* sp. B | – | – | – | – | – | + |
| Dryopidae [12] | | | | | | |
| *Heterocerus* sp. | + | – | – | + | – | – |
| Elmidae [13] | | | | | | |
| Sp. A | – | – | – | – | – | + |
| Ptilidae [13] | | | | | | |
| Sp. A | – | – | – | – | – | + |
| Staphylinidae [13] | | | | | | |
| Sp. A | – | – | – | + | – | + |
| DIPTERA [13] | | | | | | |
| Chironomidae | + | + | + | + | + | + |
| Culicidae | | | | | | |
| *Anopheles listeri* [12] | – | – | – | + | – | + |
| *A. fontinalis* [11] | – | – | – | + | – | – |
| *Anopheles* spp. [13] | + | + | – | + | – | + |
| *Culex (Culex) theileri* [12] | – | – | – | – | – | + |
| *C. (C.)* cf. *theileri* [12] | – | – | – | + | – | + |
| *Culex* sp. indet.[12] | – | + | – | – | – | – |
| *Culiseta (Allotheobaldia) longiareolata* [12] | – | – | – | – | – | + |
| *Culiseta* sp. indet.[12] | – | + | – | – | – | – |
| Psychodidae [13] | – | + | – | + | + | + |
| Empididae[13] | – | – | – | – | + | – |
| Tipulidae [13] | – | – | – | + | + | + |
| Tabanidae [13] | + | – | – | – | – | + |
| Stratiomyidae [13] | – | – | – | + | – | – |
| Ceratopogonidae [12] | | | | | | |
| *Culicoides schultzei* | – | – | – | + | – | – |
| *C. herero* | – | – | – | + | – | – |
| *Culicoides* sp. | – | – | – | – | – | + |
| *Dasyhelea* sp. | + | – | – | + | + | + |
| *Leptoconops dixi* | – | – | – | + | – | – |
| *L. interruptus* | – | – | – | + | – | – |
| Syrphidae [13] | – | – | – | – | – | + |
| Ephydridae | | | | | | |
| *Ephydra stuckenbergi* (adult) [12] | – | – | – | + | – | + |
| Sp. A (larva) [13] | – | – | – | + | – | + |
| Sp. B (larva) [13] | – | – | – | – | – | + |
| **VERTEBRATA** | | | | | | |
| AMPHIBIA [8] | | | | | | |
| *Bufo vertebralis* | – | + | – | – | – | – |
| *Phrynomerus annectans* | – | + | – | – | – | – |
| *Tomopterna delalandii* | – | + | – | – | – | – |
| Number of systems sampled | 16 | 35 | 2 | 17 | 3 | 16 |
| Number of taxa | 48 | 51 | 10 | 43 | 21 | 31 |
| Number of taxa separable to species | 41 | 45 | 9 | 42 | 13 | 25 |
| Ratio of taxa : systems | 3,0 | 1,5 | 5,0 | 2,5 | 7,0 | 1,9 |

[1] Longhurst (1955)
[2] Barnard (1929)
[3] Martens (1986 or 1988)
[4] Ris (1921)
[5] Longfield (1936)
[6] Hutchinson (1929)
[7] Grobbelaar (1976)
[8] Channing (1976)
[9] Brink (1955)
[10] Omer-Cooper (1965)
[11] Gillies and De Meillon (1969)
[12] Identifications of taxa belonging to the State Museum, Windhoek, or to the author and satisfactorily identified by systematists.
[13] Identifications of taxa belonging to the State Museum, Windhoek, or to the author and tentatively identified by her, often from unsatisfactory non-African sources.

Skeleton Coast. Most of the ephemeral waters have been sampled only once, so that temporal variations are entirely unknown. Despite these limitations, some points of interest arise.

Calculation of the ratio of the number of taxa recorded for a particular habitat type to the number of sites in that category allows the different types to be ranked according to richness of the fauna (i.e., number of taxa per site). Although the data on which the numbers are based are far too incomplete to use for anything other than such ranking, these numbers do indicate that permanent lakelets and streams are richest in taxa, followed by freshwater springs and rainpools in river-beds, with gypsous springs and endorheic rainpools supporting relatively few taxa.

Endorheic rainpools are dominated by crustaceans, especially euphyllopods and ostracods, which are able to withstand long periods of desiccation within 'egg' shells (which are actually cysts containing young larvae). Typically, they are uncommon in, or absent from, permanent waters and preliminary personal observations suggest that a dry resting period is obligatory before the eggs can hatch. Although this appears not to be true for the copepods or the cladocerans, these, too, generally occur in ephemeral waters and must also have a desiccation-resistant phase in their life-cycles. Sixteen of the 48 species of Crustacea are ostracods, reflecting both their species richness in the ephemeral waters of the Namib and the extensive recent systematic work on the group by Martens (1984, 1986, 1988). Further information on the crustaceans of desert waters is available in the reviews by Hartland-Rowe (1972) and Belk and Cole (1975).

The fauna of rainpools in river-beds comprises an element typical of ephemeral pools and, if the river has a distant origin, may also include lotic elements brought downstream from further inland. Thus some such pools may have a rather diverse fauna for this, and other, reasons. First, rainfall is more predictable inland, so that organisms able to withstand only seasonal desiccation can survive in river-beds because they are usually flooded annually. Second, at least some pools persist for long enough to be colonized by flying insects and propagules imported on the fur and feathers of vertebrates visiting the pools. Third, a number of the rivers have been dammed in their upper reaches; the resulting permanent lakes provide habitats for a variety of aquatic organisms that may be washed downstream in floods to join the temporary pond fauna. Even the obligatorily aquatic frog *Xenopus laevis* has been recorded from pools in the Kuiseb River (Channing, 1976), where fish have also been found in pools.

The insects, especially immature forms, are poorly known systematically so that the number of species must exceed the number of taxa listed. Some seem to have wide distributions, occurring in several types of waterbody. The beetles, which can generally be separated into different species or placed fairly reliably into genera even by non-coleopterists, are widespread in all types except endorheic rainpools. The only species so far found in these pools is the cosmopolitan *Eretes stictus* (Dytiscidae), a strong flier occasionally found even in very isolated and hypersaline gypsous springs, the fauna of which is otherwise restricted to surface-dwelling spiders and a few aquatic beetles and dipterans.

Interestingly, only one of the 31 taxa that occur in the gypsous springs is crustacean. A third of the taxa (mostly insects) appear to be restricted to this type of habitat, while somewhat less than a third co-occur in gypsous and freshwater springs. Five species of beetle occur both in gypsous and ephemeral waters, reflecting their ability to withstand either desiccation or extremes of salinity (or both), and their strong flying abilities.

The faunas of the two permanent lakes are, characteristically, dominated by planktonic crustaceans with the odd species of beetle, hemipteran and chironomid.

The permanent freshwater springs are dominated by insects, particularly beetles, while crustaceans are virtually absent. The relatively low ranking of taxa per pool may be an artefact caused by the number of insect taxa identified only to family. The faunal richness in freshwater springs seems to be positively correlated with their degree of permanence, although insufficient information is available to confirm this suspicion. Certainly the number of taxa is greatest in the true streams, which are also unusual for the Namib in that their fauna is typically lotic rather than lentic.

The relative similarities of the faunal communities of the six habitat types can be simply analysed (Table 2) using Sørensen's Community Coefficient (Southwood, 1966), which expresses the number of shared species in any two habitats relative to the total combined number of species:

$$CC = \frac{2j}{a + b}$$

where *CC* is Sørensen's Community Coefficient, *j* is the number of shared species, and *a* and *b* are the number of species in each habitat type.

There is an interesting contrast between the two ephemeral habitats: while those in river-beds share a good proportion of their species with all other habitat types (for reasons mentioned above), endorheic rainpools, which are generally isolated habitats, show a close similarity only with rainpools in river-beds. The similarity between these two types is determined largely by those crustaceans that are confined to ephemeral habitats. Of the permanent running waters, the freshwater springs share 30 % of their species with both the streams and the gypsous springs.

**Table 2**

Comparison of Sørensen's community coefficient (expressed as percentages) for the six habitat types. RR = rainpools in river-beds; RE = endorheic rainpools; PL = permanent lakelets; FS = permanent freshwater springs; St = permanent streams; GS = springs on gypsous beds. Taxa higher than species have been omitted from this analysis.

| | RR | RE | PL | FS | St | GS |
|---|---|---|---|---|---|---|
| RR | — | 36,8 | 20,0 | 41,0 | 40,1 | 21,2 |
| RE | | — | 7,2 | 11,4 | 6,8 | 2,8 |
| PL | | | — | 11,8 | 18,2 | 0 |
| FS | | | | — | 32,7 | 38,8 |
| St | | | | | — | 15,8 |
| GS | | | | | | — |

## FACTORS DETERMINING FAUNAL RICHNESS OF THE HABITAT TYPES

Because of their small sizes and isolated positions, and the generally perceived harshness of their physical and chemical environments, desert waters, especially temporary ones, have often been considered to be useful models for an improved understanding of distribution patterns, dispersal, isolating mechanisms, island biogeography and competition theory. The resulting hypotheses often propose that the number of taxa in desert and/or ephemeral pools will be determined by the size of the waterbody (see, for example, Weir, 1966; Pajunen and Jansson, 1969; Dehoney and LaVigne, 1984; Ebert and Balko, 1984), its isolation (e.g., Pajunen, 1986) and its chemical composition (e.g., Weir, 1966; Ranta, 1982).

These hypotheses presuppose that: either dispersal from pond to pond is limited (e.g., McLachlan, 1983*a*, *b*) or that dispersal is common (e.g., Dimentman and Margalit, 1981) and 'easy' (on the feet of birds, for instance: Maguire, 1963); that species richness will be greater in larger pools because, in the case of ephemeral waters at least, larger pools are likely to persist for longer (Ebert and Balko, 1984; Dehoney and LaVigne, 1984); and that the number of taxa will be inversely proportional to environmental 'harshness', usually some measure of a variable such as salinity (e.g., Ranta, 1982) or oxygen content of the water (e.g., Morton and Bayly, 1977).

It has generally been found that the number of taxa is most closely related to pool size, however (e.g., Weir, 1966; Dehoney and LaVigne, 1984). This is easily explained for the inhabitants of temporary pools, where size, especially depth, is proportional to longevity and therefore to the likelihood of an animal being able to complete its life-cycle. It is less easily explained for permanent systems, though, since increased size *per se* does not necessarily result in increased habitat diversity, the commonest explanation in island biogeographic theory for increased species diversity in 'islands' of increasing size (but see, for instance, Fryer, 1985).

Even with the rather limited data presently available to me, it is possible to make a preliminary assessment of the relationship between faunal richness (i.e., number of taxa) and salinity, size of system, and distance from other systems. The analyses described below and/or shown in Fig. 2 are based on data from all the sites indicated in Fig. 1 for which measurements of the other variables are available. Those from the Skeleton Coast were all collected in January 1983, while data from the central Namib Desert (inset in Fig. 1) have been collected by me from time to time over several years. Thus a major source of error in these analyses, especially for the ephemeral pools, lies in the fact that samples were collected after different intensities of, and at different times after, rainfall.

Linear regressions (Zar, 1984) of the number of taxa upon salinity (measured in the field with an American Optics refractometer) are not statistically significant for the data-set as a whole or for any of the habitat types individually ($P > 0,05$). Indeed, although a plot of the number of taxa *versus* salinity shows considerable scatter, the trend reflects, if anything, an increase in the number of taxa at least at intermediate salinities.

Surface area of each system was calculated from measured or estimated lengths and widths, and depth was measured *in situ*, both within an accuracy of about 10 %. Distances shorter than about 1 km were estimated in the field and those exceeding 1 km were measured from appropriate maps. The results can be considered only to be preliminary because of the problem of incomplete identifications of the animals, resulting

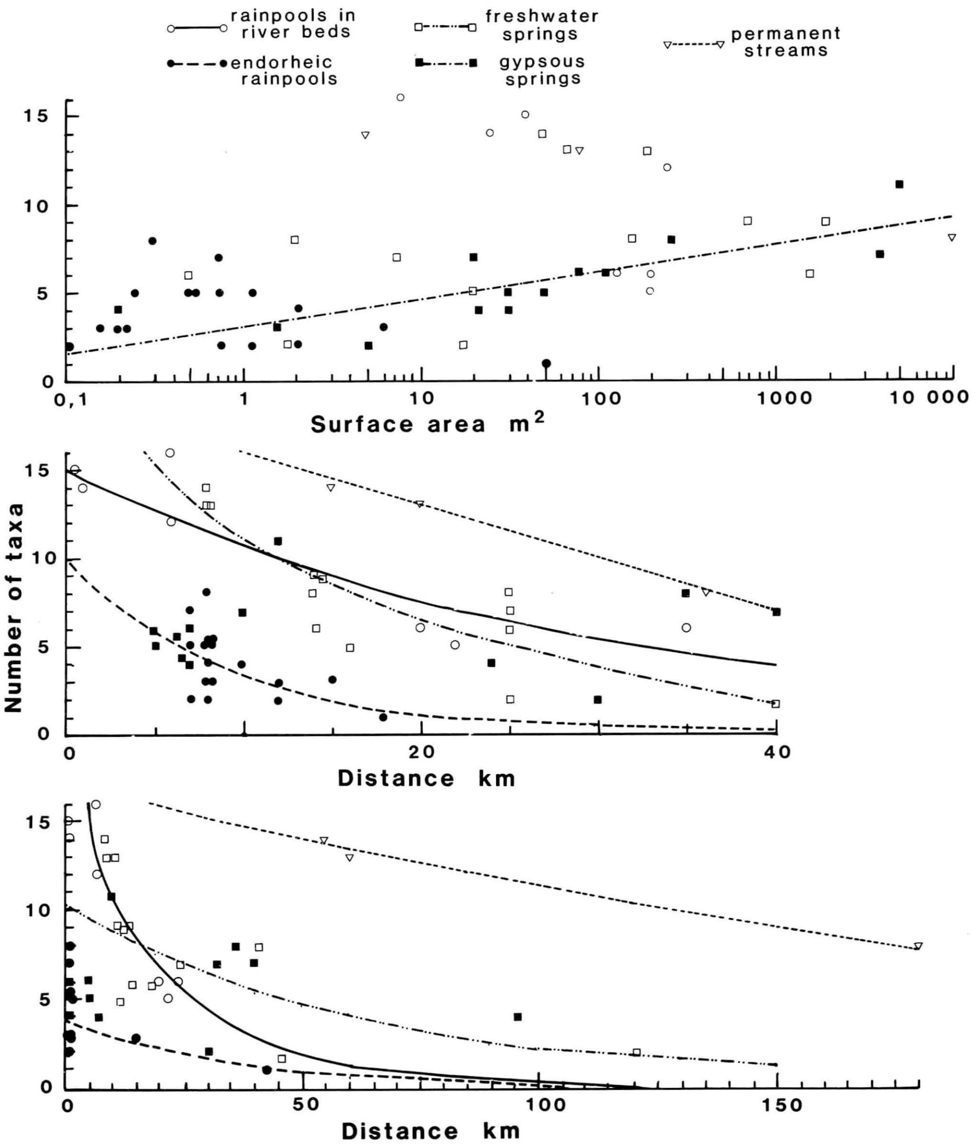

**Fig. 2**

The relationships between number of taxa recorded from each site and (a) surface area, (b) distance to any other surface water, and (c) distance to any other surface water of the same type.

in the use of various taxonomic levels in the analyses.

Regression of the number of taxa per site upon depth was not significant ($P > 0,05$) for the data-set as a whole and for each habitat type individually. Regression upon surface area (Fig. 2a) was significant only for the gypsous springs ($n = 13$, $P < 0,01$, $y = 3,03 + 0,67 \ln x$). Thus these data suggest that, for most habitat types in the Namib Desert at least, size (as reflected by depth and surface area) is not a primary determinant of faunal richness.

If, on the other hand, the geographical isolation of individual pools or springs has an effect on faunal richness, and if the individual elements of the fauna are at all able to select, or differentially to survive in, different types of habitat, then one can predict that the number of taxa in any pool should decrease with increasing distance apart of individual systems. Further, the regression lines for different habitat types should reflect their permanence: the faunas of permanent waters should be less influenced by distance from other systems than should the faunas of ephemeral pools. Finally, where faunal richness is greatly influenced by isolation, one might expect the relationship to be exponential.

Figure 2b illustrates the regression of the number of taxa upon the shortest distance from a given system to any other and Fig. 2c illustrates the regression of the number of taxa upon the shortest distance from a given system to another of the same type. Although no significant relationships exist in either case for the fauna of the gypsous springs, all the other habitat types show strongly significant ($P < 0,01$) negative correlations. The regression equations are shown in Table 3.

These results are fascinating, not least because they differ quite markedly from those of several of the authors referred to above (e.g., Dehoney and LaVigne, 1984; Ebert and Balko, 1984).

It is not clear why the richness of the fauna of the gypsous springs should be more strongly related to surface area (and therefore size) than to degree of isolation, or why these systems should be different from the others in this respect. It is possible that the habitat diversity of the larger gypsous springs is greater than that of the smaller ones; perhaps, on the other hand, the relative permanence of these systems may allow even isolated ones to accumulate species over long periods of time.

Certainly a comparison of the results for the other habitat types suggests that the richness of the fauna increases with increasing permanence and predictability, in that the curves for both types of ephemeral pool lie closer to the axes in Fig. 2c (i.e., the exponent is larger) than does the curve for the permanent springs, with that for the permanent streams lying farthest away. Finally, a comparison of the curves for the permanent springs and the rainpools in river-beds in Figs 2b and 2c suggests that the fauna of the springs is more dependent on the closeness of other springs of the same kind, while that of the rainpools responds to the closeness of any type of pool.

**Table 3**

Regression equations for the relationships shown in Figs 2b & 2c.

| | *n* | Number of taxa vs distance to any waterbody | Number of taxa vs distance to nearest waterbody of the same type |
|---|---|---|---|
| Permanent streams | 3 | $y = 18{,}58 - 0{,}29x$ | $y = 17{,}26e^{-0{,}004x}$ |
| Freshwater springs | 13 | $y = 26{,}02 - 6{,}54 \mathit{ln}\, x$ | $y = 10{,}16e^{-0{,}015x}$ |
| Rainpools (plains) | 17 | $y = 9{,}73e^{-0{,}108x}$ | $y = 3{,}90e^{-0{,}030x}$ |
| Rainpools (river-beds) | 7 | $y = 14{,}89e^{-0{,}034x}$ | $y = 15{,}81e^{-0{,}042x}$ |

In conclusion, the data strongly suggest that, with the exception of the gypsous springs, the various types of aquatic habitat in the Namib Desert are strongly dependent on neighbouring systems as sources of 'new' species. This in turn suggests that extinction in individual pools plays a significant role in the determination of community structure.

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## REFERENCES

AGNEW, J. D., 1986. Invertebrates of the Orange-Vaal system, with emphasis on the Ephemeroptera. *In:* DAVIES, B. R. and WALKER, K. F., eds, *The ecology of river systems*, pp. 123–134. Junk, Dordrecht.

BARNARD, K. H., 1929. Contributions to the Crustacean fauna of South Africa. No. 10. A revision of the the South African Branchiopoda (Phyllopoda). *Annals of the South African Museum* **29**: 181–272.

BELK, D. and COLE, G. A., 1975. Adaptational biology of desert temporary pond inhabitants. *In:* HADLEY, N. F., ed., *Environmental physiology of desert organisms*, pp. 207–266. Dowden, Hutchinson and Ross, Inc., Stroudsburg, Pa.

BERRY, H. H., 1971. Flamingo breeding on the Etosha Pan. *Madoqua* **1**: 5–32.

BRAIN, C. K. and ADAMS, C. G., 1984. Observations on Foraminifera living in a Namib spring. *South African Journal of Science* **80**: 194. (Abstract).

BRINK, P., 1955. Gyrinidae. *In:* HANSTRÖM, B., BRINK, P. and RUDEBECK, G., eds, *South African Animal Life* **1**: 329–518.

CAMBRAY, J. A., DAVIES, B. R. and ASHTON, P. J., 1986. The Orange-Vaal River System. *In:* DAVIES, B. R. and WALKER, K. F., eds, *The ecology of river systems*, pp. 89–122. Junk, Dordrecht.

CHANNING, A., 1976. Life histories of frogs in the Namib Desert. *Zoologica africana* **11**: 299–312.

DAY, J. A. and SEELY, M. K., 1988. Physical and chemical conditions in an hypersaline spring in the Namib Desert. *Hydrobiologia* **160**: 141–153.

DIMENTMAN, Ch. and MARGALIT, J., 1981. Rainpools as breeding and dispersal sites of mosquitoes and other aquatic insects in the Central Negev Desert. *Journal of Arid Environments* **4**: 123–129.

DEHONEY, B. and LAVIGNE, D. M., 1984. Macroinvertebrate distribution among some southern California vernal pools. *In:* JAIN, S. and MOYLE, P., eds, *Vernal pools and intermittent streams*, pp. 154–160. Institute of Ecology, University of California, Davis, Publication No. 28.

EBERT, T. A. and BALKO, M. L., 1984. Vernal pools as islands in space and time. *In:* JAIN, S. and MOYLE, P., eds, *Vernal pools and intermittent streams*, pp. 90–101. Institute of Ecology, University of California, Davis, Publication No. 28.

FRYER, G., 1985. Crustacean diversity in relation to the size of water bodies: some facts and problems. *Freshwater Biology* **15**: 347–361.

GEVERS, T. W., HART, O. and MARTIN, H., 1963. Thermal waters along the Swakop River, South West Africa. *Transactions of the Geological Society of South Africa* **66**: 157–189.

GILLIES, M. T. and DE MEILLON, B., 1969. Anophelinae of Africa south of the Sahara (Ethiopian zoogeographical region), 2nd edn. *South African Institute for Medical Research* Publication No. 54.

GOUDIE, A., 1972. Climate, weathering, crust formation, dunes and fluvial features of the Central Namib Desert, near Gobabeb, South West Africa. *Madoqua* (2)**1**: 15–31.

GROBBELAAR, J. U., 1976. Some limnological properties of an ephemeral waterbody at Sossus Vlei, Namib Desert, South West Africa. *Journal of the Limnological Society of Southern Africa* **2**: 51–54.

GROBBELAAR, J. U. and SEELY, M. K., 1980. The composition of water collected from the Kuiseb River, Namib Desert, at Gobabeb. *Journal of the Limnological Society of Southern Africa* **6**: 46–48.

HARTLAND-ROWE, R., 1972. The limnology of temporary waters and the ecology of Euphyllopoda. *In:* CLARK, R. B. and WOOTTON, R. J., eds, *Essays in hydrobiology presented to Lesley Harvey*, pp. 15–31. University of Exeter Press, Exeter.

HELLWIG, D. H. R., 1988. Challenging the Namib Dune Sea. *Journal of the Limnological Society of Southern Africa* **14**: 35–40.

HUNTLEY, B. J. (ed.), 1985. The Kuiseb environment: the development of a monitoring baseline. *South African National Programmes Report* No. 106. C.S.I.R., Pretoria.

HUTCHINSON, G. E., 1929. A revision of the Notonectidae and Corixidae of South Africa. *Annals of the South African Museum* **25**: 359–474.

JURGENS, J., 1985. The frogs of South West Africa. *SWA 1985: Annual Yearbook.* SWA Publications (Pty) Ltd, Windhoek.

KOK, O. B. and GROBBELAAR, J. U., 1980. Chemical properties of water-holes in the Kuiseb River Canyon, Namib Desert. *Journal of the Limnological Society of Southern Africa* **6**: 82–84.

KOK, O. B. and GROBBELAAR, J. U., 1985. Notes on the availability and chemical composition of water from the gravel plains of the Namib-Naukluft Park. *Journal of the Limnological Society of Southern Africa* **11**: 66–70.

LANCASTER, J., LANCASTER, N. and SEELY, M. K., 1984. Climate of the central Namib Desert. *Madoqua* **14**: 5–61.

LOGAN, R. F., 1960. The Central Namib Desert. South-West Africa. *National Research Council Publication* No. 758, National Academy of Sciences, Washington DC, U.S.A.

LONGFIELD, C., 1936. Studies on African Odonata with synonymy and descriptions of new species and subspecies. *Transactions of the Entomological Society of London* **85**: 467–498.

LONGHURST, A. R., 1955. A review of the Notostraca. *Bulletin of the British Museum (Natural History) (Zoology)* **3**: 3–57

MAGUIRE, B., 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. *Ecological Monographs* **33**: 161–185.

MARTENS, K., 1984. Annotated checklist of non-marine ostracods Crustacea Ostracoda from African inland waters. *Koninklijk Museum voor Midden-Afrika, Zoologische Dokumentatie N20* Tervuren, Belgium.

MARTENS, K., 1986. Taxonomic revision of the subfamily Megalocypridinae Rome, 1965 (Crustacea, Ostracoda). *Verhandelingen van de Koninklijke Academie voor Wetenschappen, Letteren en Schone Kunsten van Belgie.* Klasse der Wetenschappen, Jaargang 48, No. 174.

MARTENS, K., 1988. Seven new species and two new subspecies of *Sclerocypris* Sars, 1924 from Africa, with new records of some other megalocyprinids (Crustacea, Ostracoda). *Hydrobiologia* **162**: 243–273.

MARTIN, H., 1963. Suggested theory for the origin and a brief description of some gypsum deposits of South West Africa. *Transactions of the Geological Society of South Africa* **66**: 345–350.

MARTIN, H., 1965. *The precambrian geology of South-West Africa and Namaqualand.* Precambrian Research Unit, University of Cape Town.

McLACHLAN, A., 1983*a*. Habitat distribution and body size in rain-pool dwellers. *Zoological Journal of the Linnean Society* **79**: 399–407.

McLACHLAN, A., 1983*b*. Life-history tactics of rain-pool dwellers. *Journal of Animal Ecology* **52**: 545–561.

MORTON, D. W. and BAYLY, I. A. E., 1977. Studies on the ecology of some freshwater pools in Victoria with special reference to the microcrustacea. *Australian Journal of Marine and Freshwater Research* **28**: 439–454.

OMER-COOPER, J., 1965. A review of the Dytiscidae of southern Africa, being the results of the Lund University Expedition 1950–1951, with which are incorporated all other records known to the author. *In:* HANSTRÖM, B., BRINK, P. and RUDEBECK, G., eds, *South African Animal Life* **2**: 59–214.

PAJUNEN, V. I., 1986. Distributional dynamics of *Daphnia* species in a rock-pool environment. *Annales zoologici fennici* **23**: 131–140.

PAJUNEN, V. I. and JANSSON, A., 1969. Dispersal of the rock pool corixids *Arctocorisa carinata* (Sahlb.) and *Callocorixa producta* (Reut.) (Heteroptera, Corixidae). *Annales zoologici fennici* **6**: 391–427.

RANTA, E., 1982. Animal communities in rock pools. *Annales zoologici fennici* **19**: 337–347.

RIS, F., 1921. The Odonata or dragonflies of South Africa. *Annals of the South African Museum* **18**: 245–452.

SANDELOWSKY, B. H., 1983. Archaeology in Namibia. *American Scientist* **71**: 606–615.

SCHOEMAN, F. R. and ARCHIBALD, R. E. M., 1988. Taxonomic notes on the diatoms (Bacillarophyceae) of the Gross Barmen thermal springs in South West Africa/Namibia. *South African Journal of Botany* **54**: 221–256.

SCHOLZ, H., 1972. The soils of the central Namib Desert with special consideration of the soils in the vicinity of Gobabeb. *Madoqua* (2)**1**: 33–51.

SEELY, M. K. and SANDELOWSKY, B. H., 1974. Dating the regression of a river's end point. *South African Archaeological Society, Goodwin Series* **2**: 61–64.

SKELTON, P. H., 1986. Fish of the Orange River System. *In:* DAVIES, B. R. and WALKER, K. F., eds, *The ecology of river systems*, pp. 143–162. Junk, Dordrecht.

SOUTHWOOD, T. R. E., 1966. *Ecological methods with particular reference to the study of insect populations.* Methuen and Co., London.

STENGEL, H. W., 1964. The rivers of the Namib and their discharge into the Atlantic. 1. The Kuiseb and Swakop. *Scientific Papers of the Namib Desert Research Station* **22**: 1–49.

WATSON, A., 1979. Gypsum crusts in deserts. *Journal of Arid Environments* **2**: 3–20.

WEIR, J. S., 1966. Ecology and zoogeography of aquatic Hemiptera from temporary pools in Central Africa. *Hydrobiologia* **28**: 123–141.

ZAR, J. H., 1984. *Biostatistical analysis*, 2nd edn. Prentice-Hall, Englewood Cliffs, N.J.