Dragonfly Assemblage Dynamics and Conservation at Small Reservoirs in KwaZulu-Natal, South Africa

By

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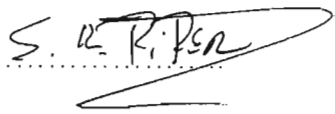Pietermaritzburg
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DECLARATION

The research described in this thesis was carried out in the School of Botany and Zoology, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Professor Michael J. Samways (currently with the University of Stellenbosch) and Professor Steven E. Piper of the School of Botany and Zoology, University of KwaZulu-Natal.

These studies represent original work by the author and have not otherwise been submitted in any form for a degree or diploma to any university. Where use has been made of the work of others, it is duly acknowledged in the text.

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General Abstract

A study of the odonate fauna was carried out at the edge of a major escarpment, in eastern South Africa, using the same methodology as has been used in the temperate regions to obtain a sub-tropical perspective. The study used the macroecology approach to compare patterns and responses of these animals (at the developmental stages of larva, tenerals and adults) to seasonal, topographical and anthropogenic disturbances. The habitats used were small, but well-established reservoirs located at five elevational gradients: Stainbank Nature Reserve (100 m), Krantzkloof Nature Reserve (450 m), National Botanical Gardens Pietermaritzburg (790 m) Cedara (1050 m) and Mondi Goodhope Estate (1350 m).

Although this is essentially a local component of a larger macroecological study, it is shown that even though species and identities differ between temperate, tropical and sub-tropical ecoregions, the general pattern of community response to these variables is similar. Odonate species phenologies in this sub-tropical study showed great similarity to their tropical counterparts by reason of their adults being highly elevation-tolerant, with long flight periods and over-lapping generations. Yet they also show temperate characteristics by over-wintering principally as larvae and eggs. The Libellulidae, followed by the Coenagrionidae were the most abundant, elevation-tolerant families, with national endemics constituting only 6.5% of the total species sampled.

Classification and ordination methods identified and characterised sub-sites to ecologically meaningful biotopes for odonates. This also allowed inferences as to how the various landscape disturbances at the five elevations affect species richness and abundance. Species that responded to these impacts were potential indicator groups that can assist in the planning and management of the landscape for conservation of biodiversity. Some management recommendations for these landscapes are given.

Individual odonate species developmental stages and their environmental relations were investigated using both univariate and multivariate analyses. The solutions to these analyses were then used to describe how odonate species are distributed along major environmental gradients. It was shown that regional processes e.g. elevation and insolation alongside local variables e.g. pH, marginal grasses, percentage shade, exposed rock, marginal forest, marsh and flow greatly accounted for adult (aerial stage) assemblage variation and distribution. Turbidity, floating/submerged vegetation and water depth (also influenced by regional factors), highly explained larval (aquatic stage) variation. Elevation has therefore, an indirect effect in that it determines climate, which in turn, determines soil and vegetation types which then determine species presence and absence. Also, although these artificial water bodies do not increase the 'extent of species occurrence', they are important in increasing their 'area of occupancy'.

Dragonflies play a major role in conservation. The Japanese culture has strongly illustrated how dragonflies feature in everyday life more than any other country in the world. While many parks and Botanical Gardens feature dragonfly trails in their nature trails in Britain, this does not necessarily cater for threatened species. Conservation of invertebrates in urban environments in South Africa for example by ecological landscaping designed to encourage dragonflies has been particularly rewarding. A core of regularly occurring odonate species occupied the dragonfly trail at the National Botanical Gardens in Pietermaritzburg, while other species visited the study site at irregular periods. This is likely to be the case for a longer term, say ten years or more. Also, the trail, with updated information on species phenologies, variability and habitat preferences continues to play a valuable role in sensitising an increasingly urbanised population to biodiversity and conservation issues.

Odonates remain a major component when assessing ecological components of aquatic biotopes, with the assemblage composition at any one locality capable of changing over time. This has been extensively illustrated in the northern hemisphere. Medium to longer term changes in odonate population at established reservoirs as demonstrated in this study at the National Botanical Gardens in Pietermaritzburg, South Africa, makes it possible to determine wheher a species in a conservation area is being given enough protection from local anthropogenic impacts and effects of unpredictable weather conditions. This in turn enables one to understand how concepts of residency and succession underpin conservation management decisions.

In conclusion, this study has addressed some salient aspects of species inventory, monitoring and conservation practice at a local scale that also play a central role in conventional biodiversity conservation practice of a global nature. Information on species phenologies enhances their awareness-raising in addition to providing valuable insights into their population dynamics and conservation, especially for those under threat. In addition, baseline data from this study and similar ones is useful in conserving biodiversity (as subjects) or in multi-taxa studies (as tools) in conserving ecosystems and/or landscapes. Finally, the macroecological approach employed in this study has great potential for teasing apart local effects from regional and/or global ones, and can contribute to the conservation of biodiversity at both small and large scales.

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Chapter One   General Introduction

1.1 Insect conservation in South Africa

South Africa now has a White Paper on Biodiversity (McGeoch 2002), with the Department of Environmental Affairs and Tourism currently developing a strategy for its implementation. Meanwhile, the environmental threats to the insect fauna show no signs of abating. Most notably, land transformation in the form of human-induced fires, livestock overgrazing and soil erosion, conversion of land to arable agriculture, deforestation, expansion of exotic forestry plantations, changes to water regimes, invasive species, urbanization and climate change pose ongoing threats (Samways 1995). These threats are not unique to South Africa but are significant in most developing, and indeed some developed nations (McGeoch 2002).

In spite of socio-economic problems resulting in uncertain prospects for insect conservation, South Africa has a strong insect conservation research record. In several instances, this research has contributed to conservation action and management decisions being made that have promoted insect conservation goals (McGeoch 2002). South Africa's insect species richness is estimated at twice to three times the presently described number i.e. 43565 (Scholtz and Chown 1995). Of those species described, an assessment of IUCN conservation status has been conducted for butterflies (Henning and Henning 1995) and dragonflies (Samways 1996; 1999; 2002).

Insects have a long history of being highly valued among a number of groups of people in South Africa, including for example, their regard as spiritual icons (praying mantids among the Cape San (Schoeman 1984, Fourie 1994)), their use as sources of toxins for hunting (e.g. larvae of *Diamphidia* spp. (Coleoptera: Chrysomelidae) (Scholtz 1984)), food (Partridge 1973) and aphrodisiacs (Clark et al. 1996). Where insects or their products are or have the potential to be used as resources in this way, unique and interesting conservation challenges arise. Insect conservation in South Africa must therefore involve not only the globally more traditional approaches of habitat conservation and the establishment and maintenance of protected areas, but must also consider issues of sustainable resources utilization for some species.

Indeed, with less than 6% of South Africa's land area conserved (Siegfried 1989), the theatre for insect conservation lies firmly outside protected areas. Although reserves in South Africa are likely to perform an important role in insect conservation (Henning 1994; Chown et al. 1995; Stewart and Samways 1998), even within them the conservation requirements of invertebrate fauna are not always met (Clark and Samways 1996; Van Rensburg et al. 1999). Furthermore, limited taxonomic knowledge and large gaps and biases in available information on distribution patterns of South Africa's insect fauna are among the greatest challenges to its conservation (Scholtz and Chown 1993; Koch et al. 2000).

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1.2 Insects as bioindicators

To be useful for conservation management, an ecological indicator should readily reflect environmental state, represent the response of other taxa to that state and be temporarily and spatially robust within the context of the bioindication objective (McGeoch 2001). Article seven of the Convention on Biological Diversity (1992), has stressed the identification of components of biological diversity important for the long-term conservation and sustainable use of biodiversity (Glowka et al. 1994). Among the recommended categories of such listed components are those with 'importance for research into the conservation and sustainable use of biological diversity, such as indicator species'. Independently of the mandate set by the Convention, bioindicators have in the past and continue to be used today to determine the state of environmental health and to be tested as potential predictors of biodiversity and of the impact of environmental change on natural systems.

The traditional approach to indicator studies, where the indicator taxon is monitored so that changes in environmental conditions can be detected (i.e environmental indication) has most commonly been applied using soil invertebrates as bioindicators of soil fertility and pollutant levels (e.g. pesticides, heavy metal levels) (Paoletti and Bressan 1996). However, the use of biota to indicate changes in physical or chemical environmental conditions or vegetation when the changes can be measured directly and far more accurately using instrumentation, or by other means, is futile (Kremen 1992). Also, when subtle, complex environmental changes occur, direct measurement of the stressor is often more useful because it may be difficult to distinguish anthropogenic influence from the inherent dynamics of the system being examined (Underwood 1989, Stork and Samways 1995).

The use of groups of taxa as indicators of the impact of environmental stressors on biotic communities (ecological indicators) is arguably perhaps the more critical objective in the field of bioindication. They indicate that a particular stressor does (or does not) have a biotic impact, and they provide critical information for the conservation of the indicator taxa or group, particularly when the species are known to be rare and endangered (e.g. Butterfield et al. 1995). The utility of ecological indicators would be substantially greater if their representativeness of other taxa could be demonstrated (Noss 1990, Dufrêne and Legendre 1997). Areas for conservation are prioritised by identifying optimal sets of viable but threatened areas for maximising overall diversity (Margules et al. 1988). Since the knowledge of the taxonomy and distribution of most invertebrates is poor (Vane-Wright et al. 1994), the only alternative is to use taxa (groups of invertebrates or other organisms) that are better known and that will, with some predetermined degree of accuracy, represent wholesale biodiversity (Savage 1982, Vane-Wright 1996, Williams et al. 1997). This concept may be applied by using biodiversity indicator groups to identify priority areas for conservation (McGeoch 1998).

In South Africa, dragonflies (e.g. Clark and Samways 1996; Samways et al. 1996b, Samways 1999, 2002), moths (McGeoch and Chown 1997; Grout 1998; Rösch et al. 2001) and dung beetles (Van Rensburg et al. 1999) have been identified as potential

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bioindicators of a variety of sources of environmental change (see also Kotze and Samways (1999) and Wessels et al. (1999) for other bioindicator-related issues). While these bioindicator systems continue to be studied by the academics that identified them and the ways in which they reflect aspects of environmental quality, unless they are adopted by conservation management agencies, their potential values will never be realised (McGeoch 1998; 2002). Such bioindicator systems stand to contribute not only to more informed management decisions, but can also contribute significantly to increasing public awareness of the role and particular plight of insects as a component of biodiversity.

1.3 Montane ecosystems and insects

Topographic variation has important conservation biology implications, especially for ectotherms such as insects. The shape of the land surface provides temporal and spatial perspectives for examining soil, vegetation and aquatic ecosystems, and for interpreting ecosystem processes (Swanson et al. 1988). In montane ecosystems, where climate variations and natural habitat fragmentation are common traits (Olson 1994; Haslett 1997, Roy et al. 2003), it is important to understand the variations in species distribution within and between habitats, its ecological meaning and its relevance to species conservation (Janzen 1973, Warren 2001).

Distribution of insect species richness along environmental gradients corresponds to some extent, to the patches in the environmental matrix (Dempster 1991). Therefore, consideration of specific habitat characteristics in studies of gradients may elucidate ecological processes in natural ecotones and human expanded habitat edges (Ribeiro et al. 1998; Samways, 1994). While most studies point to a negative correlation between species richness and elevation, mid-elevation peaks of insect richness have been reported for tropical mountains (Janzen 1976; McCoy 1990). Severe physical conditions associated with high elevations have been used to explain the decrease in species number in mountain ecosystems (Wolda 1987, Augustin et al. 1996, Ribeiro et al. 1998, Roy et al. 2003). However, the importance of spatial complexity of mountain ecosystems and its effects on invertebrate communities has been recognised (Haslett 1997) and may nullify a gradual decrease in species number along gradients where the climate is not too severe (Ribeiro et al. 1994; Ribeiro et al. 1998). Significant changes in insect species richness are greater on mountain tops or on rough slopes due to conspicuous rise in climatic severity or the harshness of the habitat (Sarmiento 1986).

1.4 Specific threats to dragonflies

Modification of the environment may cause habitat loss and fragmentation (e.g. Saunders et al. 1987; Marsh and Pearman 2001, Fahrig 2003) or a reduction in habitat suitability (e.g. Pausas et al. 1995; Pearman 1997). Dragonflies have been particularly affected by these anthropogenic landscape changes (Corbet 1980; 1999, Samways 2003).

Wetlands (potential dragonfly habitats) are one of the most threatened of wildlife habitats (Biggs et al. 1994), they have been lost on a large scale during the twentieth century,

reaching 40-90% for various northwestern European countries (Hull 1997). In Switzerland, the proportion of wetlands (including ponds) lost since 1800 has been estimated at 90% (Imboden 1976). Hence the two flagship taxa –Amphibia and Odonata are highly threatened, and in most European countries for which data are available, 20-40% of their species are generally classified as being at least vulnerable (Oertli et al. 2002). With intensification of agriculture, many stenotopic dragonfly species are under severe threat (Samways 1999).

Species losses are incurred mainly as a result of pollutants, high water requirements for crop production and the conversion of riverine wetland vegetation into crop-land as well as into built-up areas (Moore 1991, Corbet 1999). The clearing of tropical rainforests in particular, imposes the greatest threat to dragonflies (Moore 1997). Furthermore, drainage and excessive water extraction destroy many freshwater habitats, while lowering the water table can turn permanent water bodies into temporal ones, and as a result, they cannot support dragonflies with a long developmental period. In some streams and ditches, changes in the flow rate can cause local loss of species. In KwaZulu-Natal, the greatest threat is the conversion of wetlands for agricultural purposes (Begg 1986).

1.4.1 Beneficial anthropogenic changes to dragonflies

Modification of the environment also creates habitat (Hazell et al. 2001). One such example in the Australian environment is the construction of farm dams. These small, earthen structures are designed to impound water for irrigation or domestic purposes, to water stock or assist in erosion control (Timms 1980). Farm dams may also be considered as cultivated ponds providing potential breeding habitat for frogs and dragonflies in the modified agricultural landscape. In a dry country like South Africa, construction of ponds and small farm dams has substantially increased the overall abundance of some ecologically-generalist odonate species (Samways 1989a; 1999).

Small impoundments, although locally excluding some lotic species of dragonflies, generally increase species richness in the vicinity of the impoundment (Steytler and Samways 1995). In the Kruger National Park, South Africa, partial damming of the Sabie River increased species richness and local population levels of certain Odonata species. The impoundments have created more varied biotopes through slowing water flow (Clark and Samways 1996).

1.5 Increasing awareness of dragonflies as conservation subjects

It is well-known that invertebrates are relatively neglected in comparison with plants and vertebrates in conservation action (Horwitz et al. 1999). The educational value of country parks, botanical grounds and nature reserves could be also applied to public awareness of invertebrates. The small-scale nature of most insect habitats lends itself to the development of nature trails which are becoming increasingly popular within these parks, reserves and botanical grounds.

Even large, highly visible and attractive invertebrates like dragonflies still do not stimulate sufficient funding to assure their effective conservation (Moore 1999). Nevertheless, efforts are being made in various countries to create reserves for them (Asahina 1974, Moore 1976, Watson 1979, Wells et al. 1983, Tyagi 1985, Fry and Londsdale 1991). Also, one of the key points in the IUCN/SSC status survey and conservation action plan for dragonflies (Moore 1997) is that it is crucial to raise public awareness about these insects.

This is easier in Japanese culture (Primack et al. 2000) where dragonflies feature more strongly in everyday life than is the case in most countries. However, many parks and botanical gardens already feature butterflies and dragonflies in their nature trails in Britain and South Africa respectively (although this does not necessarily cater for threatened species) and other interpretative presentations (Fry and Londsdale 1991, Suh and Samways 2001). One way to increase public awareness of invertebrates has been to give them vernacular names. Such names for dragonflies are well-established in Britain (Miller 1995) and recently have been agreed upon for the USA (Paulson and Dunkle 1999). English vernacular names for South African dragonflies developed over the years via Pinhey's Heritage African Odonata Network (PHAON) (Kddijkstra@hetnet.nl) have also been established, and listed in Samways (2002)

1.6 The Odonata in conservation

1.6.1 Biogeographical species richness and distribution

The world distribution pattern of the Odonata is sufficiently wide for comparisons to be made between different areas (Samways 1993). Also, many of the families and even genera are widespread, making for meaningful taxonomic comparisons between continents or areas. The main difficulty from a practical point of view is that recognition of the species, especially of many Zygoptera, can be difficult. Another short-coming with the Odonata at a global scale is that the few species that occur in the deserts are generally widespread and eurytopic (Watson 1962; Aguesse 1968; d'Aguilar et al. 1986) and therefore of a lesser value in monitoring these ecosystems. But nevertheless, these species can be indicative of eroded, disturbed conditions, albeit that these conditions may be highly self-evident.

Davies and Tobin (1984, 1985) list 4877 described species of Odonata (Zygoptera 2362; Anisozygoptera 2; Anisoptera 2513) while Bridges (1991) lists 5667 species, probably about 80% of the actual world total. A recent and ongoing attempt to assemble all the valid Odonata species of the world on a website has been made by Schorr and Lindeboom (2003). Odonata are distributed from the tropics, where the greater number and diversity occur, to the tree-line in the polar regions. Both the moderate size of the taxon and the proportion of the species known to science, make Odonata a useful taxon in biodiversity assessment. There is a sufficient number of species to give variety, yet there is not an unwieldy number of unnamed species necessitating resort to long series of difficult-to-recognise morphospecies (Samways 1993). This is illustrated by the following data: only 11 species of odonates occur in New Zealand, and 194 species in the

whole of Canada. In contrast, at least 62 species were recorded from a single hill-stream in Malaysia (Bishop 1973). The Neotropical Region has the greatest diversity of odonates together with the greatest number of endemic species, many of them damselflies. The next richest region is the Oriental, where the Calopterygidae (Zygoptera) form a significant part of the fauna, and where many of the major islands have rich and characteristic faunas (Tillyard 1917).

The odonate fauna of the Australasian region has several features including a rich complex of archaic forms (Gondwana relicts), particularly among the stream-dwelling species. Part of the fauna has similarities with the Oriental region, and some forms are shared with the Neotropics, while the Cordulegasteridae are absent (Watson 1982). The Nearctic is relatively poor in zygopteran families (apart from the Coenagrionidae) but certain anisopteran families contain considerable numbers of species, for example the Gomphidae (93 spp.), Libellulidae (93), Corduliidae (50) and Aeshnidae (38) (Westfall 1984).

The Palaearctic Region has the poorest fauna, despite its vast area, and some species are shared with the Nearctic. Japan however, has a relatively high diversity. Dragonflies also feature strongly among the boreal faunas (Cannings and Stuart 1977; Askew 1988). Island endemics are also numerous (e.g. Preston-Mafham 1991).

The Afrotropical region is not particularly rich, with about 900 species having been recorded to date (Samways pers comm.). Being a largely dry continent, it has many widespread, vagile species, although some islands and mountainous areas are rich in local endemics. South Africa has about 160 species, divided roughly equally between Anisoptera and Zygoptera. It is relatively rich in national endemics, which account for about a fifth of the national fauna.

1.6.2   Odonata as conservation subjects and/or tools

Dragonflies are part of the world's biodiversity and therefore must be conserved (Earth Summit at Rio de Janeiro 1992). Both larval and/or adult Odonata have proved to be useful monitors of anthropogenic disturbance to river systems (Watson et al. 1982, Carchini and Rota 1985, Schmidt 1985, Chovanec et al. 1997). Additionally, their localised distribution pattern has been related to landscape changes, with the dragonflies being both the subjects and the monitoring tools (Ormerod et al. 1990, McGeoch and Samways 1991). The IUCN worldwide conservation strategy for dragonflies has been developed by the Species Survival Commission (SCC), Odonata Specialist Group (Moore 1982). This body has been active over the years (Moore 1999), and has produced an Action Plan (Moore 1997).

Additionally, there have been regional surveys assessing conservation status and proposing protection measures in parts of Africa including North Africa (d'Aguilar et al. 1986), Southern Africa (Pinhey 1951; Samways 1992; 1999, 2002, 2003), West Africa (O'Neil and Paulson, 2001, Dijkstra and Lempert 2003), East Africa (Clausnitzer 1999; 2001, 2003), Central Africa (Vick 1997; 1999), Republic of Equatorial Guinea (Brooks

and Jackson 2001), Gulf of Guinea Islands (Dijkstra 2002), the Comoro Islands (Samways 2003), Australia (Watson 1982) and Europe (van Tol and Verdonk 1988). Certain selected threatened species have also been studied specifically with their conservation in mind (e.g. Sant and New 1988). Additionally, Odonata have featured strongly in The IUCN Invertebrate Red Data Book (Wells et al. 1983, Samways 2003) and The 2002 IUCN Red List of Threatened Species (IUCN 2002).

The importance of focussing on the last-stage larva, exuviae or adults is that it means they have successfully almost completed larval development within a particular biotope. Observation of reproduction and/or breeding behaviour provides valuable supplementary information (Corbet 1993; 1999). Young Odonata larvae, on the other hand are cryptic, inconspicuous and difficult to identify, making the larval stages often impractical as conservation monitoring tools especially in Africa. Nevertheless, Hawking and New (1999) have shown that adults are good surrogates for the larvae.

Yet the use of adults alone, especially as indicators, must be done with caution as the occurrence of an adult and observed oviposition at a water body does not always imply successful breeding and larval survival at that particular water body. For example, *Pantala flavescens* (Fabricius) can often be observed ovipositing in artificial ponds but with little chance of breeding success (Samways and Caldwell 1989). Odonata are particularly well suited to monitor landscape physiognomy and quality assessment of freshwater. They are also valuable in decision making for conservation of endemism on the one hand, and typicalness on the other. Ideally however, their use should be in congruence studies, where other biotic groups are employed alongside them (Samways 1993).

1.6.3 Aspects of dragonfly biology relevant to their suitability as indicators

An important aspect of Odonata biology is the distinctive range of species biotope preferences (Samways and Steytler 1996; Corbet 1999). The vegetational conditions of water and nature of the substrate, determine the local and regional distribution of Odonata larvae (Pinhey 1978). Localised species are restricted by adult preferences as well as those of the larvae. The adults being the dispersal and reproductive stage, must select suitable breeding/oviposition sites that are structurally and ecologically preferred to ensure the completion of larval development. For example, most Zygoptera and Aeshnidae, insert their ovipositors into often submerged plant tissue to lay their eggs (endophytically).

The entire adult life centres around reproduction (Corbet et al. 1960; 1999). Between the aquatic and aerial stages in Odonata life history, there are two transitional events: emergence and oviposition. Whereas a population scatters after emergence, it aggregates before oviposition. The males arrive at the breeding grounds before the females, tending to become localised within it i.e. they set up territories within which they court females and defend the area from intruding males. Mature males often remain at the rendezvous, making short daily movements to nocturnal roosting sites, unless displaced by strong winds or by aggressive interaction with other males. For the majority, the rendezvous is

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at or near the oviposition site, serving as a focus for copulation and subsequent oviposition (Corbet 1980; 1999). This aggregation behaviour at oviposition sites can be used as a basis in determining biotope selection. In terms of practical monitoring, the females and pre-reproductive individuals are not always suitable, mostly because they are difficult to identify on the wing, especially African species. Pre-reproductive individuals often move away from the breeding ground to feed and mature, and therefore have no reliable association with a specific biotope unless ovipositing. In this study, males are used because they are conspicuous and usually easily-identified on the wing using binoculars.

1.7 Effects of elevation on dragonfly assemblages

It has long been known that more species of dragonflies occur in southern England than in the north of Britain. This is an example of a common trend in many parts of the world, whereby species richness declines at higher latitudes (Schall and Pianka 1978; Pianka 1966). The thoroughness of recording has only recently become sufficient for more detailed patterns of species richness to be explored (Lawton et al. 1994). The general pattern, of a decline in species-richness from S or SE to N or NW, is found in many taxa, and is correlated with several environmental factors (Eversham and Cooper 1998). In Britain, many physical variables such as temperature, rainfall, sunshine, topography, geology and soils show a strong SE to NW gradient, the SE being warmer, drier, sunnier, predominantly lowland, with more basic rocks and alluvial soils (Vincent 1990). Probably as a result of these trends in environmental factors, Odonata diversity 'hotspots' are concentrated in southern England, although several of the scarcer species are confined to the north (Aspinall et al. 1994; Prendergast et al. 1993). Large-scale patterns in species-richness have thus been explained in terms of major gradients, whereas small-scale variations are considered to be due to current and historical land use (Eversham 1993; Lawton et al. 1994). Diversity 'hotspot' distribution is probably caused by an interaction between the two (Eversham and Cooper 1998). Biogeographers have previously suggested that the effects of climate are much greater than other factors (such as soil) in determining large-scale patterns of dragonfly species distributions (Cain 1944; Hill and Dominguez-Lozano 1994).

The highest elevation (at a given latitude) at which adult Odonata have been observed exceeds those at which they are known or assumed to maintain resident populations (Corbet 1999). Furthermore, species assemblages at a given latitude reflects, but is not a simple function of, elevation (Corbet 1999). Excluding species that sometimes occupy thermal springs far above their elevational limits in non-thermal waters (Borisov 1987), a common pattern revealed by faunistic studies of dragonflies across vertical gradients is for the number of taxa to decrease with increasing altitude (Samways 1989b; Corbet, 1999), diminishing abruptly above a certain level. For example, above 1000 m in Taiwan, (Ubukata et al. 1992), 1300 m in Tadzhkistan (Borisov 1987), 1400 m in KwaZulu-Natal, South Africa (Samways 1989a; 1989b) and 3000 m in Nepal (Vick 1989). Within an elevational gradient occupied by Odonata, there are zones characterised by species assemblages and correlated with vegetation cover and climate (e.g. Belyshev 1961, Kepka 1971, Vick 1989, Hoffman 1991). Furthermore, in the tropics, biogeographical

faunal elements may segregate according to elevation. In Venezuelan Guiana, at 5-6° N, a typical Amazonian forest fauna exists between 100 and 700 m (e.g. *Dicterias cothurnata, Hetaerina mortua*) a mixed fauna between 700 and 1100 m, and many endemics, probably of autochthonous origin, between 1100 m and 2400 m (e.g. *Euthore montgomeryi, Iridictyon myersi* (Racenis 1968). Elevation-related changes in species composition usually entail progressive disappearance of species commoner at lower elevation, but some taxa have their centres of distribution at high elevations. In KwaZulu-Natal, the indigenous, and predominantly montane family Synlestidae occurs mainly above 1400m, and *Aeshna minuscula* primarily between 1800 and 2000 m (Samways 1989a).

1.8 Aims of the present study

Ponds can be constructed which inevitably attract dragonflies but these are mostly vagile, widespread and abundant species (Osborn and Samways 1996). Moore (1991), in a study in England, has shown that dragonfly assemblages change at an artificial pond over time. Such artificial ponds, however, are also important for introducing the public to invertebrates and increasing awareness of invertebrate conservation.

Against this background, an earlier ecological landscaping research project was carried out in South Africa as a collaborative project between the Invertebrate Conservation Research Centre (ICRC), University of Natal, and the then Natal National Botanical Gardens, Pietermaritzburg in 1989. The principal subjects under study were dragonflies which were being used to demonstrate to the public the importance of ecological landscaping (Samways 1989d). This group of insects was chosen because they are particularly conspicuous and are biologically tied to water bodies. A lily pond virtually guarantees that at least some dragonflies will be seen at any time of the year. Also, as the males are generally brightly coloured, it means that they have a high visual profile to the human eye. Additionally, they are umbrella species, and where they are being conserved, many other insects, particularly those that are less conspicuous are inevitably also being protected. KwaZulu-Natal is rich in dragonfly species and some two-thirds of the species are found in this eastern part of the country (Samways 1992; 1999). The reasons for this richness include high rainfall, warm seaboard winter climate, varying terrain, and through the altitudinal gradient providing a variety of micro-bioclimatic areas. This preliminary research laid the groundwork for the design, in 1999, and implementation in 2000, of the first dragonfly awareness trail in an African botanical garden (Suh and Samways 2001). However, it should be noted that awareness here does not always equate with meaningful conservation in terms of saving threatened species.

Interestingly, the social research leading to implementation of the trail pointed to the elderly and to children as showing most interest, with children being potential conservationists of the future. The trail, now operational at the National Botanical gardens, Pietermaritzburg, begs the question as to how and in what way does the dragonfly assemblage composition along the trail change from year to year and what are the seasonal and spatial trends followed by typical adult dragonfly species assemblages sampled along the trail. These questions are addressed in chapter two.

Little information exists in the southern hemisphere on longer-term changes in dragonfly assemblages compared to the north. Such longer-term studies are crucial for determining whether a species in a conservation area is being afforded protection from varying local anthropogenic impacts over time, especially in an El Niño-prone area. The overall aim in chapter three is to assess a reservoir which was created 13 years earlier to determine the changes that have taken place. The reason for this is to understand how concepts of residency and succession underpin conservation decisions. This third chapter specifically aims to document the physical biotope changes and also how these have affected the dragonfly assemblage over time and to ascertain how the assemblage has responded to the altered ecological conditions. As this reservoir is also part of a dragonfly conservation awareness trail (Suh and Samways 2001), the study also makes recommendations for future management of the reservoir.

Certain farm landscapes in southern Africa are important in promoting insect diversity. In particular, small farm dams, which are characteristic features of the southern African agricultural landscape are important miniature reserves. Four Zygoptera species out of 17 records and seven Anisoptera out of 23 were found in a local elevational sampling study, to occur only at farm dams. This indicates the importance of elevation in selecting sites for construction of artificial water stands for dragonfly species conservation. Many species found in high elevations do not necessarily breed (or maintain resident populations) there. Neither are high elevations generally taxa-rich (Samways 1989a; Corbet 1999). This leads to the questions: How restrictive are high elevations to species richness? Is the change in species richness with increasing elevation gradual or discontinuous, and why? Also, how does species phenology change relative to elevation in the sub-tropical African contexts? Elevation remains a significant factor in determining changes in species population dynamics and phenology, especially in South Africa with its considerable variation in topography. Chapter four therefore aims to address the above questions and at the same time, look at effects of elevation on dragonfly assemblage dynamics on a spatial and temporal scale with a view to making management recommendations for species conservation.

Any changes in landscape will, in effect, have an impact on Odonata. It will affect both the aquatic larva and aerial adult. Chapter 2-4 focus mostly on the adult, which is the final product of the landscape filtering effect on dragonfly development. But what aspects of artificial water bodies encourage Odonata larvae of particular species? Chapter five therefore focuses on species richness and abundance along different elevational sites gradients comprising of farm dams and ponds with a view to establishing exactly what factors encourage or discourage dragonfly larvae within the modified landscape, at the spatial scale of reservoirs.

10

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Chapter Two   Phenology of dragonflies along a dragonfly trail

2.1 Abstract

A dragonfly awareness trail was developed and implemented in 2000 at the National Botanical Gardens, Pietermaritzburg, South Africa. The trail, having been established was not likely to always have had the same number of dragonfly species either throughout the year or from year to year. In response to this dearth of information, the aim was to assess dragonfly assemblage changes that occurred along the trail from 2000 to 2003, so as to fine-tune expectations that the public may have as regards species to be seen at any particular time during the year. This was done by selecting the main representative sites along the trail: 1) waterfall and forested river, 2) shaded reservoir and associated small stream, and 3) an open reservoir for used in the study. The biotope requirements of an odonate species may be temporally or spatially defined. This was shown using a two-way ANOVA of sites variables-by-year interactions. Only marginal grasses, floating and submerged vegetation, marginal herbs, sedges and reeds and pH resulted in statistically significant differences at sites during the three-year study. However, multivariate analyses, using all thirteen measured site variables and dragonfly species data over two of the three years (2001/2002), selected in addition to the above-mentioned variables: percentage shade, exposed rock, marginal forest and water flow characteristics. A cumulative species variance for species (CA) and species-environmental relation (CCA) of 82% in 2001 and 70.3% in 2002, strongly indicated that the measured site variables were responsible for the main variation in dragonfly species patterns during each of the two years. There were no statistically significant differences in dragonfly species richness at the three sites over the three sampling years. However, abundance changed significantly. Accumulative species curves over the three-year study period showed that all the resident species can be seen along the trail after two visits each month from January to April (or eight times during the whole of this peak abundance period). Such information is useful for raising dragonfly awareness and conservation in general.

2.2 Introduction

There is a lack of general support for insect conservation from the public, politicians, administrators and even many non-invertebrate conservation scientists (Yen and Butcher 1992). To overcome this conceptual barrier, a public awareness campaign emphasising the taxonomic and functional diversity of beneficial invertebrates is needed as a necessary and integral part of invertebrate conservation (Yen and Butcher 1992; Kellert 1996; Horwitz et al. 1999).

The educational value of country parks lies in part in their stimulating public awareness of invertebrates (Gilbert 1989). The small-scale nature of most insect habitats lends itself to the development of ponds, reservoirs and nature trails which are becoming increasingly popular within parks. In Britain, many parks already feature butterfly and dragonfly trails (Hill and Twist 1998). These parks and trails may not necessarily be for threatened species, but rather for enjoyment of the insect subjects (Fry and Lonsdale 1991) and to enhance conservation efforts through increased awareness (Harrison and Burgess 2000).

From a conservation standpoint, artificial dragonfly reservoirs are a significant addition to the Japanese landscape. In particular, dragonfly reservoirs next to schools are successfully encouraging an appreciation for nature and conservation in a new generation of Japanese (Primack et al. 2000). Elsewhere also, reservoirs have been created and modified for dragonfly conservation (Moore 1991, Steytler and Samways 1995). Additionally, such artificial reservoirs are also important for introducing the public to invertebrates in general and increasing awareness of the need to conserve them. Indeed, the IUCN Action Plan on dragonfly conservation (Moore 1997) identifies the importance of increasing public awareness of dragonflies, which has been pioneered in Japan. In response to this Action Plan, a dragonfly trail was developed and implemented in the year 2000 at the National Botanical Gardens in Pietermaritzburg, South Africa (Suh and Samways 2001). The trail, having been established, could not be expected to always have the same number of dragonfly species either throughout the year or from one year to the next. This has general applicability with development of such awareness trails, so as to maintain their bona fide through guarantees that particular species will always be present, although not necessarily seen on any one visit. The aim here was to assess dragonfly assemblage changes that occur along the trail throughout the year and between years, so as to fine-tune expectations that the public may have as regards species to be seen at any particular time during the year.

2.3 Materials and methods

2.3.1 Site

The study area (Fig.1) was the National Botanical Gardens, Pietermaritzburg, 29°35' S, 30° 25' E, 790 m a.s.l. Three sites were selected à priori along the dragonfly trail designed in 1998/99 and implemented in 2000. These sites represented the fundamental components of habitat and hence dragonfly diversity at the location (Suh and Samways 2001), and comprised of: 1) 'Open reservoir' (Opp). This site, located at the beginning of the trail, was made up of floating, submerged and marginal vegetation. Vegetation at the reservoir edges was periodically cleared over the years, most of which was subsequently replaced with indigenous ornamental plants in 2002. 2) 'Shaded reservoir and small stream' (Shps). This site (located at the middle of the trail) had floating and submerged vegetation, and a small stream inlet and outlet, all shaded by marginal trees and medium-height over-hanging macrophytes. 3) 'Waterfall and forested river' (Wffr). This, located at the end of the dragonfly trail, was at the outlet from a reservoir (hence a waterfall), forming a small stony river with semi-forested banks, and a high diversity of marginal herbs and over-hanging macrophytes.

2.3.2 Methods

Each of the three sites was further stratified into four sampling units (SUs), each measuring 10 m length (along a line transect parallel to the water's edge) by 2 m width (1 m into water and 1 m on land). Adults were sampled from each SU for three years from January 2000 to January 2003 on 63 sampling occasions. Data collected for adult male dragonflies and measured environmental variables were collected twice a month, but once a month in June, July and August when few dragonflies were present. Only males were counted, as females are not always in close association with the water and can be difficult to identify in the field.

By walking the 10 m transect lines per SU in 6 min, all male dragonfly individuals identified to species level and patrolling or perched within a SU were recorded, using close-focus 8 x 24 binoculars. Sampling was mostly before noon to avoid the very hot (25^0C - 30^0C shade temperatures) midday temperatures when territorial males are less active (Steytler and Samways 1995; Schmidt 1985; Corbet 1999). Visual observation of adults gave reliable population estimates. Moore (1991b) has shown that even though individuals may leave without being counted or return and be counted twice, he found counts to be over 80% correct for Zygoptera and 100% for Anisoptera. Where identification of specimens was difficult in the field, odonate individuals were captured for identification and then released.

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Key

—··— Botanical Gardens Boundary

—— Service road

★ Trail

🐾 Water Bodies

Sampling Sites:

● Waterfall & Forested Stream (Wffr)

▪ Open reservoir (Opp)

✛ Shaded reservoir & Small Stream (Shps)

0   250   500 metres

Cartographic Unit, University of KwaZulu-Natal, Pietermaritzburg, 16/07/04
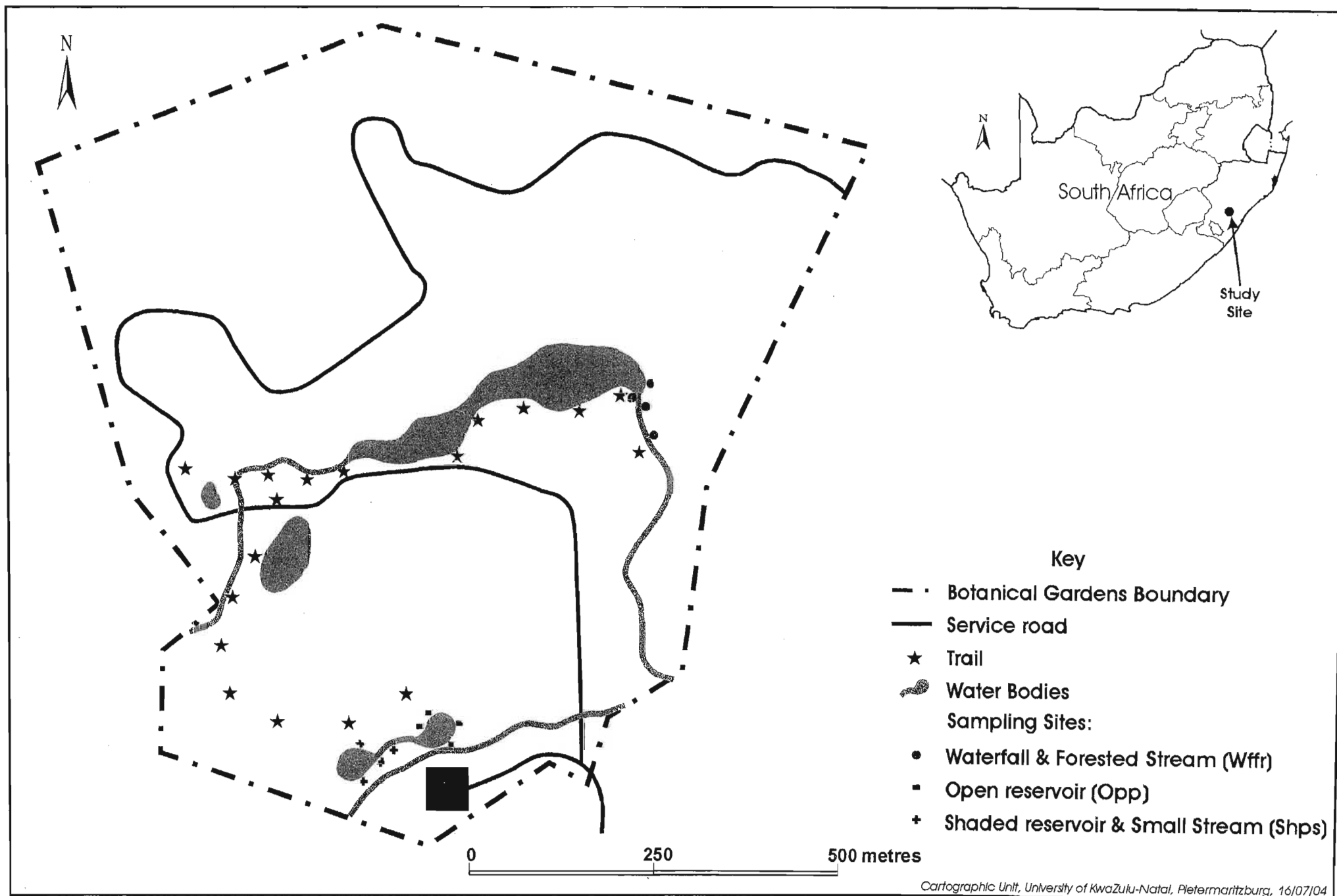
Fig. 2.1 Map showing the study site at the National Botanical Gardens, Pietermaritzburg, South Africa

2.3.3 Environmental variables and their measurement

Many dragonfly species prefer water of a certain pH (Weir 1974; Osborn 1992). Water flow may influence oxygen concentration in water. Vegetation along with substrate may serve many important functions for dragonflies (Buchwald 1992; Steytler and Samways 1995; Corbet 1999) e.g. flight perches for food, mating, oviposition, and even refuge from predators. The thermal requirements of the species further results in different responses to sunlight and shade (McGeoch and Samways 1991). Against this background, two one-monthly measurements of variables were made in sunny, warm conditions mostly just before noon. Water depth (Wd) was measured using a V.C 1456 meter rule. Acidity (pH) was measured using a Jenway 3405 electrochemistry analyser calibrated just before use. Water flow characteristics were measured as 1 = Flow (i.e. a slow meander) and 0 = reservoir. Turbidity (Tur) was estimated visually at midday as the results became less reliable near dawn or dusk because of reduced surface illumination. Percentage estimation ranged between 0% (totally transparent) to 100% (totally muddy conditions) using a secchi disc. The degree of shading (%Sh) of SUs was estimated by mean percentage shade cover at midday for each SU. Water temperatures (Wt) were measured using a Delta Trak hand thermometer at midday by immersing the probe by 2 cm below the water surface. Atmospheric temperatures (At) were taken from the botanical gardens daily records. These records were cross-checked with readings from the hand thermometer for each sampling day. Exposed rocky (Erock) conditions were useful perching sites for a variety of dragonfly species. This variable wherever it occurred was measured as a percentage of the total SU it covered.

2.3.4 Site vegetation description

Vegetation (structural and compositional) varied in summer from submerged, semi-aquatic and emergent plants through marginal grasses and sedges to deciduous forest, and showed marked variations in plant species richness, diversity and architecture. Winter was characterised by a drop in water levels at the reservoirs and streams. Percentage estimates in all 12 SUs were therefore made using the following four dominant vegetation categories:

i) Marginal herbs, sedges and reeds – Mhsr, ii) Marginal grasses – Mgra, iii) Floating and submerged vegetation – Fsv, iv) Marginal forest – Mfor, and v) Marginal ornamental plants – Mop.

In all, thirteen environmental variables were measured during the whole study period and both data sets (dragonfly species occurrences and SU variables) recorded in data matrices.

2.3.5 Statistical analyses

Data were collated for each site and arranged in matrices as proposed by Ludwig and Reynolds (1988). All dragonfly abundance data were square-root-transformed to maintain normality and to satisfy the requirements of ANOVA and multivariate analyses.

Data were analysed in two steps. Firstly, univariate methods for species richness and abundance relationships using diversity indices, distributional models and graphical methods. Species spatial and temporal variability was analysed using analysis of variance (ANOVA). Secondly, multivariate methods of classification and ordination were used.

a) Univariate methods

The full set of species counts at sub-sites was reduced to single coefficients to enable comparisons at site levels. Hill's (1973) Diversity number (N1) was used. It measures the effective number of species '$\underline{S}$' present in a sample as a degree to which proportional abundances are distributed among the species. The function's N1 = $e^{H'}$, where N1 is a measure of the diversity of abundant species. H' (Shannon's index) is a measure of the average degree of uncertainty in predicting to what species an individual chosen at random from a collection of S species and N individuals will belong. When H'=0, it means there is one species in the sample indicating low diversity. H' is maximum (indicating high diversity) when all S species are represented by the same number of individuals i.e. a perfectly even distribution of abundances. These two indices were selected for this study as they made the interpretation of species diversity at sites and sub-sites more meaningful. Pielou's Evenness index J' was also selected above other evenness indices as being least unambiguous (Ludwig and Reynolds 1988). This index expresses the degree to which individuals are evenly distributed among the species at sampling sites/SUs. As J' approaches 1, so does the diversity of that site/SU decrease. Hill's, Shannon diversity and Evenness indices were calculated using the software program BIODIVERSITY PROFESSIONAL (McAleece et al. 1997).

The difficulty was recognised here of interpretations arising from diversity indices, because parameters such as species richness, evenness and number of individuals and the area sampled are compounded when a single diversity index is used (Ludwig and Reynolds 1988, Curry 1994). An alternative approach that avoids these difficulties is the use of rank-abundance curves in which both species richness and evenness are graphically displayed. The curves are drawn such that the percentage (dominance) is plotted against ranked species sequence (Ludwig and Reynolds 1988; Curry 1994).

Rank abundance curves were used to establish the relationship between abundance and number of species having that abundance graphically. Plots of abundance of each species in the samples in order of its rank from the most to the least abundant for each site were used. This method was a more explicit illustration of species abundance patterns, rather than using simple diversity/evenness measures. Species percentage dominance patterns were calculated using the program DOMPLOT, and the program CLUSTER used to calculate Bray-Curtis similarity indices between SUs at sites, using the software package PRIMER (Ludwig and Reynolds 1988).

MINITAB and SPSS software were used to run ANOVA, relating species to sites and site variables

b) Multivariate methods

Although the sampling design would allow for ANOVA-type approaches, the presence of may zeros in the data set made this approach not very reliable. This problem was solved using ordination techniques in multivariate analyses. Classification and ordination methods were used to analyse patterns across sites in the study area. These methods are characterised by the fact that they base their comparison of samples on the extent to which these samples share particular species, at comparable levels of abundance. Similarity coefficients calculated between every pair of samples helped facilitate a classification or clustering of samples into groups which are mutually similar or an ordination plot in which the samples are 'mapped' into multidimensional space in such a way that the distances between pairs of samples reflect their relative dissimilarity of species composition.

i) Classification

Hierarchical agglomerative clustering was used. The program 'Cluster' in the computer software PRIMER (Clark and Warwick, 1994) was used. The species by sub-site (SS) data matrix was transformed using 4th root-transformation to balance rarer and commoner species. The Bray-Curtis similarity index was then used on these data to produce a similarity matrix and then fused successively through hierarchical clustering using group-average linking. The results of this clustering were represented by a dendrogram with the x-axis defining a similarity level at which two samples or groups are considered to have fused, and the y-axis representing the full set of samples.

ii) Ordinations

Ordination is a term used to describe a set of techniques in which sub-sites are arranged in relation to one or more co-ordinate axes such that their relative positions to the axes and to each other provides maximum information about their ecological similarities. When sub-sites that are most similar or dissimilar are identified based on coordinate positions, underlying biotic and abiotic factors that might be responsible for the patterns are determined.

Correspondence analysis (CA), as an ordination technique, operates on a site and species data matrix and represents it on a two-dimensional plane (ter Braak and Smilauer 1998, ter Braak 1986, 1987). It uses a site-by-species scores data matrix and summarises it such that increasing distance between the sites on the ordination plane means decreasing similarity in the species assemblages at the respective sites. Conversely, from a species-by-site matrix, CA ordinates the data such that the closer two species are to one another on the same ordination plane, the greater the likelihood that they will occur at the same or similar sites and vice versa. Canonical Correspondence Analysis (CCA) was used to relate species and site scores to underlying environmental variables. The length of an arrow representing an environmental variable is equal to the rate of change in the weighted average as inferred from the bi/triplot, and is therefore a measure of how much the species distribution differs along that environmental gradient. Important environmental gradients therefore tend to be represented by longer arrows than less

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important ones (ter Braak and Looman 1995). The software CANOCO version 4 and CANODRAW version 3.1 (ter Braak and Smilauer 1998) were used.

2.4 Results

2.4.1 Seasonal changes in species richness and abundance throughout the study period

2.4.1.1 Trends in higher taxonomic groupings of Odonata at the study site

Proportionate species richness of each odonate family as a percentage of total Odonata sampled from January 2000–December 2002 showed that Libellulidae ranked highest with slightly above 45% in summer and late spring peaks followed by Coenagrionidae with 27%. Aeshnidae, with only two species made up less than 10% of total Odonata, also appearing in summer and late spring. The remaining seven families, with single species representations, maintained a less than 5% representation, most appearing in all seasons except during winter periods.

2.4.1.2 Species trends

A total of 31 species, with 987 individuals were recorded in 2000; 30 species, with 652 individuals in 2001; and 25 species, with 275 individuals in 2002 (Table 2.1a, b). Patterns of species flight periods or occurrences during the whole study period are as shown in Table 2.2a, b, with *Lestes plagiatus, Pseudagrion kersteni* and *P. salisburyense* occurring throughout the three years of sampling although in very low numbers (1-3 individuals) during winter. *Orthetrum abbotti* occurred only in January and February 2000; *Phaon iridipennis* only in January 2000 and February 2001. Generally, peak species and individual counts were recorded in January 2000; December 2001 and December 2002 with the least counts made in July and August each year as shown in Fig. 2.2.

Accumulation species counts for the three-year study period (Fig. 2.3) showed years 2000 and 2001 curves levelling off after January with 31 and 30 species respectively, while curves for 2002 reached a near asymptote after January, with 25 species.

2.4.1.3 Spatio-temporal changes in adult dragonfly assemblages at sites

The mean number of species (Fig. 2.4a) of adult Odonata recorded each year at the three sites during the whole study period showed that most species were recorded at the waterfall and forested river site (Wffr) during the second year (Wffr2). The location of this biotope probably offered optimal conditions for most species. The least number of species was recorded along the shaded reservoir and small stream site (Shps) which maintained constant species richness throughout the study period. At the open reservoir site (Opp), the least species counts were made in 2002 (Opp3). Individuals recorded (Fig. 2.4b) showed that the open reservoir site had the highest individual counts, occurring in 2000 (Opp1). The least counts at this site were in 2002 (Opp3). The overall least counts at all the sites were at the shaded reservoir site in 2002 (Shps3).

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Table 2.1a Species list and abundance categories of Anisoptera recorded at 12 sampling units along the dragonfly trail at the Pietermaritzburg National Botanical Gardens during the three -year sampling period, with code names of species used in analyses.

Species	Species Code	2000	2001	2002
Aeshnidae				
Anax imperator Leach, 1815	Aimp	4*	3	3
Anax speratus Hagen, 1867	Aspe	2	2	0
Gomphidae				
Paragomphus cognatus (Rambur, 1842)	Pcog	3	2	2
Libellulidae				
Crocothemis erythraea (Brullé, 1832)	Cery	5	5	5
Nesciothemis farinosa (Förster, 1898)	Nfar	5	4	2
Notiothemis jonesi Ris, 1919	Njon	3	2	2
Orthetrum abbotti Calvert, 1892	Oabb	1	0	0
O. julia falsum Longfield, 1955	Ojul	5	5	5
Pantala flavescens (Fabricius, 1798)	Pfla	3	3	3
Palpopleura lucia portia (Drury, 1773)	Pluc	4	3	3
Philonomon luminans (Karsch, 1893)	Plum	2	2	0
Sympetrum fonscolombii (Sélys, 1840)	Sfon	3	2	2
Trithemis arteriosa (Burmeister, 1839)	Tart	5	5	5
T. dorsalis (Rambur, 1842)	Tdor	4	3	3
T. stictica (Burmeister, 1839)	Tsti	5	5	3
Zygonyx natalensis (Martin, 1900)	Znat	3	3	2

*Abundance categories: 1: 1-5 individuals, 2: 6-20, 3: 12-49, 4: 50-100, 5: >100 within each year.

Table 2.1b Species list and abundance categories of Zygoptera recorded at 12 sampling units along the dragonfly trail at the Pietermaritzburg National Botanical Gardens during the three-year sampling period, with code names of species used in analyses.

Species	Species Code	2000	2001	2002
Calopterygidae				
Phaon iridipennis (Burmeister, 1839)	Piri	1*	1	0
Chlorocyphidae				
Platycypha caligata (Sélys, 1853)	Pcal	5	4	3
Coenagrionidae				
Africallagma elongatum (Martin, 1907)	Aelo	4	3	3
A. glaucum (Burmeister, 1839)	Aglm	5	5	5
Agriocnemis falcifera Pinhey, 1959	Afal	4	3	4
Ceriagrion glabrum (Burmeister, 1839)	Cglm	5	5	5
Ischnura senegalensis (Rambur, 1842)	Isen	5	5	4
Pseudagrion hageni Karsch 1893	Phag	4	4	4
P. kersteni (Gerstäcker, 1869)	Pker	5	5	5
P. massaicum Sjöstedt, 1909	Pmas	5	4	4
P. salisburyense, Ris, 1921	Psal	5	5	5
Lestidae				
Lestes plagiatus (Burmeister, 1839)	Lplg	5	5	5
Platycnemididae				
Allocnemis leucosticta Sélys, 1863	Aleu	5	5	4
Protoneuridae				
Elattoneura glauca Sélys, 1860	Egla	2	3	0
Synlestidae				
Chlorolestes tessellatus (Burmeister, 1839)	Ctes	3	3	2

*Abundance categories: 1: 1-5 individuals, 2: 6-20, 3: 12-49, 4: 50-100, 5: >100 during each of the three sampling seasons.

Table 2.2 Seasonal appearances of dragonfly Anisoptera (a) and Zygoptera (b) species along the dragonfly trail at the National Botanical Gardens, Pietermaritzburg from January 2000 to December 2002.

(a)

Year	2000	2001	2002
Species/Months	J F M A M J J A S O N D	J F M A M J J A S O N D	J F M A M J J A S O N D
O. julia	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - - -
T. dorsalis	- - - - - - - -	- - - - - - -	- - - - - -
P. lucia portia	- - - - - - - -	- - - - -	- - - - -
C. erythraea	- - - - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - - - -
T. arteriosa	- - - - - - - -	- - - - - - - - -	- - - - - - -
N. jonesi	- - -	- - -	- - - -
A. imperator	- - - - - -	- - - - - - -	- - -
N. farinosa	- - - -	- - - - - - - - - - - -	-
P. flavescens	- - -	- - - - - - - - - -	-
P. cognatus	- - - -	- - - - - - -	-
T. stictica	- - - - - -	- - - - - - - - - - - - - -
A. speratus	- - - -	- - - - - -
P. luminans	- -	- -
S. fonscolombii	- - -	- - - - -	-
O. abbotti	- -
Z. natalensis	- - - - - -	- - - - - - - - - - - -

(b)

Year	2000	2001	2002
Species/Months	J F M A M J J A S O N D	J F M A M J J A S O N D	J F M A M J J A S O N D
A. glaucum	- - - - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - - - -
L. plagiatus	- - - - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - - - -
P. caligata	- - - - - - - -	- - - - -	- - - -
C. glabrum	- - - - - - - - - -	- - - - - - - - -	- - - - - - - - - -
P. kersteni	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -
P. salisburyense	- - - - - - - - - - - -	- - - - - - - - -	- - - - - - - - - -
C. tessellatus	- - - - - - - - - - -	-
A. leucosticta	- - - - - - - - - - - - - - -
P. iridipennis	- -
P. massaicum	- - - - - - - - - - - - - - - - - - - - - - -
A. falcifera	- - - - - - - - - - - - - - - - - - - - -
I. senegalensis	- - - - - - - - - - - - - - - - - - - - - -
P. hageni	- - - - - - - - - - - - - - - - - - -
A. elongatum	- - - - - - - - - - - - - - - -
E. glauca	- - - - - -

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a
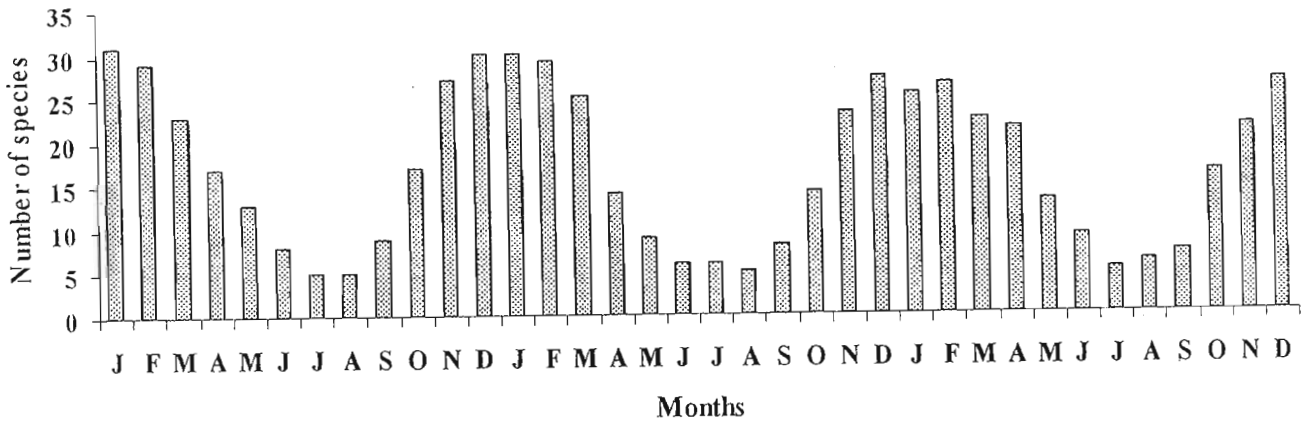
b
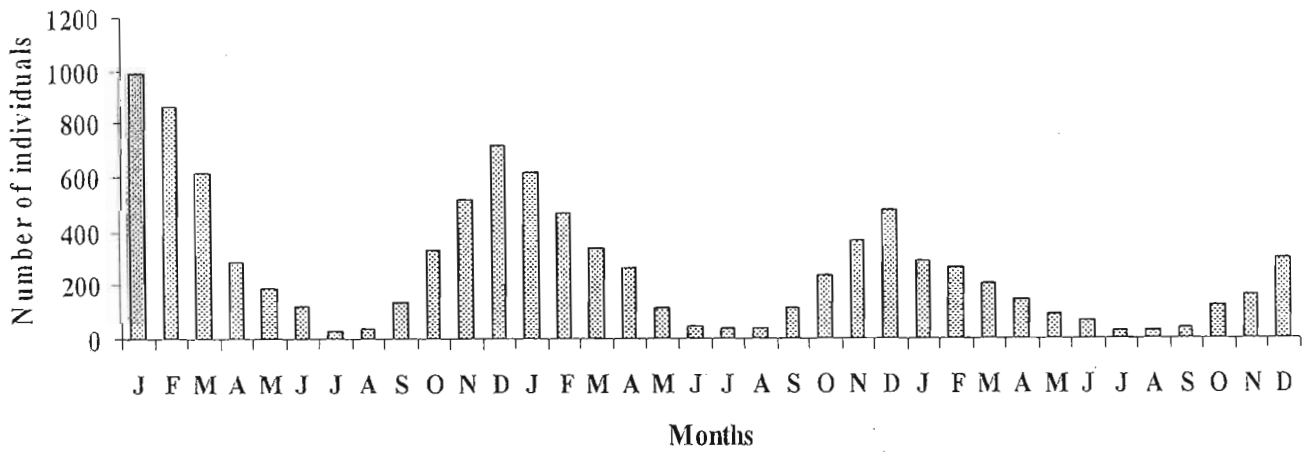
Fig. 2.2 Total number of Odonata species (a) and individuals (b) sampled each month across the three-year sampling period along the dragonfly trail in the National Botanical Gardens, Pietermaritzburg.

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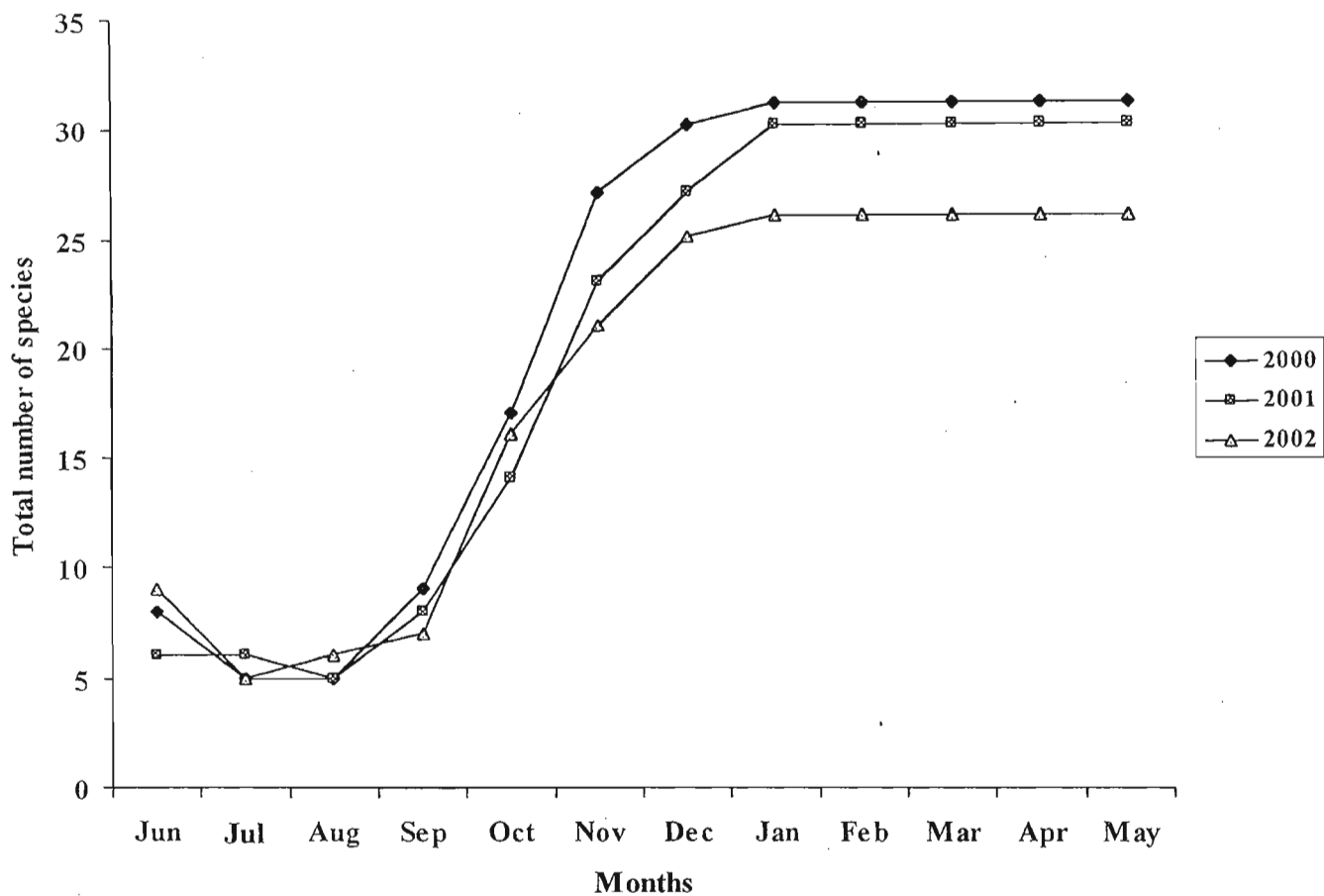
Fig. 2.3 Accumulative number of dragonfly species recorded during the first, second and third sampling years along the dragonfly trail in the National Botanical Gardens, Pietermaritzburg.

a

b
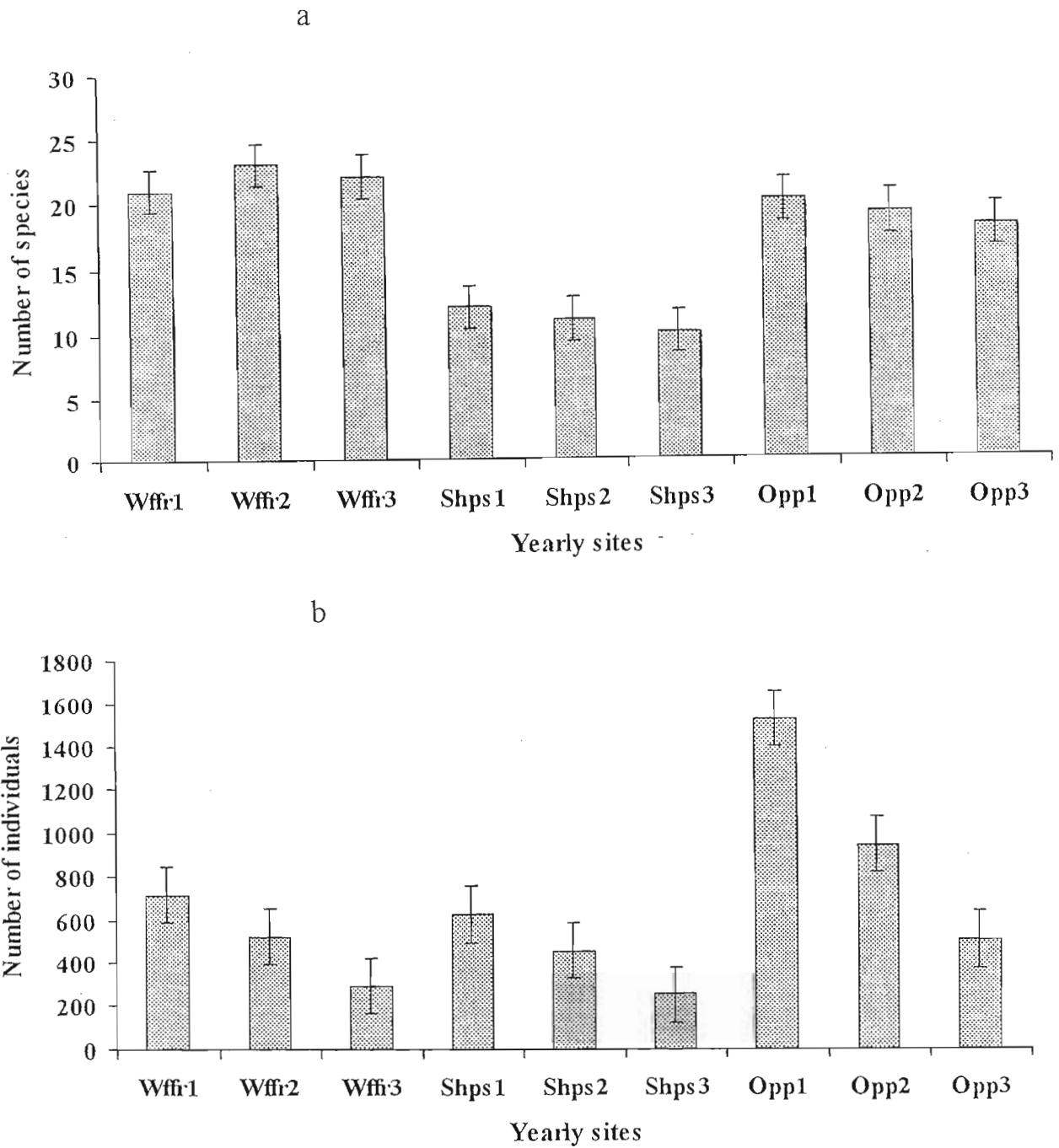
Fig. 2.4 Mean (+/- SE) number of (a) species and (b) individuals of adult Odonata recorded at the three sites (Waterfall and forested river – Wffr; Shaded reservoir and small stream – Shps and Open reservoir – Opp) in three separate years (1, 2, 3) over the whole three-year sampling period along the dragonfly trail at the national Botanical Gardens in Pietermaritzburg.

2.5 Spatial trends

Proportionate species richness of higher odonate groupings at SUs showed the Libellulidae as the most abundant family, peaking at (28%) at SU Wffr4 and at 35% at SU Opp3. The coenagrionids followed with a peak abundance of 23% at SU Wffr3. Least representations of these two families were seen at the shaded reservoir and stream site. The rest of the families showed species representations of less than 10%. Seven families were represented by one species each, while Aeshnidae was represented by two species at the open reservoir site with about 5% representation.

2.5.1 Adult dragonfly species dominance patterns at sites

Adult dragonfly species dominance patterns varied slightly among sites and years but general patterns were similar for the three-year study period. In 2000 *Ceriagrion glabrum* was the most dominant of all species sampled at the shaded reservoir and small stream (Shps) site, at 23%. In 2001 and 2002 at this same site, *L. plagiatus* was dominant at 21% and 18% respectively (Fig. 2.6a, b, c). The next two site levels of species dominance were very similar in pattern at the waterfall/forested river (Wffr) and at the open reservoir (Opp) sites between 2000 and 2002 except that at the open reservoir biotope in 2002 *Crocothemis erythraea* showed dominance levels of 12.5% (Fig. 2.6c). Sites generally showed high species evenness. High evenness values with low species richness at sites during the study period probably indicated that these sites had a few species with very similar number of individuals. Wffr had more dominance (less evenness) than the other two sites.

2.5.2 Site sampling unit clusters

Clustering of all site SUs using the Bray-Curtis index (Fig. 2.7) showed that SUs Wffl; Shps3; Shps4 had the highest similarity (68%) followed by Wffr4; Opp1 and Opp2 at 65%. Wffr2 showed the least similarity to the rest of the sites probably due to it being very shaded, with tall, over-hanging macrophytes, densely packed trees and stony river conditions.

2.5.3 Dragonfly species and their abundance at sites

There were no statistically significant differences among sites with respect to dragonfly species richness even the shaded reservoir and small stream (Shps) had the least species count. However, there was significant difference for abundance ($F = 4.15$; $P<0.05$). The mean number of individuals was the same at the Wffr and Shps sites. Diversity measures using Hill's (N1), Shannon (H') and evenness measures using Pielou's Evenness index (J') showed variation among sites SUs. SU Wffr4 had the highest N1 and H' in all the three years of sampling (January 2000- December 2002). In contrast, SU Wffr1; SU Shps4 and Opp402 had the lowest N1 and H'. This trend was also shown by the patterns revealed in Figs. 2.6 in which sites with lower dominance patterns showed higher evenness and vice versa (Table 2.3).
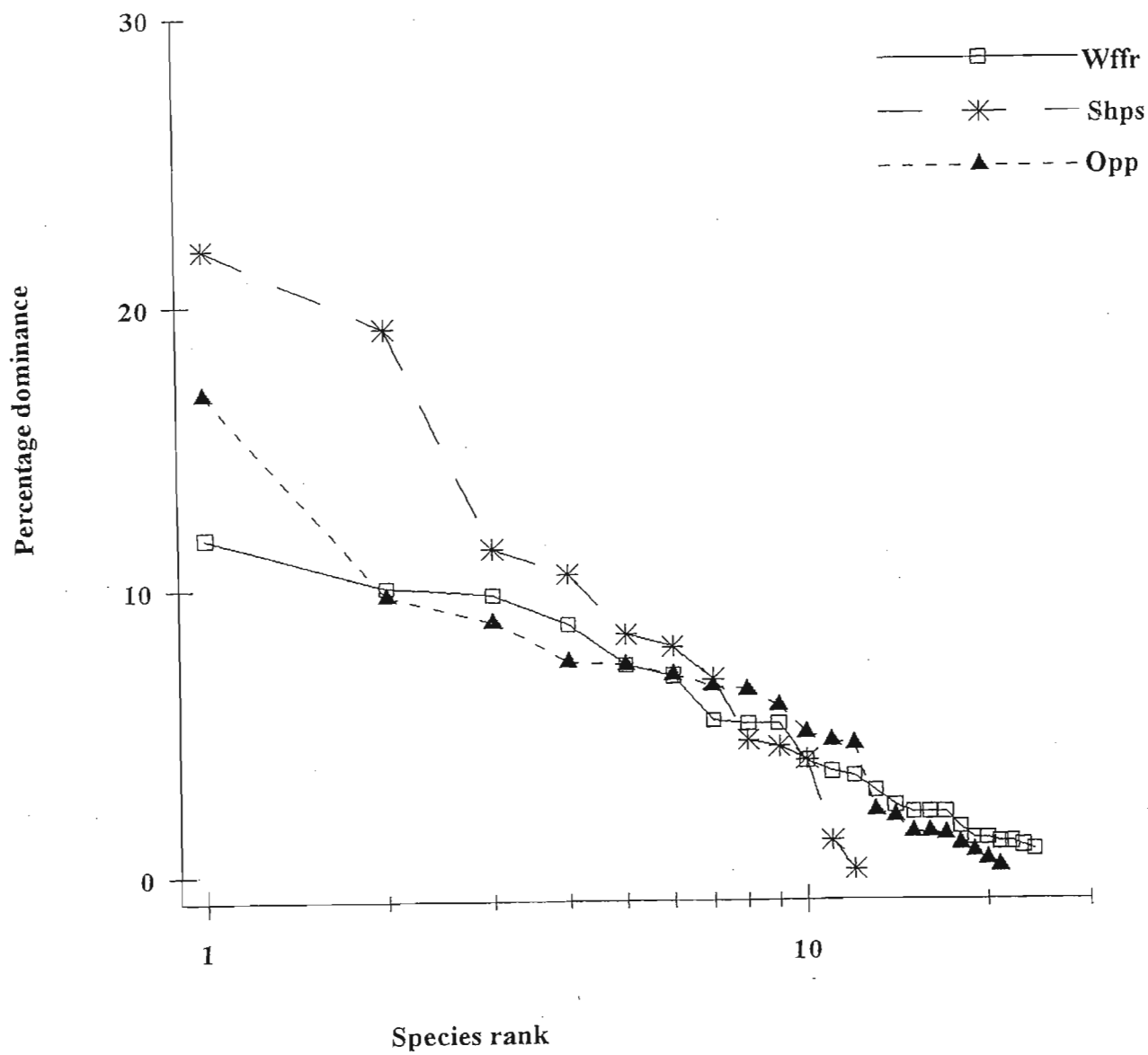
Fig. 2.5a Species rank abundance curves in the year 2000. Species are ranked in decreasing order of their importance from the most common to rarest, and shown for each of the three sites (Wffr, Shps and Opp).
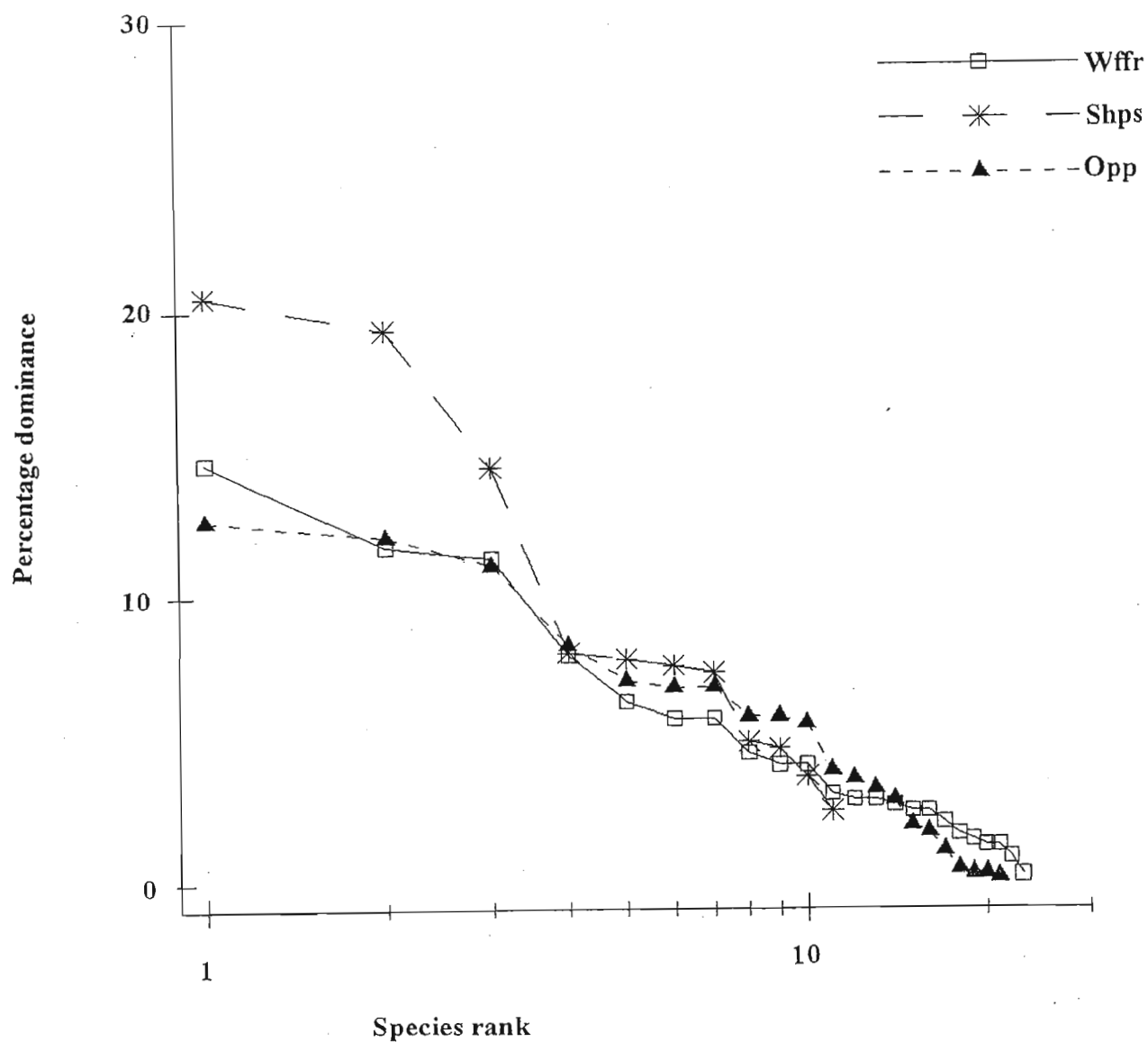
Fig. 2.5b Species rank abundance curves in the year 2001. Species are ranked in decreasing order of their importance from the most common to the most rare and shown for each of the three sites (Wffr, Shps and Opp).
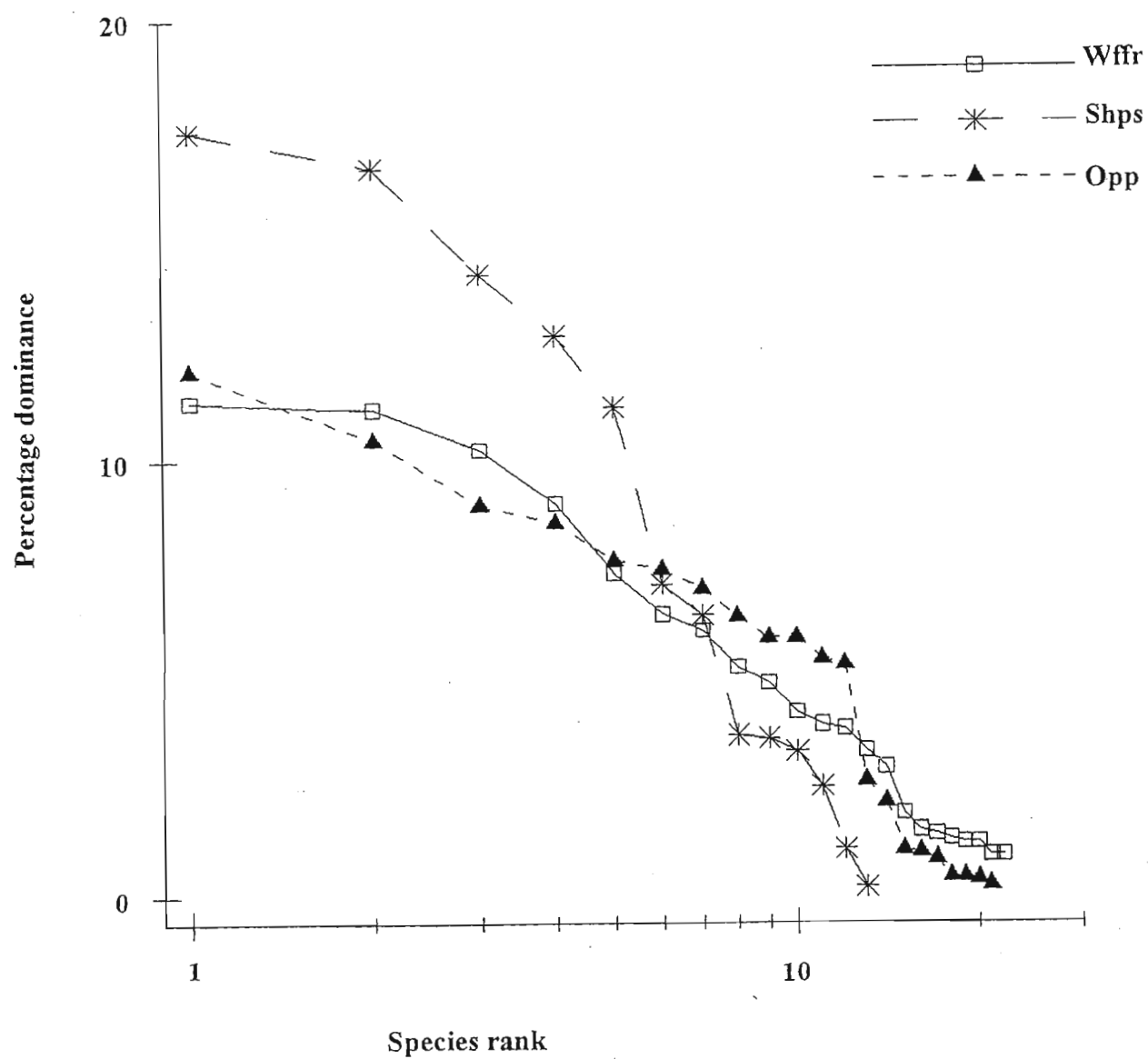
Fig. 2.5c Species rank abundance curves in the year 2002. Species are ranked in decreasing order of their importance from the most common to the most rare and shown for each of the three sites (Wffr, Shps and Opp).
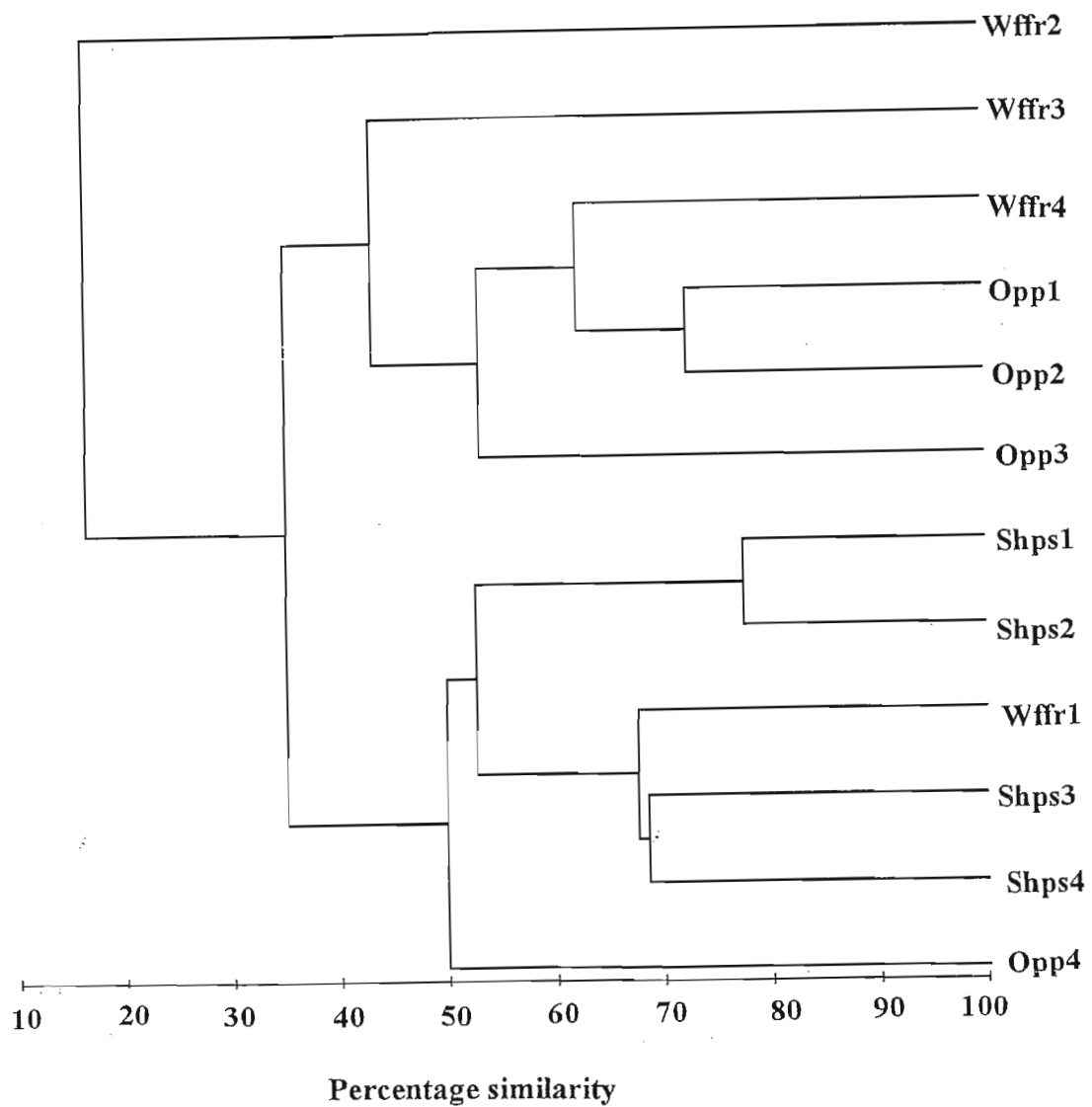
Fig. 2.6 Dendrogram showing hierarchical clustering of the twelve sampling units, using group-average linking of the Bray-Curtis similarity calculated on 4th root transformed odonate species abundance data, pooled for all three sampling years.

Table 2.3 Diversity measures (Hill -N1; Shannon -H' and Evenness-J') indices for all 12 SUs at the three sites: Waterfall and forested river (Wffr); Shaded reservoir and stream (Shps) and Open reservoir (Opp) along the dragonfly trail during the three-year study period.

Year	2000				2001				2002			
SS^a00	S	N1	H'	J'	SS^a01	S	N1	H'	J'	SS^a02	S	N1	H'	J'
Wf100	3	6.61	0.45	0.96	Wf101	6	12.9	0.66	0.85	Wf102	4	8.63	0.53	0.89
Wf200	4	7.12	0.48	0.79	Wf201	4	10.0	0.58	0.96	Wf202	3	6.75	0.46	0.97
Wf300	10	32.2	0.93	0.93	Wf301	12	37.9	0.98	0.91	Wf302	11	43.4	0.95	0.98
Wf400	21	86.7	1.23	0.93	Wf401	23	96.6	1.26	0.93	Wf402	22	84.7	1.25	0.91
Shp100	11	30.5	0.91	0.88	Shp101	11	33.9	0.95	0.91	Shp102	10	32.0	0.93	0.93
Shp200	12	34.8	0.95	0.88	Shp201	9	28.0	0.89	0.93	Shp202	8	23.6	0.84	0.93
Shp300	7	18.4	0.76	0.90	Shp301	6	12.6	0.65	0.84	Shp302	4	9.66	0.57	0.96
Shp400	5	8.56	0.53	0.76	Shp401	3	6.2	0.43	0.91	Shp402	2	3.86	0.29	0.98
Op100	20	72.0	1.17	0.90	Op101	19	69.0	1.16	0.91	Op102	18	71.9	1.17	0.93
Op200	14	48.6	1.05	0.92	Op201	14	49.8	1.06	0.93	Op202	14	51.2	1.07	0.93
Op300	10	31.6	0.92	0.93	Op301	8	27.0	0.88	0.97	Op302	6	14.3	0.77	0.88
Op400	5	10.5	0.59	0.86	Op401	8	21.5	0.81	0.90	Op402	3	6.4	0.41	0.91

SS^a00; SS^a01; SS^a02 = Sub-sites groupings of all three sites used during the first; second and third year (2000, 2001 and 2002) of data collection. $\underline{S}$ = number of dragonfly species at each sampling unit.

2.5.4 Sites, variables and year interactions

Most of the measured environmental variables were significantly different (Table 2.4) at the three sites using ANOVA differences in means. Marginal herbs, sedges and reeds (Mhsr): $F = 64.17$; $P = 0.001$, was significantly lower at Shaded reservoir/stream (Shps) than at open reservoir (Opp) and waterfall/forested river (Wffr) sites. Floating/submerged vegetation (Fsv): $F = 90.67$; $P = 0.001$, was significantly lower at Wffr. Water depth (Wd): $F = 65.06$; $P = 0.001$, was higher at Opp than at the other two sites. Percentage shade (%Sh): $F = 14.76$; $P = 0.001$, was higher at Shps and Wffr than at Opp. Marginal grasses (Mgra): $F = 3.46$; $P = 0.046$, showed a lower value at Opp. Two-way ANOVA results of all site variables-by-year interactions (Table 2.5) only selected Mgra: $F = 8.56$; $P = 0.001$, Mhsr: $F = 11.20$; $P = 0.001$, Fsv: $F = 8.57$; $P = 0.001$ and pH: $F = 16.28$; $P = 0.001$ as statistically significant environmental variables. Mean dragonfly individuals were statistically significant ($F = 9.56$; $P = 0.038$). The rest of the environmental variables, and species means, were not significant at the 5% level of probability.

2.5.5 Dragonfly assemblage correlation with environmental variables

The list of dragonfly species sampled in 2001 and 2002 and their codes used in the multivariate analyses are given in Table 2.1a/b. only data from 2001 and 2002 was used in multivariate analyses as data trends for 2000 and very similar to those in 2001. CA of sites and dragonfly species showed that the three sites had clearly different patterns that are similar to the Bray-Curtis clusters in Fig. 2.6. While the Open reservoir (Opp) assemblage formed a separate assemblage of several dragonfly species, the waterfall/forested river (Wffr) and shaded reservoir and small stream (Shps) sites appeared to form another assemblage of closely similar species. The two CA ordinations representing data collected in 2001 (Fig. 2.7a) and 2002 (Fig. 2.7b) showed that SUs Opp401 and Wffr101 shared some similar species with the shaded reservoir and small stream (Shps) site. However, two species still maintained a high preference for the Shps biotope. In the 2002 ordination, open reservoir (Opp) site species were clearly distinct due probably to biotope modification. This ordination, like the one for 2001 also showed typical species associated with SUs Wffr3 and Wffr4.

CCA revealed the patterns of relationships between the measured environmental variables, sampling units and dragonfly species in tri-plot ordinations. In the 2001 ordination (Fig.8a), the open reservoir biotope appeared to be dominated by increasing gradients of floating and submerged vegetation as opposed to Wffr and Shps biotopes, which appeared to occur along increasing gradients of Flow, Mhsr; Mfor and %shade. The Exposed rock and Flow gradients were vital biotope components of the waterfall/forested river (Wffr) site that attracted typical dragonfly species like *Platycypha caligata, Zygonyx natalensis* and *Paragomphus cognatus*. The shaded reservoir and stream (Shps) site also shared some important characteristics of the waterfall/forested river (Wffr) site but attracted only typical species like *Chlorolestes tessellatus* and *Notiothemis jonesi*. Some species e.g. *Pseudagrion hageni* preferred the forested water edges of shaded reservoir and stream (Shps) and waterfall/forested river (Wffr) sites. The 2002 ordination (Fig. 8b), produced similar results, except at the open reservoir (Opp) site

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Table 2.4 ANOVA results of mean dragonfly species richness $\underline{S}$ and abundance $\underline{N}$ and measured site variables collected at all three sites (Wffr, Shps, and Opp) along the dragonfly trail during the study. Means followed by the same letter across rows are not significantly different at 5% level of probability.

Site Variables[a]	Wffr	Shps	Opp	F-ratio	P-value
$\underline{S}$	10.1	7.3	11.6	1.32	0.28 (ns)
$\underline{N}$	76c	347d	377d	4.15	0.027
Mhsr	78.4a	30.4b	52.6a	64.17	<0.001
Mgra	33.3a	29.6a	12.8b	3.46	0.046
Fsv	18.3a	62.8b	26.7a	90.67	<0.001
pH	7.2a	6.54b	7.15a	72.28	<0.001
Tu	66.42	40.83	59.92	1245.44	<0.29 (ns)
At	26.02	25.21	28.8	45.21	<0.38 (ns)
% Sh	38.3b	50.2b	0.4a	14.76	<0.001
Wd	6.29a	4.24a	15.80b	65.06	<0.001

[a]S = Mean number of species; N = number of individuals; Mhsr = Marginal herbs, sedges and reeds; Mgra = Marginal grasses; Fsv = Floating/submerged vegetation; Tu = Turbidity; %Sh = Percentage shade; Wd = Water depth and At = Atmospheric temperature.

Table 2.5 Two-way ANOVA results of site-by-year interaction for species richness $\underline{S}$, abundance $\underline{N}$ and measured site variables along the dragonfly trail during the whole sampling period (Jan 2000 – Dec 2002). Means followed by the same letter in a row are not significantly different at 5% level of probability.

Site variables*	WfY1	WfY2	WfY3	ShY1	ShY2	ShY3	OpY1	OpY2	OpY3	F-ratio	P-value
$\underline{S}$	9.2	11	10	8.8	7.2	6	12.2	12.2	10.2	0.10	0.98 (ns)
$\underline{N}$	71a	96a	62a	491d	350c	200b	589d	356c	185b	9.54	0.038
Mhsr	82.8a	76.2a	76.2a	65a	21.2b	5c	75a	63a	19b	11.20	<0.001
Mgra	32.5b	31.2b	36.2b	23.8b	30b	35b	34.2b	3c	1.2c	13.56	<0.001
Fsv	63.2	62.5	62.5	16.2	11.2	27.5	36.2	36.2	7.5	8.57	<0.001
pH	7.1a	7.1a	7.4a	6.6b	5.92b	7.1a	7.25a	7.05a	7.15a	16.28	<0.001
Tu	60.5	73.75	65	30	22.5	70	45	59.75	75	503.38	0.213 (ns)
At	26.35	26.1	25.6	27.07	24.27	24.2	29.62	29.5	28.15	2.12	0.105 (ns)
% Sh	33.8	37.5	43.8	57.5	53.8	39.5	1.2	0.0	0.0	0.39	0.81 (ns)
Wd	6.4	6.2	6.27	3.78	4.82	4.12	17.22	18.57	11.6	2.53	0.063 (ns)

*Abbreviation as in Table 4
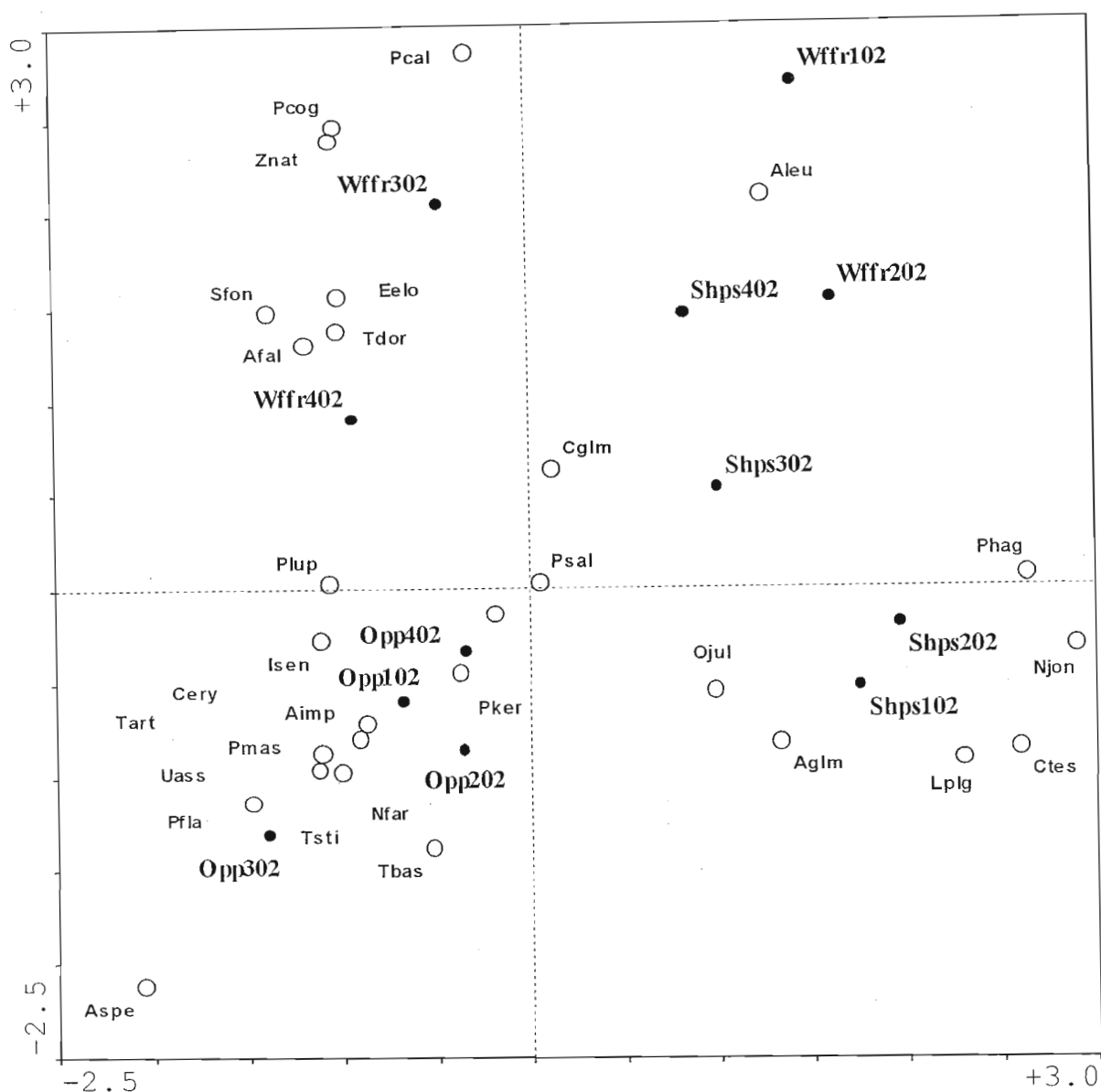
Fig. 2.7a CA biplot of dragonfly species (open circles) and site sampling units (closed circles) along the dragonfly trail in 2001. Species codes are as in Table 2.1a/b. Site and sampling unit abbreviations are: Wffr = Waterfall and forested river (Wffr101; Wffr201; Wffr301; Wffr401), Shps = Shaded reservoir and stream (Shps101; Shps201; Shps301; Shps401), Opp = Open reservoir (Opp101; Opp201; Opp301; Opp401).

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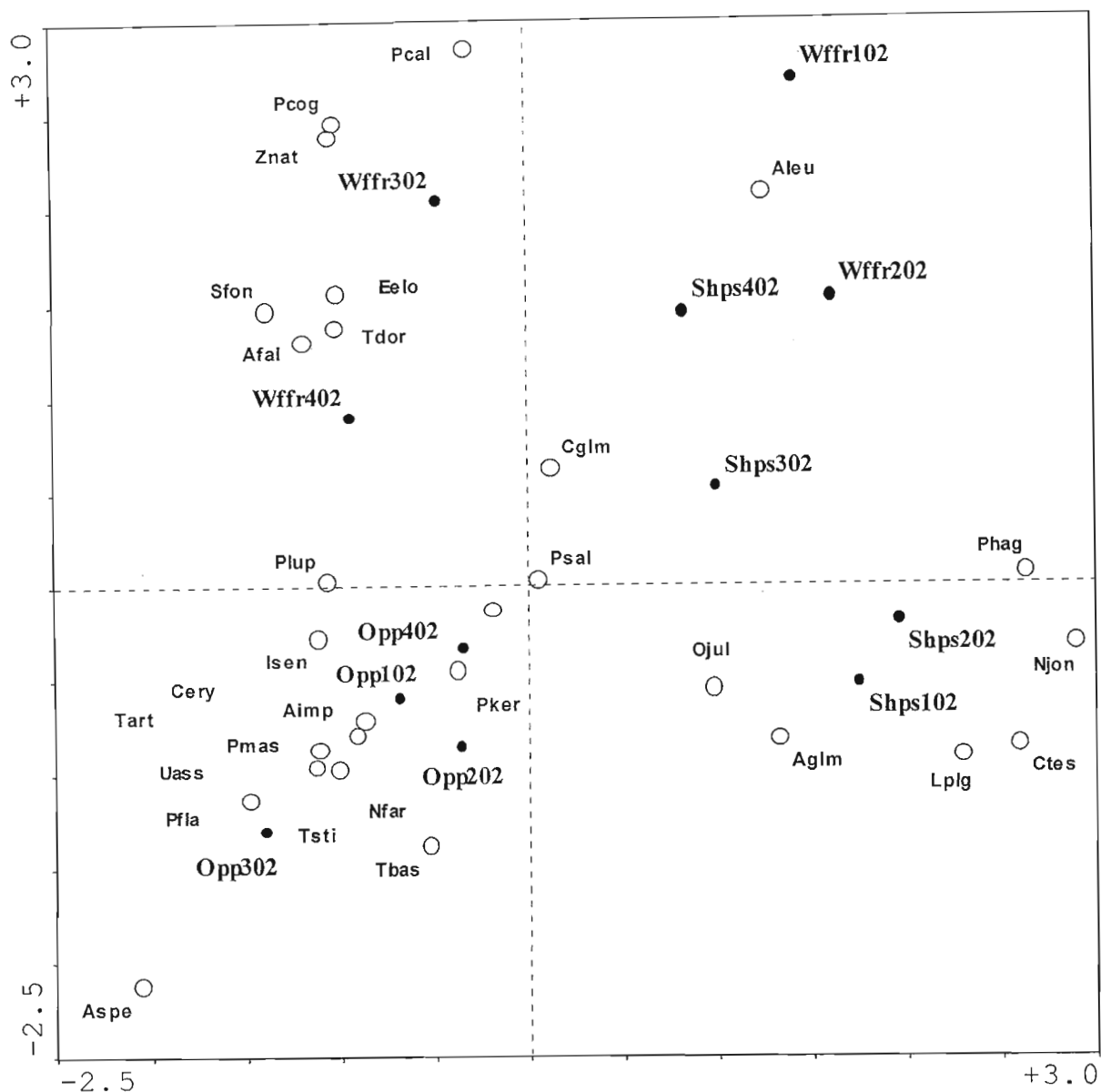
Fig. 2.7b CA biplot of dragonfly species (open circles) and sites sampling units (closed circles) along the dragonfly trail in 2002. Species codes are as in Table 2.1a/b. Site and sampling unit abbreviations are: Wffr = Waterfall and forested river (Wffr102; Wffr202; Wffr302; Wffr402), Shps = Shaded reservoir and stream (Shps102; Shps202; Shps302; Shps402), Opp = Open reservoir (Opp102; Opp202; Opp302; Opp402)

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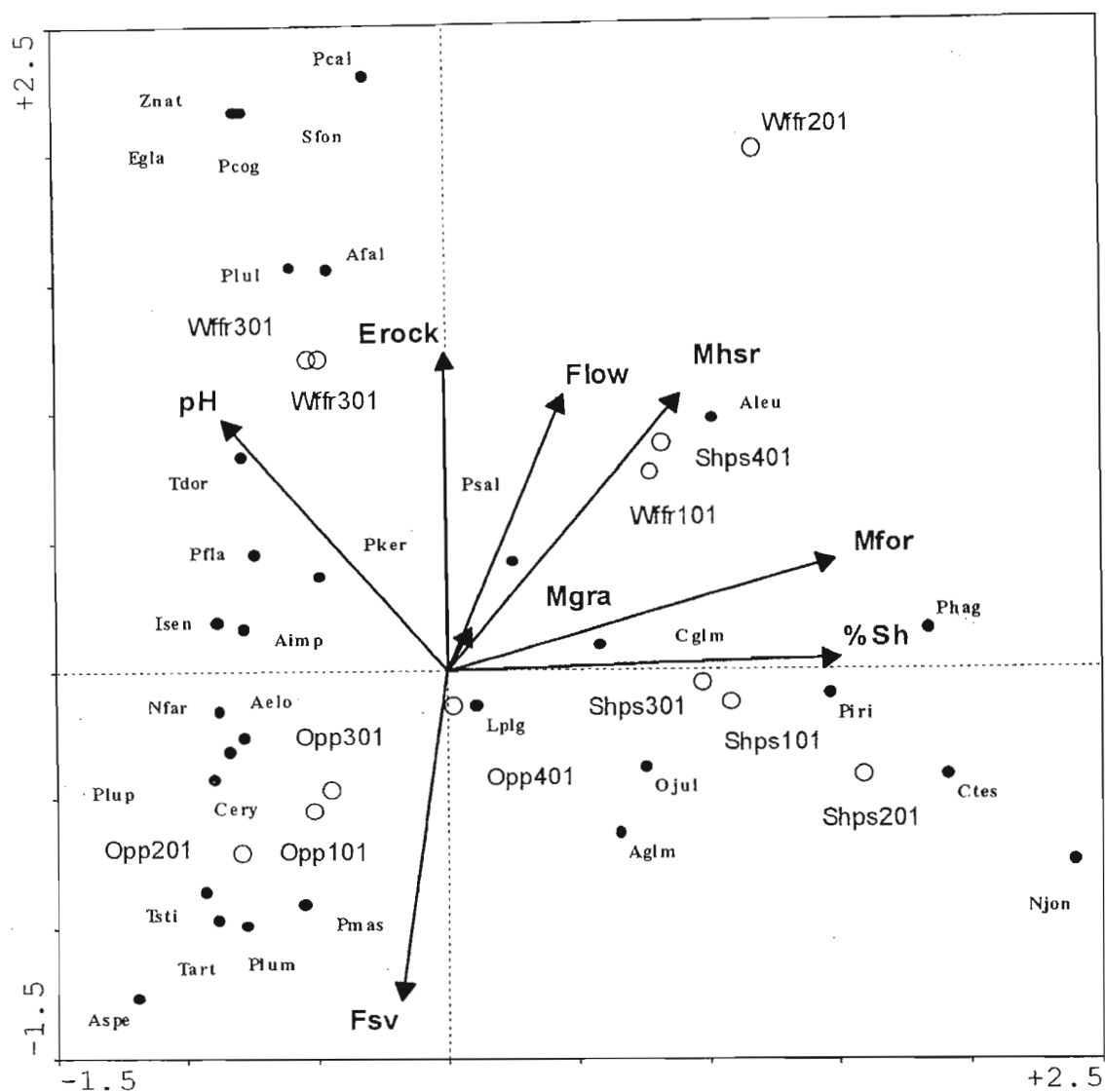
Fig. 2.8a CCA triplot of dragonfly species (closed circles); site sampling units (open circles) and environmental variables (arrows) in 2001. Axis 1 is horizontal and axis 2 vertical. Species codes are as in Tables 2.1a/b. Sub-site abbreviations are : Waterfall = waterfall and forested river; Shps = shaded reservoir and stream; Opp = open reservoir. Environmental variable abbreviations: Fsv = floating and submerged vegetation; %Sh = percentage shade; Mfor = marginal forest; Mgra = marginal grasses; Mhsr = marginal herbs, sedges and reeds; Erock = exposed rock.
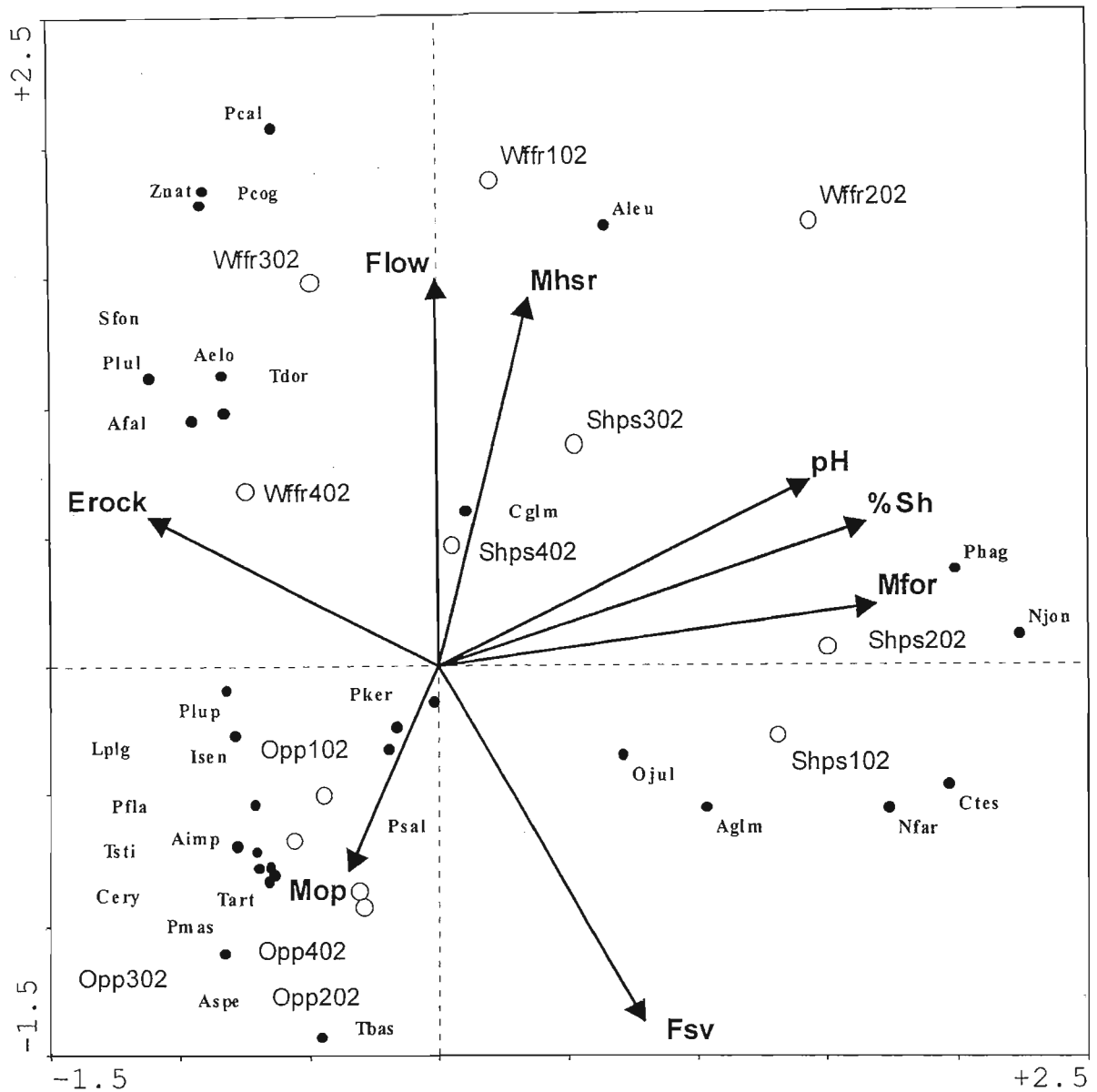
Fig. 2.8b CCA triplot of dragonfly species (closed circles); site sampling units (open circles) and environmental variables (arrows) in 2002. Axis 1 is horizontal and axis 2 vertical. Species codes are as in Tables 2.1a/b. Sub-site abbreviations are : Waterfall = waterfall and forested river; Shps = shaded reservoir and stream; Opp = open reservoir. Environmental variable abbreviations: Fsv = floating and submerged vegetation; %Sh = percentage shade; Mfor = marginal forest; Mhsr = marginal herbs, sedges and reeds; Exrock = exposed rock; Mop = marginal ornamental plants. Only important variable gradients have appeared on the ordination.

Table 2.6a Summary of weightings of the first two axes of CA and CCA for Odonata sampling years of 2001 and 2002 along the dragonfly trail in Pietermaritzburg National Botanical Gardens. Variances explained by the two axes are given. Monte-Carlo probability tests of significance are shown for the first canonical axis (AX1) and all four axes. *P<0.05; **P<0.01.

Year	2001					2002				
Axes Weightings	CA		CCA		All 4 axes	CA		CCA		All 4 axes
AXES	AX1	AX2	AX1	AX2		AX1	AX2	AX1	AX2	
Eigenvalues	0.460	0.349	0.448	0.368		0.450	0.315	0.442	0.310	
SP-ENC[1]			0.990	0.986				0.991	0.987	
CPVS[2]	30.3	53.3	29.5	53.8		35.7	60.7	34.7	59.1	
CPVS-EN[3]			35.5	64.1				39.5	67.2	
F-Ratio			1.258		1.860			1.596		2.721
P-value			0.01*		0.01*			0.015*		0.005**

[1] Species-environment correlations; [2] Cumulative species variance of species data; [3] Cumulative species variance of species-environment relations

Table 2.6b Intra-set correlations between each of the environmental variables and Canonical Correspondence Analysis axes during both years (2001 and 2002) for Odonata sampled along the dragonfly trail in the Pietermaritzburg National Botanical Gardens.

Year	2001		2002	
Variables[a]	CCA axis 1	CCA axis 2	CCA axis 1	CCA axis 2
Eigenvalues	0.442	0.310	0.448	0.368
pH	-0.5463	0.6815	0.7889	0.4132
%Sh	0.9617	0.0267	0.9103	0.3184
Flow	0.2857	0.7372	-0.003	0.858
Mhsr	0.5683	0.7385	0.1918	0.8174
Mgra[1]	0.0556	0.1133	-	-
Mfor	0.9515	0.0916	0.9299	0.1341
Fsv	-0.1190	-0.8844	0.4374	-0.7903
Erock	-0.0034	0.8583	-0.6153	0.3349
Mop[2]	-	-	-0.1937	-0.4550

[a] See Methods. [1] Marginal grasses only measured in year 2001 [2] Marginal ornamental plants only measured in year 2002. Note that only important environmental variables are included in the table.

which underwent major physical changes to its biotope. Marginal vegetation diversity was replaced by two alien ornamental plants: *Agapanthus orientalis* and *Watsonia* spp. along the reservoir edges. The marginal ornamental plant (Mop) gradient was important in this regard, as was probably variation in water levels, both affecting dragonfly richness and diversity.

The eigenvalues of axes one and two of CCA for each of the two ordinations (using 2001 and 2002 species and environmental variable data) are given in Table 2.6a. Intra-set correlations of environmental gradients with axes (Table 2.6b) showed that percentage shade, pH and marginal forest were highly correlated with axis one for both years. Floating and submerged vegetation (Fsv) and Exposed rock (Exrock) were correlated with axis one for year 2002 only. Flow was highly correlated with axis two for both years and marginal herbs, sedges and reeds (Mhsr) was highly correlated with axis two of year 2002. Marginal ornamental plant (Mop) was only slightly correlated with axis two of year 2002. Axis one for the two ordinations was therefore important in accounting for the observed species distribution in both years. The species-environment correlation coefficients were also very strong for the two ordinations (always greater than 0.96). Measured environmental variables were therefore responsible for the main variations in species patterns as indicated by cumulative percentage variances for species and species-environment relations (2001 CCA: 82%; 2002 CCA: 70.3%). Monte-Carlo probability tests (first axis) were significant for 2001 ordination (F = 1.258; P = 0.01) and 2002 ordination (F = 1.596; P = 0.015). These tests were significant for all four ordination axes in 2001, (F = 1.860; P = 0.01) and highly significant for all four ordination axes in 2002, (F = 2.721; P = 0.005).

2.6 Discussion

2.6.1 Dragonfly population dynamics across sampling years at the study site

A total of 31 species (15 Zygoptera and 16 Anisoptera) were recorded in total, accounting for 19% of South Africa's 160 odonate species records and about 25% of KwaZulu-Natal's 117 species. This number is slightly lower than the 35 records (20 Anisoptera and 15 Zygoptera) in 1998/99, when the trail was designed (Suh and Samways 2001). The four species not recorded in this study were *Orthetrum trinacria*, *O. caffrum*, *Anax tristis*, and *Palpopleura jucunda*. Absence of the highly mobile *A. tristis* may also have simply been a chance effect, while for *O. trinacria* and *P. jucunda*, conditions may have been marginally too cool, and for *O. caffrum*, a montane species, marginally too warm. Species accumulation curves and tables of species flight periods indicate that three species were found in all months throughout the three year sampling period. These were *Ceriagrion glabrum*, *Pseudagrion salisburyense* and *P. kersteni* although in very low numbers during winter (1-4 individuals each).

This study showed that prolonged sampling periods over the years for species inventory purposes does not necessarily lead to the discovery of more 'resident' species at least in

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this medium-term time frame. There were no statistically significant differences obtained with respect to species richness (although not so for numbers of individuals) during the three sampling seasons. The species accumulation curves for the three-year sampling period further confirms this. A near asymptote was reached from December when dominant species were accounted for, implying that representative species can be inventoried with a 90% accuracy in about two visits/month from January to March/April during optimal conditions. *Orthetrum abbotti* appeared only in January and February 2000; *Phaon iridipennis* appeared in January 2000 and February 2001. Peak records for most species were made in early summer (December – February) and late spring (November). These months are characterised by the highest ambient and water temperatures (McGeoch and Samways 1991) but also high light intensity, high water levels and abundant vegetation. These conditions are suitable for larval development, adult dispersal and aggregation (Corbet 1962; 1999, Miller, 1987; Gibbons, 1986). The months of June to October were species-poor and characterised by cold winter conditions, with low water/ambient temperatures, and low water levels which do not favour oviposition, dispersal or aggregation in adults. Low water levels may act alone or synergistically with other factors in causing population fragmentation of odonates during these dry times of the year (Moore, 1997).

2.6.2 Biotope preference and dragonfly dominance during the study

The waterfall and forested river (Wffr) site had the highest species richness and diversity (N1 and H') during all three seasons, with SU Wffr4 contributing the most to this feature. Increased species richness and diversity in this SU was correlated with a number of environmental factors, particularly increased sunshine and fewer trees. Its low species dominance and abundance, and high species richness was attributable to the compositional and structural complexity of this sampling unit, part of which is a waterfall with an embankment of exposed rock. These rocks served as basking sites for many dragonfly species from adjacent water bodies.

The Open reservoir (Opp) site had the greatest number of individuals in both 2000 and 2001, dominated by *Crocothemis erythraea*, *Lestes plagiatus* and *Africallagma glaucum*. The reservoir also showed a high species turn-over, due to occasional, deliberate clearing of vegetation at its edges and the possible influx of individuals from adjacent reservoirs. The lowest species and individual counts at this site were made in 2002 when three-quarters of the plant diversity at the reservoir edges was replaced with a single ornamental plant and water levels were lowered for dredging purposes. SUs Wffr1 and Wffr 3 equally recorded a high number of lotic species. However, the recovery was remarkably rapid, with the full complement of species returning as soon as the water level was restored.

Species levels at the shaded reservoir and stream (Shps) and Wffl were low. Wffr2 had the lowest species and individual counts during the whole study period due to the dense tree canopy and overhanging macrophytes at this biotope.
Clearly, overall biotope heterogeneity has played a major role in preserving local species richness and diversity, also shown elsewhere (Osborn and Samways, 1996; McGeoch and

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Samways, 1991, Samways, 1999; Stewart and Samways, 1993; Corbet, 1999). The presence of many trees, shady conditions and very shallow water were not suitable for most reservoir species. Some, however, sought shade, with *P. iridipennis* and *Chlorolestes tessellatus* occurring at the edges of the shaded reservoir.

General trends observed in each of the three sampling seasons showed similar levels of dominance at sites. At percentage dominance levels of less than 15%, there were no significant differences between species dominance curves for all three sites (Wffr; Shps and Opp) during the study period.

2.6.3 Environmental variables determining dragonfly assemblage patterns at sites

Environmental changes over time may cause an increase or decrease in species richness (Moore 1991; Osborn and Samways 1996), relative to the requirements of each species. Adults libellulids select suitable oviposition sites by visual assessment, and later tactile examination of the biotope (Wildermuth 1991; 1992). Adults reacted to the presence of certain types of vegetation and to smooth surfaces when selecting suitable oviposition sites (Wildermuth 1992). Steytler and Samways (1995) found that the biotope requirements of a biotope-specific species are multi-dimensional for sun/shade, flow/reservoir and vegetation among other factors. Also, that biotope requirements of any one odonate species may be temporarily or spatially defined (Steytler and Samways 1995). Most of the environmental variables measured during this study were statistically significant at 5% level of probability using ANOVA, therefore providing useful and interpretable interactions with corresponding species data when used in multivariate analyses.

Trends of the effects of these variables on species assemblage compositions across all sampling units, showed that increased gradients of floating and submerged vegetation alongside sunshine encouraged typical open reservoir species like *C. erythraea, Nesciothemis farinosa, Trithemis arteriosa, A. glaucum* and *Palpoleura lucia portia.* Gradients of flow, marginal herbs, sedges and reeds, marginal forest and shade encouraged species at the waterfall/forested river (Wffr) site like *Platycypha caligata, Zygonyx natalensis, Paragomphus cognatus, Chlorolestes tessellatus* and *Notiothemis jonesi. C. tessellatus* and *N. Jonesi* were attracted to the shaded reservoir and stream (Shps) site, confirming earlier studies (Suh and Samways, 2001; Steytler and Samways, 1995).

The chance of adults selecting the incorrect sites for oviposition may depend on the nature and specificity of the cues that the species uses when selecting sites Corbet 1999; Osborn and Samways 1996). In this study, environmental gradients from vegetation structure to abiotic variables were the main determinants of the Odonata assemblage patterns

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2.7 Conclusion

2.7.1 Temporal changes

Although the dragonfly species richness count of 35 species in 1998/99 when the trail was designed dropped to 25 species in 2002, most of the ten species not recorded in 2002 were vagrants. This study found that there were no statistically significant differences in dragonfly species richness (at all the three sites: waterfall/forested river (Wffr), shaded reservoir and small stream (Shps) and open reservoir (Opp)) between the years of 2000, 2001 and 2002. However, significant changes were observed for abundance sampled during this period. The drop in counts of some of the vagrant species in 2002 may have been attributable to biotope modification and overall sub-optimal biotope conditions as well as chance effects. Species accumulation curves observed during the three years showed also that all the resident species can be seen along the trail at the study area in about two visits each month from January to April (or eight times during the whole of this period) during optimal dragonfly activity period of the day. This is useful information for raising dragonfly awareness through reliability of opportunities for observing species and for species conservation.

2.7.2 Management recommendations

Awareness-raising and subsequent conservation of dragonflies are socio-cultural activities, with the clear objective of maintaining species diversity. Therefore, conserving a wider range of habitats, preferably in nature reserves is a priority (Corbet 1999, Moore 1969; 1978a; 1978b, Ratcliffe 1977). With this perspective in mind, the following management recommendations arose from this study.

Firstly, botanical gardens are inherently valuable for drawing public attention to invertebrates, especially dragonflies, which like butterflies, have iconic value. Management should therefore aim to provide optimal conditions for a wide range of observable species. To do this, it is essential to maintain the natural heterogeneity of vegetation along reservoir margins. This study illustrated, as was the case in Britain (Fry and Londsdale 1991), that removal of marginal vegetation for aesthetics or a sense of tidiness, reduces local dragonfly diversity. Furthermore, it is essential to maintain constant water levels at reservoirs, again so as to promote, relatively stable, natural submerged vegetation structures, suitable for a range of dragonfly species. Nevertheless, this study clearly showed that to maintain habitat heterogeneity and reset ecological succession, a reservoir can be partly drained, dredged and refilled with almost no effect on the odonate assemblage. Without this intervention, deposition continues and habitat homogenisation takes place, which then results in an impoverished odonate fauna.

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Chapter Three Significance of medium-term temporal changes when designing a reservoir for conservation of dragonfly diversity

3.1 Abstract

A study was undertaken at a reservoir formed from an impounded stream in 1988 for the purpose of insect and plant conservation at the National Botanical gardens, Pietermaritzburg. While little information exists in the southern hemisphere on longer-term changes in dragonfly assemblages, this study was important in determining whether a species in a conservation area is being afforded protection from varying local anthropogenic impacts over time, especially in an El Niño-prone area like KwaZulu-Natal. The overall aim here was to assess the reservoir created 13 years earlier to determine the changes (if any) that have taken place, and specifically to document the physical biotope changes and also how these have affected the dragonfly assemblage over time. The reason for this is to understand how concepts of residency and succession underpin conservation decisions. A total of 30 dragonfly species wAS recorded in this study, compared to 12 species before the reservoir was constructed in 1988, and 26 species in 1993, with 25 species resident in both 1993 and 2001. Two of these are local endemics. One other endemic was lost to succession in 1993 but reappeared in 2001. Three other species never reappeared after succession in 1993, yet six other species appeared after this date. Multivariate analyses identified structural and compositional vegetation especially marginal forest, percentage vegetation cover, percentage shade as the most important environmental variables determining dragonfly species composition. Other important environmental variables were grasses of tall, medium and short height categories, submerged vegetation, water flow and amount of open water. Not surprisingly, successional changes in vegetation physiognomy and in water conditions significantly increased Odonata species richness and diversity over the years. More importantly, the study shows that to maintain high species richness, including endemics, it is essential to maintain a variety of biotopes using selective management of the marginal vegetation without allowing succession to proceed to a point where overgrowth of the bank and silting of the bottom begin to impoverish the fauna.

3.2 Introduction

After spatial selection of areas and sites for conservation, the next question becomes to what extent is a site managed to maintain a particular assemblage of organisms in the successional process. Furthermore, the success of conservation programmes often depends on developing an approach tailored to the particular culture and circumstances of a place and its inhabitants (Primack et al. 2001). Artificial dragonfly ponds are a significant addition to Japanese and more recently, British landscapes. While dragonflies are a major component when assessing ecological composition of aquatic biotopes (Chelmick et al. 1980; Watson et al. 1982, Buchwald 1993; Samways 1992; 1993; 1999), the assemblage composition at any one locality can change over time (Moore 1991; 2001). The significance of this is that short-term inventory of species may not present a faithful picture of the dragonfly assemblage which is dynamic over time (Schmidt 1985).

Nevertheless, quantitative short-term studies on dragonfly colonisation and vegetational succession for newly-established ponds yielded information needed to understand habitat requirements of species associated with specific stages of succession, and to derive appropriate management practices (Corbet 1999). Also, such assessments form an essential starting point for the applied science of restoration ecology, which, in turn, requires recognition of the changes to be expected in species abundance and diversity as ecological succession proceeds. Information is being accumulated on medium to long-term changes in dragonfly populations after conservation ponds have been established, especially in some European countries (Schmidt 1985; Moore 1991, 2001; Chovanec 1994; Chovanec and Raab 1997).

In South Africa, Samways et al. (1996), Steytler and Samways (1995) and Osborn and Samways (1996), have documented early changes at an urban reservoir which was constructed in 1988 for insect and aquatic plant conservation. Nevertheless, little information exists in the southern hemisphere on longer-term changes in dragonfly assemblages. Such longer-term studies are crucial for determining whether a species in a conservation area is being afforded protection from varying local anthropogenic impacts over time, especially in an El Niño-prone area. The overall aim here therefore, is to assess a reservoir which was created 13 years earlier to determine the changes that have taken place. The reason for this is to understand how concepts of residency and succession underpin conservation decisions. This study specifically aims to document the physical biotope changes and also how these have affected the dragonfly assemblage over time and to ascertain how the assemblage has responded to the altered ecological conditions. As this reservoir is also part of a dragonfly conservation awareness trail (Suh and Samways 2001), the study also makes recommendations for future management of the reservoir.

3.3 Site

The study area was the National Botanical Gardens, Pietermaritzburg, $29^0 35'$ S, $30^0 25'$ E, 790 m a.s.l. The site is an impounded stream with an inlet and outlet, forming a small reservoir with a 550 m circumference (Fig. 3.1). It was impounded in 1988. Prior to this, the former stream was assessed for its dragonfly fauna, and five years later, the reservoir was studied and the dragonfly assemblage recorded in detail (Steytler and Samways 1995). The site was visited to record presence/absence of species in 1996-2001, while this detailed quantitative study took place in 2001.

3.4 Methods

3.4.1 Dragonfly sampling

Thirty-one sampling units (SUs), each measuring 20 m x 2 m (1 m either side of the water's edge), were marked in the same positions as in Steytler and Samways (1995). The SUs were sampled twice a month from February to April 2001, making six replicates during the peak flight period of the species known to occur in the area (Suh and Samways 2001). Adult male Odonata were recorded by walking the 20 m SUs and noting in 6 min all male individuals patrolling or perching within each SU. Preliminary sampling indicated that it was necessary to avoid the very hot (25^0C - 30^0C shade temperatures) mid-day period when territorial males were less active (Schmidt 1985; Corbet 1999). Only males were counted because females and pre-reproductive individuals are not always in close association with the water and their identification can be uncertain and unreliable. Where identification of a male was difficult, the individual was captured, identified with a hand lens and then released. Details of the behaviour and biotope preferences of species at the site have been given by Samways and Steytler (1996) and Osborn and Samways (1996).

3.4.2 Physical environmental variables

Since adult dragonflies respond primarily to visual cues (Corbet 1999), each SU was described according to the percentage of shaded (%SH) area, which was recorded at mid-day. Water flow characteristics (FLOW as reservoir = 0, stream = 1) were also recorded.

3.4.3 Vegetation sampling

Eight predominant types of vegetation physiognomy (structural and compositional) occurring in the 2 m marginal recording zone were identified à priori and code-named for the purpose of statistical analysis. The proportions of the eight vegetational types in each of the 31 SUs are given in Table 3.1.

Two additional variables related to water conditions were also measured. These were percentage proportions of water vegetation cover %VEC) and open water (%OW). These parameters were obtained by estimating the proportion of water surface per SU that was covered by emergent vegetation and the remaining water surface where some open water

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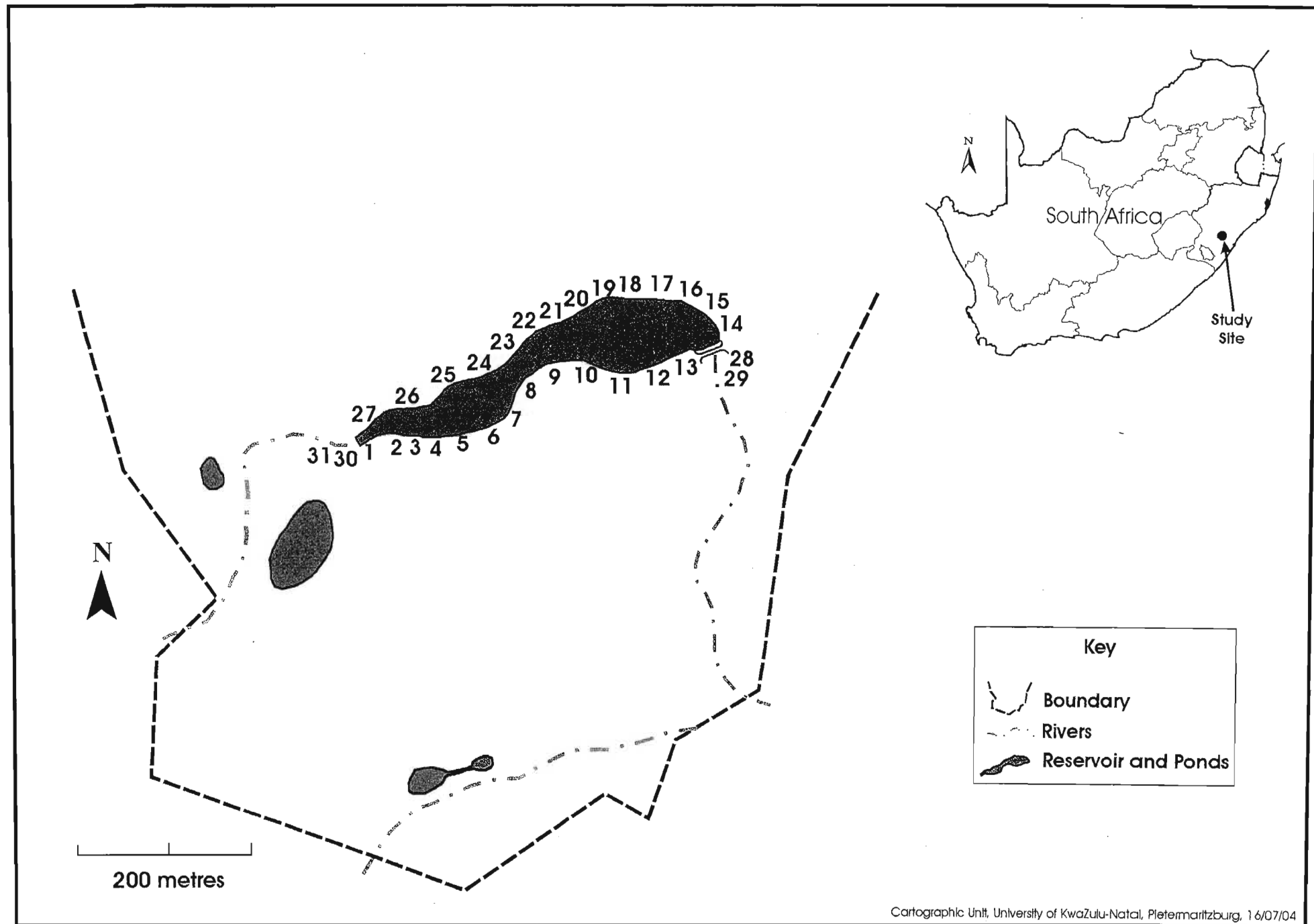
Fig. 3.1 Map of site showing reservoir circumference subdivided into 27 sampling units (SUs) with SUs 28 & 29 located on outflowing stream (waterfall) & SUs 30 & 31 located further upstream

Table 3.1 Habitat description of vegetation in the 31 sampling units (SUs).

Group	Vegetation structure	Code name	Dominant vegetation	SUs category
1	Marginal Forest	LUSH	Large tree species	15-19, 23-27, 30-31
2	Submerged	SUVG	*Chara* spp.	6-13, 15-19
3	Emergent/floating	EFVG	*Commelina africana* L., waterlilies.	5-13
4	Mixture of sedges herbs and broad-bladed grass	BUSH	*Cyperus papyrus* L. *Setaria* spp. *Ludwigia octovalvis* Jacq.	1-7
5	Grass height*	SGRA 0-25cm	*Paspalum urvillei* Steud.	8-14, 28-31
6		MGRA 25-50cm	*Sporobolus pyramidalis* Beauv.	8-14, 28-31
7		TGRA >50cm		8-14, 28-31
8	Exotic plants	EXOT	*Pontederia cordata* L. *P. purpureum* Schumach.	1-5, 20-22

* Grass height according to cutting regimes.

occurred respectively. In all, twelve environmental variables were measured during the study, and both sets of data (Odonata occurrences and environmental variables) recorded in data matrices.

3.4.4 Statistical analyses

Data from the six replicated transect walks were pooled for each SU and arranged in matrices as proposed by Ludwig and Reynolds (1988). The species data were not transformed to normality as there were many zero values (Ter Braak 1987). The environmental data were also not transformed. Nevertheless, the data were standardized to zero mean and unit variance for interpreting the canonical coefficients. Canonical Correspondence Analyses (CCA) (Ter Braak 1986) and CANOCO for Windows were used to relate the species abundance data to environmental variables. Diversity, richness and evenness indices were computed for species data. The indices were Pielou's evenness, Shannon's diversity and Margalef's and Hill's richness indices (Clark and Warwick 1994). These indices were calculated using the statistical program Diverse in PRIMER version 4.

3.5 Results

3.5.1 Odonata assemblage

A total of 30 dragonfly species (14 Zygoptera and 16 Anisoptera) representing eight families were recorded in the 31 SUs (Table 2). Of these 30 Odonata species, 13 species (five Anisoptera and eight Zygoptera) occurred in high numbers (>100 individuals); 11 species had intermediate numbers (10-100 individuals) and six species occurred in low numbers (<10 individuals) (Table 3.2).

SUs 1, 2, 21 and 22 had the lowest number of species, while SUs 1-4 and 21 recorded the least abundance in 2001. Highest species counts in 2001 were recorded at SUs 10-12, with higher individual counts made at SU 12 during this period. In 1993, highest species records occurred at SU 11 while highest individual records occurred at SU3. Least species and individual records during this period were made at SUs 30, 31 and SU 31 respectively (Fig. 3.2).

Species diversity in 2001 was similar in SUs 8, 9 and 11, probably due to the fact that a greater number of species was represented by a relatively equal number of individuals. Species diversity was low in SUs 1-3 and 21-22, probably due to absence of open water during the study period. SU 10-12 had a high diversity value of 2.49, while the rest of the SUs had values ranging from 1.04 - 2.45.

High evenness values were recorded in SUs 1, 2 and 21, with low species richness probably being related to dominance by a few species with very similar numbers of individuals.

Generally, species richness was higher at most SUs in 1993 than in 2001, probably due to higher structural and compositional plant diversity and availability of more open water. These conditions might have been suitable for mating, oviposition and foraging behaviour patterns for most dragonfly species at the study site.

Table 3.2 Odonata species and number of individuals (in brackets) recorded in this study.

Zygoptera	Code name	Anisoptera	Code name
Chlorocyphidae		**Aeshnidae**	
Platycypha caligata (Sélys) (26)	*Pcal*	*Anax imperator* Leach (14)	*Aimp*
		Anax speratus Hagen (4)	*Aspe*
Coenagrionidae			
Agriocnemis falcifera (Pinhey) (243)	*Afal*	**Gomphidae**	
A. elongatum (Martin)	*Aelo*	*Paragomphus cognatus* Rambur (10)	*Pcog*
Africallagma glaucum Burmeister (278)	*Aglm*		
Ceriagrion glabrum Burmeister (372)	*Cglm*		
Elattoneura glauca (Sélys) (2)	*Egla*	**Libellulidae**	
Ischnura senegalensis Rambur (31)	*Isen*	*Crocothemis erythraea* Brullé (323)	*Cery*
Pseudagrion kersteni (Gerstäcker) (325)	*Pker*	*Nesciothemis farinosa* Förster (198)	*Nfar*
P. massaicum (Sjöstedt) (169)	*Pmas*	*Orthetrum julia* Kirby (125)	*Ojul*
P. salisburyense Ris (432)	*Psal*	*O. abbotti* Calvert (7)	*Oabb*
P. hageni Karsch (169)	*Phag*	*O. caffrum* Burmeister (2)	*Ocaf*
		O. trinacria (Sélys)	*Otri*
Lestidae		*Palpopleura lucia* (Drury) (85)	*Pluc*
Lestes plagiatus Burmeister (272)	*Lplg*	*Pantala flavescens* (Fabricius) (7)	*Pfla*
		Philonomon luminans Karsch (2)	*Plum*
Platycnemididae		*Trithemis arteriosa* Burmeister (457)	*Tart*
Allocnemis leucosticta (Sélys) (11)	*Aleu*	*T. dorsalis* Rambur (86)	*Tdor*
		T. stictica Burmeister (431)	*Tsti*
Synlestidae		*Zygonyx natalensis* (Martin) (16)	*Znat*
Chlorolestes tessellatus Burmeister (14)	*Ctes*		
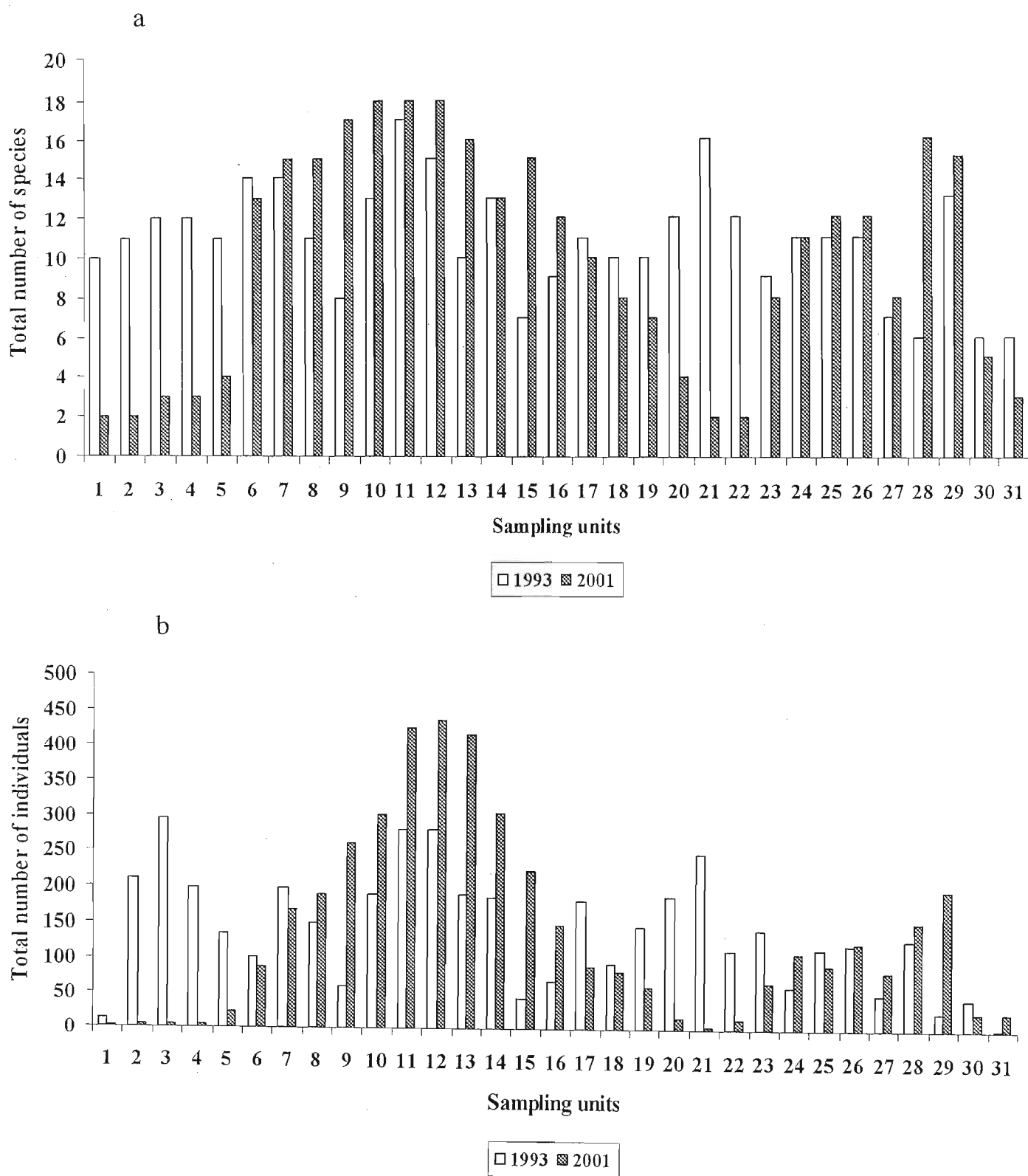
Fig. 3.2 Dragonfly species richness (a) and abundance (b) from 31 sampling units at the study site in 1993 and 2001 (Data for 1993 obtained from Steytler N. S. 1993).
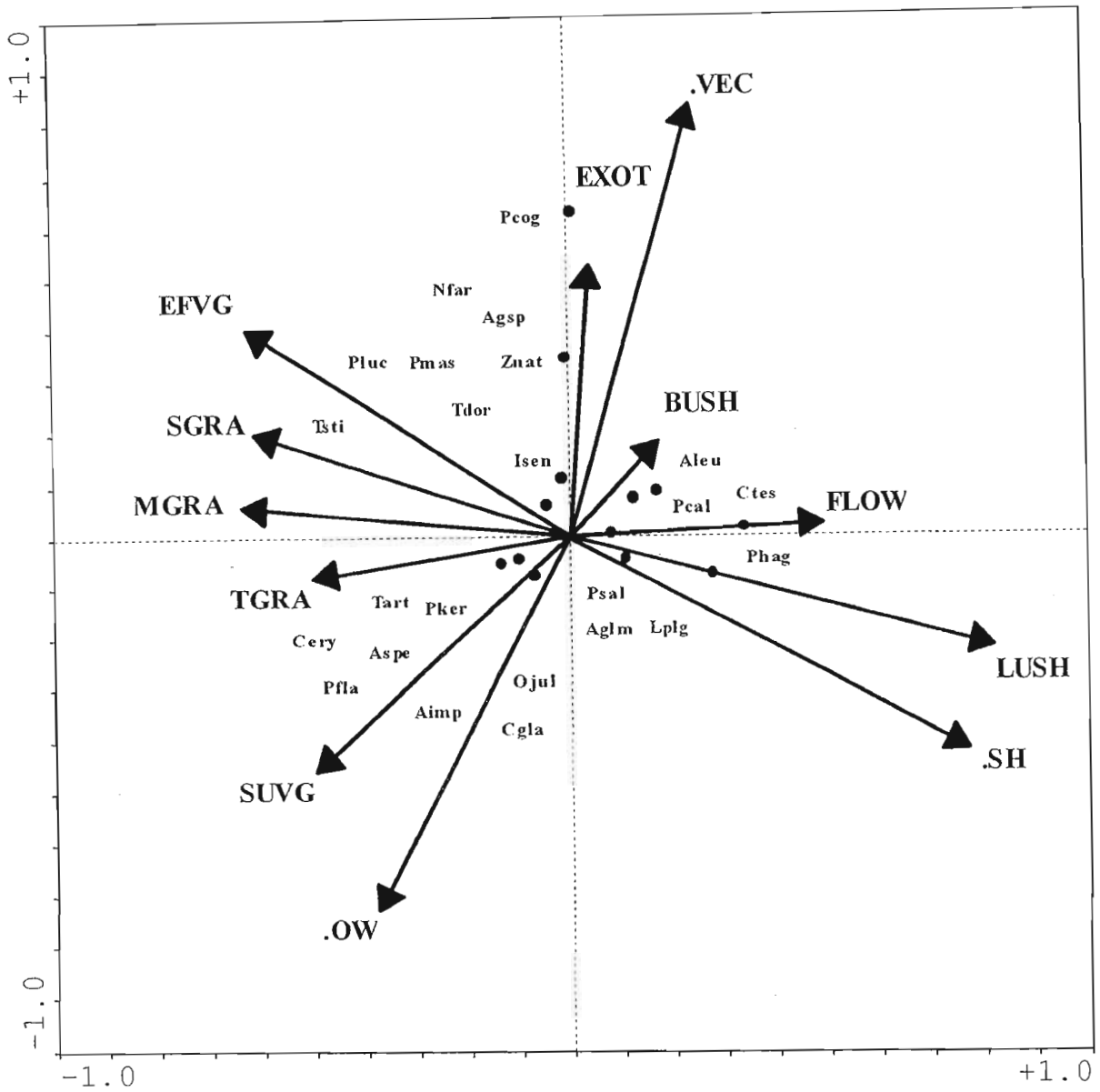
Fig. 3.3 CCA ordination of Odonata species (abbreviated in Table 3.1) and 12 measured environmental variables in 2001. SGA (short grass 0-25 cm), MGRA (medium grass 25-50 cm), TGRA (tall grass >50 cm), percentage of BUSH, emergent/floating vegetation (EFVG), submerged vegetation (SUVG), exotic plants (EXOT), trees (LUSH), open water (OW), water surface vegetation cover (VEC), sunshine/shade (SH) and FLOW characteristics. The first axis (Axis 1 = 0.352) is horizontal and the second axis (Axis 2 = 0.225) is vertical.

Table 3.3a Summary results for all four ordination axes of CCA.

| Axes | Eigenvalues | Species-environ. correlations | Cum. % variance[a] for | | Monte Carlo test: |
			Species	Spp/Env.	F-Ratio/P-value
1	0.352	0.952	25.5	36.1	F= 6.15; P<0.005*
2	0.225	0.944	41.7	59.2	All 4 axes
3	0.140	0.853	51.9	73.5	F= 3.596; P<0.005*
4	0.850	0.828	58.0	82.2	

[a] Cumulative species variance of species data and of species-environment relation
*High statistical significance at the 5% level of probability.

Table 3.3b Intra-set correlations between environmental variables and first two ordination axes of CCA.

Environmental variable[a]	Axis I	Axis II
SGRA	-0.5880*	0.0981
MGRA	-0.6048**	0.0565
TGRA	-0.4760*	-0.0771
BUSH	0.1645	0.1720
EFVG	-0.5672*	0.1886
SUVG	-0.4720*	-0.4298*
EXOT	0.0411	0.4907*
VEC	0.2290	0.7793**
LUSH	0.7785**	-0.2074
OW	-0.3594	-0.6858**
SH	0.8267**	-0.2799
FLOW	0.4676*	0.0219

[a] SGA (short grass 0-25 cm), MGRA (medium grass 25-50 cm), TGRA
(tall grass >50 cm), percentage of BUSH, emergent/floating vegetation (EFVG),
submerged vegetation (SUVG), exotic plants (EXOT), trees (LUSH), open water (OW),
water surface vegetation cover (VEC), sunshine/shade (SH) and FLOW characteristics.
**, High statistical significance, * Low statistical significance of measured
environmental variables at the 5% level of probability.

Table 3.4 Significant correlations between individual abundant Odonata species and measured environmental variables.

Species	Correlations	
	Positive	Negative
A. falcifera	SGRA, MGRA	SHADE
A. glaucum	GRASSES, OW (reservoir), EFVG	NONE
A. leucosticta	LUSH, FLOW, SHADE	SUVG, OW (reservoir)
C. glabrum	NONE	NONE
C. tessellatus	LUSH, FLOW, SHADE	OW (reservoir)
I. senegalensis	SGRA	SHADE
L. plagiatus	TGRA, MGRA, BUSH	EXOTIC PLANTS, FLOW
P. caligata	LUSH, FLOW, BUSH	SUVG, OW (reservoir)
P. hageni	LUSH, SHADE	OW (reservoir)
P. kersteni	FLOW	NONE
P. massaicum	SUVG, OW (reservoir), EFVG	SHADE
A. imperator	SUVG, OW (reservoir)	NONE
C. erythraea	OW (reservoir), TGRA, BUSH	SHADE, FLOW
N. farinosa	OW (reservoir), BUSH	SHADE, FLOW
O. julia	NONE	SHADE, LUSH
P. cognatus	FLOW	SHADE
P. lucia	OW (reservoir), MGRA, BUSH	SHADE
T. arteriosa	OW (reservoir), SGRA, MGRA, BUSH	SHADE
T. dorsalis	OW (reservoir)/FLOW	SHADE
T. stictica	OW (reservoir), BUSH, SGRA	SHADE, FLOW
Z. natalensis	FLOW	SHADE

3.5.2 Odonata species recorded in 2001 and sampling unit ordination

Four species (*Elattoneura glauca, Philonomon luminans, Orthetrum caffrum* and *O. trinacria*) were omitted from the analyses as they were too scarce at the site to provide meaningful correlations. Species points on the ordination diagram did show a great deal of overlap. CA and CCA ordinations were not fundamentally different. The four axes of the CCA (Fig.3) accounted for 63% of the species/SU variation accounted for by CA, which suggested that important environmental factors were included in the analyses. Furthermore, the Monte Carlo permutation tests were highly significant for the first axis (CCA: $F = 6.150$; $P < 0.005$) and for all four canonical ordination axes together (trace CCA: $F = 3.596$; $P < 0.005$). This implied that the null hypothesis was rejected for the option that there was a statistically significant relationship between the dragonfly species sampled during the study and the whole set of measured environmental variables.

The measured environmental variables therefore explained a significant proportion of the Odonata assemblage variation. The first CCA ordination axis (Axis 1 = 0.352) explained about 36% of the variation (Table 3.3a, b), being strongly correlated with percentage shade (%SH, r = 0.83), marginal forest (LUSH, r = 0.78) and MGA, r = -0.604, and less strongly correlated with certain grass heights (SGRA, r = -0.588, TGA, r = -0.476), emergent/floating vegetation (EFVG, r = -0.567), submerged vegetation (SUVG, r = -0.472) and flow characteristics (FLOW, r = 0.46). The second axis (Axis 2 = 0.225) explained about 23% of the variation, but was more highly significant for percentage vegetation cover (%VEC, r = 0.77) than for percentage amount of open water (%OW, r = -0.685). The ordination axes identified vegetation (both structural and compositional), comprising marginal forest, emergent and floating vegetation, medium height and short grasses, shade, water flow and amount of open water characteristics as the most effective environmental variables that separated the SUs and species (Table 3.4).

Tall grasses (TGA), percentage exotic plants (EXOT) and submerged vegetation (SUVG) appeared to have a lower effect on species and site separation. High plant diversity and constant /stable water conditions appeared to act synergistically to encourage the heterogenous habitat conditions at SUs located on either side of the stream, reservoir and waterfall. These factors, among others, probably influenced high odonate diversity at the study site.

3.5.3   Species responses to environmental conditions

Even though most species appeared at the centre of the ordination diagram suggesting high species tolerance to most of the measured variables, species patterns could still be interpreted statistically using intra-set correlation coefficients and CCA axes. *Allocnemis leucosticta, Chlorolestes tessellatus* and *P. hageni,* were positively correlated with shade: intra-set correlation coefficient : r = 0.83; Monte Carlo P-value axis 1: P< 0.005. Conversely, twelve species showed no correlation with shade characteristics, suggesting an affinity for sunshine.

These were: *Agriocnemis falcifera, Crocothemis erythraea, Ischnura senegalensis, Nesciothemis farinosa, Orthetrum julia, Palpopleura lucia, Paragomphus cognatus, Pseudagrion massaicum, Trithemis arteriosa, T. dorsalis, T. stictica,* and *Zygonyx natalensis.*

Eight species were positively correlated with flowing water characteristics (intra-set correlation coefficient: r = 0.46, Monte Carlo axis 1: P-value: P<0.005), these were *A. leucosticta, Anax imperator, C. tessellatus, P. cognatus, Platycypha caligata, Pseudagrion kersteni, T. dorsalis* and *Zygonyx natalensis.* Seven species correlated with short grasses whose intra-set correlation coefficient: r = 0.588, Monte Carlo axis 1: P-value: P<0.005, and medium grasses (intra-set correlation: r = -0.604, Monte Carlo axis 1: P-value P<0.005). These were *A. falcifera, C. erythraea, I. senegalensis, L. plagiatus, O. julia, P. lucia,* and *T. arteriosa.* These grassy biotopes served as foraging and perching sites alongside emergent objects such as sticks. Four species, *A. leucosticta, C. tessellatus, P. caligata* and *P. hageni* were positively correlated with marginal forest (intra-set correlation coefficient r = 0.78 and Monte Carlo P-value for axis 1: P<0.005). Also, four species, *P. salisburyense, P. kersteni, Ceriagrion glabrum* and *O. Julia,*

showed very weak or non-significant correlations with the main environmental variables considered in this study, including flow/reservoir, vegetation (structural/compositional) and sun/shade.

3.6 Discussion

3.6.1 Comparison of this study with earlier studies

A total of 30 dragonfly species recorded in this study compares to 12 species before the reservoir was constructed in 1988 and 26 species in 1993. Impoundment of the stream immediately increased suitable conditions for certain lentic species. In 13 years, Anisoptera species increased from seven to 16, and Zygoptera from five to 13. Eleven Zygoptera and 13 Anisoptera species were recorded as resident species in both 1993 and 2001, with *A. falcifera* and *C. tessellatus*, being South African endemics. Another South African endemic, *A. leucosticta*, was lost to damming in 1993, but reappeared in 2001. Three Anisoptera species (*Notiothemis jonesi, Phyllomacromia picta* and *Urothemis edwardsii*) were lost to succession after 1993. Three Zygoptera species *Allocnemis leucosticta, Pseudagrion massaicum, Africallagma elongatum* and three Anisoptera *Palpopleura lucia, Orthetrum abbotti* and *Pantala flavescens* were gained with successsion through damming (Tables 3.5a, b). Higher species richness and diversity at SUs 1-6 and 20-23 was recorded in 1993 (Steytler and Samways 1995) than in this (2001) study, probably due to the presence of more open water and only a low density of alien plants at these SUs in 1993. Conversely, higher species richness and diversity occurred in SUs 7-15 and 28 in the 2001 study, probably due to more optimal biotope conditions, especially increased sunlight penetration and vegetation diversity (Figs 3.2a, b). It appears that several species are highly vagile and sporadic, because visits to the study site from 1996 to 2001 indicated that several species, not recorded in either the 1993 study or the previous ones occasionally occurred there.

Table 3.5a Odonata species resident at the study site

Resident species (1993/2001)	
Zygoptera	Anisoptera
Africallagma glaucum [1]	*Anax imperator* [1]
Agriocnemis falcifera [4]	*A. speratus* [1]
Ceriagrion glabrum [1]	*Crocothemis erythraea* [1]
Chlorolestes tessellatus [4]	*Nesciothemis farinosa* [1]
Elattoneura glauca [1]	*Orthetrum caffrum* [1]
Ischnura senegalensis [1]	*O. julia* [1]
Lestes plagiatus [1]	*O. trinacria* [1]
Platycypha caligata [1]	*Paragomphus cognatus* [1]
Pseudagrion hageni [2]	*Philonomon luminans* [3]
P. kersteni [1]	*Trithemis arteriosa* [1]
P. salisburyense [1]	*T. stictica* [2]
	T. dorsalis [1]
	Zygonyx natalensis [2]

[1] African species very common throughout much of South Africa, [2] African species locally common in South Africa, [3] Common African species that are rare in South Africa, [4] Species endemic to South Africa.

Table 3.5b Odonata species response to vegetational succession.

Species lost to succession after 1993		Species gained with succession in 2001 but not 1993	
Zygoptera	Anisoptera	Zygoptera	Anisoptera
*Allocnemis leucosticta**	*Phyllomacromia picta*	*Allocnemis leucosticta*	*Palpopleura lucia*
	Urothemis edwardsii	*Pseudagrion massaicum*	*Orthetrum abbotti*
	Notiothemis jonesi	*Africallagma elongatum*	*Pantala flavescens*

* Species lost to vegetational succession in 1993 but not in 2001.

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These included *Aeshna subpupillata* McLachlan, *Anax ephippiger* (Burmeister), *Azuragrion nigridorsum* (Sélys), *Brachythemis leucosticta* (Burmeister), *Ceratogomphus pictus* (Sélys), *Crocothemis sanguinolenta* (Burmeister), *Diplacodes lefebvrii* (Rambur), *Lestes virgatus* (Burmeister) *Notogomphus praetorius* (Sélys), *Orthetrum chrysostigma* (Burmeister), *O. icteromelas* Ris, *Palpopleura jucunda* Rambur, *Phaon iridipennis* (Burmeister), *Rhyothemis semihyalina* (Desjardins), *Sympetrum fonscolombii* (Sélys), *Tramea basilaris* (Beauvois) and *Trithemis kirbyi* (Sélys).

3.6.2 Odonata response to vegetational succession

Major changes in vegetational succession can alter the Odonata assemblage (Moore 1991; 2001). High vegetation diversity at different stages of succession recorded at SUs 8-14, 28 probably accounted for high odonate species richness and diversity. Vegetation has various important functions for adults, which include concealment from predators (Askew 1982), as well as for mating and feeding perches (Buchwald 1992). The use of different types of vegetation and perching heights may allow species to co-exist (Sternberg 1994). Some impacts such as invasive plant growth enter the ecological succession (Corbet 1999), and can increase the complexity of local plant architecture (Samways 1999). This, in turn, encourages establishment of certain odonate species e.g. *C. glabrum*, *I. senegalensis*, *P. kersteni* and *P. salisburyense*.

The extent of establishment and biotope modification by these exotics can lead to them out-competing indigenous plants species, thereby reducing overall plant diversity, and consequently Odonata species richness and diversity (Kinvig and Samways 2000). Furthermore, vegetation was important for species which have endophytic oviposition e.g. *Anax imperator*.

3.6.3 Reservoir construction as a strategy for dragonfly conservation

South Africa is a dry country and anthropogenic impacts such as construction of reservoirs and small farm dams has substantially increased the overall abundance of some ecologically generalist species (Samways 1989). Small impoundments, although locally excluding some lotic species, generally increase species richness in the vicinity of the impoundment (Steytler and Samways 1995). Impoundments with a fairly constant water level and especially ones that are well vegetated (on the bank, at the margins, and in the water) have high dragonfly species richness (Osborn and Samways 1996). From a conservation management standpoint, the National Botanical Gardens in Pietermaritzburg are located at the edge of a major escarpment, so recruiting faunal elements from both higher and lower elevations with a potential to encourage an exceptional variety of dragonfly species at one location is possible. Furthermore, the reservoir here is part of a dragonfly awareness trail, making management an important feature.

This study has shown that changes due to succession in vegetation physiognomy and in water conditions significantly increased the Odonata species richness and diversity over the years. However, leaving the succession to continue further would lead to both overgrowth of the reservoir margins and silting up through deposition. Therefore to

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maintain the current Odonata species richness requires the following management: 1) Rotational clearing of marginal vegetation, (i.e. cutting back of vegetation at different spot locations in different years), 2) Removal of exotic plants e.g. *P. purpureum* (SUs 1-5) and *P. cordata* (SUs 20-23), 3) Encouraging indigenous marginal vegetation diversity while allowing sufficient sunlight penetration, 4) Maintaining a constant level and extent of open water at the stream and reservoir and 5) Dredging of the reservoir at the inlet section (SUs 1-9, 20-24). Periodic monitoring would keep track of species population fluctuations in this El Niño area and determine whether the management activities are being successful. Above all, this study shows that it is essential to provide a wide range of biotopes (with various micro-habitat conditions) for rare stenotopic species as well as the common eurytopic species. Finally, fine-tuning of conservation for particular species requires detailed knowledge on requirements for all life stages, as adults and larvae can occur in different biotopes.

3.7 Conclusion

Impoundment of the stream in 1988 increased dragonfly species richness from 12 to 26 in 1993 and 30 species in 2001, that included South African endemics e.g. *Agriocnemis falcifera* and *Chlorolestes tessellates*. *Allocnemis leucosticta* was lost to damming in 1993, but reappeared in 2001. Three Anisoptera species: *Phyllomacromia picta*, *Urothemis edwardsii* and *Notiothemis jonesi* were lost to succession after 1993 while six species were gained with succession through damming. It appeared that several species are highly vagile and sporadic because visits to the study site from 1996 to 2001 indicated that several species not recorded in either the 1993 study or the previous ones also occasionally occurred there. Multivariate analyses identified structural and compositional vegetation especially marginal forest, percentage vegetation cover and percentage shade as the most important environmental variables determining dragonfly assemblage variation and distribution. Other important environmental variables were grass height categories, submerged vegetation, water flow and open water conditions. Not surprisingly, successional changes in vegetation physiognomy and in water conditions significantly increased odonate species richness and diversity over the years. More importantly, the study shows that to maintain high species richness, including endemics, it is essential to maintain a variety of biotopes using selective management of marginal vegetation without allowing succession to proceed to a point where overgrowth of the bank and silting of the bottom begin to impoverish the fauna.

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Chapter Four   Dragonfly (Odonata) phenology and assemblage response to elevation

4.1 Abstract

Studies were conducted at a series of moderately-sized artificial but well-established reservoirs in KwaZulu-Natal, South Africa where data on dragonflies and environmental variables were collected over two years across an elevation gradient from 100 m to 1350 m a.s.l. The aim here was to determine the extent to which elevation and climate (as regional processes), alongside local factors, influence species assemblage variability and habitat preference in dragonflies. The aim was also to determine how phenology might vary with elevation. Dragonfly species including mature adults, tenerals and larvae were recorded over two years. Seven families and 46 adult species were recorded. Libellulidae, closely followed by Coenagrionidae, were the most abundant families throughout the sampling period, while the Chlorocyphidae and Platycnemididae were least represented, occurring only in summer and only at the mid-elevations. Larvae showed positive correlation in species richness and abundance with increasing elevation, while teneral and adult species richness did not. Teneral (but not adult) abundance was positively correlated with increasing elevation. Results of multivariate analyses of the two sub-orders (Anisoptera and Zygoptera), when analysed separately, showed that certain measured site variables strongly explained the main variation in species assemblages. These included local factors e.g. pH, marginal grasses, percentage shade, exposed rock, marginal forest and to a lesser extent, marshes and flow. Different species showed various tolerance levels to these process influencing differences among assemblages. Factors such as behaviour of larvae, tenerals and adults may also have been important in this regard. These conditions varied from one season to another, being optimal in summer, and minimal in winter, and influenced dragonfly species phenologies accordingly. Although more widespread and elevation-tolerant species ($\underline{S}$=43) were sampled in the study than national endemics ($\underline{S}$=3), management recommendations were made to include these endemics as far as possible. This study also offered baseline information against which to compare future global climate change scenarios.

4.2 Introduction

Insect phenology usually varies with topo-climatological and micro-climatological differentiation (Byoko 1947, Geiger 1965, Wolda 1987). Interactions between temperature-dependent development and microclimate are important features of insect life-history, leading to the maintenance of considerable genetic variation in populations (Bradshaw and Holzapfel 1990, Roff 1990). Studies of insects and other arthropods suggest that microclimatic gradients can have larger effects on emergence phenology than do annual fluctuations in weather conditions (e.g. Kingsolver 1979, Weiss 1993). Because adult emergence times can determine reproductive success, these phenological predictions can provide valuable insights into population dynamics that can be used in reserve design and management, especially for threatened species (Murphy et al. 1990).

Furthermore, field evidence (Thomas et al. 2001) supports theoretical predictions (Thomas et al. 1999), that certain types of thermophilous insects have expanded to occupy broader niches, and hence larger patch sizes near their northern range margins during some warm summers in recent years (Roy et al. 2003). Understanding the mechanisms responsible for these shifts is important not just to predict how species populations and ranges may respond to climate warming (Roy et al. 2001, Warren 2001) but also, in conservation, to ensure that appropriate management is applied to maintain optimal habitat and metapopulation structures for threatened species under different local climates.

Small reservoirs are a characteristic feature of the South African agricultural landscape, acting as important miniature nature reserves (Samways 1989b; 1999). These reservoirs have been shown to be important in promoting the conservation of insect diversity, particularly habitat-tolerant dragonflies (Samways 1996, Samways and Steytler 1995).

When a population occupies a patchy habitat, it may form a network of small, local populations collectively called metapopulations (Hanski and Gilpin 1991). Within a metapopulation, density-dependent dispersal may moderate internal patch dynamics (Hasson 1991, Fahrig and Merriam 1994) and the dispersal between local populations will influence their persistence and the rate of colonisation of vacant patches (Hasson 1991, Dias 1996).

Considering odonates, which need water to complete the larval part of their life cycle, isolated ponds separated by terrestrial landscape constitute a patchy habitat. Ponds can in this case be compared to islands (Levins 1969). In this context, the population dynamics operate at two levels: within patches and between patches. Odonates only disperse between ponds in the mobile winged adult stage, and although egg transport and larval dispersal have been reported, they can be considered as rare and insignificant events (Corbet 1962). Adult life can be divided into three phases: 1) the maturation period, 2) the reproductive period and 3) the post-reproductive period. Typically, the first phase is spent away from water. When sexually mature, individuals return to the water bodies to reproduce (Corbet 1980).

The landscape topography of KwaZulu-Natal, South Africa, ranges in elevation from 0m to 3000 m along an approximately 200 km E-W transect. This area is strongly modified by montane climate at higher elevations and has a sub-tropical/tropical climate at sea level. The study area within KwaZulu-Natal is situated at the edge of a major escarpment comprising a highly heterogeneous landscape structure with a wide variety of habitat components e.g. streams, rivers, temporary pools, farm reservoirs and nature reserve ponds with adjoining marshland. These landscape characteristics in turn recruit faunal elements from lower, medium and higher elevations, giving rise to a high diversity of dragonfly species that constitute close to three-quarters of the South African odonate fauna. This provides a basis for measuring how species phenologies and distribution respond to the seasonal (temporal) and elevational changes. This information can be useful for subsequent conservation action, and for providing baseline data for future studies on the impacts of global warming.

Using a series of five moderately-sized artificial, but well-established reservoirs, the aim here was to determine the extent to which elevation (as a regional process), alongside local factors, influence habitat preferences and species distribution. Furthermore, as there is no information on the effects of seasonal changes on southern African odonate species, the aim was also to determine how phenology might vary with elevation. Insights for management recommendations are also addressed.

4.3 Materials and methods

4.3.1 Study area

4.3.1.1 Brief physiography of KwaZulu-Natal

Climate change and variability in South Africa has been discussed by Tyson (1986), and veld characteristics by Acocks (1988). The province of KwaZulu-Natal is the portion of the coastal slopes sandwiched between the Drakensberg escarpment (<3000 m), marking the edge of the plateau, and the coast (King 1982). According to Turner (1973) and Thorrington et al. (1978), there are 43 physiographic regions in KwaZulu-Natal, each of which has homogenous characteristics, grouped into six headings, five of which are related to this study and are briefly described as follows:

a) Coastal region
The coastal belt of KwaZulu-Natal is taken to mean the strip of land up to 150 m a.s.l. The region is underlain by Ecca and Dwyka Series folded down to sea level by the monocline, through south of Durban, Table Mountain Sandstones and rocks of Basement Complex are exposed. Rainfall patterns of up to 1000 mm have been recorded.

b) Low-lying region
The Valley of a Thousand Hills and Mvoti River valley are bounded on all sides by a large escarpment of pink sandstones and quartzites. Further north of the Mvoti valley are large upstanding blocks of Table Mountain Sandstones, while the low-lying granite is an

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intricate maze of hills and valleys. The crests of the watersheds vary in elevation from 300–750 m a.s.l.

c) Intermediate region

These areas are intermediate between the interior upper and the coastal regions. These include the Pietermaritzburg and the Richmond Benchland, partly made up of undulating Table Mountain Sandstone plateau. At an elevation of 610-1220 m a.s.l., rainfall rises to 1000 mm but drops to about 800 mm per annum in the valleys.

d) Upland region

The KwaZulu-Natal midlands comprise a broad stretch of country, mainly Tall Grassveld, between 1200–1700 m a.s.l., stretching to the south west virtually from Mooi River to Richmond. Beds of Ecca Series outcrop at lower levels but are succeeded at higher elevations by sandstones, shales and mudstones. Rainfall varies from 900-1000 mm per annum.

e) Mountainous region

Both the high and Low Drakensberg escarpment are of great importance because it is these features which deflect the moist air from the Indian Ocean upwards, and which bring about the high rainfall in the summer and snowfall in the winter, which in turn feed the rivers flowing through KwaZulu-Natal. The spurs and foothills of the High Drakensberg are characterised by their steep grass slopes, vast stream networks, sandstone outcrops and overhanging cliffs. Rainfall is 1000-1200 mm per annum.

4.3.1.2 Elevation

Palmer (1991) describes elevation as an indirect gradient that correlates with the direct environmental gradients of temperature and rainfall. This variable exerts major influences on climatic features at all scales by acting as a barrier to rain bearing air masses, by altering temperature through lapse rates, and through aspect. The four major characteristics dominating the distribution of elevation across southern Africa are provided by Schulze (1997) as follows: (i) there is a narrow coastal strip of low elevation, widening only along the north-east coast of KwaZulu-Natal and the flats of the Western Cape, (ii) the Great Escarpment with highest elevation occurring in the Drakensberg and Maluti mountain ranges, (iii) the interior plateau inland of the escarpment, which drops gently from approximately 1500 m in the east to approximately 1000 m in the west, and (iv) high variabilities in elevation are present in the Western and Eastern Cape, Swaziland and KwaZulu-Natal. It is the wide elevational gradient between 0 and 1500 m a.s.l. in which farm reservoirs have been extensively established, and it is in this belt that this study was therefore conducted.

4.3.1.3 Description of study sites

Reservoirs were selected within KwaZulu-Natal (Fig. 4.1) to be relatively comparable (as shown in Table 4.1), with the following details:

1) Stainbank Nature Reserve (SB) reservoir
Reservoir with a circumference of 300 m marginal vegetation comprising mostly diverse species of grasses, herbs, marginal forest making up about a third of the reservoir margins. Floating vegetation e.g. *Imperata cylindrical* (L.), *Commelina africana* (L.), *C. benghalensis* (L.) and *Limnophyton parvifolium* Peter., submerged vegetation included the genus *Chara* and other species of algae. Marshes and fish are present. Water level maintained by a pipe outlet.

2) Krantzkloof Nature Reserve (KL) reservoir
Reservoir with a circumference of 127 m formed as an impoundment with diverse marginal vegetation made up of almost equal proportions of grasses and herbs. Floating vegetation of a few creeping grasses Impoundment surrounded by hills characteristic of the 'Valley of a Thousand Hills topography'. Marginal forest present, with a cascading stream outlet from the reservoir.

3) Pietermaritzburg Botanical Gardens (BG) reservoir
Impounded stream. Marginal forest takes up almost half of the pond circumference of about 550 m. Marginal vegetation comprises herbs, sedges and reeds, few grasses and exotic plants. Floating e.g. *Commelina africana* (L.), *Zantedeschia aethiopica* (L.) and submerged vegetation e.g. *Elodea densa* (Planchon) and various algae. Water level maintained constant by overflowing channel.

4) Cedara (CE) reservoir
Reservoir of circumference 162 m with marginal vegetation composed mainly of medium height (<1 m) marginal grasses, floating vegetation e.g. *Zantedeschia aethiopica* (L.) and submerged vegetation e.g. the genus *Chara*. Reservoir fenced, hence no major anthropogenic disturbances. Adjacent reservoirs <500 m away. Water level maintained by a pipe outlet.

5) Mondi Goodhope Estate (GH) reservoir
Largest reservoir with circumference of about 934 m. Diverse marginal vegetation mostly composed of short grasses and herbs (<1 m in height) and medium to tall grasses (>1 m in height). Sparse submerged vegetation e.g. the genus *Chara* and various algae. No floating vegetation. Marsh making up a width <1.5 m of the reservoir margin. Other reservoirs 1 km away. Water level maintained by an outlet.

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KEY

☐ KwaZulu-Natal Province
ⓒ Major Towns
■ Study Sites:

A - Kenneth Stainbank Nature Reserve (100 m a.s.l.)
B - Krantzkloof Nature Reserve (450 m a.s.l.)
C - Botanical Gardens (790 m a.s.l.)
D - Cedara (1050 m a.s.l.)
E - Mondi Goodhope Estate (1350 m a.s.l.)

Cartographic Unit, University of KwaZulu-Natal, Pieternaritzburg, 16/07/04
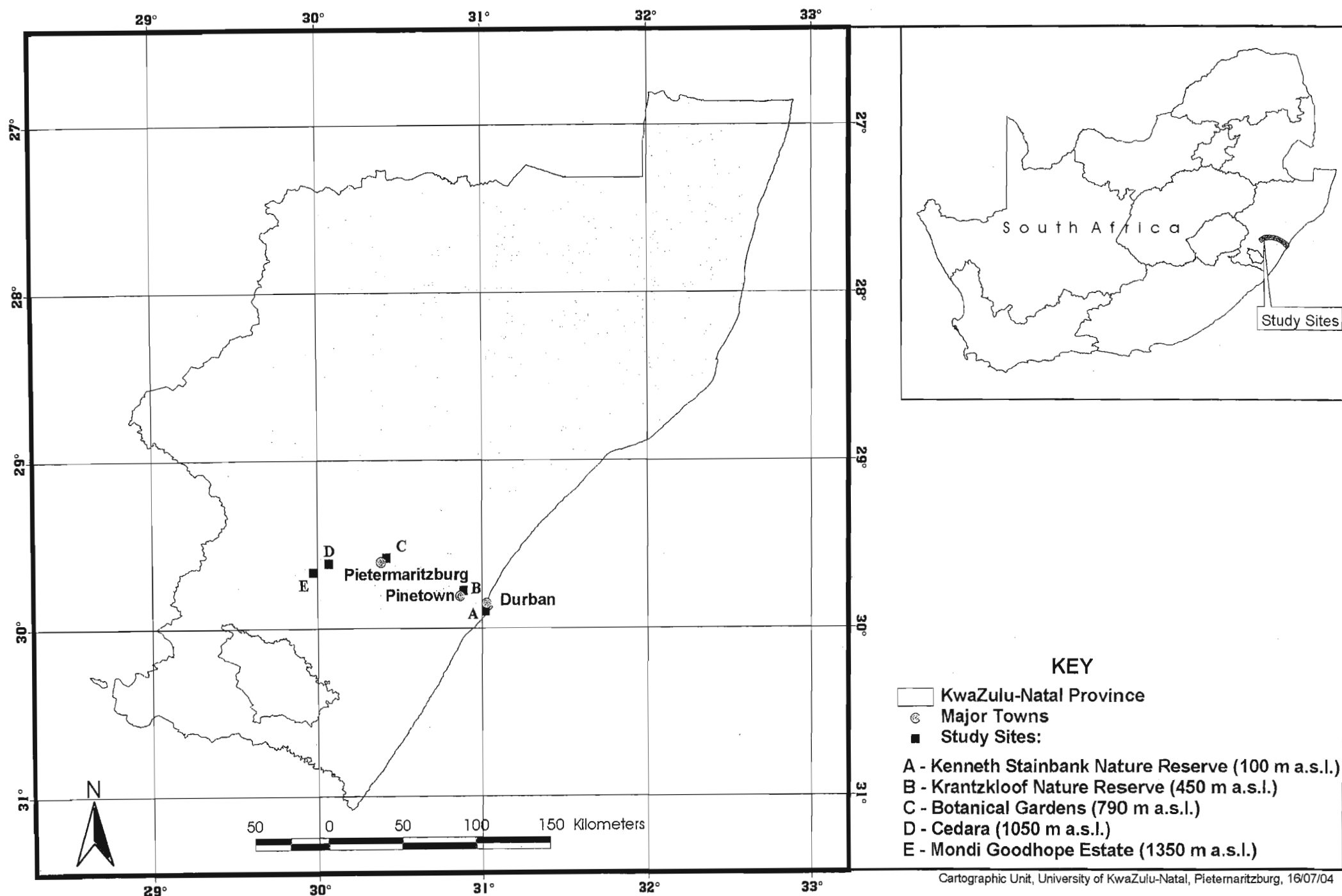
Fig. 4.1 Geographical location of study sites.

Table 4.1 Study sites within KwaZulu-Natal.

Site name/code	Elevation/Location	Land use	Source (s) of disturbance
Stainbank Nature Reserve (SB) (Low elevation)	29°50'S; 30°55'E; 100 m a.s.l.	Nature reserve with diverse species of flora and fauna	Minor effects of animal trampling of marginal vegetation when drinking. Very minor fluctuations of water levels during winter.
Krantzkloof Nature Reserve (KL) (Mid-low elevation)	29°46'S, 30°5'E; 450 m a.s.l	Nature reserve with indigenous flora and fauna.	Occasional clearing of marginal vegetation and minor winter fluctuations in water levels.
Botanical Gardens, PMB (BG) (Mid-elevation)	29°35'S; 30°25'E; 790 m a.s.l.	Botanical grounds with recreational facilities for visitors, a wide variety of alien trees and an adjacent natural forest patch.	Minor winter water fluctuations and deliberate clearing of marginal vegetation.
Cedara (CE) (Mid-high elevation)	29°61'S; 29°06E; 1050 m a.s.l.	Agricultural experimentation and extensive farming	Minor water level fluctuations during winter
Mondi Goodhope Estate (GH) (High elevation)	29°40'S; 29°58'E; 1350 m a.s.l.	Commercial pine plantation and less extensive cattle rearing.	Occasional burning of marginal vegetation, some cattle trampling. Minor water level fluctuations during winter.

4.4 Methods

4.4.1 Site stratification

The five reservoirs were in a narrow latitudinal band (26'), providing an elevational comparison without latitudinal influence. Each reservoir was stratified into six sub-sites, each measuring 20 m length (along a line transect on the reservoir edge) by 2 m width (1 m on land and 1 m into water). Data were collected on 42 sampling occasions, and covered various stages of dragonfly development (adults, tenerals, larvae and exuviae). Mating or oviposition were also recorded (mostly tandem flights and occasional dipping of ovipositors). The site environmental variables were also recorded when dragonfly recordings were made. This was done twice a month running from January 2001 to December 2002 except for the winter months of June, July and August when data were collected once each month.

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4.4.2 Sampling of adults

Adult males were sampled by slowly walking along the 20 m sub-sites and counting within 6 min individuals found perching or flying. Counts of Anisoptera at sub-sites can be virtually 100% accurate and accuracy of counts of Zygoptera exceeds 80% (Moore 1953, 1991). For comparable and reliable estimates of territorial males, counts had to be done within 2 hours before noon during sunny, high activity periods of the day i.e. when the sun was shining most of the time and there was no strong wind (Schmidt 1985, Suh and Samways 2001). Accordingly, all visits to the sites were made under these conditions.

4.4.3 Sampling of tenerals

Exuviae and tenerals were also recorded as an indication of successful breeding. In this study, population changes were indicated by comparing the maximum numbers of individuals (adults, tenerals and larvae) observed each month for the whole sampling period. Unidentified tenerals from the field were collected and reared in the laboratory until their body colour (with genitalia morphology) could be used for subsequent identification.

4.4.4 Sampling of larvae

Larvae were sampled using a dip-net (41 cm diameter x 1 mm mesh sieve). Two dips per sub-site (12 dips/site) were done within 20 min. Each dip was followed by vigorously shoving the net back and forth in water once among water weeds, along rushes and besides banks. Individual larvae in the net were identified using a 9x hand lens, counted and released back into water except where individuals could not be identified in the field in which case, they were picked out with very soft, flexible forceps (to prevent damage to their fragile body) and placed in aerated plastic cages containing reservoir water. Usually only last-instar larvae were collected for subsequent rearing and identification in the laboratory.

4.4.5 Measured environmental variables

Marginal vegetation (both structural and compositional) was estimated using percentages of sub-sites they covered. At all sub-sites, aquatic plants were recorded as: marginal forest stands (Mfor), marginal grasses (Mgra), Floating and submerged vegetation (Fsv), Marginal herbs, sedges and reeds (Mhsr).

Meteorological data e.g. Rainfall, air and water temperatures (At/Wt) collected at Stainbank (SB) and Krantzkloof (KL) Nature Reserves were compared with those collated by the Durban Airport weather station. Also, rainfall and temperature data for Cedara (CE), the Botanical Gardens (BG) and Goodhope Estate (GH), were compared with that collated by the weather bureau at Cedara Agricultural station. Other environmental variables measured were percentage exposed rock in the sampling sub-site

(Exrock %), percentage shade (% Sh), water depth (Wd), turbidity (Tur %), pH, flow (1 = running, 0 = still), reservoir circumference (Pcir (m)) and elevation (Elev (m)).

4.4.6 Data analyses

Data were analysed in two steps. Firstly, univariate methods for species richness and abundance relationships using calculation of diversity indices, distributional models and graphical methods. Species spatial and temporal variability was analysed using analysis of variance (ANOVA). Secondly, multivariate methods of classification and ordination were used.

a) Univariate methods

The full set of species counts at sub-sites was reduced to single coefficients to enable comparisons at site levels. Species diversity indices (Hill's N1) and evenness (Pielou's Evenness J') (discussed in chapter two) were calculated using the software program BIODIVERSITY PROFESSIONAL (McAleece et al. 1997).

Rank abundance curves were used to establish the relationship between abundance and number of species having that abundance graphically. Plots of abundance of each species in the samples in order of its rank from the most to the least abundant for each site were used. This method was a more explicit illustration of species abundance patterns, rather than using simple diversity/eveness measures.

Spearman's rank correlation coefficients were used to measure the association between variables and species abundance and richness. These correlations were calculated using the software SPSS version 6.1

MINITAB and SPSS software were used to run ANOVA, relating species to sites and site variables

b) Multivariate methods

Correspondence analysis (CA) was used to explore possible trends between sub-sites and species. Canonical Correspondence Analysis (CCA) was used to relate species and site scores to underlying environmental variables. The length of an arrow representing an environmental variable is equal to the rate of change in the weighted average as inferred from the bi/triplot, and is therefore a measure of how much the species distribution differs along that environmental gradient. Important environmental gradients therefore tend to be represented by longer arrows than less important ones (ter Braak and Looman 1995). The software CANOCO version 4 and CANODRAW version 3.1 (ter Braak and Smilauer 1998) were used.

4.5 Results

High rainfall patterns from September to May (Fig. 4.2) encouraged vegetation growth (dominant plant and algal species are shown in Table 4.2) and high dragonfly richness (Table 4.3a/b) that comprised mostly vagile, widespread species.

4.5.1 Species temporal trends across sampling sites during the study period

Only at Mid (BG) elevation were adults recorded during winter (June-July). These were *Ceriagrion glabrum*, *Lestes plagiatus* and *Crocothemis erythraea*.

Table 4.2 Dominant plant and algal species sampled in this study.

Species name	Family	*	**	**	Sub-site
Utricularia vulgaris L.	Lentibulariaceae	+	-	-	SB1, KL2
Juncus lomatophyllus (Spreng)	Juncaceae	+	-	-	KL2
Setaria megaphylla Thur. Dur.	Graminaceae	+	-	-	KL5, BG4
Paspalum notatum Fluegge	Graminaceae	+	-	-	All sites
Alisma acanthocarpum F.	Alismataceae	+	-	-	KL, SB
Pontederia lanceolata Nutt.	Pontederiaceae	+	-	-	CE3
P. cordata L.	Pontederiaceae	+	-	-	BG6
Paspalum urvillei Steud.	Graminaceae	+	-	-	All sites
Chara (genus)	-	-	-	+	GH, CE, BG, SB
Commelina africana L.	Commelinaceae	-	+	-	CE, BG, SB
Panicum maximum (Jacq.)	Graminaceae	+	-	-	BG, KL, SB
Juncus exsertus Buchen	Juncaceae	+	-	-	CE3
Zantedeschia aethiopica L.	Araceae	-	+	-	CE, BG, SB
Cyperus papyrus L.	Cyperaceae	+	-	-	BG, SB
Imperata cylindrica L.	Poaceae	-	+	-	SB
Digitaria eriantha Steud.	Graminaceae	+	-	-	KL, SB
Leersia hexandra Sw.	Poaceae	-	+	-	BG
Limnophyton parvifolium Peter	Alismataceae	-	+	-	BG, SB
Typha capensis Rohrb	Typhaceae	+	-	-	CE, BG, SB
Algae spp.	-	-	-	+	All sites
Nymphaea capensis Thunb.	Nymphaeaceae	-	+	-	BG, CE
Elodea densa (Planchon).	Hydrocharitaceae	-	-	+	BG, SB, CE
Commelina benghalensis (L.)	Commelinaceae	-	-	+	SB, BG, CE, GH

* Emergent plants, ** Floating plants, *** Submerged plants

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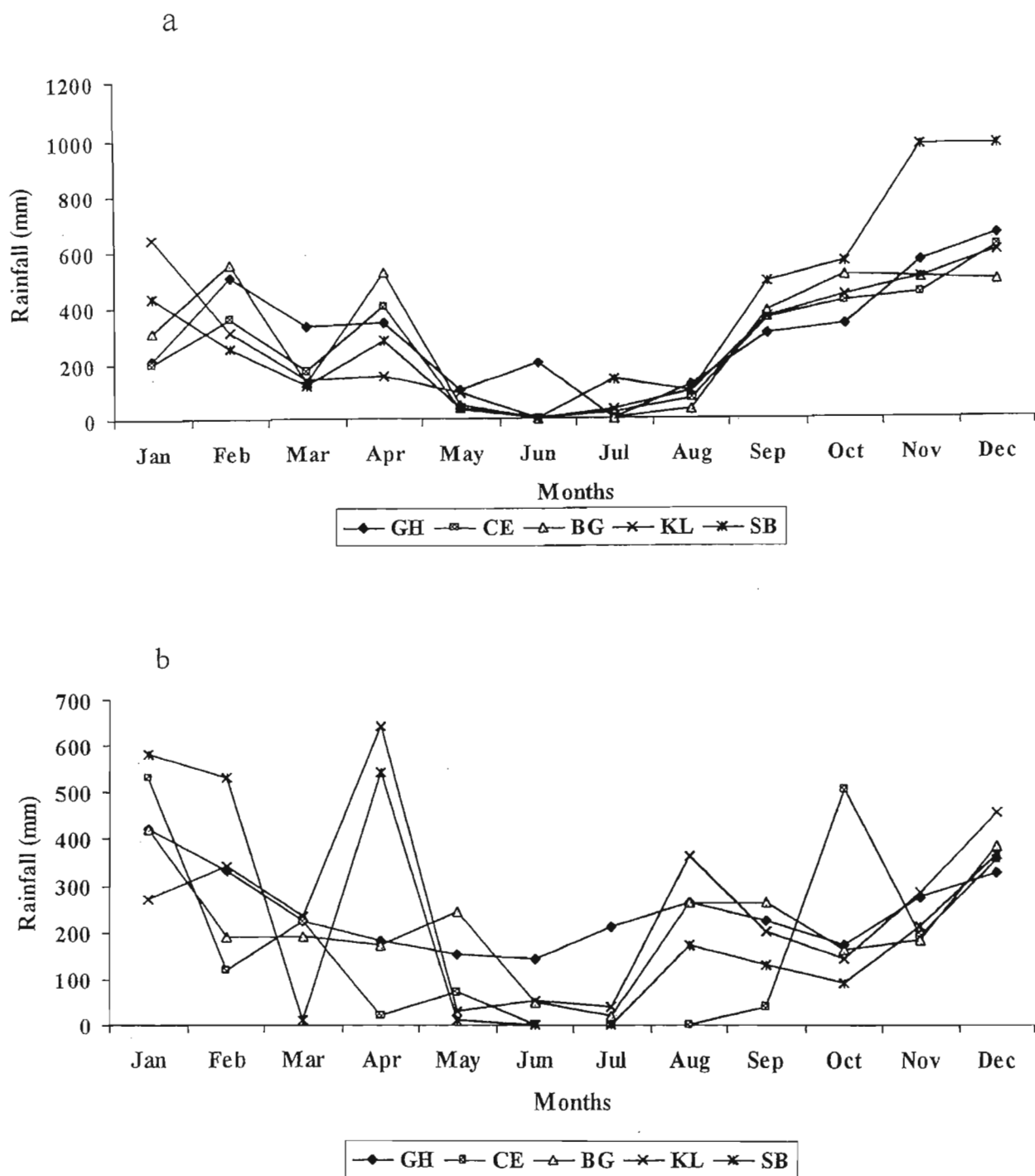
Fig. 4.2 Mean monthly rainfall (mm) at each of the five elevations: GH= High elevation (1350 m), CE= Mid-high elevation (1050 m), BG= Mid elevation (790 m), KL= Mid-low elevation (450 m), and B= Low elevation (100 m) in (a) 2001 and (b) 2002.

Table 4.3a   Anisoptera species recorded (as adult, teneral and/or larva) from all sites across the elevation gradient during the whole two-year sampling period with species code names used in analyses.

Species	Code	Elevations				
		SB	KL	BG	CE	GH
Aeshnidae						
Anax imperator Leach, 1815[3]	Aimp	AL	AL	AL	AL	AL
A. speratus Hagen, 1867[3]	Aspe	A	A	A	A	A
A. tristis Hagen, 1867[1]	Atri	A	-	-	-	-
Gomphidae						
Ceratogomphus pictus Sélys, 1854[3]	Cpic	-	-	-	A	A
Ictinogomphus ferox (Rambur, 1842)[2]	Ifer	A	-	-	-	A
Notogomphus praetorius (Sélys, 1878)[2]	Noto	-	AT	-	-	AT
Paragomphus cognatus (Rambur, 1842)[3]	Pcog	-	-	A	-	-
Libellulidae						
Acisoma panorpoides Rambur, 1842[2]	Acis	ATL	-	-	ATL	ATL
Brachythemis leucosticta Burm., 1839[3]	Bleu	A	-	-	-	-
Chalcostephia flavifrons Kirby, 1889[1]	Chfl	A	-	-	-	-
Crocothemis erythraea (Brullé, 1832)[3]	Cery	ATL	ATL	ATL	ATL	ATL
Diplacodes lefebvrii (Rambur, 1842)[2]	Dlev	A	-	-	-	-
Hemistigma albipunctum Rambur 1842[2]	Halb	A	-	-	-	-
Nesciothemis farinosa (Förster, 1898)[3]	Nfar	AT	AT	AT	AT	AT
Notiothemis jonesi Ris, 1919[1]	Njon	-	A	-	-	-
Orthetrum caffrum (Burmeister, 1839)[3]	Ocaf	-	-	-	ATL	ATL
O. hintzi Schmidt, 1951[1]	Ohin	-	-	-	-	A
O. julia falsum Longfield, 1955[3]	Ojul	ATL	ATL	ATL	ATL	A
Pantala flavescens (Fabricius, 1798)[3]	Pfla	A	A	A	A	A
Palpopleura lucia portia (Drury, 1773)[3]	Pluc	AT	AT	AT	-	-
P. jucunda jucunda Rambur, 1842[2]	Pjuc	-	-	-	-	AT
Philonomon luminans (Karsch, 1893)[1]	Plum	AT	AT	AT	-	-
Sympetrum fonscolombii (Sélys, 1840)[2]	Sfon	A	A	A	A	A
Rhyothemis semihyalina Desjardins, 1832[2]	Rshy	AT	-	AT	AT	-
Tetrathemis polleni Sélys 1877[1]	Tpol	A	-	-	-	-
Tramea basilaris (Beauvois, 1817)[2]	Tbas	AL	AL	A	AL	AL
Trithemis arteriosa (Burmeister, 1839)[3]	Tart	A	A	A	AL	AL
T. dorsalis (Rambur, 1842)[3]	Tdor	-	ATL	ATL	ATL	ATL
T. stictica (Burmeister, 1839)[2]	Tsti	-	ATL	ATL	ATL	ATL
Urothemis assignata (Sélys, 1872)[2]	Uass	A	A	A	A	A
Zygonyx natalensis (Martin, 1900)[2]	Znat	-	A	A	-	-

[1]Common African species whose range extends south just over the border into South Africa, but are local or rare in the country, [2]African species that are widespread and/or locally common in South Africa, [3]African species that are regularly seen in the right habitats. Some of these are very common throughout South Africa (Samways 2002).

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Table 4.3b Zygoptera recorded (as adult, teneral and/or larva) from all sites across the elevation gradient during the whole two-year sampling period with species code names used in analyses.

Species	Code	Elevations				
		SB	KL	BG	CE	GH
Coenagrionidae						
Africallagma elongatum (Martin, 1907)[1]	Aelo	-	-	A	-	-
A. glaucum (Burmeister, 1839)[3]	Aglm	ATL*	ATL	ATL	ATL	ATL
A. sapphirinum (Pinhey, 1950)[4]	Asap	-	-	-	-	A
Agriocnemis falcifera Pinhey, 1959[4]	Afal	ATL	ATL	ATL	ATL	ATL
Azuragrion nigridorsum (Sélys, 1876)[2]	Azn	AT	-	-	-	-
Ceriagrion glabrum (Burmeister, 1839)[3]	Cglm	ATL	ATL	ATL	ATL	-
Ischnura senegalensis (Rambur, 1842)[3]	Isen	ATL	ATL	ATL	ATL	ATL
Pseudagrion citricola Barnard, 1937[4]	Pcit	-	-	-	-	A
P. hageni Karsch 1893[2]	Phag	AT	AT	AT	-	-
P. kersteni (Gerstäcker, 1869)[3]	Pker	ATL	ATL	ATL	ATL	ATL
P. massaicum Sjöstedt, 1909[3]	Pmas	ATL	-	ATL	ATL	-
P. salisburyense, Ris, 1921[3]	Psal	ATL	ATL	ATL	ATL	A
Chlorocyphidae						
Platycypha caligata Sélys, 1853[3]	Aleu			A	-	-
Platycnemididae						
Allocnemis leucosticta Sélys, 1863[2]				A		
Lestidae						
Lestes plagiatus (Burmeister, 1839)[3]	Lplg	-	ATL	ATL	ATL	ATL
L. tridens McLachlan, 1895[1]	Ltri	AT	-	-	-	-

[1]Common African species whose range extends south just over the border into South Africa, but are local or rare in the country, [2]African species that are widespread and/or locally common in South Africa, [3]African species that are regularly seen in the right habitats, some of these are very common throughout South Africa, [4]Species endemic to South Africa (i.e. South of the Limpopo River) (Samways 2002).

Accumulation curves reached asymptotes for tenerals with 10-14 species and for adults with 21-25 species (Fig. 4.3).

4.5.2 *Relative proportions of adults, tenerals and larvae during sampling months*

Larvae stayed at about the same level all year round (Fig. 4.4). This elevation also featured highest larval records in winter. Tenerals and adults showed the same trends as in Fig. 4.3. i.e. none in July and August. However, there was a trend for maximum numbers to be reached later at higher elevations, from October to December for tenerals and November to February for adults. (Fig. 4.4)

a.

Low (SB) elevation site

b.

Mid-low (KL) elevation site

c.

Mid (BG) elevation site

d.

Mid-high (CE) elevation site

e.

High (GH) elevation site
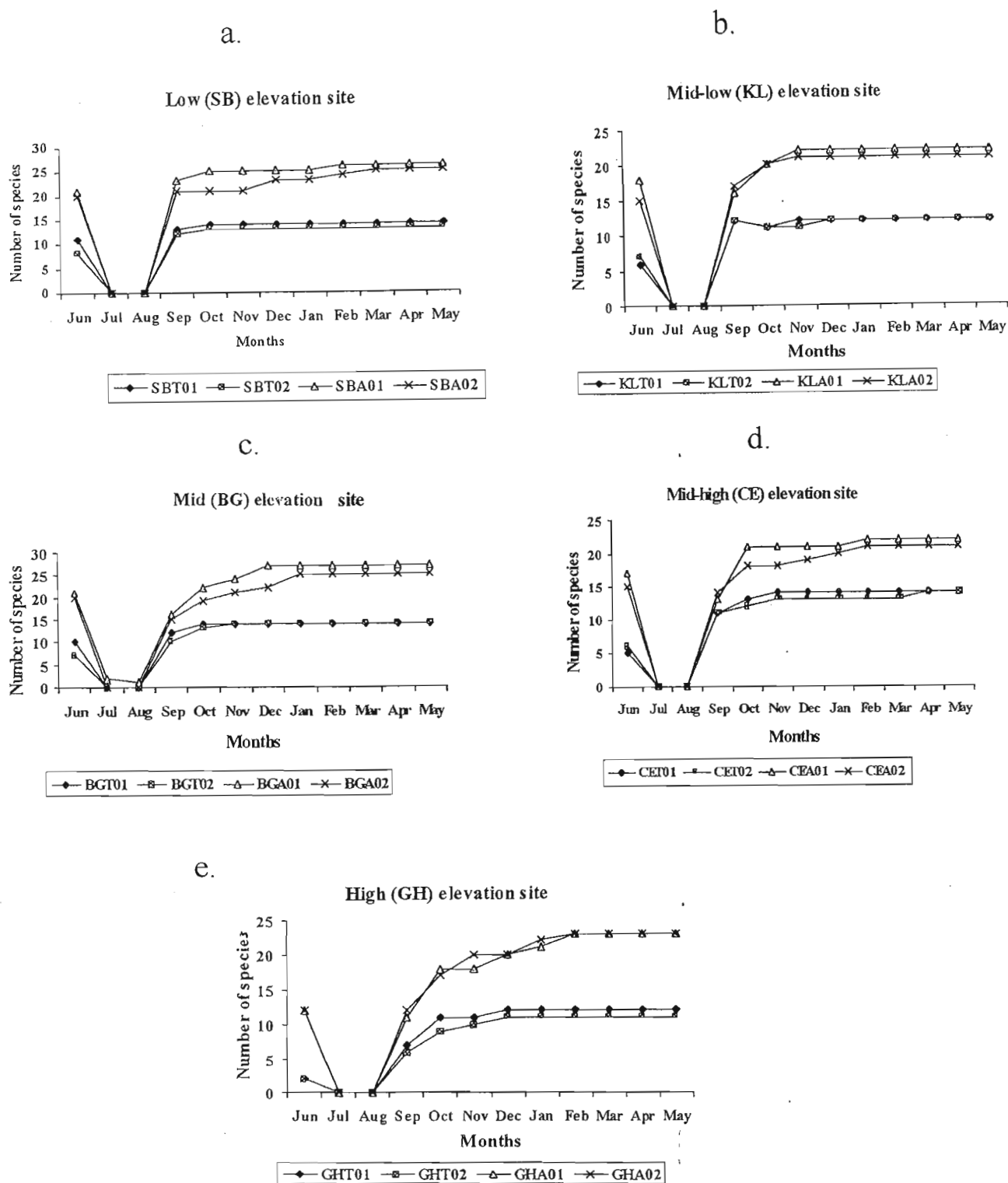
Fig. 4.3 Accumulative dragonfly tenerals (T) and adults (A) species recorded at (a) Low (SB), (b) Mid-low (KL), (c) Mid (BG), (d) Mid-high (CE) and (e) High (GH) elevations during the first (01) and second (02) year of the study.
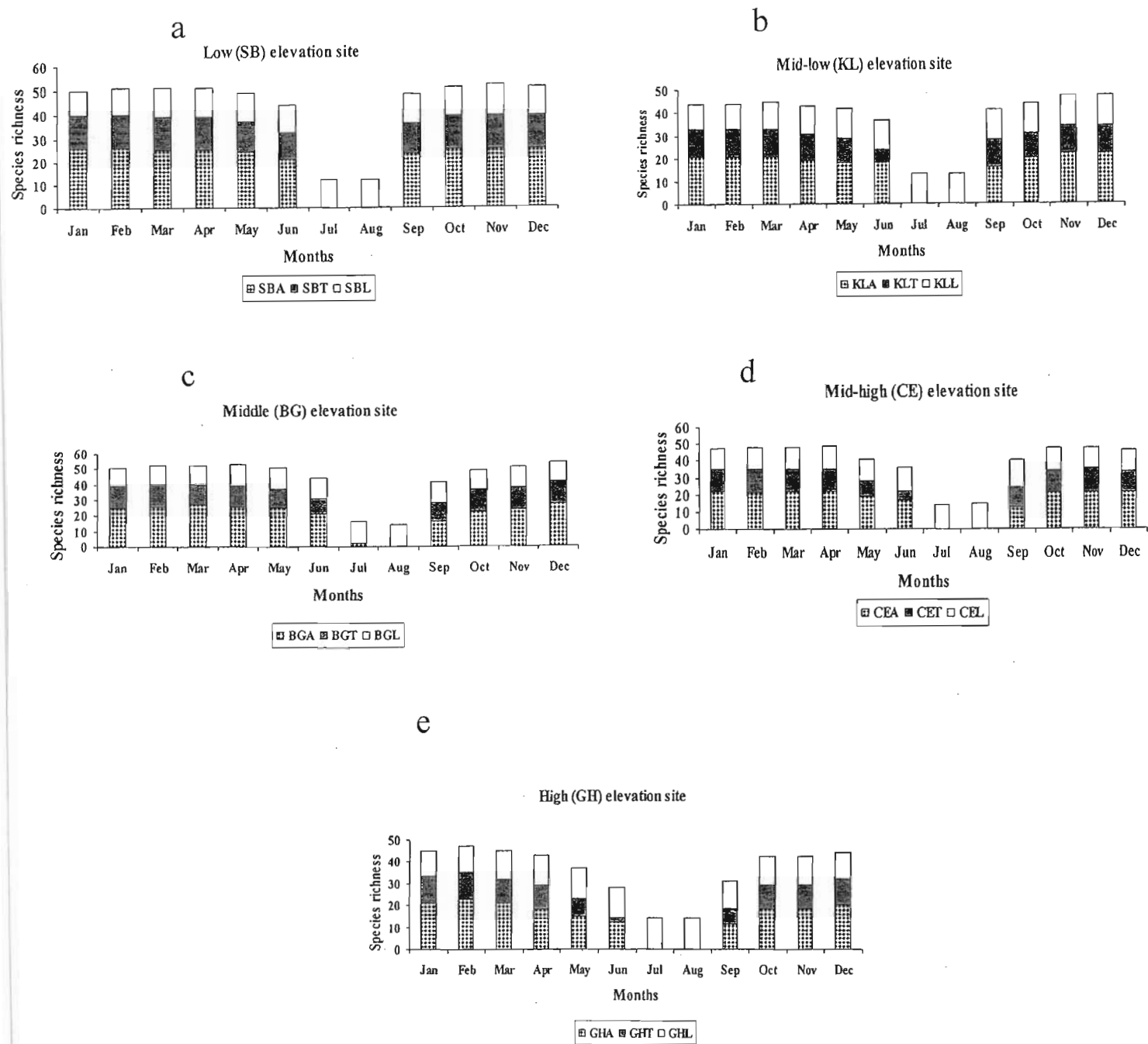
Fig. 4.4 Dragonfly species recorded at (a) Low (SB), (b) Mid-low (KL), (c) Mid (BG), (d) Mid-high (CE) and (e) High (GH) in terms of adults (A), tenerals (T) and larvae (L), and during the two-year sampling period.

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Larval abundance varied from 20 individuals in January at Mid-low (KL) elevation (Fig. 4.5b) to 138 in April at Mid-high (CE) elevation (Fig. 4.5d). Teneral counts also varied from two individuals in June at High (GH) elevation to 175 individuals in November at Mid-high (CE) elevation (Fig. 4.5d). Thereafter, trends at all elevations were high in November for both years. No teneral individuals were recorded at any elevations during winter (July to August). Adult abundance was greatest in November and in December.

4.5.3 Peak occurrence periods

There was continual emergence during the study period except in the winter months of July and August and all three developmental stages of dragonfly species were present between September and June.

Tables 4.4 summarises the months when peak counts for adults, tenerals, larval stages and mating/oviposition in Anisoptera and Zygoptera species were made (see Appendix to Chapter Four). These are arranged according to elevations. The table illustrates that most Anisoptera adults from High (GH), Mid-high (CE) and Low (SB) elevations were similar in trends for both years, with peak occurrences mostly from December to March, even though most species peaked in occurrence in November during the first sampling year at High (GH) elevations. Species peaks in Mid (BG) and Mid-low (KL) elevation were also similar, occurring in November in both sampling years. Double peaks occurred at the Mid-high (CE) elevation for *C. erythraea*, occurring in March/November 2001 and January/November 2002. *Trithemis stictica* peaked in March/November 2001 and April/November 2002.

Zygoptera species on the other hand were largely similar, with peak occurrence periods at High (GH), Mid (BG) and Low (SB) elevations from December to March in both years. Members of this sub-order showed peak occurrence in April to May and in April at Mid-high (CE) and Mid-low (KL) elevations respectively for both years.

Zygoptera species with two peaks per year were *I. senegalensis* and *C. glabrum*, each occurring at various elevations (with *C. glabrum* absent at High (GH) elevation). Also, *A. glaucum* and *P. massaicum* had two peak appearances in Mid-high (CE) elevation. *L. plagiatus* had two peaks per year at Mid (BG) and Mid-low (KL) elevation, while *L. tridens* and *P. massaicum* had two peak abundances per year in Low (SB) elevation during both years. *L. tridens* from Stainbank had four peaks at different times during the two sampling years: April/December 2001 and March/November 2002. yearly double peak species occurrences probably indicate the presence of more than one generation in a year.

Observations of intensive mating and oviposition behaviour for both sub-orders showed great variations during the months in which this behaviour occurred, and only slight variations between different elevations.

a

Low (SB) elevation site

Mid-low (KL) elevation site

b

c

Middle (BG) elevation site

d

Mid-high (CE) elevation site

e

High (GH) elevation site
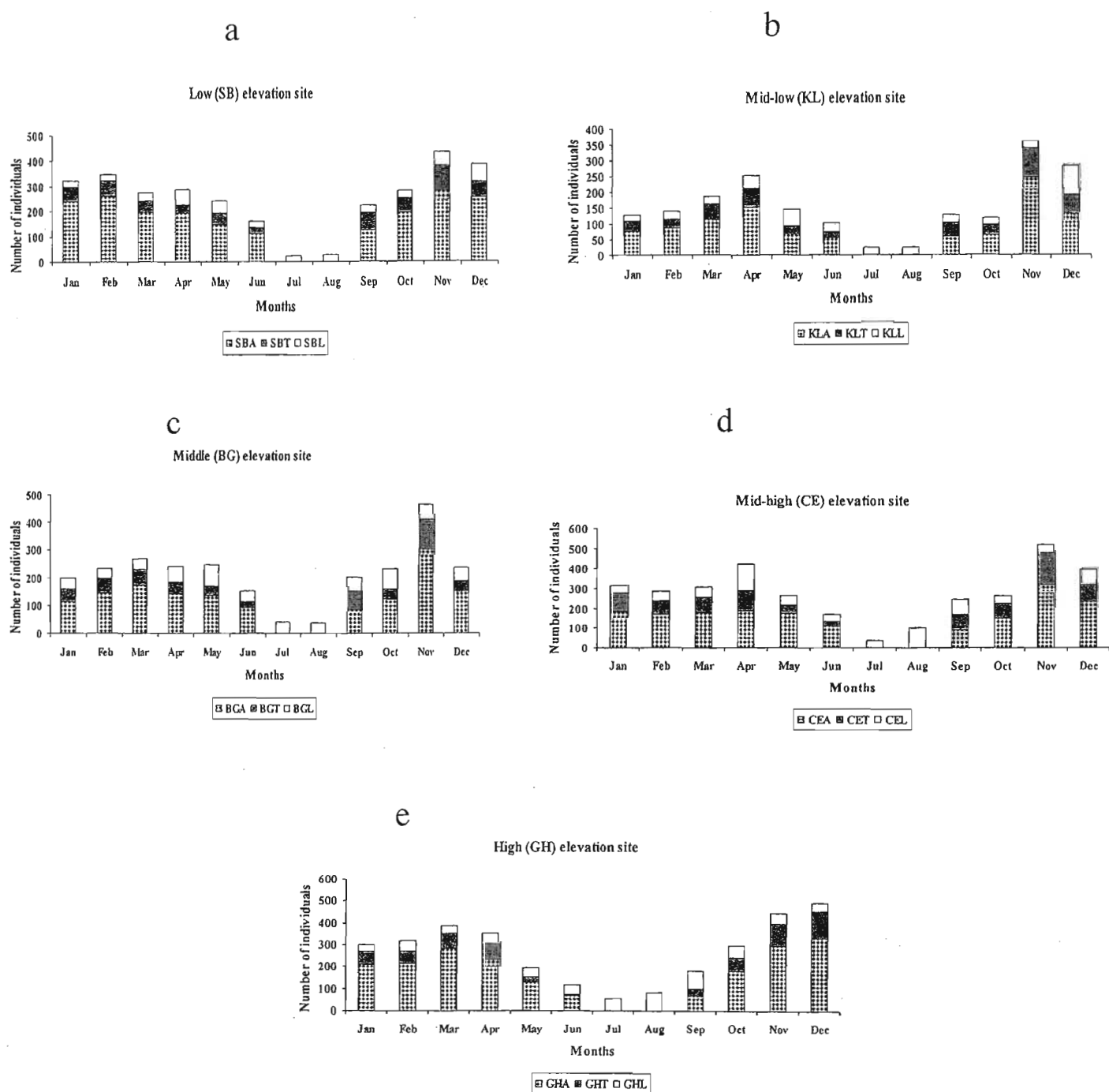
Fig. 4.5 Odonata individuals recorded at (a) Low (SB), (b) Mid-low (KL), (c) Mid (BG), (d) Mid-high (CE) and (e) High (GH) in terms of adults (A), tenerals (T) and larvae (L), and during the two-year sampling period.

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Table 4.4 Summary of species phenology patterns showing mating/ oviposition, larvae and adult peak occurrences in 2001 and 2002.

Site Elevation (m a.s.l.)	Adults		Mating/oviposition		Larvae	
	Zygoptera	Anisoptera	Zygoptera	Anisoptera	Zygoptera	Anisoptera
Low (SB) 100 m	Dec-Mar 2002 Dec-Mar 2001	Dec-Mar 2002 Dec-Mar 2001	Feb-Jun	Jan-Apr	Apr-May Dec	Apr-May Dec
Mid-low (KL) 450 m	Nov 2002 Nov 2001	Apr 2002 Apr 2001	Feb-Mar	Feb-Mar Oct-Nov	Apr-Jun Dec	Apr-May Dec
Middle (BG) 790 m	Nov 2002 Nov 2001	Jan-Mar 2002	Feb-Mar Sep-Nov	Feb-Mar	Mar-Apr, Jul, Nov-Dec	May, Sep-Oct
Mid-High (CE) 1050 m	Dec-Mar 2002 Dec-Mar 2001	Apr-May 2002 Apr-May 2002	Jan-May Oct-Nov	Feb-May	Mar-May Sep-Dec	Apr, Jul-Aug
High (GH) 1350 m	Dec–Mar 2002 Nov 2001	Dec – Mar 2002 Feb-Apr 2001	Jan-May	Feb-Jun	Feb-Sep	Feb-Sep

4.5.4 Overall family/species trends at the different elevations

A total of 46 species in seven families were recorded during the study at all elevations. Libellulidae accounted for 52% of all species, declining from 34% at 0-300 m (SB) to between 27-29% within 301-1350 m (KL, BG, CE, GH). The Coenagrionidae accounted for 32%, fluctuating between 19% at <300 m and 14% at 1350 m (GH). Aeshnidae made up 6.5% of all species and were all represented at the <300 m belt, declining to 4.3% within 301-1350 m (KL, BG, CE, GH). The Gomphidae accounted for 8.6% of all Odonata sampled, with 6.5% at 1350 m, declining to 2% within 0-1200 m (SB, KL, BG, CE). The Lestidae remained fairly constant at about 2% from 0-1350 m (Fig. 6). The Platycnemididae and Chlorocyphidae accounted for 2% each of the total Odonata and were only represented at the 601-900 m (BG) range with the former being a rare mid-elevation family. There were generally, only slight differences in species numbers among

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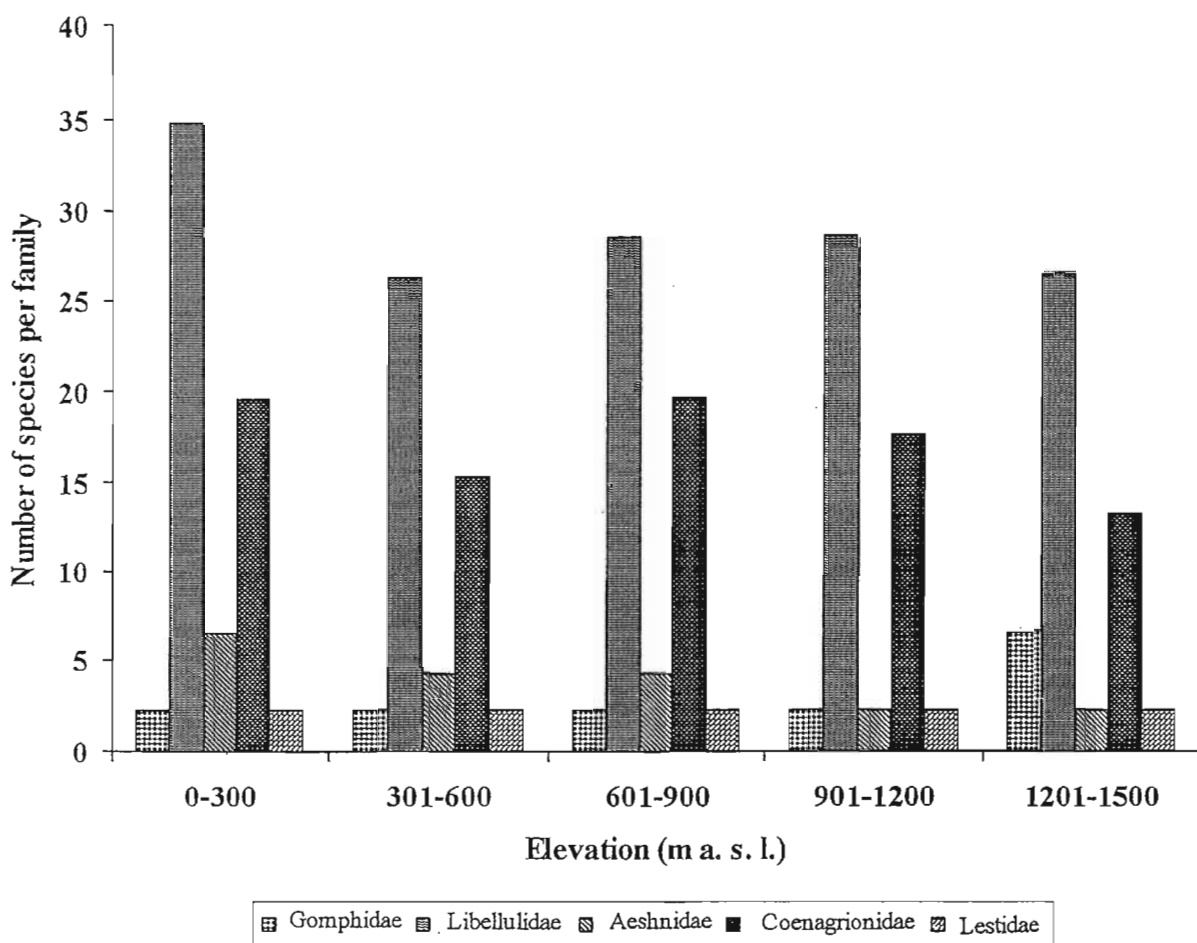
Fig. 4.6 Proportionate species richness of each odonate family as a percentage of total odonates sampled per 300m belt across all five elevations: Low (0-300 m), Mid-low (301-600 m), Mid (601-900 m), Mid-high (901-1200 m) and High (1201-1500 m) elevations.

elevations. Species restricted to one elevation occurred in Low (SB), High (GH), Mid (BG) and Mid-low (KL) elevations, decreasing in that order (Fig. 7).

Fourteen species occurred at all five elevations, while 17 species were restricted to only one elevation: eight in Low (SB); four each at High (GH) and Mid (BG) and one only occurred at Mid-low (KL), while 15 species occurred over at least two elevations of all five elevations (Table 5a)

Diversity (Hill's H') measures (Table 5b) showed that Low (SB) elevation sub-site 1 had the highest species diversity of all the 30 sub-sites. Mid-low (KL) elevation had the least diverse sub-sites, with SS3 having only one species record, as it was located at a stony waterfall biotope, with a very low density of both structural and compositional vegetation. Most SSs had almost similar evenness (J') measures.

The dominant species at the Low (SB) elevation site was *L. tridens* (22%) while *T. stictica* dominated in Mid-high (CE) elevation. Both elevations had relatively high percentage levels of species dominance patterns compared to the other elevations. Mid-low (KL) elevation and High (GH) elevation showed some similarity in patterns of species dominance, with *T. arteriosa* (17%) and *T. stictica* (18%) being the dominant species at respective elevation sites (Fig. 4.8)

4.5.5 Cluster analysis groupings of sub-sites using adult data

Clustering of the 30 sub-sites from five elevational sites using Bray-Curtis similarity index (Fig.4.9) revealed that sub-sites BG3 and SS KL3 shared very similar biotope conditions (and therefore species) comprising a waterfall with semi-forested banks and stony running stream flowing from an impoundment. Sub-sites BG4 and SB4 were characterised by tall trees with over-hanging macrophytes, and shady conditions. The remaining sub-sites were situated at sections of open water, attracting a broad diversity of dragonfly species.
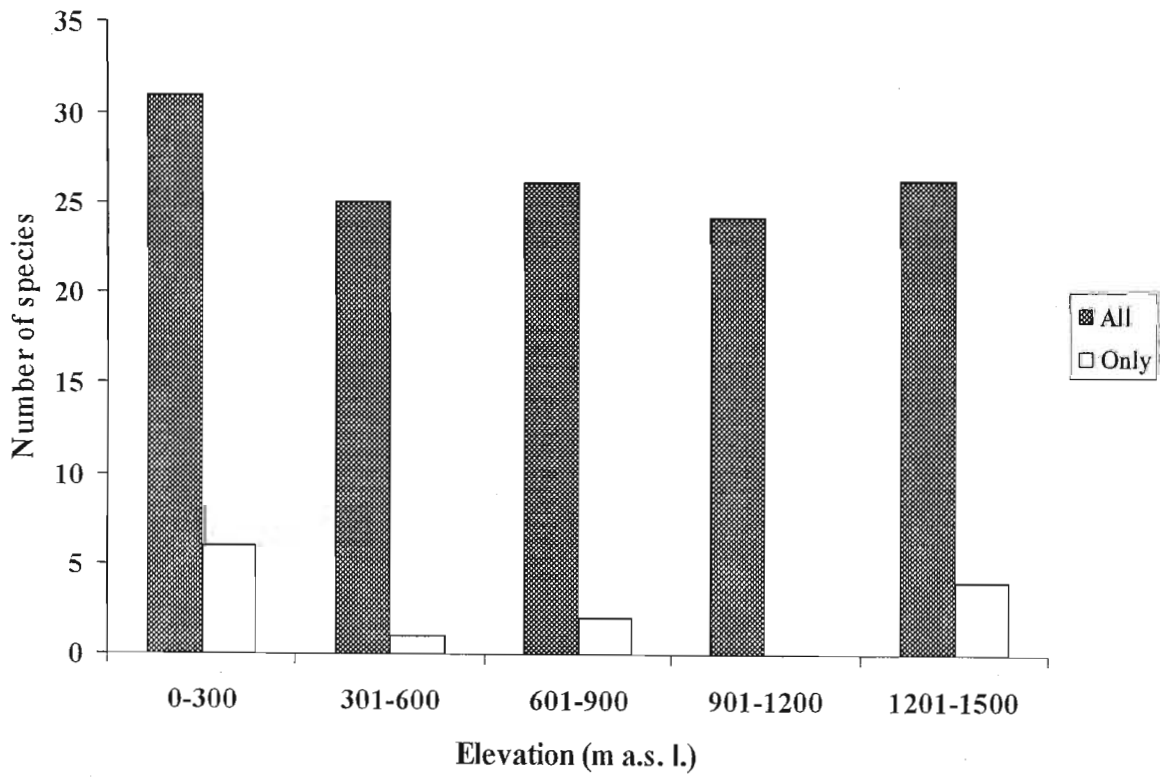
Fig. 4.7 Total number of dragonfly species ('All') and number of species restricted to particular elevations ('Only'), recorded in Low (0-300 m), Mid-low (301-600 m), Mid (601-900 m) and High (1201-1500 m) elevations. Note that species restricted to particular elevations are not confined to either low or high elevations.

Table 4.5a Elevation and dragonfly species associations. Note that species-elevation associations are based more on availability of preferred microhabitat than elevation per se.

Elevations	Species associated with specific elevations in this study
100 m (SB)	Asap, Pcit, Ohin, Pjuc
450 m (KL)	None
790 m (BG)	Pcal, Aleu, Aelo, Pcog
1050 m (CE)	Njon
1350 m (GH)	Azn, Ltri, Atri, Bleu, Chfl, Halb, Dlev, Tpol
CE, GH	Cpic, Ocaf
BG, KL	Znat
KL, GH	Noto
SB, GH	Ifer
SB, CE, GH	Acis
SB, BG, CE	Pmas, Rshy
SB, KL, BG	Phag, Pluc, Plum
KL, BG, CE, GH	Lplg, Tdor, Tsti
SB, KL, BG, CE	Cglm
All sites (0-1350 m)	Uass, Tart, Sfon, Pfla, Ojul, Nfar, Cery, Aspe, Pker, Psal, Isen, Afal, Aglm, Tbas

SB (Low) = (100 m), CE (Mid-high) = (1050 m), BG (Mid) = (790 m), KL (Mid-low) = (450 m) and GH (High) = (1350 m)

Table 4.5b Diversity measures (Hill - N1) and Evenness (J') indices at sub-sites across all five elevations during the whole sampling period (January 2001 – December 2002).

Site	SB			KL			BG			CE			GH		
Sub site	S	N1	J'	S	N1	J'	S	N1	J'	S	N1	J'	S	N1	J'
SS1	25	111.5	0.92	21	102.2	0.97	21	91.55	0.94	23	102.4	0.92	24	106.5	0.94
SS2	16	64.2	0.94	14	59.08	0.97	18	84.22	0.97	19	89.16	0.97	21	88.14	0.93
SS3	7	21.39	0.96	-	-	-	3	6.22	0.92	12	44.34	0.95	19	73.74	0.92
SS4	7	20.05	0.93	4	10.48	0.99	7	17.00	0.87	8	27.51	0.98	21	43.87	0.95
SS5	14	51.76	0.94	4	10.14	0.97	6	17.52	0.96	8	26.52	0.97	9	27.64	0.93
SS6	14	48.52	0.92	4	10.58	0.99	5	12.93	0.94	5	14.63	0.99	10	37.05	0.97

SB (Low) = (100 m), CE (Mid-high) = (1050 m), BG (Mid) = (790 m), KL (Mid-low) = (450 m) and GH (High) = (1350 m)
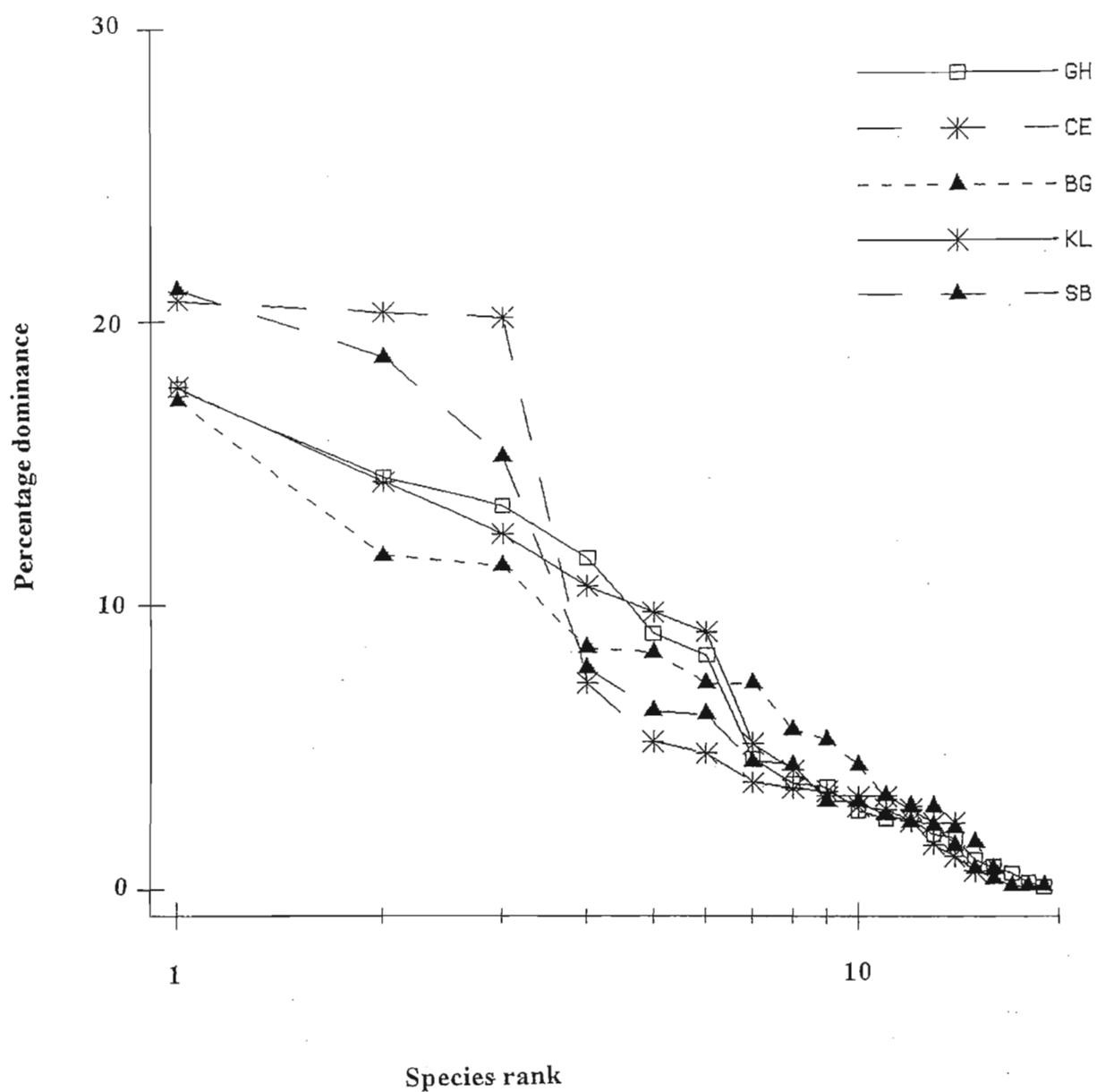
Fig. 4.8 Species rank abundance curves, using adult odonate species sampled at: SB= Low (100 m), KL= Mid-low (450 m), BG= Mid (790 m), CE= Mid-high (1050 m) and GH= High (1350 m) elevations. Species are ranked in decreasing order of their importance in terms of abundance from the most common to the most rare. Data are pooled for the whole sampling period.
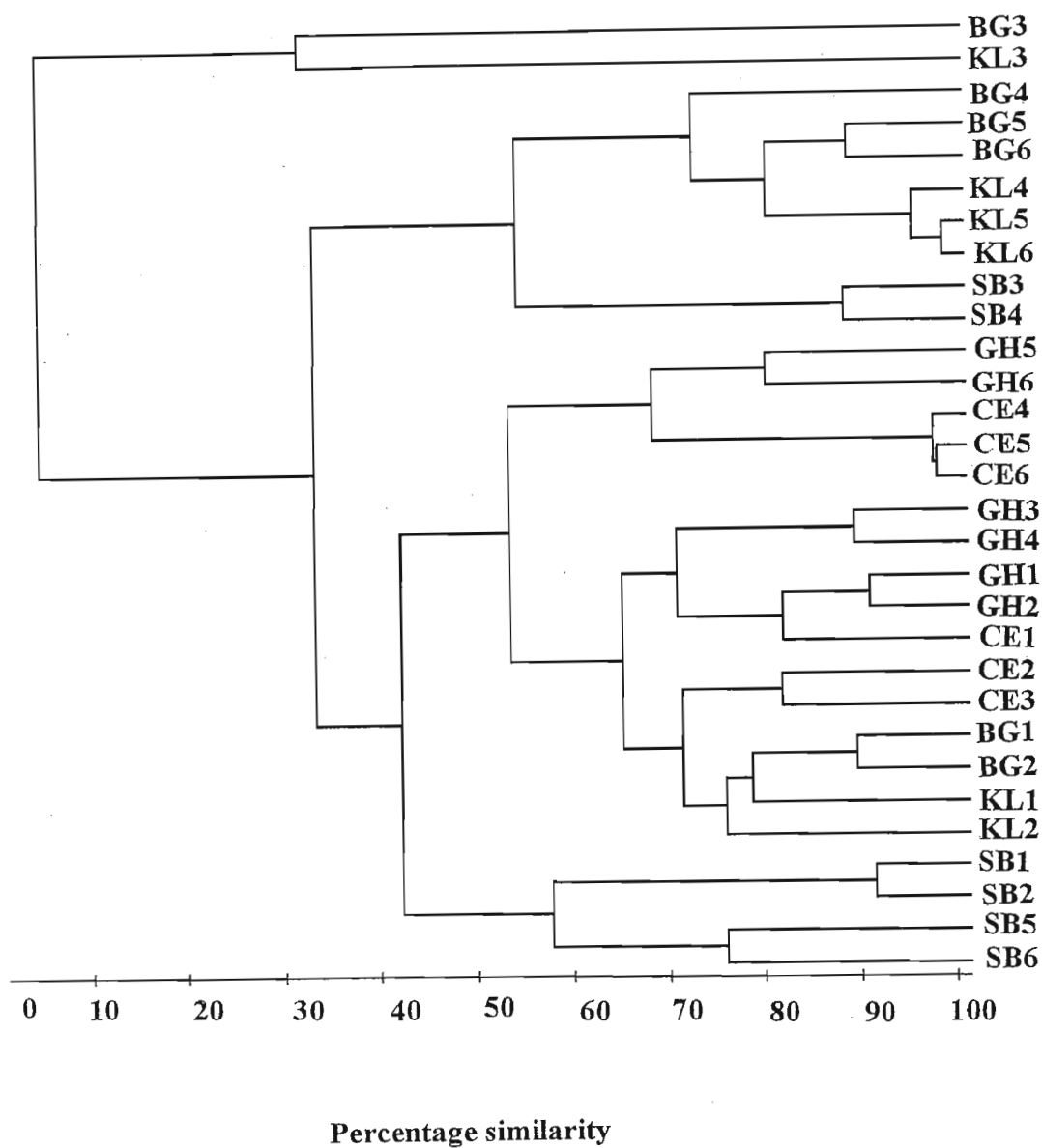
Fig. 4.9 Hierarchical clustering of the 30 sampling sub-sites across all five elevations: SB= Low (100 m), KL= Mid-low (450 m), BG= Mid (790 m), CE= Mid-high (1050 m) and GH= High (1350 m) elevations. Bray-Curtis similarity (wit group-average linking), is calculated on 4th root transformed odonate species abundance data pooled for the whole sampling period.

4.5.6 *Spatial variations in adult, teneral and larvae with elevation*

Larval species counts (Fig. 4.10a) were higher in Mid-high (CE) elevations than the rest of the elevations. This was accompanied by high individual abundance, perhaps attributable to optimal conditions available to a wide number of species (Fig. 4.10a1).

Patterns of teneral species richness across elevations ranged between 14 and 16 species per elevation during the study, with Mid-low (KL) again recording lowest individual counts (Fig. 4.10b1).

Overall number of adult dragonfly species varied slightly across elevations, with Stainbank supporting the most species (Fig. 4.10c). The rest of the elevations recorded slightly different number of species during the study period. Adult individuals showed great variation across elevations, with the Mid-low elevation (KL) having the smallest individual records (Fig. 4.10c1).

Larvae species richness was positively correlated with elevation (F = 19.25; P = 0.002). Larval abundance was also significantly correlated with elevation (F= 7.69; P=0.024) (Fig. 4.11). Teneral showed a similar trend to adults in species richness, being negatively correlated with elevation but not statistically significantly (Fig 4.12a). A rather weak positive correlation was observed for teneral individuals with elevation (F = 4.73; P= 0.056) (Fig. 4.12b). Regressions of adult dragonfly species richness (P=0.27) and abundance (P=0.32) on elevation were not statistically significant even though there was a generally decreasing trend in species numbers as elevation increased (Fig. 4.13a, b)

Two-way ANOVA results to determine the response of adult, teneral and larvae to elevation across seasons showed no statistically significant effect on adult species (F=1.2, P=0.31) and teneral individuals (F= 1.6; P= 0.41). However, there were statistically significant responses for adult individuals (F = 2.9; P = 0.01), teneral species (F = 2.1; P = 0.05), larval species (F = 4.2; P = 0.002) and larval individuals (F = 10.0; P = 0.001) (Table 4.6).
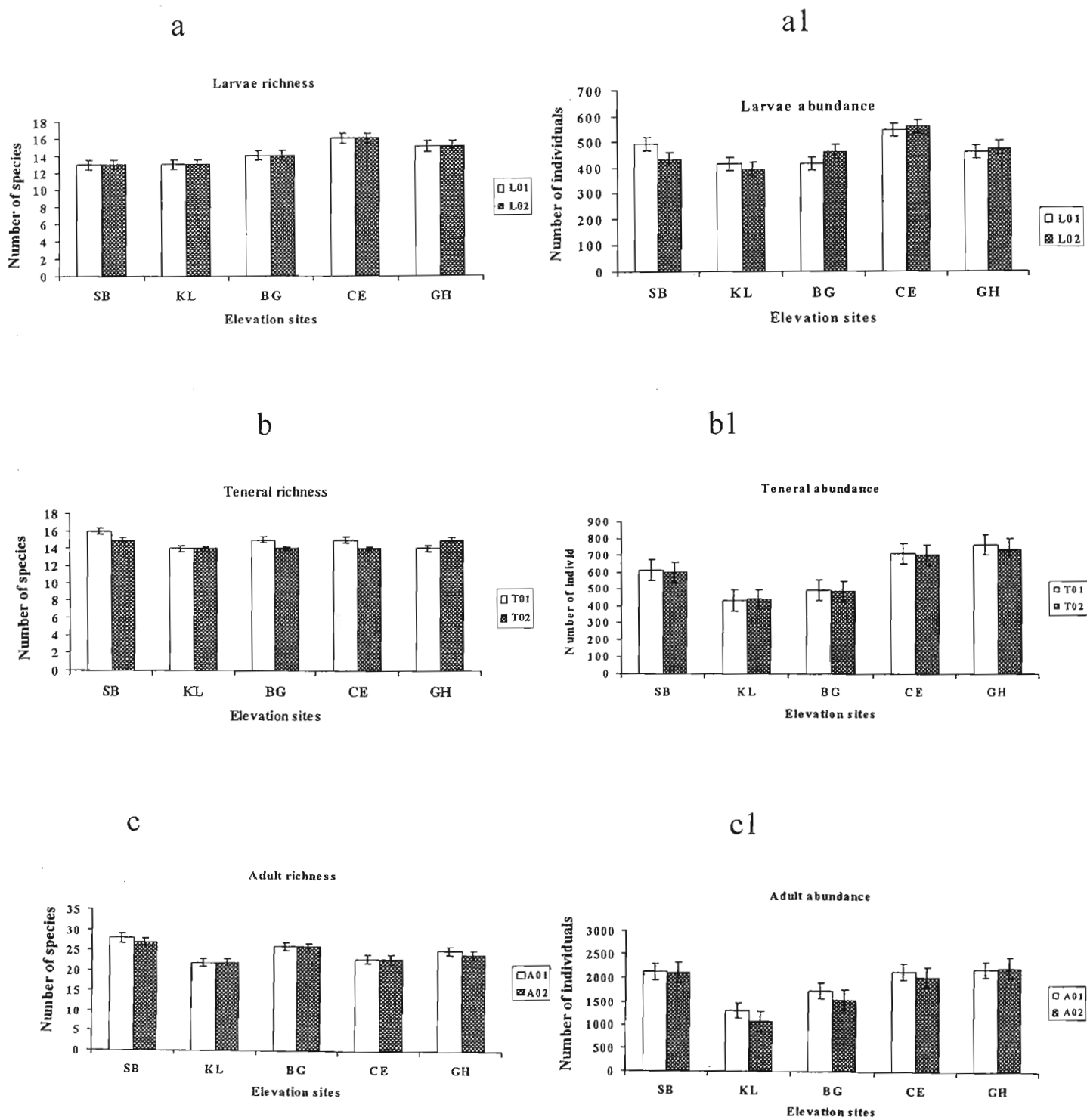
Fig. 4.10 Mean (+/-SE) of odonate species richness and abundance for larvae, tenerals and adults at the five elevations during the two sampling years (01, 02).
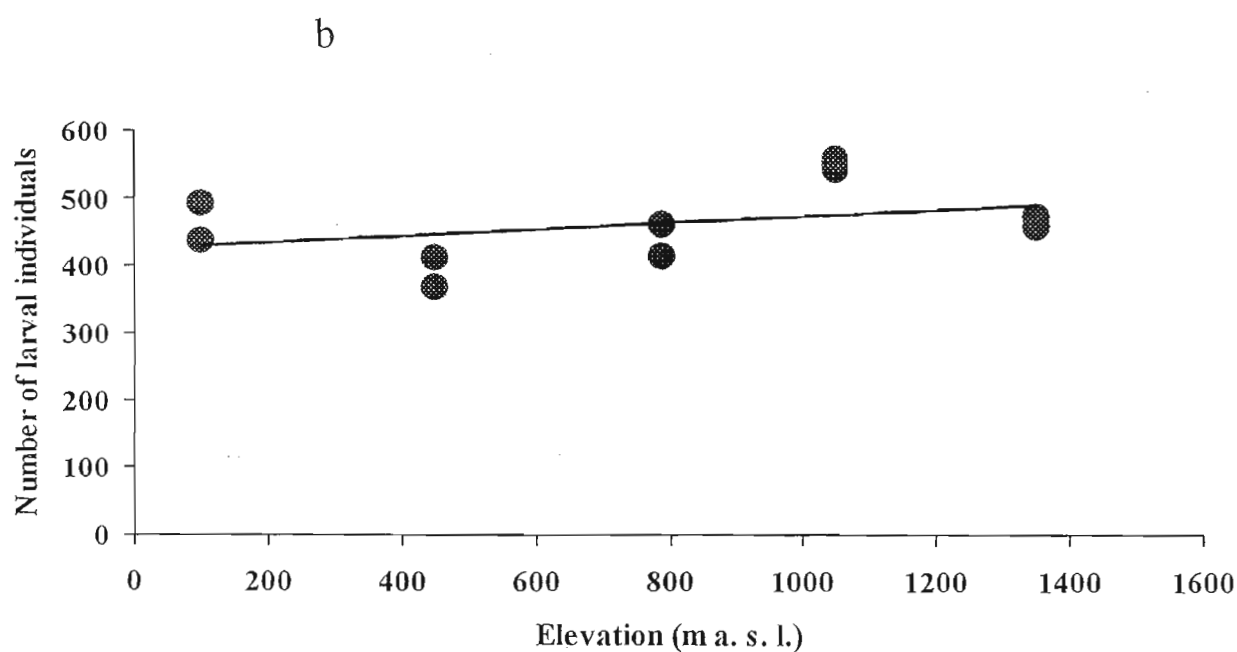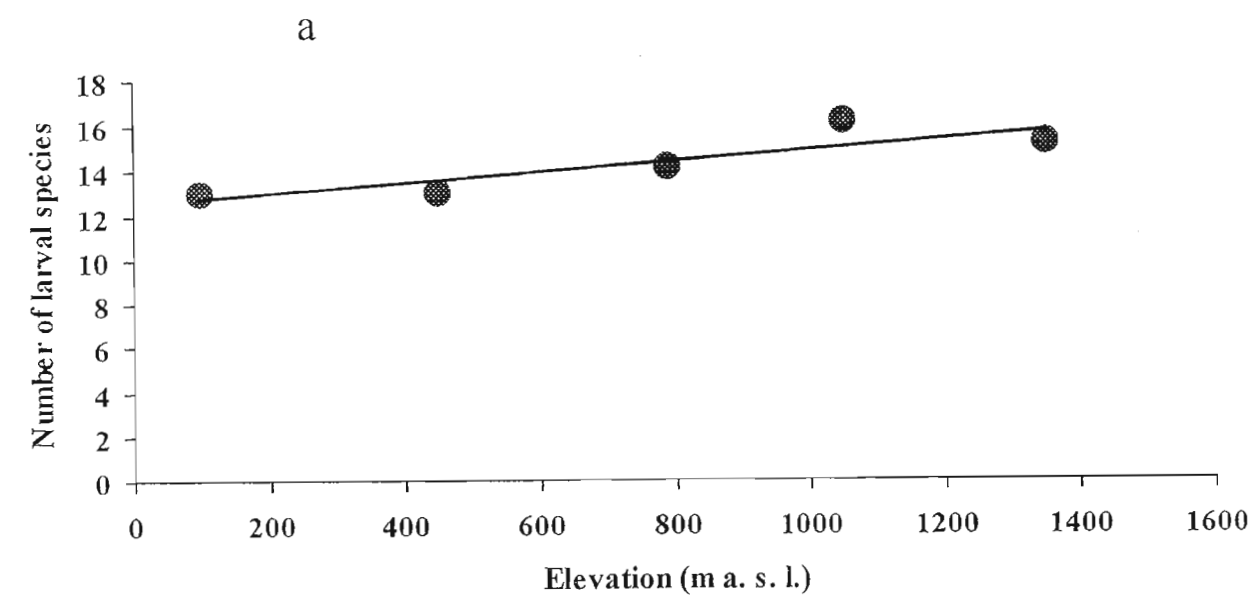
Fig. 4.11 Linear regression of odonate larvae on elevation. Both species richness (a) (model: y= 0.0022x + 12.53) and abundance (b) (model: y= 0.0431x + 424.43) are significant at P= 0.002 and P= 0.024 respectively.
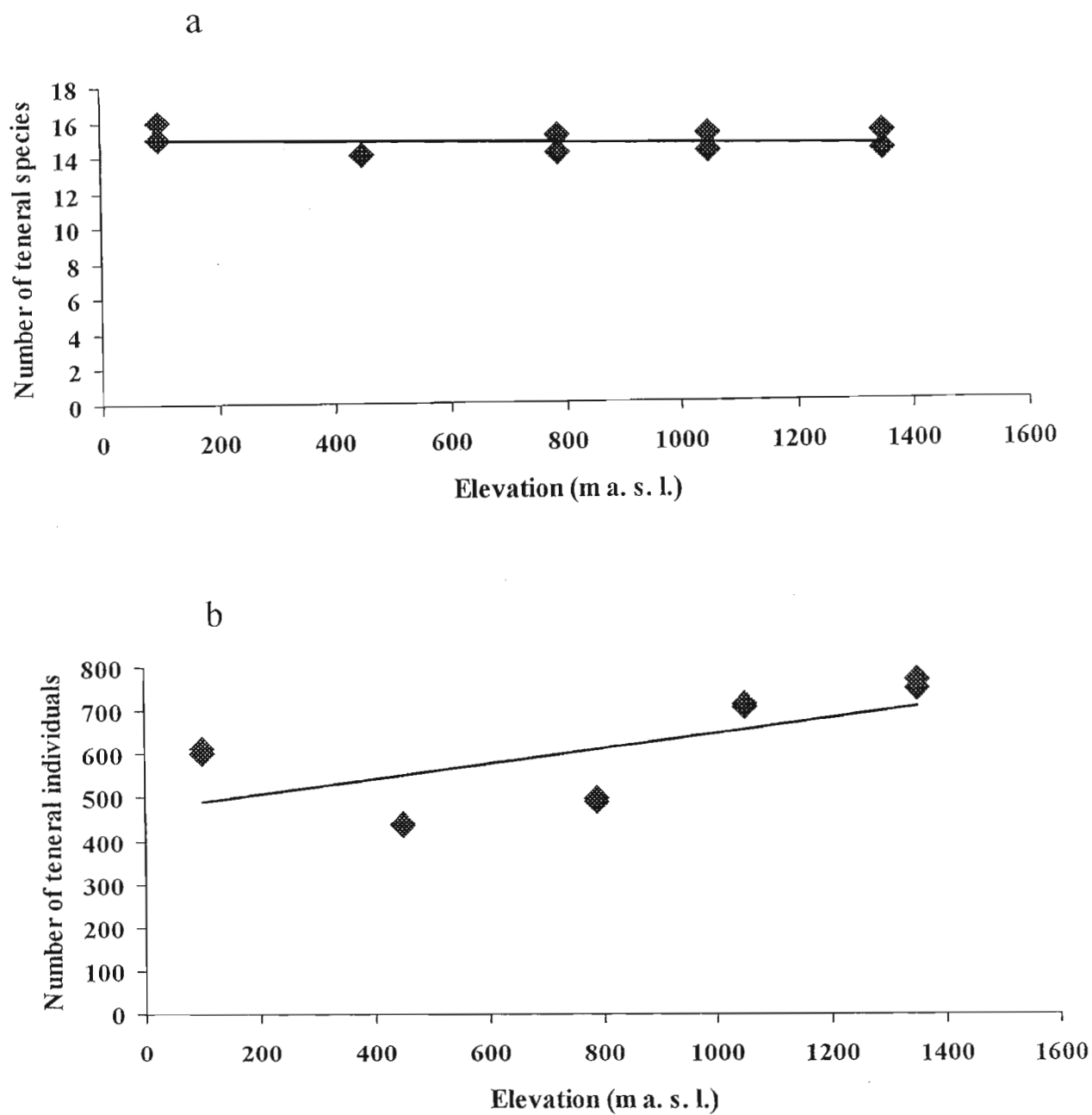
Fig. 4.12 Linear regression of odonate tenerals on elevation. Species richness (a) (model: y= -0.003x + 14.987) is not significant at P= 0.33, while abundance (b) (model: y= 0.1677x + 472.24) is significant at P= 0.046.
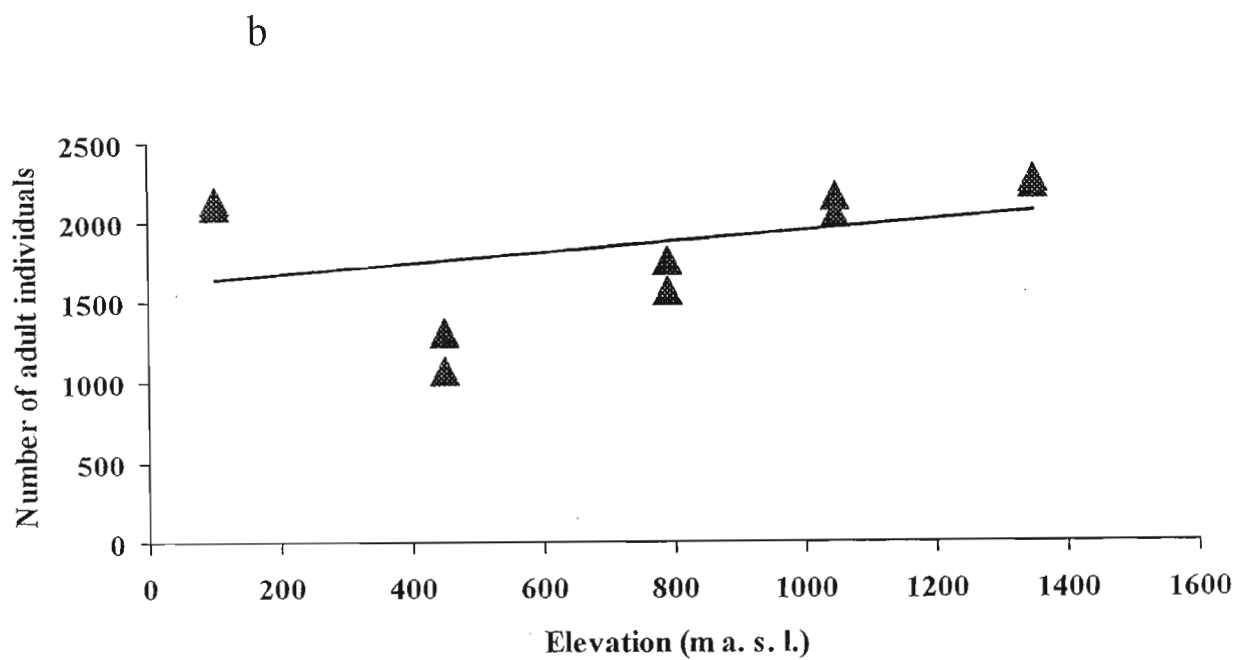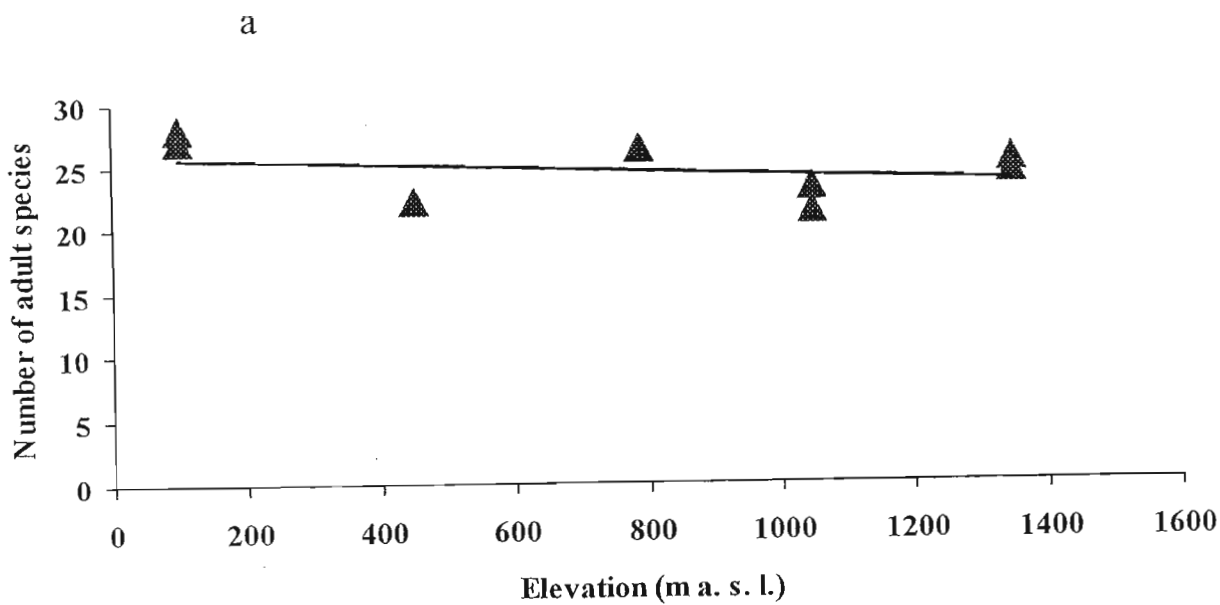
Fig. 4.13 Linear regression of adults on elevation. Both species richness (a) (model: y= -0.002x + 25.86) and abundance (b) (model: y= 0.3198x + 1609.7) are not significant at P= 0.27 and P= 0.32 respectively.

Table 4.6 Two-way-ANOVA results of elevation and seasonality interaction for mean dragonfly adults, tenerals and larvae richness and abundance, and measured site variables during the whole sampling period. Significance levels: *0.05>P>0.01; **0.01>P>0.001.

Site variable	Summer SB	KL	BG	CE	GH	Autumn SB	KL	BG	CE	GH	Winter SB	KL	BG	CE	GH	Spring SB	KL	BG	CE	GH	F	P
Asp	25	21.5	24	21	21	25.5	21	26	21.5	23	20	16	20	16	12	23	21	22.5	20	19	1.2	.31
Aind	700	351	418	296	790	572	374	480	567	648	130	62	98	112	75	600	404	552	554	534	2.9	.01
Tsp	13.5	12	14	13	11	13.5	11	13	14	11.5	9.5	6.5	8.5	6.5	2	13.5	12	14	13	11	2.1	.05
Tind	172	94	132	230	215	122	125	137	223	200	25	15	20	19	5	216	162	190	243	200	1.6	.14
Lsp	12.5	13	13	13	13	12	12.5	14	14.5	14	12	13	14	15	13.5	13	12.5	13	16	13	4.2	.002
Lind	124	141	84	93	77	145	120	146	193	83	83	70	89	131	135	121	75	147	134	151	10.	.001
% Sh	19	12.4	16.5	0	0	12	15.8	11	0	0	11	16	10	0	0.	17	11	14.6	0	0	1.3	.26
At	24.5	30	30	29	30.4	28	29.3	29	30.5	30	17	17	18	20	21.9	26	28	26.3	28	25.5	0.8	.59
Fsv	30.8	17	24	21	11.3	30	2	28	20.5	6	18	0.6	15	14	3.7	24	1.9	21.8	16	6.8	0.7	.6
Mfor	30	40	25	0	0	30	50	25	0	0	30	50	25	0	0	30	50	25	0	0	1.0	.44
Mgra	27.5	16	12.5	22	21	25	4.8	12	23.4	22	11	2.2	5.5	10	8.3	22	6.2	11.7	22	26.2	1.0	.46
Marsh	27	27	23	12	7.5	29	29	24	14.8	7.3	12	5.5	12	6.6	4.2	26	28	15.6	11	8.2	7.4	.001
pH	7.2	6.9	6.9	7.2	7.0	7	7	7.3	7.1	7.1	6	7.2	7.1	7	6.8	6	7.1	7.1	6.9	7.2	0.8	.58
Tur	18	25	20.5	23	20	15	26	24	17	25	22	28	20	19	28.8	20	21	20	19	17.4	0.5	.86
Wd	25	28	29.3	26	24	24	25	22.8	25	20	15	15	16	16	18.9	24	24	24	23.4	20.2	1.4	.24

Asp = Adult species, Aind = adult individuals, Tsp = teneral species, Tind = teneral individuals, Lsp = larval species, Lind = larval individual. SB (Low) = (100 m), KL (Mid-low) = (450 m), BG (Mid) = (790 m), CE (Mid-high) = (1050 m) and GH (High) = (1350 m).

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4.5.7 *Summary of Anisoptera and Zygoptera Ordinations*

Species associations with elevation were strongest on ordination plots when all Odonata were separated into their component sub-orders (Anisoptera and Zygoptera grouping). CA results for Anisoptera (Fig. 4.14a) showed most open water species clumped at the centre of the ordination. Zygoptera species showed various trends as species were more dispersed from the centre of the ordination (Fig. 4.14b). They were more tolerant of diverse conditions of shade, open water, running and still. Separate CCA ordinations were also run for species belonging to Anisoptera and Zygoptera again for better interpretation of the effects of measured variables and elevation on patterns of dragonfly assemblage composition and distribution. Species-site-variable triplots for Anisoptera (Fig. 4.15a) and Zygoptera (Fig. 4.15b) showed that most assemblages were related to a number of environmental variables, and indicated how species responded or not to gradients of these variables in space.

Accordingly, elevation, marginal grasses, pH, and percentage shade appeared on the first (horizontal ordination axis) as the more important variables, while floating /submerged vegetation, marginal forest and turbidity occurred on the second axis (vertical) and are less important in determining Anisoptera species assemblage distribution patterns.

Marginal forest, percentage shade, and floating/submerged vegetation were the more important variables while marginal grasses, elevation and pH were important for Zygoptera.
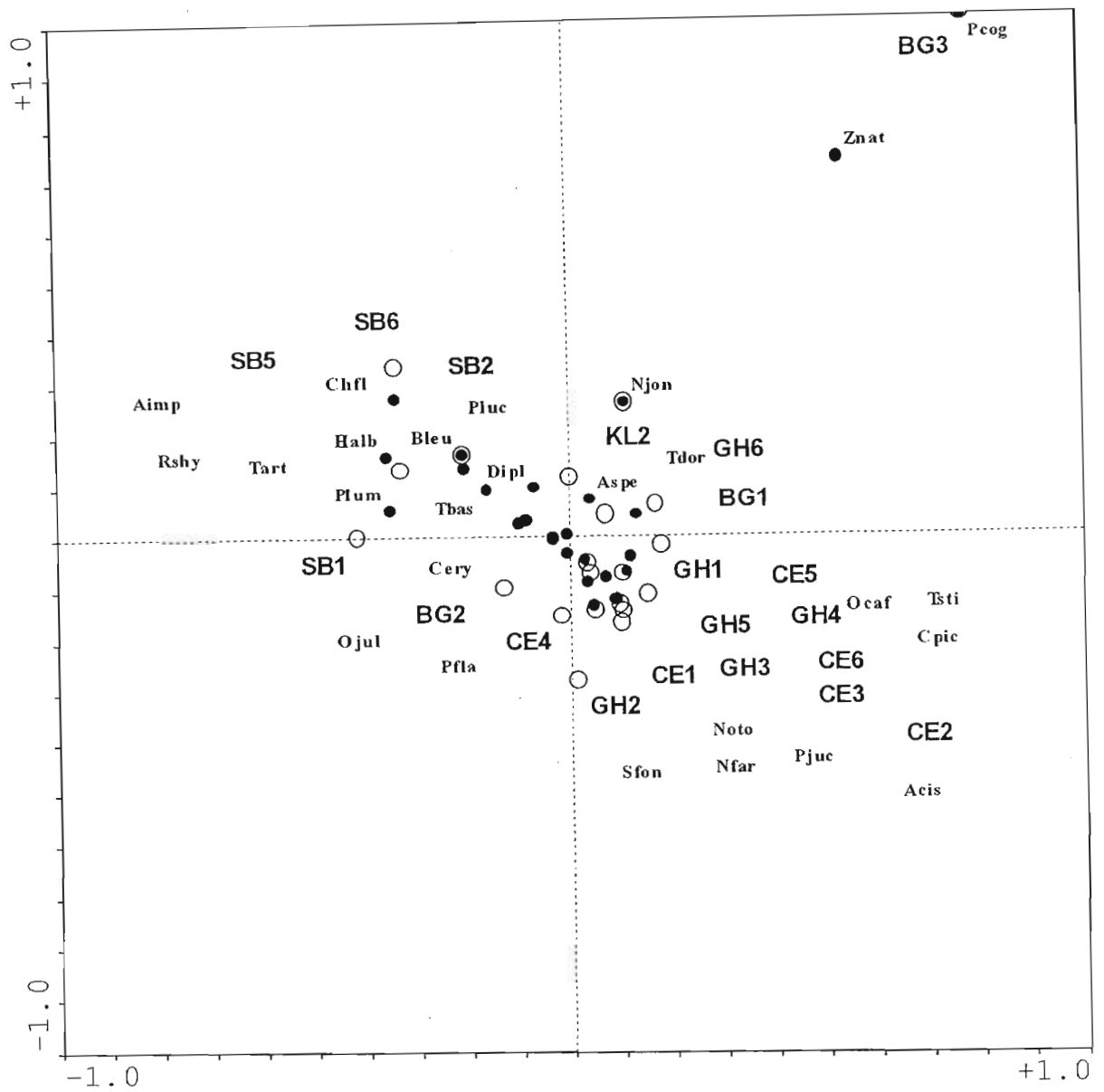
Fig. 4.14a CA biplot of Anisoptera species (closed circles) and sampling sites (open circles) for pooled 2001 and 2002 data. Site abbreviations are: SB (Low) = (100 m), KL (Mid-low) = (450 m), BG (Mid) = (790 m), CE (Mid-high) = (1050 m) and GH (High) = (1350 m). Species codes are as in Table 4.2a.

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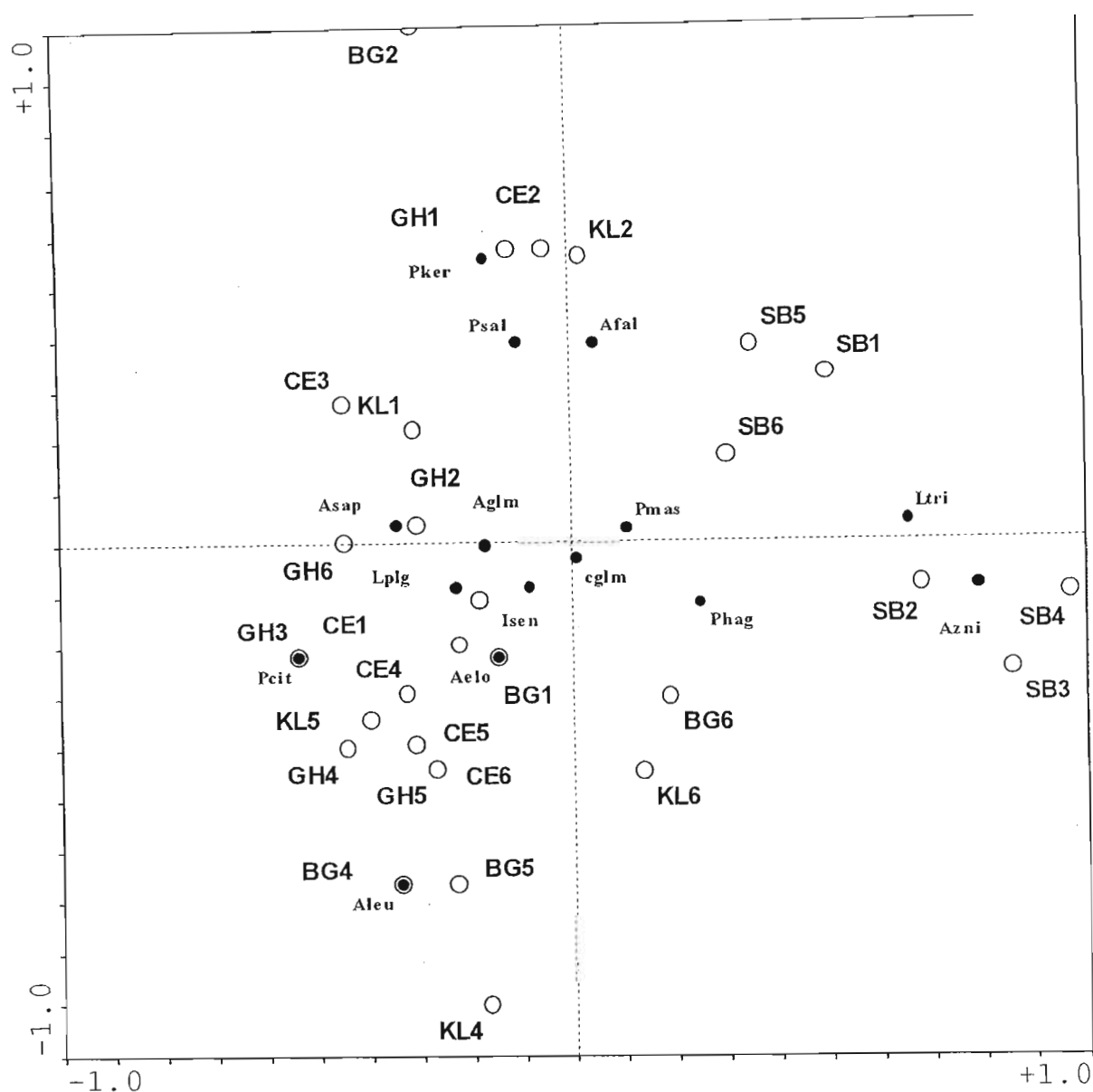
Fig. 4.14b CA biplot of Zygoptera species (closed circles) and sampling sites (open circles) for pooled 2001 and 2002 data. Site abbreviations are: SB (Low) = (100 m), KL (Mid-low) = (450 m), BG (Mid) = (790 m), CE (Mid-high) = (1050 m) and GH (High) = (1350 m). Species codes are as in Table 4.2b.

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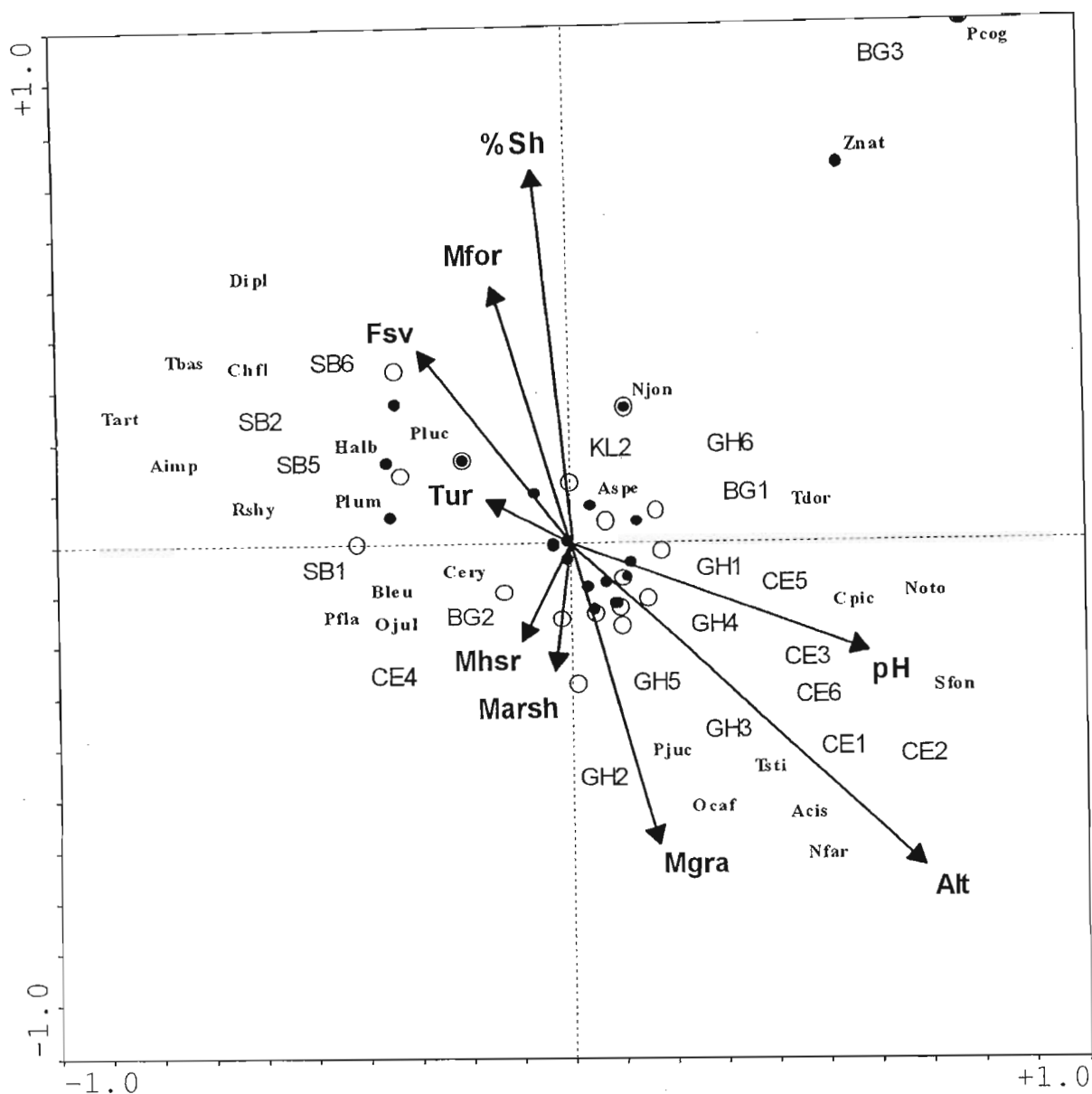
Fig. 4.15a CCA triplot of Anisoptera species (closed circles), elevation sites sampling units (open circles) and site variables (arrows) for pooled 2001/2002 data. Axis 1 is horizontal and axis 2 vertical. Site abbreviations are: SB (Low) = (100 m), KL (Mid-low) = (450 m), BG (Mid) = (790 m), CE (Mid-high) = (1050 m) and GH (High) = (1350 m). Site variables are: Elev = elevation, Mgra= marginal grasses, Mhsr= marginal herbs, sedges and reeds, Mfor= marginal forest, Tur= water turbidity, Fsv= floating and submerged vegetation, %Sh= percentage shade. Species codes are as in Table 4.2a.

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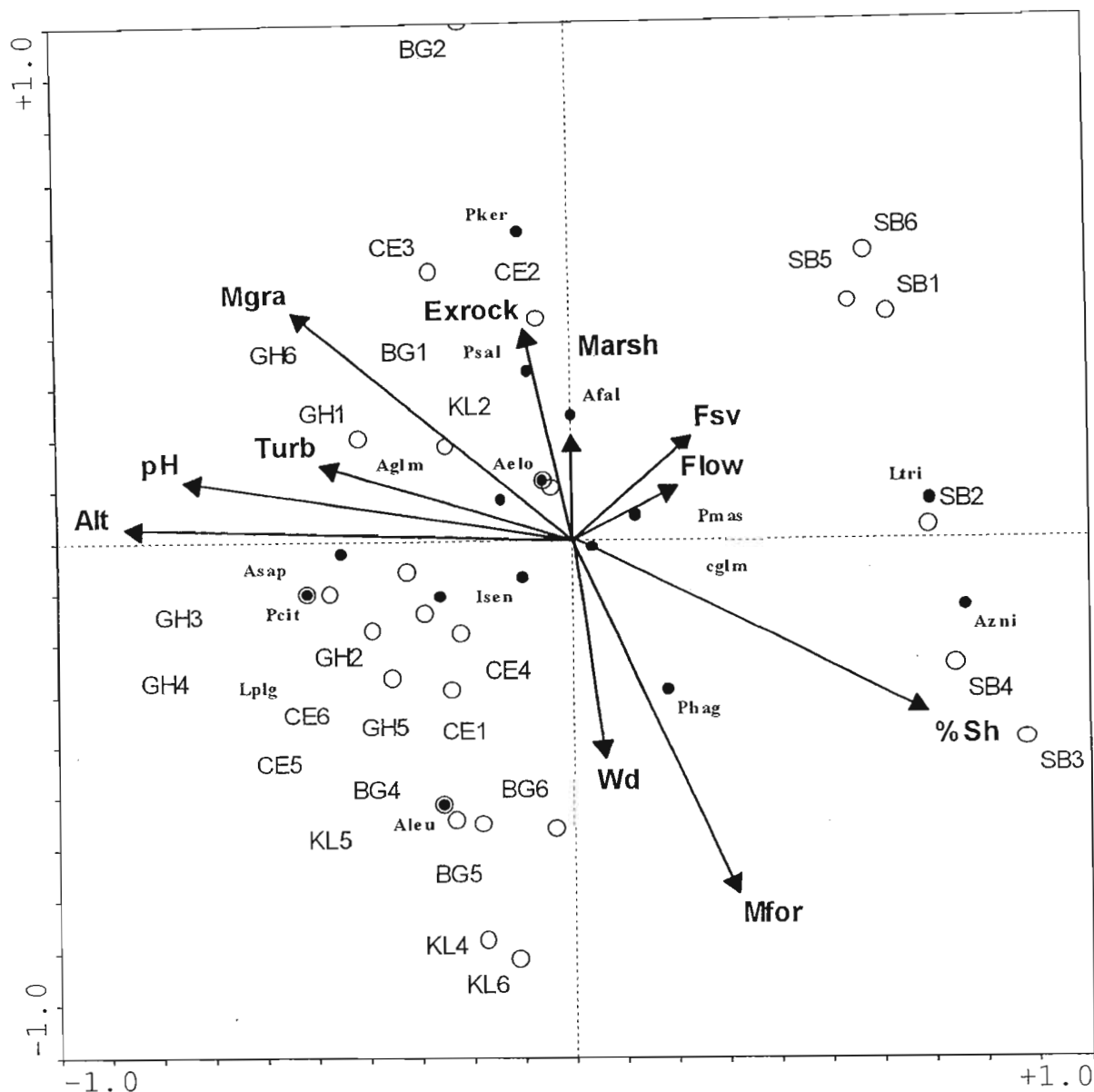
Fig. 4.15b CCA triplot of Zygoptera species (closed circles), elevation sites sampling units (open circles) and site variables (arrows) for pooled 2001/2002 data. Axis 1 is horizontal and axis 2 vertical. Site abbreviations are: SB (Low) = (100 m), KL (Mid-low) = (450 m), BG (Mid) = (790 m), CE (Mid-high) = (1050 m) and GH (High) = (1350 m). Site variables are: Elev= elevation, Mgra= marginal grasses, Mhsr= marginal herbs, sedges and reeds, Mfor= marginal forest, Turb= water turbidity, Fsv= floating and submerged vegetation, %Sh= percentage shade, Wd= water depth, Exrock= exposed rock. . Species codes are as in Table 4.2b.

The following Anisoptera species were also associated with marginal grasses of reservoirs at High (GH) and Mid-high (CE) elevations: *T. stictica, Palpopleura jucunda, Acisoma panorpoides, Orthetrum caffrum*. Otherwise, *N. jonesi* was associated with highly shaded conditions of sub-site three at Mid-low (KL) elevation.

Low (SB) elevation species (when the elevation gradient is projected backwards on the ordination triplot) had typical species like *Hemistigma albipunctum, Chalcostephia flavifrons, Tetrathemis polleni, Diplacodes lefebvrii, Rhyothemis semihyalina* and *Tramea basilaris,* even though the last three species were also present at higher elevations.

Open reservoirs (or their sections) at all elevations had the following species in common, located mostly at the centre of the ordination for Anisoptera: *O. julia, C. erythraea, T. arteriosa, P. lucia, A. speratus, A. imperator, T. dorsalis, N. farinosa* and *P. flavescens.* These species also tolerated moderate to low conditions of marshes and marginal herbs, sedges and reeds.

High (GH) elevation zygopterans like *Pseudagrion citricola,* and *Africallagma saphirinum* were strongly associated with sunny conditions, high pH and marginal grasses. Low (SB) elevation species were *L. tridens* and *A. nigridorsum* while *P. hageni* was associated with Middle (BG) to Low (SB) elevation shade conditions. *A. elongatum, P. kersteni* and *P. salisburyense* were associated with minimal flow, exposed rock and marshy conditions at such elevation sub-sites

Intra-set correlations of environmental gradients with axes (Table 4.7a) showed that elevation, pH, percentage shade and marginal grasses were highly correlated with axis one for both odonate sub-orders, with marginal forest being an additional correlate to this axis for Zygoptera. Reservoir circumference for Anisoptera and exposed rock for Zygoptera were the only important correlates with axis two in both ordinations. Axes three and four were not important. A summary of weightings attributed to the first two axes of ordinations for Anisoptera and Zygoptera showed that species-environment correlations using CANOCO were strong. The respective eigenvalues, cumulative species variances and Monte-Carlo tests for CCA are given in Table 4.7b.

With a cumulative percentage variance for species data and for species-environment relations of 89%, it can be inferred therefore that measured site variables were probably responsible for the main variation in species patterns for Anisoptera. A Monte Carlo permutation test of probability further strengthened this inference as the first axis (Ax1: F= 5.98; P< 0.005) and all four axes (global: F= 3.140; P< 0.005) were highly significant. A cumulative species variance for species data and for species-environment relation of 39.9% for Zygoptera probably indicates a very weak inferences that measured site variables in this case accounted for the main variation in species assemblage distribution patterns. Although a Monte Carlo permutation test of probability showed that the first axis (Ax1 :F= 1.99; P< 0.01) was significant, the overall test using all four ordination axes (global: F= 1.75; P< 0.4) was not significant. This indicates that the main variation in Zygoptera species assemblage distribution patterns could have been accounted for largely by chance or other behavioural factors not included in the present study.

Table 4.7a Intra-set correlations between each of the site variables and Canonical Correspondence Analysis axes 1 and 2 for adult Anisoptera and Zygoptera species and site variables sampled over two years across five elevations.

Odonata Variables[a]	Anisoptera CCA axis1	CCA axis 2	Zygoptera CCA axis 1	CCA axis 2
Eigenvalues	0.358	0.319	0.318	-0.127
Mfor	-0.3923	0.1912	0.5049	0.2924
Fsv	-0.279	0.3370	0.2001	0.0900
Mgra	0.6625	0.1082	-0.5586	0.2150
Erock	0.1777	-0.0413	-0.0947	0.5153
Marsh	-0.2967	-0.1065	0.0274	0.2826
%Sh	-0.5394	-0.3895	0.5454	-0.2373
Wd	0.1248	-0.1075	0.3524	0.0642
Tur	-0.2375	-0.0261	-0.5051	-0.0390
pH	0.5495	0.2382	-0.7604	-0.0177
At	-0.1793	-0.0333	0.0526	-0.0476
Mhsr	0.1714	0.0286	0.0490	-0.1449
Flow	0.0776	0.1496	0.2145	-0.2579
Elev (m)	0.7523	-0.3495	-0.8522	0.0251
Pcir (m)	-0.2418	-0.3889	-0.29990	0.0141

SB (Low) = (100 m), KL (Mid-low) = (450 m), BG (Mid) = (790 m), CE (Mid-high) = Cedara (1050 m) and GH (High) = (1350 m). [a]Variable abbreviations as in Methods.

Table 4.7b Summary of weightings of the first two axes of CA and CCA for both Anisoptera and Zygoptera adults sampled during the study in terms of variances accounted for by the two axes. Monte Carlo probability tests of significance are given for the first canonical axis (AX1) and all four axes. *P<0.05; **P<0.01.

Axes Weightings	Anisoptera					Zygoptera				
	CA		CCA		All 4 axes	CA		CCA		All 4 axes
AXES	AX1	AX2	AX1	AX2		AX1	AX2	AX1	AX2	
Eigenvalues	0.457	0.343	0.358	0.319		0.352	0.186	0.318	0.127	
SP-ENC[1]			0.949	0.905				0.954	0.897	
CPVS[2]	28.9	50.6	22.7	42.9		31.7	48.3	28.5	39.9	
CPVS-EN[3]			27.5	52.1				39.9	55.8	
F-Ratio			5.989		3.140			1.992		1.759
P-value			0.005**		0.005**			0.01*		0.4 ns

[1]:Species-environment correlations; [2] Cumulative species variance of species data; [3] Cumulative species variance of species-environment relationship

4.6 Discussion

4.6.1 General changes in adults, tenerals and larvae of dragonflies at sampling sites in two years

Seasonal rhythms with dormant (over-wintering) periods during winter/summer are an integral part of the life history of temperate dragonflies (Corbet 1999). A similar trend was observed in this study, larvae being the only developmental stage sampled in winter.

Sufficient free water as a result of high rainfall from September to May in addition to encouraging vegetation growth at sites, can also influence richness and diversity in dragonfly adults and larvae (Weir 1974, Happold 1968, Corbet 1999).

High ambient (and consequently water temperatures) recorded during the study especially during December to March influenced dispersal by providing sufficient warmth for

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maiden flights in tenerals (May 1976, 1978, McGeoch and Samways 1991). These conditions also influenced moulting from one instar to the next in larvae and egg development in most species (Masseau and Pilon 1982, Pritchard 1982).

Winter periods (June and July) were characterised by low temperatures low vegetation cover and low rainfall, and no adult and/or tenerals occurred at any elevation during this period of the year except at Mid (BG) elevation where adults of three species, *Ceriagrion glabrum*, *Lestes plagiatus* and *Crocothemis erythraea* were recorded in early winter (Suh and Samways (2001).

Larvae of sub-tropical dragonflies as observed in the present study occurred (at various stadia) throughout the year at all elevations but varied in diversity, richness and abundance. This was also the case for temperate regions where the larval stage is the most common over-wintering stage in Odonata (Norling 1984a, Corbet 1957d, 1999).

Most species sampled in this study showed a high frequency of mating and oviposition, especially the Zygoptera species. Some species e.g. *I. senegalensis*, *L. plagiatus*, *C. erythraea*, and *T. stictica* indicated a tendency towards one or more generations per year. This may be the situation where the larval population is provided for by the synchronised return of adult residents, and oviposition occurring early enough to allow occasionally for one or more generations in a year (Corbet 1999). Other species may also have followed the same trend or taken more than a year to complete their life cycles.

4.6.2 Seasonal patterns and species peak occurrences

The present study showed a general overlap of cohorts of larvae. Nevertheless, there were some peaks in adult emergence. Dragonfly species peak occurrences during some months, (using adult flight periods) revealed three distinct seasonal categories of species at all five elevations: 1) Spring peak (September–November), 2) Summer peak (early: December, middle: January/February and late: March), and 3) Autumn peak (April-May)

Spring species probably over-wintered between June and August as final-instar larvae, to emerge when temperatures rise from September. Summer species on the other hand may have spent the winter as intermediate stadia, resuming growth to subsequent higher-instar larvae as favourable climatic conditions and food become available from September.

Autumn species perhaps over-wintered as eggs e.g. members of the family Lestidae (Corbet 1999, Norling 1984), or as early-instar larvae. There was the possibility that most species belonging to the Anisoptera were elevation-tolerant and univoltine, being sub-tropical, this meant that there was prolonged emergence. In addition to being elevation-tolerant, most Zygoptera were multivoltine.

However, it is important to note here that there was no direct correlation between species peak occurrence and number of generations in a year as species peaking at the same period of the year could possibly belong to different age cohorts. Therefore, a detailed

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autecological study of individual species over an appreciable length of time is necessary to accurately determine voltinism in these dragonfly species.

4.6.3 Possible reasons for phenological changes at elevations

Climatic changes associated with seasons act locally and their effects will be most apparent on the level of populations and meta-populations (McCarty 2001). Only six species (*A. imperator, C. erythraea, O. julia, P. flavescens, N. farinosa* and *S. fonscolombii*) showed irregular patterns in peak seasonal occurrence during the study. They appeared to have spring peaks in Mid (BG) to Mid-low (KL) elevations, but early summer peaks at High (GH), Mid-high (CE) and Low (SB) elevations.

Many factors may have accounted for these phenological variations e.g. 1) mean annual precipitation affects the long-term quality and quantity of water available (Dent et al. 1989, Finch 2003, Pinhey 1978), and, rainfall seasonality in KwaZulu-Natal is dominated by mid-summer rains, 2) as there are temperature irregularities usually attributed to topographical variation (Schultze 1997) in KwaZulu-Natal, this usually results in warm coastal climate with high precipitation levels versus the cooler climates in higher elevations; or 3) simple chance migrations can be important in causing variation. Some regional, local and behavioural processes may also have been important and will be further explored in the spatial component of the study. These aspects clearly bring out the fact that dragonfly assemblage distribution can be useful in determining effects of climate change especially when used alongside well studied insect groups like butterflies (Parmesan 1996, 2001).

4.6.4 Aspects of dragonfly species adaptations in the sub-tropics

The centre of biogeographical distribution of a dragonfly species is very important in determining the number of generations the species can go through in a year (Corbet 1999); hence species in the tropics and temperate eco-regions tend to have life cycles that reflect this. Most dragonflies colonising the temperate zone have evolved a life cycle where winter is spent in the larval stage.

Usually a wide spectrum of instars is resistant to cold (e.g. Paulson and Jenner 1972, Norling 1984b, c). It is possible that the first step in the colonisation of the temperate zone on many occasions has been to evolve a mechanism for regulation wherein the larval stage coincides with the adverse season. According to Corbet (1957a,d; 1954; 1964; Norling, 1984a), two important ecological demands are imposed upon aquatic insects like dragonflies in temperate climates: 1) the need for all members of a population to pass the winter in a stage resistant to cold, and 2) the need for the adult, reproductive stage to be restricted to the warm season. Also, there is the subsidiary need for the adult stage to be restricted to a certain period in the warm season in order that competition with other species inhabiting the same body of water may be reduced. All these demands involve the process of synchronisation or the reduction of temporal variation at certain stages of development. Larval photoperiodic responses, interacting with temperature, also

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provide the framework for seasonal regulation in dragonflies (Norling 1984b, Srivastava and Suri Babu 1994; Suri Babu and Srivastava 1990).

Though this work was carried out in a sub-tropical region very close to the tropical centre of species distribution, dragonfly species temporal trends reflected some aspects of synchronisation as with their temperate counterparts. Both the temperate and sub-tropical regions are characterised by four seasons with cold or cool winters.

In the tropical and temperate species, there are changes in the relative duration of larval and adult stages, with the larval lifespan being very short in the tropics where growth is usually rapid and the adult life often fairly long, bridging the dry season (Happold 1968, Gambles 1960; 1963, Corbet 1957b; 1957c; 1960; 1999, Hassan 1981). This is perhaps because of a) the absence of appropriate fluctuations in environmental conditions (especially temperature) leading to unsynchronised emergence, and b) the fact that long-lived dispersal stages are probably a prerequisite for species which inhabit temporary pools in the tropics.

The present study showed that most odonate species sampled were on the wing for about nine to 10 months of the year from September to May/June, and showed marked monthly variations in richness and abundance during this period. This phenomenon is characteristic of sub-tropical species, showing very close similarity to their tropical counterparts in duration of adult flight periods where these species have been shown to be on the wing throughout the year (Parr 1984). Odonata fauna of the tropics and sub-tropics provide possible models from which most temperate species life-histories have evolved (Corbet 1960, Danks 1978), with sub-tropical odonates possibly showing the most evolutionarily advanced adaptation of the three eco-regions.

Species that regularly move between habitats may need to adjust to climate changes that are occurring at different rates in different areas, such as between high, medium and low elevations (Inouye et al. 2000) and this has been illustrated in the present study. Overall, the subtropical species studied here are characterised by wide elevational tolerance and long flight period with overlapping generations.

4.6.5 Implications of species populations dynamics at elevations

The Lestidae, Libellulidae and Gomphidae in this part of Africa at least have mostly moderate-climate species, while some of the Coenagrionidae and Aeshnidae are tolerant of a wide range of all climatic conditions (Samways 1989a). The Libellulidae were well represented at all the elevations studied here. Overall, odonate species richness ranged from 24 to 27 species between 301 and 1350 m a.s.l. However, below this (<300 m (SB)), richness increased to 31 species. Factors that may account for the high numbers of species at Low (SB) elevations include high primary productivity (Connell and Orias 1964), decreasingly harsh, variable and unpredictable environments (Sanders 1968, MacArthur 1975, Hebert 1980, Thiery 1982) and increased resource diversity (Gilbert 1984) at lower elevations. Other processes (competition, predation and evolutionary time) may have also influenced species richness. Also, besides the advantages of a warm

climate promoting larval development, the Low (SB) elevation site had a wide range of habitat types. Additionally, there are no mountain chains that might otherwise prevent either temporary or permanent movement south from the species-rich northern areas (Pinhey 1951; 1978; 1984a; 1985), thus maximising regional recruitment.

Elevation may therefore be an important factor controlling odonate distribution (Samways 1989b, Samways 1992). However the influence of elevation on distribution patterns is highly dependent on latitude (Corbet 1999, Finch 2003 MacDonald 2003, Koleff et al. 2003). This is illustrated by species which are found at progressively lower elevations farther south. For instance, the intolerance of low temperatures by tropical species (e.g. *Tetrathemis polleni*) causes them to contract their northern range into a narrow lowland strip, extending down the eastern seaboard of southern Africa (Pinhey 1978). In the present study, possible reasons for differential responses of larvae, tenerals and adults to increasing elevation may be that tenerals have limited spatial dispersal abilities at least compared to mature adults. Larvae are more restricted and habitat-specific, being entirely aquatic.

4.6.6 Odonate species distributions and endemism in KwaZulu-Natal

In this study, 46 species making up 39% of the total dragonfly fauna in KwaZulu-Natal and 28% of the South African odonate fauna (Samways 1999) were sampled. Fourteen species (30% of all species sampled in this study) occurred at all elevations while 15 species (32%) occurred at two or more of all five elevation. Seventeen species (36%) occurred only at particular elevations, with Stainbank Nature Reserve SB (Low) having the most elevation-restricted species. However, many species recorded here at particular elevations are not necessarily elevation-dependent, being rather a sampling effect due to suitable habitat at a particular elevation.

Overall, only three (6%) of species sampled were national endemics, accounting for just 10% of all South African odonate endemics. *Pseudagrion citricola* and *Africallagma saphirinum* occurred only at the High (GH) elevation, while and *Agriocnemis falcifera* was throughout all elevations, suggesting that regional endemism does not necessarily equate to elevational intolerance. Otherwise, most species sampled were widespread, being common African species that are either rare or common in South Africa (Samways 2002). Although more widespread and elevation-tolerant species ($\underline{S}$=43) than national endemics ($\underline{S}$=3) were sampled in the study, management recommendations should be designed to include these endemics as far as possible. This is baseline information against which to compare future global climate change scenarios.

4.6.7 Response of species developmental stages to local and regional variables

This study illustrated that site (habitat) variables on both a local and a regional scale were important in explaining species assemblage variation and distribution. This macroecological approach (Blackburn and Gaston 1996) has been illustrated in sub-tropical Africa by Balinsky (1967), Pinhey (1978), Samways et al. (1996), Kinvig and Samways (2000), and in the temperate regions by Malmqvist and Hoffsten (2000),

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Sandin (2003), Schultz et al. (2003). The effects of thermal conditions resulting from climate, alongside elevation, seemed to be important to odonate development, assemblage variations and distribution. Local factors e.g. vegetation (of varying structure and composition) was also an important habitat component (Clark 1992, Samways and Steytler 1996, Steytler and Samways 1995, Osborn and Samways 1996, McGeoch and Samways 1991, Suh and Samways 2001). Water depth was an important variable for larval stages of species in this geographical area (Samways et al. 1996). This illustrates that local as well as regional factors accounted largely for the variation in species developmental stages. Correspondence Analyses (CA) reflected similar trends in sub-sites/species distributions obtained using cluster analyses for adult species. Most adult species responded to sub-sites reflecting pH, open sunny versus shady, waterfall (flow) versus still water conditions at reservoirs, with *Z. natalensis* and *Paragomphus cognatus* being associated with Mid (BG), Mid-low (KL) elevations characterised by a waterfall and cascading conditions, while *Notiothemis jonesi* was found only at the shady lower elevation gradient of Mid-low (KL). However, the other sites did not have the features that attract these species. Typical Low (SB) elevation species like *B. leucosticta, H. albipunctum, C. flavifrons* and *T. polleni* were associated with sunny parts of the reservoir at this site. The rest of the Anisoptera species preferred sunny conditions, and are elevation-tolerant.

Most Zygoptera species were strongly elevation dependent, and showed more association to this gradient than did Anisoptera species. *A. saphirinum, A. elongatum, P. citricola, L. tridens* and *Azuragrion nigridosum* were highly elevation-sensitive species, with the first two species being endemics. The apparent restriction being rather a sampling effect. Elevation- tolerant species were *L. plagiatus, I. senegalensis, C. glabrum, A. falcifera, Pseudagrion massaicum, P. salisburyense* and *P. kersteni*.

Zygoptera species mostly showed a higher degree of habitat specificity than the Anisopteran species. This may be as a result of their lower dispersal abilities and because they are generally more habitat specific (Brink 1955, Samways 1989b, Corbet 1999). *Allocnemis leucosticta*, for example, was restricted only to SS4 and 5 at the Botanical Gardens.

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4.7 Conclusions

The sub-tropical odonate species studied here are similar to their tropical counterparts in that they have long flight periods with overlapping generations. Yet they also showed temperate characteristics by over-wintering principally as larvae. This was the case across all elevations, from 100 m to 1350 m a.s.l.

Most species were relatively abundant, and may be described as widespread, opportunistic habitat generalists. This is not surprising in some respects, because natural ponds and lakes are very scarce in this part of South Africa, and the species that prefer this habitat are, by default, likely to have this life-style. The national endemics: *Pseudagrion citricola* and *Africallagma saphirinum* only occurred at high elevations, while *Agriocnemis falcifera* was throughout all elevations, suggesting regional endemism does not necessarily equate to elevational intolerance.

As most species here appeared to be ready colonizers, and habitat and elevation-tolerant, the construction of farm reservoirs has a major population-filling effect by increasing 'area of occupancy', thereby improving odonate metapopulation size, and increasing chances of survival during times of adverse climatic conditions. Both regional processes (e.g. elevation and insolation) and local factors (habitat characteristics), accounted for dragonfly species assemblage variations at sites.

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Appendix to Chapter Four

A) Months when peak occurrences of adult, tenerals (T), larvae (L), mating/ oviposition (+, *) were made for species in 2001 and 2002 at Low (SB) elevation. [a]See Table 1a/b for species names.

Anisoptera: += 1-5 observations of mating and/or oviposition /species/month *=> 5 observations of mating and/or oviposition/species/month

Odonata stages / Species	Adult month peaks 2001	Adult month peaks 2002	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
								2001											2002							
Cery	Dec	Feb			L*	*	*			T		L					L	*	*			T				TL
Ojul	Dec	Jan				+	L			T		L			T						+					
Acis	Dec	-				+				T																
Nfar	Dec	Jan				*	*				T				T						+					
Plup	Feb	Dec	T																							T
Chfl	Feb	Jan							T															T		
Aimp	Feb	Feb		+	*	*	L			L						*	*	*	L							
Pfla	Mar	Jan																								
Uass	Nov	-																								
Plum	Nov	Dec																								
Rshy	Nov	-																								
Tart	Dec	Jan			*	*																+	+	+		
Tbas	Mar	Nov			L						L						L									
Halb	Dec	-																								

Zygoptera: += 1-10 observations of mating and/or oviposition/species/month *= >10 observations of mating and/or oviposition/species/month

Odonata / Species	Adult month peaks 2001	Adult month peaks 2002	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
								2001											2002							
Isen	Mar/Nov	Feb/Oct	+	*	*	L							*	LT	*	T+	L		*	+					T	L
Ltri	Apr/Dec	Mar/Nov			T		T*				*		*	T	+	+	T							+	+	T
Pmas	Feb/Nov	Feb/Nov	T	+			+							LT	T	+			L							L
Psal	Dec	Dec			L			+						L						+	L					L
Aglm	Dec	Nov				T	+							L		+	*	T								L
Afal	Nov	Nov	+	*									T	L	+	*									T	L
Cglm	Apr/Nov	May/Nov	*	*	TL					+	*	T*	L		+	*	T*	L							T*	*
Pker	Dec	Dec				+								T							*					T
Phag	Dec	Jan			*									T	T						+					

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B) Months when peak occurrences of adult, teneral (T), larvae (L) and mating/oviposition (+, *) were made by species in 2001 and 2002 at Mid-low (KL) elevation. See Table 1a/b for species names

Anisoptera: += 1-5 observations of mating and/or oviposition /species/month *= > 5 observations of mating and/or ovipositionspecies/month

Odonata Species	Adult month peaks 2001	Adult month peaks 2002	2001 J	F	M	A	M	J	J	A	S	O	N	D	2002 J	F	M	A	M	J	J	A	S	O	N	D
Aimp	Nov	Nov	+	*	*		L						L		*	+			TL						L	
Cery	Nov	Nov	+	L*							T	L			*	*	*		L						L	
Ojul	Nov	Nov			+	+	L+				T					*			L						T	
Tsti	Dec	Dec				L	*					LT				*			L							LT
Znat	-	-																								
Tdor	Nov	Nov				+			L		T												*		T	L
Nfar	Nov	Nov	*								T						+	+							T	
Pfla	Dec	Dec				+	+																			
Uass	-	-																								
Tbas	-	-																								
Tart	Nov	Nov	*	*															*							
Njon	-	-																								

Zygoptera: += 1-10 observations of mating and/or oviposition /species/month *= >10 observations of mating and/or oviposition /species/month

Odonata Species	Adult month peaks 2001	Adult month peaks 2002	2001 J	F	M	A	M	J	J	A	S	O	N	D	2002 J	F	M	A	M	J	J	A	S	O	N	D
Isen	Apr	Apr/Nov			TL						*	*	L		*	*	T							+	*	L
Lplg	Apr/Nov	Apr/Nov	*	*	T	L					*	*	L		+	L+		T						*	*	L
Pker	Nov	-	+						L																	L
Phag	Mar	Mar			T					*	*						T							*		
Aglm	Nov	Nov	*	+							T	L							*						T	L
Afal	Mar	Apr			T				+	+		L												*	*	L
Cglm	Apr/Nov	Apr/Nov	+	*	*	TL					*	T*	L		*	*	L							*	L*	T

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C) Months when peak occurrences of adult, teneral (T), larvae (L) and mating/oviposition (+, *) were made by species in 2001 and 2002 at Mid (BG) elevation. [a]See Table 1a/b for species names.

Anisoptera: += 1-5 observations of mating and/or oviposition /species/month *= > 5 observations of mating and/or oviposition/species/month

Odonata Species	Adult month peaks 2001	Adult month peaks 2002	2001												2002											
			J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Aimp	Nov	Dec	*	*	+		L					L						L	L*	+						L
Cery	Nov	Nov		+	*	L							TL		*		*	L								TL
Ojul	Nov	Nov	+	*	L								T			+	+	TL								T
Tsti	Nov	Nov	+	*	*	L					TL				+	+	L*									TL
Znat	Nov	Nov																								
Tdor	Nov	Nov		+	*	+				TL					*	*	+								TL	
Nfar	Nov	Nov	+	*	*					T									*							TL
Pfla	Nov	Nov	+	+	+													+	+							
Aspe	Oct	-																								
Tbas	Oct	-																								
Tart	Dec	Dec	+	*	*														*	+						
Sfon	Nov	Nov																								
Pcog	Dec	Dec																								

Zygoptera: += 1-10 observations of mating and/or oviposition/species/month *= >10 observations of mating and/or oviposition/species/month

Odonata life stages Species	Monthly adult peaks 2001	Monthly adult peaks 2002	2001												2002											
			J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Isen	Mar/Nov	Mar/Nov	+	*	*		L			*			L+T		*	+	*		L						T+L*	
Lplg	Mar/Nov	Mar/Nov	+	*	T+		L			*			L*	T	*		T*		L					+	L*	
Pmas	Mar	Feb			T		L				L		*				T		L*						L	
Psal	Nov	Oct	*		+									T	*		+						L			
Aglm	May/Nov	May	+		*		T				T+		*		*										+	*
Afal	Apr	Apr				T	L			L	*	*														
Cglm	May/Nov	Apr/Nov	*		+		L			T	L	*	*		*	*		+		L				*	*	T*	
Pker	Nov	Nov	+												+									L	*	*
Phag	Mar	Mar			T						*	+					T								+	*

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D) Months when peak occurrences of adult, teneral (T), larvae (L) and mating/ oviposition (+, *) were made by species in 2001 and 2002 at Mid-high (CE) elevation. See Table 1a/b for species names.

Anisoptera: += 1-5 observations of mating and/or oviposition/species/month *= > 5 observations of mating and/or oviposition species/month

Odonata	Adult month peaks	Adult month peaks	2001												2002											
Species	2001	2002	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Aimp	Dec	Jan	+	+	*	*			L									+	*	*		L				
Cery	Mar/Nov	Jan/Nov	*	*	+	L			L			+	*	T	*	*	L	*	+			L	T			
Ocaf	Nov	Nov			*				L			T					L						L	T		
Tsti	Mar/Nov	Apr/Nov		*	+	LT					*	*			+	+	*	LT				L		*		*
Acis		Apr								*	+															
Tdor	Nov	Dec	+	+	T	L		L											L	*			L		T
Nfar	Nov	Nov	+	+						T						*	*								T
Pfla	Dec	Dec				+	+																		
Tbas	Jan	Feb				+			L													+		L		
Tart	Feb	Dec			*	*	+													+	*	+				

Zygoptera: + 1-10 observations of mating and/or oviposition /species/month * >10 observations of mating and/or oviposition /species/month

Odonata life stages	Monthly adult peaks	Monthly adult peaks	2001												2002											
Species	2001	2002	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
Isen	Apr/Dec	Apr/Nov			T*	L*					*	+			+	*	*	L	*	+						T
Lplg	Apr	Nov	+	+		TL						*	*	T	+	*	T+L					L				T
Pmas	Jan/Nov	Nov	+	*	+	+	*			L			T		+	*	*	L				L				T
Psal	Jan	Feb				L	*	+												*	+			L		
Aglm	Apr/Nov	Apr/Nov		*	*	LT					+	*	LT					+	*	L			*	*	T	
Afal	Apr	Apr				L					*	*	L					L					+	*	L*	
Cglm	Apr/Nov	May/Dec	+	*	L*							*	T*				L	*	+			L			*	T
Pker	Mar	Mar			LT						*	*	+				T							*	L	+

E) Months when peak occurrences of adults, teneral (T) , larvae (L) and mating/ oviposition (+, *) were made by species in 2001 and 2002 at High (GH) elevation. See Table 1a/b for species names.

Anisoptera: += 1-5 observations of mating and/or oviposition/species/month *= > 5 observations of mating and/or oviposition/species/month

Odonata Species	Adult month peaks 2001	Adult month peaks 2002	2001 J	F	M	A	M	J	J	A	S	O	N	D	2002 J	F	M	A	M	J	J	A	S	O	N	D
Aimp	Nov	Dec	+	*	+				L									*	*		L			+		
Cery	Apr	Apr		+	+	L					*	*							L			*	*	+	
Ocaf	Nov	Dec		L	+	*				T					L				+		*				T	
Tsti	Nov	Mar		*	+				L		T							T					L	+	*	
Acis	Dec	Nov				*	*		L						+	*	*					L				
Tdor	Nov	Nov	+	*	+				L			T			+	+	*					L				T
Nfar	Nov	Nov	*		*	T+									*		*	*								T
Pfla	Mar	Mar								*	*														+	+
Uass	Oct	Feb	*	*	+													*	+							
Tbas	Mar	Mar						L	+	*	+												L	*	+	
Tart	Dec	Dec				*	*													+	+					
Sfon	Nov	Dec	*	*	+													*	*	+						

Zygoptera: += 1-10 observations of mating and/or oviposition/species/month *= >10 observations of mating and/or oviposition/species/month

Odonata Species	Adult month peaks 2001	Adult month peaks 2002	2001 J	F	M	A	M	J	J	A	S	O	N	D	2002 J	F	M	A	M	J	J	A	S	O	N	D
Isen	Mar	Jan	+		T	L					L	*	*	T	T	+	*	L	*	+			L			T
Lplg	Mar	Dec									L	*	*	T				*	*				L			T
Pmas	Feb	Feb		+				*	*			L							*	+				L		
Psal	Mar	Apr									L+	*												L	*	+
Aglm	Apr	Nov		*		T					*	L+			T	+	*					L				
Afal	Jan	Jan				*	*	+					T		*											T

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Chapter Five Elevational tolerance of dragonfly larvae (Odonata) in an African El Niño prone area.

5.1 Abstract

Any changes in landscape will, in effect, impact on both the aquatic larvae and aerial stages of adult odonates. Previous chapters focussed on the adult, which is the final product of dragonfly development but little is known of aspects of artificial water bodies that encourage odonate larvae in South Africa. In response, I investigated here, the spatial patterns in species richness and abundance of odonate larvae at a series of reservoirs at different elevations, to establish which spatial factors determine species distributions at these reservoirs. Larvae of 18 dragonfly species in four families (Coenagrionidae, Lestidae, Aeshnidae and Libellulidae) were sampled in small reservoirs across a 1350 m elevation in KwaZulu-Natal in 2001 and 2002. Most species occurred throughout all elevations, indicating that this subtropical odonate assemblage as a whole is remarkably tolerant of elevational changes. Anisoptera larval richness and abundance increased significantly with increasing elevation. There was no change in Zygoptera richness. However, Zygoptera abundance decreased significantly with increasing elevation. Species-site-variable triplots for Anisoptera and Zygoptera larvae, clumped species at the centre of ordination plots, indicating that no measured site variable on an individual basis clearly accounted for larval species assemblage distribution patterns. Nevertheless, canonical axes and their respective intra-set correlation coefficients showed that some measured site variables e.g. floating/submerged vegetation, turbidity, pH, water temperature (resulting from sunny or shade habitat conditions), marginal grasses, water depth and elevation appeared to strongly explain the main variation in species assemblage composition/distribution in a broadly similar manner for both sub-orders. Generally, the reservoirs recruited species from the regional pool, irrespective of the elevation of the pool. These species were all geographically widespread species that took advantage of the presence of these man-made reservoirs, and included only one national endemic. Although these artificial water bodies are not increasing the 'extent of species occurrence', they play a major role in increasing 'area of occupancy'. Furthermore, it appears that these species are remarkably habitat-tolerant and elevationally widespread through many millennia of impact and natural selection through El Niño Southern Oscillation (ENSO) events.

5.2 Introduction

Reservoirs provide an increase in the area of occupancy for aquatic invertebrates, thereby increasing regional invertebrate biomass, which inevitably, leads to increases in water bird and trout populations (Ward 1984, McCafferty 1984).

Aquatic environments often contain large assemblages of co-existing resident Odonata species, as well as transient species (Corbet, 1999, Brownett 1994, Sternberg 1994). Dragonfly larvae are very conspicuous invertebrate components of the fauna of many freshwater habitats (Samways 1989a, Johnson and Crowley 1980, Wissinger 1988, Watson 1982, Hawking and New 1999, Schriddle and Suhling 1994). In small, still-water habitats, they are found mostly in the littoral zone (Benke and Benke 1975, Johnson and Crowley 1980, Crowley and Johnson 1982), and play an important role in pond food webs as predators of other invertebrates (Benke 1976, 1978, Thorp and Cothran 1984, Samways et al. 1996) and even some vertebrates (Caldwell, Thorp and Jervey 1980, Travis, Keen and Juliana 1985), and are prey for fish (Benke 1978, Thorp and Bergey 1981, Johnson et al. 1984, Morin 1984a; b, Pierce et al. 1985).

Microhabitat preferences differ from one species to another, and even between larval instars of a species (Crowley and Johnson 1982). The larvae may be cryptic or nocturnal and yet nevertheless suffer high natural mortality, so that the numbers of larvae in a given cohort decrease substantially as development proceeds. Also, as dragonfly larvae are predators, their numbers may be low (Corbet 1962, 1980, Benke and Benke 1975, Benke 1976, Macan 1977). There are few quantitative data on their population dynamics. Some studies describe patterns of larval abundance and survivorship for a single species (Corbet 1957, Lawton 1970, Ubukata 1981), and a few provide information on a number of co-existing species in still-water habitats (Benke and Benke 1975, Carchini et al. 1992, Wissinger 1988).

In South Africa, taxonomic difficulties have been a significant challenge in dragonfly larval studies, as the larvae of many species are unknown and virtually all early-instar larvae are unidentified (Carchini et al. 1992, Samways et al. 1993). This means that it is difficult to determine the dragonfly assemblage in a habitat, let alone their numbers.

Any changes in landscape will, in effect, have a double impact on Odonata. They will affect both the aquatic larva and aerial adult. Previous chapters focused on the adult, which is the final product of dragonfly development. But little is known of aspects of artificial water bodies that encourage Odonata larvae of particular species. In Africa, there is also virtually no information on microhabitat selection and phenology, especially in relation to elevational gradients. This is particularly important on the east coast of South Africa which is subject to extreme climatic variation as a result of El Niño Southern Oscillation (ENSO) events. The aim here therefore is to:

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i)   Investigate spatial patterns of species richness and abundance of dragonfly larvae sampled within stratified sites at a series of reservoirs and elevational gradients.

ii)   Undertake a study of some of the spatial factors that determine dragonfly larval species distributions within these reservoirs.

iii)   Provide baseline information for future studies on the impact of global climatic change.

5.3 Site and methods

5.3.1. Study sites

Five reservoirs were chosen across a 1000 m-1350 m elevational gradient in KwaZulu-Natal, South Africa (see map in Fig. 4.1 of Chapter Four). Descriptions of these sites are summarised in Table 4.1 of Chapter Four, where abbreviations for these sites and their elevations are also given. They are: SB= Stainbank Nature Reserve (100 m), KL= Krantzkloof Nature Reserve (450 m), BG= Pietermaritzburg Botanical Gardens (790 m), CE= Cedara (1050 m) and GH= Goodhope Estate (1350 m).

5.3.2 Elevation and climate

Elevation is an important factor controlling odonate distribution (Samways 1989b). Although the influence of elevation on distribution patterns is highly dependent on latitude (Corbet 1999, Finch 2003, Koleff et al. 2003). The overall feature of mean annual precipitation distribution across South Africa is generally uniform, decreasing westwards from the escarpment across the interior plateau. Complex rainfall patterns are evident on the southern and eastern coastal margins as a result of irregular terrain (Schulze 1997). The highest mean annual temperature values of 21^0C are distributed along the north-eastern and to a lesser extent the northern border of South Africa. Temperature irregularities across the remainder of the country are as a result of topographical variation (Schulze 1997). KwaZulu-Natal and Lesotho are dominated by mid-summer rainfall. The effects of El Niño (also known as the southern oscillation), results from the fact that the surface air pressures from the Pacific and Indian Ocean regions are 180^0 out of phase over this eastern escarpment (Nash 2002). These effects have been associated with adverse weather patterns, particularly in the 1980s, and aggravated by anthropogenic changes (Van Heerden and Hurry (1990).

5.3.3 Vegetation

Acocks (1988) has described the veld categories in South Africa. There are many examples of where vegetation cover governs odonate species distribution (Balinsky 1967, Pinhey 1978, Samways 1994, 1999, Moore 1991, Corbet 1999).

5.4 Methods

5.4.1 Site stratification

The five reservoirs were at elevations of 100 m –1350 m and were selected à priori within a narrow latitudinal band, providing an elevational comparison without any latitudinal influence. Each reservoir circumference and area was measured using a line transect and later was stratified into six sub-sites (SS) measuring 20 m length (along a line on the reservoir edge) by 2 m width (1 m on land and 1 m into water). Data were collected on 42 sampling occasions. This was twice a month running from January 2001 to December 2002, except for the winter months of June, July and August when data were collected once. Corresponding sub-site environmental variables were also measured.

5.4.2 Sampling of larvae

The abundance of larvae was estimated at each SS. Last instar larvae were recognised as such by having well-developed wing sheaths extending to the third leg (Gardner 1960, Corbet 1999, 2002). Larvae were sampled during the warm time of the day between 11h00 and 13h00 using a dip-net of constant dimensions (41 cm diameter x 1 mm mesh sieve). Two dips per SS (12 dips/site) were done within 20 min. Each dip was followed by vigorously shoving the net back and forth in the water and among water weeds, along rushes and beside banks. The net was then removed and examined, and the larvae identified using a 9 x hand lens, counted and released back into water. Where individuals could not be identified, they were picked out with very soft, flexible forceps (to prevent damage to their fragile body structures) and placed in aerated plastic cages containing reservoir water. Usually, last-instar larvae were collected for subsequent rearing and identification.

5.4.3 Larval identification

Pinhey (1962), Carchini et al. (1992) and Samways and Wilmot (Pers comm.) were used alongside voucher specimens in the Invertebrate Conservation Research Centre (ICRC), University of Natal, for identification. Diagnostic larval features used in this exercise were abdominal shape, thoracic markings and the relative development of the dorsal abdominal spines.

5.4.4 Rearing and identification of larvae

Larvae of most species were reared relatively easily in an airy, shaded room. Trays were set up containing 2-3 cm depth of dechlorinated water (water that has been left to stand overnight). Larvae were then transferred from the collecting phials to small rearing cages made out of plastic netting (mesh size about 2-3 mm) rolled into cylinders of about 6 cm width and 15 cm height and sealed at the top with an inverted plastic petri-dish (Fig. 2). To avoid cannibalism and to ensure correct association of larvae and adults, only one larva was placed in each cage (onto the sides of which the emerging adult can climb).

The water inside the cage was artificially aerated. Food was provided principally as mosquito larvae and young tadpoles netted from a nearby pool or rain barrel. Food was

Petri-dish

Net cage

Aerator

water level
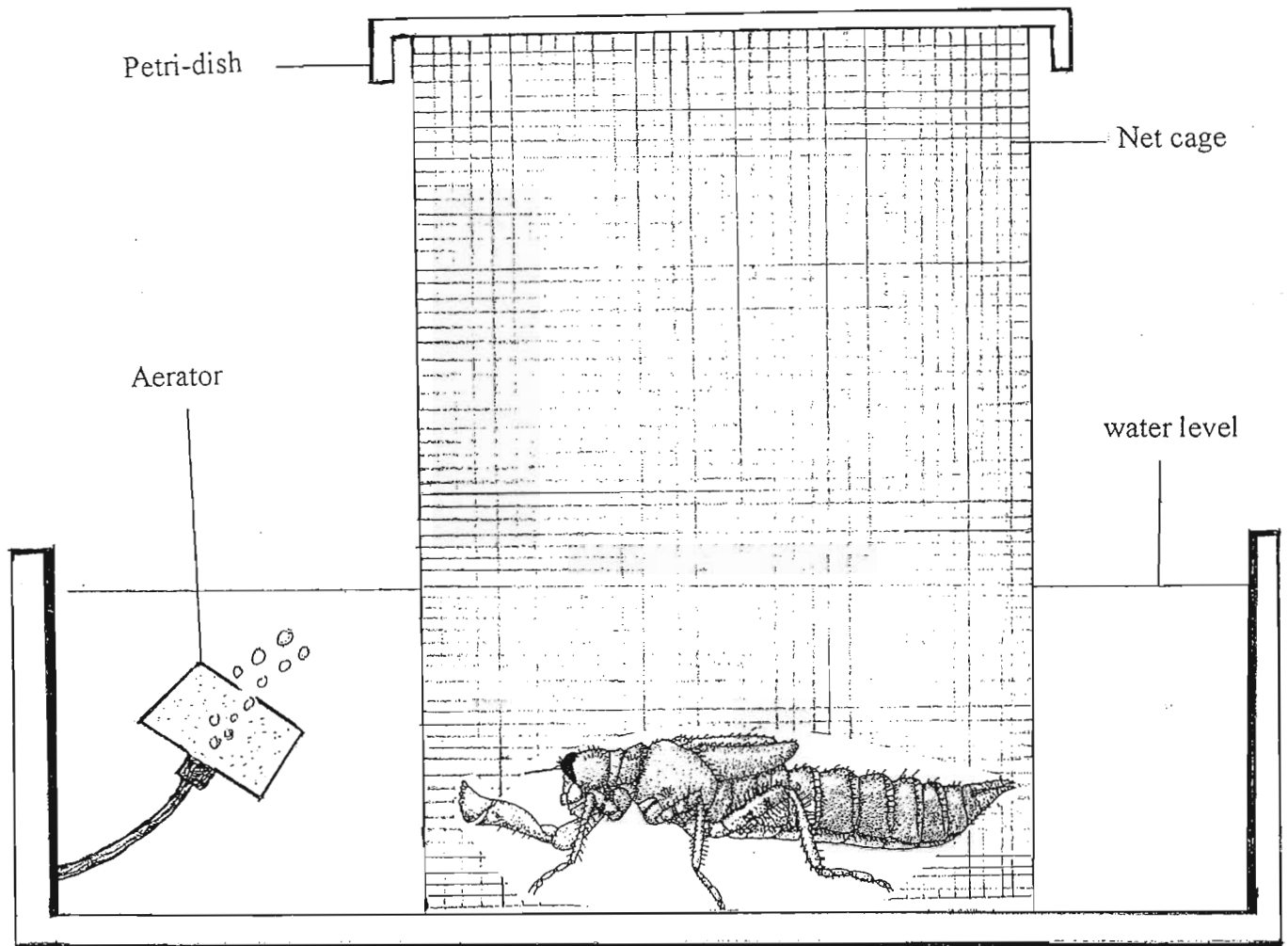
Fig 5.2 Apparatus used for rearing an odonate larva through to the adult stage.

placed inside the mesh cage by lifting the petri dish. Larvae were fed daily and uneaten or rotten food was regularly removed from the cage. After several hours, and usually during the night or early morning, the larva would leave the water and climb up the side of the cage. It usually stopped at the highest point where it emerged. The remaining exuviae were collected and retained in a phial containing 75% ethyl alcohol. After a couple of days, the adult was identified relative to the exuvium.

5.4.5 Environmental variables

Dissolved oxygen and temperature infuences the development of dragonfly larvae (Corbet 1962, 1999, Samways et al. 1996), making shallow water particularly important for them. Many Odonata also prefer water of a certain pH (Weir 1974, Osborn 1992, 1995). High turbidity may reduce visual detection of prey, and current rate may influence oxygen concentration. Vegetation serves important functions for larval Odonata (Buchwald 1992, Samways 1999, Corbet 1999), and along with substrate, provides refuge from predators. The thermal requirements of the species results in different responses to sunlight and shade (Osborn 1992).

Against this background, two one-monthly measurements of variables were made in sunny, warm conditions. Water depth was measured using a V. C 1456 meter rule. Acidity (pH) was measured using a Jenway 3405 electrochemistry analyser. Turbidity was estimated at midday as the results became less reliable near dawn or dusk because of reduced surface illumination. Percentage estimation was done visually, and ranged between 0% (totally transparent) to 100% (totally muddy conditions) aided by using a secchi disc. The degree of shading of SSs was estimated by mean percentage shade cover at midday for each SS. Water and ambient SS temperatures were measured using the Delta Trak hand thermometer at midday, two cm below water. Ambient temperature records were cross-checked with the weather bureau. Rainfall and ambient and water temperature (At/Wt) data for Stainbank (SB) and Krantzkloof (KL) Nature Reserves were compared with that collated by the Durban Airport weather station. Similar meteorological data for the Botanical Gardens (BG), Cedara (CE) and Goodhope Estate (GH), were compared with that collated by the weather bureau at Cedara Agricultural station in Cedara. Sub-sites also classified on the amount of open water and whether aquatic vegetation covered the bottom of the water body. Vegetation was therefore classified into: Submerged (Sveg), emergent/floating (EFveg) and marginal (Mgra) vegetation and was estimated using percentages of sub-sites they covered. Other environmental variables measured were percentage of marsh, Shade (% Sh) and elevation Elev (m a.s.l.)

5.4.6 Data analyses

Data were analysed in two steps. Firstly, with univariate methods using species accumulation curves, abundance relationships, using distributional models and graphical methods. Analyses of species spatial variability was done using Linear Regression and non-parametric methods. Secondly, multivariate techniques using ordination were employed.

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1) Brief description of univariate methods used

Gotelli and Colwell (2001) have suggested that for patchy distributions, individual based rarefactions curves inevitably overestimate the number of species that would have been found with less effort. They recommend species accumulation curves that take into account between-sample heterogeneity (Colwell and Coddington 1994, Ugland et al. 2003).

Relationships between abundance and the number of species having that abundance was shown graphically using plots of abundance of each species in the samples in order of its rank from the most to the least abundant for each site. This method presented a graphical and more explicit way of determining species abundance patterns at sites instead of just index numbers used in diversity and evenness measures.

The rank abundance curves and x2 geometric plots were used to obtain various information from the distribution patterns for each site and to detect the effects of disturbance or stress at the sites.

In using x2 geometric plots, Gray and Pearson (1982) have reported that in undisturbed situations, there are many rare species giving smooth curves with the mode well to the left. In disturbed situations, there are fewer species and more abundant species, so that the higher geometric abundance classes are more strongly represented, giving more irregular curves. They also suggested that it is the species in the intermediate abundance classes 3–5 that are the most sensitive to pollution induced changes and might best illustrate the differences between polluted and unpolluted sites, and therefore a way of selecting 'indicator' species objectively.

Spearman's correlation coefficients were used to measure the association between SS variables and species abundance and richness. These correlations were calculated using SPSS version 6.1

Species abundance and richness across the series of sites was measured using the software MINITAB.

2) Brief description of multivariate methods used

Ordination describes a set of techniques in which sub-sites are arranged in relation to one or more coordinate axes such that their relative positions to the axes and to each other provides maximum information about their ecological similarities. When sub-sites that are most similar or dissimilar are identified based on coordinate positions, underlying biotic and abiotic factors that might be responsible for the patterns are determined.

The computer software CANOCO (Ter Braak 1986) which combines into one algorithm correspondence analysis (CA) on species data with weighted multiple regressions on environmental data were used. This technique relates species composition to known variations in the environment. CANOCO leads to an ordination diagram in which points

represent species and sites, and vectors (arrows) represent environmental variables (Hill, 1979; Ter Braak and Simlauer 1998). Such a diagram shows the patterns of variation in species composition that can be explained best by the environmental variables and also visualises approximate 'centres' of the species distributions along each of the environmental variables (Ter Braak and Looman 1995). In this study, all dragonfly abundance and environmental variable data were long-transformed to maintain normality and to satisfy the requirements of ANOVA and multivariate analyses.

5.5   Results

5.5.1 Overall family/species trends at the different elevations

Four families (Coenagrionidae, Lestidae, Aeshnidae and Libellulidae) with 18 species (nine Anisoptera and nine Zygoptera) were sampled during the study period (Table 5.2) alongside dominant sub-site vegetation made up of mostly indigenous plants (see Table 4.3 of Chapter Four). The Coenagrionidae comprised the species: *Ischnura senegalensis, Ceriagrion glabrum, Agriocnemis falcifera, Africallagma glaucum, Pseudagrion salisburyense, P. massaicum* and *P. kersteni*. Lestidae was represented by *Lestes plagiatus* and *L. tridens*. Libellulidae species included *Crocothemis erythraea, Acisoma panorpoides, Orthetrum julia, O. caffrum, Trithemis dorsalis, T. stictica, T. arteriosa* and *Tramea basilaris. Anax imperator* was the only Aeshnidae larval species sampled. The elevational tolerance of larval odonates shows that most species, except *L. tridens,* occurred across a wide elevational band.

An estimation of total species richness across sites using sub-site-groupings showed that both sub-orders had broadly similar trends as illustrated in accumulation curves in Fig 5.3a, b. At 100 m a.s.l. (SB), *A. imperator,* followed by *C. erythraea* larvae were the most dominant Anisoptera species at 35% and 33% dominance levels respectively. Otherwise the remaining elevation sites were similar in patterns of larval species dominance, ranging for the most dominant species from 19% at 1350m a.s.l. (GH) to 29% at 450m a.s.l. (KL) (Fig. 5.4). Dominant species of the Zygoptera showed narrower trends compared to Anisoptera with dominant species ranging from 18% at 790 m a.s.l. (BG) and 1050 m a.s.l. (CE) with *C. glabrum* and *L. plagiatus* respectively to 25% at 450 m a. s. l. (KL) and 1350 m a. s. l. (GH) with *I. senegalensis* and *P. kersteni* respectively (Fig.5. 5).

Pooled data for Anisoptera during the whole sampling period (Fig. 5.6) showed that elevation ranges of High (GH) and Mid-high (CE) elevations had the highest species percentage at abundance classes four and five of about 50%, while Mid (BG) elevation showed the highest species percentage of 62% at size class five for Zygoptera (Fig. 5.7).

5.5.2 Measured site variables and elevation

Preliminary ANOVA results (Table 5.4) selected percentage shade (F= 53.52; P<0.001), floating and submerged vegetation (F= 20.43; P<0.001) marsh (F= 90.02; P<0.001), marginal forest (F= 335.39; P= 0.001, and marginal grasses (F= 15.56; P= 0.001) as showing highly significant differences across elevations.

Table 5.2 Family and species list of Odonata larvae recorded from all sites across the five elevations during the whole sampling period (January 2001 – December 2002) with species code names used in analyses.

Species	Code	Site abbreviations and Elevation (a.s.l.)				
		SB (100 m)	KL (450 m)	BG (790 m)	CE (1050 m)	GH (1350 m)
Aeshnidae						
Anax imperator Leach, 1815 [3]	Aimp	L	L	L	L	L
Libellulidae						
Acisoma panorpoides Rambur, 1842 [2]	Acis	L	-	-	L	L
Crocothemis erythraea (Brullé, 1832) [3]	Cery	L	L	L	L	L
Orthetrum caffrum (Burmeister, 1839) [3]	Ocaf	-	-	-	L	L
O. julia falsum Longfield, 1955 [3]	Ojul	L	L	L	L	-
Tramea basilaris (Beauvois, 1817) [2]	Tbas	L	L	-	L	L
Trithemis dorsalis (Rambur, 1842) [3]	Tdor	-	L	L	L	L
T. stictica (Burmeister, 1839) [1]	Tsti	-	L	L	L	L
T. arteriosa (Burmeister, 1839) [3]	Tart	-	-	-	L	L
Coenagrionidae						
Africallagma glaucum Burmeister, 1839) [3]	Aglm	L	L	L	L	L
Agriocnemis falcifera Pinhey, 1959 [4]	Afal	L	L	L	L	L
Ceriagrion glabrum (Burmeister, 1839) [3]	Cglm	L	L	L	L	-
Ischnura senegalensis (Rambur, 1842) [3]	Isen	L	L	L	L	L
Pseudagrion kersteni (Gerstäcker, 1869) [3]	Pker	L	L	L	L	L
P. massaicum Sjöstedt, 1909 [3]	Pmas	L	-	L	L	-
P. salisburyense, Ris, 1921 [3]	Psal	L	L	L	L	-
Lestidae						
Lestes plagiatus (Burmeister, 1839) [3]	Lplg	-	L	L	L	L
L. tridens McLachlan, 1895 [1]	Ltri	L	-	-	-	-

- L = larval stage sampled January 2001-December 2002. [1]Common African species whose range extends south just over the border into South Africa, but are local or rare in the country [2] African species that are widespread and/or locally common in South Africa [3]African species that are regularly seen in the right habitats. [4] Species endemic to South Africa i.e. south of the Limpopo River (Samways 2002).

a

b
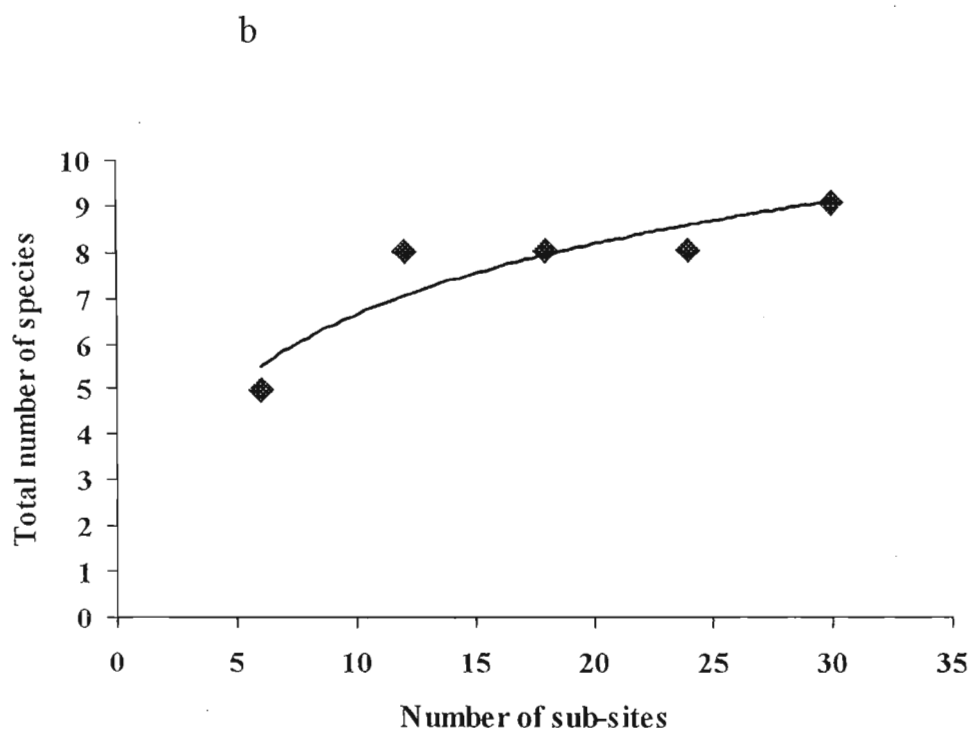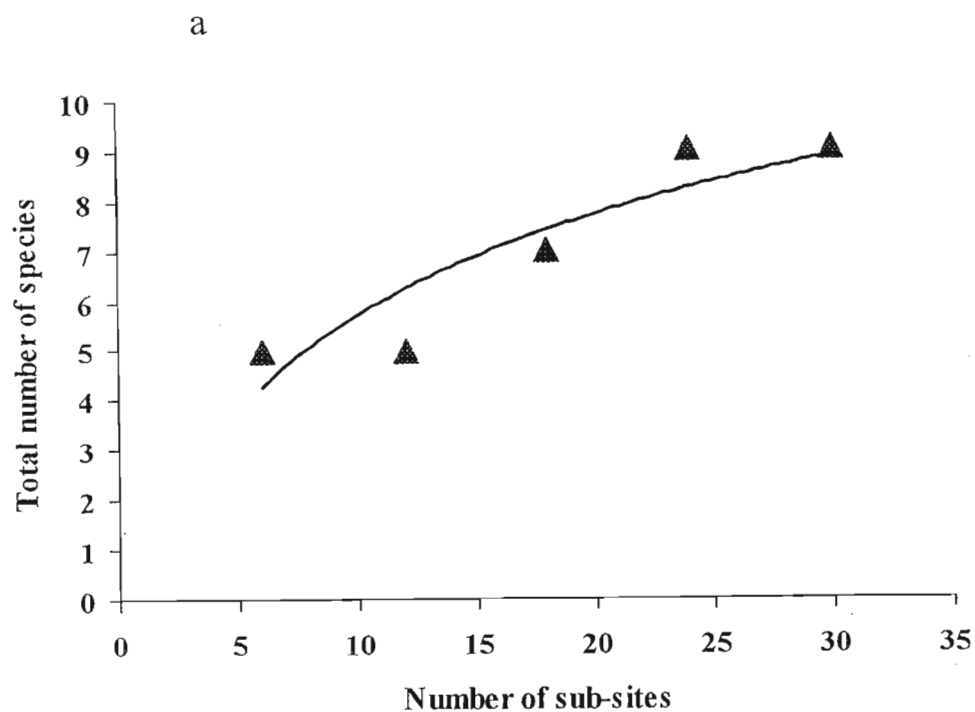
Fig. 5.3 Species accumulation curves for (a) Anisoptera and (b) Zygoptera using all 30 sub-sites.

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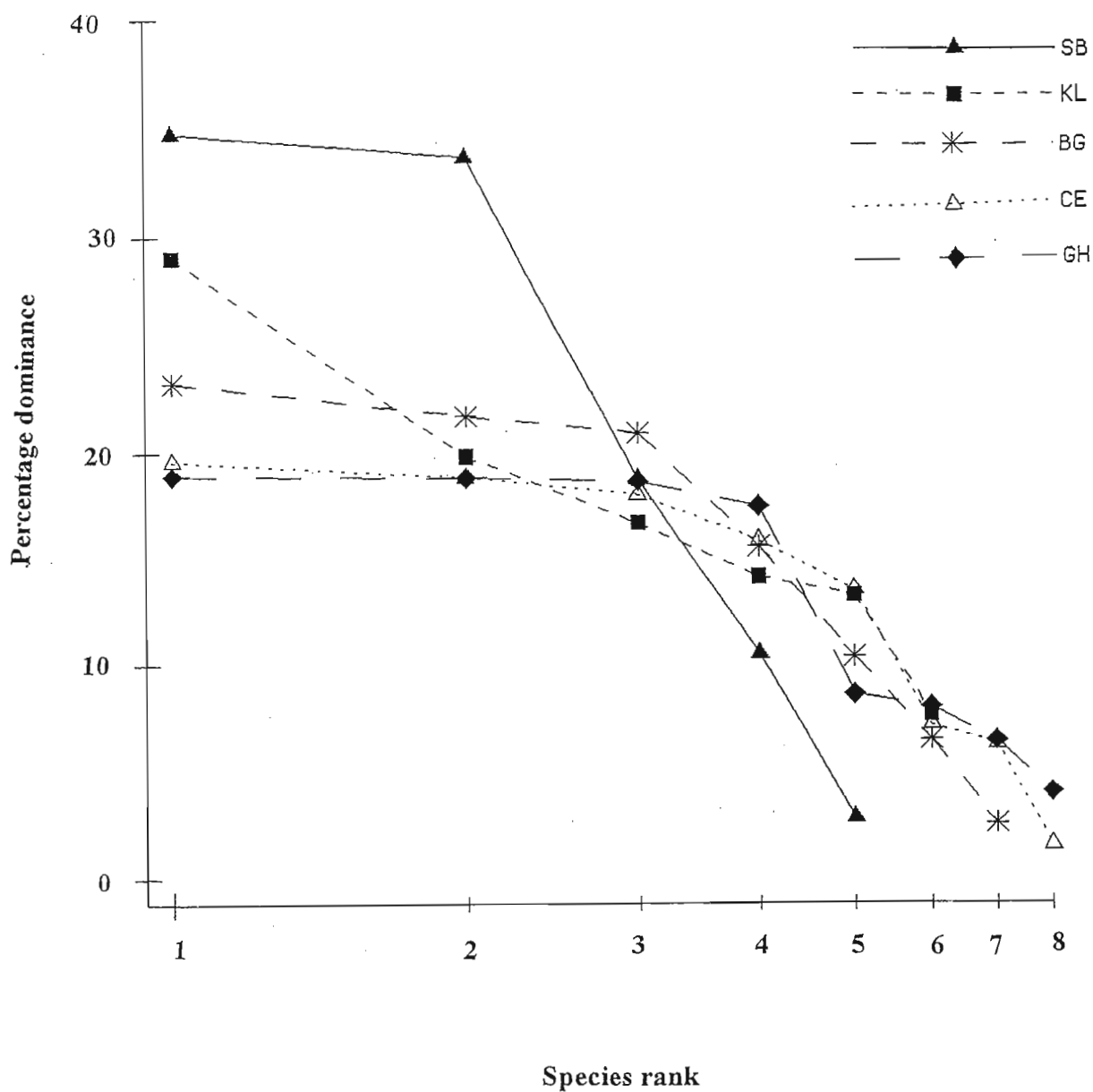
Fig. 5.4 Species rank abundance curves, using larval Anisoptera species sampled at the five elevations: SB= Stainbank Nature Reserve (100 m), KL= Krantzkloof Nature Reserve (450 m), BG= Botanical gardens (790 m), CE= Cedara (1050 m), and GH= Goodhope Estate (1350 m). Species are ranked in decreasing order of their importance in terms of abundance from the most common to rarest.
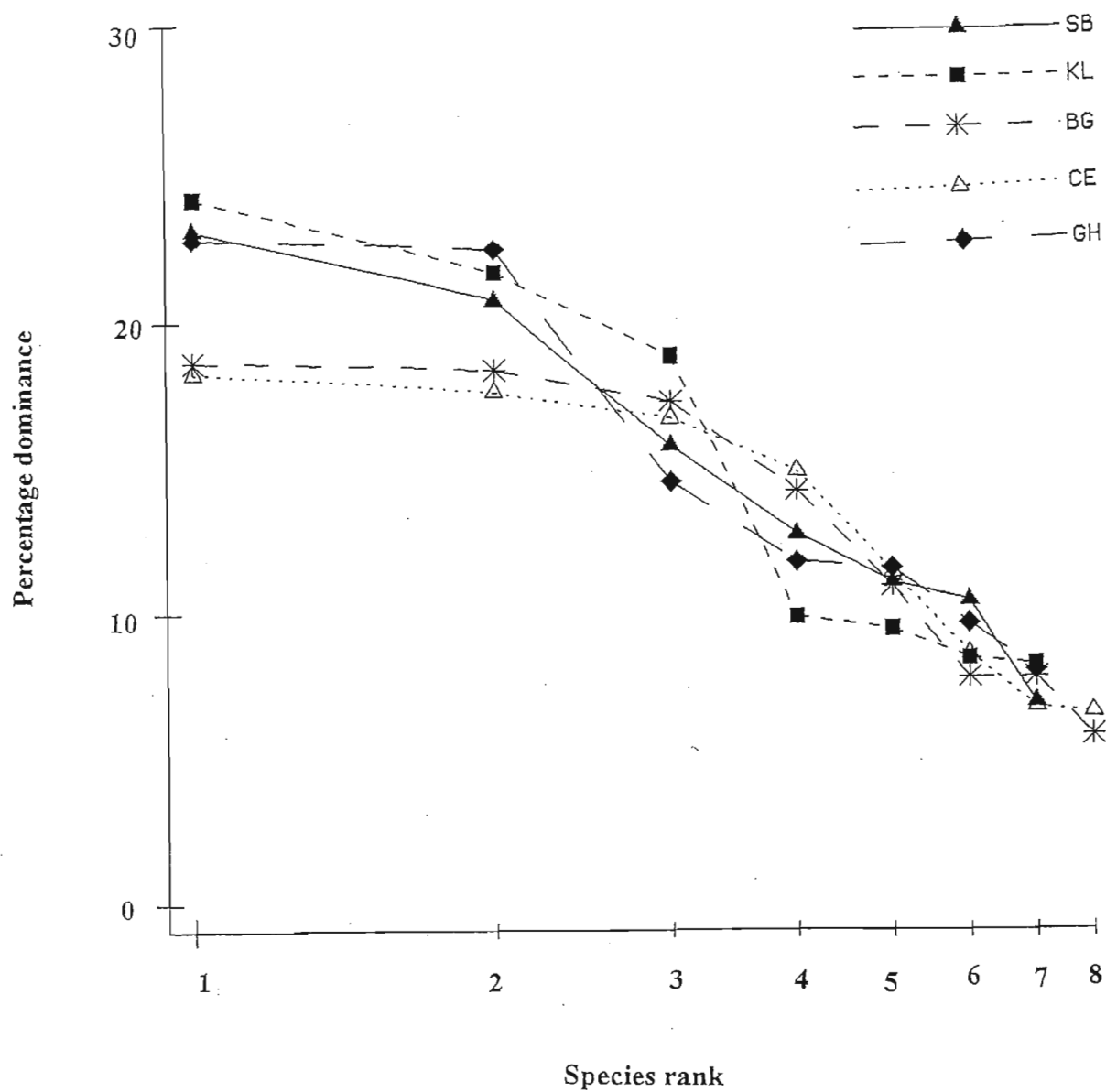
Fig. 5.5 Species rank abundance curves, using larval Zygoptera species sampled at the five elevations: SB= Stainbank Nature Reserve (100 m), KL= Krantzkloof Nature Reserve (450 m), BG= Botanical gardens (790 m), CE= Cedara (1050 m), and GH= Goodhope Estate (1350 m). Species are ranked in decreasing order of their importance in terms of abundance from the most common to rarest.
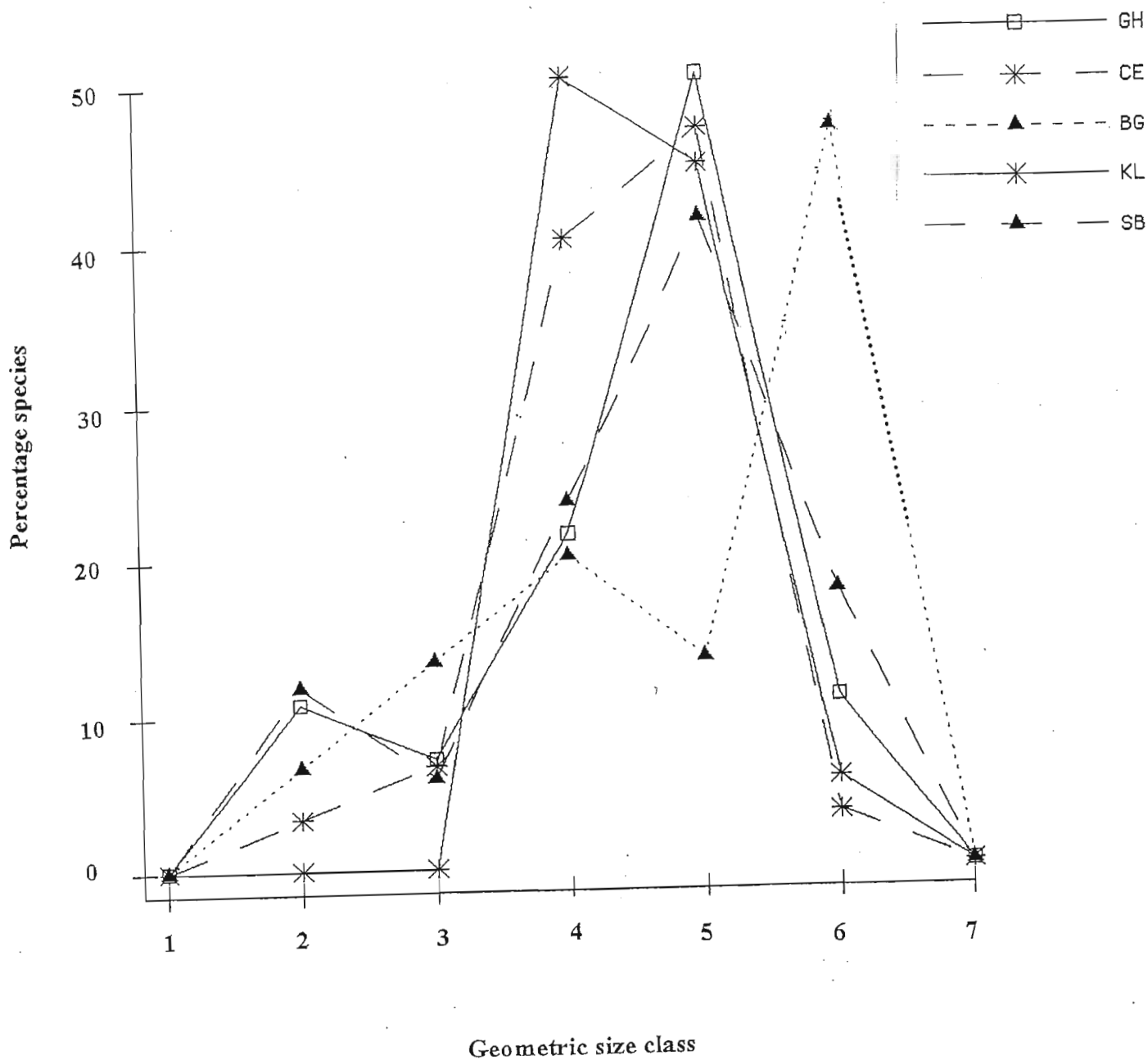
Fig. 5.6 x2 Geometric plots of larval Anisoptera species sampled at the five elevations: SB= Stainbank Nature Reserve (100 m), KL= Krantzkloof Nature Reserve (450 m), BG= Botanical gardens (790 m), CE= Cedara (1050 m), and GH= Goodhope Estate (1350 m).
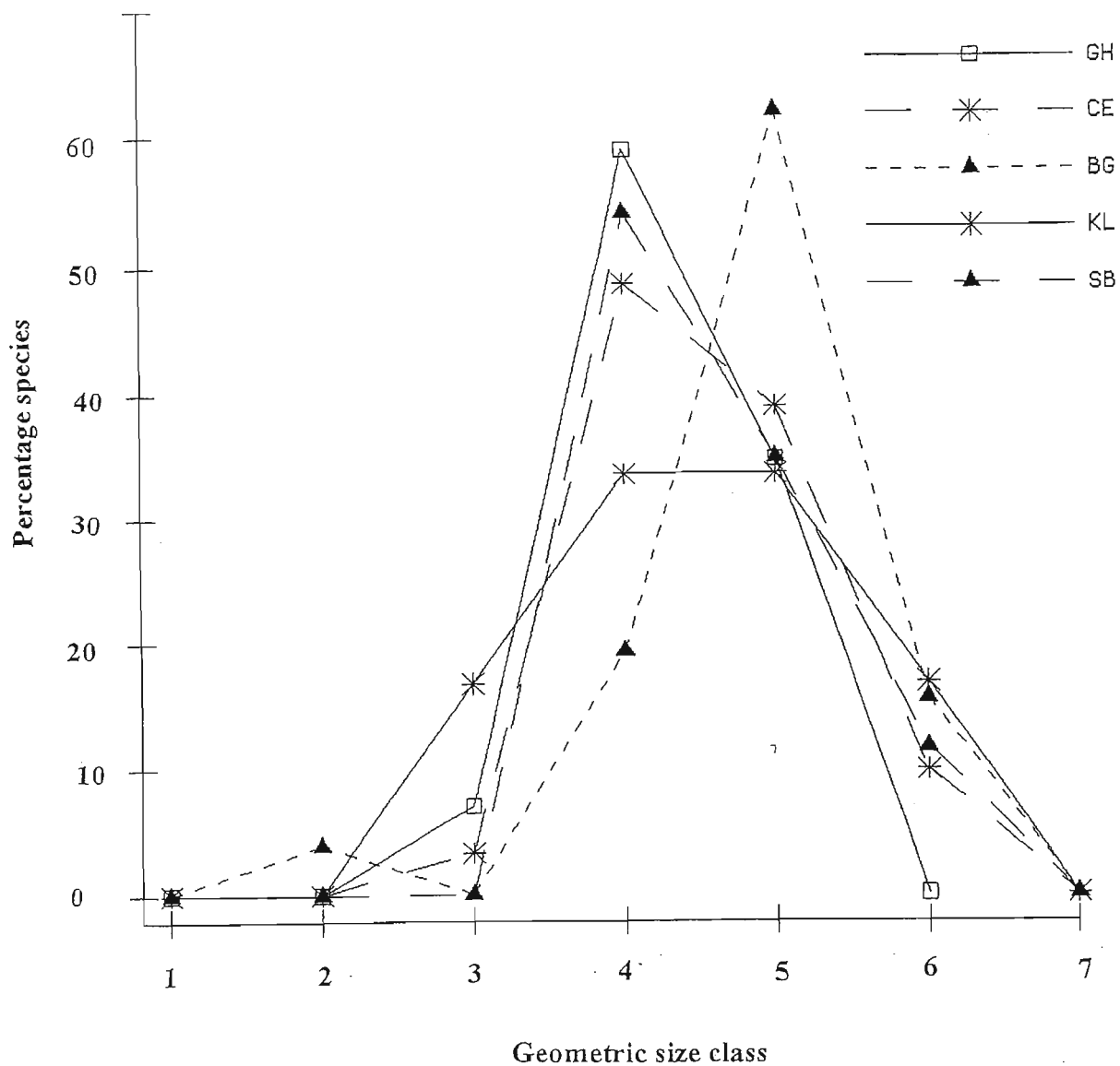
Fig. 5.7 x2 Geometric plots of larval Anisoptera species sampled at the five elevations:
SB= Stainbank Nature Reserve (100 m), KL= Krantzkloof Nature Reserve (450 m), BG=
Botanical gardens (790 m), CE= Cedara (1050 m), and GH= Goodhope Estate (1350 m).

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Table 5.4 ANOVA results of measured site variables across all five elevations. Means followed by same letter across rows are not significantly different at 5%level of probability.

Site variables	Sites					F-ratio	P-values
	SB	KL	BG	CE	GH		
%Sh	15.25b a	13.91b	13.24b	0.00a	0.00a	53.52	<0.001
At	24.21e	26.26e	26.14e	27.06e	27.06e	1.85	0.16 ns
Fsv	26.05d	5.60c	22.44d	18.28d	6.95c	20.43	<0.001
Mfor	30.0b	47.5b	25.12b	0.00a	0.00a	335.39	<0.001
Mgra	21.94	7.39	10.46	19.50	19.66	15.56	<0.001
Marsh	23.89g	22.70g	19.30g	11.44f	6.88f	90.02	<0.001
pH	7.013	7.075	7.088	7.063	7.041	0.18	0.948 ns
Tur	19.14	25.76	21.61	19.86	22.89	1.60	0.213 ns
Wd	22.30	23.52	23.31	22.79	21.21	1.43	0.26 ns

SB= Stainbank Nature Reserve (100 m), KL= Krantzkloof Nature Reserve (450 m), BG= Botanical Gardens (790 m), CE= Cedara (1050 m) and GH= Goodhope Estate (1350 m). At= atmospheric temperature, Fsv= floating and submerged vegetation, Mfor= marginal forest, Mgra= marginal grass, Tur= turbidity, Wd= water depth.

5.5.3 Larval species richness, abundance and elevation

Overall, larval Anisoptera species richness and abundance varied significantly positively with increasing elevation from 100 m (SB) (larval species richness: F= 53.06; P= <0.001, larval abundance: F= 16.25; P= 0.004) (Fig. 5.8). Zygoptera species on the other hand showed a generally negative correlation in richness with elevation, although this trend was not statistically significant (larval species richness: F= 2.17; P= 0.179), and a significantly negative correlation in abundance with elevation (larval abundance: F= 8.69; P=0.049) (Fig. 5.9).

While there were significant differences in species richness and abundance between elevational ranges of 100-900 m and 901-1500 m for Anisoptera (Fig. 5.10), only abundance in Zygoptera showed slightly significant differences across elevations (Fig 5.11).

5.5.4 Spearman's rank correlation of variables and larvae

Anisoptera larval species richness was strongly positively correlated with elevation (Elev: r= 0.894; P<0.01), with floating and submerged vegetation (Fsveg: r=0.9; P<0.001), with turbidity (Tur: r=0.894; P<0.01), and with pH (r= 0.89; P<0.01). Anisoptera larvae however, were negatively correlated with percentage shade (%Sh: r= -0.803; P<0.01). They showed a weak positive correlation with water temperature (Wt: r= 0.44; P<0.05) and marsh (r=0.57; P<0.05).

Zygoptera larvae species richness was correlated with floating and submerged vegetation (Fsveg: r=0.866; P<0.01), with marsh (r=0.8; P<0.001), with turbidity (Tur: r= 0.87; P<0.01), pH (r=0.8; P<0.01) and water temperature (r=0.5; P< 0.01). There was negative correlation with percentage shade (%Sh: r= -0.44; P<0.01). These factors appeared to be chosen at varying degrees by larval species (Table 5.5) i.e. elevation was more important for Anisoptera than for Zygoptera species.

5.5.5 Results of multivariate analyses

Species-site-variable triplots for larvae of Anisoptera (Fig. 5.12a) and Zygoptera (Fig. 5.12b) showed that most assemblages related to certain site variables and indicated how species responded or not to gradients of these variables. Important variables tended to be represented by longer arrows than less important ones (Ter Braak 1986). Accordingly, for the Anisoptera ordination, the first axis (horizontal) explained about 43.5% of the variation, with emergent and floating vegetation (EFveg), elevation (Elev) and marginal grasses (Mgra) being most important. Less important variables were turbidity (Tur), and submerged vegetation (Sveg). The second axis (vertical) explained only 24.8% of the variation, with percentage shade (%Sh), marsh, water depth (Wd) and water temperature (Wt) being selected for.

For the Zygoptera ordination, the first axis explained 40.6% of the total variation, with percentage shade (%Sh) being the main variable, and elevation less important in this axis.
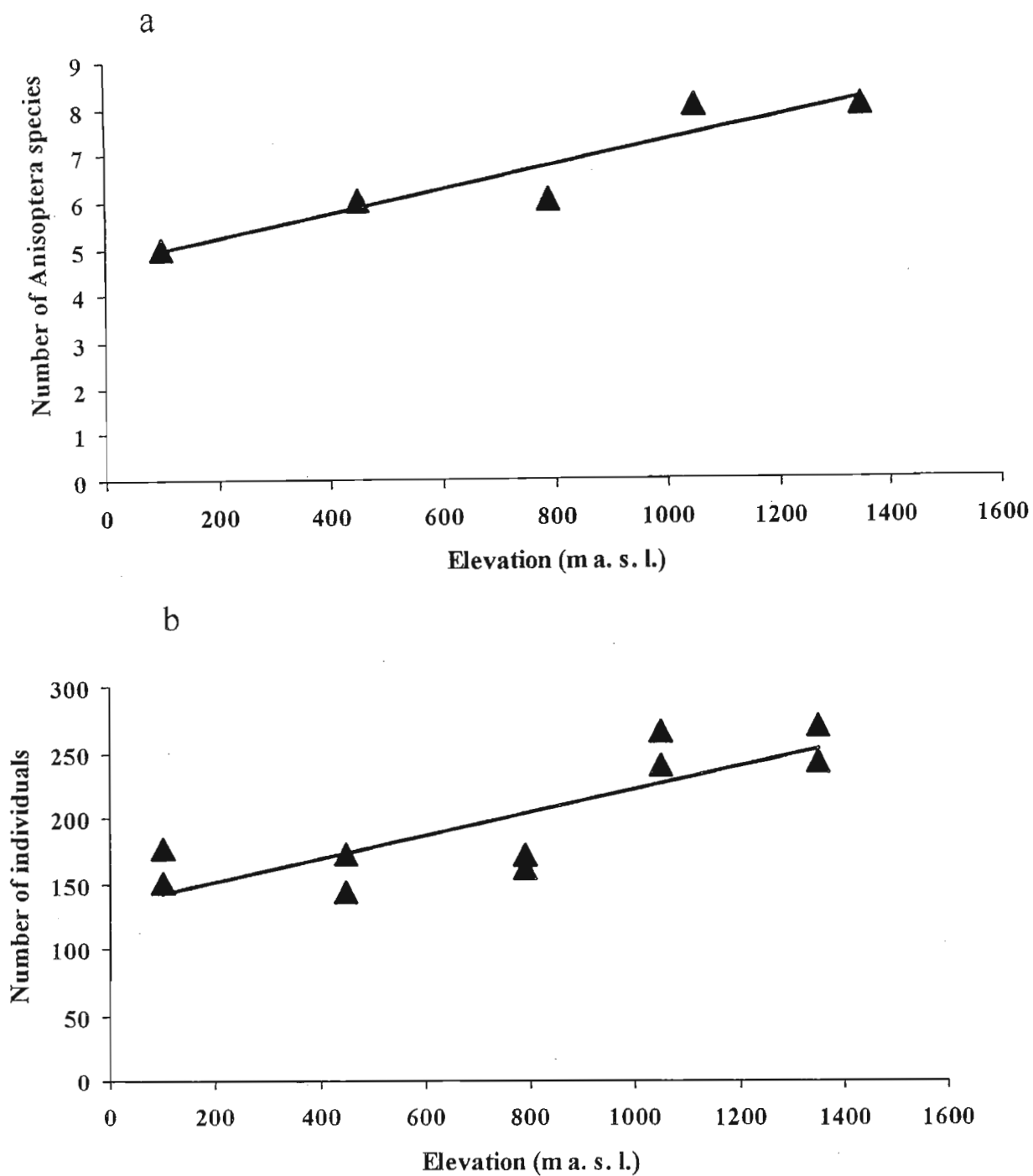
Fig. 5.8 Linear regression of Anisoptera larvae on elevation. Both species richness (a) (model: y= 4.96 + 0.00255x) and abundance (b) (model: y= 134 + 0.0863x) are significant at P= <0.001 and P= 0.004 respectively.
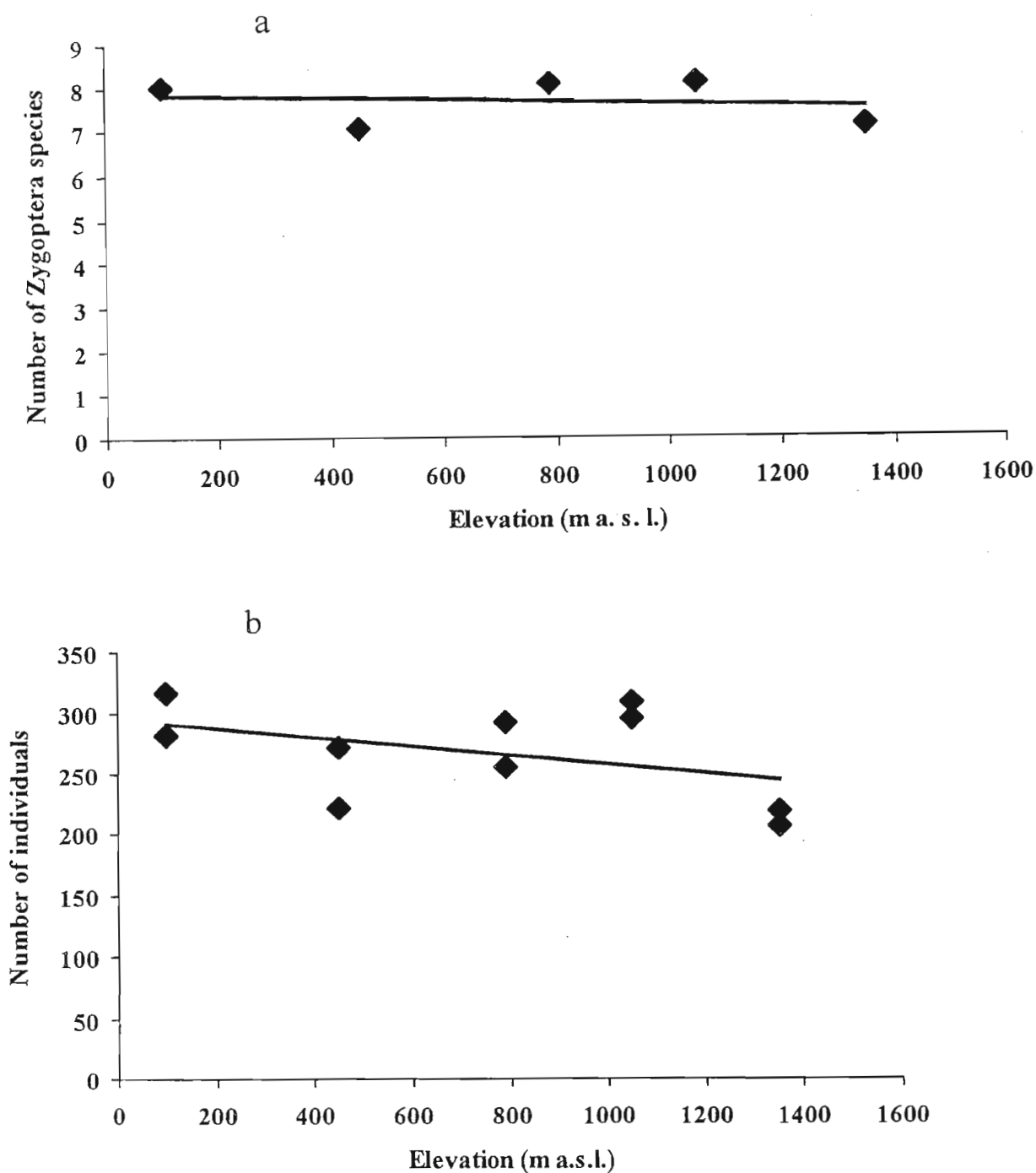
Fig. 5.9 Linear regression of Zygoptera larvae on elevation. Species richness (a) (model: y= 7.8-0.00054x) is not significant at P= 0.179, and abundance (b) (model: y= 296-0.099x) is significant at P= 0.049 respectively.
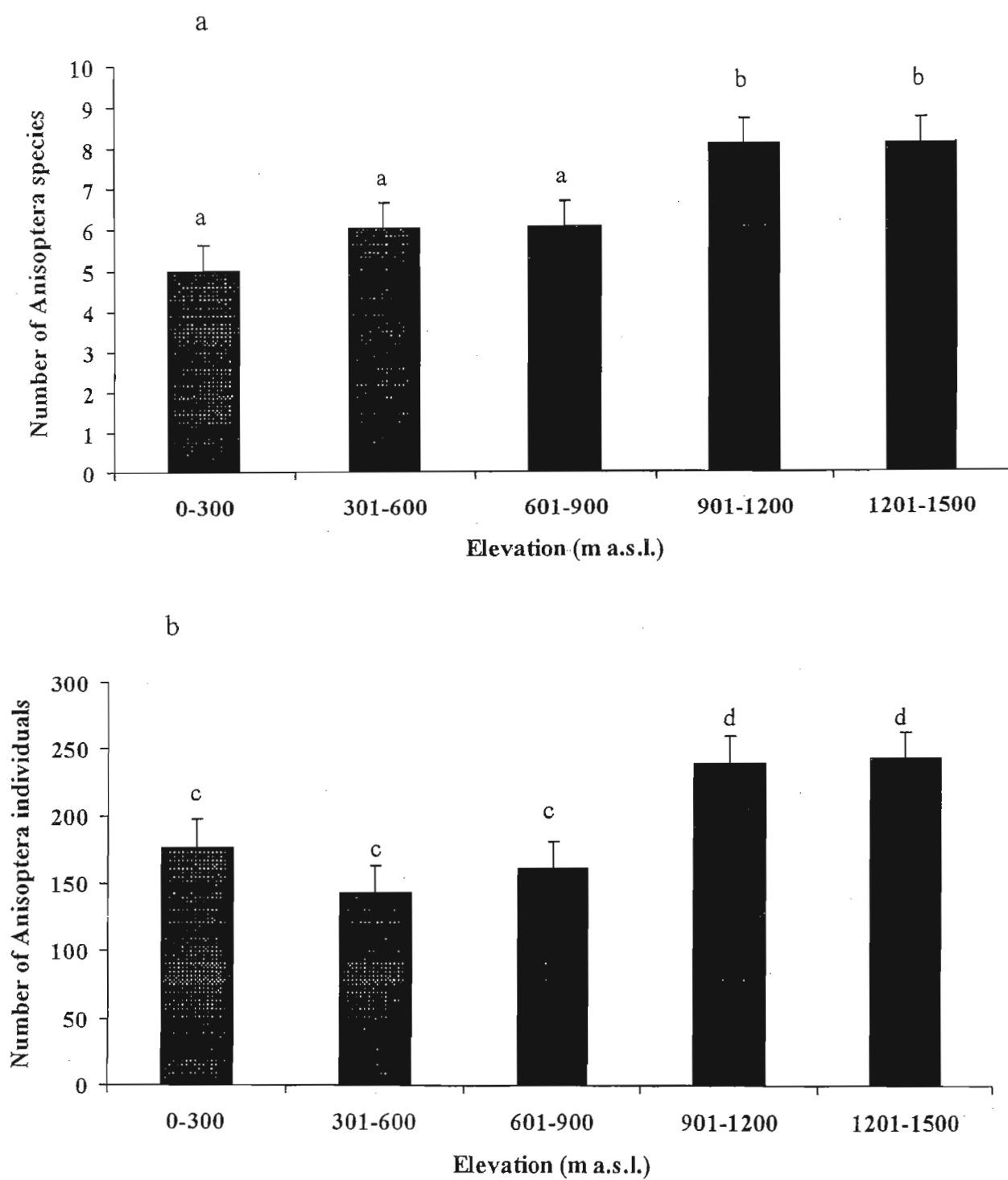
Fig. 5.10 Mean (+/-SE) number of Anisoptera larvae (a) richness and abundance (b) at sub-sites across all elevations during the whole sampling period. Means followed by the same letter are not significantly different at 5% level of probability.

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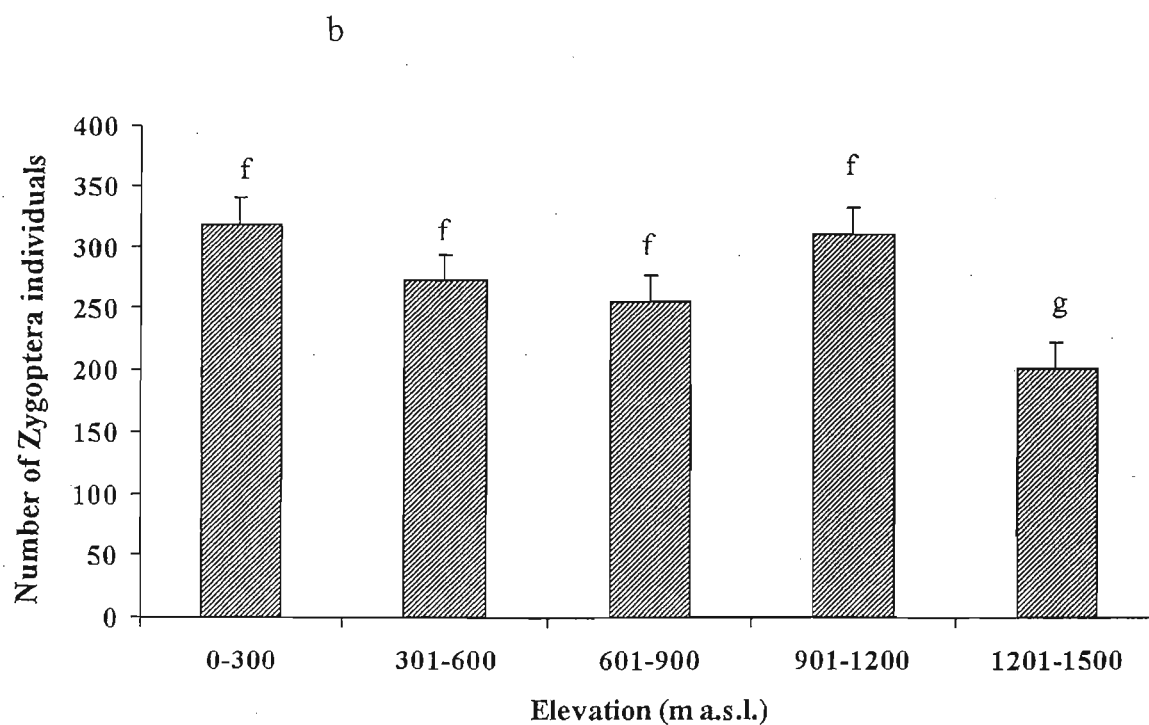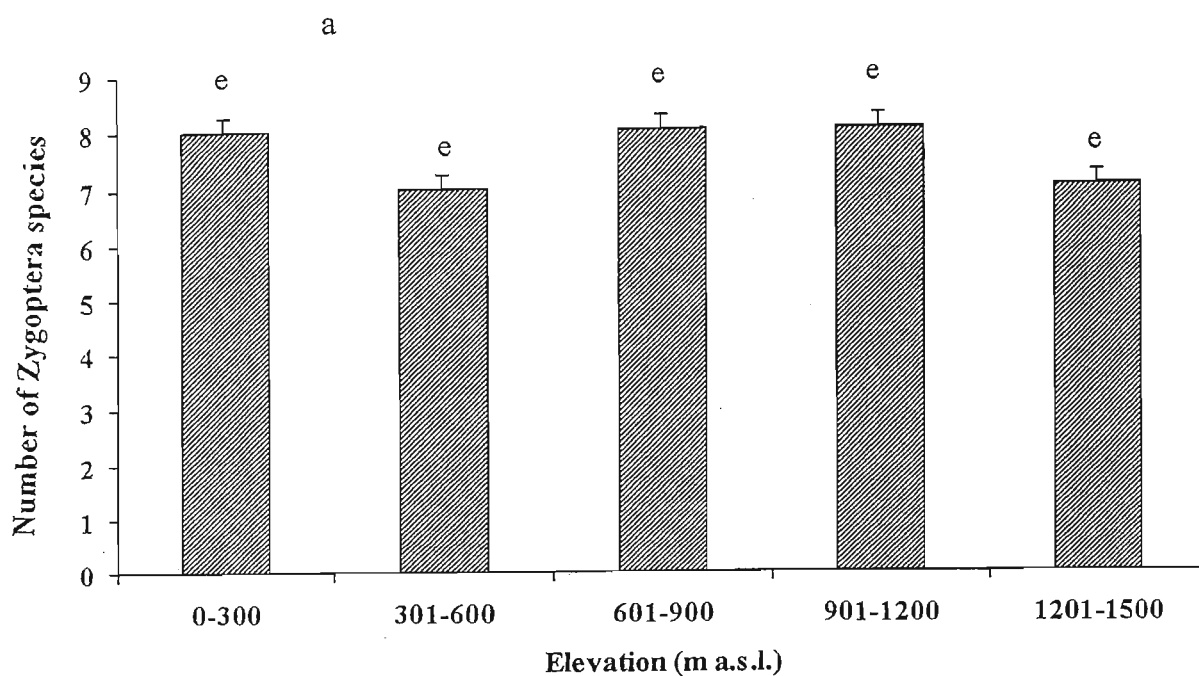
Fig. 5.11 Mean (+/- SE) number of Zygoptera larval species (a) richness and (b) density at all sub-sites across all elevations during the whole sampling period. Means followed by the same letter are not significantly different at 5% level of probability.

Table 5.5 Spearman's Rank Correlation coefficients between Anisoptera, Zygoptera larvae, odonate larvae richness/abundance, and measured site variables across all elevations.

Site variables	AniS	AniN	ZygS	ZygN	TOS	TON
Elev (m)	0.894**	0.900***	0.289	-0110	0.667**	0.700**
Pcir (m)	0.112	-0.600**	-0.287	-0.600**	-0.154	-0.20
Mfor	-0.229	0.300	0.148	-0.335	-0.026	-0.205
Fsveg	0.900***	0.100	0.866**	0.800**	0.564*	0.600**
Mgra	0.205	0.224	0.00	0.00	0.205	0.30
Marsh	0.574*	0.100	0.866***	-0.900**	-0.667**	-0.700**
%Sh	-0.803**	-0.975***	-0.444*	-0.051	-0.658**	-0.718**
Wd	-0.477*	-0.800**	-0.289	0.200	0.359	-0.500*
Tur	0.894**	0.500*	0.866**	0.700**	.821***	0.900***
pH	0.894**	0.500*	0.866**	0.700**	0.975***	0.900***
Wt	0.447*	0.900***	0.500*	-0.500*	0.447*	-0.667**

*, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$
Elev = elevation, Pcir = reservoir circumference, Mfor = marginal forest, Fsveg = floating and submerged vegetation, Mgra = marginal grass, %Sh = percentage shade, Wd = water depth, Tur = turbidity, Wt = water temperature, Asp = AniS = Anisoptera species, AniN = Anisoptera individuals, ZygS = Zygoptera species, ZygN = Zygoptera individuals, TOS= total Odonata species, TON = total odonate individuals.

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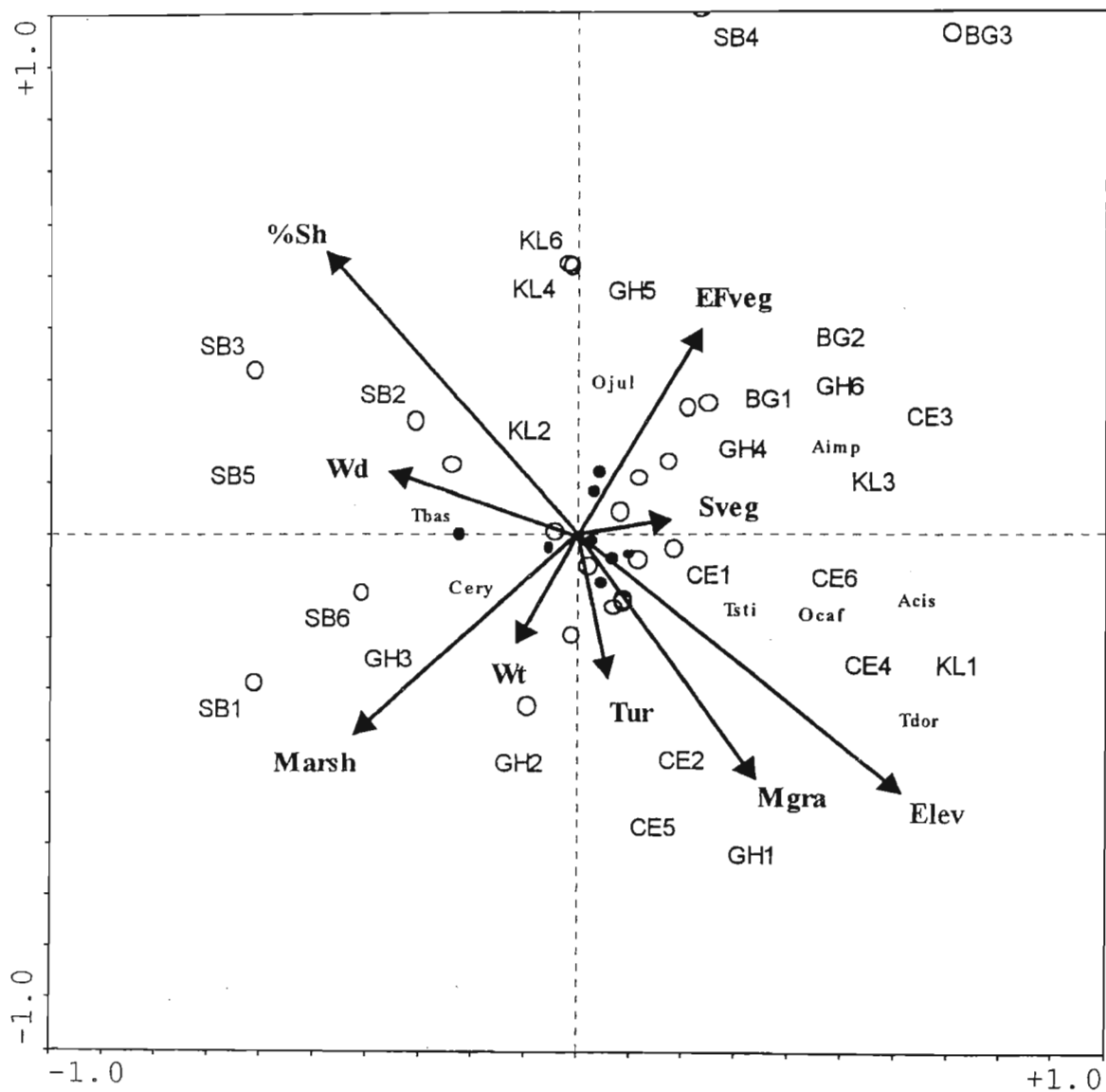
Fig. 5.12a CCA triplot of Anisoptera larvae species (closed circles); sub-sites at elevations (open circles) and site variables (arrows) for pooled (2001 and 2002) data. Axis 1 is horizontal and axis 2 vertical. Species codes are as in Table 5.3a. Site abbreviations are: SB = Stainbank Nature Reserve (100 m), BG = Botanical Gardens (790 m), CE = Cedara (1050 m), and GH = Goodhope Estate (1350 m). Important site variables are: Elev = Elevation; Mgra = marginal grasses; Sveg = submerged vegetation, Wd = water depth, %Sh = percentage shade.

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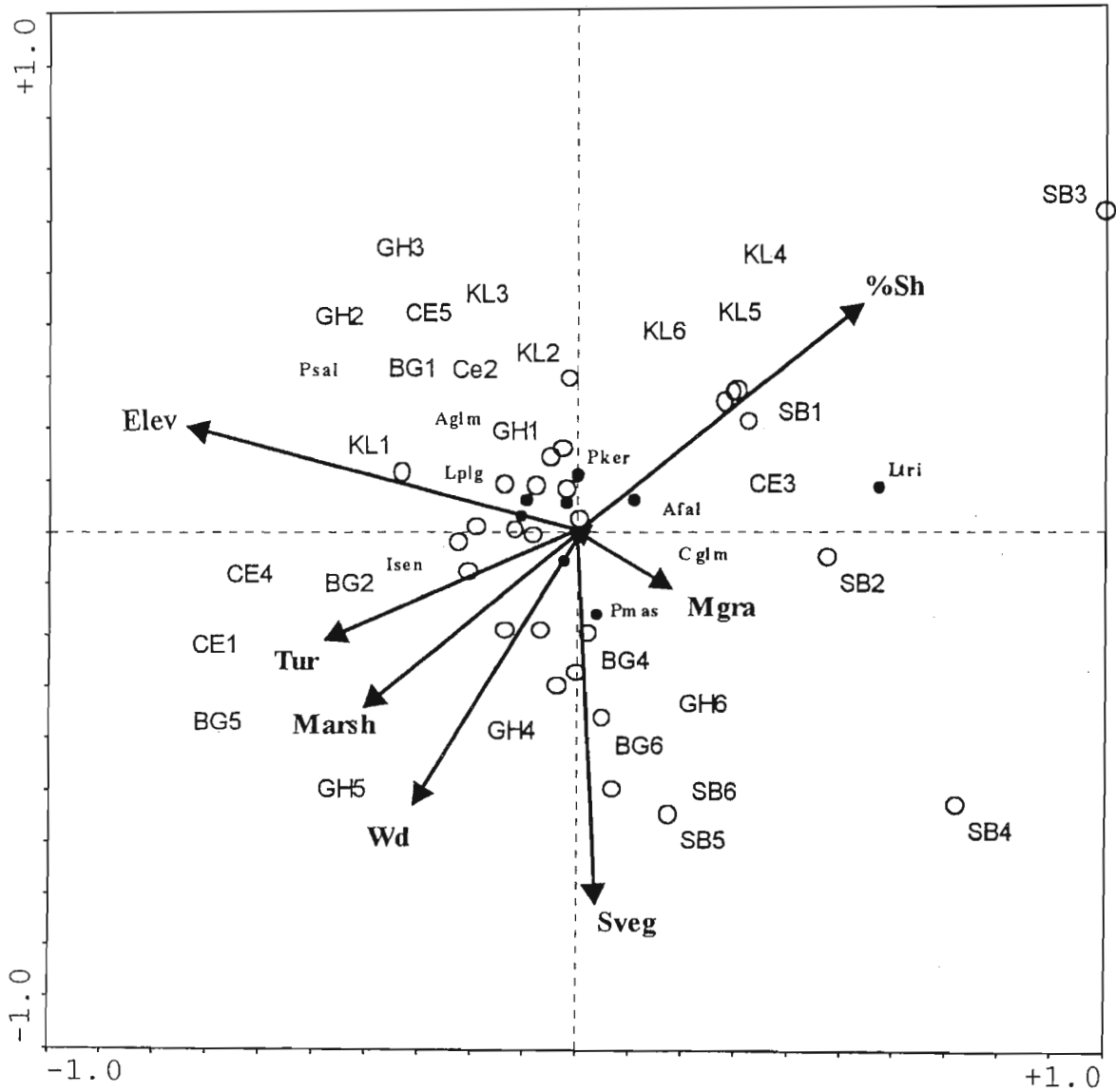
Fig. 5.12b CCA triplot of Zygoptera larvae species (closed circles); sub-sites at elevations   (open circles) and site variables (arrows) for pooled (2001 and 2002). Axis 1 is horizontal and axis 2 vertical. Species codes are as in Table 5.3b. Site abbreviations are: SB = Stainbank Nature Reserve (100 m), BG = Botanical Gardens (790 m), CE = Cedara (1050 m), and GH = Goodhope Estate (1350 m). Important site variables are: Elev = Elevation; Mgra = marginal grasses; Sveg = submerged vegetation, Wd = water depth, %Sh = percentage shade.

The second axis explained about 24.1%, of the total variation, selecting for submerged vegetation (Sveg), marginal grasses (Mgra), water depth (Wd), marsh, turbidity (Tur) in decreasing order of importance.

Both sub-orders showed great similarity with respect to broad biotope requirements, even though minor variations occurred with individual species preferences to site variables, which were usually synergistic with one another instead of having a singular effect.

5.5.6 Summary of sub-order larvae correlation with environmental variables

Results of intra-set correlations (Table 5.6a) and a summary of weightings attributed to the first two ordination axes for larvae of Anisoptera and Zygoptera (Table 5.6b) indicated that species site variable correlations using CANOCO were strong. Cumulative percentage variance for larval species data and for larval species-environment relations was 57.03% for Anisoptera and 59.4% for Zygoptera ordinations. This implies that measured site variables significantly accounted for the main variation in assemblage composition and distribution of larval species for both sub-Orders. The respective eigenvalues, cumulative species variances and Monte Carlo tests for CCA are given in Table 5.6b.

Table 5.6a Intra-set correlations between each of the site variables and Canonical Correspondence Analysis axes for all Odonata larvae species (Anisoptera and Zygoptera) and site variables across all five elevations combined.

| Variables | Anisoptera Larvae | | Zygoptera larvae | |
	CCA axis1	CCA axis 2	CCA axis 1	CCA axis 2
Eigenvalues	0.221	0.126	0.214	0.128
Sveg	0.0812	0.0867	0.5544	-0.0304
EFveg	0.6112	0.0235	-0.0561	0.0016
Mgra	0.41050	-.3232	0.2932	-0.2045
Marsh	-0.2108	-0.5634	-0.0757	-0.5174
%Sh	-0.4425	0.4760	0.4478	0.3357
Wd	-0.3130	-0.6026	-0.1966	-0.5729
pH	-0.0415	-0.0707	-0.1671	-0.3081
Wt	0.1985	0.1181	0.2179	0.1701
Elev (m)	0.5656	-0.4348	-0.4716	-.0630
Tur	-0.3160	-0.5543	-0.1896	-0.4388

SB= Stainbank Nature Reserve (100 m), KL= Krantzkloof Nature Reserve (450 m), BG= Botanical Gardens (790 m), CE= Cedara (1050 m) and GH= Goodhope Estate (1350 m).

Table 5.6b Weighting summaries of the first two axes of CA and CCA for larvae in terms of variances accounted for by the two axes. Monte Carlo probability tests of significance are given for the first canonical axis (AX1) and all four axes. *P<0.05; **P<0.01.

Axes Weightings	Anisoptera larvae				All 4 axes	Zygoptera larvae				All 4 axes
	CA		CCA			CA		CCA		
AXES	AX1	AX2	AX1	AX2		AX1	AX2	AX1	AX2	
Eigenvalues	0.264	0.186	0.221	0.126		0.314	0.24	0.214	0.128	
SP-ENC[1]			0.932	0.877				0.835	0.777	
CPVS[2]	32.2	54.9	27	42.4		32.4	57.3	22.2	35.4	
CPVS-EN[3]			43.6	68.4				40.7	65	
F-Ratio			2.446		5.557			4.840		2.033
P-value			0.005**		0.005**			0.03*		0.005**

[1] Species-environment correlations; [2] Cumulative species variance of species data; [3] Cumulative species variance of species-environment relations

5.6   Discussion

5.6.1 Family and species trends

A total of 18 dragonfly larval species in four families accounting for 36% of the total adult dragonfly species (see Chapter 4) were recorded. Seventy-six percent of larvae recorded occurred within elevation ranges of 790m-1350m a.s.l., being mostly widespread species. Six species occurred at all elevations, 11 in two or more elevations, and only one species (*Lestes tridens*) occurred at only one (SB) elevation. Even though curves for both sub-orders were broadly similar, the rate at which new Zygoptera species occurred as sub-site groupings increased was lower than for Anisoptera, perhaps due to more microhabitat specificity in this sub-order. Although the reservoirs were not necessarily increasing the extent to which species occurred, they probably played a role in increasing the area for larval occupancy.

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5.6.2 Ecological implications of larval species responses to elevation

Even though this study was done within a narrow sub-tropical latitudinal band, general features within species assemblage distribution patterns and biotope attributes reflected more of tropical than temperate characteristics. A common pattern revealed by faunistic studies of dragonflies across vertical gradients is for the number of taxa to decline with increasing elevation, diminishing abruptly above a certain level (Corbet 1999, Ribeiro et al 1998, Mcoy 1990, Pianka, 1966, Dempster 1991, Hasslett 1997, Ribeiro et al 1994, Olson, 1994, McGeoch and Chown 1998, Samways 1994).

This study showed that Zygoptera species richness and abundance steadily declined with increasing elevation from 100 m to 1350 m, although not statistically significantly. This trend was also observed by Samways (1989a). Most species occurred throughout all elevations, with a few exceptions e.g. *Ceriagrion glabrum* which was not at 1350 m and *Lestes tridens* was only at 100 m, being at its southern limit in this study. The elevational range of some species is likely to be found to be wider than reported in this study (Samways 1989b).

Anisoptera larval species richness and abundance increased significantly with increasing elevation. This contrasts with the trend for adults in chapter 4, where species richness declined with increasing elevation and with the widely held view that most insect species decrease with increasing elevation. Perhaps some species immediately dispersed as adults from the higher elevations. Perhaps also, some species of larvae at higher elevations never reached adulthood due to high predation by fish. Lack of suitable larval habitat, could also have influenced larval species variations. While *Trithemis stictica* and *Orthetrum caffrum* were easy to sample in the marshy shallows of pond edges at higher elevations, this was not the case at low to middle elevations where the reservoir edges were steep, with little or no marshy shallow patches.

Exactly where larval species do best may have depended on many factors among which are climate (Parmesan 2001, Roy et al. 2001), evolutionary adaptations (Roff 1990), landscape changes (Samways 1993, 1989c), food and habitat quality (Steytler and Samways 1995, Osborn and Samways 1996), competitive and predatory interactions (Morin 1983) and predation by fish (Morin 1984).

5.6.3 Co-variation of species richness with environmental variables at elevations

Species richness in both odonate sub-orders had strong positive correlations with floating/submerged vegetation (Fsveg), pH and water temperature, while negatively correlated with shade conditions. Zygoptera species richness was positively correlated with marshy conditions e.g. *Pseudagrion kersteni*, *P. salisburyense* and *P. massaicum* being found in these areas, whereas Anisoptera species richness was weakly correlated with this gradient, although Larvae of *Tramea basilaris* and *Anax imperator* were mostly found in these marshy habitats.

5.6.4 Ecological implications of multivariate results

The physical environment profoundly influences the ecology and behaviour of Odonata (Wright 1943, Osborn 1995, Corbet 1999), but the precise action of individual factors is difficult, and often inappropriate to characterise, because factors interact with one another and have long-term as well as short-term effects (Corbet 1999). Species-site-variable triplots for Anisoptera and Zygoptera respectively showed generally that species clumped at the centres of ordination diagrams, further implying that no measured site variable on an individual basis could clearly define species assemblage distribution patterns. However, degrees of importance of variable gradients (denoted by length of arrows) could still be selected by using canonical ordination axes with their related intra-set correlation coefficients. Results revealed that certain measured site variables could convincingly explain the main variations in larval species distribution patterns, for species in both sub-orders (although varying in magnitude for individual species). Marginal grasses (Mgra), elevation (Elev) and emergent/submerged (EFveg) were the most important gradients for Anisoptera species while percentage shade (%Sh) was very important for Zygoptera. Other important variables for both sub-orders were water depth (Wd), marsh and submerged vegetation.

Measured local variables e.g. vegetation (structural and compositional), pH, water depth, turbidity and marshiness as well as regional (large-scale) processes e.g. climate (water and ambient temperatures, elevation and reservoir size), best explained the variability in larval assemblage (Sandin 2003, Sandin and Johnson 2000, Heino et al. 2002). Here, measured variables accounted for slightly over half of the variability in species assemblage distribution patterns even though some of the variation could be accounted for by adult and larval behavioural patterns. For example, some areas of larval territory may expose the residents to higher predation risk or may allow for easier prey detection than other locations and consequently cause a shift in space use (Krams 2001).

5.6.5 Ecological importance of site variables to larvae

It is important for adult Odonata to select and colonise reservoirs where conditions for larvae are optimal, because larvae live longer and are often unable to move away from a habitat in times of adversity (Osborn 1992, 1995). Wildermuth (1992) has already suggested that Odonata may react to visual cues when selecting for oviposition sites. Larger water areas are also of greater permanence than smaller areas, with the degree of permanence of a water body influencing the distribution of larvae (Canning and Canning 1987).

The habitat preferences of adults could be explained by a combination of thermoregulatory requirements and selection of oviposition sites. Selection of micro-habitats suitable for thermoregulation is probably the most common form of thermoregulation in ectothermic insects (May 1976, 1984). The presence of larvae of *T. stictica, Crocothemis erythraea, Anax imperator, Africallagma glaucum, Ishnura senegalensis* and *Ceriagrion glabrum* in shallow marshes at reservoir edges at higher elevation (1050 m and 1350 m) probably showed that insolation strongly influenced

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growth and development in some species. Larvae of *Tramea basilaris* and *P. massaicum*, among other species on the other hand, tolerated warm, shady conditions at the 100 m site.

Individuals of some species may have moved from source (productive) habitats to less productive (sink) habitats (Pulliam and Danielson, 1991). Larvae occur where they obtain most of their preferred food, and be simultaneously protected from predators (Corbet 1999). There were fish, e.g. *Tilapia sparrmanii* in the reservoirs, that probably fed on the odonate larvae (Skelton 1993), especially in the shallows. There was perhaps also habitat and micro-habitat partitioning among larvae that may reflect past competition (Osborn 1995).

Linked with food partitioning is substrate and vegetation, because prey would occur on specific substrates and vegetation. Most larvae were closely associated with submerged vegetation. This was observed in *Trithemis* spp., *C. erythraea* and some coenagrionids which clung onto partially submerged plants (Osborn 1995). Submerged vegetation of the genus *Chara* and *Elodea densa* may have been chosen because of a greater chance of finding food such as Ephemeroptera, Zygoptera and Culicidae. Also, although *E. densa* is an invasive alien plant, it probably increased the complexity of local plant architecture (Samways 1999). This in turn encourages establishment of certain species.

Bank (marginal) vegetation of mostly grasses were used by last-instar larvae of for example *A. imperator*, *T. stictica*, *C. erythraea* and *Lestes plagiatus*, which usually climbed onto this vegetation for emergence to take place. Evidence was the presence of exuviae on marginal grasses. Larvae of *T. basilaris* clung to submerged stems of emergent vegetation or occurred on the substrate beneath vegetation (Corbet 1962). Larvae inhabiting plant beds near the water surface were probably more exposed to higher temperatures necessary for rapid growth than are bottom dwellers.

5.6.6 Habitat preference and elevation in larvae

Findings in Chapter 4 showed that local habitat variables as well as regional processes were important in determining adult dragonfly species assemblage composition and distribution. Results of statistical analyses in the present study showed that elevation as a regional process alone was not as strong as its indirect influence on local environmental factors in explaining Anisoptera larval assemblage variations and distribution.

Zygoptera species distributions also depended largely on local habitat, and indirectly on regional processes. However, odonate larvae in general, being the product of aerial dispersal in vagile adults, find themselves restricted to particular habitats that they cannot change, even in adverse conditions. Since larvae sampled were mostly eurytopic species, distribution of species for both sub-orders therefore largely depended on corresponding adult dispersal characteristics, most of which were elevation tolerant. But similarly, the larvae were also tolerant of a wide range of ecological conditions. Except for *Agriocnemis falcifera* larvae, most species also occur in large areas of Africa, and are regularly seen in the right habitats. Some of them are very common throughout South

Africa (Samways 1999; 2002), although some species, e.g. *L. tridens*, is limited to warm coastal areas.

The question then becomes: why are these species in this part of Africa so remarkably tolerant of elevational changes, both as adults and larvae? The reason seems to lie with the fact that this is an El Niño Southern Oscillation (ENSO) area, which receives continual short-term and long-term climatic variation, with fluctuating water trends. Minimally fluctuating water levels at reservoirs resulting from high rainfall during September to May, in addition to encouraging vegetation growth at sites, also influences richness and abundance in larvae (Weir 1974, Happold 1968, Corbet 1999). In addition, high ambient (and water) temperatures during this period, also influence odonate egg development, as well as larval moulting from one instar to the next (Masseau and Pilon 1982, Pritchard 1982, McGeoch and Samways 1991, Corbet 1999). Winter periods (June-August) on the other hand are characterised by very low rainfall, resulting in low vegetation cover and minimal water levels at reservoirs. These conditions are usually less optimal for larval growth and development, most of which over-winter during these periods (Corbet 1999). This means that only the most habitat tolerant species (as larvae as well as adults) can survive in the long-term. This appears to be the case, with species probably having survived many millennia of impacts and natural selection through these ENSO events.

5.7 Conclusion

The larvae that were studied here over this wide elevational gradient (1350 m in all) were mostly geographically widespread habitat-tolerant species. There were a few exceptions e.g. *Lestes tridens*, which is a low-elevation species. *Agriocnemis falcifera* (the only national endemic species sampled in this larval study out of the three adult species in Chapter Four) was elevation-tolerant. Community composition showed that there were no truly distinct larval assemblage at the various elevations. Despite the apparent diversity and heterogeneity of habitat types, the micro-habitat conditions favoured by most larval species were remarkably common to many sites. A clear understanding of this is important if site management is to conserve and protect species (Fox and Cham 1994). While local environmental variables and behaviour were important in explaining variations in larval assemblage structure and taxon richness for the reservoirs at sub-sites, there were no major differences between sites at the regional level. The upshot of this is that reservoirs in this part of Africa may be very rich in dragonfly species, but all species are geographically widespread and locally common species. The end result is that although these artificial water bodies are not increasing the 'extent of occurrence' (IUCN 2001), they play a major role in increasing 'area of occupancy'. Whether this has genetic value for these already common species is uncertain. Furthermore, it appears that these species are remarkably habitat-tolerant and elevationally widespread through many millennia of impact and natural selection through ENSO events. Survival is about vagility and colonization, with these artificial reservoirs being an ideal and relatively sole and permanent local home for them.

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Chapter Six General conclusions

Although Chapters 2-5 are complete studies in their own right, there is some merit in exploring some common threads to highlight significant findings of the study as a whole.

6.1 Phenology of dragonflies along an awareness trail

The theoretical and practical underpinnings of the 'focal species' concept has been argued by most researchers who suggest that the use of this approach in biodiversity conservation to restore landscapes may lead land managers to assume incorrectly that all other elements of the biota have been conserved (Lindenmayer et al. 2002). However, the present approach, which aims to manage a landscape for a suite of focal species, each of which is thought to be sensitive to a particular threatening process (Lambeck 1997, 1999) is now being applied in some states in Australia, and has been cited as a tool that can aid landscape restoration in other parts of the world (Noss et al 1997, Miller et al. 1999, Noss 1999, Foreman 2000).

In South Africa, conservation of insects in urban environments, by ecological landscaping designed to encourage particular insect groupings, e.g. dragonflies, has been particularly rewarding in many ways. For example, in Chapter 2, a core of regularly occurring species formed the trail while others visited the study site at irregular periods. This is likely to be the case for a longer term, say ten years or more. Also, the dragonfly trail, with updated information on species phenologies, variability and their habitat requirements continues to play a valuable role in sensitising an increasingly urbanised population to biodiversity and conservation issues.

This trend is of significance to primary and secondary schools and even the elderly and disabled as education budgets in the country are severely limited. It is worth noting that without education and public awareness, the loss of touch with the environment in which most modern and developing societies seem to find themselves, would continue (Terblanche and Van Hamburg 2003, Glazewski 2000). Conservation in South Africa however, has shifted in recent years from a protectionist approach towards one that involves the community (Wynberg 2002), and this study supports this.

6.2 Significance of medium-term temporal changes when designing a reservoir for conservation of dragonfly diversity

While dragonflies are a major component when assessing ecological components of aquatic biotopes, the assemblage composition at any one locality can change over time. Odonate species richness and diversity were shown in Chapter 3 to significantly increase, largely due to succession in vegetation physiognomy and water conditions at an artificial reservoir over 13 years. Such assessments form an essential starting point for the applied science of restoration ecology, which in turn requires recognition of the changes to be expected in species abundance and diversity as ecological succession proceeds.

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As information on medium to longer-term changes in dragonfly populations at established reservoirs is being accumulated in South Africa, it would be possible to determine whether a species in a conservation area is being given protection, especially from local anthropogenic impacts over time, especially in El Niño-prone areas.

6.3 Dragonfly (Odonata) phenology and assemblage response to elevation

Regional processes e.g. climate, elevation, insolation (and perhaps behavioural factors resulting in dispersal and colonisation) were found in Chapter 4 to strongly influence locally-measured site variables in determining dragonfly assemblage variation and distribution at different spatial and temporal scales, and differentially affected species phenologies accordingly. The study also found that dragonfly assemblages can be used to characterise various landscape types and disturbance levels along different topographical gradients. Furthermore, dragonfly larvae, tenerals and adults are complementary along both spatial and temporal scales and can therefore be used to monitor and evaluate changes in freshwater habitat quality (with species acting as conservation tools), or in multi-taxa studies (with species as subjects) for biodiversity conservation at landscape level. Species that are widespread, localised and/or endemic have been identified, and this should provide baseline information against which to measure climate change scenarios in KwaZulu-Natal in the future.

6.4 Elevational tolerance of dragonfly larvae (Odonata) in an African El Niño prone area

Larvae sampled belonged to mostly vagile and widespread species. Chapter 5 found that regional processes (acting locally), largely explained larval assemblage variations. The 1350m elevational gradient has surprisingly little effect on most species which is related to them being widespread in Africa. Generally, the reservoirs recruited species from the regional species pool, irrespective of the elevation of the pool. These species were geographically widespread species that took advantage of the presence of these man-made reservoirs, and did include only one national endemic. Although these artificial water bodies are not increasing the 'extent of species occurrence', they played a major role in increasing 'area of occupancy'. Furthermore, it appears that these species are remarkably habitat-tolerant and elevationally widespread throughout many millennia of impact and natural selection through El Niño Southern Oscillation (ENSO) events.

6.5 General comments

It has been suggested that since animal movement is likely constrained by processes operating at different scales, extrapolation of information on fine-scale movement across broad scales may provide poor quantitative prediction of the spatial dynamics of populations. Even the most detailed spatially explicit population models cannot predict the exact location of individuals across a landscape, or reproduce precise statistical properties of population distribution (Wiens 1989, Borcard et al. 1992, Legendre and Legendre 1998, Smith and Peacock 1990, Augustin et al. 1996, Dunning et al. 1995). The best application of this type of modelling approach is in making comparative and

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quantitative statements about likely population responses to a set of potential or real landscape scenarios (Legendre 1993, Underwood and Chapman 1998, Hellmann et al. 2003). Indeed such is the case with the interaction between dragonfly assemblages at reservoirs in KwaZulu-Natal as presented in this study. While local (small-scale) studies e.g. at reservoir sites or at the level of sub-sites in the present study serve to show a fine-scale picture of habitat preferences of individual dragonfly species, regional-level studies will make qualitative as well as quantitative comparisons between major physical elements of the landscape and their influence (if any) on species assemblage patterns and phenologies more illuminating.

6.6 Management recommendations

Because most studies of odonates have been of reproductive behaviour or single population dynamics, there may be the impression that the aquatic habitat is the only important patch affecting odonate reproduction and demographics. Foraging areas and suitable roosting shelter may be equally important to odonate survival and reproduction. Many species, especially non-territorial ones spend much of the reproductive lives away from water (Conrad et al. 1999, Corbet 1999, Samways 2004).

Dispersal across the intervening spaces or marshland between these water bodies is an important feature of odonate life-history and therefore the habitat between reservoirs at Mid-high (CE) and High (GH) elevations may be as important as the reservoirs themselves. Management should therefore maintain a network of reservoirs and the intervening fields to form a continuum of habitats as odonate population dynamics at reservoirs could be greatly influenced by the landscape containing them. Also, odonate species expand in geographical range in wet seasons or years and contract/withdraw to permanent water bodies in dry seasons/years. Thus it is recommended that reservoirs be regularly sampled to account for temporal variations (Samways 2002).

6.7 Future research

o Although studies on individual species contribute to the overall argument that climate change is having effects (McCarty 2001), analyses of odonate species assemblages, alongside well-studied taxa e.g. butterflies (Parmesan 2001) can be used in monitoring climate changes, especially as effects of weather are ongoing.

o It will be necessary to evaluate the dragonfly trail on a periodic (3-year) basis to be able to ascertain species presence and the impact of the trail on community awareness/education of dragonflies and other invertebrates.

o The effects of large-scale regional processes and/or local habitat conditions over a longer term, and their effects on dragonfly assemblage variation and phenology needs to be investigated further at the sub-tropical level. This would provide valuable information on other invertebrate fauna besides dragonflies, and even vertebrates e.g. fish and birds which depend on insects for food.

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o Assemblage responses of dragonfly larvae to other functional groups e.g. freshwater predators (tadpoles and fish) and prey (mosquito larvae and early stages of tadpoles) needs further investigation.

o Data on various groups of organisms (including plants) would be useful for formulating predictive models on strategies for conserving a wider cross-section of biodiversity. But as the dragonfly fauna varies so much during and between years, it means that any meaningful changes in overall biodiversity patterns could be determined through longer-term studies.

o The identification of all instars of dragonfly larvae has been attempted successfully in some temperate regions characterised by fewer species in these areas. In the tropics and sub-tropics with higher species richness, autecological studies are still needed of individual species and especially all diagnostic features of larval stages of all species.

o Larval assemblage composition and distribution appears to be intricately linked to adult dispersal characteristics. Therefore, detailed adult behavioural studies are needed to clarify their distribution patterns and how they influence larval assemblage composition, over a larger spatial scale and during a longer term.

6.8 Final comments

• Although the aim of the National Botanical Gardens in Pietermaritzburg is to maintain indigenous vegetation, they also play an important role in invertebrate biodiversity conservation as indicated by the presence of suitable habitat conditions for many odonate species e.g. several small and medium size open lily reservoirs, shaded reservoirs, small streams, waterfalls, a rich diversity of submerged, floating and marginal vegetation. These heterogenous habitat conditions account for a high diversity and abundance of dragonflies at a single location as demonstrated in Chapter 2. Also, the gardens have played a pioneering role in initiating awareness-raising for conservation (through education) of dragonflies and other little-known invertebrates.

• Vegetation succession and hydrological changes influence dragonfly assemblage compositon and variability, all of which are strongly associated with temporal factors e.g. climate and seasonality. The fact that periodic adverse winter conditions are spent in the larval stage for most species at all reservoirs in the present study further illustrates the usefulness of these habitat types in sustaining a variety of species, most of which appear to spend a greater part of their lifespan in the larval stage in these sub-tropics.

• Most dragonfly species at sites are less biotope-specific compared to damselflies, which appears to be associated with their greater mobility. This in turn dictates the scale at which individual species interact with the landscape. It was clear in

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Chapter 4 that regional processes, local factors and to a certain extent behavioural patterns accounted for species variability across the elevational gradients.

- With major threats to biodiversity in South Africa, and with few reserves or protected areas, and also a lack of pond habitats, farm reservoirs such as those studied here increase the area of occupancy for a wide range of species. However, none of these species are currently threatened.

- The variability in level of insolation across all five elevations creates thermally heterogenous shady and sunlit patches, especially at middle to low elevation, and allows some dragonfly species to move between shady and sunlit patches to survive excessive heat loads by means of behavioural thermoregulation.

- Sub-tropical species have characteristics of both tropical and temperate species and they are remarkably tolerant of elevational change.

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