

REMARKABLE ELEVATIONAL TOLERANCE IN AN AFRICAN ODONATA LARVAL ASSEMBLAGE

A.S. NIBA¹ and M.J. SAMWAYS²

¹ School of Botany and Zoology, University of KwaZulu-Natal, P/Bag X01, Scottsville,
Pietermaritzburg-3209, South Africa

² Department of Conservation Ecology and Entomology & Centre for Agricultural Biodiversity,
University of Stellenbosch, P/Bag X1, Matieland-7602, South Africa

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The spatial patterns in species richness and abundance were investigated here at a series of reservoirs at different elevations, to establish which factors determine species distributions along this topographic gradient. Larvae of 18 spp. were sampled in small reservoirs across a 1250 m elevational gradient at one latitude. Most spp. occurred throughout all elevations indicating that this subtropical odon. assemblage as a whole is remarkably tolerant of elevational changes. Although Anisoptera larval species richness and abundance increased significantly with increasing elevation, there was no change in Zygoptera species richness, while Zygoptera abundance decreased significantly. Species-site-variable triplots for Anisoptera and Zygoptera larvae indicated 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 as well as elevation to some extent, explained the main variation in species assemblage composition/distribution in a broadly similar manner for both suborders. Generally, the reservoirs recruited spp. from the regional pool, irrespective of the elevation of the pool. These spp. were all geographically widespread spp. 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, these spp. are remarkably vagile, habitat-tolerant, as well as elevationally-widespread. A reasonable explanation is that this assemblage is the historical survivor over many millennia of oscillating wet/dry periods and natural selection. The present-day spp. are those that readily recolonise pools after drought has been broken, and are pioneering residents of new water bodies over a wide elevational range.

INTRODUCTION

Reservoirs, being artificial, provide an increase in the area of occupancy for aquatic invertebrates. This increases regional invertebrate biomass which inevitably leads to increases in water bird and fish populations (WARD, 1984; McCAFFERTY, 1984). Aquatic environments often contain large assemblages of co-existing resident Odonata species and more transient species (CORBET, 1999; STERNBERG, 1994). In small, still-water habitats, they are found mostly in the littoral zone (JOHNSON & CROWLEY, 1980; CROWLEY & JOHNSON, 1982), and play an important role in pond food webs as predators of other invertebrates (BENKE, 1976, 1978; THORP & COTHRAN, 1984; SAMWAYS *et al.*, 1996) and even some vertebrates (CALDWELL *et al.*, 1980; TRAVIS, *et al.*, 1985), and in turn, are prey for fish (BENKE, 1978; THORP & BERGEY, 1981; JOHNSON *et al.*, 1984; MORIN, 1984a, 1984b; PIERCE *et al.*, 1985).

Within the larger aquatic habitat, microhabitat preferences differ from one species to another, and even between larval instars of a species (CROWLEY & JOHNSON, 1982). Larvae may be cryptic or nocturnal but still 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 (BENKE & BENKE, 1975; BENKE, 1976; MACAN, 1977). There are relatively little 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 others provide information on a number of co-existing species in still-water habitats (BENKE & BENKE, 1975; CARCHINI *et al.*, 1992; WISSINGER, 1988).

In South Africa, taxonomic difficulties have been a significant challenge in dragonfly larval studies. The larvae of many species are unknown and virtually all early-instar larvae are unidentifiable. This means that it is difficult to determine the dragonfly assemblage in a habitat, let alone their abundance.

Any changes in landscape will affect both the aquatic larva and the aerial adult. Little is known about which aspects of artificial water bodies encourage particular species of African larval odonates either over space or time. The east coast of South Africa is interesting in this regard, because as well as having a major elevational gradient (0-3000 m a.s.l.) at one latitude along a 200 km transect, it is also subject to major changes in water on a periodic basis, as a result of El Niño Southern Oscillation (ENSO) events. The aim here was therefore to determine the rate of species turnover with elevation, and to establish which environmental factors might be responsible for any assemblage change. It was postulated that wide elevational and habitat tolerance was the end-product of considerable fluctuations in weather and climate.

METHODS

Five reservoirs, across a 1250 m elevational gradient (100–1350 m a.s.l. in KwaZulu-Natal, South Africa, were selected (Fig. 1, Tab. I). They were: SB = Stainbank Nature Reserve (100 m a.s.l.), KL = Krantzkloof Nature Reserve (450 m a.s.l.), BG = Pietermaritzburg Botanical Gardens (790 m a.s.l.), CE = Cedara (1050 m a.s.l.) and GH = Goodhope Estate (1350 m a.s.l.).

Each reservoir was stratified into six sub-sites (SS) measuring 20 m length (along the pond edge) by 2 m width (1 m on land and 1 m into water). Data were collected on 42 sampling occasions from January 2001–December 2002. Abundance of larvae was estimated at each SS between 11h00 and 13h00 using a dip-net (41 cm diameter \times 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. Larvae were identified using a hand lens and released back into water. Where individuals could not be identified, they were retained for subsequent rearing and identification. Larvae of most species were reared in 2–3 cm depth of dechlorinated water. Larvae were then transferred from the collecting phials to small rearing cages made out of plastic netting rolled into cylinders of about 6 cm width and 15 cm height and sealed at the top with an inverted plastic petridish. To avoid cannibalism and to ensure correct association of larvae and adults, only one larva was placed in each cage. 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.

Larvae were fed daily and uneaten or rotten food 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 was collected and retained in a phial containing 75% ethyl alcohol. After a few days, the adult was identified relative to the exuviae.

ENVIRONMENTAL VARIABLES. – Dissolved oxygen and temperature influence the development of dragonfly larvae (CORBET, 1999), making shallow water particularly important for them. Many Odonata also prefer water of a certain pH (WEIR, 1974; OSBORN, 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), and along with substrate, provides refuge from predation.

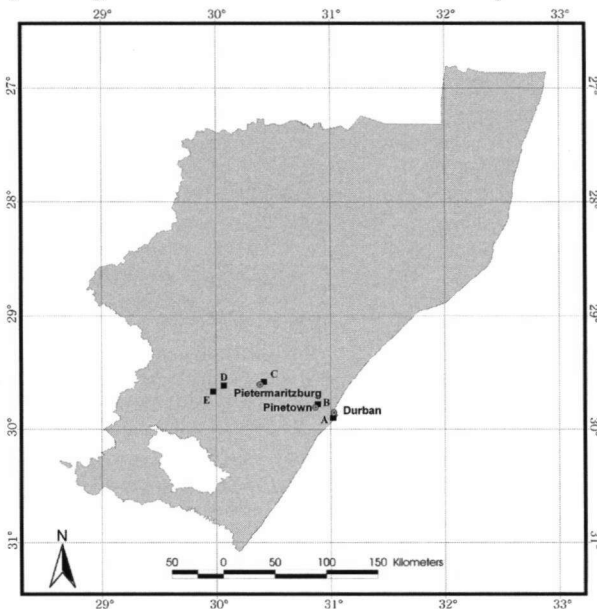


Fig. 1. Geographical location of study sites (KwaZulu, Southern Africa): (A) Kenneth Stainbank Nature Reserve [SB] (100 m a.s.l.); – (B) Krantzkloof Nature Reserve [KL] (450 m a.s.l.); – (C) Botanical Gardens [BG] (790 m a.s.l.); – (D) Cedara [CE] (1050 m a.s.l.); – (E) Mondi Goodhope Estate [GH] (1350 m a.s.l.).

Table I
The five elevational sites used in this study

Site name/code	Grid reference and Elevation	Land use
Kenneth Stainbank Nature reserve (SB) (Low elevation)	29°50'S; 30°55'E; 100 m a.s.l.	Nature reserve
Krantzkloof Nature Reserve (KL) (Mid-low elevation)	29°46'S; 30°5'E; 450 m a.s.l.	Nature reserve
Botanical Gardens, Pietermaritzburg (BG) (Mid-elevation)	29°35'S; 30°25'E; 790 m a.s.l.	Botanical gardens
Cedara (CE) (Mid-high elevation)	29°61'S; 29°06'E; 1050 m a.s.l.	Low-intensity agricultural area
Mondi Goodhope Estate (GH) (High elevation)	29°40'S; 29°58'E; 1350 m a.s.l.	Extensive grassland corridors (natural state) among pine stands

tors. The thermal requirements of the species results in different responses to sunlight and shade.

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) 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 the water surface. 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 college. Sub-sites also classified on the amount of open water and whether aquatic vegetation covered the bottom of the water body. Vegetation was 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 (Marsh), Shade (% Sh) and elevation (Alt) (m a.s.l.)

DATA ANALYSES. – Analyses of species spatial variability was done using linear regression and non-parametric methods. 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. GOTELLI & COLWELL (2001) have suggested that for patchy distributions, individual based rarefaction 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 & CODDINGTON, 1994; UGLAND et al., 2003). Relationships between abundance and the number of species having that abundance was shown graphically.

cally 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.

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 was 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. 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 & LOOMAN, 1995). All abundance and environmental variable data were log-transformed to maintain normality and to satisfy the requirements of ANOVA and multivariate analyses.

RESULTS

OVERALL FAMILY/SPECIES TRENDS AT THE DIFFERENT ELEVATIONS

A total of 18 species were sampled (Tab. II) alongside dominant subsite vegetation made up of mostly indigenous plants. The elevational tolerance of larval odonates shows that most species, except *Lestes tridens*, occurred across a wide elevational band. An estimate of total species richness across sites using subsite-groupings showed that both Anisoptera and Zygoptera had broadly similar trends (Fig. 2a, b). The asymptote was not reached for either suborder, despite much sampling, suggesting other species were still present but not sampled. On the whole, there was much evenness between abundance of species. At 100 m a.s.l. (SB), *Anax imperator*, followed by *Crocothemis erythraea* larvae were the most dominant Anisoptera species at 35% and 33% dominance levels respectively. The remaining elevation sites had high evenness and were similar in patterns of larval species dominance, ranging from 19% at 1350m a.s.l. (GH) to 29% at 450m a.s.l. (KL). Dominant species of the Zygoptera showed narrower trends compared to Anisoptera with most dominant species ranging from 18% at 790 m a.s.l. (BG) and 1050 m a.s.l. (CE) with *Ceriagrion glabrum* and *Lestes plagiatus* respectively to 23% at 100 m a. s. l. (SB) and 1350 m a. s. l. (GH) with *Ischnura senegalensis* and *Pseudagrion kersteni*, respectively.

SITE VARIABLES AND ELEVATION

ANOVA results (Tab. III) 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 ($F = 15.56$; $P =$

Table II

Species of Odonata larvae recorded from all sites across the five elevations during the whole sampling period with species code names used in analyses

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

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).

0.001) as showing highly significant differences across elevations. These results showed that habitats varied to a large extent across different elevations.

LARVAL SPECIES RICHNESS, ABUNDANCE AND ELEVATION

Larval Anisoptera species richness and abundance varied significantly positively with increasing elevation (SB) (larval species richness: $F = 53.06$; $P = 0.000$, larval abundance: $F = 16.25$; $P = 0.004$). Zygoptera species showed a generally negative correlation in richness with elevation, although this trend was not statistically sig-

nificant (larval species richness: $F = 2.17$; $P = 0.179$), and a significantly negative correlation in abundance with elevation (larval abundance: $F = 8.69$; $P = 0.049$).

**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 ($r = 0.8$; $P < 0.01$), with turbidity (Tur: $r = 0.87$; $P < 0.01$), and with pH ($r = 0.8$; $P < 0.01$), although weakly correlated with water temperature ($r = 0.5$; $P < 0.01$). There was a weak negative correlation with percentage shade (%Sh: $r = -0.44$; $P < 0.01$). These factors appeared to be selected for at varying degrees by larval species (Tab. IV) i.e. elevation was more important for Anisoptera than for Zygoptera species.

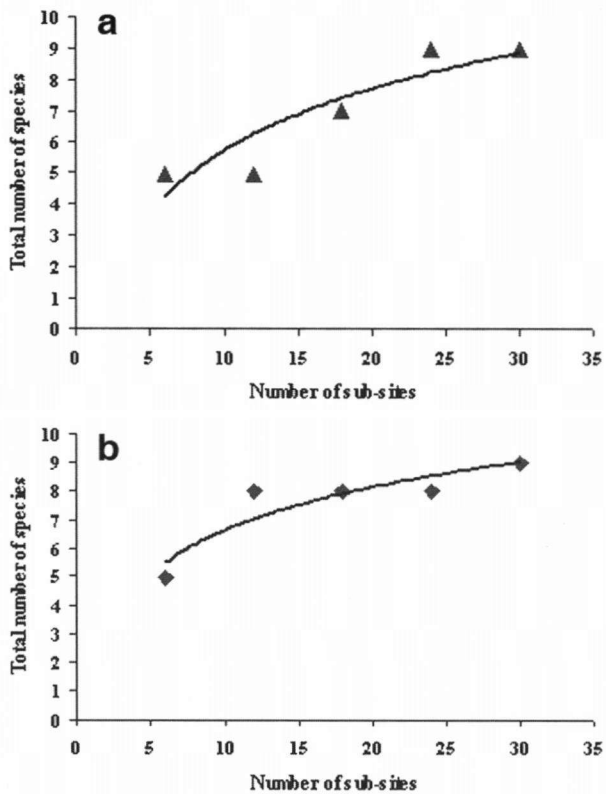


Fig. 2. Species accumulation curves for (a) Anisoptera, (b) Zygoptera larvae species using all 30 sub-sites.

MULTIVARIATE ANALYSES

Species-site-variable triplots for larvae of Anisoptera (Fig. 3) and Zygoptera (Fig. 4) showed that most assemblages related to certain site variables and indi-

Table III

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	SB	KL	Sites BG	CE	GH	F-ratio	P-values
%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 a.s.l.), KL= Krantzklloof Nature Reserve (450 m a.s.l.), BG= Botanical Gardens (790 m a.s.l.), CE= Cedara (1050 m a.s.l.) and GH= Goodhope Estate (1350 m a.s.l.).

cated how species responded or not to gradients of these variables. Important variables tended to be represented by longer arrows than less important ones. 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. 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 suborders 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.

Anax imperator preferred emergent, floating and submerged vegetation conditions at biotopes. Most species preferred all conditions as explained by Anisoptera species clustering at the centre of the ordination. *Pseudagrion massaicum* preferred increasing shady conditions while the remaining Zygoptera species also tolerated a combination of variables acting together hence are also clustered at the centre of the ordination.

Intra-set correlations (Tab. V) and a summary of weightings attributed to the first two ordination axes for larvae of Anisoptera and Zygoptera (Tab. VI) indicated that species site variable correlations using CANOCO were strong. Cumu-

Table IV

Spearman's Rank Correlation coefficients between Anisoptera, Zygoptera larvae, odonate larvae richness/abundance, and measured site variables across all elevations. *, $0.05 > P > 0.01$; **, $0.01 > P > 0.001$; ***, $P < 0.001$

Site variables	AniS	AniN	ZygS	ZygN	TOS	TON
Elev (m)	0.894**	0.900***	0.289	-0.110	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**

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 Odonata individuals.

lative 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 suborders. The respective eigenvalues, cumulative species variances and Monte Carlo tests for CCA are given in Table VI.

DISCUSSION

FAMILY AND SPECIES TRENDS

The elevational tolerance of these species was remarkable. Six occurred at all elevations, 11 in two or more elevations, and only one species (*Lestes tridens*) occurring only at the low (SB) elevation. Even though these species were common, at least as adults, considerable sampling was required to detect them. Although species accumulation curves for both suborders were broadly similar, the rate at which new Zygoptera species appeared was higher than for Anisoptera, perhaps due to more microhabitat specificity in this suborder.

The responses of pre-adult stages of temperate-centred species to low temperatures, show odonates to be principally tropical insects (NORLING, 1984),

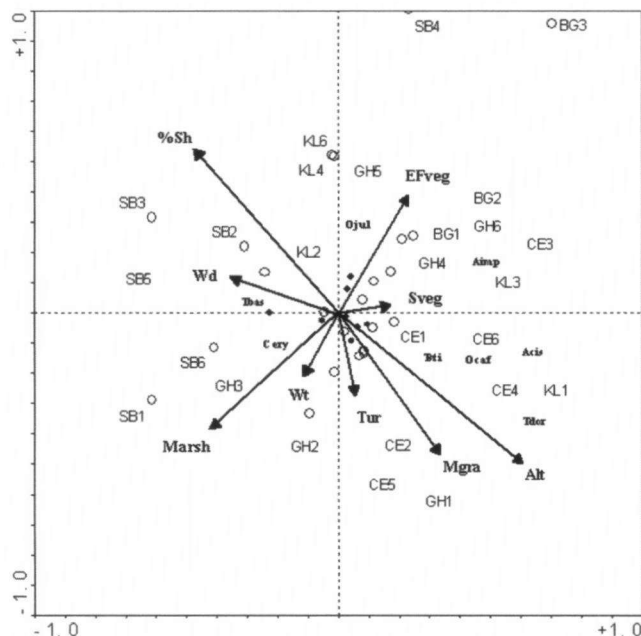


Fig. 3. CCA triplot of Anisoptera Zygoptera larvae species (closed circles); sub-sites at elevations (open circles) and site variables (arrows) for pooled (2001 and 2002) data. Axis 1 is horizontal and axis 2 vertical. Species codes are as in Table II. Site abbreviations are: SB = Stainbank Nature Reserve (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.

and abundance, as recorded here, increased significantly with increasing elevation. This contrasts with the trend for adults where species richness declined with increasing elevation. Of the 47 adult species sampled during that study, larval stages of only 18 were identified here. Lack of suitable larval habitats, could have influenced larval species variations. While *Trithemis stictica* and *Orthetrum cafrum* 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. Also, *Africallagma* spp. occurred in very shallow, marshy spots, could not be sampled as easily as open water. *Anax speratus* and *Nesciothemis farinosa* were rare as larvae and may have occurred among weed in the reservoirs.

which decline in species richness with increasing elevation. In this study, Zygoptera species richness and abundance steadily declined with increasing elevation from 100 m to 1350 m, although not statistically significantly. Most species occurred throughout all elevations, with a few exceptions e.g. *Ceriatagria glabrum* which was not at 1350 m and *L. tridens* which was only at 100 m, being at its southern limit in this study. In contrast to Zygoptera, Anisoptera larval species richness

SPECIES RICHNESS AND ENVIRONMENTAL VARIABLES

Species richness in both odonate suborders 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. Larvae of *Tramea basilaris* and *Anax imperator* were mostly found in these marshy habitats.

Species-site-variable triplots for both Anisoptera and Zygoptera indicated that as species clumped at the centres of the ordination diagrams, no particular measured site variable clearly defined 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 showed that 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 suborders 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 ambi-

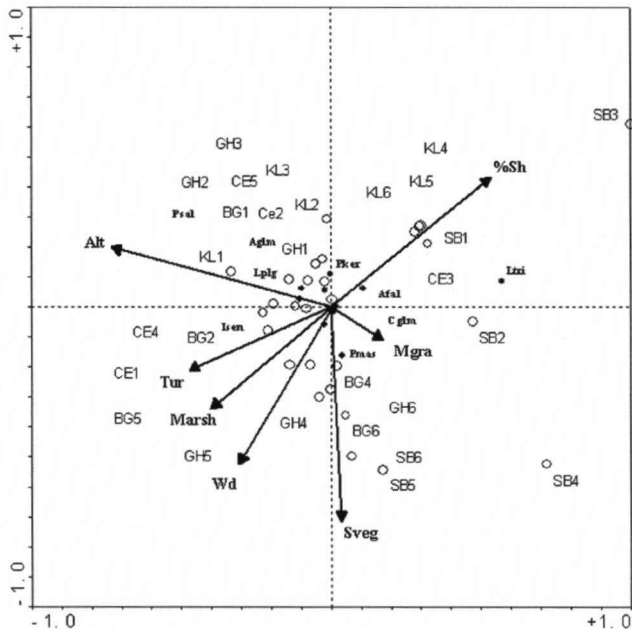


Fig. 4. CCA triplot of Zygoptera larvae species (closed circles); sub-sites at elevations (open circles) and site variables (arrows) for pooled (2001 and 2002) data. Axis 1 is horizontal and axis 2 vertical. Species codes are as in table 2. Site abbreviations are: SB = Stainbank Nature Reserve (100 m), 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.

Table V

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 axis 1	CCA axis 2	CCA axis 1	CCA axis 2
Eigenvalues	0.221	0.126	0.214	0.128
Sveg	0.0812	0.0867	0.0304	-0.5544
EFveg	0.6112	0.0235	-0.0561	0.0016
Mgra	0.41050	-0.3232	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
Alt (Elev) m)	0.5656	-0.4348	-0.4716	-0.0630
Tur	-0.3160	-0.5543	-0.1896	-0.4388

ent temperatures, elevation and reservoir size), explained variability in larval assemblages (SANDIN, 2003; SANDIN & JOHNSON, 2002). In this study, 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.

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, 1995). WILDERMUTH (1992) 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 (CANNINGS & CANNINGS, 1987).

Adult habitat preferences can 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 *Trithemis stictica*, *Crocothemis erythraea*, *Anax imperator*, *Africallagma glaucum*, *Ischnura senegalensis* and *Ceriagrion glabrum* in shallow marshes at reservoir edges at higher elevation (1050 m and 1350 m) probably showed that insolation strongly influenced growth and metamorphosis in some species. Larvae of *Tramea basilaris* and *Pseudagrion massaicum*, among other species, tolerated warm,

shady conditions at the 100 m site. Larvae occur where they obtain most of their preferred food, and be simultaneously protected from predators (CORBET, 1999). There were fish e.g. *Tilapia sarrmanii* in these 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 selected to enable greater chance of finding prey. 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.

HABITAT PREFERENCE AND ELEVATION

Elevation as a regional process alone was not as strong as its indirect influence on local environmental factors, especially on the Anisoptera larval assemblage. Zygoptera species distributions depended largely on local habitat, and indirectly on regional processes. However, odonate larvae in general, being the product of

Table VI

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				Zygoptera larvae			
	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				4.840	2.033
P-value			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

aerial dispersal in vagile adults, are restricted to particular habitats that they cannot change, even in adverse conditions. Since larvae sampled were mostly eurytopic species, distribution of species for both suborders therefore largely depended on corresponding dispersal of adults, most of which were elevation tolerant. Similarly, the larvae were also tolerant of a wide range of ecological conditions.

Except for *Agriocnemis falcifera*, most species recorded here also occur across large areas of Africa, and many are common throughout South Africa (SAMWAYS, 1999; 2002), although *Lestes 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 may 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. This means that only the most habitat tolerant species (as larvae as well as adults) can survive in the long-term.

CONCLUSION

The larvae over this wide elevational gradient (1350 m) were mostly geographically widespread habitat-tolerant species. There were a few exceptions (e.g. *Lestes tridens*, which is a low-elevation species). Even *Agriocnemis falcifera* (the only national endemic species sampled here) was elevation-tolerant. Community composition showed that there were no truly distinct larval assemblages at the various elevations. Despite the apparent diversity and heterogeneity of habitat types, the fine-scale micro-habitat conditions favoured by most larval species were remarkably common to many of these habitats. While local environmental variables and behaviour were important in explaining variations in larval assemblage structure and taxon richness for the various reservoirs, there were no major differences between these reservoir sites at the regional level. The implication of this is that reservoirs in this part of Africa may be very rich in dragonfly species, but all of these species are geographically widespread and locally common. The upshot is that although these artificial water bodies are not increasing the 'extent of occurrence', 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 over many ENSO events. Survival is about vagility and colonization, with these artificial reservoirs being an ideal and relatively permanent local habitat for them.

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