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Spatial and Temporal Patterns of Waterbird Assemblages in the Wilderness Lakes Complex, South Africa

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Abstract.—Environmental changes in estuaries resulting from resource use and management actions can detrimentally affect waterbirds. This study examined the distribution and abundance of 54 waterbird species from 1992 to 2010 in six intensively used and managed estuarine waterbodies, relative to four environmental variables (salinity, turbidity, depth variability and submerged macrophyte biomass) undergoing periodic and directional changes. Multivariate analyses enabled distinctions to be made between waterbirds associated with environmental conditions characteristic of either estuaries or estuarine lakes, and revealed spatial and temporal differences in waterbird abundances between and within waterbodies. Ducks and grebes were more abundant in low salinity deeper waterbodies, while waders, cormorants and gulls were more abundant in high salinity shallow waterbodies. Higher quantity and quality of food sources attract herbivorous waterbirds to saline lakes rather than estuaries. Water depth variability influences accessibility of feeding areas, with decreased variability in water levels increasing habitat suitability for herbivores, and reduced open periods in the estuaries decreasing habitat suitability for waders. Turbidity did not significantly influence the distribution of waterbirds, whereas disturbance from human activities and vegetation of sandbanks were considered to be important factors. The estuarine lakes systems provide a mosaic of different habitat conditions, essential for maintaining a diverse waterbird community. *Received 10 May 2013, accepted 5 August 2013.*

Key words.—depth variability, salinity, submerged macrophytes, Swartvlei Estuary, Touw Estuary, turbidity, waterbird communities.

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The Swartvlei and Wilderness systems of estuarine lakes, collectively known as the Wilderness Lakes Complex (WLC), are rare wetland types in South Africa, with only eight (3.1%) of the approximately 250 estuarine waterbodies in the country being classified as estuarine lakes (Whitfield 2000). The conservation importance of the WLC is demonstrated by its incorporation into the Garden Route National Park, while most of the Wilderness system was declared a Ramsar site in 1991, having met the criteria for waterbird abundance (Ramsar Bureau 1990). In spite of this high conservation value, these estuarine wetlands and the waterbirds they support are, like many other estuaries in South Africa, under mounting threat due to a combination of climatic change and resource use pressures, in addition to invasive management actions such as artificial breaching, which reduce disturbance and hence temporal and spatial heterogeneity in the structure and dynamics of natural communities (Whitfield *et al.* 2012). Besides natural variability in water quality (Russell 1999), submerged macrophytes (Weisser and Howard-Williams 1982; Allanson and Whitfield 1983) and fishes (Whitfield 1984, 1986), there is the disturbing longer term trend of directional changes in several abiotic and biotic variables. These include a reduction in marine connectivity, decreased water depth in channels, reductions in salinity and pH (Russell 2013), loss of wetland vegetation (Russell 2003), and invasion by alien fish (Olds *et al.* 2010). All such environmental changes can detrimentally affect waterbird communities either directly or indirectly through alteration of habitats and availability of resources.

The global populations of many waterbirds that use estuarine wetlands are in decline (Stroud *et al.* 2004), particularly in Africa (Dodman 2007; Wetlands International 2012), emphasizing the urgency for the conservation and correct management of these ecosystems. Regular surveys of waterbird abundances in the WLC have been undertaken since 1992 as part of a program to identify and understand long-term ecosystem changes. Identifying the causes for changes, and formulation of management strategies for the protection of wetlands and the waterbirds they support, requires comprehensive knowledge of the links between the life history patterns of waterbirds and the physical, chemical and biological attributes of the wetlands.

The aim of this study was to describe the distribution and abundance of waterbirds in the waterbodies of the WLC and to interpret the patterns observed in relation to relevant environmental factors. This entailed: 1) examining the spatial distribution of abundant species; 2) investigating of correlations between waterbird distribution and highly variable environmental factors; 3) spatial and temporal grouping of waterbodies according to the similarity of the waterbirds they support; and 4) grouping the waterbird species according to the similarity of their distribution on different waterbodies within the WLC.

METHODS

Study Area

The WLC is situated on the Cape south coast of South Africa (33° 59' to 34° 02' S and 22° 35' to 22° 46' E) and comprises two estuarine systems (Fig. 1). The Wilderness System consists of three estuarine lakes: Rondevlei (~1.38 km^2), Langvlei (~2.83 km^2) and Eilandvlei (~1.78 km^2), and the Touw Estuary (~0.45 km^2), all of which are interconnected by shallow channels. The Swartvlei System consists of Swartvlei Lake (~11.0 km^2), which is directly connected to the Swartvlei Estuary (~2.12 km^2), but excludes the lower reaches of the Karatara River. Lakes in the Wilderness System are relatively shallow with maximum depths ranging between 4.0 and 6.5 m (Hall *et al.* 1987), whereas Swartvlei Lake, with a maximum depth of 16.6 m (Whitfield *et al.* 1983), is relatively deep. Both estuaries are shallow with maximum depths seldom exceeding 4.0 m. Much of the upper reaches of the Swartvlei Estuary consist of intertidal saltmarshes and sandflats, whereas these habitats are largely absent from the Touw Estuary. Both Touw and Swartvlei estuaries are naturally temporarily open/closed estuaries, which are regularly artificially breached at water heights substantially below (approximately -1.5 m) the level that would be reached if breaching were to occur naturally.

Submerged macrophytes occur in all of the estuarine waterbodies, though they are generally confined to waters less than 3.0 m deep (Whitfield 1984). Lake communities are dominated by fennel-leaved pondweed (*Potamogeton pectinatus*), water hornwart (*Ceratophylum*

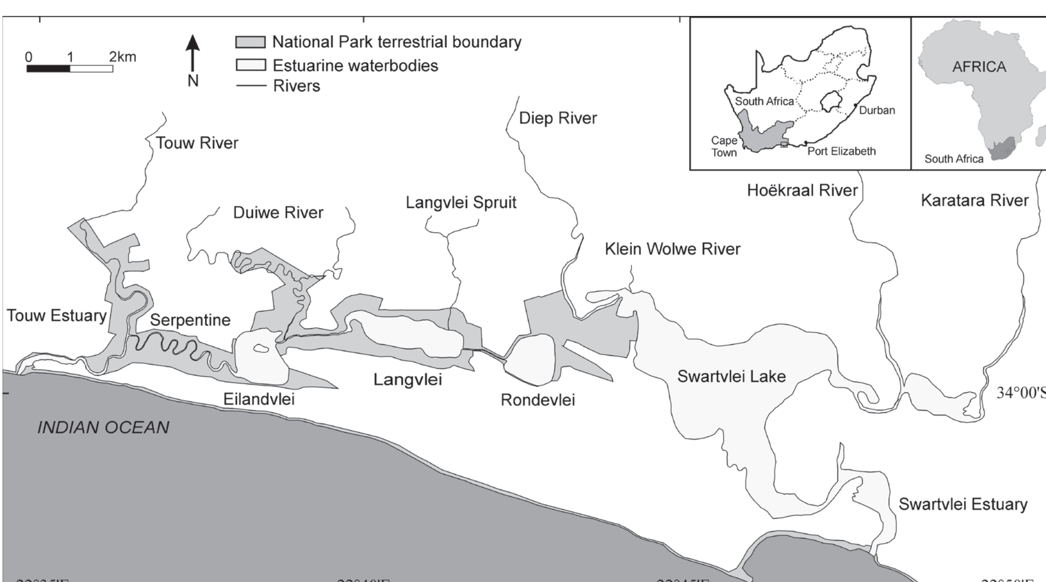


Figure 1. Study area of two estuarine lake systems in the Garden Route National Park, consisting of two temporarily open/closed estuaries (Touw and Swartvlei) and four estuarine lakes (Eilandvlei, Langvlei, Rondevlei and Swartvlei).

demersum), stoneworts (Charophyta) and filamentous algae (Howard-Williams and Liptrot 1980; Weisser and Howard-Williams 1982; Whitfield *et al.* 1983). Cape dwarf-eelgrass (*Nanozostera capensis*) and spiral ditch-grass (*Ruppia cirrhosa*) are abundant in Swartvlei Estuary (Whitfield *et al.* 1983), and occur sporadically in the Touw Estuary (Allanson and Whitfield 1983). The lakes are fringed by a narrow margin of emergent macrophytes of which common reed (*Phragmites australis*) and clubrush (*Schoenoplectus scirpoides*) are widespread and abundant. The fish fauna consists of a combination of estuarine (Whitfield 1984; Hall *et al.* 1987; Russell 1996) and alien freshwater species (Olds *et al.* 2010).

Waterbird Counts

Waterbird abundance was determined biannually during mid-summer (January-February) and mid-winter (July-August) in all estuarine waterbodies from 1992 to 2010. Counts were conducted by four observers using binoculars and a spotting scope from a boat following a standardized route. The route allowed for surveillance of all open water areas, as well as an estimated 90 to 95% of marginal areas with emergent macrophytes. Variability in observer error was minimized by use of the same observers wherever possible throughout the study period, with observers specializing in different species. Each species was counted once per waterbody in each survey. Counts were conducted from 08:00 to approximately 12:00, in low wind conditions, and on high tides in the Touw and Swartvlei estuaries when the estuary mouths were open. Most counts were conducted over three or four consecutive days.

All species used in analyses are listed in Tables 2 and 3 (including scientific names and species grouping terms). Vernacular names follow Hockey *et al.* (2005).

Environmental Variables

Water quality parameters of surface waters were measured in the same month as waterbird counts at five localities each in Rondevlei, Langvlei and Eilandvlei, six localities in Swartvlei Lake, and eight localities each along the length of Touw and Swartvlei estuaries (Fig. 1). Salinity was measured in the field at 30 cm depth using YSI Model 33 (1992 to 2005) and Model 30 (2005 to 2010) S-C-T meters. Turbidity (Nephelometric Turbidity Units or NTUs) was measured in a laboratory with Hach Model 16800 (1992 to 2008) and Model 2011N (2008 to 2010) turbidimeters. Median values of all samples within a waterbody were used in analyses.

Water height data were obtained from the South African Department of Water Affairs (unpubl. data), which maintains continuous water level recorders in all waterbodies in the WLC with the exception of Swartvlei Estuary. As Swartvlei Lake and Swartvlei Estuary are permanently linked, water height variability in the two systems is likely to be similar. Consequently, water height data for Swartvlei Lake were also used for Swartvlei Estuary.

Standing biomass of submerged macrophytes (g/m^2) was determined during May and June from 1992 to 2010. Assessments were undertaken biennially between 2000 and 2004 in the Touw Estuary, Langvlei and Rondevlei, and between 1998 and 2005 in Swartvlei Lake and Swartvlei Estuary. Stratified random sampling was used to position four littoral transects around each lake, the limits of which were the inner edge of the emergent macrophyte zone and the 2 m depth contour. In the Touw and Swartvlei estuaries, five transects were positioned in each waterbody from shoreline to shoreline across the width of the primary channel. A submerged macrophyte sampler (Howard-Williams and Longman 1976) was used to collect the above ground portions of plants at five 0.063 m^2 sample points along each transect. Living plant tissue was oven-dried at 55 °C for approximately 7 days and weighed to the nearest gram on an electronic balance. Missing data points were estimated by interpolation.

Analysis

The association between the bird assemblage and environmental variables was examined using Canonical Correspondence Analysis (CCA) (Kovach Computing Services 2005) on log(x+1) transformed waterbird abundance data (Ter Braak 1986; Palmer 1993) grouped by waterbody and season. Species that were recorded in less than 10% of waterbodies surveyed over the entire study period were excluded from this analysis. The output of the CCA was displayed in an ordination diagram, with species represented as points and environmental variables represented as vectors. The directions of vectors represent gradients of the corresponding environmental variables, with vector length representing how much the species distributions differ along that environmental variable (Ter Braak 1986). Perpendicular projection of the species points in the direction of the vectors indicates their position along the gradient. Cluster analysis (Kovach Computing Services 2005) was undertaken based on the Wards' minimum variance method using the scores of the first two axes of CCA to facilitate visualization of the distribution of species along gradients generated by the CCA.

The spatial and temporal similarity of waterbodies in terms of waterbird assemblages was examined using cluster analysis (Wards minimum variance method) on log(x+1) transformed waterbird abundance data grouped by waterbody and season. As with CCA analyses, uncommon species were excluded.

RESULTS

The estuarine lakes had lower mean salinities, but higher values of turbidity and submerged macrophyte biomass than estuaries (Table 1). Depth variability was largest in the Touw Estuary, less extreme in the lakes of the Wilderness system, and least in the Swartvlei system (Table 1).

A total of 75 waterbird species were recorded during the surveys, of which 54 were

Table 1. Average of environmental variables in the period 1992-2010 (SE).

Waterbody	Salinity	Turbidity (NTU)	Plant Biomass (g/m^2)	Depth Variability (m)
Rondevlei	9.63 (0.35)	5.61 (0.45)	708 (105)	0.47 (0.03)
Langvlei	6.97 (0.27)	5.34 (0.45)	936 (133)	0.40 (0.03)
Eilandvlei	6.55 (0.39)	6.57 (0.85)	708 (175)	0.52 (0.04)
Touw Estuary	13.6 (1.35)	3.09 (0.23)	46 (16)	0.66 (0.06)
Swartvlei Lake	11.21 (0.91)	4.08 (0.51)	913 (117)	0.33 (0.04)
Swartvlei Estuary	19.93 (1.10)	3.20 (0.17)	175 (23)	0.33 (0.04)

recorded in 10% or more of the waterbodies surveyed over the study period (Tables 2 and 3). Frequency of occurrence of waterbirds during surveys (Table 2), as well as abundance on different waterbodies (Table 3), varied widely between species.

Relationship with Environmental Variables

The canonical axes I and II collectively explained 88.9% of the variance (54.8% and 34.1%, respectively). The first axis showed a contrast between species associated with high salinity, low turbidity, and low submerged macrophyte biomass (estuaries) and those that occurred predominantly in less saline, deeper waterbodies with extensive submerged macrophyte stands (estuarine lakes) (Fig. 2). The second axis displayed predominantly a gradient of water depth variability.

Species more frequently associated with higher salinity waters supporting submerged macrophyte stands (Swartvlei Estuary) included African Black Oystercatcher, Common Greenshank, Curlew Sandpiper, Caspian Tern, Marsh Sandpiper, Kittlitz's Plover, Black-winged Stilt, Cape Teal, Osprey and African Sacred Ibis (Fig. 2). By contrast, species associated predominantly with higher salinity waterbodies with little or no submerged macrophytes (Touw Estuary) included Half-collared Kingfisher, Giant Kingfisher and Water Thick-knee (Fig. 2). Waterbirds more commonly occurring in higher turbidity waters with abundant submerged macrophytes and relatively lower salinity, which were conditions characteristic of several of the lakes, included most of the herbivorous ducks and geese and Common Moorhen. In addition, there were open water piscivores such as grebes and Common Tern, as well as shorebirds, waders and raptors that occur in or adjacent to the emergent macrophyte stands on the edges of waterbodies, such as the Black Crake, Glossy Ibis, Yellow-billed Egret, Wood Sandpiper, African Purple Swamphen and African Marsh-Harrier.

Waterbirds more commonly associated with waterbodies where water depth variability was lowest included small, invertebrate-feeding waders such as Common Greenshank, Kittlitz's Plover, Marsh Sandpiper, Curlew Sandpiper and Ruff, as well as some larger waders such as African Spoonbill and Greater Flamingo, and the herbivorous Cape Teal. By contrast, species more commonly associated with waterbodies that experienced larger variability in water depth included plunge divers such as the kingfishers, visual pursuit piscivores species such as cormorants, darter and grebes, and herbivorous waterbirds such as ducks and rallids (Fig. 2). Also associated with these more depth variable waterbodies were some waterbirds which, due to their largely terrestrial or waters-edge feeding habits, were unlikely to have their feeding efficiency significantly affected by water depth, such as Water Thick-knee and African Marsh-Harrier.

Species Associations

Cluster analysis reveals 10 main groups of waterbirds that differed in terms of both the abundance and distribution of composite species. These 10 main groups could be broadly graded as consisting predominantly of species that occur almost exclusively on estuaries, through to those that occur almost exclusively on lakes, with a range in between that occur with varying frequency and abundance on different waterbodies (Fig. 3). Group 1 contained the Water Thick-knee and kingfishers, which occurred predominantly on estua-

Table 2. Frequency of occurrence and mean number (in brackets) of waterbirds on waterbodies in the Wilderness Lakes Complex during all surveys conducted between 1992 and 2010. Species grouped according to occurrence in cluster groups of CCA scores in Figure 3. Waterbodies ordered with estuaries on the left and saline lakes on the right.

			Touw Estuary		Swartvlei Estuary		Swartvlei Lake		Eilandvlei		Langvlei		Rondevlei	
Group	Waterbird		%	No.	%	No.	%	No.	%	No.	%	No.	%	No.
1	Water Thick-knee	*Burhinus vermiculatus*	88	(4)	43	(2)	3	(< 1)	43	(1)	0	(0)	0	(0)
	Giant Kingfisher	*Megaceryle maximus*	68	(1)	38	(< 1)	33	(< 1)	13	(< 1)	5	(< 1)	3	(< 1)
	Half-collared Kingfisher	*Alcedo semitorquata*	45	(< 1)	5	(< 1)	5	(< 1)	5	(< 1)	0	(0)	3	(< 1)
2	African Black Oystercatcher	*Haematopus moquini*	0	(0)	70	(2)	0	(0)	0	(0)	0	(0)	0	(0)
	Kittlitz's Plover	*Charadrius pecuarius*	0	(0)	60	(8)	3	(< 1)	0	(0)	43	(3)	38	(3)
	Common Greenshank	*Tringa nebularia*	8	(< 1)	80	(22)	10	(< 1)	0	(0)	28	(1)	38	(1)
	Caspian Tern	*Sterna caspia*	3	(< 1)	78	(4)	45	(< 1)	5	(< 1)	30	(< 1)	15	(< 1)
3	Cape Teal	*Anas capensis*	0	(0)	73	(5)	53	(3)	18	(< 1)	50	(5)	58	(5)
	Marsh Sandpiper	*Tringa stagnatilis*	0	(0)	35	(15)	8	(< 1)	0	(0)	43	(3)	35	(2)
	Curlew Sandpiper	*Calidris ferruginea*	3	(< 1)	40	(36)	3	(< 1)	0	(0)	25	(3)	15	(2)
	Black-winged Stilt	*Himantopus himantopus*	0	(0)	100	(38)	38	(10)	5	(< 1)	85	(19)	75	(8)
4	Grey Heron	*Ardea cinerea*	68	(1)	100	(14)	85	(5)	55	(1)	83	(4)	73	(2)
	Black-headed Heron	*Ardea melanocephala*	13	(< 1)	68	(1)	43	(< 1)	30	(< 1)	48	(< 1)	25	(< 1)
	Little Egret	*Egretta garzetta*	38	(< 1)	98	(19)	75	(6)	58	(2)	90	(12)	80	(6)
	African Sacred Ibis	*Threskiornis aethiopicus*	0	(0)	73	(4)	13	(< 1)	5	(< 1)	10	(< 1)	3	(< 1)
	Osprey	*Pandion haliaetus*	0	(0)	38	(< 1)	23	(< 1)	0	(0)	15	(< 1)	15	(< 1)
	Common Sandpiper	*Tringa hypoleucos*	30	(< 1)	33	(< 1)	8	(< 1)	0	(0)	0	(0)	0	(0)
5	White-breasted Cormorant	*Phalacrocorax lucidus*	98	(11)	100	(21)	100	(26)	98	(18)	95	(27)	95	(9)
	Cape Cormorant	*Phalacrocorax capensis*	55	(2)	85	(5)	53	(3)	45	(41)	20	(12)	20	(21)
	Reed Cormorant	*Phalacrocorax africanus*	93	(25)	100	(81)	98	(95)	100	(48)	98	(83)	100	(36)
	Blacksmith Lapwing	*Vanellus armatus*	95	(5)	100	(19)	78	(4)	95	(5)	100	(12)	88	(7)
	Kelp Gull	*Larus dominicanus*	100	(11)	100	(22)	100	(8)	100	(4)	88	(3)	75	(2)
	Pied Kingfisher	*Ceryle rudis*	75	(2)	80	(3)	70	(3)	45	(1)	73	(2)	65	(2)
	Cape Wagtail	*Motacilla capensis*	50	(1)	75	(2)	48	(1)	55	(2)	63	(2)	43	(< 1)
6	Little Grebe	*Tachybaptus ruficollis*	83	(9)	85	(101)	98	(122)	98	(36)	100	(269)	98	(81)
	Little Bittern	*Ixobrychus minutus*	10	(< 1)	3	(< 1)	10	(< 1)	10	(< 1)	35	(< 1)	10	(< 1)
	Egyptian Goose	*Alopochen aegyptiaca*	48	(2)	65	(5)	88	(9)	95	(13)	90	(62)	95	(86)
	Yellow-billed Duck	*Anas undulata*	100	(20)	100	(108)	100	(153)	100	(71)	100	(299)	98	(228)
	African Fish-Eagle	*Haliaeetus vocifer*	20	(< 1)	38	(< 1)	90	(3)	50	(< 1)	80	(3)	45	(< 1)
	Red-knobbed Coot	*Fulica cristata*	70	(9)	100	(695)	100	(4,174)	100	(601)	100	(1,994)	100	(950)

Table 2. (Continued) Frequency of occurrence and mean number (in brackets) of waterbirds on waterbodies in the Wilderness Lakes Complex during all surveys conducted between 1992 and 2010. Species grouped according to occurrence in cluster groups of CCA scores in Figure 3. Waterbodies ordered with estuaries on the left and saline lakes on the right.

			Touw Estuary		Swartvlei Estuary		Swartvlei Lake		Eilandvlei		Langvlei		Rondevlei	
Group	Waterbird		%	No.	%	No.	%	No.	%	No.	%	No.	%	No.
7	Great Crested Grebe	*Podiceps cristatus*	5	(< 1)	58	(2)	98	(40)	100	(23)	100	(67)	100	(55)
	African Darter	*Anhinga rufa*	50	(4)	60	(2)	95	(25)	93	(7)	83	(8)	48	(3)
	Purple Heron	*Ardea purpurea*	43	(< 1)	18	(< 1)	70	(2)	93	(3)	93	(4)	63	(3)
	Hottentot Teal	*Anas hottentota*	0	(0)	3	(< 1)	3	(< 1)	15	(< 1)	50	(3)	23	(1)
	African Marsh-Harrier	*Circus ranivorus*	0	(0)	23	(< 1)	48	(1)	58	(< 1)	83	(2)	45	(< 1)
	Black Crake	*Amaurornis flavirostris*	13	(< 1)	0	(0)	20	(< 1)	40	(< 1)	73	(2)	40	(< 1)
	Common Moorhen	*Gallinula chloropus*	65	(2)	28	(2)	88	(9)	100	(25)	100	(47)	88	(14)
	Malachite Kingfisher	*Alcedo cristata*	38	(< 1)	18	(< 1)	50	(2)	38	(1)	80	(3)	45	(< 1)
8	African Spoonbill	*Platalea alba*	3	(< 1)	55	(3)	50	(3)	20	(< 1)	80	(10)	58	(5)
	Greater Flamingo	*Phoenicopterus ruber*	0	(0)	15	(2)	15	(20)	0	(0)	5	(< 1)	23	(3)
	Cape Shoveler	*Anas smithii*	10	(< 1)	95	(153)	98	(212)	100	(45)	100	(221)	100	(121)
	Three-banded Plover	*Charadrius tricollaris*	5	(< 1)	23	(1)	8	(< 1)	3	(< 1)	53	(2)	35	(1)
	Ruff	*Philomachus pugnax*	0	(0)	18	(4)	10	(2)	0	(0)	53	(17)	40	(16)
9	Yellow-billed Egret	*Egretta intermedia*	0	(0)	15	(< 1)	15	(< 1)	0	(0)	45	(1)	18	(< 1)
	Glossy Ibis	*Plegadis falcinellus*	0	(0)	18	(< 1)	10	(< 1)	15	(< 1)	73	(6)	48	(2)
	Red-billed Teal	*Anas erythrorhyncha*	0	(0)	38	(3)	43	(22)	35	(1)	85	(17)	80	(10)
	Spur-winged Goose	*Plectropterus gambensis*	0	(0)	10	(< 1)	30	(2)	5	(< 1)	58	(5)	13	(1)
	African Purple Swamphen	*Porphyrio madagascariensis*	8	(< 1)	30	(< 1)	90	(5)	85	(3)	98	(5)	80	(2)
	Wood Sandpiper	*Tringa glareola*	0	(0)	10	(< 1)	5	(< 1)	15	(< 1)	50	(2)	23	(1)
	Common Tern	*Sterna hirundo*	5	(< 1)	18	(< 1)	13	(< 1)	35	(2)	50	(4)	50	(7)
10	Black-necked Grebe	*Podiceps nigricollis*	0	(0)	0	(0)	15	(< 1)	18	(1)	53	(18)	55	(17)
	White-backed Duck	*Thalassornis leuconotus*	0	(0)	0	(0)	53	(20)	33	(5)	88	(40)	63	(17)
	Southern Pochard	*Netta erythropthalma*	0	(0)	10	(< 1)	35	(4)	35	(8)	100	(69)	83	(60)
	Maccoa Duck	*Oxyura maccoa*	0	(0)	0	(0)	3	(< 1)	8	(< 1)	93	(34)	55	(7)

Table 3. Mean abundance of waterbirds in all samples comprising waterbody groupings 1-13 as per cluster analysis of waterbodies in Figure 4. Heading abbreviations for waterbodies TE, EV, LV, RV, SVL, SVE refer respectively to Touw Estuary, Eilandvlei, Langvlei, Rondevlei, Swartvlei Lake and Swartvlei Estuary, and for sample season S and W respectively to summer and winter. Superscript Δ indicates dabbling ducks, Φ indicates diving ducks, and * indicates Palearctic migrants.

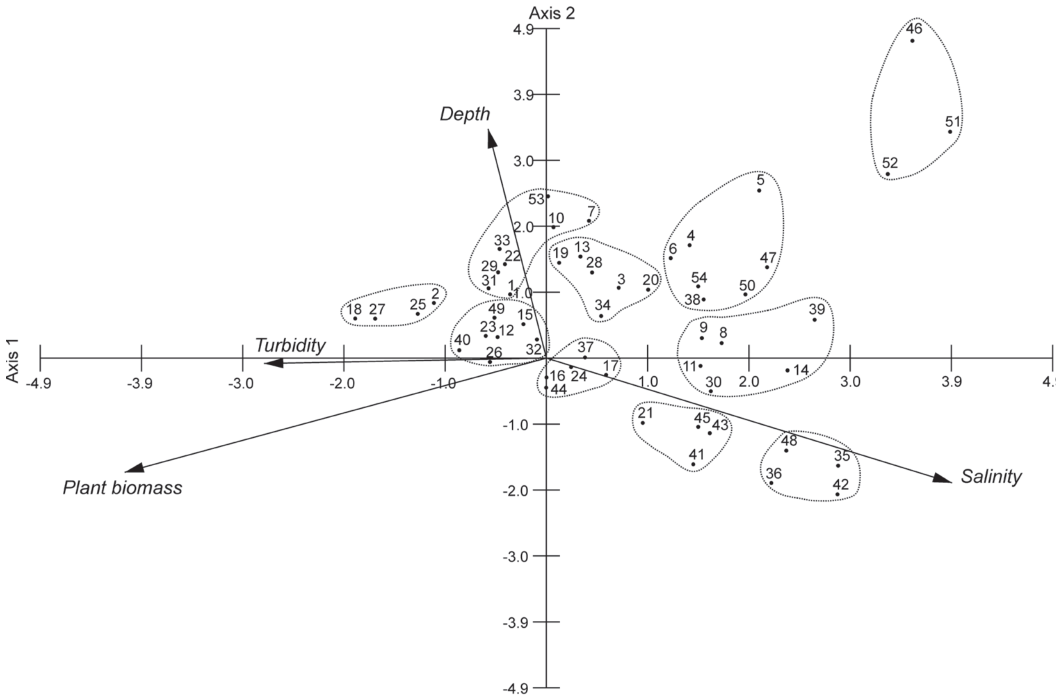
	Group, Waterbody and Season												
	1	2	3	4	5	6	7	8	9	10	11	12	13
	TE	TE	RV	LV	RV & LV	EV	EV	SVL	SVL	SVE	SVE	SVE	SVE
Waterbird	W	S	W	W	S	W	S	W	S	W	S	S	S
Grebes													
Great Crested Grebe	0	0	61	53	58	30	20	41	46	2	11	1	0
Black-necked Grebe	0	0	29	38	2	1	0	1	0	0	0	0	0
Little Grebe	18	4	175	434	103	66	18	164	82	202	51	12	7
Ducks and geese													
Yellow-billed Duck $^{\Delta}$	20	19	140	236	375	43	61	155	203	112	151	28	140
Cape Shoveler $^{\Delta}$	0	0	45	211	305	14	46	59	435	148	300	86	112
Red-billed Teal $^{\Delta}$	0	0	12	69	10	1	1	4	7	5	2	0	0
Cape Teal $^{\Delta}$	0	0	8	7	4	0	1	2	5	6	7	5	2
Hottentot Teal $^{\Delta}$	0	0	1	1	2	0	1	0	0	1	0	0	0
White-backed Duck $^{\Phi}$	0	0	25	98	12	5	1	27	2	0	0	0	0
Southern Pochard $^{\Phi}$	0	0	70	69	67	9	1	6	6	0	1	0	0
Maccoa Duck $^{\Phi}$	0	0	11	72	4	0	0	0	0	0	0	0	0
Egyptian Goose	2	1	31	54	99	12	27	8	12	3	4	24	0
Spur-winged Goose	0	0	0	3	5	0	1	1	1	0	0	2	2
Cormorants and darter													
White-breasted Cormorant	19	6	10	41	19	31	8	39	12	26	16	16	12
Cape Cormorant	5	0	43	1	0	111	1	2	1	10	1	4	2
Reed Cormorant	45	9	43	147	52	90	21	111	76	94	114	38	65
African Darter	7	1	4	30	3	13	5	25	19	2	4	1	1
Large non-migratory/nomadic waders													
Grey Heron	2	1	3	7	2	1	1	4	4	10	19	11	16
Purple Heron	1	0	2	6	2	2	2	2	1	0	2	0	0
Little Egret	1	1	6	5	13	3	2	2	12	26	21	12	6
Yellow-billed Egret	0	0	0	2	1	0	0	0	0	0	1	0	0
African Sacred Ibis	0	0	0	0	0	0	0	0	0	6	6	1	2
Glossy Ibis	0	0	1	4	6	0	0	0	0	1	1	0	0
African Spoonbill	0	0	2	6	12	1	0	1	4	2	5	3	0

Table 3.(Continued) Mean abundance of waterbirds in all samples comprising waterbody groupings 1-13 as per cluster analysis of waterbodies in Figure 4. Heading abbreviations for waterbodies TE, EV, LV, RV, SVL, SVE refer respectively to Touw Estuary, Eilandvlei, Langvlei, Rondevlei, Swartvlei Lake and Swartvlei Estuary, and for sample season S and W respectively to summer and winter. Superscript Δ indicates dabbling ducks, Φ indicates diving ducks, and * indicates Palearctic migrants.

	Group, Waterbody and Season												
	1	2	3	4	5	6	7	8	9	10	11	12	13
	TE	TE	RV	LV	RV & LV	EV	EV	SVL	SVL	SVE	SVE	SVE	SVE
Waterbird	W	S	W	W	S	W	S	W	S	W	S	S	S
Large migratory wader													
Greater Flamingo	0	0	3	37	2	0	0	13	0	3	1	0	0
Small non-migratory/nomadic wader													
Black-winged Stilt	0	0	11	22	18	0	1	0	9	54	20	22	38
Small migratory waders													
Common Sandpiper *	0	1	0	0	0	0	0	0	0	0	1	0	1
Wood Sandpiper *	0	0	0	0	2	0	0	0	0	0	1	0	0
Marsh Sandpiper *	0	0	0	0	5	0	0	0	1	0	15	5	70
Common Greenshank *	0	0	0	0	2	0	0	0	0	4	14	22	81
Curlew Sandpiper *	0	0	0	0	6	0	0	0	0	1	14	0	221
Ruff *	0	0	0	0	34	0	0	0	4	0	15	0	4
Shorebirds													
Black-headed Heron	0	0	1	1	1	0	0	1	2	1	2	1	1
Little Bittern	0	0	0	0	0	0	0	0	0	0	0	0	0
African Black Oystercatcher	0	0	0	0	0	0	0	0	0	1	1	3	2
Kittlitz's Plover	0	0	2	2	4	0	0	0	0	11	0	11	13
Three-banded Plover	0	0	1	4	1	0	0	0	0	2	0	0	2
Blacksmith Lapwing	3	5	5	11	11	4	4	3	5	20	20	15	15
Water Thick-knee	5	4	0	0	0	2	0	0	0	3	1	0	1
Cape Wagtail	2	1	1	3	1	1	2	1	1	2	2	2	3
Rallids													
Red-knobbed Coot	10	6	1,367	4,167	1,341	1,142	540	4,834	3,505	680	1,496	120	135
Common Moorhen	3	1	27	78	17	31	13	17	5	3	1	0	0
African Purple Swamphen	0	0	3	5	4	3	3	4	4	0	1	0	0
Black Crake	0	0	1	3	2	1	0	0	1	0	0	0	0

Table 3.(Continued) Mean abundance of waterbirds in all samples comprising waterbody groupings 1-13 as per cluster analysis of waterbodies in Figure 4. Heading abbreviations for waterbodies TE, EV, LV, RV, SVL, SVE refer respectively to Touw Estuary, Eilandvlei, Langvlei, Rondevlei, Swartvlei Lake and Swartvlei Estuary, and for sample season S and W respectively to summer and winter. Superscript Δ indicates dabbling ducks, Φ indicates diving ducks, and * indicates Palearctic migrants.

	Group, Waterbody and Season												
	1	2	3	4	5	6	7	8	9	10	11	12	13
	TE	TE	RV	LV	RV & LV	EV	EV	SVL	SVL	SVE	SVE	SVE	SVE
Waterbird	W	S	W	W	S	W	S	W	S	W	S	S	S
Raptors													
African Fish-Eagle	1	0	1	2	3	1	1	2	3	0	1	0	1
African Marsh-Harrier	0	0	1	2	1	1	1	1	1	0	1	0	0
Osprey	0	0	0	0	0	0	0	0	0	0	1	1	0
Gull and terns													
Kelp Gull	9	12	3	6	2	6	3	8	6	23	16	32	20
Caspian Tern	0	0	0	1	0	0	0	1	1	3	6	6	4
Common Tern *	0	0	4	2	7	5	2	0	0	1	0	0	2
Kingfishers													
Pied Kingfisher	2	2	2	2	2	1	2	2	3	4	3	3	3
Giant Kingfisher	1	1	0	0	0	0	0	1	0	1	0	1	0
Half-collared Kingfisher	1	1	0	0	0	0	0	0	0	0	0	0	0
Malachite Kingfisher	1	1	1	3	2	2	1	2	1	0	0	0	0



1	Great Crested Grebe	19	Egyptian Goose	37	Three-banded Plover
2	Black-necked Grebe	20	Yellow-billed Duck	38	Blacksmith Lapwing
3	Little Grebe	21	Cape Teal	39	Common Sandpiper
4	White-breasted Cormorant	22	Hottentot Teal	40	Wood Sandpiper
5	Cape Cormorant	23	Red-billed Teal	41	Marsh Sandpiper
6	Reed Cormorant	24	Cape Shoveler	42	Common Greenshank
7	African Darter	25	Southern Pochard	43	Curlew Sandpiper
8	Grey Heron	26	Spur-winged Goose	44	Ruff
9	Black-headed Heron	27	Maccoa Duck	45	Black-winged Stilt
10	Purple Heron	28	African Fish-Eagle	46	Water Thick-knee
11	Little Egret	29	African Marsh-Harrier	47	Kelp Gull
12	Yellow-billed Egret	30	Osprey	48	Caspian Tern
13	Little Bittern	31	Black Crake	49	Common Tern
14	African Sacred Ibis	32	African Purple Swamphen	50	Pied Kingfisher
15	Glossy Ibis	33	Common Moorhen	51	Giant Kingfisher
16	African Spoonbill	34	Red-knobbed Coot	52	Half-collared Kingfisher
17	Greater Flamingo	35	African Black Oystercatcher	53	Malachite Kingfisher
18	White-backed Duck	36	Kittlitz's Plover	54	Cape Wagtail

Figure 2. Plot of first two axes of Canonical Correspondence Analysis (CCA) ordination based on (log transformed) waterbirds abundance data (·) and environmental variables (arrows), with superimposed waterbird groups from cluster analyses of CCA scores as illustrated in Figure 3. Numbers assigned to waterbirds listed below the CCA plot correspond to those in the CCA plot.

rine systems and particularly the Touw Estuary (Table 2) and occasionally on some lakes but only in low numbers. Of the waterbirds in Group 2, the African Black Oystercatcher was only recorded on Swartvlei Estuary (Table 2), whereas small waders and Caspian Tern were at times abundant on this estuary, and to a lesser extent some of the lakes, particularly Langvlei, but occurred infrequently on the Touw Estuary (Table 2). Group 3 comprising Cape Teal and several small wading birds was similar to Group 2 in terms of spe-

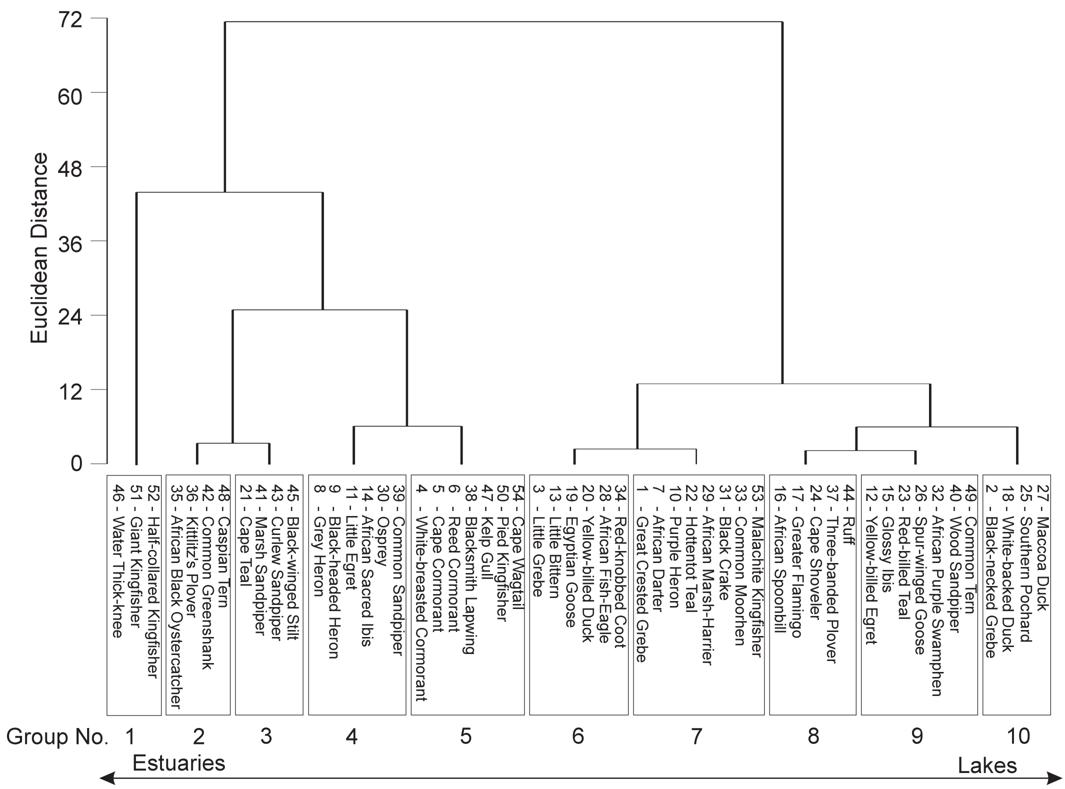


Figure 3. Dendrogram representing the similarity amongst waterbird species in the space defined by the first two axes of the CCA plot illustrated in Figure 2. Waterbird groups numbered 1 to 10 are arranged roughly from those characteristic of estuaries to those characteristic of estuarine lakes, as indicated by the horizontal line at the base of the figure.

cies distribution, but differed in that at times these species were generally more abundant than those of Group 2. Group 4 consisted of several large wading birds as well as Osprey and Common Sandpiper, which were generally widespread throughout the WLC, though with the exception of Little Egret were usually not abundant (Table 2). Common Sandpiper had the most restricted distribution of the waterbirds in Group 4, occurring principally on the estuaries and occasionally on Swartvlei Lake but always in low numbers, whereas the larger wading birds were generally more widespread and abundant. Groups 5 and 6 included the cormorants, abundant ducks, geese and rallids, resident shorebirds, a raptor and a gull. These groups could be described as spatial generalists in that they were frequently recorded on all waterbodies, though with species in Group 5 having moderately higher abundance on Touw and Swartvlei estuaries and Eilandvlei, and species in Group 6 generally being more abundant on the vegetated inner lakes than the estuaries (Table 2). Group 7 comprised species that generally had relatively low abundance on both Touw and Swartvlei estuaries, with Great Crested Grebe, Common Moorhen and African Dater being relatively abundant on the four lakes, and Purple Heron, African Marsh-Harrier and Malachite Kingfisher, while not abundant, were frequently recorded on these waterbodies. Group 8 comprised African Spoonbill, Greater Flamingo, Cape Shoveler, Three-banded Plover and Ruff that were also spatial generalists that have been recorded on most waterbodies. Most species in this group were more abundant on the four lakes, and in some instances Swartvlei Estuary, but all were seldom recorded on the Touw Estuary, and when present there occurred in very low numbers (Table 2). Group 9 consisted of Yellow-billed Egret, Glossy Ibis, Red-billed Teal, Spur-winged Goose, African Purple Swamphen, Wood Sandpiper and Common Tern of which all, with the occasional exception of Red-billed Teal, occurred in relatively low numbers, and far more frequently on the lakes (Table 2). Most of the species in Group 9 were not recorded on Touw Estuary during surveys. Group 10 comprised Black-necked Grebe and three diving ducks that occurred almost exclusively on the lakes, and particularly Rondevlei and Langvlei. None of these species were recorded on Touw Estuary, and only Southern Pochard occurred infrequently and in low numbers on Swartvlei Estuary (Table 2).

Waterbody Similarity

Cluster analysis separated the count data for the various waterbodies into 13 main groups (Fig. 4) revealing both spatial differences between waterbodies, and temporal variations within waterbodies in terms of waterbird abundances. The Touw Estuary was the only waterbody represented in Groups 1 and 2, with many waterbirds occurring either in low numbers or being absent (Table 3). Group 1 consists predominantly of sites surveyed in winter, and Group 2 in summer. The difference lay principally in the increased abundance of Little Grebe, Reed Cormorant and White-breasted Cormorant in winter surveys (Table 3).

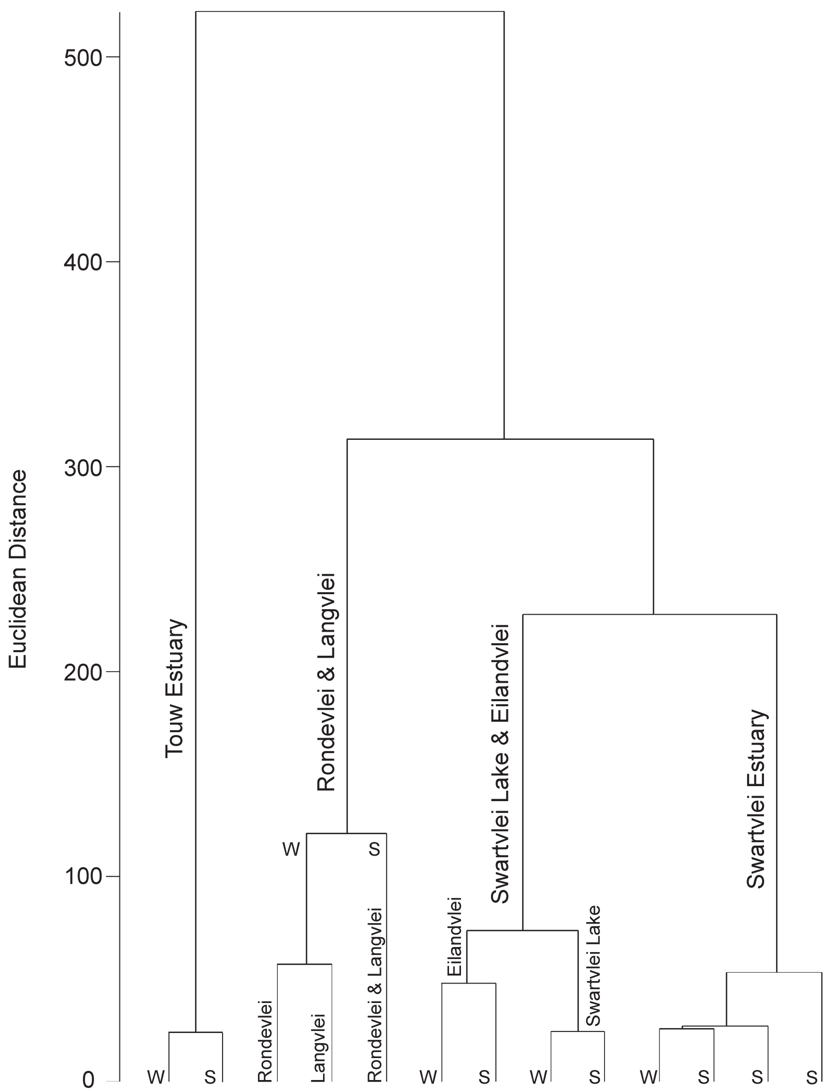
Groups 3 to 5 consisted predominantly Rondevlei and Langvlei counts that were distinctive in terms of the relatively high abundances of several ducks and geese and the almost exclusive occurrence of Maccoa Duck and Black-necked Grebe (Table 3). Summer and winter groupings differed, as in most waterbodies, mainly in terms of higher abundances of cormorants, Little Grebe, White-backed Duck and Red-knobbed Coot during winter, and higher abundance of Egyptian Goose, Yellow-billed Duck and Cape Shoveler during summer. Palearctic migrants also occurred on both Langvlei and Rondevlei during summer months (Table 3), with a relatively high abundance of Ruff. Group 3 representing predominantly Rondevlei winter counts differed from Group 4, which represented predominantly Langvlei winter counts, mainly in terms of a lower abundance of the most numerically dominant waterbirds.

Groups 6 to 9 consisted mostly of counts from Eilandvlei and Swartvlei Lake that differed from other waterbodies mostly in terms of the low abundance or absence of waterbirds characteristic of other waterbodies, namely Half-collared Kingfisher and Water Thick-knee that were characteristic of Groups 1 and 2 (Touw Estuary), African Black Oystercatcher, Kittlitz's Plover, Three-banded Plover, African Sacred Ibis and Palearctic migrants that were characteristic of Groups 10-13 (mostly Swartvlei Estuary), and Glossy Ibis, Southern Pochard and Maccoa Duck that were characteristic of Groups 3-5 (mostly Rondevlei and Langvlei) (Table 3). Seasonal differentiations were largely based in increased abundance of Little Grebe, Cape Cormorant and Red-knobbed Coot in winter, and Yellow-billed Duck and Cape Shoveler in summer.

Groups 10 to 13 consisted mostly of counts from Swartvlei Estuary. Group 10 comprised only winter surveys in this waterbody, which were characterized by an increased abundance of Little Grebe, and the low abundance or absence of Palearctic migrants (Table 3). Summer counts were scattered in three groups with Group 11 consisting of counts where there was a high abundance of Little Grebe, Reed Cormorant, Yellow-billed Duck, Cape Shoveler and Red-knobbed Coot (five summers -estuary closed, three summers - estuary open), and Group 13 consisting of counts where there was high abundance of most Palearctic migrants (six summers - estuary open). By contrast, species that were abundant in Groups 11 and 13 occurred in low numbers in Group 12, despite the estuary being open during all four summer counts in this group.

DISCUSSION

The environmental variables investigated in this study have frequently been found to be important in affecting habitat use by



Group No.	1	2	3	4	5	6	7	8	9	10	11	12	13
Touw Estuary Winter	15	4	-	-	-	-	-	-	-	-	-	-	-
Touw Estuary Summer	-	18	-	-	-	-	-	-	-	-	-	-	-
Eilandvlei Winter	-	-	2	-	-	13	2	2	-	-	-	-	-
Eilandvlei Summer	-	-	1	-	-	-	17	-	-	-	-	-	-
Langvlei Winter	-	-	5	12	2	-	-	-	-	-	-	-	-
Langvlei Summer	-	-	-	-	18	-	-	-	-	-	-	-	-
Rondevlei Winter	-	-	17	1	-	-	1	-	-	-	-	-	-
Rondevlei Summer	-	-	-	-	15	-	3	-	-	-	-	-	-
Swartvlei Estuary Winter	-	-	1	-	-	-	-	-	-	16	1	1	-
Swartvlei Estuary Summer	-	-	-	-	-	-	-	-	-	-	8	4	6
Swartvlei Lake Winter	-	-	-	3	-	2	2	11	1	-	-	-	-
Swartvlei Lake Summer	-	-	-	-	-	-	3	3	11	-	1	-	-

Figure 4. Dendrogram representing the similarity amongst waterbodies in summer and winter surveys in terms of the abundance of waterbird species. Waterbody groups numbered sequentially from 1 to 13. Waterbody names in the dendrogram are used to describe the numerically dominant waterbody in each group or cluster of groups. W = winter surveys and S = summer surveys are used to describe the dominant sample season for each waterbody group. The table below the dendrogram lists the number of surveys from different waterbodies in both summer and winter survey periods that comprise each waterbody group.

waterbirds in both artificial and natural wetlands (Ma *et al.* 2010). It needs to be borne in mind, however, that no single research project can cover all potential variables influencing habitat use by birds (Jones 2001). Furthermore, non-habitat phenomena, not addressed in this study, such as nest predation (Martin 1993), competition (Svärdson 1949) and intraspecific attraction (Danchin *et al.* 1998; Pöysä *et al.* 1998), may also influence habitat selection and hence use.

The relationship between water depth and foraging habitat use by waterbirds has been well documented (Velasquez 1992; Colwell and Taft 2000; Isola *et al.* 2002; Ntiamoa-Baidu *et al.* 2008). Water depth directly determines the accessibility of foraging habitats because of restrictions of bird morphology such as leg (in the case of waders) and neck (in the case of dabblers) lengths, with few non-diving species foraging in waters greater than 25 cm (Colwell and Taft 2000). In the WLC, however, the largest concentrations of non-diving waterbirds occurred on the deeper lakes. The reason for this lies in the growth form of the dominant submerged macrophytes that are a food source for herbivorous ducks and rallids, either directly or indirectly via associated invertebrates. The dominant submerged macrophyte in the lakes is fennel-leaved pondweed, which roots in waters up to 3 m deep (Whitfield 1984) and has an upright growth form, with the upper leaves of mature plants either on or just below the water surface. The majority of ducks, geese and herbivorous rallids occur in this vegetated zone. Thus, for dabbling herbivorous birds the issues of relative depth to the food source would be more significant in determining food availability rather than actual water depth. Both Wilderness and Swartvlei are temporarily open/closed estuarine systems that experience large temporal variability in water levels and hence water depth, which would be expected to influence food availability (Heÿl and Currie 1985). During open periods, shallow and exposed sandflats used by smaller waders increase, as do the accessibility of submerged macrophytes in deeper waters. Increased accessibility of shallow intertidal habitats may also partially explain the differentiation of predominantly summer surveys in Swartvlei Estuary into three groupings with periods of high wader abundance always coinciding with open periods.

The regular artificial breaching of Touw and Swartvlei estuaries has resulted in a substantial reduction in maximum water levels (approximately -1.5 m) and the duration of high water periods. In addition, reduced sediment scouring due to lower breaching heights has resulted in more rapid closing of estuaries, thereby also reducing the duration of low water periods (Fijen and Kapp 1995a, 1995b; South African National Parks, unpubl. data). Decreased spatial and temporal variability in water levels may have increased the suitability of the WLC for some waterbird groups, notably herbivores, which are positively affected by high stability in water (Heÿl and Currie 1985). However, detrimental impacts could also be expected, with reduced open periods in the estuaries being unfavorable for species that utilize shallow water habitats.

Increased stabilization of water levels is also facilitating the establishment of emergent macrophytes on sandbanks (Russell 2003), with resulting loss of habitat for waterbirds that use these areas for feeding and maintenance. Waterbird surveys conducted in the 1980s recorded extensive use of exposed and shallow sandbanks on the eastern shoreline of Eilandvlei (Boshoff and Palmer 1989). These shallows have subsequently been colonized primarily by common reed and bullrush (*Typha capensis*) (Russell 2003), with a concurrent reduction in shorebird and wader numbers. Tall emergent macrophytes can limit accessibility of wetlands and hence adversely affect foraging (Fujioka *et al.* 2001; Bancroft *et al.* 2002). The inverse has also been observed, particularly on Langvlei where, following a localized die-back of clubrush in shallow areas, the exposed mudflats were heavily used principally by small waders until such time as the plants became re-established (I. A. Russell, pers. obs.). Thus, the existence of shallow areas alone is insufficient for small waders, as they also need to be relatively free of tall emergent macrophytes.

The lakes in WLC support dense stands of submerged macrophytes (Russell 2013) with positive correlations observed between macrophyte and herbivorous waterbird biomass (Russell *et al.* 2009), which offers an explanation why the herbivorous and graminivorous Anatidae species together with the herbivorous Red-knobbed Coot (Fairall 1981) are numerically dominant. Macrophyte communities in the lower salinity lakes were dominated by fennel-leaved pondweed and stonewarts that are higher quality food for waterbirds than ditchgrass (Holm 2002) which, due to its higher salt tolerance (McMillan and Moseley 1967), occurs predominantly in the estuaries (Whitfield *et al.* 1983).

Although several waterbird species in the WLC were more abundant on the estuaries compared to the less saline lakes, high salinity water can potentially be harmful (Ma *et al.* 2010) by causing dehydration when consumed (Hannam *et al.* 2003) and reducing waterproofing of feathers (Rubega and Robinson 1997). The use of saline habitats by waterbirds may be less about some species favoring high salinity water and more about using the food resources that it provides. Water salinity influences the distribution and abundance of zoobenthos (Velasquez 1992) and the species composition of submerged macrophyte communities (Adams *et al.* 1999), and hence will influence the use of foraging sites by waterbirds. In large hydrologically complex systems such as the WLC, spatial variability in salinity is likely to be critical in supporting a range of foraging habitats for diverse waterbird communities.

The low influence of turbidity on waterbird distribution in the WLC was likely due to the waterbodies in the WLC being relatively clear, except following the inflow of sediment laden flood waters. The rivers entering the systems are naturally stained with brown humates, the flocculation of which increases at higher salinities. The lower salinity lakes would thus be expected to naturally be more turbid than the higher salinity estuaries. The distribution of piscivorous waterbirds should be affected by water clarity due to its impact on prey accessibility (Abrahams and Kattenfeld 1997). Henkel (2006) found that visual pursuit waterbirds such as cormorants favor clear waters due to increased visual acuity, whereas shallow plunge diving piscivores such as terns favor more turbid conditions (Hanley and Stone 1988). Cormorants in the WLC followed the expected trend of being more abundant in the less turbid estuaries, and Common Tern more plentiful on the relatively turbid lakes. Countering this trend was the strong association of the piscivorous Black-necked and Great Crested grebes with more turbid waterbodies, notably Rondevlei and Langvlei. It could be argued that so long as the waterbodies of the WLC remain relatively clear of suspended sediments, factors other than relatively small spatial variations in turbidity may be more influential in determining habitat suitability and hence waterbird distribution.

The similarity of waterbird communities on Rondevlei and Langvlei, particularly during summer months, was in agreement with the findings of Boshoff and Piper (1993). The occurrence of Maccoa Duck, White-backed Duck and Southern Pochard virtually exclusively on these two waterbodies is noteworthy, as their largely herbivorous diets suggests that Swartvlei Lake and Eilandvlei should also provide suitable habitat, as for other herbivorous ducks. A possible explanation for their restricted distribution could lie in their sensitivity to disturbance. Several studies undertaken elsewhere have demonstrated the sensitivity of some waterbirds to disturbance by recreational activities (Tuite *et al.* 1984; Keller 1991; Fox *et al.* 1994; Cardoni *et al.* 2008), in particular power-boating and the presence of people on shorelines. All boating activity and public access to both Rondevlei and Langvlei are restricted thereby limiting disturbance, whereas power-boating, sailing and other water sport activities are permitted on both Eilandvlei and Swartvlei Lake. Reedbeds are also thought to mitigate human disturbance to waterbirds in urban areas (Hattori and Mae 2001), and it is likely that dense emergent macrophytes, including reeds, that surround both Rondevlei and Langvlei, along with recreation restrictions, help reduce disturbance on these waterbodies and create a favored habitat for disturbance sensitive waterbirds.

The similarity of waterbird communities on Eilandvlei and Swartvlei Lake was in agreement with the findings of Boshoff and Piper (1993). However, Boshoff and Piper (1993) described waterbird communities between 1981 and 1984 as being dominated by diving piscivorous species, whereas in surveys described here, conducted 10 to 30 years later, herbivorous species were numerically dominant. Changes in the abundance of submerged macrophytes were probably primarily responsible for this difference, with a die-back of submerged macrophytes having occurred in 1981 at the commencement of surveys undertaken by Boshoff and Piper (1993) that resulted in a substantial reduction in herbivore numbers, particularly in Swartvlei Lake (Boshoff *et al.* 1991). Submerged macrophytes were more abundant during the 20 years of this study, particularly in Swartvlei Lake, creating conditions more favorable for herbivorous waterbirds. Reduced feeding opportunities for both herbivorous and insectivorous waterbirds in the Touw Estuary caused by low biomass of submerged macrophytes, and the absence of saltmarshes and mudflats due to extensive shoreline development and reedbed encroachment (Russell 2003) were likely the reasons for the dominance of piscivorous species and scavengers on this waterbody. By contrast, extensive saltmarsh and intertidal mudflats still remained in Swartvlei Estuary, which presented feeding opportunities for invertebrate feeding waders, several of which occurred predominantly on this waterbody.

Seasonal changes in community composition and species abundance were apparent on all waterbodies and corroborate the expected fluctuations due to movement and migration (Heÿl and Currie 1985; Underhill 1987b). Seasonal movements of ducks in southern Africa are not well understood, and numbers on the WLC can vary substantially between years. Similarly, intensive use of the estuaries by Palearctic migrants does not occur every year, even in times when conditions are apparently suitable, such as the estuary being open and water levels low. Factors external to the WLC, and general population trends taking place on a much broader scale, may well drive this variability with, for example, inter-annual changes in nest predation at breeding areas on the Siberian tundra during the austral summer affecting migrating and overwintering waterbird numbers in southern Africa (Summers and Underhill 1987; Underhill 1987a).

This study has demonstrated variability in both the spatial and temporal distribution of waterbirds in the WLC. While many waterbird species were ubiquitous, there were a few that were largely restricted to one or a few waterbodies, or waterbody type. Overall spatial variation in community composition is mainly driven by differences in relative abundance, and temporal variation by the seasonal movements of several waterbirds. Environmental variables that affect habitat use differed between waterbodies of the WLC, with the temporarily open/closed estuaries differing from both one another and the lakes in several attributes, and the whole wetland system thus providing a mosaic of different habitat conditions. Care must be taken to conserve this diversity through the maintenance of environmental processes, and particularly fresh and marine water inflows and movements, the alteration of which is leading to long-term changes in water chemistry (Russell 2013) and wetland loss (Russell 2003), and creating conditions suitable for alien invasions (Olds *et al.* 2010). Effective management of the full complex of interlinked wetlands in the WLC, notably improving marine and inter-waterbody connectivity, and selected macrophyte control (Russell 2013), will provide different habitats suitable for supporting diverse and abundant waterbird communities.

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