KOEDOE - African Protected Area Conservation and Science
ISSN: (Online) 2071-0771, (Print) 0075-6458

Waterbird community changes in the Wilderness Lakes, South Africa (Part 3 of 3): Diving piscivores and scavengers

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Dates:
Received: 13 Apr. 2023
Accepted: 06 Oct. 2023
Published: 06 Dec. 2023

How to cite this article:
Russell, I.A., 2023, 'Waterbird community changes in the Wilderness Lakes, South Africa (Part 3 of 3): Diving piscivores and scavengers', *Koedoe* 65(1), a1772. https://doi.org/10.4102/koedoe.v65i1.1772

Estuarine waterbodies typically support diverse and abundant waterbird communities. However, global environmental degradation as a result of anthropogenic activities is leading to species level changes in biodiversity, with top predators such as piscivorous waterbirds being particularly vulnerable to ecosystem changes. The study aimed to document long-term spatial and temporal patterns of abundance of piscivorous and scavenging waterbirds in the Wilderness Lakes Complex (WLC) in the Garden Route National Park, South Africa, and where possible identify potential causes for observed trends. The abundance of waterbirds on these wetlands was determined biannually from 1992 to 2019, with counts conducted from a boat following a standardised route. Historical waterbird abundance data from the 1980s were also used to describe long-term abundance changes. Eight of the species exhibited seasonal variability in abundance with most, excluding Common Tern *Sterna hirundo*, being more abundant in winter. Substantial changes occurred in the abundance of several species over the four-decade study period, notably increases in Cape Cormorant *Phalacrocorax capensis* and Great Crested Grebe *Podiceps cristatus*, and decreases in Common Tern and Black-necked Grebe *Podiceps nigricollis*. Long-term abundance trends indicate a combination of declining, increasing, and stable populations. Although some species have undergone contrasting abundance changes on different waterbodies in the WLC the dominant pattern was a similar direction of change on most or all waterbodies and in different seasons. Local reasons for changes probably include loss of sandbanks, changing prey availability, and the absence of recreational disturbance on some waterbodies.

Conservation implications: Drivers of changes in the abundances of piscivores are likely to be multifaceted, functioning on multiple spatial and temporal scales, and affecting different species in different ways. Recommended local corrective actions include managing emergent macrophyte encroachment on sandbanks, reducing recreational disturbance, managing processes affecting indigenous fish stocks, and protecting nesting sites.

Keywords: Touw system; Swartvlei system; waterbird community change; species abundance; causes of change; wetlands; recreational disturbance.

Introduction

Piscivorous waterbirds are frequently abundant in estuarine ecosystems where they are, in many instances, top predators. While many waterbirds have fish as a component of their diet, their reliance on fish as a primary food source, and their methods of capture differ. This study investigates changes in the abundance of waterbirds that capture fish through either underwater pursuit (grebes, cormorants, and darters) or plunge-diving (terns, kingfishers), as well as one scavenger and generalist forager (Kelp Gull *Larus dominicanus*) whose diet also includes fish (Crawford & Hockey 2005; Duffy, Duffy & Wilson 1984).

The Wilderness Lakes Complex (WLC) consisting of the Touw and Swartvlei estuarine systems, is a mosaic of wetlands in the Garden Route National Park in South Africa, and regularly supports populations of up to 68 waterbird species (Randall, Randall & Kiely 2007). Waterbird abundance assessments have been undertaken over four decades since 1980 in both this and previous (Boshoff, Palmer & Piper 1991) studies. In this time, several directional physical and biological changes have occurred in the WLC that could potentially either directly or indirectly affect waterbird abundance, including changes in water chemistry and clarity (Russell 2013, 2015; Taljaard, Van Niekerk & Lemley 2018), loss of some exposed sandbanks, and open shorelines because of increased water level stabilisation (Russell 2003), variability in the abundance of submerged aquatic plants (Russell et al. 2019:8), and herbivorous fishes (Whitfield 1984, 1986), and proliferation of new and established alien fishes (Olds et al. 2011).

Environmental changes on a broader landscape scale also potentially affect piscivorous waterbird abundances in the WLC. These include increases in the number and area of artificial wetlands, such as farm dams, which may provide new feeding and breeding opportunities (Froneman et al. 2001), as do the eastward displacement in the southern coastal waters of South Africa of some marine pelagic fish preyed upon by marine feeding cormorants (Coetzee et al. 2008; Roy et al. 2007).

The quantity of fish removed from an estuary by piscivorous birds can be substantial and these birds are likely to have a large predatory impact on juvenile marine fishes in estuaries (Cowley, Whitfield & Terörde 2017:152). It has been estimated that in the WLC cormorants and darters alone can remove nearly 61 000 kg of fish (wet mass) annually (Williams & Randall 1995). Energy removal and nutrient mobilisation resulting from predation by waterbirds on fish in the WLC and adjacent marine areas and inland wetlands are likely to have significant effects on wetland ecology.

Many piscivorous waterbirds, and particularly communally nesting cormorants, face a unique set of survival challenges including high susceptibility to pollution-induced reproductive failure (Walker & Knight 1981), wilful destruction of nesting sites (pers. obs.), and vulnerability to environmental disturbance from anthropogenic activities (Williams & Randall 1995) resulting in high chick and egg loss. Most of the waterbodies in the WLC and adjacent coastline continue to support intensive human recreation, which has the potential to disturb feeding and breeding piscivorous waterbirds.

The effects of wetland habitat transformation on waterbird abundances frequently remains unclear (Ma et al. 2004) with few long-term studies occurring where both ecosystem transformation and species abundance changes have been monitored and documented. The objectives of this study were to: (1) document long-term spatial and temporal patterns of abundance of frequently occurring and abundant piscivorous and scavenging waterbirds (hereafter referred to collectively as piscivorous waterbirds) within the WLC, (2) where possible identify potential causes for the observed trends, and (3) consider the conservation implications of observed spatial and temporal changes. This entailed examining seasonal differences in the abundance of species, assessing changes in the abundance of species between surveys conducted in the periods 1980–1983 (Boshoff et al. 1991) and 1992–2019, and examining the trends in species abundances both seasonally between summer and winter surveys, and spatially between waterbodies for the latter 28-year survey period.

Research methods and design

Study site

The WLC is situated on the Cape south coast of South Africa and comprises two estuarine systems (Figure 1). The Touw system consists of three interconnected estuarine lakes (Rondevlei, Langvlei, Eilandvlei) and the Touw Estuary.

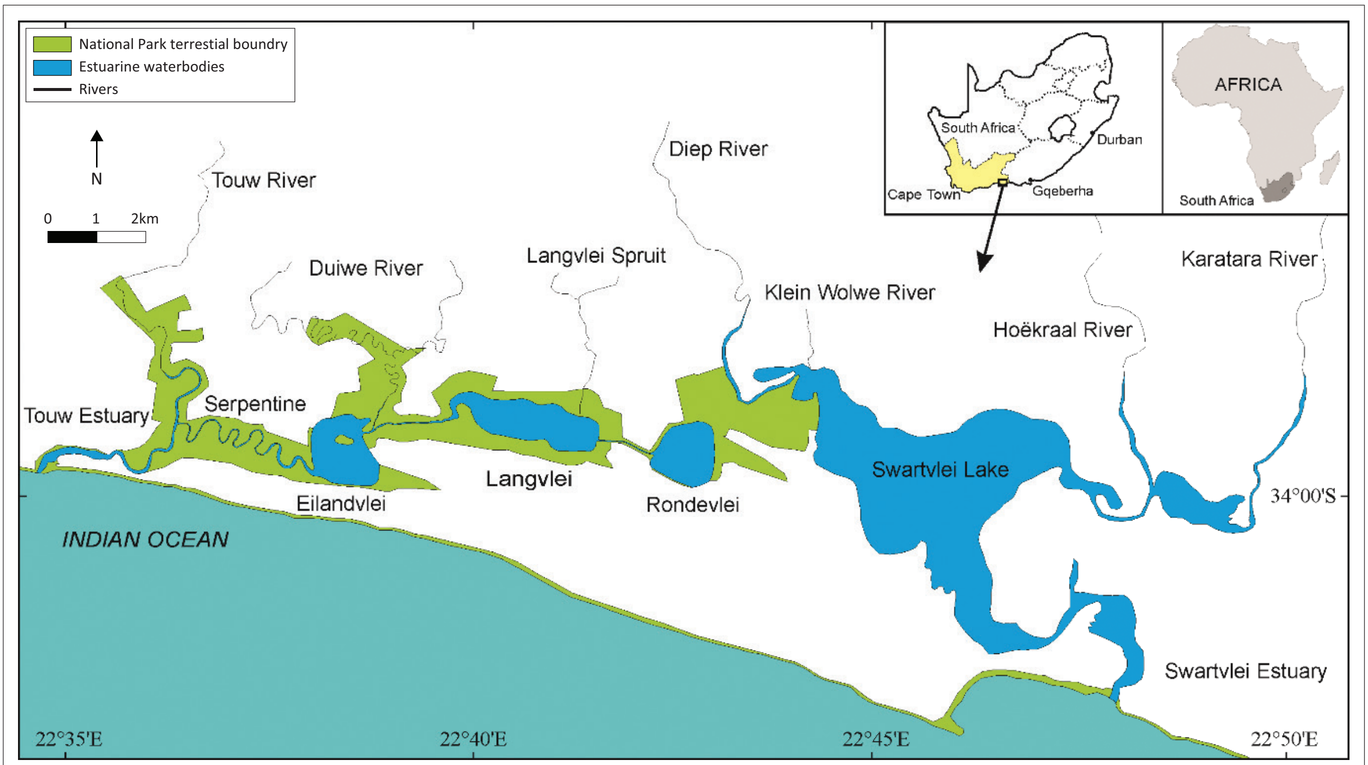


FIGURE 1: Map of study area showing relative position of estuaries and estuarine lakes within the Wilderness Lakes Complex.

The Swartvlei system consists of the Swartvlei Lake and Swartvlei Estuary. Both Touw and Swartvlei estuaries are naturally temporarily open/closed waterbodies. Artificial breaching of the estuary mouths along with reductions in freshwater inflows have reduced the average percentage of time both estuaries are open (SANParks unpublished data). Six rivers flow into the lake system (Figure 1). The lower catchment of the larger perennial rivers (Touw, Hoëkraal, Karatara), and majority of the catchments of the smaller intermittently flowing rivers (Duiwe, Langvlei Spruit, Klein Wolwe) are intensively utilised for agriculture, plantations, and urban development (Filmalter & O'Keeffe 1997). Dissolved inorganic nutrients (NOx-N, NH4-N, and PO4-P) in the Touw system are variable although typically low, with external catchment fluxes likely not the dominant drivers of long-term nutrient patterns in the lakes (Taljaard et al. 2018:65). Submerged macrophytes occur in all waterbodies, although they are generally confined to waters less than 3.0 m deep (Whitfield 1984). Emergent aquatic plants occur on the margins of the lakes. The fish fauna consists of a combination of estuarine (Hall, Whitfield & Allanson 1987; Russell 1996; Whitfield 1984) and alien freshwater species (Olds et al. 2011, 2016). The entire WLC forms a component of the Garden Route National Park, and the Touw system, with the exclusion of Touw Estuary, is a designated Ramsar site. Recreational fishing and boating is permitted on all estuaries and lakes except Langvlei and Rondevlei. Walking is possible and permitted along portions of the shorelines of Touw and Swartvlei estuaries.

Waterbird counts

Assessments of changes in waterbird abundances were based on waterbird counts undertaken in two separate surveys periods.

Firstly, monthly waterbird counts on all waterbodies in the WLC, with the exception of Touw Estuary, were undertaken for 4 years (January 1980 to December 1983) by staff of the then named Chief Directorate: Nature and Environmental Conservation. These counts were undertaken either by using binoculars from a boat following a fixed route (Swartvlei Lake), using a zoom telescope from fixed shore sites (Eilandvlei, Rondevlei, Swartvlei Estuary), or a combination of these methods (Langvlei) as described by Boshoff et al. (1991). The lead of these surveys, Dr Andre Boshoff, made all of the original waterbird abundance data from these counts available to SANParks in the mid-1990s, for unrestricted use in future assessments of changes in waterbird abundances.

Secondly, waterbird abundances were determined biannually during summer (January–February) and winter (July–August) for 28 years (1992 to 2019) by the author and co-workers. Fifty six surveys on each of six waterbodies were undertaken in the 28-year study period. Counts of all waterbirds were conducted separately on each waterbody by four observers using binoculars, from a boat following a fixed and repeated route parallel to the shoreline of each waterbody. The routes allowed for surveillance of all open water areas on each waterbody, as well as sparsely vegetated areas on the waterbody floodplains. Boat speeds were low and stands of dense emergent vegetation supporting high abundances waterbirds were avoided to minimise disturbance of waterbirds on the water surface. Variability in observer error was minimised by use of the same observers wherever possible throughout the study period, with observers specialising in different taxa. Accurate counts could only be undertaken on days with little or no wind. Online long-term weather forecasts (7 days) were used to select suitable consecutive sample days with little or no wind and low probability of precipitation on four consecutive days within a 3-week window. Counts were undertaken in the morning when wind speeds are typically low, commencing at 08:00, and usually ending at approximately 13:00, with counts undertaken on either one or two waterbodies in a day. In a few instances when wind speeds unexpectedly increased substantially during surveys, thus reducing the accuracy of counts, the survey was abandoned for the day and restarted on the next day, or period, with predicted suitable weather. All counts in the entire WLC were conducted over a maximum of four consecutive days in each survey. The scientific and common names of waterbird species are based on those used by Hockey, Dean and Ryan (eds. 2005).

Analysis

The non-parametric Mann–Whitney test was used to assess differences in the abundance of individual bird species in different seasons (summer and winter) using pooled data from all waterbodies collected in the 1992–2019 surveys. The data were tested for normality using the Shapiro-Wilk test.

The mean abundances of waterbirds in four different decades from the years 1980 to 2019, thus spanning all available waterbird abundance records, were used to assess long-term changes in abundance on the Touw and Swartvlei estuarine systems. Defined decades, and years in which data were collected were the 1980s (data 1980–1983), 1990s (data 1990–1999), 2000s (data 2000–2009), and the 2010s (data 2010 to 2019). To achieve consistency in the calculation of mean abundances across the entire 1980–2019 study period only data collected in January and July surveys in the 1980s period were used in analyses. Comparisons of species abundances in different decades excluded all data collected on the Touw Estuary as surveys were not undertaken on this waterbody during the 1980s (Boshoff et al. 1991).

The Mann–Kendall trend analysis test was used to determine the significance (p) and direction (increasing or decreasing) of long-term non-seasonal trends in the abundances of waterbirds on both individual waterbodies in the WLC as well as pooled abundance data for the WLC as a whole, with analyses conducted separately for summer and winter count data collected in the 1992–2019 surveys.

The selection of reliable estimators of population change is essential in monitoring programmes generating trend data (Ortiz-Velez & Kelley 2023). Zero-inflation resulting from the inclusion of rare species in datasets can bias statistical estimates and trend detection (Cunningham & Lindenmayer 2005), and data screening prior to analysis can typically include exclusion of species with few observations (Thomas & Martin 1996) by setting arbitrary thresholds of percent presence among samples (Ortiz-Velez & Kelley 2023). Count data of only abundant and regularly occurring waterbirds were used in analyses, defined here as those that from the 1992 to 2019 surveys demonstrated an average abundance of five or more individuals on at least one waterbody as well as on all waterbodies combined, and were recorded in 50% or more of surveys on at least one waterbody. Data were analysed using Systat Version 13 (Systat 2009).

Ethical considerations

This article followed all ethical standards for research without direct contact with human or animal subjects.

Results

Seasonal differences in waterbird abundances

Of the eight piscivorous waterbirds that demonstrated seasonal variability in abundance all, with the exception of Pied Kingfisher *Ceryle rudis*, are either nomadic or undertake local movement for breeding, and seven were significantly more abundant during surveys undertaken in winter (Table 1). Common Tern *Sterna hirundo*, a non-breeding migrant, was the only species significantly more abundant during summer surveys. The abundance of Great Crested Grebe *Podiceps cristatus* and Kelp Gull did not differ significantly between summer and winter surveys.

Variation in waterbird abundances between survey periods

Piscivorous waterbirds could be categorised into one of four groups depending on the pattern of change in abundance across the four decades in the study period. These included: (1) increasing significantly in most or all decades; (2) decreasing significantly over time and particularly relative to abundances in the 1980s; (3) species with a low-high-low pattern, with significant increases in the decades after 1980s, a high in either the 1990s or 2000s, followed by a decline in the following decade or decades; and (4) species with consistently low abundance, and for whom no substantial change in average abundance between decades was apparent.

Most abundant piscivorous species on the Swartvlei system (7 out of 10) underwent similar changes, namely relatively low abundance in the 1980s, higher abundance in the 1990s (Common Tern) (Figure 2f) and/or 2000s (Little Grebe *Tachybaptus ruficollis*, Great Crested Grebe, Reed Cormorant *Phalacrocorax africanus*, White-breasted Cormorant *Phalacrocorax lucidus*, African Darter *Anhinga rufa*, Kelp Gull) (Figures 2a–e, g), followed by a decline in the 2010s (Figure 2a–f). The abundance of Cape Cormorant *Phalacrocorax capensis* increased over time, with significant increases in both the 1990s and 2010s (Figure 2i). Alternatively Black-necked Grebe *Podiceps nigricollis* exhibited an overall decrease in abundance (Figure 2h) and was seldom recorded on the Swartvlei system (average < 1 every three surveys) from the 1990s onwards. The abundance of the Pied Kingfisher on the Swartvlei system has remained relatively unchanged over time, with the average abundance being only two individuals higher in the 2010s compared with the 2000s (Figure 2j).

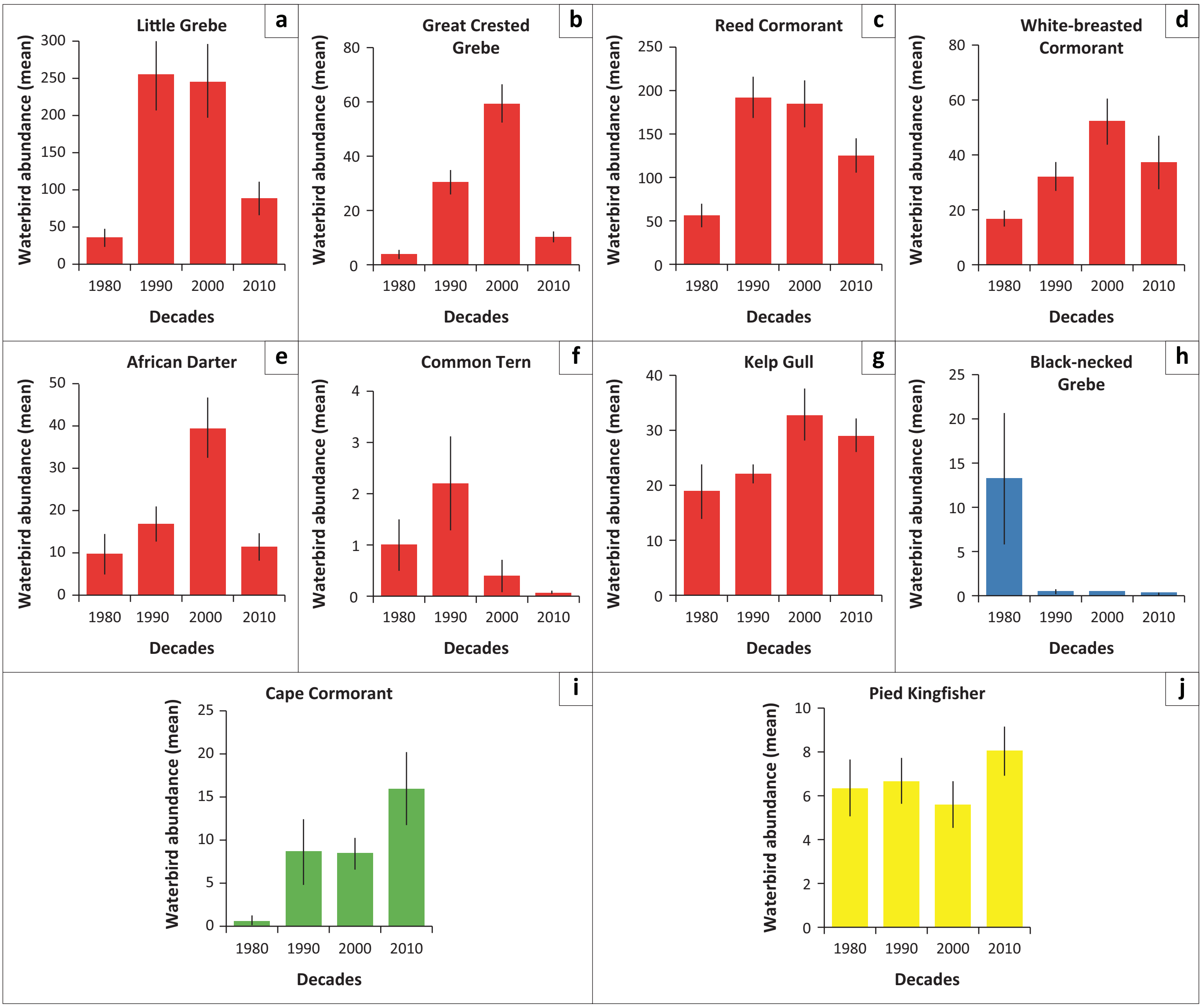
The abundance of only one piscivorous waterbird on the Touw system (Little Grebe) showed a low–high–low pattern, with low abundance in the 1980s, higher abundance in the 1990s, followed by decreasing abundance in the 2000s and 2010s (Figure 3a), in contrast to the Swartvlei system where the majority of the species had similar patterns of change in average abundance across the study period. Six species have undergone long-term declines on the Touw system (Black-necked Grebe, White-breasted Cormorant, African Darter, Pied Kingfisher, Common Tern, Kelp Gull) with prominent declines noted for all in the 1990s (Figure 3b–g), and continuing declines of Pied Kingfisher and

TABLE 1: Seasonality of piscivorous waterbirds on waterbodies in the Wilderness Lakes Complex, with species grouped according to season of higher abundance.

Seasonality	Species	Average abundance - Summer							Average abundance - Winter							Test statistics for WLC	
		RV	LV	EV	TE	SL	SE	WLC	RV	LV	EV	TE	SL	SE	WLC	Mann-Whitney (*U*)	*p* <
Winter	Black-necked Grebe	9	2	0	0	0	0	11	45	26	2	0	0	0	74	62.0	0.000
	Little Grebe	33	124	15	2	42	14	230	119	369	55	15	141	181	881	30.0	0.000
	White-breasted Cormorant	7	23	6	6	7	13	61	10	25	24	18	36	26	139	60.0	0.000
	Cape Cormorant	0	0	0	1	0	3	5	102	66	280	16	6	12	483	18.5	0.000
	Reed Cormorant	40	68	13	8	49	71	249	31	115	72	50	114	95	477	102.0	0.000
	African Darter	0	4	3	0	13	1	22	4	10	9	7	28	4	62	138.0	0.000
	Pied Kingfisher	2	2	1	1	2	3	11	1	2	1	2	4	5	15	236.5	0.017
Summer	Common Tern	9	4	1	0	0	1	15	2	2	3	0	0	0	8	543.5	0.005
Non-seasonal	Great Crested Grebe	46	74	19	0	31	3	174	85	77	26	0	30	2	221	269.0	0.066
	Kelp Gull	1	2	3	15	5	23	49	2	4	5	8	8	21	48	428.5	0.395

Note: Average abundances are given of waterbirds on lakes and estuaries in both summer and winter surveys undertaken from 1992 to 2019. Test statistics are given for the seasonal difference in the abundance of waterbirds within the entire Wilderness Lakes Complex for the Mann–Whitney (*U*-test), where *p* = probability value.

RV, Rondevlei; LV, Langvlei; EV, Eilandvlei; TE, Touw Estuary; SL, Swartvlei Lake; SE, Swartvlei Estuary; WLC, Wilderness Lakes Complex.



Note: Vertical whiskers show 95% confidence limits of means in each decadal period. Colouring of bars is used to categorise species into one of four groups depending on the pattern of change in abundance across the study period, where red = species with a low–high–low pattern, with significant increases in the decades after 1980s, a high in either the 1990s or 2000s, followed by a decline in the following decade or decades, green = species increasing significantly in one or more decades, blue = species decreasing significantly over time and particularly relative to abundances in the 1980s, and yellow = species with consistently low abundance, and/or for whom no substantial change in average abundance between decades was apparent.

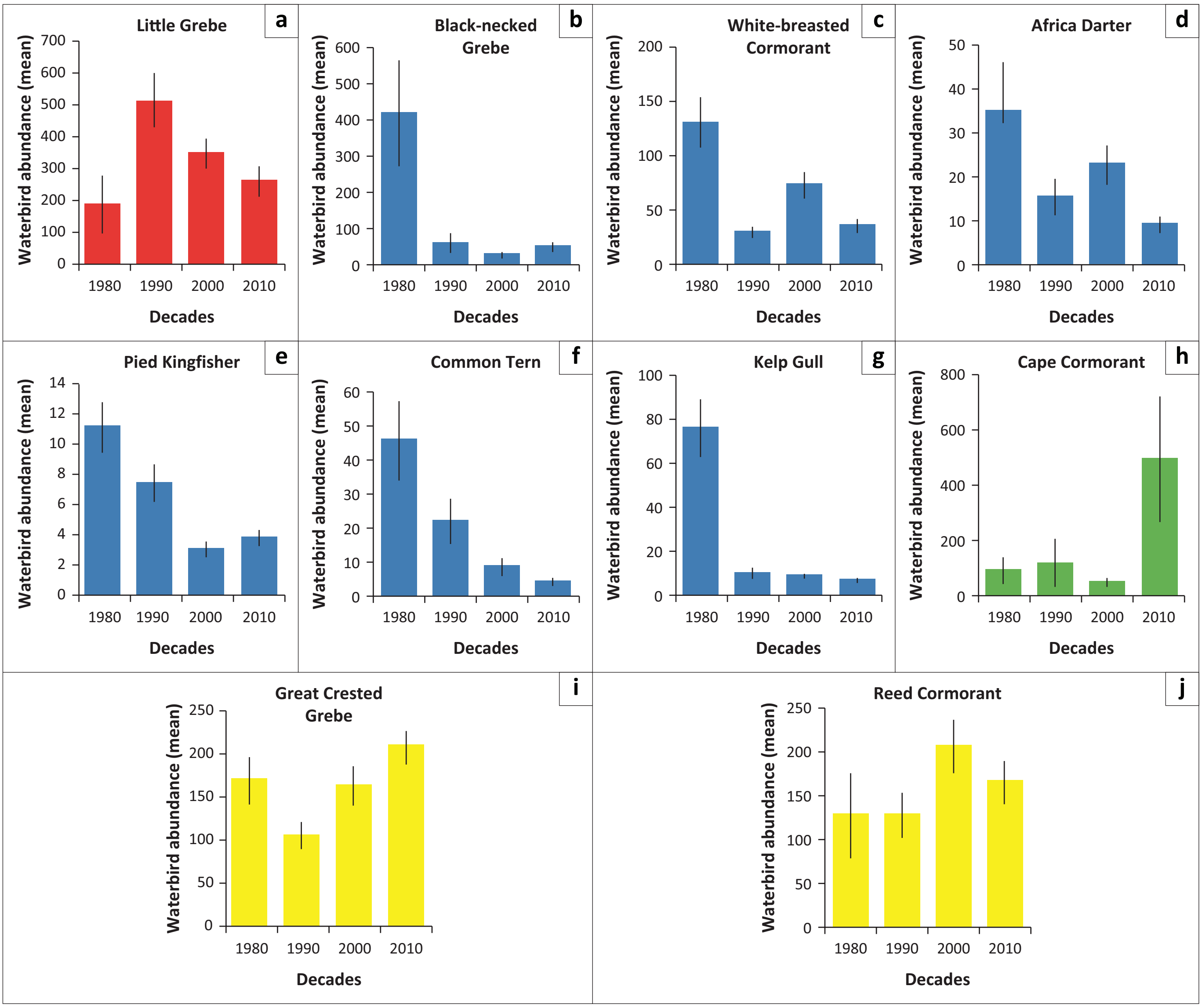
FIGURE 2: (a–j) Average abundances of piscivorous waterbirds on the Swartvlei system over four decades, where 1980 = period 1980–1989, 1990 = period 1990–1999, 2000 = period 2000–2009, and 2010 = period 2010=2019.

Common Tern also occurring in later decades (Figure 3e and Figure 3f). The abundance of Cape Cormorant has increased significantly on the Touw system in the 2010s (Figure 3i). The average abundance of the Great Crested Grebe decreased significantly from the 1980s to the 1990s, but thereafter increased in successive decades (Figure 3i). The abundance of Reed Cormorant on the Touw system has remained relatively unchanged over time, although with increases occurring in the 2000s compared with earlier decades (Figure 3j).

Abundance trends: 1992 onwards

Decreases have occurred in the abundance of Little Grebe in the WLC during both summer and winter surveys (Figures 4a) with declines being most prominent on Langvlei ($Z = -1.897$, $p < 0.01$), Eilandvlei ($Z = -2.753$, $p < 0.01$), and Swartvlei Lake ($Z = -3.596$, $p < 0.01$) during summer, and both Swartvlei Lake ($Z = -3.735$, $p < 0.01$) and Langvlei ($Z = -2.687$, $p < 0.01$) during winter when this species is typically more abundant (Table 1). Similarly, the abundance of the Black-necked Grebe has also decreased on both Langvlei ($Z = -2.644$, $p < 0.01$) and Swartvlei Lake during winter ($Z = -2.334$, $p < 0.05$), although this did not lead to a significant reduction in abundance in the WLC as a whole. Significant decreases have occurred in the abundance of Common Tern in the WLC in both summer ($Z = -2.301$, $p < 0.05$) and winter survey periods ($Z = -2.925$, $p < 0.01$) (Figure 4d) driven by declines on all waterbodies in the Touw system (Figure 5).

Overall increases have occurred in the abundance of two diving piscivores. Cape Cormorant increased significantly in the WLC in both summer ($Z = 2.883$, $p < 0.01$), as well as in winter ($Z = 2.312$, $p < 0.05$) during which they are typically substantially more abundant (Table 1). Increases



Note: Vertical whiskers show 95% confidence limits of means in each decadal period. Colouring of bars is used to categorise species into one of four groups depending on the pattern of change in abundance across the study period, where red = species with a low–high–low pattern, with significant increases in the decades after 1980s, a high in either the 1990s or 2000s, followed by a decline in the following decade or decades, green = species increasing significantly in one or more decades, blue = species decreasing significantly over time and particularly relative to abundances in the 1980s, and yellow = species with consistently low abundance, and/or for whom no substantial change in average abundance between decades was apparent.

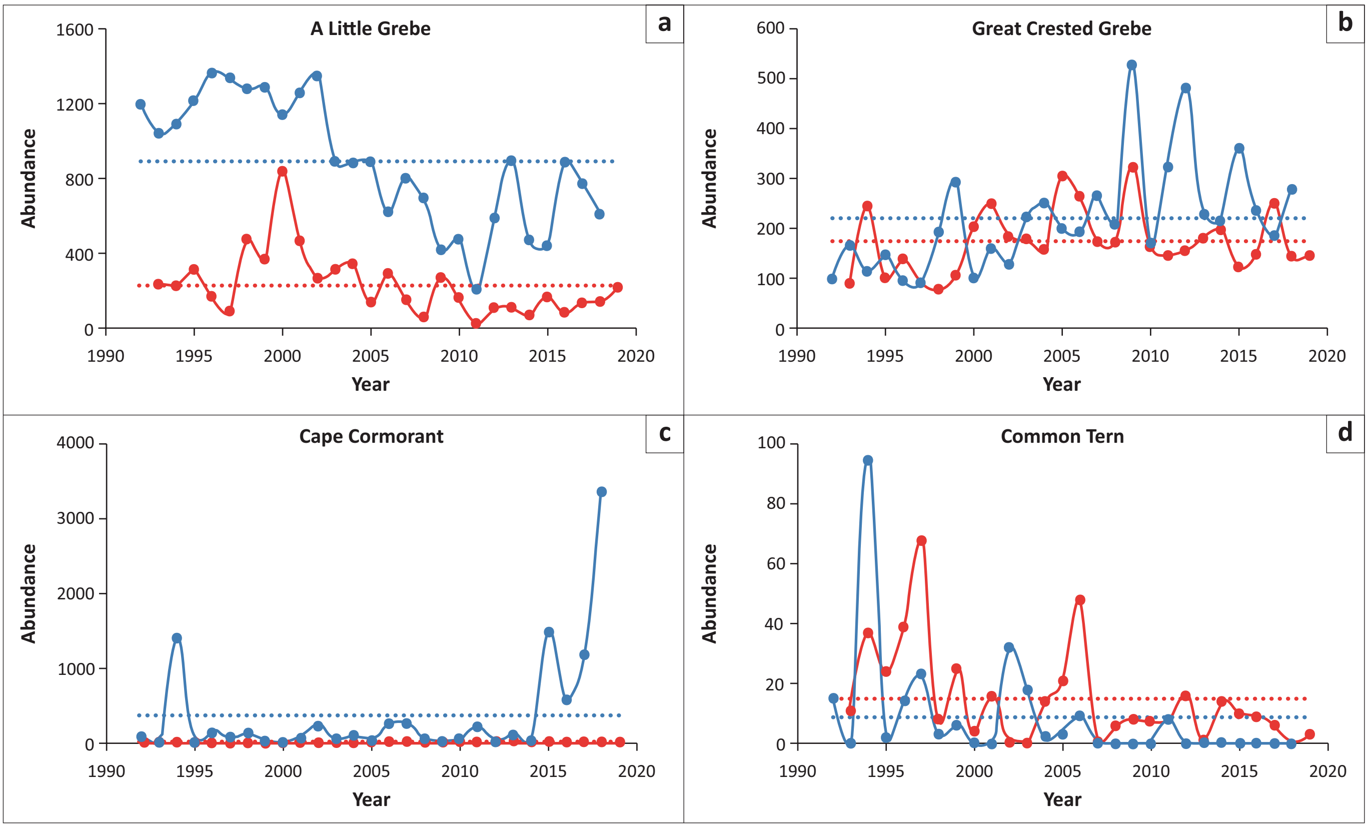
FIGURE 3: (a–j) Average abundances of piscivorous waterbirds on the Touw system over four decades where 1980 = period 1980–1989, 1990 = period 1990–1999, 2000 = period 2000–2009, and 2010 = period 2010=2019.

of Cape Cormorant have occurred on all waterbodies except Rondevlei (Figure 5) and with the most notable increases from 2015 onwards (Figure 4c) when the presence of large flocks during winter became a regular occurrence. The abundance of the Great Crested Grebe increased in winter surveys on all waterbodies except Swartvlei Lake (Figure 5), as well as overall in the WLC in this period ($Z = 3.536$, $p < 0.01$). Increases occurred in the abundances of the Great Crested Grebe during summer on Touw Estuary ($Z = 1.650$, $p < 0.05$) and Rondevlei ($Z = 3.856$, $p < 0.01$), which contrasted with Swartvlei Lake where declines during summer surveys were recorded ($Z = -2.711$, $p < 0.01$).

Several piscivorous waterbirds have undergone contrasting abundance changes in different systems, with the Black-necked Grebe, Reed Cormorant and Kelp Gull all declining in abundance on Swartvlei Lake during at least one season (Figure 5), though increasing in abundance on one or more waterbodies in the Touw system. The abundance of the Black-necked Grebe increased on Rondevlei in both summer ($Z = 2.346$, $p < 0.05$) and winter ($Z = 2.471$, $p < 0.05$) with the most notable increases occurring from 2016 to 2019, the last 4 years of the sampling period.

Declines have occurred in Pied Kingfisher on Eilandvlei ($Z = -2.702$, $p < 0.01$) during winter, although abundances are typically low (average one individual) (Table 1) and hence unlikely to be ecologically significant. No significant changes were recorded in the abundance of White-breasted Cormorant on any waterbody (Figure 5).

It is noteworthy that of the piscivorous species that have undergone significant changes in abundance on Swartvlei Lake all, with the exception of Cape Cormorant, have



Note: Blue solid lines and markers depict average annual abundances in winter surveys, and red solid lines and markers depict average annual abundances in summer surveys. Stippled lines show average abundances across the study period.

FIGURE 4: (a–d) Abundances of piscivorous waterbirds in the Wilderness Lakes Complex showing significant changes in abundance from 1992 onwards in at least one season.

Seasonality	Species	WLC		RV		LV		EV		TE		SVL		SVE	
		Slope		Slope		Slope		Slope		Slope		Slope		Slope	
		S	W	S	W	S	W	S	W	S	W	S	W	S	W
Winter	Black-necked Grebe	-	-	↑	↑	-	↓	-	-	-	-	-	↓	-	-
	Little Grebe	↓	↓	-	-	↓	↓	↓	-	-	-	↓	↓	-	-
	White-breasted Cormorant	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Cape Cormorant	↑	↑	-	-	↑	-	↑	↑	↑	↑	-	↑	↑	↑
	Reed Cormorant	-	-	↑	-	↑	-	-	-	-	-	↓	-	-	-
	African Darter	-	-	-	-	↑	-	-	↓	-	-	↓	-	-	↑
	Pied Kingfisher	-	-	-	-	-	-	-	↓	-	-	-	-	-	-
Summer	Common Tern	↓	↓	-	↓	↓	↓	↓	↓	↓	-	-	-	-	-
Non-seasonal	Great Crested Grebe	-	↑	↑	↑	-	↑	-	↑	↑	↑	↓	-	-	↑
	Kelp Gull	-	-	↓	-	-	-	-	-	↑	-	↓	↓	-	-

Note: Red down arrow = significant decline in abundance within the study period; Green up arrow = significant increase in abundance within the study period; dash = no significant trend within the study period. WLC = Wilderness Lakes Complex. Test statistics provided in Appendix 1.

RV, Rondevlei; LV, Langvlei; EV, Eilandvlei; TE, Touw Estuary; SL, Swartvlei Lake; SE, Swartvlei Estuary; S, summer counts, W, winter counts.

FIGURE 5: Graphic depiction of the test results of the Mann–Kendall tests performed on selected piscivorous waterbird abundance data collected on each waterbody between 1992 and 2019, and combined- data for all waterbodies, per season, to test for the significance and direction of non-seasonal trends.

declined in abundance, whereas on other waterbodies in the WLC both increases and decreases occurred across the spectrum of assessed species. Of the four species that have undergone significant abundance changes in the WLC, the dominant pattern has been a similar direction of change in most or all waterbodies as well as in different seasons, rather than the type of change differing either spatially or temporally (Figure 5).

Discussion

Seasonal differences in piscivorous waterbird abundances

Of the considered species the only true migratory piscivorous waterbirds in the WLC are firstly, the Common Tern, which overwinters in the northern hemisphere, predominantly in the Baltic region (Underhill et al. 1999) and occurs in southern

Africa in summer months (September to May) (Tree 2005); and secondly Cape Cormorant, which undertakes post-breeding migrations from the west to the south and east coastlines of southern Africa, with large flocks occurring in the WLC during mid-winter. These seasonal long-distance movements are described by Boshoff et al. (1991), although the winter influx of Cape Cormorant to the WLC appears to have increased with time. The Little Grebe, Black-necked Grebe, White-breasted Cormorant, Reed Cormorant, and African Darter all undertake local seasonal movements, with many dispersing away from the WLC during the summer breeding period. Some White-breasted Cormorants breed on local coastal cliffs and marine stacks, although most seasonally moving piscivorous waterbirds are thought to breed predominantly on inland freshwater wetlands (Boshoff & Palmer 1989), and are significantly more abundant in the WLC during the largely non-breeding winter months. Seasonality of these species is the same as given by Boshoff et al. (1991). The movement patterns of the Kelp Gull appear to be poorly understood, and the non-seasonality of this species, as well that of Great Crested Grebe and Pied Kingfisher, are the same as in published accounts (Boshoff et al. 1991; Randall et al. 2007).

Changes in piscivorous waterbird abundances

There are two broad patterns of change among piscivorous waterbirds in the WLC, firstly similar changes in abundance by most species on Swartvlei Lake, and secondly, similar changes in abundance of individual species on different waterbodies in the WLC. On Swartvlei Lake, the numbers of all regularly occurring and abundant piscivores, with the exception of the regionally increasing Cape Cormorant, which is typically uncommon on this waterbody, have declined over time. These changes have been described in Russell and Randall (2017) and were the consequence of atypical meteorological conditions in 2007 and 2008 that resulted in significant increases in seawater inflows along with reduced freshwater inflows, causing substantial increases in water salinity over several years and resultant near complete loss of once abundant submerged macrophytes. Numerically dominant littoral fish species such as Cape stumpnose *Rhabdosargus holubi* and oval moony *Monodactylus falciformis* feed predominantly on filamentous algae, macrophytes, and associated invertebrates (Whitfield 1984, 1986), and mullet species (Mugilidae) feed mainly of plant detritus and associated unicellular algae and diatoms (Whitfield 1982). The prolonged senescence of macrophytes in Swartvlei Lake is thus expected to have caused substantial decline in littoral fish populations, as observed in the early 1980s by Whitfield (1984), which in turn could account for observed declines in most piscivorous waterbirds on this waterbody (Russell & Randall 2017).

The Common Tern is a long-distance seasonal migrant prevailing during the austral summer mostly in the Baltic States and Western Europe (Underhill et al. 1999). The global abundance of the Common Tern is described as 'Declining?' (Nagy & Langendoen 2018), although there appears to be no perceived increased risk of global extinction as the species remains red-listed as Least Concern (IUCN 2022). Whilst the abundances of birds in some breeding colonies of Common Tern in Europe are considered to be either stable (Soerensen & Faxneld 2020) or increasing (Ottvall et al. 2008 cited in Söderström 2013), others are thought to be declining (Scarton 2010; Szostek & Becker 2012) as is the abundance of this species in the southern Cape (Ryan 2013). The Baltic Sea is a highly disturbed ecosystem with declines in fish communities affecting the abundances of piscivorous birds (Ottvall et al. 2008 cited in Söderström 2013). Like most Palearctic migrants, declines of Common Tern in southern Africa including the WLC, are likely because of multiple causes across its range rather than just changing conditions within habitats used during non-breeding periods in the southern hemisphere.

The increasing proportion of Cape Cormorants breeding on the South African south coast compared with the western coastline of southern Africa has been well-documented (Crawford et al. 2015, 2016) and follows the eastward displacement of their main prey species anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* (Coetzee et al. 2008:1680; Crawford et al. 2014:115; Roy et al. 2007:316). Cape Cormorant do not breed in significant numbers in close proximity to the WLC, and increases in abundances within these waterbodies occurs in winter months (mostly from June to September) and most likely consist of migratory non-breeding individuals who use the lakes for fishing and resting.

The lack of significant seasonal difference in the abundance of Great Crested Grebe indicates that it is generally resident in the WLC, although the species can be nomadic dependent on environmental conditions (Dean 2005). Although breeding can occur throughout the year (Randall et al. 2007), a marked summer (November–February) peak occurs in the south-western portions of South Africa (Dean 1997b). Significant increases occurred on most waterbodies in the WLC, particularly in winter counts, potentially indicating inter-lake dispersal of individuals successfully raised in summer months. Consistently high and increasing abundance occurred particularly on Langvlei and Rondevlei, with low abundance on lakes with more intensive human use, namely Swartvlei Lake and Eilandvlei.

Possible reasons for changes in piscivorous waterbird abundances

Boshoff and Palmer (1989) describe the high utilisation of sandbanks on Eilandvlei during the 1980s for loafing and roosting, particularly by waterfowl and gulls, with Kelp Gull preferring waterbodies with exposed sandbanks (Boshoff et al. 1991). These exposed banks have largely disappeared following their colonisation by emergent macrophytes, particularly the common reed *Phragmites australis* (Russell 2003), and may have contributed to the decline of Kelp Gull in the WLC. The abundance of the Kelp Gull along the South African coastline has increased (Crawford et al. 2009;

Whittington et al. 2016) although local breeding, which occurs on the mainland (Crawford, Cooper & Shelton 1982), is low (Whittington et al. 2016) and may be disrupted by increasing usage of coastal areas for recreational pursuits, potentially also contributing to reduced abundance of this species in the WLC.

Environmental conditions during the 1980–1983 surveys were atypical, with high rainfall events in 1980 leading to elevated turbidity levels, prolonged opening of estuary mouths and associated elevations of salinity in the Swartvlei system, and resultant reductions in plant biomass (Weisser, Whitfield & Hall 1992; Whitfield 1982) and likely fish, which utilise plant matter either directly or indirectly for food (Whitfield 1982, 1984, 1986). Substantially lower abundances of many piscivorous birds in the 1980s compared with later surveys, particularly on the Swartvlei system, are likely to have been a result of these system changes. The reasons for the declines of several piscivorous birds on the Touw system, notably Reed Cormorant, White-breasted Cormorant, African Darter and Pied Kingfisher, as well as substantial declines in Black-necked Grebe on both Swartvlei and Touw systems remains unclear, although changing environmental conditions such as fish community composition (Olds et al. 2016) and reduced sandbanks (Russell 2003) for basking by cormorants and darters, may be contributory factors.

Mixed species feeding associations, including cormorants, gulls, grebes, and terns, may occur to effectively harvest more mobile, mid-water fish (Williams & Randall 1995) and likely shoaling species. Piscivorous birds may differ in terms of fish species taken, with larger species generally able to capture and consume larger fish species (Whitfield & Blaber 1979). Changing fish communities within the WLC resulting from the introduction and proliferation of several alien fishes (Olds et al. 2011) could potentially have differing impact on the feeding success of different sized waterbirds.

Great Crested Grebe are highly susceptible to boat-based disturbance, showing both agitation and displacement when approached (De Blocq Van Scheltinga 2017). Although there is some suggestion that the species is able to adapt their flight behaviour on waterbodies with high disturbance (Keller 1989), no such habituation has been observed on the regularly disturbed Rietvlei (Western Cape) (De Blocq Van Scheltinga 2017) and nesting success is lower on waterbodies with recreation than on undisturbed waterbodies (Keller 1989). The absence of recreational disturbance on Rondevlei and Langvlei, which have the species preferred habitat of deep water with abundant vegetation (Russell, Randall & Hanekom 2014) has likely contributed to the increasing abundance of Great Crested Grebe on these waterbodies.

Little Grebe undergo seasonal movements by dispersing to smaller or ephemeral waterbodies during summer, with movements typically dependent on seasonal changes in environmental conditions (Dean 1997a). Within the WLC, Little Grebe are typically most abundant on Langvlei, and it is on this waterbody where substantial long-term declines have occurred. Reasons for such declines remain unclear, but could potentially be linked to changing local conditions such as increased competition from other diving piscivores, as well as changing fish communities resulting from the establishment of several large alien fish species notably Mozambique tilapia *Oreochromis mossambicus* and common carp *Cyprinus carpio* (Olds et al. 2011), which are habitat modifiers and can result in reduced vegetative cover and water clarity (Weber & Brown 2009) and may, because of their large adult size, be less suitable prey species. Further study into the factors causing a decline of the Little Grebe population is warranted.

Conclusions

Changes in the abundances of several piscivorous waterbirds species in the WLC over the four decade study period are substantial. Periodic changes in salinity, plant biomass, and fish communities in Swartvlei Lake appear to have contributed to the decline of many piscivorous birds on this waterbody. Drivers of change in species abundances and wetland usage, particularly of highly mobile or migratory species, are likely to be multifaceted, function on multiple spatial and temporal scales, and affect different species in different ways. Many such cause and effect relationships are poorly understood and require further investigation.

From a conservation perspective most of the observed trends and particularly abundance declines, are concerning. Increases in the abundance of Cape Cormorant are indicative of a species changing its behaviour and movement patterns in response to widespread ecosystem changes. One positive note is the increasing abundance of the Great Crested Grebe, particularly on the waterbodies where human disturbance is minimised. The Touw system was proclaimed a Ramsar site in 1991 primarily because it regularly supported globally significant (> 1% global populations) numbers of waterfowl (Randall 1990). The abundances of these species have, however, declined substantially and the Ramsar criteria, in terms of waterfowl abundance, has not been regularly achieved for many years (Russell 2023). One per cent of the southern African population of Great Crested Grebe is estimated as 100 individuals (WPE 2012), which has been achieved intermittently in the Touw system between 1992 and 2007, and thereafter was exceeded in all counts in both seasons.

The conservation of vagile species such as waterbirds is a national concern, extending beyond the boundaries of individual waterbodies, with likely drivers of change such as the national degradation of wetlands (eds. Van Deventer et al. 2019) and estuaries (eds. Van Niekerk et al. 2019) including the overutilisation of fish, changing pelagic fish stocks (Coetzee et al. 2008; Roy et al. 2007) and disturbances in remaining wetlands and breeding sites, requiring urgent attention at a regional and national scale. On a local scale there are several actions that could be implemented to potentially reduce anthropogenic impact on waterbodies in the WLC and restore and reinstate their suitability for several declining waterbird species. These could include:

- Arresting the encroachment of emergent macrophytes into the lakes and reinstatement of open sand banks away from high-intensity recreational areas, which can be used by piscivorous birds for resting and roosting.
- Reducing both the extent and intensity of disturbance from recreational pursuits and resource use activities. Use zonation within national park and estuary management plans could be used to restrict high-disturbance activities to areas and times of low importance to waterbirds. The area of low or no usage or impact within the lakes as a whole should be increased.
- Preventing the establishment of additional alien fish species, and where feasible managing populations of existing alien and introduced fish species through the selective removal of large breeding individuals, and maintenance of environmental conditions, notably salinity, such that it is unsuitable for the mass breeding of introduced primarily freshwater species such as common carp.
- Responsible management of estuary breaching to both prevent significant artificial variability in estuarine conditions and enable regular and timeous movement of fish between the estuarine and marine environments. Recruitment of fish from the marine environment likely mostly affects the availability of small size classes, which would form the bulk of fish consumed by birds. The estuaries need to remain temporarily open/closed systems, with open and closed durations broadly mimicking that which would reasonably be expected to occur under natural conditions.
- Channels between lakes in the WLC need to be maintained to enable the movement of water and free migration of indigenous fish between waterbodies.
- Strict management of recreational and subsistence fishing so as to prevent overexploitation. Illegal fishing, and particularly the use of gill nets which not only capture large numbers of fish but can also entangle and drown waterbirds and particularly pursuit piscivores such as grebes, cormorants and darters, must be actively prevented.
- The cormorants unique incubation method of holding eggs and small chicks on top, between, or under their large webbed feet makes their eggs and chicks vulnerable to being thrown out of nests by disturbed and frightened brooding adults (Williams & Randall 1995) making it essential to eliminate human disturbance of nesting cormorant colonies.
- Deliberate removal of nesting trees must be prevented wherever possible. Where these trees occur on public lands they must be protected, and safeguarding of nesting trees on private properties must be actively encouraged.

Acknowledgements

Several persons have participated in the approximately 232 waterbird surveys through the years, including Beate Holscher, Jenny Harding, Nick Hanekom, Bridget Randall, Rod Randall, and Jessica Hayes. They are thanked for their dedication and professionalism on both the good and bad weather days. The late Andre Boshoff provided full access to waterbird abundance data collected in the 1980s without which components for this study would not have been possible. Kyle Smith and anonymous reviewers are thanked for helpful comments on an earlier draft of this article.

Competing interests

The author declares that he has no financial or personal relationship(s) that may have inappropriately influenced him in writing this article.

Author's contributions

'I.A.R. is the sole author of this research article.

Funding information

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

Data availability

The data that support the findings of this study can be made available by the author upon reasonable request.

Disclaimer

The views and opinions expressed in this article are those of the author and not an official position of South African National Parks and the publisher.

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Appendix starts on the next page →

Appendix 1

TABLE 1-A1: Test results of the Mann–Kendall tests performed on selected piscivorous waterbird abundance data on each waterbody collected between 1992 and 2019, and combined data for waterbodies, per season, to test for the significance and direction of non-seasonal trends.

Species	Season	Rondevlei		Langvlei		Eilandvlei		Touw Estuary		Swartvlei Lake		Swartvlei Estuary		All waterbodies	
		Z	*p*	*Z*	*p*	*Z*	*p*	*Z*	*p*	*Z*	*p*	*Z*	*p*	*Z*	*p*
Great Crested Grebe	Summer	3.856	0.000	0.831	0.203	1.129	0.129	1.650	0.049	-2.711	0.003	1.272	0.102	0.688	0.246
Great Crested Grebe	Winter	2.510	0.006	2.154	0.016	2.174	0.015	2.228	0.013	-1.544	0.061	2.572	0.005	3.536	0.000
Black-necked Grebe	Summer	2.346	0.009	0.144	0.443	-	-	-	-	-	-	-	-	1.264	0.103
Black-necked Grebe	Winter	2.471	0.007	-2.644	0.004	-0.698	0.243	-	-	-2.334	0.010	1.609	0.946	-0.178	0.429
Little Grebe	Summer	0.217	0.414	-1.897	0.029	-2.753	0.003	1.284	0.100	-3.596	0.000	0.316	0.376	-2.585	0.005
Little Grebe	Winter	-0.850	0.198	-2.687	0.004	-0.336	0.368	-1.407	0.080	-3.735	0.000	-0.968	0.166	-4.011	0.000
White-breasted Cormorant	Summer	-0.576	0.282	0.655	0.256	0.139	0.555	-0.837	0.201	-0.945	0.172	-0.836	0.202	0.000	0.500
White-breasted Cormorant	Winter	1.472	0.071	0.238	0.406	-1.406	0.080	0.674	0.250	-1.325	0.093	1.148	0.126	0.158	0.437
Cape Cormorant	Summer	0.593	0.277	2.334	0.010	1.693	0.045	2.169	0.015	-0.806	0.210	2.240	0.013	2.883	0.002
Cape Cormorant	Winter	1.021	0.154	0.879	0.190	2.177	0.015	2.340	0.010	2.552	0.005	2.206	0.014	2.312	0.010
Reed Cormorant	Summer	2.909	0.002	1.916	0.028	0.496	0.310	-1.269	0.102	-2.379	0.009	-1.209	0.113	-0.709	0.761
Reed Cormorant	Winter	-1.028	0.152	0.277	0.391	-0.672	0.251	0.969	0.166	-1.225	0.110	0.296	0.383	0.988	0.162
African Darter	Summer	0.752	0.226	2.885	0.002	-0.521	0.301	1.363	0.086	-1.671	0.047	-0.849	0.198	-0.773	0.220
African Darter	Winter	0.364	0.358	-0.878	0.190	1.711	0.044	1.134	0.128	-0.099	0.461	2.108	0.017	-0.376	0.354
Kelp Gull	Summer	-1.944	0.026	-0.650	0.258	-1.388	0.083	1.900	0.029	-3.002	0.001	1.462	0.072	0.814	0.208
Kelp Gull	Winter	-1.067	0.143	0.684	0.247	0.729	0.233	0.497	0.309	-1.988	0.023	0.951	0.171	0.020	0.492
Common Tern	Summer	-1.436	0.075	-2.116	0.017	-1.773	0.038	-1.693	0.045	-1.424	0.077	1.019	0.154	-2.301	0.011
Common Tern	Winter	-1.663	0.048	-2.394	0.008	-1.822	0.034	-	-	-1.426	0.077	-1.297	0.097	-2.925	0.002
Pied Kingfisher	Summer	-1.173	0.120	-0.597	0.275	-0.204	0.419	-0.937	0.174	0.675	0.250	-0.809	0.209	-1.109	0.134
Pied Kingfisher	Winter	-0.667	0.252	-0.955	0.170	-2.702	0.003	-0.630	0.264	1.197	0.116	-0.996	0.061	-1.406	0.080