Effects of prolonged elevated water salinity on submerged macrophyte and waterbird communities in Swartvlei Lake, South Africa

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ABSTRACT

Large fluxes in the physico-chemical characteristics of estuarine lakes can have profound effects on biota and processes. Where salinity in Swartvlei Lake usually ranges between 5 and 12, extended open conditions post–2007 floods, coupled with reduced freshwater inflows due to drought, resulted in salinity exceeding the upper tolerance of dominant submerged macrophytes. A resulting die-back of macrophytes equated to a 99% decline in standing crop, and was followed by a 95% decline in the biomass of waterbirds. Significant positive correlations exist between the biomass of macrophytes and both piscivorous and herbivorous waterbirds. Whereas Swartvlei Lake is expected to, in the short term, revert to its former (pre–2007 flood) state, inevitable environmental changes such as global warming and resulting changes in local climatic and marine conditions, along with increased freshwater abstraction from feeder rivers, could cause the observed large fluctuation in the abundance of aquatic biota to become more frequent.

Keywords: Swartvlei Lake, estuarine lake, drought, flood, macrophyte senescence, biotic interactions, environmental change, global warming

INTRODUCTION

Estuarine submerged macrophyte communities can be highly variable at both spatial and temporal scales, with many studies from around the world describing community changes along spatial and temporal salinity gradients (Verhoeven, 1975; Bayley et al., 1978; Verhoeven and van Vierssen, 1978a, b; Vaquer and Heurteaux, 1989; Lazar and Dawes, 1991; Quammen and Onuf, 1993). In South African estuarine systems, substantial community changes occurring in conjunction with elevated salinity have been recorded, mostly in estuarine lakes (Whitfield, 1984; Cyrus et al., 2011).

Only 8 estuarine lake systems occur in South Africa (Whitfield, 1995), which, considering that there are in excess of 250 estuaries in the country (Van Niekerk and Turpie, 2012), makes them relatively uncommon ecosystems. What estuarine lakes lack in number, however, they make up for in size, collectively comprising more than 62% of estuarine area in the country (Van Niekerk and Turpie, 2012). Most have a high conservation value, with 5 of the 8 ranking in the top 10 estuaries in South Africa in terms of conservation importance, and with 7 of the 8 in the top 40 (Turpie et al., 2002). The Swartvlei system ranks 7th. Estuarine lakes vary in the permanency of their marine connection, from permanent (e.g. Kosi) to seldom (e.g. St. Lucia), with the Swartvlei system lying between these two extremes, being open 68% of the time (1969–2016) and more frequently in summer (Russell, 2015). Salinity in estuarine lakes is determined primarily by the balance between marine and freshwater inflows (volume and timing), as well as evaporation.

Salinities in estuarine lakes can vary both spatially and temporally, with arguably the most extreme example in South Africa being St. Lucia, where salinity ranges up to 200 (Cyrus et al., 2011) and spatial variation of salinity across the waterbody at times exceeds 100 (Taylor et al., 2006). By contrast Swartvlei Lake is usually relatively stable, with salinity fluctuation typically not exceeding 16 (1991–2006) and with little spatial variability across the waterbody (Russell, 2015).

Large fluxes in the physico-chemical characteristics of estuarine lakes can have a profound effect on biota and process (Taylor, 1983; Davies, 1982; Whitfield, 1984; Heÿl and Currie, 1985; Cyrus et al., 2011). This paper describes the effects of an 8-year period of above-average salinity, resulting from extended open mouth conditions and drought, on the submerged macrophytes and avifauna of Swartvlei Lake.

METHODS

Study site

The Swartvlei system is situated in the Garden Route National Park (33°58′ to 34°02′S and 22°43′ to 22°50′E) on the Cape south coast of South Africa. It comprises two connected estuarine lakes, namely, Swartvlei Lake and so-called Karatara Lake, and the Swartvlei Estuary (Fig. 1). One small seasonal river, the Klein Wolwe (catchment area approx. 17.2 km^2) and three larger perennial rivers, namely the Wolwe (approx. 98.3 km^2) Hoëkraal (approx. 111.0 km^2) and Karatara (approx. 101.6 km^2) flow into the Swartvlei system. Mean annual rainfall in the catchments is between 900 and 1 000 mm·yr^{-1} (Adamson, 1975), with no identifiable seasonal variation (Whitfield et al., 1983).

Swartvlei Lake is temporarily connected to the sea via the Swartvlei Estuary, with frequent mouth closure of the estuary caused by south-westerly wave conditions and longshore sand transport (Whitfield et al., 1983). Artificial breaching of the system is undertaken when rising water levels achieve 2.0 m amsl and threaten developed properties on the estuary floodplain.

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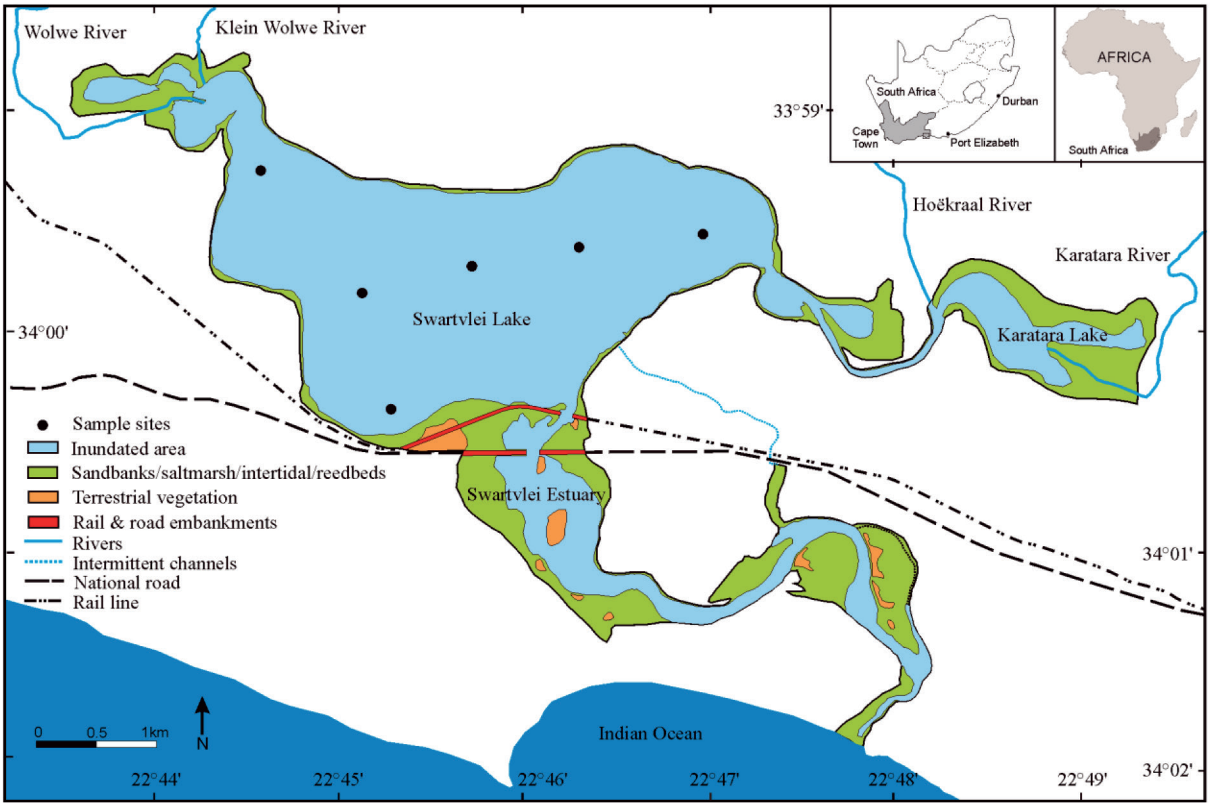

Figure 1
Locations of water quality sample sites within Swartvlei Lake over the period 1991–2016.

Swartvlei Lake is meromictic (Robarts and Allanson, 1977). The monimolimnion often has a higher salinity than the mixolimnion (Allanson and Howard-Williams, 1984). The 1% level of photosynthetically-active radiation is generally about 5 m (Allanson and Howard-Williams, 1984), hence large portions of the lake, which is up to 17 m deep, are unable to support rooted macrophytes. Stratification is maintained by the inflow of higher salinity water from the estuary during open-mouth phases that accumulates in the deeper portions of the lake, which lie well below sea level. During closed phases, wind mixing of surface waters can cause the erosion of this stratification and, if prolonged, its breakdown (Allanson and Howard-Williams, 1984).

Submerged macrophytes are usually widespread and abundant in the shallow (< 3 m) littoral zone of Swartvlei Lake. Communities consist predominantly of pure and mixed stands of *Stuckenia pectinata* syn., *Potamogeton pectinatus* (Fennel-leaved Pondweed), Charophyta (stoneworts) and filamentous algae (Howard-Williams and Liptrot, 1980; Weisser and Howard-Williams, 1982; Whitfield et al., 1983). Estuarine and marine fish (Whitfield, 1984; Russell, 1996) and waterbirds (Boshoff et al., 1990a, 1990b, 1990c; Russell et al., 2014) inhabit the lake system.

Sample collection

Surface water salinity was measured monthly from 1991 to 1999 and quarterly from 2000 to 2016 at 6 localities (Fig. 1). Measurements were undertaken in the field during daylight hours (08:00 – 13:00) at 30 cm depth using YSI Model 33 (1991 to 2005) and Model 30 (2005 to 2016) S-C-T meters.

The South African Department of Water and Sanitation provided unpublished flow data for rivers. Data from the Karatara River were used for flow descriptions, as they were the most complete. Monthly flow trends in the adjacent systems are likely to be similar because river catchments are relatively small, arise in the Outeniqua Mountain chain and are hence similarly affected by rainfall events.

The standing biomass of submerged macrophytes was determined during May and June from 1991 to 2016. Assessments were undertaken biennially between 2000 and 2004. Stratified random sampling was used to position 6 littoral transects around the lake, the limits of which were the inner edge of the emergent macrophyte zone and the 2 m depth contour. A submerged macrophyte sampler (Howard-Williams and Longman, 1976) was used to collect the above-ground portions of macrophytes at five 0.0625 m^2 sample points along the length of 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.

Waterbird abundance was determined biannually during summer (January–February) and winter (July–August) from 1992 to 2016. Counts were conducted by 4 observers using field glasses, from a boat following a standardised 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 minimised by use of the same observers wherever possible throughout the study period, with observers specialising in different taxa. Mean biomass of waterfowl from summer and winter abundance assessments within a calendar year was taken to represent annual average biomass. Biomass of waterbird species was calculated from the mean of the masses for males and females obtained from Fairall (1981) for *Fulica cristata* (Red-knobbed Coot) and Hockey et al. (2005) for the other species.

Analysis

Salinity did not differ significantly between sample sites (Russell 2015); therefore, mean salinity of all sites was used to display change in salinity over time. The association between the waterbird and macrophyte biomass was examined using regression analysis.

RESULTS

River runoff broadly correlates with rainfall, with low rainfall periods resulting in periods of sustained low runoff (2009) and, alternatively, high rainfall years (2006–2007) resulting in high runoff, which typically includes one or more high-intensity flooding events (Fig. 2a, b). High runoff events during closed phases leading to a rapid rise in water level in the system invariably triggered artificial breaching of the estuary mouth. High freshwater inflow events during closed phases result in a reduction in lake salinity (Fig. 2b, c), though this is short-term if followed by breaching which enables the inflow of marine waters into the system once river flow has subsided. Progressive increases in salinity in Swartvlei Lake are usually associated with extended open phases (Fig. 2b, c), with decreases in

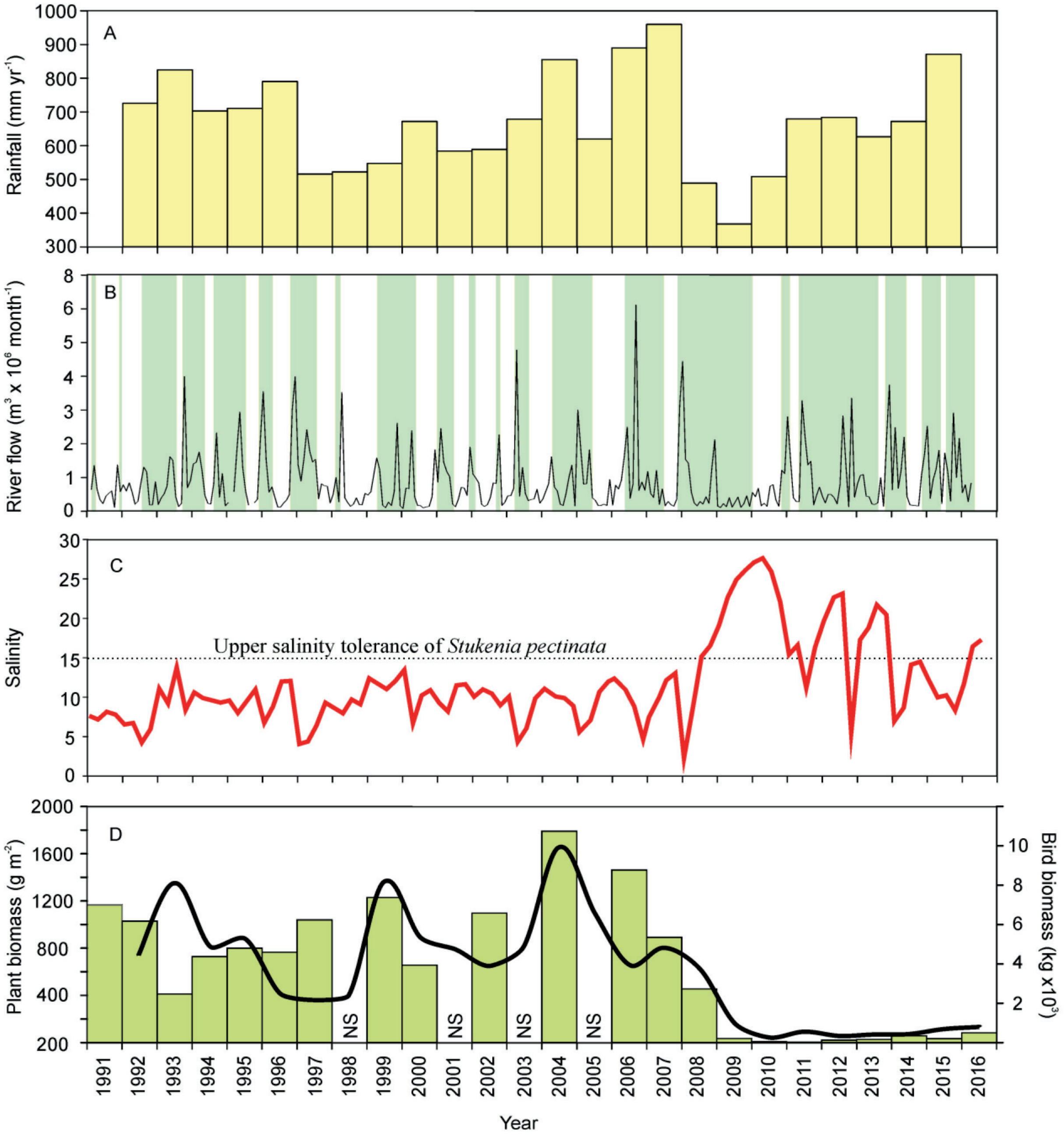

Figure 2

(A) Total annual rainfall (1991-2015) measured at Rondevlei 2nd order meteorological station. (B) Time-series of the total monthly flow in the Karatara River. Shaded vertical bars indicate periods when the Swartvlei Estuary was open. (C) Time series of the average salinity of surface mixolimnion waters in Swartvlei Lake measured at 3-month intervals from 1991 to 2016 (D) Solid line indicates total biomass of all waterbirds on Swartvlei Lake averaged from surveys conducted bi-annually in January and July. Shaded vertical bars indicate the biomass of submerged macrophytes determined annually in the period of maximum biomass (May–June). NS = macrophytes not sampled.

salinity at times associated with extended closed phases, but more commonly associated with high freshwater inflows during both closed and open phases.

During the period 1991 to 2007 surface salinity typically fluctuated between 5 and 12 (Fig. 2c), with occasional deviations beyond this range being short-lived and generally associated with high freshwater inflows (< 5) or extended open conditions (> 12). A high-intensity rainfall event occurred in November 2007 (Fig. 2b) with 260 mm falling in a 48-h period (Rondevlei meteorological station). Salinity of surface waters in Swartvlei Lake dropped from 13.1 to 2.3 during this event (Fig. 2c). Swartvlei Estuary was breached on 22 November 2007, and remained open until 4 January 2010. This extended open phase coincided with a period of exceptionally low rainfall in 1999 (Fig. 2b), which together resulted in a substantial increase in the salinity of the lake's surface waters (2.3 to a high of 27.6) during the 775 days the estuary was open (Fig. 2c). Higher than average salinity also occurred during much of the period 2011 to 2013 (Fig. 2c), when the estuary also remained open for an extended period (max = 831 consecutive days) (Fig. 2b), with short-term decreases occurring only during high-runoff events.

The biomass of submerged macrophytes in Swartvlei Lake littoral decreased substantially during the period of increasing and high salinity, declining from 892.0 g·m^{-2} in 2007 prior to salinity increases, to 34.8 g·m^{-2} 2 years later in 2009 during the low freshwater inflow period, and reaching a low of 3.0 g·m^{-2} in 2011 (Fig. 2d). This equated to a 99% decline in standing crop. Exceptionally low plant biomass has persisted up until 2016, though with some relatively small increases (3.0 to 83.7 g·m^{-2}) during this 5-year period (Fig. 2d).

A substantial decline in the biomass of waterbirds coincided with the decline of submerged macrophytes (Fig. 2d). The biomass of all waterbirds in Swartvlei Lake decreased from 4 775 kg in 2007 to 217 kg 3 years later in 2010, representing a 95% decrease. Low overall waterbird biomass has persisted up until 2016. A significant ($F = 26.996$, $p < 0.000$) regression is present between plant biomass and the biomass of all waterbirds. Both piscivorous waterbirds and the predominantly herbivorous waterfowl underwent declines (Fig. 3a, b). The mean biomass of waterfowl during years prior to plant declines

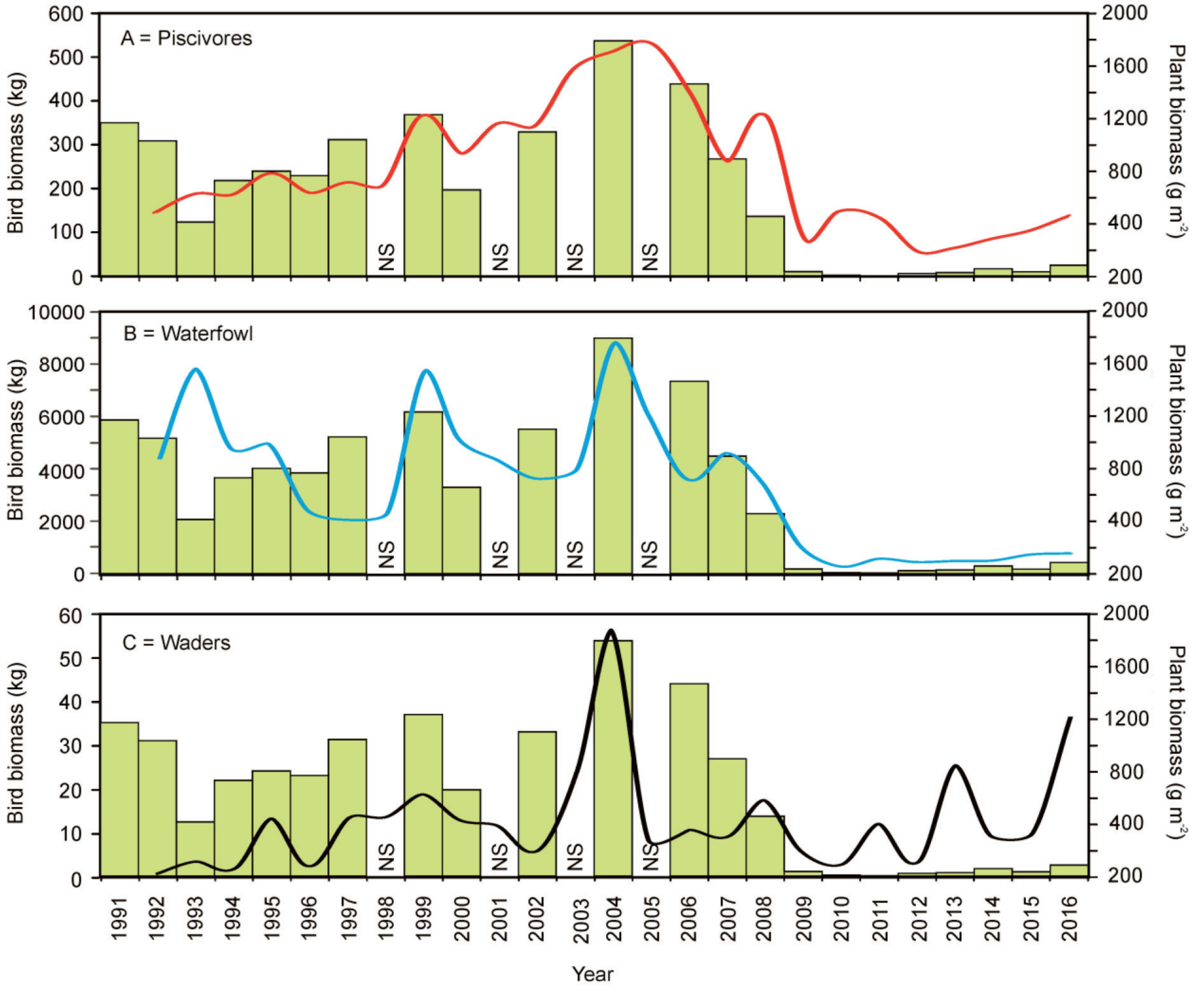

Figure 3

(A-C) Solid lines indicates total biomass of (A) piscivorous waterbirds comprising grebes, cormorants, darter, herons, egrets, night heron, bittern, raptors, gulls, terns and kingfishers, (B) waterfowl comprising ducks, geese, crake, swamphen, moorhen and coot, (C) waders comprising ibises, spoonbill, rail, jacana, oystercatcher, plovers, sandpipers, lapwing, greenshank, stint, ruff, snipe, avocet, stilt and thick-knee on Swartvlei Lake. Annual totals are averaged from surveys conducted bi-annually in January-February and July-August. Shaded vertical bars in all panels indicate the biomass of submerged macrophytes in Swartvlei Lake determined annually in the period of maximum biomass (May–June). NS = macrophytes not sampled.

(1992–2007) was 4 684 kg, which decreased to an average of 403 kg during the phase of low plant abundance (2009–2016), equating to a decline of 91%. Regression between plant biomass and the biomass of waterfowl is significant ($F = 24.470$, $p < 0.000$). Over the same period, the biomass of piscivorous waterbirds declined from 304 kg to 99 kg, equating to a decline of 67%. Regression between plant biomass and the biomass of piscivorous waterbirds is highly significant ($F = 48.970$, $p < 0.000$). By contrast, the mean biomass of wading birds, excluding greater flamingos which occur intermittently, though at times in sufficiently large numbers to completely dominate wader biomass, remained low (average = 12.8 kg) during both high and low macrophyte biomass phases (Fig. 3c). No significant correlation existed between plant biomass and wader biomass ($F = 1.890$, $p = 0.185$).

DISCUSSION

The upper salinity tolerance of the dominant macrophytes *S. pectinata* and Charophyta is considered to be 15 (Howard-Williams and Liptrot, 1980). It is presumed that the prolonged exposure of these species to high salinities in Swartvlei Lake from 2008 onwards was the cause of their temporarily corresponding dieback. The close link between zoobenthos and submerged macrophytes in Swartvlei Lake has been demonstrated by Davies (1982), when in the 1980s macrophyte senescence over a 3-year period, characterised by a 60% decline in primary production (Taylor, 1983), resulted in a 74% decline in littoral invertebrate biomass, reducing food availability for invertebrate-feeding fish and birds. An analogous decline could be expected to have occurred post-2007 which, due to dominant taxa and diatoms being tolerant of high salinities (Nel et al., 2015; Bate et al., 2013), would likely have been due to the loss of macrophytes and associated detritus production.

Most waterfowl (ducks and rallids) are dependent on macrophytes, either directly or indirectly, for food. The most abundant of these waterfowl on Swartvlei Lake is the Red-knobbed Coot (Russell et al., 2014), which feeds almost exclusively on *S. pectinata* and *Chara* spp. (Fairall, 1981). Of the 7 duck species that have been regularly recorded, 5 (*Anas undulata* Yellow-billed Duck, *Anas erythrorhyncha* Red-billed Teal, *Netta erythropthalma* Southern Pochard, *Thalassornis leuconotus* White-backed Duck, and *Alopochen aegyptiaca* Egyptian Goose) are primarily herbivorous (Siegfried, 1981; Brickell, 1988), though the Egyptian Goose feeds predominantly on terrestrial vegetation (Halse, 1984). Aquatic invertebrates form the major component of the diet of *Anas smithii* (Cape Shoveler) and *Anas capensis* (Cape Teal) (Siegfried, 1981; Brickell, 1988). The relationship between macrophyte biomass and both herbivorous and invertebrate-feeding waterfowl has been demonstrated in the Wilderness lakes (Russell et al., 2009), and the substantial decline in waterfowl on Swartvlei Lake can with some confidence be ascribed to a local decline in their food source.

Estuarine fishes are able to tolerate salinity ranges in excess of those recorded in Swartvlei Lake (Whitfield, 1998). The diet of many estuarine fishes, however, is linked to the presence of macrophytes, with juveniles and adults of numerically dominant littoral species (Whitfield, 1984) such as *Rhabdosargus holubi* (Cape Stumpnose) feeding mainly on filamentous algae, macrophytes and epibenthic invertebrates (Whitfield, 1984, 1986). The abundant *Monodactylis falciformis* (Oval Moony) feed on invertebrates associated with macrophytes (Whitfield, 1984), and the diet of Mugilidae (mullet spp.) comprises mainly plant detritus and associated unicellular algae and diatoms (Whitfield, 1982). A substantial decline in macrophytes is thus expected to result in an associated decline in littoral fish populations, as observed by Whitfield (1984) in Swartvlei Lake in the early 1980s. Abundant zooplanktivorous species such as *Atherina breviceps* (Cape Silverside) and *Gilchristella aestuarius* (Estuarine Round-herring) (Whitfield, 1984) are likely to be less affected. Although changes in littoral fish communities were not assessed in this study, their probable decline following prolonged macrophyte senescence could account for substantial declines in piscivorous waterbirds.

Howard-Williams and Allanson (1979) described how the ratio of food production to consumption in Swartvlei Lake is approximately 1:1 and hypothesized that any change in production would have a corresponding change in the number of consumer organisms. The significant positive correlations between macrophyte plant biomass and the biomass of waterbirds either directly or indirectly dependent on littoral plants supports this hypothesis.

The question arises whether the observed changes are likely to persist over the long term. Expectations are that cyclical rainfall patterns, including the reduction of the El Niño phenomenon, could, in the short term, lead to periods of above-average rainfall and hence freshwater inflows. In addition, the periods of atypically prolonged open estuary phases following large-scale flooding in 2006 and 2007, and as also observed following floods in 1980 (Whitfield et al., 1983), could also be expected to decline, resulting in future shorter open phases. These two processes would result in deceasing salinity, and the possible shifting of the system back to a state where macrophytes intolerant of high salinity re-establish, and in turn support, either directly or indirectly, a high biomass of waterbirds.

Alternatively, the current changes that are occurring in Swartvlei Lake may provide a glimpse of what the long-term future holds for this system. Climate change and resulting changes in the marine environment, such as sea level rise and increased hydrostatic, wave and wind set-up, will affect estuaries in several ways, including increased intrusion of seawater (Theron and Rossouw, 2008). Although pollen analysis of the adjacent Groenlvlei Lake sediments provides some evidence to suggest that global cooling is associated with drier conditions in the southern Cape (Martin, 1968), and hence by default global warming is associated with wetter conditions, climate change models widely forecast increases in the intensity and frequency of droughts in South Africa resulting from global warming (Cook et al., 2014; Dia, 2013), with only the eastern subtropical portions of the country likely to experience generally wetter conditions (Engelbrecht et al., 2009; Shongwe et al., 2009; Tadross et al., 2005). Thus periodic reduction in rainfall and river flow, coupled with increased abstraction of freshwater from rivers to meet growing demand, in conjunction with increased seawater intrusion, may place Swartvlei Lake on a trajectory of becoming more saline more frequently.

If the above scenario plays out it is unsure if existing biota will adapt, or if more salinity-tolerant species will establish or dominate. The epiphytic *Brachidontes virgiliae* (Brackwater Mussel) which is the dominant bivalve in the system (Davies, 1982), comprising 95 to 99% of the benthic standing stock (Allanson, 1981), has a preferred salinity tolerance range of 0 to 20, though is able to survive salinities in excess of seawater (~35) when exposure to increasing concentration is gradual (Nel et al., 2015). Similarly, epipelic diatoms show a high tolerance to variability in salinity (Bate et al., 2013). Thus, given appropriate substrate and food sources they possibly could persist. However, it is unsure if current *S. pectinata* and *Chara* spp. dominated macrophyte communities would be replaced by species that are abundant in the typically more saline Swartvlei Estuary, such as *Ruppia cirrhosa* (Spiral Ditchgrass) or *Zostera capensis* (Eelgrass), which can tolerate salinity levels up to 50 and 45, respectively (Adams and Bate, 1994), or whether they would be able to support comparable waterbird and other estuarine biota communities.

Humphries et al. (2016) have provided evidence of historic (~1 100 and 1 750 cal year BP) severe drought events in St Lucia to the north, demonstrating that El Niño driven desiccation cycles and resultant elevated salinity are a long-standing natural process, and a driver of environmental flux in systems sensitive to changes in water balance. Even though long-term (25-year) data indicate that the Swartvlei system, including Swartvlei Lake, is not undergoing a rapid deterioration in water quality (Russell, 2015), but rather exhibiting both short- and long-term fluxes characteristic of estuarine systems, these results do emphasise the ability of Swartvlei Lake to undergo substantial changes in ecological state. This in turn emphasises the need for wise use of resources, particularly freshwater, and awareness of the consequences of radically altering estuarine processes, such as artificial estuary breaching, lest we wish to observe ecological changes that become either a more regular occurrence, or possibly even a permanent state.

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