Wetland- and waterbirds as indicators of ecosystem productivity in the Incomati Delta, Mozambique in relation to hydrology and river hydraulics

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Abstract

Wetland- and waterbirds were counted, mostly from vehicles, on 3400 hectares of the low-lying floodplains of the Incomati Delta, the Macaneta wetlands between January 2021 to February 2023. Over 300 bird species have been observed in and around these wetlands of which 153 species were considered wetland- and waterbirds, yielding a total of 61089 birds from 92 counts (664 birds per count). The counted area was divided into 21 zones according to altitude Above Mean Sea Level (all are below 4m AMSL) and vegetation characteristics. but not all zones could be accessed at each count (average 15.4 zones per count) resulting in a total of 1415 zones counted. Average duration of the counts was 3hrs 30min and covered 25 km of road. The counts were converted to monthly average biomass per countplot using average weight for each individual species. The species were divided into 10 feeding guilds on the basis of feeding spectrum from literature sources. Piscivores and herbivores were the dominant guilds, followed by aquatic invertebrate feeders, a specialized molluscivore, etc.
The data were analysed using principal component analysis with the environmental variables collected: river discharge, salinity (monthly average per countplot), peak tide within 72 hours prior to the count, local rainfall (monthly total), altitude and vegetation type.
In February 2021, almost the entire floodplain was covered by a >1000 m^3s^{-1} river flood while 2022 was characterized by an exceptionally strong and extended rainy season.
Both piscivore and raptor biomass correlated with river discharge 7 months prior to the counts, indicating a positive impact of flooding on floodplain productivity.
As waterbird biomass, and in particular the piscivores, can be considered a proxy for fish and crustacean production these correlate with human well-being as fisheries are an important livelihood component in the delta, Maputo Bay and adjacent coastal waters. Maintaining such floodpeaks is thus essential for maintaining and enhancing the livelihoods of the vulnerable users of the area. In addition, it is suggested that managed flood releases prior to the equinox tides of September would be beneficial to both biodiversity values and ecosystem services of the delta, including by preventing high salinities destroying floodplain vegetation and thus increasing the risk of erosion.

1. Introduction

The wetland- and waterbird counts of January 2021 to February 2023 were conducted on the 3400 ha of low-lying floodplain (Fig. 2), situated below 4 m Above Mean Sea Level (AMSL), between Hobjana and the Macaneta Beach Club, south of the village of Macaneta, where the coastal dune narrows down to the 20 km long sandspit that extends to the Incomati river mouth. Additional counts were made on the river during the salinity transects of 2021 and occasional boat trips for school excursions or awareness raising such as during the Macaneta festival of mid-October 2021.

The northern limit of this floodplain is formed by sandy dunes situated at 6-12 m AMSL, stretching west from the coastal dune to the Incomati River over about 5 km. The floodplain curves strongly towards the North here, possibly scoured out from the coastal dune by a former river meander. Along the river's edge, the dune narrows down to a 200 m wide strip, separating the river from the floodplain for about 3 km to the village of Hobjana, situated on a dune "island" of about 1.7 km East to West and about 1 km North to South. The eastern limit is formed by about 10 km of originally forested coastal dune (6-10 m altitude) of between 1.5 to 2 km width until, towards its southern limit, it narrows to a 100 m wide vegetation-less sandy strip that closes a former river mouth and that can be overtopped during high tides with strong wave action. According to Allport (2021), late 19th century maps show an open river mouth here. The western limit of the Macaneta floodplain is formed by the meandering Incomati River (Fig. 2).

The floodplain soils are predominantly fine clay, deposited by river flooding with some sandier parts of reworked dune terraces, intensively used for rainfed agriculture (maize, cabbages, bananas, etc.). There are many signs of historical attempts for irrigated rice cultivation (pumphouses, ditches, embankments), mostly from colonial times, but also more recent attempts with fresh canals dug even during the counts. During the counts, in 2022, the main road from the bridge to Macaneta village was raised to be permanently above the tidal range and broadened using sand from the terraces west of the River, surfaced with bricks and its slopes covered with clay extracted from the floodplain. More information on the historical timelines of agriculture in the Macaneta floodplain will come through the PhD work of Dércio Alberto (this volume).

The lowest lying areas of the floodplain are reached by the highest tides (>2.5 m AMSL) and can therefore accumulate salt when the tidal water subsequently evaporates, especially during the dry season (June to October). When diluted by rainfall or by river flooding, some of these salts are released again into the surface waters, creating brackish conditions favourable to estuarine species, including mud-probing waders.

Under prolonged dry conditions, the salts can cause mortality of the vegetation with increasing loss of soil cohesion and increased vulnerability to wind erosion. Possibly this explains why some of the lowest-lying areas are the saltiest through a self-strengthening process. Only series of years with high rainfall and/or flooding with river water from upstream can reduce the salt by exporting it back to the river as could be observed in 2022. It is our hypothesis that the northern wetlands, the lowest lying and saltiest area have been created through this process, probably reinforced by the reduction in discharge observed in the Incomati Basin since the 1950s (Saraiva Okello et al. 2015). Indeed, as discharge decreased, salty water would move further upstream by the tides and, especially during the dry season equinox tides (August to November), bring in large quantities of salt unto the floodplain, subsequently washed into the lowest lying areas by rain and flooding. Other, smaller low-lying areas where high salinities can be observed are probably subject to similar trends. These depressions are vegetation-less or covered with halophytes (the wetland on the edge between Z2 and Z4, the large vegetation-less seasonal lakes in Z7 and just to the West of the northern wetlands). This hypothesis is based on the observations of the salinity in the Macaneta wetlands since 2019 in conjunction with bird observations.

2. Birdcounts in Macaneta

2.1 Development of birding in Macaneta

As explained in Allport (2021), Macaneta was rather inaccessible to birdwatchers until the completion of the Marracuene bridge over the Incomati in October 2016, with only a handful of observers entering data into the citizen science platform eBird (eBird - Discover a new world of birding...) prior to that (around 100 species observed until 2014). Over the year 2017, the number of bird species observed in Macaneta increased substantially to reach 198 (Fig. 1). The next event, which put Macaneta on the map for amateur birders, as well as for professionals (guides who take clients on birding tours of Southern Mozambique), was the first observation for continental Africa of a migrant from Eastern Siberia, the Vulnerable Sharp-tailed Sandpiper *Calidris acuminata* (February-March 2018). From its breeding grounds in Siberia, this species normally flies south-easterly to Oceania. The species has seen strong declines thought to be caused mainly by the loss of habitat along the eastern seaboard of the South China Sea (development of aquaculture, harbour expansion, industry, etc.) as well as increasing droughts in Australia. In addition to adding substantial tourism revenue, this event also increased the number of observers and records and, by the end of 2018, the number of species observed had jumped to 257.

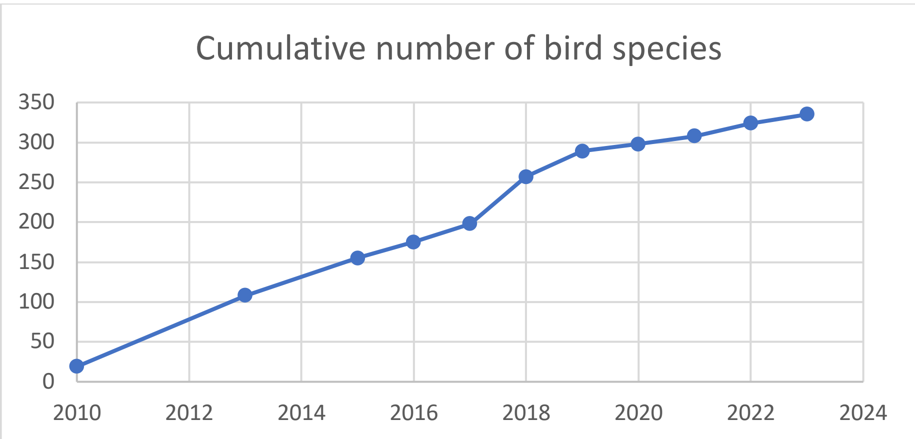


Figure 1. Cumulative number of bird species at Macaneta as recorded in eBird.

Since then, the number of species observed has been slowly rising, reaching 335 in late 2023. This is almost half of the total number of bird species observed in the whole of Mozambique.

Figure 2. Map of the birdcount zones of Macaneta with Zones 1 to 8 (Z1-Z8) along the main road from the bridge over the Incomati River to Macaneta village, Zones 9 and 10 along the road extending South from there, Zones 11 and 12 at the start of the track towards Hobjana village. MO the main outlet, RR the River Reedbeds, RF Rice Fields, DT Diagonal Track, CW Canal Wetlands, FLNW First Lake North Wetlands, CNW Core North Wetlands, BH Beyond Hobjana and DGS Dune Gardens South.

2.2 Methodology of the birdcounts from January 2021 to February 2023

The birdcounts in 2021-2022, extending slightly into 2023, we report on here have concentrated on the 3400 ha Incomati floodplains of Macaneta between the villages of Hobjana and the southern tip of the Macaneta 2 village, between the dune edge and the Incomati River (Fig. 2).

Depending on the season, these wetlands are supplied with water from various sources in related to:

- the river stage linked to rainfall in the catchment,
- abstractions by irrigation schemes and releases from dams upstream,
- the tides (highest around the March and September equinoxes),
- local rainfall and
- groundwater flows.

This mix of water sources creates a mosaic of productive ecosystems with varying water depth and quality, attractive to waterbirds. It is precisely this attractiveness to the waterbirds, in particular through the provision of food, which we are trying to capture through the birdcounts across these different habitats. In addition, we attempt to establish correlations between the bird community present and the available quantity of water as well as its quality as both of these will be affected by modifications of the (environmental) flows. The measurements of the salinity of the surface waters started in March 2019, when the Sharp-tailed Sandpiper was again present, expanding gradually from its preferred section of the floodplain to the wider birdcount areas and systematically monitored during the birdcounts.

Other environmental variables obtained are River Discharge at Magude from AraSul data and the Tidal Height at the Maputo Harbour tidal gauge. Rainfall data were obtained from a rain gauge at a private farm in Marracuene.

We consider waterbird presence and abundance as indicators of the productivity (food availability) of the system. The (known) food preferences of the different species can give us clues to the nature of these food sources and to their correlations with water quality. Thus, by identifying and counting the different bird species in the various habitats, we can infer the underlying ecological processes (primary and secondary production) that have made these food sources available to the waterbirds. Human interventions on environmental flows can be expected to modify salinity and therefore productivity and food availability and this will be reflected in the abundance and diversity of waterbirds. We can therefore use the waterbirds as proxies to predict and monitor the effectiveness of various potential management measures affecting environmental flows.

Of these 3400 ha of floodplains, around 1900 ha are the central floodplains, to the East of the Hobjana Road and to the North of the main Marracuene Bridge to Macaneta Road. Around 800 ha are strongly tidally influenced floodplains (to the South of the bridge to Macaneta road). Of the remaining 600 ha of floodplains to the West of the Hobjana Road, between this road and the river, only the easternmost edge along the Hobjana Road was part of the birdcounts.

A small triangle of about 100 ha, just north of the bridge has some higher ground with built infrastructure and a coconut palm plantation where high numbers of White-breasted Cormorants (*Phalacrocorax carbo lucidus*) and some Pink-backed Pelicans (*Pelecanus* *rufescens*), mainly feeding in the estuary, can roost at night. Sometimes they also fly upstream in fairly large groups on the incoming tide (e.g. 56 on 02/11/2021), presumably to feed in the contact zone between brackish and freshwaters around Hobjana, which conveniently also has sandbanks where they can digest at low tide. This is also a zone intensely fished with gillnets by the user communities. For example, around Hobjana during the salinity transect of 22/09/2021, there were several boats operating multiple very long gillnets – almost closing the entire breadth of the river. This was then in the brackish water zone below 10 PSU (Practical Salinity Unit). We report on this here as these piscivores do not appear in our results of the floodplain counts as they are not feeding locally.

This part of the Incomati Delta is comparatively easily accessible, especially since the building of a bridge in 2016 that led to substantial development of tourism, mostly day or weekend tourism (both domestic and expatriate) from Maputo. Macaneta is also popular with South Africans for longer stays during holidays. The lodges of Macaneta are a favoured venue for meetings and conferences. The roads, constructed to facilitate tourism, make observing and counting the waterbirds relatively straightforward.

Many of the waterbird concentrations can be observed directly from roads and tracks and thus the system was divided into count plots along these axes. The first set of count plots are situated along the 5 km road ("the main road", paved in 2022) that bisects the floodplains from the Marracuene Bridge to Macaneta 2 village on the coastal dune (Fig. 2). These plots are numbered Zones 1 to 8 (odd numbers North of the main road, even numbers South of the main road). Most are wet grassland with patches of Salicornia-type vegetation and bordered along deeper channels by reeds. The visible sections of Zones 5 and 6 are almost entirely covered by *Phragmites* reedbeds, harvested for roof thatch. The reedbeds of Zone 5 are about 100 m wide, while in Zone 6 they stretch several hundred meters to the South to reach the river. During the dry season, some sections are occasionally burned to rejuvenate the vegetation.

The said main road abuts at a roundabout on the coastal dune and then heads southwards for another 2.5 km along the inhabited dune edge, with many bars and restaurants, to where it meets the river. Zone 9 is along the main tidal creek that supplies the wetlands along the road and has a boat club from where sports fishing boats can be chartered to go fish on the Ocean or, alternatively, go on birdwatching tours along the estuary. Zone 10 is where the villagers from across the river land their fishing and ferry boats. It overlooks a stretch of river and some *Avicennia* and *Rhizophora* mangroves with a small breeding colony of Pink-backed Pelicans and Grey Herons. Groups of Gulls, Terns, White-breasted and Long-tailed Cormorants can often be observed roosting on sandbanks there at low tide or seen migrating up or down the river to feed. Some, especially the Terns, also feed in the inshore coastal waters.

Around 2 km from the bridge, a track heads north to the village of Hobjana along a series of abandoned and active fishponds on its western side (Zone 11) and wet grasslands on the eastern side (Zone 12). After about 1 km, the road reaches the river and crosses an important culvert ("MO") that connects the river to the central floodplain and also supplies some active fishponds. Situated at around 2.5 m AMSL, this connection establishes even at moderate tides. Its main channel links up with a set of smaller channels that, through the culverts under the main Marracuene to Macaneta road, connect to the 800 ha of strongly tidal wetlands south of the road and to the northern wetlands.

These two stretches, covering zones 1 to 12 (Z1 to Z12 on the map), are the easiest to count as they are accessible in almost any weather. During the river floods of early 2021, many stretches of the main road were shallowly covered by the floodwaters for over a week. In 2022, the main road was raised to 1 m above the surrounding floodplain and paved.

North of the MO culvert, the 3 km of track to Hobjana village, is often flooded by the highest tides (equinoxes) and the countplots along it can be inaccessible also when there is a lot of rain. For about 1 km, the track passes through reedbeds (“River Reedbeds”, RR), stretching all the way to the river on the western side (maximum 200 m wide) and around 100 m wide on the eastern side. Next, there are abandoned rice fields (“Rice Fields”, RF) on both sides, though some small plots can be cultivated when there is sufficient rainfall.

A major canal bisects this road about 1 km South of Hobjana and the low-lying wetlands (“Canal Wetlands”, CW) along this canal are often flooded, either from the river (through a sluicegate that can be managed by the users) or from rainfall. Two side tracks head East from the Hobjana Road into the central wetlands and can be travelled upon when conditions are favourable. Firstly, the “Diagonal Track” (DT), a slightly elevated ridge that, in the dry season, connects to the main road in the count plot “Zone 7” on the main bridge to Macaneta Road. The second side track stretches for about 300m from the Canal Wetlands to a viewpoint of the surrounding “North Wetlands First Lake” (NWFL), a shallow depression very attractive to birds when flooded. The soils are quite saline here with Salicornia-type vegetation and bare mud. From the viewpoint it is possible to walk and wade for some 500 m into the “Core North Wetlands” (CNW), the deepest depression surrounded by Reedmace (*Typha*) and that collects water from a wide range of sources through connecting channels with the central wetlands.

From Hobjana to Macaneta 2 there is a track that edges along the dune edge farms (pineapple, maize, vegetables) to the Macaneta Secondary School (birdcount plot “Beyond Hobjana”, BH) with a lot of rice cultivation and reedbeds in the floodplain and onwards, from the school along the coastal dune to the roundabout (birdcount plot “Dune Gardens South”, DGS). Here a relatively narrow strip (300 to 600 m) of land is cultivated with bunds (rice) and raised beds (bananas, vegetables). Both of these countplots BH and DGS are mainly fed from groundwater seepage from the dune with low (less than 0.2 PSU) and relatively constant salinity. This inflow is estimated to be around 4 cubic metres per hour.

In the westernmost section of BH, a small channel can collect fresh water from the river upstream of Hobjana, mainly to supply extensive banana cultivation in this area.
The people managing this canal by and large seem to be able to keep the salinity below 1.5 PSU, probably by opening the canal when the river is very high and the tides do not push the salt water up beyond Hobjana. Drops in salinity were noticed in late 2021, March 2022 and early 2023 (Fig. 3).

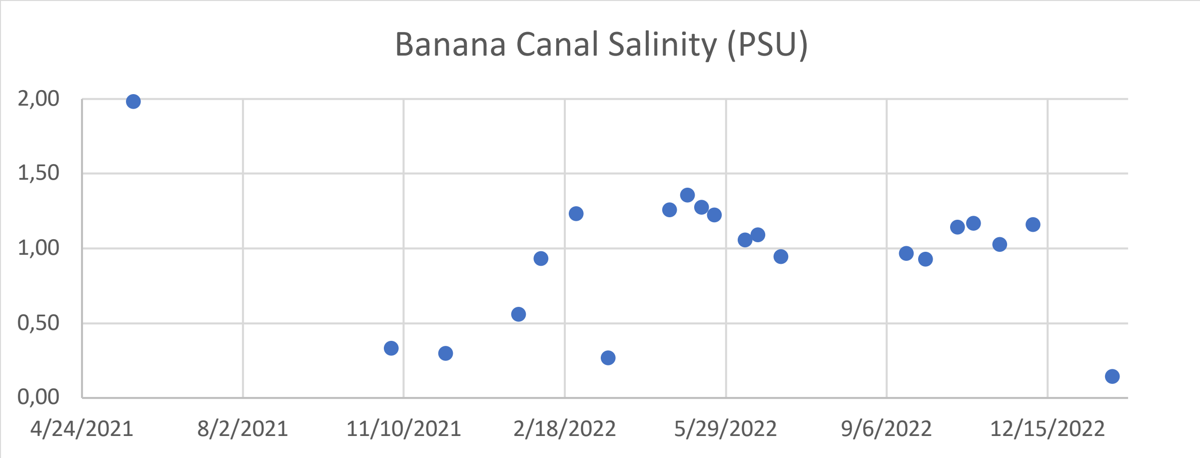


Figure 4. Salinity in the "Banana Canal" just upstream of Hobjana.

All wetland and waterbirds, defined as birds purposely using the wetlands for feeding and/or breeding, perceived as active in the plots were identified (about 150 species) and counted. Recording was done either by writing in notebooks, using a Sony voice recorder or directly online in ebird. Notebook and voice recorder data were subsequently transcribed into Excel worksheets and, with the support of VLIZ Ostend, converted into a searchable Excel database with pivot tables for both numbers and biomass (using the average weight per individual from Gibbon 2019). Birds flying over the plots were counted separately but only those feeding on the wing (Pratincoles, Swallows, Swifts, Terns, Raptors) were considered as being active within the plots. Roosting birds that could clearly not have been feeding in the plots (water depths too shallow) were excluded from the counts.

Though most of the counts were conducted from 4WD vehicles, they were completed by surveys on foot in the flooded wetlands to record more cryptic species such as snipes, rales and crakes, to close in on hard to identify species, to take salinity measurements in the various water bodies, etc.

The dates of the counts were chosen opportunistically but there is a bias towards choosing dates with tides predicted to surpass 3.5 m AMSL as these will reach the main Marracuene-Macaneta road. Such tides will flood into zone 8 and push waterbirds, especially waders to the high water roost of the Sharpie Spot/Common Ringed Roost with often some spillover of waterbirds into Zone 7 north of the road. The tidal waters themselves can cross the road through the culverts connecting Z8 to Z7 or, before the raising of the road in 2022, even flow over the road.

This distinction between feeding and non-feeding birds is important as it separates presence from use. A case in point are the Pelicans and the Great White Pelican (*Pelecanus onocrotalus*) in particular. Weighing almost 10 kg, this is by far the heaviest bird in the system. When they are feeding, they can form dense groups that will surround a school of fish and then synchronously dip their heads under water to create a sort of fyke from which they can scoop up the fish (Fig. 4).

Figure 5. Feeding Pelecanus onocrotalus in the Northern Wetlands in September 2021.

In contrast, when they are roosting, they will mostly stand in shallow water and preen or they will sleep lying down in the grasslands (Fig. 5).

Figure 6. Roosting Pelecanus onocrotalus in the Northern Wetlands in March 2022.

Additional observations were made to assess the roosting behaviour of birds as, at dawn and dusk, groups of birds, especially communal roosters such as cormorants, egrets and herons, can be seen migrating to roosts situated in the vast inaccessible areas between the Northern Wetlands and Beyond Hobjana. Early morning they will do the inverse journey. Black-crowned Night Heron (*Nycticorax nycticorax*) that feeds at night inverses these movements, towards the roost in the morning and from the roost in the evening. There may also be a breeding colony of this species in some 4-5 m high shrubs there as a high percentage of juveniles is sometimes present. Long-tailed Cormorant (*Microcarbo africanus*) may also be breeding in the same general area. As is the case for the White-breasted Cormorant (*Phalacrocorax carbo lucidus*), Long-tailed Cormorant movements may also be partially inked to the tides, both species heading towards the river at the incoming tide. Little Egret (*Egretta garzetta*), some of the Anatidae and many waders also show movements related to the tides as they head to the mudflats to feed at low tide.

Roost counts allow an estimate of the total number of birds actively feeding in the floodplains. For example, at night, Glossy Ibis (*Plegadis falcinellus*) roosts communally in Zone 7 but will disperse into small groups just before sunrise and, as they often forage in high grass, become partially invisible. On 27/05/2022 485 were recorded at the roost, before dispersal. Similarly, Wood Sandpiper (*Tringa glareola*) is a solitary feeder of rather vegetated flooded areas and therefore hard to count accurately. After a high rainfall event, 40 were counted on a wader roost at the cattle pens, mixed in with other species. This number is higher than in any of the cumulative counts. Thus, depending on size, colouration, behaviour, habitat, etc. the “detectability” of each species differs and, except for the largest species, the numbers observed in the counts represent a variable fraction of the birds active in the plot.

2.3 Summary results of the bird counts

Birds were counted in the plots on 92 days between 27/01/2021 and 12/02/2023 (on average every 8 days) adding up to over 60,000 wetland and waterbirds (over 600 individuals per count). On average, the counts took 3hrs 30min and covered 25 km of road. In total 1415 zones were counted, i.e. on average 15 zones (out of 21) were counted per date. These counts are not evenly spread in time, being less frequent during the dry season (June-September) when fewer birds are present. Spatially also some plots are counted much more regularly then others. For example, the Core North Wetlands can only be accessed on foot, often wading to a depth of about 0.8m and have only been counted a few times.

Table 1. Most abundant and highest biomass species in the Macaneta birdcounts (totals).

Species	Number	Species	Biomass (kg)
Glareola pratincola	9400	*Pelecanus onocrotalus*	73922
Dendrocygna viduata	6814	*Dendrocygna viduata*	48621
Bubulcus ibis	5048	*Anastomus lamelligerus*	44985
Anastomus lamelligerus	4181	*Plectropterus gambensis*	31220
Hirundo rustica	3765	*Plegadis falcinellus*	21921
Plegadis falcinellus	3690	*Bubulcus ibis*	18215
Euplectes axillaris	2303	*Threskiornis aethiopicus*	14031
Ardea intermedia	1399	*Glareola pratincola*	7344
Ploceus cucullatus	1254	*Ardea intermedia*	5948
Cypsiurus parvus	1210	*Dendrocygna bicolor*	5055

The most abundant species was the Collared Pratincole (*Glareola pratincola*) with 9400 individuals counted, followed by White-faced Whistling Duck (*Dendrocygna viduata* 6814), Cattle Egret (*Bubulcus ibis* 5084), Openbill Stork (*Anastomus lamelligerus* 4181), Barn Swallow (*Hirundo rustica* 3765), Glossy Ibis (*Plegadis falcinellus* 3690), Fan-tailed Widowbird (*Euplectes axillaris* 2303), Intermediate Egret (*Ardea intermedia* 1399), Village Weaver (*Ploceus cucculatus* 1254), Palm Swift (*Cypsiurus parvus* 1210), etc. A number of these most abundant species are small insectivores and granivores that, from a food chain perspective, represent relatively low consumption in comparison to the much larger aquatic fish, frog and aquatic invertebrate feeders.

Thus, from a functional perspective, bird biomass is a more relevant variable than number. When bird numbers are converted to biomass (using the average weight per individual from Gibbon 2019), a different picture emerges with the Great White Pelican (*Pelecanus onocrotalus*) the dominant species (Table 1). Other newcomers in this list are Spur-winged Goose (*Plectropterus gambensis*), Sacred Ibis (*Threskiornis aethiopicus*) and Fulvous Whistling Duck (*Dendrocygna bicolor*).

3. Waterbird feeding guilds

From biomass data these can be converted to energy use or fresh weight consumption (Hean et al. 2017) and, on the basis of the preferred food items from Gibbon 2019 and supplemented by the occasional direct observations of predation events, the wetland and waterbird species in Macaneta can be grouped into 10 feeding guilds.

These are:

- Specialised feeders on fish (Piscivores) such as the Pelicans, Cormorants, large Herons (with Little Egret and Black Heron), Hamerkop, Yellow-billed Stork, most Terns and the aquatic Kingfishers. The African Fish Eagle is also included here though, in Macaneta, it was often seen attacking the Openbill flocks (unsuccessfully).
- Herbivores mostly Ducks, Geese, Coots and also Francolins (on the edges of the wetland). These will also consume animal matter either inadvertently or targeted.
- Partially specialised aquatic invertebrate feeders with most of the waders, Jacanas, Ibises, Rails and Crakes, but also the Greater Flamingo and the more terrestrial kingfishers (Striped, Brown-hooded). They will also feed on small vertebrates (frog tadpoles, fish) when these are abundant.
- Insectivores mostly hunt insects on the wing (Collared Pratincole, Bee-eaters, Swifts and Swallows, Amur Falcon, Nightjars) but some glean insects from the wetland vegetation (Cattle Egret, Buttonquail, Warblers, Stonechat, Pipits, Longclaws and Wagtails, Cuckoos as well as most Cisticolas).
- A specialised Mollusc eater, the Openbill, feeding exclusively on *Lanistes ovum* in Macaneta.
- Broadspectrum species feeding in particular on frogs, small fish and aquatic invertebrates. Prominent species are the small squat Ardeidae (Intermediate Egret, Squacco, Rufous-bellied and Striated Heron, Little and Dwarf Bittern, Black-crowned Night Heron) but also Whiskered Tern, Grey-hooded Gull and Woolly-necked Stork.
- A rodent specialist, the Black-headed Heron. This species will also feed on large insects and some aquatic fauna and other large Herons will also consume rodents.
- Two types of Omnivore, the aquatic Moorhens and the rare Pied Crow.
- Seed-eaters such as Waxbills, Weavers, Mannikins, Bishops, Widowbirds, Whydahs and Queleas. These are the bane of the user communities as they can invade the rice fields in large groups and cause substantial damage.
- Carnivorous birds such as the Raptors (diurnal and nocturnal) plus Lilac-breasted Roller and Burchell's Coucal.

3.1 Piscivores

Specialised feeders on fish (Piscivores) dominated by the Pelicans, Cormorants and Herons. The latter include the huge but rare Goliath Heron, *Ardea goliath* (probably a pair is always present but they are quite cryptic mostly hiding in dense reedbeds), large common herons such as Grey Heron, *Ardea cinerea* (with a small breeding colony in Marracuene), Purple Heron, *Ardea purpurea* and Great Egret, *Ardea alba* as well as the medium-sized Little Egret, *Egretta garzetta* and the Black Heron *E. ardesiaca*. Others are African Spoonbill, *Platalea alba*, Hamerkop, *Scopus ombretta*, Yellow-billed Stork, *Mycteria ibis*, most Terns and the aquatic Kingfishers. The African Fish Eagle, *Haliaeetus vocifer* - with only 6 observations a rare species in Macaneta - is also included here even though it was observed attacking the Openbill flocks (unsuccessfully).

We consider the piscivorous species as the best proxies for fish productivity in the system, a key ecosystem service and an important component of local user livelihoods. Aquatic invertebrates, especially adult stages of Penaeid shrimp and crabs, also feature prominently in the fisheries, together representing over 20% of income (Machava et al., this volume). Birds mostly consume juvenile stages of both fish and aquatic invertebrates. Because of the very high natural mortality rates in these groups, piscivorous birds are rarely in direct competition with the fisheries but are good indicators of the production of juveniles. These will either hatch on the floodplains or move in from the river and feed there until they return to river and, for many of those, add to the stocks fished in the coastal waters of Maputo Bay and beyond.
With an average monthly biomass of 102.7 kg, the piscivores are the dominant feeding guild in Macaneta over the study period (but only 10% more than the Herbivores). The seasonal pattern shows a very high peak in September-October 2021 when hundreds of Great White Pelicans, probably from the breeding colonies in the Maputo National Park, would be actively fishing in the remaining and disconnected (through evaporation) water bodies, especially in the Northern Wetlands (Fig. 6). It is thought this is linked to the successful fish breeding in the floodplains after the February 2021 river flood, with an extended connection between the river and the floodplain allowing adult fish to move in and spawn and the juveniles finding favourable feeding and growth conditions in the flooded grasslands. At the end of the dry season, we suspect these fish aggregated in the residual, by then slightly brackish, water bodies (around 6 PSU) and thus become comparatively easy prey for the coordinated fishing by groups of pelicans.

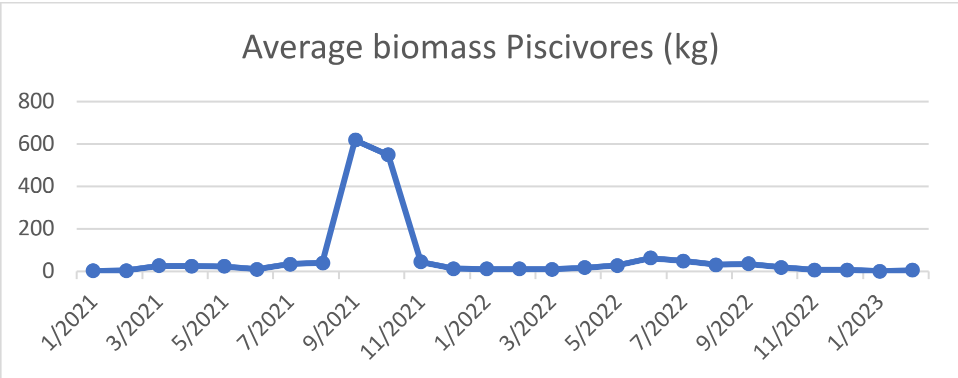


Figure 7. Monthly average biomass of piscivorous waterbirds present in the counted plots at Macaneta over the study period.

In 2022, there is a much smaller (max 63 kg) peak in May to September, mostly made up of Long-tailed Cormorants and the larger herons (Grey, Purple, Great Egret) feeding in the harvested rice fields beyond Hobjana as well as the presence of African Spoonbills and Yellow-billed Storks in the flooded areas throughout the system. Possibly, there was an active breeding colony of Long-tailed Cormorants, *Microcarbo africanus* close to the rice fields (display and mating behaviour observed). It is thought that the extended wet season, with significant rainfall even in July, allowed for a protracted presence of small fish.

3.1.1 Great White Pelican

The Great White Pelican (*Pelecanus onocrotalus*) is, in biomass terms (Fig. 7), by far the dominant piscivore feeding on the Macaneta floodplain (75 %). Weighing on average 9.5 kg it is amongst the heaviest flying birds. Most likely, the birds visiting Macaneta come from the breeding colonies in the Maputo National Park to the South of Maputo Bay. They are gregarious birds mostly flying in large groups and descending on wetlands to collectively feed on fishes. Through cooperative feeding, they can efficiently harvest fish stocks when these are concentrated in relatively restricted wetlands, especially towards the end of the dry season.

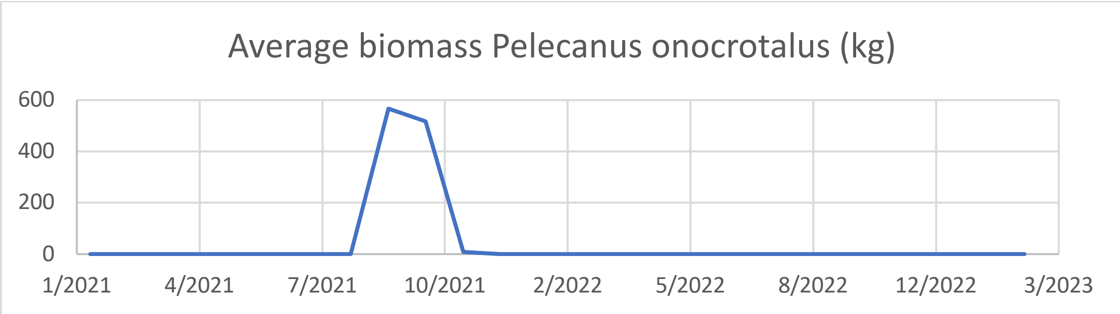


Figure 8. Monthly average biomass of Great White Pelican, Pelecanus onocrotalus feeding in the Macaneta floodplains during the birdcounts.

Groups of up to 300 Pelicans were observed actively feeding in the Northern Wetlands (see Fig. 4) between early September and early November 2021. By that time they had probably fished out most of the small disconnected wetlands on the floodplain. In early 2024, smaller groups were observed but always only roosting, either in the Northern Wetlands or in Zone 7. It is our hypothesis that, in 2022, as there was no flooding from the river there was much less fish biomass available on the floodplain than in 2021.
The top 10 piscivorous species in monthly average biomass terms (averaging over 1%) are shown in Table 1.

Table 2. Highest ranking species in terms of percentage of monthly average piscivores biomass feeding in the Macaneta floodplain count plots during the study period.

Species name	**Vernacular**	**%**
Pelecanus onocrotalus	Great White Pelican	75
Ardea cinerea	Grey Heron	4.3
Microcarbo africanus	Long-tailed Cormorant	4
Platalea alba	African Spoonbill	2.9
Mycteria ibis	Yellow-billed Stork	2.5
Ardea alba	Great Egret	2.2
Phalacrocorax carbo lucidus	White-breasted Cormorant	2.1
Ardea purpurea	Purple Heron	1.9
Egretta ardesiaca	Black Heron	1.3
Egretta garzetta	Little Egret	1.2

3.1.2 Grey Heron

The Grey Heron (*Ardea cinerea*) is a constant presence (usually 10 to 30 birds) with an average biomass of 2 to 8 kg (average 4.4 kg) spread throughout the floodplains and especially along the hydraulic axes. It breeds both in the mangrove and in Marracuene (where its breeding precedes the season of the Black-headed Heron).

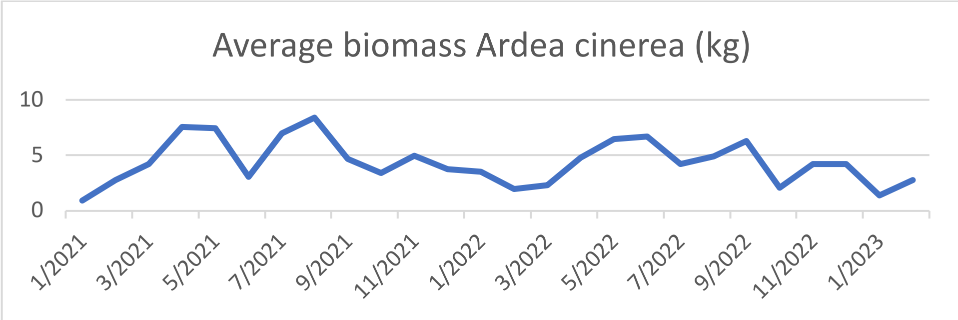


Figure 9. Monthly average biomass of Grey Heron, Ardea cinerea feeding in the Macaneta floodplains during the birdcounts.

3.1.3 Long-tailed Cormorant

The long-tailed Cormorant (*Microcarbo africanus*) is present in small numbers feeding in the hydraulic axes of the floodplains but the highest numbers are observed during the migrations to and from the roost/suspected breeding colony (Beyond Hobjana). These migrations can be linked to the incoming tide when they head to the estuarine part of the river generally upstream from the White-breasted Cormorant groups. Average biomass is around 4.2 kg but with a clear difference between 2021 and 2022 with much higher values May to July (Fig. 9) but there may be a bias here. In 2021, because of the floods and thus access issues, the northern wetlands were visited less intensely than in 2022. Once we had better knowledge of where they would be and when, they were counted more accurately in some of the rice fields beyond Hobjana close to the suspected breeding colony where they were feeding before heading out on the floodplains and to the estuary.

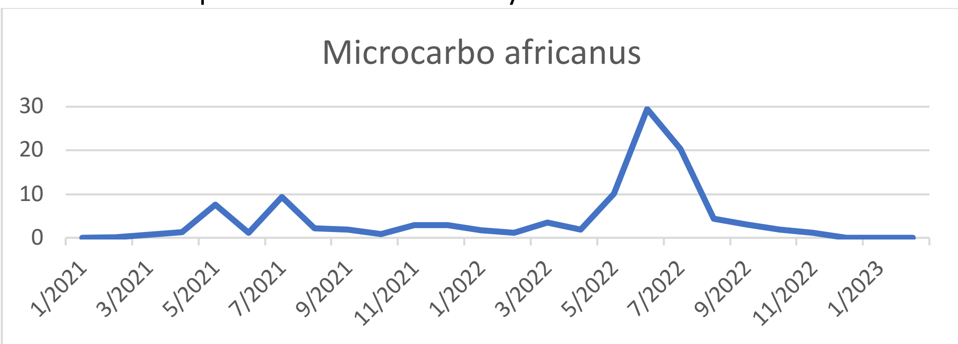


Figure 10. Monthly average biomass of Long-tailed Cormorant Microcarbo africanus feeding in the Macaneta floodplains during the birdcounts.

3.2 Herbivores

Predominantly plant-eating waterbirds mostly comprise the Anatidae (Ducks and Geese). Coots are an exceptional occurrence in Macaneta (2 Red-knobbed Coots, *Fulica cristata* in February 2022). A small number of Francolins are also included here, mostly foraging in the agricultural fields on the edges of the wetland between Hobjana and the coastal dune.

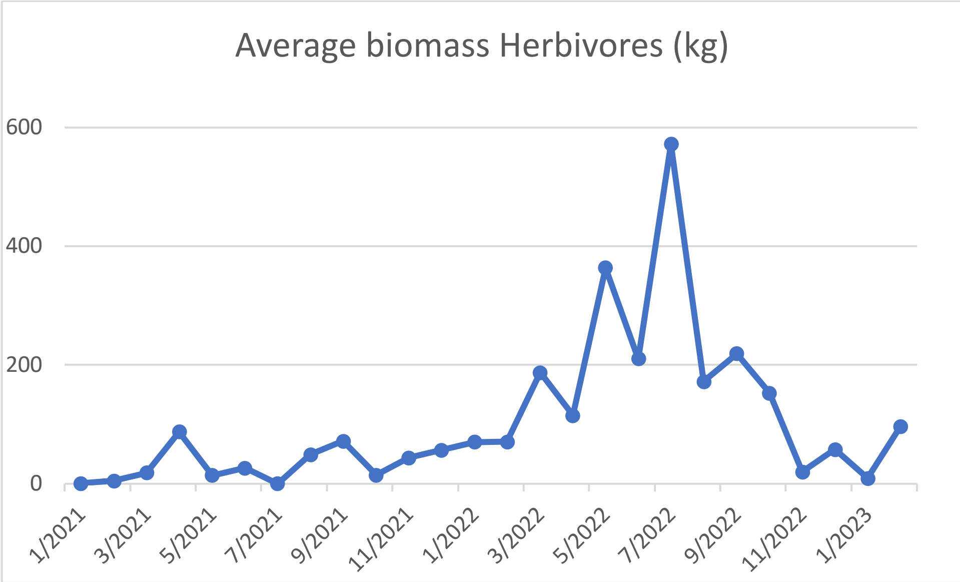


Figure 11. Monthly average biomass of herbivorous waterbirds present in the counted plots at Macaneta over the study period.

With an average monthly biomass of 93.6 kg, the herbivores are a close second to the specialised piscivores over the study period. The seasonal pattern (Fig. 10) is quite the opposite of the piscivores with a broad peak (over 100 kg) between March and October 2022, largely made up of Whistling ducks (both White-faced, *Dendrocygna viduata* and, to a lesser extent Fulvous, *Dendrocygna bicolor*) as well as groups of Spur-winged Goose, *Plectropterus gambensis* (highest ever count – since 2013 – of 149 in March 2022). For the latter species, the adults were often accompanied by numerous juveniles thought to have been locally bred and raised. The highest ever count of Knob-billed Duck (50), an irregular visitor, also occurred in 2022 (July). The broad peak of plant-eating waterbirds is made up of 4 smaller peaks and troughs that are probably linked to the capacity of these Anatidae to effectively hide in the vegetation rather than a genuine change in abundance. Also, there was only a single count in July 2022 creating a bias (peaks and troughs are usually smoothed by averaging multiple counts in a single month).

It is thought this pattern reflects the significant increase of the vegetation both in biomass and cover after 7 years of local drought. In the absence of flooding, this led to a relatively high salinity in the water bodies of the system limiting the growth of vegetation, especially in the central grasslands frequented by the herbivores. For example, in Zone 5, just North of the main road, the average salinity in 2019 and 2020, prior to the February 2021 flood, was 18.3 PSU (1/10/2019-24/12/2020, N=14, Standard Deviation=8.02, 99% Confidence limits 12.78-23.82), limiting the food source for the herbivorous species. After the February 2021 flood, salinities were significantly lower (17/02/2021-12/02/2023, N=40, Standard Deviation=4.85, 99% Confidence limits 3.46-7.41). The substantial and protracted rainfall in 2022 allowed for a spectacular development of the vegetation with bare ground being colonised by Salicornia, the Salicornia areas taken over by grasses and sedges, reedbeds of both *Typha* and *Phragmites* growing to much greater heights - for example - obscuring the Core North Wetlands that used to be countable from the Hobjana dune road, etc. In the rice fields of Hobjana and the Dune Gardens South, the comparatively deep freshwater bodies harboured extensive water lily patches, attractive to Pygmy Goose, *Nettapus auritus* and White-backed Duck, *Thalassornis* *leuconotus* both recorded for the first time in the Macaneta wetlands in 2022 (mid-February and Mid-March respectively).

It would be worthwhile to include flooded surface area and duration in the multivariate analysis if such data is available (LIDAR). Normalised Difference Vegetation Index (NDVI) from Sentinel imagery, covering the floodless pre-2021 years (since 2014) could also be a relevant variable for this guild.

3.2.1 White-faced Whistling Duck

The White-faced Whistling Duck (*Dendrocygna viduata*) is, in biomass terms, the dominant herbivore (54%) in the Macaneta floodplains (Fig. 11). As most ducks and geese it is gregarious and often mixed in with the Fulvous Whistling Duck (*Dendrocygna bicolor*).

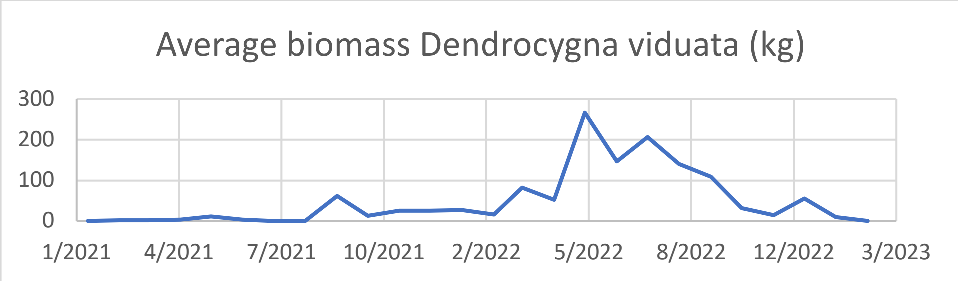


Figure 12. Monthly average biomass of White-faced Whistling Duck, Dendrocygna viduata feeding in the Macaneta floodplains during the birdcounts.

3.2.2 Spur-winged Goose

Second, with 35% of the average herbivore biomass is the Spur-winged Goose (*Plectropterus gambensis*).

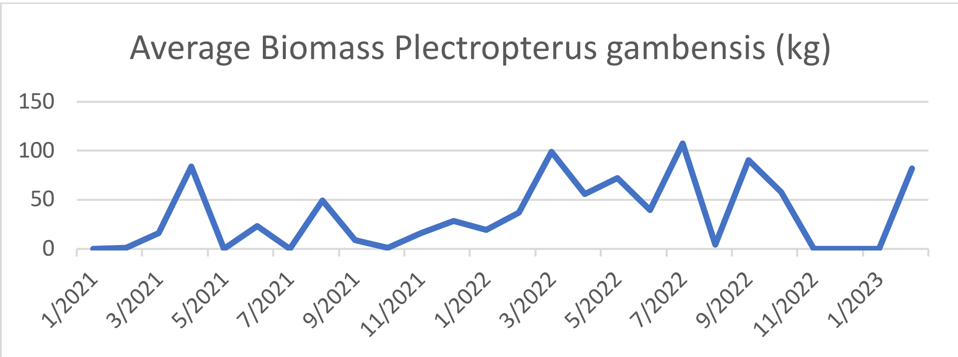


Figure 13. Monthly average biomass of Spur-winged Goose, Plectropterus gambensis feeding in the Macaneta floodplains during the birdcounts.

It is clear that this is both species were much more abundant (8 times and 2 times respectively) in the high rainfall year 2022 when very large surface areas of the floodplain were under water for many months and vegetation was thriving.

The top 6 herbivorous species in monthly average biomass terms (averaging over 1%) are shown in Table 2.

Table 3. Highest ranking species in terms of percentage of monthly average herbivore biomass feeding in the Macaneta floodplain count plots during the study period.

Species name	Vernacular	%
Dendrocygna viduata	White-faced Whistling-duck	54
Plectropterus gambensis	Spur-winged Goose	35
Dendrocygna bicolor	Fulvous Whistling-duck	5.6
Anas erythrorhyncha	Red-billed Duck	1.5
Sarkidiornis melanotos	Knob-billed Duck	1.4
Spatula hottentota	Blue-billed Teal	1.3
Anas undulata	Yellow-billed Duck	1.1

3.3 Aquatic invertebrate feeders

With a monthly average biomass of 47.6 kg, the partially specialised aquatic invertebrate feeders are the third feeding guild. In comparison to the two previous guilds, the seasonal pattern seems relatively weak, which is probably related to the wide taxonomic, biogeographical and functional range of this guild. There is higher biomass in May-June and Nov-Dec 2022.

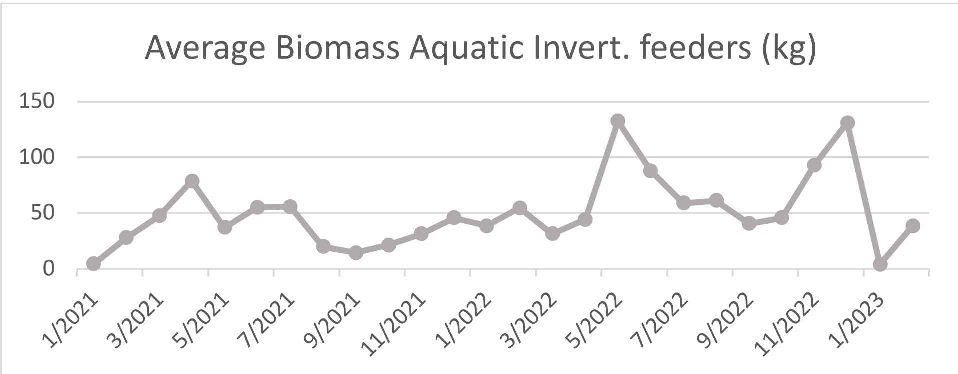


Figure 14. Monthly average biomass of aquatic invertebrate feeding waterbirds present in the counted plots at Macaneta over the study period.

As mentioned, this guild is constituted by several taxonomic groupings with distinct feeding habits and distinct biogeographical status.

The higher values in May-June 2022, in comparison to the previous year, are possibly linked to the extensive and prolonged flooding of the grassy plains that the Glossy Ibis prefer for feeding.

3.2.1 Resident Aquatic invertebrate feeders

The dominant subgroup (90% of the biomass) are resident invertebrate feeding species, especially the Ibises with the Glossy Ibis, *Plegadis falcinellus*. The Glossy Ibis makes up the bulk of the May and December 2022 peaks, while the Sacred Ibis, *Threskiornis aethiopicus* is responsible for about 75% of the March 2021 peak (Fig. 12).

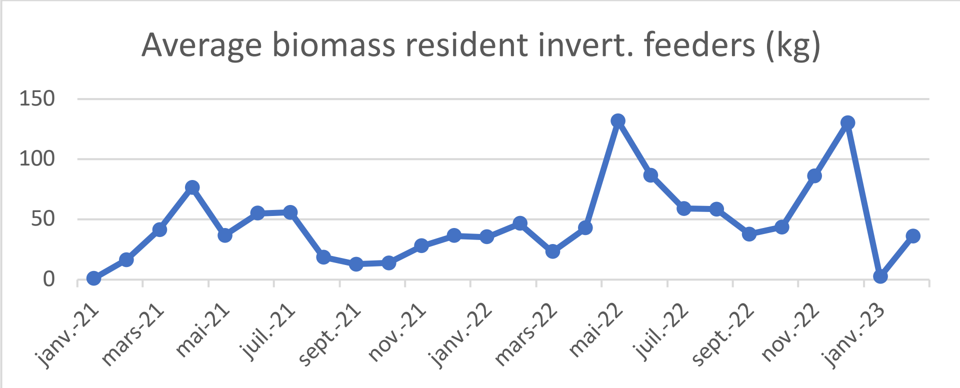


Figure 12. Monthly average biomass of the resident invertebrate feeding waterbirds present in the counted plots at Macaneta over the study period.

Possibly, with less predaceous fishes in the floodplain in 2022, aquatic invertebrates provided a richer food source.

3.2.1.2 Glossy Ibis

This species is mostly seen walking through the flooded grasslands, usually in small flocks of a few tens of individuals, picking up items from the vegetation, from shallow water or probing into mud. Up to about 500 can be present on the floodplains, communally roosting at night on the edges of water bodies and spreading out to feed just before sunrise. This species also preferred the conditions of the high rainfall year 2022 (Fig. 13) when flooded grasslands were present extensively and for long durations.

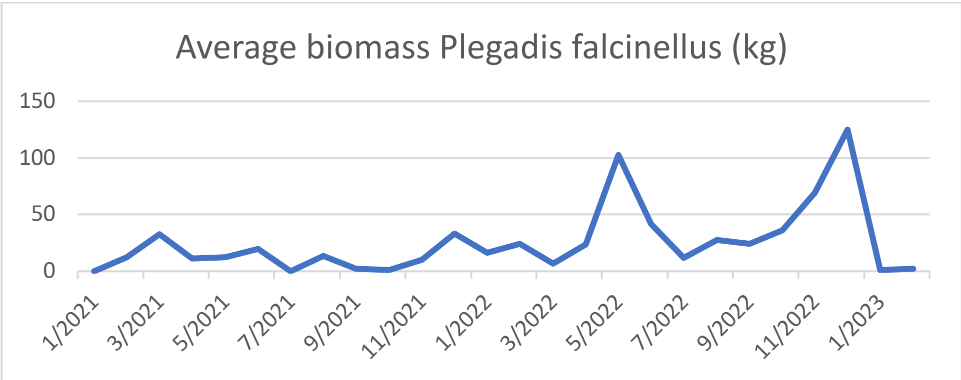


Figure 13. Average monthly biomass of Glossy Ibis, Plegadis falcinelles feeding in the Macaneta floodplains present in the counted plots at Macaneta over the study period.

Possibly, with less predaceous fishes in the floodplain in 2022, aquatic invertebrates provided a richer food source.

3.2.2 Palearctic waders

Another obvious subgroup are the Palearctic waders that breed in the Northern hemisphere (Eurasia) and migrate to winter in the Southern African Region. They represent about 10% of the biomass of the guild but are one of the main ornithological attractions of the system because of the regular occurrence of species that are rare or unique (Sharp-tailed Sandpiper, White-rumped Sandpiper, Pectoral Sandpiper). As discussed in Allport (2018, 2021) twitchers bring in non-negligible tourism expenditure into the area.

Logically, there is quite a strong seasonal pattern (Fig. 15) with a lower biomass during the Palearctic breeding season when the adults are absent. Higher biomass occurs between October and March when these return from the breeding grounds with the juveniles. The smaller species mostly eat either invertebrates hiding in the mud (sandpipers) or picked up from the surface (plovers). The heavier Whimbrel, *Numenius phaeopus* often feed on small crabs.

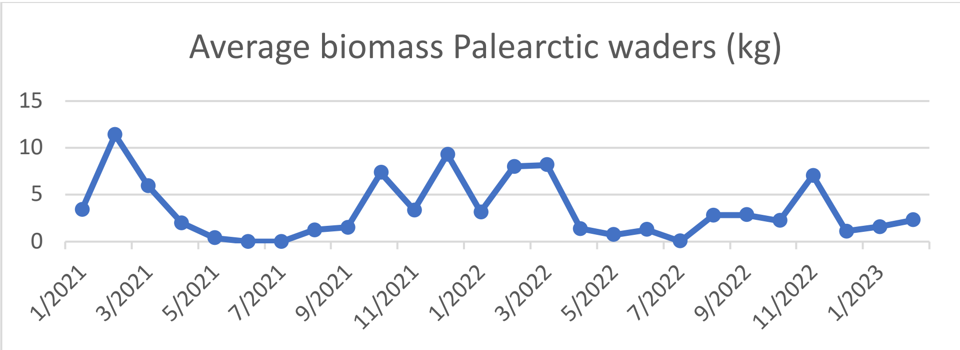


Figure 15. Monthly average biomass of Palearctic waders present in the counted plots at Macaneta over the study period.

3.4 Molluscivore

With an average monthly biomass of 43.7 kg, the Openbill, *Anastomus lamelligerus* constitutes the fourth and peculiar single-species-feeding "guild". Possibly, in the lower parts of the estuary, other species (gulls, waders) also consume molluscs in the intertidal areas where the villagers collect bivalves. Peak numbers were present in November 2021.

3.4.1 Openbill

The Openbill (*Anastomus lamelligerus*) is a specialised molluscivore that, in Macaneta feeds almost exclusively on the indigenous *Lanistes ovum* "apple snail". Between September and November 2021, large groups of Openbills were seen flying in at sunrise from, as yet unidentified, roosts west of the Incomati River to feed in the floodplains. Smaller groups can roost on sandbanks and in the mangroves of the estuary.

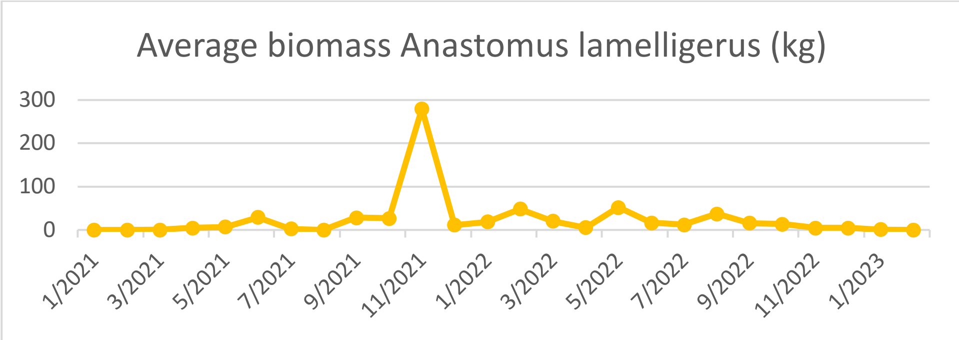


Figure 16. Monthly average biomass of the molluscivore specialist Openbill, Anastomus lamelligerus present in the counted plots at Macaneta over the study period

Though "Apple Snails" (Ampullariidae) are well known as crop pests (Joshi et al 2017), especially on rice as they eat the new shoots soon after sowing, this is in fact mostly the case for the South American species introduced elsewhere (especially in South-East Asia where rice growing and exports are of global significance) where they have become invasive and destructive, requiring substantial investment into control measures, including molluscicides (Horgan 2018).

Figure 17. Lanistes ovum, the prime food of Openbill in Macaneta with characteristic damage of operculum removal.

Although the impact on rice cultivation by indigenous apple snails is less pronounced, because of the lower densities of the snails, it has been documented in Southern Africa (Crossland 1965). It is possible that the Openbill play a significant role in the control of *Lanistes* damage. The species is not perceived negatively by the wetland user communities. It seems likely that many other species exert a level of biological control on the juvenile *Lanistes* (<20 mm) when their shells are still thin and they are easily digestible. Fish such as "Tilapia", ducks, ibises and other waterbirds are thought to consume them in numbers (Hayes et al. 2015).

Openbill numbers in the Macaneta floodplains were slow to react to the February 2021 flood and peaked in late 2021. In 2022 the maximum counted was 139 on 22/05/2022, very similar to the highest count (130) recorded between 2016 and 2020 (Allport 2021). Our hypothesis is that, with dead plant material accumulating in the floodplain in the absence of flooding since 2014, this became available to the snails as edible detritus during the 2021 floods, resulting in high densities of snails attractive to the Openbill. Alternatively, the nutrients from the detritus might have been recycled and used by microphytobenthos (microscopic algae growing on the soil surface) in these areas. Perhaps, using stable isotopes, the signal from these would allow to elucidate the food chain and distinguish between the microphytobenthos versus young shoots of grasses and sedges as the basis for the high density of apple snails.

3.5 Insectivores

With an average monthly biomass of 28.9 kg, the Insectivores are the fifth feeding "guild", with a strong dominance (86%) of two species: the Cattle Egret accounting on average for 59% of the biomass and the Collared Pratincole for 27%.

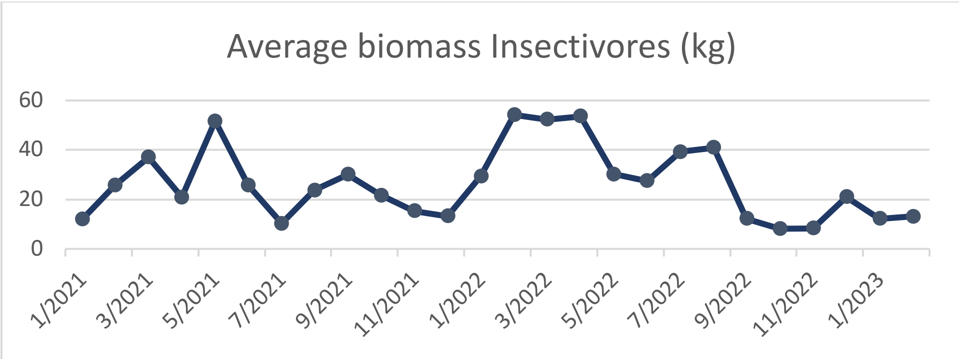


Figure 18. Monthly average biomass of the insectivorous waterbirds present in the counted plots at Macaneta over the study period.

3.5.1 Cattle Egret

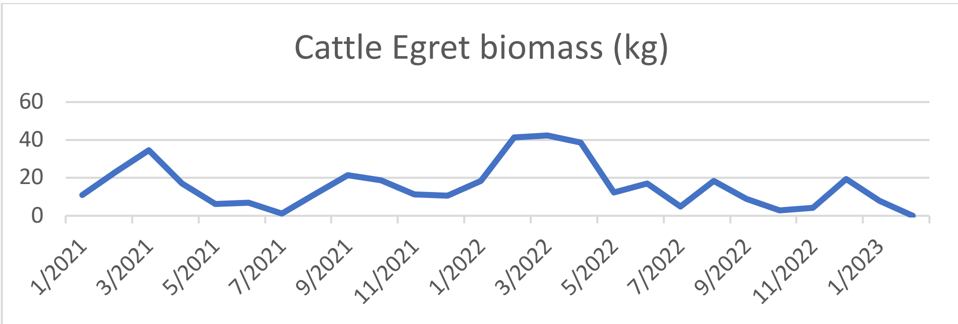


Figure 19. Monthly average biomass of the Cattle Egret, Bubulcus ibis present in the counted plots at Macaneta over the study period.

3.5.2 Collared Pratincole

The Collared Pratincole (*Glareola pratincola*) is a wader specialised on the capture of insects in flight and can reach high numbers (up to 2000) in the Macaneta floodplains, occasionally harbouring over 1% of the regional population of the species. Together with the Whiskered Tern (*Chlidonias hybrida*) and the White-breasted Cormorant (*Phalacrocorax carbo lucidus*) this means that the Incomati Delta qualifies for the status of Wetland of International Importance under the Ramsar Convention) (see https://www.ramsar.org/).

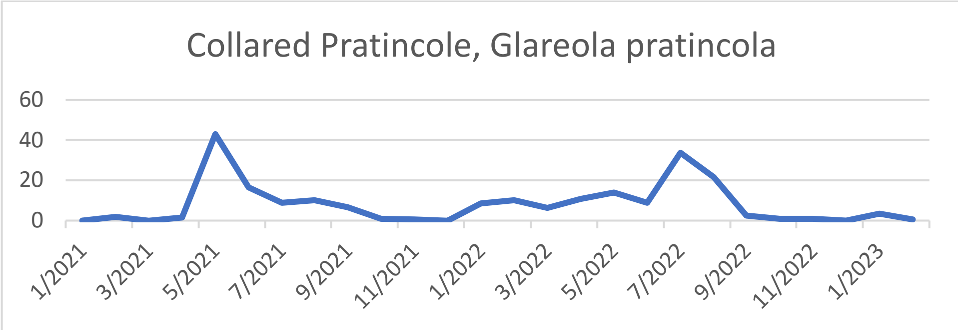


Figure 20. Monthly average biomass of the Collared Pratincole, Glareola pratincola present in the counted plots at Macaneta over the study period.

Two peaks can be observed in the graph (Fig. 9), a first in May 2021 post flood. It is our hypothesis that it takes a while for the aquatic larvae of flying insects to develop in the newly flooded areas and that the flying stages become available to the insectivores.

3.6 Broadspectrum feeders or Opportunists

These feed on a mix of whatever animal protein is abundant in particular frogs, small fish and aquatic invertebrates. Prominent species are the small squat Ardeidae (Intermediate Egret, Squacco, Rufous-bellied and Striated Heron, Little and Dwarf Bittern, Black-crowned Night Heron) but also Whiskered Tern, Grey-hooded Gull and Woolly-necked Stork.

With an average monthly biomass of 10.2 kg, the Broadspectrum feeders are the sixth feeding "guild". On average, 54% of this guild are Intermediate Egret, but this goes up to 82% in May 2021 and 78 % in February 2022 when average monthly biomass of the guild is highest (Fig. 21). Exceptionally, in July 2021, 75% were Black-crowned Night Heron, possibly indicating a successful local breeding season.

3.6.1 Intermediate Egret

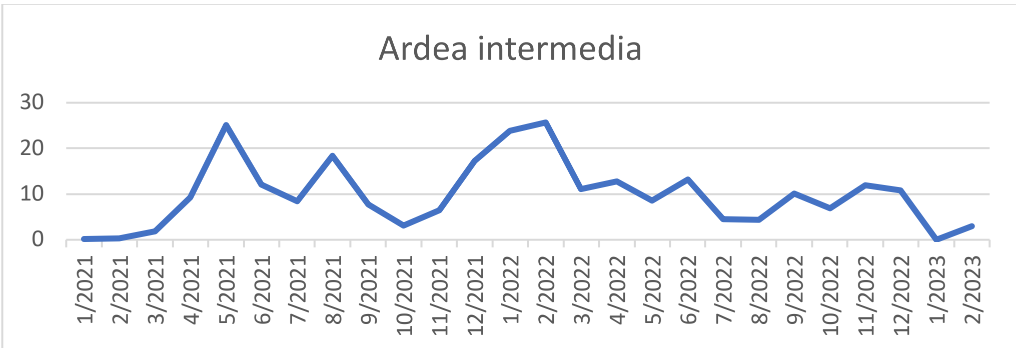


Figure 21. Monthly average biomass of the Intermediate Egret, Ardea intermedia present in the counted plots at Macaneta over the study period.

3.7 Marginal feeding guilds

The last 4 feeding guilds are comparatively marginal, totalling 5% or less of the average biomass of the birds over the study period.

1. A rodent specialist, the Black-headed Heron is a solitary hunter in the grasslands. There is a peak in April 2021 post-flood and a much broader peak from January to November 2022. There is a breeding colony in Marracuene from which most of these birds derive.

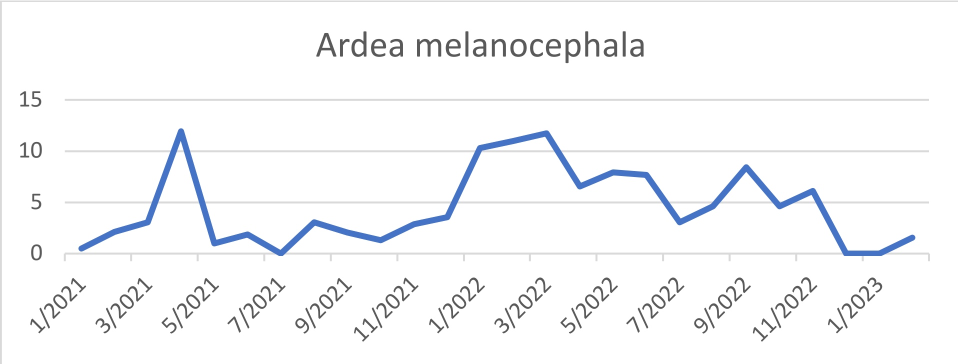


Figure 22. Monthly average biomass of the Black-headed Heron, Ardea melanocephala in the counted plots at Macaneta over the study period.

2. Two types of Omnivore, the aquatic Moorhens (especially the heavy African Swamphen *Porphyrio madagascariensis*) and the rare Pied Crow in the wetlands mostly feeding on food discarded by the road workers). Their maximum occurs in April to December 2022, possibly related to the high rainfall that year.

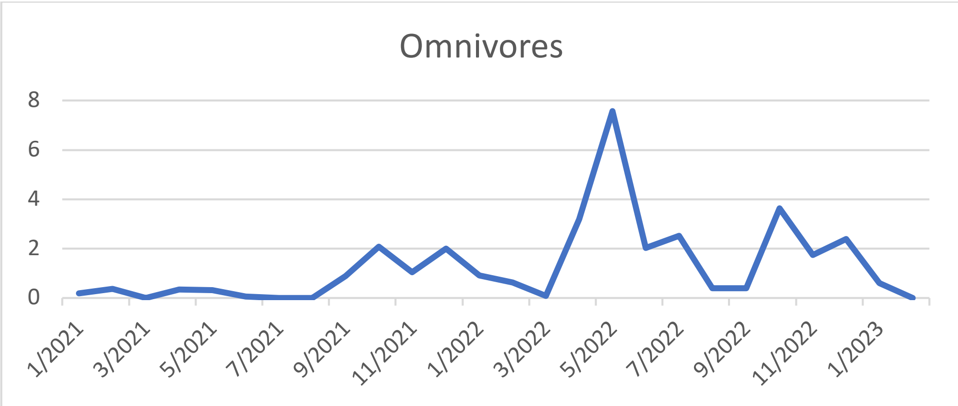


Figure 23. Monthly average biomass of the Omnivores present in the counted plots at Macaneta over the study period.

3. Carnivorous birds such as the Raptors (diurnal and nocturnal) plus Lilac-breasted Roller and Burchell's Coucal.

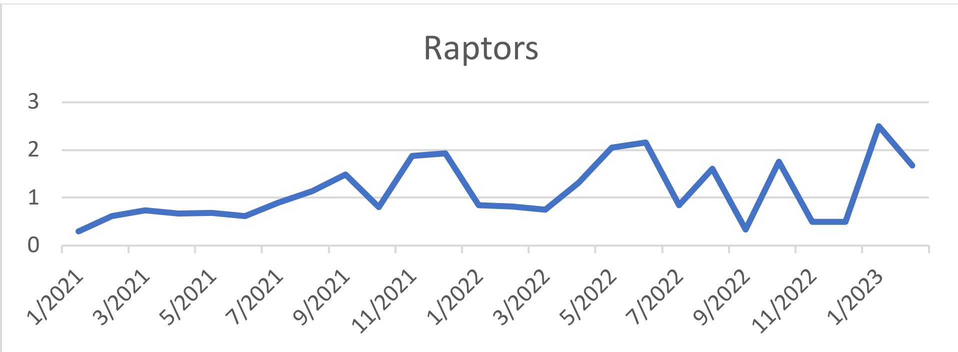


Figure 24. Monthly average biomass of the Raptors present in the counted plots at Macaneta over the study period.

4. Seed-eaters such as Waxbills, Weavers, Mannikins, Bishops, Widowbirds, Whydahs and Queleas. These are the bane of the user communities as they can invade the rice fields in large groups and cause substantial damage. In order to prevent this damage, a lot of (wo-)man

power is mobilised to scare the seedeaters away using arrays of plastic bottles attached to lines suspended over the wetland and that can be made to rattle when shaken. There is also a lot of whistling and loud vocal calls made by the bird chasers. Many chasers are armed with catapults with stocks of clay balls at their feet to target trespassing birds (that will be eaten when hit). The economic impact is therefore largely indirect through the time that bird scaring that prevents them from doing other productive work.

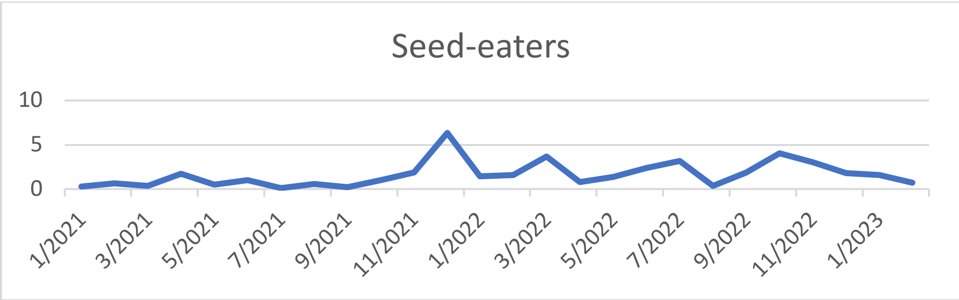


Figure 25. Monthly average biomass of the Seed-eaters present in the counted plots at Macaneta over the study period.

4. Relations with hydrology and hydraulics

The area is low-lying, between 0 and 4 m AMSL, and can therefore be flooded by tides exceeding 2.5m (especially those exceeding 3.5 m around the March and September equinoxes), by river floods exceeding 1000 m^3/s^{-1} or by substantial local rainfall which also increases groundwater seepage from the dunes which is the basis of the agriculture on the northern and eastern edges of the floodplain.

The predominant origin of the water covering the floodplain allows a subdivision of the system into different subsystems.

4.1 Flooding from the Incomati River

According to the findings of the hydrological modelling (Nhantumbo, Juizo et al. this volume) floods of over 1000 m^3/s^{-1} (cumecs) will cover the Macaneta floodplain. Discharge data have been recorded at Magude (Station E43, situated above the tidal limit) since 1954 but with missing data for 1961 to 1964.

Prior to the birdcounts in 2020-2022, discharges exceeding or closely approaching 1000 cumecs have occurred in 24 years of the 57 years of available data, i.e. every 2.4 years on average.

However, between the previous flood (2014) and the one observed in 2021 there was no flooding for 7 years and maximum discharge was less than 400 cumecs in any year.

This may explain why the postbridge birdcounts (since 2016) observed a relatively dry and saline floodplain with low vegetation and substantial stretches of Salicornia type halophytic vegetation and also extensive vegetationless patches.

4.2 Flooding from tides

The Incomati Delta is connected to Maputo Bay that has a very pronounced tidal regime with one of the highest amplitude differences between the spring and neap tides. On the equinox spring tides, and especially those of the dry season, marine waters can penetrate inland for several tens of km and flood the lowest lying areas of the floodplains. Main entry points for the birdcount area are the various tidal creeks in the plots south of the main road, with the main channel adjacent to the Boat Club. These can cross into the central floodplains through the culverts under the main road at tides >3.5 m AMSL. There are also some entry points upstream of the bridge, especially the Main Outlet (MO), situated around 2.5 m AMSL but tides can also cross the Hobjana Road and through the culverts of the adjacent River Reedbeds. As mentioned previously, tidal freshwaters can also be manipulated to enter the floodplains south of Hobjana through a canal that can be closed off with sandbags and through the "Banana Canal" sluicegate.

4.3 Flooding from rainfall

Since 1914, a rain gauge has been operating intermittedly at Marracuene, 5 km to the southwest of the centre of the Macaneta floodplain in 3 distinct periods: 1914-1920, 1941-1984 and 1990-2023. Since 2021, an additional rain gauge in a private compound a bit further west has been in operation, allowing to fill in missing records during the birdcounts. The daily

records are in general incomplete with only 53 years out of 109 years complete enough to be used to calculate total rainfall.
For ecological/agricultural purposes, calendar years (January 1st to December 31st) are not especially meaningful. The growing season for vegetation starts with the first significant rainfall (>20 mm) after the dry season. Indeed, the months of June, July and August have virtually no rain with the vegetation in a resting stage. In most years, this first significant rainfall occurs in mid-October thus, for our analysis, the "agro-ecological" year has been set to October 1st to September 30th of the subsequent year and the "year" will be designated by the end date. This first significant rainfall is also the signal for the local farmers to plant maize. However, in some years, significant rainfall occurs in late September and, under such circumstances, these last days of September have been included in to cumulative rainfall for the "year".

In the first operating period, 1914-1920, only 2 agro-ecological years can be used: "1915" (October 1st 1914 to September 30th 1915 with 1409.5 mm and 1918 with 1887.3 (data for July missing), a cumulative rainfall that has never been reached afterwards during the time series. These 2 years have not been included in the analysis.
For the 51 complete data years after 1942 the average rainfall is 827 mm.
Growth years 2018 and 2019, the only available years just prior to the birdcount dataset (January 2021- February 2023), are comparatively dry with 653.1 mm (79% of the average) and 556.2 mm (67%) respectively, while the year 2022 was exceptionally wet with 1233.6 mm, 49% more than the average.

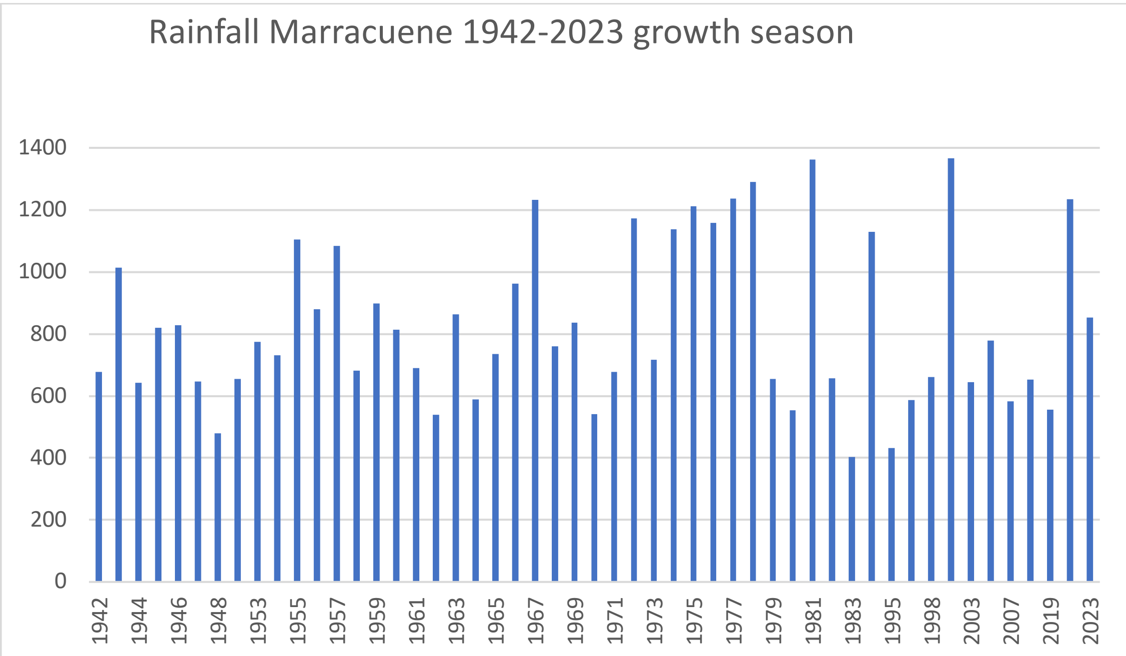


Figure 26. Annual rainfall in Macaneta between October of year N to September of year N+1, corresponding to the vegetattion growing season.

For the multivariate analysis the private raingauge dataset is used as it is continuous and seems more reliable than the official raingauge (Table 4). For example, the data for January to April 2015 are identical to those for 2016. The measurements started on 18/01/2021 but, as the birdcounts started only on 27/01/2021, the first half of January is considered less relevant. Unfortunately, there are no rainfall data available for the "growth year" months of

2020 preceding the birdcounts (October-December) so it is not possible to use cumulative rainfall for the growth year to directly compare between 2021 and 2022.

Table 4. Monthly total rainfall (Marracuene) in mm for the birdcount months.

Month	2021	2022	2023
January	125.2	204.5	79.5
February	310.2	128.5	370
March	101.5	129.9	
April	31.5	157.5	
May	16.5	168.5	
June	67.4	6.3	
July	6.1	109.3	
August	15.0	5.8	
September	6.6	19.5	
October	89.9	39.0	
November	135.0	101.0	
December	97.5	112.3	

While in 2021 February and June were much wetter than in 2022, April, May and July were much wetter in 2022. February 2023 was also very wet.

5. Salinity

As mentioned previously, the surface water salinity measurements on the floodplains started in March 2019 in the area where the Sharp-tailed Sandpiper (*Calidris acuminata*) was being observed at the time. As this is a very exceptional species for Africa, but observed almost annually in Macaneta, it was deemed interesting to assess its habitat preferences. The area, colloquially known in the ornithological lore of southern Africa as "the Sharpie Spot" (Allport 2021), was initially (in 2018 when the bird made its first appearance) a patchwork of Salicornia and open mud that would be flooded at Spring Tides of over 3.5 m that would push the Sharp-tailed Sandpiper and other waders, especially Palearctic migrants, towards the main road where they would roost and/or feed. Thus, concentrations of Common Ringed Plover (*Charadrius hiaticula*), Common Sandpiper (*Actitis hypoleucos*), Vulnerable Curlew Sandiper (*Calidris ferruginea*), Little Stint (*Calidris minuta*), Whimbrel *Numenius phaeopus*, various *Tringa* species, as well as rarities (vagrants) of suspected Nearctic origin (White-rumped Sandpiper, Pectoral Sandpiper) could be observed there around 2 hours after the high tide in Maputo Harbour (the tidal gauge on which predictions are made). Many piscivorous and aquatic invertebrate feeding birds can also concentrate there on the incoming tide. This was especially the case in 2021.
As from late September 2019, the salinity measurements were expanded to other sites of ornithological interest and gradually became part of a routine monitoring of the floodplain during bird counts (854 manual measurements in total).
One particularly interesting site is what is called the "first wetland", because it is the first birdrich spot that one encounters after driving into the floodplains from the bridge (S -25.731893, E 32.7031) on the edge between Zones 2 and 4. It consists of a series of small vegetationless depressions that only dry out exceptionally as, in addition to collecting rain

water from the neighbouring areas, is also supplied by the highest tides (estimated at >3.7 m) through a complex of channels coming from the main tidal creek of the boatclub. As such it has become a kind of barometer of the low lying areas of the southern floodplain influenced by the tides but without the variability of a direct daily tidal influence (Fig. 27).

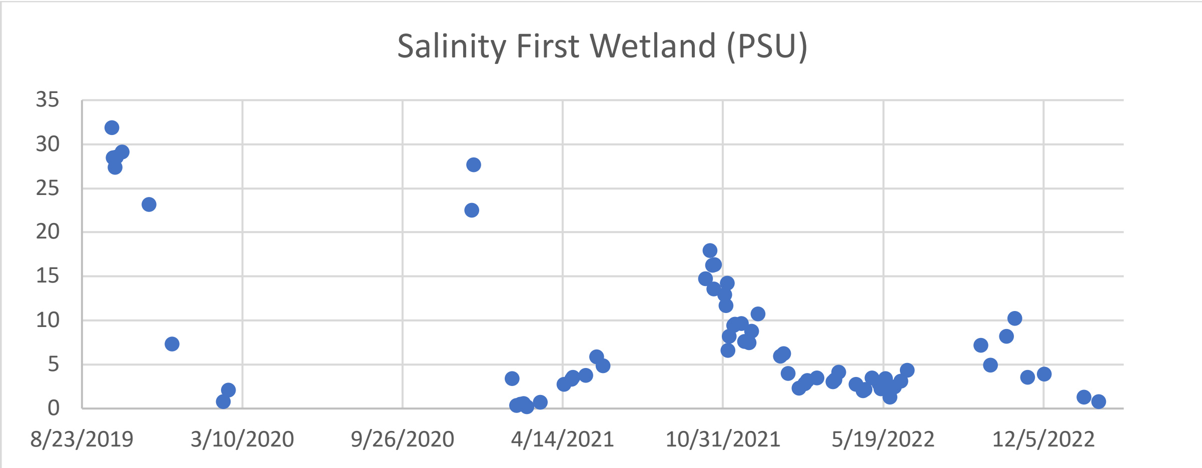


Figure 27. Salinity at the "first wetland" (edge Zone 2 - Zone 4) monitored from 29/09/2019 to 12/02/2023.

The site allows us to characterise the main hydraulic events prior to and during the bird counts. First of all, in late September 2019, the salinity almost reaches 32 PSU (over 90% of full strength sea water at 35 PSU). This is during the equinox tides that most likely brought in high salinity sea water as similar salinities were observed at the "Sharpie Spot" around the same dates. Subsequently, as the rainy season gains strength, the salt is diluted and drops to near zero (0.8 PSU) in February 2020 when equinox tides are again approaching (4.5 PSU at the Sharpie Spot) and the river has high discharge. Unfortunately, there is a COVID related gap in the data until December 2020 with comparable salinities as recorded in late 2019.

The main difference between the pre-birdcount data (2019-2020) and the measurements during 2021-2022 is that the highest salinities are much lower post the February 2021 flood (18 PSU in October 2021) and, especially in the high rainfall year 2022 (10.24 PSU in October 2022). These changes have been reflected in the vegetation at Macaneta.

For example, in late 2019 during some of the early visits to the North Wetlands Core (NWC), the birds could be observed from the terraces of the dunes just north of Hobjana and they were typically salt-tolerant waders such as Black-winged Stilt (*Himantopus himantopus*). The salinity there on 03/10/2019 was 20.1 PSU. There were patches of reedmace *Typha* at the water's edge but the main depressions of the North Wetlands were vegetationless. In contrast, after the February 2021 floods, counting birds in the NWC required wading into them to get past the screen of *Typha* and salinities were much lower (between 3.44 and 4.82 PSU in October and November 2021.

Similarly, the neighbouring "North Wetlands First Lake" (NWFL) is low-lying with, initially a large vegetationless salty expanse that floods after intense local rainfall and, in 2021 post-flood, started being colonised by Salicornia. The Salicornia greatly expanded in 2022. When it floods, salinity can go down to 1.94 PSU as on 21/06/2022 after the series of unusually late rains and rising to 14.36 PSU on 06/12/2022. The bare ground is much appreciated by the large flocks of Collared Pratincole (*Glareola pratincola*), that roost and, most likely, also breed there as behaviour to distract predators was observed (pretending to be unable to fly to attract the predator away from the nest).

Likewise, the "Sharpie Spot" in zone 8 became progressively more overgrown with Salicornia and subsequently gradually with salt-tolerant sedges and grasses. A screen of Phragmites reeds also developed on the edge of the road, reducing visibility. Increasingly waders and especially the shorter legged species like Plovers would roost a bit further East on what became known as the "Common Ringed Roost". Both areas are flooded by the same water at high tides >3.5 m and therefore the salinity measurements have been combined (Fig. 28).

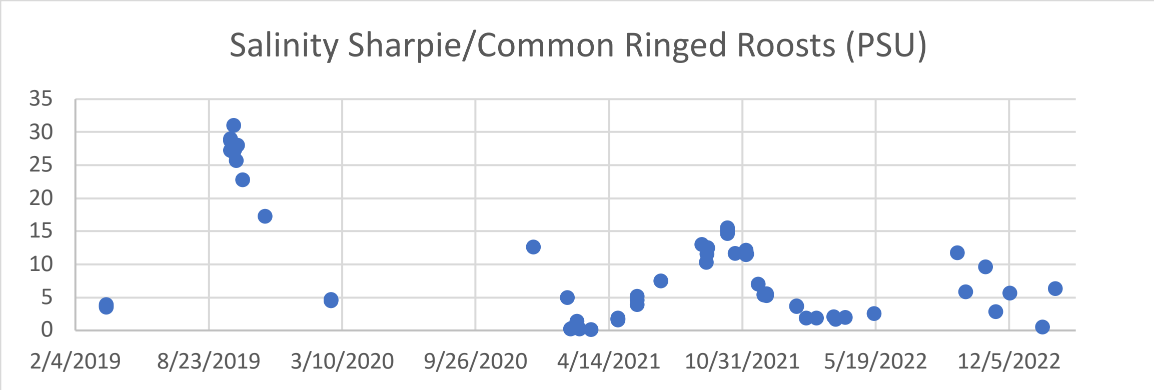


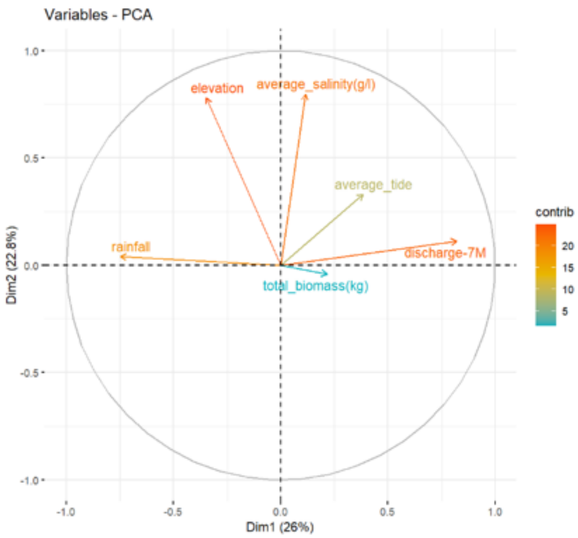
Figure 28. Salinity at the "SharpieSpot/Common Ringed Roost" (Zone 8) monitored from 21/03/2019 to 20/03/2022.

As was the case for the "first wetland" (Fig. 27), the highest salinities were recorded before the start of the 2021-2022 birdcounts. They went down to almost zero during and just after the February 2021 flood (0.13 PSU on 17/03/2021). During 2021, salinity only marginally exceeded 15 PSU (15.54 on 08/10/2021) and we think that the lower salinities explain most of the observed vegetation changes. As there was no flooding in 2022, salinity stayed slightly higher than in 2021 with a minimum of 1.76 PSU on 20/03/2022.

6. Multivariate analysis of bird observations with environmental variables

In order to analyse which environmental variables correlate, and to what extent, with the bird observations, the birdcount dataset partitioned into feeding guilds (monthly average bird biomass per species observed in the countplot) was combined with data on vegetation type at the countplot, local rainfall (monthly average at the Marracuene private raingauge), surface water salinity in the countplots (monthly average), highest tide within 72 hours before the birdcount (monthly average from the tidal gauge of Maputo harbour) and discharge as measured at Magude (daily average from 3 measurements) 7 months prior to the birdcount (in order to allow time for the ecosystems to respond to the hydraulics, building up the food chain from primary production) was subjected to a Principal Component Analysis (PCA) (Abdi & Williams 2010) using R scripts.
In order of the importance in biomass terms of the feeding guilds:

6.1 Piscivores



For the piscivores, the PCA biplot shows that piscivores biomass is, amongst the set of variables used, most closely correlated with the Discharge 7 months prior to the count, i.e. the flooding in February 2021. Mostly the signal comes from the Great White Pelican concentrations towards the North Wetlands where fish were concentrating in the remaining water bodies but Grey and Purple Herons and Little Egret and Black Heron also partake.

6.2 Herbivores

The herbivore biomass (mostly Spurwing Goose and White-faced Whistling Duck) also correlates most closely with Discharge 7 months prior to the count but again the explanatory power is relatively weak. Possibly the deposit of fine sediments, the recycling of the old vegetation reflooded after a prolonged drought and the recharge and freshening of the groundwater allowed for a vigorous vegetation growth season as well as providing good cover for nests.

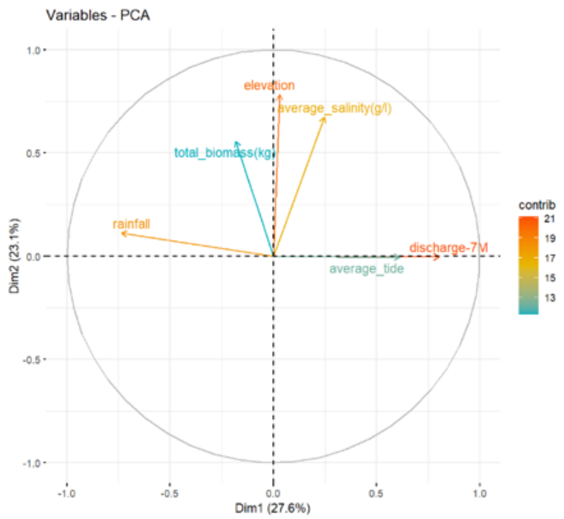
6.3 Aquatic invertebrate feeders

Biomass of this guild (a mix of resident Ibises and migratory waders) has only the slightest of signals inversely correlated with elevation. As they probe into soft mud it makes sense for them to be in the wettest lowest lying places.

6.4 Molluscivore

The biomass of the Openbill Stork correlates positively and relatively strongly (contribution to the variance 13%) with elevation. The birds tend to aggregate feeding on the apple snails in the relatively high-elevation grasslands around the Diagonal but also around the Canal Wetlands.

We think the correlation with surface water salinity might be spurious as there are no surface water salinity data from the Diagonal (so the PCA uses the overall average creating a bias), as this area is inaccessible during flooding or after big rains as the Canal Wetlands cut them off from the road creating a bias. When reachable by car these areas are basically dry salty land with a lot of bare patches, chenopodiacea (Salicornia) and short grasses/sedges. The salinity signal in the biplot we think comes from the Canal Wetlands and other areas where surface salt dissolves with rain or flooding and then concentrates with evaporation.



6.5 Insectivores

There is only the tiniest of correlation between Insectivore biomass and the environmental variables (in the direction of elevation and surface water salinity). Cattle Egrets are joining the cows that graze all over the place except in the deep, and therefore fresh, water from the dune groundwater seepage. Similarly, the Collared Pratincoles feed on insects while flying and are very mobile so there isn't much of a spatial pattern.

6.6 Broadspectrum feeders or Opportunists

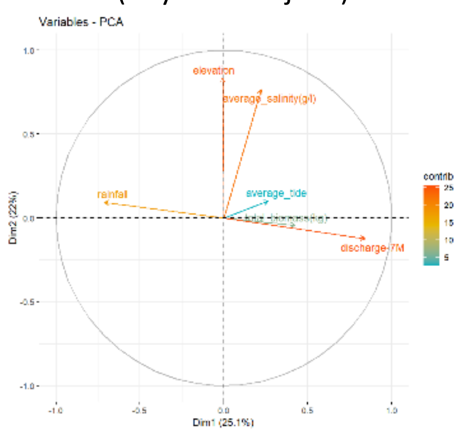
Biomass in this feeding guild correlates quite strongly (over 10% contribution) with surface water salinity and elevation but also, to a lesser extent, with discharge 7 months prior to the bird count. This group is dominated by the Intermediate Egret, feeding abundantly in zones 4 and 7, as well as close to the North Wetlands as do the Whiskered Terns.

6.7 Marginal feeding guilds

The Black-headed Heron is feeding on rodents in the higher elevation areas (again correlating with higher surface water salinity) in Zones 3, 5 and 7 especially.

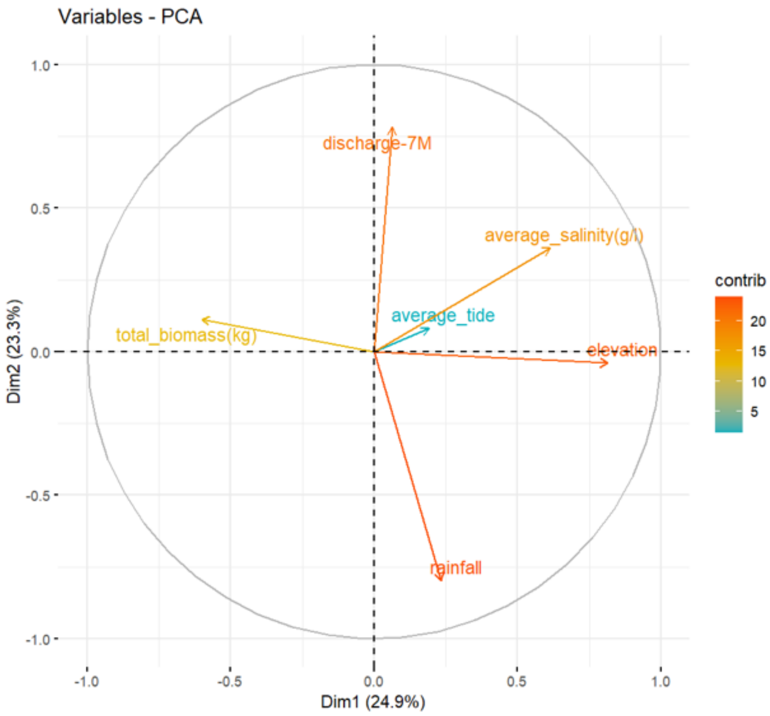
Omnivore biomass (dominated by the Moorhens, especially the African Swamphen) is relatively strongly correlated with low lying fresh water areas (Beyond Hobjana).

The Raptors are quite strongly correlated with the Discharge 7 months prior to the bird count. Being at the top of the food chain this possibly signals the positive impact of the flooding on general productivity in the area. Dominated by the Marsh Owl, the Black-winged Kite and the African Marsh Harrier they like the medium height grasslands with reeds around the northern wetlands where both the Owls and the Harriers breed, but



they also hunt around the main road (e.g. in Zones 4 and 6) . Mostly they target rodents but they also take small birds.

The Seed-eaters biomass shows some of the strongest correlations of all the single guild PCAs, in low-lying low salinity areas, mostly targeting the farmland used for growing rice (Beyond Hobjana). This is the area where chasing small birds is a time-consuming activity for the farmers.



7. Possible changes under managed Environmental flows

6.1 Flooding

Flooding as a main driver of floodplain productivity can be seen from the numbers of large piscivorous birds, such as the Great White Pelicans actively feeding in the lowest lying areas of the Macaneta wetlands in September and October 2021. It is thought that these were attracted by high concentrations of fish generated on the floodplain during the February 2021 flood, growing throughout the season and concentrating in the lowest lying water bodies during the dry season. Such concentrations were not observed during 2022.

Figure29. High density of juvenile Penaeid shrimp observed in the tidal ditches at Macaneta on 21/02/2021.

Indirect evidence also exists, e.g. the presence of high densities of juvenile Penaeid shrimps (Fig. 29) – in the ditches of Z12 linked to the MOCFP canal on 21/02/2021, just after the flood. Schools of Mozambique Tilapia *Oreochromis mossambicus* were also observed moving through the main road culverts during and after the flooding. The hypothesis is that the flooding creates connectivity between the river and the floodplain and allows spawning fish to access the floodplain and reproduce there while also creating favourable habitat for juvenile shrimp, and probably other crustaceans such as crabs. These can then, at least partially, return to the estuary where they can be caught by humans and also feed the high numbers of piscivorous birds observed there during the salinity transects of May 2021 (average 12.5 piscivorous birds counted per km of transect). Though birdcounts were not repeated during the corresponding transects of 2022, the tourism operators halted guided bird tours of the estuary in early 2022 as there were no longer the numbers and variety of birds to attract tourists (Roy Vermaak, *pers. comm*). Also, on a school excursion in the estuary on 21/06/2022 only 2.2 piscivorous birds per km were observed, 5 times less than during the salinity transects of late May 2021.

It is therefore important to maintain, enhance or create the possibility of floods exceeding the 1000 cumecs reaching the lower Incomati. Obviously, flooding is also required to maintain the deposition of fine elements and thus the landbuilding functions of the Delta. Without these, the entire floodplain would in the medium to long term disappear.

6.2 Reducing salinity during the dry season equinox

One of the major risks to the Incomati Delta is further salinization and loss of the productive brackish water habitat. Indeed, it is well known that the maximum turbidity zone, where organic material from the upstream flocculates and settles is an important driver of productivity. Similarly, the brackish water zone is a haven from predation as access to both marine and freshwater adult predatory fish is limited by the physiological constraints these conditions pose. Thus, juveniles of a wide range of vertebrate and invertebrate species find abundant resources in combination with low predation levels.

With sea level rise it can be predicted that salt water will penetrate further and further upstream and, on the Equinox tides can penetrate in to the floodplains. This is especially the case for the dry season equinox tides. It might be advisable to use environmental flows to reduce the salinity during this critical time period, e.g. through managed flood releases from upstream dams.

8. Conclusion

Field ecology is a discipline that, at the scale of Macaneta, does not allow controlled experiments that would allow us to test hypotheses. Ideally, we would apply a series of floods of different height and duration while keeping all the other hydrological variables constant e.g. an identical rainfall regime over several years and then compare the use of the area by different bird feeding guilds. In reality, one just has to make the best of a given situation, sometimes euphemistically designated as “a natural experiment”. This is why long time series of ecological observations are so important: more observation years mean an increasing range of situations in a number of variables can be tracked and analysed. A great example are the weekly counts of wintering Pink-footed Geese, *Anser brachyrhynchus* conducted in the polders of the Belgian Coast since 1959 by Eckhart Kuijken (65 years) providing information on breeding success in the Arctic long before snow cover images became available.

For Macaneta it was “lucky” that, early into the first year of the systematic counts reported here, there was an impressive flood of over 1000 m^3s^{-1}, almost entirely covering the study area. Moreover, this flood in 2021 happened after a long (7 year) drought without significant flooding and this in a setup where regular bird observations had been conducted and entered in eBird by, mainly, Gary Allport who also encouraged visiting birders to do the same. Thus, decent background knowledge was available. The next year, 2022 did not have any flooding but was characterised by very high rainfall that extended much longer than is usual. This meant a lot of waterbirds were present in the central floodplains in high numbers for much longer in 2022 than in 2021, making it hard to distinguish the effect of flooding from simply the presence of water, especially as many species are at least partially opportunistic. In the field it is hard to distinguish piscivory from feeding on other aquatic vertebrates, such as tadpoles and frogs even though circumstantial evidence, such as a marked abundance of frogs in the floodplains and direct observations of birds taking frogs suggests that the food chain was more strongly amphibian than fish-oriented in 2022. Still, we are fairly confident that the 2021 flood was key to the presence of higher numbers and especially biomass of piscivorous birds on the floodplains later in the year. Similarly, the multivariate analysis points to a positive correlation between flooding and raptor biomass. The mass influx of juvenile Penaeid shrimp observed in the floodplain channels by James Hogg in 2021 and not noticed in any other year, suggests a higher crustacean productivity in the flood year.

The case for the importance of flooding for fish and crustacean productivity would have been much stronger if we had been able to conduct a similar boat-based count of the lower estuary in May 2022 as we did in 2021. All the indirect evidence points to much lower numbers of piscivorous birds, especially Caspian Tern in that area in the non-flood year, especially the boat bird tour operator giving up on the venture as clients came back disappointed.

We think therefore that our conclusions are robust and that flooding is indeed a key driver of fish and crustacean productivity in Macaneta in spite of the lack of hard data to prove this.

Acknowledgements

Numerous volunteers participated in the counts but special mention should be made of Anne-Marie and Tom Moore, Dave Minney, Zèv Hamerlynck and Samuel Liebert who were often joining in the “dawn patrol” and also added (and continue to add) data into eBird. Further support was provided by Danilo Makers, Stéphanie Duvail, Thomas Bruneau, Gary Rowan, Lynette Polson, Olivier Vilaça, Ken Behrens, Alice Marque, Yara Tibirica, Carlos Bento, Héloïse Hamerlynck, Bahati Moseti, James Watson, Alex Caron, Cathy and Etienne La Roux.

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