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ORIGINAL PAPER

Characterising benthic diatom community responses to abiotic variability in a tropical Ramsar estuarine lake

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Abstract Benthic diatoms are reliable indicators of estuarine ecosystem health. These communities can be used to track water quality changes in estuarine lakes that are unique, yet highly susceptible to anthropogenic perturbations due to their high accumulation potential. This study investigated the abiotic drivers of the benthic diatom community structure in the near-natural Kosi Bay Estuarine Lake, a Ramsar Wetland of International Importance in summer/spring of 2016 and 2022. A total of 159 taxa, belonging to 57 genera were recorded. The composition of benthic diatom assemblages was related to salinity variability, with marine species dominating the tidal lower estuarine reaches and freshwater taxa in the distal and oligohaline lake compartments. Taxa capable of attachment to different substrates that enable resilience to tidal disturbance, such as *Amphora*, *Halamphora*, *Mastogloia*, and *Seminavis*, were dominant in the tidally influenced lower lake compartments. Higher species diversity (H' > 2) was observed in proximity to the estuarine mouth, with regular sediment disturbance favouring increased diversity. An increased availability of DIP (≥ 0.01 mg L^{-1}) and sediment organic content (1.1–3.7%), coupled with low flow velocities, favoured the proliferation (RA > 10%) of *Cocconeis* spp. in the *Phragmites*-dominated upper lake compartments. Nutrient tolerant taxa, such as *Navicula gregaria*, *Nitzschia frustulum,* and *Tabularia tabulata,* were present in the estuarine lake. However, further investigations are required to determine whether their presence is due to inherent estuarine variability or a precursor to future anthropogenic change. Studies such as these that provide baseline information are essential to help inform effective management and recovery plans of rare estuarine ecosystem types.

Keywords Habitat heterogeneity · Indicator species · Oligotrophic · Salinity gradient · Water quality

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Introduction

Estuaries are complex ecosystems defined by the interaction between the physical and biological processes that vary over spatial and temporal scales (Adams et al. 2016; Van Niekerk et al. 2020). The interrelationship between these key processes facilitates habitat heterogeneity that shapes a diverse biotic community along the river to ocean continuum (Elliott et al. 2017; Paerl et al. 2018). In South Africa, nine estuary types, occurring across four biogeographical zones (i.e. cool temperate, warm temperate, subtropical and tropical), are recognised (Van Niekerk et al. 2020). These include estuarine lakes, estuarine bays, estuarine lagoons, predominantly open estuaries, large and small temporarily closed estuaries, large and small fluvially dominated estuaries, and arid predominantly closed estuaries (Van Niekerk et al. 2020). Estuarine area (ha), degree of connectivity to the marine environment, mean annual runoff, salinity regime, and mixing processes (i.e., wind, riverine, tidal, seepage or evaporation) are key features and physical processes that define the estuary types (sensu Van Niekerk et al. 2020). Estuarine lakes mostly evolved from drowned river valleys and are rare, representing less than 5% (13 of 290 systems) of the country's estuaries (Van Niekerk et al. 2020). Yet, despite their rarity, these larger systems collectively cover more than 60% of the South African estuarine habitat and contribute a significant proportion of critical nursery habitats (e.g., submerged aquatic macrophytes) (Van Niekerk et al. 2022a).

The Kosi Bay Estuarine Lake supports the largest area (652 ha) of submerged aquatic macrophyte habitat in South Africa (Adams et al. 2016). Part of the UNESCO World Heritage iSimangaliso Wetland Park and listed as a RAMSAR Wetland of International Importance since 1991, this natural to near-natural system is an important fish nursery and bird area (i.e., migratory and nomadic birds) (SAR 2022; Van Niekerk et al. 2022a). However, increasing human activities and development within the catchment, ranging from informal housing, subsistence agriculture (e.g., transformation and cultivation of swamp forest habitat), and afforestation (*Eucalyptus* spp. plantations), pose a potential threat to the pristine state of the system (Kyle 1995; Van Niekerk et al. 2022d). Estuarine lakes are typically characterised by prolonged water residency that stems from large surface-area-to-volume ratios, proportionately low mean annual runoff, and intermittent periods of marine connectivity (Sheaves and Johnston 2008; Van Niekerk et al. 2022a). The marine connectivity (extent and duration), variable freshwater sources (surface and groundwater), and evaporation rates drive highly variable salinity regimes (fresh to hypersaline) in estuarine lakes (Van Niekerk et al. 2020, 2022a). Mixing processes within these lake systems are primarily wind-driven because of the limited connectivity to the sea and low tidal amplitudes (15 to 20 cm) (Van Niekerk et al. 2020). The resultant low flushing potential culminates in ecosystems inherently vulnerable to the build-up of land-derived pollutants (Van Niekerk et al. 2022a).

Science-based interventions supported by spatial and temporal predictions of ecosystem health trends are required to prevent the loss of functional diversity that affects the resilience of estuaries to multiple stressors (Mahoney and Bishop 2017; Leruste et al. 2018). Abiotic variables to which biota are known to respond in a predictable manner, or reliable structural metrics (abundance, species richness, biomass) of characteristic biotic communities are effective indicators for assessing risk of ecosystem change (Elliot and Quintino 2007; Mahoney and Bishop 2017). Adverse effects of human-induced stressors often lead to reductions in species richness, evenness, diversity, as well as a loss of rare taxa (Clark et al. 2021). Diatoms, unicellular photoautotrophic eukaryotes, that inhabit the intertidal and subtidal estuarine sediments are usually the dominant microalgal component of the microphytobenthos (MPB) communities (Round 1981; Round et al. 1990; MacIntyre et al. 1996). Benthic diatoms are widely implemented as bioindicators due to their limited dispersal potential, short generation times, ubiquity in aquatic ecosystems, rapid response to environmental change, suitability to different methodologies (i.e., microscopy, molecular), and relative ease of sample collection from a range of different microhabitats (e.g., scrubbing rocks, agitating submersed macrophyte stems, or scraping sediments) (Kafouris et al. 2019; Nunes et al. 2021; Plante et al. 2021; Taurozzi et al. 2024). Species abundance and presence mostly depend on habitat type, nutrient and light availability, temperature and salinity, hydrodynamic conditions, competition, and/or grazing pressure (MacIntyre et al. 1996; Liu et al. 2022; Da Rosa et al. 2023). Individual species

responses to specific environmental tolerances, coupled with categorising diatom taxa using their functional classification (e.g., low-profile, high profile and motile species), provides valuable information on the conservation status of an ecosystem under data-poor conditions (Mbao et al. 2020; Heine-Fuster et al. 2021; Weilhoefer et al. 2021; Oliveira et al. 2022).

Yet, the value of environmental inferences based on benthic diatom metrics are reliant on consistent and sound taxonomy, as well as knowledge regarding the abiotic variables that control the composition and distribution of diatom communities (Pérez et al. 2013; Vélez-Agudelo and Espinosa 2021). Despite the conservation importance of the Kosi Bay Estuarine Lake, little is known about the benthic diatom community and the abiotic variables driving their structure and composition (Van Niekerk et al. 2022a). Rapid anthropisation of the coastal zone necessitates identifying reference conditions for contemporary and future studies to monitor, assess, and manage change to ecosystem structure and function for the continued provision of ecosystem services (Little et al. 2017). This is particularly important in estuarine lakes that are less resilient to change given that their biophysical processes function over prolonged temporal scales (annual to decadal) (Van Niekerk et al. 2022a). As such, this study aimed to examine how abiotic variables influence the composition and distribution of benthic diatom assemblages in the Kosi Bay Estuarine Lake. Such information is critical to assess whether anthropogenically-driven change is evident, as well as provide a baseline of how these unique ecosystems function under near-natural conditions. In eutrophic systems, nutrient availability predominantly drives benthic diatom community dynamics (Agatz et al. 1999). Therefore, it was hypothesised that, in the near-natural Kosi Bay Estuarine Lake, changes in the benthic diatom community structure will be influenced by the interaction of multiple site-specific abiotic variables, such as salinity, nutrient supply, and sediment characteristics.

Materials and methods

Study area

The Kosi Bay Estuarine Lake (26°53′44.70"S; 32°52′51.06"E) is situated on the northeast coast of the KwaZulu-Natal Province of South Africa (Fig. 1) (Begg 1978; Van Niekerk et al. 2020). Characterized by a humid subtropical climate, temperatures range from 11 to 29 °C. Yearly average rainfall is estimated at 980 mm and rainfall occurs predominantly in the austral spring and summer months (i.e., October to March) (Wright et al. 1997; Rajkaran and Adams 2011; Ndlovu and Demlie 2016). Kosi Bay consists of four tidally influenced, interconnected lakes and a broad channel that leads into an estuary which is connected to the Indian Ocean (Fig. 1) (Begg 1978; SAR 2022). In terms of zonation, the estuary was divided into five compartments, namely the shallow estuary, Lake 1 (Makhawulani), Lake 2 (Mpungwini), Lake 3 (Nhlange), and Lake 4 (Amanzimnyama). The mouth of the system is generally open throughout the year and experiences regular and strong tidal exchange (Begg 1978). While two principal rivers, the Sihadla and Nswamanzi rivers, a semi-perennial KuKhalwe stream, and outflow into the estuary from Lake KuZilonde supply surface water flow to the system, it is primarily groundwater driven (Begg 1978; Ndlovu and Demlie 2016; Van Niekerk et al. 2022a). Substrate materials consist predominantly of white sands that are characterised by a lack of fine particulate matter and low nutrients, while unconsolidated organic matter derived from fragmented plant material accumulates in the sediments of Lake 4. The Sihadla River and Lake 4 are considered important sources of organic debris for Lake 3 (Begg 1978). Key habitat types include freshwater swamp forests, reeds and sedges, submerged macrophytes, and mangrove forests. The Kosi Bay mangrove forests are the only community in South Africa to encompass five species of mangrove trees, namely *Avicennia marina*, *Bruguiera gymnorrhiza*, *Rhizophora mucronata*, *Ceriops tagel,* and *Lumnitzera racemosa* (Rajkaran and Adams 2011). The system is mainly impacted by subsistence agriculture, commercial plantations (e.g., *Eucalyptus* spp.), invasive terrestrial species (e.g., *Casuarina equisetifolia* and *Tarebia granifera*), over-exploitation of natural resources (e.g., traditional

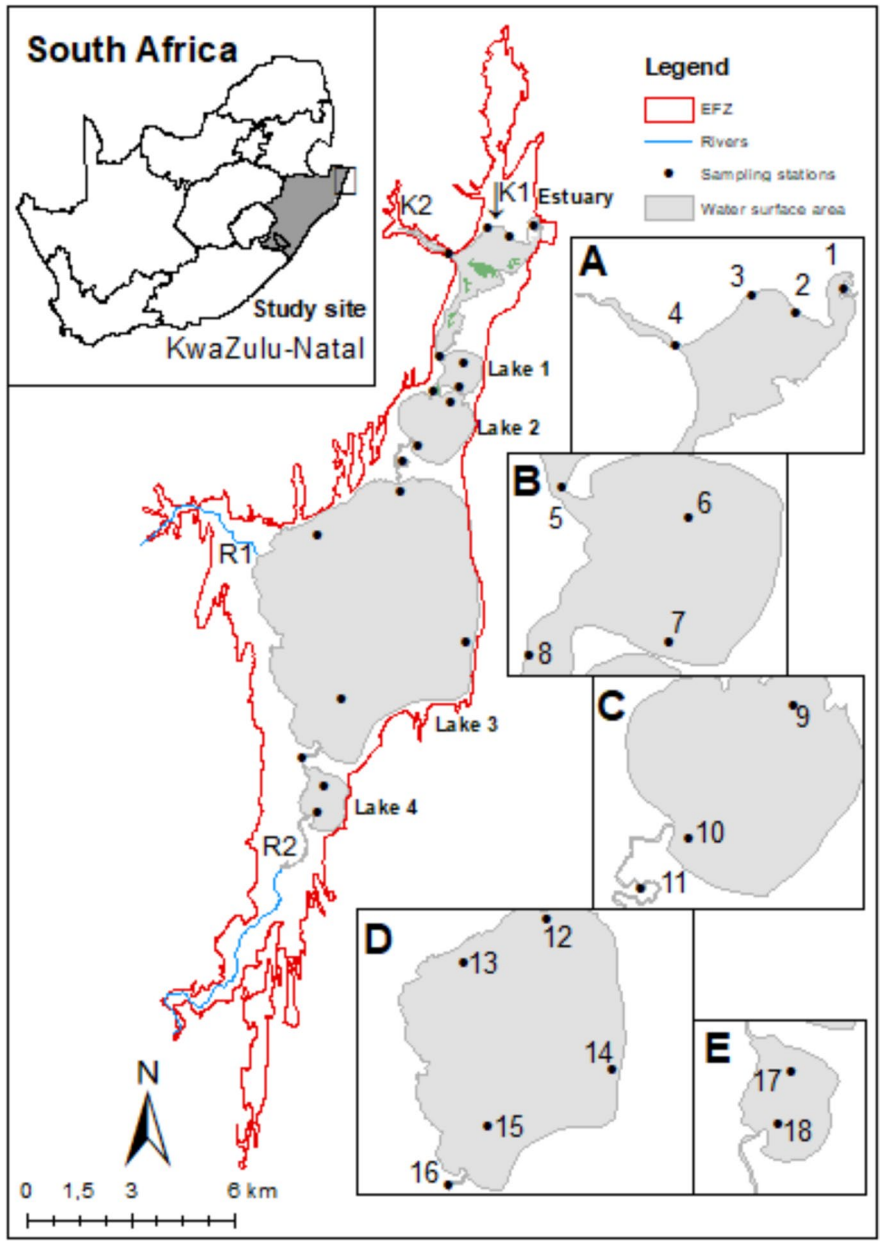

Fig. 1 Map indicating the location of the Kosi Bay Estuarine Lake along the northeast coast of the KwaZulu-Natal Province (South Africa), the two principal rivers (R1—Nswamanzi; R2—Sihadla), the position of the Lake KuZilonde outflow to the estuary (K1), the semi-perennial KuKhalwe stream (K2) as well as the position of the respective sampling stations in the estuary (**A**) and interconnected lakes (**B**–**E**). B—Makhawulani (Lake 1), C—Mpungwini (Lake 2), D—Nhlange (Lake 3), and E—Amanzimnyama (Lake 4)

fish traps, mangrove harvesting), and DDT pollution (Begg 1978; SAR 2022).

The environmental and benthic diatom community composition data were collected as part of Environmental Water Requirement (EWR) studies of the Department of Water and Sanitation. The EWRs quantify the quality, quantity and timing of freshwater required to ensure the adequate functioning and future persistence of estuaries and is generally conducted every 5–10 years (Adams et al. 2016). Therefore, surveys were conducted in the summer of 2016 (7–11 February) and spring of 2022 (29 September to 01 October). Eighteen sampling stations, representative of the typical salinity gradient, were sampled along the length of the estuarine lake (Fig. 1).

Land cover classification

The 2017 KZN Land-Cover Sentinel 2 Equivalent dataset was used to extract and calculate (in hectares) the land-use type distribution of the Kosi Bay Estuarine Lake, using ESRI ArcMap 10.5.1 software. The land-use for the system was obtained using both the quaternary catchment area and the estuarine functional zone (EFZ). A quaternary catchment is the fourth-order hydrological unit boundary in the hierarchal catchment classification system that is being used for fine-scale water resource management in South Africa (Maherry et al. 2013). The EFZ is a well-defined area that includes the estuary waterbody along with supporting physical and biological processes and habitats that are essential for estuary function and health (Van Niekerk et al. 2019a). Both the quaternary catchment and EFZ included in this assessment as size and intensity of land-use upstream of a system may, in some instances, supersede the water quality signal from the larger catchment and subsequently become the key determinant of the water quality status of freshwater inflow (Taljaard et al. 2017). The 2017 KZN Land-Cover Sentinel 2 Equivalent dataset was selected as it represents an overall mapping accuracy of 97.7% due to the incorporation of enhanced spectral content provided by the Sentinel 2 imagery, as well as multi-seasonal imagery that covers the full dynamic range of seasonal landscape characteristics. A total of 47 different land-cover classes have been delineated, of which the individual class mapping accuracy level ranges between 86 and 100% (EKZNW and GeoTerraImage 2018).

Environmental variables

Physical and chemical variables

Measurements for temperature (°C), salinity, dissolved oxygen (mg L^{-1}), pH, and turbidity (NTU) were recorded from the surface to the bottom of the water column at 0.5 m depth intervals at each sampling station using a YSI 6920 V2 and YSI ProDSS multiparameter during the 2016 and 2022 survey, respectively. Water samples for inorganic nutrient analysis were collected in duplicate at the specified depths using a 500 ml weighted pop-bottle. Each water sample was first gravity-filtered through Munktell© MGC glass-fibre filters (1.2 µm pore size). The filtrate was then filtered through sterile GVS© cellulose acetate syringe filters (0.45 µm pore size) into low-density polyethylene (LDPE) bottles. The filtrate was frozen and stored in the dark until it was analysed in the laboratory for dissolved inorganic nitrogen (NO_x-N, i.e., $NO^-_3 + NO^-_2$), orthophosphate (PO_4^{3-}-P), and ammonium (NH_4^+-N). The 2016 samples were measured colourimetrically using a four-channel flow injection autoanalyzer (detection limit 5 ug L^{-1}) according to the methods described in CSIR (2002), whereas the 2022 samples were measured using a SEAL Auto-Analyzer 3 HR (SEAL Analytical, Inc., Germany) (Murphy and Riley 1962; Grasshoff et al. 1999).

Sediment organic content

Triplicate sediment samples were collected using a dual Perspex corer with extension at a depth of 5 cm at each sampling station during each survey. The sediment samples were stored in polyethylene containers and kept cold (~2 °C) until processing in the laboratory. For sediment organic content, the sediment was weighed (10 g), placed in crucibles, and dried at 105 °C for 24 h. Thereafter, the dried samples were weighed before being placed in a furnace at 550 °C for 8 h. All sediment samples were weighed again afterwards and organic content (%) was calculated as the loss of weight of the sample (Briggs 1977).

Microphytobenthos biomass

Triplicate subtidal sediment samples were collected for the analysis of microphytobenthos (MPB) biomass using a dual Perspex corer (i.e., 20 mm internal diameter) with extension to a depth of 1 cm at sampling station during each survey. The triplicate sediment samples were transferred to individual 60 ml polyethylene containers and frozen until analysis of MPB biomass, measured as chlorophyll-a concentration (mg Chl-*a* m^{-2}), in the laboratory. Chlorophyll-*a* was extracted by first adding 15 ml of 95% ethanol (Merck 4111) to each sample and then storing each sample in a cold, dark room for 6 h (Brito et al. 2009). The extract was filtered through microglass fibre filters (Munktell© MGC glass-fibre filters, 1.2 µm pore size) and the filtrate was subsequently used to determine the Chl-*a* concentrations using the

standard spectrophotometric method described by Nusch (1980).

Benthic diatom community composition

A replicate sediment sample for the identification of the benthic diatom community was also collected at each sampling station during each survey. This was collected using the same method described for the MPB biomass and was immediately transferred to a petri dish. The sediment sample was homogenised and left to settle for 1 h in light. Five glass cover slips (22 × 22 mm each) were subsequently positioned on the surface of the damp sediment following the 1 h settling period and left for 12 h (equivalent to one tidal cycle) (Bate et al. 2013). The glass coverslip method is globally used to harvest motile epipelic diatoms from a variety of freshwater and marine systems (Yang et al. 2010). While this method is designed to target epipelic taxa specifically, sand/mud mixtures provide the ideal habitat for a combination of epipelic (motile taxa) and epipsammic (non-motile/slow motile) benthic diatoms (Yang et al. 2010; Morelle et al. 2020; Serôdio et al. 2023). In addition, a study by Thomson and Manoylov (2019) showed the benthic habitat to consist of epipelic epipsammic and planktonic species. This method was used consistently across the two sampling dates to measure diatoms. The glass coverslips were removed from the sediment and stored dry in 60 ml polyethylene containers. All samples were stored in the dark until analysis in the laboratory. Sample preparation for benthic diatom identification was performed according to the method described by Bate et al. (2013). The permanently mounted diatom frustules were examined and counted using a Zeiss Axioplan light microscope with differential interference contrast (DIC) optics. Images of the dominant species were visualised for taxonomic identification using a television camera (The Imaging Source DFK 41F02) and the Imaplan 2.06 image analysis program (IMATEC Elektronische Bildanalysesysteme GmbH ©2016). Diatom community analysis was performed by counting 400 diatom valves and by identifying the taxa to the lowest possible level (species or genus) using taxonomic guides by Round et al. (1990), Sims (1996), Witkowski et al. (2000), Bate et al. (2004), Taylor et al. (2007), Álvarez-Blanco and Blanco (2014), Cantonati et al. (2017), and John (2020). To ensure that all the diatom species present were recorded and included in the analysis, the entire surface area of the permanent mount was scanned once the initial valve counts were completed (Manoylov et al. 2016). Relative abundance (RA) of all species was calculated and then used to determine the dominant (RA > 10%) and subdominant species (RA 5–10%). The World Register of Marine Species (WoRMS Editorial Board 2024), AlgaeBase (Guiry and Guiry 2024), Round et al. (1990), and Taylor et al. (2007) were used to obtain the most recent taxonomic names and the salinity/habitat preferences of all diatoms identified per taxonomic inventory.

Data analysis

All statistical analysis and graphical illustrations were performed using R (version 4.3.0, R Core Team 2024). An a priori significance level of $\propto < 0.05$ was specified. Data were tested for normality and homogeneity of variance using the Shapiro-Wilks test and Levene's test, respectively (see Table 3A and 4A, Supplementary material). The paired t-test was used to compare the physicochemical measurements, sediment organic content (SOC), inorganic nutrient concentrations, and the benthic diatom community variables (biomass, diversity, evenness, and richness) between 2016 and 2022. The Shannon diversity index (H'), evenness of species distribution (J'), and species richness (S) were determined for the benthic diatom communities (Shannon and Wiener 1949). The non-parametric Spearman's rank correlation was used to test relationships between the environmental variables and the benthic diatom community variables. Non-metric multidimensional scaling (NMDS) was applied ("vegan" package) to the benthic diatom abundance data using the Bray–Curtis index to assess the similarity in community structure between 2016 and 2022. A five-dimensional solution (k = 5) was chosen to reduce high stress value. To test whether these groupings were significantly different, analysis of similarities (ANOSIM, permutations = 999) was used. Diatom species that were found more often in one survey compared to another were identified using indicator species analysis (package: "indicspecies," permutations = 1000). The relative occurrence and abundance of these indicator species reflect the abiotic state of the

environment (De Cáceres 2022). Additional ecological descriptors for the benthic diatom taxa were determined using the "DiaThor R package", specifically the "diat_guilds" that classifies the proportion of each ecological guild (i.e., planktonic, low-profile, high-profile and motile; see Table 1A in Supplementary Material) and "diat_vandam" related to ecological indicator indices (see Table 2A in Supplementary Material) functions. This R package has been developed for the assessment of freshwater systems (Gelis et al. 2022). Thus, the two functions with the best results were selected as the number of taxa included in the analyses was low (total benthic diatom community $\leq 33\%$). The relationship between the environmental parameters, system compartments, and benthic diatom species abundance between 2016 and 2022 was described using canonical correspondence analysis (CCA) ('vegan': Oksanen et al. 2022). CCA was used as it provides a better evaluation than generalised linear modelling when species presence recorded between the total number of sampled points are relatively low (Guisan et al. 1999). Stepwise model selection was performed, and collinear predictors ('vif.cca' function; VIF > 10) were excluded. The significance of variation in benthic diatom species abundance explained by the predictor variables was tested using Monte Carlo permutation tests (999 permutations) (Borcard et al. 2011).

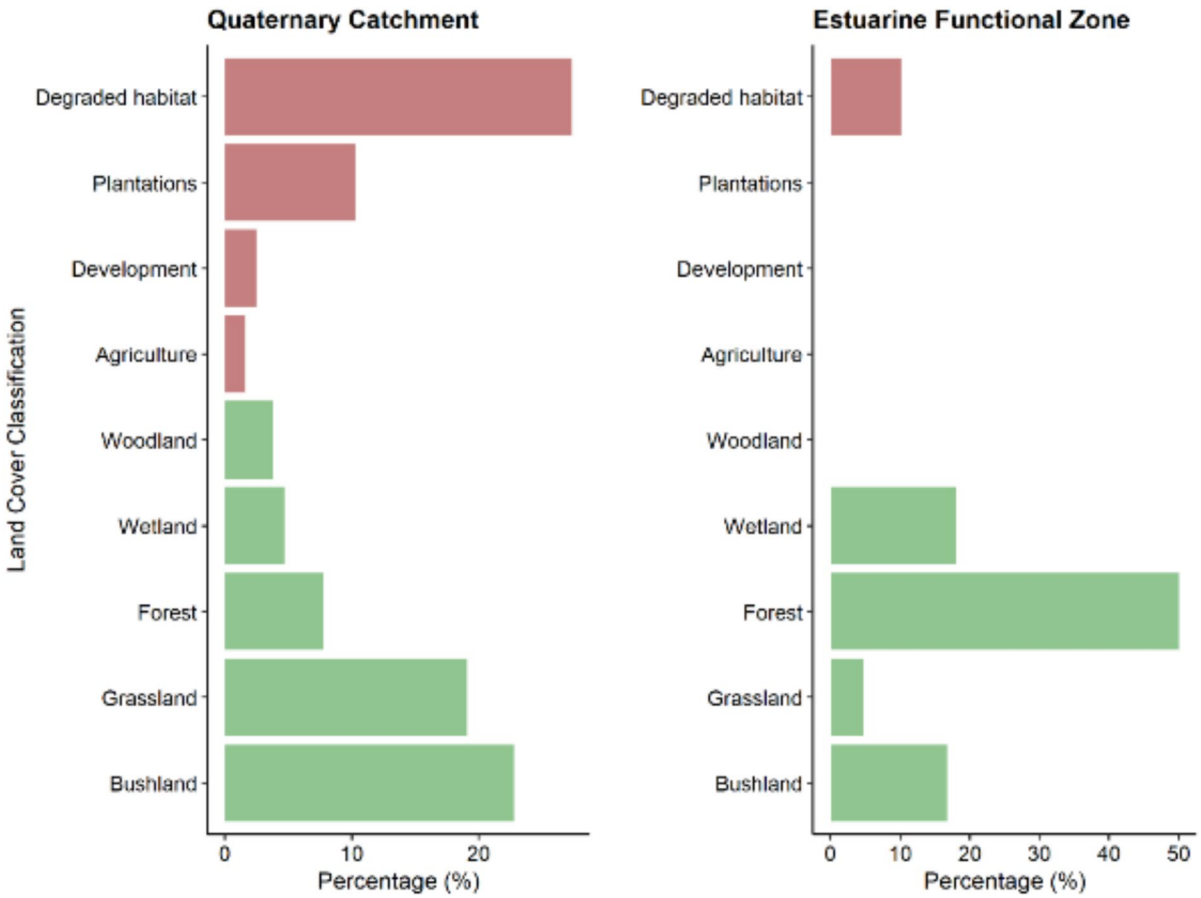

Fig. 2 The land cover classification of the Quaternary Catchment and EFZ of the Kosi Bay Estuarine Lake

Results

Land cover classification

Nine primary land-use types were identified within the quaternary catchment and five primary land-use types were identified within the estuarine functional zone (EFZ) using the KZN Land-Cover Sentinel 2 Equivalent dataset (Fig. 2). The quaternary catchment consisted predominantly of degraded habitat (i.e., degraded bushland, forest, and grassland; 27%), bushland (23%), and grassland (17%). Agriculture, commercial plantations, and development only represented 14% of the total land cover. In the EFZ, forest (50%), wetland (18%), and bushland (17%) represented the largest portion of the total land cover. Degraded habitat (10%) and agriculture (0.1%) were identified as the primary land-use pressures. No development or commercial plantations were present (Fig. 2).

Physical and chemical variables

Water temperatures reflected conditions characteristic of the warmer months (i.e., spring and summer) and varied from 23 to 29 °C. Higher water temperatures were recorded in 2016 (Table 1), specifically in the Estuary (28.7 ± 0.7 °C) and Lake 4 (28.2 ± 0.4 °C) (Fig. 3). Salinity displayed the typical longitudinal trend by gradually decreasing towards the river. Overall, salinity was lower in 2022 (11.5 ± 7.6) compared to 2016 (19.5 ± 11.8) (Table 1). Additionally, salinity intrusion was more pronounced in 2016, with polyhaline conditions (18 to 30) extending into Lake 2 and only into Lake 1 in 2022 (Fig. 3). The estuarine lake was well oxygenated (> 5 mg L^{-1}) in both years, with an isolated hypoxic event recorded in the river (1.3 ± 0.6 mg L^{-1}) in 2022. The pH typically exceeded 8 from the Estuary to Lake 3 (Fig. 3), while lower values were recorded in Lake 4 (L4) and the river (R) during 2016 (L4: 7.6 ± 0.2; R: 7.2 ± 0.02) and 2022 (L4: 7.4 ± 0.2; R: 7.3 ± 0.2). Dissolved inorganic nitrogen (DIN) fluctuated (range: 0.03–0.32 mg L^{-1}) between sampling stations, while dissolved inorganic phosphorus (DIP) steadily increased (range: 0.001–0.026 mg L^{-1}) towards the river (Fig. 3). Differences were observed for DIN concentrations recorded in 2016 and 2022 (Table 1). Higher DIN concentrations (0.07 ± 0.04 mg L^{-1}) were recorded in 2016. Most of the DIN concentrations were below the 0.1 mg L^{-1} threshold that indicates oligotrophic conditions (see Lemley et al. 2015). DIN concentrations were consistently higher in the Estuary (2016: 0.08 mg L^{-1}; 2022: 0.05 mg L^{-1}), Lake 1 (2016: 0.08 mg L^{-1}; 2022: 0.05 mg L^{-1}), and Lake 2 (2016: 0.10 mg L^{-1}; 2022: 0.07 mg L^{-1}), compared to the distal Lake 3 and Lake 4. DIP concentrations differed between years (Table 1), with higher concentrations (0.007 ± 0.004 mg L^{-1}) recorded in 2016. DIP concentrations indicative of mesotrophic conditions (≥ 0.01 but < 0.1; see Lemley et al. 2015) were recorded for both years in Lake 4 (2016: 0.011 mg L^{-1}; 2022: 0.012 mg L^{-1}) and the river (2016: 0.012 mg L^{-1}; 2022: 0.026 mg L^{-1}). A positive association ($P < 0.05$) was recorded between DIN and salinity ($r = 0.45$), while a negative association was recorded between DIP and salinity ($r = -0.35$).

Turbidity was higher in 2016 (2.4 ± 3.0 NTU) than in 2022 (1.3 ± 1.1 NTU), while no differences between years were recorded for total water column depth and sediment organic content (Table 1). Higher turbidity (> 1.5 but < 7.9 NTU) and an increased availability

Table 1 Comparison between the physico-chemical measurements, sediment organic content (SOC), and nutrient concentrations (mean ± SD [min; max]) recorded in 2016 and 2022 in Kosi Bay. Significant *P*-values are indicated in bold

Variable	2016	2022	*Score*	*P*-value
Temperature (°C)	27.4 ± 0.8 [25.5; 30.0]	25.3 ± 1.0 [22.5; 27.5]	15.12	**< 0.001**
Salinity	19.5 ± 11.8 [0.7; 35.2]	11.5 ± 7.6 [0.6; 28.4]	5.38	**< 0.001**
DO (mg L^{-1})	6.8 ± 1.4 [1.0; 9.3]	7.3 ± 1.4 [0.9; 10.3]	28.74	**< 0.001**
pH	8.1 ± 0.2 [7.2; 8.4]	8.2 ± 0.4 [7.1; 8.8]	− 3.34	**< 0.001**
Turbidity (NTU)	2.4 ± 3.0 [0.6; 18.1]	1.3 ± 1.1 [0.01; 7.1}	− 13.56	1
Total depth (m)	4.2 ± 4.4 [1; 18]	3.2 ± 3.8 [0.5; 15]	0.80	0.09
SOC (%)	0.7 ± 0.2 [0.2; 1.2]	1.1 ± 2.1 [0.1; 10.6]	− 1.01	0.21
DIN (mg L^{-1})	0.07 ± 0.04 [0.02; 0.23]	0.05 ± 0.03 [0.001; 0.21]	2.99	**< 0.05**
DIP (mg L^{-1})	0.007 ± 0.004 [0.004; 0.02]	0.006 ± 0.004 [0.001; 0.02]	1.75	**< 0.05**

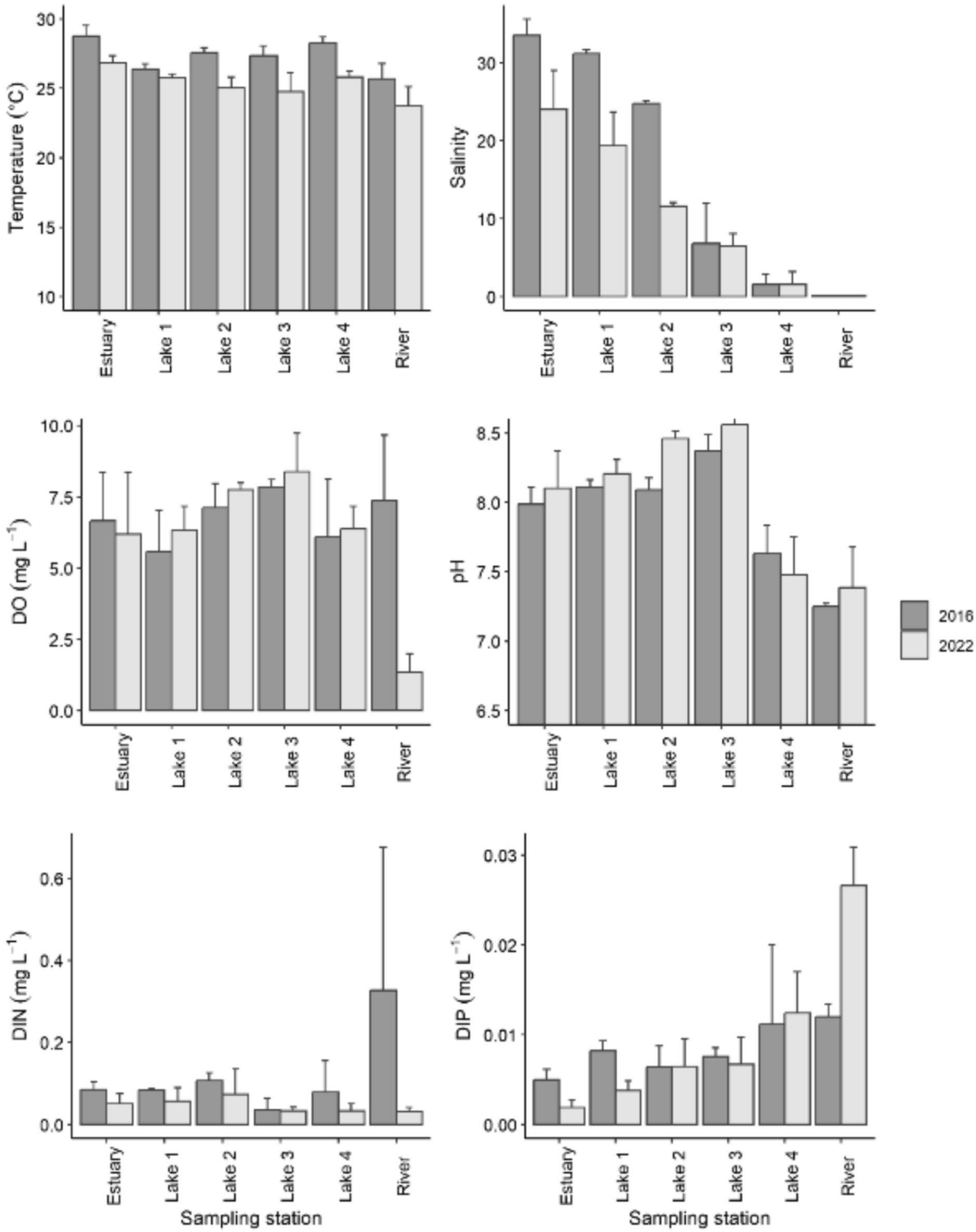

Fig. 3 The physical and chemical variables (mean ± SD) recorded in the estuary, the four interconnected lakes, and river of the Kosi Bay Estuarine Lake for 2016 and 2022

Table 2 The nephelometric turbidity unit (NTU), total water column depth and sediment organic content (SOC) recorded in the estuary and the four lakes of the Kosi Bay Estuarine Lake for 2016 and 2022

Date	Variable	Estuary	Lake 1	Lake 2	Lake 3	Lake 4
2016	Turbidity (NTU)	1.84 ± 0.52	1.24 ± 0.23	1.53 ± 1.90	2.43 ± 1.78	7.83 ± 5.50
	Total depth (m)	1.13 ± 0.25	5.9 ± 1.96	7.93 ± 7.95	4.04 ± 3.56	2.5 ± 0.46
	SOC (%)	0.86 ± 0.38	0.48 ± 0.20	0.65 ± 0.35	0.80 ± 0.11	1.07 ± 0.24
2022	Turbidity (NTU)	0.84 ± 0.12	1.06 ± 0.21	1.16 ± 0.08	1.56 ± 1.45	1.83 ± 2.29
	Total depth (m)	0.76 ± 0.21	3.92 ± 2.67	5.83 ± 4.80	3.88 ± 5.47	1.83 ± 0.29
	SOC (%)	0.81 ± 0.38	0.31 ± 0.09	0.34 ± 0.07	0.75 ± 0.81	3.69 ± 4.45

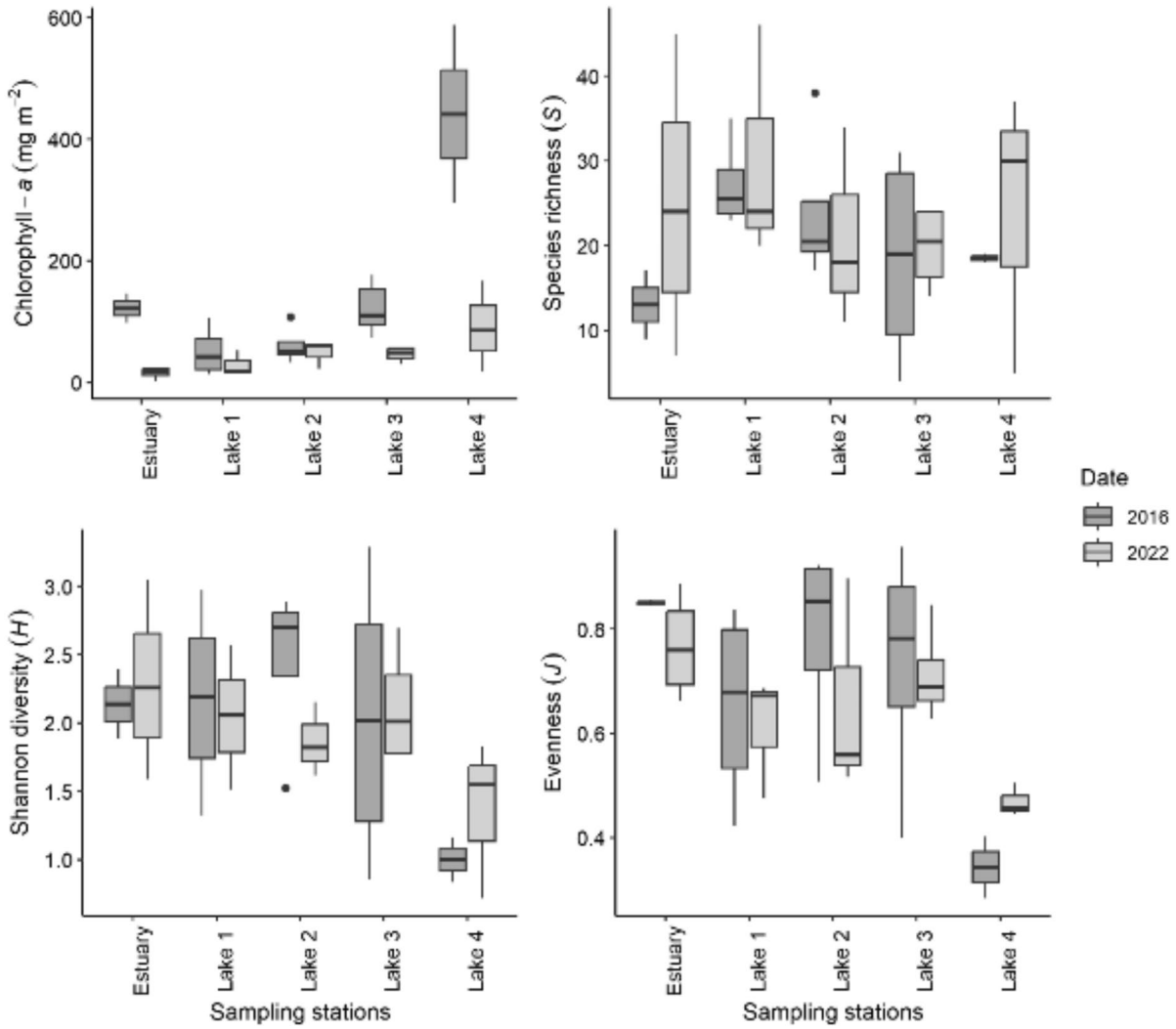

Fig. 4 The microphytobenthos biomass (Chl-*a* concentrations), species richness (*S*), Shannon diversity index (*H'*) and evenness index (*J'*) recorded in the estuary and the four lakes of the Kosi Bay Estuarine Lake for 2016 and 2022. Box-plots represent median values (solid line), interquartile range (IQR = 25th and 75th percentiles; box), ± 1.5 × IQR (whiskers) and outlier values

Table 3 Comparison between the microphytobenthos biomass, species richness (S), Shannon diversity index (*H'*), and evenness index (*J'*) (mean ± SD [min; max]) recorded in 2016 and 2022 in Kosi Bay. Significant *P*-values are indicated in bold

Variable	2016	2022	*Score*	*P*-value
MPB biomass (mg Chl-*a* m^{-2})	127.9 ± 132.6 [13.7; 587.2]	44.2 ± 38.8 [2.3; 166.8]	2.5	**< 0.05**
Species richness (S)	21.0 ± 9.1 [4; 38]	23.7 ± 12.1 [5; 46]	-0.74	0.77
Diversity (*H'*)	2.0 ± 0.7 [0.8; 3.2]	1.9 ± 0.5 [0.7:3.1]	0.35	0.36
Evenness (*J'*)	0.7 ± 0.2 [0.2; 0.9]	0.6 ± 0.1 [0.4;0.9]	.0.7	0.24

of sediment organic content (≥ 0.75 but < 4%) were recorded in Lake 3 and Lake 4 (Table 2). Total water column depth fluctuated between 0.75 and 7.93 m, with deeper waters recorded in Lake 1, Lake 2, and Lake 3 (Table 2). A positive association ($P < 0.001$) was recorded between NTU and DIP (r = 0.39).

Benthic diatom community composition

The microphytobenthos (MPB) fluctuated between 2.3 and 587.2 mg m^{-2} (Fig. 4). High MPB biomass concentrations (> 100 mg Chl-*a* m^{-2}) were recorded in 2016 (Table 3) in the Estuary (121.9 ± 34.5 mg Chl-*a* m^{-2}), Lake 3 (121.5 ± 41.7 mg Chl-*a* m^{-2}), and Lake 4 (441.1 ± 206.6 mg Chl-*a* m^{-2}). While MPB was lower (< 100 mg Chl-*a* m^{-2}) in 2022, MPB biomass concentrations were higher in Lake 2 (49.0 ± 23.1 mg Chl-*a* m^{-2}), Lake 3 (46.1 ± 12.9 mg Chl-*a* m^{-2}), and Lake 4 (90.0 ± 74.8 mg Chl-*a* m^{-2}) compared to the tidally influenced Estuary and Lake 1. In 2016, MPB biomass demonstrated positive associations ($P < 0.001$) with sediment organic content (r = 0.73) and turbidity (r = 0.72). In 2022, MPB biomass displayed a positive association with DIP (r = 0.63, $P < 0.05$) only. Additionally, MPB biomass decreased in response to increasing salinity in both 2016 (r = − 0.51) and 2022 (r = − 0.63). No statistical differences ($P > 0.05$) were recorded for species richness (*S*), diversity (*H'*), and evenness (*J'*) between 2016 and 2022 (Table 3). Species richness ranged between 4 and 46, with peak values recorded in Lake 1 ($S_{2016} = 27$; $S_{2022} = 30$). Mean species

Table 4 The relative abundance of the dominant (> 10% RA; in bold) benthic diatom species identified in the estuary and the four lakes of the Kosi Bay Estuarine Lake for 2016 and 2022. S = salinity preference, M = marine, B = brackish and F = freshwater taxa according to Guiry and Guiry (2024) and WoRMS Editorial Board (2024)

Year	Species	S	Estuary	Lake 1	Lake 2	Lake 3	Lake 4
2016	*Amphora obtusaeformis* Cholnoky, 1961	B	0	**23.5**	**15.6**	1.0	0
	Amphora praelata Hendey 1973	M	0	**14.3**	0.4	0.2	0
	Cocconeis lineata Ehrenberg 1849	F	1.5	0	1.9	**32.3**	**72.9**
	Cocconeis scutellum Ehrenberg 1838	B/M	**10**	2.1	3.8	**10.7**	**16.1**
	Mastogloia halophila J.John 1981	F	1.4	3.6	**16.1**	0.8	0
	Planothidium engelbrechtii (Cholnoky) Round & Bukhtiyarova 1996	M	**27.8**	0.2	0.1	2.1	1.3
	Seminavis eulensteinii (Grunow) D.B.Danielidis, K.Ford & D.Kennett 2003	M	**10.8**	8.2	1.8	2.8	0
2022	*Amphora abludens* Simonsen 1960	M	**11.8**	0	0	0	0
	Amphora proteus W.Gregory 1857	M	6.8	2.8	**20.5**	2.5	0.1
	Cocconeis lineata Ehrenberg 1849	F	0.7	3.7	**22.0**	**22.3**	**70.7**
	Cocconeis scutellum Ehrenberg 1838	B/M	0.8	**13.1**	2.9	1.2	7.1
	Halamphora coffeiformis (C.Agardh) Mereschkowsky 1903	B	6.8	4.7	7.9	**12.0**	0.1
	Halamphora luciae (Cholnoky) Levkov 2009	B	**10.4**	**12.1**	**14.3**	**26.1**	0
	Melosira nummuloides C.Agardh 1824	M	0	**16.0**	0	1.9	0
	Melosira subsetosa Manguin 1957	M	1.2	**11.5**	0.2	0	0
	Navicula salinicola Hustedt 1939	F/B/M	4.2	0.1	0.8	**11.7**	0.5

diversity (range: 0.7 to 3.2 *H'*) and evenness (range: 0.2 to 0.9 *J'*) were above 2 and 0.5, respectively, for all sampling stations except for Lake 4. In the most distal Lake 4, benthic diatom community indices were lower in both 2016 ($H' = 0.9$; $J' = 0.3$) and 2022 ($H' = 1.3$; $J' = 0.4$) (Fig. 4).

A total of 159 taxa, belonging to 57 genera, were recorded in the Kosi Bay Estuarine Lake**.** The dominant species are listed in Table 5. The salinity preference of the dominant species differed between system compartments and followed the typical longitudinal salinity gradient by shifting from marine taxa (i.e., *Planothidium engelbrechtii* and *Amphora abludens*) proliferating in the estuary to the accumulation of freshwater taxa (i.e., *Cocconeis lineata*) in Lake 4 (Table 4). *Cocconeis lineata* was the only taxa identified as dominant (> 20%) in Lake 3 and Lake 4 for both years. Despite the difference in dominant species between years, 38% of the total number of diatom species identified were present in both years (Table 5A; Supplementary Material) representing 82% of the total relative abundance, while similarity between system compartments ranged between 9 and 70% (Table 6A; Supplementary Material). The indicator species analysis revealed 15 species (Table 7A; Supplementary Material) specific to the different system compartments ($P < 0.05$). Indicator species with the highest indicator value (IV ≥ 0.6) for 2016 include the freshwater taxa *Nitzschia palea* in the estuary, the marine taxa *Nitzschia prolongata* var. *hoehnkii* in Lake 1 and the marine taxa *Amphora robusta* in Lake 3. In 2022, the freshwater taxa *Nitzschia tonoensis* were identified in the estuary, the marine taxa *Caloneis liber* in Lake 1, the freshwater taxa *Cocconeis engelbrechtii* in Lake 3, and the freshwater taxa *Fragilaria delicatula* in Lake 4. No unique indicator taxa were identified for Lake 2.

Results from the diatom ecological classification indices revealed the presence of taxa with variable salinity tolerances ranging from brackish to freshwater throughout the system compartments for both years (Fig. 5a). Oxygen requirements ranged from high (> 100% saturation) to low (> 30% saturation) for both years (Fig. 5b). No taxa indicative of very low oxygen requirements (± 10% saturation) was recorded. The motile guild (> 45%) was higher throughout the system compartments in 2016. In 2022, the dominant guild composition fluctuated between system compartments (Fig. 5c). The most abundant (> 50%) guilds included the low-profile guild in the Estuary and Lake 2, the planktic guild in Lake 1, the motile guild in Lake 3, and the high-profile guild in Lake 4. System compartments in 2016 showed α-mesosaprobity with a higher presence of eutraphentic taxa (i.e., indicative of eutrophic conditions) that were either tolerant (class 2) to or continuously needed (class 4) elevated concentrations of organic nitrogen compounds (Fig. 6). In 2022, the Estuary and Lake 1 showed α-meso-/polysaprobity, Lake 2 showed β-mesosaprobity, and Lake 3 and Lake 4 showed α-mesosaprobity (Fig. 6a). The presence of eutraphentic taxa were higher in the Estuary, Lake 1, Lake 3, and Lake 4, while the presence of meso-eutraphentic taxa were higher in Lake 2 (Fig. 6b). Despite the variability in trophic state, most taxa appeared to be tolerant (class 2) to elevated concentrations of organic nitrogen compounds (Fig. 6c).

The NMDS displayed a significant overlap regarding the composition of the benthic diatom community in the Kosi Bay Estuarine Lake for 2016 and 2022 (Fig. 7). This was verified by the analysis of similarity (ANOSIM) which highlighted the similarity between system compartments but with minor differences (Global $R = 0.29$, $P < 0.001$) as Lake 4 separated from the Estuary, Lake 1, Lake 2, and Lake 3. The CCA model results ($F = 1.36$, $P < 0.001$) showed that the constrained components explained 39% of the total variation of the benthic diatom community structure (Fig. 7). The first four axes explained 22% of the cumulative variation of which three axes yielded a significant result ($P < 0.05$). Salinity, temperature (°C), DIP (mg L^{-1}), and SOC (%) were identified as the significant environmental variables ($P < 0.05$). *Amphora praelata*, *Plagiotropis lepidoptera,* and *Seminavis eulensteinii* were associated with the higher salinity characteristic of conditions recorded in the estuary to Lake 2. Lake 4 presented with an increased availability of SOC and DIP which favoured predominantly freshwater taxa (RA < 2%), namely *Nitzschia clausii*, *Stephanocyclus meneghinianus*, *Gomphonema parvulum*, *Gomphonema gracile,* and *Aulacoseira granulata*. *Cocconeis scutellum* was associated with higher water temperatures, while lower salinity was also favoured by *Cocconeis lineata* and *Hyalodiscus radiatus* (Fig. 7).

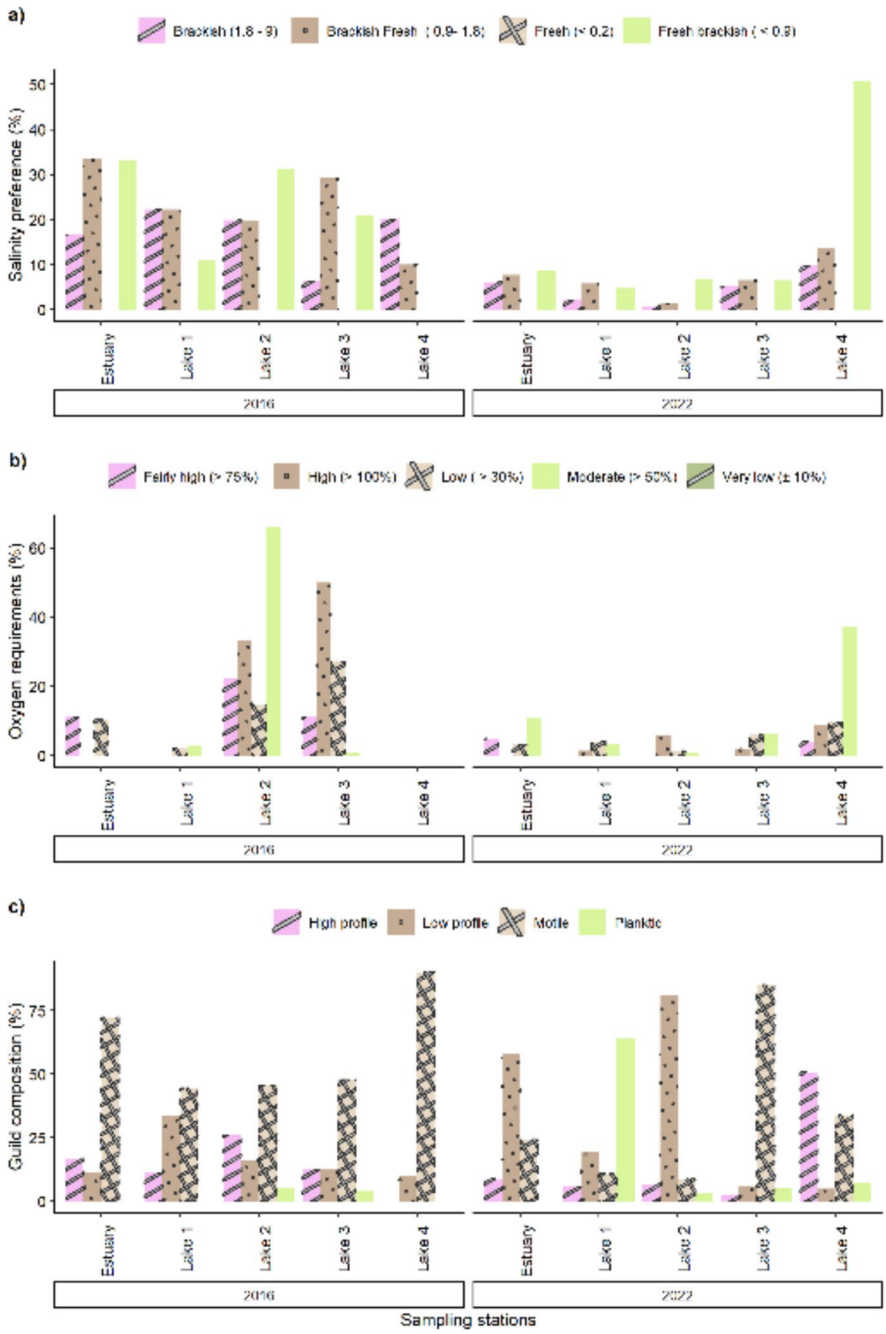

Fig. 5 The salinity preference ($n_{2016} = 18$; $n_{2022} = 29$), oxygen requirements ($n_{2016} = 13$; $n_{2022} = 19$), and the ecological guilds ($n_{2016} = 10$; $n_{2022} = 16$) of the benthic diatom assemblages recorded in the estuary and the four lakes of the Kosi Bay Estuarine Lake for 2016 and 2022

Discussion

Anthropogenic deterioration of water quality is a key threat to the structure and function of South African estuaries (Adams et al. 2020; Van Niekerk et al. 2019a, 2022b). However, the tropical estuaries are less impacted by nutrient pollution largely due to the absence of extensive catchment development (Adams et al. 2020). This was highlighted in this study where the extent of land-use modifications (i.e., commercial plantations, development and agriculture) in the Kosi Bay catchment (14%) and estuarine functional zone (0.1%) were minimal. Thus, nutrient concentrations recorded throughout

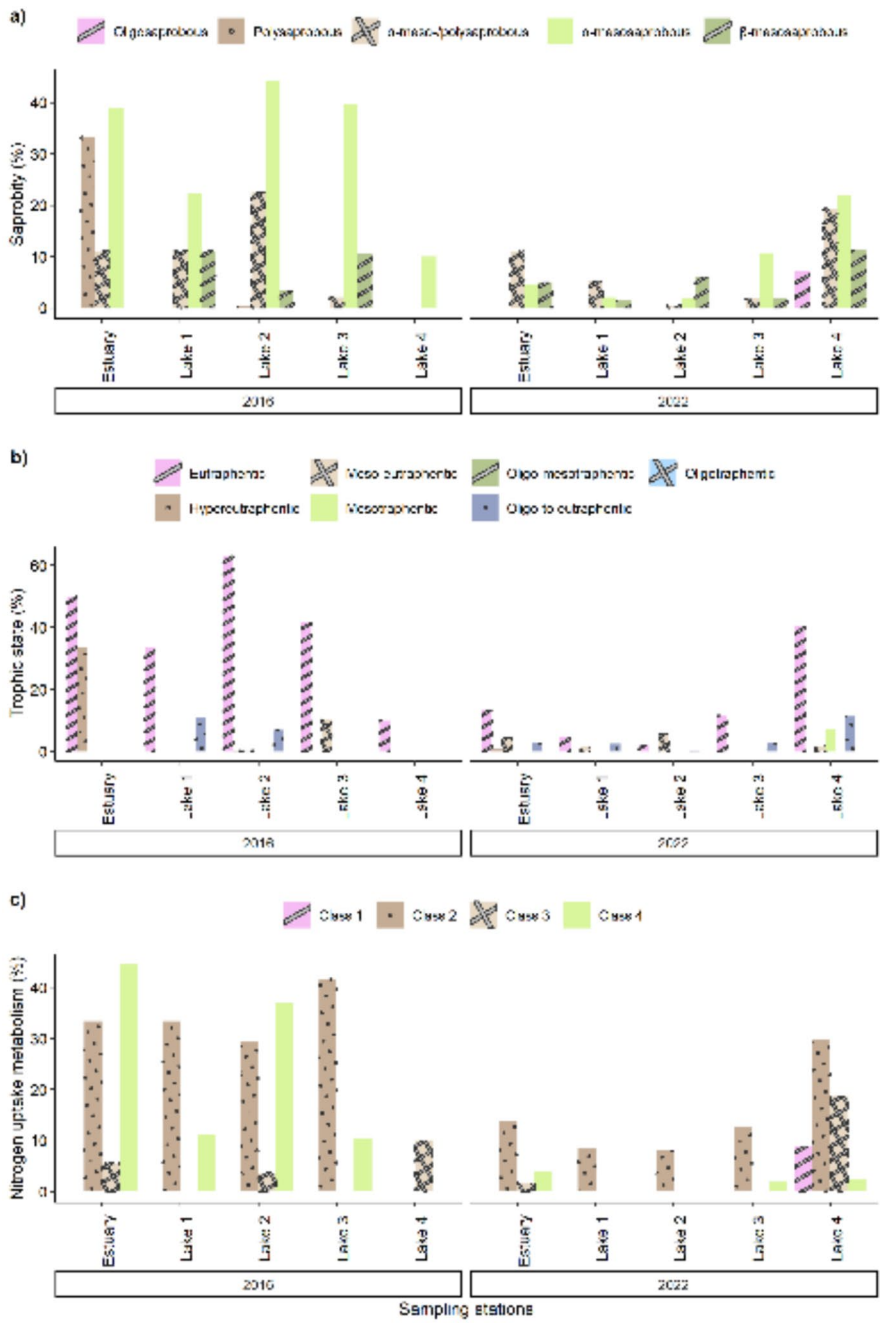

Fig. 6 The saprobity ($n_{2016} = 13$; $n_{2022} = 22$), trophic state ($n_{2016} = 14$; $n_{2022} = 24$), and the nitrogen uptake metabolism ($n_{2016} = 12$; $n_{2022} = 20$) of the benthic diatom assemblages recorded in the estuary and the four lakes of the Kosi Bay Estuarine Lake for 2016 and 2022. Organically bound nitrogen requirements include Class 1: nitrogen-autotrophic taxa, tolerating very small concentrations; Class 2: nitrogen-autotrophic taxa, tolerating elevated concentrations; Class 3: facultatively nitrogen-heterotrophic taxa, needing periodically elevated concentrations and Class 4: obligately nitrogen-heterotrophic taxa, needing continuously elevated concentrations (Van Dam et al., 1994)

the interconnected estuarine lake system were low (< 0.3 mg L^{-1}) and did not exceed the eutrophic thresholds (DIN > 1 mg L^{-1}; DIP > 0.1 mg L^{-1}, see Lemley et al. 2015). This is in contrast to the St Lucia Estuarine Lake, also situated within the iSimangaliso Wetland Park, that is subject to a high degree of anthropogenic pressures in the catchment that exacerbate the consequences (i.e., mouth closure, turbidity and eutrophication) of the natural climatic cycle (Whitfield and Taylor 2009; Chrystal and Scharler 2014; Nunes et al. 2017).

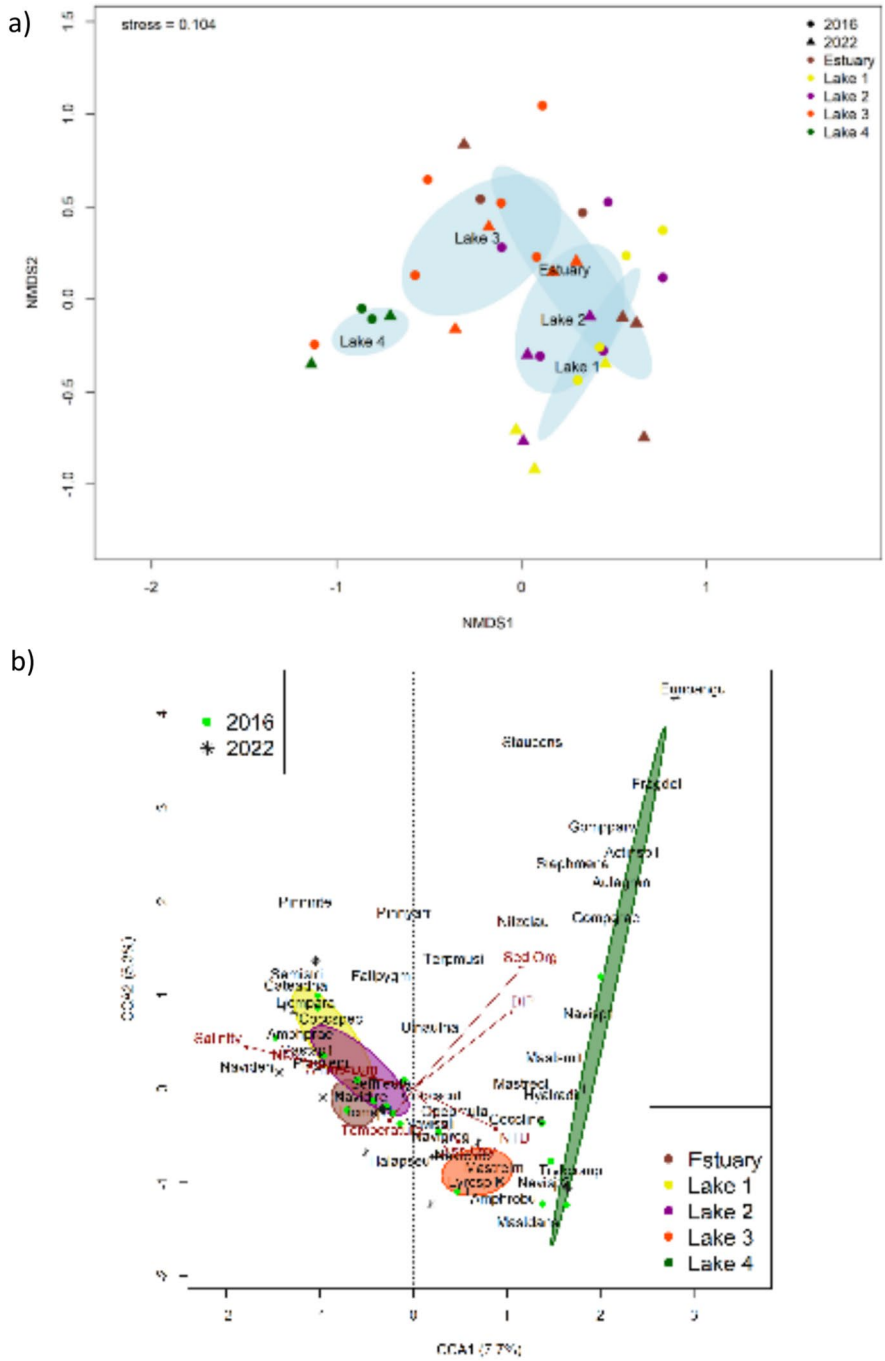

Fig. 7 A 2-dimensional non-metric multidimensional scaling (NMDS) plot using the Bray–Curtis similarity metric of the benthic diatom community recorded in the estuary and the four interconnected lakes of the Kosi Bay Estuarine Lake (**a**) and a canonical correspondence analysis plot (CCA) of the benthic diatom species which shows the most influential environmental variables affecting the species distribution in the estuary and the four interconnected lakes of the Kosi Bay Estuarine Lake (**b**). Ellipses represent the system compartments as specified in the bottom right corner. Benthic diatom species abbreviations are listed in Table 5A in the Supplementary Material

The influence of the abiotic variables on the benthic diatom community composition

In less-impacted, near-pristine estuaries the structure of benthic communities is shaped by natural variability (e.g., salinity, detritus inputs, and tidal variation) (Brauko et al. 2020). In this study, the benthic diatom assemblages in the near-pristine Kosi Bay Estuarine Lake responded to marked salinity and DIP gradients and therefore, the hypothesis was accepted. As visualised by NMDS ordination, the benthic diatom community present in the estuarine lake partly overlapped,

with the exception of distinct taxa unique to Lake 4 the most distal of the interconnected lakes. The highest MPB biomass and DIP concentrations (≥0.01 mg L^{-1}), as well as the lowest benthic diatom diversity ($H' \leq 1.3$), were consistently recorded in the oligohaline Lake 4. Soil erosion caused by human activities (e.g., agriculture, forestry) has been linked to phosphorus (P) enrichment originating from erosion and transport of P-amended soils and organic matter into water bodies (Ekholm and Lehtoranta 2012; Xiong et al. 2021). Results showed an inverse relationship between salinity and DIP suggesting allochthonous, river-borne delivery of P to the estuarine lake. Since P is naturally limiting in most aquatic ecosystems, an influx of P tends to support higher primary productivity (Correll 1999; Marshall and Montagna 2025).

As previously indicated, peak MPB biomass levels were recorded in Lake 4 in 2016 (441 mg Chl-*a* m^{-2}) and 2022 (90 mg Chl-*a* m^{-2}). Concentrations exceeding 100 mg Chl-*a* m^{-2} are typical of impacted or eutrophic systems (Lemley et al. 2015). However, the high-retention zones of estuarine lakes are ecologically unique (i.e., annual to decadal biophysical processes) and, thus, any system-wide inferences about ecosystem health should be made with caution. This is highlighted in Kosi Bay where the inorganic nutrient concentrations remain within the natural nutrient balance of the system (Van Niekerk et al. 2022c). Low ambient nutrient conditions are typical of oligotrophic estuaries, as nutrients are effectively recycled and retained within the sediment (Heip et al. 1995; Hope et al. 2020a). Many benthic species are believed to be facultative heterotrophs that consume organic matter in the sediment during heterotrophic growth (Patrick 1977; Virta et al. 2019). This was evidenced in the more organically-enriched sediments (1.1–3.7%) of the α-mesosaprobic Lake 4 where MPB biomass was positively association with sediment organic content and facultative heterotrophic diatom taxa (Class 3; genus *Cocconeis* spp.) were present. Lower MPB biomass (≤60 mg Chl-*a* m^{-2}) was consistently recorded in the tidally influenced Lake 1 and Lake 2, where the available sediment organic content was low (≤0.65%). Furthermore, the motile guild was recorded as the dominant functional group (>75%) in 2016 and the high-profile guild (>50%) in 2022. The high-profile guild favours habitats characterised by low current velocities (Passy 2007; Rimet and Bouchez 2012). Redzuan and Underwood (2021) reported the presence of high MPB biomass on an intertidal mudflat in the Colne Estuary, UK owing to reduced sediment and MPB resuspension. Resuspension of the fine sediments by wind-driven circulation has been shown to limit MPB biomass accumulation in the shallow northern lake basins of the nearby St Lucia estuarine system, with reported concentrations ranging between 0.6 and 9.8 mg m^{-2} (Perissinotto et al. 2013; Nunes et al. 2017). Calm conditions favour MPB development (Hope et al. 2020b). Thus, the nutritive value of the organic matter coupled with high-water residency facilitates MPB biomass accumulation in estuarine lakes.

Low species diversity ($H' \leq 1.3$) characterised Lake 4, while elevated diversity ($H' > 2$) was typically observed throughout the remainder of the tidally influenced lake compartments. This is similar to the St Lucia Estuarine Lake where benthic diatom diversity fluctuated between 0 and 2.7 H' due to inherent system dynamism such as variable salinity and circulation patterns (Bate and Smailes 2008; Perissinotto et al. 2013; Nunes et al. 2017). Intermediate levels of sediment disturbance enhance MPB composition and diversity (Connell 1978; Collins and Glenn 1997; Ribeiro et al. 2013). Moreover, sandier habitats promote a more diverse mix of epipelic and epipsammic diatoms, stemming from the constant resuspension of sediments that prevents any one taxon of becoming dominant (Rivera-Garcia et al. 2018; Weilhoefer et al. 2021). Motile epipelic taxa typically dominate stable mudflat communities, and these dense diatom biofilms tend to be more susceptible to interspecific competition and/or herbivory (Ribeiro et al. 2013). The CCA multivariate analysis indicated that a large part of the variation (61%) remained unexplained suggesting the possible influence of grazing pressure or competition for resources among species comprising benthic diatom assemblages (Resende et al. 2005). Interspecific competition has been found to lower diversity of mudflat diatom communities in the Loire Estuary, France, resulting in an inverse relationship between MPB biomass and diversity (Ribeiro et al. 2021).

The freshwater *Cocconeis lineata* ($RA_{2016} = 72.9\%$; $RA_{2022} = 70.7\%$) and brackish/marine *Cocconeis scutellum* ($RA_{2016} = 16.1\%$) dominated the benthic diatom community in Lake 4. Generally considered epiphytic (attached to macrophytes), *Cocconeis* spp. are effective competitors in tropical (>25 °C)

oligotrophic systems given their efficiency in incorporating limiting nitrogen resources (Round et al. 1990; De Nicola 1996). In the subtropical Mdlotane Estuary, South Africa, the dominance (RA = 50.7%) of *C. lineata* in subtidal habitats was associated with the presence of the submerged macrophyte species *Stuckenia pectinata* (L.) Böerner and *Ceratophyllum demersum* L. (Nunes et al. 2024). The presence of *C. scutellum* within the intertidal mudflat habitat of the Dourduff Estuary, France was found to originate from the epiphytic community on *Zostera marina* (Riaux-Gobin 1991). Notably, lower abundances of *C. lineata* (RA_{2016} = 32.3%; RA_{2022} = 22.3%) and *C. scutellum* (RA_{2016} = 10.7%) were recorded in the mesohaline Lake 3 where submerged macrophytes like *S. pectinata* and *C. demersum* also occur. Results from the Bray-Curits index (Tabe 6A, Supplementary material) revealed a similarity value of > 40% for these lake compartments between years. However, key differences between these lake compartments are the reduced depth and widespread abundance of emergent macrophytes (i.e., *Phragmites australis, Schoenoplectus scirpoides,* and *Typha capensis*) in the littoral zone characteristic of Lake 4. The common reed, *Phragmites australis* has been shown to support higher epiphyte biomass compared to submerged macrophytes (e.g., *Zostera capensis*) in tidal estuaries (Lemley et al. 2017; Van Niekerk et al. 2022a). Surface sediment often contains planktonic, epipelic, epipsammic, and epiphytic diatoms that are free-living in mudflat communities (Admiraal et al. 1984; Thomson and Manoylov 2019). Epiphytic algal growth on littoral macrophytes can contribute substantially to whole-ecosystem productivity in lakes (Vander Zaden and Vadeboncoeur 2020). As such, the increased availability of emergent macrophyte and submerged macrophyte (e.g., *C. dermersum*, *Najas horrida*, *Najas marina*, *Potamogeton sweinfurthii*) habitats explains the increased abundance of the epiphytic taxa, such as *C. lineata* and *C. scutellum*, in Lake 4.

Salinity was a strong driver shaping the benthic diatom community in the tidal and meso- to euhaline portions of the system. Regular and strong tidal movements through the open mouth extend from the lower estuary to Lake 2, shaping the longitudinal salinity regime in the estuarine lake (Van Niekerk et al. 2022a,b). Results from the salinity classification index showed that brackish and brackish-fresh taxa gradually decreased from the lower estuary to Lake 2 in 2016 (50 to 39.5%) and 2022 (13.8 to 2.1%). Marine species (e.g., *Amphora praelata*, *Amphora abludens*, *Melosira nummuloides*, *Melosira subsetosa*, *Planothidium engelbrechtii, Seminavis eulensteini*) were dominant (RA > 10%) in the lower estuary and Lake 1, while Lake 2 was characterised by brackish (e.g., *Amphora obtusaeformis*, *Halamphora lucia*) and freshwater (e.g., *Mastogloia halophila*) species. The gradual replacement of marine to freshwater diatom species along a longitudinal salinity gradient is generally driven by their salinity optima (Hassan et al. 2006).

Nutrient concentrations and current velocity are important factors structuring the composition and prevalence of diatom ecological guilds (Passy 2007; Liu et al. 2025). As such, seasonal variation in freshwater inflow and mixing processes likely drove the differences in ecological guilds between the sampling occasions, as the DIN and DIP concentrations were consistently low. Increased current velocity driven by summer rainfall may have favoured the proliferation of the motile guild in summer 2016 in the Kosi Bay Estuarine Lake (Van Niekerk et al. 2022a,e). This diatom guild typically consists of fast-moving species that are well-adapted to high flow (Passy 2007; Rimet and Bouchez 2012). However, in spring 2022 the guild diversity shifted to a dominance of the slow-moving low-profile guild in the Estuary and Lake 2, and the planktic guild in Lake 1. In the Kosi Bay Estuarine Lake, wind driven circulation is more pronounced in the lake system during the low-flow, cooler months (Van Niekerk et al. 2022a). Wind-generated wave action and current induced shear stresses cause sediment resuspension (Zikhali et al. 2015). The settling of phytoplankton cells increases with increased turbulence in lakes (Ruiz et al. 2004). Furthermore, the low-profile guild is typically associated with environments characterised by low nutrients and high disturbance stress (Passy 2007; Liu et al. 2025). Taxa that can withstand the abrasion and physical damage by moving between sand grains, such as the low-profile guild, are more likely to establish viable populations in disturbed habitats. These taxa usually consist of short stature diatoms with firm attachment such as the dominant genera recorded in this study (i.e., *Amphora*, *Halamphora*, *Mastogloia*, and *Seminavis*) that can attach to substrates (Round et al. 1990; Passy 2007).

Benthic diatom indicator values and indices

Taxa with the highest indicator value (IV ≥ 0.6) in the estuary were the freshwater species, *Nitzschia palea* and *Nitzschia tonoensis*. Planktonic algae in river systems mainly originate from benthic algae via detaching from substrates due to flow abrasion, self-detachment processes, and/or grazing by invertebrates, and tend to move passively to downstream habitats with water flow (Roeder 1977; Tekwani et al. 2013; Hu et al. 2022). According to Round et al. (1990), the genus *Nitzschia* is usually epipelic or planktonic while the study by Hu et al. (2022) showed *N. palea* became dominant in the planktonic community of the Jinsha River, China because it was unable to attach firmly to the substratum. The KuZilonde freshwater lake, that lies directly north of the Kosi Bay Estuarine Lake, and the semi-perennial KuKhalwe stream draining from the north-west are a direct source of freshwater to the lower estuary (Van Niekerk et al. 2022a). Directional flow affects planktonic diatoms by causing species living in favourable habitats ("source") to disperse to unfavourable environments ("sink") (Hu et al. 2022). Thus, it is probable that the freshwater species recorded in the Kosi Bay estuary originated from the KuKhalwe stream and KuZilonde freshwater lake.

Results from the trophic and saprobic indices indicated that the benthic diatom assemblages in the lower estuary, Lake 1, Lake 3, and Lake 4 were mesosaprobic with a high presence of eutraphentic taxa, signalling that these system compartments are possibly under threat of eutrophication. This is contradictory to the near-natural state of the Kosi Bay Estuarine Lake. It is important to note that these assumptions are based on a subsample (15%) of the total benthic diatom community, of which 75% of the incorporated taxa were exclusively freshwater species (Table 9A; Supplementary Material). Many benthic diatom indices have been developed based on the abundance, frequency, and autecology of species in both lentic and lotic freshwater ecosystems, thus limiting their application in estuaries (Rimet and Bouchez 2012; Rovira et al. 2012; Szczepocka et al. 2018). Rovira et al. (2012) reported the exclusion of several ecologically important brackish/marine species in most of the indices used in the Ebro Estuary and advocated for more research to be done before implementation in transitional waters. Species responses may differ between aquatic systems (Resende et al. 2005). For example, considered good indicators of high nutrient concentrations, *Navicula veneta* and *Gomphonema parvulum* were abundant at river sites characterised by low total phosphorus concentrations in the Northern Piedmont ecoregion, USA, while the presence of *Gomphonema* in different urban rivers in the Shanghai district, China was considered indicative of a macrophyte-dominated state following restoration efforts (Potapova et al. 2004; Chen et al. 2019). Similarly, in this study, *Gomphonema gracile* and *Gomphonema parvulum* were present in Lake 4 where emergent macrophytes dominate the littoral zone, while *N. veneta* was present under low nutrient conditions.

However, while it is evident that the perceived ecological status derived from these indices should be interpreted with caution, the appearance of nutrient tolerant taxa in a low-nutrient environment can serve as an early warning sign of declining water quality (Wachnicka et al., 2010; Desianti et al. 2019). DIP concentrations recorded in the Sihadla River and Lake KuZilonde (see Table 7A, supplementary material), two sources of freshwater input to the system, were indicative of mesotrophic conditions (DIP ≥ 0.01 mg L^{-1}; Lemley et al. 2015). A study by Bate et al. (2018) in the nearby Mgobezeleni Estuarine Lake showed high inorganic concentrations of N (2.94 mg l^{-1}) and P (0.06 mg L^{-1}) in groundwater feeding into the system. Despite low in-situ nutrient levels, the potential impact of these nutrient-enriched (e.g., sewage from informal residential developments) groundwater inflows were highlighted by cyanophyte blooms (*Aphanocapsa planctonica*) and nutrient tolerant diatom species (*Aulacoseira ambigua*) in the lake and estuary compartments, respectively (Kling 1998; Bate et al. 2018). Therefore, the close association between surface and groundwaters in the Kosi Bay Estuarine Lake infers an inherent vulnerability of the system to any potential catchment land-use modifications that increase nutrient loading (Van Niekerk et al. 2022a). This is particularly relevant given the presence of nutrient tolerant taxa (i.e., *Fallacia pygmaea*, *Navicula gregaria*, *Nitzschia frustulum,* and *Tabularia tabulata*) observed in 2016 and 2022 (Table 6A; Supplementary Material). Additionally, taxa indicative of organic enrichment and low oxygen conditions (> 30% saturation) were present

throughout the estuarine lake in both years (Van Dam et al., 1994; Barletta et al. 2019). Nutrient-enriched freshwater inflows from the agriculturally impacted uMfolozi River were shown to drive the dominance (RA ≥ 40%) of the nutrient tolerant taxa, *Cyclotella atomus* and *Diatoma vulgaris* in the St Lucia Estuarine Lake (Nunes et al. 2019). Therefore, it is essential that future research endeavours investigate the water quality of source inputs to determine if the presence of these nutrient tolerant taxa in the estuarine lake is a precursor to anthropogenic change or simply indicative of natural estuarine conditions (e.g., salinity gradient, remineralisation processes, directional dispersal) (Rovira et al. 2012; Brauko et al. 2020; Hu et al. 2022).

Future outlook

Water quality is considered a good predicator for future estuarine resilience since anthropogenic stressors (e.g., eutrophication, flow modifications) are expected to intensify under future climate scenarios (Van Niekerk et al. 2022a). In the case of the Kosi Bay Estuarine Lake, reduced water levels, warmer temperatures, more frequent mouth closure (i.e., reduced habitat complexity), and increased salinity have been predicted (Van Niekerk et al. 2022c). Under these circumstances, higher salinity is expected to change the dominant benthic diatom species based on their salinity optima, higher temperatures are likely to shift the proportions of algal growth forms towards large-sized, adnate, non-colonial, low-profile taxa, and a loss of habitat heterogeneity will reduce species richness (Mahoney and Bishop 2017; Virta and Hedberg 2024). However, irregular investigations of the diatom community composition make it challenging to elucidate temporal variations given the broad environmental tolerance of some taxa (Anderson 2000; Fontaine and Rynearson 2023). This study revealed temperature as an overall important driver of change, with *Cocconeis lineata* proliferating (RA > 10%) in summer 2016 (~ 27.4 °C) and *Halamphora coffeiformis* in spring 2022 (~ 25.3 °C). Yet, a study by Tuchman and Blinn (1979) that investigated the diatom community structure along a thermal gradient revealed the competitive advantage of taxa *C. lineata* at temperatures < 26 °C and *H. coffeiformis* at temperatures > 26 °C. The effects of temperature are unlikely to be independent of other factors and a short period covered by monitoring data impedes the interpretation of temperature as a controlling variable (Anderson 2000). Seasonal sampling is necessary to separate the response of taxa to anthropogenic versus natural stressors (Costa-Böddeker et al. 2017). Long-term studies (i.e., seasonal and annual) are necessary to develop an in-depth understanding of shifts in the benthic diatom community in response environmental change and the effects of climate change in the Kosi Bay Estuarine Lake.

Conclusion

This study investigated the abiotic drivers responsible for shaping the benthic diatom community in the Kosi Bay Estuarine Lake. Due to the near-natural condition of the system, the longitudinal salinity gradient, availability of DIP, sediment organic content, the dispersal of freshwater taxa downstream, and habitat characteristics (disturbance versus macrophyte-dominated state) were identified as being responsible for the observed differences in benthic diatom community metrics between the system compartments. Thus, the hypothesis that the benthic diatom community structure will be influenced by the interaction of multiple site-specific abiotic variables was accepted.

Diatoms are useful indicators of change. Benthic diatom community metrics, (i.e., abundance, biomass, diversity) are routinely used to assess estuarine health in South Africa (Lemley et al. 2015). This study provides an important baseline regarding the drivers of benthic diatom community dynamics in near-pristine estuarine lakes. Such information is critical for contextualising any potential ecosystem shifts that may occur in response to increased anthropogenic pressures on these unique ecosystem types. It is estimated that approximately 58% of estuarine lakes are currently subjected to water quality pressures derived from urban and/or agricultural developments (Van Niekerk et al. 2022a). Thus, conservation managers could consider using the Kosi Bay Estuarine Lake as a baseline to help inform and assess restoration efforts in severely modified systems.

Conflict of interest

The authors declare no competing interests.

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Data availability We did collect data in field and analysed these datasets and it can be made available on request.

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