Ecological networks reveal important taxa for ecosystem function in two subtropical South African estuaries

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ABSTRACT

Biodiversity is essential for estuarine ecosystems' functioning, resilience, and persistence. While biodiversity assessments provide some insight into the ecosystem state, they cannot quantify every aspect of ecosystem-level function. We assessed aspects of estuarine ecosystem function and pinpointed taxa of interest that fulfil specific roles in estuarine ecosystems, using a series of novel food web model ensembles and Ecological Network Analysis. We investigated emergent network properties of two subtropical South African estuaries, the anthropogenically impacted large temporarily closed uMdloti Estuary and the 'near natural' predominantly open uMlalazi Estuary, during a drought period induced by the El Niño Southern Oscillation. In addition, important network components were identified to elucidate the importance of estuarine/marine taxa in maintaining ecosystem function. The key findings included (1) estuaries exhibit system-specific functional responses under drought conditions, and (2) estuarine/marine taxa are critical for overall ecosystem function. Both estuaries showed seasonal differences in ecosystem activity and reliance on trophic level I (microalgae and detritus) to fuel the food web, and persistently low cycling (<9.3 %). However, compared to uMdloti Estuary, uMlalazi Estuary showed less variation in mean seasonal activity (1597–2095 mgC m^{-2} d^{-1}), and higher reliance on detritus to fuel the food web (D:H > 2.02), indicating greater ecosystem functional resilience to external perturbations. uMlalazi Estuary ecosystem function could be attributed to predominantly open mouth conditions maintaining a salinity gradient, and subsequent large contributions to overall ecosystem function from typically estuarine/marine invertebrate taxa. In contrast, the uMdloti Estuary, dominated by freshwater/brackish taxa under prolonged closed mouth conditions, showed greater seasonal variations in mean system activity (1084–2289 mgC m^{-2} d^{-1}) and generally high reliance on microalgae (D:H < 1.26), indicative of decreased resilience to external perturbations. During this study, a single mouth breach acted as a 'biological reset' of uMdloti Estuary, enabling recruitment of estuarine/marine taxa, and a temporary recovery in ecosystem function reflected in increased system cycling (FCI >14.05 %) and decreased reliance on microalgae (D:H > 1. 41). These findings suggest that future predicted drought impacts on estuarine ecosystem function may be partially system-specific due to differing estuarine types, anthropogenic impact, and invertebrate community composition. This study provides a scientific link between ecosystem-level indicators and the role of individual taxa within the system, which is a valuable complement to biodiversity assessments and ecosystem state evaluation.

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1. Introduction

The complexity and dynamic nature of ecosystems is especially exemplified in estuaries. Mixing riverine freshwater and saline marine water creates naturally variable environmental conditions (Adams and van Niekerk, 2020), supporting diverse habitats and unique biodiversity underpinning their ecosystem function (Elliott and Quintino, 2007). Since overall estuarine ecosystem productivity and function arise from ecological interactions (Ulanowicz, 1986), reductionist approaches (e.g., species diversity and abundance surveys) that do not consider the ecological interactions cannot assess whole-ecosystem function. Instead, a cornerstone approach of holistic ecosystem function assessment is to embed taxa interactions as flows of energy or material (e.g., trophic interactions and egestive flows) into static 'snapshot' food web network models. Thereafter, application of network analysis to the food web models allows one to quantify emergent ecosystem properties (e.g., system cycling) that emerge as a function of the interactions between ecosystem components, which otherwise cannot be estimated from examining them in isolation (Borrett and Lau, 2014; Fath et al., 2019; Ulanowicz, 1986). A series of 'snapshot' models, and their network analysis metrics, can provide insight into the fundamental functioning of the ecosystem over time or space, and can complement reductionist approaches focusing on specific species populations or communities (D'Alelio et al., 2016; Ludovisi and Jørgensen, 2009).

Holistic assessments of estuarine ecosystem function with food web models are gaining popularity in the local (Banerjee et al., 2017; Lechman, 2020; Mukherjee et al., 2015; Scharler, 2012) and international (Le Guen et al., 2019; Mukherjee et al., 2019; Tecchio et al., 2016) literature. However, they generally do not elucidate the taxa responsible for changes in ecosystem function. A comprehensive view of ecosystem-level functioning and the contributing role of individual taxa is essential from both biodiversity and management points of view, as ecosystem function cannot be directly managed, but arguably, the ecosystem components (e.g., taxa) are more tangibly manageable. Quantifying ecosystem function, together with identification of 'important' ecosystem compartments for overall ecosystem function (Borrett, 2013), can potentially provide complementary information to biodiversity surveys and add new knowledge to the system's state.

Estuaries are often heavily impacted by various anthropogenic activities and stressors (van Niekerk et al., 2020), with climate change possibly further compounding stress factors that affect estuarine ecosystem function and biodiversity (Chevillot et al., 2019; Day and Rybczyk, 2019). Shifts in natural rainfall patterns and water abstractions from catchments impact salinity gradients and estuarine mouth conditions (open, closed) (Adams and van Niekerk, 2020; Elliott et al., 2019) and, thus, the environmental conditions for estuarine biota. Drought, defined as extended periods of reduced rainfall and water scarcity (World Meteorological Organization, 1992), is a frequent occurrence in South Africa, with historical records indicating intense and extensive droughts lasting several years (Malherbe et al., 2016), and predicted increases in drought frequency and intensity for the region (IPCC, 2021). A holistic understanding of estuarine ecosystem-level function during drought is critical to understanding how these systems may function under future such occasions (Mahoney and Bishop, 2017; O'Brien et al., 2016).

A typically healthy estuarine environment provides different environmental niches for its species. For instance, typical zooplankton species in South African estuaries with a salinity gradient include *Pseudodiaptomus hessei* (Mrázek, 1894) or *Acartiella natalensis* (Connell and Grindley, 1974) as the dominant species (Deale et al., 2013; Hart, 1978; Jerling and Wooldridge, 1991) whereas typically, freshwater species such as many cladocerans are restricted to the upper reaches, and a few marine species (e.g., *Mesopodopsis africana* (Tattersall, 1952) are found near the estuarine inlet (Deale et al., 2013). During drought, the zooplankton diversity may shift to favour oligohaline or freshwater species (e.g. Cladocera) in low salinity conditions or favour marine taxa when the salinity gradient is restricted to higher salinities. Likewise there is a typical core group of sediment macrofauna in South African estuaries across the Crustacea and Polychaeta, of which some species are ubiquitous across salinity gradients and estuary types e.g. *Halmyrapseudes cooperi* (Brown, 1954), *Grandidierella lignorum* (Barnard, 1935), *Americorophium triaeonyx* (Stebbing, 1904), *Melita zeylanica* (Stebbing, 1904), *Iphinoe truncata* (Hale, 1953), *Ceratonereis (Composetia) keiskama* (Day, 1953) and *Dendronereis arborifera* (Peters, 1854; MacKay et al., 2010; Sheppard and MacKay, 2018; Teske and Wooldridge, 2004). During drought, elements of the estuarine core community may be retained or shift spatially, but overall diversity is depressed (Pillay and Perissinotto, 2013). Moreover, following the theory that disturbance (or high human pressures) favour invasions (Strayer, 2010) estuaries with lower health scores (van Niekerk et al., 2019) can become susceptible to non-native species invasions (Whitfield et al., 2021) (e.g., *Tarebia granifera* Lamarck, 1816) that are direct competitors for resources for native species (Miranda and Perissinotto, 2012; Tagliarolo and Scharler, 2018). In degraded or highly freshwater-influenced estuaries, the macrobenthos is typically dominated by Oligochaeta and Chironomidae (Scharler et al., 2020) and may include representatives of tolerant Polychaeta families, especially the Spionidae (Mackay and Cyrus, 2001).

Our taxon and ecosystem-level study was conducted in 2015/2016, during and just after Southern Africa experienced prolonged drought induced by a strong El Niño Southern Oscillation (ENSO), with the most severe below-average rainfall observed in 2015 (Ndlovu and Demlie, 2020). This was particularly serious for estuaries on the subtropical east coast of South Africa (Roffe et al., 2021; Scharler et al., 2023). These estuaries depend on the usually high mean annual rainfall (600–1200 mm) to maintain adequate freshwater flow volumes (van Niekerk et al., 2022). During the study period, the large temporarily closed uMdloti Estuary experienced prolonged states of mouth closure and subsequent shifts towards freshwater-dominated invertebrate communities (Scharler et al., 2020). In the same region, drought-induced decreased freshwater flow led to salinity gradient contraction (i.e., loss of oligohaline conditions) in the uMlalazi Estuary, a predominantly open estuary (PrOE), with potential implications for estuarine biota niche availability (Scharler et al., 2023).

Using food web models and Ecological Network Analysis (ENA), we aimed to quantify the ecosystem function of these two subtropical South African estuaries to better understand each system's functional capacity under drought conditions. We compared 1) seasonal emergent properties of system-specific ecosystem activity, cycling, and reliance on trophic level I (microalgae and detritus) to

fuel the food web and 2) identified ecosystem components to elucidate the importance of selected taxa on overall ecosystem function. We hypothesized that the two estuarine ecosystems show different system-level responses under drought conditions given their prevailing mouth status and associated invertebrate communities.

2. Methods

2.1. Case study sites

The subtropical east coastal zone of South Africa, influenced by the warm Agulhas Current, experiences an austral subtropical climate regime, characterized by warm summers with higher rainfall (i.e., wetter conditions) and cool winters with decreased rainfall (i.e., drier conditions) (Walker, 1990). Estuaries, therefore, typically receive larger volumes of freshwater during summer compared to winter. uMdloti Estuary (29° 39′ 2.1348″ S, 31° 7.' 44.9328″ E) is a perched, large, temporarily closed estuary (LTCE) (van Niekerk et al., 2020), approximately 25 km north of Durban (Fig. 1). The estuary (0.58–1.4 km²) (Forbes and Demetriades, 2008; van Niekerk et al., 2019) has a catchment area of 486 km² (DWA, 2013) with variable water depth (0.5 m to > 2 m) between open and closed mouth conditions (Scharler et al., 2023). uMdloti Estuary has a category 'D' Present Ecological State (PES) rating, describing the system as 'heavily modified' due to wastewater (WW) pollution and freshwater flow modification, among others (van Niekerk et al., 2019). Before and during the study, uMdloti Estuary experienced prolonged mouth closure (July 2014–June 2016), except for a single mouth breach event in one dry season (July 2015) (Scharler et al., 2020). uMlalazi Estuary (28° 56′ 40.995″ S, 31° 49′ 22.8971″ E) is a predominantly open estuary (PrOE) (van Niekerk et al., 2020) near Richards Bay (Fig. 1). The relatively larger estuary (4.69 km²) (van Niekerk et al., 2019) has an estimated catchment area of 420–570 km² (DWS, 2015) and a category 'B' PES, describing a 'largely natural' system state (van Niekerk et al., 2019), with a large area of the estuary located within uMlalazi Nature Reserve, a biodiversity conservation priority area (DWS, 2015). uMlalazi Estuary experienced open mouth conditions and a constant sea connection for the months selected for this study.

2.2. Food web model construction and parameterization

To capture seasonal ecosystem function via food web processes during the drought, we constructed a series of six food web models per estuary using existing network construction guidelines (for details see Fath et al., 2007; Scharler and Borrett, 2021). In brief, a food web model is a network map of several *compartments* (i.e., who is in the system), and numerous *flows* or *links* between the compartments, within a spatially delineated ecosystem. Each flow represents one of: consumption (who eats who), egestion (unused energy flows to detritus sinks), respiration (by-product of metabolism), and import and export flows across the system boundary (e.g., immigration, emigration). Once the network model topography is defined (number of compartments and flows between them), the model can be parameterized with empirically or ecologically valid weights, such that each compartment is given a biomass (how much of each compartment there is), and each flow a rate (how much energy moves along each flow).

2.2.1. Data availability

We defined food web models for months typically representative of the drier season (June, August, September 2015)[1] and the wetter season (December 2015, January 2016, February 2016). We used empirical data and secondary sources (as recommended by Scharler and Borrett, 2021) to construct food web models representing lower trophic levels (microalgae, detritus, bacteria, small invertebrates). Monthly *in situ* data were available for three sites in the uMdloti Estuary and four in the uMlalazi Estuary for 2014–2016 (Tables A1–A2) (Scharler et al., 2020). Collected data included microalgae chlorophyll-*a* concentrations (microphytobenthos and phytoplankton), invertebrate abundance surveys (meiofauna, macrozoobenthos, zooplankton), and concentrations of total suspended solids (TSS), and sediment organic matter (SOM). We averaged the data across all sites for each monthly model. In addition (detailed below), we consulted several open-source databases and various unpublished and published literature for carbon conversions, diet and unassimilated energy flow information and proportions, and rates of metabolic parameters and flows. We excluded birds, fish, and larger carnivores (e.g., crocodiles in the uMlalazi Estuary) due to a lack of data from the same time period, and/or temporal resolution. However, for each invertebrate compartment, we account for the potential predation by birds, fish, and larger carnivores by defining an 'Export' compartment for each invertebrate (see Section 2.2.2). To ensure model reproducibility (Scharler and Borrett, 2021), we report and reference all model data in this manuscript and Appendix A.

2.2.2. A priori models and parameters

For each food web model, we defined the model topography (i.e., internal compartments, internal and boundary flows) and then parameterized each with equalities and inequalities within ecologically derived ranges from *in situ* data, published and unpublished data, and open-source databases. We constrained each compartment's biomass with an equality to delineate stock quantity. We incorporated ecological flow variability into each model by constraining the magnitude of defined flows with inequalities to reflect the lower and upper empirical data ranges. We calculated all parameters to a thermodynamically conserved model currency (Fath et al., 2007), expressing compartment biomasses in mgC m⁻², and flows in mgC m⁻² d⁻¹.

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[1] Due to a lack of empirical datasets, we did not define a July 2015 food web model.
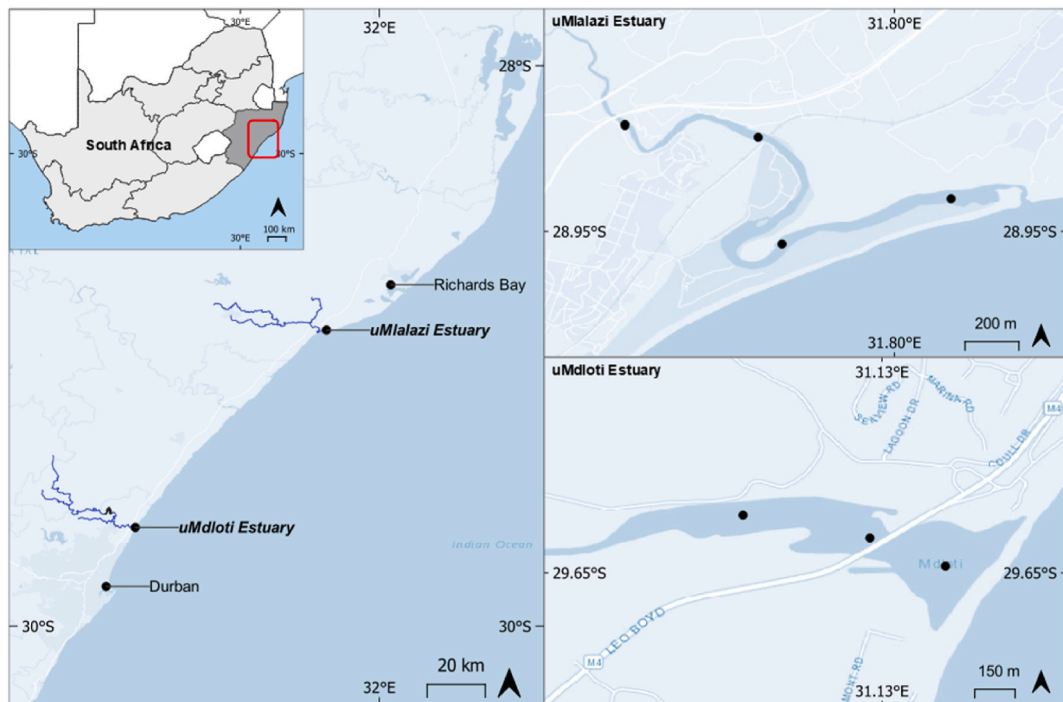
Fig. 1. uMdloti and uMlalazi estuaries in KwaZulu-Natal, on the east coast of South Africa, and proximity to major cities. Data from sample sites (●) within each estuary (lower, middle, and upper reaches) were used to construct networks for this study.

For primary-producing microalgae (phytoplankton and microphytobenthos), we calculated biomass from *in situ* chlorophyll-*a* concentrations and carbon regression conversions (Sathyendranath et al., 2009) (Table A3). For detrital compartments, we calculated suspended particulate organic carbon (susPOC) biomass from *in situ* TSS concentrations, local carbon estimates (Ortega-Cisneros and Scharler, 2015), and estuary depth (Table A3), and sedimented particulate organic carbon (sedPOC) biomass from *in situ* SOM, sediment bulk density (Hay and Flemming, 1984), sediment core sample depth, and local carbon estimates (Ortega-Cisneros and Scharler, 2015) (Table A3). We parameterized the bacteria compartment with *n situ* biomass and respiration estimates (Reddy, 2017) and standardized to the model currency. For consumers, we estimated biomass using *in situ* abundances and taxa-specific individual body masses derived from laboratory measurements, local studies, and general carbon conversion factors (Tables A4–A5).

We defined internal (i.e., within the system boundary) directed energy flows into and out of each living compartment as diet flows ('who eats who') and flows to detrital compartments as unassimilated energy (U) consisting of egestive and natural mortality flows. Diet and U flow information were estimated from local stable isotope analysis, published literature, and databases (Tables A6–A7). We assumed pelagic compartment U flows entered the susPOC compartment, and benthic compartments U flows entered the sedPOC compartment. For benthopelagic compartments, we assumed U flows to enter both susPOC and sedPOC compartments (de la Vega et al., 2018) without specified proportion. We constrained total consumption (Q), the sum of all diet inflows into a compartment (Tecchio et al., 2016), and total (U), the sum of all egestive and mortality flows, with inequalities calculated from allometric equations and conversions (Table A3).

We defined input boundary flows as carbon gain into the system via material imports (IM) to susPOC and phytoplankton (through riverine input) and Gross Primary Production (GPP), defining carbon import from an external CO_2 sink to microalgae via photosynthesis (Tecchio et al., 2016). We constrained GPP with inequalities estimated from compartment biomass, potential growth rates (Tirok and Scharler, 2014), and mean daily sunlight hours (Table A3). We defined export boundary flows as the carbon loss from the system (Scharler and Borrett, 2021) via material exports (EX) and respiration (R) from each compartment. We defined EX flows to account for boundary losses via emigration and potential undocumented carbon loss e.g., predation by fish, birds, and larger carnivores (Le Guen et al., 2019), but did not constrain them due to a lack of reliable data. We defined R as the carbon loss from living compartments to an external CO_2 sink (Le Guen et al., 2019; Tecchio et al., 2016). We constrained microalgae R flows with inequalities estimated from compartmental biomass, potential basal and activity-dependent respiration rates (Baretta et al., 1995; Geider, 1992; Tirok and Scharler, 2014), and consumer R flows with taxon-specific R/B ratios (Brey, 2001, 2010) (Table A3).

For all consumer compartments, we defined outflow Production (P) as the carbon available for predation by other living compartments (Tecchio et al., 2016). We constrained P with inequalities derived from allometry (Huntley and Lopez, 1992) and taxon-specific P/B ratios (Brey, 2001, 2012) (Table A3). For microalgae, we defined Net Primary Production (NPP) instead of P, indicating the energy produced by primary producers available for consumption by trophic level II herbivores.

We defined mass balance equations for each internal compartment as the sum of compartmental inputs equal to the sum of outputs

and a zero net gain in biomass (Fath et al., 2007; Scharler and Borrett, 2021). For living consumer compartments, the mass balance was defined as $= P + R + U + EX$, and for primary producers, $IM + GPP = NPP + R + U + EX$ (Table A8).

2.2.3. Aggregation

Before aggregating multiple taxa to reduce model complexity into a manageable size for interpretation (Johnson et al., 2009), for each food web model, we considered differences in body sizes and metabolic rates by first calculating all taxon−specific parameters within each invertebrate community. Thereafter, we aggregated taxa across communities into compartments based on biomass and abundances (e.g., (Saint-Béat et al., 2020), functional feeding (Du et al., 2020; van der Heijden et al., 2020), or taxonomic classification (Robson et al., 2018). We kept the microalgae compartments (phytoplankton and microphytobenthos) and detrital compartments (susPOC and sedPOC) disaggregated to account for invertebrate diet niche partitioning (Allesina et al., 2005; Johnson et al., 2009; Saint-Béat et al., 2020). The final list of aggregated compartments and biomasses are summarized in Table A9. We provide an example of final visualized model structure in Fig. 2 and summarize the final aggregated compartments and biomasses in the Appendices (Table A9 and Figures C1–C12).
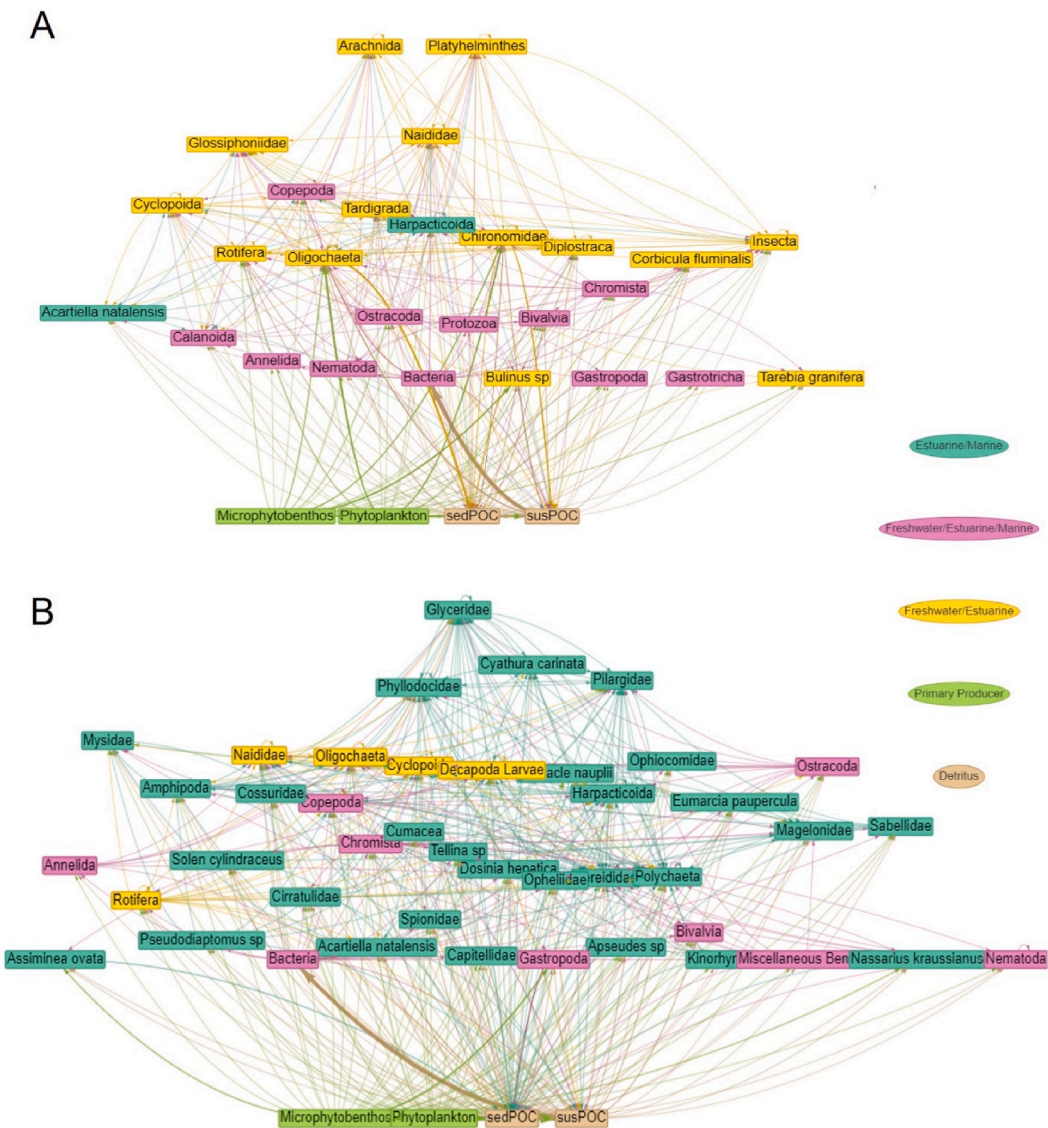

Fig. 2. (A) uMdloti Estuary and (B) uMlalazi Estuary June 2015 food web model structure, showing internal compartments and the energy flows between them. Boundary flows of gross primary production, respiration, imports, and exports are omitted for figure clarity. All twelve food web models used in this study are visualized in Appendix C.

2.3. Flow uncertainty analysis

Before ENA, we quantified each food web flow within mass-balance assumptions, where compartmental *inflows = outflows* (Fath et al., 2007; Scharler and Borrett, 2021), using Linear Inverse Modelling and Markov Chain Monte Carlo (LIM-MCMC) techniques (van Oevelen et al., 2010). The LIM-MCMC approach describes food web models as a mathematical function of the flows, allowing the specification of equality and inequality constraints on flow values to reflect uncertainty in empirical measurements.

To use LIM−MCMC, we coded all twelve food web models into individual 'LIM Declaration Files' using the function `autoGen` in R package **autoLIMR v3.0.1** (Gerber et al., 2023). The LIM declaration file content is summarized in Table 1, and the complete files are available online (https://github.com/gemmagerber/uMlalazi-Estuary-LIM and https://github.com/gemmagerber/uMdloti-Estuary-LIM). Next, we solved ensembles of plausible food webs (n = 10,000) for each model with the LIM-MCMC function `multi_net` (Gerber et al., 2023), using arguments of the default Least Squares with Equalities and Inequalities starting solution (Haskell and Hanson, 1981), and a jump size (distance between samples) of 0.05 mgC m^{-2} d^{-1}.

The selected sample size (n = 10,000) was based on previous considerations that such a sample size adequately captures input data variability (Bentley et al., 2019; Olli et al., 2019; Zhang et al., 2022). We selected the jump size based on preliminary assessments of analyzing food web ensembles solved with the LIM-MCMC algorithm of different jump sizes (0.001, 0.01, 0.05, 0.5 mgC m^{-2} d^{-1}) with *post hoc* MCMC convergence diagnostics (Gerber et al., 2023). This approach justified a 0.5 mgC m^{-2} d^{-1} jump size as it incorporated more data variability into the food web ensembles.

2.4. Ecological Network Analysis

For each solved plausible food web (n = 10,000 per month), we calculated ENA indicators using functions enaAscendency and enaFlow in R package **enaR v3.0.0** (Lau et al., 2017), returning 10,000 values of each indicator per month. We selected three macro-scale network indicators related to trophic level I to describe overall ecosystem function (Table 2), which are interrelated and recommended for policy inclusion (de Jonge and Schückel, 2021; Fath et al., 2019; Safi et al., 2019).

Total System Throughflow (TST$_{flow}$) is the sum of compartmental inputs or outputs (i.e., compartmental throughflow T_i, Table 2) under mass balance assumptions excluding boundary flows (de Jonge and Schückel, 2021; Fath et al., 2019) and characterizes system size and activity (Patten, 1995). TST$_{flow}$ is related to trophic level I as primary producers and detritus are often dominant compartments contributing to ecosystem TST$_{flow}$ (Borrett, 2013). Given the greater total biomass stocks in the uMlalazi Estuary, we expected a larger TST$_{flow}$ in the uMlalazi Estuary than in the uMdloti Estuary.

The Finn Cycling Index (FCI, %) measures the system's cycled TST$_{flow}$ fraction (Finn, 1976, 1980). It is calculated by weighing the total system activity (TST$_{flow}$) by the sum of the compartments cycling (C_i, Table 2), or total system cycling (TST$_c$), and characterizes the degree of carbon cycling within the system. It is related to trophic level I because detritus consumption (by trophic level II consumers) cycles energy/material back into the system. Given the higher detritus stocks, we expected more system cycling in the uMlalazi Estuary than in uMdloti Estuary.

The Detritivory: Herbivory ratio (D:H) quantifies the relative importance of trophic level I (primary producers or detritus) transfers of energy to trophic level II (detritivores and herbivores) in a food web (Ulanowicz and Kay, 1991). Trophic level II consumers rely on two feeding modes: 1) consumption of non-living detritus (detritivory) and 2) consumption of living primary producers (herbivory). We expected that D:H would (1) be larger in uMlalazi Estuary, given higher detritus stocks than in uMdloti Estuary, and (2) decrease during the wet season due to increased microalgae biomass and availability as a food source for herbivores.

Table 1

Monthly food web model LIM declaration file input of uMdloti and uMlalazi estuaries for the seasonal time series, consisting of internal living (primary producers, consumers) and non−living (detritus) compartments; external compartments (CO$_2$ sink, import and export compartment); internal (diet and egestive/mortality) and boundary flows between external and internal compartments (respiration, material imports, material exports); mass−balance equalities; and inequalities constraining the flows. Months are formatted as 'MMM YYYY".

Estuary	Month	Number of Compartments			Number of Externals	Number of Flows			Number of Constraints	
		Living	Non−Living	Total		Internal	Boundary	Total	Equalities	Inequalities
uMdloti	Jun 2015	29	2	31	34	300	64	364	29	159
	Aug 2015	22	2	24	27	210	50	260	22	119
	Sep 2015	30	2	32	35	339	66	405	30	192
	Dec 2015	27	2	29	32	308	60	368	27	170
	Jan 2016	31	2	33	36	362	68	430	31	194
	Feb 2016	29	2	31	35	307	65	372	29	180
uMlalazi	Jun 2015	45	2	47	50	465	96	561	45	315
	Aug 2015	42	2	44	47	531	90	621	42	240
	Sep 2015	37	2	39	42	425	80	505	37	219
	Dec 2015	24	2	26	29	203	54	257	24	192
	Jan 2016	33	2	35	38	333	72	405	33	200
	Feb 2016	43	2	45	48	467	92	559	43	267

Table 2
Summary of ecological indicators characterizing ecosystem function tied to trophic level I calculated with Ecological Network Analysis (ENA).

Indicator	Formula	Units	Reference
Total System Throughflow (TST$_{flow}$)	$TST_{flow} = \sum_{i=1}^{n} T_i$, where $T_i^{in} = z_i + \sum_{j=1}^{n} f_{ji}$; $T_i^{out} = y_i + \sum_{j=1}^{n} f_{ij}$ At steady state, $T_i^{in} = T_i^{out} = T_i$	mgC m^{-2} d^{-1}	Patten (1995)
Finn Cycling Index (FCI)	$FCI = \dfrac{TST_{Ci}}{TST_{flow}} *100$ Where the cycled flow of compartment i is: $C_i = \left(\dfrac{n_{ii}-1}{n_{ii}}\right) T_i$ And total system cycling is: $TST_C = \sum_{i=1}^{n} C_i$	%	(Finn, 1976, 1980)
Detritivory: Herbivory ratio (D:H)	$DH = \dfrac{\sum Detritivory}{\sum Herbivory}$	None	Ulanowicz and Kay (1991)

2.5. Statistical analyses

Given the large monthly sample sizes (n = 10,000) and non−independency of samples (Niquil et al., 2020), we used the non-parametric effect size measure Cliff's Delta (δ) (Cliff, 1993) to statistically compare ecological indicators between months and seasons for both estuaries following previous approaches (Meddeb et al., 2019; Nogues et al., 2021). We used the function cliff.delta in R package **effsize v3.4.3** (Torchiano, 2020) to calculate Cliff's δ magnitudes. We considered statistically significant differences between groups if there was a 'medium' ($0.33 \geq |\delta| < 0.474$) or 'large' ($|\delta| \geq 0.474$) overlap between groups (Nogues et al., 2021; Tecchio et al., 2016). As Cliff's δ does not compare mean and standard deviations, we display results with box and density plots (Fig. 3) and report mean ± SD within the text to aid interpretation.

2.6. Compartment contributions to ecosystem function

We used a node-focused approach (Borrett, 2013) to determine the relative importance of individual food web compartments for monthly ecosystem activity (characterized by TST$_{flow}$) and cycling (characterized by FCI). We calculated monthly compartmental
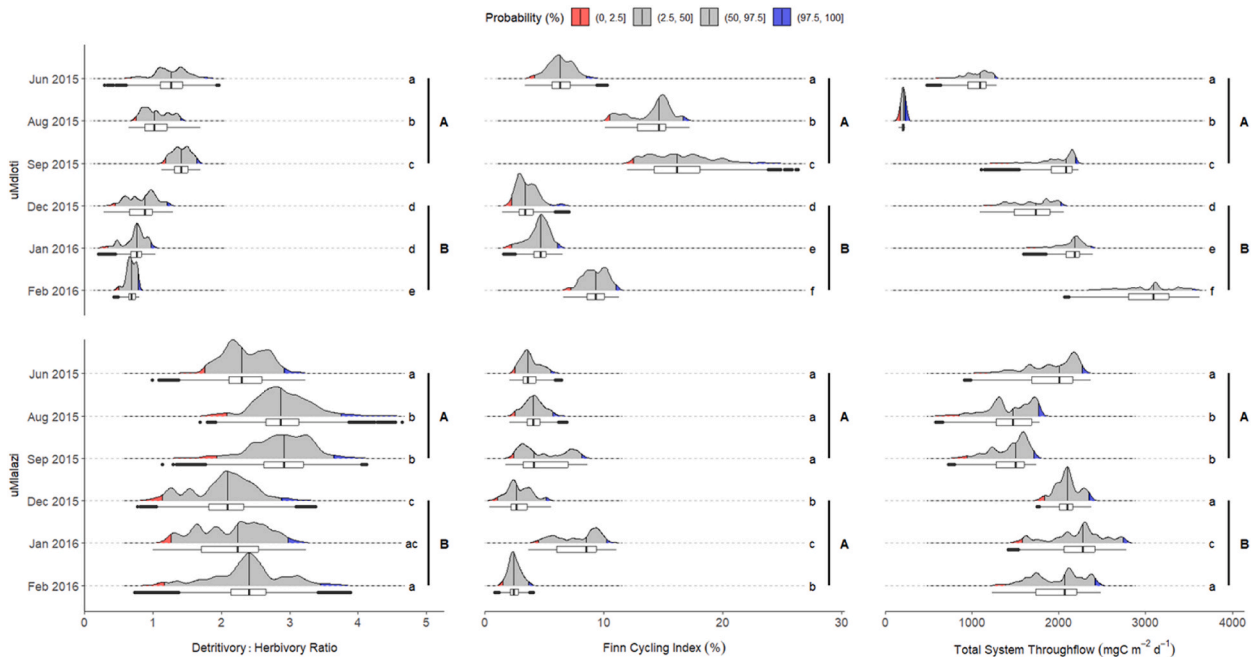

Fig. 3. Temporal variation of uMdloti and uMlalazi Estuary ecosystem function characterized by select ecological indicators (n = 10,000). The y-axes are standardized between months and estuaries. Density distributions show 95 % confidence intervals in grey, with lower (2.5 %) and upper (97.5 %) tails highlighted in red and blue. As a visualization alternative, box plots represent the median as the line inside the box, 25th and 75th percentiles by lower and upper box boundaries, ±1.5 * IQR (Interquartile Range) by error lines, and outliers by filled circles. Statistically significant differences (|Cliff δ| > 0.33) between months denoted by lowercase letters and between seasons with uppercase letters.

throughflow (mgC m^{-2} d^{-1}) using function enaFlow from **enaR** (Lau et al., 2017) and divided each by TST$_{flow}$ to determine relative compartment contributions to ecosystem activity (T$_i$, %). We calculated monthly compartmental cycling (mgC m^{-2} d^{-1}) using a custom function (Appendix B). We divided each by Total System Cycling (TST$_c$) to determine the relative compartment contributions to overall ecosystem cycling (C$_i$, %). We only report on consumer compartments for compartment cycling, as the carbon they consume originates within the system.

3. Results

3.1. Reliance on trophic level I (primary producers and detritus)

Compared to the uMdloti Estuary, the uMlalazi ecosystem generally relied more on detritus than on microalgae (phytoplankton and microphytobenthos) to fuel the food web (mean monthly D:H ratios 2.03–2.90; Fig. 3). Both uMdloti and uMlalazi Estuaries showed significant seasonal differences in reliance on microalgae, with higher reliance on detritus during the drier season (1.2 ± 0.3 and 2.70 ± 0.47, respectively) and on microalgae during the wetter season (0.8 ± 0.2 and 2.19 ± 0.51, respectively, Fig. 3). In uMdloti Estuary, the relatively larger D:H in the drier season can be attributed to increases in D:H after the July 2015 mouth breach in August 2015 (1.0 ± 0.2) and September 2015 (1.4 ± 0.1), suggesting that D:H may be influenced by mouth status rather than seasonality.

3.2. Ecosystem activity

uMlalazi Estuary had generally higher system activity, characterized by Total System Throughflow (TST$_{flow}$; mgC m^{-2} d^{-1}) than uMdloti Estuary (Fig. 3). Both estuaries showed significantly increased ecosystem activity during the wetter season (uMdloti Estuary = 2288.9 ± 602.1; uMlalazi Estuary = 2094.7 ± 277.4) compared to the drier season (uMdloti Estuary = 1083.9 ± 747.8; uMlalazi Estuary = 1597.2 ± 344.0).

In both estuaries, ecosystem activity was primarily driven by large compartmental throughflow contributions (T$_i$, %) from microalgae (phytoplankton and microphytobenthos), detrital compartments (susPOC and sedPOC), and bacteria (Figs. 4 and 6). The uMdloti Estuary had a relatively low number of taxa, and core taxa represented in many regional estuaries were few to absent. Changes in taxa composition and biomass were rapid between sampling events, particularly after the mouth breach (Fig. 4). Generally, there were more freshwater/estuarine consumer taxa with larger contributions to TST$_{flow}$ than estuarine/marine taxa, most notably freshwater/estuarine Oligochaeta and Chironomidae. Before the breach, the largest contributors to TST$_{flow}$ were microalgae, detritus, bacteria, and freshwater/estuarine taxa (Fig. 4). Immediately after the mouth breach in August 2015, the significantly low TST$_{flow}$ (207.2 ± 16.6) was attributed to decreased throughflow of all compartments (Figure C15) and concomitant loss of several freshwater/estuarine taxa, including Bivalvia, Diplostraca, and Naididae (Fig. 4). Simultaneously, we noticed small contributions to TST$_{flow}$ from

Fig. 4. Mean monthly compartmental contribution to Total System Throughflow (TST$_{flow}$) (%) in the uMdloti Estuary ecosystem in the drier (June, August, September 2015) and wetter (December 2015, January, February 2016) seasons (n = 10,000). Error bars indicate ±1 SD. Monthly TST$_{flow}$ (mgC m^{-2} d^{-1}) is depicted in Fig. 3, and compartment throughflow (mgC m^{-2} d^{-1}) in Appendix C Figure C15.

previously absent estuarine/marine Sabellidae (0.25 ± 0.04 %), and other polychaetes (1.70 ± 0.29 %). In the following month, September 2015, TST_{flow} significantly increased, with increased contributions from re-established freshwater/estuarine Bivalvia, Naididae, and Diplostraca, and estuarine/marine calanoid copepod *Pseudodiaptomus* sp. (Herrick, 1884), polychaetes Sabellidae and Nereididae, and the bivalve *Brachidontes virgiliae* (Barnard, 1964) (Fig. 4). During the wetter season (December 2015, January 2016, February 2016) under closed mouth conditions, there were increased contributions to TST_{flow} from phytoplankton (14.98–24.42 %), microphytobenthos (17.25–19.23 %), and again of other freshwater/estuarine taxa, notably Oligochaeta, Chironomidae, Rotifera, and the invasive gastropod *Tarebia granifera* (Lamarck, 1816) (Fig. 4). Throughout the wetter season, contributions to TST_{flow} from estuarine/marine taxa decreased again, with some disappearing entirely, notably Sabellidae and Calanoida.

In contrast to uMdloti Estuary, there were a larger number of estuarine/marine taxa in uMlalazi Estuary, which contributed more to TST_{flow} than freshwater/estuarine taxa (Fig. 6). The increased system activity during the wetter season could be attributed to increased contributions from phytoplankton (15.57–30.41 %), microphytobenthos (16.99–18.36 %), and detrital compartments susPOC (15.32–17.88 %) and sedPOC (7.25–11.34 %) (Fig. 5). In addition, there were seasonal shifts in the T_i of dominant estuarine/marine taxa, best illustrated by the increased T_i of the bivalve *Eumarcia paupercula* (Holten, 1802) during the drier season (2.20–4.03 %) and decrease in the wetter season (0.36–1.74 %). The opposite trend was exhibited by the bivalve *Assiminea ovata* (Krauss, 1848), which showed higher T_i in the wetter season (2.04–4.40 %) than in the drier season (0–2.18 %).

3.3. Ecosystem cycling

Under drought conditions, both uMdloti and uMlalazi estuaries cycled small fractions of total energy (monthly mean Finn Cycling Index FCI <9.28 %), except for a significant increase in cycling in uMdloti Estuary in the months after the breach (14.05–16.42 %; Fig. 3). Throughout the study period, the largest compartment contributions (C_i, %) to total system cycling (TST_c, Table 2) in uMdloti Estuary were generally from freshwater/estuarine compartments Oligochaeta and Chironomidae, and bacteria (Fig. 6).

In uMdloti Estuary, the significantly higher cycling during the drier season (12.3 ± 4.7 %) than the wetter season (5.8 ± 2.7 %) may be related to the breach event. In August 2015 (one month after the mouth breach), there was significantly increased system-level cycling, but overall decreased compartment cycling (mgC m^{-2} d^{-1}) of dominant compartments and the loss of some freshwater/ estuarine taxa (Figure C16). Thus, the increased FCI was not related to increased compartmental cycling, but rather a relative reduction in TST_{flow} (Fig. 3). However, during September 2015, significantly increased cycling (FCI, 16.4 ± 2.6) could be attributed to a wider complement of taxa with comparable relative cycling, notably Chironomidae (8.72 ± 1.12 %), Diplostraca (5.14 ± 0.60 %), and estuarine/marine *P. hessei* (12.23 ± 1.33 %) and *B. virgiliae* (5.47 ± 0.46 %) (Fig. 6). During the wetter season, the low FCI was concomitant with decreased compartment cycling of estuarine/marine taxa (Figure C16). In December 2015, FCI significantly decreased, but taxa contributions to system cycling were more evenly distributed among taxa (Fig. 6). FCI in January 2016 and February 2016 significantly increased, with more than half the compartmental contributions to cycling concentrated in a few dominant
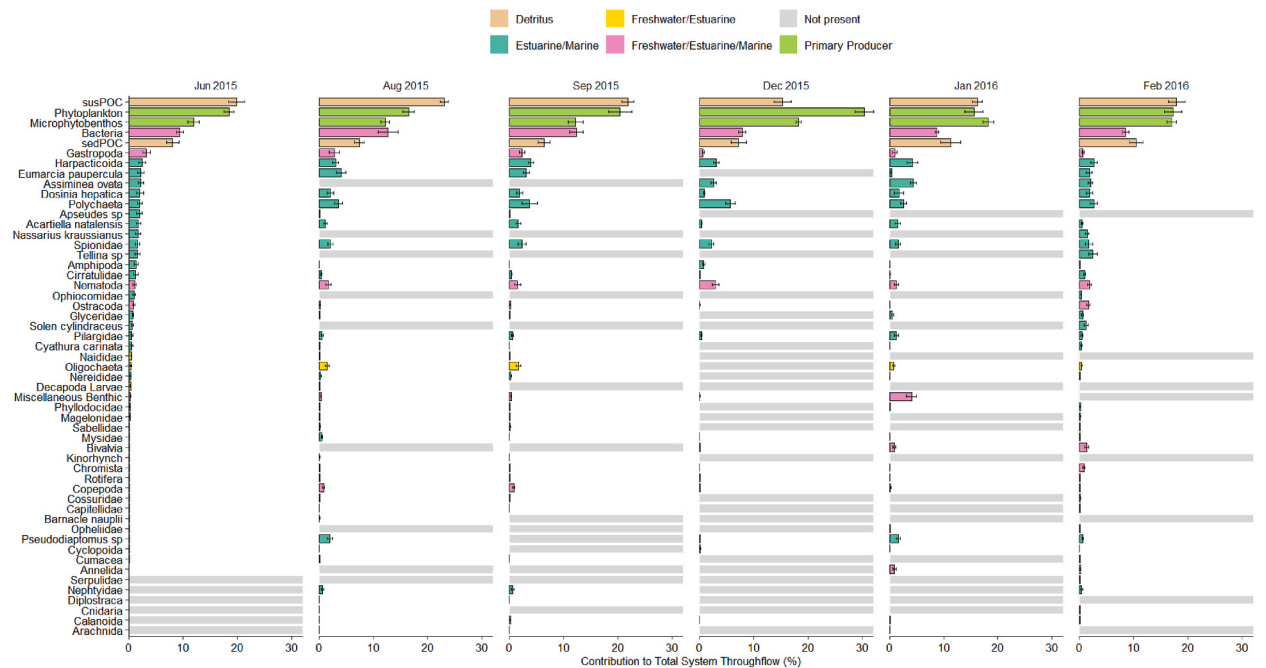

Fig. 5. Mean monthly compartmental contribution to Total System Throughflow (%) in the uMlalazi Estuary ecosystem in the drier (June, August, September 2015) and wetter (December 2015, January, February 2016) seasons (n = 10,000). Error bars indicate ±1 SD. Monthly TST_{flow} (mgC m^{-2} d^{-1}) is depicted in Fig. 3, and compartment throughflow (mgC m^{-2} d^{-1}) in Appendix C Figure C17.
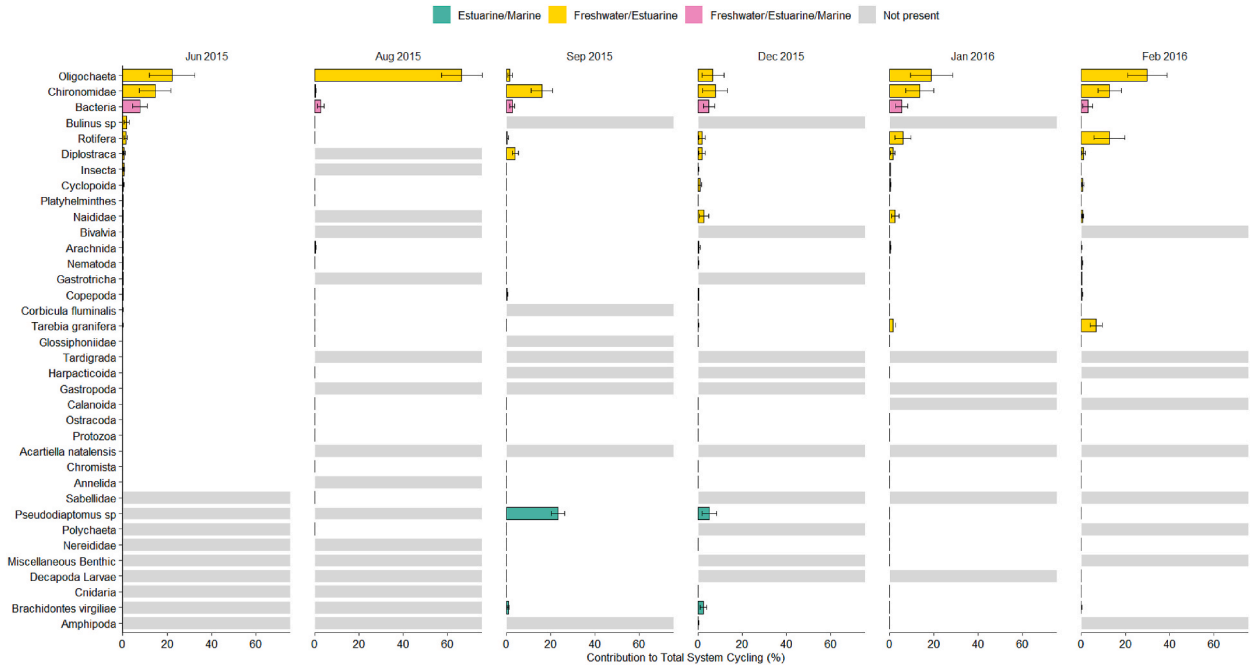
Fig. 6. Mean monthly compartmental contribution to Total System Cycling (TST_c) (%) in the uMdloti Estuary ecosystem in the dry (June, August, September 2015) and wet (December 2015, January, February 2016) seasons (n = 10,000). Error bars indicate ±1 SD. Monthly Finn Cycling Index (%), calculated from TSTc (mgC m^{-2} d^{-1}) and Total System Throughflow (TST$_{flow}$, mgC m^{-2} d^{-1}) is depicted in Fig. 3, and compartment throughflow (mgC m^{-2} d^{-1}) in Appendix C Figure C16.
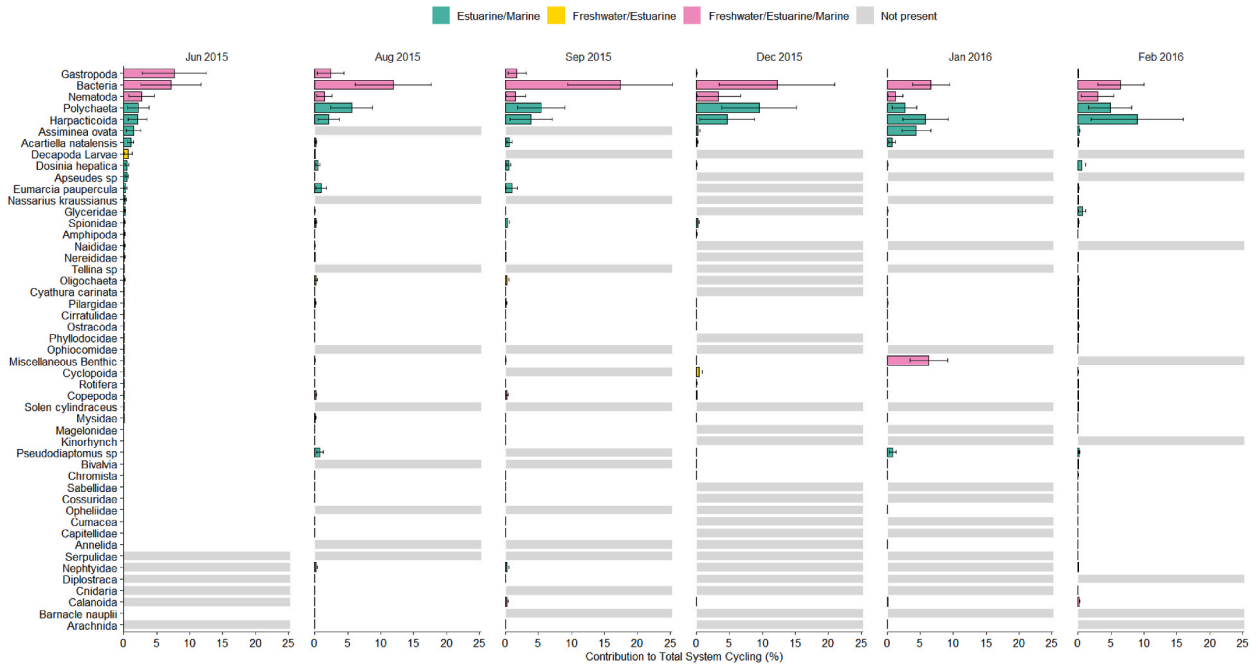

Fig. 7. Mean monthly compartmental contribution to Total System Cycling (%) in the uMlalazi Estuary ecosystem in the drier (June, August, September 2015) and wetter (December 2015, January, February 2016) seasons (n = 10,000). Error bars indicate ±1 SD Monthly Finn Cycling Index (%), calculated from TSTc (mgC m^{-2} d^{-1}) and Total System Throughflow (TST$_{flow}$, mgC m^{-2} d^{-1}) is depicted in Fig. 3, and compartment throughflow (mgC m^{-2} d^{-1}) in Appendix C Figure C18.

taxa, specifically freshwater/estuarine Oligochaeta (18.89–29.71 %), Chironomidae (12.71–13.57 %), Rotifera (6.04–12.64 %), *T. granifera* (1.38–6.66 %), and bacteria (2.95–5.39 %) (Fig. 6). During these months, the contribution from estuarine/marine taxa was extremely limited (<0.11%).

In uMlalazi Estuary, there was generally higher compartmental cycling (mgC m^{-2} d^{-1}) exhibited by all compartments during the wetter season (Figure C18). Overall system cycling was dominated by estuarine/marine compartments, notably Polychaeta (2.19–9.59 %), Harpacticoida copepods (2.08–8.95 %), and *A. ovata* (0.13–1.46 %), and compartments that could not be identified as either "freshwater/estuarine" or "estuarine/marine", specifically Gastropoda (0.01–7.62 %), Bacteria (7.87–12.24 %), and Nematoda (1.22–3.40 %) (Fig. 7). In contrast to uMdloti Estuary, there were limited contributions from freshwater/estuarine taxa throughout the study period (<0.70 %).

4. Discussion

4.1. Ecosystem function under drought conditions

In this study, we constructed monthly carbon food web models of quantified trophic flows for the uMdloti and uMlalazi estuaries, primarily investigating changes in seasonal ecosystem function and compartment contributions under drought conditions. Under these conditions, ecosystem activity, cycling, and relative reliance on trophic level I (microalgae and detritus) to fuel the food web of uMdloti and uMlalazi estuaries were generally influenced by mouth conditions, and to a lesser extent, seasons. Mouth state is critical for estuaries as it influences physico-chemical gradients, residence time and substrates, affecting biodiversity and productivity of water column and benthic compartments (Froneman, 2018; Perissinotto et al., 2010).

In the uMdloti Estuary (large temporarily closed estuary LTCE), the decreased freshwater inflows during the drought period were exacerbated by abstraction from the Hazelmere Dam ± 20 km upstream from the estuary (Forbes and Demetriades, 2008; Umgeni Water, 2022; van Niekerk et al., 2019). As a result, the mouth was nearly continuously closed, resulting in prevailing oligohaline salinity conditions typical of perched estuaries with low freshwater additions (Scharler et al., 2023), and the dominance of fresh-water/estuarine taxa within the invertebrate community (Scharler et al., 2020). In contrast, uMlalazi Estuary (predominantly open estuary PrOE) experienced open mouth conditions. In PrOEs, critical drivers of ecological function are the relative dominance of saline marine waters and freshwater inflows determined by seasonal rainfall and evaporative loss (Keith et al., 2020).

In LTCEs, prolonged closed-mouth conditions influence primary productivity. The generally low D:H (0.68–1.41) in the uMdloti Estuary indicates a higher reliance on microalgae to fuel the food web (Chrystal and Scharler, 2014; Luong et al., 2014), especially during the wetter season when higher water temperatures and more daylight hours are conducive for higher primary productivity. Additionally, D:H decreased with prolonged mouth closure duration from September 2015 until February 2016 (Fig. 3), corroborating previous research that shows that in LTCEs, D:H is lower during closed mouth phases (Ortega-Cisneros et al., 2016) and decreases with increasing duration of mouth closure (Scharler, 2012).

In contrast, the uMlalazi Estuary (PrOE) showed a greater reliance on detritus to fuel the food web (D:H 2.03–2.90). The larger reliance on detritus (D:H > 1) and relative decrease during the wetter season (Fig. 3) corroborates previous research describing overall high D:H of uMlalazi Estuary and decreases during the wet season related to high microphytobenthos stocks (Ortega-Cisneros et al., 2016). Persistently high D:H indicates greater detritivory by trophic level II consumers (detritivores), which is related to ecosystem maturity (Christensen, 1995; Odum, 1969) and a larger degree of functional resilience to perturbations (Lassalle et al., 2011).

In both estuaries, a decrease in D:H during the wetter season and proportional increase in herbivory matches the overall higher ecosystem activity (TST$_{flow}$) during the same period. The latter corroborates findings for other estuaries such as Chesapeake Bay, USA (Baird and Ulanowicz, 1989), Apalachee Bay, USA (Baird et al., 1998), or Brouage mudflat, France (Leguerrier et al., 2007), where the ecosystems showed higher activity during warmer periods. In uMdloti Estuary, increased TST$_{flow}$ with increasing mouth closure duration (September 2015–February 2016) signals the influence of mouth status on ecosystem activity, in line with previous research that shows larger system activity during closed mouth phases in warm temperate (East Kleinemonde) and subtropical (uMpenjati) South African LTCEs, which was related to increased primary producer biomass (Ortega-Cisneros et al., 2016). While both estuaries show seasonal fluctuations in system activity, the generally larger system activity of uMlalazi Estuary compared to uMdloti Estuary, suggests a larger, more productive ecosystem (Patten, 1995). High system activity of PrOEs (e.g., uMlalazi Estuary) has previously been attributed to increased imports and exports of energy/material due to permanently open mouth conditions, and during the wetter season, increased rainfall (Ortega-Cisneros et al., 2016). We did not quantify import and export flows during this study, however, the permanently open mouth state that allows for constant exchanges with the sea can be interpreted as a 'buffer' of ecosystem activity under drought conditions.

In both estuaries, a few dominant compartments contributed proportionally more to overall ecosystem activity, corresponding with previous findings that ecosystem activity is concentrated within a handful of dominant compartments (Borrett, 2013; Scharler and Fath, 2012). The uMlalazi had a higher diversity of taxa from the typical estuarine/marine groups than the uMdloti (van Niekerk et al., 2019), which is expected with the predominantly open mouth status. The open mouth status, mediated by tide and seasonal changes in freshwater flow, allows a salinity gradient to develop along the estuary. Different species occupy the different salinity niches along this gradient, allowing for higher biodiversity of estuarine/marine taxa than estuaries with predominantly oligohaline conditions (Wolanski and Elliott, 2016). During this study, the open mouth conditions, together with drought-induced reduction in freshwater flow, led to the contraction of oligohaline zone, extended the suitable habitat for the predominantly mesohaline species in this group, notably Crustacea, Polychaeta, Gastropoda and Bivalvia that contributed highly to the ecosystem activity. These taxa have feeding traits that correlate with high sediment organic loads (surface and subsurface deposit feeders), and that forage on detritus or on

bacterial films.

In uMdloti Estuary, the prolonged mouth closure and the resulting oligohaline conditions during this study favored taxa preferring oligohaline conditions and, consequently, their compartmental activity. The large contributions to system activity from Oligochaeta and Chironomidae indicate either overriding freshwater conditions as both are affiliated with freshwater/brackish waters and/or the poor condition of the estuarine ecosystem. Chironomidae are global indicators of degraded conditions, under which they become ubiquitous and can proliferate due to the plasticity of their inherent responses to the prevailing ecological conditions (Serra et al., 2017). Whereas, better known from estuaries in the Global North, Oligochaeta have exceptional physiological (haemoglobin) and morphological adaptations (gills) and thus can thrive in hypoxic conditions (Martin et al., 2008) typically developed by prolonged mouth closure in uMdloti Estuary (Scharler et al., 2020).

The decreased system-level activity of uMdloti Estuary after the mouth breach shown by this study corroborates previous findings (Scharler, 2012). During a breach, perched LTCEs drain rapidly into the marine environment (Cooper, 2001), and due to the loss of several compartments from the estuary associated with system flushing (Froneman, 2018) TST_{flow} and compartmental activity decreases. Such breaches act as a 'biological reset' (Adams and van Niekerk, 2020; Whitfield et al., 2008), significantly affecting system function through temporarily reduced productivity and biodiversity (Deale et al., 2013; Lemley and Adams, 2020; Scharler et al., 2020). A recovery from the breach was apparent by September 2015 through increased abundances of specific compartments, and its benefits in the form of recruitment of previously absent estuarine/marine taxa. During this time, contributions to system activity from estuarine/marine taxa had increased. The re-established estuarine-marine connectivity is a catalyst for creating diversity through increasing salinity and estuarine-associated fauna recruitment. However, contributions from compartmental throughflow of the estuarine/marine taxa to overall ecosystem activity declined towards February 2016, with increased freshwater/brackish infauna (Chironomidae/Oligochaeta) associated with high sediment organic loading (sedPOC) and increased microphytobenthos.

The generally low amount of cycling of both estuarine ecosystems suggests that system function is dependent on external energy inputs (e.g., increased primary production, detritus inputs) to maintain function (de Jonge and Schückel, 2021; Finn, 1976), and that it therefore has lower resilience to external perturbations (de Jonge and Schückel, 2019). In uMdloti Estuary, low cycling may be caused by a combination of low freshwater input that still carried relatively high nutrient loads (Brooker and Scharler, 2020). However, as we did not parameterize import and export flows in this study, future research is required to elucidate whether freshwater inflow and WWTW effluent are important drivers of uMdloti ecosystem cycling. The increased cycling after the breach can be interpreted as a stress response (Odum, 1985; Raoux et al., 2019; Scharler and Baird, 2005; Tecchio et al., 2015), where the system increases cycling to support overall activity as a response to the loss of energy and material.

Previous research shows that in subtropical South African LTCEs (uMdloti, uMhlanga), cycling initially increases after a breach event during open mouth phases, but decreases with prolonged mouth closure (Ortega-Cisneros et al., 2016; Scharler, 2012). After the mouth breach, the high fraction of cycling during August 2015 was related (Fig. 6) to a low TST_{flow} (Fig. 3). Cycling increased during September 2015, with increased contributions from almost all existing compartments, and newly established estuarine/marine taxa, notably *P. hessei*. As a notably diverse group in subtropical estuaries, the presence and persistence of estuarine/marine taxa exhibiting higher contributions to system cycling after the mouth breach indicate their importance in enabling system function and recovery.

In uMlalazi Estuary, while there was high compartmental cycling of estuarine/marine taxa compared to freshwater/estuarine taxa, the low overall fraction of cycling and lack of seasonal differences could be a result of high system activity (TST_{flow}) maintained by a constant input of energy and materials, lowering the need for recycling (Ortega-Cisneros et al., 2016). This constant resource input was presumably from the open mouth conditions allowing exchanges with the sea or from inputs of organic detritus and nutrients via WW effluent from the Mtunzini Municipal Sewage Treatment Works and the Mtunzini Aquaculture Projects Kob Farm (DWS, 2015). However, since the input flows were not parameterized (i.e., weighted) due to a lack of data, we cannot explicitly attribute high system activity to high input flows. Thus, further research is needed to (1) adequately quantify estuarine boundary inputs through improved monitoring, or simulations, or both, and (2) include the quantified boundary flows in the models to elucidate their role.

While we discuss and compare the study results to trends found in previous research, the results cannot be compared directly due to differences in model aggregation and calculation of ecological indicators. Aggregation of compartments is an important determinant of whether ENA model outputs can be compared with confidence (Abarca-Arenas and Ulanowicz, 2002; Allesina et al., 2005; de Jonge et al., 2019). While the degree of aggregation was similar between models in this study, previous comparative studies used different aggregation methods (Ortega-Cisneros et al., 2016; Scharler, 2012; Scharler and Baird, 2005). Additionally, ecological (ENA) indicators between this study and others cannot be directly compared, given that some ecological indicators can be calculated slightly differently. For example, TST_{flow} (used here to characterise ecosystem activity) is calculated by the sum of all inflows or outflows of internal compartments (Borrett and Scharler, 2019; Fath et al., 2019). However, other studies characterise estuarine ecosystem activity with Total System Throughput (TST_p) (Ortega-Cisneros et al., 2016; Scharler, 2012; Scharler and Baird, 2005), which is the sum of all inflows and outflows (de Jonge and Schückel, 2021; Fath et al., 2019). Since TST_p is always larger than TST_{flow}, (Fath et al., 2019), the results of TST_{flow} from this study cannot be directly compared to studies reporting TST_p. Further, the Finn Cycling Index (%) used in this study was calculated as the sum of total system cycling (TST_{Ci}) divided by TST_{flow}. In contrast, other studies calculate FCI based on TST_p (Ortega-Cisneros et al., 2016; Scharler, 2012). For these reasons, the relative *trends* of ecological indicators calculated in this study are discussed and compared with previous studies.

4.2. Insights for future estuaries & assessments

For the KwaZulu-Natal province, historical data shows decreasing rainfall volumes from 1987 to 2016 (Roffe et al., 2021), whereas predictive models show slight to large increases in rainfall delivered through more frequent storm events during summer and spring

(Dunning et al., 2018; Engelbrecht et al., 2009, 2013; Lumsden et al., 2009). These rainfall events are predicted to be interspersed with more frequent and severe drought periods (IPCC, 2021). This will likely severely affect the timing and volume of runoff received by estuaries, with potential implications for mouth closure frequency and subsequent effects on ecosystem function (van Niekerk et al., 2022). The effects of these changes on estuarine taxa and ecosystem function may be compounded by future predicted shifts in land and air temperatures (CSIR, 2019) and their influence on river and estuarine temperature (James et al., 2013; van Niekerk et al., 2022). In addition, water abstraction from catchments, a major determinant of freshwater input to estuaries in South Africa, exacerbates the impact of drought periods (Scharler et al., 2023).

Depending on each estuary's unique geomorphic and hydrological regimes, regional climate, and anthropogenic impacts, drought-induced freshwater flow reduction can have short-term and multi-year influences on system hydrology and water chemistry (Clark et al., 2022; Scharler et al., 2023), nutrients and microalgae productivity (de Oliveira et al., 2022; Wetz et al., 2011), and species biomass and community composition (Carrasco et al., 2010; Cyrus et al., 2011; Mackay and Cyrus, 2001; Scharler et al., 2020). Through food web models and network analysis, our study is the first to show that the unique context of each estuary influences system-specific functional responses to the same drought conditions, which can indicate the systems *functional resilience* to future predicted conditions.

Under drought-induced prolonged mouth closure, the anthropogenically impacted, large temporarily closed uMdloti Estuary ex-hibits decreased ecosystem functional capacity, demonstrated by low D:H, low cycling, and high seasonal fluctuations in ecosystem activity. This infers vulnerability to external perturbations affecting ecosystem function. Under predicted drought conditions, and associated prolonged mouth closure periods, our results suggest that future uMdloti Estuary ecosystem activity may fluctuate largely due to predicted changes in atmospheric and water temperatures (James et al., 2013; van Niekerk et al., 2022), and changes in rainfall affecting freshwater flow and WWTW outflow (van Niekerk et al., 2022). The single mouth breach allows insight into how connections with the sea are important for maintaining estuarine/marine taxa in the system by evaluating their role in overall ecosystem function. In contrast, the permanently open mouth conditions of uMlalazi Estuary provides a constant connection to the sea, allowing tidal mixing processes to regulate nutrient status (Snow and Taljaard, 2007) and continuous exchanges of estuarine/marine taxa and energy despite limited freshwater flow under drought conditions. Thus, the system maintained less variable seasonal differences in D:H, cycling, and activity, which infers increased resilience capacity to maintain function under drought conditions. Therefore, future predictions of increased land temperatures (CSIR, 2019) and drought frequency and severity (IPCC, 2021) are, to some extent, mitigated by the constant connection to the sea, whereas oligohaline reaches may be lost or reduced (Scharler et al., 2023; van Niekerk et al., 2019; Wooldridge and Deyzel, 2012).

Through this study, we show that network analysis can complement biodiversity surveys and assessments of ecosystem function. Our approach extends the knowledge gained from invertebrate biomasses and community composition surveys, which tell us *who* is in the system, to how important these taxa are, and which role they play in a whole ecosystem context. This contributes to a better understanding of system-specific responses to drought and highlights the need to account for unique system contexts (estuarine type, complement biotic communities. and anthropogenic impacts) in future modelling studies. Modelling studies that examine temporal estuarine ecosystems function under past or present drought can elucidate the impacts of such conditions and provide insights to facilitate holistic management strategies. However, such an approach requires an enormous amount of data, often lacking in the South African context due to a lack of established monitoring programs, among others (Scharler et al., 2024). Thus, we recommend more concrete targets for monitoring to increase data availability, thereby enabling improved holistic estuarine ecosystem function assessments.

In this study, we used Ecological Network Analysis (ENA) indicators to quantify whole-ecosystem functional properties. While such indicators provide a high-level, holistic overview of emergent ecosystem function, emergent properties cannot be directly managed, nor is there a consensus on 'good' indicator reference points (Fath et al., 2019). Further, the large number of existing ecological in-dicators and ongoing debate as to which ones are practically useful for ecosystem management (de Jonge and Schückel, 2021; Fath et al., 2019; Safi et al., 2019) provide few clear, practical recommendations for monitoring and management. A recent pilot study showed that some ENA indicators can be used to provide key information on food web structural and functional variability for the OSPAR North-East Atlantic region (Schückel et al., 2022). Previous work has attempted to use ecosystem indicators to communicate the effects of fishing on the state of marine upwelling ecosystems (Shannon et al., 2010). However, how these findings can be used in ecosystem management is still in development. Therefore, according to this study's findings, we suggest that the first step in using whole-system ecological indicators for ecosystem management is to relate the indicators to the practically manageable individual ecosystem components (e.g., taxa). For example, we used the node-focused approach (Borrett, 2013) to identify ecosystem components important to system activity and cycling. In both systems, estuarine/marine taxa were important contributors to ecosystem activity and cycling, highlighting the importance of maintaining estuarine/marine biodiversity no matter the estuarine type. Therefore, a practical management strategy to improve estuarine/marine biodiversity in uMdloti Estuary, and thereby ecosystem function, is better management of the freshwater inflow quantity and quality and to allow more natural breaching frequencies for recruitment of estuarine/marine taxa into the estuary (James et al., 2013; Whitfield et al., 2012). A deeper investigation into the theoretical best-attainable communities under good ecosystem functioning conditions and their concomitant habitat and ecological requirements would additionally address management requirements for restoration. These are not new suggestions in themselves, but we clarified the importance of taxa in the context of ecosystem-level function.

Further, the node-focused approach can be used to monitor the contribution of compartments of interest to the ecosystem, such as that of invasive species. For example, in this study, the invasive gastropod *T. granifera* was present in all months in uMdloti Estuary and increased their relative contributions to overall ecosystem activity over time. While *T. granifera* is officially classified as a freshwater gastropod (Perissinotto et al., 2014), this study classifies it as freshwater/estuarine, given its high salinity tolerance (Miranda et al.,

2010) and prevalence as an invasive species in many South African estuaries (MacKay and McKelvey, 2022; Perissinotto et al., 2014). As a highly adaptable species, *T. granifera* thrives in estuarine environments with high local abundances, potentially resulting in reduced growth rates and biodiversity of cohabiting macroinvertebrate species (Appleton et al., 2009; Jones et al., 2017; Riley and Dybdahl, 2015). This study shows, for the first time, the role of *T. granifera* within a whole-system context, which could potentially be used to indicate degradation of overall estuary health and loss of biodiversity. For instance, under prolonged mouth closure and stable (but poor) environmental conditions, the snails exhibit higher metabolic performance at the expense of poorer-performing local species (Tagliarolo and Scharler, 2018). However, further research is required to elucidate how the increased importance of *T. granifera* within an ecosystem (via contributions to overall system activity/cycling) affects the ecosystem function and the activity of cohabiting invertebrates.

5. Conclusions

Using food web model ensembles and Ecological Network Analysis (ENA), we quantified the seasonal ecosystem function under drought conditions of two South African subtropical estuaries, the large temporarily closed uMdloti Estuary, and the predominantly open uMlalazi Estuary. The study presents novel findings of emergent ecosystem function during drought conditions, and how ecosystem component behavior underpins emergent ecosystem-level behavior. Key findings include (1) estuaries exhibit system-specific functional responses to drought, depending on their unique context, and (2) estuarine/marine taxa are critical for maintaining or improving overall ecosystem function and resilience to perturbations. During the study, uMdloti Estuary experienced prolonged drought-induced closed mouth conditions, except for a single breach. During prolonged mouth conditions, the system was dominated by freshwater/brackish taxa, which contributed to large seasonal differences in ecosystem activity, low cycling, and high reliance on microalgae. This infers decreased functional resilience to predicted drought conditions, increased temperatures, and perturbations affecting primary producers (e.g., nutrient input). The mouth breach event allowed a temporary 'biological' reset of the system, whereby recruitment of estuarine/marine invertebrates temporarily improved system function via increased cycling and decreased reliance on microalgae to fuel the food web. uMlalazi Estuary generally showed less seasonal variation in ecosystem activity, higher system activity overall, and higher reliance on detritus to fuel the food web than the uMdloti Estuary. Together with low cycling, these findings can be related to the open mouth conditions and continuous exchanges of energy/material and recruitment of estuarine/marine taxa. The high contributions of estuarine/marine taxa, compared to freshwater/brackish taxa, highlight their role in driving ecosystem function in this system. These findings suggest that uMlalazi Estuary has a degree of functional resilience to decreased freshwater flow under drought due to the constant open-mouth conditions. Together, these results provide critical insight into system-specific responses of estuaries to drought and highlights the need to account for unique system contexts (estuarine type, complement biotic communities. and anthropogenic impacts) in future modelling studies.

CRediT authorship contribution statement

Gemma Gerber: Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Fiona MacKay:** Writing – review & editing, Writing – original draft. **Ursula M. Scharler:** Writing – review & editing, Writing – original draft, Supervision, Funding acquisition, Conceptualization.

Data statement

The data used in this study can be accessed by any individual, granted that the data is not used for commercial purposes. To access any data used in this publication at no financial cost, interested parties are encouraged to submit a request via email to the corresponding author.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:Gemma Gerber reports financial support was provided by National Research Foundation. Ursula M Scharler reports financial support was provided by National Research Foundation. Gemma Gerber reports a relationship with University of KwaZulu-Natal, School of Life Sciences that includes: employment. Ursula M Scharler reports a relationship with University of KwaZulu-Natal, School of Life Sciences that includes: employment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envdev.2024.101090.

Data availability

Data will be made available on request.

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