

Variability and temporal stability of communities in estuaries (Mlalazi and Mpenjati, South Africa)

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ABSTRACT: Estuaries are considered stressed environments because of the high variability in their physico-chemical properties; however, estuarine biota are able to thrive in this perceived stressful environment. The environmental homeostasis hypothesis states that this natural stress provides estuarine communities with the ability to reach stability by compensating for changes in the environment. Species diversity is one of the most important mechanisms contributing to community stability, although its influence is less evident in environments exposed to high environmental forcing. This study aimed to determine the variability and temporal stability of community-level properties such as phytoplankton biomass and zooplankton and macrobenthos density and biomass over a dry/wet cycle in the Mlalazi and Mpenjati estuaries. Despite the significant seasonal changes recorded for the density and biomass of the planktonic and benthic communities of both estuaries throughout the study, the variability of these community-level properties did not differ significantly among seasons. Of the community properties analyzed, phytoplankton and macrobenthos biomass exhibited the lowest and highest variability, respectively, in both systems. The temporal stability was similar among community-level properties and systems, and species synchrony was the main driver of community stability in both estuaries, probably because of the prevalence of environmental forcing in estuaries. Our study suggests that stable variability and an asynchronous response by species could be the mechanisms used by the estuarine biota of these 2 systems to compensate for environmental changes and reach environmental homeostasis.

KEY WORDS: Variability · Temporal stability · Estuaries · Species synchrony · Environmental forcing · Environmental homeostasis hypothesis

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INTRODUCTION

Diversity has long been considered a mechanism promoting stability in a community, with high-diversity communities being more resistant to species invasion and environmental fluctuations (Tilman 1999 and references therein, Cottingham et al. 2001, Stachowicz et al. 2002). The diversity–stability relationship has been tested in diverse ecosystems such as grasslands, microbial communities and rocky shore benthic assemblages (e.g. Tilman 1999, McGrady-Steed & Morin 2000, Romanuk & Kolasa 2002, Steiner et al. 2005, Grman et al. 2010, Bulleri et al. 2012), with most authors reporting a positive relationship between

diversity and stability at the community level (but see Valdivia & Molis 2009) and a negative relationship at the population level. Consequently, diversity (e.g. species richness and evenness) is predicted to promote community stability through 2 main insurance mechanisms: (1) a buffering effect, where higher species richness reduces the temporal variance of a community-level property (e.g. abundance, biomass), and (2) a performance-enhancing effect, where higher species richness produces an increase in the temporal mean of a community-level property such as abundance or biomass (insurance hypothesis; Yachi & Loreau 1999). These 2 mechanisms are influenced by the responses of individual species to environmental

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fluctuations and the degree of asynchrony of these responses (Yachi & Loreau 1999).

Environmental variability has been shown to play an important role in influencing the strength of diversity effects on stability (Romanuk & Kolasa 2002, Campbell et al. 2011). Evidence suggests that under high environmental forcing, additional mechanisms such as species dominance and asynchrony of responses can contribute to the stability of a community (Loreau & de Mazancourt 2008, Grman et al. 2010, Langenheder et al. 2012). Species dominance can promote stability because of the effect of better-performing species, which exhibit lower temporal variance and higher capacity to resist disturbances (Grman et al. 2010, Langenheder et al. 2012, Valdivia et al. 2013). Similarly, asynchronous species fluctuations can foster stability by compensating for the decrease of less-tolerant species with the increase of better-performing ones (Tilman 1999, Loreau & de Mazancourt 2008). Stability can also be enhanced through the effect of statistical averaging of the different species fluctuations within a community by cancelling out the independent responses to environmental fluctuations (Doak et al. 1998). Statistical averaging is highly influenced by species richness and evenness because in communities with low species richness and evenness, total variances will be influenced mainly by the fluctuations of dominant species (Cottingham et al. 2001, Steiner et al. 2005). Moreover, temporal stability can be promoted by a faster increase in the mean of a total community property with increasing species diversity when compared to its variance. This mechanism, known as overyielding, takes place when a species performs better in a multispecific than a monospecific assemblage (Lehman & Tilman 2000).

Finally, other mechanisms such as species traits (Flöder & Hillebrand 2012), food chain length and omnivory (Long et al. 2011) can also determine the stability of community properties. The interaction effect of these different mechanisms in community stability in relation to different environmental forcing is not yet clear. Stability and its mechanisms have been studied in a wide range of ecosystems; however, no studies have evaluated the stability of communities in environments with a high degree of environmental forcing, such as estuaries. An exception is the study by Pinto et al. (2013), who specifically evaluated the temporal stability of the macrobenthic community to determine if it can be used as a measure of estuarine stability in relation to ecosystem services provision in the Mira and Mondego estuaries, Portugal.

Estuaries are considered naturally stressed systems because of the high variability in their physico-chemical characteristics. Estuarine biota are exposed to strong fluctuations in salinity, tidal influence, pH, nutrient levels, river inflow and even mouth status, but they are able to survive and even thrive in this stressful environment (Elliott & Quintino 2007). It has been hypothesized that this natural variability constitutes a subsidy for estuarine biota to flourish rather than a stress (Costanza et al. 1992, Elliott & Quintino 2007), which provides estuarine communities with an opportunity to persist under the fluctuating environmental conditions rather than perish, exhibiting high resilience after disturbances (e.g. floods, droughts). Consequently, the environmental homeostasis hypothesis (Elliott & Quintino 2007) suggests that the variable, and perceived stressful, estuarine environment might provide estuarine communities with the capacity to reach stability by compensating for the changes in the environment. However, this natural stress typical of estuaries constitutes an advantage only for those species that are able to tolerate the variable environmental conditions. These are relatively few when compared to, for example, oceanic environments, and estuaries are thus characterized by a comparatively low species diversity (Elliott & Whitfield 2011, Whitfield et al. 2012). As stated by Elliott & Quintino (2007), estuarine ecosystems are able to function successfully despite their low diversity, although diversity has been put forward as a necessity for efficient ecosystem function in the biodiversity–ecosystem functioning debate (Loreau et al. 2001).

Estuarine systems are influenced by numerous environmental factors and are characterized by a large range of physico-chemical fluctuations at various spatial and temporal scales (McLusky & Elliott 2004). Estuaries are also controlled by cyclic changes, e.g. seasonal fluctuations of temperature, salinity and river inflow. River inflow constitutes one of the most important factors influencing estuaries and its communities (Adams et al. 1999, Wooldridge 1999, Montagna et al. 2002). One example of such marked seasonal changes occurs along the KwaZulu-Natal coast, South Africa, which experiences a subtropical climate with 2 marked seasons. The rainy season is characterized by strong river inflow to estuaries (October to April), and the dry season (May to September) is characterized by lower rainfall and negligible river inflow to estuaries. This marked seasonal variation in environmental conditions produces spatio-temporal changes in the estuarine planktonic and macrobenthic invertebrate communities in this region

(Perissinotto et al. 2010 and references therein). It can be expected that this natural variability will influence the stability of these estuarine communities.

In this study, 2 KwaZulu-Natal estuaries were used as examples to determine the variability and temporal stability of community-level properties such as phytoplankton biomass and zooplankton and macrobenthos density and biomass over a dry/wet cycle. Specifically, our objectives were to (1) determine if the studied community-level properties (i.e. phytoplankton biomass and zooplankton and macrobenthic invertebrate density and biomass) vary significantly through time and space in both estuaries; (2) determine if the variability (as coefficient of variation, CV) of these community-level properties through time; and (3) estimate the temporal stability of these community-level properties and determine the main drivers of stability in these estuaries.

MATERIALS AND METHODS

To determine spatio-temporal changes and temporal stability of the planktonic and benthic communities in the Mlalazi and Mpenjati estuaries, time-series of planktonic and macrobenthic communities were produced. Biological and environmental samples were collected at both estuaries between May 2010 and May 2011. Quarterly samplings (5 seasons) were conducted at 3 stations in the Mpenjati Estuary and 4 stations in the Mlalazi Estuary (Fig. 1). The difference in number of stations was based primarily on the differences in estuary length. The stations were located so that representative samples were collected in the upper, middle and lower reaches of the respective estuaries. The duration of our study (13 mo) allowed us to include major seasonal environmental fluctuations and adequately describe the stability of these estuarine communities under a seasonal cycle.

Study sites

The Mlalazi Estuary (28° 56' 42" S, 31° 48' 58" E) is classified as a permanently open system (Fig. 1). The catchment area is approximately 492 km² (DEAT 2001), and the estuary length is approximately 10 km. The estimated mean annual runoff is 122×10^6 m³ (Jezewski et al. 1984), and the estuary area is 95.86 ha (van Niekerk & Turpie 2012). Subsistence farming, sugar cane farming and commercial forestry account for approximately 46% of the catchment usage, with 53% of the catchment considered unde-

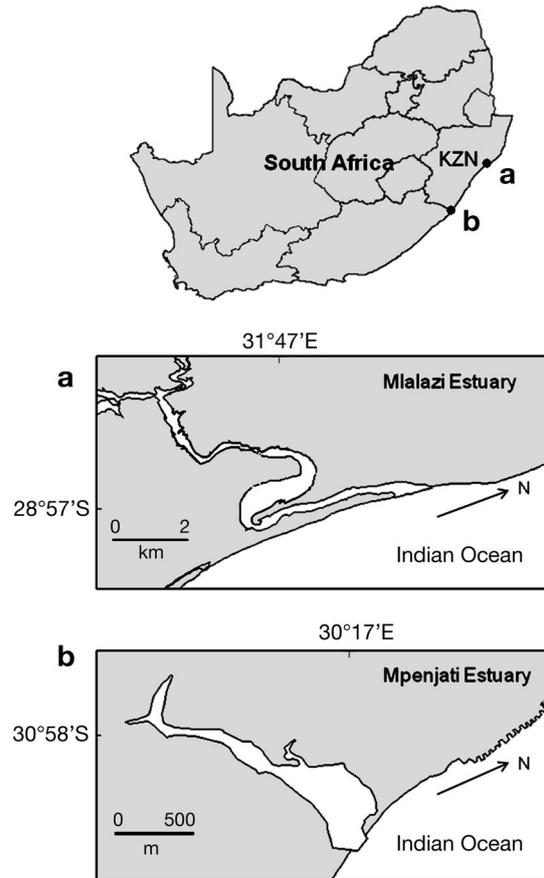


Fig. 1. The 2 study systems in KwaZulu-Natal (KZN) on the east coast of South Africa, (a) Mlalazi Estuary and (b) Mpenjati Estuary

graded and 1% urban (coastal village of Mtunzini and town of Eshowe).

The Mpenjati Estuary (30°58' 21" S, 30° 17' 02" E) is a temporarily open/closed estuary (TOCE) system (Whitfield 1992) and is also located in the South African subtropical region (Fig. 1). The catchment area is approximately 101 km², with an axial length of 1.1 km. The estimated mean annual runoff is 20.7×10^6 m³ (Jezewski et al. 1984), and the estuary area is 11.6 ha (van Niekerk & Turpie 2012). Most of the catchment is used for banana and sugar cane farming. Both systems are located in the subtropical biogeographical region and are part of nature reserves. These systems are considered to have no major negative anthropogenic impacts (Whitfield & Baliwe 2013).

Environmental variability

To determine if the seasonal fluctuations in rainfall and river inflow produce spatio-temporal varia-

tions in the abiotic environment of these estuaries, physico-chemical measurements (salinity, temperature, pH and dissolved oxygen) were taken at ca. 50 cm depth and at the bottom of the water column using a YSI 6920 water quality logger at each station to determine the variability in space and time of these parameters in both systems. Simultaneously, water samples were collected for the determination of total suspended solids (TSS), dissolved inorganic nitrogen and phosphorus and particulate organic carbon and nitrogen (POC and PON, respectively), and sediment samples were taken for the determination of sediment nutrient concentrations (particulate carbon and nitrogen) and mud content (%).

For the determination of TSS, triplicate water samples were collected in acid-washed plastic bottles from ca. 50 cm depth at each station and subsequently stored in the dark on ice. In the laboratory, the water samples were filtered through a 0.72 μ m pre-combusted and pre-weighted GF/F filter, which was then dried at 60°C for 24 h and re-weighed. POC and PON measurements were obtained from GF/F filters, on which particulate organic matter had been collected. These were analyzed using a Europa Scientific 20-20 IRMS elemental analyzer. Results for POC and PON were expressed as micrograms of carbon and nitrogen per liter. Three 100 ml samples of water filtrate from TSS determinations were collected in acid-washed bottles and frozen at -20°C for the determination of dissolved inorganic nitrogen ($\text{NO}_3^- + \text{NO}_2^-$) and phosphorus (orthophosphate) concentrations. Nutrient determinations were conducted using a Skalar San++ continuous-flow analyzer (Skalar Analytica BV).

For sediment nutrient concentrations (carbon, nitrogen), 3 sediment samples were collected at each station to a depth of 1 cm using a twin corer (internal diameter 2 cm) to determine carbon and nitrogen content in the sediment. Nutrient content in the sediment was analyzed following the procedure described above for POC and PON content of TSS. Three sediment samples were collected at each station using a Zabalocki-type Ekman grab (September 2010) and a van Veen grab (other sampling seasons) to determine grain size distributions and sediment organic content. Samples were dried at 60°C for 48 h. For sediment organic content determinations, 5 g of oven-dried sediment was weighed and combusted at 450°C for 6 h before reweighing. Organic matter content was determined as the difference in sediment weights. For grain size analysis, the remaining dried sand was analyzed to

determine mud content (%) at the Enviromap laboratory (Durban, South Africa)

Biological variability

To determine the variability and temporal stability of the planktonic and macrobenthic communities of the Mlalazi and Mpenjati estuaries, data were collected as follows.

Phytoplankton biomass. Triplicate subsurface samples were collected from May 2010 to May 2011 and serially filtered through 20 μ m Nitex mesh, 2 μ m membrane filters, and 0.72 μ m GF/F filters. The pigments were extracted using 90% acetone for 24 h in the dark at -4°C. Phytoplankton chl *a* concentrations (as a proxy for phytoplankton biomass) were estimated using a Turner Trilogy fluorometer (Holm-Hansen & Riemann 1978). Microplankton, nanoplankton and picoplankton size fractions were used as proxies for species composition for the phytoplankton community.

Zooplankton abundance and biomass. Daytime zooplankton samples were collected using a hyperbenthic sled with a 200 μ m mesh plankton net from September 2010 to May 2011. The sled was towed at a speed of 1 to 2 knots at each station for 27 m. Samples were preserved in 5% formalin with rose bengal. In the laboratory, samples were suspended in 1 to 5 l solutions, depending on the concentration of organisms. From each solution, three 20 ml subsamples were withdrawn at mid-depth, while stirring continuously to ensure homogenous suspension (Perissinotto & Wooldridge 1989, Jerling & Wooldridge 1991). Organisms were then identified to species level and counted with a dissecting microscope. The CV between subsamples was always less than 10%. Dry weight was determined for the most numerically dominant species of zooplankton in terms of density and biomass after oven drying for 48 h at 60°C.

Macrobenthic invertebrate abundance and biomass. Three replicate samples were collected with a Zabalocki-type Ekman grab (sampling area 0.024 m²) during September 2010 and with a van Veen grab (sampling area 0.025 m²) during the other sampling sessions. Both types of grabs sample the same area and depth (ca. 10 cm). Three replicate samples were collected at each station, each consisting of 3 grab samples to collect sufficient material for subsequent analysis. Samples were collected using a 500 μ m sieve and preserved in 5% formalin with rose bengal. In the laboratory, organisms were identified, counted and weighed after oven drying for 48 h at 60°C.

Data analysis

To test for significant spatio-temporal changes in the environmental and biological data at both estuaries (Objective 1), permutational multivariate analysis of variance (PERMANOVA) (Anderson et al. 2008) was performed using seasons and stations as factors. All environmental variables (see Table 1) were log transformed and normalized to account for the differences in units among variables (Clarke & Gorley 2006). A similarity matrix based on Euclidean distance was produced to represent the relationships among stations and seasons.

For the analysis of zooplankton and macrobenthos communities, only the most abundant species (collectively accounting for 99% of mean density or biomass) were considered. All groups accounting for <1% of mean density or biomass were not included in our analysis to reduce bias towards their contributions. Phytoplankton biomass and zooplankton and macrobenthos density and biomass data were square root transformed to balance the contributions between more abundant and rare taxa. Separate PERMANOVAs based on the Bray-Curtis similarity matrix were conducted using a significance level of 0.05. PERMANOVAs were conducted in PRIMER 6 (Clarke & Gorley 2006).

To determine if the variability of the community-level properties changed significantly through time in both estuaries (Objective 2), the CV, defined as the ratio between the standard deviation and its mean ($CV = \sigma \mu^{-1}$), was used. Higher values of CV represent a high variability. CVs of phytoplankton biomass and zooplankton and macrobenthos density and biomass were calculated for each station among seasons in both estuaries to determine the variability in these community-level properties. To test for significant temporal changes in the variability (CV) of each community-level property, a 1-way ANOVA was performed using seasons as factors. To test if the variability changed among community-level properties and estuaries, a 2-way ANOVA was conducted. Possible significant differences between pairs of samples were determined with a Tukey honestly significant difference post-hoc test. Normality and homoscedasticity were evaluated for each community-level property prior to the analyses, and all CV values were \log_{10} transformed to fulfill the assumptions of parametric tests. ANOVA tests were conducted using the software package IBM SPSS Statistics 21 at a significance level of 0.05.

To determine the temporal stability of the analyzed community-level properties and its stabilizing mech-

anisms (Objective 3), temporal stability was used as a stability measure. Temporal stability is an index of the stability of a community or population along time (Lehman & Tilman 2000). In this study, community stability was estimated as the ratio between the temporal mean of a particular community-level property and its standard deviation. Temporal stability is the inverse of the CV; thus, higher values indicate higher temporal stability. Temporal stability was calculated for each station and community-level property in both systems.

Four possible mechanisms contributing to temporal stability were evaluated. Community-wide synchrony (ϕ_c) (Loreau & de Mazancourt 2008), considered an important mechanism contributing to community stability, was calculated as:

$$\phi_c = \sigma_{cT}^2 / \left(\sum_{i=1}^s \sigma_{ci} \right)$$

where σ_{cT}^2 is the variance of the total community-level property (e.g. phytoplankton biomass, zooplankton density) and σ_{ci} is the standard deviation in the abundance or biomass of species i in a community with s species. ϕ_c ranges from 0 (perfect asynchrony) to 1 (perfect synchrony), with higher synchrony values meaning that most species within a community are positively correlated and fluctuate in a similar manner. This statistic is independent of the magnitude and distribution of species abundances/biomasses and variances, which allows for quantitative comparisons of communities with different species richness (Loreau & de Mazancourt 2008). Other important stabilizing mechanisms such as species richness (Margalef 1958), species evenness (Pielou 1975) and species dominance (Simpson 1949) indices were calculated for each community-level property and estuary using the routine DIVERSE in Primer 6 (Clarke & Warwick 1994). A Pearson product-moment correlation was run to determine the relationship between temporal stability and stabilizing mechanisms (i.e. dominance, species richness, synchrony). Correlation tests were conducted in IBM SPSS Statistics 21 using a significance level of 0.05.

RESULTS

Spatio-temporal changes in abiotic factors

The inlet of the Mlalazi Estuary remained open throughout the study period, whereas the mouth of the Mpenjati Estuary was primarily closed. Mouth breaching occurred twice during the study period

because of river flooding at the end of October 2010 and the beginning of May 2011. This estuary was open to the sea from the end of October to the beginning of April 2011.

All analyzed environmental variables showed significant seasonal differences at the Mlalazi Estuary, with the exception of pH and sediment mean grain size. Similarly, a significant interaction effect of season \times station was observed by TSS, POC and PON of sediment and water, mud content and sediment organic matter. Salinity showed significant differences among seasons and stations at this estuary, and lower salinities were recorded at the upper reaches of the estuary throughout the study period (Table 1). At the Mpenjati Estuary, all environmental variables showed significant seasonal differences. Significant interaction effects of season \times station were recorded by dissolved inorganic phosphorus, TSS, POC and PON of the sediment, mud content and sediment organic matter (Table 1). A marked salinity gradient was recorded along both estuaries during the wet season, with lowest salinities at the upper reaches of these systems.

Spatio-temporal changes in biological communities

Phytoplankton biomass

Mean (\pm SD) total phytoplankton biomass (as chl *a*) in the Mlalazi Estuary ranged from 0.53 ± 0.42 mg m^{-3} in May 2011 (dry season) to 9.75 ± 2.23 mg m^{-3} in

November 2010 (wet season). In the Mpenjati Estuary chl *a* concentrations ranged from 0.16 ± 0.06 mg m^{-3} in May 2011 (abnormal dry season with high rainfall) to 10.40 ± 2.26 mg m^{-3} to September 2010 (dry season).

PERMANOVA detected significant differences between seasons for phytoplankton chl *a* concentrations in the Mlalazi and Mpenjati estuaries (Tables 2 & 3). These differences are explained by the marked differences in chl *a* concentrations between the wet and dry seasons, with high chl *a* concentrations recorded during the wet season at the Mlalazi Estuary and during the dry season at the Mpenjati Estuary.

Zooplankton density and biomass

Mean (\pm SD) zooplankton density varied from 3920 ± 3150 ind. m^{-3} in June 2010 (dry season) to 58671 ± 37969 ind. m^{-3} in November 2010 (wet season) at the Mlalazi Estuary and from 6053 ± 1925 ind. m^{-3} in September 2010 (dry season) to 46264 ± 23233 ind. m^{-3} in November 2010 (wet season) at the Mpenjati Estuary.

A significant interaction effect of season \times station was detected on zooplankton density in the Mlalazi Estuary by PERMANOVA (Table 2). Contrarily, significant seasonal changes in zooplankton density were only observed at the Mpenjati Estuary (Table 3). Significant variations were based on differences between samples of low and high zooplankton density at both estuaries.

Table 1. Permutational multivariate analysis of variance for environmental parameters recorded at the Mlalazi and Mpenjati estuaries. DIN: dissolved inorganic nitrogen; DIP: dissolved inorganic phosphorus; TSS: total dissolved solids; POC: particulate organic carbon; PON: particulate inorganic nitrogen; POE: permanently open estuary; TOCE: temporarily open/closed estuary

Parameter	Significant variation	
	Mlalazi Estuary (POE)	Mpenjati Estuary (TOCE)
Water column		
pH	No significant differences	Season
Salinity	Season, Station	Season
Temperature ($^{\circ}$ C)	Season	Season
DIN (μ M)	Season	Season, Station \times Season
DIP (μ M)	Season	Season
TSS ($mg\ l^{-1}$)	Season, Station, Station \times Season	Season, Station, Station \times Season
POC (μ g l^{-1})	Season, Station, Station \times Season	Season
PON (μ g l^{-1})	Season, Station, Station \times Season	Season
Sediment		
POC of the sediment (%)	Season, Station, Station \times Season	Season, Station, Station \times Season
PON of the sediment (%)	Season, Station, Station \times Season	Season, Station, Station \times Season
Mud content (%)	Season, Station \times Season	Station, Station \times Season
Sediment organic matter (%)	Season, Station, Station \times Season	Season, Station, Station \times Season

Mean (\pm SD) zooplankton biomass varied from $0.003 \pm 0.002 \text{ g m}^{-3}$ in June 2010 (dry season) to $0.064 \pm 0.060 \text{ g m}^{-3}$ in November 2010 (wet season) at Mlalazi Estuary. At Mpenjati Estuary, zooplankton biomass ranged from $0.028 \pm 0.024 \text{ g m}^{-3}$ in February 2011 (wet season) to $0.348 \pm 0.341 \text{ g m}^{-3}$ in May 2011 (abnormally high rainfall during the dry season).

PERMANOVA found a significant season \times station interaction effect at the Mlalazi and Mpenjati estuaries (Tables 2 & 3). However, no significant pair-wise comparisons were recorded among stations at the Mpenjati Estuary.

Macrobenthic invertebrate density and biomass

Mean (\pm SD) macrobenthos density ranged from $2797 \pm 2329 \text{ ind. m}^{-2}$ in February 2011 (wet season) to $29350 \pm 30248 \text{ ind. m}^{-2}$ in September 2010 (dry season) at the Mlalazi Estuary. At the Mpenjati Estuary, macrobenthos density ranged from $4938 \pm 4619 \text{ ind. m}^{-2}$ in November 2010 (wet season) to $20044 \pm 7034 \text{ ind. m}^{-2}$ in May 2011 (abnormally high rainfall during the dry season).

m^{-2} in November 2010 (wet season) to $20044 \pm 7034 \text{ ind. m}^{-2}$ in May 2011 (abnormally high rainfall during the dry season).

A significant season \times station interaction effect in macrobenthos density was recorded at the Mlalazi Estuary (Table 2), and a significant main effect of season was recorded at the Mpenjati Estuary (Table 3). PERMANOVA reported significant differences in the macrobenthos density between dry and wet months at both systems.

Mean (\pm SD) macrobenthos biomass varied from $7.891 \pm 9.221 \text{ g m}^{-2}$ in May 2011 (dry season) to $98.039 \pm 165.54 \text{ g m}^{-2}$ in November 2010 (wet season) at the Mlalazi Estuary. At the Mpenjati Estuary, macrobenthos biomass ranged from $0.114 \pm 0.082 \text{ g m}^{-2}$ in November 2010 (wet season) to $2.055 \pm 2.088 \text{ g m}^{-2}$ in May 2011 (abnormal dry season).

A significant season \times station interaction effect was detected on the macrobenthos biomass at the Mlalazi and Mpenjati estuaries (Table 2 & 3). However, no significant pair-wise comparisons were recorded between stations at the Mpenjati Estuary.

Table 2. Permutational multivariate analysis of variance results of biological parameters for the Mlalazi Estuary. Values in **bold** indicate significant differences. p(perm): probability values from permutations; p(MC): probability values estimated by Monte Carlo simulations

Source	df	SS	MS	Pseudo- <i>F</i>	p(perm)	Unique permutations	p(MC)
Chl a concentration							
Season	4	18622	4655.4	7.3185	0.0002	4990	0.0004
Station	3	2482.2	827.4	1.3007	0.2788	4978	0.272
Residual	12	7633.4	636.11				
Total	19	28737					
Macrobenthos density							
Season	3	18765	6254.9	13.103	0.0001	9930	0.0001
Station	3	33212	11071.00	23.191	0.0001	9919	0.0001
Season \times Station	9	21229	2358.80	4.9413	0.0001	9855	0.0001
Residual	32	15276	477.36				
Total	47	88481					
Macrobenthos biomass							
Season	3	29846	9948.7	6.6358	0.0001	9891	0.0001
Station	3	51547	17182	11.461	0.0001	9886	0.0001
Season \times Station	9	36346	4038.4	2.6937	0.0001	9858	0.0001
Residual	32	47976	1499.2				
Total	47	166000					
Zooplankton density							
Season	4	7492.3	1873.1	6.9986	0.0002	4978	0.0002
Station	3	2970.6	990.21	3.6999	0.0004	4981	0.0006
Season \times Station	12	8550.3	712.53	2.6623	0.0004	4973	0.0004
Residual	18	4817.4	267.64				
Total	37	23349					
Zooplankton biomass							
Season	3	6478.4	2159.5	2.6386	0.0135	9940	0.0159
Station	3	8061.7	2687.2	3.2834	0.0016	9935	0.0032
Season \times Station	9	19414	2157.1	2.6357	0.0008	9899	0.0017
Residual	14	11458	818.42				
Total	29	43969					

Table 3. Permutational multivariate analysis of variance results of biological parameters for the Mpenjati Estuary. Values in **bold** indicate significant differences. p(perm): probability values from permutations; p(MC): probability values estimated by Monte Carlo simulations

Source	df	SS	MS	Pseudo- <i>F</i>	p(perm)	Unique permutations	p(MC)
Chl a concentration							
Season	4	21887	5471.9	14.462	0.0002	4986	0.0002
Station	2	681.28	340.64	0.9003	0.4846	4993	0.4744
Residual	8	3026.9	378.36				
Total	14	25596					
Macrobenthos density							
Season	3	19183	6394.3	8.335	0.0001	9923	0.0001
Station	2	3908.6	1954.30	2.5475	0.0257	9939	0.0279
Season × Station	6	7735	1289.20	1.6804	0.0633	9934	0.0705
Residual	21	16110	767.17				
Total	32	47340					
Macrobenthos biomass							
Season	3	26143	8714.3	10.112	0.0001	9925	0.0001
Station	2	7740.2	3870.1	4.4909	0.0001	9940	0.0004
Season × Station	5	12436	2487.3	2.8863	0.0004	9917	0.0007
Residual	19	16373	861.76				
Total	29	61565					
Zooplankton density							
Season	3	5881.9	1960.6	16.253	0.0001	9948	0.0001
Station	2	1252.4	626.22	5.1911	0.0005	9951	0.0025
Season × Station	6	1653.4	275.56	2.2843	0.0260	9924	0.0316
Residual	12	1447.6	120.63				
Total	23	10235					
Zooplankton biomass							
Season	3	20254	6751.3	17.054	0.0001	9954	0.0001
Station	2	4009.7	2004.8	5.0643	0.001	9959	0.0021
Season × Station	6	13280	2213.3	5.5909	0.0003	9933	0.0002
Residual	12	4750.6	395.88				
Total	23	42294					

Overall, significant seasonal variations were recorded for the planktonic and benthic communities of both estuaries. Marked increases in phytoplankton biomass and zooplankton density and biomass were observed during the wet season at the Mlalazi Estuary. Contrarily, significant decreases in these community properties were recorded during the wet season at the Mpenjati Estuary. At both systems, macrobenthos density and biomass were significantly higher during the dry season (or closed phase for the TOCE Mpenjati). Significant spatial differences were recorded for the zooplankton and benthic communities at the Mlalazi Estuary but not at the Mpenjati Estuary.

Variability of community-level properties

No significant seasonal differences in the CV of the different community-level properties were detected at the Mlalazi and Mpenjati estuaries ($p < 0.05$). This indicated that the changes in seasons did not influence the variability of the community-level proper-

ties, even when significant differences among seasons were reported for phytoplankton biomass or zooplankton and macrobenthic invertebrate density and biomass. Although significant seasonal changes were recorded for particular estuarine assemblages within these systems, the variability in each parameter remained relatively constant through time.

Our results indicate that phytoplankton biomass (as chl *a*) showed the lowest variability among the community-level properties in both estuaries, with CV varying from 0.16 ± 0.13 for the Mlalazi Estuary and from 0.24 ± 0.18 for the Mpenjati Estuary (Fig. 2). Contrarily, macrobenthos biomass showed the highest variability and varied from 0.82 ± 0.37 at the Mlalazi Estuary and from 0.73 ± 0.39 at the Mpenjati Estuary (Fig. 2). No significant interaction effect of type of community-level property × estuary in the CV was reported by the 2-way ANOVA test ($F_{4,141} = 1.199$, $p = 0.314$). However, significant differences were reported in the CV among community-level properties ($p = 0.019$). The CV of phytoplankton biomass was significantly different ($p < 0.01$) from the

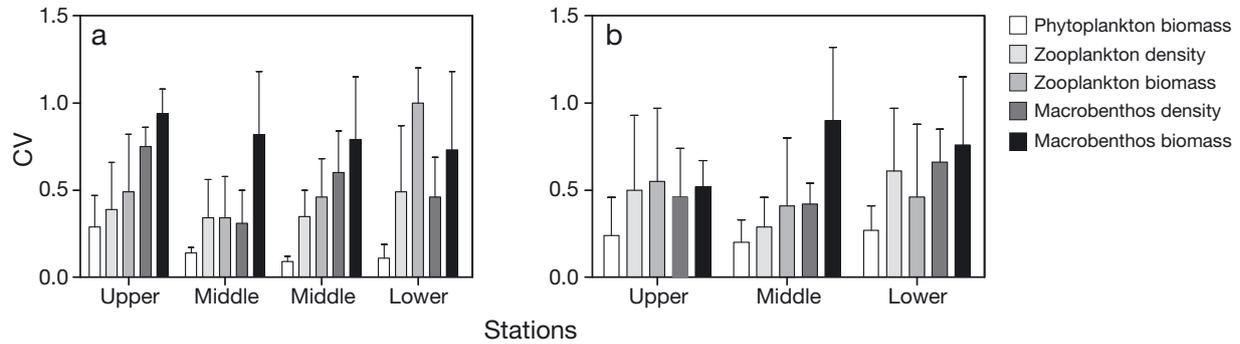


Fig. 2. Mean variability (as coefficient of variation, CV) among stations of the analyzed community-level properties at the (a) Mlalazi and (b) Mpenjati estuaries

CV of all other community properties. Significant differences were also found between the CV of macrobenthos biomass and zooplankton density and biomass ($p = 0.002$ and $p = 0.045$, respectively).

Stability of community-level properties

Temporal stability of community-level properties showed small variations but was overall slightly lower at the Mpenjati Estuary. Community stability varied from 0.87 ± 0.61 (mean among stations, zooplankton biomass) to 1.75 ± 0.31 (macrobenthos density) at the Mlalazi Estuary (Fig. 3a). Similarly, temporal stability ranged from 0.72 ± 0.09 (macrobenthos biomass) to 1.15 ± 0.58 (zooplankton density) at the Mpenjati Estuary (Fig. 3a).

Regarding the possible stabilizing mechanisms of community stability, the overall lowest and highest species synchrony were recorded for macrobenthos and phytoplankton biomass, respectively, at the Mlalazi Estuary (Fig. 3b). Zooplankton biomass and macrobenthos density exhibited the lowest and highest species synchrony, respectively, in the Mpenjati Estuary (Fig. 3b), highlighting the differences in synchrony for a given community property between systems. Macrobenthos density showed the lowest species dominance in both systems, and zooplankton density and biomass showed the highest species dominance at the Mlalazi and Mpenjati estuaries, respectively (Fig. 3c). Consequently, the lowest species richness was recorded for zooplankton density and the highest was recorded for macrobenthos biomass at both systems (Fig. 3). If phytoplankton species composition had been analyzed, it probably would have had the highest species richness among community properties. Similarly, the temporal stability of phytoplankton species could exhibit a different trend than when using size classes.

Pearson correlation analysis showed that the temporal stability significantly increased with species richness at the Mlalazi Estuary (Table 4). Temporal stability significantly decreased with an increase in species synchrony at this system (Table 4). At the Mpenjati Estuary, temporal stability showed no significant correlations with species diversity, dominance, evenness or synchrony. However, temporal stability showed a significant positive correlation with mean total community property (density/biomass) (Table 4).

When the data from both systems were pooled, species synchrony was the best predictor of species stability ($F_{1,32} = 32.70$, $p < 0.001$, $R^2_{Adj} = 0.49$); none of the other stabilizing mechanisms significantly predicted the temporal stability. This may indicate that species synchrony was the most important mechanism influencing community stability in these systems (Table 4).

DISCUSSION

In this study, we determined spatio-temporal variations of environmental variables and biological communities as well as the variability and temporal stability of 5 different community-level properties (phytoplankton biomass and zooplankton and macrobenthos density and biomass) in 2 estuaries in South Africa. Environmental variables showed significant spatio-temporal variations at both estuaries throughout the study period. Our study also detected significant spatio-temporal changes in the communities of the permanently open Mlalazi Estuary, whereas significant seasonal, but not spatial, changes were observed in the communities of the Mpenjati Estuary. Contrarily, the variability of these community-level properties did not show significant seasonal changes; however, significant differences

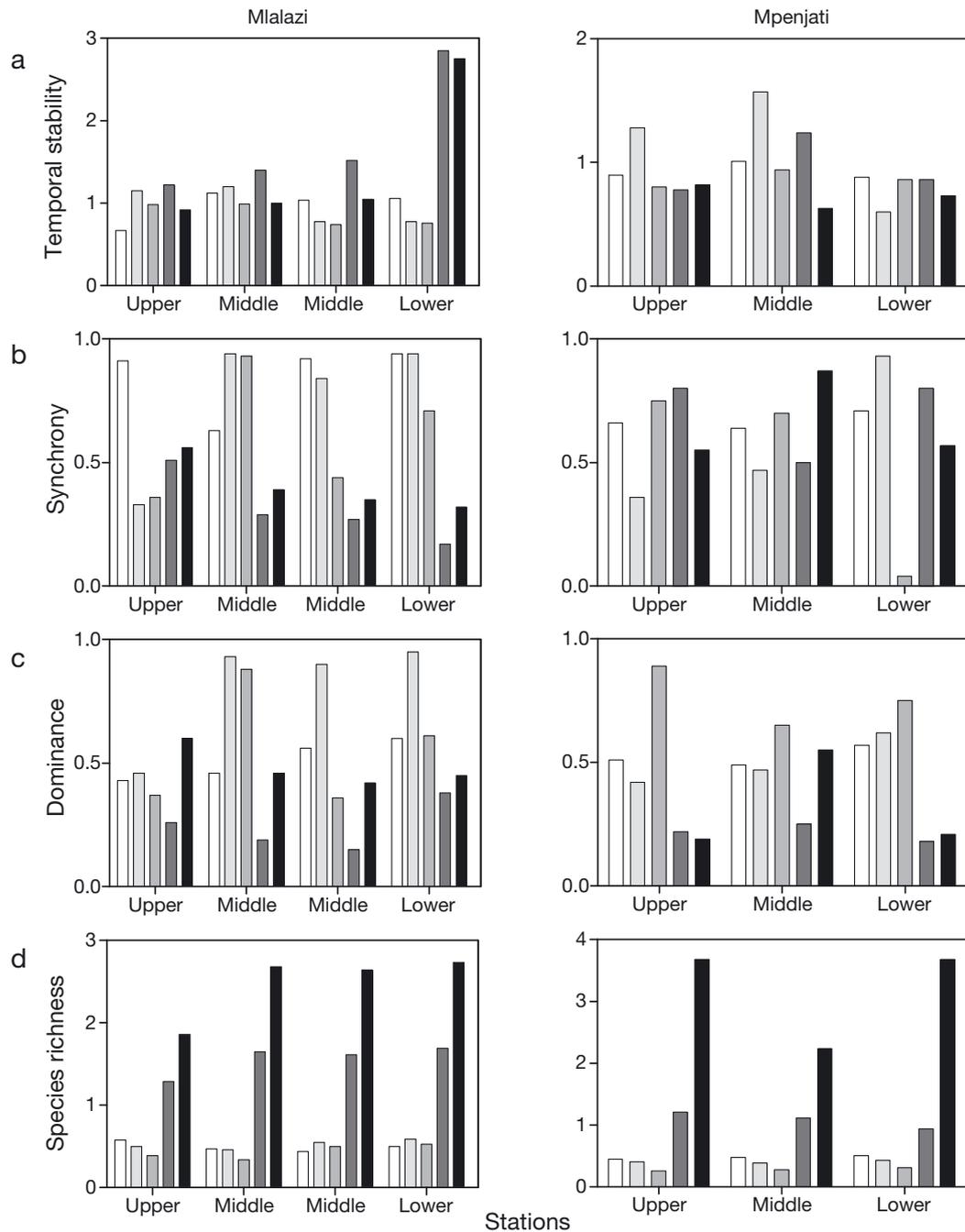


Fig. 3. Differences in community attributes at the Mlalazi (left) and Mpenjati (right) estuaries. (a) Temporal stability, (b) species synchrony, (c) species dominance and (d) species richness. Key to shading as in Fig. 2

were reported for the variability among properties, with macrobenthos biomass exhibiting the highest variability in both systems and phytoplankton biomass exhibiting the lowest. The temporal stability was similar among community-level properties and between systems, and species synchrony was found to be the main driver explaining the stability of these communities in both systems.

Phytoplankton biomass and zooplankton density and biomass responded differently to the dry/wet cycle in each type of estuary. In the permanently open Mlalazi Estuary, chl *a* concentrations and zooplankton density and biomass were significantly higher during the wet season when compared to the dry season. Similar differences were observed in the temporarily open/closed Mpenjati Estuary, except

Table 4. Pearson correlation between the temporal stability and community properties at the Mlalazi and Mpenjati estuaries. Only significant correlations are included ($p < 0.05$)

Parameter	r^2	n	p
Mlalazi Estuary			
Synchrony	-0.550	20	0.012
Species richness	0.512	20	0.021
Mpenjati Estuary			
Mean total community property	0.735	15	0.002
Both systems			
Synchrony	-0.521	35	0.001

that the highest chl *a* concentrations and zooplankton biomass were recorded during the closed phase (dry season). The highest plankton density and biomass values during the wet season in the Mlalazi Estuary are attributed to the increase in freshwater inflow and nutrient input to this estuary during the wet season (Adams et al. 1999, Wooldridge 1999). Conversely, the high water residence time and low physical disturbance during the closed phase in TOCEs are key to explaining the increased phytoplankton and zooplankton biomass recorded during this phase, despite river inflow being at a minimum (Whitfield 1980, Froneman 2006, Skinner et al. 2006).

Macrobenthic invertebrate density and biomass were significantly lower during the wet season (increased river inflow) in both systems. Contrarily, Gladstone et al. (2006) found no significant differences in the macrobenthic community structure at the entrance barriers of 4 TOCEs in New South Wales following 2 mouth breachings. However, Netto et al. (2012) reported a reduction of 50 and 90% in zoobenthic biomass and density in Camacho Lagoon, southern Brazil, because of the scouring and flushing of sediments after a mouth breaching. In this study, macrobenthic invertebrate communities, independent of estuary type, showed a similar negative response to increased river flow and mouth opening during the wet season. The significant reduction in macrobenthos density and biomass during this season could be attributed to the increased freshwater scour which created instability and habitat loss for the remaining zoobenthos.

Despite significant seasonal differences reported for planktonic and benthic density and biomass in both estuaries, the variability (as $CV = \sigma \mu^{-1}$) of phytoplankton biomass (as chl *a*) and zooplankton and macrobenthos density and biomass did not show significant seasonal differences through the study. This suggests that the marked seasonal environmental changes do not influence the variability of these

communities in both systems. We propose that the lack of significant seasonal differences in the variability of the analyzed community-level properties indicates that seasonal reductions in the mean of these properties were compensated for by a simultaneous decrease in the standard deviation. This compensatory effect ('stable' variability) has been found to be an insurance mechanism against the effects of disturbances in a rocky shore assemblage and a marine subtidal system (Long et al. 2011, Bulleri et al. 2012).

Our analysis also found that both estuaries showed similar variability (as $CV = \sigma \mu^{-1}$) in the analyzed community-level properties, with CV lowest for the phytoplankton biomass and highest for the macrobenthos biomass in both systems. These differences can be attributed to either an increase in the standard deviation, a decrease in the mean of a community-level property or both (Lehman & Tilman 2000, Bulleri et al. 2012), and in our study, the differences in the variability are attributed to an increase in the standard deviation (in relation to its mean) from phytoplankton to macrobenthos communities. Our results are in agreement with Steiner et al. (2005), who found significantly lower variability of primary producers than consumers at the population level in a multitrophic aquatic system (composed of bacteria, algae, heterotrophic protozoa and rotifers) and attributed their results to the influence of stable dominant species at lower trophic levels. In our study, the nanoplankton size fraction was consistently dominant throughout the study period despite the marked seasonal changes in biomass (K. Ortega-Cisneros unpubl. data); thus, it is probable that the effect of stable dominant taxa could also have explained the lower variability of the phytoplankton biomass reported here.

The temporal stability of the total mean density and biomass of planktonic and benthic communities was similar between estuaries. In contrast to the variability results, the temporal stability did not vary markedly among community-level properties. Temporal stability values in our study areas were considerably lower than those reported for other systems exposed to high environmental fluctuations, e.g. rocky shore benthic assemblages (Bulleri et al. 2012, Valdivia et al. 2013). Our temporal stability values, however, were comparable with those of macroinvertebrate communities in the Mira and Mondego estuaries in Portugal (Pinto et al. 2013). Unfortunately, the temporal stability of the community properties analyzed here could not be compared with those of other estuaries because of the unavailability of such studies.

Stability is mainly controlled by species synchrony, statistical averaging, species dominance and richness (Doak et al. 1998, Tilman 1999, Lehman & Tilman 2000, Loreau & de Mazancourt 2008). In this study, the temporal stability of the estuarine communities at the Mlalazi Estuary was driven mainly by species synchrony and richness. None of these mechanisms had an effect on the temporal stability of the community-level properties at the Mpenjati Estuary, but temporal stability was significantly correlated to the mean community-level property because slightly higher temporal stability values were associated with a few very high mean zooplankton densities at this estuary. Similarly, Pinto et al. (2013) reported a stronger association of temporal stability with species abundance than to species richness of macrobenthic communities at the Mira and Mondego estuaries. The lack of a significant species richness-stability relationship in the Mpenjati Estuary could be related to a higher influence of environmental variability in this system (closed and open phases, narrower range of temporal stability values) when compared to the Mlalazi Estuary (Romanuk & Kolasa 2002). The lack of a positive relationship between species richness and stability in the Mira, Mondego (Pinto et al. 2013) and Mpenjati estuaries (this study) confirms that a high diversity is not necessary for the successful functioning of complex systems as estuaries (Elliott & Quintino 2007).

In terms of species synchrony, asynchronous fluctuations are enhanced by interspecific competition and the presence of species with differential responses to stress (Tilman 1999). Synchronous fluctuations have been related to a higher degree of environmental forcing and are expected to increase with an increasing gradient of environmental stress (Bertness & Callaway 1994, Houlahan et al. 2007, Valone & Barber 2008), although biological interactions can also generate positive covariances (Steiner et al. 2005, Bulleri et al. 2012). It is thus suggested that the prevalence of environmental forcing (e.g. natural stress) in estuarine systems is key to explaining the role of species synchrony as a main driver of the community stability in these systems. Overall, we suggest that stable variability and species synchronization could be the mechanisms used by the estuarine biota of these 2 systems to compensate for environmental changes and reach environmental homeostasis (*sensu* Elliott & Quintino 2007).

Our mesoscale results did not provide support for the diversity–stability relationships in the planktonic and benthic communities of these 2 estuaries, since species richness was not the main stability driver in

both studied systems. Species synchrony was overall the most important mechanism contributing to community stability in these estuaries, and similar results have been reported in other systems exposed to a high degree of environmental forcing (Campbell et al. 2011, Bulleri et al. 2012). Despite the statistically significant variations in total community density and biomass throughout the study, the variability of the analyzed community-level properties did not vary seasonally in both estuaries. This stable variability constitutes a mechanism to cope with environmental fluctuations in these systems. In conclusion, our results suggest that species synchrony and stable variability are the mechanisms responsible for the environmental homeostasis of these 2 estuaries. Our study reiterates the need for the establishment of specific management programs for estuaries which recognize that estuarine environmental variability constitutes a subsidy to their biota and not a stress. However, it is first necessary to determine thresholds in the measures of stability which allow us to detect state changes within and across estuarine systems.

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