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Austral winter marine epilithic diatoms: Community composition and distribution on intertidal rocky substrate around the coast of South Africa

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ABSTRACT

The knowledge on the composition and spatial distribution of marine benthic diatoms around the coast of South Africa remains limited. Epilithic diatom assemblages from natural intertidal rocky substrate and physico-chemical variables were investigated during July–August in 2016 and 2017 along the South African coastline. A total of 85 diatom taxa from 31 genera were observed at 15 sites along the coast. Taxa with the highest contribution included *Nitzschia* (9 species), *Cocconeis* (7 species) and *Achnanthes* (6 species) and the observed Shannon–Wiener diversity (H') during the study varied from 0.44 (Kraalbaai) to 2.09 (Bird Island). Non-metric multidimensional scaling ordination (nMDS) separated the diatom assemblages into three groups with 20% similarity among sites (grouped according to coastal sections) and PERMANOVA analysis revealed a significant difference between the coastal sections. The observed diatom composition was shown to be influenced by both nutrient concentrations along the west coast and temperature along the east coast. This study provides insights on the abundance and distribution patterns of marine littoral diatoms along the coastline and the potential environmental drivers. The observed variations in diatom composition and distribution warrant further investigations if they are to be considered as potential indicator species of change.

1. Introduction

Globally, the marine rocky intertidal zone is considered one of the most biologically diverse environments, owing to the number of microhabitats harbouring communities, from microalgae to intertidal fauna (Stephenson, 1944; Bustamante et al., 1995; Underwood et al., 2008; Maggi et al., 2017). Intertidal rocky shores remain well studied habitats, with ecological studies covering the spatio-temporal variation of organisms along stretches of coastlines (Bustamante and Branch, 1996; Underwood and Chapman, 1996; Underwood et al., 2008). On noting the ecological importance of epilithic microphytobenthos (EMPB) in aquatic habitats, the structure and spatial distribution of rocky shore EMPBs has been studied across numerous rocky coasts (e.g. United Kingdom, Thompson et al., 2005; Australia, Jackson et al., 2010; Mediterranean, Maggi et al., 2017). To date, studies on South Africa's intertidal communities have covered trophic structure (McQuaid and Branch, 1985; Blanchette et al., 2008), effects of abiotic factors

(McQuaid et al., 2000), primary productivity and biological interactions (Branch et al., 1987; Bustamante et al., 1995), zonation and distribution of intertidal communities (Stephenson and Stephenson, 1949; Bustamante et al., 1997) and biogeography (Sink et al., 2005; Bolton, 1986). However, studies focusing on the ecology of marine microphytobenthos on rocky shores still require investigation.

Marine benthic diatoms dominate marine biofilms on hard substrata (MacLulich, 1987; Thompson et al., 2005) and play an important role in marine primary production (MacIntyre et al., 1996). Worldwide, marine epilithic diatom assemblages attached to natural or artificial substrata have been investigated, with studies ranging from those that assess the taxonomic composition to those evaluating diatom response to environmental variables (e.g. Castenholz, 1963; MacLulich, 1987; Al-Handal and Wulff, 2008; Hillebrand and Sommer, 1997, 2000; Totti et al., 2007). In South Africa, studies on benthic diatoms have been conducted from freshwater to the coastal marine environments (Cholnoky, 1958, 1963; Giffen, 1971, 1973; 1975; Schoeman and Archibald, 1976;

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Schoeman et al., 1984). Further, studies were particularly focused on the use of diatoms for biomonitoring and investigating their distribution along environmental gradients (Taylor et al., 2005; Holmes and Taylor, 2015; see review by Dalu and Froneman, 2016; Dalu et al., 2016). Despite these efforts, the knowledge on the diversity and distribution of marine benthic diatoms along the coast of South Africa remains largely unexplored.

Epilithic diatom assemblages are affected by a number of abiotic and biotic factors such as temperature, salinity, nutrients and grazing (Ulanova and Snoeijs, 2006; Hillebrand and Sommer, 2000). MacLulich (1986, 1987) investigated the colonisation of natural substrata by intertidal microflora and the subsequent variation in density along an Australian rocky shore. Bavestrello et al. (2000) discussed the possible influence of mineralogical features of rocky substrata on marine benthic communities. Furthermore, efforts to understand the response of epilithic diatoms on natural substrata to changing environmental variables and biological control (i.e. grazing) along coastal marine waters have been made (Hillebrand et al., 2000; Çolak Sabanci, 2011; Al-Harbi, 2017; Hafner et al., 2018), as well as for microflora grown on artificial substrata (e.g. Hillebrand and Sommer, 1997; Patil and Anil, 2005; Totti et al., 2007; Jackson et al., 2013). Despite the known effects of numerous factors on epilithic assemblages (e.g. surface roughness, see Hutchinson et al., 2006; Sempere-Valverde et al., 2018), Desrosiers et al. (2013) noted that marine epilithic diatoms have the potential for use as bio-indicators; however, research on the composition of epilithic diatom assemblages in coastal marine environments, which serve as fundamental baseline data, is still lacking.

Given this knowledge gap, the aim of this study was primarily to

assess and describe the relative abundance, community composition and spatial distribution of marine epilithic diatoms on natural substrata along the intertidal zone of the South African coast. Secondly, we wished to interrogate the influence of physico-chemical variables on the spatial structure of diatom communities. Due to the known coastal temperature gradient and its influence on rocky intertidal communities along the coast (McQuaid and Branch, 1984; Smit et al., 2013), we hypothesised that the diatom community composition will differ between the coastal sections. This study provides baseline data for modern quantitative studies and contributes to the knowledge of marine benthic diatom diversity and biogeography in the southern African region.

2. Materials and methods

2.1. Study region and sampling method

The South African coastline is estimated to be ca. 3100 km in length (Schlegel et al., 2017) and is comprised of rocky, sandy and mixed shores (Harris et al., 2011). Seventeen rocky shore types have been identified (see Harris et al., 2019). The coastline is influenced by two major ocean currents, the cold Benguela and the warm Agulhas currents (Fig. 1), which results in a mean coastal inshore water temperature gradient from $12.0 \pm 0.9^\circ\text{C}$ on the west coast to $24.0 \pm 1.9^\circ\text{C}$ on the east coast (Smit et al., 2017). The coastline is predominantly wave exposed, experiencing a semi-diurnal tidal regime with a tidal range of approximately 2 m (Griffiths et al., 2010). In terms of the coastal topography, the rocky substratum along the coast is comprised of different rock types that include sandstone, quartzite from the Table Mountain Group, black

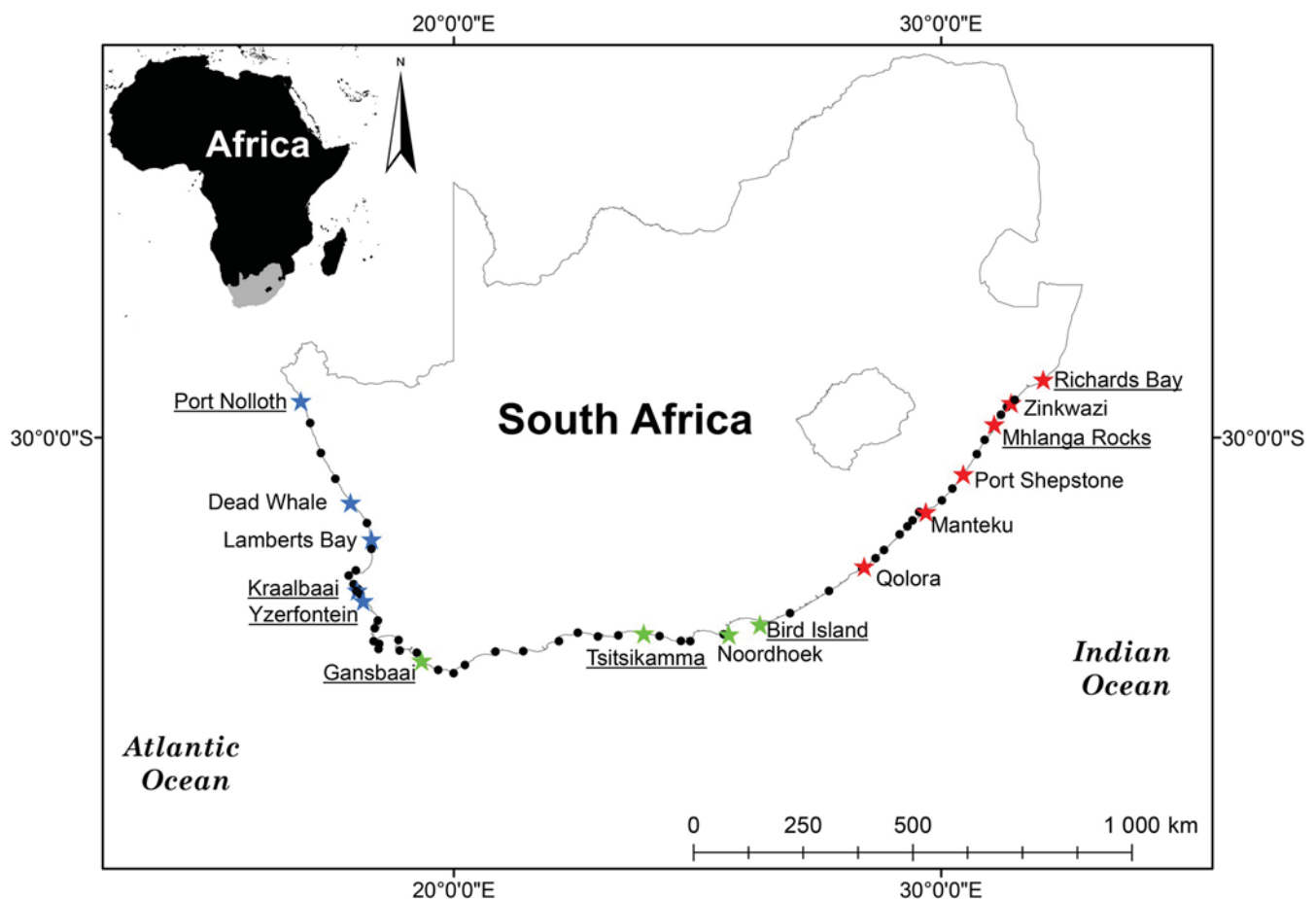


Fig. 1. Map of South African coastline indicating sampling sites visited during the study. Locations with diatom material were categorised according to coastal sections, namely; west (blue stars), south (lime) and east (red) coasts following Smit et al. (2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

shale, compact siltstone and olive-grey sandstone from the Bokkeveld Group, granite, boulders, dolerite and aeolianite beach rock (Bolton and Anderson, 1990; Rust, 1991, 1998).

Marine epilithic diatom samples were collected from the natural rocky substratum during coastal surveys conducted in July–August (winter season) of 2016 (west coast sampling) and 2017 (east coast sampling), totalling 63 sampling sites along the coast (Fig. 1). Global positioning system (GPS) coordinates of all surveyed sites are provided in Table S3 (Supplementary Material). The sampling was conducted during spring-low tide and the distances between the sampling sites varied due to the consideration of accessibility. It was not possible to collect samples from the entire coastline in the same year; however, for comparative purposes, sampling only occurred during winter to eliminate seasonal differences, and all sites were visited once. Due to variable oceanographic features and temperature differences observed along the coast, we subdivided the coastline into three coastal sections, namely the west, south and east coasts after Smit et al. (2013) and Schlegel et al. (2017).

2.2. Physico-chemical and nutrient variables

Physico-chemical variables were measured *in situ*; these included temperature (°C), salinity, dissolved oxygen (DO - mg l⁻¹), pH and turbidity (nephelometric turbidity units - NTU) using a YSI 6600-V2 multiprobe (Yellow Springs, OH). For nutrient analysis, triplicate water samples (500 ml) were collected and gravity-filtered through glass-fibre filters (Whatman® GF/F), the filtrates were then stored in 150 ml bottles and frozen (-20 °C). The filtrates were analysed for inorganic nutrient concentrations; nitrate (NO₃⁻) plus nitrite (NO₂⁻), ammonium (NH₄⁺), soluble reactive phosphorus (PO₄³⁻) and silicate (SiO₄), according to the Bate and Heelas (1975) and Strickland and Parsons (1972) methodology adapted for use with the SEAL AA3 Auto Analyser (Mostert, 1983). The inorganic nutrients were presented as dissolved inorganic nitrogen (DIN - NO₃⁻, NO₂⁻ and NH₄⁺) and phosphorus (DIP - PO₄³⁻) and the DIN:DIP and DIN:Si ratios were determined for selected sites.

2.3. Diatom sampling, preparation and counting

Epilithic diatom sample collection was conducted using a sterile toothbrush to scrape the surface of at least five randomly chosen rocks (total surface area ~100 cm²), the diatom material was homogenised into a 50 ml centrifuge tube and immediately preserved with 1 ml of 25% glutaraldehyde solution. Samples were then cleaned by removing carbonate particles and organic matter using 10% hydrochloric acid (HCl) and 37% hydrogen peroxide (H₂O₂), respectively. After thorough rinsing with distilled water, permanent slides were prepared by pipetting the cleaned material onto acid-washed coverslips and allowed to air dry overnight and subsequently mounting the cover slips onto glass slides using the Naphrax® mountant (refractive index = 1.7). The slides were examined using a Zeiss AxioScope A1 light microscope (LM) equipped with differential interference contrast (DIC) at 1000 × magnification (under oil immersion). During the current study, some samples were found to contain low numbers of diatom valves while other samples did not contain any diatom material despite two slides being examined at 1000 × magnification. For quantitative analyses, a minimum of 300 diatom valves were counted on random transects across the slides made from the eight sites that yielded sufficient material (underlined in Fig. 1). The absolute counts were converted and presented as relative abundance (RA in %). After counting, the slides were scanned for diatom taxa not encountered during the counts. All identified taxa that were not part of counts were excluded from the multivariate analysis and only recorded in the species list (Table S2 in Supplementary Material). Diatoms were identified to genus or species level (where possible) using Álvarez-Blanco and Blanco (2014); Cox (2006); Giffen (1973, 1975 and 1976); Lobban et al. (2012); Trobajo

et al. (2013), Wachnicka and Gaiser (2007), and Witkowski et al. (2000). The nomenclature of identified taxa was confirmed using AlgaeBase (Guiry and Guiry, 2019). Reference samples and slides are currently stored at the SAEON Elwandle Node, South Africa, with duplicate slides held at the Palaeoceanology Unit, University of Szczecin, Poland.

2.4. Data analyses

Diversity indices, including Shannon–Wiener diversity (H'), Pielou's evenness (J') and Simpson's dominance (λ) and diversity (1-λ), were calculated using the absolute diatom abundance from eight sites in PRIMER v.6 software (Clarke and Gorley, 2006). Further analysis was performed using square root transformed diatom abundance data to balance the effect of highly abundant and rare taxa. The spatial patterns of diatom assemblages among sampling sites (grouped according to coastal sections) were visualised using non-metric multidimensional scaling (nMDS) ordination and the permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) test was performed to test for significant differences between the coastal sections. The nMDS and PERMANOVA analyses were based on Bray-Curtis similarity resemblance matrix (Clarke and Warwick, 2001). The contribution of species (%) to the dissimilarity of diatom assemblages between the sampling sites was then assessed using SIMPER (similarity percentage analysis). Kraalbaai (west coast site) count data were dominated by only two species and therefore left out of the nMDS, PERMANOVA and SIMPER analyses. CANOCO v4.5 (Ter Braak and Šmilauer, 2002) was used to investigate the influence of the physico-chemical variables on the diatom assemblages—we first removed diatom taxa that had a relative abundance of less than 1%. This reduced the number of taxa from 61 to 47 species which accounted for 77% of the total number of species identified from the eight sites. A detrended correspondence analysis (DCA) was performed, and based on the length of the longest axis (longest gradient length = 4.1), a unimodal ordination method was selected. Collinearity among the physico-chemical variables was assessed using variance inflation factors (VIFs) and values of VIF ≥ 4 were considered to exhibit high collinearity (Zuur et al., 2009). Variables that exhibited high VIF values (DIN, DIP and DO) were subsequently omitted from the canonical correspondence analysis (CCA).

The annual mean coastal *in situ* temperature dataset from the sampled sites (>10 years daily measurements, from the South African Coastal Temperature Network - SACTN¹) was included in the CCA as an additional variable. We performed the CCA to evaluate the relationship between the diatom assemblages (square root transformed data) and measured physico-chemical variables including the annual mean coastal temperature using forward selection and Monte Carlo permutation tests (999 unrestricted permutations, *p* < 0.05) to assess the significance of the canonical axes.

3. Results

3.1. Physico-chemical and nutrient variables

Coastal water temperatures showed an increasing gradient from the west to the east coast along the coastline (Table 1 and Table A1 in Appendix A). As expected in coastal marine waters, saline conditions (range 34.8–35.5) and dissolved oxygen (DO) concentrations (~7.5 mg l⁻¹) indicative of oxygenated water were evident at all sampling sites. The pH readings were alkaline (~7.4–8.2) throughout the sampling sites. Turbidity levels also remained similar (~5.0 NTU) along the sampling sites except for Bird Island where low (< 2 NTU) turbidity conditions were recorded (Table 1). Nutrient concentrations, particularly dissolved inorganic nitrogen (DIN) and silicate, were high along the west coast sites (e.g. Port Nolloth) compared to the east coast (e.g.

¹ <https://robert-schlegel.shinyapps.io/SACTN/>.

Table 1

Physico-chemical data recorded at eight sites along the coastline. DO = Dissolved oxygen, DIN = Dissolved inorganic nitrogen, DIP = Dissolved inorganic phosphorus. DIN, DIP and Silicate values are means of three replicates (n = 3).

Variable	Sites							
	Port Nolloth (PN)	Kraalbaai (KB)	Yzerfontein (YZ)	Gansbaai (GB)	Tsitsikamma (TK)	Bird Island (BI)	Mhlanga Rocks (MR)	Richards Bay (RB)
<i>Physico-chemical</i>								
Temperature (°C)	10.3	15.9	12.7	13.8	15.4	16.5	21.0	19.5
Salinity	34.8	34.8	35.1	35.3	35.4	35.3	35.5	35.3
DO (mg l ⁻¹)	8.7	7.8	8.4	8.2	8.3	8.7	7.5	7.6
pH	7.4	8.2	7.9	7.9	8.0	7.9	8.2	7.9
Turbidity (NTU)	6.5	6.0	5.2	5.0	6.3	0.7	6.3	4.8
<i>Nutrients</i>								
DIN (µM)	31.4 ± 12.2	11.3 ± 5.6	14.1 ± 6.8	13.3 ± 6.1	3.0 ± 1.3	7.7 ± 2.7	2.3 ± 0.8	1.1 ± 0.3
DIP (µM)	2.5 ± 0.2	2.1 ± 0.56	1.1 ± 0.1	1.8 ± 0.2	0.2 ± 0.0	12.4 ± 6.2	0.8 ± 0.3	2.9 ± 2.0
Silicate (µM)	18.4 ± 0.7	12.0 ± 8.9	5.3 ± 1.5	17.0 ± 7.4	2.6 ± 0.6	7.1 ± 1.7	2.5 ± 0.7	1.4 ± 0.6

Richards Bay) (Table 1). The ratios of DIN:DIP and DIN:Si were generally low, peaking at 7:1 and 6:16, respectively, compared to the Redfield thresholds of 16:1 (DIN:DIP) and 16:16 (DIN:Si). This revealed that the coastal waters sampled sites were nitrogen limited during this study (Table S1 in Supplementary Material).

3.2. Diatom assemblages

A total of 61 diatom taxa belonging to 22 genera were identified across the eight sampling sites. Genera with the highest contribution were *Nitzschia* (9 species – spp.), *Cocconeis* (7 spp.), *Achnanthes* (6 spp.), *Amphora* (5 spp.), *Navicula* (5 spp.) and *Tabularia* (5 spp.). *Achnanthes brevipes*, *Achnanthes yaquiniensis*, *Navicula johannrossi* and *Navicula pseudosalinarum* were observed to be present across multiple sites (up to four of the eight sites) along the coastline (Table 2). Taxa varied at each site, with some species observed in high relative abundance (RA %) at only one site during this study e.g. *Nitzschia steenbergensis* (30%) in Tsitsikamma, *Craspedostauros capensis* (43.3%) in Port Nolloth and *Stricosus* sp. (60.7%) in Richards Bay. The diatom communities were dominated by taxa with low relative abundances of < 5% across sampling sites, e.g. *Amphora helenensis*, *Cocconeis dirupta*, *Nitzschia laevis*, *Seminavis strigosa* (Table 2). Of the 61 diatom taxa, 36 had a RA of < 1% and were only observed once at a particular site including *Cocconeis costata* (Port Nolloth), *Craspedostauros decipiens* (Tsitsikamma) and *Grammatophora cf. marina* (Richards Bay) (Table 2). Altogether, including sites that yielded minimum diatom material not used during the analyses, a total of 85 diatom taxa from 31 genera were observed across a total of 15 sites during the current study (Table S2 in Supplementary Material). The total numbers of taxa observed from the 15 localities varied non-systematically along the coastline, the numbers of taxa from the eight sampling sites with sufficient material are shown in Fig. 2.

Species richness (S) was high at Bird Island compared to other sites in this study and relatively similar between other sites, except for Kraalbaai, where the only taxa observed were *A. brevipes* and *A. yaquiniensis*. Shannon–Wiener diversity values (H') varied from 0.44 (Kraalbaai) to 2.09 (Bird Island); however, they were similar between other sampling sites. Pielou's evenness (J') ranged from 0.47 to 0.80 and the Simpson diversity ($1 - \lambda$) was highest at Bird Island (0.82) followed by Yzerfontein (0.78) and Port Nolloth (0.75) (Table 3).

The nMDS ordination separated the diatom assemblages into three groups and showed a 20% similarity between the sampling sites, grouped according to coastal sections. In terms of diatom assemblages, the coastal sections differed significantly (PERMANOVA; $p < 0.05$) (Fig. 3, Table 4). The SIMPER analysis revealed a high average dissimilarity of 90% between the coastal sections based on the diatom

assemblages. A total of 29 taxa were found to contribute to the dissimilarity between the west and south coasts, and the taxa with a cumulative contribution of greater than 80% included *Tabularia fasciculata*, *A. brevipes*, *N. laevis*, *Nitzschia cf. inconspicua* and *Amphora* sp. *Amphora crenulata*, *N. steenbergensis*, *Craspedostauros* sp., *Navicula* sp. and *Cocconeis scutellum* contributed to the observed dissimilarity between the west and east coasts. The average dissimilarity of 90.4% between the south and east coasts sampling sites was contributed to by *Hyalosira deliculata*, *Licmophora communis*, *C. scutellum*, *Tabularia investiens*, *Achnanthes* sp. and *A. helenensis*. When grouped according to genera abundance, *Achnanthes* spp., *Amphora* spp., *Navicula* spp. and *Nitzschia* spp. were found to be present in varying abundances across the sampling sites with 20% similarity between sites, indicating a wide distribution (Fig. 4).

With regards to the relationship between the diatom assemblages and physico-chemical variables, explored using the CCA (Fig. 5), the results showed that the first and second axes explained 23.6% and 19.7% of the species-environment relation and accounted for 0.733 and 0.609 of the eigenvalues, respectively. The CCA ordination of 47 species (RA > 1%) and six physico-chemical variables (based on their VIF values of < 4) including annual mean coastal temperature values showed diatom composition observed along the east coast sites (e.g. site 7 - Mhlanga Rocks and site 8 - Richards Bay) were associated with both elevated temperature and the annual mean temperature (e.g. *Parlibellus bennikei*, *Nitzschia angularis*, *Amphora fluminensis*, *Stricosus* sp., *Cocconeis convexa*). Meanwhile, the diatom composition along the west coast sites (e.g. site 1 - Port Nolloth and site 3 - Yzerfontein) were associated with silicate concentrations. Interestingly, the diatom assemblage observed at Bird Island (site 6 - south coast) was shown to be associated with silicate, similar to the west coast sites (Fig. 5).

4. Discussion

The existing knowledge on the marine littoral diatoms from selected locations along the coast of South Africa remains purely from taxonomic contributions (e.g. Cholnoky, 1963, 1958; Giffen, 1966, 1970, 1975 and 1976; Witkowski et al., 2011; Dąbek et al., 2014, 2019). Having noted these contributions, this study presents the first attempt, to our knowledge, at providing quantitative data and insight with regards to the composition and distribution of marine epilithic diatoms from natural substrata along the rocky intertidal zone of the South African coast.

4.1. Community composition, diversity and distribution

In this study, the intertidal diatom assemblages observed at each site revealed a contribution by both rare and highly abundant taxa. Our investigation showed that the diatom community composition across

Table 2

List of diatom taxa and their relative abundances (%) observed at eight sites along the coastline. See Table 1 for site full names.

	Taxa	Code	Sites							
			PN	KB	YF	GB	TS	BI	MR	RB
1	<i>Achnanthes brevipes</i> C. Agardh	<i>Ach bre</i>		16.0	2.7	28.3	29.3	28.3		
2	<i>Achnanthes brevipes</i> var <i>intermedia</i> (Kützing) Cleve	<i>Ach brein</i>				61.7	20.0		1.3	
3	<i>Achnanthes parvula</i> Kützing	<i>Ach par</i>			3.3					3.7
4	<i>Achnanthes sancti-pauli</i> Heiden in Heiden & Kolbe	<i>Ach sapa</i>							2.3	3.7
5	<i>Achnanthes yaquiniensis</i> McIntire & Reimer	<i>Ach yaq</i>		84.0				6.7	5.3	6.7
6	<i>Achnanthes</i> sp.	<i>Ach sp1</i>					1.7			
7	<i>Amphora crenulata</i> A.H.Wachnicka & E.E.Gaiser	<i>Amp cre</i>						5.0		
8	<i>Amphora fluminesis</i> Grunow	<i>Amp flu</i>							4.0	
9	<i>Amphora helenensis</i> Giffen	<i>Amp hel</i>	2.7			1.3				
10	<i>Amphora subacutiscula</i> Schoeman	<i>Amp sub</i>			4.0					
11	<i>Amphora</i> sp. 1	<i>Amp sp1</i>			2.0					
12	<i>Calonies fusioides</i> (Grunow) Heiden & Kolbe	<i>Cal fus</i>	2.7							
13	<i>Cocconeis alucitae</i> Riaux-Gobin & Compère	<i>Coc alu</i>								0.7
14	<i>Cocconeis convexa</i> Giffen	<i>Coc con</i>								1.7
15	<i>Cocconeis costata</i> Gregory	<i>Coc cos</i>	0.7							
16	<i>Cocconeis dirupta</i> Gregory	<i>Coc dir</i>				0.7				1.7
17	<i>Cocconeis dirupta</i> var <i>flexella</i> (Janisch & Rabenhorst) Grunow	<i>Coc dfl</i>						2.0		
18	<i>Cocconeis scutellum</i> Ehrenberg var. <i>scutellum</i>	<i>Coc scu</i>					0.3	1.3		
19	<i>Cocconeis krammeri</i> Lange-Bertalot & Metzeltin	<i>Coc kra</i>						1.3		
20	<i>Craspedostauros capensis</i> Cox	<i>Cra cap</i>	43.3		7.0					
21	<i>Craspedostauros decipiens</i> (Hustedt) Cox	<i>Cra dec</i>					0.3			
22	<i>Craspedostauros</i> sp. 1	<i>Cra sp1</i>						4.7		
23	<i>Delphineis minutissima</i> (Hustedt) Simonsen	<i>Del min</i>						0.3		
24	<i>Diploneis</i> cf. <i>vacillans</i> (A. Schmidt) Cleve	<i>Dip vac</i>							0.7	
25	<i>Fragilariopsis pseudonana</i> Haslea	<i>Fra pse</i>					0.3			
26	<i>Gomphonemopsis pseudexigua</i> (Simonsen) Medlin	<i>Gom pse</i>								10.7
27	<i>Grammatophora</i> cf. <i>marina</i> (Lyngbye) Kützing	<i>Gra mar</i>								0.3
28	<i>Grammatophora pfannkucheae</i> Giffen	<i>Gra pfa</i>						1.0		
29	<i>Grammatophora undulata</i> Ehrenberg	<i>Gra und</i>						0.3		
30	<i>Halamphora hybrida</i> (Grunow) Levkov	<i>Hal hyb</i>			7.7					
31	<i>Hyalinella lateripunctata</i> Witkowski, Lange-Bertalot & Metzeltin	<i>Hya lae</i>				0.3				
32	<i>Hyalosira deliculata</i> Kützing	<i>Hya del</i>							1.3	
33	<i>Hyalosira tropicalis</i> J.N.Navarro	<i>Hya tro</i>						1.0		
34	<i>Licmophora communis</i> (Hieberg) Grunow	<i>Lic com</i>					2.7			
35	<i>Licmophora paradoxa</i> (Lyngbye) C. Agardh	<i>Lic par</i>			1.0			18.0		
36	<i>Licmophora partita</i> Giffen	<i>Lic part</i>				0.3				
37	<i>Navicula johannrossi</i> Giffen	<i>Nav joh</i>	6.0		42.3	1.3		23.0		
38	<i>Navicula</i> cf. <i>nasuta</i> Giffen	<i>Nav nas</i>	21.3		8.3					
39	<i>Navicula pseudosalinarum</i> Giffen	<i>Nav pse</i>	7.0		5.0		12.7		55.0	8.0
40	<i>Navicula</i> sp.1	<i>Nav sp1</i>					2.7		2.0	
41	<i>Navicula</i> sp.2	<i>Nav sp2</i>				2.0				
42	<i>Neofragilaria nicobarica</i> Desikachary, Prasad & Prema	<i>Neo nic</i>				2.3				
43	<i>Nitzschia angularis</i> W. Smith	<i>Nit ang</i>							7.0	
44	<i>Nitzschia dissipata</i> (Kützing) Rabenhorst	<i>Nit dis</i>						2.0		
45	<i>Nitzschia inconspicua</i> Grunow	<i>Nit inc</i>			9.7	1.7				
46	<i>Nitzschia</i> cf. <i>inconspicua</i> Grunow	<i>Nit cinc</i>								2.0
47	<i>Nitzschia laevis</i> Hustedt	<i>Nit lae</i>	2.33					1.3		
48	<i>Nitzschia panduriformis</i> var <i>continua</i> Grunow	<i>Nit pan</i>							0.3	
49	<i>Nitzschia rorida</i> Giffen	<i>Nit ror</i>	1.7						6.7	
50	<i>Nitzschia scalpelliformis</i> Grunow	<i>Nit sca</i>	0.7							
51	<i>Nitzschia steenbergensis</i> Giffen	<i>Nit ste</i>					30			
52	<i>Parlibellus bennikei</i> Witkowski	<i>Par ben</i>							8.3	
53	<i>Seminavis strigosa</i> (Hustedt) Daniedis & Economou-Amilli	<i>Sem str</i>							2.7	0.3
54	<i>Stricosus</i> sp.	<i>Str sp</i>								60.7
55	<i>Synedra commutata</i> Grunow	<i>Syn com</i>						0.3		
56	<i>Synedra</i> sp. 1	<i>Syn sp1</i>						0.3		
57	<i>Tabularia investiens</i> (W. Smith) Williams & Round	<i>Tab inv</i>	7.0					2.7		
58	<i>Tabularia</i> cf. <i>investiens</i> (W. Smith) Williams & Round	<i>Tab cirv</i>	2.0							
59	<i>Tabularia fasciculata</i> (C.Agardh) Williams & Round	<i>Tab fas</i>	2.7					0.3		
60	<i>Tabularia ktenoeoides</i> Kuylenstierna	<i>Tab kte</i>							3.0	
61	<i>Tabularia</i> sp. 1	<i>Tab sp1</i>			7.0					

sampling sites was dominated by taxa in low relative abundance ($\leq 5\%$). Despite this, the presence of taxa with high relative abundance was evident; however, most of these taxa were observed once at one specific site during the study. The numerous rare taxa thus contributed to the relatively high species richness at seven of the eight sites (see Tables 2 and 3). Site-specific differences in composition were evident, with certain diatom species making significant contributions ($\sim 40\%$ RA) to the diatom composition found at a particular site. Examples included

C. capensis at Port Nolloth, *N. johannrossi* at Yzerfontein and *N. pseudosalinarum* at Mhlanga Rocks (Table 2). Interestingly, the diatom composition at Kraalbaai was only contributed to by *Achnanthes* taxa (*A. brevipes* and *A. yaquiniensis*), hence it was the only site with low species richness and thus, diversity compared to other sites in this study (Table 3). During this study, taxa that were only recorded along the west coast were *Amphora subacutiscula*, *C. costata* and *Halamphora hybrida*. Section-specific taxa were also evident on the south (e.g. *A. crenulata*,

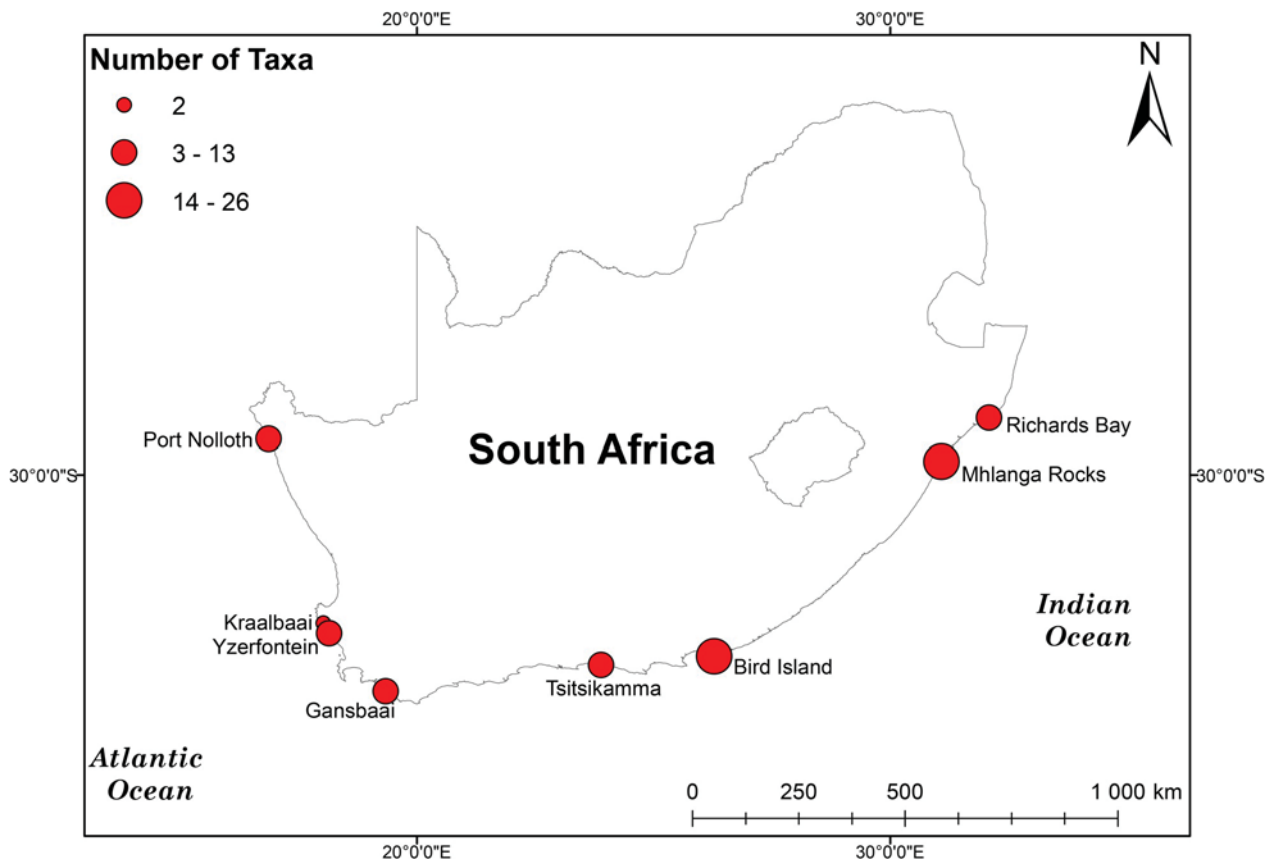


Fig. 2. Number of taxa recorded in eight sampling sites along the coastline.

Table 3

Diversity indices of the diatom assemblages observed across the eight sites along the coast. S = species richness, J' = Pielou's evenness, H' = Shannon index, λ = Simpson dominance index, 1 - λ = Simpson diversity index.

Sites	S	J'	H'	λ	1 - λ
Port Nolloth	13	0.71	1.82	0.25	0.75
Kraalbaai	2	0.63	0.44	0.73	0.27
Yzerfontein	12	0.80	1.98	0.22	0.78
Gansbaai	10	0.47	1.08	0.46	0.54
Tsitsikamma	10	0.70	1.62	0.23	0.77
Bird Island	19	0.71	2.09	0.18	0.82
Mhlanga Rocks	14	0.65	1.72	0.33	0.67
Richards Bay	12	0.58	1.45	0.39	0.61

C. capensis, and *L. communis*) and east coasts (e.g. *Diploneis cf. vacillans*, *A. fluminensis* and *Stricosus* sp.). With the exception of Kraalbaai, composition at other sites was contributed to by up to ten diatom species, comprised of both sporadic and abundant taxa. There were some spatial differences with regards to species richness and diversity, with high diversity (H' value) observed at Bird Island (south coast), followed by Yzerfontein (west coast) (Table 3). The similarity in diversity values of diatom assemblages from different sampling sites (this study) differs from Hernández-Almeida and Siqueiros-Beltrones (2012) who reported similarity in diversity values of diatom assemblages from the same locality. We argue that due to the nature of this study being a 'snapshot' and how spatially sparse our data were (few sites with diatom material), we cannot infer that there is great diatom diversity on any given scale (e.g. local, regional, etc.) along the coast of South Africa based on the current data. Baseline data (this study) and continued investigation on the changes in marine benthic diatom composition over time, will, however, enable future comprehensive studies of diatom diversity (e.g. β-diversity) along the coast (Smit et al., 2017). Notwithstanding the

limits of 'snapshot sampling' data, it can be used to measure relatively large-scale spatial patterns (Bustamante and Branch, 1996; Rivadeneira et al., 2002). Underwood et al. (2008) stressed that quantifying the patterns of species in order to understand their ecological function and response to changing environment is an important aspect towards the study of biodiversity on rocky shores.

Our results demonstrated spatial variability based on diatom assemblages as shown by the nMDS ordination. The patterns of sampling sites grouped according to coastal sections were found to be significantly different (see Fig. 3, Table 4). The SIMPER analysis revealed a high dissimilarity between the coastal sections based on diatom assemblages contributed to by a number of diatom taxa including *A. helenensis*, *C. scutellum*, *H. delicaluta*, *N. cf. inconspicua*, and *N. steenbergensis*. The observed distribution of the diatom taxa found during the current study offers insights into the cosmopolitan nature of benthic diatoms. Several diatom taxa reported in our study have been recorded in other marine regions such as *A. brevipes*, *C. scutellum*, *T. fasciculata*, *Licmophora paradoxa*, *Trachyneis aspera* and *Nitzschia dissipata* (e.g. Baltic Sea, Vilbaste et al., 2000; Mediterranean, Çolak Sabancı, 2011; Hafner et al., 2018). However, knowledge on the extent of diatom species distribution still requires further field and experimental investigations. Our observations revealed that, despite a number of diatom taxa being observed across multiple sites, the diatom genera *Achnanthes* spp., *Amphora* spp., *Navicula* spp. and *Nitzschia* spp. were widely distributed along the coastline (see Fig. 4).

The current study contributes to both the regional and global knowledge on marine benthic diatom composition and distribution, given the location and characteristics of our study area. Despite the paucity in studies on marine benthic diatom composition, the results of our study are comparable to a few, but with noticeable differences. In the South African context, the taxonomic investigations by Giffen (1966, 1970, 1971, 1973, 1975 and 1976) covered locations along the west,

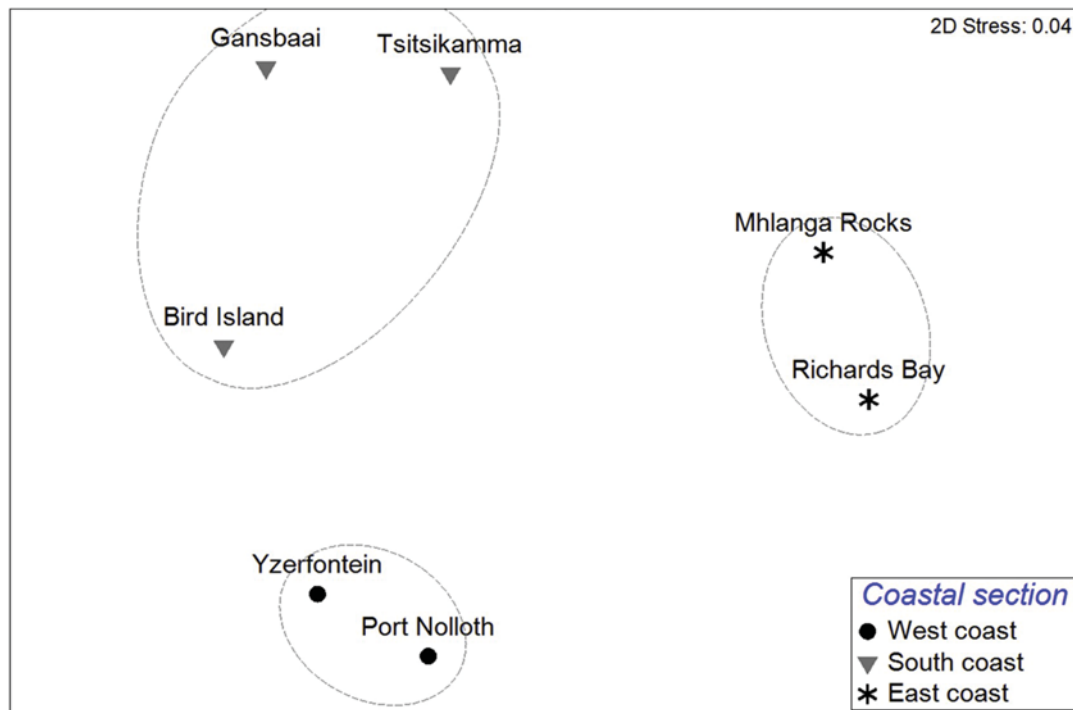


Fig. 3. Non-metric MDS ordination based on the diatom assemblages at the sampling sites. The dotted lines represent 20% similarity.

Table 4

PERMANOVA results comparing diatom assemblages across the coastal sections (west, south and east). df = Degree of freedom, MS = Mean square. Significance $\alpha = 0.05$.

Source	df	MS	F	P
Coastal section	2	5645.3	2.219	0.018
Residual	4	2544		
Total	6			

south and east coasts. These investigations described diatom taxa and some provided limited insight on quantity and distribution (e.g. “wide-spread”, “not frequent”; Giffen, 1976). However, these studies lacked quantitative data similar to the current study. In contrast, Giffen’s sample collections were mostly epiphytic microalgae on macroalgae (e.g. *Ecklonia* spp. *Laminaria* spp.; Giffen, 1970; *Cladophora* spp. *Corallina* spp.; Giffen, 1973). The epiphytic diatom community on common macroalgae along the intertidal zone of South Africa is yet to be investigated. Bate et al. (2013) recorded a total of 333 diatom taxa from intertidal sites around the coast of South Africa; however, their study was focused on estuarine epipelagic diatoms rather than epilithic assemblages. Globally, marine epilithic diatom studies from other regions have investigated diatom community composition on both natural and artificial substrates. However, these studies have stark differences based on the scope of each study, thus limiting comparison of data as noted by Totti et al. (2009). Our current study shares limited similarity with works from Çolak Sabancı (2011), Al-Harbi (2017) and Hafner et al. (2018) who studied the diversity of epilithic diatom communities on natural substrata. However, their studies were mainly focused on the seasonal changes in diatom community in relation to environmental variables, which was not the scope of this study. Ulanova and Snoeijis (2006) studied the response of epilithic diatom community from natural substrata to environmental variables off the Swedish coast. Meanwhile, Al-Handal and Wulff (2008) provided relative abundance and distribution of epilithic diatoms from an artificial substrate from Potter Cover, Antarctica, with no relation to environmental variables or other factors. The differences in study designs, methodology and substrate choices

with regards to marine benthic diatom studies hinder comparison, but do not invalidate the data from regions with poor baseline studies. At present, our knowledge on the composition of marine benthic diatoms on the rocky shoreline of South Africa remains limited and further studies are required to fully understand the diatom composition and distribution over space and time.

4.2. Diatom assemblages and physico-chemical variables

Given the highly dynamic nature of the intertidal environment, physical and biological factors are known to drive the abundance and diversity of intertidal assemblages (Underwood et al., 2008). The environmental conditions during this study exhibited a known occurrence of low temperatures coupled with high nutrient concentrations along the west coast compared to the elevated temperature and low nutrients along the east coast, as observed by Bustamante et al. (1995) and Smit et al. (2013). The CCA showed temperature as the influential variable associated with the assemblages along the east coast and silicate concentrations were associated with the assemblages along the west coast. It is worthy to note that the structure of the diatom communities found along the west coast could also be attributed to the nutrient concentrations in the form of dissolved inorganic nitrogen (DIN) and phosphorus (DIP). These inorganic nutrients along with dissolved oxygen (DO) were strongly correlated with temperature and not used in the CCA (see Methods). The DIN:DIP and DIN:Si ratios along the sites indicated nitrogen as the potential limiting nutrient during this study. This is in line with Downing (1997), where a global analysis of nitrogen to phosphorus was shown to be low in coastal ecosystems. However, the nutrient stoichiometry of benthic microalgal growth still required further investigation following (Hillebrand and Sommer, 2000).

During this study, we observed high species richness and diversity at Bird Island compared to other sites in this study, and this could be attributed to nutrients concentrations via guano from seabirds. Bird Island harbours large seabird colonies that have been shown to enhance rocky intertidal communities along the west coast of South Africa (Bosman and Hockey, 1986). The results of this study showed that salinity, which was relatively constant along the coast, did not influence

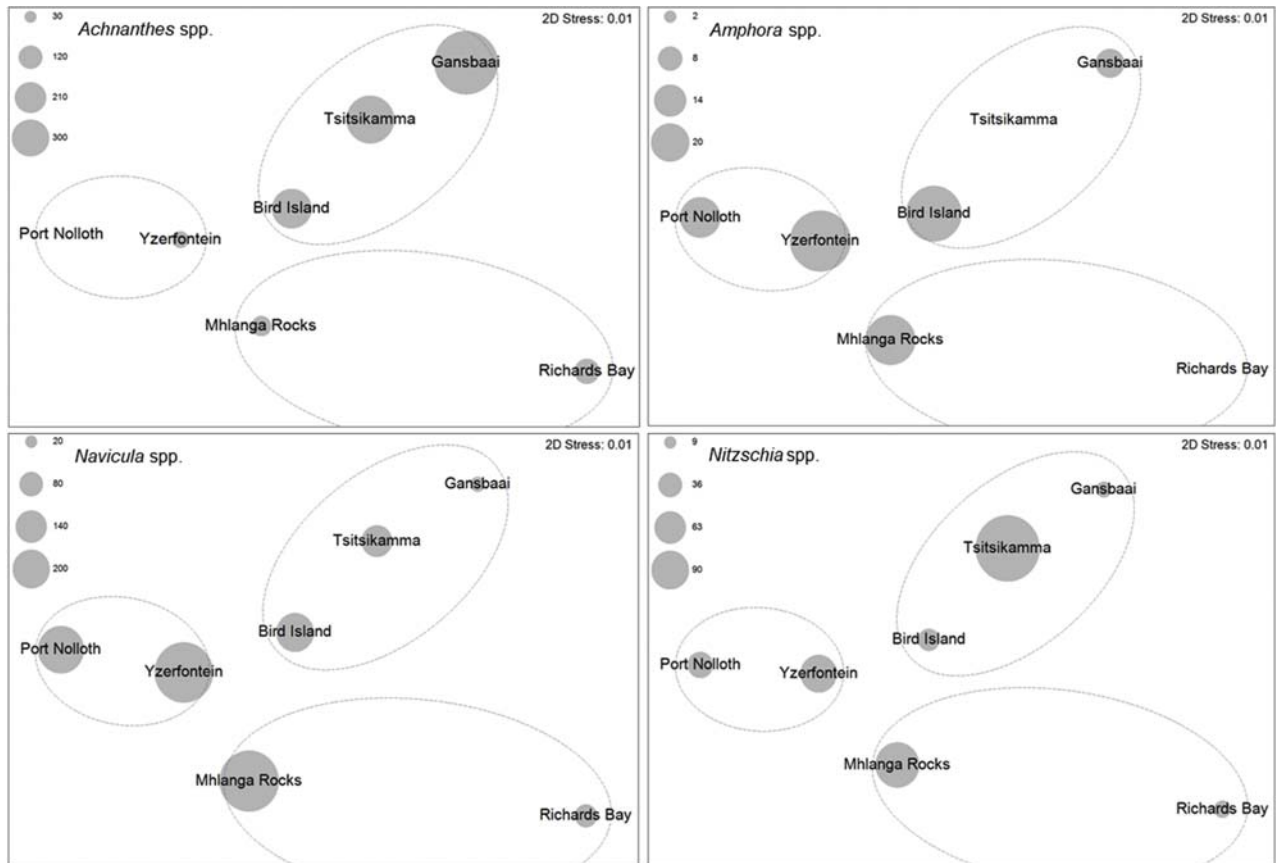


Fig. 4. Non-metric MDS bubble plots showing abundance of four genera distributed across the sampling sites. The dotted lines represent 20% similarity.

the diatom assemblages or their distribution, similar to observations made by Çolak Sabancı (2011). Due to the limited data from our study, we do not infer that the identified variables are the main drivers of the diatom assemblages and their distribution because the influence of other factors (e.g. substrate type, wave exposure) has not been accounted for. Several studies have investigated the distribution and response of benthic diatom communities to environmental variables and nutrients in estuarine (Underwood et al., 1998; Cibic et al., 2012; Dalu et al., 2016) and marine systems (Cunningham and McMinn, 2004; Çolak Sabancı, 2011; Hafner et al., 2018). Comparatively, there is a lack of similar studies in the coastal environment along the South African coast. Our study suggests that the coupling between measured physico-chemical variables and underlying site-specific processes (e.g. substrate mineralogy, grazing, competition, etc.) could explain the overall epilithic diatom composition along the coast of South Africa. During the current study, diatom composition and distribution were partly explained by the measured physico-chemical variables, particularly temperature, therefore partially supporting our hypothesis that diatom assemblages would differ across the coastal sections. Temperature has been shown to influence the composition of benthic organisms and acts as an important driver of biogeographical patterns (Blanchette et al., 2008; Tittensor et al., 2010). Bolton (1986) and Bolton and Anderson (1990) reported that the structure and composition of macroalgae (seaweeds) along the coast were correlated with temperature regimes, with substrate type having no effect on the observed composition. Further, a study by James et al. (2016) also suggested a link between coastal temperature and the abundance and distribution of mugilid fish species along the coastline. In our study, the coastal *in situ* seawater temperature (annual mean) showed a similar effect to that of the on site temperature measurements during sampling (Fig. 5). This emphasises the influential role of temperature as a potential driver of the composition and distribution of

coastal benthic microalgae, similarly to macroalgae along the coastline. An attempt to quantify changes in marine epilithic diatom community and their response to physical and chemical factors over time is under investigation. Other factors have been shown to influence organisms along intertidal rocky coastline and McQuaid and Branch (1984) found the effects of substrate on biota to be highly overridden by the effects of temperature and wave exposure. Similarly, Bustamante and Branch (1996) reported a greater diversity of autotrophs along the coast of South Africa that was driven by wave action. However, field and laboratory experimental work is required to further elucidate the effect of other factors such as grazing and substrate type on the marine epilithic diatom assemblages observed in this region, as shown elsewhere by Hillebrand et al. (2000), Totti et al. (2007), Sempere-Valverde et al. (2018). Çolak Sabancı (2011) mentioned that, due to the continual changes and interactions between biotic and abiotic factors in transitional environments such as intertidal rocky shore, it is difficult to pinpoint which factors affect the community structure.

5. Conclusion

The results showed variability in the number of diatom taxa recorded along the coastline despite some similarities in diatom assemblages between sites. With regards to distribution patterns, some diatom genera were found to be widely distributed across the coastal sections, however, section- and site-specific diatom taxa were also evident. The interplay between the measured physico-chemical variables was the potential environmental driver of the observed diatom communities and their distribution. More research is required on other physical, chemical and biological factors that may influence the marine microphytobenthos, as well as spatial variability within microhabitats and seasonal changes in response to environmental conditions. However, our results provided

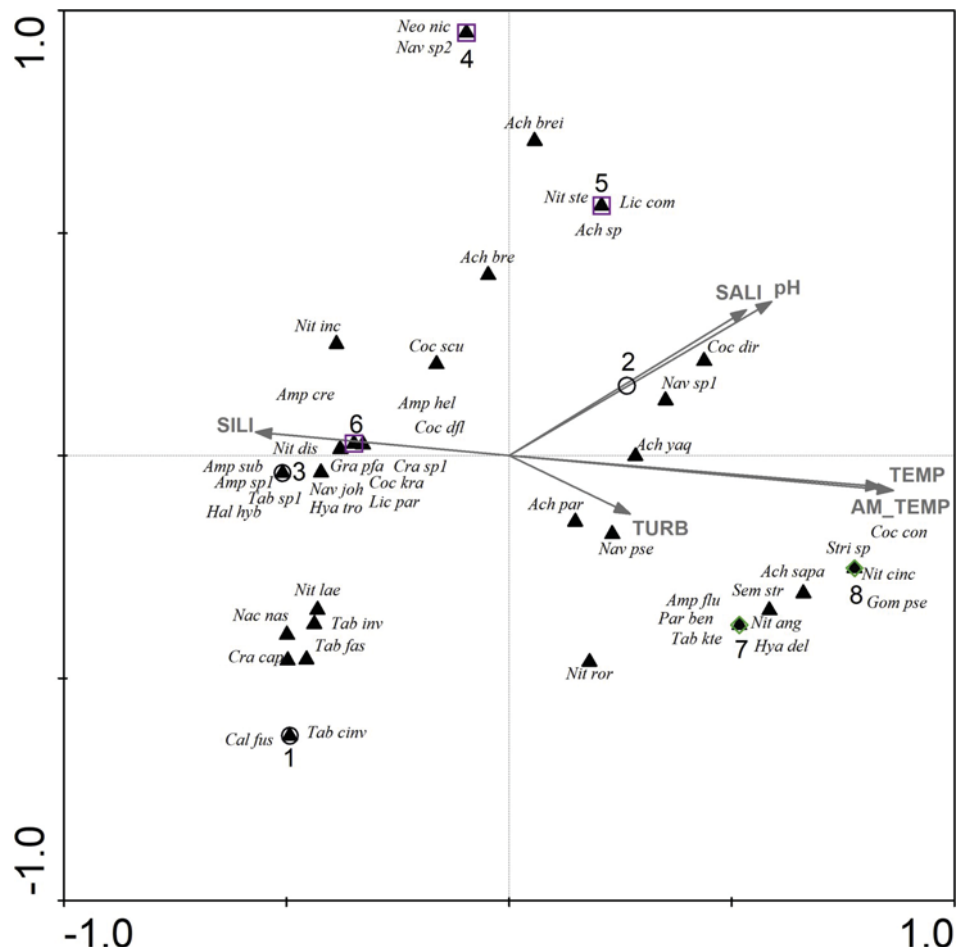


Fig. 5. CCA ordination showing diatom taxa (triangles) in relation to physico-chemical variables (arrows) recorded along the coastline. Numbers indicate sampling sites – black circles (west coast), purple squares (south coast) and green squares (east coast). Abbreviations: TEMP – Temperature; SALI – salinity; TURB – Turbidity; SILI – Silicates; AM_TEMP – Annual Mean Temperature. Codes for diatom taxa are highlighted in Table 2.

much needed quantitative data on marine epilithic diatoms in this region to improve our knowledge on the biogeography of marine diatoms and to set the baseline against which change in the community could be measured.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Phumlile Cotiyane-Pondo: Formal analysis, Conceptualization, Writing - original draft, Writing - review & editing. **Thomas G. Bornman:** Funding acquisition, Conceptualization, Supervision, Writing - review & editing. **Przemysław Dąbek:** Methodology, Writing - review & editing. **Andrzej Witkowski:** Funding acquisition, Conceptualization, Methodology. **Albertus J. Smit:** Supervision, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2020.106837>.

Table A1

Physico-chemical data recorded at sampling sites with minimum diatom material along the coastline. DO = Dissolved oxygen, DIN = Dissolved inorganic nitrogen, DIP = Dissolved inorganic phosphorus. DIN, DIP and Silicate values are means of three replicates (n = 3).

Variable	Sites						
	Dead Whale (DW)	Lamberts Bay (LB)	Noordhoek (NH)	Qolora (QO)	Manteku (MA)	Port Shepstone (PS)	Zinkwazi (ZK)
<i>Physico-chemical</i>							
Temperature (°C)	13.1	13.6	17.2	19.7	18.8	21	20.8
Salinity	34.9	35.1	35.3	35.5	35.8	35	35.6
DO (mg l ⁻¹)	8.9	8.6	8.5	8.0	8.0	8	8.3
pH	8.0	8.0	8.0	8.1	8.1	8	8.0
Turbidity (NTU)	5.8	4.1	4.1	8.4	6.5	5	6.8
<i>Nutrients</i>							
DIN (µM)	3.2 ± 0.8	3.6 ± 1.1	1.4 ± 0.4	0.9 ± 0.2	0.9 ± 0.2	0.8 ± 0.2	1.0 ± 0.3
DIP (µM)	2.4 ± 0.1	1.2 ± 0.1	0.2 ± 0.0	1.2 ± 0.4	0.7 ± 0.1	1.9 ± 1.5	2.2 ± 1.5
Silicate (µM)	5.2 ± 0.1	0.3 ± 0.0	8.6 ± 0.8	1.4 ± 0.1	1.1 ± 0.2	1.1 ± 0.2	1.9 ± 0.4

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