



Depth and inter-annual variation of crustacean diversity within *Ecklonia maxima* holdfast communities in the Benguela-Agulhas transition zone of the South African coast

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Abstract

Kelp holdfasts form complex, three-dimensional biogenic habitats that support diverse macroinvertebrate assemblages, yet the crustacean fauna within these structures which are an important contributors to secondary production and trophic transfer in kelp forest food webs remains poorly quantified. We characterised crustacean assemblages associated with holdfasts of the kelp *Ecklonia maxima* at Miller's Point, False Bay, South Africa, to test for effects of depth and interannual variation. In 2024, we compared assemblages between shallow (2–5 m) and deep (6–8 m) holdfasts. To assess temporal change, holdfasts from shallow depths (2–5 m) were sampled annually from 2023 to 2025, with the 2024 shallow holdfasts serving as the shared shallow cohort for both comparisons across a total of 29 independently harvested holdfasts. Across all holdfasts, we recorded 10,560 crustaceans representing 131 morphospecies, 60 families and 10 orders, grouped into 12 functional categories based on mobility and feeding strategy. Deeper holdfasts hosted significantly more individuals and higher species richness (458.8 ± 70.7 SE individuals and 43.3 ± 4.2 SE species per holdfast) than in shallower holdfasts. Assemblage composition also varied significantly among years, with functional-group composition tracking these taxonomic shifts. These findings show that *E. maxima* holdfasts support unexpectedly high, spatially and temporally dynamic crustacean diversity, highlighting their role as biodiversity hotspots within kelp forests and pointing to the need for additional surveys to incorporate other taxa, kelp species and regions.

Keywords Kelp forests · Benthic community structure · Biodiversity · Macroinvertebrates · False Bay

Introduction

Kelps are large brown macroalgae of the order Laminariales (Bolton 2010) and form extensive three-dimensional, multi-layered forest habitats that dominate shallow subtidal

rocky reefs in temperate regions globally (Steneck et al. 2002; Krumhansl et al. 2016). The kelp biome is present along approximately 22% of the global coastline at latitudes between approximately 25–70° in the northern hemisphere, and 25–55° in the southern hemisphere (Jayatilake and Costello 2020) with distribution predominantly driven by sea surface temperature (5–25 °C) and light availability (Steneck et al. 2002; Graham et al. 2007a, b; Bolton 2010). In South Africa, wide-spread kelp forests, colloquially termed the Great African Seaforest, are dominated by two kelp species, *Ecklonia maxima* and *Laminaria pallida*, and extend for approximately 1,300 km along the south and south-west coastline (Dunga et al. 2024). The kelp forests are also expanding eastward in response to localised cooling driven by changing wind patterns (Bolton et al. 2012).

Kelp forests provide direct, significant economic benefits through fishing and tourism (Jerardino and Navarro 2002;

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Blamey and Bolton 2018; Eger et al. 2023), and indirect services such as coastal protection, nutrient cycling, carbon sequestration, recreation and education (Velimirov et al. 1977; Duggins 1988; Bustamante and Branch 1996a; Blamey and Bolton 2018; Filbee-Dexter and Wernberg 2020; Eger et al. 2023; Rosenthal 2023). Unlike terrestrial forests that rely on soil for nutrient uptake, kelp forests are supplied with nutrients from the surrounding water, resulting in high levels of primary production, making them among the most productive biomes on earth (Mann 1973; Brady-Campbell et al. 1984; Pessarrodona et al. 2022).

Kelps function as both ecosystem engineers and foundation species, providing a physical structure within these temperate rocky reef habitats (Miller et al. 2018; Pérez-Matus et al. 2025). Through physical engineering, kelps offer a complex diversity of microhabitats, food sources, and nursery areas, which in turn facilitates an increase in available ecological niches (Anderson et al. 1997; Steneck et al. 2002; Teagle et al. 2017; Miller et al. 2018). As a foundation species, these kelp forests support a wide range of taxa ranging from fishes (Pérez-Matus et al. 2025) to benthic macroinvertebrate assemblages including crustaceans, polychaetes, bivalves, urchins and anemones, all of which characterise these ecosystems (Anderson et al. 2005; Arnold et al. 2016; Winkler et al. 2017; Teagle et al. 2018; Carbajal et al. 2022). These macroinvertebrates form a critical link in kelp forest food webs, by transforming kelp primary production to secondary production, supporting higher trophic levels (Beviss-Challinor and Field 1982; Norderhaug et al. 2005; Lorentsen et al. 2010).

Kelp habitats can be divided into three vertical layers, the upper canopy made up of fronds, the vertical stipes, and the basal holdfasts (Carbajal et al. 2022). The holdfasts, which anchor the algae to the substrate, are structurally complex, consisting of intertwined, branching, root-like haptera interspersed with small spaces that create numerous niches that support most of the kelp forest's biodiversity (Hauser et al. 2006; Christie et al. 2003). The haptera provide a complex habitat, greatly increasing surface area for colonisation (Orland et al. 2016; Velasco-Charpentier et al. 2021) and providing protection from both physical stress, such as wave action and temperature extremes (Perry et al. 2024; Christie et al. 2003), and from predation (Coull and Wells 1983). Additionally, holdfasts trap sediment and particulate organic matter from the surrounding water, increasing food availability and habitat heterogeneity (Moore 1972; Smith et al. 1996). As holdfasts age, new layers of haptera are progressively developed, enlarging and increasing the volume and complexity of the holdfast (Kain and Jones 1963) and increasing habitat available to colonising fauna (Smith et al. 1996; Hauser et al. 2006). Several studies have reported positive relationships between holdfast volume and

macroinvertebrate abundance (Smith et al. 1996; Anderson et al. 2005) or species richness (Ojeda and Santelices 1984; Smith 1996; Anderson et al. 2005). Aside from biotic factors, such as the size and complexity of the holdfast, abiotic factors like temperature, sedimentation, hydrodynamic forces, salinity and depth may also drive patterns of diversity, abundance and composition of holdfast-associated fauna (Moore 1973, 1978; Fenwick 1976; Norderhaug et al. 2012; Teagle et al. 2018; Rios et al. 2007).

There has been extensive global research on kelp holdfasts, their associated fauna and factors driving their distribution (Jones 1972; Sheppard et al. 1980; McKenzie and Moore 1981; Bell and Coen 1982; Ojeda and Santelices 1984; Smith et al. 1996; Anderson et al. 2005; Walls et al. 2016; Teagle et al. 2017, 2018; Akita et al. 2019; Velasco-Charpentier et al. 2021; Perry et al. 2024). In South Africa, a few studies have been conducted on this habitat (Velimirov et al. 1977; Beviss-Challinor and Field 1982; Anderson et al. 1997; Katharoyan et al. 2024; Nkohla and Dlaza 2024, 2026). Over the last six decades, only six publications have provided baseline data on key macroinvertebrate communities in kelp holdfasts along the South African west (Anderson et al. 1997; Katharoyan et al. 2024) and east coast (Nkohla and Dlaza 2024, 2026), investigating depth and geographic differences (Velimirov et al. 1977; Katharoyan et al. 2024; Nkohla and Dlaza 2024, 2026) and examining the trophic structure of these holdfast microhabitats (Beviss-Challinor and Field 1982). Despite these research efforts, significant gaps remain, specifically in terms of long-term trends and bathymetric variation at fine taxonomic scales. Almost all such studies investigating holdfast communities, both globally and in South Africa, rely on once-off 'snapshot' databases resulting in knowledge gaps around long-term stability. In addition, there is a critical need for research that investigates depth-related shifts at a high taxonomic resolution.

Depth plays a critical role in the composition and distribution patterns of faunal assemblages in many marine systems, including kelp forests (Fenwick 1976; Edgar 1983a; Smith et al. 1996; Coleman et al. 2007), but in South Africa, studies that have investigated the effects of depth on biodiversity are scarce. Although Velimirov et al. (1977) compared the faunal assemblages of 'inshore' and 'offshore' kelp bed localities and reported depth-related faunal differences focussed on biomass and energy flow, the role of depth in structuring macroinvertebrate communities at a fine taxonomic resolution or at a functional level has not been explored for this ecosystem.

For this reason, this study focusses only on the Crustacea associated with *E. maxima* holdfasts from a site in False Bay, South Africa. The aims of the study were to establish a high resolution taxonomic and functional baseline of crustacean

assemblages in *E. maxima* holdfasts while investigating inter-annual variability and the role of depth in structuring these communities.

Specifically, three objectives were addressed: (1) to characterise compositional and structural shifts in crustacean assemblages between two depth categories, (2) to assess the degree of inter-annual variability over a three-year period, and (3) to determine whether functional diversity patterns mirror taxonomic diversity patterns in holdfast communities.

Methods

Study site

This study was conducted at Miller's Point, False Bay, South Africa (34.228°S, 18.470°E), which lies within the Table Mountain National Park Marine Protected Area (Fig. 1). This site lies in the transition zone of the Southern Benguela and Agulhas ecoregions (Griffiths et al. 2010) where the overlap of cold-temperate and warm-temperate currents form a globally recognised marine biodiversity hotspot. While False Bay is primarily influenced by the cold Benguela Current, periodic intrusions of the warm Agulhas Current results in a sea surface temperature range of 13–22 °C (Dufois and Rouault 2012). This dynamic environment combined with the physical habitat heterogeneity and productivity created by *Ecklonia maxima* stands supports an exceptionally complex faunal assemblage. This site

was chosen as kelp grows across an accessible depth gradient (approximately 1–8 m), its MPA status, and because it is a recognised baseline kelp forest ecology research site (Kock et al. 2022).

Sample collection

Across all three years (2023, 2024, and 2025), sample collection took place between March–May. In 2023 and 2025, 10 and seven holdfasts were collected respectively from the 'shallow' zone (defined as 2–5 m in depth). In 2024, 12 holdfasts were collected in total, with six from the shallow zone and six from a 'deep' zone (6–8 m in depth). For all collections, freedivers identified a single holdfast before prying it from the substrate using a paint scraper and a dive knife to cut off the stipe. Once loose, the holdfast was immediately enclosed in a Ziplock bag to minimise loss of macroinvertebrates. In the laboratory, the holdfast was cut into smaller segments and rinsed in seawater to remove and collect the organisms present (Anderson et al. 2005; Katharoyan et al. 2024). The rinsed water was passed through a mesh sieve of 500 µm to retain smaller macroinvertebrates. Once all organisms were removed and haptera were cleaned of epibiota, holdfast volume was measured through water displacement. One holdfast was collected, processed, and measured at a time.

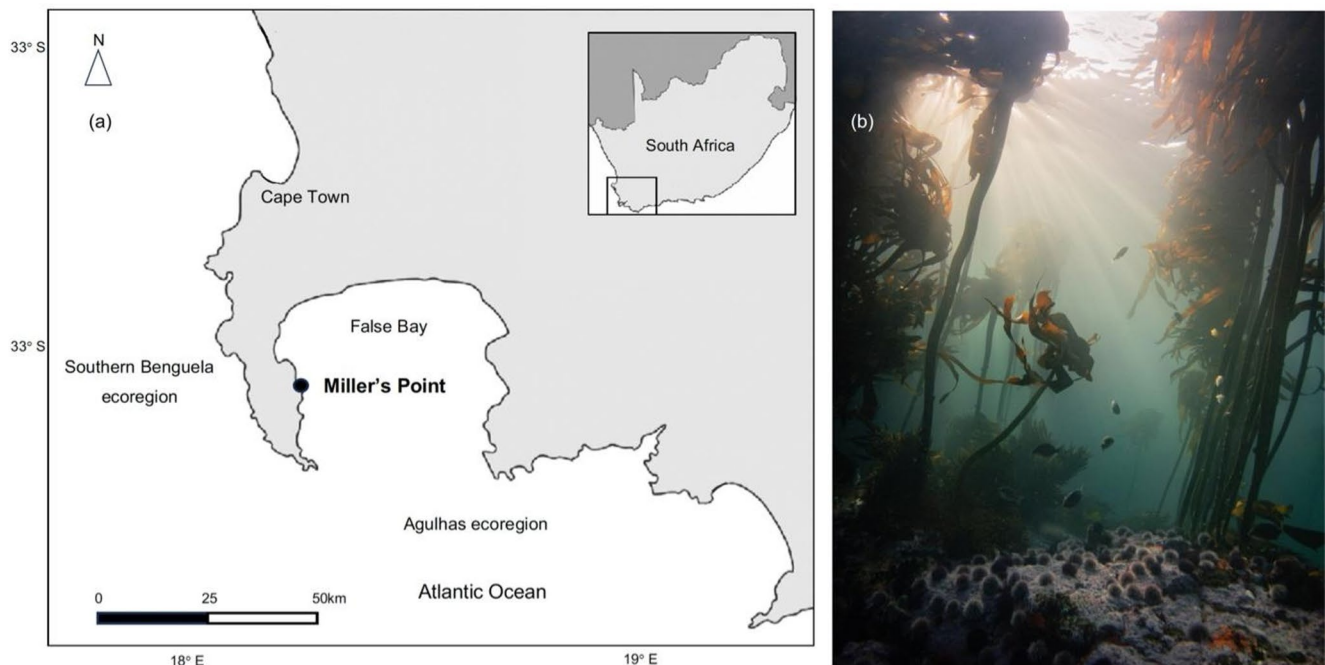


Fig. 1 Location of Miller's Point within False Bay (a), a transition zone between the Southern Benguela and Agulhas marine ecoregions. At this site, *E. maxima*, a foundation species of kelp, forms an undersea forest supporting a complex and diverse ecosystem. Photo: Jannes Landschoff

Macroinvertebrate processing and identification

Crustaceans were pre-sorted by eye, counted and identified to the lowest taxon level under a microscope using published guides (Day 1969; Griffiths 1976; Kensley 1978; Branch et al. 2022) and with the aid of taxon experts. The status of species' names was checked on the World Register of Marine Species (<http://www.marinespecies.org> accessed 26 October 2025) and updated accordingly. Selected specimens, including all rare individuals, were photographed using two camera systems; the microscope function of an Olympus TG-7 together with a BigBlue VTL4200 underwater video light, and/or a Nikon 5100 with an R1C1 Speedlight flash system. All specimens were preserved in 99% ethanol. To ensure consistency in species identification across years and research teams, all specimens were re-examined and identifications confirmed. The collection and processing of the holdfasts and the identification methods used were the same across the three years.

Functional diversity analyses

All families were characterised in terms of mobility (mobile, tube-dwelling, burrowing, sessile) and diet (detritivore, filter feeder, carnivore, deposit feeder, grazer) based on literature. Twelve functional groups were defined and count data was consolidated per group.

Statistical analysis

All analyses were conducted in RStudio and R version 4.3.3 (R Core team 2025). Species count data were used for analyses, and diversity metrics were calculated for each holdfast and analysed using the 'vegan' package, version 2.6–10 (Oksanen et al. 2022). Diversity metrics included species richness (S), Margalef index (d'), Shannon-Wiener index (H'), and Pielou's evenness index (J').

To analyse depth-related differences, only the 2024 samples were used. Diversity metrics were compared across depth with a permutational ANCOVA based on Euclidean distance. Depth was considered a fixed factor, and holdfast volume a covariable. A permutational analysis of covariance (PERMANCOVA) was used to analyse changes in community composition between depth categories. A total of 999 Permutations, under a reduced model, were based on a Bray-Curtis similarity matrix from square-root transformed abundance data. Depth was treated as a fixed factor and holdfast volume was a covariable to all analyses, as diversity and abundance are known to be related to the size (and hence volume) of the holdfast (Ojeda and Santelices 1984; Smith 1996). A SIMPER analysis was conducted

on count data to determine which species contributed to the dissimilarity between depths.

To analyse inter-annual differences, only the shallow (2–5 m) samples were used from all three years (2023: $n=10$; 2024: $n=6$; 2025: $n=7$). Diversity metrics were compared across years with a permutational ANCOVA based on Euclidean distance. Year was considered a fixed factor, and holdfast volume a covariable. A permutational analysis of co-variance (PERMANCOVA) was used to analyse changes in community composition across years. A total of 999 Permutations, under a reduced model, were based on a Bray-Curtis similarity matrix from square-root transformed abundance data. Year was treated as a fixed factor and holdfast volume was included as a covariable. A SIMPER analysis was conducted on count data to determine which species contributed to the dissimilarity between years.

Lastly, a similar multivariate PERMANOVA approach was used to analyse functional diversity across years and depth. A total of 999 Permutations, under a reduced model, were based on a Bray-Curtis similarity matrix from count data. Two models were run, one for 'Year' and one for 'Depth', with volume as a covariable in both.

Results

General crustacean diversity

Overall, 10,560 individuals belonging to 131 crustacean species from 60 families in 10 orders were retrieved from 29 holdfasts samples from 2023 to 2025 (Supplementary Table 1). On average, each holdfast contained 24 (± 9 SE) species and 325 (± 182 SE) individual crustaceans. Amphipoda was the most abundant order both in terms of number of individuals (7,979) and number of species (68), making up 76% of total individuals and 52% of species. The second most important order in terms of both abundance and species number was Isopoda with 1,285 individuals from 35 species. Two Amphipoda species, *Chevalia aviculae* Walker, 1904, and *Latigammaropsis atlantica* (Stebbing, 1888) were particularly common contributing 22% and 13% of total individual counts respectively. The most speciose families were Caprellidae (12) followed by Sphaeromatidae (8), Maeridae (7), Podoceridae, Anthuridae and Photidae (6 species per family) (Supplementary Table 1).

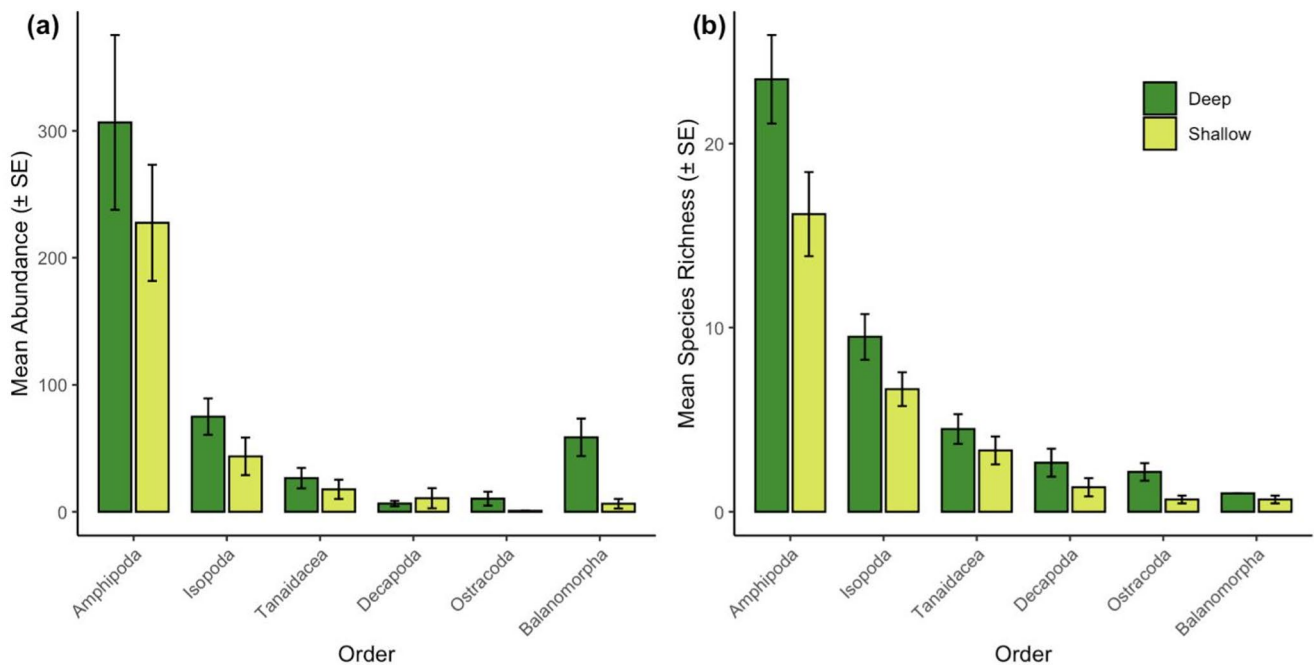
Comparisons across depth

There were significant differences in species richness between holdfasts sampled from different depth intervals in 2024 ($p=0.027$, Table 1). Holdfasts from deeper waters (6–8 m) had a higher average count, S, d' , and H' values but

Table 1 PERMANOVA results based on the Bray–Curtis similarity matrix for square-root transformed crustacean abundance data for 2024 across two depth categories, and ANCOVA results comparing Shannon–Wiener Index (H') and species richness (S) across two depth categories and *E. maxima* holdfast volume

Source	df	PERMANOVA			H' - ANCOVA			S - ANCOVA		
		MS	Pseudo-F	<i>p</i>	MS	Pseudo-F	<i>p</i>	MS	Pseudo-F	<i>p</i>
Depth	1	0.42	2.812	0.003	0.59	4.560	0.074	588.00	8.034	0.027
Volume	1	0.24	1.585	0.056	1.32	10.157	0.004	273.95	3.743	0.088
Residual	9	0.15			0.08			73.19		
Total	11									

Bold values represent significant differences (Alpha=0.05)

**Fig. 2** (a) Mean abundance of individuals and (b) mean species richness ($\pm$ SE) per holdfast of the six most abundant crustacean orders in deep ($n=6$) and shallow ($n=6$) *E. maxima* holdfasts at Millers Point, False Bay, South Africa

similar J' compared to those from shallow waters (2–5 m) (Supplementary Table 1). Overall, 61% (2,914) of all the individuals collected were from deep holdfasts and only 1,842 from shallow holdfasts. Moreover, a total of 94 species were collected from the deep holdfasts, compared to only 79 in the shallow holdfasts (Supplementary Table 1), with 31% of species exclusively found in the deeper samples and 17% of species that were exclusively found in the shallows.

While there was a greater abundance of crustaceans in holdfasts collected at greater depth (Supplementary Table 1), proportions of higher taxa appear to be similar across both depth categories (Fig. 2). Amphipoda were the most dominant order at both depths in terms of abundance and species richness, followed by Isopoda and then Tanaidacea (Fig. 2). Balanomorpha was the only Order to show a strong depth preference, with deep holdfasts contributing some 90% (352 individuals in deep samples) of all individuals collected (390 individuals in both deep and shallow

samples) (Fig. 2), however this is based on distribution of just the single species *Notomegabalanus algicola*. Although Amphipoda were more abundant in deep holdfasts (1,840 individuals) compared to shallow samples (1,365 individuals) (Fig. 2), they made up a larger proportion of the total individuals collected in shallow holdfasts (74%) compared to deep holdfasts (63%).

Volume was a significant covariable for the Shannon–Wiener Index between depths ($p=0.025$) but was not significant for community composition or species richness ($p=0.09$; Table 1). However, species richness was significantly higher at greater depths (Supplementary Table 1; Table 1).

Similarly, community composition varied significantly across depth (PERMANOVA, Table 1). Species assemblages in deep water were more even across different holdfasts compared to a more variable species composition in shallow holdfasts. The non-metric multidimensional scaling

Fig. 3 Non-metric multidimensional scaling (nMDS) ordination of the crustacean assemblages between depths in 2024 based on Bray Curtis similarity matrix for square root transformed count data



Table 2 SIMPER analysis showing average similarity between the 2024 shallow and deep *E. maxima* holdfasts with the relative contribution of the top five species to this similarity; and the inter-depth dissimilarity with the contribution of the top 10 species in Miller's Point

Depth	Average similarity (%)	Species	Contribution (%)
Shallow	30.43	<i>Chevalia aviculae</i>	35.44
		<i>Latigammaropsis atlantica</i>	14.70
		<i>Photis dolichommata</i>	13.37
		<i>Panathura serriacauda</i>	4.28
		<i>Mesanthura cf. catenula</i>	4.14
Deep	43.48	<i>Chevalia aviculae</i>	27.04
		<i>Notomegabalanus algicola</i>	11.38
		<i>Stenetrium crassimanus</i>	7.90
		<i>Paramoera capensis</i>	5.95
		<i>Aora anomala</i>	4.80
Depth comparison	Average dissimilarity (%)	Species	Contribution (%)
Shallow/Deep	73.22	<i>Latigammaropsis atlantica</i>	4.41
		<i>Notomegabalanus algicola</i>	4.28
		<i>Chevalia aviculae</i>	3.56
		<i>Maera vagans</i>	3.17
		<i>Stenetrium crassimanus</i>	3.02
		<i>Gammaropsis</i> sp. 1	2.88
		<i>Aora anomala</i>	2.49
		<i>Paramoera capensis</i>	2.44
		<i>Ceradocus (Denticeradocus) rubromaculatus</i>	2.40
		<i>Gammaropsis</i> sp. 2	2.30

plot (nMDS) (Fig. 3) showed a distinct clustering of the deep holdfasts away from the more scattered shallow holdfasts.

Deep holdfasts had an average similarity of 48.84% and shallow holdfasts an average similarity of 41.30%, indicating notable inter-sample variability (Table 2). The amphipod *C. aviculae* was the most abundant species in both shallow and deep holdfasts (Supplementary Table 1) and was the greatest contributor to the similarity between holdfasts within shallow (18.19%) and deep (11.58%)

zones (Table 2), however this species also contributed to the dissimilarity between deep and shallow zones due the higher number of individuals collected in deep holdfasts (total of 559 individuals) compared to shallow ones (327 individuals).

Table 3 PERMANOVA results based on the Bray–Curtis similarity measure for square-root transformed crustacean abundance data, and ANCOVA results comparing Shannon–Wiener Index (H') and species richness (S) of *E. maxima* holdfasts from shallow (2–5 m) habitats across three years

Source	df	PERMANOVA			H' - ANCOVA			S - ANCOVA		
		R^2	Pseudo-F	p	MS	Pseudo-F	p	MS	Pseudo-F	p
Year	2	0.17	4.56	0.001	1.03	4.25	0.035	277.33	6.67	0.012
Volume	1	0.11	2.95	0.001	1.16	4.80	0.041	479.86	11.54	0.002
Residual	19	0.73			0.24			41.58		
Total	15									

Bold values represent significant differences (Alpha=0.05)

Table 4 Post hoc pairwise comparison between years

Comparison between years	df	R^2	F	p
2023 VS 2024	1	0.13	2.17	0.017
2023 VS 2025	1	0.22	4.12	0.001
2024 VS 2025	1	0.16	2.10	0.001

Bold values represent significant differences (Alpha=0.05)

Inter-annual variability

Community assemblage, H' and S were all significantly different in shallow samples (2–5 m) across years and appear to correlate with holdfast volume (Table 3). Importantly, holdfast volume was not significantly different across years (ANOVA– $df=2$; $F=1.91$; $p=0.17$). Although the 2025 samples had the highest average count per holdfast, the 2024 samples revealed the highest S , H' , d' and J' averages per holdfast (Supplementary Table 1).

A post hoc analysis revealed that each year was significantly different in terms of community composition (Table 4). This is also evident from the nMDS which showed separation of communities between years with a distinct

clustering of holdfasts from 2024 to 2025 away from the more scattered 2023 (Fig. 4).

Amphipoda dominated in terms of counts across all years (2023: 78.7%, 2024: 74.1%, 2025: 87.2%), followed by Isopoda in 2023 (14.3%) and 2024 (14.25), but in 2025 Isopoda only accounted for 3.7% of total counts (Supplementary Table 1). Instead, Balanomorpha were the third most abundant group that year, representing 6.7% of total counts. In 2023, Ostracoda had the third-highest average relative abundance of individuals (5.6%), however this was mainly due to one holdfast having > 150 individuals (all others had < 10). In 2024 shallow samples, Tanaidacea had the third-highest relative average abundance (5.8%) but only had an average relative abundance of 0.53% in 2023 and 1.0% in 2025 (Supplementary Table 1; Fig. 5).

The species assemblages in the 2024 shallow holdfasts were more uniform across samples with a higher % similarity compared to the 2023 and 2025 samples (Table 5). In terms of specific species, the Amphipoda *C. aviculae*, *L. atlantica* and *Photis dolichommata* were major contributors to similarity across all three years. However, these three species were also the highest contributors to dissimilarity

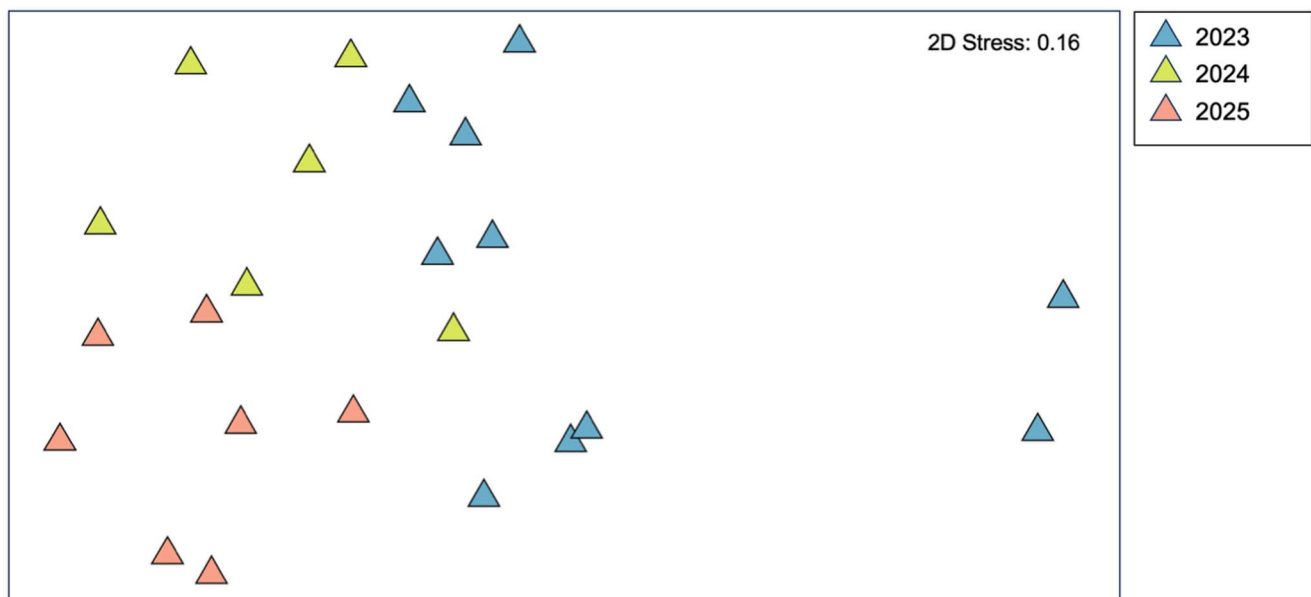
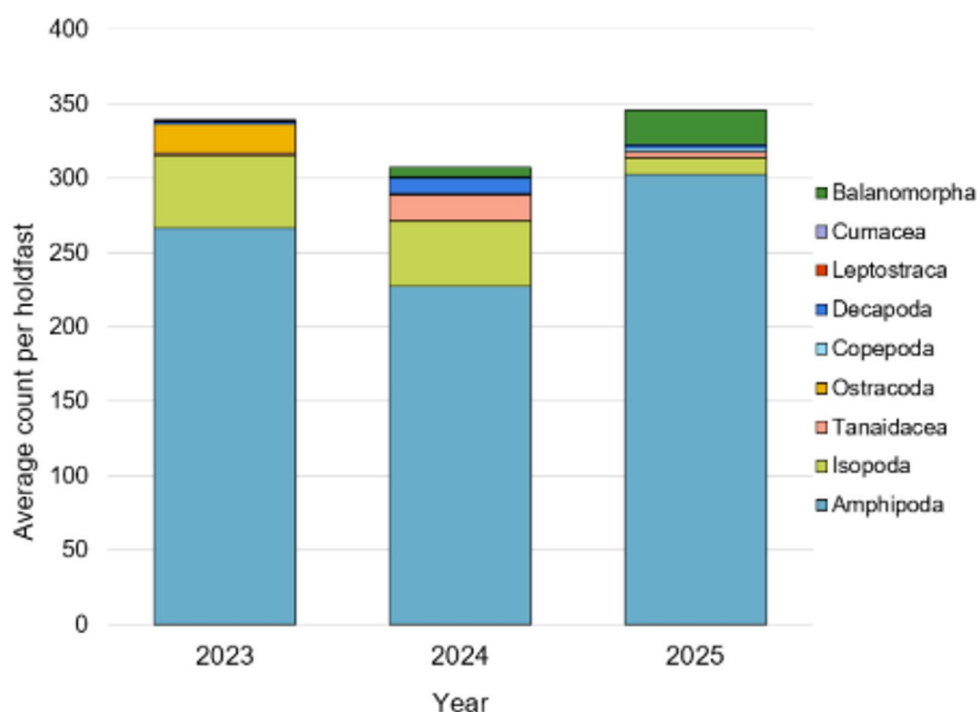
**Fig. 4** Non-metric multidimensional scaling (nMDS) ordination of the crustacean assemblages from shallow (2–5 m) habitats across three years, based on Bray Curtis similarity matrix for square root transformed count data

Fig. 5 The average numbers of Crustacea in each Order collected per *E. maxima* holdfast in 2023, 2024 and 2025 from a depth of 2–5 m in Miller's Point, False Bay



between years, because of changes in counts per holdfasts. In 2023, *L. atlantica* was the most dominant species with an average of $77.2 (\pm 23.4 \text{ SE})$ individuals per holdfast, but in 2024 *C. aviculae* became the most abundant species with $54.5 (\pm 14.9 \text{ SE})$ individuals per holdfast, increasing three-fold in 2025 to $167.0 (\pm 79.1 \text{ SE})$ individuals per holdfast (Supplementary Table 1). Similarly, *P. dolichommata* showed a consistent increase in abundance over the years (Supplementary Table 1).

Rare species and biodiversity discoveries

The majority of crustacean species in the holdfasts were $<5 \text{ mm}$, and many have rarely been previously sampled. Figures 6 and 7 show one representative specimen for each of the 16 species that contributed most strongly to the average similarities described above. For the majority of these species, no live images are available in existing local field guides. In 2024, there were 34 singleton species (only one individual found across all holdfasts), 19 collected in deep and 15 in shallow holdfasts. Furthermore, 29 species were identified only to morpho-species, but could not be named. Limited taxonomic knowledge and lack of active experts in the region make it difficult to judge if these are new to science, but at least some are almost certainly undescribed. All of the Ostracoda (5 morpho-species), Cumacea (2 morpho-species), and Copepoda (4 morpho-species), and four out of eight Tanaidacea could not be identified to species level, all of which could potentially be new and undescribed. Several species of Amphipoda, a group which one of the

authors (Griffiths) is a specialist, also contained two species of Caprellidae probably unknown to science (recorded as *Caprella* sp. 3 and *Caprella* sp. 5, Supplementary Table 1) plus an undescribed species of Podoceridae recorded as *Laetmatophilus* sp. 1 (Supplementary Table 1). Notably, one specimen of the crab *Afropinnotheres monodi* was collected from the deep zone and identified via molecular analyses (Palacios Theil, unpublished data) and is recorded from South Africa for the first time. Additionally, a species of Isopod, *Pseudojanira stenetrioides* Barnard, 1925 was collected in 2024 that has only been found previously in KwaZulu-Natal and Mozambique (Kensley 1978). Despite 2025 having the lowest abundance and diversity of Isopoda across years, three isopod species were recorded from these holdfast samples for the first time: *Haliophasma macrurum* (Barnard, 1914), *Haliophasma* sp. 1 (which did not match any known South African *Haliophasma* species), and *Stenetrium saldanha* Barnard, 1920.

Functional diversity and assemblage structure

Mobile detritivores were the most dominant functional group (Table 6), largely consisting of amphipods and isopods (Supplementary Table 2). This group accounted for approximately 30% of the total community in deep holdfasts and 20–31% in shallow holdfasts (Fig. 8). The filter feeders (comprising mobile, sessile and tube-dwelling groups) collectively made up 6–15% of all holdfasts with mobile filter feeders dominating at deeper sites (8%) while tube dwellers were more dominant at shallow sites (6%). Overall, mobile

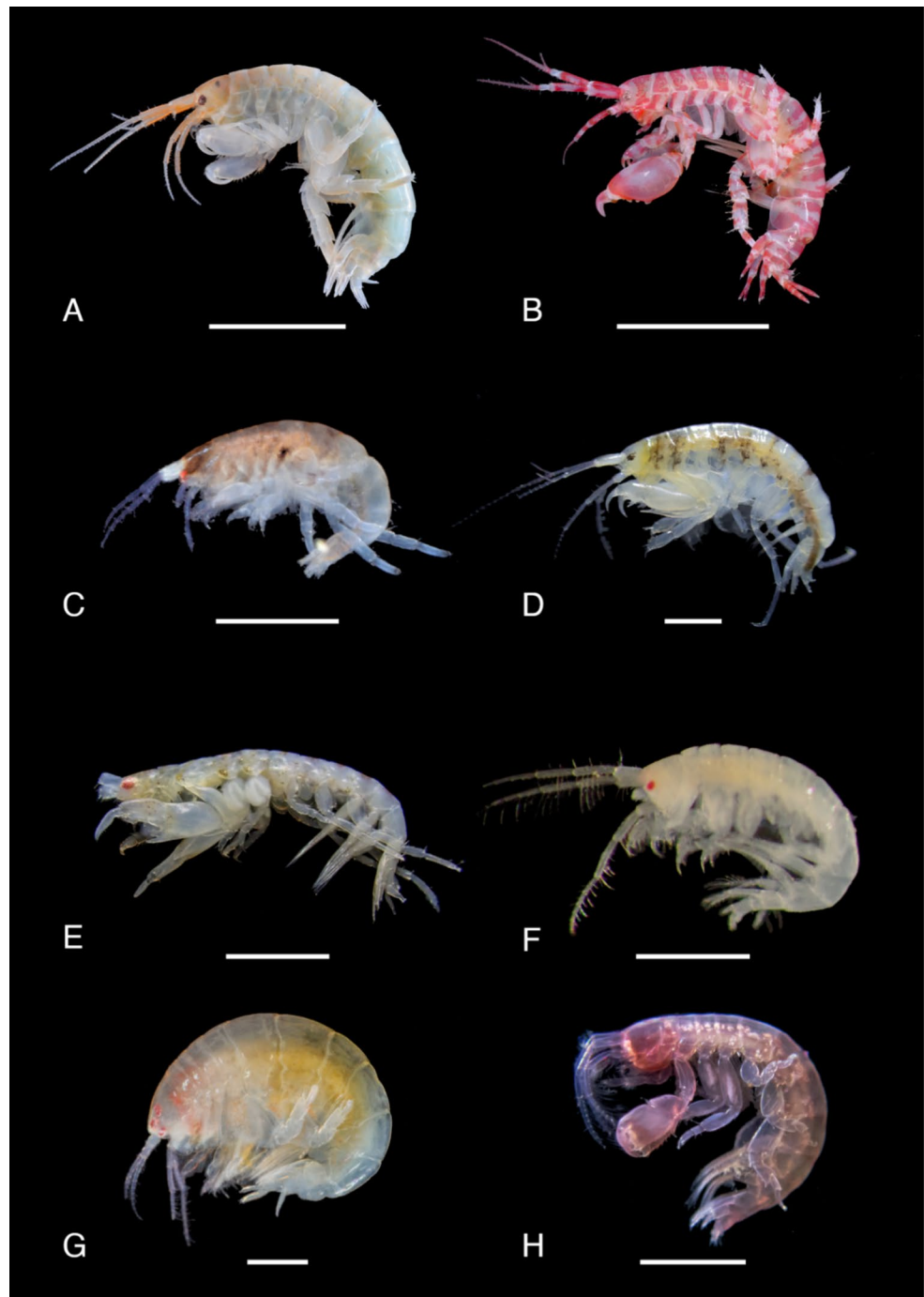
Table 5 SIMPER analysis showing average 3-year inter-annual similarity between shallow (2–5 m) *E. maxima* holdfasts with the relative contribution of the top five species to this similarity, and the inter-annual dissimilarity between 2023, 2024, and 2025, with the contribution of the top 10 species to this dissimilarity in Miller's Point

Species	Contribution to similarity within years %		
	2023	2024	2025
<i>Latigammaropsis atlantica</i>	20.43	12.33	20.26
<i>Chevalia aviculae</i>	11.31	18.41	30.56
<i>Photis dolichommata</i>	5.51	11.86	12.72
<i>Ampelisca brachyceras</i>	14.51	-	-
<i>Panathura serricauda</i>	-	6.45	-
<i>Notomegabalanus algicola</i>	-	-	9.00
<i>Aora kergueleni</i>	5.40	-	-
<i>Mesanthura cf. catenula</i>	-	5.85	5.83
Total similarity (%)	35.37	40.92	42.18
Year comparison	Total dissimilarity (%)	Species	Contribution (%)
2023/2024	66.71	<i>Latigammaropsis atlantica</i>	6.07
		<i>Chevalia aviculae</i>	4.73
		<i>Ampelisca brachyceras</i>	4.52
		<i>Photis dolichommata</i>	3.73
		<i>Maera vagans</i>	3.66
		<i>Ceradocus (Denticeradocus) rubromaculatus</i>	3.59
		<i>Cymodocella pustulata</i>	3.45
		<i>Gammaropsis</i> sp. 2	3.41
		<i>Panathura serricauda</i>	3.00
		<i>Cerapus tubularis</i>	2.78
2024/2025	62.90	<i>Chevalia aviculae</i>	8.52
		<i>Photis dolichommata</i>	5.39
		<i>Maera vagans</i>	4.78
		<i>Notomegabalanus algicola</i>	4.73
		<i>Latigammaropsis atlantica</i>	4.49
		<i>Cerapus tubularis</i>	3.21
		<i>Gammaropsis</i> sp.2	3.03
		<i>Panathura serricauda</i>	2.89
		<i>Cymodocella pustulata</i>	2.45
		<i>Leptochelia barnardi</i>	2.44
2023/2025	72.49	<i>Chevalia aviculae</i>	9.76
		<i>Photis dolichommata</i>	5.96
		<i>Ampelisca brachyceras</i>	5.82
		<i>Latigammaropsis atlantica</i>	5.80
		<i>Notomegabalanus algicola</i>	4.99
		<i>Ceradocus (Denticeradocus) rubromaculatus</i>	3.80
		<i>Cymodocella pustulata</i>	3.33
		<i>Gammaropsis</i> sp. 2	2.83
		<i>Maera vagans</i>	2.70
		<i>Aora anomala</i>	2.40

groups were most abundant followed by tube dwellers and burrowers. The most rare functional groups were the burrowers including the carnivores (1 individual of *Paraphoxus oculatus*), deposit feeders (Cumacea and two amphipod species), and detritivores (Limnoriid isopods). The sessile filter

feeders were species-poor, represented by the single Balanomorpha species *N. algicola*, but were abundant especially at greater depth in 2024 and at shallow sites in 2025. Functional redundancy was highest in the 2024 deep samples (Table 6).

Fig. 6 Crustaceans contributing most strongly to the average similarities between sites and depth. (A) *Maera vagans*, (B) *Ceradocus* (*Denticeradocus*) *rubromaculatus*, (C) *Photis dolichommata*, (D) *Aora anomala*, (E) *Cerapus tubularis*, (F) *Gammaropsis* sp. 1, (G) *Ampelisca brachyceras*, (H) *Chevalia aviculae*. Scale bars: 0.5 mm (A, B), 0.1 mm (C–H)



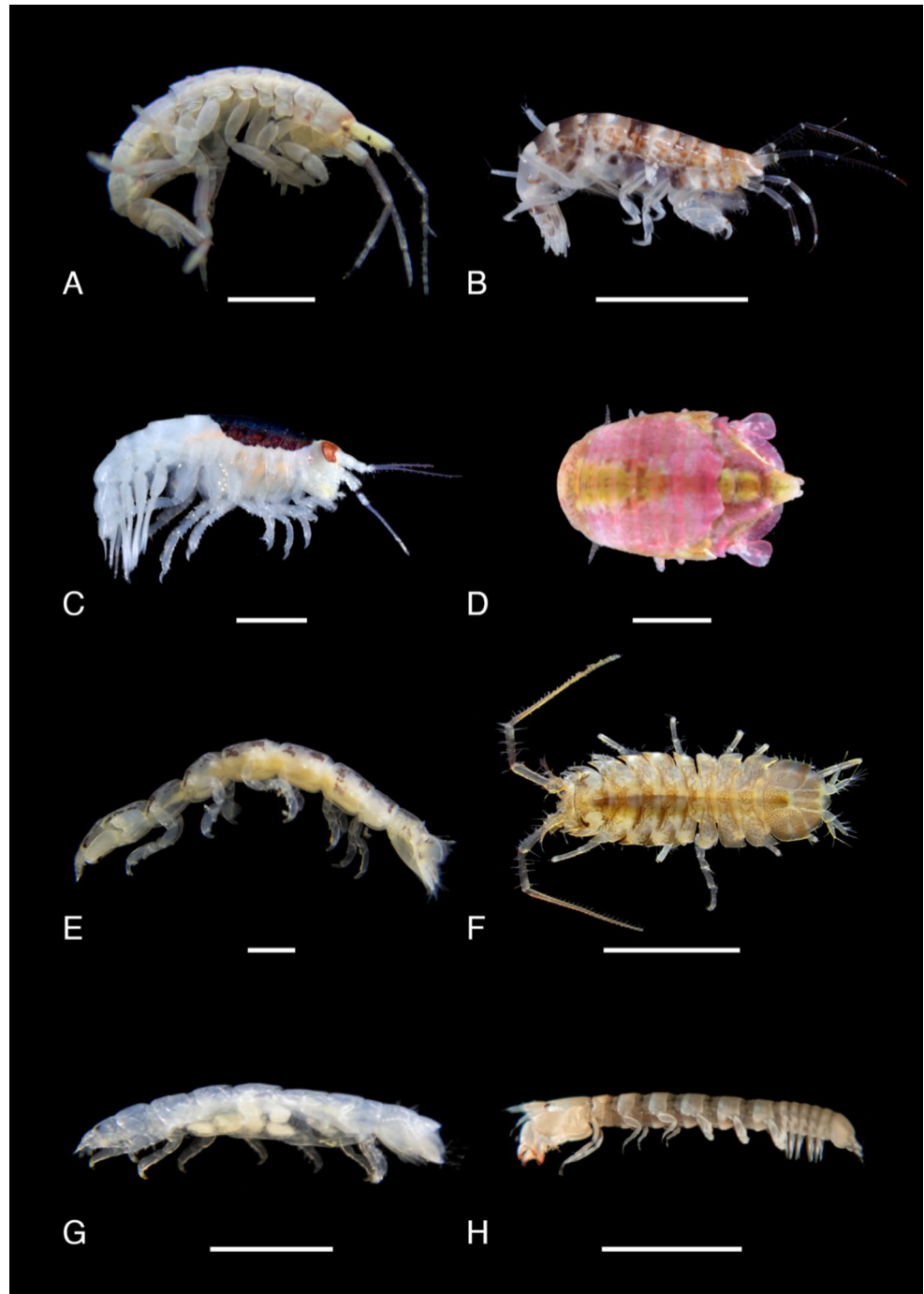
Multivariate analyses revealed that both depth and year played a role in structuring the composition of functional groups (Table 7). Inter-annual variation shows a clear shift in mobility with a decreased proportion of both mobile detritivores and filter feeders from 2023 to 2025, as tubedwelling detritivores increase in dominance (Fig. 8). In terms of depth, there was a higher proportion of both sessile and mobile filter feeders at greater depth compared to the 2024 shallow samples. These functional shifts mirror taxonomic patterns where depth and year are primary drivers of

taxonomic and functional communities and the influence of volume is more variable.

Discussion

This study adds to the growing database of South African holdfast-associated macroinvertebrate species and is the first to compare assemblages across depths and years. The study site, Miller's Point located in False Bay, falls within

Fig. 7 Crustaceans contributing most strongly to the average similarities between sites and depth. (A) *Gammaropsis* sp. 2, (B) *Latigammaropsis atlantica*, (C) *Paramoera capensis*, (D) *Cymodocella pustulata*, (E) *Mesanthura* cf. *catenula*, (F) *Stenetrium crassimanus*, (G) *Panathura serricauda*, (H) *Leptochelia barnardi*. Scale bars: 0.1 mm (A, C–E, G, H), 0.5 mm (B, F)



a transition zone between the warm-temperature Agulhas marine ecoregion and the cold-temperature Southern Benguela marine ecoregion, which each support distinct species assemblages (Griffiths et al. 2010; Awad et al. 2002). The high diversity recorded at Miller's Point (as indicated by S values and d' values > 5 – Supplementary Table 1) is likely a result of its location within this marine ecotone where a high-energy, nutrient rich, and dynamic habitat is created by the confluence of these two ecoregions. In turn, the structural heterogeneity of the *Ecklonia maxima* kelp forests

form a biogenic habitat capable of supporting such diverse communities as observed in this study.

Over three years, a total of 29 holdfasts revealed a diverse crustacean assemblage of 131 species in 60 families over 10 Orders. This is consistent with previous global and South African research reporting high numbers of crustacean species, compared to other taxa, inhabiting kelp holdfasts (Coull and Wells 1983; Gibbons 1988; Eckman et al. 1989; Hauser et al. 2006; Perry et al. 2024). Fittingly, the taxonomic biodiversity recorded at this study exceeds

Table 6 Crustacean functional groups found in *E. maxima* holdfasts sampled over three years. Average ($\pm$ SE) individual counts for each group is reported per year and per depth (2024). Functional richness (Fric), Shannon-Wiener index (H'_f), and functional redundancy are also included for each year and depth category

Functional group			2023	2024	2025	2024 Deep
Diet	Mobility	Code				
Detritivore	Mobile	MD	195.70 (51.23)	157.50 (37.13)	126.00 (44.19)	183.67 (53.74)
Detritivore	Tube-dweller	TD	43.00 (8.34)	75.50 (15.49)	172.43 (79.86)	144.50 (35.42)
Detritivore	Burrower	BD	0.60 (0.60)	4.33 (2.74)	0.14 (0.14)	8.67 (3.31)
Filter feeder	Mobile	MF	11.70 (4.35)	6.83 (3.25)	9.86 (5.85)	53.67 (24.99)
Filter feeder	Sessile	SF	0.30 (0.30)	5.33 (3.44)	23.29 (10.76)	34.67 (13.62)
Filter feeder	Tube-dweller	TF	39.70 (14.13)	19.17 (5.93)	4.14 (3.65)	8.00 (1.51)
Grazer	Mobile	MG	24.80 (9.72)	9.33 (3.17)	3.29 (1.32)	8.33 (2.23)
Grazer	Tube-dweller	TG	1.40 (0.52)	0.83 (0.65)		1.33 (0.56)
Carnivore	Mobile	MC	20.90 (10.17)	27.00 (12.86)	8.29 (3.24)	22.17 (6.37)
Carnivore	Burrower	BC		0.17 (0.17)		
Deposit Feeder	Mobile	MP	5.90 (4.71)	1.33 (1.33)	2.29 (1.02)	2.00 (0.97)
Deposit feeder	Burrower	BP	0.40 (0.22)	0.17 (0.17)		1.50 (1.31)
Functional richness			6.90 (0.72)	7.67 (0.92)	6.57 (0.48)	9.50 (0.34)
H' - Functional			1.22 (0.07)	1.25 (0.12)	1.00 (0.15)	1.43 (0.07)
Functional redundancy			3.48	3.81	2.56	4.58

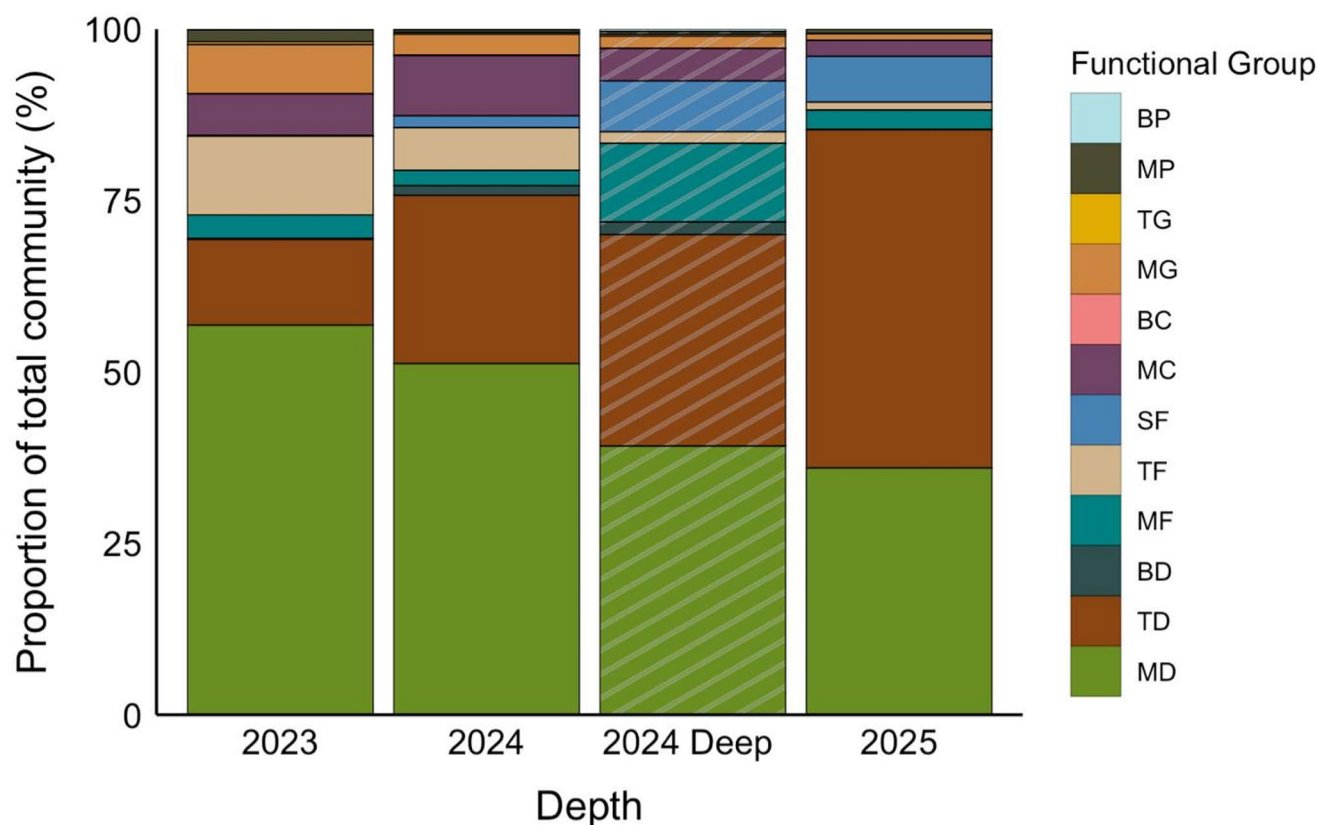


Fig. 8 The average proportion of Crustacea functional groups collected per *E. maxima* holdfast from shallow holdfasts in 2023, 2024 and 2025 and deep holdfasts in 2024 at Miller's Point, False Bay. The plain bars indicate shallow samples (2–5 m) while the patterned bar indicated the deep samples (6–8 m). Functional groups are represented as follows: MD – Mobile Detritivores; TD – Tube-dwelling Detritivores;

BD – Burrowing Detritivores; MF – Mobile Filter Feeders; TF – Tube-dwelling Filter Feeders; SF – Sessile Filter Feeders; MC – Mobile Carnivores; BC – Burrowing Carnivores; MG – Mobile Grazers; TG – Tube-dwelling Grazers; MP – Mobile Deposit Feeders; BP – Burrowing Deposit Feeders

Table 7 PERMANOVA results based on the Bray–Curtis similarity measure for square-root transformed crustacean abundance data across depth (Shallow vs. Deep) and Year (2023, 2024, 2025)

Source	Depth				Year			
	df	R ²	Pseudo-F	<i>p</i>	df	R ²	Pseudo-F	<i>p</i>
Main factor	1	0.24	3.32	0.008	1	0.18	5.38	0.001
Volume	1	0.05	1.26	0.301	1	0.17	5.08	0.001
Residual	9	0.66			20	0.66		
Total	11				22			

Bold values represent significant differences (Alpha=0.05)

larger-scale, multi-site studies from kelp holdfasts in other regions. Christie et al. (2003) reported 92 species of Crustacea from 56 *Laminaria hyperborea* holdfasts along the Norwegian coast, with Amphipoda representing the most diverse group. In New Zealand, Anderson et al. (2005) identified 77 Arthropoda species from 80 holdfasts, while Smith and Simpson (1992) documented 60 Amphipoda species from 60 holdfasts across four sites in Australia. Similarly, Ríos et al. (2007) recorded 21 Crustacea species from 136 holdfasts collected in the Straits of Magellan, Chile, in their study of spatial and seasonal variation in macrofaunal communities.

The influence of depth on crustacean assemblages

There was significantly higher diversity, abundance and species richness of holdfast-associated crustaceans found in deeper samples (Supplementary Table 1; Table 1). This is consistent with previous studies that found an increase in diversity and abundance of macroalgal-associated macroinvertebrates with depth (Fenwick 1976; Edgar 1983b; Morri et al. 1999), suggesting that depth-related stability facilitates the accumulation of more species. While some research has reported a shift in higher taxa dominance between different depths (Fenwick 1976; Edgar 1983a), this study found no depth-related pattern in the distribution of crustacean Orders, which is consistent with Smith (1996). In Australian and New Zealand kelp forests, the Order Amphipoda was found to dominate shallow waters (<2–4 m), while Isopoda and Mollusca dominated deeper (>5 m) areas (Fenwick 1976; Edgar 1983a). Similarly in this study, Amphipoda, followed by Isopoda and Tanaidacea, dominated in terms of abundance and species richness in both depth ranges (3–5 m and 6–8 m). The differences in the literature could be the result of biogeographic variation in the diversity of various groups or other interlinked environmental factors, such as differences in wave action, sedimentation and habitat complexity.

At Miller's Point the shallow site was observed to have coarse sand, medium-to-high wave exposure, and consequently high turbidity, whereas the deeper site had lower direct wave exposure, reduced turbidity, and finer sediment with high detritus levels. Wave exposure is closely

related with depth, making it one of the most likely factors explaining the differences in abundance and diversity (Edgar 1983b; McQuaid and Branch 1985; Bustamante and Branch 1996b; Smith 1996; Bué et al. 2020). High levels of wave-induced disturbance create an unstable environment, dislodging organisms and damaging algae (Fenwick 1976). The increase in abundance of individuals at greater depth (Table 1; Figs. 2 and 3) aligns with the idea that the reduced turbulence and increased water stability at a deeper site supports higher diversity.

While there was no general evidence of depth preference among the Orders of crustaceans, specific patterns of dominance may occur among some families and species. Faunistic patterns associated with feeding strategy have been reported to vary with sediment type (McQuaid and Branch 1985; Bustamante and Branch 1996b; Smith 1996). Notably, in 2024, 95% of Caprellidae individuals, categorised here as Mobile Filter Feeders (MF) were found in the deep holdfasts (6–8 m), which likely reflects the high availability of detritus and low surge or wave energy at those depths. This is consistent with Guerra-García et al. (2010) who reported higher Caprellidae diversity at depths >5 m while Guerra-García and Tierno de Figueroa (2009) found that detritus contributed 86% of the Caprellidae diet. In contrast, the shallow holdfasts were dominated by Tube-dwelling Filter Feeders (TF) such as *Latigammaropsis atlantica* (Stebbing, 1888), *Cerapus tubularis* Say, 1817 and *Photis dolichommata* Stebbing, 1910 (Table 1) that utilise the readily suspended sediment for filter-feeding (Moore and Eastman 2015) and depend on their tubes for protection and stability from the increased currents or wave energy (Fenwick 1976). The majority of the individuals of abundant tube-building species, *L. atlantica* (71%), *C. tubularis* (84%) and *P. dolichommata* (70%) were found in the shallow holdfasts.

These functional patterns closely mirror taxonomic trends, despite the high degree of functional redundancy within these holdfast communities. With a total of 131 species distributed across 12 functional groups, several ecological roles are performed by multiple distinct species, highlighting the resilience of these communities. In particular, holdfast communities appear to be more resilient at greater depths, likely due to the stability offered beyond the influence of the surge. Functional specialisation, such

as tube-dwelling, demonstrates the adaptation of these communities to dynamic, sometimes unpredictable surface conditions, whilst still maintaining ecological processes.

Change in community assemblage over time

Species diversity, species richness, and community assemblages all differed significantly in the shallow holdfasts sampled from 2023 to 2025 (Tables 3, 4 and 5), indicating that holdfast-associated communities are dynamic. This was affirmed by a clear shift in functional groups over the three-year sampling period. Specifically, the shallow holdfast communities transitioned from being Mobile Detritivore (MD) dominated systems to a more Tube-dwelling Detritivore (TD) state by 2025 (Fig. 8), largely driven by the shift from an abundance of Ostracoda and Maeridae amphipods (MD) to the dominance of Tube-dwelling (TD) *Chevalia aviculae* (Table 1).

These shifts may reflect natural variability in physical parameters, such as temperature, upwelling intensity, productivity or other environmental conditions (Teagle et al. 2018) or may be the result of biological factors such as larval supply and settlement success, differing levels of competition or predation etc. Both groups of factors are linked to unpredictable variations in upwelling, productivity and hydrodynamics around the Cape Peninsula (Bustamante et al. 1995). Since sampling occurred within the same season in all three years, shifts reflect inter-annual variability with possible successional shifts in community compositions and not seasonality. Regardless, it appears that shifts in taxonomic abundance, while mirrored by shifts in functional patterns, do not disrupt ecological processes. While the community might switch from a Mobile to Tube-dwelling state, the ecological role of the detritivore is maintained across years.

Changes over time might also be amplified by the transitional nature of Miller's Point, situated close to Cape Point, the biogeographical break between the Southern Benguela and Agulhas ecoregions. This region is known to experience environmental heterogeneity such as seasonal shifts in upwelling, wave exposure and annual variability in productivity (Griffiths et al. 2010).

Conclusion

The recent work on South African kelp holdfasts has renewed focus on this historically overlooked habitat, while revealing substantial gaps. By building on these efforts, this study provides updated records of the diverse crustacean communities at Miller's Point, an ecologically dynamic transition zone, and highlights depth as an important but

previously unexplored driver of holdfast assemblage structure. The observed year-to-year shifts in community composition underscore the need for continued monitoring to distinguish natural variability from longer-term ecological change. Furthermore, this study focussed solely on Crustacea, and it would be interesting to measure the diversity and functional biology patterns in other diverse groups, such as Mollusca and Annelida, to primarily document the taxonomic biodiversity, and to determine whether they exhibit similar patterns of depth and inter-annual variation. Additionally, sampling a wider depth range, from intertidal to the seaward extent of the kelp would provide further insights into depth-related community composition, diversity, and abundance patterns.

Given the unique biogeographical context of the Great African Seafloor and its ongoing eastward expansion under localised cooling, establishing robust biodiversity baselines and clarifying the factors shaping community structure are essential for understanding and conserving this globally significant ecosystem. Through refined taxonomic resolution, inclusion of a functional trait-based approach, and the detection of species not previously recorded, this study contributes meaningfully to that foundation and strengthens South Africa's role in global kelp forest biodiversity research.

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Author contributions NP and JL conceptualised the research. AR, NP, JL, DR, CK, JPJ conducted fieldwork, NP, AR, DR conducted analyses. CG helped with identifications and sample analysis. AR wrote the original manuscript. NP, JL, AR, DR, and CG also contributed to writing, reviewing and editing various drafts.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No animal testing was performed during this study.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements.

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