



Kelp holdfasts in the Great African Seaforest provide habitat for diverse assemblages of macroinvertebrates

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ABSTRACT: Kelp forests along the southwestern and west coasts of South Africa, dominated by the species *Ecklonia maxima* and *Laminaria pallida*, are locally termed 'the Great African Seaforest'. They form 3-dimensional biogenic habitats that provide 4 distinct microhabitats — canopy, fronds, stipe and holdfast — with the latter typically supporting the highest abundance and diversity of associated macroinvertebrates. The macrofauna inhabiting kelp holdfasts in South Africa have rarely been studied, resulting in a near complete lack of baseline data. In this study, macrobenthic assemblages from 40 *E. maxima* holdfasts were examined over 2 marine ecoregions and 4 locations. Macroinvertebrates were identified and counted for univariate and multivariate analyses using family-level data. A total of 120 families from 9 phyla were identified and were generally dominated by Arthropoda (48 families), Annelida (24 families) and Mollusca (23 families). Marine ecoregion had no significant effect on composition of macroinvertebrate assemblages, whereas location had a significant effect. There was no significant relationship between holdfast volume and macroinvertebrate diversity or abundance, suggesting that other environmental and physicochemical factors are important in determining community structure. This study serves as a baseline for future research aimed at understudied holdfast macroinvertebrate communities in the Great African Seaforest.

KEY WORDS: *Ecklonia maxima* · Biodiversity · Kelp forest · South Africa · Taxonomy · Community structure · Ecoregions

1. INTRODUCTION

Kelp forests are assemblages of large brown algae, predominantly of the order Laminariales (Blamey & Bolton 2018, Smale 2020). They are found along 25% of coastlines globally (Wernberg et al. 2019), covering an area of 49 287 km² (Eger et al. 2023), dominating rocky reefs in shallow temperate oceans and thriving in cold, nutrient-rich waters (Teagle et al. 2017, Wernberg et al. 2019, Jayathilake & Costello 2020). In

South Africa, kelp forests occur along the west and southwest coasts from the Namibian border to De Hoop, near Cape Agulhas, covering a distance of approximately 1000 km, and extending across a third of the South African coastline (Blamey & Bolton 2018). Two species of kelp dominate the southern African ecosystem, colloquially referred to as 'the Great African Seaforest', i.e. *Laminaria pallida* Greville in J. Agardh 1848 and *Ecklonia maxima* (Osbeck) Papenfuss, 1940 (Blamey & Bolton 2018).

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While global warming is causing declines in kelp forest coverage in many regions globally (Krumhansl et al. 2016), those along the South African western coastline have increased in cover over recent decades (Bolton et al. 2012, Reimers et al. 2014). Specifically, *E. maxima* has increased in density and expanded ~70 km eastwards towards De Hoop (Bolton et al. 2012), possibly due to an increase in southeasterly winds, leading to increased upwelling (Bolton et al. 2012), resulting in cooling of coastal water and a higher influx of nutrients. It is likely that these expansions may be reflected by expansions in associated biota (Bolton et al. 2012), although this has not been documented.

Kelp forests provide a wide range of biological services and offer refuge for diverse assemblages of marine species (Teagle et al. 2017, Carbajal et al. 2022). They also influence water flow, light levels and sedimentation (Smale et al. 2013), and support complex trophic webs due to their high levels of primary productivity (Dayton 1985). Ecosystem services provided include fisheries production, carbon storage, coastal protection and nutrient recycling (Blamey & Bolton 2018, Schoenrock et al. 2021, Eger et al. 2023). These services, alongside education and recreation services, are associated with high economic value, including for fisheries, tourism and climate regulation (Tegner & Dayton 2000, Bertocci et al. 2015, Bennett et al. 2016, Bayley et al. 2021). The value of kelp forests and associated rocky reefs in South Africa has been estimated at ZAR 5.8 billion (USD 434 million) per year, emphasizing their importance to the national economy (Blamey & Bolton 2018). To properly manage kelp as an economic resource and to preserve the ecosystem function of this biogenic habitat, it is essential to fully understand the diversity and ecological interactions associated with kelp forests.

Kelp forests provide 3-dimensional biogenic habitats, which can be divided into 4 components: the canopy, fronds, stipe and holdfast. Like a terrestrial forest canopy, the canopy of a kelp forest is defined as the space above and around the head and fronds (Parker 1995). This definition includes the structures themselves, the epiphytes and the environment in which the canopy is situated. The stipe supports the head, which is made up of the fronds and a gas-filled bulb, and the holdfast acts as an anchor, attaching the kelp to the rocky substrate (Teagle et al. 2017). These

4 habitats (canopy, fronds, stipe and holdfast) are each home to distinct assemblages of marine organisms, with holdfasts known to support the most diverse and abundant assemblages (Teagle et al. 2017, Shunatova et al. 2018, Carbajal et al. 2022). Kelp holdfasts have a complex structure with many crevices (Tuya et al. 2011, Teagle et al. 2017), thus providing habitat and refuge for both smaller algae and numerous marine invertebrate groups, such as polychaetes, crustaceans, molluscs, echinoderms, sponges, bryozoans and cnidarians (Anderson et al. 1997, Schoenrock et al. 2021, Velasco-Charpentier et al. 2021, Carbajal et al. 2022).

The diversity, abundance and distribution patterns of macroinvertebrate species in kelp holdfasts have scarcely been explored in South Africa, with only 3 studies to date, all focusing on *E. maxima* holdfasts and all restricted to the Cape Peninsula (Fig. 1). These studies examined the effect of depth and wave exposure on holdfast-associated macroinvertebrates (Velimirov et al. 1977), the trophic interactions within holdfasts (Beviss-Challinor & Field 1982) and the recruitment potential of kelps facilitated by holdfasts (Anderson et al. 1997).

The composition of macroinvertebrate assemblages in kelp holdfasts is thought to be influenced by several environmental and physicochemical factors (reviewed in Teagle et al. 2017). These include turbidity (Moore 1973), pollution (Sheppard et al. 1980, Smith & Simpson 1993, Smith 2000), wave exposure (Bué et al. 2020), geographic distribution (Anderson et al.

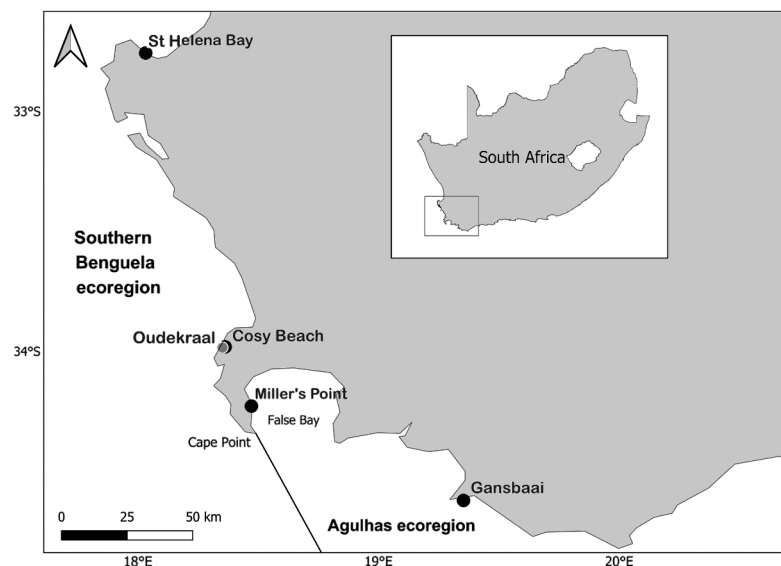


Fig. 1. Four study locations (black circles) nested within 2 marine ecoregions along the southwestern and west coasts of South Africa. Oudekraal (grey circle) is where previous studies on kelp holdfasts were undertaken

2005a,b, Bué et al. 2020), rate of sedimentation (Ronowicz et al. 2018) and depth (Velimirov et al. 1977, Smith 1996). Additionally, holdfast volume has been shown to influence faunal diversity and abundance, with larger volumes providing greater habitat availability and hence supporting a richer fauna (Sheppard et al. 1980, Ojeda & Santelices 1984, Thiel & Vásquez 2000).

The South African coast can be divided into 4 inshore and 2 offshore marine ecoregions (Sink et al. 2012, 2019), 2 of which support extensive kelp beds and hence are included in this study. The Agulhas marine ecoregion, a warm-temperature marine ecoregion along the south coast, is characterized by moderate nutrient levels and upwelling (Griffiths et al. 2010, Sink et al. 2012), while the Southern Benguela marine ecoregion, a cold-temperature ecoregion on the west coast, experiences upwelling of cold, nutrient-rich water (Sink et al. 2012). These 2 marine ecoregions support different species assemblages (Awad et al. 2002, Griffiths et al. 2010, Sink et al. 2019), with the Agulhas ecoregion being more diverse than the Southern Benguela ecoregion. According to Sink et al. (2012, 2019), Cape Point marks the boundary between the Southern Benguela and the Agulhas marine ecoregions, although some studies suggest that this boundary might vary depending on the taxa considered (Awad et al. 2002, Griffiths et al. 2010). These patterns might be reflected in the assemblages of macroinvertebrates associated with kelp holdfasts, but this has yet to be investigated.

The present study examines the biotic communities associated with *E. maxima* holdfasts across the Southern Benguela and Agulhas marine ecoregions. The objectives were to identify and quantify organisms found within holdfasts from 4 locations (Fig. 1), 2 from each ecoregion. The hypotheses were: (i) macroinvertebrate assemblages would differ between the 2 marine ecoregions, and (ii) there would be a significant difference in macroinvertebrate assemblages between individual locations, with the 2 southern sites harbouring higher biodiversity than the 2 western sites.

2. MATERIALS AND METHODS

2.1. Study locations

Ecklonia maxima holdfasts were collected from 4 locations along the southwest and west coasts of South Africa (Fig. 1): two (Gansbaai and Miller's Point) within the Agulhas and two others (Cosy Beach and St Helena Bay) within the Southern Benguela

marine ecoregion. Cosy Beach is adjacent to Oudekraal on the west of Cape Point, where previous holdfasts were collected by Velimirov et al. (1977), Beviss-Challinor & Field (1982) and Anderson et al. (1997). Both marine ecoregions differ in temperature (Griffiths et al. 2010, Sink et al. 2019), with the Agulhas being warmer, with an average sea surface temperature ranging from 14–18°C, and the Southern Benguela being cooler, with an average of 12–14°C (Smit et al. 2013). The Southern Benguela has intense upwelling along the west coast, resulting in high productivity supporting fisheries such as sardines, hake and rock lobsters (Griffiths et al. 2010), while the Agulhas has low productivity with fewer commercial fisheries (Griffiths et al. 2010). *E. maxima* holdfasts provide a sheltered environment (Velimirov et al. 1977), and even though South Africa has a high wave energy coastline (Griffiths et al. 2010), kelp forests dissipate high-energy waves, allowing for calm, low-energy onshore environments.

2.2. Fieldwork

Ten adult holdfasts were sampled during low tides from each of the 4 locations ($n = 40$) between March and May 2022. Sampling sites were chosen to be easily accessible and to reflect low wave energy, where any incoming swell was dissipated by kelp stands. Kelp holdfasts were collected from the center of these stands. Although both *Laminaria pallida* and *E. maxima* occur at each site, the sample stands at Miller's Point and Cosy Beach were nearly monospecific, while St Helena Bay and Gansbaai had mixed stands. All stands were very dense, although this was not quantified. Divers targeted stand-alone holdfasts, which were collected by SCUBA or freediving at depths of 2–5 m. Divers cut the stipe of the kelp with a dive knife, then pried the holdfast from the rock using a paint scraper and placed it immediately into an individual plastic Ziploc bag. Upon surfacing, the bag was labelled and placed in a dark cooler box until further processing.

In the field laboratory, holdfasts were cut into smaller segments, which were rinsed and shaken for 30 s in seawater to extract mobile invertebrates. The seawater was then passed through a 500 µm mesh sieve and the invertebrates were sorted into broad taxonomic groups whilst still alive, prior to preservation in 70% ethanol. The remaining holdfast pieces, with any encrusting invertebrates still attached, were placed back into plastic Ziploc bags and frozen until laboratory processing.

2.3. Laboratory processing

Encrusting invertebrates, such as Porifera, Bryozoa and Cnidaria (Hydrozoa), were removed from holdfast segments with tweezers. Thereafter, holdfast volume (ml) was determined by placing holdfast pieces in a graduated cylinder containing a measured volume of water and measuring the water displacement. Faunal samples were sorted using a stereo or compound microscope and identified using regional guides to various taxa, including Day (1969), Griffiths (1976), Kensley (1978), Samaai & Gibbons (2005), Branch et al. (2010), Milne & Griffiths (2013), Emmerston (2016), Laird & Griffiths (2016) and Olbers et al. (2019). The World Register of Marine Species (www.marinespecies.org) was used to verify scientific names, and taxonomic experts were consulted where available. To standardize specimen abundance, only whole organisms and heads were counted. Encrusting invertebrates were measured using wet weight (g). To reconcile weight, a unit was assigned to the smallest weight each for Porifera, Bryozoa and Cnidaria (Hydrozoa). Weights were then divided by this unit to provide a rank or count for the sake of statistical analyses. Combining quantitative and semi-quantitative analyses has been previously conducted for kelp holdfast communities, and is used to reconcile quantification of individual versus colonial organisms (Anderson et al. 2005b).

2.4. Statistical analysis

Variation in macroinvertebrate assemblages within kelp holdfasts was assessed using permutational analysis of variance (PERMANOVA) for multivariate analysis using PRIMER v6 software (Anderson 2001, Christie et al. 2003, Anderson et al. 2005b, Clarke & Gorley 2006). Although species-level identifications are presented where possible, family-level identification was used for all analyses. A total of 40 holdfasts was used for the multivariate abundance data, and species richness, Shannon-Wiener diversity index and Pielou's evenness index were calculated for each holdfast. The abundance data (number of organisms and presence/absence), Shannon-Wiener diversity and species richness were analyzed using a 2-factor nested design with marine ecoregions (fixed, 2 marine ecoregions) and locations (fixed, 4 locations nested within marine ecoregion), with holdfast volume added as a co-variable.

Multivariate abundance data were square-root transformed using the Bray–Curtis similarity index. A non-

metric multidimensional scaling (nMDS) was applied to visualize differences in macroinvertebrate assemblages across the 4 locations, including holdfast volume as a co-variable. Where significant differences were found among locations, a pair-wise test was performed ($p < 0.05$), using the square root of the PERMANOVA test statistic, with 999 permutations of residuals under a reduced model. Monte Carlo simulations were used to obtain p-values (Anderson et al. 2005b). A similarity percentage (SIMPER) analysis with a cut-off percentage of 90% was also performed to determine which families contributed most to dissimilarities between locations. To determine the relationship between holdfast volume (ml) and total macrofauna abundance (number of individual organisms), a Pearson's correlation test was performed in R version 4.2.1 (R Core Team 2022).

3. RESULTS

3.1. Macroinvertebrate biodiversity

A total of 9742 individual invertebrates were extracted from the 40 holdfasts dissected, and these belonged to 120 families from 9 phyla (Table 1, see Table S1 in the Supplement at www.int-res.com/articles/suppl/b033p033_supp.pdf). Out of 147 morphotypes identified, less than 50% (67) were confidently identified to species level, hence analyses were conducted at family level as we were confidently able to separate all individuals into separate families. Nevertheless, a species list is presented in Table S2 in the Supplement. Arthropoda was the most diverse group in terms of number of families (48), followed by Annelida (24), Mollusca (23), Echinodermata (11), Cnidaria (6), Porifera (3), Platyhelminthes (2), Nematoda (2) and Bryozoa (1). When assessed by location, the greatest number of families was identified from St Helena Bay (62), followed by Gansbaai (58), Miller's Point (56) and Cosy Beach (55) (Table S1).

The most abundant taxa, in terms of numbers of individuals, were usually Polychaeta, followed by Amphipoda, the only exception being at St Helena Bay, where Amphipoda and Bivalvia were both more abundant than Polychaeta (Table 1). Overall, 37% of all individuals collected were Amphipoda and 28% were Polychaeta, these 2 groups thus collectively contributing 65% of all invertebrate numbers.

Among the encrusting (sessile) invertebrates, St Helena Bay supported Porifera (2 families), Hydrozoa and Bryozoa (Table 2), while in Gansbaai only

Table 1. Total macroinvertebrate abundance for major 'taxa' found at each of the 4 study locations along the southwestern and west coasts of South Africa (n = 10 holdfasts per location)

Phyla	Major 'taxa'	Gansbaai	Miller's Point	Cosy Beach	St Helena Bay
Echinodermata	Asteroidea	1	3	—	—
	Ophiuroidea	27	128	263	114
	Echinoidea	3	13	2	81
	Crinoidea	—	2	—	—
	Holothuroidea	1	1	7	2
Arthropoda	Amphipoda	516	392	317	2376
	Isopoda	39	84	53	226
	Tanaidacea	15	103	19	368
	Decapoda	31	50	6	2
	Balanomorpha	—	—	—	2
	Cumacea	8	—	—	3
	Leptostraca	—	—	—	6
	Pycnogonida	2	—	7	—
	Ostracoda	2	8	15	88
	Mollusca	Bivalvia	15	3	92
Gastropoda		13	26	30	5
Polyplacophora		7	1	8	—
Annelida	Polychaeta	844	620	606	684
	Hirudinea	15	—	—	2
	Sipunculida	11	—	—	—
Platyhelminthes		1	—	—	3
Nematoda		4	—	—	39
Cnidaria	Anthozoa	2	4	61	59
Total		1557	1438	1486	5261

Table 2. Wet weights (g) of encrusting invertebrates by family, found at each of 4 study locations along the southwestern coast of South Africa (n = 10 holdfasts per location)

Phyla	Families	Gansbaai	Miller's Point	Cosy Beach	St Helena Bay
Porifera	Chalinidae	—	—	—	88.66
	Callyspongiidae	—	—	—	83.82
	Coelosphaeridae	8.35	—	—	—
Cnidaria (Hydrozoa)	Aglypheniidae	—	—	—	9.38
Bryozoa	Phidoloporidae	—	—	—	1.68

Table 3. PERMANOVA based on Bray–Curtis similarity on transformed abundance data, Shannon-Wiener diversity (SWD), richness and presence/absence (P/A) data for all 'taxa'. df: degrees of freedom; MS: average of sum squares; M.E.: marine ecoregion. **Bold** values represent significant differences

Source	df	MS	Abundance		SWD		Richness		P/A	
			Pseudo- <i>F</i>	p(perm)	Pseudo- <i>F</i>	p(perm)	Pseudo- <i>F</i>	p(perm)	Pseudo- <i>F</i>	p(perm)
Holdfast volume	1	3189.3	1.2034	0.269	1.2034	0.269	1.0884	0.384	1.2782	0.171
Marine ecoregion	1	10714	0.97229	0.534	0.97229	0.534	1.032	0.523	0.97168	0.64
Location (M.E.)	2	10672	3.5383	0.002	3.5383	0.002	3.6703	0.001	5.9863	0.001
Residual	31	1633								
Total	39									

Porifera (1 family) were present. Miller's Point and Cosy Beach both had no encrusting invertebrates present (Table 2).

3.2. Diversity across ecoregions and locations

Macroinvertebrate assemblages were not significantly different across the marine ecoregions (Agulhas versus Southern Benguela, $p = 0.534$) (Table 3), and the nMDS plot (Fig. 2) indicated an overlap in ordination between both marine ecoregions. However, a significant difference in macroinvertebrate community assemblage, Shannon-Wiener diversity, Pielou's evenness and presence/absence was observed between locations (Table 3, $p < 0.05$). There was considerable overlap between the macroinvertebrate assemblages from Miller's Point and Cosy Beach, while the Gansbaai and Miller's Point samples were relatively close in ordination, with all 3 locations clustering separately from St Helena Bay (Fig. 2, Table 4). The pairwise comparison revealed no significant differences in macroinvertebrate assemblages between Gansbaai and Miller's Point and between Miller's Point and Cosy Beach ($p > 0.05$) (Table 4).

The average relative abundances of the various phyla at each site are depicted in Fig. 3. Arthropoda were the dominant group at Miller's Point (44.3%) and St Helena Bay (56.27%), while Annelida dominated at Gans-

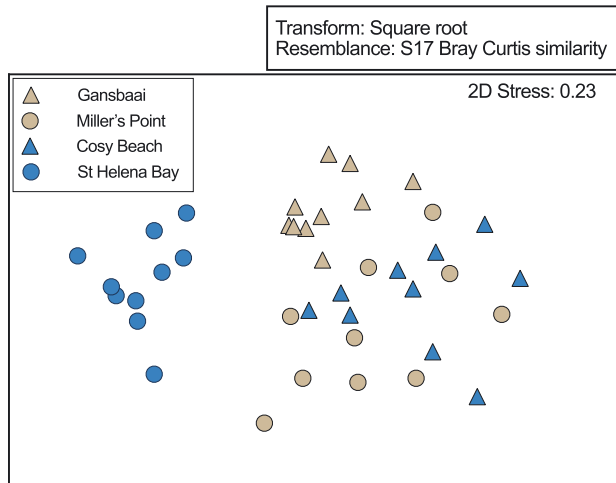


Fig. 2. Non-metric multidimensional scaling plot comparing macroinvertebrate assemblages across all 4 study locations based on Bray–Curtis similarities of fourth-root transformed abundance data (number of individual organisms). Brown represents the Agulhas marine ecoregion and blue represents the Southern Benguela marine ecoregion

baai (54.12%) and Cosy Beach (40.79%). Mollusca were most abundant at St Helena Bay (22.1%). Echinodermata (18.3%) and Cnidaria (4.1%) were most abundant at Cosy Beach. Nematoda, Platyhelminthes and Porifera were only present at St Helena Bay and Gansbaai, and made up less than 2% of the overall relative abundance. Bryozoa were only present at St Helena Bay (0.49%). Annelida appeared to decline in average abundance from warm to cool coasts (east to west), while Mollusca increased in abundance along this gradient (Fig. 3).

St Helena Bay had the highest average species richness (22.1 ± 4.2) and number of total individuals (536.6 ± 491.41), while Miller's Point had the lowest (17.6 ± 4.6 species and 143.8 ± 33.7 individuals) (Table 5). St Helena Bay also had the lowest average Shannon-Wiener diversity (1.88 ± 0.50) and Pielou's evenness (0.61 ± 0.16), while Gansbaai had the highest average Shannon-Wiener diversity (2.27 ± 0.29) and Miller's Point had the highest average Pielou's evenness (0.79 ± 0.06).

In terms of dissimilarity, the Gammariidae, a family of Amphipoda (phylum Arthropoda), and Mytilidae, a family of Bivalvia (phylum Mollusca), contributed the most to the dissimilarities between St

Table 4. Pairwise comparison test results comparing macroinvertebrate assemblages at 4 study locations for all 'taxa'. The *t*-statistic represents the average difference ratio between samples, while the *p*-values are drawn from Monte Carlo sampling. **Bold** values represent significant differences

Location comparison	<i>t</i>	<i>p</i> (MC)
Gansbaai vs Miller's Point	1.5119	0.067
Gansbaai vs Cosy Beach	1.9961	0.01
Gansbaai vs St Helena Bay	2.3446	0.004
Miller's Point vs Cosy Beach	1.285	0.176
Miller's Point vs St Helena Bay	1.9313	0.01
Cosy Beach vs St Helena Bay	2.2443	0.003

Helena Bay and all other locations (Table 6). St Helena Bay samples were characterized by high abundances of Amphipoda and Bivalvia (Table 1), which supports this dissimilarity. Amphiuroidae, a family of Ophiuroidea (phylum Echinodermata), contributed most to the dissimilarity between Cosy Beach and Miller's Point and between Cosy Beach and Gansbaai.

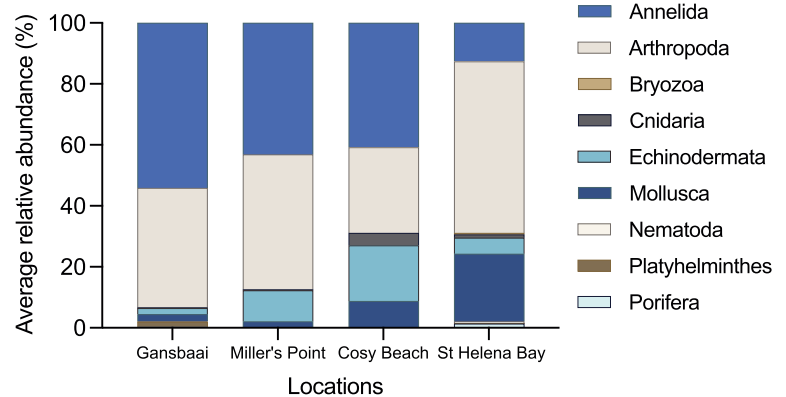


Fig. 3. Average relative abundance (%) from abundance of major phyla for each of the 4 study locations arranged from east to west. For Bryozoa, Porifera and Cnidaria (Hydrozoa), a unit was assigned to the smallest weight and then the weight was divided by this unit to provide a 'count'

Table 5. Mean (\pm SD) species richness, total number of individuals, Shannon-Wiener diversity and Pielou's evenness for each of 4 study locations along the southwestern coast in South Africa

Location	Species richness	Total number of individuals	Shannon-Wiener	Pielou's evenness
St Helena Bay	22.1 (4.2)	536.6 (491.41)	1.88 (0.50)	0.61 (0.16)
Cosy Beach	17.9 (5.4)	148.6 (60.0)	2.18 (0.30)	0.76 (0.07)
Miller's Point	17.6 (4.6)	143.8 (33.7)	2.25 (0.31)	0.79 (0.06)
Gansbaai	19.6 (4.4)	156.1 (61.1)	2.27 (0.29)	0.76 (0.07)

Table 6. Average dissimilarity of the top 5 families between locations along the southwestern coast in South Africa

Location comparison	Average dissimilarity	Family	Contribution (%)
Gansbaai vs. Miller's Point	69.14	Gammaridae	6.4
		Syllidae	5.15
		Terebellidae	4.64
		Corophiidae	4.14
		Sabellidae	4.08
Miller's Point vs. Cosy Beach	69.02	Amphiuridae	5.7
		Sabellidae	4.78
		Syllidae	4.75
		Ampeliscidae	4.73
		Nereididae	4.34
Miller's Point vs. St Helena Bay	79.40	Gammaridae	10.26
		Mytilidae	5.22
		Podoceridae	4.96
		Tanaididae	4.17
		Sabellidae	3.49
Gansbaai vs. Cosy Beach	69.73	Amphiuridae	7.66
		Gammaridae	6.78
		Syllidae	4.47
		Corophiidae	4.15
		Ampeliscidae	3.96
Gansbaai vs. St Helena Bay	74.09	Gammaridae	7.94
		Mytilidae	5.35
		Podoceridae	4.98
		Tanaididae	4.71
		Syllidae	4.49
Cosy Beach vs. St Helena Bay	77.40	Gammaridae	10.81
		Mytilidae	5.46
		Podoceridae	5.25
		Tanaididae	5.2
		Amphiuridae	4.44

3.3. Influence of holdfast volume on macrofaunal diversity

Holdfast volume had no significant relationship with total macroinvertebrate abundance (Pearson's correlation coefficient: $t = 0.15442$, $df = 38$, $r = 0.025$, $p = 0.8781$; Fig. 4a) or diversity (PERMANOVA: pseudo- $F = 1.2034$, $p = 0.269$; Table 3, Fig. 4b). The largest individual holdfast volume was measured at Miller's Point (505 ml), it contained 174 individuals and had a diversity index (H') of 2.64 (Fig. 4). The lowest individual holdfast volume was observed at Gansbaai (60 ml) and had 116 individuals, with an H' of 2.06 (Fig. 4).

4. DISCUSSION

This study is the first to describe variations in macroinvertebrate assemblages from *Ecklonia max-*

ima kelp holdfasts at different sites within the Great African Seaforest. A total of 9 phyla were recorded, which is comparable to the findings of several other international studies on other kelps. Six major phyla were found in *Macrocystis pyrifera* holdfasts from southern Chile (Ojeda & Santelices 1984, Winkler et al. 2017), 11 in *Laminaria hyperborea* holdfasts from the northeast Atlantic (Teagle et al. 2018) and 15 in *E. radiata* holdfasts from New Zealand (Anderson et al. 2005b). Only 7 major phyla were identified from *E. maxima* holdfasts in an earlier study in South Africa (Velimirov et al. 1977), but that study sampled considerably fewer holdfasts from a single site. Interestingly, that study also failed to record any Annelida, whereas Annelida were a major contributing phylum to the abundance and diversity of the fauna in the present study. The reason for this disparity is unclear, but could be a function of sampling technique, or methods of sample processing.

Ecklonia maxima holdfasts were clearly demonstrated to have a diverse macroinvertebrate assemblage comparable to those found in other biogenic marine habitats studied in South Africa (Table 7). Although not as diverse as the seagrass and algal turf communities found in northern KwaZulu-Natal on the east coast (Browne et al. 2013, Milne & Griffiths 2014), these holdfast communities have a higher species richness than other kelp microhabitats (Allen & Griffiths 1981, Lindberg et al. 2020), as well as ascidian and mussel beds (Fielding et al. 1994, Hammond & Griffiths 2004).

4.1. Implication of recording diversity at family vs species level

Taxonomic sufficiency includes the identification of organisms to the level of taxonomic resolution that is necessary to retain important information about assemblages exposed to environmental stress or changes in biodiversity (Ellis 1985). Many studies use operational taxonomic units or morphospecies rather than named species (Balmford et al. 2000, Cabeza & Moilanen 2001). In the present study, organisms were identified to species level where possible (Table S2), but this was challenging due to time and equipment constraints, and because taxonomic knowledge of South African invertebrates remains generally incomplete, outdated or scattered across the literature. This lack of baseline taxonomic knowledge, expertise and comprehensive guides forms a major challenge for conducting biodiversity surveys in systems such as the Great African Seaforest. This unsolved problem

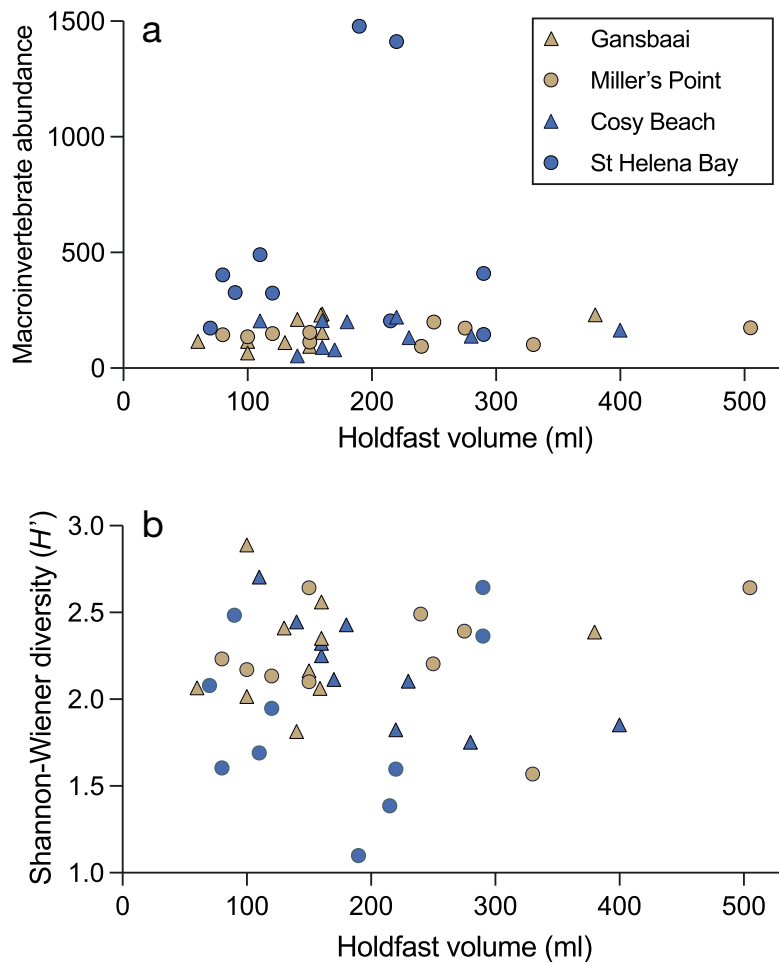


Fig. 4. Relationships between holdfast volume (ml) and (a) total macroinvertebrate abundance and (b) Shannon-Wiener diversity (H') for each holdfast from all 4 study locations ($n = 10$ per location). Brown represents the Agulhas marine ecoregion and blue represents the Southern Benguela marine ecoregion

has long been identified (Gibbons et al. 1999, Griffiths et al. 2010).

As a result, we were not always confident in the accuracy of our species identifications across the wide range of taxa examined, and hence restricted our analysis to family-level identifications, which could be made with confidence. Terlizzi et al. (2009) investigated the implications of using different taxonomic resolutions in identifying spatial patterns in various hard-bottom substrate habitats (holdfasts included). They found that family-level patterns follow species-level patterns. Furthermore, family-level identification can be used to identify significant changes, particularly in holdfasts (Anderson et al. 2005a). Volvenko et al. (2023) also emphasized that species richness can be assessed using higher taxonomic levels, such as family level, as species and supraspecies are strongly correlated. The authors discuss the importance of reporting supraspecies analyses in understudied habitats, especially where a complete species identification is not possible. However, it is possible that higher levels of taxonomic resolution (species rather than families) could have shown a difference in species diversity across ecoregions, as families could be consistent and numbers of species within these families could be very different between locations. Specifically, species numbers within these families might be greater in the east (Agulhas) than in the

Table 7. South African biogenic habitats and their associated macrofauna species diversity

Habitat type	Location	Taxa present	Dominant groups	Reference
Mussel beds of <i>Mytilus galloprovincialis</i>	West coast, South Africa	35 species	Arthropoda, Polychaeta, Gastropoda	Hammond & Griffiths (2004)
Solitary ascidian beds of <i>Pyura stolonifera</i>	Durban, KwaZulu-Natal	83 species, 10 phyla	Annelida, Arthropoda, Nemertea, Mollusca	Fielding et al. (1994)
Seagrass beds of <i>Thalassodendron leptocaula</i>	Sodwana, KwaZulu-Natal	230 species, 8 phyla	Arthropoda, Annelida, Mollusca	Browne et al. (2013)
Algal turfs	Sodwana, KwaZulu-Natal	314 species, 4 phyla	Arthropoda, Annelida, Mollusca, Echinodermata	Milne & Griffiths (2014)
Canopy and stipe of <i>Ecklonia maxima</i> kelp	False Bay and Oudekraal, Western Cape	81 species, 11 phyla	Arthropoda, Mollusca, Polychaeta	Lindberg et al. (2020), Allen & Griffiths (1981)
Holdfast of <i>E. maxima</i>	Southwestern and west coasts, Western Cape	> 146 species, 9 phyla	Arthropoda, Annelida, Mollusca	Present study

west (Southern Benguela), and this might be responsible for our unexpected result of similar diversity levels between these ecoregions.

4.2. Variation across ecoregion

Marine ecoregions appear to have no significant effect on family-level macroinvertebrate assemblages found in *E. maxima* holdfasts (Table 3); therefore, Hypothesis (i) (macroinvertebrate assemblages would differ significantly between the 2 marine ecoregions) was rejected. Generally, temperature is a major driver of marine species distribution at large spatial scales (Tittensor et al. 2010, Waldock et al. 2019, Bué et al. 2020) and across seasons (Winkler et al. 2017). Both the Agulhas and Southern Benguela marine ecoregions differ in temperature (Griffiths et al. 2010), with Cape Point being the break point between these ecoregions (Leliaert et al. 2000, Sink et al. 2012, 2019), and with lower temperatures and fewer species on the west of the Peninsula compared to the east (Leliaert et al. 2000, Awad et al. 2002, von der Heyden 2009, Griffiths et al. 2010). A higher taxonomic resolution in this study might have provided a different result, as presented by Anderson et al. (2005a), who showed that the effect of large spatial scales on macroinvertebrate assemblages are less distinct with lower taxonomic resolution. Also, several of the major groups associated with holdfasts (Amphipoda, Isopoda, Polychaeta) are exceptions to the trend observed in the biota as a whole, and rather display a diversity peak in the cooler waters of the Western Cape (Awad et al. 2002).

4.3. Variation across location

Location did have a significant effect on macroinvertebrate assemblages (Tables 3 & 4); therefore, Hypothesis (ii) (there would be a significant difference in macroinvertebrate assemblages between individual locations) was accepted. St Helena Bay was the most distinct location, having both the highest abundance and the highest diversity of families (Table 4, Fig. 2). This was unexpected, given that overall marine biodiversity tends to be lower along the west coast (Awad et al. 2002). Based on this, it was expected that the south coast sites, Miller's Point and Gansbaai, would have a higher diversity than the west coast sites (St Helena Bay and Cosy Beach).

All locations showed a significant difference in community assemblages, except for Gansbaai–Miller's

Point and Miller's Point–Cosy Beach (Table 4). Miller's Point, located between Cosy Beach to the west and Gansbaai to the east, exhibits similar macroinvertebrate assemblages to both these sites, reflecting its geographical position between them. The dominant phyla at all 3 locations were Arthropoda (mainly Amphipoda) and Annelida (mainly Polychaeta) (Table 1, Fig. 3), the same dominant phyla reported in similar studies elsewhere (Ojeda & Santelices 1984, Smith et al. 1996, Thiel & Vásquez 2000, Anderson et al. 2005b, Walls et al. 2016, Teagle et al. 2017).

The present study was designed to explore baseline biodiversity of individual holdfasts, rather than to conduct a large-scale analysis. However, our data do reveal some large-scale variations, with the most obvious being the distinct community assemblage of St Helena Bay compared to the other 3 sites. Reasons for this unexpected result, which should be explored further, could relate to environmental pollution events from the 1970s, or the frequent algal blooms, which often cause walk-outs and mass mortalities in this area (Shannon et al. 1982, Cockcroft 2001, Mouton et al. 2012, Branch et al. 2013, Pitcher et al. 2014, Ndhlovu et al. 2017).

4.4. Influence of holdfast volume

Holdfast volume sometimes plays a significant role in determining holdfast diversity (Thiel & Vásquez 2000, Anderson et al. 2005b). However, in our study, biodiversity and abundance did not increase with holdfast volume (Table 3, Fig. 4). Christie et al. (2003) also found that increases in *L. hyperborea* kelp holdfast volumes were not correlated to macrofauna diversity, but that an increase in holdfast volume led to a significant increase in macrofauna abundance. Our study contradicts several studies that found a significant relationship between holdfast volume and macrofauna species diversity (Ojeda & Santelices 1984, Smith et al. 1996, Thiel & Vásquez 2000, Anderson et al. 2005b, Walls et al. 2016), possibly because holdfasts were not sampled across a wide enough size range to demonstrate such a trend (if minute holdfasts had been sampled, these would surely have had a reduced faunal diversity).

It is worth noting that encrusting invertebrates typically reduce the available habitat for other organisms in holdfasts, resulting in a decrease in biodiversity (Anderson et al. 2005b, Fernández et al. 2022). However, this remains to be tested for *E. maxima* holdfasts. In the present study, possibly because the

encrusting invertebrates were only present in St Helena Bay ($n = 10$, primarily attached to the outer surface of the holdfasts) and Gansbaai ($n = 2$ holdfasts) (Table 2, Fig. 3), they did not lead to a corresponding decrease in diversity at family level. Future studies investigating this relationship should quantify the coverage of encrusting organisms, rather than within the holdfast crevices (C. Katharoyan, pers. obs.). As encrusting invertebrates were solely detected in St Helena Bay ($n = 10$ holdfasts) and Gansbaai ($n = 2$ holdfasts) (Table 2, Fig. 3), it is challenging to determine whether they could potentially affect the overall biodiversity and volume relationship.

4.5. Unique species

From the 67 species identified, the role of *E. maxima* holdfasts in the Great African Seaforest can be slightly better understood. An invasive species of isopod, *Limnoria quadripunctata*, was documented at all locations (Table S2). The previous known distribution range of *L. quadripunctata* was between Table Bay and Port Elizabeth (Robinson et al. 2005, Griffiths et al. 2011), indicating that the species might have expanded its western range from Table Bay to St Helena Bay, or that it was previously overlooked. The invasive mussel *Mytilus galloprovincialis* and the native brown mussel *Perna perna* dominated and co-existed at St Helena Bay, showing that holdfasts support both native and non-native marine invertebrates.

At Miller's Point, an undescribed Amphipoda species from the family Ampeliscidae was found (C. Griffiths, pers. obs.). As the species did not taxonomically match any other known species of *Ampelisca* (Griffiths 1976), it was preliminarily identified and recorded as *Ampelisca* sp. (Table S2). Another undescribed species in this study included an unknown species of nudibranch (family Dorididae, genus *Doris*) from St Helena Bay (G. Jones, pers. comm.). These 2 examples highlight the importance of documenting holdfast communities, as it is highly likely that they harbour many more undescribed species.

Furthermore, kelp holdfasts are known to act as nursery habitats (Ojeda & Santelices 1984, Tegner & Dayton 2000, Teagle et al. 2018), and the present study showed that *E. maxima* holdfasts fulfil this role for many species of Bivalvia, Echinodermata (such as the sea urchin *Parechinus angulosus*, the sea cucumber *Pentacta doliolum*, and several Ophiuroidea species) and Decapoda (such as the crabs *Pilumnus minutus*, *Guinusia chabrus* and *Pilumnoides*

rubus, hermit crabs *Paguristes gamianus*, rock lobsters *Jasus lalandii* and snapping shrimp *Synalpheus tumidomanus*) (Table S2). This was also seen in *M. pyrifera* holdfasts, where Echinodermata and Decapoda used holdfasts as refuges for reproduction and protection of their young (Ojeda & Santelices 1984).

5. CONCLUSIONS

Holdfast communities display an abundant invertebrate fauna representing considerable taxonomic diversity, making them much richer than other kelp microhabitats. Although several taxa were common at all sites, there were site-specific differences, with the west coast displaying the highest richness and the other 3 sites displaying a gradual change in richness from west to east. However, it is unclear what drives these differences. The low percentage of species identified in our study highlights the importance of continued biodiversity and taxonomic research within this microhabitat. Future research on kelp holdfast macrofauna assemblages could focus on a single phylum and work at finer scales of resolution to provide this much-needed baseline taxonomic information. Building on this, larger-scale studies could identify the ecology and interactions within holdfast communities, as well as patterns and drivers of species distribution within the Great African Seaforest. As South Africa's kelp forests expand eastwards, our research will allow us to monitor changes in kelp forest biodiversity and associated range shifts of macro-invertebrates.

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