Baited remote underwater video survey of macro-invertebrate distribution and abundance across False Bay, South Africa

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Table of contents

ABSTRACT

Assessing invertebrate species diversity and distribution based on environmental predictors is essential for conservation planning. South Africa need to understand ecological patterns to better plan for species conservation. South Africa's unique coastline requires additional protection, but the design of areas is reliant on evidence based research. South Africa has a distinctive marine environment and is host to tropical, sub-tropical and temperate invertebrate species. False Bay in the Western Cape province of South Africa is a biodiversity hotspot with high species richness due to the overlap of two bioregions. This project reports on the first comprehensive camera survey of False Bay's invertebrate population and assesses diversity across more habitat types and a greater depth range than previous dredge studies. 154 sites were sampled across summer and winter, reef and sand and three depth categories: shallow (5-15 m), intermediate (16-30 m) and deep (31-50 m). A total of 67 species from 8 phyla were recorded in this study. Winter samples showed a greater diversity than those sampled in summer (p=0.004). Intermediate depths (Shannon-H=1.184) and reef substrate (Shannon-H=1.403) support a greater diversity of invertebrate species. Habitat emerged as the most significant predictor of species distribution in the bay (p=0.01). Depth (p=0.01) and season (p=0.03) were also of influence, but to a lesser extent. Reef sites were separated from sand sites by the presence of *Jasus lalandii* and *Comanthus wahlbergi* on the former and *Bullia laevissima*, *Marthasterias glacialis* and *Ovalipes trimaculates* on the latter. Reef species *J. lalandii* and *Tropiometra carinata* and sand species *B. laevissima* and *M. glacialis* had the greatest contribution to dissimilarity between winter and summer samples. Complex granite reefs should be a main priority in invertebrate conservation as they host the greatest species diversity and abundance of all habitats sampled. BRUVs have provided a non-invasive, non-destructive method of sampling invertebrate species on all habitat types and are recommended for use in future studies of invertebrate species composition.

Introduction

Invertebrates as ecosystem indicators

Benthic invertebrates characterize the seafloor and are responsible for the modification of these environments into complex, diverse habitats (Snelgrove 1999). They play an important trophic role in marine ecosystems and are a major resource for human-beings as food, medicines and in aquaculture (Troell et al. 2006; Pawlik 1993; Lotze & Milewski 2004). Improved understanding of the patterns of invertebrate abundance and distribution as well as linking mechanisms between them will allow increased inclusion of these important interactions in conservation and management legislation (Snelgrove 1999). Past attempts at managing ecosystems have demonstrated the difficulty and complexity of such a task, but also highlight the importance of conservation (Kremen 2005).

Marine biodiversity is responsible for maintaining the ecosystem services on which the human population depends (Worm et al. 2006). Interactions between organisms plays a major role in determining the distribution and abundance of benthic communities, where changes in biodiversity often occur as a direct result of exploitation, pollution and habitat destruction (Worm et al. 2006). As well as their importance as a food source for higher trophic levels, benthic invertebrate abundance is mirrored by the state of the environment and drivers of change (Rocers & Greenaway 2005). Most species are either sessile, sedentary or move within a limited range, making them excellent indicators of ecosystem health (Rocers & Greenaway 2005).

False Bay, a dynamic ecosystem

The South African coastline is unusual in that it hosts tropical, sub-tropical as well as temperate species along its shores (Day 1970). South African coastal waters are dominated by two oceanic currents: the cold Benguela current running along the west Coast, and the warm Agulhas current that runs along the east coast (Griffiths et al. 2010). These currents play an important role in determining diversity and abundance of invertebrate species (Griffiths et al. 2010), given the importance of seawater temperature in regulating organism distribution. Day (1970) showed that the coast is divisible into three distinct bioregions with overlap zones between them. The east coast extends from the Transkei into Mozambique and is made up of tropical and subtropical species (Day 1970). The west coast extends from Cape Agulhas northward and hosts cool-temperate fauna (Day 1970), while the warm-temperate south coast extends from the Transkei to Cape Point and contains species from both east and west coastal systems, making it a rich and diverse area of study (Day et al. 1970).

The influence of both the Agulhas and Benguela currents is evident in False Bay, resulting in a unique mixture of invertebrate species (Day 1970). Previous studies have highlighted False Bay as a hotspot for biodiversity with a peak in richness due to the overlap of two bioregions (Scott 2009), making False Bay an important area for biodiversity conservation and management (Lombard et al. 2011).

False Bay is the largest true bay along the South African coastline as it is deep enough to offer significant protection from wave exposure (Spargo 1991). South Africa is known to have a high percentage of endemism (33%) and it is therefore important to fully understand the interaction of invertebrate species within their environment (Griffiths et al. 2010). Studies have shown that community composition is largely determined by depth, temperature, salinity and sediment dynamics, all factors that vary within False Bay (Atkins 1970 & Day 1970), both seasonally and annually. Most invertebrate species are benthic and have specific habitat preferences based on morphology and other limiting factors such as food availability and quality, factors also largely controlled by environmental conditions (McQuaid & Branch 1984).

The variation in substrata, from soft sediment to complex granite reefs, found in False Bay, has meant that traditional sampling methods have been limited to specific areas, restricting the extent of community studies to a specific habitat type or depth. The geology of False Bay consists of Malmesbury Shale (MS), Table Mountain Sandstone (TMS) and Granite (Du Plessis and Glass 1991). The western part of False Bay is underlain by granite and the eastern part by Malmesbury Shale, both types allowing the formation of large, complex reef systems (Du Plessis and Glass 1991). Towards the north of the Bay, there is a shift from reefs and kelp forests to broken shell and course sand with patches of fine sediment gently sloping up the beach (Du Plessis and Glass 1991).

Surface currents in the Bay are wind driven and change among seasons and within seasons as dominant wind patterns change. The southwest edge of the Bay is mostly influenced by south-easterly winds with southerly winds dominating in the northern parts of the Bay. South-westerly or south-easterlies dominate in the north-east corner of the Bay (Cram 1970). Cram (1970) showed that in summer a clockwise current is evident within the Bay, formed by easterly and south-easterly winds. During this period a gyre forms in the north-east corner, often with a reverse circulation. In contrast, winter currents are largely affected by north-west winds, causing a reversal of flow patterns to an anti-clockwise flow (Cram 1970).

In winter, surface temperatures average between 13-14 °C, dropping to about 10-12 °C at greater depths (Watson 2013). During spring, warmer water from the Agulhas bank (16 °C) flows into the bay and circulates in a clockwise manner, increasing temperatures to about 18°C in the north-east corner of the Bay (Watson 2013). The cold Benguela current is associated with short but significant upwelling events providing nutrients and decreased temperatures within the upwelling cells (Griffiths et al. 2010). Upwelling is wind driven and is most common in spring and summer when offshore south-easterly winds are at their strongest (Griffiths et al. 2010). Upwelling along the west coast invokes high productivity and supports a large biomass of marine life (Dunn 2014). The south-easterly winds cause a north-westerly drift of upwelled water into False Bay during summer months (Cram 1970). Upwelled water flowing along the western shore of the Bay results in surface temperatures that are generally slightly lower than those of the eastern shore (Cram 1970).

In contrast, the warm Agulhas current, originating in the tropics, is associated with nutrient poor waters, small stock sizes but very high diversity of species (Griffiths et al. 2010). The Agulhas current is 1500km long and 300 km wide, running from east to west down the eastern South African coast before turning east at about 40°S, 20°E (Duncan 1970). Although the main Agulhas current deflects towards the south-east, branches of warmer waters occasionally flow into False Bay (Duncan 1970). The Agulhas bank generally experiences mixed waters from the Benguela drift and Agulhas current, the same water that enters False Bay in relaxed periods of no upwelling (Day 1970).

Previous invertebrate studies in False Bay

The first study on invertebrate distribution patterns in False Bay was done by Morgans (1959, 1962), who discovered the presence of faunistic areas dominated by specific species (Field 1970). A polychaete species dominates the northern part of False Bay on coarse sand, a smaller area by an amphipod species and deeper waters are dominated by a species of urchin and a species of anemone (Field 1970). This study was limited by sample size and habitat due to the restriction of dredge sampling to sand habitats. Field (1970) performed a study based on the method used by Morgans (1962) to collect 150 dredge samples, but also included 89 grab samples.

Field (1970) found sites sampled in depths shallower than 80 m all showed similar species composition and did not show significant differences among them. Samples at depths between 80-87 m were found to be significantly different with regards to species distribution when compared with shallower samples. (Field 1970). He concluded that there are major changes in invertebrate assemblages from shallow to deep water and that there were specific species dominating at different depths.

Field (1970) also highlighted the influence of other factors, including type of substratum, in determining species diversity. Very shallow samples also showed a significant difference in diversity compared to other samples in the study, which could be a result of the influence of wave action on soft sediment species. Field (1970) also observed the pattern of varying diversity on hard and soft substrate but also noted the inaccuracy of sampling hard substrate using dredge and grab sample methods. Dredging was the only available method to sample the depths of False Bay at the time.

The parallel development of marine research and technology has provided qualitative data sets that provide information on the health of South African marine species and the effects of human activities, such as introduction of alien species, over fishing and global warming (Bax et al. 2003; Hughes 2000; Jackson et al. 2001). Most data sets provide detailed information on commercially important fish species but lack accurate, long-term data on invertebrate species. The distribution and diversity of invertebrate species is very poorly understood and is traditionally a rare focus of studies. Invertebrates play an important role in South Africa's economy and have experienced extreme levels of exploitation in the recent past (Griffiths & Branch 2010).

Since these early studies were undertaken the biology and oceanography of False Bay has been further studied. The development of technology has created non-extractive methods that can be used to survey and monitor invertebrate species in the Bay. Studies are no longer limited to soft sediments, and this has allowed the completion of the first comprehensive study on invertebrate distribution and abundance in False Bay using Baited Remote Underwater Video systems.

Baited Remote Underwater Video system (BRUVs)

Many survey methods are limited to certain habitat types, are destructive or are restricted by other environmental factors such as depth (Langlios et al. 2010; Willis et al. 2000). There is no one method that can be applied to all studies, making comparisons between areas difficult and inaccurate (Field 1970). Baited Remote Underwater Video systems (BRUVs) are a complementary method and has provided a repeatable system that has removed bias introduced by the decisions of individuals and alteration of animal behaviour (Field 1970).

Methods have been developed that have improved the assessment of the health of fish and shark populations in oceans across the world (Dulvy et al. 2008). Developments and improvements in technology have produced methods that limits biases introduced by the nature of the equipment or survey method. Some of the methods largely used today include visual census (VC), controlled angling (Willis et al. 2000), dredge sampling (Field 1970) and BRUVs (Cappo et al. 2004; Harvey et al. 2005).

The use of BRUV systems has only recently been introduced as a method to assess the community structures of fish and sharks in South Africa. This system was developed in Australia and proved successful in measuring diversity and abundance of fish species

(Watson 2013). This is a low impact, non-invasive method of survey and shows potential for long-term studies. Non-destructive methods are important for studies conducted in Marine Protected Areas (MPA's) where conservation is a main priority (Malcolm et al. 2007). South Africa is expanding its protected area network and the development of non-destructive monitoring systems is crucial to ensure conservation goals are achieved.

In addition to BRUVs evident advantages with regards to non-invasive sampling, they also provide the option of storing footage that can then be used in future studies of change, or in studies focussed on a different aspect of the community structure. BRUVs are able to sample at depths of up to 50m and is suitable for use on complex habitats (Malcolm et al. 2007). BRUV provides a useful method for surveying cryptic or shy species as animal behaviour is not affected, which allows for detection of these species (Langlois et al. 2010). The absence of divers removes the bias caused by attraction or deterring of certain species (De Vos 2012). However, the attraction of bait used in the study often skews results towards carnivorous and scavenger species (De Vos 2012). Species attracted to the activity around the bait have also been recorded in fish and shark surveys (Watson 2013). The effect of bait on invertebrate studies have not yet been studied, but is expected to influence the diversity and abundance recorded. Using video techniques will provide permanent records that can be validated where necessary (Langlois et al. 2010). BRUVS are more cost effective and have higher power and lower variability than other methods (De Vos et al. 2014).

This is the first comprehensive study on benthic macro-invertebrate distribution and abundance across False Bay. The aim of the study is to determine the diversity of macro-invertebrates and also to comment on the feasibility of BRUVs for surveying invertebrates.

Four hypotheses were tested. (1) There will be a difference in productivity among the depth categories and (2) between seasons resulting in a difference in invertebrate diversity and abundance. (3) There is a greater diversity on reef habitats and (4) diversity and abundance on east and west sides of the Bay will differ due to current patterns.

Methods

Study area

False Bay is found to the west of the Cape Agulhas and is the only true bay in Southern Africa. False Bay (34°04'-34°16'S, 18°26'-18°51'E) has an area of 1090 km^2 with the mouth width of 32 km (Spargo 1991). The mouth of the Bay extends from Cape Point in the west to Cape Hangklip in the east.

Survey sites

The survey design is described by De Vos et al. (2014). False Bay was split into nine zones of similar size, each encompassing a range of depths and habitat types (Figure 1). Winter sampling occurred during June and July of 2012 and summer sampling December 2012. Samples were collected from 185 sites that were selected using a random stratified method (Figure 1). Sites were selected to ensure that 50 % of samples were on reef habitats and 50 % on sand. Zones that has more than one type of reef were sampled to ensure all reef types were considered. To avoid pseudoreplication and the overlapping of bait plumes, BRUVs were separated by at least 250 m (De Vos et al. in press). Sampling was restricted to depths shallower than 50 m as the housing of the camera could not withstand greater pressures. Samples were limited to waters deeper than 5 m as BRUVs cannot be deployed from a boat in the surf zone or shallow waters in False Bay (De Vos et al. in press).

At each of the sites, the depth and geographical co-ordinates were recorded. The video was recorded for an hour, which has been shown to be an adequate length of time for fish sampling (De Vos 2012). The time requirement for invertebrate surveys has not been studied and one hour was therefore considered adequate.

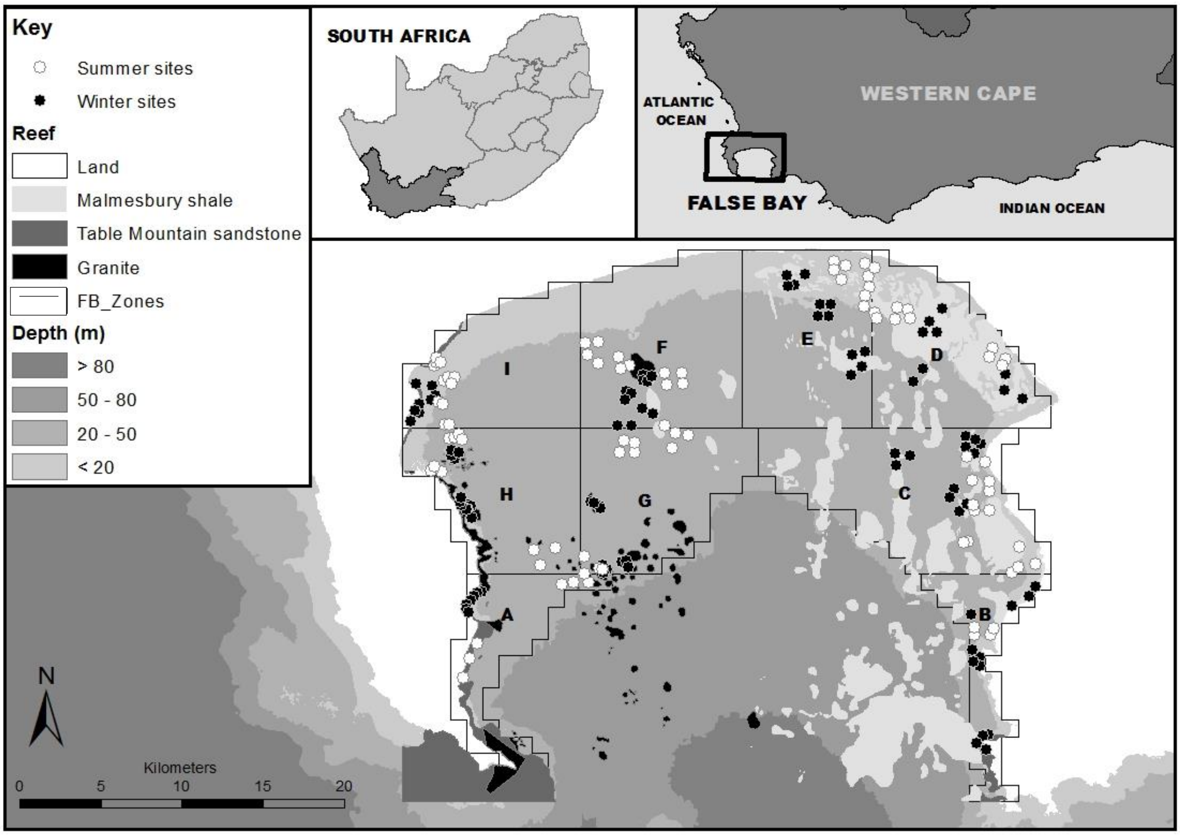

Figure 1. A map of False Bay with South Africa (insert top left) and the Western Cape (insert top right) showing the sampling sites and zones in this study (De Vos et al. in press).

Baited remote underwater video system (BRUVs)

A *GoPro Hero 2* camera in a waterproof casing was mounted horizontally onto a steel frame (Figure 2 and Figure 3). A perforated PVC bait canister (130 mm x 110 m with 10mm perforations) was mounted in view of the camera. The bait canister was filled with 1 kg of sardines (*Sardinops sagax*). The steel frame sets the camera 1m away from the bait canister and 30 cm off the ground. The steel frame was connected to a surface buoy via a rope to ensure it can be easily spotted and retrieved by the boat.

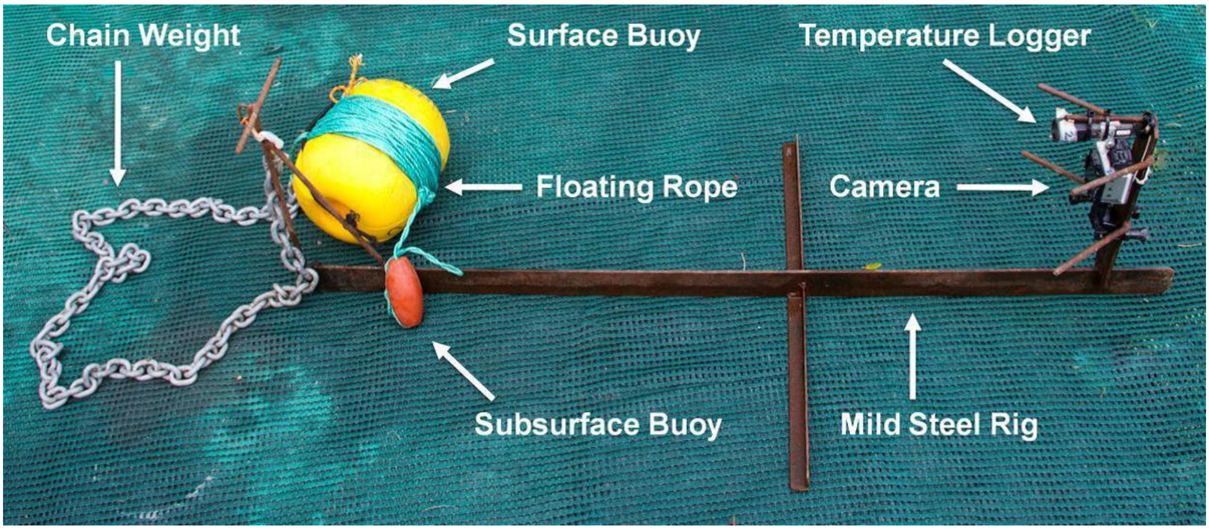

Figure 2. The baited remote underwater video system with all the components. This image does not include the bait canister (Sanguinetti 2013).

Figure 3. A baited remote underwater system in operation (Sanguinetti 2013).

Environmental variables

Depth was recorded *in situ* and was categorised into either shallow (5-15 m), intermediate (16-30 m) or deep (31-50 m). The season (summer or winter) in which the sample was collected was also considered as a factor which could influence diversity and abundance. Habitat was recorded as either sand or reef. Reefs were then classified as either Malmesbury shale, granite or Table Mountain sandstone (De Vos et al. in press).

Species identification

Videos were analysed using Apple Quicktime 7.7.1. Each species of invertebrate was identified and counted. MaxN represented the greatest number of individuals of a species in any one frame for the duration of the one-hour recording. This was done to avoid recounting individuals that swam in and out or crowded in view of the camera (Cappo et al. 2004). There were difficultulties in distinguishing between individuals of certain reef species covering a large area, thus these were recorded as either present or absent. There was no estimation of abundance for these species, which altered the accuracy of abundance analyses of reef samples. Porifera and certain Crinoidea species were therefore highly underestimated in this study.

Statistical analysis

Data was standardised and fourth root transformed to decrease the influence of abundant species. Using MaxN as a measure for abundance, Shannon-Weiner diversity index (H') was calculated for each site. To determine the similarity in species composition and abundance among different sites, a Bray-Curtis similarity matrix was calculated. A multi-dimensional scaling plot in PRIMER-E version 6 (Clarke and Gorley 2006) was used represent the similarity and show the effect of habitat, season, depth and zone on species diversity and abundance. A one-way analysis of similarity (ANOSIM) tested the influence of habitat, season, depth and zone on species composition. A permutational multivariate analysis of variance (PERMANOVA) was performed on each of the variables individually to assess the influence they have on species composition and abundance. The variables were then assessed in combination to determine the combined influence and their interactive effects. Models were assessed using the pseudo-F statistic with 999 random permutations of the data. Models were run using the extension package PERMANOVA+ in PRIMER-E version 6 (Clarke & Gorley 2006). To define which species contributed towards the dissimilarity and similarity between sites, a SIMPER similarity test was performed.

Results

Diversity and abundance

From the 185 sites that were sampled, six contained no invertebrate species, eighteen were unusable due to poor visibility and seven experienced a technical malfunction and were therefore removed from the data set. The remaining 154 sites were used, of which 75 were reef sites and 83 sand sites. 37 % of summer sites and 55 % of winter sites were reef. Total abundance in winter (2133 individuals) was significantly greater than the abundance recorded in summer (1523 individuals). Sixty seven species recorded in total (Table 9). The diversity was higher in winter (57 species) than summer (46 species).

Shannon-Weiner diversity index showed a greater diversity in winter (1.20) compared to summer (0.99) and a greater diversity on reefs (1.40) compared to sand (0.85) (Figure 4). Intermediate depths contained the greatest diversity (1.18), shallow contained the second highest value of diversity (1.10) and deep sites the lowest measure of diversity (0.99) (Figure 4).

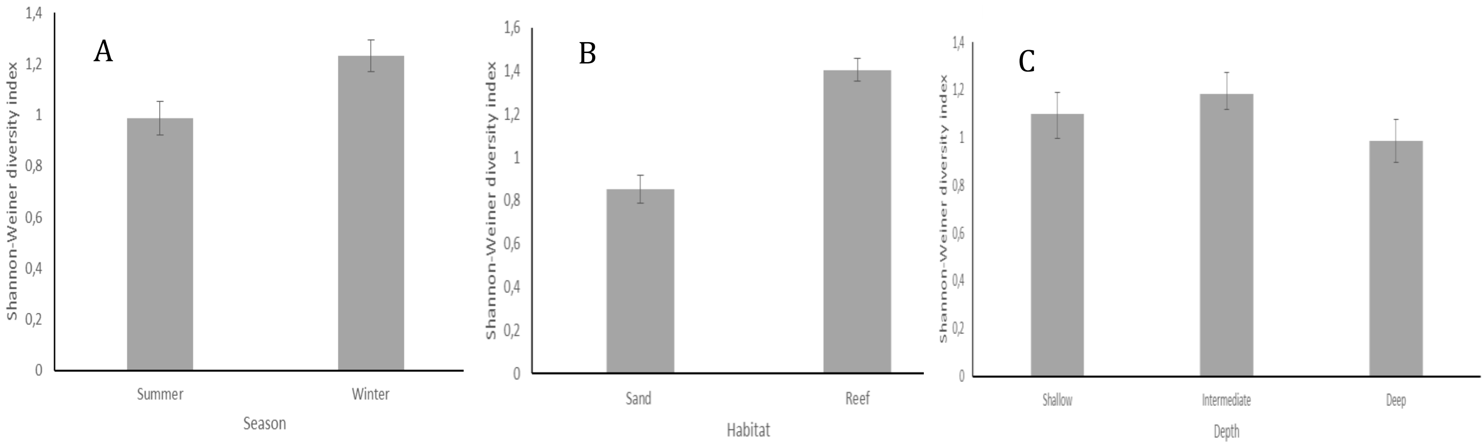

Figure 4. Shannon-Weiner Diversity Index calculated for a) winter and summer, b) sand and reef and c) shallow, intermediate and deep depths (Standard error bars are shown).

The influence of habitat

Figure5 shows the similarities in species composition between reef and sand habitats. There was a very slight overlap of sand and reef clusters, suggesting very strong differences. An ANOSIM analysis revealed a significant difference in the sites that were sampled on reef habitats compared to those sampled on sand (R=0.389, p=0.01). SIMPER similarity test results showed a high dissimilarity between the two habitat types with a value of 95.01 % dissimilarity. The five species that contributed most towards the dissimilarity are shown in Table 1, illustrating a clear separation in species composition between the two habitat types. *Bullia laevissima* was most dominant on sand habitats with *Jasus lalandii* dominating reef habitats. *Marthasterias glacialis* was be found in both habitat types but shows a greater average abundance in sand habitats. *Ovalipes trimaculatus* was mainly sampled in sand habitats with *Comanthus wahlbergi* inhabiting mainly reef habitats.

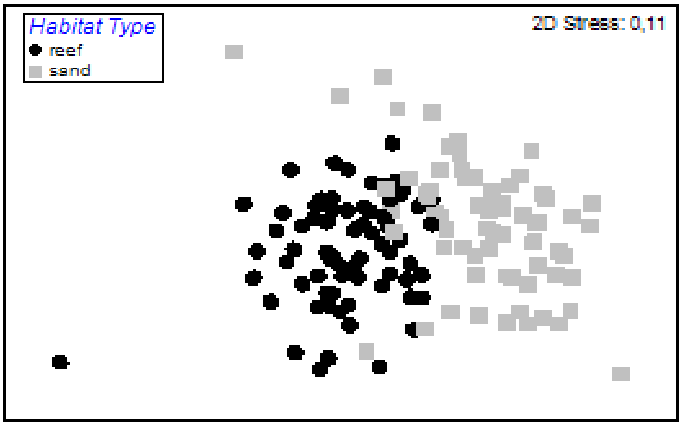

Figure 5. Multidimensional scaling plot of Bray-Curtis similarity of invertebrate assemblages sampled on reef and sand habitats in False Bay. The abundance data were transformed using a fourth root transformation.

Table 1. The top five species contributing towards the dissimilarity value are listed with their mean abundance in reef and sand sites and their contribution to dissimilarity.

Species	**Reef Average Abundance**	**Sand Average Abundance**	**% Contribution to dissimilarity**
Bullia laevissima	0.61	27.63	14.57
Marthasterias glacialis	5.46	11.5	7.13
Jasus lalandii	9.24	3.19	6.02
Ovalipes trimaculatus	1.03	10.72	5.97
Comanthus wahlbergi	9.86	1.68	5.24

The influence of season

Due to an uneven proportion of sand and reef samples, the habitat types were considered separately for the remaining analyses. Fig. 6 showed no clear separation or clustering between assemblages sampled in summer and those sampled in winter for both reef and sand habitats. However, ANOSIM results showed a significant difference of species sampled in summer compared to those in winter for both reef (R=0.065, p=0.02) and sand (R=0.082, p=0.007) samples. Season had a greater influence on species composition for sand species compared to reef species.

A SIMPER similarity test showed a high level of dissimilarity between species sampled in different seasons. All filter feeding species and 82% of Porifera species experienced a decreased abundance in summer. Table 2 shows the five species that had the greatest contribution towards the dissimilarity value. *B. laevissima* had a much greater average abundance during summer than winter. *M. glacialis* was slightly more abundant during winter in comparison with *O. trimaculatus* that was more abundant during summer. *Astropecten irregularis pontoporeus* had an average abundance that was slightly higher in summer but did not show a large change between seasons.

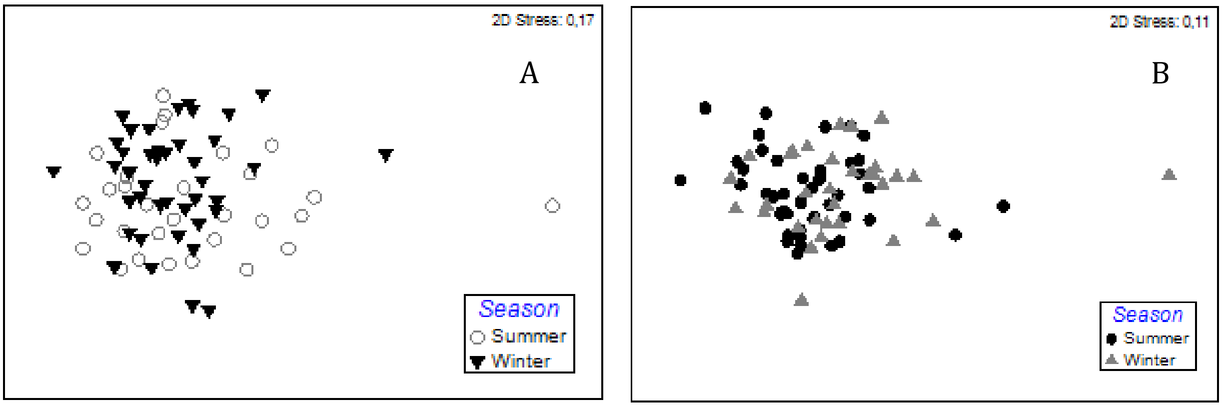

Figure 6. Multidimensional scaling plot of Bray-Curtis similarity of invertebrate assemblages sampled in winter and summer on A) reef and B) sand habitats in False Bay. The abundance data were transformed using a fourth root transformation.

Table 2. The top five species contributing towards the dissimilarity value of reef sites are listed with their mean abundance in summer and winter sites and their contribution to dissimilarity.

Species	**Summer Average Abundance**	**Winter Average Abundance**	**% Contribution to dissimilarity**
Jasus lalandii	0.27	0.63	8.89
Tropiometra carinata	0.37	0.66	6.78
Eunicella tricoronata	0.32	0.46	6.72
Comanthus wahlbergi	0.53	0.54	6.21
Ophioderma wahlbergii	0.29	0.37	6.13

Table 3. The top five species contributing towards the dissimilarity value of sand sites are listed with their mean abundance in summer and winter sites and their contribution to dissimilarity.

Species	**Summer Average Abundance**	**Winter Average Abundance**	**% Contribution to dissimilarity**
Bullia laevissima	1.20	0.55	19.62
Marthasterias glacialis	0.31	0.56	10.31
Ovalipes trimaculatus	0.39	0.40	9.69
Astropecten irregularis pontoporeus	0.31	0.43	8.68
Ophiothrix fragilis	0.05	0.51	6.54

The influence of depth

In Fig. 7 there was no clear separation or clustering of sites at different depths for reef and sand samples. However, the one-way ANOSIM showed a significant difference between invertebrate assemblages sampled at different depths. It revealed a significant difference in invertebrate assemblages across all depth categories for reef (R=0.135, p=0.01) and sand (R=0.075, p=0.32) samples. The samples collected at shallow and intermediate depths were most significantly different on reef (R=0.152, p=0.01) and sand (R=0.120, p=0.02) (Table 4). The least significant difference was between shallow and deep sites in reef (R=0.087, p=0.025) and sand (R=0.035, p=0.17) (Table 4). Samples collected at intermediate depths were also significantly different from those collected at deep depths. The difference in species composition between intermediate and deep depths was greater on reef (R=0.151, p=0.04) than sand (R=0.045, p=0.124) (Table 4).

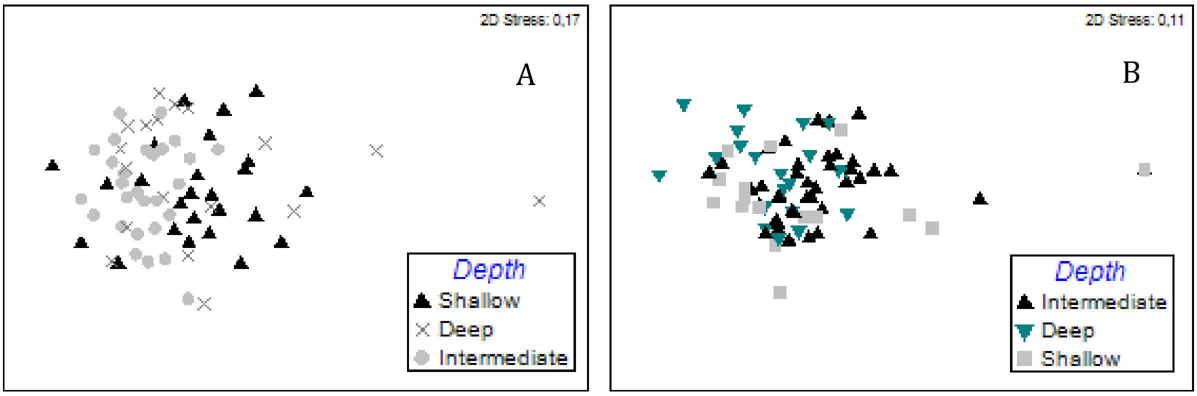

Figure 7. Multidimensional scaling plot of Bray-Curtis similarity of invertebrate assemblages sampled in three depth categories for A) reef sites and B) sand sites. Sites are categorised according to depth: Shallow (5-15 m), Intermediate (16-30 m) and Deep (31-50 m). The abundance data were transformed using a fourth root transformation.

Table 4. ANOSIM results for depth sites in False Bay including the number statistic (R) and significance level of each category calculated for reef and sand sites. Depth was categorised into Shallow (5-15 m), Intermediate (16-30 m) and Deep (31-50 m).

Groups Observed	**Number Statistic Reef (R)**	**Significance level Reef (%)**	**Number Statistic Sand (R)**	**Significance level Sand (%)**
Shallow, Intermediate	0.150	0.10	0.120	2.10
Shallow, Deep	0.087	2.50	0.035	17.0
Intermediate, Deep	0.151	0.40	0.045	12.4

The results obtained from SIMPER similarity also showed a high level of dissimilarity among all depth categories. There was a clear pattern within samples where the most abundant, mobile species contributed the most to dissimilarity among groups of sand and reef samples. Different species dominated the different depth categories. Table 5 shows the species commonly found at the three different depth categories on reefs. *Parechinus angulosus*, *Crambe acuata* and *Ophioderma wahlbergii* were common in shallow depths whereas; *Ophiothrix fragilis*, *T. carinata*, *Eunicella tricoronata* and *C. wahlberghi* were the species commonly found at intermediate depths on reefs. Deeper depths were commonly colonized by *J. lalandii*, *M. glacialis* and *Polymastia mamillaris*. In contrast, Table 6 shows the species commonly found at three different depth categories on sandy habitats. *O.*

trimaculatus, *Sabella penicillus* and *Bullia digitalis* were commonly found in shallower depths with *B. laevissima*, *M. glacialis* and *O. fragilis* at intermediate depths and *M. glacialis*, *Dardanus arrosor* and *A. irregularis pontoporeus* colonized deeper depths.

Table 5. The average Bray-Curtis similarity among reef sites per depth category are shown in the diagonal blocks. The off-diagonals list species that are common in the depth listed on the row but rare in the depth listed on the column.

		Rare Species		
		Shallow	**Intermediate**	**Deep**
Common Species	**Shallow**	18.36	*P.angulosus* *C.acuata*	*O. wahlbergii* *C. acuata*
	Intermediate	*O.fragilis* *T.carinata*	29.98	*E,tricoronata* *C.wahlbergi*
	Deep	*J.lalandii* *M.glacialis*	*J.lalandii* *P.mamillaris*	16.39

Table 6. The average Bray-Curtis similarity among sand sites per depth category are shown in the diagonal blocks. The off-diagonals list species that are common in the depth listed on the row but rare in the depth listed on the column.

		Rare Species		
		Shallow	**Intermediate**	**Deep**
Common Species	**Shallow**	16.56	*O.trimaculatus* *S.penicillus*	*O.trimaculatus* *B.digitalis*
	Intermediate	*B.laevissima* *M.glacialis*	23.54	*B.laevissima* *O.fragilis*
	Deep	*M.glacialis* *A.irregularis*	*J.lalandii* *D.arrosor*	20.51

One-way PERMANOVA analyses of habitat, season and depth showed all three to be significant in determining species composition with P-values of 0.001, 0.014 and 0.003 respectively (Table 7). Two-way PERMANOVA's showed that the combinations of habitat and depth, and season and depth had significant effects on invertebrate composition with P-values of 0.046 and 0.020 respectively.

The influence of zone

Fig.9 shows separation or clustering of some, ANOSIM results revealed a highly significant difference among the different zones sampled (R=0.221, p=0.01). Fig.10 indicates the average abundance of reef species in each of the zones, while Fig.11 shows the average abundance of the sand species. There is a clear separation in species dominance between the different zones for both reef and sand species. Zone A and B was dominated by *C. wahlberghi* and had a large relative abundance of *J. lalandii*. *O. fragilis* had the greatest relative abundance of reef species in zones C, D and H. The greatest relative abundance of *J. lalandii* occurred in zone I and had a high dominance compared to other reef species recorded in the zone. *Clathria hooperi* had the greatest relative abundance in zone F with *E. tricoronata* dominating in zone. Zone G was almost completely dominated by *J. lalandii*. Zones towards the southern tips of False Bay, in zones A and B experienced similar dominant species. Sites moving northward into zones C, D and H on either side of the Bay also showed similar species composition with the northern sites had some similar species.

Table 7. Table of results of a PERMANOVA model of environmental factors, Depth, Habitat and Season on invertebrate composition in False Bay.

Source	**df**	**Pseudo-F**	**P(Perm)**
Habitat	1	11.879	0.001
Season	1	1.8602	0.014
Depth	2	1.9118	0.003
Habitat x Season	1	1.5676	0.055
Habitat x Depth	2	1.4009	0.046
Season x Depth	2	1.5745	0.020

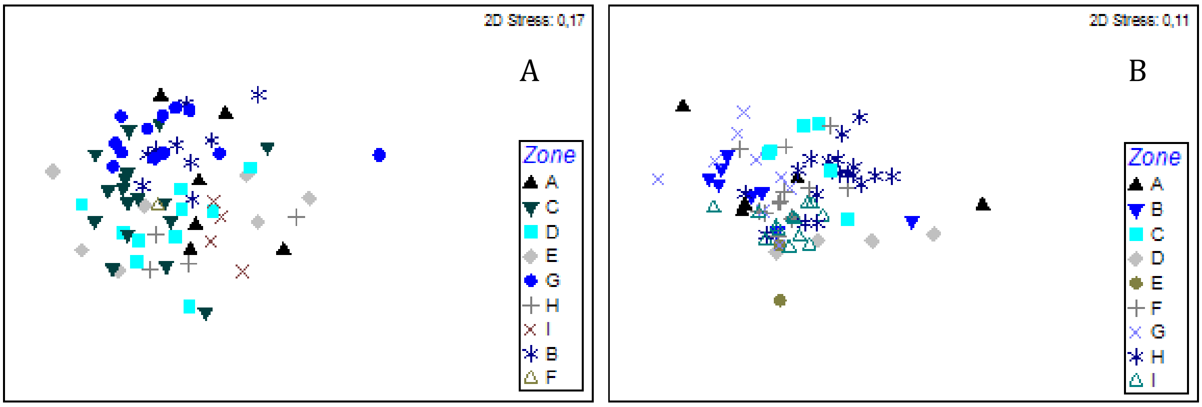

Figure 9. Multidimensional scaling plot of Bray-Curtis similarity of invertebrate assemblages sampled at 9 zones on a) reef and b) sand sites. Sites are categorised according to Zone A, B, C, D, E, F, G, H, I. The abundance data were transformed using a fourth root transformation.

Fig.11 shows the relative abundance of dominant sand species in the zones. Zones F, G and I had the greatest relative abundance of *B. laevissima* with zone A also having a relatively high abundance of this species. Zones C, D and H were dominated by *O. fragilis* that had a very high relative abundance compared to other species. *S. penicillus* had a large relative abundance in zones A and B and was also found in smaller numbers in zones C and D. Zone E showed a large relative abundance of *Bullia cincta* that was not found in the other zones. Once again there was a pattern of similar species on either sides of the Bay with the southernmost tips of the Bay having a similar species composition and the northern most stretch hosting a differing abundance of dominant species. These tips show the dominance of predatory species along with filter feeding species. The sides of the Bay are dominated by scavenger and detritivore species. There is a shift to scavengers and filter feeding species in the north-east corner of the Bay. The dominance of scavenger sand species is found throughout the Bay apart from the southern tips of the Bay where sand habitats are dominated by filter feeding species.

One-way PERMANOVA analyses of zone, habitat and season showed all three to be significant in determining species composition with P-values of 0.001, 0.001 and 0.006 respectively (table 8). A two-way PERMANOVA showed that a combination of zone and habitat, and zone and season had a significant effect on invertebrate species composition with P-values of 0.001 and 0.001 respectively

Table 8. Table of results of a PERMANOVA model of environmental factors, Zone, Habitat and Season on invertebrate composition in False Bay.

Source	df	Pseudo-F	P(Perm)
Zone	8	2.1642	0.001
Habitat	1	7.3895	0.001
Season	1	1.9716	0.006
Zone x Habitat	8	1.4970	0.001
Zone x Season	8	1.4474	0.001

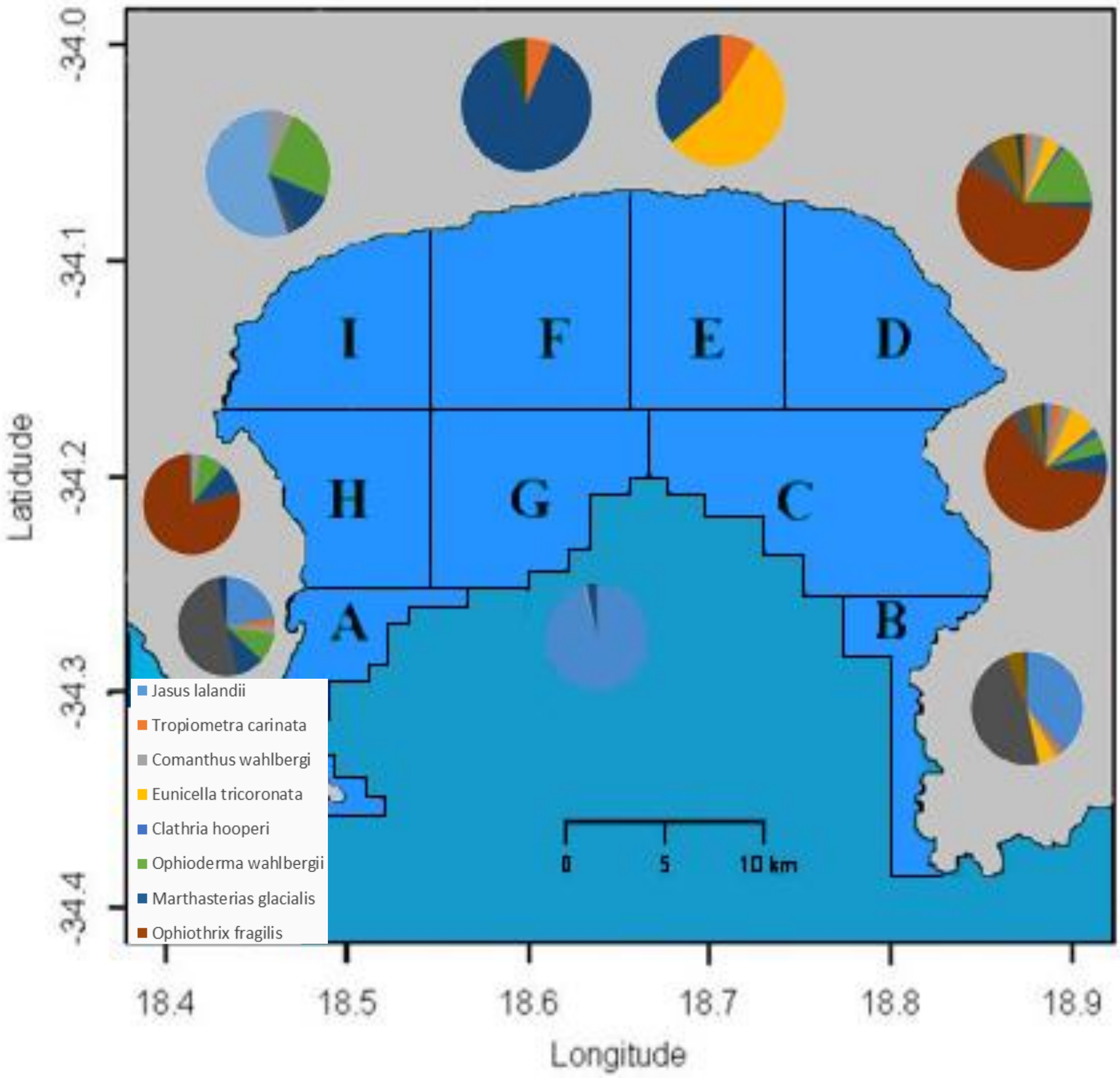

Figure 10. A map of False Bay showing a pie chart of the average abundance of the dominant reef species in each zone.

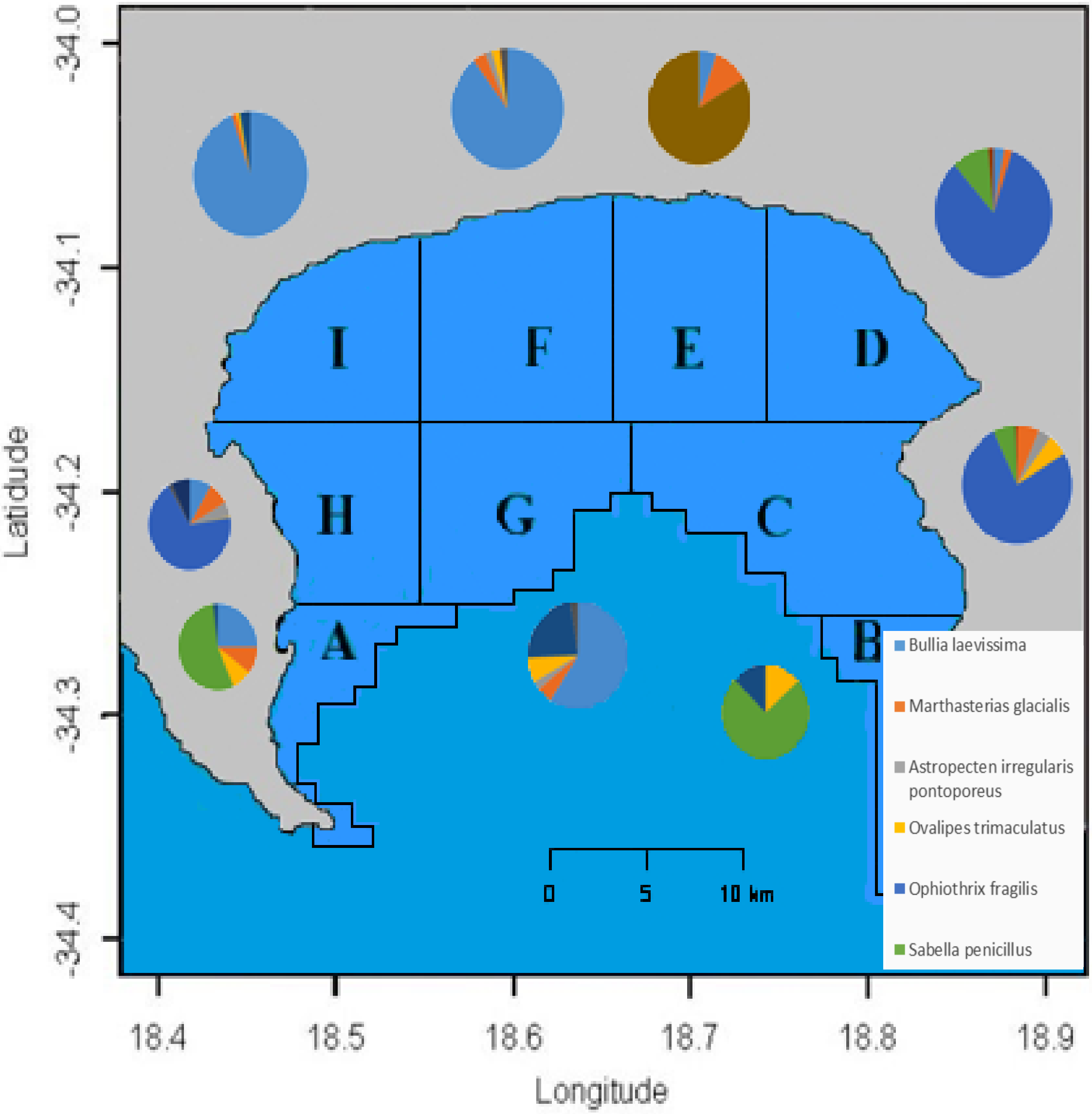

Figure 11. A map of False Bay showing a pie chart of the average abundance of the sand dominant species in each zone.

Discussion

BRUVs as a survey method

Indicator species have been identified in different zones. There is a clear distribution between the dominance of different species among the zones and future studies should incorporate the abundance of these indicator species in the evaluation of community structure and the changes within these communities. When considering species-specific data, it has to be interpreted with caution. BRUVs lack a downward facing camera and make use of bait to attract species. This causes a bias towards mobile predators that are attracted to the bait and might not provide true data on the dominance of certain species.

BRUVs will very rarely detect meiofauna or smaller species of invertebrates. Species recorded on sand in this study were large, mobile species attracted to the bait. Reef sites also comprised mostly of large mobile species but included many sessile reef species, not recorded in Field's study (1970). It is often difficult to spot and record cryptic species, which is also a limitation of SCUBA sampling. This study has provided evidence that BRUVs are a suitable method for surveying macro-invertebrates and recorded 67 species. Field (1970) sampled about 2000 species in total during a dredge study done on soft sediments in False Bay. Field (1970) achieved a higher reading of diversity but the BRUVs allowed for a greater area of coverage comprising all habitat types over a short period of time. This method was non-destructive, cheap and conventional and produced clear, significant patterns of invertebrate distribution.

The influence of habitat

There was a clear separation in species found on reef and sand habitats. Studies have shown that diversity increases with habitat complexity (Buxton 1987; Lechanteur 2004). The complexity of reefs provides greater opportunity for niche exploitation and thus allows these habitats to play host to a greater diversity of species (Gotz 2005). This has been shown for fish species around the Cape Peninsula (Gotz 2005) and this study shows similar trends for invertebrates across False Bay.

Reefs provide a hard substratum to which sessile animals such as feather stars, sponges and ascidians can attach and also provide a refuge for species within crevices or under boulders. The stability of reefs promote a greater diversity (Buxton 1987; Lechanteur 2004). Reefs are dominated by sessile invertebrates, most of which are filter feeding species and animals such as west coast lobster, that rely on the complexity of the reef for survival. They are known to hide under boulders to avoid predation and are often found in large numbers on reefs. The high abundance and diversity on reefs, provides a constant supply of food to larger mobile species.

The enormous abundance of whelks in sand habitats could be explained by their ability to burrow into the sand and remain unaffected by changing currents. The flow of water affects sand species (Parker 1956) and requires an adaptation for burrowing or possessing the ability to attach to substrate. As a result of the lack of complexity, sand habitats are largely dominated by burrowing whelk and crab species in this study. Upwelling events in summer destabilize sediment and alter the flow of water within these environments (Atkins 1968).

The decrease in all filter feeding and Porifera species can be explained by the changes in water movement patterns in summer. Many reef species are filter feeding sessile animals that rely on the movement and filtering of clear water for nutrition. With the increased upwelling, deposition and movement of material during summer, these filtration systems can easily become clogged and unable to function effectively (Schiel et al. 2006).

The influence of season

Seasonal variation has a significant influence in determining the distribution and abundance of invertebrates but is less significant than other variables. The effects of season on invertebrate abundance and diversity will be influenced by inter-annual variability of environmental conditions and the effect on the recruitment and settlement of invertebrate larvae (Gaines & Roughgarden 1985). Upwelling strength and duration varies between years and plays an important role in the transportation of larvae and produces specific spatial patterns of recruitment (Botsford 2001). Studying the influences of changing conditions over a long period of time will enable us to predict important settlement zones and incorporate dispersal patterns in the management of invertebrate species.

The increasing diversity in winter could be a result of a number of interactions with other species or the environment. Studies have shown that an increase in productivity in summer, due to upwelling, initially increases diversity (Scott 2009), but later increases the variability of environmental conditions, often leading to periods of anoxia (Scott 2009). The variability in conditions acts to decrease diversity and abundance as many invertebrate species have low tolerances to changing conditions (Scott 2009). Species that are found in large abundance in summer samples could have a greater tolerance and be better adapted to changing environmental conditions.

There are many other ecological factors that need to be considered to fully explain the varying diversity and abundance of invertebrates across False Bay during summer and winter. Predation and competition could be a major driving force behind changing diversity and abundance (Connell 1961). Predatory fish species have been shown to migrate out of the bay in winter and return in spring, coinciding with the increase in productivity (Scott 2009). Studies have shown an increase in fish abundance with increasing temperatures and visibility (Gotz 2005). Temperatures within False Bay are higher during summer (Field 1970) and therefore attract a larger abundance of fish into the Bay.

Many fish species find refuge in shallow reefs where many of them feed on invertebrate species (Gotz 2005). The predation on invertebrates during summer months may also explain the decrease abundance of invertebrates observed in this study. Lechanteur and Griffiths (2002) observed the diet of 17 suprabenthic reef fish in False Bay. They found reef dwelling prey dominated the diets of supra-benthic reef fish, with sand dwelling species likely to be consumed close to the reef. Species that showed a decrease in abundance in winter was recorded in the study as prey items of reef fish species

(Lechanteur and Griffiths 2002). The study found Crinoidea, Ophiuroidea and whelk-like gastropods species to be important constituents of these reef fish diets. *J. lalandii* was also recorded in 30 % of the reef fish species, being an important food source for these fish (Lechanteur and Griffiths 2002). In my study all reef invertebrate species in these classes showed a greater abundance in winter when predator pressure was released. The large abundance of whelks in summer can be explained by their extensive distribution and the tendency for predators only to feed on these species close to reefs, allowing for increased abundance on widespread sandy habitats.

Depth and season as a proxy for temperature

Temperature is a highly variable factor across False Bay and could explain variable patterns of species composition at different sites. Temperature is considered the most important abiotic determinant of invertebrate community composition (Scott 2009). Depth and season can be used as a proxy for temperature. Temperatures decrease with depth and winter temperatures are generally lower than temperatures experienced during summer in False Bay (Field 1970). Short upwelling events in summer periodically causes abrupt changes in temperatures within the bay (Field 1970). Temperature has a constraining effect on the metabolism of invertebrate species, as well as playing a crucial role in the settlement of invertebrate larvae (Wing et al. 1995).

Studies have linked a decrease in temperature to a decrease in the abundance of echinoderm and decapod species (Scott 2009). Upwelling is associated with abrupt decreases in temperature within False Bay (Field 1970) and could be a factor contributing to the decreased abundance of invertebrates during summer. Results from this study supported the findings of Scott (2009) with a decreased summer abundance of every echinoderm species recorded. *J. lalandii* also showed a pattern of decreasing abundance in summer that could be linked to temperature patterns within False Bay and also to the influence of temperature on predator species. Predator species have been shown to increase in summer months due to warmer temperatures and increased productivity in the Bay (Lechanteur and Griffiths 2002). *J. lalandii* was also found to be dominant on deep reefs where temperatures are lower and predation is absent (Lechanteur and Griffiths 2002).

The main mechanism resulting in the decrease of *J. lalandii* is unknown and could also be explained by the vulnerability of prey species to changes in temperature. Urchins make up a large proportion of the lobsters diet and have also been shown to be highly sensitive to changes in temperature (Scott 2009). The variability in summer would explain the declining abundance of urchins in the Bay, and in turn the decrease in lobster abundance in summer months. The importance of interactions between species and their environment needs to be better understood to ensure effective management of commercially important species such as *J. lalandii.*

Zone as a proxy for geology

Gotz (2005) explained the significance of food availability on reefs and the influence reef profile has on the availability of food. He showed that an increase in reef profile is related to a higher standing biomass of benthic organisms (Gotz 2005). He used this to explain the presence of fish abundance in relation to the availability of prey, in this case invertebrate species. Reef profile is related to reef geology, in this study classified as either granite, Malmesbury shale (MS) or Table Mountain sandstone (TMS) (Van Zyl 2011). MS has a low reef profile with granite and TMS both having a high reef profile producing a complex habitat.

Results showed that *J. lalandii* was mostly sampled on TMS reefs, which can be explained by their reliance on a complex habitat to escape predation. They were also sampled on some granite reefs that also exhibit a steep, complex habitat. *O. fragilis* and *M. glacialis* show a pattern of dominance on shale reef samples. These species are not as reliant on habitat complexity for survival and have the ability to move between habitats. A large proportion of biomass on TMS reefs are made up of *C. wahlbergi*. This species experiences a lot of interspecific competition with other sessile species and are therefore largely abundant on complex reefs where there is more habitat available.

The dominance of predatory species along the sides of the Bay could be explained by the availability of prey on reef systems. There is a great abundance of filter feeding species found in the north of the Bay where depth decreases, current speed decreases and plankton settles. The southern tips of the Bay are dominated by filter feeding species on both sand and reef habitats. Currents bringing in nutrient rich water from surrounding areas provides a continuous supply of food for filter feeding species. Sand habitats within the Bay are dominated by scavenging species. Due to the low and variable food supply in sandy habitats in comparison with the standing biomass of prey species on reefs, differences in food capture techniques are expected and could explain the dominance of scavengers in these sandy habitats.

Improvements and Future Studies

There are aspects of the equipment that could be improved to make it easier to use and will also ensure useable data is recorded each time. The BRUVs often fall over to the side and the FOV becomes blocked by sediment or behind boulders. Weighting the BRUV system accurately by lowering the centre of gravity will ensure the tripod lands upright on the substrate. The problem of visibility, especially in summer months, restricted the use of recordings that were collected. A method needs to be developed to measure the abundance of sessile invertebrate species that cover a large percentage of the reef. Individual abundance is difficult to calculate and an area cover could be a useful measurement.

This study presents the first quantification of invertebrate abundance and diversity across False Bay, South Africa and highlights the need for large-scale studies and a better understanding of the interactions between species and their environment. The possible influence of factors such as predation in determining the distribution of invertebrates should be further investigated to ensure successful conservation of all species in the ecosystem. The greater diversity and abundance found on reef habitats at intermediate depths should be considered in conservation planning and allocation of marine protected areas in False Bay. Granite reefs with a complex habitat structure should be a main priority in invertebrate conservation as it hosts the greatest diversity and abundance of species. Invertebrate species play an important trophic role in an ecosystem and provide imperative ecosystem services to higher trophic levels and important commercial fish species. BRUVs have provided a non-invasive, non-destructive method of sampling invertebrate species on all habitat types as well as providing information on species interactions.

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Appendix

Table 9. Invertebrate species recorded in a BRUVs study of False Bay.

Phylum	Class	*Genus*	*Species*
Annelida	Polychaeta	*Potamilla*	*reniformis*
		Sabella	*penicillus*
Arthropoda	Malacostraca	*Dardanus*	*arrosor*
			penduculatus
		Diogenes	*brevirostris*
		Exosphaeroma	*varicolor*
		Jasus	*lalandii*
		Mursia	*cristiata*
		Ovalipes	*trimaculatus*
		Symparagus	*dimorphus*
Bryozoa	Gymnolaemata	*Alcyonidium*	*rhomboidale*
Chordata	Ascidiacea	*Ascidia*	*incrassata*
		Pyura	*stolonifera*
		Styela	*plicata*
	Anthozoa	*Anthothoe*	*chilensis*
		Aulactinia	*reynaudi*
		Bunodosoma	*capensis*
		Drifa	*thyrsoidea*
		Eunicella	*albicans*
			papillosa
			tricoroinata
		Parazoanthus	*sp.*
		Pseudactinia	*flagellifera*
		Virgularia	*schultzei*
	Cubozoa	*Carybdea*	*branchi*
	Hydrozoa	*Allopora*	*nobilis*
	Scyphozoa	*Eupilema*	*inexpectata*
	Asteroidea	*Astropecten*	*irregularis pontoporeus*
		Callopatiria	*granifera*
		Henricia	*ornate*
		Marthasterias	*glacialis*
Echinoderamta	Crinoidea	*Patiriella*	*dyscrita*
		Comanthus	*wahlbergi*
	Echnoidea	*Tripiometra*	*carinata*
	Holothuroidea	*Parechinus*	*angulosus*
	Ophiuroidea	*Pentacta*	*doliolum*
		Amphiura	*capensis*
		Astrocladus	*euryale*
		Ophioderma	*capensis*
			wahlbergi
		Ophionereis	*dubia*
		Ophiothrix	*fragilis*

Phylum	**Class**	***Genus***	***Species***
Mollusca	Bivalvia	*Scissodesma*	*spengleri*
	Cephalopoda	*Enteroctopus*	*megalocyathus*
		Octopus	*vulgaris*
		Sepia	*typics*
	Gastropoda	*Bullia*	*digitalis*
			laevissima
			pura
		Burnupena	*cincta*
			lagenaria
			papyracea
		Nassarius	*capensis*
			speciosus
		Pleurobranchaea	*bubala*
Porifera	Calcarea	*Leucosolenia*	*sp.*
	Demospongiae	*Chondropsis*	*sp.*
		Clathria	*hooperi*
		Cliona	*celata*
		Crambe	*acuata*
		Echinoclathria	*dichotoma*
		Ircinia	*arbuscula*
		Isodictya	*frondosa*
		Latrunculia	*spinispiraefera*
		Polymastia	*atlanticus*
			mamillaris
		Tethya	*aurantium*