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Prediction of species distributions across the offshore Kimberley region.

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WAMSI Kimberley Marine Research Program

Final Report

Subproject 1.1.1.6

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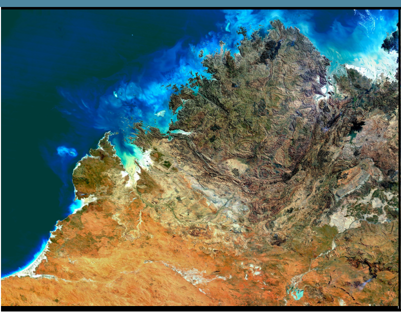
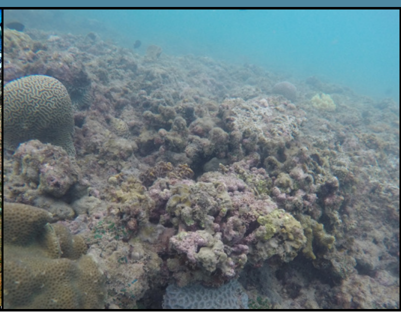

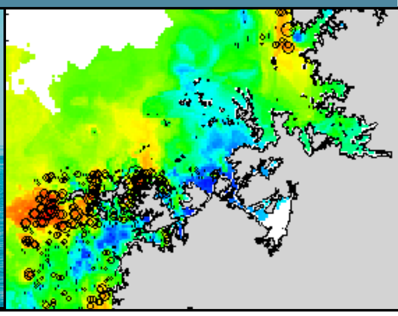

WESTERN AUSTRALIAN MARINE SCIENCE INSTITUTION

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WAMSI Kimberley Marine Research Program

Initiated with the support of the State Government as part of the Kimberley Science and Conservation Strategy, the Kimberley Marine Research Program is co-invested by the WAMSI partners to provide regional understanding and baseline knowledge about the Kimberley marine environment. The program has been created in response to the extraordinary, unspoilt wilderness value of the Kimberley and increasing pressure for development in this region. The purpose is to provide science based information to support decision making in relation to the Kimberley marine park network, other conservation activities and future development proposals.

Front cover images (L-R)

Image 1: Satellite image of the Kimberley coastline (Image: Landgate)

Image 2: Live tridacnid clams were found during the survey on the inner- to mid- reef-flats (Image: AIMS)

Image 3: Humpback whale breaching (Image: Pam Osborn)

Image 4: Figure 1. Seabed characterisation of the Kimberley survey region into nine assemblage types (See subproject 1.1.1.7)

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Contents

Executive Summary

Understanding the extent to which habitat characteristics influence species distribution patterns is an important consideration in spatial coastal and marine park planning and management in the Kimberley as elsewhere. The aim of this component of the WAMSI Kimberley benthic biodiversity study was to describe species distribution patterns and to seek to explain them on the basis of environmental drivers, principally habitat type and factors such as depth and substrate type which shape habitats. We examined differences in marine benthic communities between three study locations (Camden Sound; Maret Islands and the Eclipse Archipelago) using data collected from a towed epibenthic sled. There was no significant latitudinal trend or differences with depth among benthic assemblages (across a relatively narrow depth range, ~30 m). However there was a significant difference among Camden Sound and Maret Islands assemblages from mud and rocky substrates and a significant interaction between depth and substrate, indicating an inconsistent response by species to these factors. Highest diversity occurred in deeper > 45 m, 40 to 45 m and shallow < 20 m rocky habitat, with the lowest diversity recorded in mud habitat. Species richness in shallow stations was lower than in deeper stations. The shallow stations were also more variable than deeper stations and mud stations were more variable than rocky stations. The association between hard reef substrate and habitat forming filter feeder organisms like sponges and octocorals in the Kimberley, was reinforced in this study.

The analysis of species distributions in this chapter broadly confirmed the validity of the nine spatial habitat/species assemblages identified and mapped in 1.1.1.5. Clustering of the 50 most abundant taxa at each location identified groups of species that co-varied among substrate and depth stations. In Camden Sound 19 coherent species groups were identified, eight in the Maret Islands and 12 in the Eclipse Archipelago. Each group of species tended to occur only at a limited subset of stations although some species or group of species were more station specific than others. A combination of depth and substrate type explained the separation of species clusters.

Management Implications

The surveys confirmed the expected correlation between reef habitats and species richness indicating that hard substrate and habitat complexity are important determinants of diversity. The large number of species assemblage groupings within each of the three locations suggests that species are patchily distributed and thus our surveys probably undersampled the diversity of species and species assemblages. This reinforces the need for large spatial scale protection measures such as the marine parks and reserves that have been established in the Kimberley. Better knowledge of the relationships between habitat forming sessile invertebrates and mobile animals remains a gap in the Kimberley and closing it would lead to an improved understanding of the patterns found in this study.

1 Introduction and Methodology

Understanding the variability of species distribution patterns is important to managing and conserving Kimberley marine ecosystems. We examined species distribution patterns taking into account the role of depth and substrate in structuring species distribution and abundance in three locations (Camden Sound; Maret Islands and the Eclipse Archipelago) over a latitudinal gradient.

1.1 Depth and Substrate type

Depth was recorded at the beginning and end of each trawl. Depth categories were determined based on the pattern of CTD water column data collected:

- < 20 m: Photosynthetically Active Radiation (PAR) declined;
- 30 - 40 m: depth of the chlorophyll maximum layer; and
- > 45 m: increase in turbidity and a small spike in fluorescence observed (resuspended benthic chlorophyll).

Substrate classification was based on analysing a photograph of the sled from each station taken immediately after sled landed on the vessel's deck. Each station was categorised into location, depth and substrate. Substrate was determined as a binary variable classifying the sea-floor bottom as:

- mud (silt, mud and sand); or
- rock (cobbles to small boulders).

1.2 Species, abundance and biomass

Species diversity and distribution data were collected using benthic sleds. Collection methods are described in 1.1.1.4. Abundance and biomass of animals and plants captured by the sled was obtained on the ship by counting and weighing individuals using spring balances immediately after sorting.

1.3 Towed video habitat classifications

The towed video transect data (see 1.1.1 chapters 2 and 3) was used to classify biohabitat types and provided a quantitative assessment of the bio-physical attributes to associate the 10 most important species in terms of biomass within Arthropoda, Echinodermata, Mollusca, Soft Coral, Porifera, Fish, Bivalvia and Gastropoda with these attributes. We performed the same analysis for entire groups of Ascidiacea, Zoantharia, Worm, Hydrozoa and Bryozoa which were not identified further.

1.4 Regional environment/habitat/species assemblages identified for the Kimberley

Nine environmental parameter/habitat/species assemblages were identified for the study region in 1.1.1.5 based on a wide range of environmental variables, bio-habitat distributions from towed video and animal and plant catches from sleds (Figure 1).

1.5 Statistical analyses

Statistical analyses were undertaken using PRIMER 7 with PERMANOVA. Data were square root transformed to balance contributions of abundant and rarer taxa. Bray Curtis similarity was used in multivariate non metric MDS ordination analysis to visualise patterns of resemblance among the observations based on community composition. The analysis of similarity (ANOSIM) global R statistics was used to test the null hypothesis of no difference among groups of stations classified by depth and by substrate type with R = 1 when all pairs of samples are more similar than to any pair of samples from different groups and R = 0 expected value under the model that among and within group dissimilarities are the same on average. The null hypothesis of no structure in the data was tested using SIMPROF. A distance based PERMANOVA test was applied to test if the observed differences were significant. Unrestricted permutation of raw data was performed for one factor and permutation of residuals under a reduced model was performed for more than one factor analysis (Anderson and Ter Braak, 2003). A test of homogeneity of dispersion PERMDISP was carried out to infer if the differences are due to a location effect, a dispersion effect or both (Anderson, 2001).

2 Results and Discussion

2.1 Broad spatial patterns within the environment/habitat/species assemblages identified for the Kimberley study region

The results of the multivariate analyses broadly confirmed the validity of the nine environmental parameter/habitat/species assemblages identified for the study region in 1.1.1.5 (Figure 1). This was largely to be expected as the regional habitat modelling used the sled species catch data.

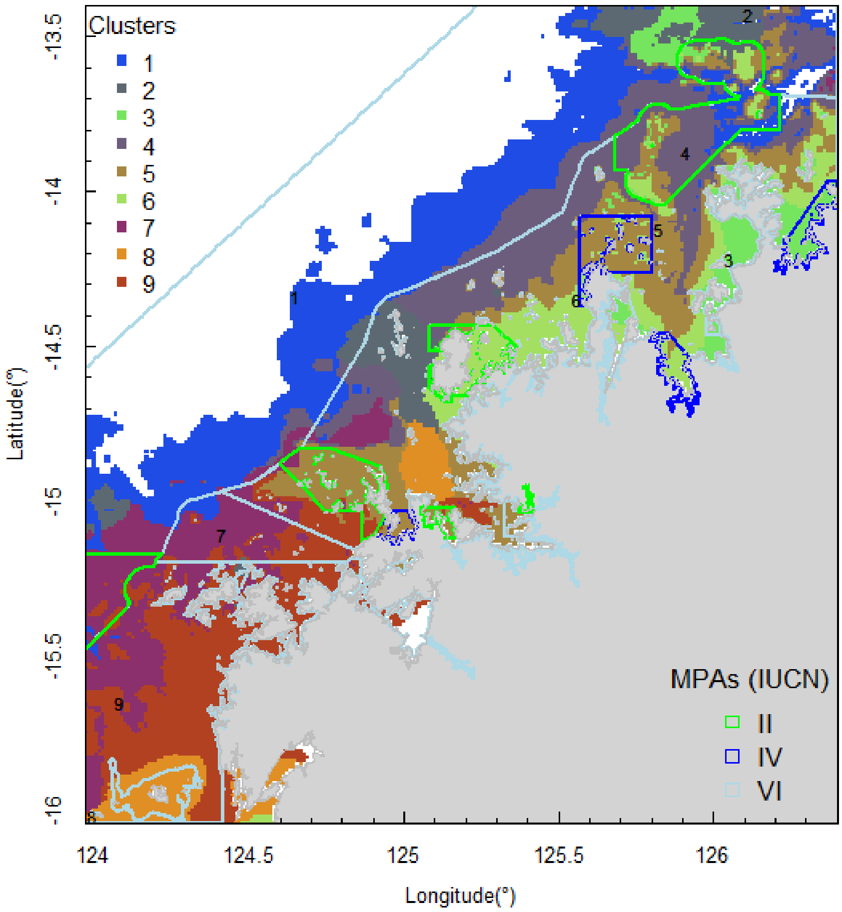


Figure 1. Seabed characterisation of the Kimberley survey region into nine assemblage types. The location of Marine Protected Areas and their IUCN classification is overlaid for reference. Note that only eight of the habitat/species assemblages had sled samples.

There was a significant difference among the groups of species abundance grouped into 8 assemblages (PERMANOVA, unrestricted permutation of raw data, 994 permutations, $p = 0.001$) (Figure 2). All assemblages were significantly different to each other except assemblage 5 was not significantly different to assemblages 3, 4 and 9 ($p > 0.050$) indicating some transition and overlap in species among these assemblages which are defined by environmental variables and habitat type as well as species diversity and abundance. Reduced space ordination patterns (Figure 2) showed that the differences among groups may be due to some or all features of the groups to make them distinct such as location (centroids), dispersion or the correlation structure of the data points being compared. PERMANOVA focuses on the specific hypothesis of no differences in location (centroids) among the groups (Anderson and Walsh, 2013) by calculating the average distance of the group centroids. PERMDISP analysis tested if one or more groups were more variable than the others by examining the differences in multivariate dispersion (Anderson, 2006). Distance based test of homogeneity of multivariate dispersion showed that differences between assemblages 1 and 2, 1 and 5, 1 and 7, 2 and 7, 3 and 6, 4 and 5, 4 and 7, 5 and 7 and 5 and 9 were due to location, and differences between other assemblages were due to location, dispersion (variability in spread) or combination of both (median-variance relationship) (PERMDISP, 999 permutations, $P > 0.05$).

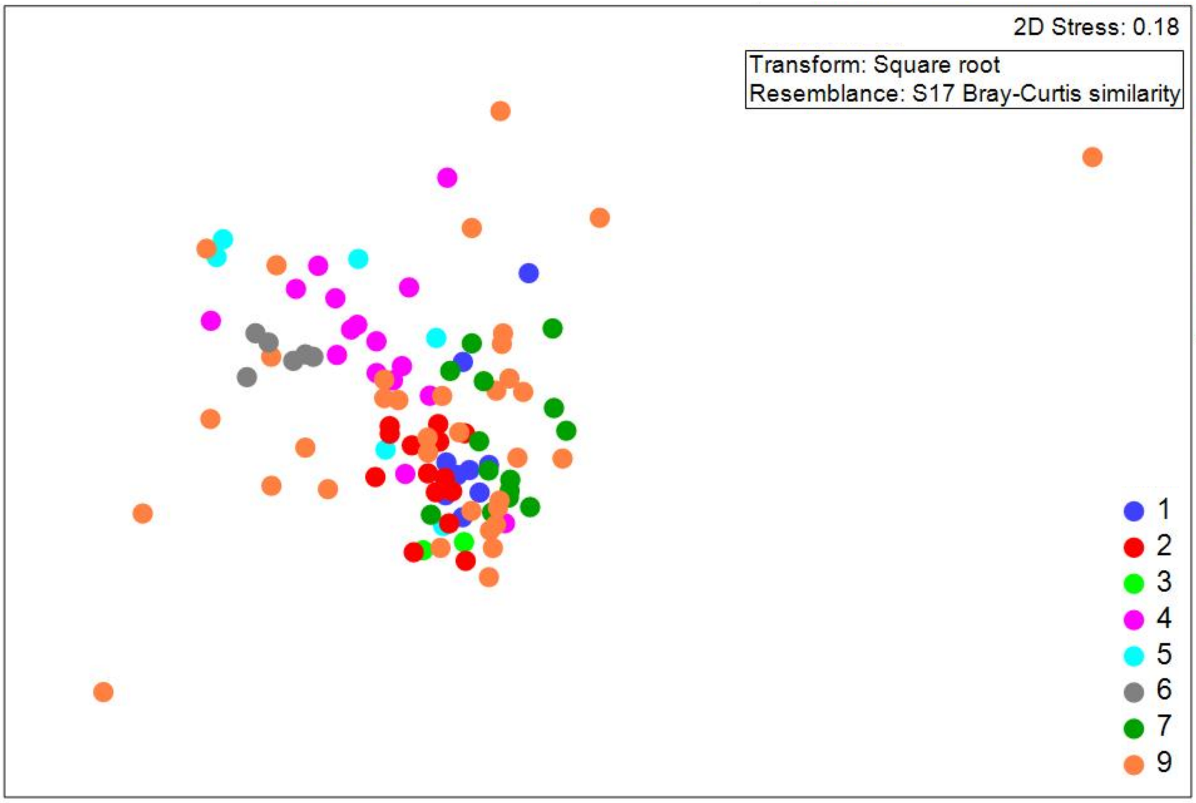


Figure 2. Non Metric Multidimensional Scaling plot of counts m^2 (closed circles) of all taxa sampled by sleds in Camden Sound, Maret Islands and Eclipse Archipelago. Factor is assemblage number (see Figure 1).

PERMANOVA on species biomasses grouped into the same 8 assemblages revealed that all the assemblages were significantly different to each other apart from assemblage 2 and 3; 3 and 5; 3 and 9; 5 and 9. Difference between assemblages 1 and 2; 1 and 5; 1 and 6; 1 and 7; 2 and 5; 2 and 7; 3 and 6; 4 and 5; 5 and 7; and 5 and 9 was due to location only while differences between other assemblages were due to location, dispersion or a combination of both (PERMDISP, $p < 0.05$) (Figure 3).

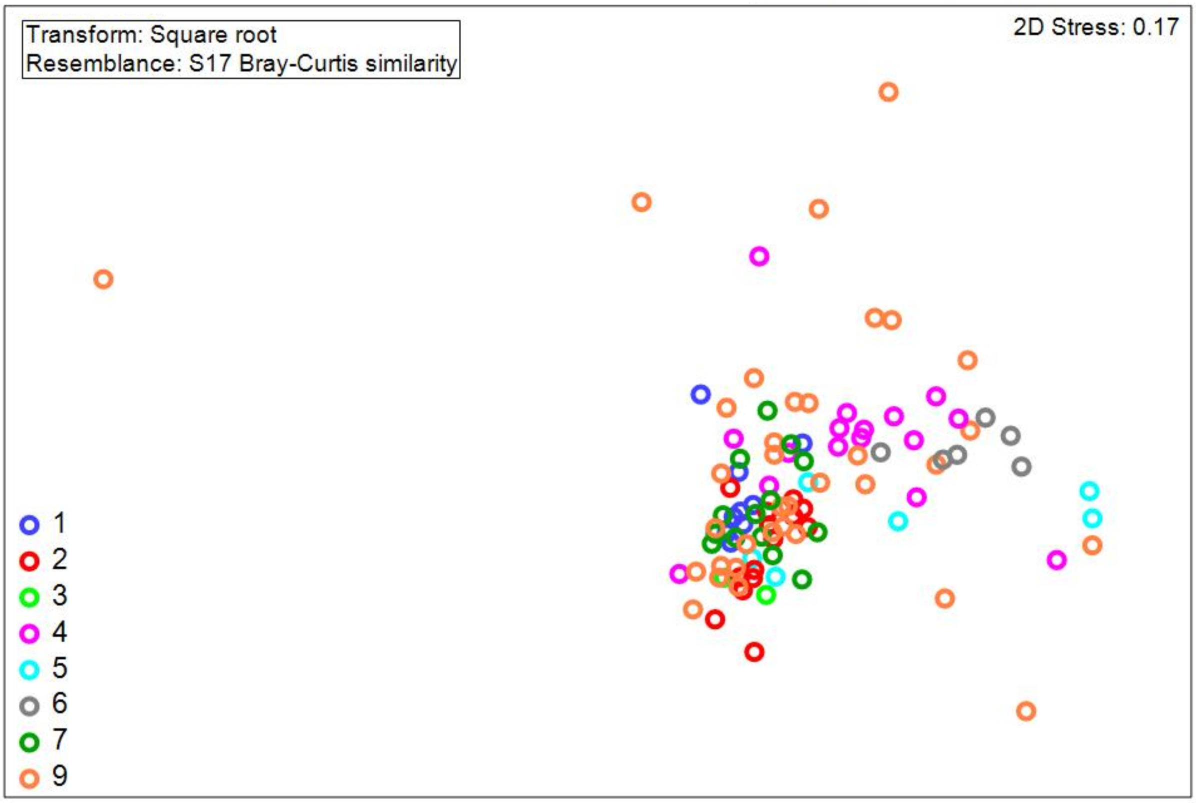


Figure 3. Non Metric Multidimensional Scaling plot of biomass g m^2 (open circles) of all taxa sampled by sleds in Camden Sound, Maret Islands and Eclipse Archipelago. Factor is assemblage number (see Figure 9.1).

2.2 Patterns among location, substrate type and depth

Abundance and biomass of the main taxa types stratified by location, substrate type and depth are shown in Figure 4 box plots which show the first to the third quartiles. The line in the box is the median. The whiskers are the minimum and maximum values. The outliers are plotted as individual points. Sessile filter feeders (Ascidiacea, Porifera, Bryozoa, and Bivalvia) were more abundant on rocky substrates. Hard Coral was relatively rare in the samples collected. Zoantharia showed no preference for substrate type but where less abundant in the two shallower depths (< 20 m; 20 – 30 m). Echinodermata occurred in both rock and mud substrates, however their abundance and biomass was higher on rocky substrates except in shallow stations at the Maret Islands where they more abundant in mud and had equally distributed biomass between both substrates. This pattern of abundance and biomass distribution was driven by Ophiuroidea, Holothuroidea and Echinoidea, while Asteroidea and Crinoidea occurred mostly in rocky substrate. Mollusca and Gastropoda had higher abundance and biomass in rocky substrate with peaks in deeper stations. Arthropoda occurred in mud and rocky substrate across all the depths with abundance peaks in Camden Sound 20 - 30 m and biomass peaks in Camden Sound 20 - 30 m mud, Maret 30 - 40 m rocky and Eclipse 20 - 30 m rocky. Worms were almost equally abundant in rocky and mud substrate with biomass peaks in Maret > 45 m rocky and abundance peaks in Eclipse 30 – 40 m mud. Fish biomass and abundance in general was higher in rocky substrate.

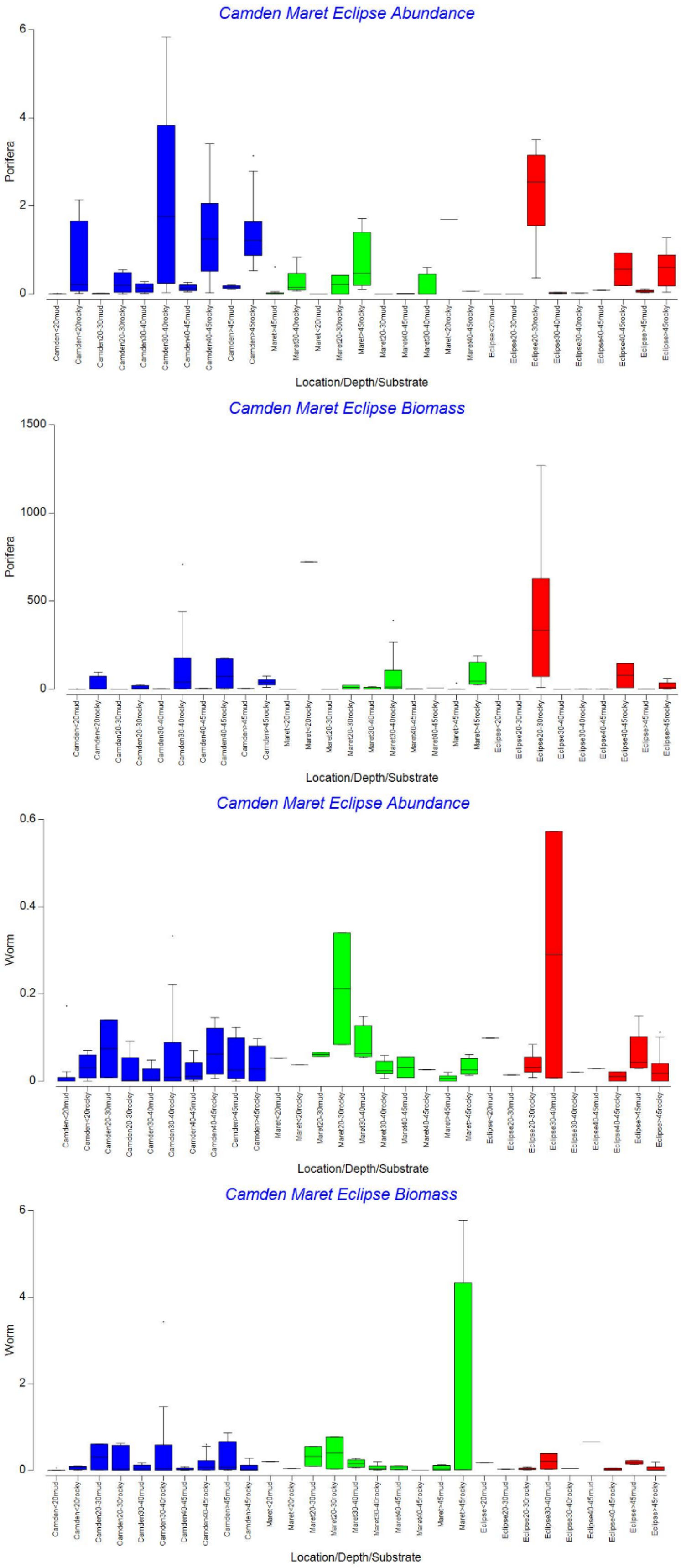
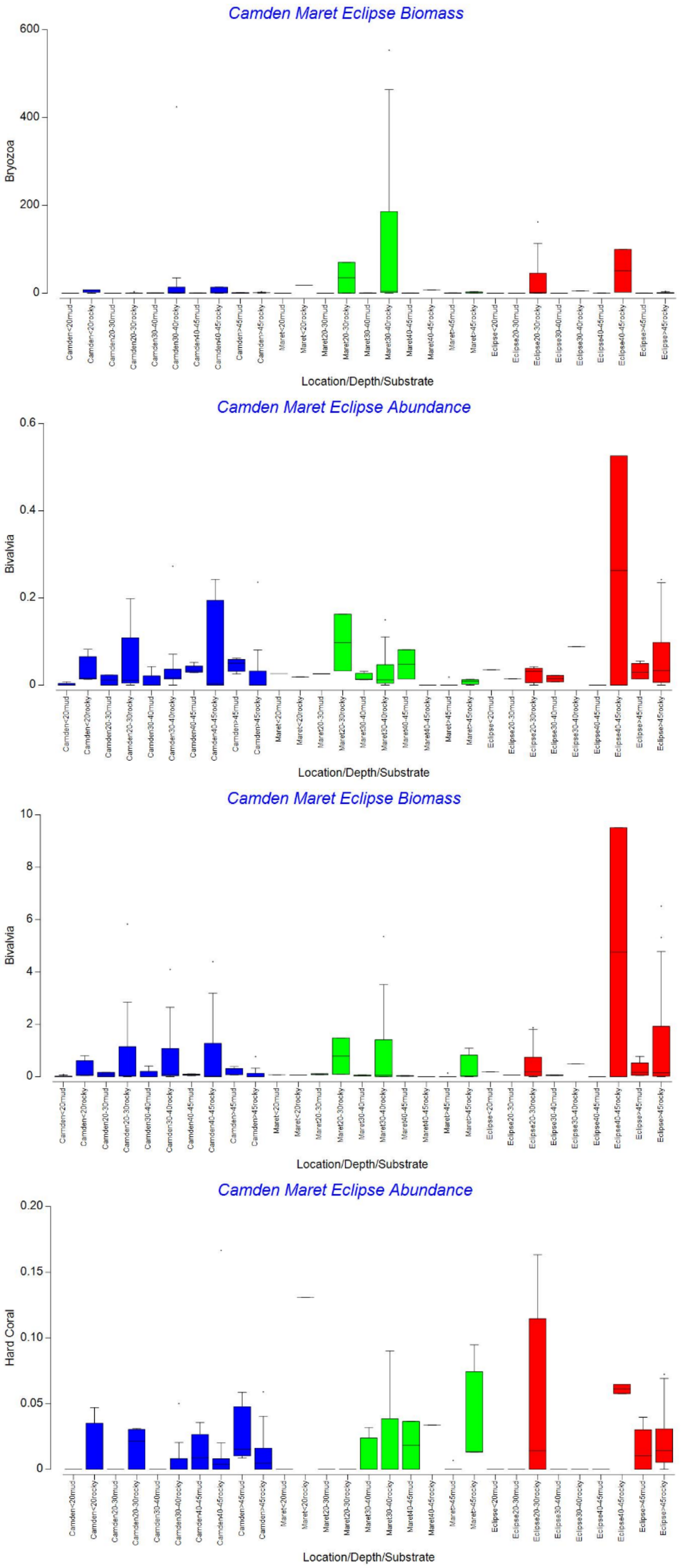


Figure 4. Box plots of abundance m² and biomass per g of wet weight m² collected in Camden Sound, Maret Islands and Eclipse Archipelago across 5 depth (m) and 2 substrate categories. Biomass only for Bryozoa and Hydrozoa as abundance is not representative for these groups.



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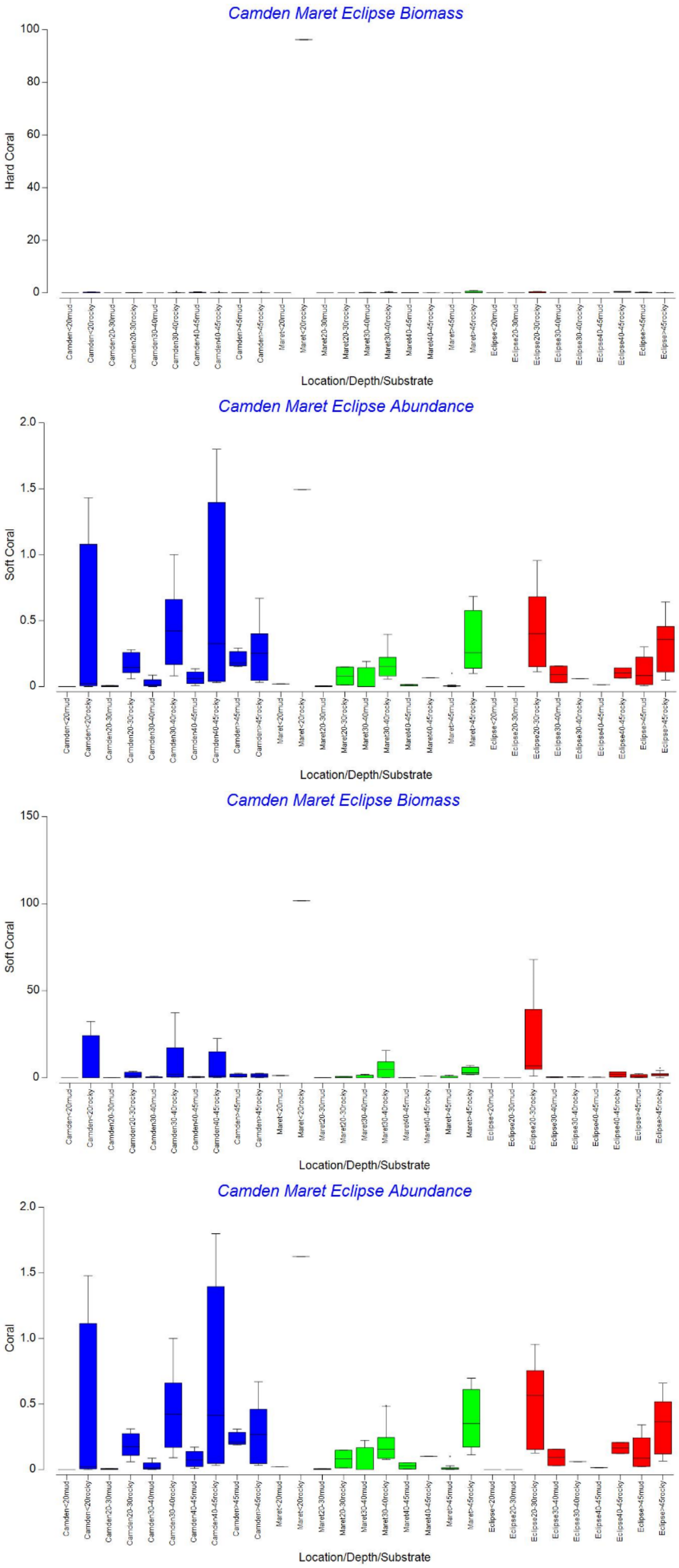

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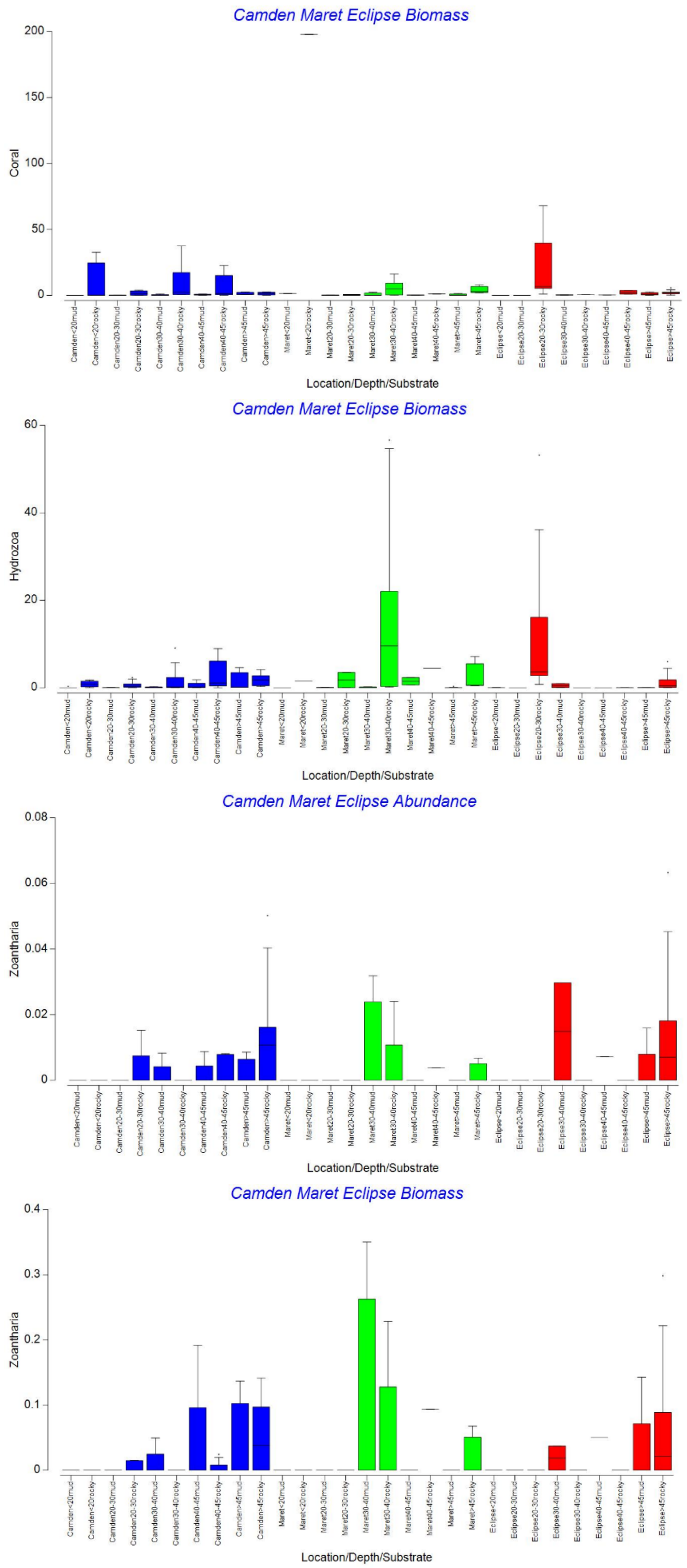

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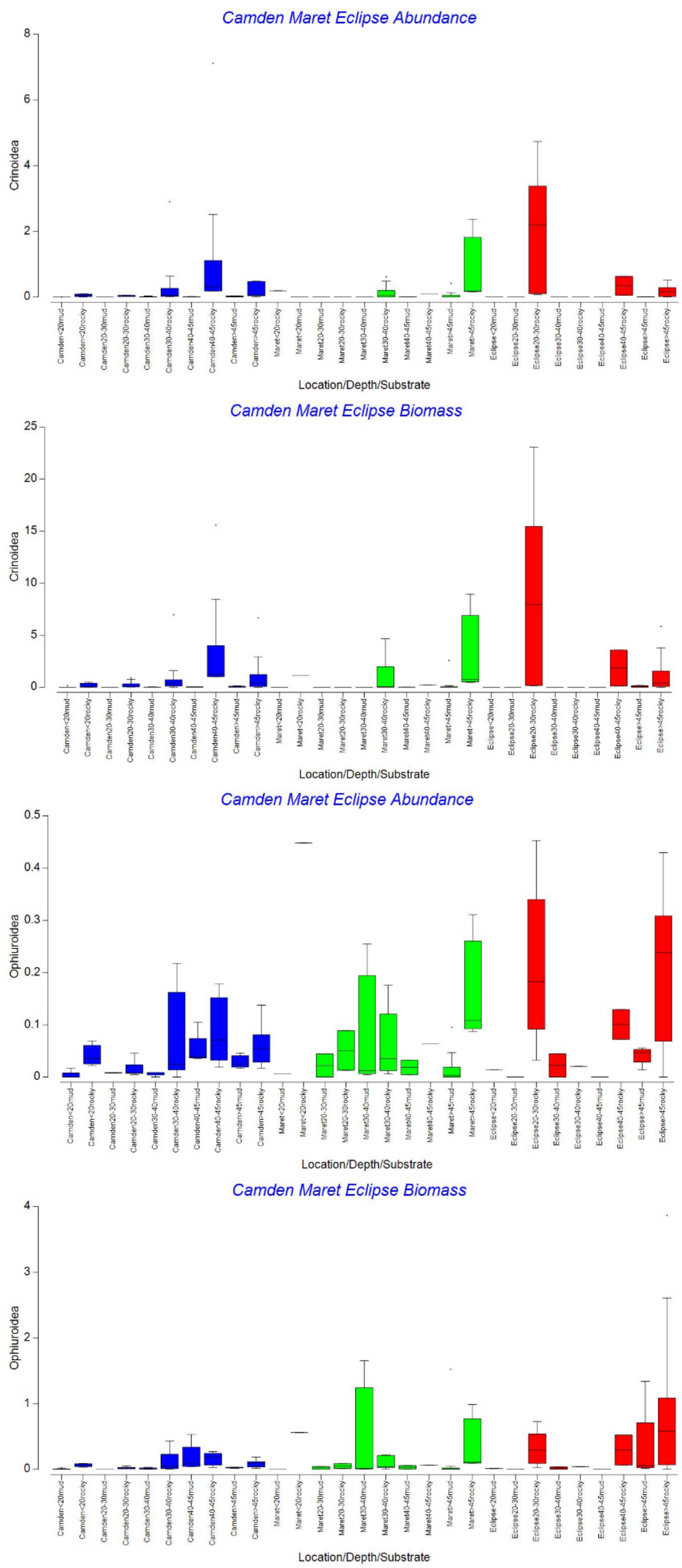

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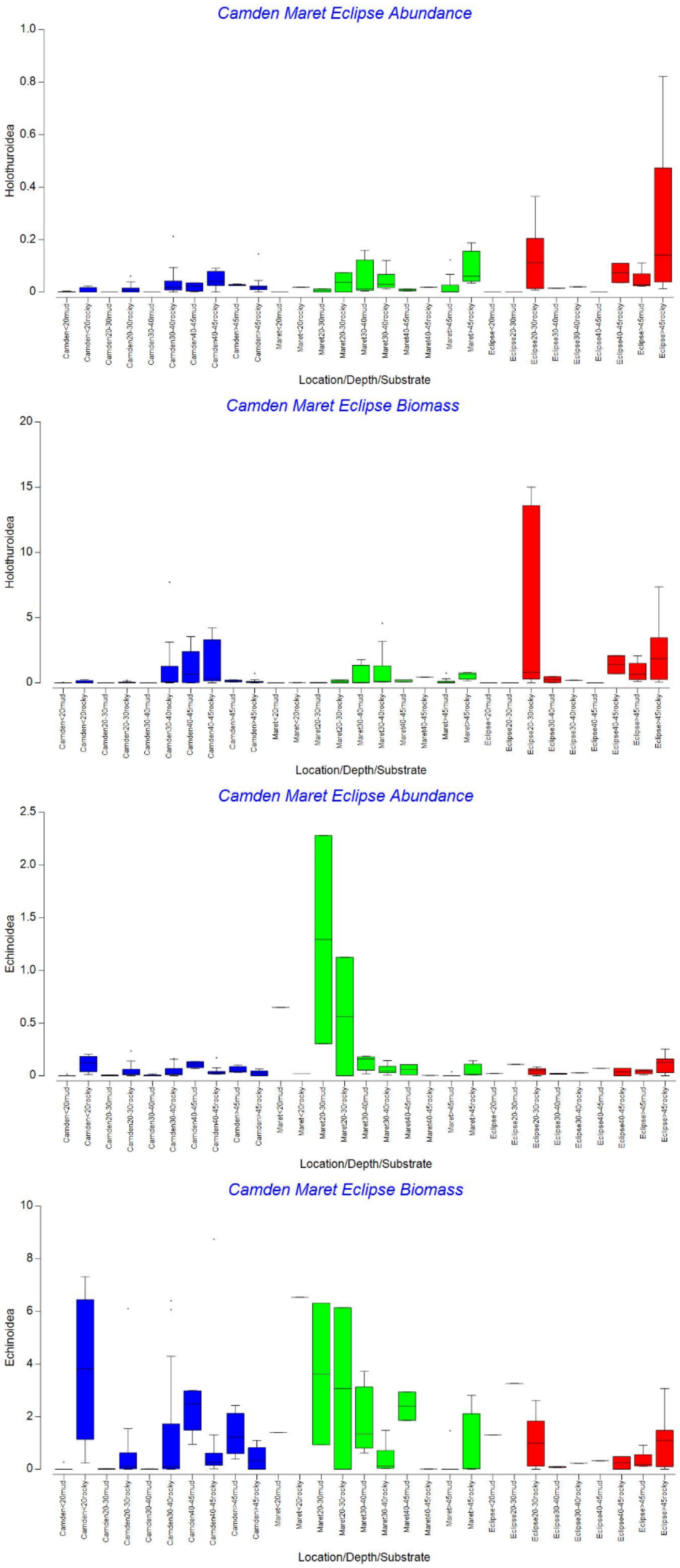

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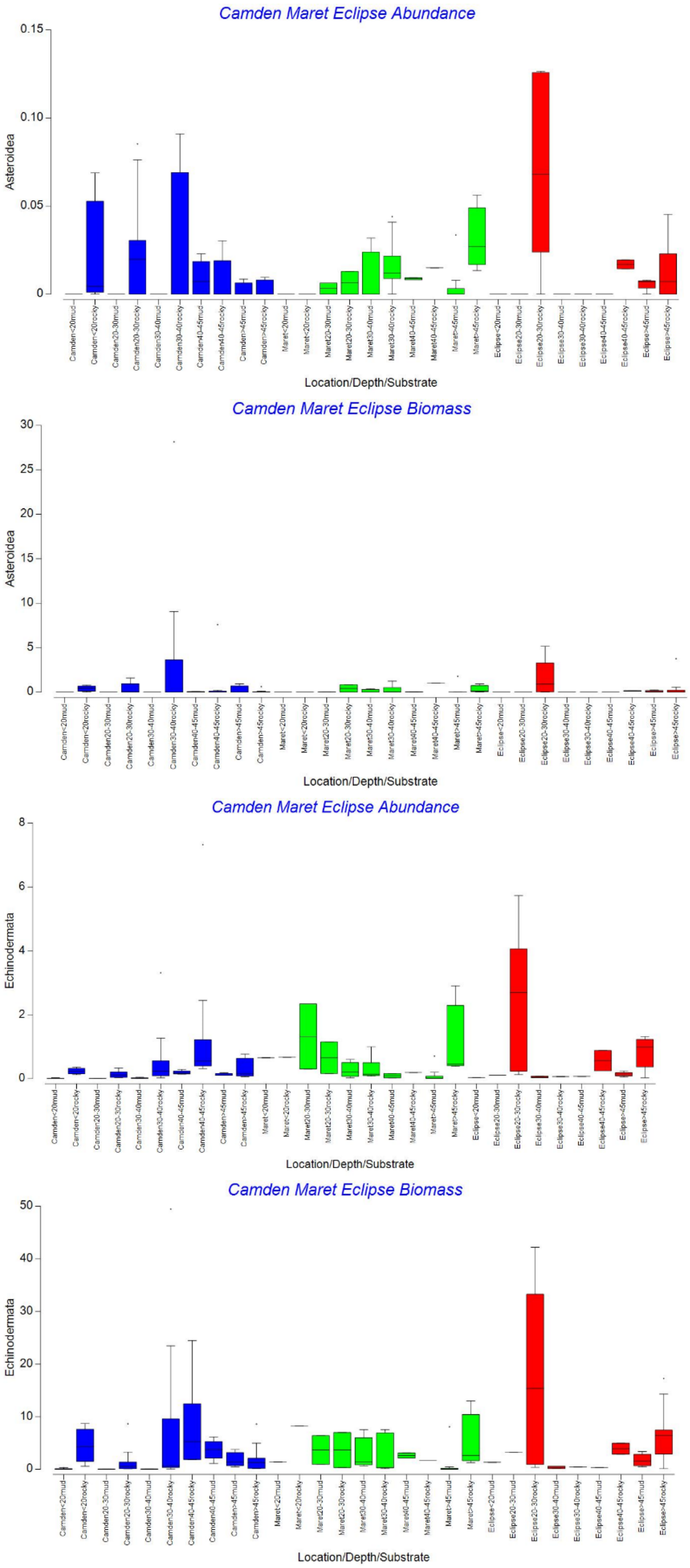

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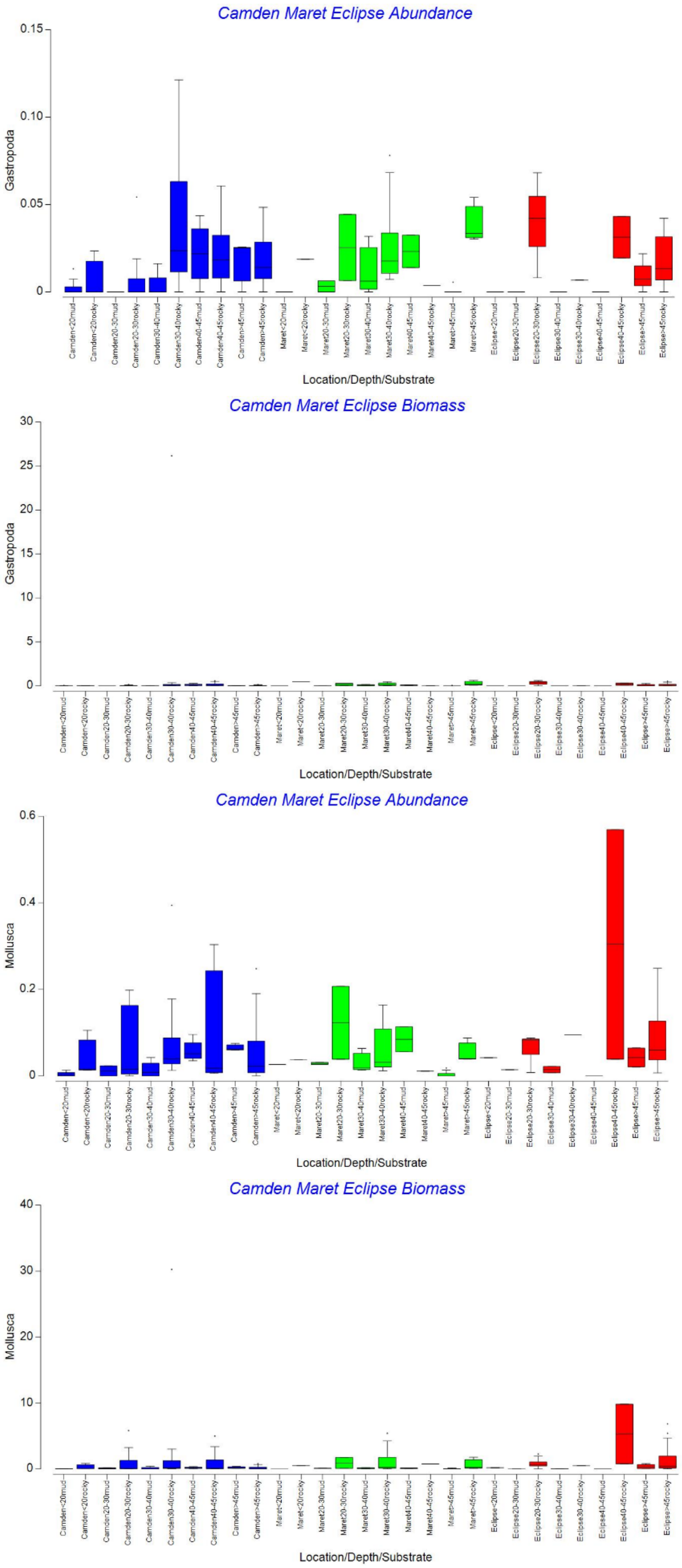

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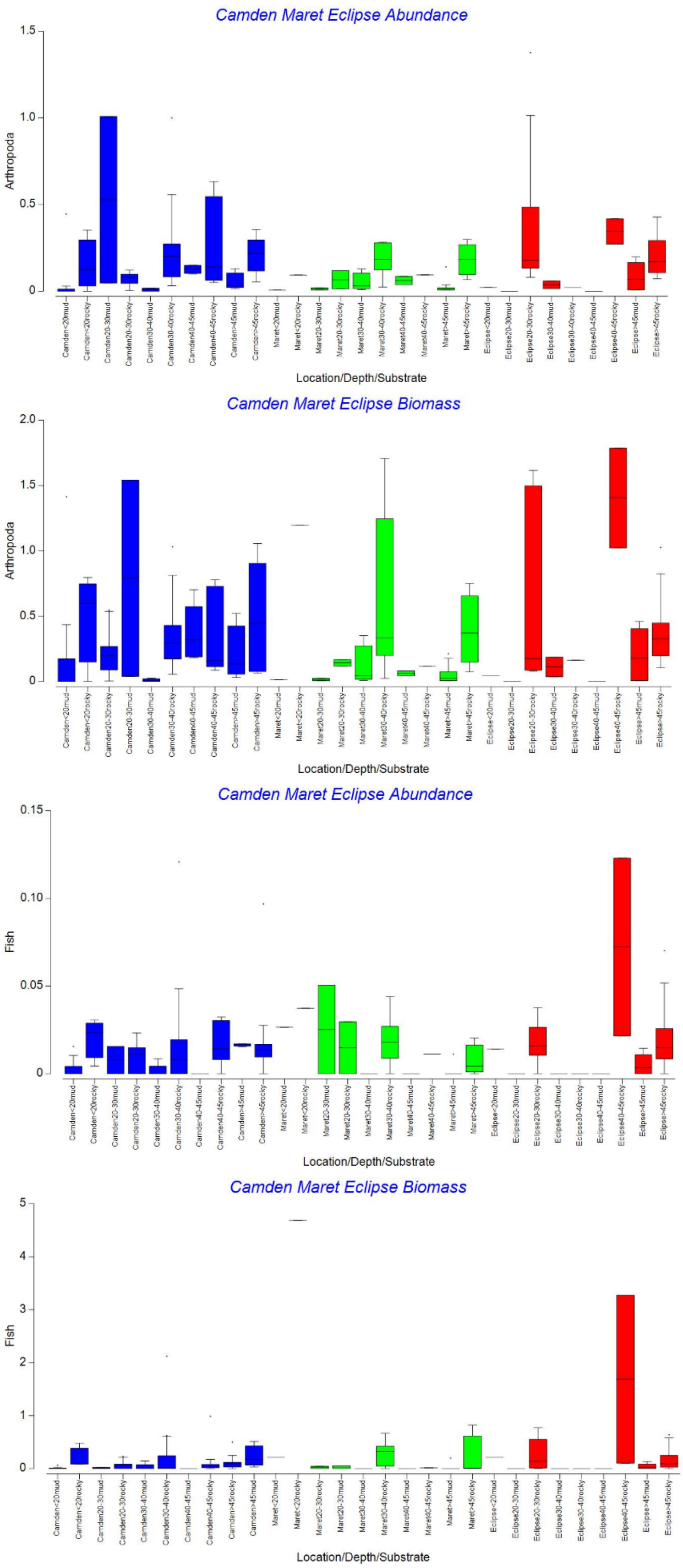

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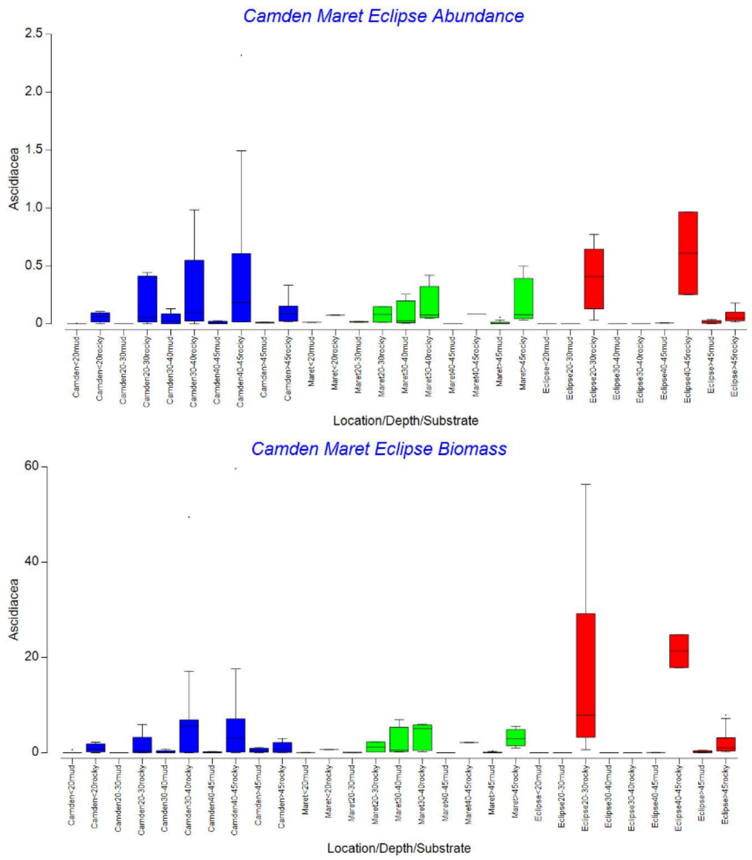

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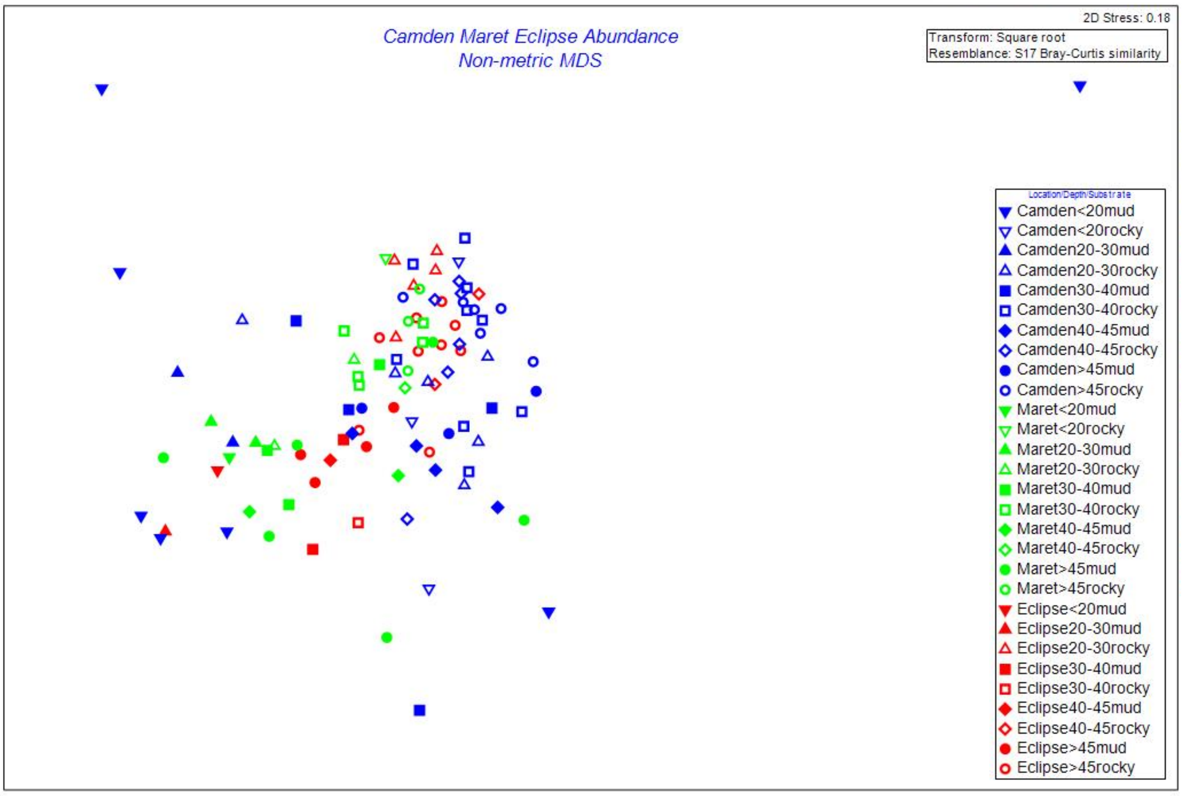
PERMANOVA analysis (permutation of residuals under a reduced model) was used to test the null hypothesis of no difference among assemblages from different locations, depth and substrate type. There was no significant latitudinal trend or depth difference among assemblages based on species count ($p = 0.600$ and $p=0.070$ respectively).

However, there was a significant difference among Camden Sound and Maret Islands assemblages from mud and rocky substrate and significant interaction between depths and substrate (PERMANOVA, p= 0.004 and 0.045 respectively). In Camden Sound assemblages from mud were significantly different to assemblages on rocky substrates at all depths except in < 20 m ($p<0.050$). Maret Islands assemblages from mud and rock from 30-40 m depth and Eclipse Archipelago assemblages from > 45 m depth were significantly different ($p<0.05$) (Figure 5).

When the stations from all three locations were combined, a significant difference between the assemblages collected at shallower depths of < 20 m and 20 – 30 m and those collected at deeper locations of 40 – 45 m and > 45 m was recorded (PERMANOVA $p < 0.050$). Assemblages from mud and rocky substrate were significantly different from all the depth categories (PERMANOVA, $p < 0.005$).

PERMANOVA analysis on biomass data revealed no significant difference among assemblages latitudinally or with depth within location but a significant difference in assemblages from mud and rocky substrate in Camden Sound and Maret Islands but not the Eclipse Archipelago. When all three locations were combined assemblages from different depths were significantly different and assemblages from mud substrate were significantly different to assemblages from rocky substrate (PERMANOVA, $p = 0.001$). Assemblages from < 20 m were significantly different to those collected at 40 - 45 m and > 45 m. Assemblages from 20 - 30 m were significantly different to those collected at 30 - 40 m, 40 - 45 m and > 45 m. Assemblages from < 20 m were not significantly different to the ones from 20 - 30 m or 30 - 40 m. Assemblages from 30 - 40 m were not significantly different from the ones from 40 – 45 m and assemblages from > 45 m were not significantly different to the ones from 30 – 40 or 40 – 45 m. Assemblages from mud were significantly different to assemblages from rock across all the depths.

Similarity Percentages – Species Contribution (SIMPER) analysis on abundance and biomass (table not shown) indicated that species richness was higher in rocky substrate stations compared to muddy stations. Species richness in shallower stations was lower than in deeper stations. Shallower stations were more variable than deeper stations and mud stations were more variable than rocky stations at same depths (Figure 5). Mud stations were dominated by worms, *Brissopsis luzonica*, *Breynia desorii*, *Prionocidaris bispinosa*, *Dendronephthya spp*. Rocky stations were dominated by sponges, ascidians and bryozoans.



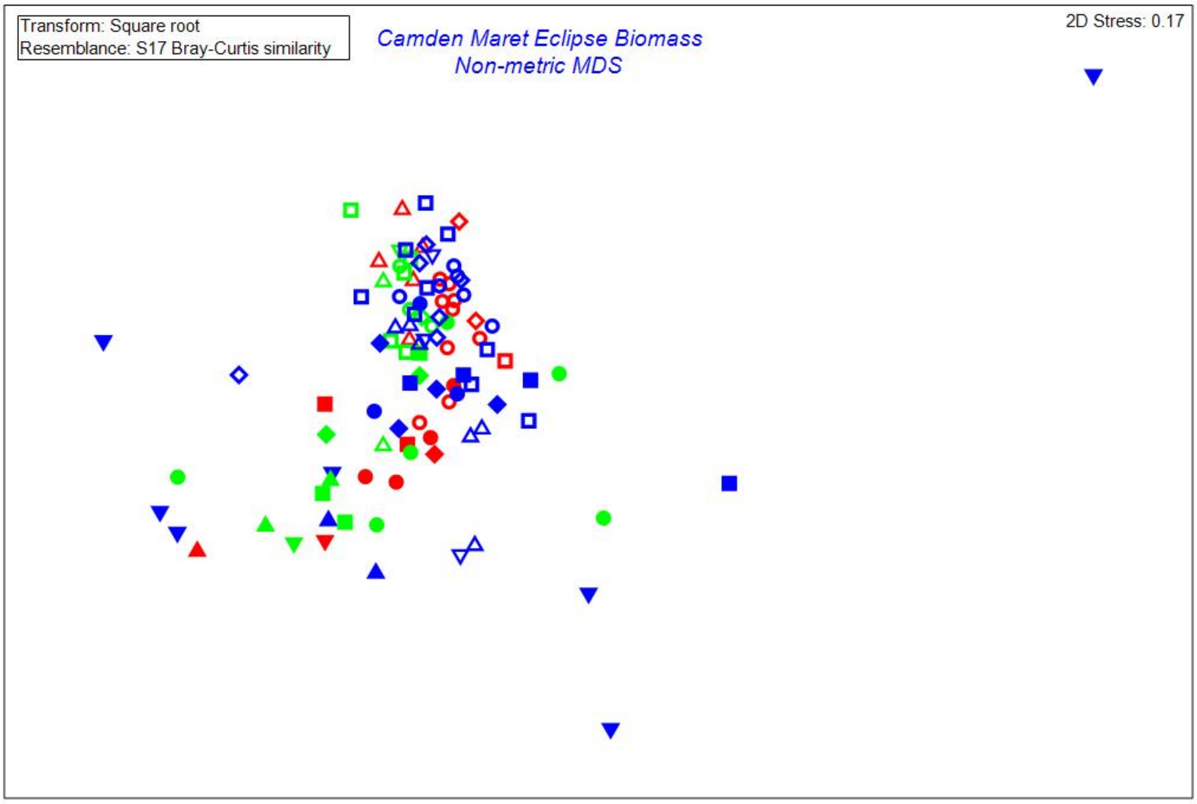
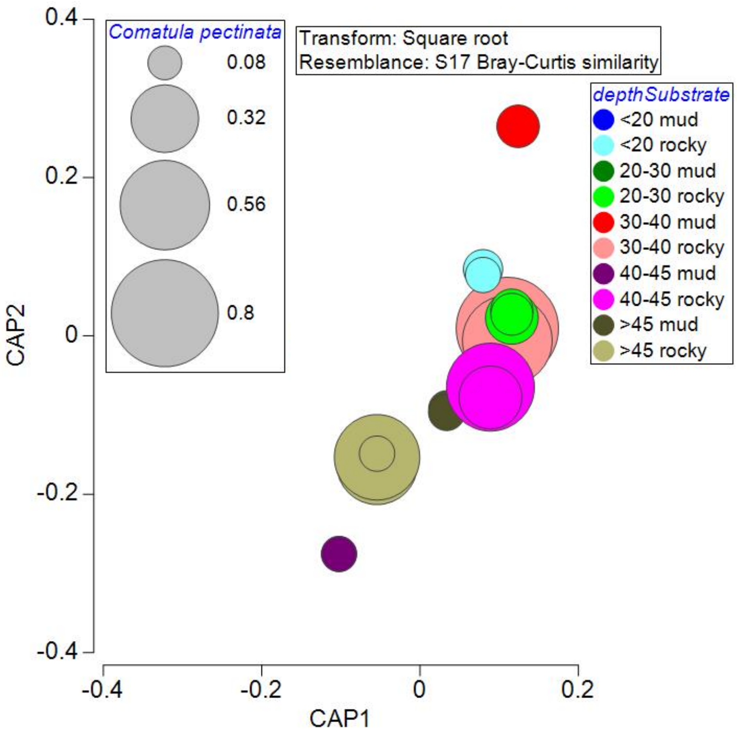


Figure 5. Non Metric Multidimensional Scaling plot of counts m² and biomass g m² of all taxa sampled by sled in Camden Sound, Maret Islands and Eclipse Archipelago. Factors are depth and substrate nested in location.

2.3 Predictor environmental variables for ten most abundant species.

It is believed that the most common species found in an assemblage are likely to be disproportionately important for ecosystem function (Winfree et al., 2015). We investigated the distribution of most abundant species across depth/substrate habitats to provide information on predictor environmental variables for these species. The plots (Figure 6) visualise species abundance (as bubble plots) as response variable with a predictor environmental variables of depth and substrate. Four crinoid species *Capillaster multiradiatus*, *Comatula pectinata*, *Heterometra cf. crenulata* and *Comatula rotalaria* were among the most abundant ones in the area. According to substrate preference and distribution depth the crinoids can be divided into two groups. *C. pectinata* and *H. cf. crenulata* occurred at all depths and substrates with peak aggregations at 30 to 40 and 40 to 45 m and rocky substrate. *C. multiradiatus* and *C. rotalaria* were also mostly aggregated in these habitats but with limited aggregations among other habitats. The three most abundant species *Dendrilla* sp. EG1, *Ianthella flabelliformis* and *Reniochalina stalagmitis* occurred in rocky substrate with *Dendrilla sp*.EG1 limited mostly to 30 to 45 m depth and the other two species occurring across the depth. Soft coral species *Dendronephthya* and Malithaeidae were distributed in all habitats except muddy <20 m but both were aggregated mostly in rocky vs muddy substrates. Blind pea crab *Xenophthalmus pinnotheroides* occurred exclusively in shallow mud habitat.



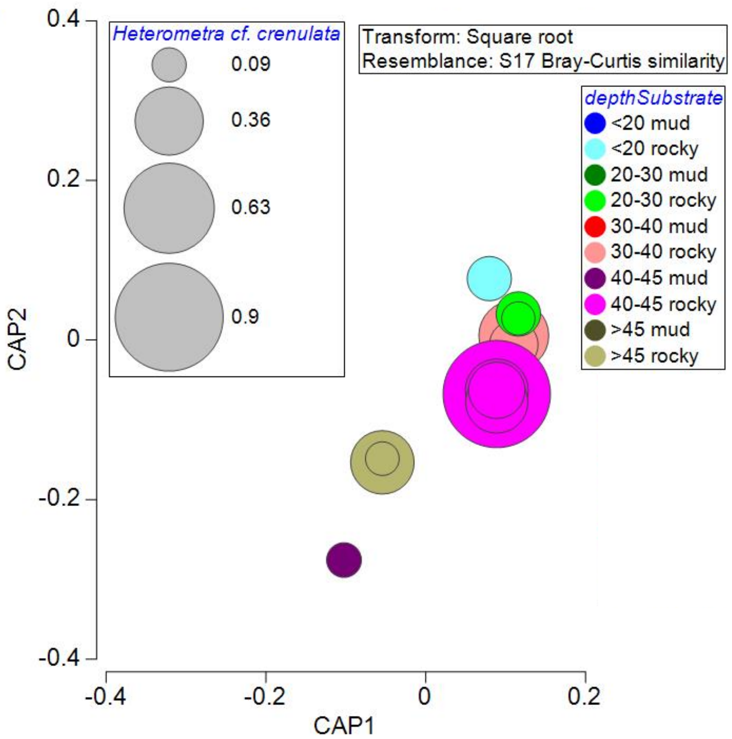
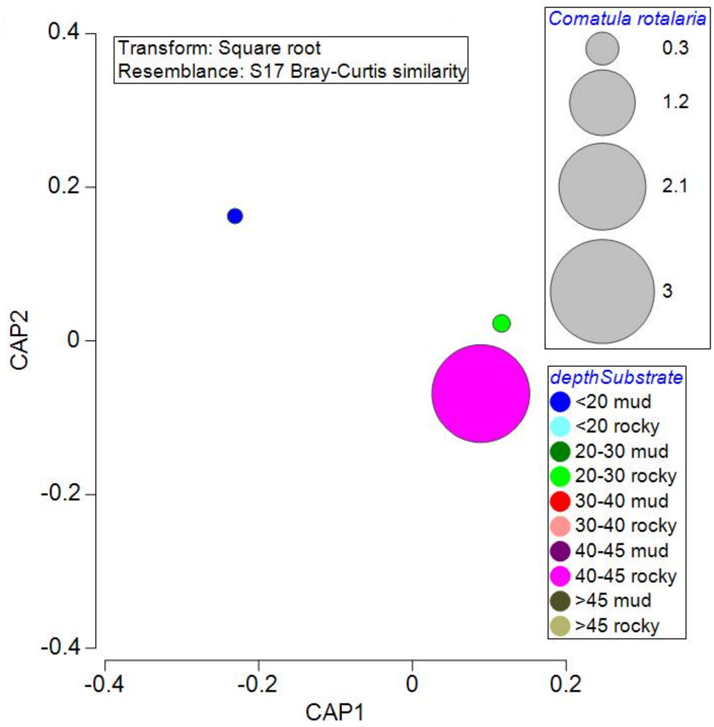
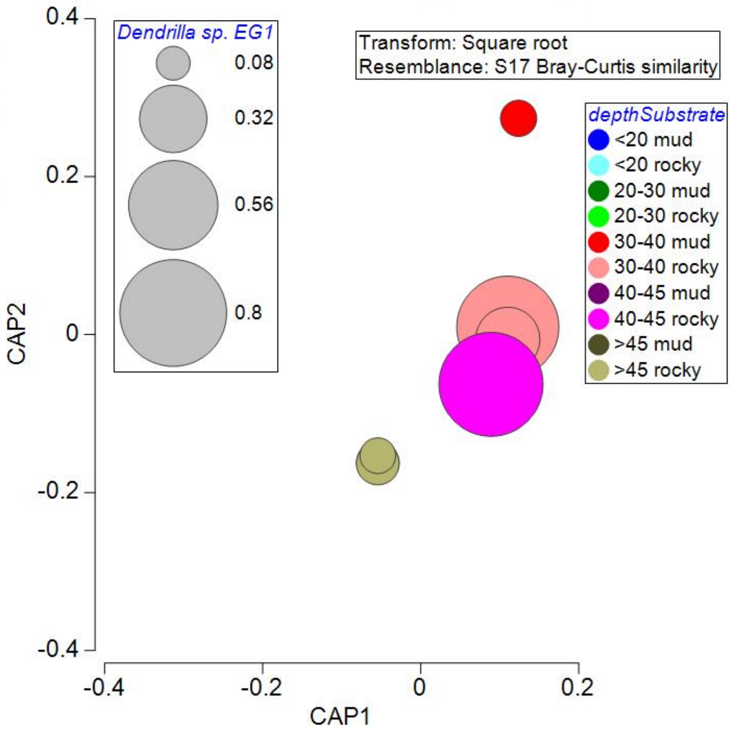


Figure 6. Bubble plot overlay of the 10 most abundant species in Camden Sound with the Constrained Analysis of Principal Coordinates (CAP) axes.





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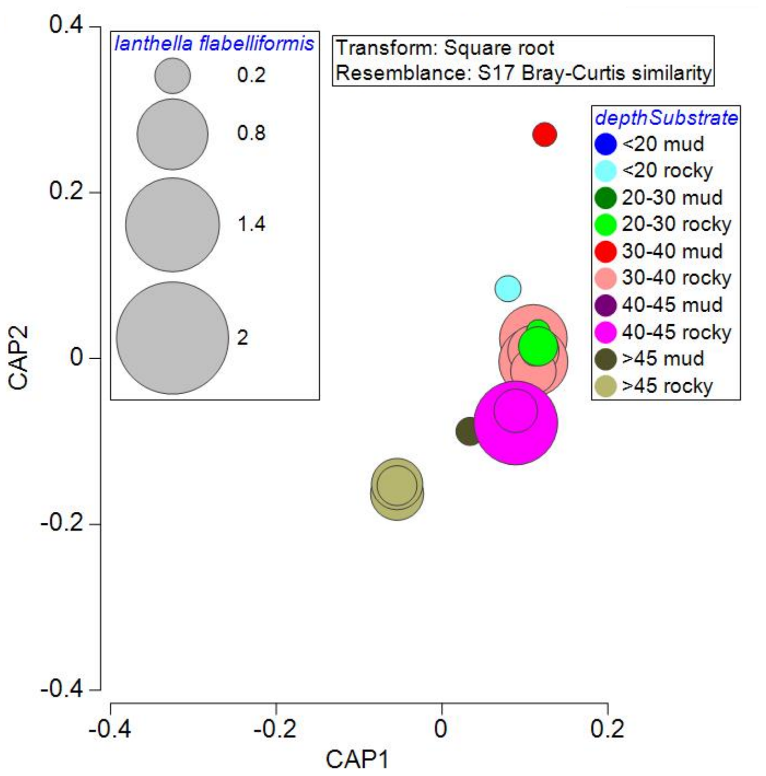

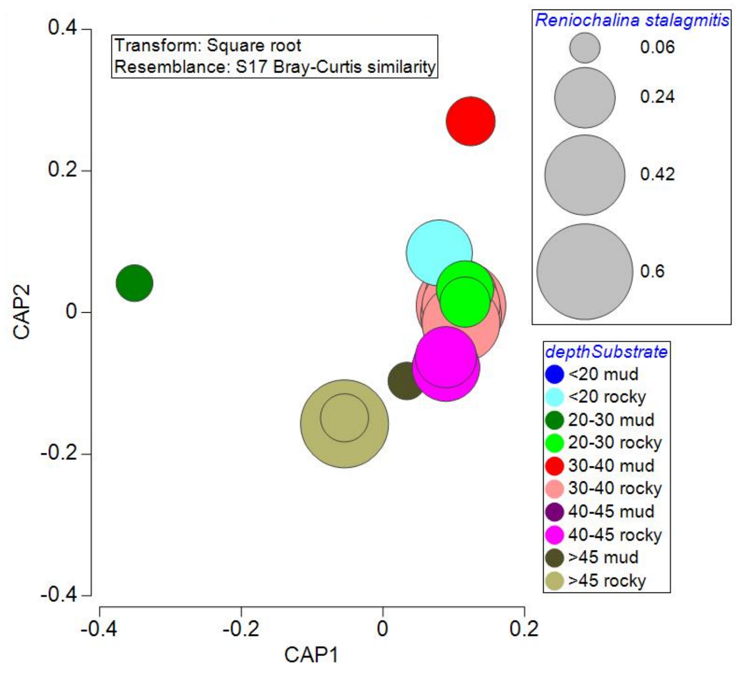

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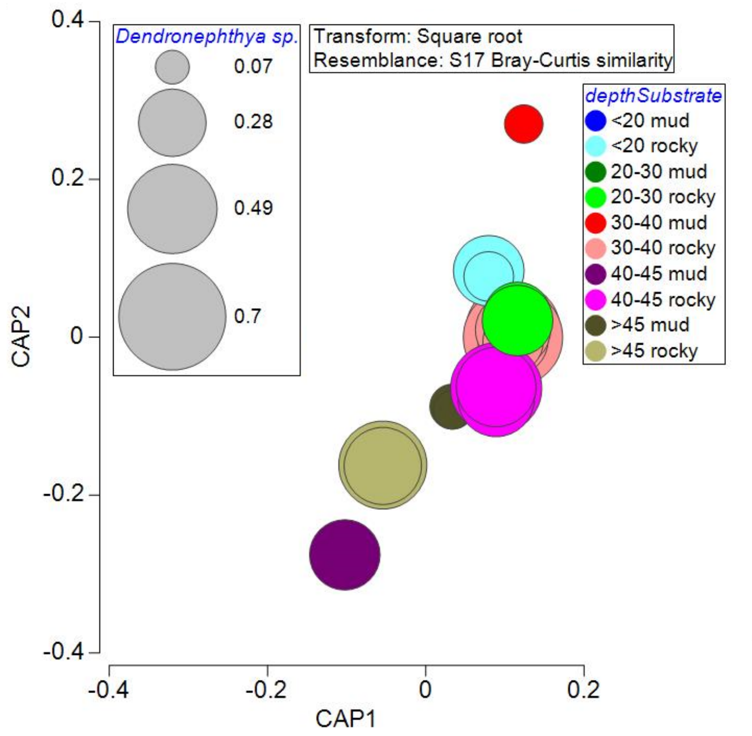


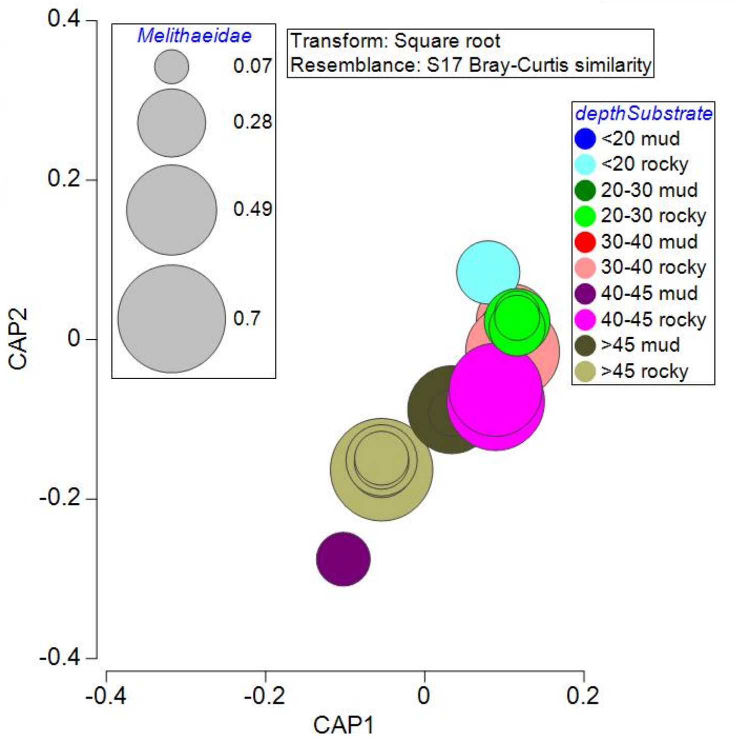
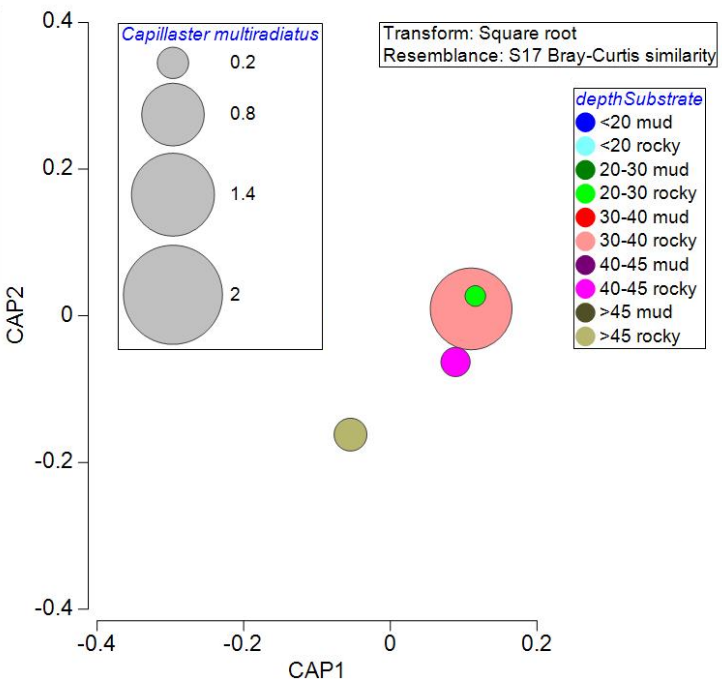


Figure 6 (continued). Bubble plot overlay of the 10 most abundant species in Camden Sound with the Constrained Analysis of Principal Coordinates (CAP) axes.



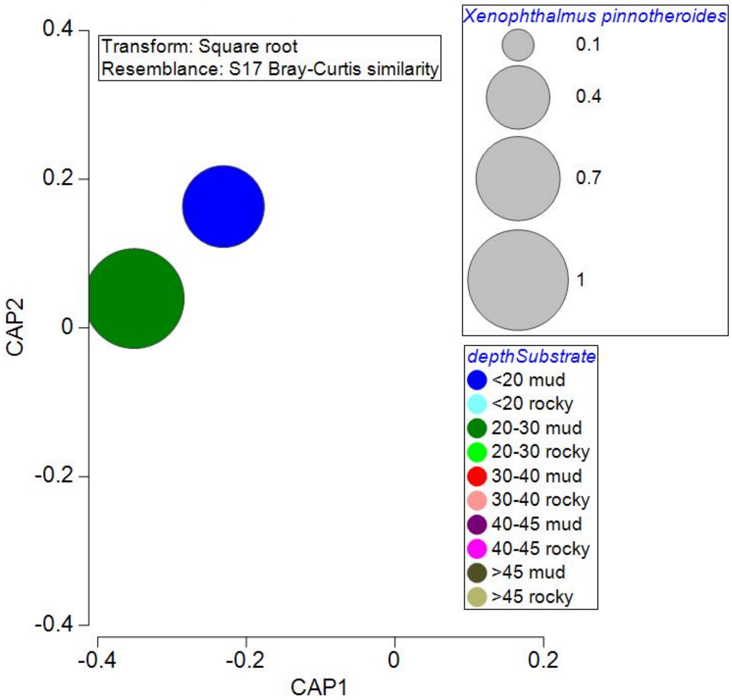


Figure 6 (continued). Bubble plot overlay of the 10 most abundant species in Camden Sound with the Constrained Analysis of Principal Coordinates (CAP) axes.

2.4 Analysis of species associations.

Species association patterns could be due to species interactions or environmental factors and may facilitate species persistence therefore are important for maintaining biodiversity. SIMPER analysis were performed to detect how species are varying across samples or more specifically which species are varying coherently across samples. Samples were characterised by their environmental characteristics of depth and substrate. Clustering of 50 most abundant taxa at each location identified groups of species that covaried coherently among substrate and depth. In Camden Sound 19 coherent species groups were identified (A to S) (Figure 7), in Maret eight groups ((A-H) (Figure 9) and in Eclipse Archipelago twelve groups (A-L) (Figure 11). Groups contained one or more species. Groups of line plots for the groups of species identified in dendrograms showed the association with a combination of environmental variables of depth and substrate (Figures. 8, 10 and 12). Each group of species tended to occur only at a limited subset of stations although some species or group of species were more station specific than others. Combination of environmental variables of depth and substrate explained the separation of each species clusters.

2.5 Camden Sound.

Species occurring in different stations but exclusively in >20 m mud habitats were gastropod molluscs of family Vermetidae, bivalve *Placamen lamellosum*, a group consisting of small snails Pyramidellidae, *Vexillum rugosum*, large predatory snail *Murex brevispina* and sea cucumber *Leptopentacts grisea* and a group consisting of northern velvet shrimp *Metapenaeopsis cf. novaeguineae*, southern rough shrimp *Trachysalambria curvirostris*, and sea cucumber *Molpadia scabra*. Blind pea crab *Xenophthalmus pinnotheroides* (group d) was found in shallow, up to 30 m habitat. Barnacle *Solidobalanus socialis* (group d) occurred at one station, 40-45 m mud. Group g consisted of species that occurred in both mud and rocky substrate from > 20 to 45 m. Blue Endeavour prawn formed group i and occurred at deep, > 45 m mud and 20-30 rocky stations. A sponge, *Guitarra* sp. and two soft corals *Alertigorgia orientalis* and *Chromonepthea* sp. (group j) occurred mostly in <20 m rocky station. Group k consisting of a crinoid and sponge occurred at rocky stations 20-30 m and 30-40 m. Group I consisted of one species of sponge occurring mostly in 40-45 m rocky stations. Group m, n, o, q, r and s contained species assemblages that were not specific. The crinoid, *Heterometra cf. crenulata* occurred in rocky habitats from 30 to > 45 m depth.

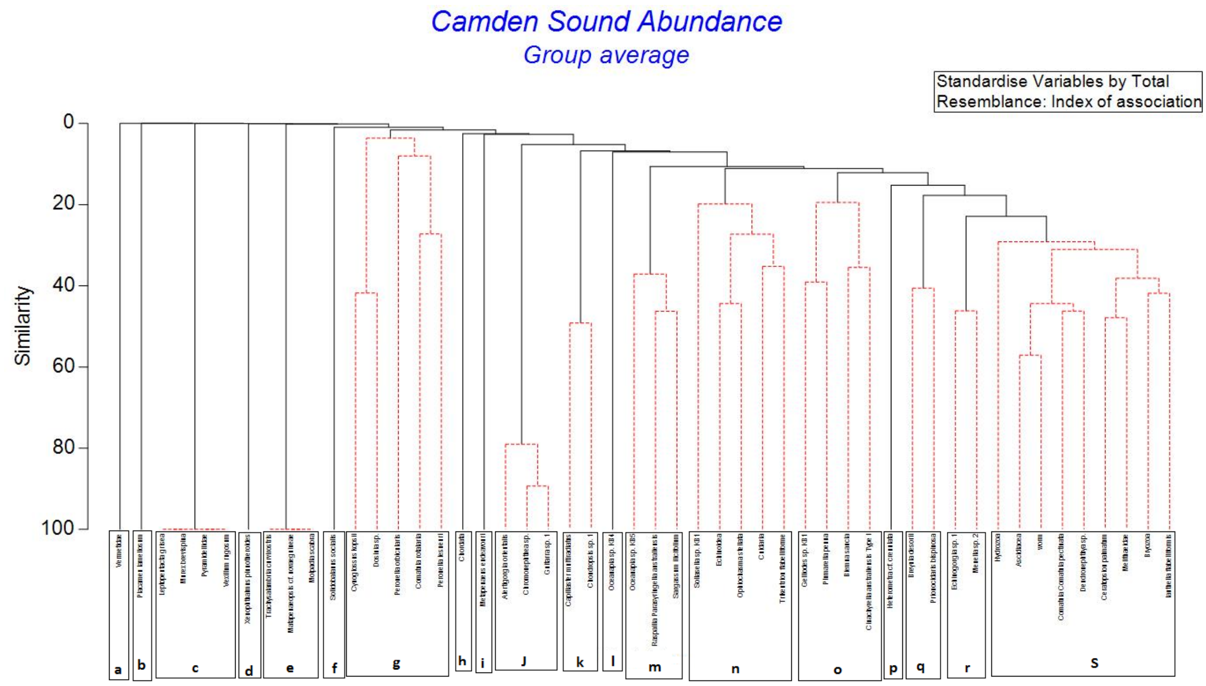


Figure 7. Dendrogram from group average clustering of the 50 most important taxa among species. Continuous lines indicate coherent groups which were significantly differentiated by SIMPROF tests (at the 5% level).

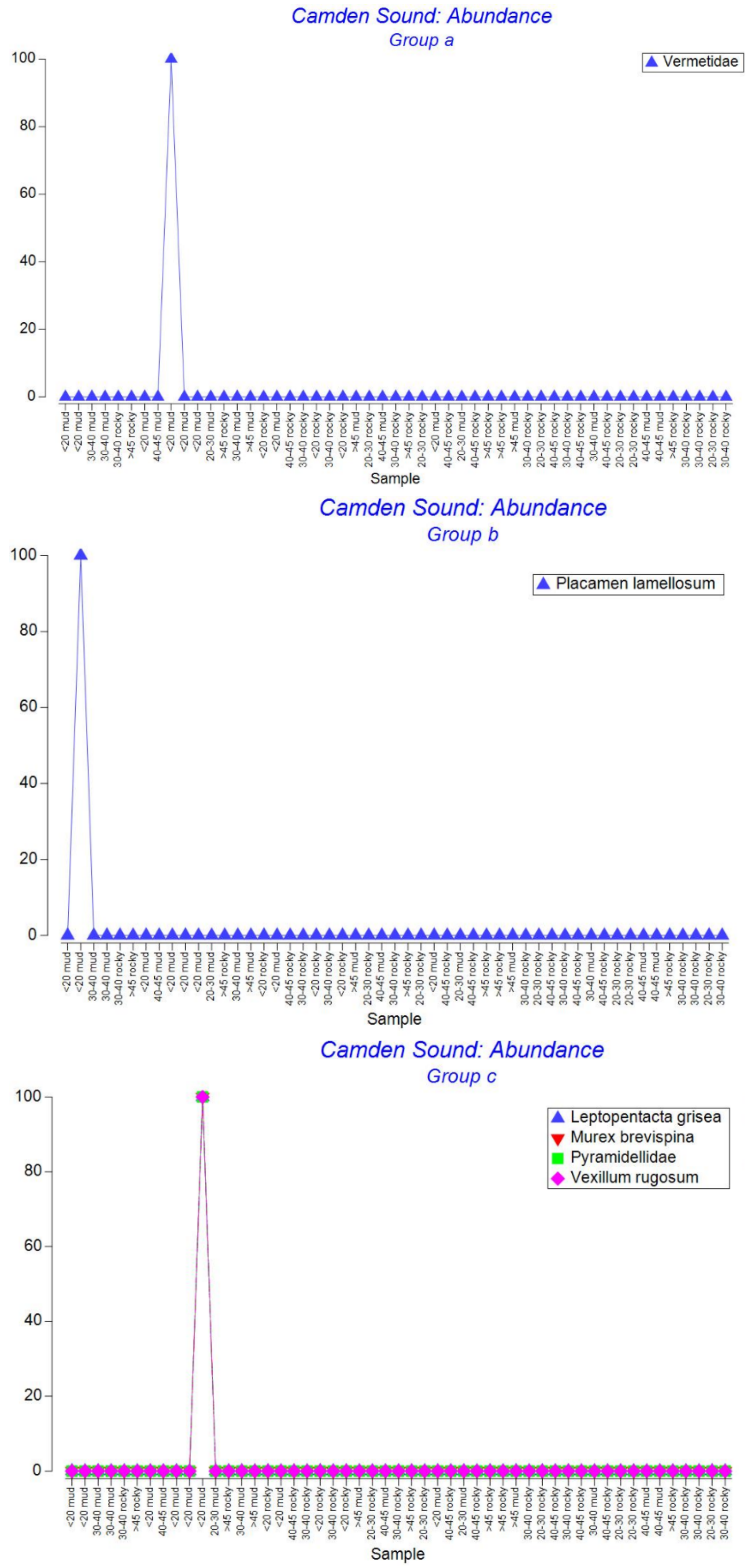


Figure 8. Line plots for the groups of species identified in the dendrogram shown in Figure 7. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

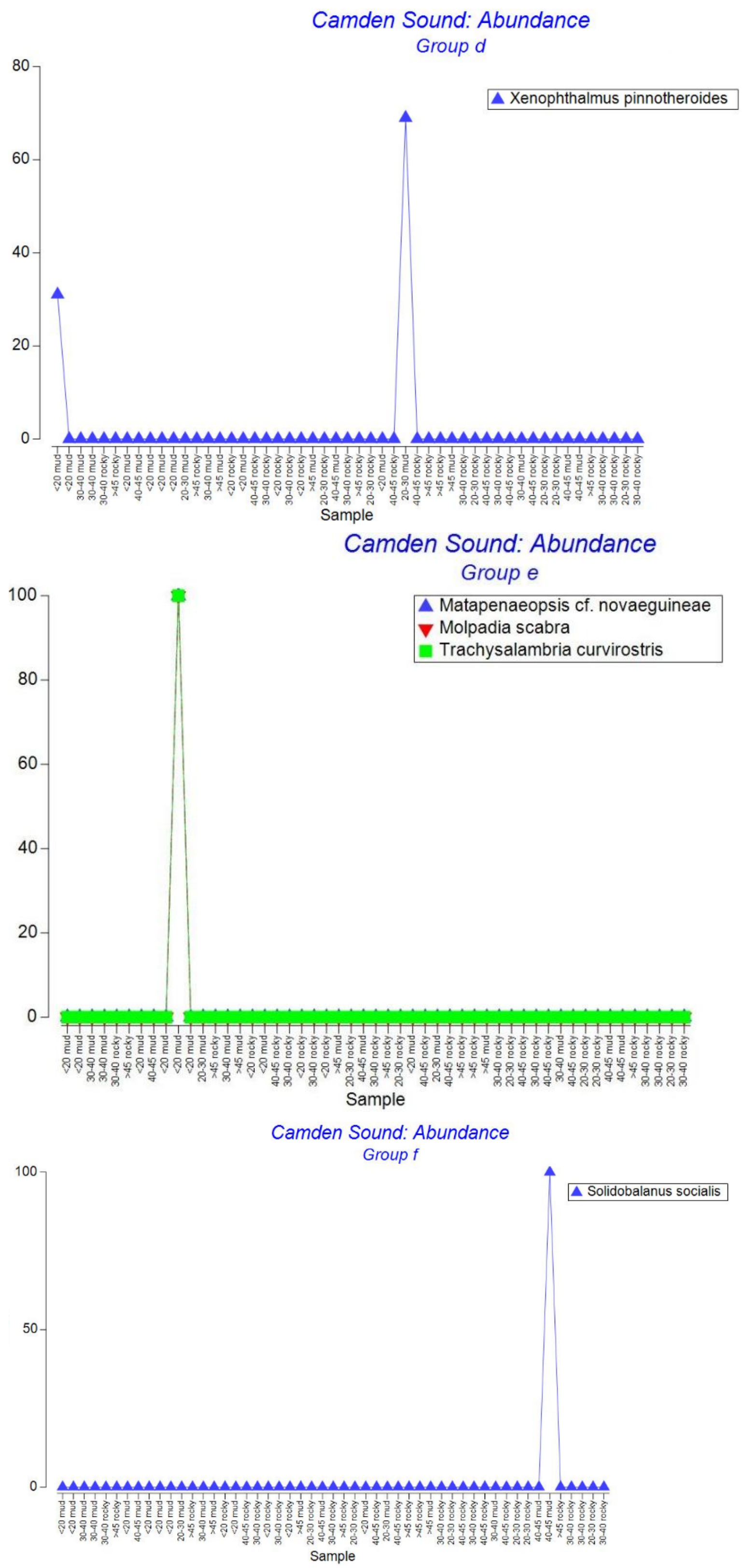


Figure 8 (continued). Line plots for the groups of species identified in the dendrogram shown in Figure 7. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

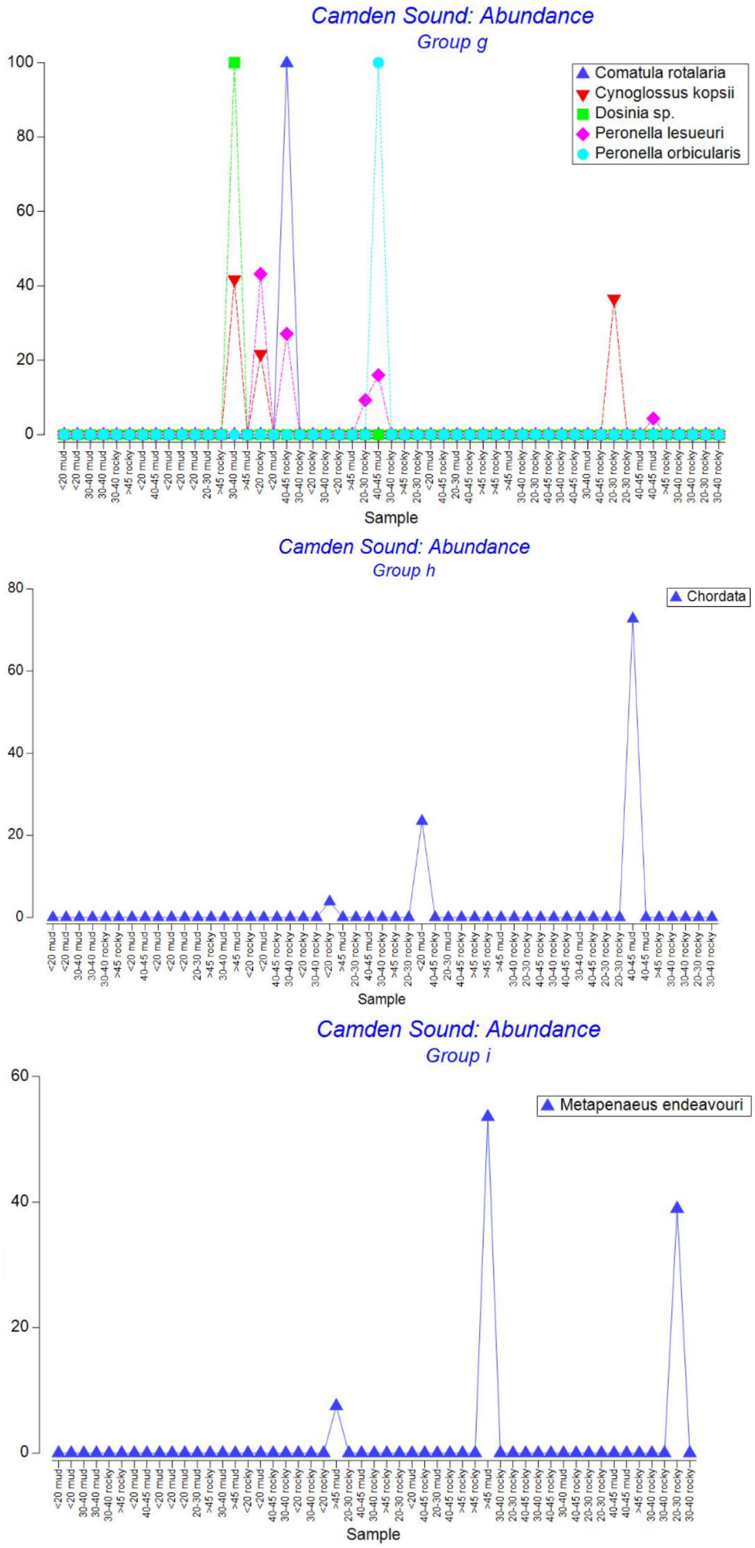


Figure 8 (continued). Line plots for the groups of species identified in the dendrogram shown in Figure 7. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

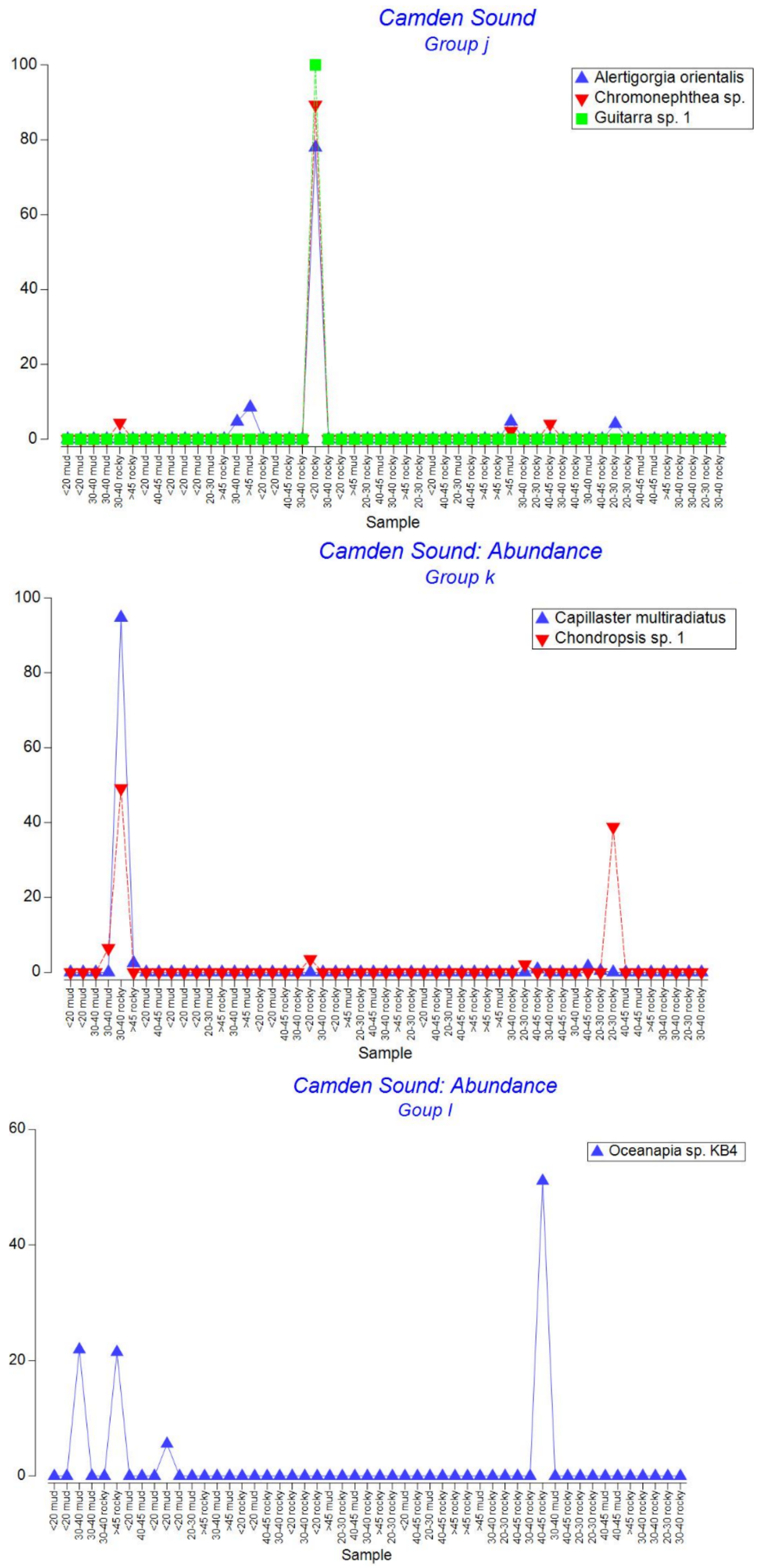


Figure 8 (continued). Line plots for the groups of species identified in the dendrogram shown in Figure 7. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

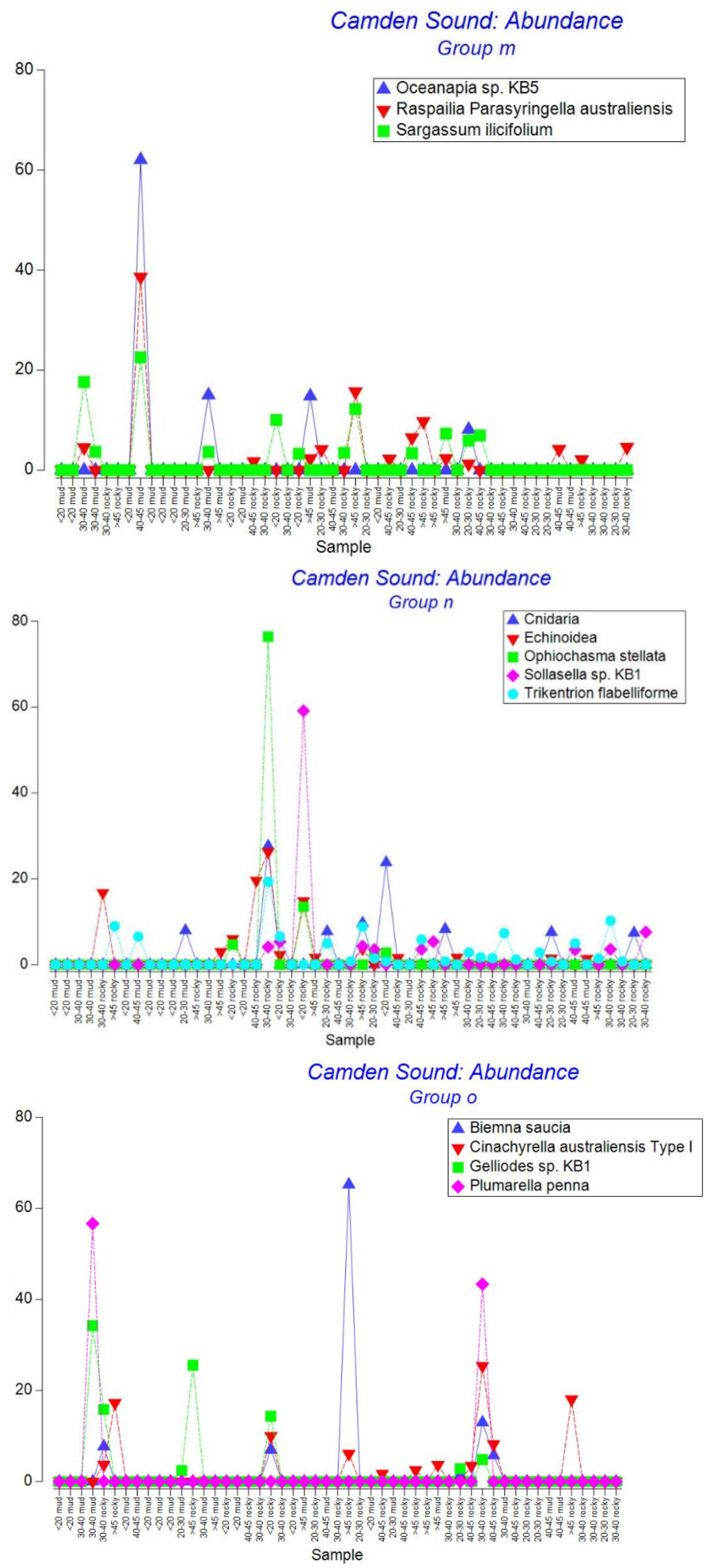


Figure 8 (continued). Line plots for the groups of species identified in the dendrogram shown in Figure 7. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axis are stations characterised by depth and substrate type.

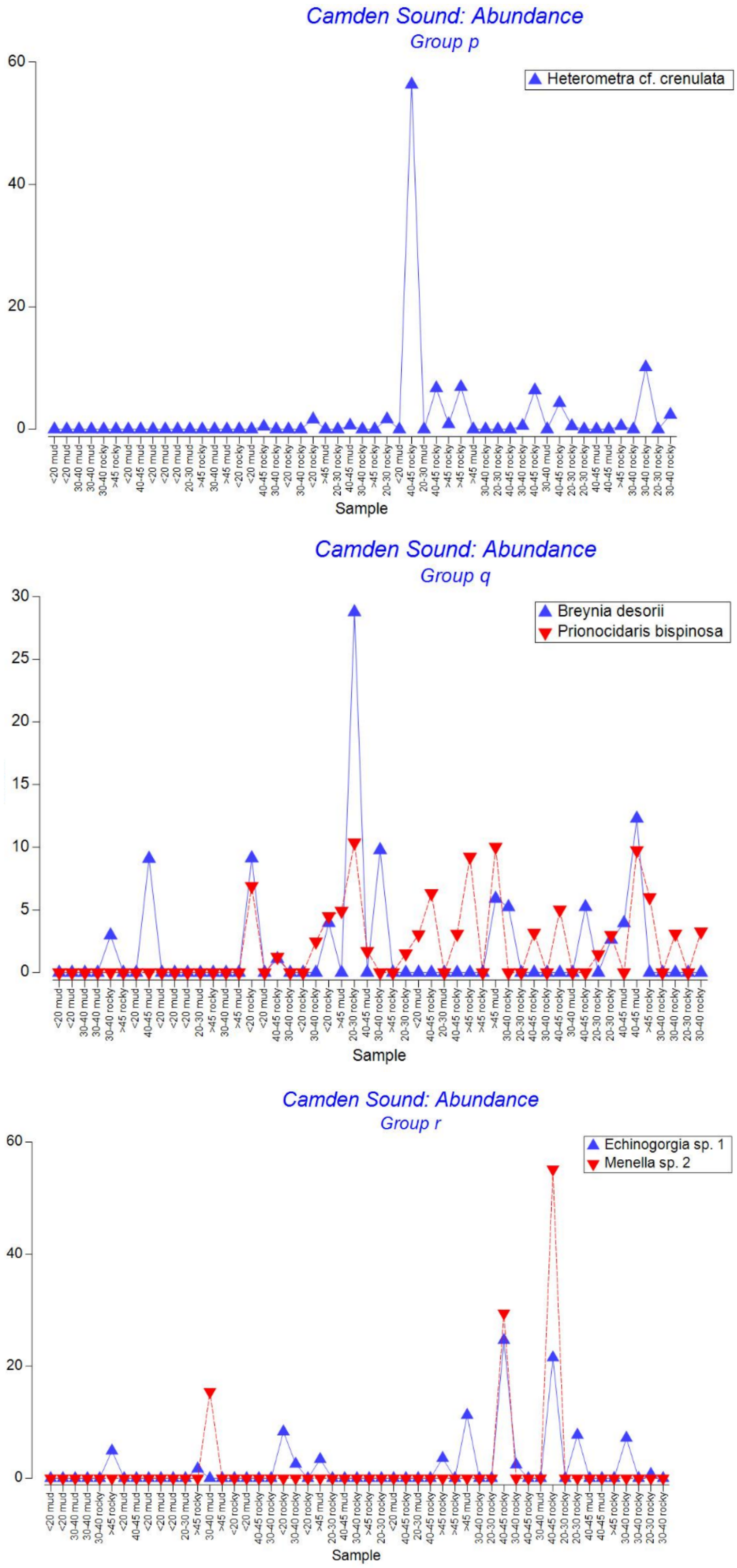


Figure 8 (continued). Line plots for the groups of species identified in the dendrogram shown in Figure 7. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

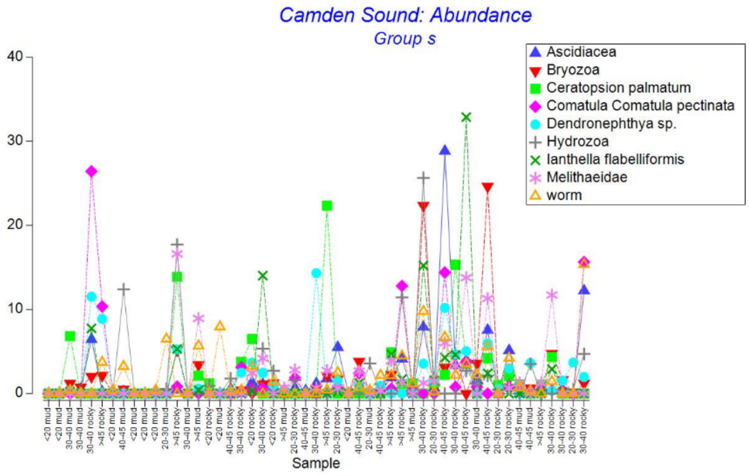


Figure 8 (continued). Line plots for the groups of species identified in the dendrogram shown in Figure 7. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

2.6 Maret Islands

There were two groups In Maret Islands stations consisting of one species each. Crab *Galene cf. bispinosa* occurred in one deep mud station and ophiuroid *Ophiocentrus verticillatus* occurred in two deep and one shallow mud stations. Other six groups consisted of associations of 5 to 15 taxa. Group d composed of five species occurred predominantly in mud with limited occurrence in few shallower rocky stations. Group e occurred mainly in rocky stations. Group f occurred mostly in 30 to 40 mud stations. Group f occurred in several 30-40 m rocky sites, few > 45 m rocky sites and 30-40 m and >45 mud station. Group h occurred across depths and substrates with peak abundance in 40-45 m and >45m stations and one <20 m rocky station.

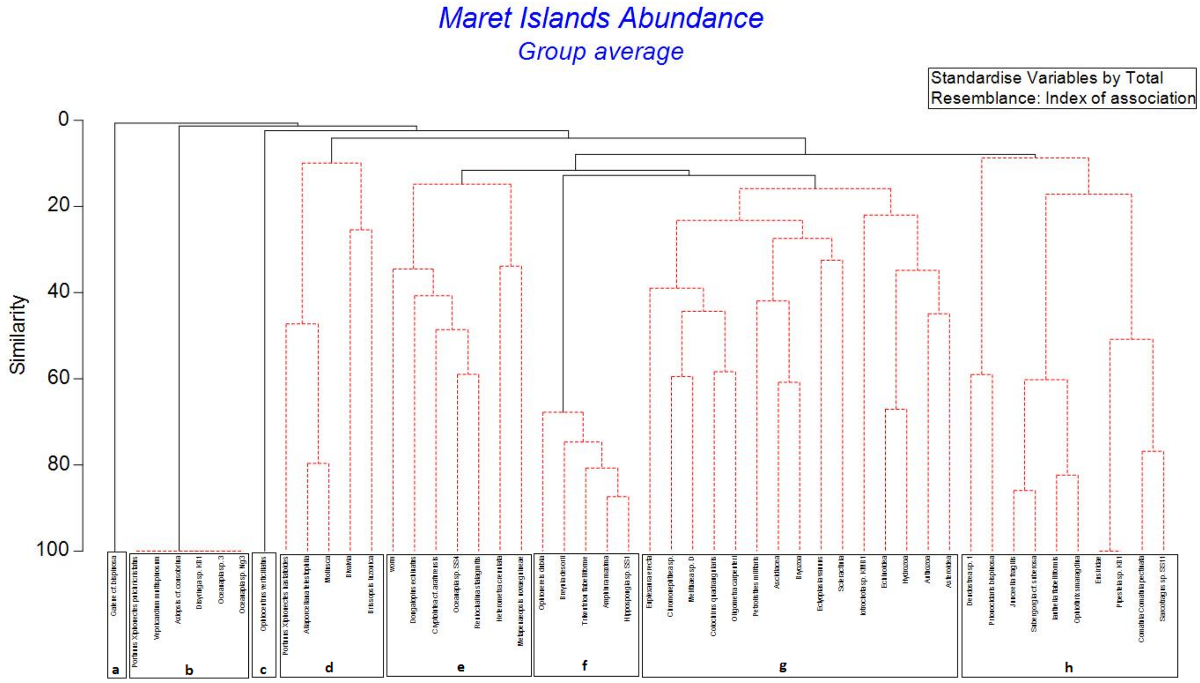


Figure 9. Dendrogram from group average clustering of the 50 most important taxa among species. Continuous lines indicate coherent groups which were significantly differentiated by SIMPROF tests (at the 5% level).

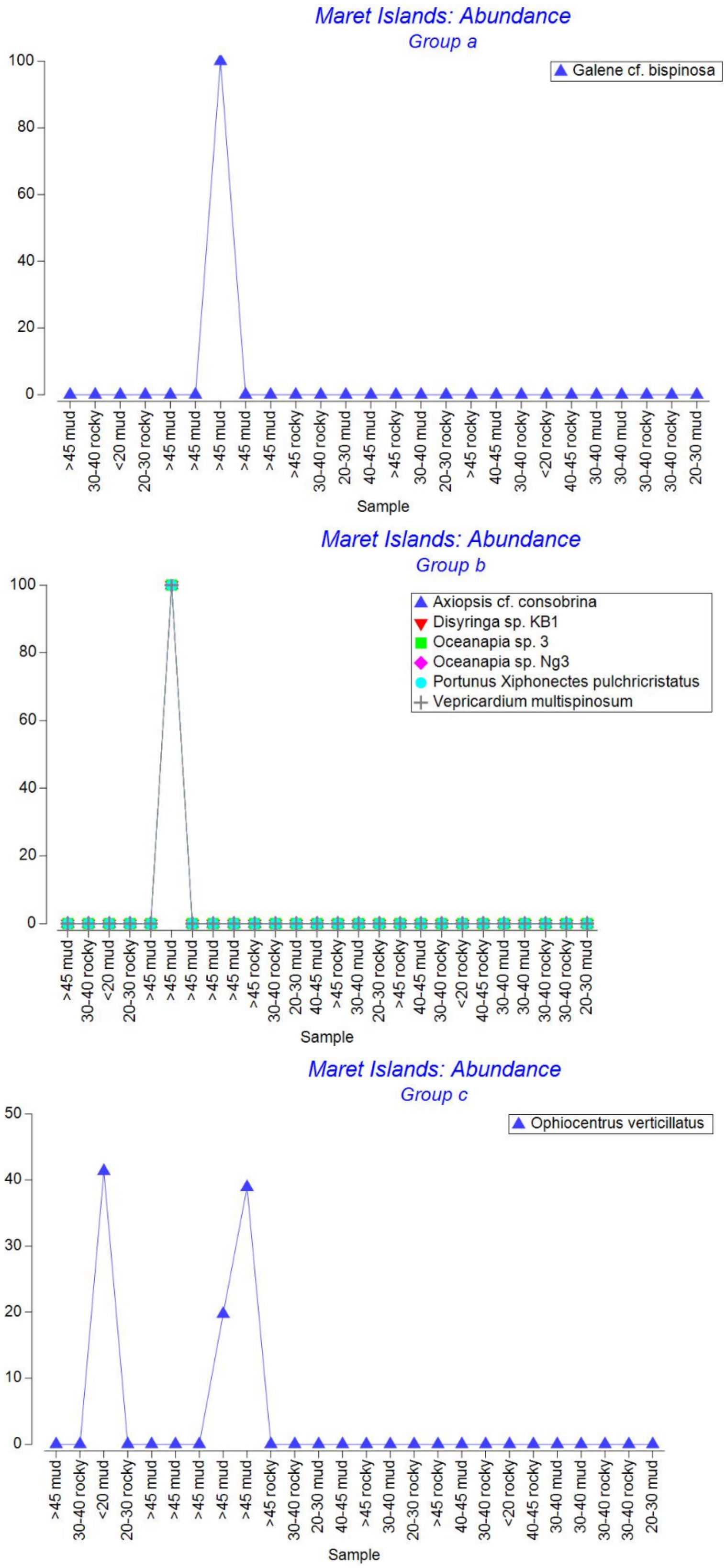


Figure 10. Line plots for the groups of species identified in the dendrogram shown in Figure 9. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

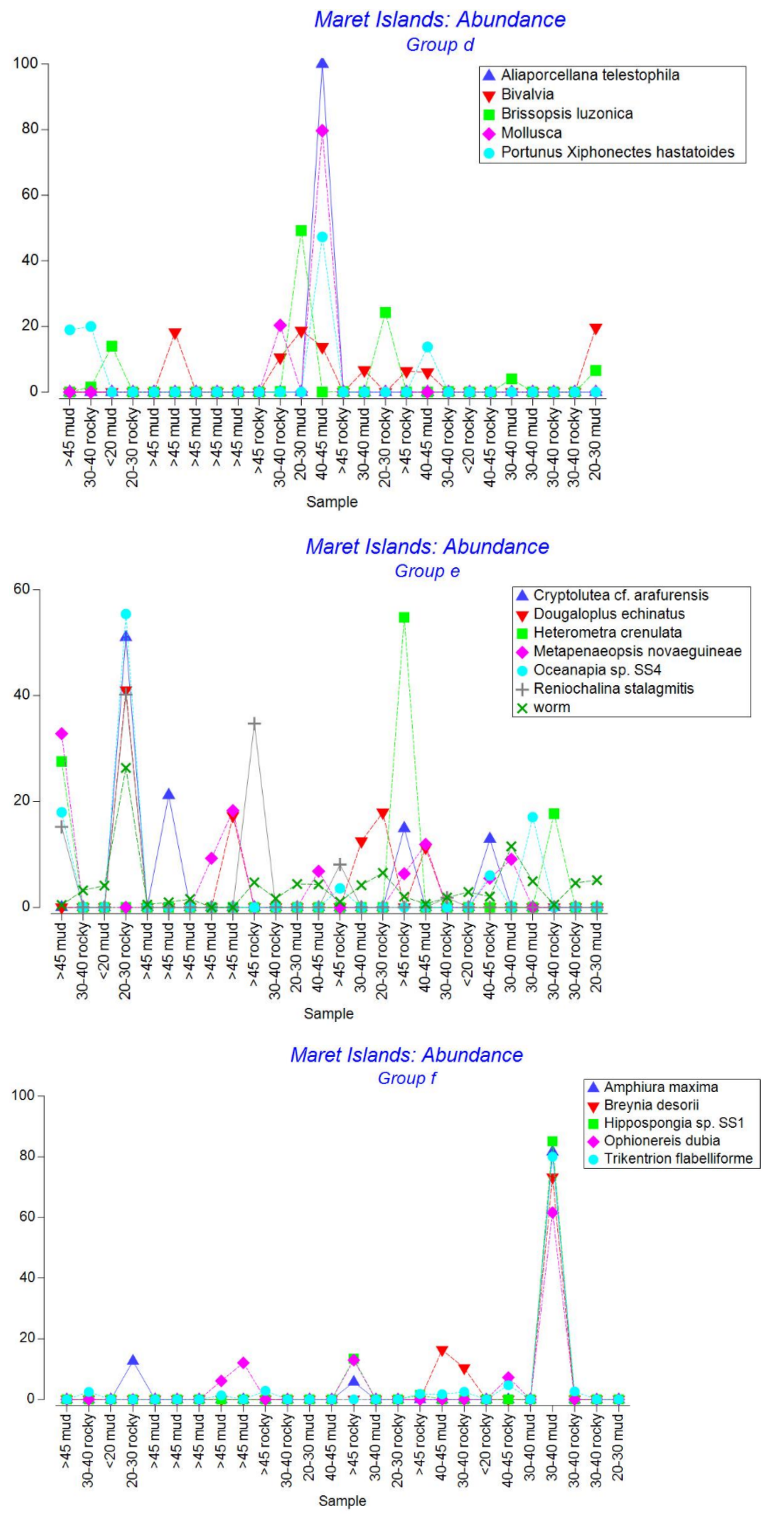


Figure 10 (continued). Line plots for the groups of species identified in the dendrogram shown in Figure 9. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

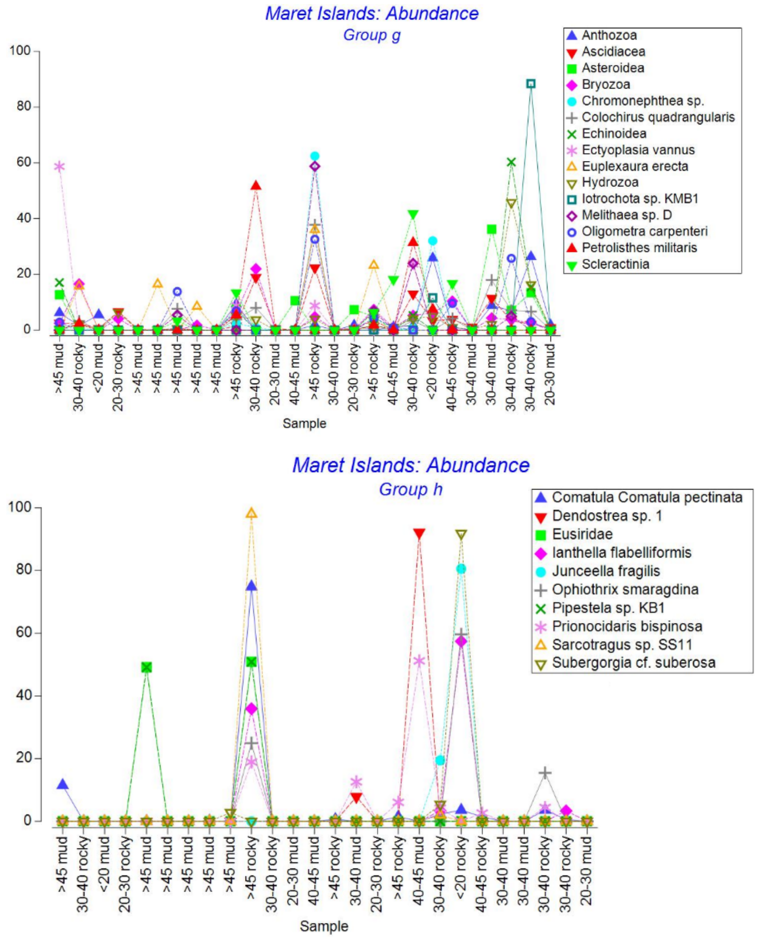


Figure 10 (continued). Line plots for the groups of species identified in the dendrogram shown in Figure 9. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

2.7 Eclipse Archipelago

Eclipse Archipelago has one group consisting of a single species and eleven groups consisting of several taxa. White hammer oyster (group d) occurred in deep rocky stations. Groups a, c, d, e, f and g occurred mainly in rocky stations while groups I and j had peak abundance in mud 30-40m and > 45 m. groups k and L occurred in both rocky and mud stations and across depths.

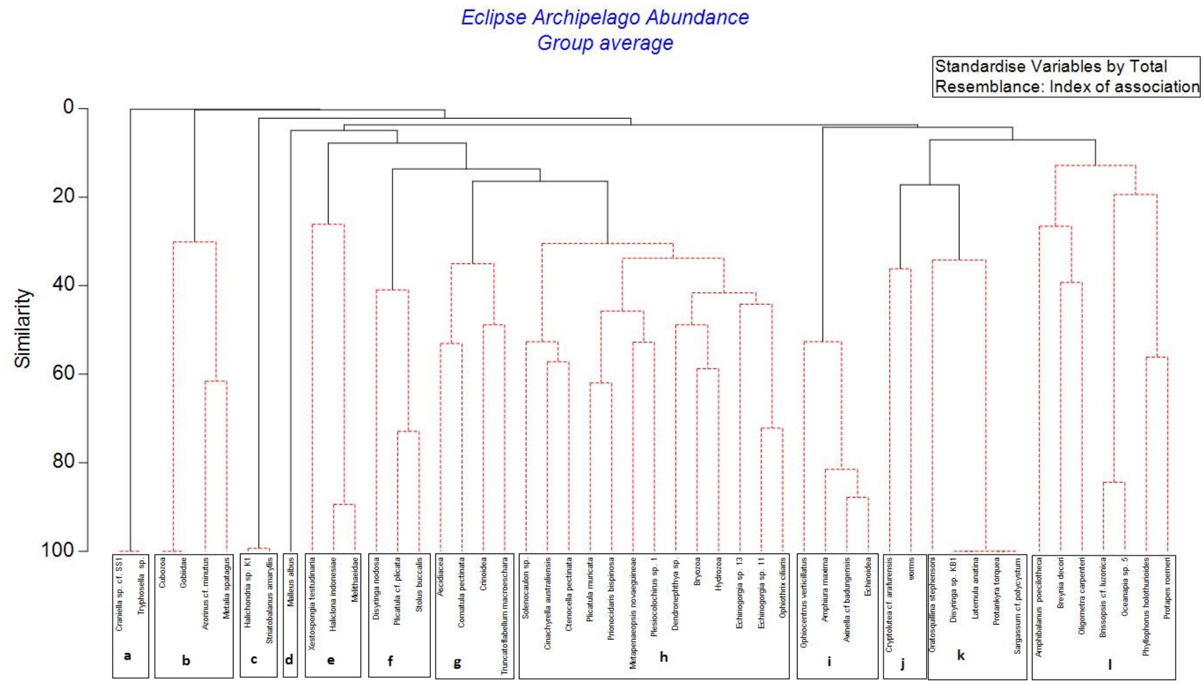


Figure 11. Dendrogram from group average clustering of the 50 most important taxa among species. Continuous lines indicate coherent groups which were significantly differentiated by SIMPROF tests (at the 5% level).

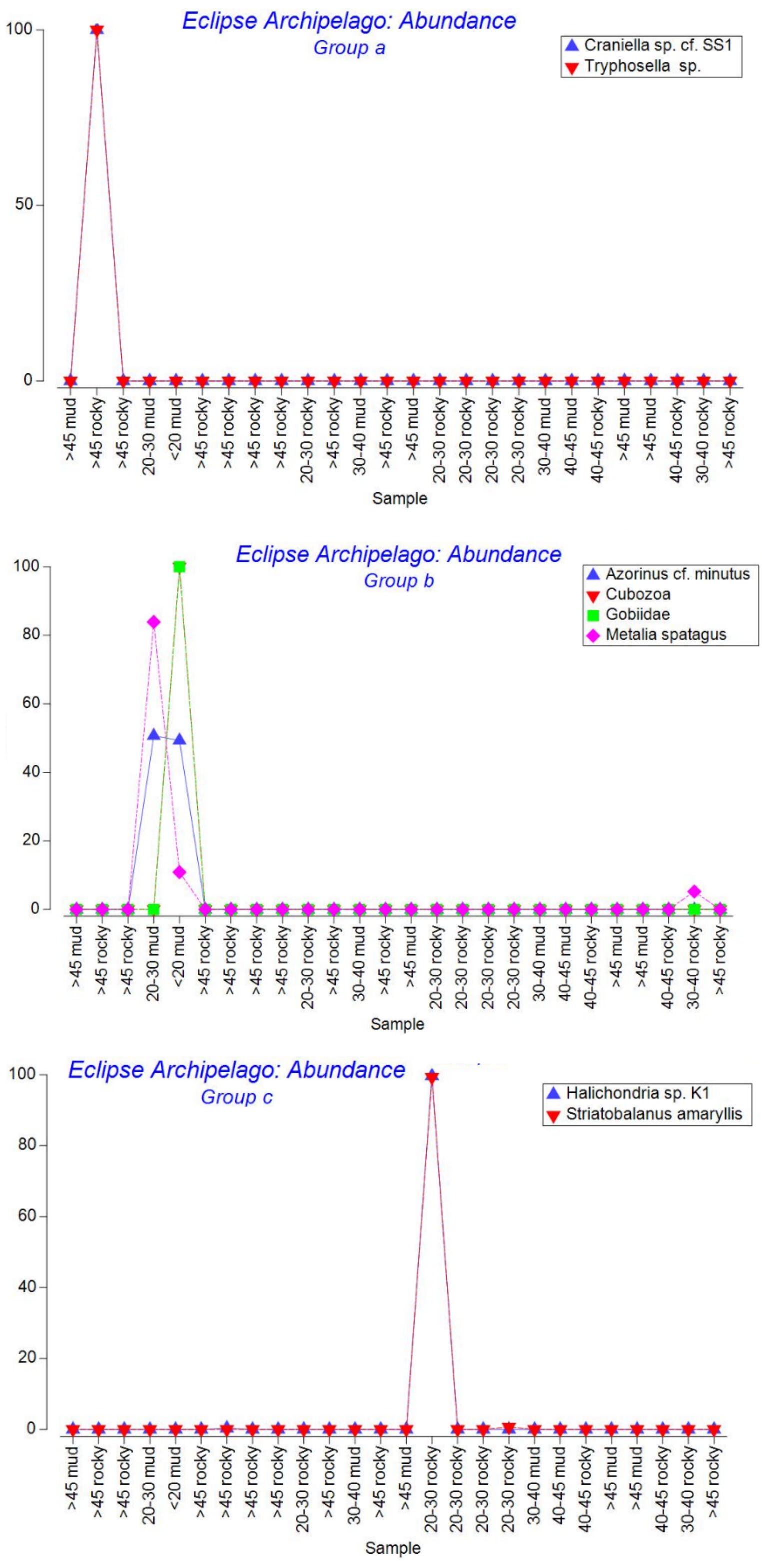


Figure 12. Line plots for the groups of species identified in the dendrogram shown in Figure 11. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

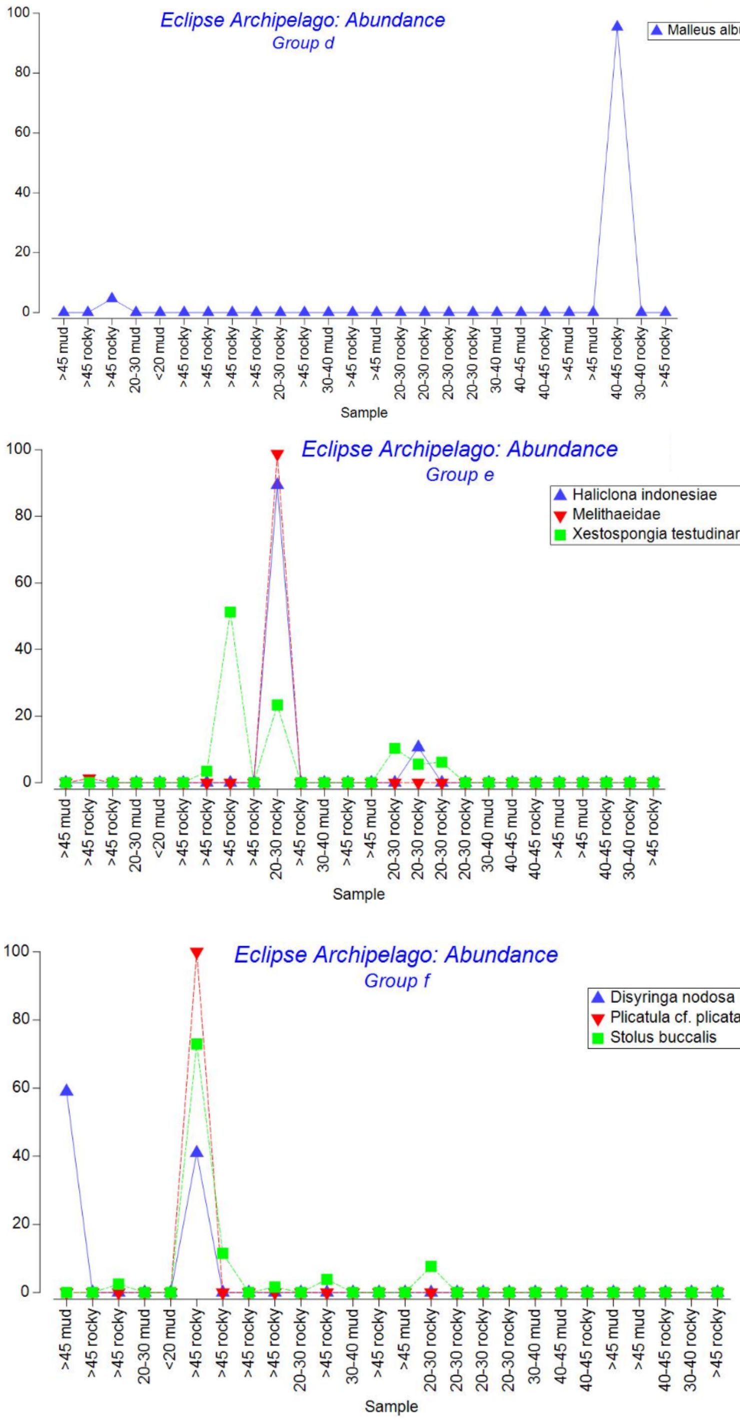


Figure 12 (continued). Line plots for the groups of species identified in the dendrogram shown in Figure 11. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

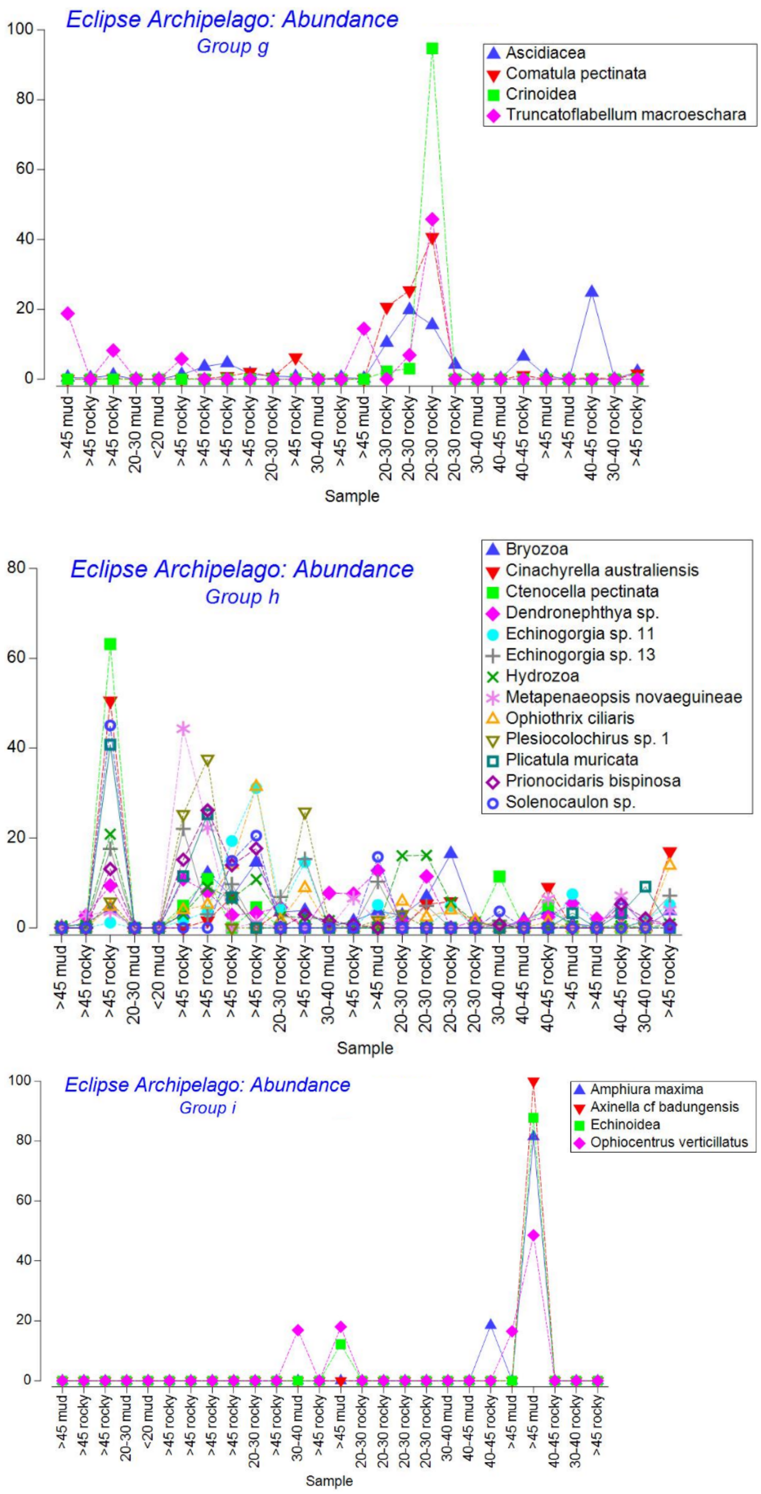


Figure 12 (continued). Line plots for the groups of species identified in the dendrogram shown in Figure 11. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

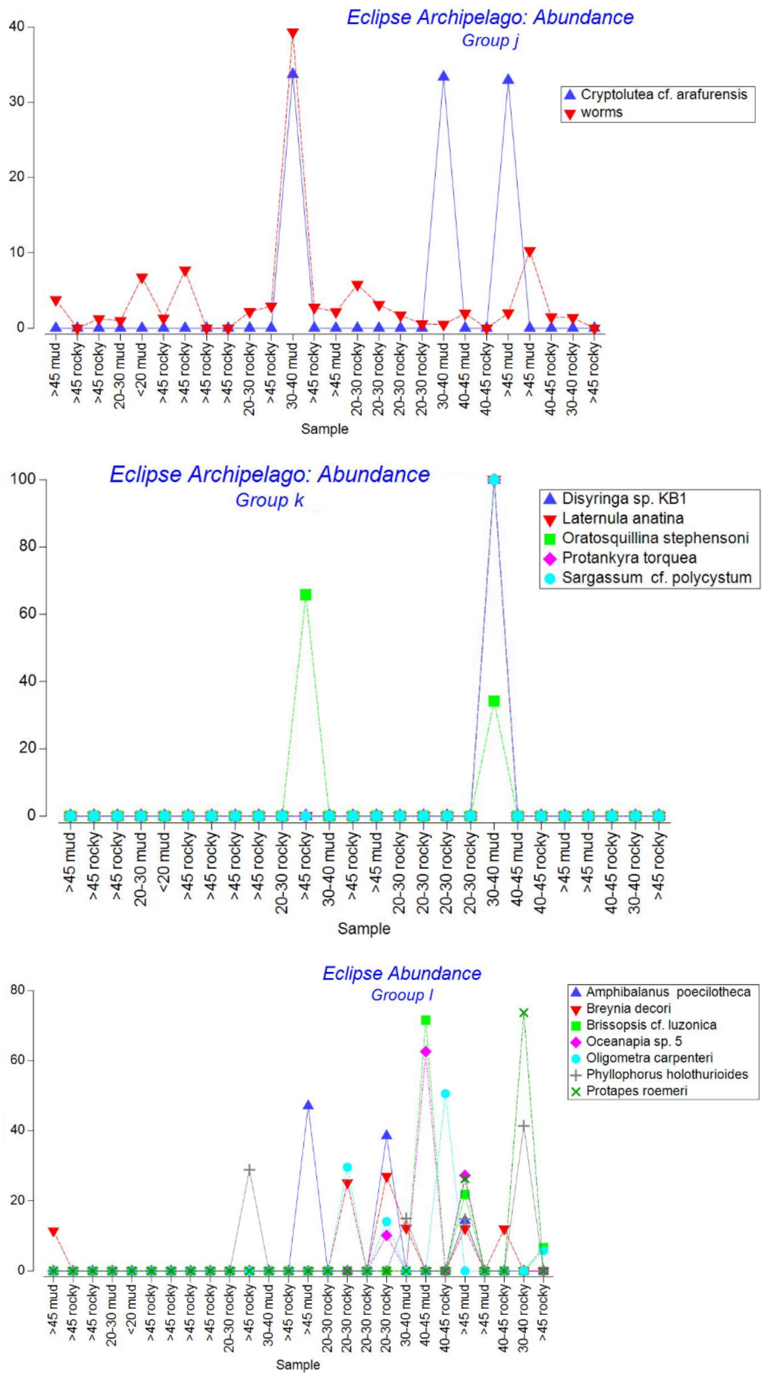


Figure 12 (continued). Line plots for the groups of species identified in the dendrogram shown in Figure 11. Plots show the consistency of species responses within groups. The y axes are percentages of total abundance of each species found in sled surveys. The x axes are stations characterised by depth and substrate type.

2.8 Associations between species and habitat type (determined by tow video) within major taxonomic groups

Figure 13 below shows the association of the 10 most important species in terms of biomass with physical habitat types showing a range of biomass (g of wet weight m^2) for each. Size of the bubble is proportionate to biomass occurring in a habitat. Principal Component (PC) 1 explained 42.1% and PC2 explained 17.2% of the variance in physical habitat type accounting together for 59. 3% of the total habitat variability. Sand, silt and low relief reef contained most of the overall variation.

The following analysis showed the association of communities with habitat structure and compared species distribution patterns across habitats. The mechanisms of habitat effects on associated organisms range from providing physical conditions, affecting biological interactions, altering hydrodynamics and nutrient flows. These comparisons provided an indication of the importance of equivalent habitat values. Some Arthropoda species showed association with all physical habitats but some were associated with a specific one like *Izanami inermis*, *Xenophthalmus pinnotheroides, Thenus parindicus* and *Lophopilumnus globosus* occurring in sand and silt only and *Striatobalanus amaryllis* in stone habitat. Asteroidea occurred in majority of habitats except silt. *Goniodiscaster rugosus* occurred in majority of habitats but the congener *G. acanthodes* in high relief reef and *G*. sp. A in coarse sand and high relief reef only. All Crinoidea were mostly associated with reefs, coarse sand, rocks, less with sand and not with silt or mud. Echinoids occur in all habitats with irregular ones (*Metalia spagatus, Peronella lesueuri, Breynia desorii* and *Brissopsis luzonica* more often associated with sand, mud and silt. Holothuroid *Phyllophorella spiculata, Massinum bonapartum* and *Globosita elnazae* were associated with sand and silt only while *Pseudocolochirus axiologus* and *C. quandragularis* were in reefs, and sand waves. Most species of ophiuroids were associated with all the habitats. Bivalvia *Antigona laqueata* were associated with sand, *Arca patriarchalis* and *Chama pacifica* with coarse sand, *C. lazarus* with low relief reef and coarse sand, *Pteria maccullochi* with stones and rocks. Gastropod *Chicoreus* spp were associated with sand, mud and coarse sand and C. *cervicornis* with low relief reef as well, *Aphelodiris cf. gigas* and *Platydoris cf. formosa* with reefs, *Bufonaria rana* with sand only. Hard coral *Turbinaria reniformis* was associated with reef only while soft coral species were associated with all the habitats. Only *Dendronephthya* and *Carijoa* spp. were associated with silt and mud but mostly with stones. All species of sponges were associated mainly with reefs, rocks and stones. Some species were associated with sand possibly attached to shells or other patchy hard substrate in sand. Fish were associated with all habitats with *Johnius borneensis* associated with reef only, *Jaydia melanopus* and *Liocranium pleurostigma* with sand and low relief reef and *Ostorhinchus melanopus* with mud. Ascidians, Bryozoa, Hydrozoa and Zoantharia were associated with sand and reef, worms with sand, coarse sand and less with reef. The associations of species with reef habitats (low and high relief reef in video data) in the Kimberley region reinforced the importance of the reef organisms like sponges creating habitats for other organisms.

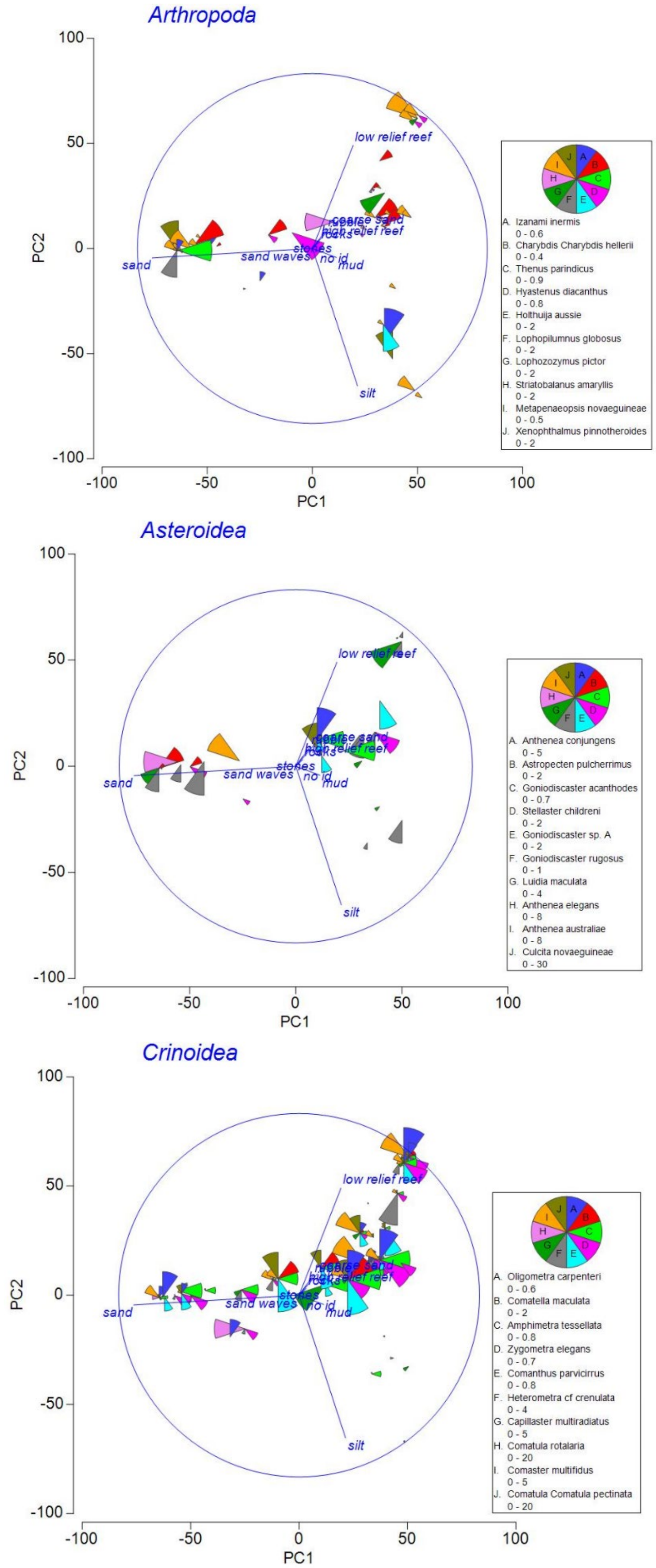


Figure 13. Habitat association of important species (by biomass) in each taxonomic group. Biomass (g wet weight m^2) shown. Size of bubble is proportionate to biomass occurring in habitat.

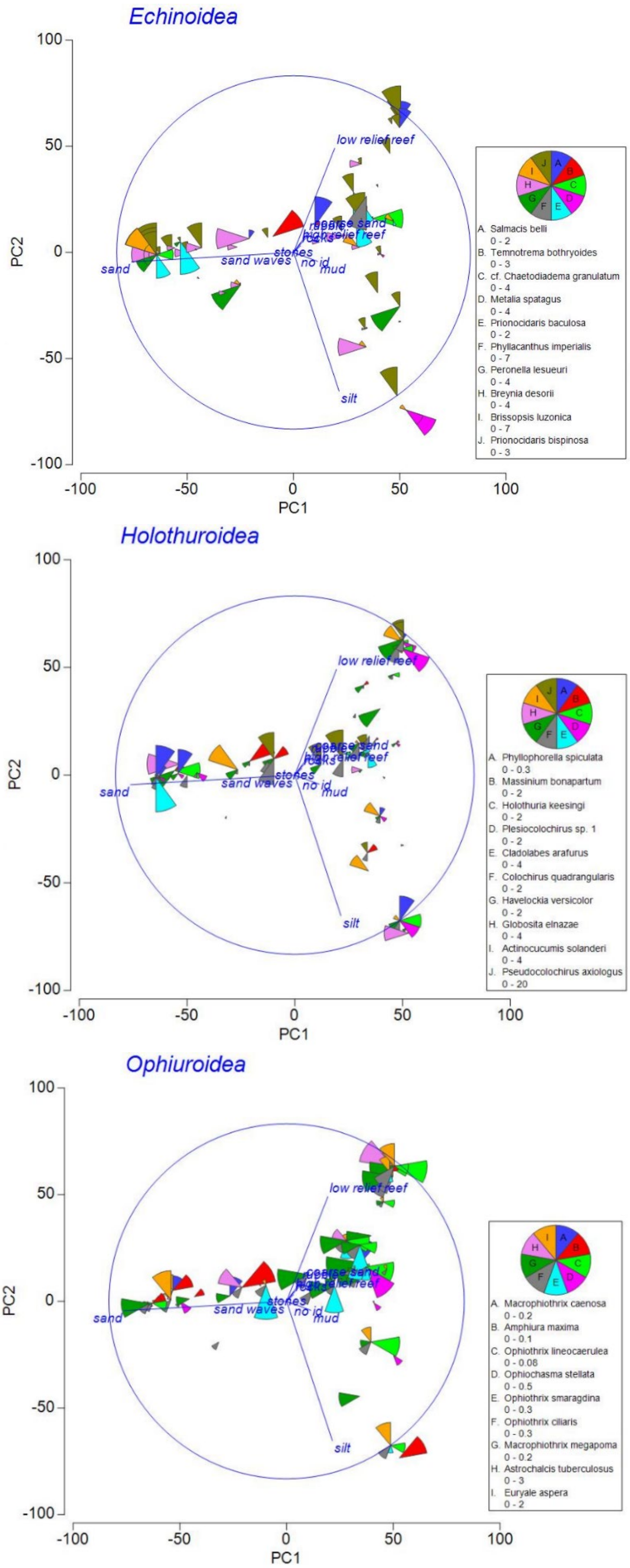


Figure 13 (continued). Habitat association of important species (by biomass) in each taxonomic group. Biomass (g wet weight m^2) shown. Size of bubble is proportionate to biomass occurring in habitat.

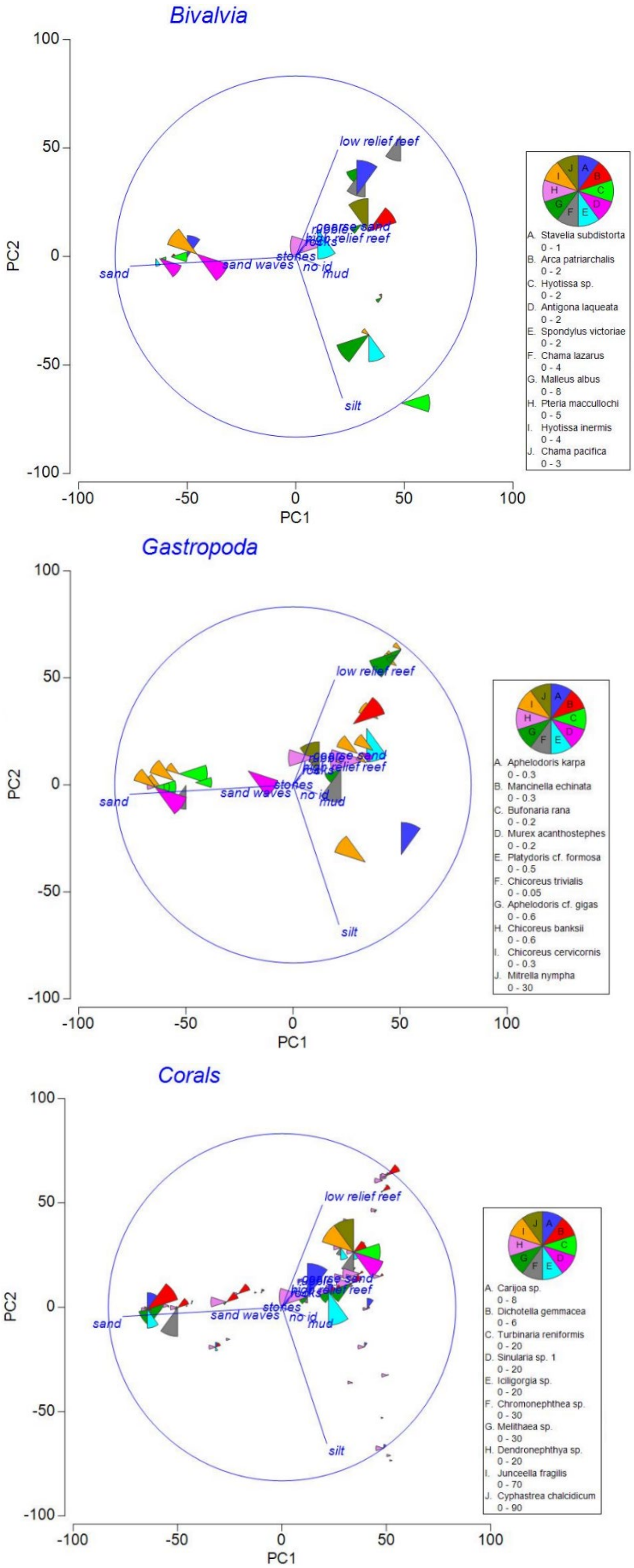


Figure 13 (continued). Habitat association of important species (by biomass) in each taxonomic group. Biomass (g wet weight m²) shown. Size of bubble is proportionate to biomass occurring in habitat.

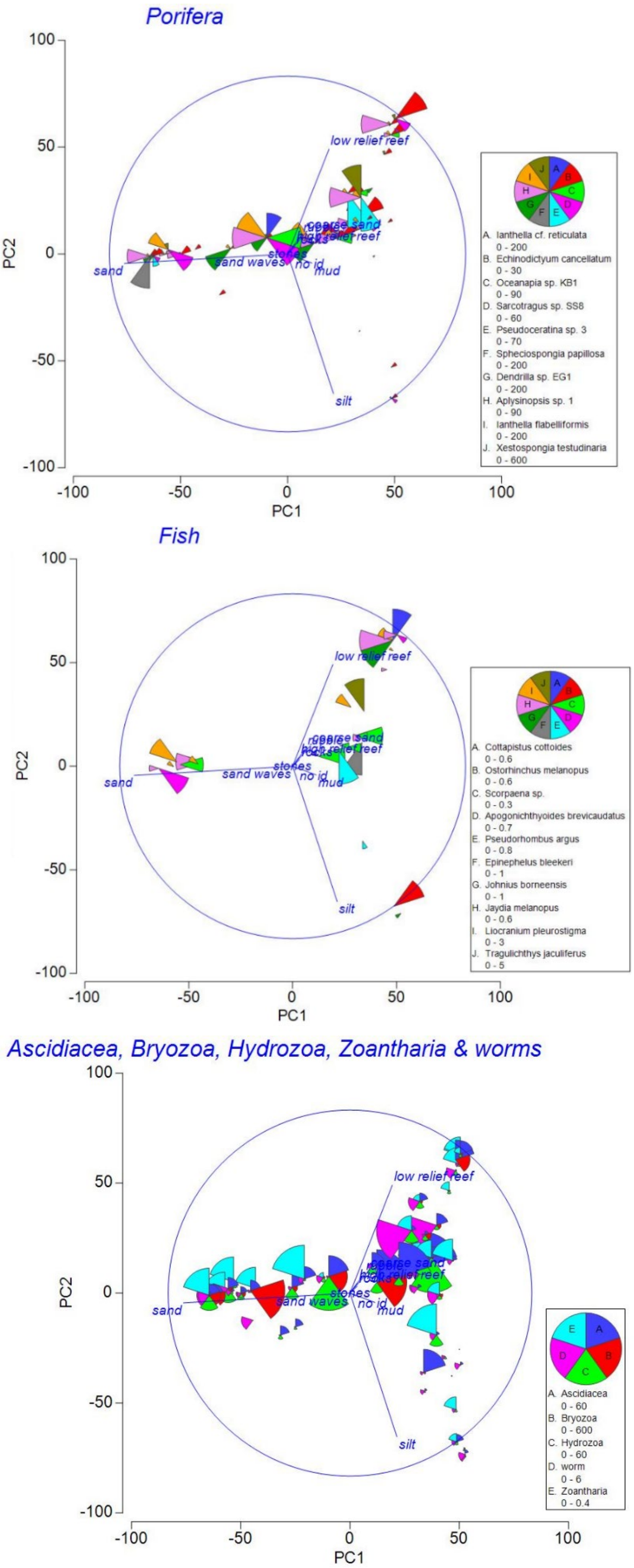


Figure 13 (continued). Habitat association of important species (by biomass) in each taxonomic group. Biomass (g wet weight m^2) shown. Size of bubble is proportionate to biomass occurring in habitat.

Figure 14 shows benthic habitat associations of major groups. PCA accounted for 57.5% of variation and 82.3% variation was accounted for by PCA 1 and PCA 2. No biohabitat contained a substantial part of the overall variation. Arthropoda were not associated with any particular biohabitat. Porifera, Ascidiacea, coral were associated with filter feeder habitat. Fish were associated mostly with sponge biohabitat and some with no biohabitat, macroalgae and bioturbated biohabitat. Zoantharia were associated with no biohabitat, filter feeder and bioturbated habitat. Worms were associated mostly with sponges and less so with macroalgae, bioturbated and no biohabitat. Bryozoa and Hydrozoa were associated mostly with other filter feeders. Bivalvia were associated with sponge habitat, bioturbated and no biohabitat while gastropoda were mainly associated with filter feeder habitat. Asteroidea and Crinoidea were associated with sponge habitat, Holothuroidea with sponge habitat and less so with no habitat, and Echinoidea and Ophiuroidea with filter feeder, macroalgae, bioturbated and no habitat.

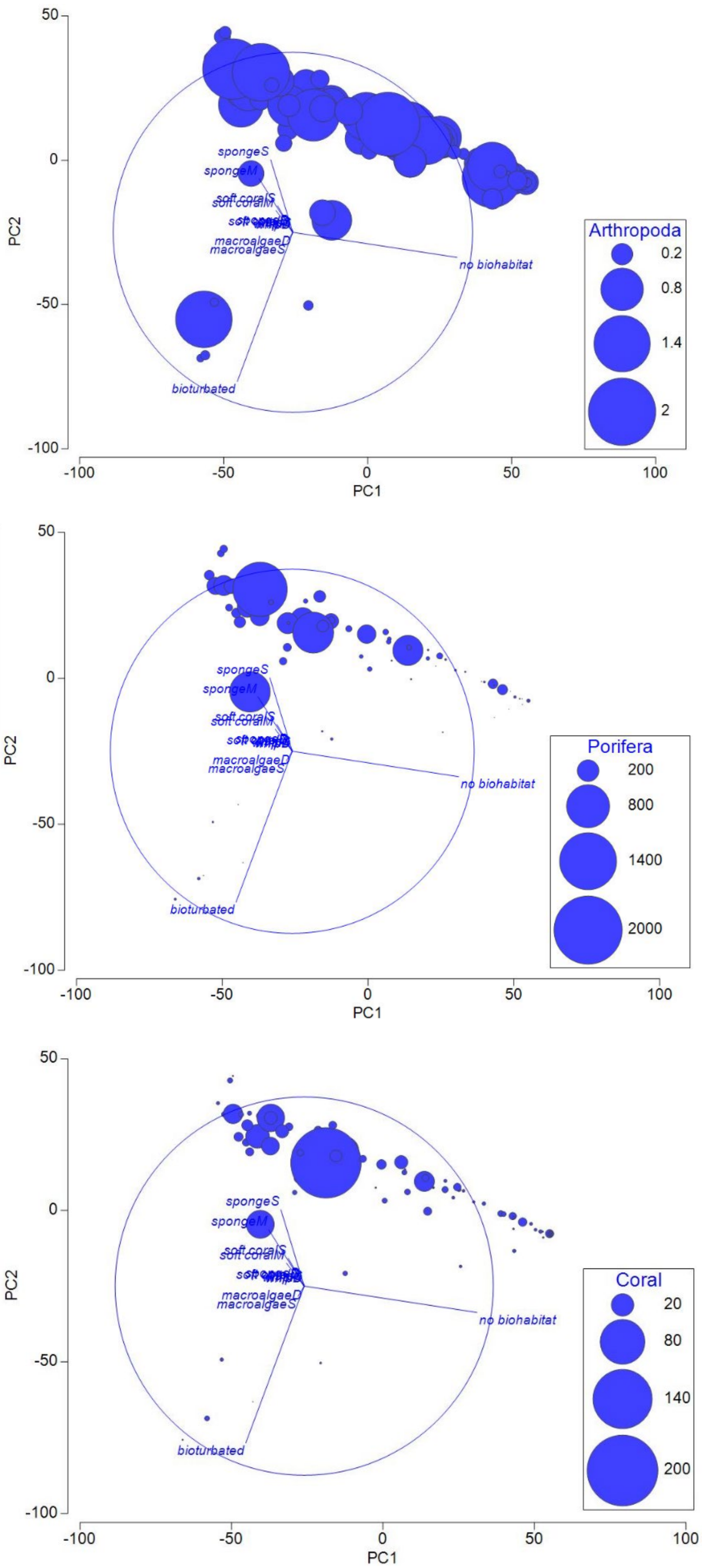


Figure 14. Habitat association of groups in each taxonomic group. Biomass (g wet weight m²) shown. Size of bubble is proportionate to biomass occurring in habitat.

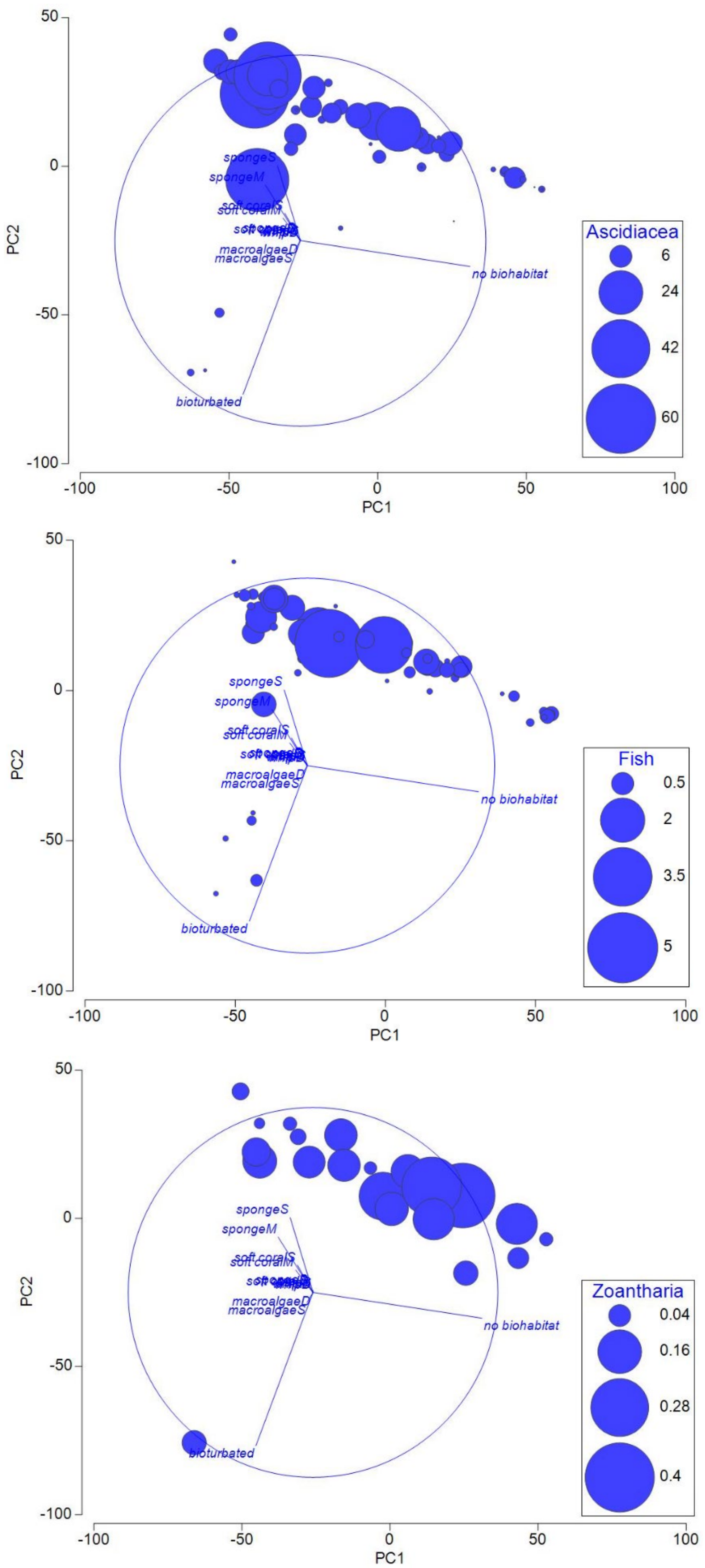


Figure 14 (continued). Habitat association of groups in each taxonomic group. Biomass (g wet weight m^2) shown. Size of is bubble proportionate to biomass occurring in habitat.

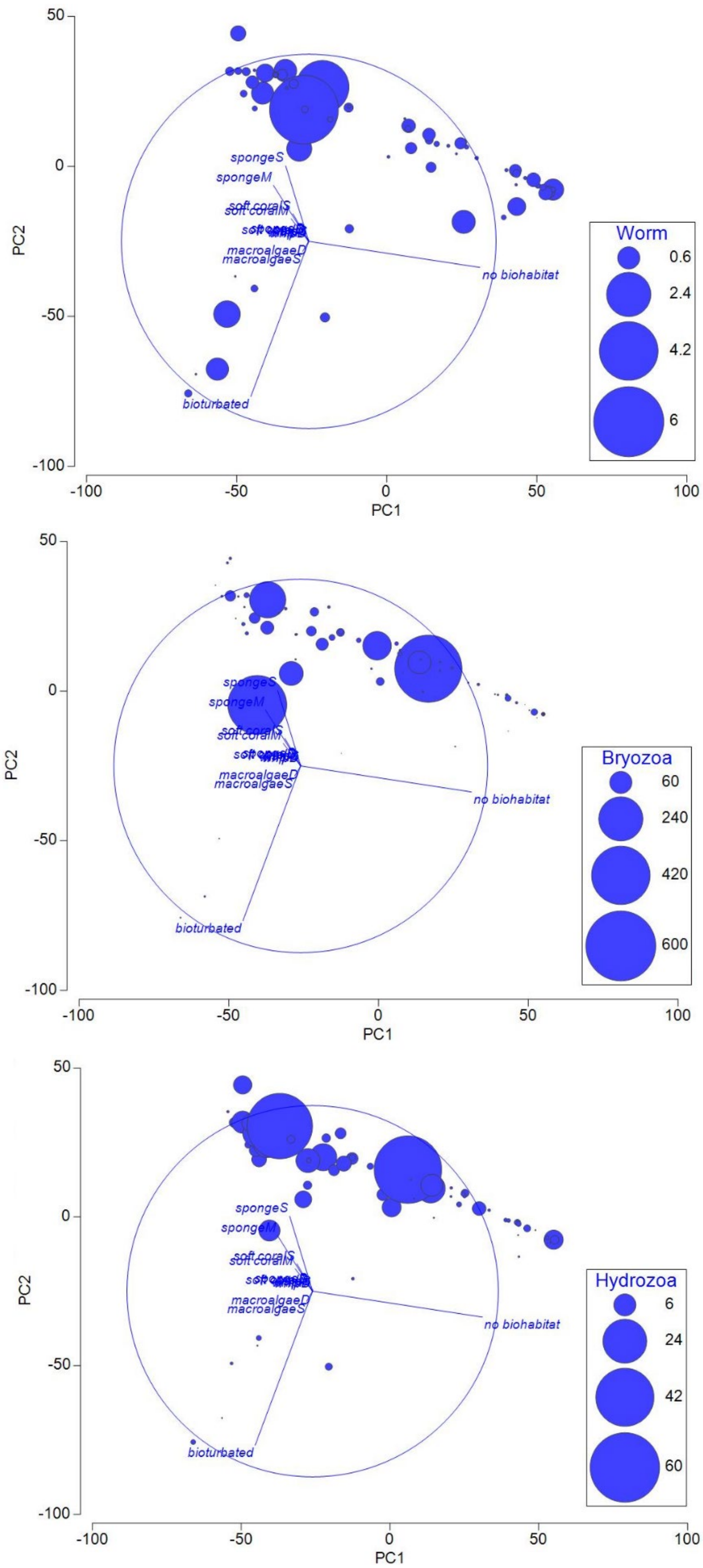


Figure 14 (continued). Habitat association of groups in each taxonomic group. Biomass (g wet weight m^2) shown. Size of bubble is proportionate to biomass occurring in habitat.

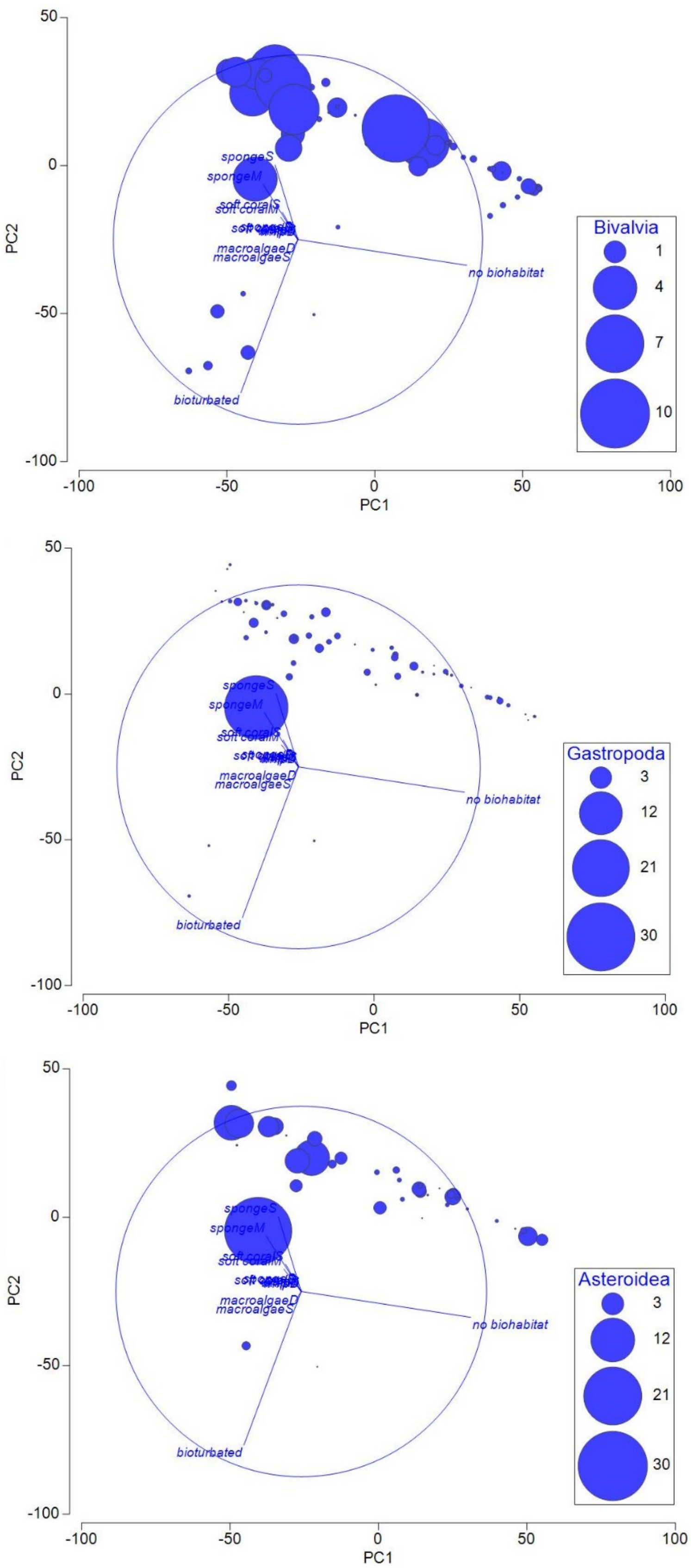


Figure 14 (continued). Habitat association of groups in each taxonomic group. Biomass (g wet weight m²) shown. Size of bubbleis proportionate to biomass occurring in habitat.

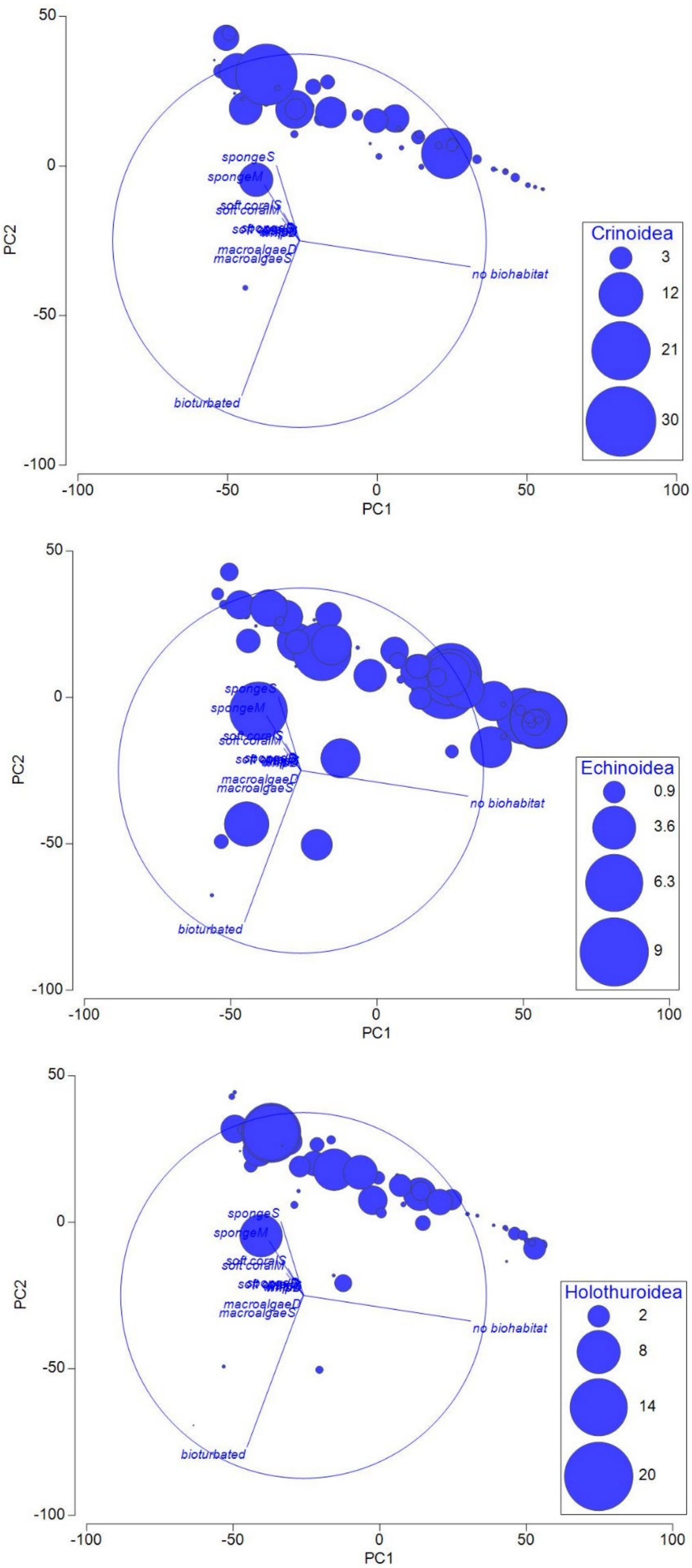


Figure 14 (continued). Habitat association of groups in each taxonomic group. Biomass (g wet weight m2) shown. Size of bubble is proportionate to biomass occurring in habitat.

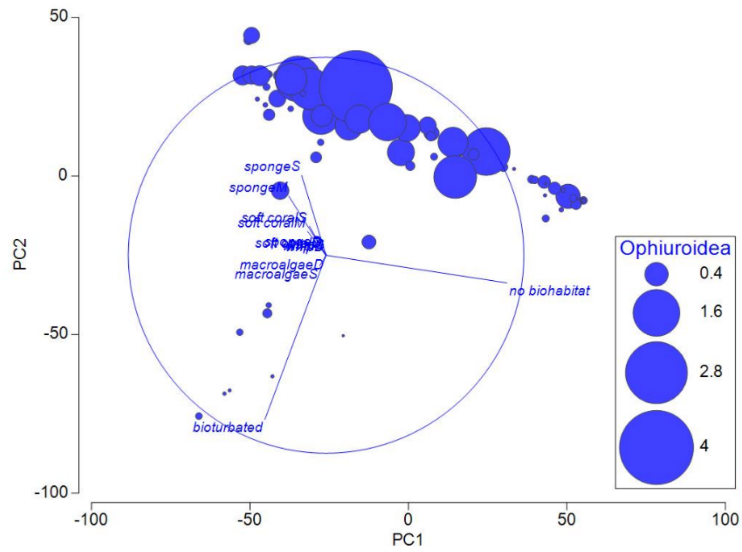


Figure 14 (continued). Habitat association of groups in each taxonomic group. Biomass (g wet weight m²) shown. Size of bubble proportionate to biomass occurring in habitat.

3 References

Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. Austral Ecology 26(1), 32-46.

Anderson, M.J., Ter Braak, C.J.F. (2003). Permutation tests for multi-factorial analysis of variance. Journal of Statistical Computation and Simlulation, 73(2), 85-113.

Anderson, M.J. (2006). Distance-based tests for homogeneity of multivariate dispersions. Biometrics, 62, 245–253.

Anderson, M.J., Walsh, D.C.I. (2013). PERMANOVA, ANOSIM, and the Mentel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecological Monographs, 83(4), 557-574.

Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18, 117-143.

Winfree, R., Fox, J. W., Williams, N. M., Reilly, J. R. & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real world ecosystem service. Ecol. Letts. 18, 626–635