Spatial variation in functional group diversity in a sandflat benthic community: implications for ecosystem resilience

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ABSTRACT

The resilience of macrobenthic communities to environmental stress depends upon the vulnerability, adaptability and connectivity of species. Recent studies suggest that the function(s) species perform may be more influential in driving community response to change than the more traditional measures of abundance and occurrence. Species that perform similar functions within a community theoretically give rise to redundancy, an important attribute of resilience. This thesis assesses the potential for functional redundancy in coastal macrobenthic communities by comparing the degree of sharing of specific functional traits, patterns of abundance and spatial distribution to provide insight into the potential for resilience. The research is focused on the functional diversity of a species rich macrobenthic community from a large intertidal area in the Kaipara Harbour, New Zealand. 400 macrofaunal and 360 sediment cores were collected using a newly developed hierarchical sampling grid covering an area of 300,000 m^2. This resulted in a data set consisting of 115 taxa and 23,682 individuals and 360 observations of sediment grain size and chlorophyll *a*. Linking species attributes such as body type, size, feeding mode, and living depth, produced 26 species functional groups that characterised important functional attributes of the macrobenthic community. These attributes relate to ecosystem functions associated with sediment biogeochemistry, stability and resilience to disturbance. Redundancy was assessed within these functional groups (ranging from 1-13 species per functional group) considering both occurrence and abundance in their spatial distribution. Various levels of redundancy were identified for different functional groups, for example, functional groups characterised by small deposit-feeding polychaetes encompassed high redundancy, whilst functional groups consisting of large suspension-feeding, highly mobile bivalves maintained low redundancy. Nevertheless, the latter functional group does contribute considerably to abundance despite its low redundancy. The spatial patterns exhibited by different functional groups (identified by correlograms using Moran's *I*) were used to provide insights to connectivity and exposure of the functional group to localised disturbance. A range of spatial patterns were apparent, reflecting small-scale homogeneity to large-scale heterogeneity with spatial arrangements including gradients and distinct patches. Density maps showed that some functional groups, such as tube worms and large mobile suspension-feeding bivalves, showed strong and opposing spatial distributions, separated by clear boundaries. Canonical correspondence analyses indicated that the measured environmental variables were not important drivers of the spatial distribution of functional groups. Thus, either biological interactions between functional groups are the driving force of spatial diversity or this sampling strategy failed to measure relevant environmental parameters. These findings emphasise a role for spatial variation in functional diversity and species redundancy in structuring community resilience. Understanding the functional roles of species, the diversity of these functions and associated biological interactions, is essential for evaluating biodiversity and resilience.

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No more saying “I can’t, I have to write my Thesis”!!!!

Bring on the Golf!!!

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1.0 INTRODUCTION

Biodiversity is defined as the variety of life on earth; it encompasses many scales of variation in biological organisation (from genes to ecosystems) which are important for ecosystem functioning and productivity (Naeem et al. 1994, Tilman et al. 1996, Bengtsson 1998). Biodiversity is a complex multidimensional concept (Purvis and Hector 2000) involving a multitude of processes and links between species, the functions they perform, and the environment. Biodiversity enables efficient use of ecosystem resources due to the diversity of functions engaged in utilising and recycling resources performed by a range of species occupying different niches (Tilman 1999). Therefore, conserving biodiversity is fundamental to maintaining the integrity of system functioning. Despite conservation efforts, biodiversity is continuing to decline across a wide range of ecosystems (Bengtsson et al. 1997). Important drivers of biodiversity loss are the increasing intensity of disturbance, such as destruction of habitats, overexploitation of species, climate change, and species invasion (see Mouillot et al. 2013). Accordingly, as information on ecological response to change is important in guiding future conservation and management there is a pressing need to understand how ecological communities are structured in ways that help them cope with disturbance.

The majority of research focused on biodiversity has been centred on terrestrial ecosystems with little effort directed at soft-sediment marine environments, despite their spatial coverage of the planet. Of particular importance are intertidal estuarine ecosystems, because they are one of the most productive systems in the world (Nixon et al. 1986, Beck et al. 2001). These intertidal estuarine ecosystems also provide essential economic, cultural, social and ecological goods and services (Levin et al. 2001). Due to the nature and location of estuaries, acting as the point of contact between the land and sea, they are threatened by a range of anthropogenic stressors (including pollution, sediment and nutrient addition from land run-off, introduced species and fisheries). Variation in type, scale and extent of these stressors, along with the potential for interactions between them, means the subsequent impacts on estuarine ecology are often difficult to predict and manage. These stressors are on-going and cause long-term environmental problems that can cause catastrophic changes in biodiversity and functioning of the benthic environments (Kennish 2002). This emphasises the importance of understanding how the attributes of these communities can influence their ability to persist and recover in the face of these stressors.

The functioning of all aquatic environments is dependent on the exchange of particles and solutes between the sediment and water (benthic-pelagic coupling) (Covich et al. 1999, Perissinotto et al. 2003, Fulweiler and Nixon 2009). The effectiveness of benthic-pelagic coupling directly impacts many ecosystem functions, e.g., organism’s dispersal and settlement, the availability of oxygen in the sediment, the recycling of organic matter and the subsequent release of nutrients back into the water column. The disruption of benthic-pelagic coupling can lead to major shifts in ecosystem functioning (Rodil et al. 2011), resulting in adverse effects on functioning and the productivity of the ecosystem. Organisms (both invertebrate and microbial) play important roles influencing the rates and processes involved in benthic-pelagic coupling (e.g. Norkko et al. 2001). Therefore, understanding these organisms’ functional roles fundamental to understanding ecosystem function and the contribution of specific species or communities. In the absence of direct measurement of ecosystem function ecologists have moved to species attributes or traits to describe important, morphological, mobility or life-style characteristics. Traits describe distinguishing characteristic or quality to act as surrogates for direct function measurements.

Traditionally, emphasis regarding the relationship between biodiversity and community function has been centred on the roles that species individually play in regulating specific community processes (Wardle et al. 2000), using species richness and evenness to explain biodiversity (Hewitt et al. 2010). The shortfall in this richness-based approach is that it assumes that all species are potentially equal with respect to function, when in reality, due to the variety of traits, species hold very different roles in contributing to ecosystem function (Posey 1987, Walker 1992, Bengtsson 1998, Luck et al. 2009). A good example of this issue is associated with animal size; size matters in the delivery of many functions but the effects of large species that can create habitat, pump large volumes of water or move a lot of sediment (see Thrush et al. 2006b, Norkko et al. 2013) are lost when the specifics of traits are ignored. Abundance, i.e., the number of individuals performing a function, is also important in linking community structure to the functional performance of the community. This too is ignored or down weighted by simple univariate community indices, such as evenness and species richness. When stressors impact species with specific traits, severely reducing their abundance, trait differences between species can drive interspecific differences in response to disturbances (Haddad et al. 2008). Accordingly, species diversity alone cannot reliably distinguish between this trait-driven, and random (where on average all species are effected equally) processes in shaping the response of communities to stressors. A trait-based approach can therefore better quantify, and therefore predict, the impacts of stressors on ecological communities (Mouillot et al. 2013).

In the marine environment, processes such as nutrient fluxes across the sediment–water interface, bioturbation and irrigation, habitat creation, secondary production, sediment stability/transport and carbon sequestration are fundamental to ecosystem function (Hewitt et al., 2008). For example, the movement of sediment from the surface to depth by deposit-feeders living deep in the sediment create nutrient-rich pockets in otherwise anoxic conditions, which in turn affects nutrient recycling and in turn ecosystem productivity. Thus, defining which traits are key contributors to maintaining system function is critical in assessing the role of biodiversity in affecting ecosystem function. The biological traits used as surrogates for the functional attributes of species reflect life history, morphology and behavioural aspects that may directly mediate energy and material fluxes or alter abiotic conditions that govern ecosystem processes. For example, in marine soft sediments, body size, feeding mode and the influence on sediment characteristics and hydrodynamics (Dıaz et al. 2003, Hewitt et al. 2008a, McGill 2013). Some species, due to their specific traits, abundance, and biomass will play a stronger role than others in delivering a specific function (Walker 1992).

Trait composition has been said to be more stable than taxonomic composition over extensive biogeographic gradients in both freshwater (Charvet et al. 2000) and marine systems (Bremner et al. 2003). Trait analysis is growing in popularity for empirical studies, with theoretical application to macro-ecology (Blackburn 2004, Webb et al. 2009, Tyler et al. 2012), and more practical application in assessing anthropogenic impacts on functioning, and evaluating conservation and management options (De Juan et al. 2007, Frid et al. 2008). In marine and freshwater studies this approach is commonly referred to as *biological trait analysis* (Townsend and Hildrew 1994, Usseglio-Polatera et al. 2000, Bremner et al. 2003) where attributes are divided into sub-categories or traits that species are assigned (see Törnroos and Bonsdorff 2012). For example, the attribute ‘mobility’ can be divided into four traits: attached, sessile, semi-mobile and mobile. Species can then be grouped based on a shared combination of traits, forming what is called a *functional group*. For example, a mobile organism that is found on the sediment surface of an intertidal sandflat is a predator and has a calcareous shell, e.g. the gastropod *Cominella glandiformis*.

As many species can occupy the same functional group defined by different traits, determining the redundancy within a functional group has important implications for resilience. Redundancy here is based on the number of species within each functional group employing similar functions. Resilience here is the effectiveness of a species, community or functional group to cope with changes relating to disturbances or stressors while maintaining a reasonable standard of productivity. The more species which contribute to a given function increases the resilience of that functional group, i.e. a larger range of species with differing levels of susceptibility to various stressors. A functional group with low functional redundancy likely exhibits lower resilience and subsequent greater susceptibility to stressors (Walker 1992, Naeem 1998, Rosenfeld 2002, Ellingsen et al. 2007).

Spatial patterns in the distribution of species may exist due to environmental conditions (i.e. sediment grain size, tidal elevation, etc.), biological interactions (i.e. competing for a common food resource, differences in habitat structures; for example, sediment stabilisers versus sediment bioturbators) (Fager 1964, Rhoads and Young 1970, Posey 1987, Thrush et al. 1994) or the interactions of the two. To develop and properly utilize the trait concept for understanding functional community dynamics on regional scales, quantifying not only the number of traits but also within-trait richness of species and variability as well as the functional role of common and rare species is urgent (Ellingsen et al. 2007, Hewitt et al. 2008b). Understanding the principal driver of spatial diversity in functionality should provide a useful framework for assessing resilience, contributions to ecosystem services, functional interdependencies and thus ultimately inform wise management.

Marine soft-sediment ecosystems are ideal for investigating the relationships between biodiversity, ecosystem function and redundancy because: they are diverse, involve a multitude of functions that play important roles in the system, these functions can be related to measurable species traits, and they are practical to sample and collect good data linking function to spatial structure in the community.

One of the major challenges in understanding the role of any community in contributing to specific functions is spatial heterogeneity (Legendre and Fortin 1989, Thrush 1991). Functional roles may fluctuate across the natural heterogeneous environments (Walker et al. 1999, Wellnitz and Poff 2001, Rosenfeld 2002). Natural spatial variation in the distribution of species and environmental conditions could result in functional hot spots due to high density or poor performance from low density areas. Species with complementary traits in terms of delivering a specific function may be isolated by variation in spatial patterns. Statistically, patterns can be defined and variation across scales quantified by spatial autocorrelation, often expressed as Moran's *I* or semi-variance (e.g. Sokal and Oden 1978, Legendre and Fortin 1989). Furthermore, autocorrelation provides additional statistical validity on patterns and enhances ecological inference (Thrush 1991, Kraan et al. 2010, Kraan et al. 2013).

Here, I apply the functional groups approach of Walker (1992) to group species into a similar functional type based on single or multiple traits across a diverse group of sandflat dwelling organisms collected in an intensive survey in Kaipara Harbour. I develop a system of characterising the macrobenthic community based on six attribute combinations each with between 3 and 6 traits, resulting in 26 functional groups representing the 115 species in the data set. By examining the potential for species to sit in the same functional group and thus perform the same process I determined the degree of redundancy within functional groups. To develop this approach I build on Species Abundance Distribution diagrams and Species Observation Distribution diagrams (SADs and SODs (Gray et al. 2006, McGill et al. 2007, McGill 2013)) to develop their functional group equivalents (GADs and GODs). This large-scale empirical study is the first to include spatial analyses of functional diversity for marine benthic systems, which are the most productive habitats in the world. Functional groups with little or no redundancy warrant priority of conservation effort as the loss of function is likely to have detrimental impacts on the system (Walker 1992, Lawton and Brown 1993, Naeem 1998, Rosenfeld 2002, Gonzalez and Loreau 2009).

The specific objectives of this study were to:

1. Identify the functional traits present within a benthic macro invertebrate sandflat community. Then group species based on these functional traits.
2. Determine differences in community abundance and occurrence distributions, before and after grouping of species by functional traits to assess redundancy and resilience across functions.

3. Quantify the spatial distribution of functional groups and the role of key environmental drivers and biotic interactions in explaining these patterns.

2.0 METHODS

2.1 STUDY AREA

Kaipara Harbour (36° 39’ S, 174° 29’ E) is the largest harbour in New Zealand (947 km^2). It is a tidally dominated inlet (43% intertidal sand flats) that is situated north west of Auckland (Heath 1975) (Figure 1). The sample site covered an area 1000 m down shore and 300 m along shore (300,000 m^2) of an extensive area of homogeneous intertidal sand flat at Tapora Bank. The entire area sampled was a similar elevation and the sediment was well-compacted medium sand largely covered by ripples (0-2 cm in height). Additionally, patches of shell hash and expanses of various densities of seagrass (*Zostera muelleri.*) were distributed throughout the site (Figure 2).

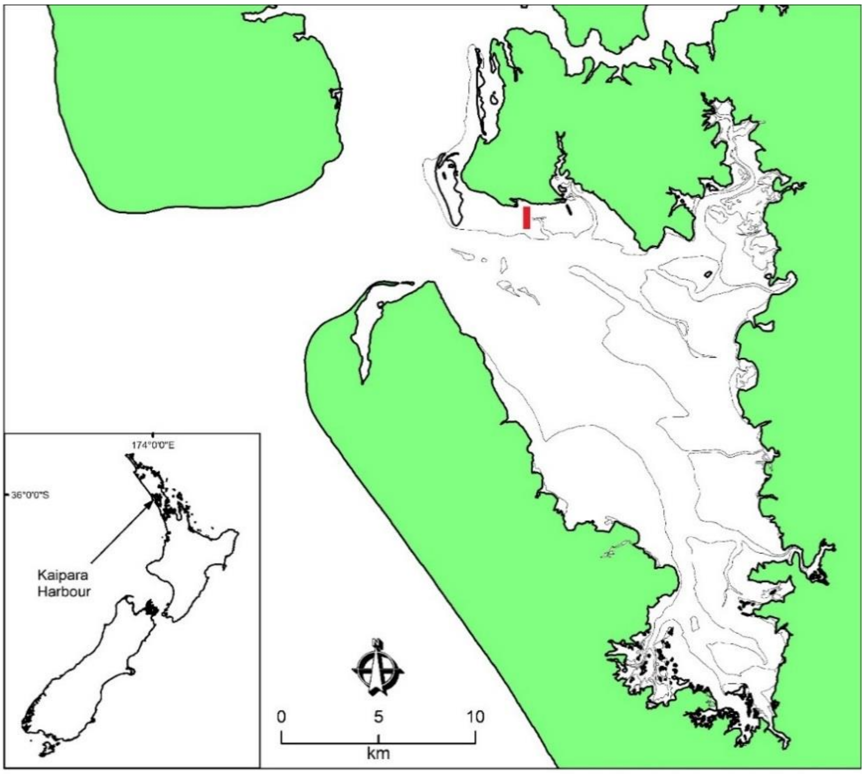

Figure 1. Location of sampling area (red rectangle) on Tapora Bank in Kaipara Harbour.

Figure 2. Photograph of the exposed site area at low tide, facing south. Surface ripples and patches of *Zostera muelleri* are evident.

2.2 DISTRIBUTION AND ABUNDANCE DATA

2.2.1 COMMUNITY DATA

Samples were collected in April 2012 at predetermined points within an extensive hierarchical sampling grid (Figure 3). This design allowed us to sample at a wide range of inter-sample distances with a reasonable balance in the number of samples for different distance classes, without excessive sampling effort. Spatial analyses at scales from 50 cm to 1044 m, was possible from the four 1 km long transects, set 100 m apart. The grid covered the intertidal area from high-tide to the low-water mark to ensure all environmental variation was included, as well as the complete range of macrobenthic species present. The sample points were distributed at varying distances along each transect. Note that on sampling locations marked as blue squares, three neighbouring cores were sampled to allow determination of variation at the finest scale. Positions were located using handheld GPS (GARMIN GPSMAP 78sc with 2 m accuracy) and a 100 m tape measure. At each point a macrofaunal core (13 cm diameter, 20 cm deep) was collected and sieved on site (500 μm mesh) and stored in 70% isopropyl alcohol (diluted with seawater). In the laboratory, samples were stained with 2% Rose Bengal, sorted and identified to the lowest practical taxonomic resolution (species in most cases).

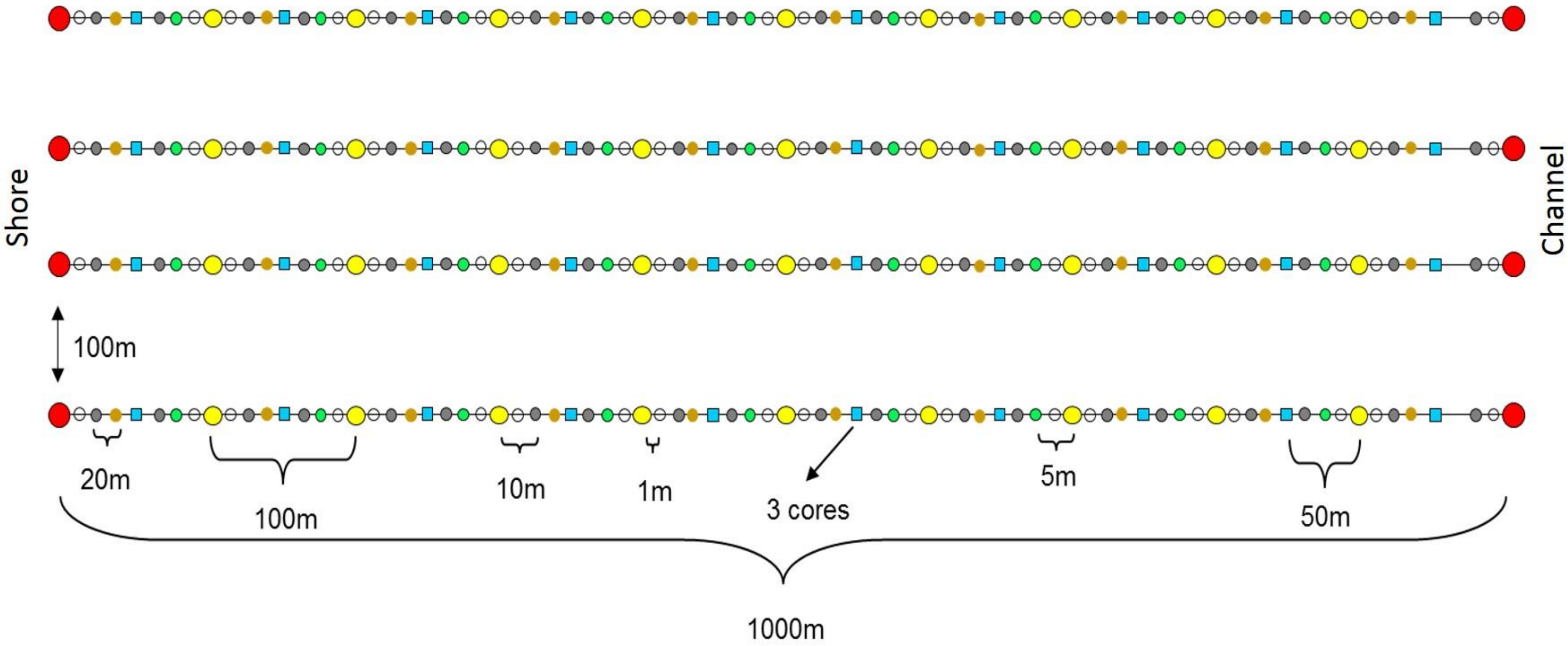

Figure 3. Hierarchical gridded sample design for benthic sampling in Kaipara Harbour. The 4 transects are each 1000 m long and are spaced 100 m apart. Points along transects are spatially varied to fit distance classes of 0.5 m (3 cores at each blue square), 1 m (white), 5 m (grey), 10 m (green), 30 m (orange), 50 m (blue square), 100 m (yellow), 500 m and 1000 m (red).

2.2.2 ENVIRONMENTAL VARIABLES

To determine surface structure of the sediment at each point, a 0.25 m^2 quadrat of the sediment surface was photographed prior to any disturbances caused by sampling. Percent coverage of seagrass (*Zostera muelleri*), shell hash and bare sand within the quadrat photo was estimated based on 75 random points using Corel Point Count with Excel extensions (CPCe) (Kohler and Gill 2006). Within the quadrat, three cores of surface sediments (2 cm wide, 2 cm deep) were amalgamated to obtain an averaged measure of sediment particle size and chlorophyll *a* (Chl-*a*). These sediment samples remained in the dark and on ice until arrival at the laboratory where they were freeze-dried for to analysis. Sediment particle size (median grain size [µm] and % fractions [silt < 63 µm, very fine 63-125 µm, fine 125-250 µm, medium 250-500 µm, coarse > 500 µm]) was measured using a MALVERN LAZERSIZER (Singer et al. 1988). Sediment for Chl-*a* analysis was freeze-dried and analysed using a Turner's 110 flurometer (Arar and Collins 1997).

2.3 TRAIT INDEX: DEFINITION OF TRAITS

Each species was assigned to at least one of the traits for each of the five functional attributes reflecting life history, morphology and behavioural aspects that act to maintain stability in soft-sediment intertidal ecosystems (Table 1). Functional groups were derived by combining species sharing the same trait combinations. Information for the groupings was derived from a NIWA (National Institute of Water and Atmospheric Research, NZ) functional traits based index (TBI) (Lohrer and Rodil 2011), taxonomic information (including, MarLIN 2013, WoRMS Editorial Board 2013), and taxonomic and field observations. As some species possessed multiple traits for a given attribute (for example, *Macomona liliana* is a known deposit feeder but is capable of suspension feeding (Olafsson 1986)), fuzzy-coding was used (Cheven et al. 1994). Thus, a species may exist in more than one functional group.

Table 1. Functional attributes, explanatory traits and corresponding letter codes used for the creation of functional groups. For each functional attribute a number of traits are assigned to a letter, from which species were grouped based on the similarity of their resultant individual trait code.

Functional Attributes	Functional Traits	Code
Body hardness	Calcified (fully calcified shell, e.g., molluscs)	B
	Soft-bodied	C
	Rigid (chitonous exoskeleton or endoskeleton)	D
Feeding behaviour	Suspension feeder	E
	Deposit feeder	F
	Predator/Scavenger	G
	Grazer	H
Living position	Attached	I
	Above surface	J
	Top 2 cm	K
	Below surface (movement between defined layers)	L
	Deep	M
Movement ability	Freely mobile on or in sediment	N
	Limited movement, usually in sediment	O
	Sedentary/movement in a fixed tube	P
Living structure created	Tube	Q
	Permanent burrow	R
	Large burrow (larger crustaceans, e.g. shrimp and crabs)	S
	None	T
Body size Longest dimension (based on adult size sourced from literature)	Small (<5 mm)	U
	Medium (5 - 20 mm)	V
	Large (>20 mm)	W

As there was a number of traits for each attribute a large number of trait combinations, forming potential functional groups, were possible and greatly exceeded the number of species recorded. However the majority of these combinations were biologically implausible. Such an impossible combination is, for example, CHMPSU, a small soft-bodied grazer that lives deep in the sediment column, has a sedentary lifestyle and builds large permanent burrows. By using relevant literature and comparable studies (e.g. Törnroos and Bonsdorff 2012) I was able to assign all 115 taxa (referred to as ‘species’ throughout) to 26 functional groups with species richness within a functional group ranging from 1-13 (Table 2).

Table 2. Trait code from Table 1 and description of traits used to generate the 26 functional groups. Example species (for the highest abundances) are given for each functional group (photographs are given in Appendix 1).

Group number	Traits Code from Table 1	Description of traits code	Example species (most abundant)
1	BEI	Calcified, Suspension feeding, Attached	*Austrominius modestus* *Crassotrea gigas*
2	BEKN	Calcified, Suspension feeding, Top 2 cm, Freely mobile	*Paphies australis* *Austrovenus stutchburyi*
3	BEKO	Calcified, Suspension feeding, Top 2 cm, Limited mobility	*Soletellina siliquens* *Arthritica bifurca*
4	BEKP	Calcified, Suspension feeding, Top 2 cm, Sedentary	*Musculista senhousia*
5	BF/G/HJN	Calcified, Deposit/Pred.Scav/Grazer, Above surface, Freely mobile	*Zeacumantus lutulentus* *Cominella glandiformis*
6	BFKO	Calcified, Deposit feeding, Top 2 cm, Limited mobility	*Linucula hartvigiana* *Lasaea parengaensis*
7	BF/GKN	Calcified, Deposit feeding, Predator/Scavenger, Top 2 cm, Freely mobile	*Eatoniella* sp. *Amalda australis*
8	BFMOTW	Calcified, Deposit feeding, Deep, Limited mobility, No habitat structure, Large	*Macomona liliana* *Mactra ovata*
9	CEI	Soft-bodied, Suspension feeding, Attached	*Anthopleura aureoradiata*
10	CEQ	Soft-bodied, Suspension feeding, Tube structure	*Euchone* sp. *Boccardia syrtis*
11	CFKN	Soft-bodied, Deposit feeding, Top 2 cm, Freely mobile	*Travisia olens*
12	CFLN	Soft-bodied, Deposit feeding, Below surface, Freely mobile	*Orbinia papillosa* *Scolecolepides benhami*
13	CFLO	Soft-bodied, Deposit feeding, Below surface, Limited mobility	*Aonides trifida* *Heteromastus filiformis*
14	CFM	Soft-bodied, Deposit feeding, Deep	*Notomastus* sp. *Barantolla lepte*
15	CFQ	Soft-bodied, Below surface, Tube structure	*Owenia petersenae* *Macroclymenella stewartensis*

Table 2. Continued

Group number	**Code from Table 1**	**Description of traits code**	**Example species (most abundant)**
16	CGKN	Soft-bodied, Predator/Scavenger, Top 2 cm, Freely mobile	*Dorvillea* sp. *Pholoe* sp.
17	CGKO	Soft-bodied, Predator/Scavenger, Top 2 cm, Limited mobility	*Trypanosyllis sp.* Oligochaeta
18	CGL/MNT	Soft-bodied, Predator/Scavenger, Below surface+Deep, Freely mobile, No habitat structure	Nemertean *Aglaophamus macroura* *Nereidae* spp.
19	CGLO	Soft-bodied, Predator/Scavenger, Below surface, Limited mobility	*Hesionid* spp. Oligochaeta
20	CJ/K/L/MPQ	Soft-bodied, Above surface, Top 2 cm, Below surface, Deep, Sedentary, Tube structure	*Owenia petersenae* *Phoronis* sp.
21	DEK	Rigid, Suspension feeding, Top 2 cm	*Corophium* spp. *Paracorophium* spp.
22	DF+GKNT	Rigid, Deposit feeding, Predator/Scavenger, Top 2 cm, Freely mobile, No habitat structure	*Paracalliope novizealandiae* *Waitangi brevirostris*
23	DJN	Rigid, Above surface, Freely mobile	*Colurostylis lemurum* *Halicarcinus whitei*
24	DJNW	Rigid, Above surface, Freely mobile, Large	*Ophiuroida* sp. *Patiriella* sp.
25	DGI	Rigid, Predator/Scavenger, Attached	*Pinnotheres novaezelandiae*
26	DGLNS	Rigid, Predator/Scavenger, Below surface, Freely mobile, Large burrow former	*Hemiplax hirtipes* *Alpheus* sp. *Squilla armata*

2.4 REDUNDANCY AND RESILIENCE: FUNCTIONAL GROUP RESILIENCE INDEX (GRI)

Like most diversity studies, a Shannon-Wiener diversity analysis was conducted during preliminary data assessment. However, it did not take into account all variables (abundance, occurrence and functional groupings) and the successive distribution of functional groups. To assess the necessary variables I created the functional Group Resilience Index (GRI) for each functional group using abundance, occurrence and functional group richness (redundancy within a functional group), as a method to evaluate the resilience. Functional groups with a high number of species coupled with high abundance or occurrence are considered to be robust and therefore have a high GRI rank (denoting high resilience). Whereas, functional groups with low species richness and low abundance and occurrence are considered to be at high risk to environmental change due to fact that species with potentially different tolerance to stress are not delivering the specific function expressed by the functional group. Total functional group richness, abundance and occurrence (i.e. from the 400 cores) was categorised as high/medium/low. Abundance was based on the average number of individuals of a functional group where high was >2 ind. core^{-1}; medium 0.25-2 ind. core^{-1} and low <0.25 ind. core^{-1}. How many times an individual from any species representing the functional group was found in the 400 cores, (i.e., occurrence) was classified as high 50%, medium 10-50% or low <10% of the cores. Functional group richness, the number of species per functional group was classified as high > 6, medium 3-6 or low, < 2.

2.5 STATISTICAL ANALYSIS

Standard community structure analyses (e.g. species accumulation curves) were conducted using both species and functional group data (Table 3).

To verify that both the community and the functional groups were sampled adequately, a species accumulation curve (SAC) and a functional group accumulation curve (GAC) were generated using PRIMER (Clarke and Warwick 2001) with PERMANOVA+ (Anderson et al. 2008a, b). I chose to construct the SAC using Ugland, Gray and Ellingsen (UGE) distribution (Ugland et al. 2003) as it recognises that heterogeneity in species richness can occur within subareas and that this may have important consequences for estimating species richness (see Colwell and Coddington 1994, Mao and Colwell 2005, Thrush et al. 2006a). Species distribution data were analysed according to (Gray 1981, Gray et al. 2006). Species were arranged by relative abundance (% of total number of species identified) from highest to lowest, and plotted. This reveals the distribution of common and rare species within the community. The same technique was used to show the distribution of relative abundance of functional groups (group abundance distribution: GAD). To indicate occurrence (presence/absence), the process was repeated for species occurrence distribution (SOD) and functional group occurrence distribution (GOD) where rankings were assigned based on occurrence (presence) out of 400 cores.

Table 3. Community structure analyses conducted for both species and functional group data

Analysis	**Plot**	**Purpose**
Species accumulation curve (SAC)	Species accumulation relative to number of cores required to encompass all species identified.	Determines if species richness was adequately sampled.
Functional group accumulation curve (GAC)	Functional group accumulation relative to number of cores required to encompass all functional groups identified.	Determines if functional group richness was adequately sampled.
Species abundance distribution (SAD)	Species ordered by relative abundance.	Community distribution and an indication of common and rare species.
Functional group abundance distribution (GAD)	Functional groups ordered by relative abundance of combined species of group.	Community distribution of functional groups.
Species occurrence distribution (SOD)	Species ordered by occurrence (presence/absence) out of 400 cores.	Occupancy of species throughout the site.
Functional Group occurrence distribution (GOD)	Functional groups ordered by occurrence (presence/absence) of any species within the group out of 400 cores.	Occupancy of functional groups throughout the site.

Point samples of functional group abundances were interpolated using Kriging (e.g. Kraan et al. 2010) in ArcGIS (ESRI 2009) and plotted to visualise spatial distribution. To allow clear comparisons between functional groups, the total group abundances were Log (x + 1) transformed. On the resulting contour plots graduated circles were added to represent the number of species per functional group at each sample point.

Moran's *I* coefficient was used to quantify the degree of spatial correlation between neighbouring units over different spatial scales (Dray et al. 2006, Dray et al. 2012, Legendre and Legendre 2013). Isotropic (all-directional) Moran's *I* correlograms were generated using Spatial Analysis in Macroecology (Rangel et al. 2010). To warrant similar power to detect significant differences at all distance classes, equal number of pairs were used (number of pairs ranged from 9812-10080) in each distance class. Consequently, 16 distance classes (Table 4) were created. Significance of individual Moran's *I* values were determined using 999 permutations at a significance level of 0.05.

Table 4. Distance classes determined by equal number of pairs for correlograms using Moran's *I* analysis.

Distance Class	Lower limit (m)	Upper limit (m)
1	0	100
2	100	140
3	140	181
4	181	210
5	210	242
6	242	279
7	279	311
8	311	342
9	342	378
10	378	420
11	420	469
12	469	529
13	529	594
14	594	668
15	668	767
16	767	1044

Canonical Correspondence Analysis (CCA) was used to assess the relationship between the 26 functional groups and environmental variables (grain size (% silt, fine, medium and coarse sand), Chl-*a*, organic content, and sediment coverage (% seagrass, shell hash and bare sand) using CANOCO 4.5 (ter Braak and Smilauer 2002). Raw abundances with down weighting of rare species were used as this gave the greatest amount of variation explained by the first 2 axes and a better spread between them.

3.0 RESULTS

3.1.1 SAMPLING EFFORT

The species accumulation curve, although it never completely levelled off, indicated that the community was sampled adequately after I had collected about 100 samples (Figure 4A). Sampling the range of functional groups was achieved with less sampling effort as seen in Figure 4B, which indicated we could characterise the functional groups within the system after collecting about 30 samples. Nevertheless collecting more samples is needed to characterise the redundancy in functional groups.

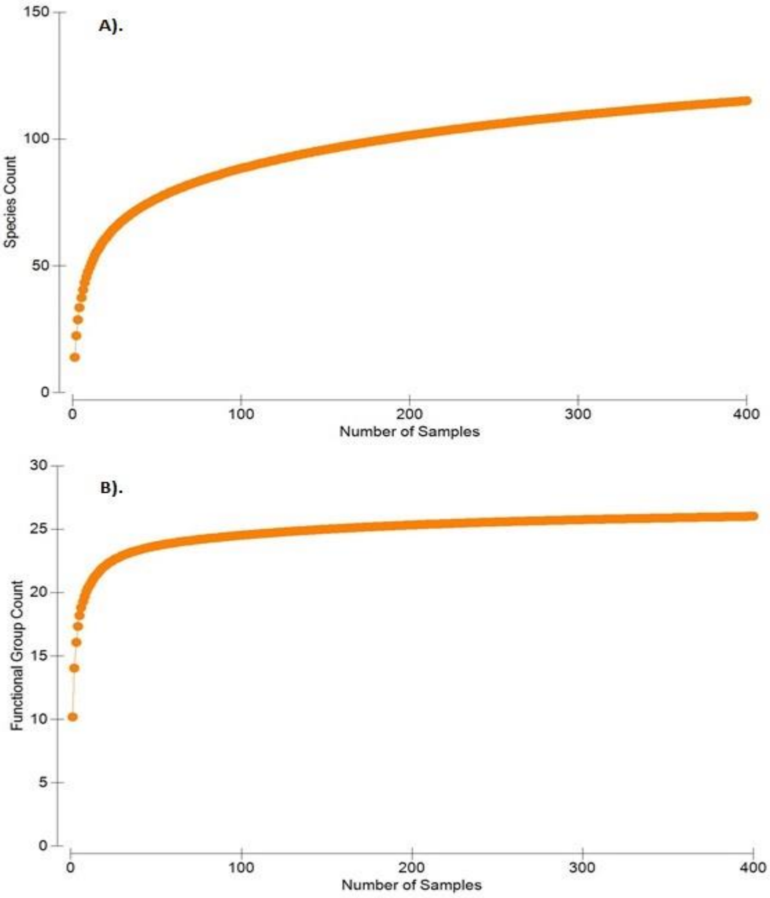

Figure 4. (A) Species accumulation curve (SAC) and (B) functional group accumulation curve (GAC) based on 400 samples.

3.2 COMMUNITY DISTRIBUTION

3.2.1 SPECIES DISTRIBUTIONS

115 species were identified at the site with 1 to 144 individuals of a single species occurring in one core. The total number of individuals sampled was 23,682. There is a high degree of skewedness in the species abundance distribution (SAD), characteristic of most communities, indicating that a few species are very common (e.g., *Aonides trifida*, *Macomona liliana*, and *Paphies australis* where total number of individuals = 3915, 1952 and 1542 individuals respectively), whilst most species are rare, (e.g., *Caprellidae, Squilla armata, Ophiuroida* and *Patiriella* where n = 1-2) (Figure 5 A). Species occurrence distribution (SOD) were not as strongly skewed as the SAD, suggesting that although a species may have a high abundance it does not imply that it will also have a high occurrence. For example *Austrominius modestus* (species rank = 7) has a total abundance of 778 individuals, but was only found in 68 out of 400 cores (17%) (Figure 5).

The 10 most abundant species made up 61 % of the community and 91 out of the 115 species contributed <1 % abundance. The 10 species with the highest occurrence throughout the site were found at 40-95 % of the cores and accounted for 57 % of the abundance (Table 5).

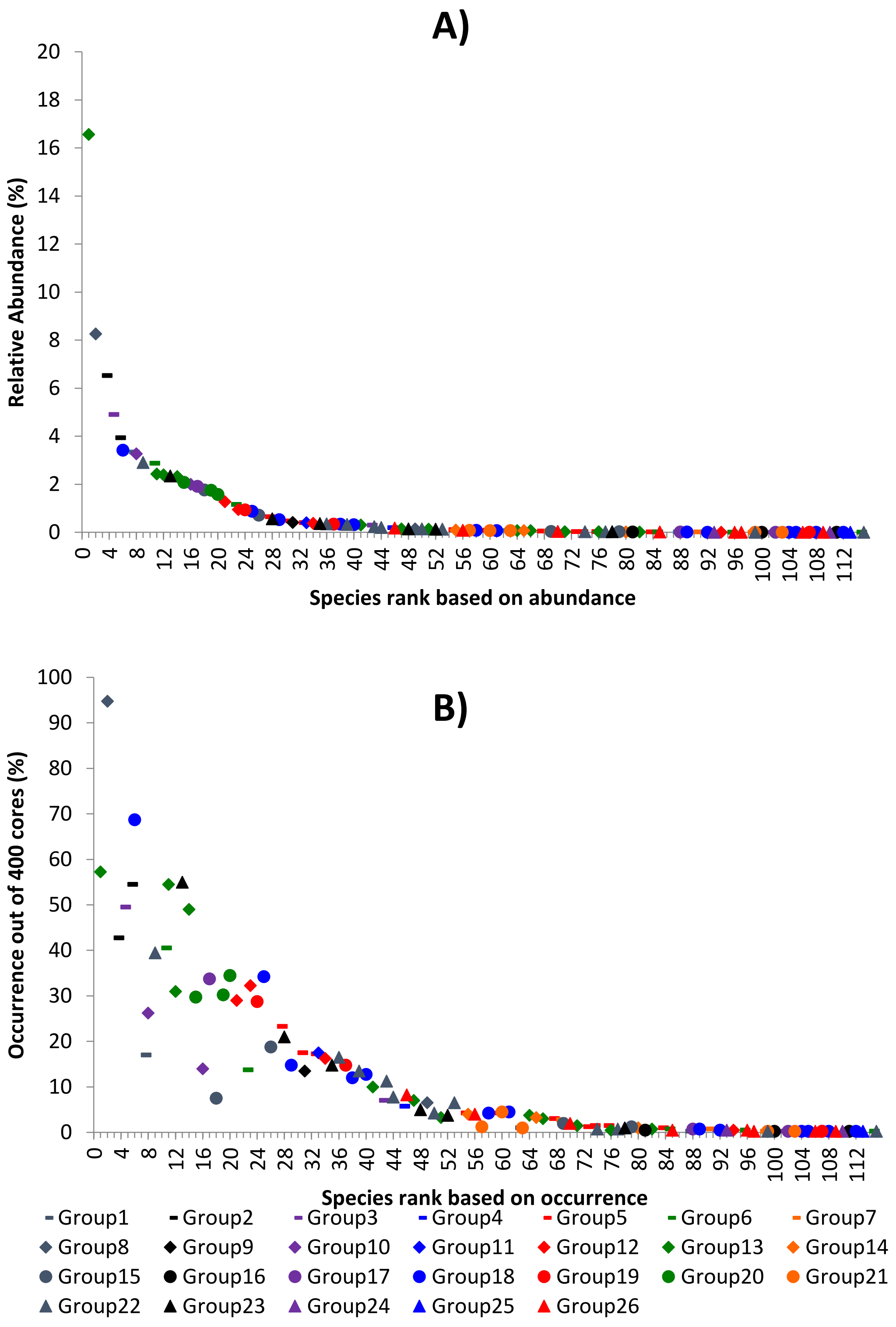

Figure 5. (A) Species abundance distributions (SAD) and (B) species occurrence distribution (SOD). Shape and colour-coding for the 26 functional groups indicates whether specific functional groups are rare or common and the level of redundancy

Table 5. Ten most abundant species and those with the highest occurrence. Percent relative abundance given in brackets.

Abundance	**Occurrence**	**% occurrence (400 cores)**
Aonides trifida (18%)	*Macomona liliana* (9%)	95
Macomona liliana (9%)	Nemertean (4%)	69
Paphies australis (7%)	*Aonides trifida* (18%)	57
Soletellina siliquens (5%)	*Colurostylis lemurum* (3%)	55
Austrovenus stutchburyi (4%)	*Austrovenus stutchburyi* (4%)	55
Nemertean (4%)	*Heteromastus filiformis* (3%)	55
Austrominius modestus (4%)	*Soletellina siliquens* (5%)	50
Euchone sp. (4%)	*Magelona dakini* (3%)	49
Paracalliope novizealandiae (3%)	*Paphies australis* (7%)	43
Linucula hartvigiana (3%)	*Linucula hartvigiana* (3%)	41

3.2.2 FUNCTIONAL GROUP DISTRIBUTIONS

Functional group abundance distributions (GAD) and group occurrence distributions (GOD) (Figure 6) yield similar distribution patterns to that observed in the SADs and SODs. However, as expected, community composition appears more evenly distributed when species are placed in functional groups due to the merging of the rare and common species (Figure 6). The four most common functional groups were small deposit-feeding polychaetes (27% abundance), large suspension-feeding bivalves (11% abundance), tube-forming polychaetes (9% abundance) and deep-living deposit-feeding bivalves (9% abundance) (see Table 6 for the top ten). Although grouping species resulted in a more even spread of abundance of function, 17 functional groups had <5% total abundance and 10 had abundances <1%. Only four species (the polychaete *Aonides trifida*, and the bivalves *Macomona liliana, Paphies australis* and *Soletellina siliquens*) had abundances greater than 5% of the total population (Figure 5). When grouping species by function (Figure 6), this 5% margin included eight functional groups (13, 2, 10, 8, 15, 18, 20 and 3) with a combined total of 43 species representing 74.7% of the total abundance. Comparing SOD and GODs, a similar pattern emerges whereby pre-grouping show 48 species were found in more than 50 cores, and after-grouping the margin included 19 functional groups (8, 13, 18, 23, 22, 2, 12, 3, 6, 15, 5, 20, 17, 10, 19, 1, 11, 26 and 9) with a total of 105 species that occur in 85% of the total cores collected.

Redundancy occurs where more than one species is performing the same function. Therefore overall redundancy is high with 85% of functional groups containing >1 species, 63% with 3 or more and 50% containing 4 or more species. The 3 functional groups with the highest redundancies are small deposit-feeding polychaetes (13 species), predator/scavenger polychaetes (13 species), isopoda/amphipoda top 2 cm (11 species) and surface-dwelling mobile gastropods (11 species). The large suspension-feeding mobile bivalves (functional group 2), deep-living deposit-feeding bivalves (functional group 8) and the large above surface mobile Asterozoa (functional group 24) had only 2 species per functional group. With such high abundance and occurrences (Table 6), this low redundancy of functional groups 2 and 8 is very concerning for resilience of the community. The mean number of species per functional group was 5 and median was 4 species per functional group. Four functional groups showed no redundancy, functional groups 9 (*Anthopleura aureoradiata*), 11 (*Travisia olens*), 4 (*Musculista senhousia*) and 25 (*Pinnotheres novaezelandiae*).

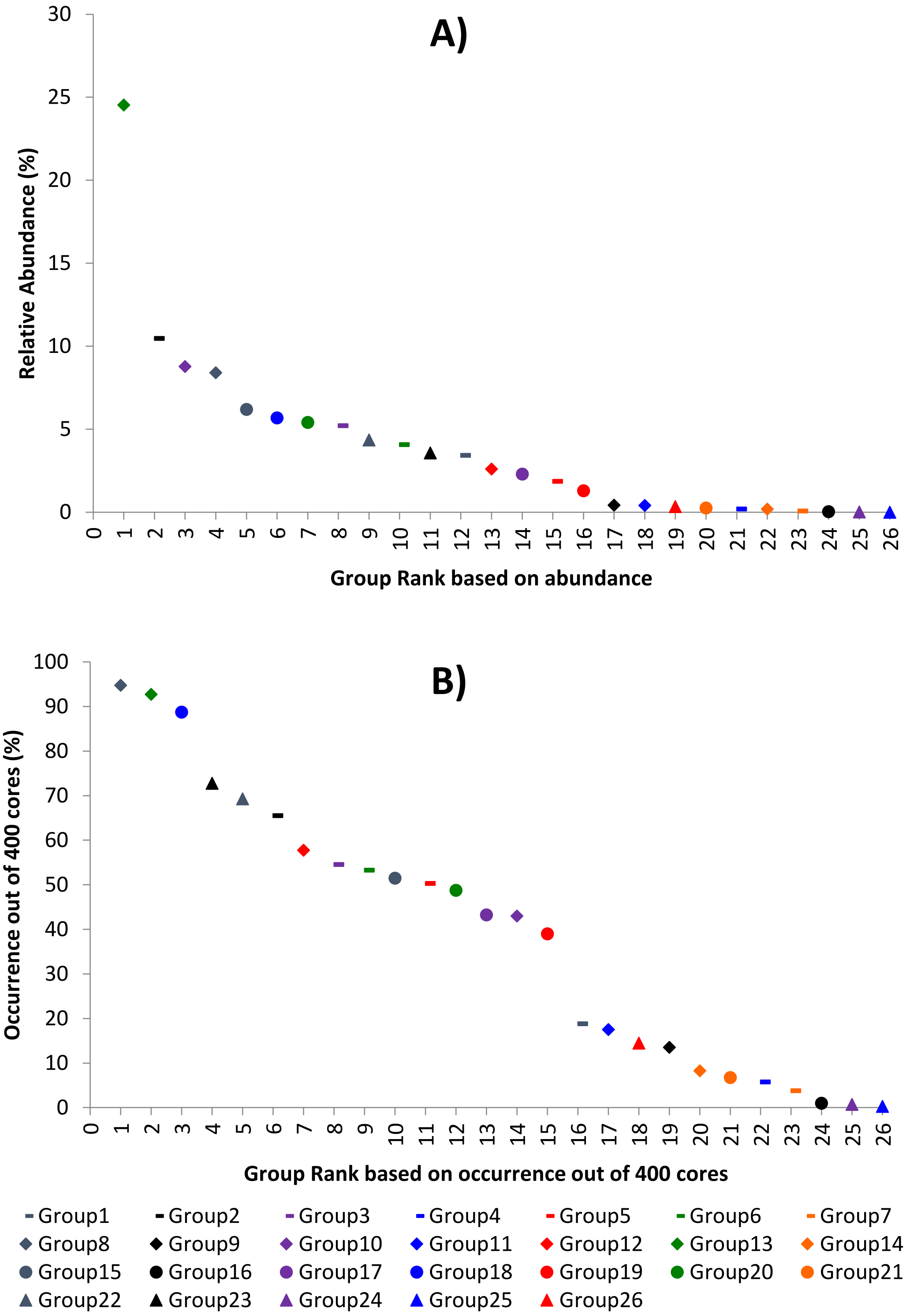

Figure 6. (A) Functional group abundance distribution (GAD) and (B) Functional group occurrence distribution (GOD). Shape and colour-coding for the 26 functional groups indicates whether specific functional groups are rare or common and the level of redundancy.

Table 6. Ten most abundant and occurring functional groups. Functional group richness is number of species per functional group. Percent relative abundance given in brackets.

Abundance	Richness	Occurrence	Richness	% occurrence (400 cores)
Group 13 (27%)	13	Group 8 (9%)	2	95
Group 2 (11%)	2	Group 13 (27%)	13	93
Group 10 (9%)	4	Group 18 (6%)	13	89
Group 8 (9%)	2	Group 23 (4%)	6	73
Group 15 (7%)	6	Group 22 (5%)	11	69
Group 18 (6%)	13	Group 2 (11%)	2	66
Group 20 (6%)	3	Group 12 (3%)	4	58
Group 3 (6%)	4	Group 3 (6%)	4	55
Group 22 (5%)	11	Group 6 (4%)	5	53
Group 6 (4%)	5	Group 15 (7%)	6	52

3.2.3 FUNCTIONAL GROUP RESILIENCE INDEX

There were notable differences in trait diversity, that is, that some traits were more common than others. For example, deposit- and suspension-feeding bivalves, tube-forming polychaetes and predator/scavenger polychaetes were common across many groups, whilst deep-living and attached traits were typically associated with rarer groups (with the exception of functional group 8, which included *M. liliana*, a deep-living bivalve, which was very abundant and had high occurrence). However, this functional group only had 2 species in it and may therefore be rare in this respect.

Some functional groups have high resilience with respect to functional group abundance and occurrence (Table 7), for example, functional groups 13 (small deposit-feeding polychaetes), 15 (below surface tube structure polychaetes), 18 (mobile predator/scavenger polychaetes), 22 (isopoda/amphipoda top 2 cm) and 23 (surface-dwelling mobile crustaceans). Conversely, functional groups 4 (sedentary top 2 cm bivalve), 24 (large above surface mobile Asterozoa) and 25 (attached scavenger crab) showed low abundance and low occurrence inferring that they are highly vulnerable to stressors. Some functional groups were abundant but had lower occurrence rank implying a restricted distribution on the sandflat (functional groups 1 (Oyster and barnacles), 10 (tube polychaetes) and 20 (deep-living tube polychaetes)). Conversely, greater spatial distribution and lower abundance was observed for functional groups 5, 9, 11, 12 and 26. This distribution indicates that although these functional groups have low abundance they are widely dispersed across the study site and are therefore likely more resilient to localised disturbances and/or stressors.

Table 7. Functional group resilience index (GRI) derived from measures of average abundance per core, occurrence of functional group out of 400 cores and functional group richness.

GRI	Average abundance per core	Occurrence of functional group in 400 cores	Functional group richness	Functional group number
11	High	High	High	13, 15, 18, 22, 23
10	High	High	Medium	3, 6
9	High	High	Low	2, 8
8	High	Medium	Medium	1, 10, 20
7	Medium	High	High	5
6	Medium	High	Medium	12
5	Medium	Medium	Medium	17, 19
4	Low	Medium	High	26
3	Low	Medium	Low	9, 11,
2	Low	Low	Medium	7, 14, 16, 21,
1	Low	Low	Low	4, 24, 25

3.3 SPATIAL DIVERSITY AND CORRELOGRAMS

I have focused on 12 functional groups that display clear spatial structuring, rather than discussing the spatial variation in abundance displayed by all 26 functional groups (see Appendix 1 for abundance maps and correlograms of all functional groups). Spatial patterns were interpreted from the correlograms using the guidelines provided by Legendre and Fortin (1989) and Thrush et al. (1989). Three general distribution patterns were apparent in this study.

Gradient distribution (Figure 7). Characterised by short-distance positive autocorrelation coupled with very negative autocorrelations at the largest distance classes in the correlogram. That is, community composition becomes increasingly different as the distance between samples increases, shown by points farther apart having very different Moran's *I* coefficients. Functional groups 2 (large mobile suspension-feeding bivalves), 17 (limited mobility predator polychaetes), 15, 20 and 10 (various tube-forming polychaetes) demonstrated such a gradient. Furthermore, the corresponding interpolated abundance maps (Figure 7) show that these functional groups have a gradient from high to low abundance. A change is often apparent in these maps that is consistent with the insignificant distance classes in the correlogram. For functional groups 17, 15, 20 and 10 the area of highest abundance is situated low on the shore. However, functional group 2 displays the opposite distribution. This gradient is also observed in the grain size data (see Figures 10 and 11) where functional groups 17, 15, 20 and 10 occupy finer sediments, whereas functional group 2 was located in coarser sediments.

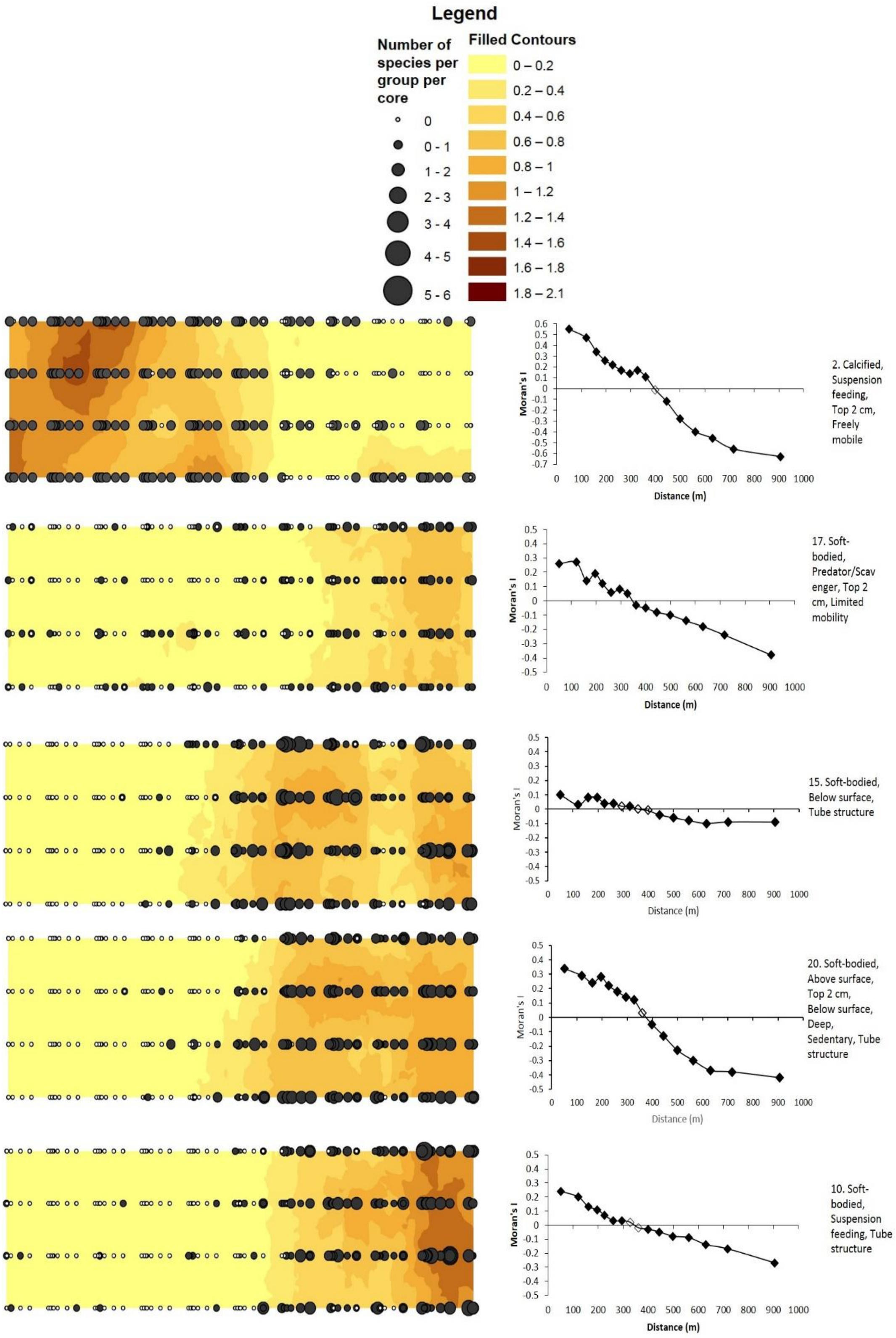

Figure 7. Interpolated Kriging abundance (data transformed Log(x+1)) contour maps (1000 m x 300 m) and Moran's I correlogram for functional groups (2, 17, 15, 20 and 10) displaying a gradient spatial distribution. Darker areas indicate higher abundances and larger dots higher species richness in the functional group. The x-axis on the correlogram represents distance class.

Large patch (Figure 8). Correlograms show significant positive autocorrelations at the shortest and longest distances, with negative correlations in the intermediate distance classes. These correlograms are typical of either spatial patterns dominated by one large patch or a saddle shaped pattern. The spatial maps confirm these patterns to be based on large patch structures. Functional group 12 (deposit-feeding mobile polychaetes), and to a degree Functional group 8 (deposit-feeding deep-dwelling bivalves), displayed this distribution.

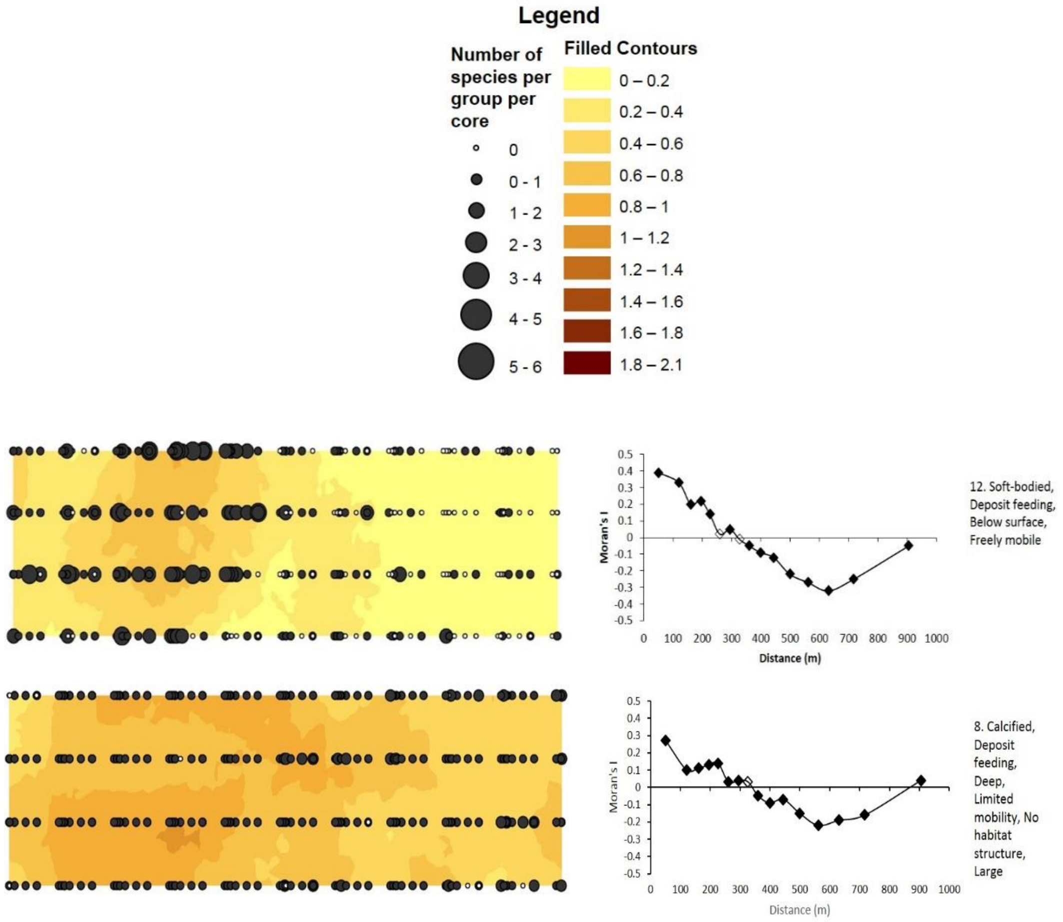

Figure 8. Interpolated Kriging abundance (data transformed Log(x+1)) contour maps (1000 m x 300 m) and Moran's *I* correlogram for functional groups (12 and 8) displaying large patch distribution. Darker areas indicate higher abundances and larger dots higher species richness in the functional group. The x-axis on the correlogram represents distance class.

Multiple patches (Figure 9); where an oscillation of significant positive autocorrelation is followed by negative autocorrelation. This indicates a landscape dominated by small patches and is shown by functional groups 3, 5, 13, 18 and 22 in the corresponding abundance maps.

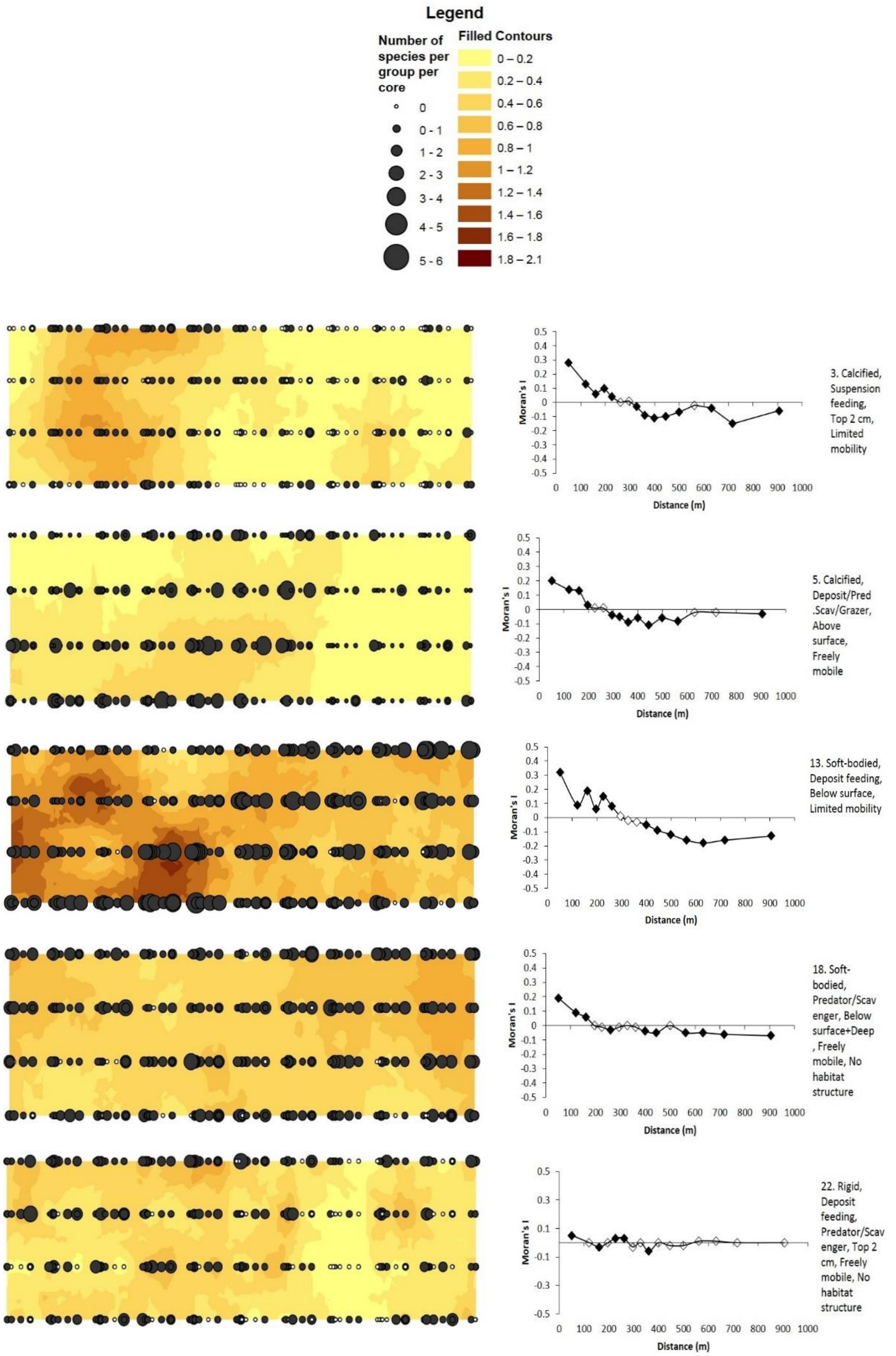

Figure 9. Interpolated Kriging abundance (data transformed Log(x+1)) contour maps (1000 m x 300 m) and Moran's *I* correlogram for functional groups (3, 5, 13, 18 and 22) displaying multiple patches distribution. Darker areas indicate higher abundances and larger dots higher species richness in the functional group. The x-axis on the correlogram represents distance class.

3.3.2 ENVIRONMENTAL VARIABLES

There were subtle variations in both Chl-*a* and median sediment grain size across the site (Figure 10) with coarser sediments at the shore and finer sediments near the channel with higher Chl-*a* concentrations associated with larger grain size. Organic matter appears to be correlated with seagrass coverage. Shannon-Wiener diversity of functional groups encompasses both functional group richness and abundance. The greater diversity of functional groups and the abundance of organisms with these functional groups at the channel end of the site implies greater functional redundancy low on the shore.

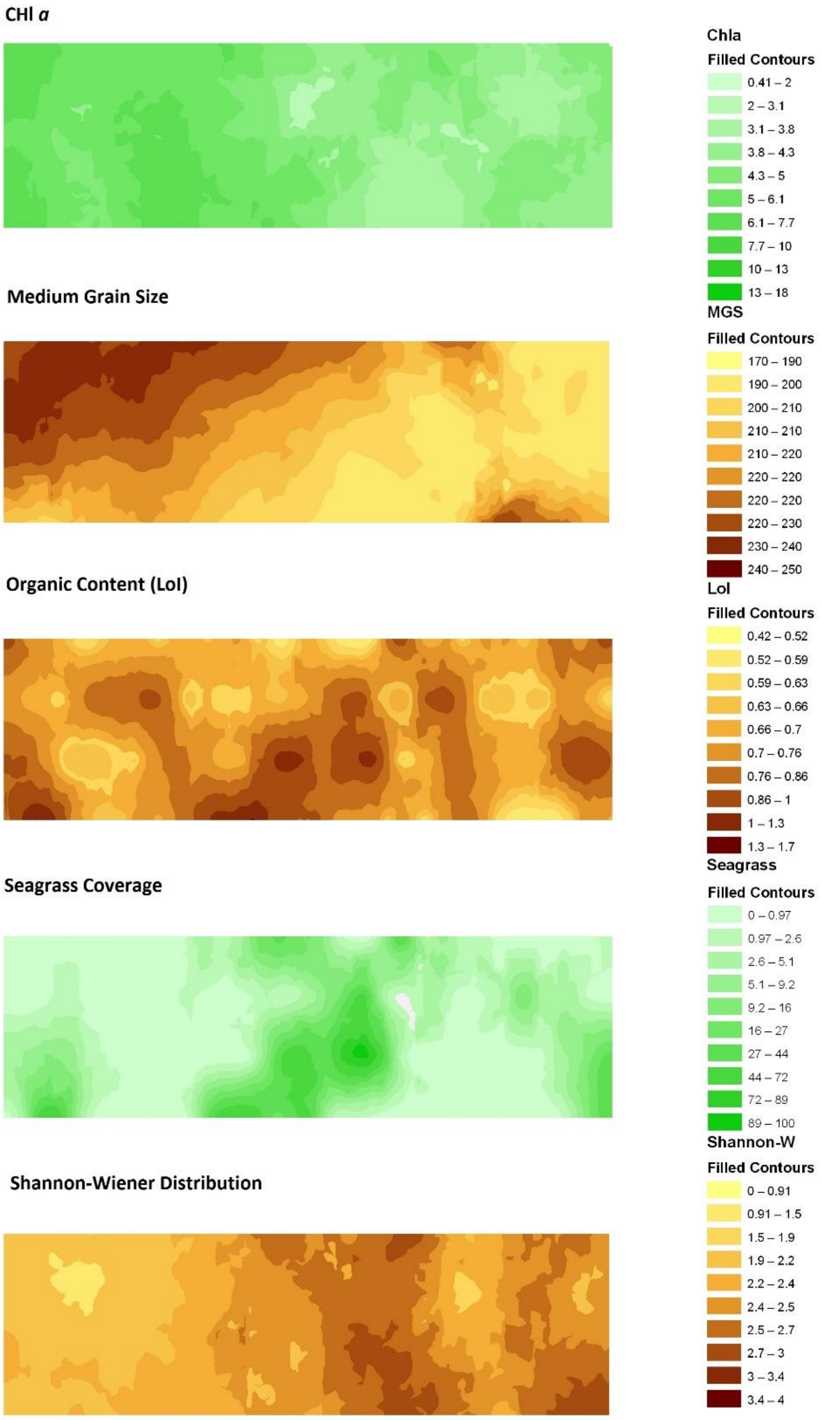

Figure 10. Interpolated Kriging maps of site area (1000 m x 300 m) for environmental variables: Chlorophyll *a* concentrations (µg/g), sediment median grain size (µm), LoI (%), Seagrass coverage (%) and Shannon-Weiner distribution.

3.3.3 CANONICAL CORRESPONDENCE ANALYSIS (CCA)

The canonical relationship between the 26 functional groups and environmental variables (Chl-*a* content, organic content and sediment characteristics: % silt, fine, medium and coarse) is shown in Figure 11. The distribution of some functional groups (such as tube-forming polychaetes vs. large mobile suspension-feeding bivalves) along the x-axis of the ordination are comparable to non-overlapping pattern apparent in the abundance maps (Figures 7, 8 and 9). Where, these functional groups, which are shown to have negatively correlating distributions in Figures 7, 8 and 9, appear negatively correlated to each other relative of correlation with environmental variables (see Figure 11). For example, the CCA shows that functional group 2 (large mobile suspension-feeding bivalves) is weakly positively correlated with medium/coarse sand and weakly negatively correlated with fine particles, whereas, functional groups 10, 15 and 20 (variations of tube-forming polychaetes) are weakly and negatively correlated to the preferences of functional group 2. One of the two most species-rich functional groups, group 18 (mobile predator/scavenger polychaetes), is negatively correlated with Chl-*a*, organic content and prefers finer sediments. The other, functional group 13 (small deposit-feeding polychaetes), is an outlier and may be due to its extensive spatial range seen in Figure 9. Functional group 25 is also an outlier, however, this may be as it consists of a single specimen of *Pinnotheres novaezelandiae*. Functional groups 5 (surface-dwelling gastropods), 7 (top 2 cm mobile deposit-feeding gastropods), 16 (top 2 cm mobile predator polychaetes), 22 (isopoda/amphipoda top 2 cm), 24 (large above surface mobile Asterozoa) and 26 (large burrow-forming crustaceans) appear more similar in distribution than the functional groups found towards that of the main cluster. This appears to be related to seagrass cover and silt concentration (supported by spatial distributions in previous figures for functional groups 5 and 22, and in Appendix 2 for functional groups 7, 16, 24 and 26). It is important to note that there is greater pattern of variation present across the community than can be explained by the environmental variables alone (tight clustering of environmental variables around the 0,0 origin). The percent variation explained by the x-axis was 25.7% (p=0.002) and by the y-axis 11.7% (p=0.002). The total amount of variation explained by environmental and spatial variables was low at 28% suggesting that the diversity observed is related more so to the biological interactions between functional groups.

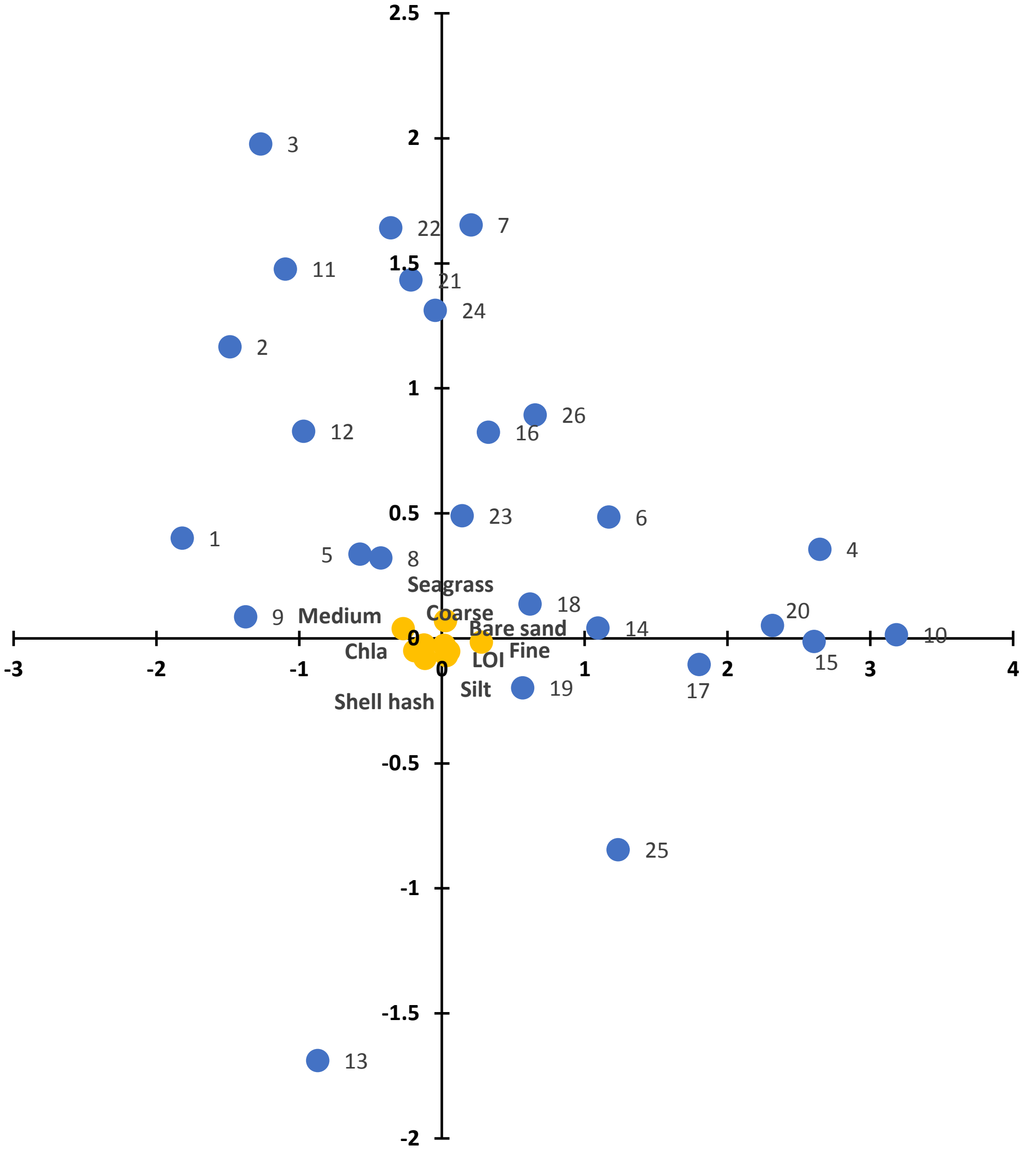

Figure 11. Canonical Correspondence Analysis (CCA) between the 26 functional groups (blue) and environmental variables (yellow): sediment grain size - % silt, fine, medium and coarse sand (µm); Chl-*a* content (µg/g); organic content (LoI) (%); and surface coverage of bare sand, shell hash and seagrass (% coverage). The proximity of a blue dot to a yellow signifies the strength of relationship.

4.0 DISCUSSION

The study of heterogeneity in diversity, e.g. Hewitt et al. (2010), is particularly important in modern times as increased anthropogenic stressors leading to habitat homogenisation is a major threat to biodiversity (Loreau et al. 2001, Naeem 2002). Thus, studying spatial patterns in functional diversity and defining functional redundancy, as determined in this study, is an important direction for improving our knowledge of resilience in coastal ecosystems. This study builds on the findings of Wellnitz and Poff (2001) who state that quantifying ecological redundancy within communities is essential to implement strategies to maintain ecosystem integrity. This large-scale empirical study is the first to include spatial analyses of functional diversity for marine benthic systems. I identified, and grouped, biological traits from a species-rich benthic macrofaunal community in a large intertidal harbour in New Zealand. Analyses showed that the spatial variation of biological traits could be assessed for various functional groups across a range of environmental conditions. Two important caveats on the use of traits to assess function are, firstly, that trait function relationships are often not mechanistically demonstrated and, secondly, although a species may appear to perform the same function (i.e. be redundant) their functional roles may vary in naturally heterogeneous environments (Walker 1992, Wellnitz and Poff 2001). However, defining the mechanistic trait function relationships across all possible traits is a major tasks and until it is completed traits are the best surrogates for function we have. The functional trait database I have developed and the insight gained on redundancy and spatial variation in functional trait diversity can help guide future *in-situ* experimental research on biodiversity ecosystem function relationships in benthic marine communities. The spatial element of functional redundancy and distribution may also enable more precise selection of experimental sites and focal areas of intertidal sandflats.

The most common functional groups were groups 13 (small deposit-feeding polychaetes), 2 (large mobile suspension-feeding bivalves), 10 (tube-forming polychaetes), 8 (deep-living deposit-feeding bivalves) and 18 (mobile predator polychaetes) (Table 6). These functional groups consist of species regarded as important drivers of community structure (e.g. the bivalves *A. stutchburyi* and *M. liliana*, the tube-forming polychaetes *B. syrtis* and *Euchone* sp. (e.g.Thrush et al. 2006b, Hewitt et al. 2008a). The rarest functional groups contained the most specialised species. These were functional groups 16 (top 2 cm mobile predator polychaetes), 24 (large above surface mobile Asterozoa) and 25 (attached scavenger crab).

4.1 COMMUNITY DISTRIBUTION

Abundance and occurrence distributions of taxa are an influential aspect in determining community resilience (Gray et al. 2005, Ellingsen et al. 2007, Heegaard et al. 2013, Mouillot et al. 2013). Analyses of species abundance and occurrence distributions (Figure 5) indicate that my data is typical of an ecological community (Gray 1981, Ellingsen et al. 2007) whereby most individuals belong to a small number of highly abundant species and the majority of the species are represented by a small number of individuals (e.g. Gaston 1994, Schlacher et al. 1998, Heegaard et al. 2013). Many of the rarer species have been found to contribute much the same functions as the common species (Ellingsen et al. 2007, Törnroos and Bonsdorff 2012). A community with a high proportion of rare species may prove less resilient, as indicated by early studies of species abundance distributions (Whittaker 1975, Gray and Mirza 1979). Following low but consistent levels of anthropogenic stressors, these more vulnerable species may decline in both richness and evenness while the less vulnerable, more robust species can an increase (Ellingsen et al. 2007, Hewitt et al. 2010). In their *niche hypothesis* of community composition, Mouillot et al. (2013) refer to this process as *functional specialization*. This change in community distribution to one more homogeneous in nature endangers the rare, often habitat-specific, species which make up a large proportion of species richness (e.g. Hewitt et al. 2010).

Redundancy is an important element of resilience, where a greater number of species performing the same function acts to reinforce that function against the negative impacts of stressors. With 85% of groups consisting of 2 or more species and 50% containing 4 or more species most functional groups in this study show a degree of redundancy whereby species are relatively evenly distributed across functional groups. Some functional groups (for example large mobile suspension-feeding bivalves and large, deep-living deposit-feeding bivalves) consist of only 2 species but have very high abundances (n = 2471 and 1986 individuals respectively). Each of the potentially least resilient functional groups on the Kaipara Sandflat are dominated by a single bivalve species – *A. stutchburyi* and *M. liliana* respectively. With such high abundances the two functional groups appear resilient. However, high abundance does not always confer resilience, the low redundancy still indicates vulnerability. This has been demonstrated for parrotfish assemblages on the Great Barrier Reef, where loss or drastic reduction of a single species may lead to a loss of a whole functional group and thus greatly effects ecosystem functioning ((Micheli and Halpern 2005).

Functional groups that are highly abundant and have high occurrence across the site (for example, small deposit-feeding polychaetes) are expected have greater resilience to large-scale stressors (Brown 1984, Crist et al. 2003, Ellingsen et al. 2007). Functional groups that have a high abundance coupled with low occurrence may be more vulnerable to small-scale or point-source stressors that can devastate a local population (De Juan et al. 2007, Rodil et al. 2011). Functional groups with low abundance per core and high occurrence across the site exhibit resilience, as although they are not locally abundant *per se*, they have a high degree of redundancy provided by their broad-scale occupancy of the site. Low abundance can occur for a number of reasons, including the match between animals size and core size; you will not find many in a single core as the sample size is too small to incorporate more than a few individuals. Large shrimps, crabs and predator/scavenger polychaetes fall into this category. However, in the latter case abundance is also limited by trophic position, i.e. prey are far more abundant than predators (Rosenzweig and MacArthur 1963). The most vulnerable functional groups are those with low abundance and low spatial dispersal. Consequently, these functional groups are very susceptible to both small-scale and large-scale stressors (Menge and Olson 1990, Gray et al. 2005, Thrush et al. 2005, Hamaide et al. 2006, Ellingsen et al. 2007, Cao et al. 2011, Heegaard et al. 2013, Mouillot et al. 2013).

The spatial extent of the stressor is a very important aspect of predicting changes in resilience (Legendre et al. 1997, Thrush et al. 2000, Thrush et al. 2005, Hewitt et al. 2010). It is therefore necessary to determine the spatial distribution and environmental range of these functional groups in order to appropriately assess their overall resilience (Legendre and Fortin 1989). My preliminary spatial analysis relied on presence/absence data to give an indication of occurrence throughout the site. However, further spatial measures were required as this provided no qualitative assessment. For example, a functional group may be found in 200 out of 400 cores suggesting a high occurrence, but, the location of these samples is also important when assessing resilience. The samples may be evenly-spaced throughout the site or all clumped in one place. The spatial location of functional groups was quite diverse across the site. Small deposit-feeding polychaetes, amphipoda, and isopoda were distributed throughout the site in various abundances. Whereas, large deposit- and suspension-feeding bivalves and tube-forming polychaetes showed aggregations and marked boundaries to their distribution. This suggests that the latter may be vulnerable to small-scale stressors. Functional groups that cover a greater spatial area may be able to tolerate a broader environmental range and therefore be more resilient to stressors. Consequently, the diversity of functional groups relative to environmental variables using spatial analyses (Figure 11) was required to assess resilience to stressors and degree of resilience.

A range of stressors may impact my study site, including storms, thermal stress or desiccation events which are likely linked to tidal elevation, but likely to influence the whole site. Other stressors such as predator impacts (eagle rays and shorebirds), are likely to be much more spatially specific even though predators tend to target prey patches (Sutherland 1982, Thrush et al. 1994, Cummings et al. 1997). Additionally, the surrounding land is used for farming sheep and cattle and therefore, the typical stressors associated with farming are likely to impact the area (nutrient and sediment runoff).

4.2 ENVIRONMENTAL VARIABLES

Functional groups may have apparent resilience due to their abundance and occupancy characteristics but may in fact still be highly vulnerable due to their low tolerance to environmental stress (Walker 1992, Walker et al. 1999). Environmental variables are typically a major influence on the spatial distributions and diversity (Menge and Olson 1990, Hewitt et al. 1998, Blackburn and Gaston 2002, Borcard et al. 2004, Thrush et al. 2005, Kraan et al. 2010, McGill 2013). On sandflats, common environmental drivers are organic content, grain size, hydrodynamics and disturbance (Hewitt et al. 2010). However, CCA on my data indicated that environmental parameters are only weakly affecting the distribution of functional groups in the ordination space (depicted by clustering of environmental variables around 0,0 on Figure 11). Within the study site environmental variation was low (Chl-*a* 0.41-18 μg/g, organic content ranged from 0.42-1.7 %, medium grain size ranged from 170-250 µm and seagrass coverage ranged from 0-100 % coverage), this suggests that biological interactions between functional groups are likely to be the principal driving forces behind the spatial structure of functionality for the scales at the site (see Borcard et al. 2004, Legendre and Legendre 2013) or that the environmental variables important for structuring benthic communities at this scale have not been measured.

Differences in biological (physical and behavioural) use of habitat structure is the likely influence causing the opposing spatial structure of functional group 2 with functional groups 10, 15 and 20 (see Figure 7). Functional group 2, large suspension-feeding, surface-dwelling, highly mobile bivalves (*Austrovenus stutchburyi* and *Paphies australis*) cause destabilisation of the sediment (Posey 1987). Whilst functional groups 10, 15 and 20, consisting of tube worms (including

Macroclymenella stewartensis, *Boccardia syrtis* and *Pseudopolydora sp.*) act to stabilise the sediment (Fager 1964, Posey 1987) and are therefore in direct conflict with functional group 2. Another biological interaction that may be causing functional diversity is the spatial distribution of functional group 18 (large predatory polychaetes including *Ceratonereis sp.*, *Glycinde spp.*, and G*lyceridae spp.*) and functional groups 10, 15 and 20. Functional group 18 prey on other polychaetes and the sedentary lifestyle of the tube-forming functional groups make them easy prey.

5.0 CONCLUSIONS

The biological trait analysis proved to be useful in describing the functional patterns and distribution of traits across a large intertidal sandflat area. Analysis showed that there were clear gradients and boundaries of abundance and occurrence spatial distributions separating function on the Kaipara sandflat. An important finding from this study was that two of the least resilient functional groups on the Kaipara Sandflat are dominated by a single bivalve species – *A. stutchburyi* and *M. liliana* functional group 2 and 8 respectively. Both functional groups had such high abundances that they appear resilient, however this does not always infer resilience, for the low functional group redundancy still indicates vulnerability.

The species and traits data set developed can hopefully aid further research on functional diversity in this region and between regions since the traits described are not location specific. Development of my attributes and traits of species database as more information becomes available would be integral to the advancement of our understanding of spatial diversity of functionality. Future research into the distribution of functionally important traits, for example, nutrient fluxes between the sediment-water interface will complement this research significantly. Trait identification and spatial diversity of functional traits is expected to be the way forward in our understanding of the processes concerning biodiversity and subsequent management of our environmental resources.

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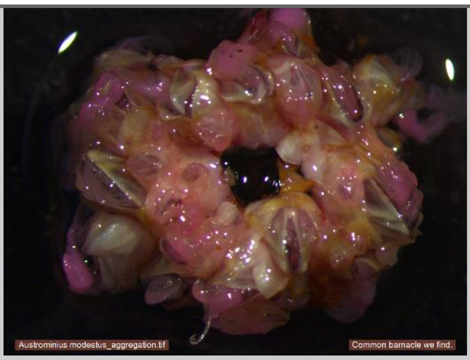
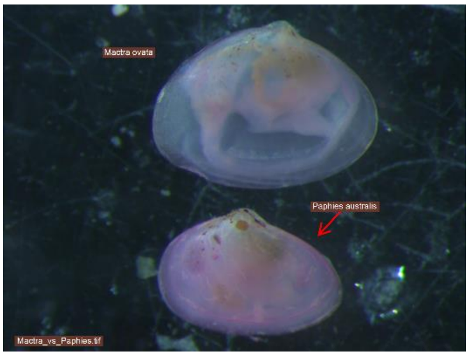
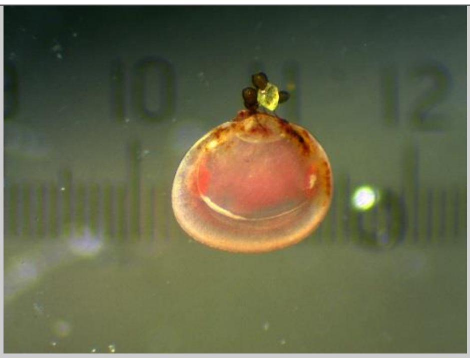
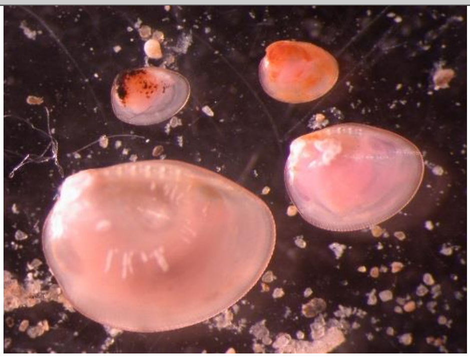
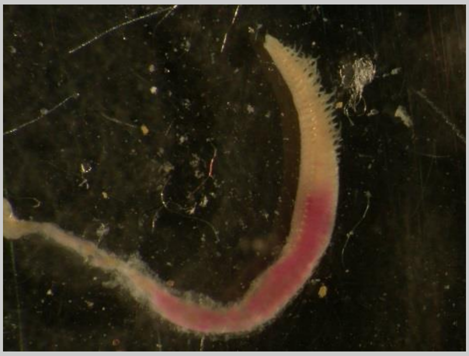
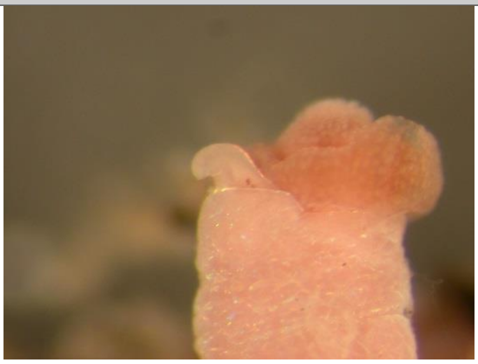
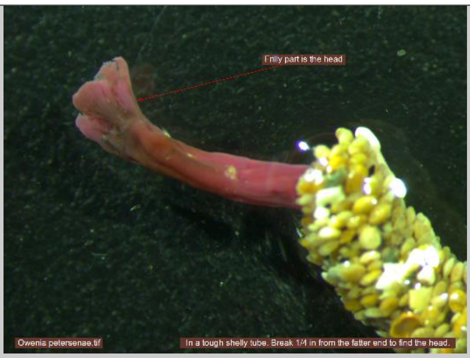
APPENDIX 1: SPECIES PHOTOGRAPHS

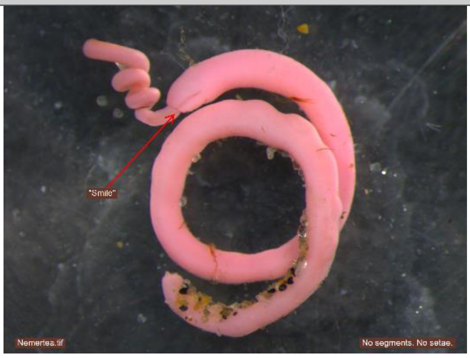
Functional group number	**Description of traits**	**Photo**	**Example species (highest contributors)**
1	Calcified, Suspension feeding, Attached		*Austrominius modestus* *Crassotrea gigas*
2	Calcified, Suspension feeding, Top 2 cm, Freely mobile		*Paphies australis* *Austrovenus stutchburyi*

3	Calcified, Suspension feeding, Top 2 cm, Limited mobility	 	*Soletellina siliquens* *Arthritica bifurca*
4	Calcified, Suspension feeding, Top 2 cm, Sedentary		*Musculista senhousia*
5	Calcified, Deposit/Pred .Scav/Grazer, Above surface, Freely mobile		*Zeacumantus lutulentus* *Cominella glandiformis*
6	Calcified, Deposit feeding, Top 2 cm, Limited mobility		*Linucula hartvigiana* *Lasaea parengaensis*

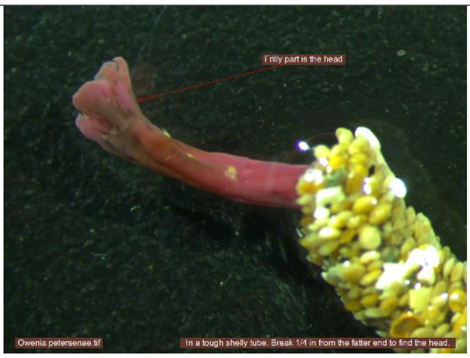
7	Calcified, Deposit feeding, Predator/Scavenger, Top 2 cm, Freely mobile		*Eatoniella* sp. *Amalda australis*
8	Calcified, Deposit feeding, Deep, Limited mobility, No habitat structure, Large		*Macomona liliana* *Mactra ovata*
9	Soft-bodied, Suspension feeding, Attached		*Anthopleura aureoradiata*
10	Soft-bodied, Suspension feeding, Tube structure		*Boccardia syrtis* *Euchone* sp.

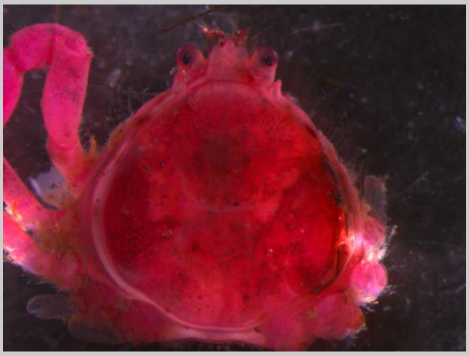
		 	
11	Soft-bodied, Deposit feeding, Top 2 cm, Freely mobile		*Travisia olens*
12	Soft-bodied, Deposit feeding, Below surface, Freely mobile	  	*Orbinia papillosa* *Scolecolepides benhami*

13	Soft-bodied, Deposit feeding, Below surface, Limited mobility	 	*Heteromastus filiformis* *Aonides trifida*
14	Soft-bodied, Deposit feeding, Deep		*Notomastus* sp. *Barantolla lepte*
15	Soft-bodied, Below surface, Tube structure		*Owenia petersenae* *Macroclymenella stewartensis*

16	Soft-bodied, Predator/Scavenger, Top 2 cm, Freely mobile		*Dorvillea* sp. *Pholoe* sp.
17	Soft-bodied, Predator/Scavenger, Top 2 cm, Limited mobility	 	*Trypanosyllis sp.* Oligochaeta (middle specimen is Capitella sp.)
18	Soft-bodied, Predator/Scavenger, Below surface+Deep, Freely mobile, No habitat structure		Nemertean *Aglaophamus macroura* *Nereidae* spp.

		  	
19	Soft-bodied, Predator/Scavenger, Below surface, Limited mobility		*Hesionid* spp. Oligochaeta

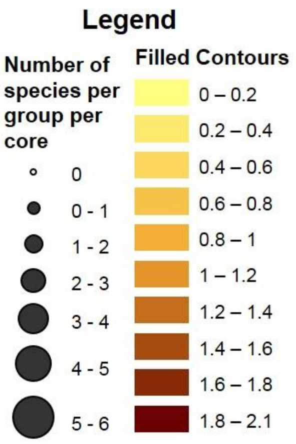
20	Soft-bodied, Above surface, Top 2 cm, Below surface, Deep, Sedentary, Tube structure	 	*Owenia petersenae* *Phoronis* sp.
21	Rigid, Suspension feeding, Top 2 cm		*Corophium* spp. *Paracorophium* spp.

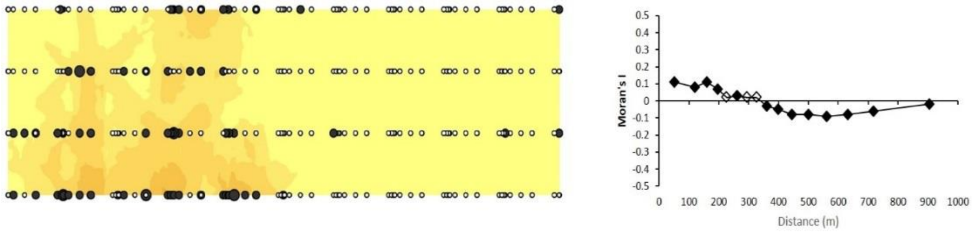
22	Rigid, Deposit feeding, Predator/Scavenger, Top 2 cm, Freely mobile, No habitat structure	 	*Paracalliope novizealandiae* *Waitangi brevirostris*
23	Rigid, Above surface, Freely mobile	 	*Colurostylis lemurum* *Halicarcinus whitei*

24	Rigid, Above surface, Freely mobile, Large		*Ophiuroida* sp. *Patiriella* sp.
25	Rigid, Predator/Scavenger, Attached		*Pinnotheres novaezelandiae*
26	Rigid, Predator/Scavenger, Below surface, Freely mobile, Large burrow former		*Hemiplax hirtipes* *Alpheus* sp. *Squilla armata*

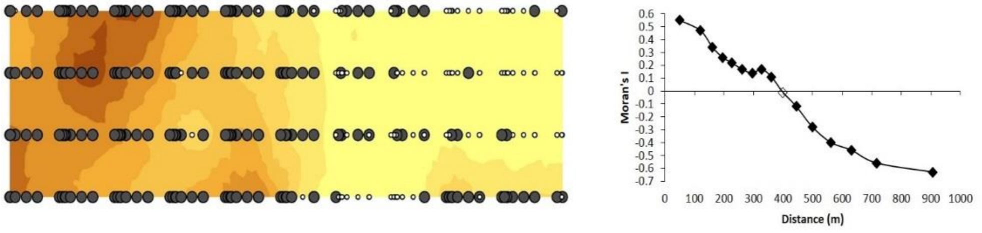
APPENDIX 2. ABUNDANCE SITE MAPS AND CORRELOGRAMS

Appendix 1: Correlograms (Moran's *I* co-efficient) and interpolated abundance area maps for all 26 functional groups.

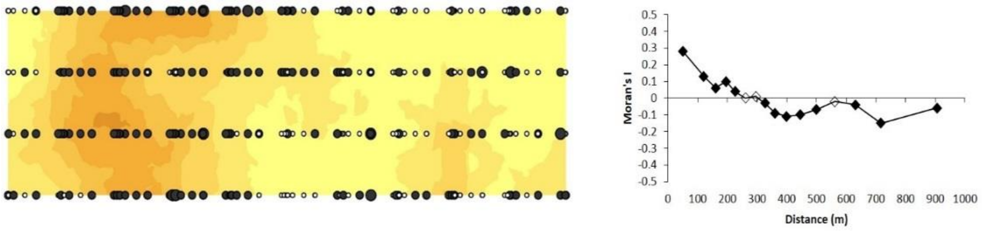




1. Calcified, Suspension feeding, Attached



2. Calcified, Suspension feeding, Top 2 cm, Freely mobile



3. Calcified, Suspension feeding, Top 2 cm, Limited mobility

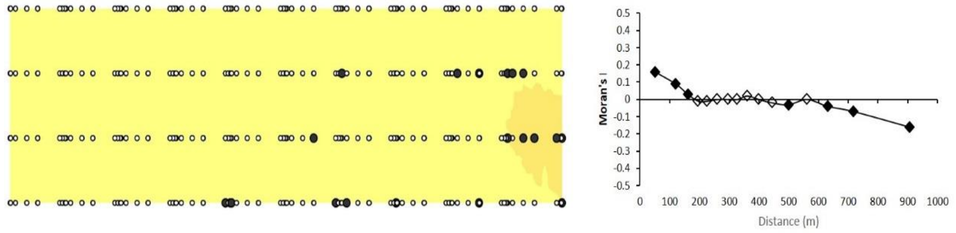
Legend

Number of species per group per core

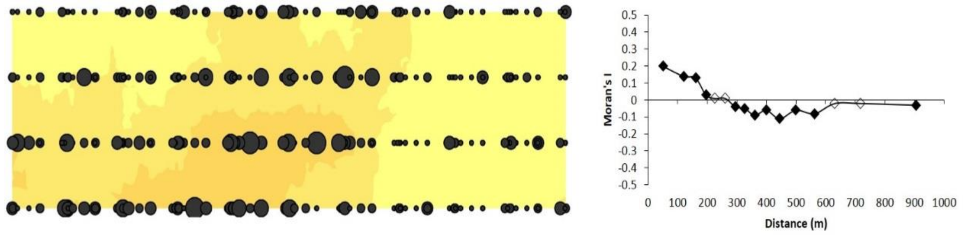
- ○ 0
- ● 0 - 1
- ● 1 - 2
- ● 2 - 3
- ● 3 - 4
- ● 4 - 5
- ● 5 - 6

Filled Contours

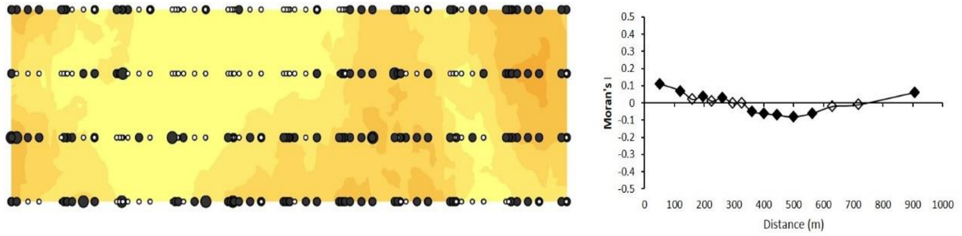
- ▨ 0 – 0.2
- ▨ 0.2 – 0.4
- ▨ 0.4 – 0.6
- ▨ 0.6 – 0.8
- ▨ 0.8 – 1
- ▨ 1 – 1.2
- ▨ 1.2 – 1.4
- ▨ 1.4 – 1.6
- ▨ 1.6 – 1.8
- ▨ 1.8 – 2.1



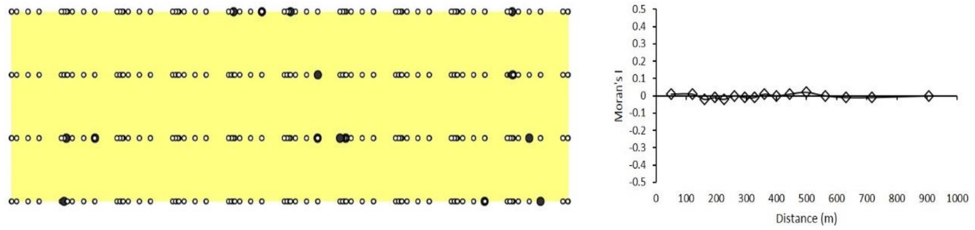
4. Calcified, Suspension feeding, Top 2 cm, Sedentary



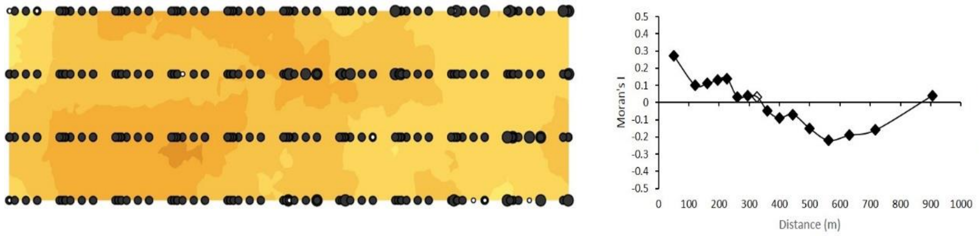
5. Calcified, Deposit/Pred.Scav/Grazer, Above surface, Freely mobile



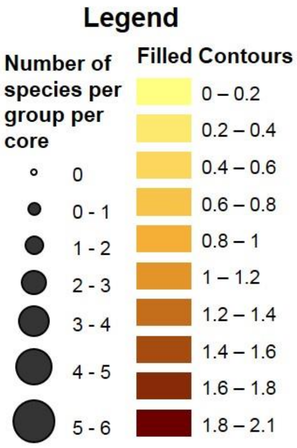
6. Calcified, Deposit feeding, Top 2 cm, Limited mobility

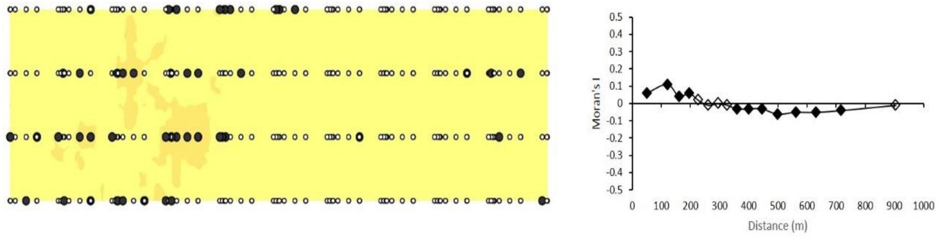


7. Calcified, Deposit feeding, Predator/Scavenger, Top 2 cm, Freely mobile

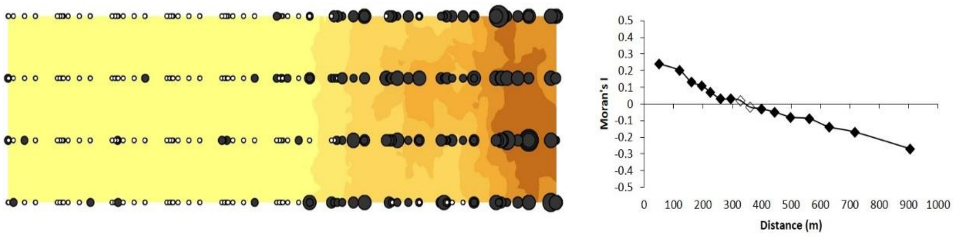


8. Calcified, Deposit feeding, Deep, Limited mobility, No habitat structure, Large

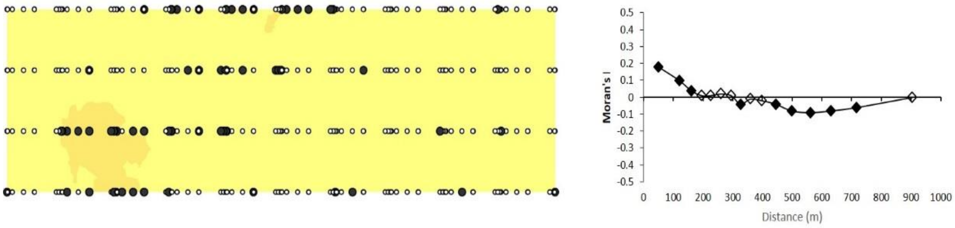




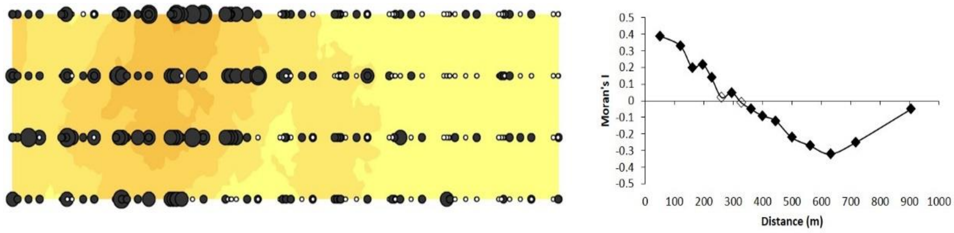
9. Soft-bodied, Suspension feeding, Attached



10. Soft-bodied, Suspension feeding, Tube structure

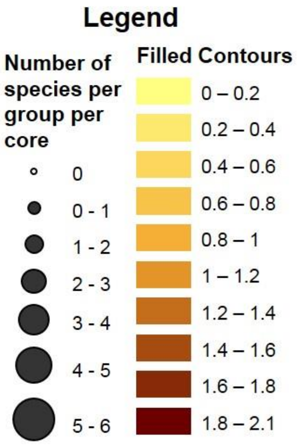


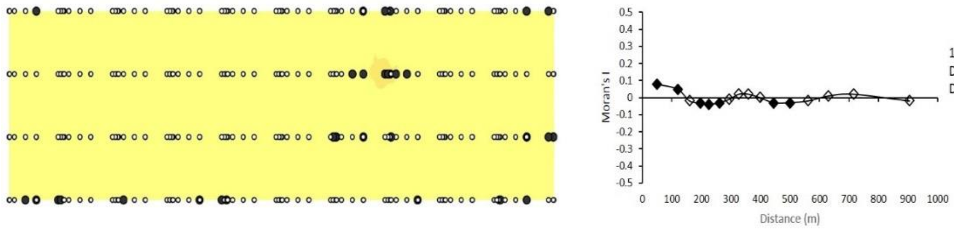
11. Soft-bodied, Deposit feeding, Top 2 cm, Freely mobile



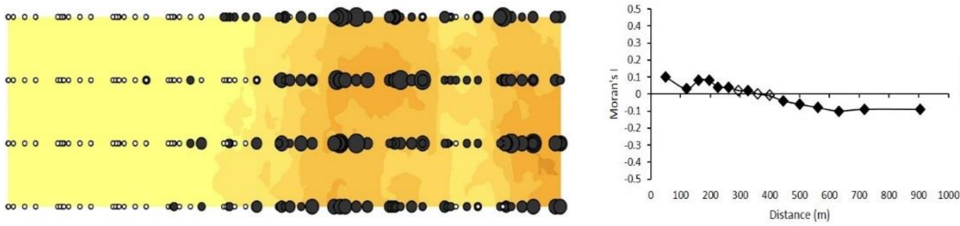
12. Soft-bodied, Deposit feeding, Below surface, Freely mobile

13. Soft-bodied, Deposit feeding, Below surface, Limited mobility

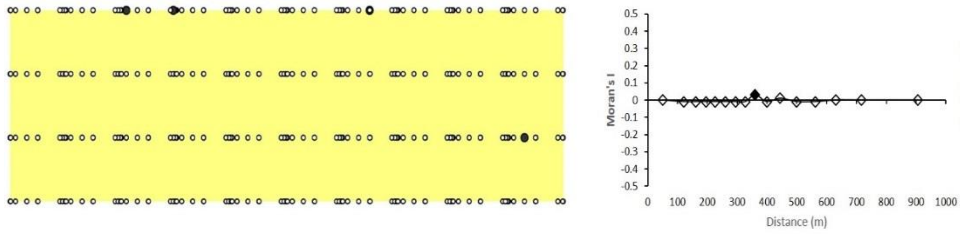




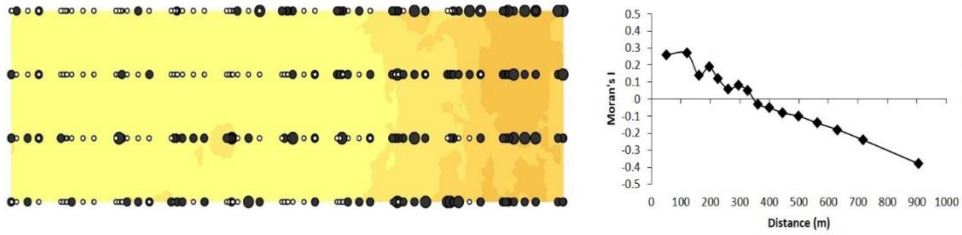
14. Soft-bodied, Deposit feeding, Deep



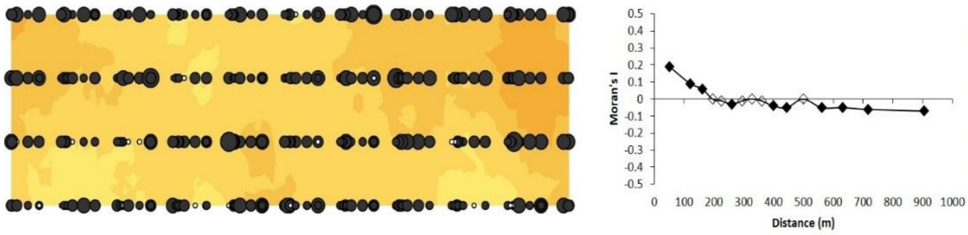
15. Soft-bodied, Below surface, Tube structure



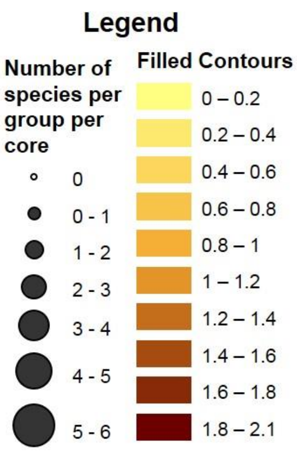
16. Soft-bodied, Predator/Scavenger, Top 2 cm, Freely mobile

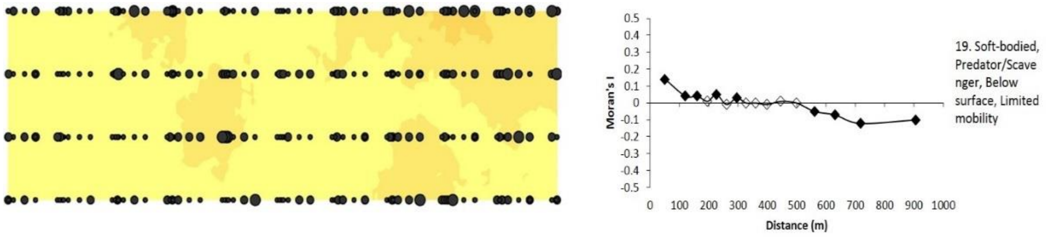


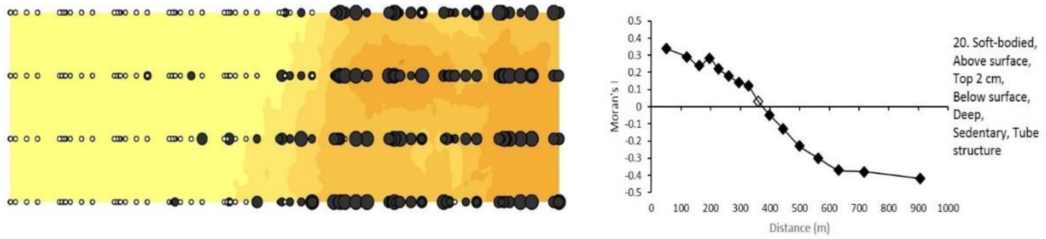
17. Soft-bodied, Predator/Scavenger, Top 2 cm, Limited mobility

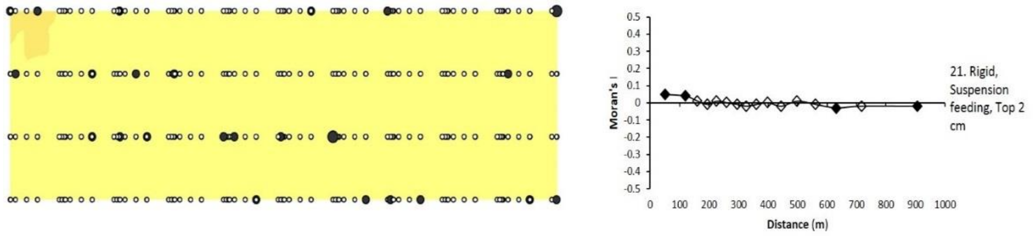


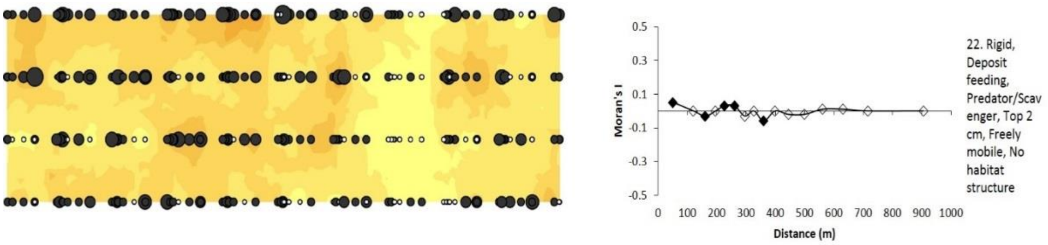
18. Soft-bodied, Predator/Scavenger, Below surface+Deep, Freely mobile, No habitat structure

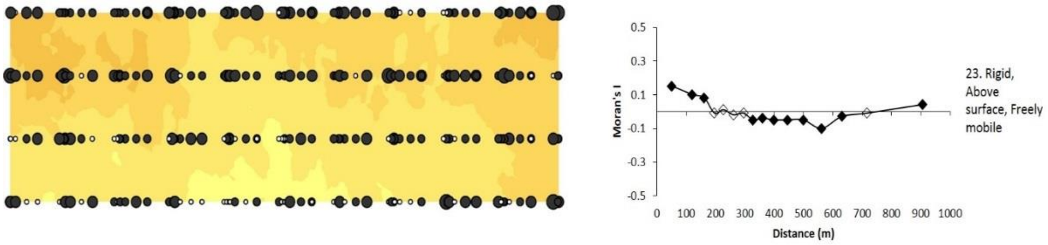


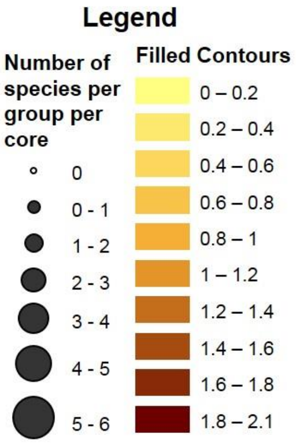

19. Soft-bodied, Predator/Scavenger, Below surface, Limited mobility

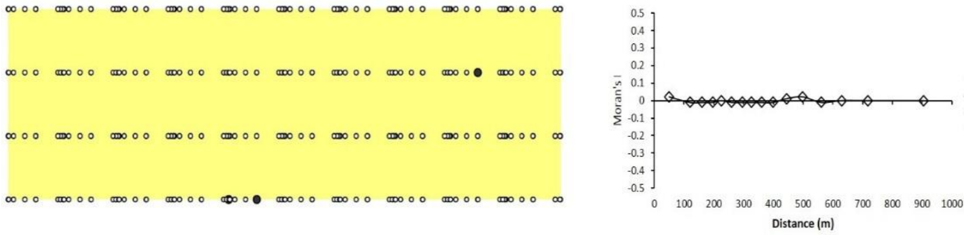

20. Soft-bodied, Above surface, Top 2 cm, Below surface, Deep, Sedentary, Tube structure


21. Rigid, Suspension feeding, Top 2 cm

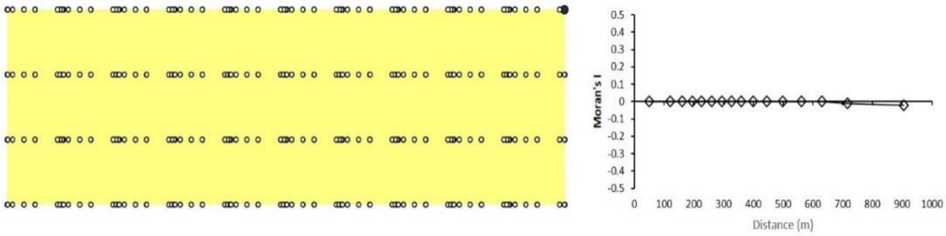

22. Rigid, Deposit feeding, Predator/Scavenger, Top 2 cm, Freely mobile, No habitat structure


23. Rigid, Above surface, Freely mobile

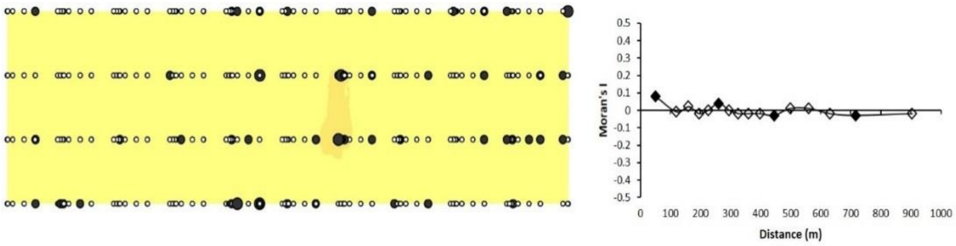




24. Rigid, Above surface, Freely mobile, Large



25. Rigid, Predator/Scavenger, Attached



26. Rigid, Predator/Scavenger, Below surface, Freely mobile, Large burrow former