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ECO-FUNCTIONAL BENTHIC BIODIVERSITY ASSEMBLAGE PATTERNS IN THE GUINEA CURRENT LARGE MARINE ECOSYSTEM

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A

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DECLARATION

This PhD thesis is original and independent research work conducted under supervision of Dr. George Wiafe, Prof. Elvis Nyarko and Mr. A.K. Armah of the Department of Marine and Fisheries Sciences. This research has not been included in any thesis or dissertation submitted to other institution for a degree, or any other qualifications. Authors whose works were used have been duly referenced/recognised.

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DEDICATION

I dedicate this piece of work to God Almighty and my family.

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LIST OF ABBREVIATIONS AND ACRONYMS

ABC:	Abundance-Biomass Comparison
ABC:	Abundance Biomass Curve
ANOSIM:	Analysis of Similarities
ANOVA:	Analysis of Variance
BC:	Benguela Current
B-EF:	Biodiversity Ecosystem Function
BIO-ENV:	Biological and Environment
BN:	Benin
BTA:	Biological Trait Analysis
CANOCO:	Canonical Community Ordination
CBD:	Convention on Biological Diversity
CC:	Canary Current
CCA:	Canonical Correspondence Analysis
CD:	Cote D'ivoire
CI:	Chlorine Index
CR:	Cameroon
DBM:	Dendrogram Based Measure
EA:	Equatorial Anticyclonic
EAF:	Ecosystem Approach to Fisheries
EAM:	Ecosystem Approach to Management
EcoQO's:	Ecological Quality Objectives
FAD:	Functional Attribute Diversity
FD:	Functional Diversity

FE:	Functional Evenness
FGR:	Functional Group Richness
FR:	Functional Richness
FS:	Functional structure
FWHM:	Full Width at Half Maximum
GA:	Gabon
GB:	Guinea Bissau
GC:	Guinea Current
GCE:	Guinea Current Ecosystem
GCLME:	Guinea Current Large Marine Ecosystem
GH:	Ghana
GNP:	Gross National Product
GU:	Guinea
HCL:	Hydro Chloric Acid
HPGe:	High Purity Germanium
INAA:	Instrumental Neutron Activation Analysis
ITCZ:	Intertropical Convergence Zone
KCl:	Potassium Chloride
LI:	Liberia
MCA:	Multi Channel Analyzer
MDS:	Multi-dimensional Scaling
MFAD:	Modified Functional Attribute Diversity
MLRA:	Multiple Linear Regression Analysis
MNSR:	Miniature Neutron Source Reactor
NAS:	North Atlantic Subtropical

NEC:	North Equatorial Cyclonic
NECC:	North Equatorial Counter Current
NG:	Nigeria
OC:	Organic Carbon
OM:	Organic Matter
POC:	Particulate Organic Carbon
RDA:	Redundancy Analysis
SEC:	South Equatorial Cyclone
SECC:	South Equatorial Counter Current
SIMPER:	Similarity Percentages
SL:	Sierra Leone
SOPs:	Standard Operation Procedures
SR:	Species Richness
STA:	Species Trait Analysis
TG:	Togo
TG-BN:	Togo-Benin
TOC:	Total Organic Carbon
TN:	Total Nitrogen

ABSTRACT

Functional diversity, an important component of biodiversity, has in recent years engaged global attention. This is in great part due to the mechanistic understanding achieved from functional diversity studies in the face of accelerated global biodiversity changes ascribed primarily to anthropogenic drivers. The exigency of the situation has stimulated biodiversity-ecosystem functions (B-EF) studies to elucidate ecosystem processes and services that are at threat notably in the marine ecosystem. The marine benthos is the largest ecosystem on earth and supports the highest phylogenetic diversity but has rather witnessed comparatively low attention in the B-EF studies than the terrestrial counterpart. This thesis is aimed at i) quantifying benthic functional diversity (using biological trait analysis) and assemblages along abiotic gradients in the Guinea Current Large Marine Ecosystem (GCLME); and ii) examining the impact of bottom trawling for demersal fishes on the functional structure of epibenthic fauna along bathymetric gradients.

In achieving the above-mentioned objectives, epibenthic fauna of bottom trawl samples were collected from Ghana to western Nigeria's continental shelf in 2003. Further, macrobenthic infauna and abiotic samples were collected from coastal waters of Guinea Bissau to Gabon in 2007. Each processed dataset was treated as a stand-alone in the thesis. In decomposing the assemblage patterns, suites of univariate and multivariate statistics were employed. The results indicated 381 macobenthic species comprising polychaetes (61.15% richness and 55.15% abundance), crustaceans (18.64% richness and 28.02% abundance), molluscs (9.19% richness and 2.23% abundance), echinoderms (2.63% richness and 1.84% abundance) and 'others' (8.39% richness and 12.76% abundance). Functional diversity analysis indicated spatial differences in eco-functional traits namely small body size, solitary lifestyle, burrowing and deposit-feeding, and these traits dominated the assemblage especially from Ghana to Benin. The results suggest that these areas are potential surrogates of allochthonous organic material possibly driving pelagic productivity that is translated to the benthos. Significant (p<0.05) relationship was found between functional traits (also species diversity) and sediment parameters (i.e., nitrate, calcium, magnesium, organic carbon, silt & clay). These abiotic variables largely implicate productivity and climate change models as principal community drivers, and are likely to impact ecosystem functions directly by altering B-EF relationship. Inferentially, the results indicated an unstable, dynamic, productive and low biomass-supported ecosystem Guinea Current Large Marine Ecosystem (GCLME), reflecting in the small body size solitary burrow-dwelling deposit-feeding organisms, which potentially exert the strongest influence on ecosystem processes (e.g., nutrient remineralization). These species used multiple adaptative strategies including trophic, lifestyle, anatomical and morphological in the prevailing environment.

Bottom trawled epibenthic sample analysis showed significant difference (p=0.002; ANOSIM) of assemblages along bathymetric gradient, notably between shallow-depth (11-30m) and deep-depth (51-70m). Functional analyses showed dominance of carnivores (28% contribution), opportunistic/scavenging (9%) and herbivore (9%) in shallow waters, while filter-feeders (18%) dominated deep waters suggesting gradient in structuring forces. The high abundance of motile epibenthic fauna (64%) is suggestive of an unstable substrate and turbulent system supporting motile carnivores and filter-feeding organisms. The evidence of trophic interactions between demersal fishes and epibenthic fauna occurred ideally in most tolerable and favorable zone (i.e. mid-depth). Abundance-Biomass Comparison (ABC) analyses indicated an ecosystem which is stressed (66.56%) with the degree of stress inversely related to increasing water depth. The findings of this thesis have important implications for marine biodiversity conservation and resource management approach in the GCLME.

CHAPTER ONE

GENERAL INTRODUCTION

Biodiversity, from genes through species to ecosystems, play an important role in the evaluation of the resilience of natural systems to environmental changes (Naeem *et al.*, 1999; Mant *et al.*, 2014). Understanding the patterns and processes of biodiversity at the primary, secondary and tertiary trophic levels is fundamental to sustainable management of marine living resources (Sherman and Duda, 1999; Costello, 2000; Hooper *et al.*, 2005). Biodiversity loss is defined as a sudden change to natural ecosystem setting due to human interventions. This is because natural changes of biodiversity are a much slower and longer-term process (Kessler *et al.*, 2007), which may be reversible**.** Human activities have contributed to variability in global climate, land cover and biodiversity at unprecedented rates (Steffen *et al.*, 2004). Human activities that affect biodiversity are referred to as *critical environmental issues* (National Research Council, 1995). The world is facing accelerated and apparently inevitable loss of species (Pimm *et al.*, 1995) and populations (Hughes *et al.*, 1997) through anthropogenic impact on the world's ecosystems.

The socioeconomic consequences of global biodiversity changes from *critical environmental issues* will depend on how they translate into altered ecosystem processes and services (Costanza *et al.*, 1997; Balmford *et al.*, 2002; Millennium Ecosystem Assessment, 2003). Impact of biodiversity loss under economic terms will mean that humankind will have to technically compensate for the services ecosystems provide (e.g. CO_2/O_2 gas regulation, food production, raw material production, prevention of soil erosion, genetic resources for pharmacy development, regulation of hydrological flows) (Costanza, *et al*., 1998; Edwards and Abivardi, 1998). Nonetheless, the ecological impacts of biodiversity loss are poorly understood (Solan *et al*., 2004).

Concerns of biodiversity loss are more amplified in the marine ecosystem due to the uncertainties associated with the effects of the loss on the basic functioning of the ecosystem and the oceans' capacity to withstand multiple human disturbances (Snelgrove *et al*., 1997). Available information indicates that the oceans account for approximately two-thirds of the value of global ecosystem services (Snelgrove, 1999), which is estimated to average $33 trillion US dollars/yr compared to the Global GNP of $18 trillion/yr (Costanza *et al*., 1997). As a result, of the ecosystem services , a large and increasing proportion of the world's population lives close to the coast; thus the loss of services such as flood control and waste detoxification can have disastrous consequences to coastal dwellers (Danielsen *et al*., 2005; Adger *et al*., 2005). The marine seafloor is the largest ecosystem on earth (Snelgrove *et al*., 1997) supporting high phylogenetic diversity (Snelgrove, 1999; Giller *et al*., 2004) and key ecosystem services (Bremner, 2008) and as a consequence biodiversity alterations/changes may have wider ecological and socio-economic implications. Marine ecosystems provide a wide variety of goods and services, including food resources for millions of people (Peterson and Lubchenco, 1997; Holmlund and Hammer, 1999). The maritime domain has also been used by society for different activities including fishing, aquaculture, shipping, tourism, renewable energies, extraction of minerals etc. (Borja *et al*., 2013).

Marine biodiversity alterations at both local and global scales can disrupt the ecological functions that species assemblages perform (Hughes *et al*., 2003). These changes make differentiation between effects of species richness *per se,* and the effects of functional group richness (i.e., functional diversity) on ecosystem function a major issue in ecology (Solan *et al*., 2004). This is because, although biodiversity generally enhances many process rates, such as resource use or biomass production, across a wide spectrum of organisms and ecosystems, the evidence for positive effects of biodiversity on ecosystem functioning (i.e., ecosystem processes, properties and their maintenance, (Reiss *et al*., 2009) is neither ubiquitous nor unequivocal (Thompson and Starzomski, 2007; Jiang *et al*., 2008).

Marine benthic faunal diversity, therefore, provides an ideal tool for exploring the relationship between biodiversity and ecosystem functioning in the marine environment (Snelgrove, 1999). Ecosystem functioning involves several processes, which can be summarized as production, consumption and transfer of organic matter to higher trophic levels, organic matter decomposition, and nutrient regeneration (Danovaro *et al*., 2008). According to Jax (2005) ecosystem functioning refers to the overall performance of ecosystem, and has been variously defined as incorporating, individually or in combination, ecosystem processes (such as biogeochemical cycles), properties (e.g. pools of organic matter), goods (food and medicines) and services (e.g. regulating climate or cleansing air and water) as well as temporal resistance or resilience of these factors over time in response to disturbance (Biles *et al*., 2002; Hooper *et al*., 2005; Duffy and Stachowicz, 2006).

The assemblage patterns of the marine macrobenthos and associated functional diversity, and their spatial and temporal variations as well as the drivers of functional traits remain poorly understood. The importance of the marine macrobenthic functional diversity includes roles in the structure and functioning of the systems, particularly their productivity and resilience in the potential human-induced disturbances/perturbations context (Solan *et al.*, 2006). Essentially, the global biodiversity concerns, exemplified by the predictions that species loss might impair the functioning and sustainability of ecosystems (Naeem *et al*., 1994; Sala *et al*., 2000; Loreau *et al*., 2001; Hooper *et al*., 2005; Worm *et al*., 2006;) have stimulated ecosystem-based and experimental efforts to: i) understand the synergy between biodiversity and ecosystem functioning, and ii) devise sustainable management strategies (Levin, 2001).

The apparent failure of diversity conservation tactics (Soulé, 1991; Faith, 2011), and the need to gain more profound understanding about the factors governing and/or governed by biodiversity is urgent and crucial. Diversity indices are relevant tools on which far-reaching decisions are based on in conservation science (Walker and Faith, 1994; Reid *et al*., 2004). Indices derived from phylogeny play an important role in this area, where decisions frequently have to be taken on basis of a limited data about the system in question. Previously, the tendency was to focus on species diversity in one dimension using a single parameter (e.g., species richness) (Gaston, 2000). However, current studies employ different descriptors, and example of two of such descriptors that are improving description and understanding of diversity are *macrophysiology* and *trait* approaches. Macrophysiology describes how physiological traits are distributed in space (Chown *et al.*, 2004); while morphological traits enable exploration selection pressures between different species assemblages (Vermeij, 1978; Ricklefs and Miles, 1994; Roy *et al*., 2004; McGill *et al*., 2006). The functional trait approach is interested in explaining the abundances and distributions of species (McGill *et al*., 2006). It advocates for the examination of numerous functional traits and also species' abundance and trait distributions across environmental gradients (McGill *et al*., 2006). The goal of the functional trait approach is to explore how the fundamental niche is determined by physiological and morphological traits and consequently how organismal traits and the fundamental niche are related to the realized niche (McGill *et al*., 2006). A functional trait is defined as an attribute of an organisms' morphology or physiology that affects fitness indirectly via growth, reproduction and survival (Violle *et al*., 2007). A trait-based approach in combination with an understanding of where species occur in relation to environmental gradients may provide new perspectives to species diversity; especially because most spatial and temporal patterns of diversity are based solely on the unit of species richness (Roy *et al*., 2004).

Morphological traits are useful tools for detecting different selection pressures at species-rich and species-poor systems (Vermeij, 1978). For example, gastropod shell armour is more elaborate in species-rich tropical system than in species-poor temperate rocky intertidal environments (Vermeij, 1978). This relationship infers a gradient of protection against predation to tropical species (Vermeij, 1978). Although most diversity measures are likely to correlate with species richness, e.g. genetic diversity, in some cases the relationship between species richness and the traits of species can be complex and non-linear (Foote, 1997; Roy and Foote, 1997). Morphological diversity in most species-rich systems is not higher than in systems with half the number of species, suggesting that species-poor systems can still harbor a great variety of morphological trait diversity (Roy *et al.*, 2001). Morphological traits have also been used to examine differences between species-rich and species-poor systems (Ricklefs and Miles, 1994). From basic principles, morphological traits of species in species-rich systems, relative to species-poor systems, could be expected to display either (a) increased morphological trait variety, i.e., a greater occupied morphospace, and trait differences between species, (b) minimized trait differences between species within a larger or similar occupied morphospace as temperate species or (c) have similar traits, i.e. show morphological overlap, in an occupied morphospace similar to temperate species (MacArthur, 1972; Ricklefs and Miles, 1994).

Measures of ecological functioning emphasize the roles played by organisms and include information on their interactions with their chemical and physical environment (Bremner, 2005). Measuring changes in the rates of ecological processes in the presence of anthropogenic impacts will, therefore, incorporate information on the chemical and biological components of ecosystems (Bremner, 2005). Hence, investigation of ecological functioning focus on the types of taxa present in marine communities and their responses to anthropogenic impacts. Taxa interact in various ways with their physical and chemical environment depending on the characteristics they express, and changes in the occurrence of these taxa have implications for ecological processes (Bremner, 2005). Organisms sharing particular characteristics are not always affected in the same way (Ramsay *et al.*, 1996) and as the methods also do not examine the responses of every taxon expressing a particular characteristic; it is difficult to determine their general responses. This thus compromises the ability of the methods to determine anthropogenic effects at the ecosystem level (Bremner, 2005).

Nonetheless, a promising method for evaluating the ecological functioning of marine benthic assemblages is the use of biological traits analysis (Bremner; 2005), which originated from terrestrial and freshwater ecosystems studies (Olff *et al.*, 1994; Townsend and Hildrew, 1994; McIntyre *et al.*, 1995). Many terrestrial ecosystem studies have found positive effects of plant diversity on ecosystem processes, but this pattern has been less general in marine systems, where many studies find weak or no effects (Stachowicz *et al.*, 2007). The biological trait analysis approach explicitly incorporates information on the attributes of all members of the species assemblage, and on a wide range of attributes connected to organisms' interactions with each other and their physical and chemical environments, as well as their perceived responses to anthropogenic stress (Bremner, 2005). It can also accommodate intraspecific variation in trait expression (Chevenet *et al.*, 1994); thereby overcoming the problems encountered in trophic or functional group analyses where taxa fit into more than one functional category. Characters such as reproduction type, larval type, body size, movement, body form, growth rate, feeding type, attachment etc. are substituted for species names and multivariate analyses are conducted (Fleddum, 2010). Ostensibly, several factors influence the number of traits selected for inclusion in biological trait analysis, such as the length of the taxon list utilized, the amount of information available on biological characteristics of these taxa and the time required for gathering the information (Bremner, 2005). The use of the biological trait analysis (BTA) makes it possible to compare assemblage patterns of species and traits analyses, and also can reveal relationship of structure and functional properties (Chevenet *et al.*, 1994; Charvet *et al.*, 2000; Bremner *et al.*, 2003b). The BTA can better discriminate environmental differences in comparison with taxonomic composition. The traditional biodiversity data analysis methods tend to underestimate the importance of rare species although it has provided useful information of benthic community structure over the years (Bremner, 2005; Fleddum, 2010). The use of BTA together with traditional biodiversity analysis is helpful in identifying impact-driven alterations to ecological functioning as well as providing information for ecosystem monitoring, management and conservation (Fleddum, 2010). For example, Bremner *et al*. (2003b) compared traditional analysis technique using relative taxa composition and trophic guilds with BTA in investigating the functioning diversity of macrobenthic fauna in the southern North Sea and eastern English Channel. They concluded that BTA can offer information on assessing ecosystem functioning in benthic environments on both large and small scales, and that there is a significant relationship between habitat and traits.

According to Usseglio-Polatera (2000b) the species trait approach has the potential to evaluate the actual state of ecosystems, discriminate among different types of human impact, and help to develop monitoring tools for ecological communities. However, the use of the BTA in the marine benthic ecosystems has received little attention (Bremner, 2005) and lags behind the freshwater and terrestrial counterparts (Bremner, 2008). Of much concern is the lack of study in the Guinea Current Large Marine Ecosystem (GCLME) focusing on functional species assemblages employing the BTA approach. Where information on general benthic biodiversity in the region has been carried out, the literature is widely dispersed and inadequate. The GCLME is one of the productive large marine ecosystems in the world’s ocean (Ukwe, 2003;

Ukwe *et al.*, 2006). The fishery and the plankton have received some attention (Bainbrige, 1972; Bakun, 1978; Mensah, 1995; Koranteng, 1998; Wiafe, 2002; Wiafe 2008). However, very little is known about the dynamics of the macrobenthic community, especially its functional diversity and community structure. Knowledge of macrobenthic functional diversity and community structure will contribute immensely to understanding the overall trophic dynamics, biodiversity and ecosystem functioning of the GCLME.

1.1 Study Objectives and Hypothesis

The primary aim of this research is to investigate macrobenthic functional traits diversity and community assemblages along spatial scales in the GCLME. The research further explored whether environmental gradient, on spatial scale, correlated with local species diversity and their functional attributes. The study aimed at testing the hypothesis that the marine benthic functional biodiversity effects on ecosysem processes/properties were the results of established environment gradient in the ecosystem . Specifically, the following predictions were tested as part of the overall hypothesis:

- Dominant macrobenthic functional trait assemblages rather than species richness exert the strongest control on ecosystem properties/process; and
- abiotic stressors/drivers/factors select for differences in functional traits and species assemblages.

In order to evaluate the central predictions of the study hypotheses, the following objectives were formulated:

- Identify and quantify dominant functional traits and elucidate their influence on ecosystem functions;

- Ascertain how macrobenthic faunal communities and eco-functional trait assemblages are influenced by abiotic factors. This will assist in understanding and predicting how benthic communities and ecosystem properties might be affected by environmental variability and disturbance;
- Identify dominant epibenthic functional traits across bathymetric gradients;
- Investigate the effects of bottom trawling for demersal fishes on species diversity and functional structure of epibenthic communities; and
- Evaluate the ecological quality status of the GCLME using epibenthic macrofauna species.

1.2 Study Justification

The past several decades have witnessed a soaring research interest on earth's biodiversity across all environments, including studies that assessed trends in biodiversity and the underlying mechanisms that produced and maintained such trends. Escalating concerns over the loss of marine biodiversity and associated consequences have increased the urgency for research for a better mechanistic understanding.

Many of such studies/research have been carried out in short-term and on local scale with findings (species diversity and the driven forces) which still limit our understanding. Nonetheless, a growing body of research has addressed the functional consequences of diversity for ecosystem processes (Stachowicz *et al.*, 2008). The primary goals of Biodiversity-Ecosystem functioning research have been to investigate how biodiversity and ecosystem functioning are linked and to understand the mechanisms that inform such relationships. In accordance, recent biodiversity researches have principally focused on important links between number of species and ecosystem functioning (Hooper *et al*., 2005; Worm *et al*., 2006; Solan *et al*., 2008, 2009).

Earlier studies on biodiversity-ecosystem functioning tested whether ecosystem functioning was enhanced in species-rich versus depauperated assemblages (Srivastava and Vellend, 2005), but was demonstrated that biodiversity generally enhances many process rates such as resources use or biomass production, across a wide spectrum of organisms and ecosystems (Balvanera *et al*., 2006). However, the evidence for positive effects of biodiversity of ecosystem functioning is neither ubiquitous nor unequivocal (Thompson and Starzomski, 2007; Jiang *et al*., 2008), stimulating conservable scientific debate (Loreau *et al*., 2002). Following from this, four research themes namely: functional traits, environmental gradients, interactions milieu and performance currencies have been suggested (McGill *et al*., 2006) as a cornerstone of modern ecology in order to fully understand the biodiversity–ecosystem functioning.

There have been many studies investigating the relationship between species diversity, functional diversity and ecosystem function (Petchey and Gaston, 2002; Petchey and Gaston, 2006; Bremner, 2008). In marine benthic ecosystems, however, only a few studies have examined that relationship and most of them have shown a strong correlation between species diversity and functional diversity (Bremner *et al*., 2003b; Micheli and Halpern, 2005; Hewitt *et al*., 2008). Furthermore, there are studies investigating how biotic and abiotic components affect the temporal and spatial variability in functional diversity (Emmerson *et al*., 2001; Raffaelli *et al*., 2003; Micheli and Halpern, 2005; Ieno *et al*., 2006; Bell, 2007; Norling *et al*., 2007), but it seems that such processes affect species diversity and functional diversity in a similar way (Bremner *et al*., 2003b; Micheli and Halpern, 2005; Hewitt *et al*., 2008).

1.3 Datasets for the Thesis

The datasets used for this thesis research included the following:

- Epibenthic trawl samples collected along the continental shelves of Ghana, Togo, Benin and western part of Nigeria in 2003 as part of the West Africa Gas Pipeline Project (WAPCo, 2003). This data was used for the assessment of the impacts of bottom trawling on epibenthic faunctional assemblage patterns.
- Macrobenthic fauna and sediment samples collected from Guinea Bissau to Gabon in 2007 as part of the Guinea Current Large Marine Ecosystem (GCLME) project comprising 16 countries (GCLME, 2006). This data was used to investigate soft-bottom macrobenthic infauna functional assemblage patterns and their response to environmental variability.

1.4 Organization of Thesis

The thesis comprises five chapters. Chapter 1 presents a general introduction to the thesis, with a brief background information on marine biodiversity, functional diversity, trait analysis, level of macrobenthic information in the GCLME, scientific hypothesis and study objectives. The various data sets used in the analyses have also been presented. Chapter 2 presents a detailed review of relevant literature on the subject, biodiversity structure and functions of macrobenthic communities as well as environemntal factors influencing benthic biodiversity assemblages. Chapter 3 describes the ‘macrobenthic functional traits diversity and community structure along environmental gradient. Chapter 4 focuses on impact of demersal fish trawling on the structure and functional assemblages of epibenthic fauna along bathymetric gradient. Chapter 5 gives general conclusions and recommendations. The species list and biological trait database are presented as Appendices I & II. Appendix III shows the carbon:nitrate ratios and the sources of organic load, while statistical descriptions are annotated in Appendix IV.

CHAPTER TWO

LITERATURE REVIEW

2.1 Marine Benthic Biodiversity

The idea of biodiversity has taken hold on science and society with its multifaceted concepts (Zajac, 2008) and has also emerged as a major field within ecological research. Biodiversity has been variously defined as the variety of life and collectively referred to variation at all levels of biological organization (Sheppard, 2006). According to Harper and Hawksworth (1994), biodiversity refers to the extent of genetic, taxonomic and ecological diversity over all spatial and temporal scales. However, the Convention on Biological Diversity (CBD) gave the most important and far-reaching definition in its Article 2 to mean '*the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this include diversity within species, between species and of ecosystem*' (Convention on Biological Diversity, 1992). In seeking to describe the "variety of life" or "nature," biodiversity includes three components of diversity, namely, "within species," "between species" and "of ecosystems" (Costello, 2000). The usage of the term is value laden connoting that biodiversity is *per se* a good thing, that its loss is bad, and that something should be done to maintain it.

Diversity is usually designed as being α-diversity (the diversity within a given habitat), β-diversity (the degree to which communities show spatial variability in species composition from place to place) and γ-diversity (the overall diversity in a whole region; (Whittaker, 1975). At the species level in a given assemblage, α-diversity can be regarded as either the number of species present ("species richness"), the proportional abundance or homogeneity of individual species ("evenness" or "equitability") or more commonly a combination of both (Terlizzi and Schiel, 2009).

The marine benthic biodiversity comprise organisms that span a wide range of sizes, including micro-, meio-, macro- and megafauna (Clarke and Warwick, 1994; Dittmann, 1995; Zajac, 2008). These organisms are operationally classified as microbenthos (< 63 µm), meiobenthos (from 63 µm to 500 µm) and macrobenthos (> 500 µm or > 1000 µm) according to the sieve mesh size used for extracting them from sediment cores or grabs. The macrofaunal forms are by far the better known and are the main essential component of environmental impact studies (Clarke and Warwick, 1994). Marine macrobenthos are a diverse group of organisms composed mainly of molluscs (bivalves and snails), polychaetes (bristle worms), crustaceans (amphipods, shrimps, and crabs) and echinoderms (sea cucumbers, brittle stars, sea urchins) (Gray, 1981a). These organisms are central elements of marine ecosystems and provide excellent indicators of environmental health. They also play multiple ecological roles within the marine ecosystem and are a critical part of environmental monitoring and evaluation programmes. Most macrobenthic animals are relatively long lived (several years) and thus integrate changes and fluctuations in the environment over a longer period of time. Changes in soft bottom zoobenthic communities in response to the environmental impact have been successfully implemented world-wide in pollution assessment studies and monitoring programs (Pearson and Rosenberg, 1978).

Variations in species composition, abundance and biomass can be used to assess environmental disturbance. Comparatively rich and diverse shallow-water benthic communities are amenable for more sensitive analyses of eutrophication effects. The potential benefits of using macro-invertebrates include quick detection of pollution through differences between predicted and actual faunal assemblages (Ormerod and Edwards, 1987). Of relative importance, benthic invertebrates are relatively sessile (therefore allowing spatial patterns to imply causation), can be sampled quantitatively without high cost, are well described taxonomically, and reveal ecologically meaningful and important patterns, even at coarse levels of taxonomic discrimination (Warwick, 1988c). Analysis of differences in macrobenthic community structure is one of the mainstays of detecting and monitoring the biological effects of marine pollution and habitat disturbance (Warwick and Clarke, 1993) as well as for ecological modeling (Tumbiolo and Downing, 1994; Josefson and Rasmussen, 2000).

In most environmental studies of impacts, benthic invertebrates are the principal targeted organisms (78 percent of all studies), reflecting their suitability as ecological indicators (Clarke and Warwick, 1994; Peterson and Bishop, 2005). The macrobenthic infaunal communities are especially suited for long-term comparative investigations since many of the constituent species are of low mobility, relatively long lived and integrate effects of environmental changes over time. Consequently, macrobenthic fauna constitute good biological candidates for monitoring ecosystem health and processes. Cury and Roy (2002) have stressed that studies that link the different components of the trophic web or the spatial and temporal dynamics of the interaction between the environment and marine resources are needed as they have important implication for managing the resources.

Marine biodiversity is of direct benefit to society as a food source, potential pharmacopoeia (Hunt and Vincent, 2006), stabilizer of inshore environments (Jie *et al*., 2001) and regulator of atmospheric processes (Murphy and Duffus, 1996). Marine biodiversity provides indirect benefits to society through ecological stability (Menge *et al*., 1999) and benthic-pelagic coupling (Ponder *et al*., 2002) which contribute to self-sustaining marine ecosystems. Marine biodiversity also has recreational, aesthetic and intrinsic value (Wilson, 1994; Ponder *et al*., 2002).

2.2 Functional Role of Benthic Communities

Benthic communities perform numerous ecological functions to the systems they inhabit. Benthic organisms continually process, transport, and modify marine sediments. There are those that bind, protect and stabilize near-surface sediment and those that loose and destabilize the sediment (Nichols and Boon, 1994). They also play a vital role in organic matter processing and nutrient cycling at the water/sediment interface (Aller and Yingst, 1985; Rosenberg, 2001) and decomposition of dead matter or waste materials (Snelgrove *et al*., 1997). Sediment organic matter is a causal factor of infaunal distribution (Snelgrove and Butman, 1994) being the dominant source of food for deposit-feeders (Pearson and Rosenberg, 1978), and indirectly (e.g., through re-suspension) for suspension feeders (Snelgrove and Butman, 1994). Benthic organisms also improve the conditions within the sediment, such as oxygenation (Reise, 1985) and loosen subsurface sediments and render them inhabitable by other macrofauna (Flint and Kalke, 1986).

Benthic invertebrate assemblages are heavily involved in the regulation of ecosystem processes (Snelgrove, 1998), so provide a useful study unit. Functioning in these assemblages will be dependent on the biological characteristics, or traits, exhibited by constituent species, because these determine how the species contribute to ecological processes.

Woodin and Jackson (1979) have proposed five functional groups of benthic organisms in relation to their effects on the sediment: (i) mobile burrowers that destabilize the sediment (including their feeding activity) such as crustaceans, amphipods & tanaids, and Maldanid polychaetes; (ii) sedentary organisms that cause the sediment to be more easily resuspended (e.g., infaunal holothurian, *Molpadia oolitica,* Crustacean *Callianassa*); (iii) sedentary organisms that do not inhabit tubes that still straddle the sediment-water interface and modify the local hydrography such as to reduce re-suspension and, by virtue of buried parts, bind the subsurface particles together (e.g., seagrasses such *Thalassia* & *Zostera*, Sabelid polychaete worms); (iv) tube builders that stabilize the sediment by incorporating it, often in mucus-bound form into their tubes (e.g., mud snail *Illyanasa obsolete*, polychaete *Polydora)*; and (v) neutral species having no impact on sediment deposition or re-suspension. The feeding type of the benthic community is considered as an adaptation to the sediment characteristics (Rosenberg, 1995).

However, it has been suggested that animal and sediment correlation is a result of hydrological and geological processes associated with sediment granulometry rather than a function of organism in available space within sediment (Parry *et al*., 1999). For macro-invertebrates, the requirements of life in unconsolidated sediments inevitably involve the need to move particles around in some way, whether as a consequence of locomotion through the sediments, or feeding upon the organic material associated with them. This is known as bio-turbation (Hall, 1994). Bio-turbation occurring in sediments regulates carbon degradation and bentho-pelagic nitrogen cycling (Biles *et al.*, 2002; Widdicombe *et al.*, 2004).

Benthic species also affect the microbial processes in the sediments by modifying particle distribution, sediment porosity, and solute transport (Krantzberg, 1985). Bio-turbation of sediments by burrowing or deposit-feeders through processes such as irrigation, pelletization and tube construction, usually increases sediment pore space and thus, water content in the upper sediment layer (Rhoads, 1974; Rhoads and Young, 1970). Bio-turbation lowers erosion resistance of the surface, and thus destabilizes the bed sediment. Bio-turbation can be important in excluding particles and pore water nutrients across the sediment-water interface as well as through various vertical chemical gradients in the sediment (Nichols and Boon, 1994).

The impacts of invertebrates on biogeochemical processes are often due to biogenic structure in marine sediments (Aller and Aller, 1986, Kristensen *et al.*, 1991; Mayer *et al.*, 1995; François *et al.*, 1997) and infaunal activity (Holst and Grunwald, 2001). Biogenic structures can modify organic matter distribution and solute transport at the water-sediment interface (Krantzberg 1985, de Vaugelas and Buscail, 1990). Solute transport is enhanced by animal movement and burrow ventilation, which is a process known as bio-irrigation (Riisgård and Banta, 1998). Bioturbation (i.e., sediment biogenic activities) does not only play a crucial role in the stabilization of marine benthic environments (Woodin and Jackson, 1979; Kristensen *et al.*, 1985) but, also in recycling of nutrients that enhance ocean productivity. Oceanic productivity is related to abundance of commercially important species such as fishes thereby depicting a coupling between benthic biodiversity (functional effects) and fisheries (Hodson *et al.*, 1981; Bell and Woodin, 1984; Josefson and Rasmussen, 2000) through primary production (Kjerve, 1994).

The health of marine ecosystems is often assessed in terms of the taxon composition of faunal communities, or on the distribution of abundance/biomass between the species present (e.g., Warwick and Clarke, 1991; Bonsdorff and Blomqvist, 1993). Marine macrobenthic fauna are used in pollution and ecosystem health monitoring studies to ascertain pollution effects on the ecosystem (Sherman and Anderson, 2002). Potential benefits of research on macro-invertebrates include quick assessment of biological resources for conservation purposes and the detection of pollution through differences between predicted and actual faunal assemblages (Ormerod and Edwards, 1987). Macrobenthic communities have the capabilities to integrate into their system both short-, and long-term environmental changes and thus are excellent candidates for monitoring environmental impacts (Borja *et al.*, 2000). Snelgrove (1998) reported that the roles performed by benthic species are important in regulating ecosystem processes and that these roles can be portrayed by biological traits they exhibit.

2.3 Biodiversity Indices and Measurements

Measurements of biodiversity are often used as bases for making decisions on planning and conservation actions. In conservation, diversity indices become mighty tools on which far-reaching decisions are based on (Walker and Faith 1994; Reid *et* *al*., 2004). It is evident from the biodiversity definition that there could be no clear single all-embracing measure of biological diversity owing to its great complexity. The breadth of ways in which differences can be expressed is infinite. The most practical and relevant measures of biodiversity within species are the phenotypic or visible attributes of populations. Nevertheless, measurements of biodiversity are based on three assumptions (http://www.coastalwiki.org):

- *All species are equal in abundance:* meaning that richness measurement makes no distinctions amongst species and treats the species that are exceptionally abundant in the same way as those that are extremely rare species. The relative abundance of species in an assemblage is the only factor that determines its importance in a diversity measure.

- *All individuals are equal in size:* this means that there is no distinction between the largest and the smallest individual; in practice however the smallest animals can often escape for example by sampling with nets. Taxonomic and functional diversity measures, however, do not necessarily treat all species and individuals as equal.

    - *Species abundance has been recorded in using appropriate and comparable units.* It is clearly unwise to use different types of abundance measure, such as the number of individuals and the biomass, in the same investigation. Diversity estimates based on different units are not directly comparable.

Biodiversity has many facets, yet three generally different concepts in its quantification can be distinguished (Purvis and Hector, 2000):

(i) Richness: was probably the first measure used for assessing diversity. Counting the number of taxa in the sample under consideration is always the first step. Often richness or an estimate of it is the only measure available for large unexplored regions;

(ii) Evenness- often the individuals are not evenly distributed among species. A site containing dozens of species may not seem particularly diverse if 99.9% of the individuals belong to the same species. Evenness is defined as the ratio of observed diversity to maximal possible diversity if all species in a sample were equally abundant (Purvis and Hector, 2000); and

(iii) (iii) Phylogeny: difference between the observed organisms is another facet of diversity. Phenotypic and genetic variability are reflected in phylogeny. A community consisting of 30 species of polychaeta is intuitively less diverse than one consisting of 30 benthic macrofaunal species of 5 different classes. These three principal concepts can be applied not only at the species level, the definition of the term species being a problem of its own (Hey, 2001), but also on higher taxonomic levels or arbitrary divisions like functional groups. Species is the unit of diversity most easily conceptualized and is therefore most commonly considered (Willig *et al*., 2003).

Many diversity indices combine two or even all three concepts into one number, in order to summarize information for decisions and comparisons. However, information is always lost in this process and none of the three concepts should be held in low regard.

2.3.1 Diversity Indices

Species richness: The oldest and most straightforward measure, where: ***s***, the sum of species in the sample, ***d'***, Margalef's species richness, ***n***, number of individual species, and $\log_e$ is the natural logarithm. Margalef (1958) proposed a richness index which is standardized against the ***n*** in the formula below, following information theory.

$$d = \frac{s-1}{\log_e n}$$

(Margalef, 1958)

Shannon's diversity index: The Shannon-Weaver diversity index is one of a so called family of heterogeneity indices. These indices do not only take taxa richness into account but also depend on the relative distribution of individuals. The logarithm can be taken to any base but taken to the base of two gives H' a special meaning: bits per species. It is the mean number of binary decisions necessary to determine the taxum of an individual. Originally derived from communication theory (Shannon and Weaver, 1949), this index was severely criticized by Hurlbert (1971) for containing no ecologically valuable information. Apart from the problem of interpreting the ecological meaning of bits per species, all heterogeneity indices share the drawback that information is lost by merging two concepts. It is not possible to tell from the final value, if it is high or low due to species richness or relative abundances or a combination of both.

$$H' = -\sum_{i=1}^{s} p_i \log_2 p_i$$

(Shannon and Weaver, 1949)

Simpson's index of diversity: The Simpson's index D also belongs to the class of heterogeneity indices and is a probability measure. Therefore it ranges between 0 and 1 but it appears in three similar formulations: D, 1-D and 1/D. Each one has its own name but often they all use the symbol D and are simply called Simpson's index, so attention is advisable at comparisons. In the formulation of 1-D, the Simpson's index of diversity is the probability of encountering two different species when randomly picking two individuals of a sample.

$$D = 1 - \sum_{i=1}^{s} p_i^2$$

(Simpson, 1951)

Pielou's evenness: Pielou (1966) defined this equitability measure for the Shannon weaver index. J' will approach 1 if H' will approach the maximal possible value for the given set of species, meaning that all species in the sample will be equally abundant.

$$J' = \frac{H'}{H'_{max}} = \frac{H'}{log_2 s}$$

(Pielou, 1966)

Taxonomic diversity Δ: Proposed by Warwick and Clarke (1995), the taxonomic diversity index delta is derived from the Simpson index. ij is the "distinctness weight" and has no fixed syntax. It could be simple as a number for relatedness (1=same genus, 2= different genus same family, etc.) or a measure of distance between species in a phylogenetic tree.

$$\Delta = \frac{\sum_{i=1}^{s}\sum_{j=1}^{s} \omega_{ij}\, x_i\, x_j}{\left(\frac{n(n-1)}{2}\right)}$$

(Warwick and Clarke, 1995)

Taxonomic distinctness Δ +: Taxonomic diversity calculated only on presence/absence data. If all xi are assumed to equate to unity then taxonomic diversity reduces to taxonomic distinctness.

$$\Delta + \; = \frac{\sum_{i=1}^{s}\sum_{j=1}^{s}\omega_{ij}}{\left(\frac{s(s-1)}{2}\right)}$$

(Warwick and Clarke, 1995)

Sum of phylogenetic diversity Φ +z: Introduced by Faith (1992). The total branch length of the phylogenetic tree.

Average phylogenetic diversity Φ +: This is simply the total phylogenetic diversity divided by the number of species.

Although this is not exhaustive list, the selection shows representation of all the three concepts (richness, evenness, difference), as well as indices which incorporate concepts. Other common indices have not been used because they are in one way or the other inappropriate for the dataset, like Fisher's α, which assumes a log series distribution of species abundances, or the rarefaction method of Saunders which allows comparisons of samples of unequal size.

2.3.2 Functional Diversity

With the unprecedented nature of biodiversity changes, science is faced with the challenge of predicting how ecological systems will respond. Predicting future changes based on relationships and patterns in the current environment records offers one way to address this question. While this approach has yielded important insights, it is largely correlational, making the identification of the roles of specific drivers of change (e.g. climate, atmospheric chemistry, land use, biota) difficult (Osmond *et al.*, 2004). A complementary approach is to identify the functional or mechanistic basis of the links between ecosystem functioning and global changes by scaling processes (Woodward *et al.*, 1991; Field *et al.*, 1992; Iverson and Prasad, 2001).

Functional diversity can be quantified using a variety of indices that capture different aspects of the distribution of trait values within a community (Bótta-Dukàt, 2005; Ricotta, 2005; Petchey and Gaston, 2006). Functional groups describe organisms that share a similar physiological or ecological function e.g. deposit-feeders, bioturbators, predators (Bonsdorff and Pearson, 1999). The validity of using functional groups has been questioned because analyses based on such divisions may be meaningless without more comprehensive knowledge about life history and biology of marine biota than is currently available for most species (Pearson, 2001). In addition, some evidence points to species identity being closely linked to ecosystem services such as bioturbation (Norling *et al*., 2007).

In a broad scale functional diversity research, Naeem and Wright (2003) proposed four step-wise factors:

i. determination of species composition across sites through regional biotic inventory of species pool and application of environmental filters (Woodward and Diament, 1991; Keddy, 1992) (hierarchy of abiotic and biotic factors that constrain the distribution and abundance of the species, see Diaz *et al*., 1999; Lavorel and Garnier, 2002) to obtain local species composition.
ii. Species abundance determination through relative abundance or common and rarity.
iii. Determination of functional traits by selecting driver of biodiversity impacts, ecosystem process, screening the local biota for relevant functional traits, establishing response traits relevant to the selected driver, and also establishing effect traits relevant to selected ecosystem function.
iv. Determination of ecosystem functioning.

Nonetheless, functional diversity (utilizing functional/biological traits analysis) has assumed increased prominence in biodiversity ecosystem function (e.g. Petchey and Gaston, 2002; Bremner, 2006). According to Mason *et al*., (2005), functional diversity is a measure (or group of measures) of the distribution of species and abundance of a community in functional attribute space that represents the following:

- the amount of functional attribute space filled by species in the community (***functional richness***),
- the evenness of abundance distribution in filled niche space (***functional evenness***), and
- the degree to which abundance distribution in niche space maximizes divergence in functional attributes within the community (***functional divergence***).

In their perspective, Tilman, (2001) and Hooper *et al*. (2005) refer to functional diversity to mean the range and value of organism traits that can influence ecosystem properties. According to Hooper *et al*. (2005), functional diversity can be expressed in a variety of ways including the number and relative abundance of functional groups (Tilman *et al*., 1997, Hooper and Vitousek, 1998) and (Spehn *et al*., 2000), the variety of interactions with ecological processes (Martinez, 1996), and the average difference among species in functionally related traits (Walker *et al*., 1999). Functional groups are defined as groups of taxa which share a range of similar attributes and have analogous effects on major ecosystem processes (Bonsdorff and Pearson, 1999).

Functional diversity results from the different ways by which different species exhibit similar functional traits, or the number of different functional groups sharing biological traits (Wright *et al*., 2006). Functional attributes of species are therefore crucial to understanding the effects of marine biodiversity and its role in ecological patterns and processes. Functional categorization of marine species is a useful approach for comparing communities over large scales in a way that transcends taxonomic boundaries, and for linking changes in structure to effects on ecological function (e.g. Bellwood *et al*. 2003; Floeter *et al*. 2004; Micheli and Halpern, 2005). An effective functional classification could be a cost-effective way of predicting effects of loss (or restoration) of particular taxa on ecosystem functioning and could have valuable implications for management and conservation (Micheli and Halpern, 2005). Functional classifications can enable meaningful comparison of the roles of biodiversity in different ecosystems as they transcend taxonomic differences (Micheli and Halpern, 2005; Bremner, 2006).

Functional classification of organisms can also improve mechanistic understanding of community assembly (Micheli and Halpern, 2005). This is because diversity is manifest in species identities (e.g., variations in form and functions) and therefore variations in species traits is a key element in biological diversity (Crowe and Russell, 2009). Reiss *et al*. (2009) emphasized that biodiversity-ecosystem functioning (B-EF) experiments regarding traits, could hold species identity constant, and alter traits and functional diversity to demonstrate whether species provide unique contributions to ecosystem processes. Ecosystem functions (e.g., nutrient cycling, sediment stabilization etc.) are moderated by the functional attributes of species in a community. To understand how an ecosystem will function and its ability to provide crucial ecosystem services as well as its capacity to respond to environmental changes, functional diversity of the assemblages are critical fundamental steps.

Thus, there have been increased interests in examining ecosystem consequences of biodiversity loss in marine systems (e.g., Emmerson and Raffaelli, 2000; Duffy *et al*., 2001, Emmerson *et al*., 2001; Stachowicz *et al*., 2002; Solan *et al*., 2004; Hooper *et al*., 2005; Worm *et al*. 2006; Bracken *et al*., 2008) especially in high latitude locations. However, the biodiversity ecosystem function (B-EF) relationship can be dependent on environmental conditions for specific ecosystem functions (Hiddink *et al*., 2009), which differ in spatial scales. Functional diversity incorporates interactions between organisms and their environment into a concept that can portray ecosystem level structure in marine environments (Bremner *et al*., 2003a). The functional traits of benthic species are modified on many temporal and spatial scales (Solan *et al*., 2004) due to the effects of physical, chemical and biological characteristics. Environmental gradients may form geographic patterns of diversity by influencing local processes such as predation, resource partitioning, competitive exclusion, and facilitations that determine species co-existence (Levin *et al*., 2001).

2.3.3 Functional Diversity Indices

Recently, several methods have been proposed and described on how to calculate functional diversity (Mason *et al*., 2003, 2005; Botta-Dukát, 2005; Ricotta, 2005; Petchey and Gaston, 2006; de Bello *et al*., 2006). Some consider species presence/absence, whereas others are based on abundance data (e.g., Bady *et al*., 2005; Botta-Dukát, 2005; Mason *et al*., 2005). However, incorporating species abundances into a measure of functional diversity poses several questions on weighing the relative contribution of richness and evenness components (Hurlbert, 1971), and on the relationship of trait dissimilarity (Walker *et al*., 1999) to the ecological diversity of species (Magurran, 1988). It is therefore a more complex problem than previously thought (Mouillot *et al*., 2005; Ricotta 2005; Petchey and Gaston, 2006).

Petchey *et al*. (2004) compared four presence/absence measures of functional diversity: (i) species richness (SR), (ii) functional group richness (FGR), (iii) a dendrogram-based measure (DBM) and (iv) functional attribute diversity (FAD). Although the simplest measure is SR, it assumes that all species are equally different and the contribution of each species to functional diversity is independent of species richness (Petchey *et al*., 2004). Functional group richness (FGR) is the number of functional groups present in the community. FGR assumes that the species within the same group are identical in function (Lawton and Brown, 1993) and assigning a species into a category is unambiguous. However, many animal species use, for instance, a variety of feeding strategies and show omnivory (Lancaster *et al*., 2005; Woodward *et al*., 2005ab). Thus, measuring functional diversity based on FGR is not always meaningful, even if its application can be fruitful when no taxonomical information on the fauna of the study area is available (Cummins *et al*., 2005).

A further problem is that the number of functional groups is arbitrarily determined. Petchey and Gaston (2002) applied cluster analysis from a matrix of functional traits, and then used the sum of branch lengths of the dendrogram as a multivariate measure of functional diversity (DBM). This function does not suffer from the problem of species categorization since it uses the functional traits of the species (Walker *et al*., 1999; Petchey and Gaston, 2002; Petchey *et al*., 2004; Botta-Dukát, 2005; Ricotta, 2005; Podani and Schmera, 2006), and can be defined as a continuous measure (Petchey and Gaston, 2006). However, DBM also has limitations. For instance, Petchey and Gaston (2002) suggest that after removing a group of species from the community, the functional diversity of the new community should be calculated by deleting those parts of the dendrogram which pertain to the removed objects and then by summing the branch lengths for the remaining part. When a new group of species is captured, a new dendrogram should be calculated for all species (i.e., the original species and the new species). Accordingly, the same community could have different functional diversity if measured by the DBM value, depending upon the original community and the dendrogram from which it was derived.

Functional attribute diversity (FAD) (Walker *et al*., 1999; Petchey *et al*. 2004) is the sum of the pairwise functional dissimilarities of species. FAD can be calculated as follows

$$FAD = \sum_{h=1}^{S} \sum_{k=1}^{S} d_{hk},$$

(Walker *et al*., 1999):

where S is the number of species, and d_{hk} is the dissimilarity between species h and k. Thus, FAD measures the dispersion of species in the functional traits space (Ricotta, 2005) and similarly to DBM, it is also a continuous measure of functional diversity (Petchey and Gaston, 2006).

Among the many methods, the Rao coefficient (another measure of functional diversity proposed by Rao, (1982)) is gaining currency as a good candidate as an efficient functional diversity index, because it is a generalization of the Simpson's index of diversity, it is easy intuitively understandable, and it can be used with various measures of dissimilarity between species (both those based on a single trait, and those based on many traits (Ricotta, 2005; Petchey and Gaston, 2006). However, when intending to quantify the functional diversity, various methodological decisions such as how many and which traits to use, how to weight them, how to combine traits that are measured at different scales and how to quantify the species' relative abundances in a community have to be made.

The Rao index uses species traits to calculate dissimilarity among species (Botta-Dukát, 2005; Lepš *et al*., 2006; Lavorel *et al*. 2008). The Rao index generally reflects the probability that, picking randomly two individuals in a community (i.e., a sample), they are different. For trait diversity, the Rao index represents the probability that they are functionally different (e.g. for single traits, either they have different trait values or different trait categories). The Rao coefficient is very flexible, and can be used with various dissimilarity measures. For example, Shimatani (2001) used it with taxonomic dissimilarity when exploring taxonomic diversity and amino acid diversity; asymmetrical measures can be also used. The main methodological decisions are mainly i) how to measure the species dissimilarity, and ii) how to characterize the proportion of a species in the community. These methodological decisions are also made even if other indices of functional diversity other than Rao's coefficient are being used (Lepš *et al*., 2006).

The mechanistic models concerning the functional consequences of diversity have been based on the fact that species differ from each other (and thus function differently; MacArthur, 1955). Similarly, the importance of the differences among species for maintaining species coexistence was explicitly expressed by the concept of limiting similarity (MacArthur and Levins, 1967). Ecologists have thus progressively realized that species differ from each other in terms of some traits (Díaz and Cabido, 2001) and thus that the effect of ecological diversity might be based on the “extent of trait dissimilarity among species in a community” (or functional diversity; Tilman, 2001; Petchey and Gaston, 2002). Traditionally, species diversity has been considered a surrogate for functional diversity in most studies linking biodiversity to ecosystem functioning (Díaz and Cabido, 2001; Loreau *et al*., 2003). However, some pairs of species are very similar to each other, while some are very different. Consequently, the relationship between species diversity and functional diversity is expected to be positive (Petchey and Gaston, 2002) but not necessarily very tight (Díaz and Cabido, 2001; Petchey and Gaston, 2006).

Other two widely used continuous measures of functional diversity are the dendrogram-based measure (DBM) and the functional attribute diversity (FAD). In contrast to DBM, FAD does not require the knowledge of the entire species pool before the analysis, and hence FAD is a more ideal tool for measuring functional diversity. However, the original form of FAD and its variants have several undesirable properties (Schmera *et al*., 2009). A modified FAD (denoted by MFAD) has therefore been suggested (Schmera *et al*., 2009). The MFAD allows for calculating functional diversity without violating the twinning and monotonicity criteria such that the number of species collected is compensated for (Schmera *et al*., 2009). These requirements are met by replacing the original species by so-called functional species and then by dividing FAD by the number of functional units.

Accordingly, MFAD measures the dispersion of species in the functional traits space so that MFAD values for different communities can directly be compared if the same set of functional trait is used.

2.3.4 Functional Trait Analysis

One of the most promising of the recently proposed approaches to measure functional diversity is biological traits analysis (BTA) (Statzner *et al*., 1994). A biological trait is a character of an organism that may be inherited or environmentally determined. The character can be genotypic or phenotypic i.e., size, body form, movement, feeding, larval type. These characteristics strongly influence ecosystem properties. The contribution of a benthic species to ecosystem processes may be determined by a suite of biological characteristics (Webb and Eyre, 2004a), suggesting the involvement of a number of traits in ecological functioning.

Biological traits analysis uses a series of life history, morphological and behavioural characteristics of species present in assemblages to indicate aspects of their ecological functioning (here defined as the maintenance and regulation of ecosystem processes (Naeem *et al*. 1999)). The roles performed by benthic species are important for regulating ecosystem processes (Snelgrove, 1998) and these roles are determined by the biological traits species exhibit (Bremner *et al*., 2006). Several characteristics can be involved in organisms’ responses to individual environmental variables. For example, responses to benthic trawling have been linked to traits such as feeding methods, body size, flexibility, mobility and burrowing activities (Kaiser *et al*., 1998; Rumohr and Kujawski, 2000; Bradshaw *et al*., 2002; Thrush and Dayton, 2002).

The approach aims to provide a description of multiple aspects of functioning based on features of the biological ecosystem component. It does this by utilising specific species traits as indicators of functioning (Diaz and Cabido, 2001) and examining the occurrence of these traits over assemblages (Bremner, 2008). Biological Traits Analysis (BTA) is based on habitat templet theory, which states that species' characteristics evolve in response to habitat constraint (Southwood, 1977). Community structure is governed by habitat variability and the biological traits exhibited by organisms will provide information about how they behave and respond to stress (Lavorel *et al*., 1997), thereby indicating the state of the environment (Usseglio-Polatera *et al*., 2000b). BTA uses multivariate ordination to describe patterns of biological trait composition over entire assemblages (i.e., the types of trait present in assemblages and the relative frequency with which they occur) (Bremner *et al*., 2006).

Species trait analysis (STA) focuses on defining biological and ecological characteristics of faunal assemblages. It incorporates information on species' distributions and the biological characteristics they exhibit, to produce a summary of the biological trait composition of assemblages (Bremner *et al*., 2005). The approach provides a link between species, environments and ecosystem processes, and is potentially useful for the investigation of anthropogenic impacts on ecological functioning (Bremner *et al*., 2005). Species diversity indices do not take into account functional differences between species, though some authors pointed out the necessity of including these differences between species to estimate a diversity related to changes in environmental conditions or influencing ecosystem processes (Diaz and Cabido, 2001; Mouillot *et al*., 2005). Alternative groups, functional diversity and productivity descriptors are proposed (Bremner *et al.*, 2003; Mouillot *et al.*, 2006). These methods offer the opportunity to compare sites with different taxonomic compositions and allow derivation of indicators related to ecological status of communities under scrutiny.

Ecological functions can be described by a variety of biological traits that reflect the adaptations of species to environmental conditions (Townsend and Hildrew, 1994). It is thus promising to quantify the functional diversity in ecological communities to study both the response of diversity to environmental gradients and the effects of diversity on ecosystem functioning (Lepsˇ *et al.*, 2006). The distinction between functional effect groups and functional response groups is directly analogous to the distinction between the functional and habitat niche concept (e.g., Leibold, 1995) where the functional niche encompasses the effects that a species has on community and ecosystem dynamics, and the habitat niche encompasses the environmental parameters necessary for species survival (Hooper *et al.*, 2005).

Changes in the environment can affect ecosystem processes directly through effects on abiotic controls and indirectly through effects on the physiology, morphology, and behavior of individual organisms, the structure of populations, and the composition of communities (Suding *et al.*, 2008)**.** Changes of the functional components of the communities represent the adaptations of the organisms to the environment and their response to stress (de Juan *et al.*, 2007). For instance, the response of benthic fauna to organic enrichment depends on the biological traits of the organisms (Papageorgiou, *et al.*, 2009; Villnӓs *et al.*, 2011). Different species have different activity patterns and the importance of faunal activities for system regulation is frequently associated with individual species traits (Norling *et al*., 2007). For example, opportunistic species are less affected by sedimentation and likely to respond positively to it (Tomassetti and Porrello, 2005).

2.4 Disturbance of Marine Biodiversity

Disturbance relates to the disruption of system's stability resulting from events including natural and anthropogenic. It is often not possible to decide what has been changed by anthropogenic stress and what is natural. This is because anthropogenic stresses are superimposed on stresses caused by natural environmental factors (Raffaelli and Hawkins, 1996). Anthropogenic stress is the response of a biological entity (individual, population, community etc.) to an anthropogenic disturbance or stressor. Stress can be any factor that negatively affects the physiology, growth, reproduction and survival of an organism or that has consequences affecting populations or communities (Shiel, 2009). Stress at one level of organization (e.g. individual, population) may also have an impact on other levels, for example, causing alterations in community structure. However, it is sometimes difficult to detect the effects of anthropogenic stress at the level of individual organisms, and impacts are more often investigated at a population or community level (Crowe *et al*., 2000).

There is little doubt that anthropogenic disturbance have extensively altered the global environment, leading to a decrease in biodiversity. Changes in marine biodiversity are directly caused by exploitation, pollution and habitat destruction, or indirectly through climate change and related perturbations of ocean biogeochemistry (Jackson *et al*., 2001; Dulvy *et al*., 2003; Lötze *et al*., 2006).

Disturbance of the community by physical and biological factors may reduce the number of organisms in the community to the point at which there is less competition for resources, and hence less competitive exclusion and greater species diversity (Dether, 1984).

Jackson and Chapman (2009) indicated a tendency to associate current biodiversity changes with contemporary causes such as pollution, global warming and invading species. In reality, impacts may be temporally disconnected from their causes; long-term or historic activities may have precipitated chains of events, causing what we see today. Anthropogenic influence and their consequences may also be disconnected spatially (Jackson and Chapman, 2009).

Useful conclusions of Worm *et al*. (2006) indicate that high biodiversity in the marine environment is associated with ecosystem stability and resilience, and with the productivity and recovery potential of vital fisheries, although this was criticized for two shortcomings (Hölker *et al*., 2007). In the marine environment, changes are often assumed to be smaller, more localized or more easily reversed, although this may not be the case-e.g., large fishing grounds take decades to recover (Thrush and Dayton, 2002). Many impacts on ecosystem have now become global in scale (e.g., declines in major fisheries; Brander, 2007); others are limited to a local sphere of influence. According to Worm *et al*. (2006) and Hölker, *et al*. (2007) the number of overexploited or depleted fish stocks has been increasing over several decades and the United Nations Food and Agriculture Organization (FAO) reports an increase from about 10% in the mid-1970s to around 25% in the early 1990s (FAO, 2006). The FAO data indicate, however, that the increasing trend has stabilized since the early 1990s, whereas the Worm *et al.* (2006) data indicate that the increasing trend continues.

Enhanced fisheries recovery occur at high diversity due to the fact fishers can switch more readily among target species, potentially providing overfished taxa with a chance to recover (Worm *et al.*, 2006). Also taxonomically related species play complementary functional roles in supporting fisheries productivity and recovery (Worm *et al.*, 2006). Another useful finding from Worm *et al.* (2006) indicated that collapse of LME fisheries occurred at a higher rate in species-poor ecosystem compared with species-rich ones, giving credence to the effects of biodiversity loss on the ecosystem. Removal of mature fish affects the supply of juveniles elsewhere in the system, with consequences for species richness and diversity, marine predator populations, and food web functionality (Worm *et al.*, 2006) that extend over a far greater area and range of ecosystems than the fishing activity itself.

Recent evidence suggests that coastal and open-water systems can rapidly flip from being dominated by fish (that keep jellyfish in check through competition or predation) to a less desirable ‘gelatinous’ state (Richardson *et al.*, 2009). This new ecosystem state is resistant to returning to its original state because jellyfish are voracious predators of fish eggs and larvae, and effectively prevent fish from returning. This flip to a jellyfish-dominated system once a critical threshold is reached has been termed ‘the jellyfish joyride’. Thus, natural ecosystems can be slowly degraded by the combination of continued overfishing, eutrophication and climate change to one where there are few fish, marine mammals and seabirds (Fig.

2.1). This change to jellyfish is consistent with the ‘rise of slime’ (Pandolfi *et al*., 2005).

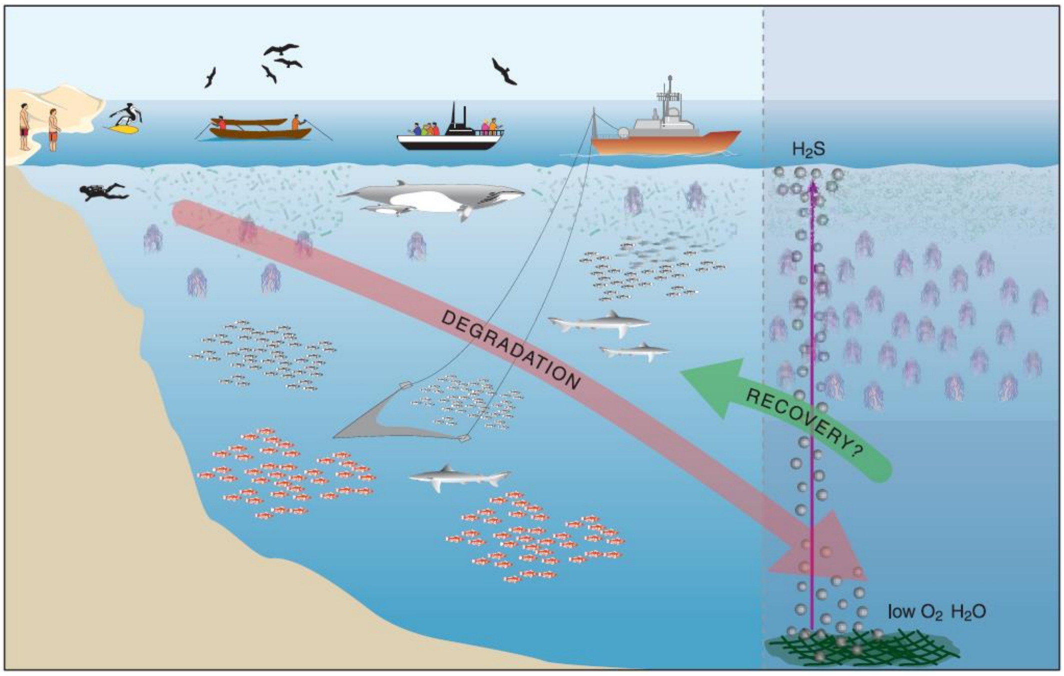


Figure 2.1 Human-induced processes of change from fish to jelly-fish domination (after Richardson *et al*., 2009).

These tipping points for ecosystems (illustrated in Fgiure 2.1) are generally unknown and the new ecosystem state is resistant to returning to its original state (Richardson *et al*., 2009). A pervasive and irreversible impact of human activity on natural marine ecosystem is introduction of non-indigenous species. The opportunities for species introduction have steadily increased over recent centuries (Hewitt and Campbell, 2007). Non-indigenous species are now common inhabitants of most geographic regions of the world. For example, up to 230 introduced species have been documented for a single estuary (Loxahatchee River estuary in Florida, USA) and about 400 are established in marine and estuarine habitats in the US alone (Ruiz *et al*., 1997). Although the ecological effects of introduced species to the native assemblage are not clearly fully understood, they pose a significant stress to marine communities, particularly in areas already stressed by loss of habitat or high levels of contamination (Clynick *et al*., 2009).

The degrading effects of fishing, habitat destruction, introduced species, and eutrophication reinforce each other through positive feedbacks (Jackson, 2001; Jackson *et al*., 2001; Lötze *et al*., 2006). For example, oysters were nearly eliminated by overfishing, but their recovery is now hampered by hypoxia due to eutrophication, by introduced species that compete for space and cause disease, and by the explosive rise of formerly uncommon predators that were previously kept in check by now overfished species in the Neuse River estuary, North Carolina, USA (Lenihan and Peterson, 1998; Myers *et al*., 2007). Much of the overall decline of the 80 species reviewed by Lötze *et al*. (2006) was due to multiple suites of drivers: 45% of depletions and 42% of extinctions involved multiple impacts. Nowhere have these drivers been brought under effective regulation or control.

Trawling is the most important factor affecting the structure and function of soft-bottom communities globally (Watling and Norse, 1998; Thrush and Dayton, 2002; Gray *et al*., 2006). A number of studies have investigated the impacts of trawling on different components of the marine ecosystem (e.g., Drabsch *et al*., 2001; Spark-McConkey and Watling 2001; Thrush and Dayton, 2002; Nilsson and Rosenberg, 2003; Rosenberg *et al*., 2003). McConnaughey *et al*. (2000) further demonstrated that there are chronic effects, which result in lower diversity in the sedentary macrofauna in the heavily trawled areas of the eastern Bering Sea. Tillin *et al*. (2006) found that chronic bottom trawling can lead to large-scale shifts in the functional composition of benthic communities, with likely effects on the functioning of coastal ecosystems.

Another important factor of disturbance to benthic communities is euthrophication. Benthic eutrophication is defined as an increase in the rate of supply of organic matter to benthic environment (Nixon, 1995). One of the most important effects of eutrophication on aquatic organisms is the reduction in the concentration of dissolved oxygen. Hypoxia or anoxia (low or nil oxygen content) can cause direct mortality and reduced growth rates in organisms (Weston, 1990). Many studies have documented changes in biodiversity of macrofaunal benthic communities under hypoxia conditions (Nilsson and Rosenberg, 1994; Ritter and Montagna, 1999; Craig *et al*., 2000; Meyers *et al*., 2000; Nilsson and Rosenberg, 2000; Rosenberg *et al*., 2001) and into the behavioral or physiological responses of species to hypoxia (Rosenberg *et al*., 1991; Holmes *et al*., 2002; Wu and Or, 2005). These studies showed decreased biodiversity, alterations of species composition and reductions in biological responses, when the benthic environment is subjected to short or long-term hypoxia events. Although the effects of hypoxia on biodiversity, physiology and behavioral responses have been extensively studied (Widdows *et al*., 1989; Vaquel-Sunyer and Duarte, 2008; Hondorp *et al*., 2010), there has not been any research into the combined effects of trawling and hypoxia on the biological traits of benthic communities.

The intermediate disturbance hypothesis of Connell (1978) predicts maximum biodiversity at a frequency of disturbance where recruitment is able to replace lost individuals but inter-specific processes do not have time to exclude species. This response has been recorded in many marine systems (Begon *et al*., 1996; Svensson *et al*., 2007). Disturbance, both anthropogenic and natural, may act as a potential abiotic drivers/surrogate for diversity at an appropriate spatial scale and temporal scale (Harris *et al*., 2008). The stability of the seabed sediment surface exerts a major control on benthic community structure (Newell *et al*., 1998). Species diversity tends to be highest on stable rocky shores and on cohesive muddy shores, with the more mobile sandy or fine gravel substrates typically showing much lower richness. Sediment stability is dependent on slope, particle size and the degree of water motion on the bed (Bagnold, 1963). The shape and roundness of sediment grains are additional properties that determine the stability of a deposit (Lewis and McConchie, 1994) but grain shape is difficult to measure and is rarely recorded despite its likely importance. Stability may also be influenced by the presence of biota through biological armouring of the bed and binding of sediment by faunal mucus (Murray *et al*., 2002). The stability of a sediment surface as a habitat is difficult to quantify, particularly given that one of the key proxies, sediment grain size, is determined on disaggregated samples which have been dislodged from their environment and may have little physical resemblance to what an organism actually encounters (Snelgrove and Butman, 1994).

2.5 Environmental Drivers of Marine Benthic Diversity

The goal of ecological research is to determine which easily measured characteristics best describe the species assemblage of a particular space and time (Moore *et al*., 1991). Models which have been suggested for understanding community dynamics or species assemblages include ‘‘environmental stress models’’ and either ‘‘nutrient/productivity models’’ or the ‘‘food chain dynamics hypothesis’’ (Connell, 1975; Oksanen *et al*., 1981; Fretwell, 1987; Menge and Olson, 1990; Menge, 2000). Environmental stress models assume that community structure results from species interactions and disturbances, and how these are modified by underlying gradients of environmental stress (where stress is a consequence of environmental conditions such as temperature, moisture, salinity) (Menge *et al*., 2002). The two models postulate that communities can be ordered along environmental gradient. McGill *et al*. (2006) argued that general principle in community ecology may not be achieved if research continues to focus on pair-wise species interactions independent of the environment. Global species distributions are generally believed to be determined by abiotic influences related to oceanographic and physiographic properties (Sanders, 1968; Ricklefs and Schluter, 1993). For instance, water motion affects biology by acting as a transport mechanism for organisms and their propagules, as a dynamic boundary between regimes, and as a force to which organisms must adapt or respond, for example, in their feeding and locomotor activities (Nowell and Jumars, 1984; Denny, 1993).

The abiotic characteristics are expected to act as predictors of species assemblages in unexplored areas (Franklin, 1995). Pitcher *et al*. (2007) identified grain size, carbonate composition, available space, benthic irradiance, sheer stress, bathymetry, bottom water physical properties, nutrient concentrations and turbidity as abiotic surrogates of biotic distributions on the Great Barrier Reef; but these variables, while useful predictors, may not be the forces driving the patterns they describe. The influence of abiotic factors on species assemblages is due to the effect they exert on fundamental niches. A species' fundamental niche was defined by Austin *et al.* (1990) as “that hypervolume defined by environmental dimensions within which a species can survive and reproduce.” Fundamental niches are rarely fully realized by species because interspecific competition, disease and disturbance events displace individuals and populations, resulting in a reduced occupied hypervolume, often referred to as the realized niche (Austin and Smith, 1989).

The environmental gradients that describe a species' fundamental niche can be broadly grouped into resource gradients – e.g. chemicals or energy consumed by a species; direct gradients – variables with a physiological influence on a species but not consumed by it – e.g. sediment grain size or temperature; and indirect gradients – variables correlated with direct and resource gradients but with no physiological connection to the species – e.g. depth and latitude (Meynard and Quinn, 2007). When niche theory was first proposed, species were expected to exhibit a Gaussian distribution to environmental gradients but skewed distributions are more common in ecological studies as the effects of additional variables express their influence (Karadzic *et al*., 2003).

The abiotic variables which have been historically ascribed the greatest direct influence over benthic organism distributions are temperature, salinity, oxygen concentration, light availability and sediment composition (Snelgrove, 2001). Environmental variables (such as sediment structure, organic matter content, temperature, salinity, dissolved oxygen, nutrient concentrations, pH, turbidity, water transparency and depth) have been found to correlate with abundance, density and diversity of macrofauna and these variables may vary seasonally (Nicolaidou *et al*., 1988; Arvanitidis *et al*., 1999; Hagberg and Tunberg, 2000; Mistri *et al*., 2000; Mistri *et al*., 2001).

A model describing the influences of these factors and some of their potential synergies is given in Figure 2.2. The figure depicts the influence of interdependency of physical processes and potential surrogate abiotic drivers on biological community structure. Olabarria (2006) found depth accounted for as much as a quarter of the variance in benthic diversity in deep systems but, as benthic organisms lack an apparent mechanism for measuring depth, some correlated water quality parameter or seafloor characteristic most likely influences the settlement, recruitment and survival processes that result in the observed depth related patterns. Lamptey *et al*., (2010) identified nitrate-nitrogen, dissolved oxygen, salinity and water temperature as suite of abiotic drivers of rocky intertidal biodiversity in Ghana. Gray (2002) reduced Snelgrove's list of direct drivers (2001) to productivity, temperature and sediment composition as the dominant variables in determining regional benthic richness, noting that temperature and productivity are often correlated to depth and latitude. Combinations of these driving influences occur with varying spatial and temporal consistency, in turn producing semi-regular patterns of biodiversity. The validity and origin of several identified general benthic biodiversity patterns are the focus of much recent debate. For example, the latitudinal (spatial) richness gradient, widely accepted as a rule for benthic fauna since the mid twentieth century (Thorson, 1957) has been shown to be weaker than previously thought (Snelgrove, 2001) or entirely incorrect for some taxa or systems (Rex *et al*., 2005) due to the driving influence of complex biotic and abiotic factors.

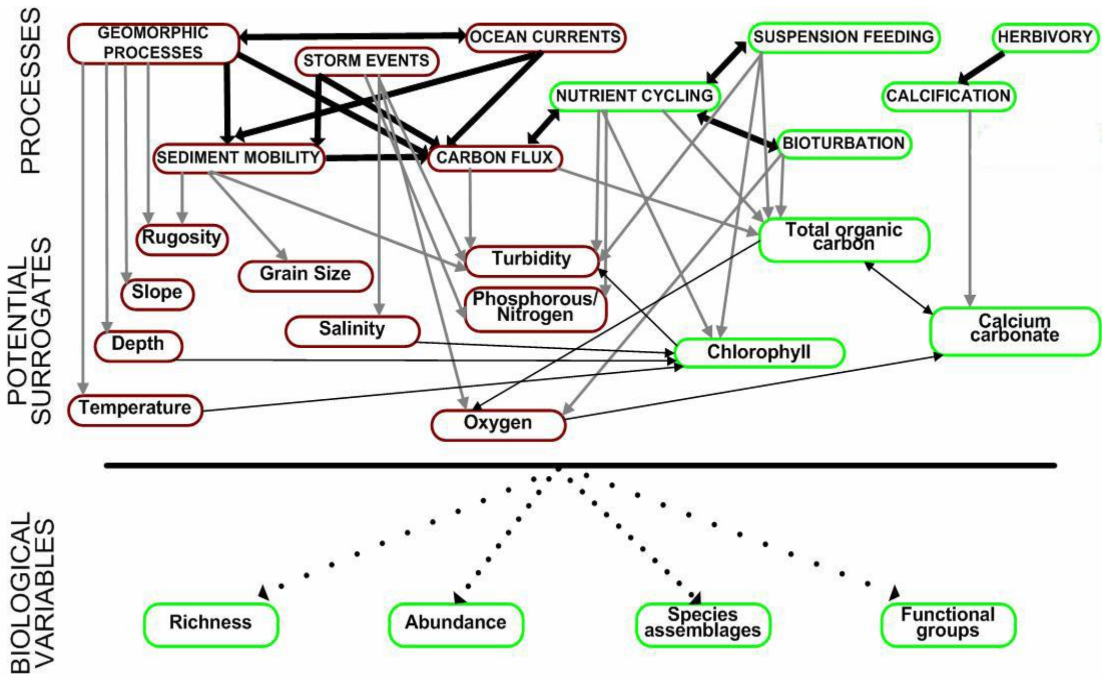


Figure 2.2. Conceptual map of the relaionships between drivers of biodiversity in marine systems and potential surrogates (after .McArthur *et al*., 2009).

2.5.1 Spatial and Temporal Patterns of Environmental Drivers

An important goal in community ecology is to understand factors contributing to species assemblage patterns at variety of spatial and temporal scales. Benthic faunal communities vary considerably in time and space (Carriker, 1967; Boesch, 1973), due, in great part, to the patchiness of species occurrences (Pearson and Rosenberg, 1978) and overall heterogeneity of the benthic habitat (Mistri *et al*., 2000). This heterogeneity has been ascribed to such factors as bottom sediment, spatial variability (Tenore, 1972), climatic irregularity (Hessle and Sanders, 1967; Bourcier, 1995), anthropogenic perturbations (Rosenberg, 1973; Kröncke *et al.*, 1992) and biogenic structures (Woodin, 1981). According to Alongi (1990), temporal and spatial patterns of benthos are determined by primary production in the water column and by sediment types and associated physico-chemical conditions. Changes in environmental conditions promote changes in species assemblages at variety of spatial scales (Lamptey *et al*., 2010). Many environmental factors affecting species performance and interactions vary with spatial scale (Noda, 2009). There is, however, no particular scales of change that are consistent among taxa (Burrows *et al*., 2002), congruently demanding ambitious ecological models to decipher spatial patterns. Physical or environmental factors, such as water depth and sediment type and movement, are considered to determine large-scale patterns of distribution (e.g. Thorson, 1957; Barry and Dayton, 1991). Within these patterns, however, spatial heterogeneity exists at various scales, forming a mosaic of patches.

Spatial heterogeneity is often cited as a diversity driver, with high inshore species richness being promoted by the variety of habitats available on a broad scale and deep water benthic and planktonic richness occurring in spite of low biomass as a result of small scale shifts in sediment or water composition in habitats which otherwise appear homogenous (Snelgrove, 2001). Spatial pattern is difficult to quantify and often refers to the spatial character and arrangement, position or orientation of patches within a landscape (Li and Reynolds, 1993).

A greater understanding of the distribution and complexity of benthic habitats and a common approach to measuring and describing this complexity will provide a spatial framework within which to properly address spatially explicit research and management goals (Kendall *et al*., 2005). The decline of many species has been linked directly to habitat loss and fragmentation. Identifying what characteristics make an area preferentially habitable for particular species has been examined by many landscape ecologists and is being increasingly taken up by marine ecologists to describe patterns of benthic diversity (Barrett *et al*., 2001). Recent advances in image processing and GIS technologies have made it possible to link indices of landscape pattern to ecological functions. However, the uncertainties in mapping the pattern and extent of marine habitats have, until recently, been behind the rarity of habitat-scale studies in marine ecology

Increasing species richness with increasing proximity to the equator is a long recognized biogeographic pattern (Cox and Moore, 2005). While this pattern has been documented in the marine environment (Attrill *et al*., 2001) it has recently been found to be less general than previously thought (Gray, 2001). Hawkins *et al*. (2003) and Willig *et al*. (2003) each cite thirty hypotheses to explain latitudinal richness gradients. These were categorized by Mittelbach *et al*. (2007) into ecological, historical and evolutionary groups. The ecological hypotheses concentrate on the different adaptive challenges faced by organisms living in different climatic zones: polar and temperate organisms must adapt to environmental conditions (Schemske, 2002) while tropical organisms, dealing with less harsh abiotic extremes, adapt to biotic interactions (Crame, 2000). Historical explanations concentrate on the age and stability of richness hotspots (Alongi, 1990).

Evolutionary models incorporate several possible drivers for high rates of speciation including the wide variety of microhabitats available in tropical regions (Rex *et al*., 2005) and higher rates of molecular evolution (Kerswell, 2006). Attempts to measure and explain the extent of a latitudinal richness gradient in taxa other than molluscs on broad geographic scales have found less evidence for a marine equivalent to the terrestrial pattern (Gray, 2001) and brought into question the treatment of data in describing such patterns. For example, Thorson's (1956) pattern of increasing richness in benthic epifauna toward the equator was based only on the 140,000 marine taxa known at the time (Snelgrove, 2001). Diversity responses to pure spatial gradients can vary depending on how assemblage data are treated. Ellingsen *et al*. (2005) determined that latitude could account for variance in richness of molluscs (11.8 % explained), annelids (9.6 %) and crustaceans (13.7 %) in Norwegian shelf benthos.

2.5.2 Water Depth

Water depth has been a consistently powerful explanatory variable in benthic studies (Nicolaidou and Papadopoulou, 1989; Gogina *et al*., 2010). When generalizing from shallow to deep, intertidal and estuarine systems exhibit high biomass and low species richness caused by high productivity and extreme environmental conditions (Edgar, 2001), coastal shelves have moderate biomass and species richness (Snelgrove, 2001), and the deep sea shows a decrease in biomass and increase in richness (Levin *et al*., 2001). Peak benthic species richness values have been recorded seaward of the continental rise, excluding the deep sea (Snelgrove, 2001). The lower slope and abyssal plains become comparatively depauperate for some groups, and species turnover tends to be high (Paterson *et al*., 1992). Levin *et al*. (2001) stated that the deep sea houses greater diversity than coastal shelf systems, although at far lower abundances. Areas with low abundance and high species turnover require greater sampling effort to reliably account for diversity (Etter and Mullineaux, 2001).

2.5.3 Substrate Types

Numerous studies have provided evidence to show significant differences in the species composition between ‘hard’ and ‘soft’ substrata (Beaman *et al.*, 2005; Beaman and Harris, 2007; Williams and Bax 2001). For practical purposes, ‘soft substrate’ is usually defined as detrital mineral or biogenic sediment comprising grains with a mean diameter less than 2 mm, although gravel size fractions are often included (Lewis and McConchie, 1994). The term ‘hard substrate’ is typically used to represent rock outcrops but may include sediments with large grain size (e.g. cobbles, boulders) since these materials can provide a surface that is functionally comparable to bedrock. While the contrast between soft and hard substratum is conceptually simple, defining the boundary between soft and hard substrates can be complex in practice because some rock types are friable or semi consolidated and may be partly covered by sediment (Ryan *et al.*, 2007). In addition, because the boundaries between adjacent soft-sediment environments are not always sharp as those across hard and soft substrate features, the associated boundaries between biological assemblages may be gradational and spatially complex (Beaman and Harris, 2007).

Sediment particle size distribution and composition on the seabed express a strong influence on the morphology and life history of species living in soft sediments (Jones, 1950). These variables are determined by complex interactions between local geology, rates of sediment production and supply, actions of bioeroders, current and wave induced bed stress, and slope (Reineck and Singh, 1980). Generally, in high-energy areas, coarse sediments (gravel) will predominate, whereas lower energy (depositional) areas are muddy, although there are exceptions (Foster, 2001; Hart and Kench, 2007) which have led to a highly complex and variable distribution of seabed sediment types on the shelf and slope. Although several sediment surrogacy relationships are well documented (Brown *et al*., 2001; Beaman and Harris, 2007; Degraer *et al*., 2008), the nature and strength of sedimentary surrogates for species composition within soft sediment environments remains a subject of debate (Dye 2006; Inoue *et al*., 2008; Stevens and Connolly, 2004). Soft substrates are home to epifauna and infauna and plant life may include sea grasses (and their epiphytes) or microphytic algae occurring at the sediment-water interface. Hard substrates can act as habitat for epifauna and encrusting or macro-algae, but infauna are excluded.

The most basic way of characterizing any community is by the habitat type and for benthic community habitat normally means sediment type (Hall, 1994). The distribution of many of the benthic communities shows a clear correlation with sediment type. Early studies suggested that macrobenthic communities could be distinguished on the basis of sediment composition (Thorson, 1957; Buchanan *et al*., 1978; van Dalfsen *et al*., 2000). Other studies, however, have shown little correlation (Day *et al*., 1971; Sneiderer and Newell, 1999) and suggested that the distribution of macrofuana in many sedimentary habitats is controlled by complex interaction between physical and biological factors at the sediment–water interface, rather than by the granulometric properties of the sediments themselves (Snelgrove and Butma, 1994). However, density-dependent variables play a minor role in structuring the macrobenthic communities, which were probably affected more by other variables, such as the kind of habitat and sediment structure (Mistri *et al*., 2000). Many apparent relationships between sediment type and biota remain untested in an experimental sense (Whitlatch, 1981) and have been challenged (Snelgrove and Butman, 1994).

Storms and current eddies may contribute to primary space being made available in a system in two fashions: increasing sheer stress at the benthos/water interface, which can remove sediment, algal cover and motile fauna; and mechanical abrasion or damage caused by moving sediment or projectiles (Sousa, 2001). Benthic organisms continually process, transport, and modify seafloor bed sediments. There are those that bind, protect and stabilize near-surface sediment and those that loose and destabilize the sediment (Nichols and Boon, 1994).

Depending upon its life style, an organism may require a given size range of sediment for tube building, burrowing or feeding (Wieser, 1959). The feeding type of the benthic community is considered as an adaptation to the sediment characteristics (Rosenberg, 1995). Certain mechanisms result in sediment-specific distribution. One of these is the preferential ingestion or retention of specific grain sizes during feeding. Adults of a variety of deposit-feeders have been shown to ingest specific grain sizes of sediments (Whitlatch, 1977; 1980). For instance, newly settled larvae may be restricted to feeding on the finest material within the bed or on particular rich food items (Jumars *et al*., 1990) thus, optimal grain size may be different for settling larvae and adults. Larger particles may be preferred by larger organisms within a given species (Whitlatch and Weinberg, 1982 cited in Snelgrove and Butman, 1994). Some species show little affinity with any one particular sediment type, and the fauna within different sediment environments invariably show some degree of overlap, which might be due to the grain size being a correlate of the actual causative factor(s) (Snelgrove and Butman, 1994).

Much of the potential food for benthic organisms are located within the upper 2 cm of the sediment (Whitlatch, 1977, 1980) and most of the organisms produce faecal pellets that are deposited at or near the sediment surface. This process may result in a change in the grain size of surface sediments (Hall, 1994). In mud, for instance, this can result in a pelletised silt-clay matrix. It is therefore, evident that physical processes impact upon biological features to structure the benthic organisms and its habitat. Habitat selection based on the availability of a preferred grain size in feeding is difficult to conceptualise in view of the ontogenic and hydrodynamic changes in feeding behaviour and particle selectivity (Snelgrove and Butman, 1994). It has been suggested that animal and sediment correlation is a result of hydrological and geological processes associated with sediment granulometry rather than a function of organism‘s available space within sediment (Parry *et al*., 1999). Benthic space can also be made available in the wake of acute pollution events (Scanes *et al*., 1993), fishing activity (Currie and Parry, 1996) and eutrophication (Tett *et al*., 2007), but the effects tend to be locally focused.

2.5.4 Primary Productivity

Contrary to observed patterns in terrestrial systems (Currie *et al*., 2004), high primary productivity in near shore waters tends to promote low species richness (Snelgrove, 2001) and high evenness (Hillebrand *et al*., 2007). In these areas, the role of producer tends to be dominated by a small number of species able to monopolise resources under ambient conditions. Corresponding benthic communities are dominated by the taxa best able to use the associated products (Lenihan and Micheli, 2001) or withstand periods of anoxia imposed by excess organic input (Dell'Anno *et al*., 2002). In contrast, oligotrophic waters are often home to low biomass assemblages with high species richness, including a large proportion of endemic taxa (Poore *et al*., 2008). Coral reefs, areas of high biomass and species richness occurring in oligotrophic waters, are an exception. The symbiosis between coral polyps and their resident zooxanthellae allows higher productivity than would otherwise occur in the ambient conditions and the spatial complexity and diversity of habitats provided by hard corals competing for space and light promotes a high corresponding richness of invertebrate and fish life, in turn supporting a rich community of predators (Cribb *et al*., 1994). Primary production can be estimated from satellite or airborne spectral analysis of chlorophyll in surface waters (Parmar *et al*., 2006). While productivity is directly linked to marine biodiversity, the relationship has yet to be fully explored as a predictive surrogate over large scales.

2.5.5 Organic Carbon

Detrital matter derived from primary productivity and the wastes of secondary production comprise a valuable resource in the photic zone and, excepting chemosynthetic systems, almost the only energy input to the aphotic zone (Vetter, 1995; Carney, 2005). This material settles in particles of various sizes, among which larger particles such as faecal pellets (Angel, 1984) and marine snow (Alldredge and Silver, 1988) are particularly important. It is generally accepted that the flux of particulate organic carbon (POC) from the euphotic zone controls the biomass and abundance of deep-sea benthos. This notion was originally based on observations of high benthic standing-crops beneath productive equatorial and near-shore waters, and low standing-crops underlying oligotrophic gyres (Belyayev *et al*., 1973; Gage and Tyler, 1991; Rowe *et al*., 1991; Blake and Hilbig, 1994). However, a direct coupling between pulse-like sedimentation events and the activity of benthic fauna has become clear (Aberle and Witte, 2003 and references therein). The detailed nature of this coupling remains poorly understood because there have been few studies which combine both types of measurements. One good example is a study by Smith *et al*. (1997) in the equatorial Pacific, in which strong and significant correlations ($r^2>0.9$) were found between both megafaunal (phototransects) and macrofaunal (enumerated from box core samples) abundances and annual POC fluxes.

An interesting conclusion from this study was that macrofaunal abundance might potentially serve as a proxy (i.e., surrogate) for POC flux in low energy abyssal habitats, implying that the macrofauna themselves are either more widely or more easily measured than POC fluxes (see also Rowe *et al*., 1991; Cosson *et al*., 1997). The main technique to directly measure POC fluxes is using sediment traps. Seiter *et al*. (2005) drew on particle-trap data from 61 locations, and produced a global map of minimum POC flux to the seafloor which was based on global estimates of diffusive oxygen uptake. This map, and the global map of total organic carbon (TOC) concentrations that underpins it (Seiter *et al*., 2004), may prove useful in making first order approximations of benthic productivity over broad scales, assuming that benthic communities are not compromised by sediment de-oxygenation. Indeed, the relationships between diversity and POC fluxes (or other productivity proxies) are scale-dependent and may be complicated by other variables that influence diversity including bottom-water oxygen concentration, hydrodynamic regime and the stability of the physical environment (Levin *et al*., 2001).

Proxies of POC fluxes such as TOC, TOC:TN (total nitrogen) ratios, biochemical markers and pigments in sediment have proven useful in explaining more localized patterns of biodiversity. TOC is undoubtedly the most widely measured of these parameters (Seiter *et al*., 2005), and, where a consistent and robust method (Galy *et al*., 2007) has been applied to its measurement, TOC can be a useful surrogate for biomass, deposit-feeding taxa, and community structure (Gogina *et al*., 2010). However, its application is limited to interpolations from physical samples (Levin and Gage, 1998) as no remote sensing proxy is available. Moreover, correlations between TOC and diversity measures are not always found (Cartes *et al*., 2002) because a large proportion of TOC in sediment may be refractory and thus resistant to bacterial degradation. Sediment grain size can also affect the amount of biologically available organic matter (OM) in shallow soft sediments (Taghon, 1982). Small particles have larger surface area per unit volume than large particles, offering greater habitat for micro-organisms (Fauchald and Jumars, 1979; Petch, 1986; Neira and Hoepner, 1994) and associated organic matter. Some deposit-feeding species use size-specific foraging mechanisms to select and ingest fine sediments (Butman and Grassle, 1992; Sebesvari *et al*., 2006), but both selective and non-selective deposit-feeders exhibit settlement preferences for sediments with high concentrations of readily available organic carbon (Snelgrove and Butman, 1994; Post *et al*., 2006).

The organic matter content of bottom sediments may be a more likely causal factor than sediment grain size in determining infaunal distribution (Snelgrove and

Butman, 1994). This is because it is a dominant source of food for deposit-feeders (Pearson and Rosenberg, 1978), indirectly (e.g., through resuspension) for suspension feeders (Snelgrove and Butman, 1994). The sediment must be considered as an indicator of the availability of food, and not as a first order factor directly determining the distribution of feeding types (Snelgrove and Butman, 1994). Nichols (1970) and Field (1971) have suggested that there is a strong relationship not only between animal and grain-size distribution but also between animal and organic-carbon distributions as well. However, a similarity between the type of sediment and the percentage of organic matter, which have been ascribed to the hydrodynamic conditions established during heavy rains, has been observed (Estacio *et al.*, 1999).

Several deposit-feeding opportunistic species have been shown to colonize, preferentially, organic-rich sediments over non-enriched sediments with comparable grain size in shallow-water (Grassle *et al.*, 1985; Tsutsumi *et al.*, 1990) and in associated slow water movements (Mistri *et al.*, 2001). Organic matter was also found to be correlated with annelid distribution (Arvanitidis *et al.*, 1999). Seasonal variations in particulate organic matter are greatly influenced by monsoonal rains. Total organic matter levels decrease during the monsoon season as a result of increase in river discharge and scouring of surface silt and clay and associated organic matter (Alongi, 1990). The highest concentrations of organic matter in sediments are in regions of upwelling and in proximity to rivers and more generally, relate to the patterns of pelagic primary production (Alongi, 1990).

The availability, freshness or quality of organic matter (OM) pertains to the labile fraction, which consists mainly of lipids, carbohydrates, proteins and nucleic acids

(Danavaro *et al*., 1993, 1995, 2001). Several useful biochemical parameters have been derived to describe the lability of OM (Danavaro *et al*., 1995; Dauwe *et al*., 1999), and some of these have proven useful for explaining different diversity indices (Cartes *et al*., 2002). Such measures, however, often require a high degree of discipline expertise (and advanced techniques), and as such are unlikely to be widely employed in the capacity of surrogates. However, the Chlorin Index (CI) (Schubert *et al*., 2005) is a simple analytic measurement of OM lability, whose reliability has been demonstrated by comparison to more advanced techniques (e.g., Dauwe Index, total hydrolysable amino acids, and % ß-alanine as non-protein amino-acid, and sulfate reduction rates) (Schubert *et al*., 2005). The Chlorin Index (CI) is a measure of the amount of chlorophyll (and its degradation products) that could be transformed to phaeophytin, and is expressed as the ratio of the fluorescence intensity of a sediment sample extracted in acetone and subject to HCl treatment to that of the original sediment sample (Schubert *et al*., 2005). CIs have been found to correlate well with an index of track richness developed from photographic stills of seabed sediments, which conveyed differences in the diversity of tracks, faecal casts, burrows and mounds of benthic biota in deep-sea sediments of the Lord Howe Rise (Dundas and Przeslawski, 2009). Comparison with this index shows a greater diversity of animal traces, and potentially more metazoan activity, in sediments of apparently higher food quality. CIs thus show promise as an easily measured geochemical surrogate of biodiversity for regions where organic loads are not expected to give rise to significant sediment anoxia.

2.5.6 General Oceanography

Oceanographers measure and model variables that directly influence the physiology and behavior of marine organisms (temperature, salinity, pH), variables affecting productivity (nutrient concentrations, temperature and light intensity: see section 2.5.4 on productivity) and the currents that affect larval distributions. Some factors such as pH and salinity vary sufficiently over regional and global scales to show correspondence to biological patterns (Williams and Bax, 2001) but are sufficiently uniform at a local scale (with the exception of estuarine systems) to preclude their use in local surrogacy analyses (Bamber *et al*., 2008). Dissolved oxygen has been identified as a key predictor of biodiversity in deep sea sediments (Levin and Gage, 1998).

In addition to determining local water properties and delivering food and oxygen, ocean currents are important to the dispersal of many marine organisms which, in turn, determines the potential distribution of many benthic taxa. Most larvae and algal propagules spend their early development adrift and must attempt to settle where the prevailing currents take them. With larval periods ranging from hours (e.g., tropical ascidians in Cloney *et al*., 2006) to four and a half years (e.g., gastropod of the Tropical Atlantic Ocean in Strathmann and Strathmann, 2007), the scope for currents to act as a surrogate for potential richness is substantial where both life histories and water movements are well known. The relative rarity of long larval life histories make local currents (~tens of kilometers) more important than regional currents in determining benthic larval supply (Palumbi, 2001), but even groups with well-known life histories have frustrated attempts to predict geographic assemblies (Shulman and Bermingham, 1995). Stevens and Connolly (2004) considered local scale current speed as an abiotic variable in their assessment of surrogates in Moreton Bay, Australia, but found its predictive capacity negligible. In addition to understanding larval supply patterns, the proximity of any given sample to diversity hotspots must be taken into consideration (Bellwood *et al*., 2005). Further information on biodiversity patterns as they relate to oceanographic variables can be found in reviews by Hall (1994), Wolanski (2001), and Levin *et al*. (2001).

2.5.7 The Guinea Current Ecosystem

The oceanography of the Guinea Current Ecosystem (GCE) is dominated by the Guinea Current (GC), but also the Benguela Current (South Equatorial), the Canary (Counter Equitorial) play important roles in the regional oceanography that influence coastal upwelling. The GCE and adjacent areas of the eastern tropical Atlantic, bounded to the north by the Canary Current (CC) coastal upwelling region and to the south by the Benguela Current (BC) coastal upwelling region, are affected by five major basin-wide wind-driven cells of ocean circulation (Longhurst, 1962). These are the North Atlantic Subtropical (NAS), North Equatorial Cyclonic (NEC), Equatorial Anticyclonic (EA), and South Equatorial Cyclonic (SEC) gyres (Henin *et al*., 1986). The circulation cells are formed due to latitudinal variations in the wind stress that is due to the existence of the subtropical anticyclones and Intertropical Convergence Zone (ITCZ), which separates the belts of the northeast and southwest trade winds.

The major surface currents forming the peripheries of the gyres are the North Equatorial Current (NEC), South Equatorial Current (SEC), North Equatorial Counter Current (NECC), South Equatorial Counter Current (SECC), GC, and

Angola Current (Moroshkin *et al*., 1970; Stramma and Schott 1999). Other current systems that may affect near surface circulation in the region are the equator-ward CC feeding the NEC in the north and the BC feeding the SEC in the south (Arnault, 1987). The NEC, SEC, NECC, and SECC are the westward and eastward cross-basin flows while the CC, GC, AC, and BC form the system of the tropical eastern boundary currents (Richardson and Walsh, 1986).

Three narrow coastal sedimentary basins, with a few volcanic intrusions and outcrops of hard rock forming the major capes, have developed on the edges of the coastline along the GCE: from north to south, they include the Cote d'Ivoire basin, the Niger basin (Delta) and the coastal basins from Gabon to Angola (Allen and Wells,1962, Quelennec,1984). The Volta, Niger and Congo basins dominate the coastal geology of the GCE. The continental shelf widens towards the east reaching its widest part of about 90 km off Cape Coast in Ghana. The shelf narrows again further eastwards between Tema (Ghana) and Lagos (Nigeria). Off Nigeria, the middle shelf configuration is modified by the Avon, Mahin and Calabar canyons, as well as pockets of dead Holocene coral banks (Awosika and Ibe,1998). East of Lagos, the shelf widens to about 85 km off the Niger Delta beyond which it narrows to an average width of 30–40 km. The shelf generally breaks at depths of between 100 and 120m (Awosika and Ibe, 1998).

Generally, the northern subsystem of GCE is thermally unstable and is characterized by intensive seasonal upwelling (around Cote d'Ivoire—Ghana) while the southern subsystem is mostly stable depending on nutrient input originating from land drainage and river flood and oceanic turbulent diffusion, although periodic upwellings have been reported (Bakun, 1978; Ukwe, 2003). The GC is a geostrophically balanced current with isotherms sloping upwards towards the coast and as the current intensifies, the slope becomes steeper bringing the thermocline closer to the surface near the coast (Henin *et al*., 1986).The coastal upwelling and the boreal summer intensification of the GC are thus related (Philander, 1979)

Although oceanography has been identified as a major driver of benthic biodiversity, there are limited studies in the GC relating it to biodiversity distribution. Lœuff and Cosel (1998) in their investigation of the benthic biodiversity pattern across hydroclimatic conditions in the Tropical eastern Atlantic concluded the following:

i) five different hydroclimatic regions existed in the tropical eastern Atlantic namely: the northern altemance region (Cape Blanc -Cape Verga), the atypical tropical region (Cape Palmas - border Benin/Nigeria), the southern altemance region (Cape Lopez - Cape Frio), all with periodical upwelling of colder water, and two intercalated typical tropical regions with warm water and reduced salinity.

ii) the fauna1 richness in the regions with upwelling is higher than in the typical tropical regions because many benthic species avoid warm and reduced salinity water;

iii) faunistic exchange and affinity are greater between the upwelling zones and the areas bordering temperate zones;

iv) the cold regions are also more similar in fauna1 composition;

v) benthic communities in both tropical and temperate eastern Atlantic are not fundamentally different;

vi) species diversity of benthic invertebrates in tropical West Africa is about the same order of magnitude as in Europe and the Mediterranean; and

vii) hydro-climatic conditions do not favor the establishment of stenohaline and stenotherm fauna in West Africa. Lœuff and Zabi (2002) also demonstrated the existence of major types of faunal bionomic variations at different spatial and temporal scales in benthic ecosystem of tropical Atlantic coast of Africa.

Figure 2.3. Guinea Current Ecosystem Region (Google Earth Image).

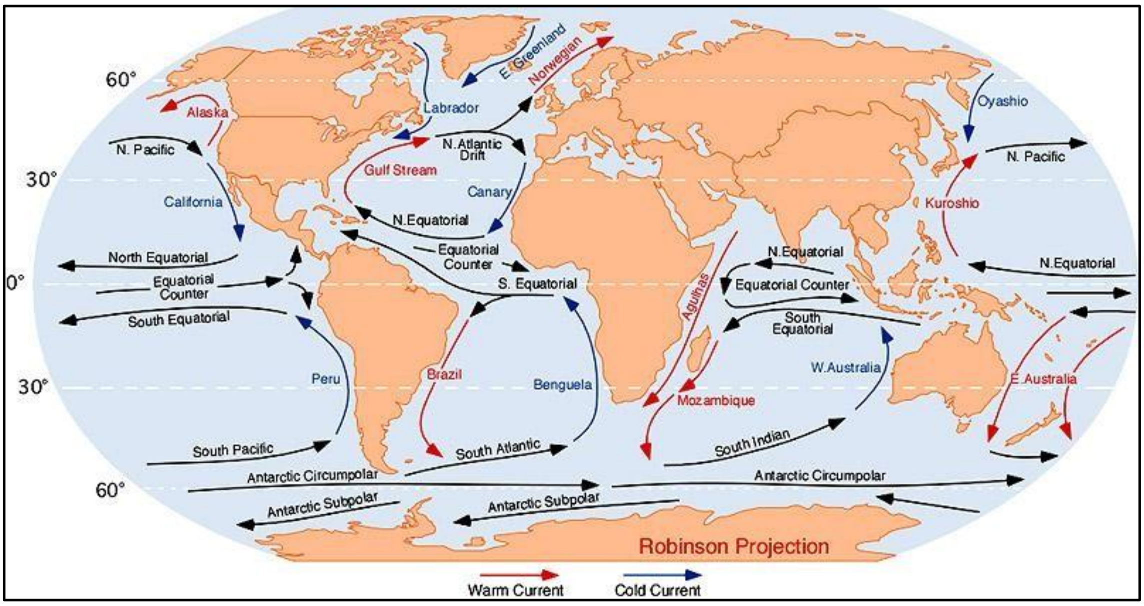


Figure 2.4. Large-scale oceanic circulation in the Atlantic Ocean including the Guinea Current Ecosystem region. (Image Source: NASA)

CHAPTER THREE

MACROBENTHIC FUNCTIONAL TRAIT DIVERSITY AND COMMUNITY STRUCTURE ALONG ENVIRONMENTAL GRADIENT

3.1 Introduction

The distribution of species and species' traits across environmental gradients can provide an understanding of how assemblages that differ in diversity are composed and their relative selection pressures (McGill *et al*., 2006). Comparing assemblages at local scales can often yield more insights into processes that drive diversity compared to global or regional scales (Gaston, 2000). However, a challenge to understanding various local processes is the comparison of assemblages with differing abundances in space and time, different histories (Underwood and Petraitis, 1993) and differing climatic and environmental settings. One approach for comparing diversity is to compare the spatial distributions of species at different geographic localities to look for generalities in community composition or habitat use (MacArthur, 1972; Warwick and Ruswahyuni, 1987, Thrush *et al*., 2005). Many of these approaches have been employed in most terrestrial ecosystems with the marine counterparts lagging behind.

The marine ecosystems are composed of three units: (i) the physical environment (e.g. seabed structure, sediment composition, waves, currents and water temperature), (ii) the chemical environment (e.g. substances such as carbon, oxygen, nitrogen and phosphorus and properties such as salinity and pH) and (iii) the biotic environment (the assemblages of living organisms present in the system, ranging from micro-organisms up to macroalgae, large marine mammals and humans) (Bremner, 2005). Recent evidence suggests that environmental conditions are intricately linked to biological traits, and hence ecological functioning (Bremner, 2006). Environmental conditions are all the things outside an organism that affect it but, in contrast to resources, are not consumed by it (Begon *et al*., 1990). The environment of an organism consists of all those phenomena outside an organism that influence it, whether those factors are physical (abiotic) or are other organisms (biotic) (Olff *et al*., 2009). Increasing moderation in environmental conditions leads to increased abundances, more complex trophic structure, and increased influence of species interactions on structure (Menge, 2000; Menge and Branch, 2001).

The main environmental gradients that have been associated with variation in species diversity are energy-related variables (*i.e*., temperature), precipitation, productivity and habitat heterogeneity (Currie, 1991; Rahbek and Graves, 2001; Hawkins *et al.*, 2003). Models which have been suggested for understanding community dynamics include ‘‘environmental stress models’’ and either ‘‘nutrient/productivity models’’ or the ‘‘food chain dynamics hypothesis’’ (Connell, 1975; Oksanen *et al*., 1981; Fretwell, 1987; Menge and Olson, 1990; Menge, 2000). Environmental stress models assume that community structure results from species interactions and disturbances, and how these are modified by underlying gradients of environmental stress (where stress is a consequence of environmental conditions such as temperature, moisture, salinity, etc.) (Menge *et al*., 2002).

The two models postulate that communities can be ordered along environmental gradient. McGill *et al*. (2006) argued that general principle in community ecology may not be achieved if research continues to focus on pair-wise species interactions independent of the environment. They suggested four research themes: functional traits, environmental gradients, interactions milieu and performance currencies, in order to bring general patterns to community ecology. Relatively few studies have explicitly incorporated structuring abiotic (environmental gradient) and biotic (movement, dispersal) features that are key to species co-existence and vital for the maintenance of species diversity (Loreau *et al*., 2003). The number of species in a community are influenced by a variety of factors (e.g., physical stress, nutrient availability, consumer pressure, habitat destruction), which result in non-random diversity gradient in natural habitats (Zavaleta, 2004; Srivastava and Vellend, 2005).

From a theoretical point of view, functional diversity decreases with increasing environmental constraints or stress (Mouillot *et al*., 2006). When environmental constraints increase, coexisting species are more likely to be similar to one another because environmental conditions (i.e., abiotic properties of the habitat) act as a filter, allowing only a narrow spectrum of species to survive. The species that make it through the environmental filters are likely to share many biological/ecological characteristics through the niche filtering concept (Franzen, 2004; Statzner *et al*., 2004). More precisely, environmental factors could limit the presence of certain functional traits at certain sites and thus decrease functional diversity of local communities in sites under environmental pressure such as confined parts in lagoons (Mouillot *et al*., 2006).

Global species distributions are generally believed to be determined by abiotic influences related to oceanographic and physiographic properties (Sanders, 1968;

Richlefs and Schluter, 1993). For instance, water motion affects biology by acting as a transport mechanism for organisms and their propagules, as a dynamic boundary between regimes, and as a force to which organisms must adapt or respond, for example, in their feeding and locomotor activities (Nowell and Jumars, 1984; Denny, 1993). Thus mechanisms of species assemblages depend strongly on various environmental conditions. However, the variability of species along major environmental gradients in many components of biodiversity remains poorly understood.

Nevertheless, environmental conditions and processes that occur at a variety of spatial scales are critical elements to understand patterns of species assemblages. Analysis of spatial patterns along environmental gradient at different scales is seen as a logical requirement to deal with spatial and temporal confounding (Hurlbert, 1984), and provides tests for generality of models of species assemblages. There are limited studies that have tested the consistency of patterns along sharp environmental gradients at hierarchies of spatial scales (e.g., Benedetti-Cecchi, 2001). A better understanding of the role played by abiotic factors is a key prerequisite for forecasting the effects of shifts in environmental conditions on species diversity (or species traits), as a result of human pressure, and for setting up adequate policies for marine conservation and management (Terlizzi and Schiel, 2009).

The use of traits to predict functional response to environmental change has developed rapidly over the last two decades (Grime *et al*., 1988; Woodward and Diament, 1991; Chapin *et al*., 1993; McIntyre *et al*., 1995; Gitay and Noble, 1997; Poff, 1997; Purvis *et al*., 2000), including studies on traits related to the probability of extinction (e.g. Davies *et al*., 2000; Williams *et al*., 2005) and invasion (e.g.

Grotkopp *et al*., 2002; Hamilton *et al*., 2005; Olden *et al*., 2006). The community assemblage that will affect ecosystem properties is the result of sorting processes among individuals with appropriate response traits (Weiher *et al*., 1998; Grime, 2006). These response traits may encompass response to environmental change, directly and response through compensatory dynamics due to consequent changes in species interactions. The altered community will impact ecosystem processes via changes in the representation of ecosystem-effect traits. Suites of effect on traits are often reliable predictors of ecosystem function (Chapin *et al*., 1996; Diaz and Cabido, 2001; Garnier *et al*., 2004) across a wide range of ecosystem types (Grime *et al*., 1997; Reich *et al*., 2003; Diaz *et al*., 2004; Kremen, 2005), and understanding of how traits affect various ecosystem properties is a currently growing area of research (Suding *et al*., 2008).

The species trait diversity effects on ecosystem processes are the degree to which abiotic conditions constrain the functional variations within communities that influence the processes within the system (Hopper *et al*., 2002). Consequently, merging our understanding of ecosystem level controls with our understanding of community dynamics and assembly is an important focus of future study (Thompson *et al*., 2001). Functional diversity is increasingly used to understand the biodiversity-environment relation and biodiversity-ecosystem functioning and to decipher the effect of anthropogenic activities on ecosystem (Dimitriadis and Koutsoubas, 2011).

Studies using functional traits to test the strength of different processes of community assembly often find that habitat filtering plays a key role in the communities' formation (Paine *et al*., 2011; Katabuchi *et al*., 2012; Shipley *et al*., 2012). However, it is important to recognize that in many cases there is also evidence that in varying degrees, other processes (e.g. limiting similarity, dispersal limitation) play a role in the formation of the community structure (Cornwell and Ackerly 2009; Katabuchi *et al*., 2012; Shipley *et al*., 2012).

There has been an overall lack of studies accounting for the fact that communities assemble across environmental gradients (McGill *et al*., 2006). This chapter of the thesis focuses on quantifying assemblage patterns of functional traits and assesseses whether those patterns are the results of gradient in abiotic factors. The study hypothesizes that multiple functional traits influence macrobenthic community structure, and that traits relating to primary strategy or ‘ecological syndrome’ (sets of traits that are collectively associated with adaptation to particular environment change (or gradient) (see Grime, 2001; Lavorel *et al*., 2007), will be similar among species; and also, the dominant traits exert the strongest control on ecosystem processes.

3.2 Materials and Methods

3.2.1 Study Area

The study locality is within the Guinea Current Large Marine Ecosystem (GCLME) which borders 16 countries from Bissagos Island in Guinea Bissau to Angola in Western Africa. It is number 28 of the 66 globally delineated large marine ecosystems (LMEs) (IOC, 2013). The sampling extended from Bissagos Island to Cape Lopex in Gabon and comprised of 11 countries (Figs. 2.3 and 3.1).

The GCLME is characterized by distinctive bathymetry, hydrography, chemistry and trophodynamics. The Guinea Current System represents a Large Marine Ecosystem (LME) ranked among the five most productive coastal and offshore waters in the world with rich fishery resources, oil and gas reserves, precious minerals, a high potential for tourism and serves as an important reservoir of marine biological diversity of global significance (Sherman, 1993; Ukwe, 2003).

3.2.2 Field Sampling

Soft-bottom macrobenthic fauna samples were collected in replicate from the Bissagos Island (Guinea Bissau) in the north to Cape Lopez (Gabon) in the south of the GCLME onboard RV Fritdjorf Nansen as part of the GCLME fisheries resource survey from May to July 2007. In all four stations were sampled for sediment in each of the GCLME country, using a van Veen grab of surface area of $0.1m^2$. At each station, two replicate sediment samples were in order to ensure sample representativeness due to the patchiness in the macrobenthic community.

The sediment samples were washed through a 0.5 mm mesh size sieve using filtered seawater.

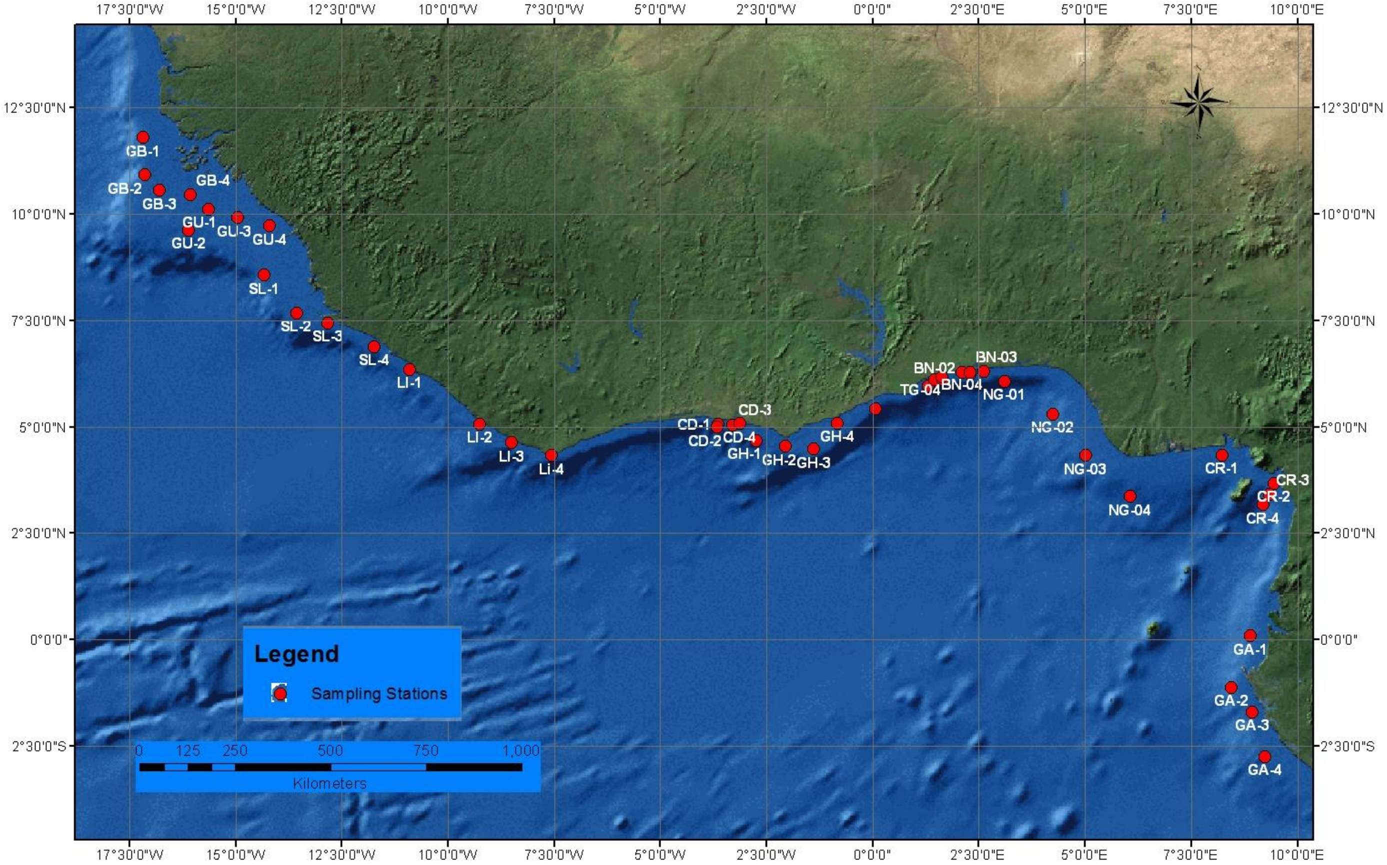


Figure 3.1 Map of the study area showing sampling points.

The retained samples on the sieve were transferred in turns into inner and outer-labeled wide neck plastic sample holding containers and fixed with borax pre-buffered with 10% formaldehyde solution for taxonomic identification in the laboratory. The labeling followed a format of the station name and number (i.e. country first 2 initial letters), date, replicate type, and fixative used (e.g. GB-03, 08/05/06, 1/3, Formalin). Each grab sample was evaluated on suitability of acceptance as good grab sample. For instance, an acceptable grab sample has the top layer of the sediment intact and not disturbed and also if +51% of the sample were retrieved from the grab (Holme and McIntyre, 1971; Eleftheriou and Holme, 1984).

The top 2cm of each sediment sample was sub-sampled for physical and chemical analyses. This was done using a 2 cm deep Kynar-coated scoop and placed into separate jars as follows:

- 500 ml container for organic carbon content analysis (samples were frozen);
- 250 ml container for chemical analyses (samples were frozen);
- ziplock bag for grain size analyses.

3.2.3 Field Quality Control

Basic quality control measures were followed for sediment macro-infauna sampling. These measures were based on internationally accepted Standard Operation Procedures (SOPs) in benthic sampling to ensure quality of the information gathered (Holme and McIntyre, 1971; Eleftheriou and Holme, 1984; ASTM, 2006). Among others, the following field quality control procedures and measures were observed:

- Sediment samples collected at each station were ensured that they meet international sample acceptance criteria. These include:

  - Incomplete closure of grab
  - Inadequate sediment samples
  - Lack of surficial water
- Only experienced persons assisted with the sediment sampling, sieving, fixation and preservation.
- Sediment was sieved with gentle flowing water hose to avoid squashing of organisms.
- All sieves were backwashed into storage containers after sieving to ensure that organisms at the crevices of the sieve are removed.
- Chemicals solutions such as formalin and ethanol for fixation and preservation respectively were carefully and properly prepared.
- Injurious and harmful chemicals were adequately labelled and stored in appropriate cabinet.

3.2.4 Laboratory Processing of Samples

The processing and analyses of samples were performed in the Department of Fisheries and Marine Science , University of Ghana laboratory for the sediment biota and the activities included sorting of organisms (picking target organisms from the sediment grains), preservation and taxonomic identification. For the abiotic component both physical and chemical analyses were carried out on the sediment samples and these are described in section 3.4.

The sample sorting involved emptying the contents of the fixed samples into 0.5 mm mesh sieves and thoroughly washing with fresh water to get rid of all silt/clay particles, as well as the formaldehyde fixative. The samples were then put into a tray with a white background and macrobenthic faunal organisms sorted into preservation vials containing 70% ethanol premixed with glycerol to prevent evaporation of the ethanol.

3.2.4.1 Taxonomic Identification

The preserved organisms were put into petri dishes and identified to the lowest taxonomic units as possible using Leica 2000 dissecting and compound microscopes. Enumeration of individual species was carried out after the identification. Various taxonomic guides were used in the species identification including Day, (1967ab); LeLœuff and Intes, (1974); Fauchald, (1977); Edmunds, (1978); Intes and Lœuff (1984); Kirkegaard, (1988); Cosel, (2006) and Rakel, (2007).

With regards to taxonomic identification, quality assurance measures were observed in the laboratory to ensure that the quality and the integrity of the data from the laboratory processes were not compromised. The following procedures were used.

- Each sorted sample was crosschecked by other benthic expert to ensure that all organisms had been picked before sample was discarded.
- Species identification was verified independently by a colleague expert.
- Unidentified species were assigned the genus name followed by 'sp.' (if only one species, e.g. *Glycera* sp.) or 'spp.' (i.e. more than one species, e.g. *Eunice* spp.) and put separately into vials for later identification.
- Organisms preserved in vials were annotated with relevant information on non-wettable sheets.
- Data entering into computers were verified by another person to avoid wrong entering.

3.2.4.2 Laboratory Analysis of Abiotic Data

The abiotic data collected were physical (grains size), and chemical (total organic carbon, nutrients [i.e. nitrate, phosphate], calcium, sodium, potassium and magnesium).

3.2.4.3 Analyses of Physical Parameters

Prior to the sediment grain size fraction analysis, the sediment samples were air-dried, sieved through 200 mm mesh size sieve. The Bouyoucos Methods (Bouyoucous, 1934) was used for the grain-size analysis. The method is based on the principle that sediment particles were expected to settle in water at a speed directly related to the square of their diameter and inversely related to the viscosity of the water. As regards the Bouyoucous Method, forty grams (40 g) of the air-dried, homogenized and sieved samples were transferred into polyethylene containers and then 100 ml of calgon solution was added to disperse the particles. The solution was stirred on a mechanical shaker for 90 minutes and then transferred into a sedimentation cylinder after sieving through 45 µm.

The retained sand fraction was put in a moisturizing container and 5ml of hydrogen peroxide was added to dissolve any organic matter present. The sample was oven dried overnight at a temperature of 105^{o} C, each sample was weighed afterwards. The suspension was poured into a cylinder and made up to the 1 litre mark with distilled water. The sediment particles were thoroughly stirred with a hand stirrer and after five hours a hydrometer was carefully inserted into the suspensions and the readings were taken. The hydrometer readings for a blank were also taken. This was subtracted from the original hydrometer readings to give the actual weight of the clay fractions. The weights of both the clay and sand fractions were calculated in terms of percentages with respect to the initial weight taken, and the sum of their combined weight was subtracted from 100 to give the percentage weight of the silt.

3.2.4.4 Chemical Analysis

Total Organic Carbon

The organic carbon content determination was carried out at the Ecological Laboratory of the University of Ghana using the ELTRA 5500 C-S determinator. The samples were pretreated with 10% hydrochloric acid to remove the inorganic carbonates. The sediment samples were oven-dried at $60^{o}C$ for 12 hours to get rid of the moisture. The samples were then weighed individually and transferred into a weighing boat of size 1.5 x 0.15 cm. The samples were then sent into an ELTRA C5500 C-S determinator, with a furnace combustion temperature of about $1100^{o}C$. After the combustion the percent organic carbon of the samples were determined and recorded.

Sediment Nutrient Determination

Five grams (5 g) of each sediment sample was weighed into a beaker and 0.75M KCl solution was added for extraction, after which the samples were shaken vigorously for 1 hour. The resultant solution was filtered and 25ml of it taken for analysis of nitrate and using the HACH DR/2010 Spectrophotometer following the methods in A.P.H.A. *et al*., (1998). However, for phosphate analysis the EDTA method (Golterman, 1996) was used for the P-extraction.

Elemental Analysis

The sediments were first dried to get rid of excess water and later oven-dried at a temperature of 50^{o}C to attain a constant mass. Sediments were then pounded into powder form using a mortar and pestle. They were later passed through a 63µm sieve (silt fraction) and later kept in labeled transparent polythene bags for analysis. One hundred milligrams (100 mg) of each sample was enveloped via thermal sealing inside 5×5 cm^{2} polyethylene thin film, which was heat-sealed in 8.9 cm^{3} rabbit capsule for irradiation. Initially, the polyethylene film and rabbit capsules were cleaned by soaking them into dilute nitric acid for three days and washed with de-ionized water.

The sediment samples were analyzed by Instrumental Neutron Activation Analysis (INAA). The neutron flux used for the irradiation was approximately $5.0 \cdot 10^{11}$ n·cm^{-2}·s^{-1}. The samples were sent into the Miniature Neutron Source Reactor (MNSR) by means of a pneumatic transfer system operating at a pressure of 25 atmospheres. The scheme of the irradiation was chosen so as to take into account the half-lives of the radionuclides under investigation. In that regard, the following irradiation times were selected: 10 seconds for the short-lived radionuclides; 3600 seconds for the intermediate radionuclides; and 14400 seconds for long-lived elements.

After a short decay period the activity of the gamma-ray emitting radionuclides with short and medium half-lives were measured. The measurements of the gamma-ray spectral intensities were made using a spectroscopy system of high purity germanium (HPGe) N-type coaxial detector Model GR 2518; high voltage power supply Model 3105; and a spectroscopy amplifier Model 2020 (all manufactured by Canberra Industries, Inc.). The detector system at fixed geometry was coupled to an 8k Ortec multichannel analyzer (MCA) emulation card and a 486 microcomputer.

The resolution of the detector system which operates at a bias voltage of –3000 V full width at half maximum (FWHM) was 1.8 keV for ^{60}Co 1332 keV gamma-ray with 25% relative efficiency.

The output spectral intensities of both the analytical samples and the standards were processed and stored in the microcomputer software by means of the MCA card. Qualitative analysis of the radioisotopes was achieved by means of identifying their spectral intensities. The evaluations of the areas through integration under the photo peaks of the identified elements were converted into their concentrations using the comparator method (Dampare *et al*., 2005).

3.2.5 Functional Trait Analysis

The statistical analyses of the data was preceded by functional trait categorization as described in the ensuing sections. The macrobenthic fauna species were categorized using biological traits. The selection of biological traits and their categorization was dictated by i) available information, ii) ecological functions and iii) perceived sensitivities to environmental disturbance. The selected biological traits reflect morphology (e.g. body size and form) and behaviour (adult mobility, sociability and feeding habit). Some of these traits directly reflect ecological functions (e.g. food and feeding habits), whereas others are indirect indicators. For example, body size indicates the ratio of production/biomass and of production/respiration, beacuase for invertebrate populations in most aquatic systems, the ratios of production/biomass and of production/respiration are closely related to the maximum size achieved by the different taxa (Statzner, 1987). Size also has implications for many other ecological functions and considered to be an important trait of organisms because it correlates with many aspects of its biology (e.g. metabolism, growth and reproduction) (Calder, 1984). The selected biological traits were further divided into categories as indicated in Table 3.1.

Table 3.1 Biological traits categorization

Numbers	**Adult Body Size [BS]**	**Adult Mobility [AM]**	**Feeding Habit [FH]**	**Feeding Structure [FS]**	**Sociability [S]**	**Adult Body Form [BF]**
1	0.5-20mm	Sessile	Deposit-feeding	Mandible	Solitary	Vermiform
2	20.5-40mm	Crawl	Filter/suspension	Jaw	Gregarious	Cylindrical
3	40.5-60mm	Burrow	Opportunist/scavenger	Proboscis	Colonial	Slender
4	60.5-80mm	Swim	Predator	Palp	Commensal	Flattened
5	80.5-100mm	Creep	Herbivore	Pharyngeal		Elongated
6	>120mm	Glide	Omnivore	Tentacle		Tapered

3.2.5.1 Ecological and Biological Traits

Characteristics describing living modes of the organisms were classified in the ecological traits. These traits have a strong effect on ecosystem functioning and occur in most of the macrobenthic organisms. Mobility was described in the scale of the capacity of the organisms to move in and outside of the sediment. Semi-mobile organisms have the ability to move but they do so only if necessary and usually very slowly. Mobility is an important ecological trait because it affects the capture method of prey organisms or other food resources and defines the trophic relationships of a benthic community.

The chosen morphological traits are important indicators of sediment condition (sediment type and organic loading concentration). The average weight of an adult individual was used to assign the organisms to the body size categories. The second characteristic of the morphological traits was the body form. The attribute "shell" describes all the organisms having external protecting structures while vermiform are considered all the worm-like organisms with or without segmentation (length ≫ width) (Papageorgiou *et al.*, 2009).

3.2.5.2 Functional Trait Classification and Categorization

For every species, information was assigned in each trait catogory. The data on the species traits was gathered from a variety of literature and internet sources. The functional composition of the samples was determined using biological (morphological) and ecological traits based on the fact that traits that affect resources use (e.g., energy and nutrients), feeding interactions, habitats modification (bioturbation and habitat providers) are recognized for their functional importance (Pearson, 2001; Meysman *et al.*, 2006; Hastings *et al.*, 2007) and are wide ranging (Bremner, 2008). As a result, six biological and ecological traits were used in the functional classification analysis. These described the morphology and behaviour of the macrobenthic invertebrates, reflecting their involvement in ecosystem processes and perceived sensitivities to environmental disturbance (see Snelgrove *et al.*, 1997; Jennings and Kaiser, 1998; Bolam *et al.*, 2002; Coleman and Williams, 2002; Thrush and Dayton, 2002). Each of the six traits were sub-divided into categories, for example the trait ‘feeding habit’ contained the categories deposit-feeder, filter/suspension feeder, opportunist/scavenger and predator (Table 3.1). As a result, each species at each sampled station was assigned its biological and ecological traits (see Appendices I & II), and the total traits were determined for each station under each of the selected trait in Table 3.1. Further, statistical analyses of the traits and their categorization were carried out as described in section 3.3.

The selected traits are likely to bring out the effect and response to environmental drivers. For instance traits such as adult size is likely to change with severity of disturbance (Pearson and Rosenberg, 1978), feeding type of the species determine its ability to utilize/tolerate a new diet (Fauchald and Jumars, 1979). Mobility and and sociability can be related to recovery patterns and resilience to disturbance (Thrush and Whitlatch, 2001). Size and living habits indicate the ability to rework the sdiment affecting sediment biogeochemistry (Michaud *et al.*, 2006) providing a link to ecosytem function.

3.3 Statistical Analysis

The data sets were analysed using suites of univariate and multivariate statistics. Basic statistics of the species abundance were calculated as well as distributional trends of the major macrobenthic taxa and dominant functional traits across the sampled stations. Macrobenthic species abundance data were grouped into major taxa namely polychaeta, mollusca, crustacea, echinodermata and ‘Others’. Wet-weight biomass of these major taxa were determined across the stations.

The frequency of occurrence of the data sets (taxonomic diversity and functional richness) were calculated using the F index described by Guille (1970):

$$F=p_a/P \times 100 \qquad (1)$$

where: p_a, is the number of stations where the species occurred and P is the total number of stations. Using this formula the species (and also functional traits) data were classified as: constant ($F>50\%$), common ($10\%<F<49\%$) and rare species or traits ($F<10\%$). The data sets were refined and all the rare taxonomic species and functional traits ($F<10\%$) were eliminated from the data sets as they could potentially introduce ‘noise’ in the statistical analyses. In certain instances, only data for constant taxonomic species and functional traits were used in the statistical analyses. These have been indicated in the appropriate sections of the thesis.

For multivariate analysis, dendrograms of Bray-Curtis similarity index of the composite station data for the GCLME countries were calculated for taxonomic species abundance and fucntional trait richness using the PRIMER v6 package (Clarke and Gorley, 2006). The data sets were first fourth-root transformed to stabilize and normalize the variance (Clarke and Green, 1988). Using a complete linkage, sample (country and biological traits) classifications were produced and thereafter samples (i.e., countries and traits) related to each other identified based on the resulting similarity matrix. The differences in the samples (i.e., GCLME countries) were assessed with one-way ANOSIM (Clarke and Warwick, 1994).

In order to demonstrate the most important abiotic variables related to assemblage patterns of the taxonomic and functional traits, various statistical tools were employed. Forward selection in a Canonical Correspondence Analysis (CCA) and Redundancy Analysis (RDA) ordinations in the CANOCO package and rank correlations between cluster matrix with the program BIO-ENV (Clarke and Ainsworth, 1993) in the PRIMER package and Multiple Linear Regression Analysis (MLRA) were utilized.

In the CCA and RDA analyses, the proportion of the total faunal variance (= sum of all eigenvalues, called total inertia in CANOCO) which can be accounted for by the environmental variables can be estimated as the ratio of eigenvalues of constrained versus unconstrained axes. From this ratio, the percentage value which indicates the percentage explanation of each separate environmental variable to the total fauna and trait variance was calculated. Constrained axes are constructed to maximise the fit with linear combinations of environmental variables, and remaining, unconstrained axes represent a residual variation in data after extracting the constrained axes.

For the functional trait data, the RDA was performed (Ter Braak, 1986) for only identified dominant functional trait data (the identified dominant trait contributed

35.6% and their selection as dominant traits was based on the F index, i.e., F>85%) (Guille, 1970) and trait richness >4%. This technique ensured that rare traits and/or traits with low spatial occurrence and contribution were eliminated so that the analysis was refined and 'noisy' data were not included. It is the author's view that functional traits (or taxonomic species) with the highest spatial coverage (based on the F-index) possess valuable ecological information, having adapted naturally possibly through ecological filtering to the varied environmental gradient, are key in unearthing the main environmental drivers of community assemblages.

The RDA was run using the package CANOCO 4.5 (Ter Braak and Smilauer, 2002), which combines both ordination and regression to ascertain relationships between species (and also species traits) and environmental variables (Ter Braak, 1986). None of the environmental variables utilized reported inflation factor >20 (Ter Braak and Smilauer, 2002) and as a result none was eliminated from the RDA and CCA analyses. All the environmental variables used for the analysis were transformed (Log $(x + 1)$) to stabilize and normalize the variance. In the RDA biplot, the first and second axes represent the most important environmental gradient along which the macrobenthic functional traits are linearly distributed. The direction of each environmental vector represents the maximum rate of change for that particular environmental variable and its length indicates the relative importance to the ordination.

The significance of all primary RDA axes was determined by a Monte Carlo permutation test (199 permutations) of the eigenvalues (Ter Braak and Smilauer, 2002). A forward selection procedure ordered the environmental variables according to the amount of variance they captured in the trait data (Ter Braak and Verdonschot, 1995). In the first step of this method, all environmental variables were ranked on the basis of the fit for each separate variable. Each variable was treated as the sole predictor variable and all other variables were ignored; hence, the variance explained represents marginal effects. At the end of the first step of the forward selection, the best variable was selected. Hereafter, all remaining environmental variables were ranked on the basis of the fit (amount of variance explained) that each separate variable gave in conjunction with the variable(s) (covariables) already selected (conditional or unique effects). At each step, the statistical significance of the variable added was tested using a Monte Carlo permutation test (199 unrestricted permutations) (Ter Braak and Smilauer, 1998). This description of RDA is similar to the CCA used for the taxonomic species and functional trait data sets except that the RDA is a linear ordination whilst CCA is unimodal (weighted averaging).

Bio-Env analysis was the second method used for extracting important explanatory variables from the taxonomic species and functional traits data. This harmonic analysis uses a weighted Spearman's rank correlation between the resulting ranked similarity matrices which underlie the MDS ordinations (or the dendrogram) of species or traits and correlation-based. The variable or combinations of variables which give the highest correlation coefficient is assumed to be the most important explanatory vanable(s).

In order to confirm the explanatory variables and develop a simple model, the taxonomic species and functional traits data were subjected to step-wise linear multiple regression analysis. The analysis not only select the best explanatory environmental variable to the dependent variable (ie., species diversity, functional richness, and dominant functional traits) but also create a significant predictive model of the dependent variables.

3.4 RESULTS

3.4.1 Macrobenthic Fauna Community Structure

The analysis of the taxa resulted in a numerical abundance of 3,048 individuals (mean density = 693±579 indi/m^2) comprising 381 species that belong to five major taxonomic groups namely: Polychaeta, Crustacea, Mollusca, Echinodermata and ‘Others’. Of the total numerical abundance, polychaetes contributed 55.15%, crustaceans accounted for 28.02%; 12.76% was contributed by species placed in “Others” category, while molluscs and echinoderms accounted for 2.23% and 1.84% respectively (Table 3.2). Species placed in ‘Others’ category included cnidarians, sponges, sipunculids etc.

In terms of number of species, polychaetes comprised 233 species (61.32%), crustaceans consisted 71 species (18.64%), 35 species (9.19%) were molluscs, whereas echinoderms and “others” category constituted 10 (2.63%) and 32 (8.39%) species respectively. Polychaetes taxa contributed substantially and ranked highest in terms of species richness and numerical abundance among the major macrobenthic taxa in the study area. Crustaceans ranked second highest in terms of species richness and numerical abundance. The dominant polychaete and crustacean species could constitute important food resources for many commercially important demersal fish species.

Table 3.2 Abundance and richness of major macrobenthic faunal groups.

Taxa	**No. of Species**	**Abundance (No. of indi.)**	**Abundance (%)**
Polychaeta	233	1681	55.15
Crustacea	71	854	28.02
Mollusca	35	68	2.23
Echinodermata	10	56	1.84
Others	32	389	12.76
Total	**380**	**3048**	**100**

The distribution pattern of these macrobenthic fauna may therefore determine the abundance of demersal fish stocks on the continental shelves of the GCLME as the fish prey on these. The spatial pattern of all the major macrobenthic faunal taxa is shown in Figures 3.2-3.13. The distribution pattern generally depicts two abundance peaks especially for polychaetes, crustaceans and molluscs (Fig. 3.2). The lowest abundances were noted from Guinea Bissau to Sierra Leone, with Guinea being exception, while the highest abundances occurred in the central sections from Ghana to Benin. Cameroon and Gabon recorded the lowest numerical abundance (Fig. 3.2). The highest abundance of echinoderms occurred at Guinea Bissau (Fig. 3.2) but with low species richness (Fig. 3.3) depicting dominance of few species, which could suggest conditions tolerable to few species. The highest crustacean abundance and richness was noted at Guinea (Figs. 3.2 and 3.3). Nonetheless, the composite abundance and richness data indicated that Togo, Benin and Ghana, and Guinea ranked highest. The composite data indicated considerable differences in species abundances and richness in Togo, Benin, Ghana and Guinea with the other GCLME countries (Figs. 3.2 and 3.3).

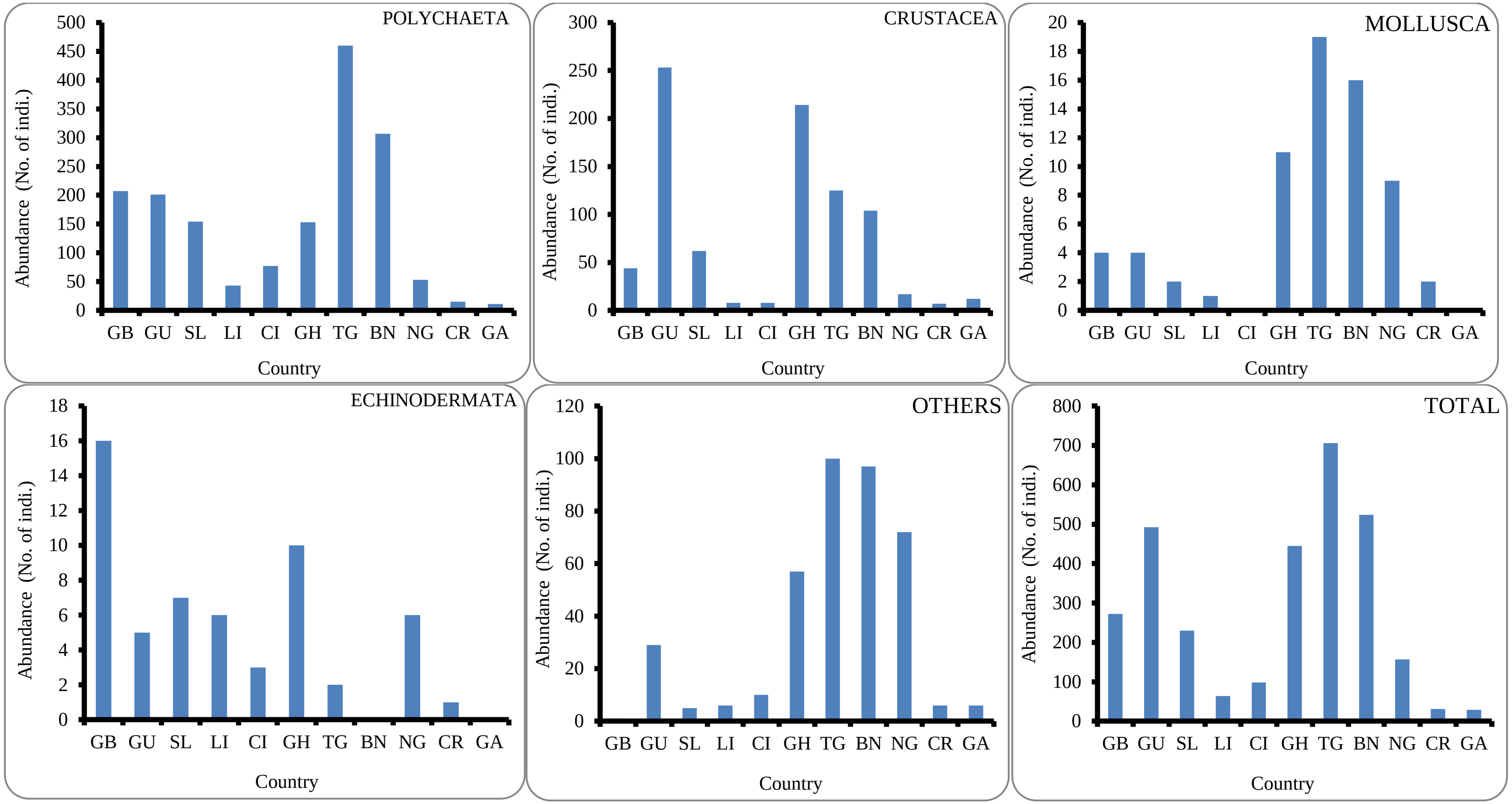


Figure 3.2 Spatial distribution of major macrobenthic fauna abundance on the continental shelves of the GCLME countries. See Table 3.3 for the codes used on the x-axis.

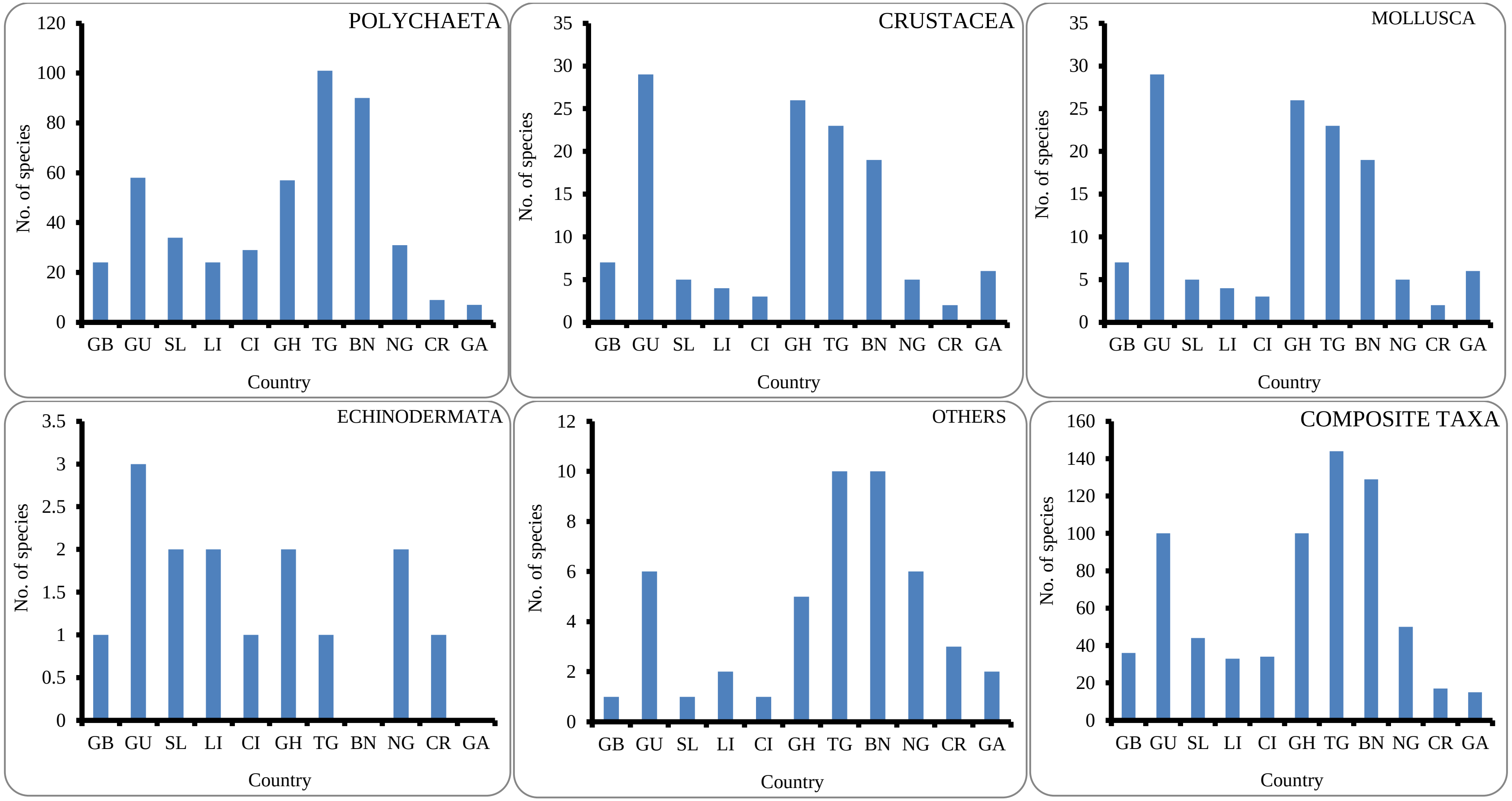


Figure 3.3 Spatial distribution of number of species (species richness) across continental shelf of the GCLME countries. See Table 3.3 for the codes used on the x-axis

3.4.2 Macrobenthic Faunistic Density

The total densities for the respective countries are presented in Table 3.3. The overall total density for the study area was 9,525 indi/m^2 (mean density = 865.9±723.2 indi/m^2). The highest densities were sequentially observed with polychaetes, crustaceans, 'other' taxa, molluscs and echinoderms, which are consistent with the pattern of the species abundance data. The densities of polychaetes, crustaceans and molluscs across the GCLME countries showed similar patterns to that of the species abundance (Figure 3.2). The patterns indicated two peaks and troughs. The highest densites occurred between Ghana and Benin, followed by Guinea Bissau to Sierra Leone, whiles lowest densities were noted between Liberia-Cote d'Ivoire, and Cameroon-Gabon

Table 3.3 Densities (Ind./m^2) of major macrobenthic faunal groups in the continental shelves of countries bordering the GCLME.

Country	**Country ID**	Polychaeta	Crustacea	Mollusca	Echinodermata	'Others'	**Total**
Guinea Bissau	**GB**	647	138	13	50	3	**850**
Guinea	**GU**	628	791	13	16	91	**1538**
Sierra Leone	**SL**	481	194	6	22	16	**719**
Liberia	**LI**	134	25	3	19	19	**200**
Cote d'Ivoire	**CD**	241	25	0	9	31	**306**
Ghana	**GH**	478	669	34	31	178	**1391**
Togo	**TG**	1438	391	59	6	313	**2206**
Benin	**BN**	959	325	50	0	303	**1638**
Nigeria	**NG**	166	53	28	19	225	**491**
Cameroon	**CR**	47	22	6	3	19	**97**
Gabon	**GA**	34	38	0	0	19	**91**

3.4.3 Dominant Macrobenthic Taxa

The analysis of frequency of occurrence (F-index) of the 381 identified macrobenthic faunal species across the 44 sampling locations, indicated that 15 species (contributed 35% to species abundance) occurred in >20% of the sampling stations. They may constitute cosmopolitan species with greater geographical coverage and could be excellent biological candidates for monitoring the health of the GCLME. These species were predominantly polychaetes, however, the highest occurrence species (59.0%) was noted for a crustacean, *Ampelisca* spp. The polychaete with the highest frequency of occurrence was *Glycera* sp. and *Eunice vittata* in that order with 41% and 39% respectively (Table 3.4).

Table 3.4 Frequency of Occurrence for 15 numerical dominant macrobenthic fauna. For brevity only taxa contributing >20% were selected. P= Polychaete, C=Crustacean, O= 'Others' taxa .

Taxa	**Frequency of Occurrence (%)**
Ampelisca spp. (C)	59.0
Glycera sp.(P)	41.0
Eunice vittata (P)	39.0
Sipunculid spp. (O)	39.0
Lumbrinereis aberrans (P)	32.0
Tanaid spp. (C)	30.0
Mysid sp. (C)	27.0
Armandia intermedia (P)	25.0
Prionospio pinnata (P)	25.0
Scoloplos madagascariensis (P)	25.0
Aricidea fauveli (P)	23.0
Lumbrinereis latrelli (P)	23.0
Lumbrinereis coccinea (P)	23.0
Nepthys lyrochaeta (P)	23.0
Prionospio sexoculata (P)	23.0

The spatial distribution of the abundance of the 15 most occurred species is presented as Figure 3.4. A striking feature of the distribution was the high numbers of *Prionospio pinnata* (Spionidae) at Guinea Bissau (Fig. 3.4), which also revealed higher numerical abundance for echinoderm but low taxa richness (Figs. 3.2 and 3.3) suggesting the existence microhabitats that support certain species. *Eunice vittata* (Spionidae) was also highest at Togo followed by Guinea Bissau (Fig. 3.4).

There were numerical dominance of different species across the GCLME countries suggesting the existence of abiotic gradients supporting organismal life. *Ampelisca* spp. for instance ranked highest in Togo followed by Guinea. Ostensibly, the 3 most occurred crustaceans (*Ampelisca* spp., Tanaid & mysid) were collectively dominant numerically in Guinea, which thus rank the country highest in terms of crustacean abundance. *Sipunculid* spp. was dominant in Ghana but was visibly absent in Guinea Bissau, Togo, Benin and Nigeria (Fig. 3.4). The countries with the lowest representation of these most occurred species were Nigeria, Gabon, Cameroon, Liberia, Cote d’ Ivoire and to some extent Sierra Leone.

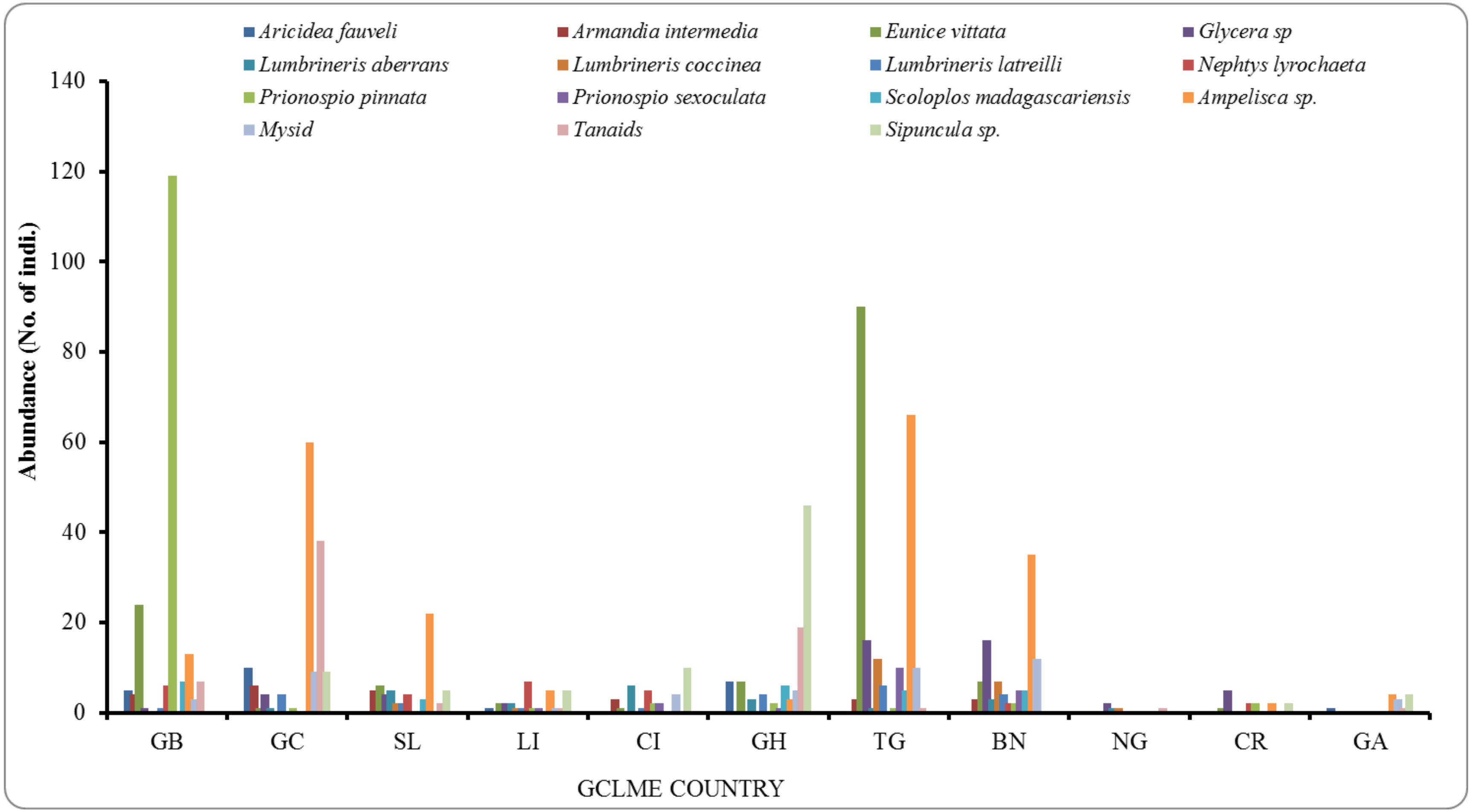


Figure 3.4 Distribution of abundance of dominant macrobenthic faunal species across GCLME countries using F-index, F>20. Codes on x-axis are provided in Table 3.3.

3.4.4 Spatial Pattern of Sediment Abiotic Variables

The water depth the for the various sample stations ranged between 16 m and 153 m (Appendix V) with the mean water depth of 54.7±33.7 m. However, 50% of the stations had an average depth of 49 m.

The mean concentration levels and the distribution of the sediment abiotic variables are presented in Figure 3.5. All the sediment parameters showed spatial differences with peaking and troughing between the countries, but without discernible east-west pattern. Average nitrate levels were higher at both west (Guinea Bissau, Guinea and Sierra Leone) and east (Nigeria, Cameroon and Gabon) of GCLME than at the central (Benin, Togo, Ghana, Cote d'Ivoire and Liberia). There were considerable within country spatial variations in the sediment parameters. Certain GCLME countries, reported the highest mean concentrations namely phosphate in Benin, sodium and organic carbon in Ghana, nitrate in Guinea Bissau, and silt in Cameroon

Calcium showed three spatial peaks at Sierra Leone, Gabon and Ghana in that decreasing order. The lowest concentrations of calcium were noted at Togo, Benin and Nigeria. However, the levels within Nigeria depicted the highest variations. Total organic carbon and clay showed relatively similar pattern with Ghana recording the highest mean concentrations.

Magnesium levels ranked highest at the western sections of the GCLME depicting a similar pattern to ccalcium distribution. The lowest magnesium and calcium levels occurred in Togo and Benin, which also depicted the highest species and dominant trait richness. Higher phosphate levels were noted at Togo, Benin and Ghana (Fig. 3.5b).

Table 3.5 Average water depth of the sampled GCLME countries

Country	**Country Code**	**Average (m)**	**Standard Deviation**
Guinea Bissau	GB	89.8	58.9
Guinea	GU	47.5	32.0
Sierra Leone	SL	40.5	12.0
Liberia	LI	41.5	15.0
Cote d'Ivoire	CD	59.5	32.6
Ghana	GH	66.3	29.8
Togo	TG	32.8	19.2
Benin	BN	21.3	5.4
Nigeria	NG	58.2	23.6
Cameroon	CR	51.5	36.8
Gabon	GA	92.8	25.5

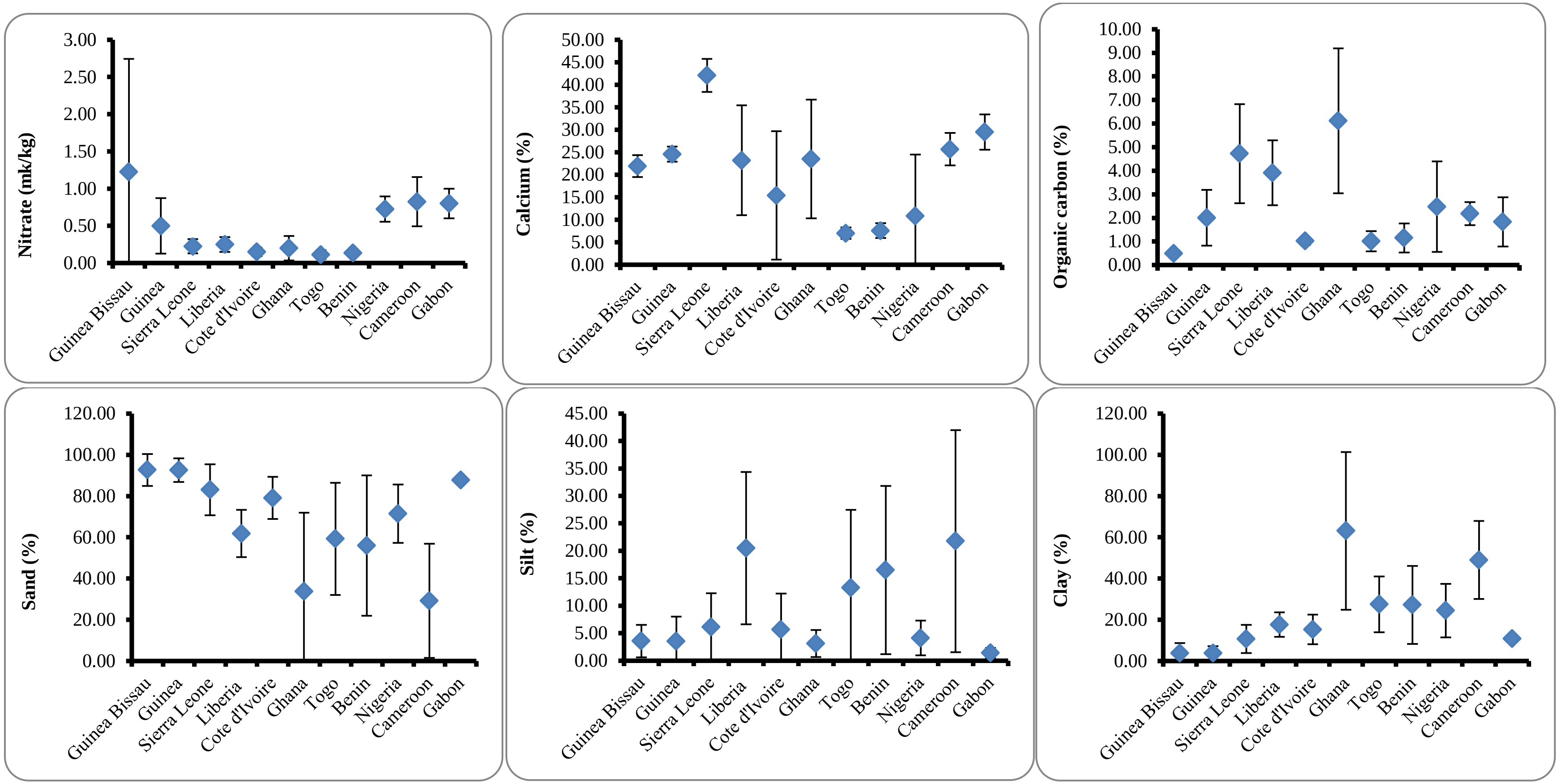


Figure 3.5a. Mean concentration of nitrate, calcium, organic carbon, sand, silt and clay contents of sediments across the GCLME countries. The error bars indicate 95% confidence intervals.

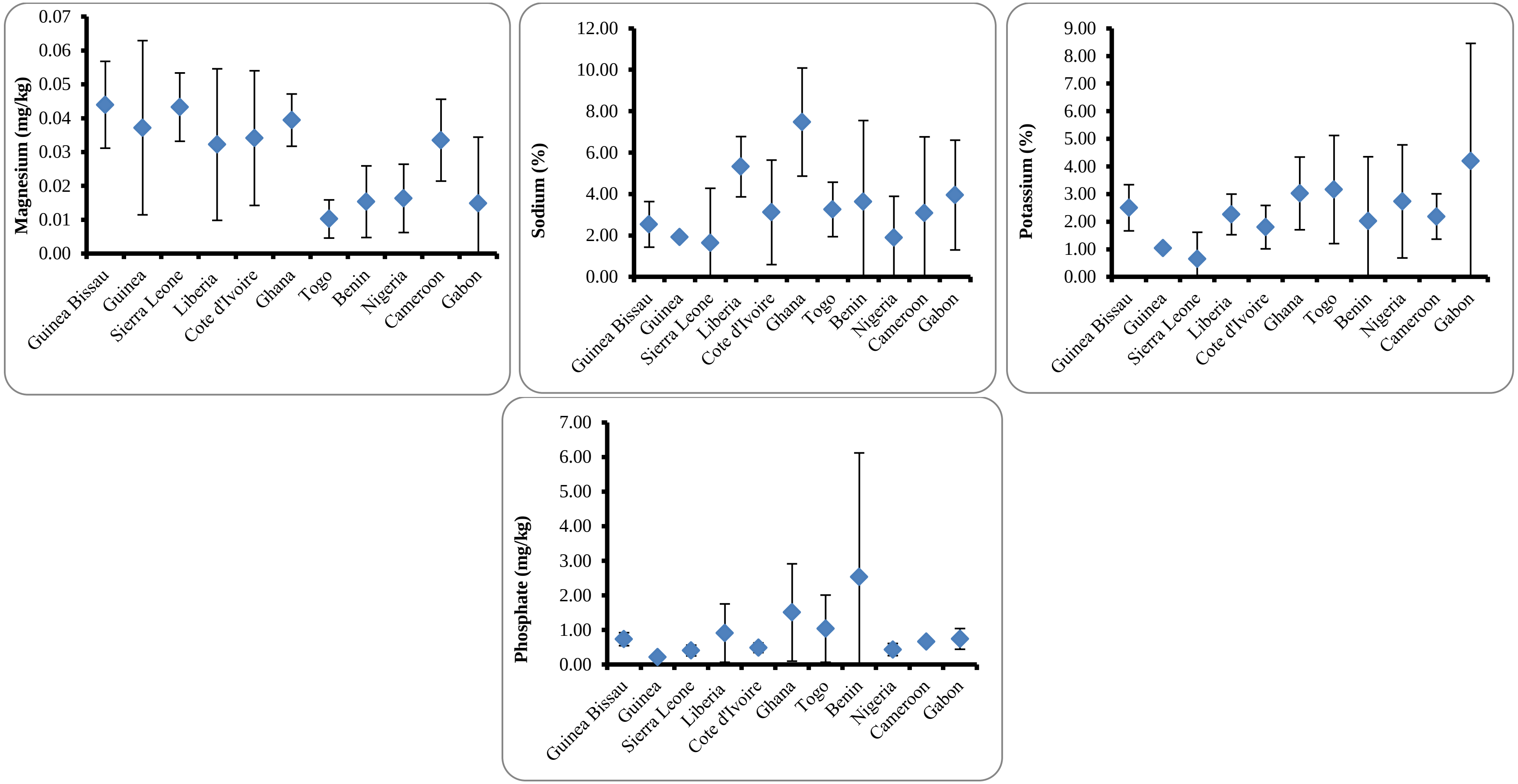


Figure 3.5b. Mean concentrations of magnesium, sodium, potassium and phosphate across the GCLME countries. The error bars indicate 95% confidence intervals.

3.4.5 Community Structural Analysis

An agglomerative Bray–Curtis similarity dendrogram of the pooled station species abundance data to represent countries revealed three significant ($p<0.05$) groupings based on the faunistic data (Fig. 3.6). Only Nigeria showed non-significant faunistic structure with the other countries indicating either unique condition supporting unique fauna or a stressful ecosystem. The first cluster ground (Group A) comprised Cameroon, Liberia and Gabon. Cluster Group B is made up countries located at the western part of the GCLME namely Guinea Bissau, Guinea, Sierra Leone, Cote d' Ivoire and Ghana. Ghana and Cote d'Ivoire formed one sub-group under Group B just as Guinea Bissau, Guinea and Sierra Leone. The last cluster Group C composed of Benin and Togo, which showed the highest similarity index of 58%, followed by Sierra Leone and Guinea at 54%, and together with Guinea Bissau at 47% (Fig. 3.6). Liberia and Cameroon followed at 43% similarity before Ghana and Cote d' Ivoire 36%. The pattern shows high degree of spatial differences in the macrobenthic fauna composition and abundance possibly due to prevailing gradients in environmental conditions creating varied tolerable regimes for the organisms.

In order to test the level of similarity between the countries, the analysis of simlarity (ANOSIM) test was run and the results indicated significant differences ($p=0.001$) between the countries with the global R=51.2% (Table 3.6). However, the pairwise test showed non-significant differences ($p>0.05$) between some countries notably those bordering the western sections of the GCLME suggesting that the macrobenthic fauna composition at those countries are relatively similar than the the central and eastern sections of the GCLME.

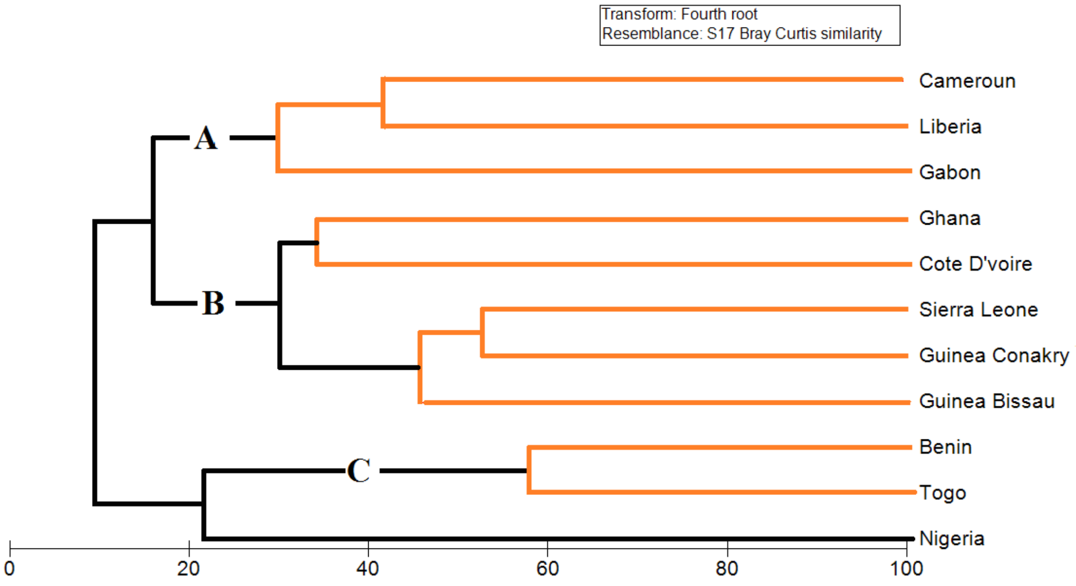


Figure 3.6 Complete-linkage of agglomerative dendrogram of Bray–Curtis similarity of macrobenthic faunal abundance data for GCLME countries. Thin red lines indicate significant evidence of structure (SIMPROF test, *p*<0.05) and thick black lines indicate no evidence of structure.

Table 3.6 Pairwise ANOSIM analysis

Global Test
Sample statistic (Global R): 0.512
Significance level of sample statistic: 0.1%
Number of permutations: 999 (Random sample from a large number)
Number of permuted statistics greater than or equal to Global R: 0

Pair Country	R Statistic	Significace level (%)	Significance
Guinea Bissau, Cote d' Ivoire	0.672	2.9	Yes
Guinea Bissau, Ghana	0.516	2.9	Yes
Guinea Bissau, Togo	0.766	2.9	Yes
Guinea Bissau, Benin	0.771	2.9	Yes
Guinea Bissau, Nigeria	0.635	2.9	Yes
Guinea Bissau, Cameroon	0.479	2.9	Yes
Guinea, Cote d' Ivoire	0.625	2.9	Yes
Guinea, Togo	0.719	2.9	Yes
Guinea, Benin	0.750	2.9	Yes
Guinea, Nigeria	0.740	2.9	Yes
Sierra Leone, Ghana	0.427	2.9	Yes
Sierra Leone, Togo	0.615	2.9	Yes
Sierra Leone, Benin	0.677	2.9	Yes
Sierra Leone, Nigeria	0.604	2.9	Yes
Sierra Leone, Cameroon	0.339	2.9	Yes
Liberia, Ghana	0.604	2.9	Yes
Liberia, Togo	0.958	2.9	Yes
Liberia, Benin	0.958	2.9	Yes
Liberia, Nigeria	0.677	2.9	Yes
Cote d' Ivoire, Ghana	0.469	2.9	Yes
Cote d' Ivoire, Togo	0.969	2.9	Yes
Cote d' Ivoire, Benin	0.969	2.9	Yes
Cote d' Ivoire, Nigeria	0.740	2.9	Yes
Cote d' Ivoire, Gabon	0.385	2.9	Yes
Cote d' Ivoire, Cameroon	0.557	2.9	Yes
Ghana, Togo	0.927	2.9	Yes
Ghana, Benin	0.917	2.9	Yes
Ghana, Nigeria	0.719	2.9	Yes
Ghana, Gabon	0.333	2.9	Yes
Ghana, Cameroon	0.776	2.9	Yes
Togo, Nigeria	0.635	2.9	Yes
Togo, Gabon	0.458	2.9	Yes
Togo, Cameroon	0.854	2.9	Yes
Benin, Nigeria	0.625	2.9	Yes

Benin, Gabon	0.479	2.9	Yes
Benin, Cameroon	0.828	2.9	Yes
Nigeria, Cameroon	0.693	2.9	Yes
Guinea Bissau, Guinea	0.078	25.7	No
Guinea Bissau, Sierra Leone	0.005	57.1	No
Guinea Bissau, Liberia	0.490	8.6	No
Guinea, Ghana	0.323	5.7	No
Guinea, Sierra Leone	-0.042	60	No
Guinea, Liberia	-0.073	74.3	No
Guinea, Gabon	0.036	37.1	No
Guinea, Cameroon	0.266	8.6	No
Sierra Leone, Liberia	-0.219	94.3	No
Sierra Leone, Cote d' Ivoire	0.396	8.6	No
Sierra Leone, Gabon	0.198	17.1	No
Liberia, Cote d' Ivoire	0.313	8.6	No
Liberia, Gabon	0.146	14.3	No
Liberia, Cameroon	0.292	5.7	No
Togo, Benin	0.146	25.7	No
Nigeria, Gabon	0.375	8.6	No
Gabon, Cameroon	0.167	20	No

3.4.5.1 Community Structure-Environmental Relation

The relationship between benthic macrofaunal community structure and the abiotic variables were determined using suite of multivariate statistical analysis including BIO-ENV routine in PRIMER software v6. This was done to obtain best combination of explanatory environmental variables for the species assemblages. Further, canonical correspondence analysis (CCA) in CANOCO package was used for ordination and correlation of environmental variables, and lastly a multiple linear regression model for a predictive model of species diversity.

The results of the BIO-ENV analysis indicated four environmental variables (silt, nitrate, sodium and calcium) as best explanation variables for the data of the ‘constant’ species (constant species are based on F-index, with F>50) with

Spearman's correlation of 24.3% (Table 3.7). Silt and nitrate combination gave a signifcant ($p<0.05$) correlation of 23.5%. However, when only the ten most occurred species (i.e., species with the highest occurence) were used in the analysis, similar abiotic variables (i.e., silt, nitrate, sodium and calcium) combined to give a correlation of 28.6% although the overall analysis was not signficant ($p=0.164$).

Table 3.7 BIO-ENV results for dominant 'constant' species with F>20.

No of variables	Best variable Combination	Correlation (p_w)
	'Constant' Species with F>20 (p=0.047; Rho=0.243**)**	
4	Silt-Nitrate-Sodium-Calcium	0.243
3	Silt-Nitrate-Calcium	0.241
2	Silt-Nitrate	0.235
	Ten Most Dominant 'Constant' Species with F>25 (p=0.164; Rho=0.204**)**	
4	Silt-Nitrate-Sodium-Calcium	0.286
1	Nitrate	0.201
2	Silt-Nitrate	0.199

The forward selection of the CCA indicated that six environmental variables namely magnesium, organic carbon, nitrate, sand, sodium and silt explained significant variations in the species abundance data ('constant' species). The highest significantly ($p=0.005$) explained species variance was the effect of magnesium (35%), total organic carbon (31%) and nitrate (18%) (see Table 3.8). In the CCA ordination the first two ordination axes showed 66.2% relationship between the species and environment indicating that the species data is constrained on the environment data. The first axis alone explained 19.2% variance in the species data and together with the second axis 33.6% of the species variance data is explained. The Monte Carlo test indicated that the first axis was significant (p=0.01) while all the four axes showed higher significance (p=0.005). All the four axes indicated 92% relation between the species and environment data but only 46.7% variation in the species data was explained (Table 3.9).

Table 3.8 Canonical Correspondence Analysis (CCA) results. Marginal effects denote percentage variance explained (percentage of the total variance in the species data explained) by using each environmental variable as the sole predictor variable. Conditional (unique) effects denote variance explained by each environmental variable with the variable (s) already selected and treated as covariable(s) based on forward selection. Environmental variables are listed by the order of their inclusion into the model. Significant levels are based on a Monte Carlo permutation test with 199 restricted permutations.

Abiotic variable	Marginal Effect Lambda1	Conditional Effect Lambda1	*p*-value	*F-ratio*
Magnesium	0.35	0.35	0.005*	6.40
Organic carbon	0.33	0.31	0.005*	6.25
Nitrate	0.18	0.18	0.005*	4.00
Sand	0.11	0.12	0.025*	2.67
Sodium	0.16	0.13	0.005*	3.15
Silt	0.13	0.09	0.015*	2.17
Clay	0.08	0.07	0.070	1.83
Potassium	0.18	0.04	0.375	1.12
Calcium	0.19	0.02	0.870	0.51
Phosphate	0.06	0.02	0.945	0.41

The ordination biplot (Fig. 3.7) showed important correlations between organic carbon and *Lumbrineries aberrans*, tanaid spp. and mysid spp. These species showed preference to higher sediment organic carbon. *Ampelisca* spp. *Glycera* spp. and *Amandia intermedia* also showed positive preference for clay, whereas higher silt content correlated with *Eunice vittata* and *Scoloplos madagascariensis*.

Table 3.9 Summary of CCA results.

Axes	1	2	3	4	Total inertia
Eigenvalues	0.502	0.378	0.202	0.141	2.622
Species-environment correlations :	0.887	0.848	0.751	0.715	
Cumulative percentage variance					
of species data:	19.2	33.6	41.3	46.7	
of species-environment	37.8	66.2	81.4	92.0	
Sum of all eigenvalues					2.622
Sum of all canonical eigenvalues					1.330

***** Monte Carlo test *****

Significance of first canonical axis: eigenvalue (p= 0.010; F-ratio = 7.585)

Significance of all canonical axes : (p= 0.005; F-ratio =3.293)

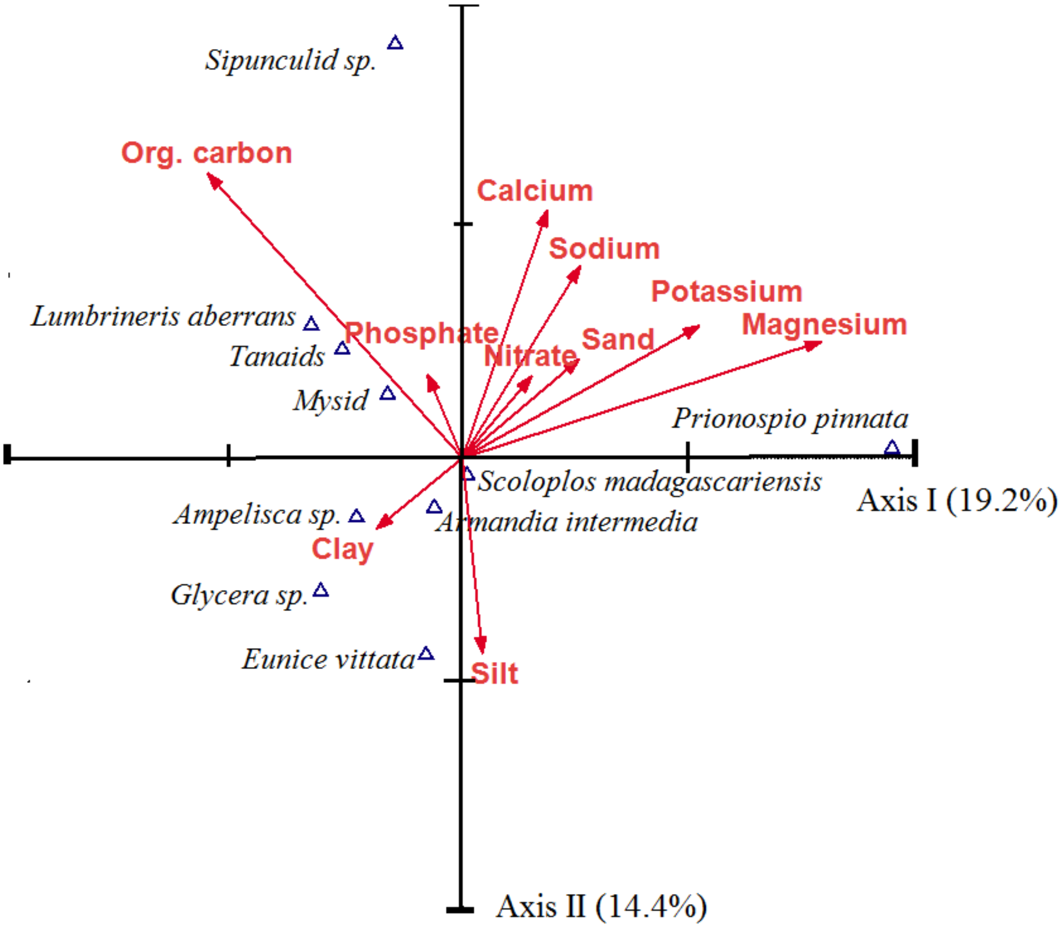


Figure 3.7 CCA ordination biplot for taxon-environment relationship

Predictive Linear Regression Model

To further test the interactions between diversity indices (species assemblages) and abiotic variables, a multiple predictive regression model was run using the Business Spreasheet Excel software. The result of this analysis showed that species assemblages were significantly influenced by suite of abiotic variables ($p<0.05$). Shannon-Wiener species diversity index was influenced by nitrate and calcium, and these two variables explained 41.37% of the variance in the data (Table 3.10) and are therefore important parameters predicting Shannon-Wiener's diversity in the GCLME. The regression model depicted that the independent variables of nitrate and calcium were correlated negatively with the dependent variable. This suggests that low levels of the variables influence the species diversity but there could be a threshold to these low levels. The variations in Margelef's species richness were also explained by nitrate and calcium accounting for 41.71%. The model relationships were indirect (negative) for nitrate and calcium and similar explanation as in the Shannon-Wiener diversity could be adduced. Since none of the explained variances (R squared) were 100%, the unexplained variances could constitute surrogate of unmeasured environmental variables. This means that other factors such as biological (competition and predation), physical (waves and tides), chemical (pollutants), human disturbances, nature of the topography could all be critical in seeking influence of environmental gradients to species community assemblages.

Table 3.10 Step-wise multiple regression model (using the Business Spreadsheet Excel software) for taxon assemblages and abiotic variables, $p<0.05$.

Diversity index	Equation (independent parameters)	R^2
Shannon-Wiener's diversity index	-1.13*nitrate + -0.50*calcium+ 4.06 ± 0.66	0.4137
Margalef's species richness	-4.43*nitrate +-1.91*calcium+11.81 ± 2.55	0.4171

3.4.5.2 Functional Trait Richness And Distribution

The functional trait richness data were catogorised into constant, commom and rare traits using the F-index proposed by Guille (1970) (see Tables 3.11 and 3.12). The analysis showed that the highest functional trait group were sociability (solitary trait category dominate contributing 14.89% and F=92%); mobility (burrow traits being dominant category contributing 11.09% and F=90); adult body size (the dominant trait category was small adult size of 0.5-20 mm contributing 4.98% and F=85%); and feeding habit (deposit-feeding as the dominant category contributing 4.71% and F=81%) (see Table 3.12). The total contributions of the functional trait groups under the 'constant', 'common' and 'rare' categories were 72.72%, 23.65% and 3.63% respectively (Table 3.11). This indicates that the contributions to the functional group richness of the 'rare' species were marginal and will not influence the traits structural analyses, and to some extent the influence of the 'common' species to the analyes may be marginal. Essentially, the influence of the 'constant' functional traits to communtiy assemblage is deemed important due to the total percent contribution and as such dominant traits within the category may exert the strongest influence on ecosystem processes in the GCLME region.

Of the biological traits (see Appendix II), the 4 most dominant were solitary, burrow, small body size and deposit-feeding, which together contributed 35.67% to the functional richness (Table 3.12). The dominant traits were selected based on an individual trait contribution >4% and F>80% (Table 3.12) The individual and combined influences of these traits will determine to a very large large extent the nature of the subtrate, prevailing environment conditions, environmental drivers of community assemblages, effect and response of community and key ecosystem processes in the GCLME.

Table 3.11 Percentage functional trait group richness using the F-index described by Guille (1970): $F=p_a/P \times 100$, where: p_a, is the number of stations where the funtional traits occurred and P is the total number of stations, thus classified as: constant (F>50%), common (10% <F<49%) and rare traits (F<10%).

Trait Group	**Constant**	**Common**	**Rare**	**TOTAL**
Feeding Habit	12.03	4.62	0.23	**16.88**
Feeding Structure	8.48	6.98	0.98	**16.44**
Adult Mobility	14.44	2.08	0.28	**16.79**
Sociability	15.87	1.00	-	**16.87**
Adult Body Size	16.65	-	-	**16.65**
Adult Body Form	5.26	8.97	2.14	**16.37**
TOTAL	**72.72**	**23.65**	**3.63**	**100**

Table 3.12 Dominant traits with respective percent richness and frequency of occurrence. Trait category's richness contribution >4% and F>80% concurrently are highlighted.

Functional Trait Group	Trait Category	% Richness	% Freq. of occurrence
Feeding Habit	**Deposit-feeder**	**4.71**	**81**
	Carnivore	3.82	79
	Detritivore	1.44	65
Feeding Structure	Proboscis	2.12	67
	Mandible & Jaw	1.72	65
	Pharynges & Proboscis	1.08	63
Adult Mobility	**Burrow**	**11.09**	**92**
	Burrow & Sessile	1.02	54
	Burrow & Swim	0.91	50
Sociability	**Solitary**	**14.89**	**92**
	Commensal	0.98	56
Adult Body Size	**0.5- 20mm**	**4.98**	**85**
	20.5- 40mm	3.42	83
	40.5- 60mm	2.89	83
Adult Body Form	Vermiform & flattened	1.61	65
	Slender and Elongated	0.91	56
	Slender	0.83	50

The Bray-Curtis similarity clustering of the 'constant' functional traits revealed significantly important pairings that lend evidence/support to combined effect of trophic, lifestyle, anatomical and morphological adaptations to the prevailing environmental conditions. This may suggest that habitation and subsequent survival of macrobenthic organisms in their environment require multiple adaptive strategies including biological and ecological, which may be determined by prevailing environmental conditions. The dendrogram clustering depicted the highest cluster pairs betwen madibular palps (feeding structure) and laterally-flattened (adult body form) (Fig. 3.8) giving an indication of body form playing an important role in organism's feeding strucutre as well as the feeding type.

Further, the results may suggest that species with elongated and tapered body form are mainly carnivores or detritivores and that possibly facilitate their food acquision mechanism. Slender and elongated species may also be commensal, which could mean better attachment to host to ensure efficient feeding or optimal foraging. The benthic solitary species and burrowing type (see Appendix I) indicated strong signficant relationship (Fig. 3.8). The dendrogram also suggests that deposit-feeding species range from different body sizes (Fig. 3.8) due possibly to the different forms/types of organic carbon (refractory & labile) or sources (authotonous and allochthonous) of organic carbon. The results also suggest that benthic carnivorous species in the GCLME are of medium body size (i.e., 20.5-40.0mm) possibly to facilitate quick movement for preys as well as adequate body size to handle the prey items. Filter-feeders are species with maximum body size (i.e., 100.5- 120mm) probably because they require greater amount of energy for active filter feeding in possibly the high water current.

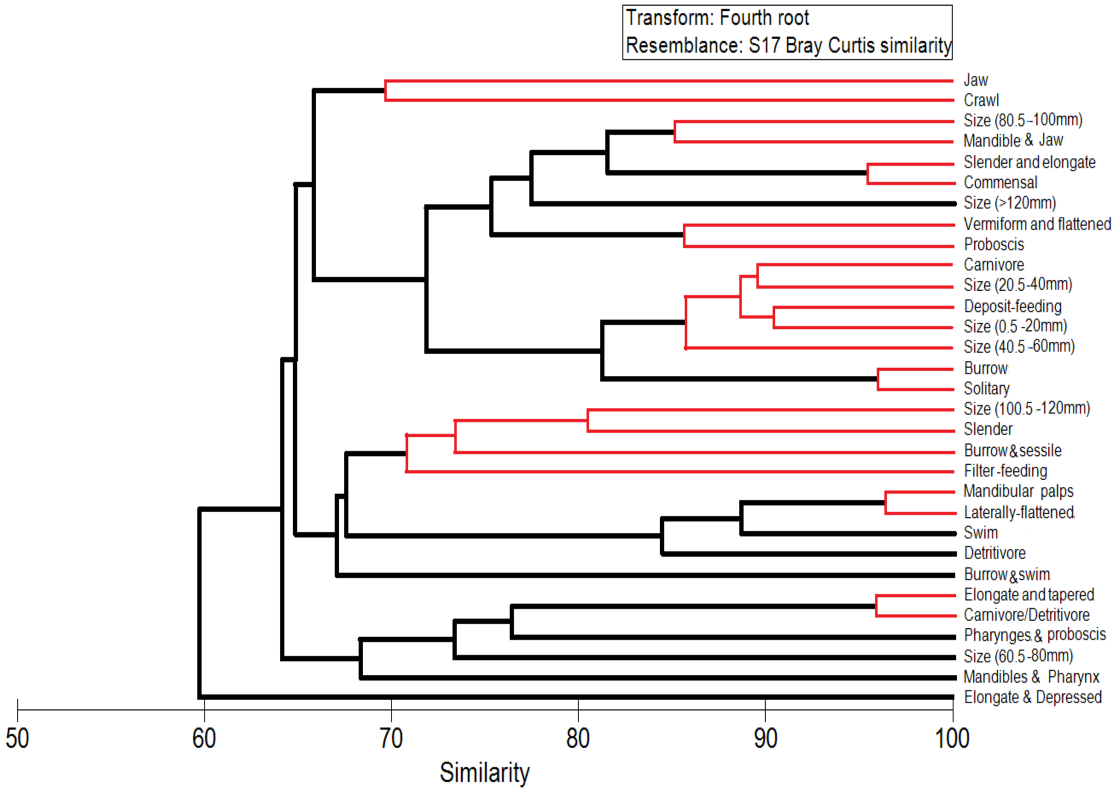


Figure 3.8 Group-average agglomerative dendrogram of Bray-Curtis similarity of 'constant' functional biological traits. Thin red lines indicate significant evidence of structure (SIMPROF test, *p*<0.05) and thick black lines indicate no evidence of structure

3.4.5.3 Distribution of Most Dominant Functional Traits

The distribution of the 4 most dominant traits across the countries bordering the GCLME showed higher abundance of solitary trait followed by burrowing traits (Fig. 3.8). The sequence of dominance for the functional traits were solitary>burrow>small body size>deposit-feeding. The highest richness of the dominant traits occurred at Togo followed by Benin, Guinea and Ghana. The countires with the least in dominant trait richness were Gabon and Cameroon. The distribution pattern of the 4 most dominant traits (Fig. 3.9) is a resemblance of the distribution of taxonomic species abundance (Fig. 3.2), taxonomic species richness (Fig. 3.3) and the 15 most abundant species (Fig. 3.4) strongly suggesting that the dominant species reflect in dominant traits and exert the strongest influence on ecosystem properties/processes in the GCLME.

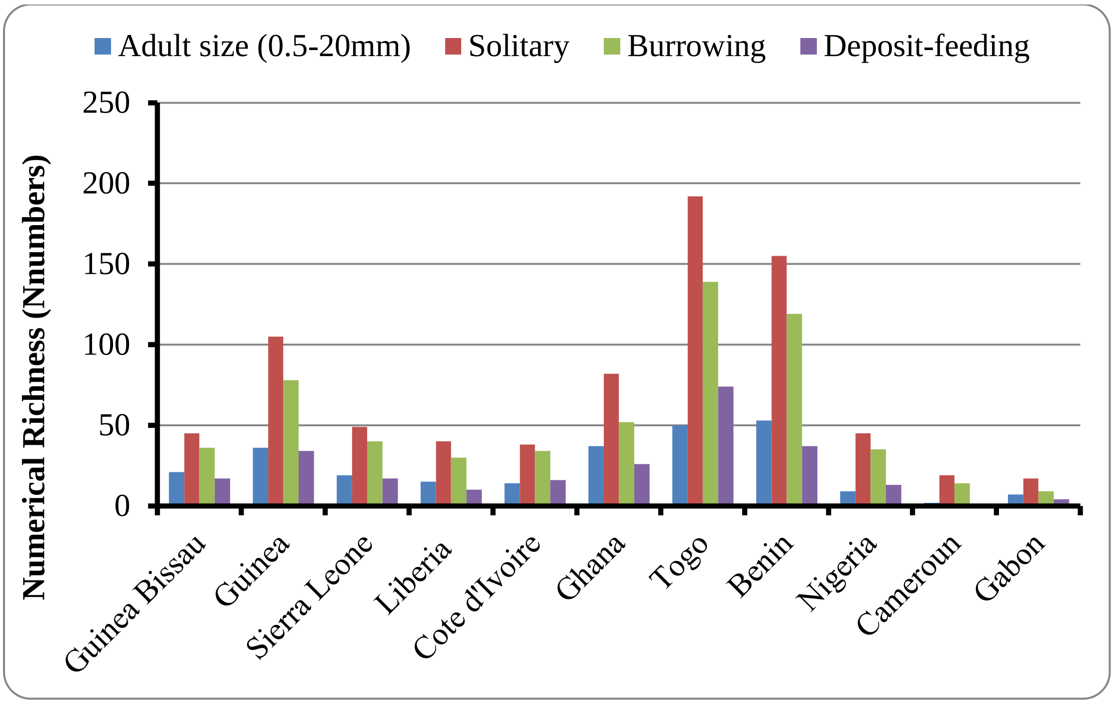


Figure 3.9 Distribution of dominant functional trait richness across GCLME country stations.

3.4.5.4 Multivariate Structural Analysis of Functional Traits

Bray-Curtis similarity analysis of the functional richness data for countries in the GCLME indicated two major significant ($p<0.05$) cluster groups (Group A & B) distinguished at 52% similarity level. Group A comprised Cameroon and Gabon, located far east of the GCLME. Group B is made up of two subgroups namely B1 and B2, which is distinguished at 73% Bray-Curtis similarity level. Subgroup B1 comprised Liberia, Sierra Leone, Guinea Bissau, Nigeria and Cote d'Ivoire in that decreasing order of similarity, and these are mainly countries located west of the GCLME except for Nigeria (Fig. 3.10). Group B2 comprised Ghana, Guinea (subgroup B2i), Benin and Togo (subgroup B2ii), which with the exception of Guinea, are countries located at the central part of the GCLME. In effect, the analysis significantly categorized the countries bordering the GCLME into Eastern Zone (i.e., Gabon & Cameroon), Central Zone (Benin, Togo & Ghana) and Western (Guinea Bissau, Sierra Leone, Liberia & Cote d'Ivoire). Guinea and Nigeria presented macrobenthic functional structure that mimic the Central Zone and Western Zone respectively. The similarity between the groups showed a sequential declension from Central GCLME >Western GCLME>Eastern GCLME. The analysis suggests that the eastern GCLME is low (poor) in benthic biodiversity, the western GCLME moderately rich benthic biodiversity and the central GCLME rich benthic biodiversity relatively.

Nonetheless, the highest Bray-Curtis similarity was noted between Togo and Benin clustering at 97%. This was followed by the similarity of 96% between Liberia and and Sierra Leone. Ghana and Guinea followed with 94% similarity (Fig. 3.10).

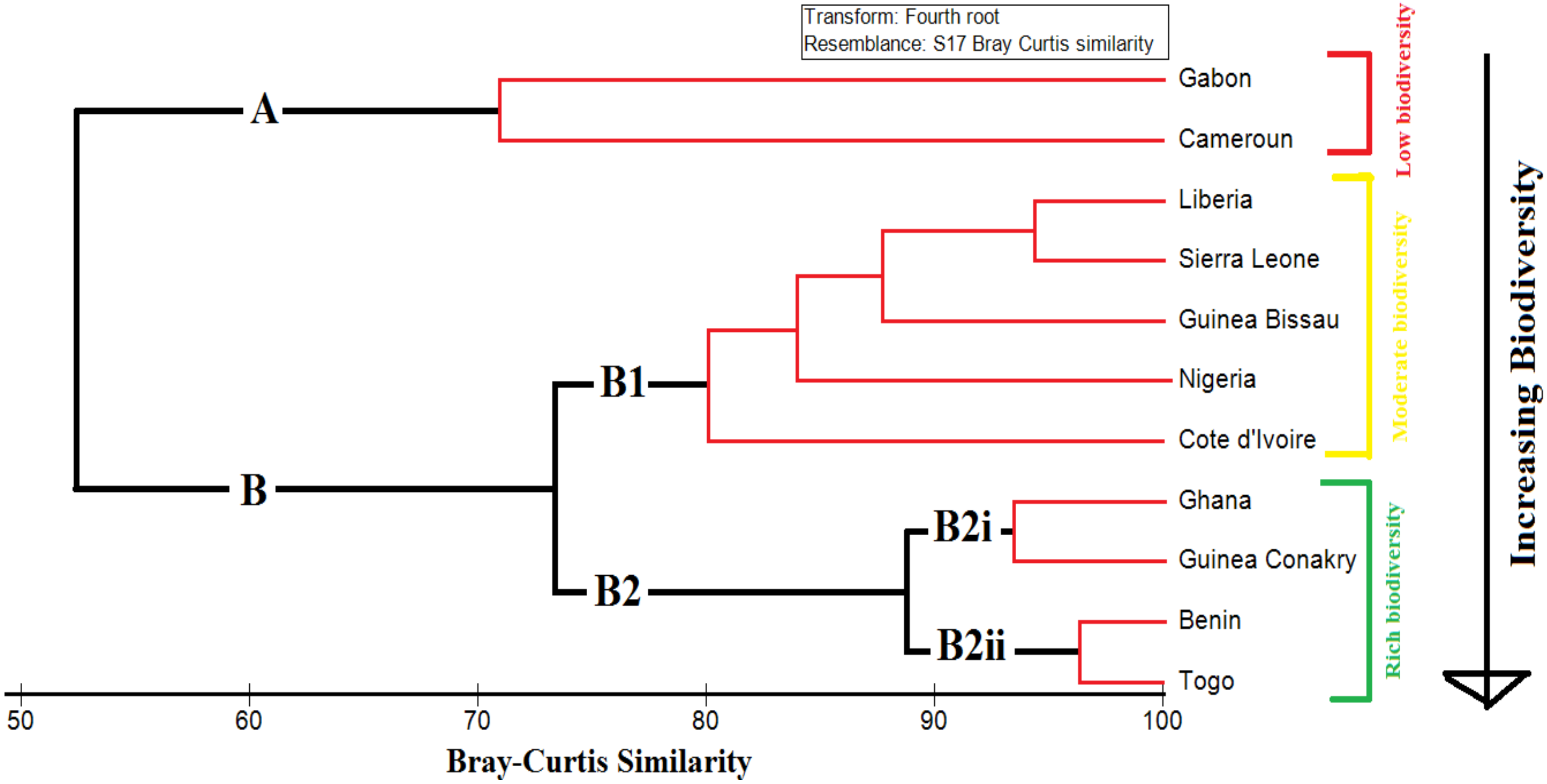


Figure 3.10 Complete-linkage of agglomerative dendrogram of Bray–Curtis similarity of GCLME countries based on functional richness data of ‘constant’ trait. Thin red lines indicate significant evidence of structure (SIMPROF test, $p<0.05$) and thick black lines indicate no evidence of structure.

3.4.6 Functional Trait-Environment Interactions

The relationships between the functional trait and environment were examined using the BIO-ENV procedures in the PRIMER v6 program (Clarke and Gorley, 2006). The BIO-ENV procedure identified two variables as 'best explaining' the dominant benthic functional traits assemblages in the study area (Table 3.13). Nitrate and magnesium produced the highest significant correlation (p=0.005) of 34.8%. Nitrate alone showed 34.7% correlation with the dominant functional traits. However, for the 4 dominant functional trait distribution, the 'best match' was obtained with sand, nitrate and potassium (ρ_w=0.286) (Table 3.13). Here also, nitrate alone indicated good correlation (ρ_w=0.275).

Table 3.13 Bio-Env results for 'constant' functional traits.

No of variables	Best variable Combination	Correlation (ρ_w)
	'Constant' Traits (p=0.005; Rho=0.348)	
2	Nitrate-Magnesium	0.348
1	Nitrate	0.347
4	Silt-Nitrate-Potassium-Magnesium	0.210
	Four Most Dominant 'Constant' Traits (p=0.042; Rho=0.286)	
3	Sand-Nitrate-Potassium	0.286
4	Sand-Nitrate-Potassium-Sodium	0.278
1	Nitrate	0.275

In the RDA, the environmental variables are shown as arrows, the lengths of which indicate the relative importance and the directions of which are obtained from the correlation of the variable to the axes. The orthogonal projection of a trait linear to an environmental arrow represents the approximate center of the traits distribution along that particular environmental gradient.

In the RDA, the first four ordination axes accounted for 50.1% of explained total variance in the dominant trait richness data. The first ordinantion axis accounted for 49.5% of the trait variance, but the ordination axes showed 98.7% relationship between the traits and environment indicating that the trait data is strongly constrained on the environment data. The first ordination together with the second axis accounted for 49.9% of the variance and 99.5% of the variance explained by the environmental variables. This indicates that the first axis alone and the environmental variables associated with it are important in explaining large portion of the trait variance. The first ordination axis reflected environmental samples with a gradient largely related to nitrate, calcium, organic carbon, magnesium and sand at the positive end of the axis, which are linearly related to all the dominant traits at the negative end of the axis (Fig. 3.11). The entire RDA analysis resulted in a significant model as depicted by the Monte Carlo test ($p \leq 0.005$) (Table 3.15).

The results of forward selection environmental explanatory covarible(s) (marginal effect) was significantly ($p<0.05$) noted for nitrate (21% explained variance), organic carbon (11% explained variance) and clay (6% explained variance) (Table 3.14). However, for the sole predictor environmental variables (marginal effect), the highest explained variances were noted for nitrate (21%), calcium (18%), organic carbon (8%), magnesium and silt (each 5%) (Table 3.14).

Table 3.14 Results of Redundancy Analysis (RDA). Marginal effects denote percentage variance explained (percentage of the total variance in the functional trait data explained) by using each environmental variable as the sole predictor variable. Conditional (unique) effects denote variance explained by each environmental variable with the variable (s) already selected and treated as covariable(s) based on forward selection. Environmental variables are listed by the order of their inclusion into the model. Significant levels are based on a Monte Carlo permutation test with 199 restricted permutations

Environmental variable	Marginal Effect Lambda1	Conditional Effect Lambda1	*p*-value	*F-ratio*
Nitrate	0.21	0.21	0.005*	11.08
Organic carbon	0.08	0.11	0.010*	6.78
Magnesium	0.05	0.05	0.065	3.29
Sand	0.01	0.05	0.100	3.25
Clay	0.01	0.06	0.035*	4.48
Phosphate	0.02	0.01	0.575	0.62
Silt	0.05	0.01	0.180	0.48
Potassium	0.00	0.00	0.620	0.21
Sodium	0.01	0.00	0.000	0.05
Calcium	0.18	0.00	1.000	0.01

Table 3.15 Summary of Redundancy Analysis (RDA) results:

Axes	1	2	3	4	Total variance
Eigenvalues	0.495	0.004	0.002	0.001	1.000
Traits-environment correlations:	0.715	0.543	0.334	0.376	
Cumulative percentage variance					
of traits data:	49.5	49.9	50.0	50.1	
of traits-environment :	98.7	99.5	99.8	100.0	
Sum of all eigenvalues					1.000
Sum of all canonical eigenvalues					0.501

*** Summary of Monte Carlo test ***

Significance of first canonical axis: *(p = 0.005; F-ratio = 32.32)*

Significance of all canonical axes: *(p = 0.005; F-ratio = 3.32)*

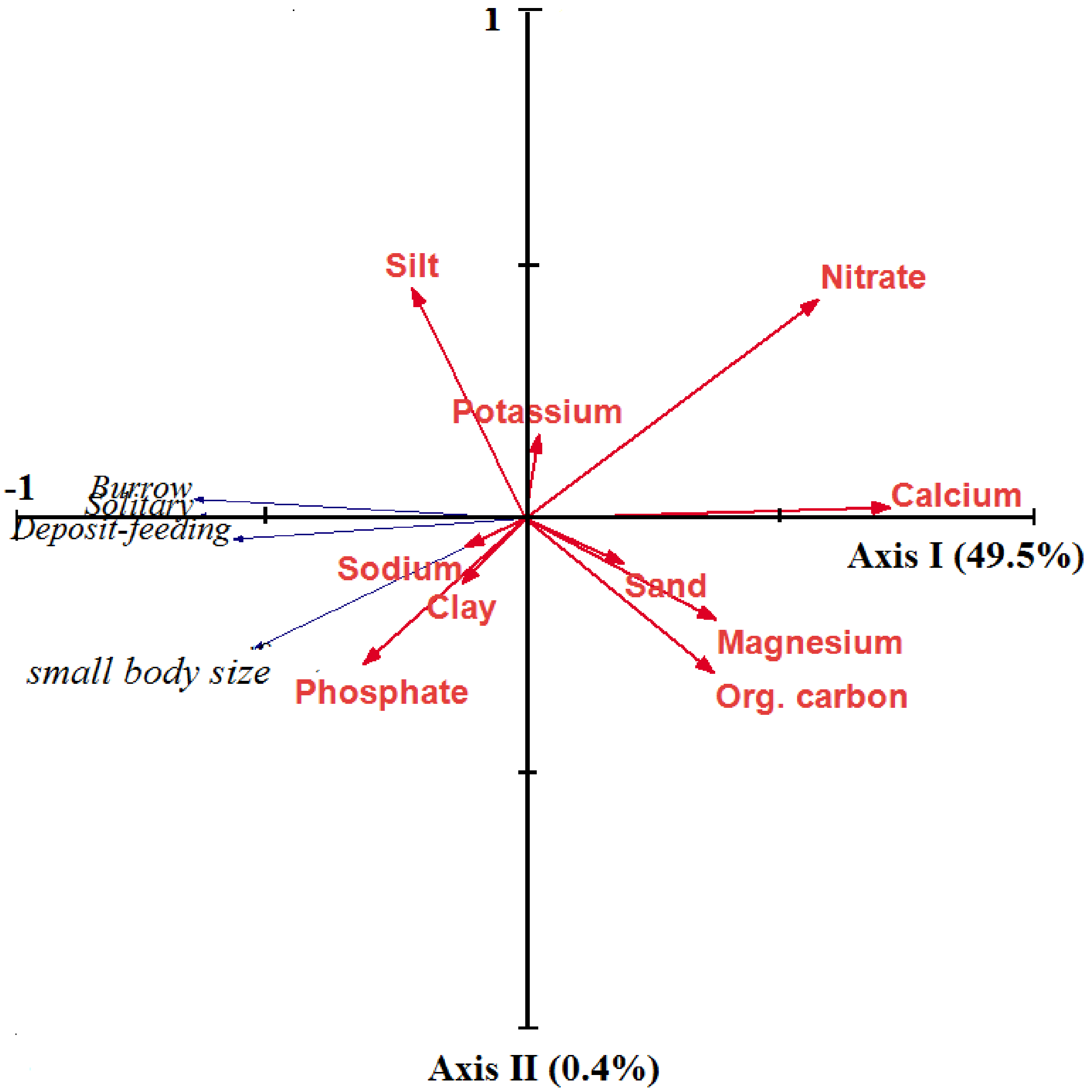


Figure 3.11 RDA ordination of functional trait-environment biplot.

3.4.6.1 Functional Trait-Environment Model

The functional trait assemblage and their relationship with the environmental variables were modeled using the Business Spreadsheet Excel software for multiple linear predictive regression. The regression models were run for the functional richness and diversity for the composite data sets and also for ‘constant’ data only. The result showed that functional assemblage (i.e., functional richness and diversity) for the composite data were explained by three environmental variables namely nitrate, calcium and silt, whereas the ‘constant’ functional trait assemblage was explained by nitrate and silt (Table 3.16). The model was significant (p<0.05) and thus the explanatory variables could predict the assemblage patterns of these traits (Table 3.16). Nonetheless, the percent explained variance for the two scenarios were relatively low, although in all cases marginally higher in the functional richness than the functional diversity.

Table 3.16 Step-wise multiple regression model (using the Business Spreadsheet Excel software) for dominant functional trait and abiotic variables, $p<0.05$.

Functional Trait Assemblage	**Model for independent environmental variables**	**R-squared**
Functional Richness (composite traits)	-6.83*nitrate+ -1.63*calcium+0.55*silt + 17.44 ± 3.93	0.3401
Functional Diversity (composite traits)	-0.98*nitrate + -0.6*calcium+0.07*silt + 4.33 ± 0.54	0.3142
Functional Richness (constant traits)	-2.94*nitrate +0.26*silt + 6.81 ± 1.37	0.3343
Functional Diversity (constant traits)	-0.84*Nit +0.06*Silt + 3.15 ± 3.96	0.2825

The step-wise multiple linear regression model was also developed for the the dominant functional traits namely burrow (adult mobility), solitary (sociability/degree of attachment), small adult body size (0.5-20mm) and deposit-feeding (feeding habit). The model results showed nitrate, organic carbon and calcium as significant abiotic variables explaining the trait variance and could predict the numerical abundance of these dominant functional traits (Table 3.17).

The model indicated that for burrowing trait, nitrate, total organic carbon and calcium were the main environmental factors that could predict their richness (Table 3.17). All these variables depcited inverse relationship with the burrowing trait. The results were also consistent with the other dominant traits, viz. deposit-feeding, solitary, and small body size but with varying degrees of explained predictive variances. The low R-sqaured values suggest the influence of other important variables biological (competition and predation), physical (currents and temperatures), chemical (organic and inorganic substances), and anthropogenic disturbances as surrogates, which were probably not assessed in this study.

Table 3.17 Step-wise multiple regression model for dominant functional trait and abiotic variables. TOC=total organic carbon

Dependent Functional Trait	**Model for independent environmental variables**	**R-squared**
Burrow	-17.48*nitrate + -5.24*TOC+-3.48*calcium + 34.92± 9.09	0.3796
Solitary	-23.30*nitrate +-6.42*TOC+-4.72*calcium+ 46.29± 12.55	0.3580
Small Body Size (0.5-20mm)	-8.72*nitrate + -1.62*TOC+-1.09*calcium + 13.83 ±3.96	0.3617
Deposit-feeding	-8.68*nitrate + -3.19*TOC+-1.08*calcium + 15.18 ± 5.04	0.3068

3.6 Discussion

3.6.1 Species Composition and Abundance

The species composition and dominance were noted for the polychaetes, crustaceans and molluscs with numerical abundance, richness and density varying spatially across the countries in the GCLME. Ecological variability is regarded as ubiquitous patterns in marine benthos regardless of the habitats or taxa especially on the small-scale level (Fraschetti *et al*., 2005). However, according to Benedetti-Cecchi (2009) it is pertinent to address the issues of the variability of the processes driving the change in the species assemblage (i.e., ecological drivers), and the variables that are influenced by the forces (i.e., ecological response). The environmental changes promoting fluctuations in species and assemblages are important ecological forces (Benedetti-Cecchi, 2009), as spatial heterogeneity in species assemblage may enhance productivity and increase resistance to disturbance (Hutchison *et al*., 2003).

The species assemblage (notably polychaete, crustaceans and molluscs) patterns across sampled stations (countries) showed variations with higher taxa abundances, richness and densities occuring in the central section of the GCLME (Benin, Togo and Ghana) (see Figs. 3.2-3.3 and Table 3.2 and 3.3). These areas (country stations) corresponded with moderate levels of sediment nitrate, calcium, magnesium and higher total organic carbon at some areas. These areas showed surrogates of allochthonous and autochthonous organic matter input (Appendix III). The macrobenthic community structure was influenced by the abiotic variables namely: nitrate, total organic carbon, silt, calcium and magnesium. These variables may be influenced by the interactions with other environmental factors to create favourable conditions for the organisms. For instance, the primary food source for benthos originates, with a few localized exceptions, in euphotic surface waters. The movement of water driven by currents, wind and other forces transports food particles in the water mass and causes resuspension of bottom sediments (Pearson and Rosenberg, 1987), which essentailly distribute food to benthic animals. Essentially, benthic infaunal communities are organized structurally, numerically and functionally in relation to gradients of resource availability, and are modified by interactions with other environmental factors (Pearson and Rosenberg, 1987; Wieking and Kröncke, 2005). Thus species distribution may be recognised as a response to the varying effects of these modified environmental gradients in tandern with other factors. According to Angel (1984) sedimentation of faecal pellets is generally considered to be the major means of transporting phytogeneous primary production to the benthos.

Nitrate is known to drive marine primary production (Camargo and Alonso, 2006), thus the low levels of nitrate observed to influence species diversity, could be the result of denitrification and nitrate uptake for pelagic primary production, with the latter driving benthic diversity. In marine sediments, nitrate is often consumed within the zone of denitrification (Lehmann *et al.*, 2005) possibly as a result of organic matter remineralization, which is also influenced by the conditions in the overlying water. The observation and interactions between the organisms and the abiotic variables suggest a more complex ecological driver-species assemblages relations in the GCLME. This is because the assumed reason for high nitrate abstraction and subsequent utilization reflecting in higher species abundance and diversity, could be the result of complex interactions. The low correlation values realized in the BIO-ENV matrix, CCA ordination and the predictive regression models (see Tables 3.7-

3.10, Fig. 3.6) support the assertion of a complex environmental stressors/drivers of species and functional assemblage patterns in the GCLME.

3.6.2 Functional Structure and Assemblage Patterns

Functional biodiversity encompassed functional richness (FR– the number of functional groups derived from a combination of functional feeding groups and habit trait groups), functional diversity (FD – the number of functional groups and division of individuals among these groups, and functional evenness (FE– the division of individuals among functional groups). Furthermore, functional structure (FS) comprised the composition and abundance of functional groups at each site. The results of the functional biodiversity analysis revealed dominance of small size (0.5-20 mm) burrow-dwelling solitary deposit-feeding organisms (dominated by polychaetes), which potentially exert the strongest influence on the ecosystem properties/processes in the GCLME region such as biogeochemical nutrient remineralization of nitrate from organic matter. These traits further provide clear indication/information about prevailing environmental conditions, nature of the substrate, key ecosystem processes and possible response to ecological disturbances. In the ecological processes, the interactions and feedback among species and their respective environment are important elements in elucidating synergies.

The prevalence and dominance of small body size (0.5-20 mm) traits inferred habitat instability (see Schwinghamer, 1983) and may result in high production relative to total biomass (given the high turnover rates of member organisms (Bougdreau *et al.*, 1991). This suggests that the GCLME region is characterized by high productivity but low total biomass as a result of small adult body size dominance. Essentially, the size structure of marine macrobenthic communities is affected by anthropogenic stressors such as organic enrichment (Pearson and Rosenberg, 1978; Gray, 1989; Weston, 1990; Warwick and Clarke, 1994) and trawling (Jennings *et al*., 2001; Duplisea *et al*., 2002), and thus size-dependent relationships provide objective basis for understanding ecology and predicting conservation outcomes (Calder, 2001). According to Calder (2001), adult body size exerts a quantitative dominance over how an animal lives and for how long and on its rate of living and extraction of resources from its environment, and consequently on how many of its kind can live simultaneously on a unit of habitat.

The small body size organisms are closely related to the burrow-dwelling species, and are well known to play key roles in ecosystem functioning of soft-bottom temperate habitats (Austen and Widdicombe, 1998; Amaro *et al.*, 2010). Macrobenthic burrowers can affect recruitment, growth and survival of a variety of organisms, and thus influence community biodiversity (Macdonald *et al.*, 2012). The profound effects of their burrowing and feeding activities can include the delivery of food and solutes (e.g., oxygen) to subsurface sediments, alteration of sediment geochemical and physical makeup (Braeckman *et al.*, 2011), and increased potential for grazing and subduction of smaller organisms (Needham *et al*., 2011). The dominance of small body size burrow-dwelling species (e.g., *Prionospio sexoculata Prionospio cirrobranchiata, Paraonides lyra capensis*) indicates characteristics of short lifespans due possibly to habitat instability as large surface burrowers have limitations on their ability to maintain an optimal burrow position in shifting sediments (Bromley, 1990).

Small size organisms are mainly opportunistic species that respond to habitat perturbations. According to Villnäs *et al*. (2011), such opportunistic species may endure stress and take advantage of extra resources through processing the upper-most layers of the sediments. Small body size burrow-dwelling traits are likely to influence secondary production due to their short generations and may play essential roles in sediment biogeochemistry (an important ecosystem process) due to their bioturbatory activities. Further, burrowing deposit-feeding traits give lucid indication of sediment characteristics including fine-grained soft substrate with potentially high organic matter (i.e., silt or clay) supporting burrowing and deposit-feeding. The retention for organic matter in sediment is influenced by the particle size (Milliman, 1994). Subsurface deposit-feeders tend to be common in muddier sediments (Macdonald *et. al*., 2012b). Deposit-feeders play important role in bioturbation, which is a critical process in biogeochemistry that ensures mineralization of nutrients (e.g., nitrate) to drive primary production. This thus makes the GCLME a productive ecosystem as acknowledged by Ukwe *et al*. (2006).

It has been demonstrated that macrobenthic fauna create burrow networks that penetrate the sediment anoxic zone (Anderson and Meadows, 1978) and create burrow ventilation (Webb and Eyre, 2004), which impact on the sediment (Rhoads, 1974) thus affecting sediment biogeochemistry (Aller and Aller, 1998; Wenzhӧfer and Glud, 2004). The importance of benthic macrofauna in nutrient dynamics and benthic-pelagic coupling have been noted in several studies (Pilskaln *et al*., 1998; Thrush and Dayton, 2002; Lohrer *et al*., 2004) suggesting that benthic bioturbators have large-scale ecosystem implications (Bonsdoff and Rosenberg, 2007). The results of this study lend potential evidence to benthic-pelagic coupling clearly demonstrating the functional significance of marine macrobenthic species.

3.6.3 Functional Trait-Environment Relationship

Marine benthic biodiversity–environment relationships are well-understood in the context of taxonomic species richness and species composition, whereas other component of biodiversity, including functional richness (FR) and functional diversity (FD) lag behind in scientific literature. Most studies to date have examined either taxonomic assemblage patterns with few giving prominence to functional diversity especially in the marine environment (Bremner *et al.*, 2005 and 2008). The relationships between functional diversity (and also taxonomic diversity) of marine macrobenthic fauna and environmental factors showed synergistic association and can give evidence of effect and response mechanisms. This present study established strong association between functional diversity (also taxonomic diversity) and suites of environmental parameters namely nitrate, calcium, organic carbon, mangesium, silt and clay. These abiotic variables, which significantly influence the functional and taxonomic species diversities, are largely related to primary productivity and climate change factors. The spatial variations (or gradient) in these abiotic factors explained and can predict the species abundance and functional stucture of macrobenthic organisms in the GCLME. It is possible that the functional and community assemblages of the macrobenthic fauna are tolerable to these abiotic variables, and have as such emerged as dominant component through the habitat filteration process (Mouillot *et al.*, 2006).

It has been indicated that the adaptation of certain species to unpredictable environments can be related in part to their life history (Grassle and Grassle, 1976) and biological traits characteristics (Mouillot *et al.*, 2006). Newell (1970) further pointed out that where the tolerance limits for a particular environmental variable have been determined for an organism, the organism's realized distribution is much more restricted than its potential distribution. It is reasonable, therefore, to presume that the gradients (spatial differences) in the environmental variables probably ensured that only tolerant species or traits are selected and hence their distribution.

Among the many best matched environmental factors with species and functional communities, sediment nitrate emerged as key abiotic driver. Nitrate is an important nutrient in primary production (Camargo and Alonso, 2006) and thus productivity models could be implicated here in influencing assemblage patterns. Nonetheless, the possible reasons for the nitrate influence may include:

i) nitrogen is the most abundant chemical element on the earth atmosphere (almost 80%) and essential components of many key biomolecules (e.g., amino acids, nucleotides) (Camargo and Alonso, 2006) and also ranked fourth behind carbon, oxygen and hydrogen as the commonest chemical element in living tissues (Campbell, 1990);

ii) most inorganic reactive nitrogen is in the form of nitrate and nitrate drives aquatic productivity by increasing cyanobacteria (an important autotroph) as they efficiently uptake nitrate for fast growth,, and

iii) less toxicity of nitrate in seawater animals probably because of the ameliorating effect of water salinity (sodium, chloride, calcium and other ions) on the tolerance of aquatic animals. Also nitrate has to be converted into nitrite under internal body conditions for its toxicity to be realized but owing to the low branchial permeability to nitrate ions by most marine organisms (Cheng and Chen, 2002), the nitrate uptake in aquatic animals is more limited than the nitrite uptake, thus contributing to the relatively low toxicity of nitrate (Jensen, 1996; Cheng and Chen, 2002; Alonso and Camargo, 2003; Camargo *et al.,* 2005a).

Nitrate has been found to be a strong predictor of marine benthic assemblages (Lamptey *et al*., 2010) due in part to their influence on primary productivity. Aquatic animals are, in general, better adapted to relatively low levels of inorganic nitrogen since natural (unpolluted) ecosystems often are not N saturated (Camargo *et al.*, 2005a), and that explains the low nitrogen correlation with benthic biodiversity (see Tables 3.10 and 3.16).

Calcium and magnesium also emerged as important variables best explaining and predicting functional biodiversity patterns in the GCLME. These parameters implicate climate change effects on the benthic species and functional diversities. The main climate change impact on the marine ecosystem is triggered by the atmospheric CO_2 dissolution in the ocean. Absoprtion of CO_2 into the ocean leads to low pH and decreased concentration of CO_3^{-2}. The decreased concentration of CO_3^{-2} means low $CaCO_3$ saturation, which is important in calcification of benthic organisms. According to Fabry *et al.* (2008), elevated partial pressure of CO_2 (pCO_2) in seawater (also known as hypercapnia) impact on marine organisms both via decreased $CaCO_3$ saturation, which affects calcification rates, and via disturbance to acid–base (metabolic) physiology. Some studies have indicated that the oceanic uptake of anthropogenic CO_2 and the concomitant changes in seawater chemistry have adverse consequences for many calcifying organisms, and may result in changes to biodiversity, trophic interactions, and other ecosystem processes (Kleypas *et al.*, 2006; Royal Society, 2005). Evidence from freshwater systems suggests climate warming could also cause significant shifts in benthic community size structure (Yvon-Durocher *et al.*, 2011). Such shifts in size structure could have significant impacts on marine ecosystems, affecting sediment production, geochemistry, and the amount of food available to predators at higher trophic levels (Jennings and Kaiser, 1998).

Further, during calcification, element such as magnesium is incorporated into biogenic calcium carbonate (Dissard *et al.*, 2010) and thus decalcification would lead to the release of magnesium. Magnesium occurred in seawater to nearly constant ratios to calcium (for the last 1Myrs, Broecker and Peng, 1982) and variations in Mg/Ca in benthic shelly organisms (e.g., foraminiferans) on shorter timescale are shown to be mainly related to changes in temperature (Anand *et al.*, 2003; Reichart *et al.*, 2003; Barker *et al.*, 2004), which is resultant effect of climate change. Other environmental parameters such as pH or (CO_3^{2}) may influence magnesium incorporation into shelly organisms (Dissard *et al.*, 2010). Higher temperature result in higher amounts of magnesium incorporated into the shell matrix (Fergusson *et al.*, 2008; Dissard *et al.*, 2010). Shells with higher Mg:Ca ratios are more soluble, so even organisms with primarily calcite (less soluble than aragonite) skeletons may be heavily impacted by future conditions.

The precipitation of $CaCO_3$ in the upper ocean through the formation of calcareous skeletons by marine organisms creates more acidic conditions which decrease the capacity of the upper ocean to take up atmospheric CO_2 (Kleypas *et al.*, 2006). Conversely, the dissolution of marine carbonates at depth, including biogenic magnesium calcites (from coralline algae), aragonite (from corals and pteropods), and calcite (from coccolithophorids and foraminifera), raises pH and increases the capacity of the oceans to take up and store CO_2 from the atmosphere (Feely *et al.*, 2004). The results of the analysis herein indicated that the selection of magnesium and calcium as drivers of species and functional diversity supports the view of carbonates dissolution at depth leading to the possible release of magnesium and calcium.

In general, magnesium (Mg) calcite minerals with a significant mole percent (mol %) $MgCO_3$ are more soluble than aragonite and calcite, and it is therefore likely that Mg-calcite, high latitude and cold-water calcifying organisms will be the first to be affected by increasing ocean acidification (Andersson *et al.*, 2008). The mole percent of magnesium deposited by marine organisms varies from a few mol% to as much as 30 mol% between different species (Andersson *et al.*, 2008), resulting in a significant response variation among taxa to changing ambient conditions (Hoffmann *et al.*, 2008). In tropical and sub-tropical environments, the dependence of calcareous algae, and other important reef calcifiers like echinoderms and benthic foraminifera, on high-magnesium calcite, the most soluble of all calcium carbonate minerals, would make these likely early casualties of climate change effect. The importance of magnesium is seen on its influence on calcium carbonate precipitation. According to Holmes-Farley, 2003), magnesium binds to the calcium carbonate crystals' growing surface, when the latter begins to precipitate. The magnesium effectively clogs the crystals' surface so that they no longer look like calcium carbonate, making them unable to attract more calcium and carbonate, so the precipitation stops. Without the magnesium, the abiotic (i.e. non-biological) precipitation of calcium carbonate would likely increase enough to prohibit the maintenance of calcium and alkalinity at natural levels.

Sea urchins and crustaceans, including lobsters and shrimp, exert higher biological control by gradually accumulating intracellular stocks of ions; between moults crustaceans are thought to harden their chitin and protein exoskeletons by continually depositing calcite minerals (Convention on Biological Diversity, 2009). The shell chemistry and mineralization of crustaceans suggest that they may withstand climate change effect (e.g., ocean acidification) and saturation state decreases better than molluscs, however the response of organisms is likely to be a function of individual history and genetic variability (Cooley and Doney, 2009).

Organic carbon and sediment particles have been demonstrated as playing important structuring role in marine species assemblages (Gray, 1989 and 2002; Lamptey and Armah, 2008; Pearson and Rosenberg, 1978 and 1987; Snelgrove and Butman, 1994) as they are associated with productivity and nutrition. It is therefore corroborating the selection of these abiotic factors as key environmental drivers of taxonomic and the functional assemblages in the GCLME. Organic matter is the main food source for deposit-feeders (Pearson and Rosenberg, 1978), which were the dominant feeding trait identified. The sediment type gives an indication of availability of food rather and not as a first order factor determining species assemblages (Snelgrove and Butman, 1994).

CHAPTER FOUR

IMPACT OF DEMERSAL FISH TRAWLING ON THE STRUCTURE AND FUNCTIONAL ASSEMBLAGES OF EPIBENTHIC FAUNA ALONG BATHYMETRIC GRADIENT IN THE GUINEA CURRENT LME

4.1 Introduction

The global biodiversity concerns (i.e., accelarated loss and decline) and the predictions of impaired ecosystem functioning and sustainability (Naeem *et al*. 1994; Sala *et al*., 2000; Loreau *et al*., 2001; Hughes *et al*., 2003; Hooper *et al*., 2005; Worm *et al*., 2006; Hooper *et al*., 2012), have increased interests of investigating the wider impacts of commercial fishing on non-target species (e.g. Alverson *et al*., 1994; Dayton *et al*., 1995). The effects of mobile fishing gears on marine benthic productivity and biodiversity are a global concern both for the fishing industry and government regulators (Dayton *et al*., 1995; Auster and Langton, 1999; McConnaught *et al*., 2000; Kaiser *et al*., 2002; Hiddink *et al*., 2007). The socioeconomic consequences of the biodiversity changes depend on how they translate into altered ecosystem processes and services (Costanza *et al*., 1997; Balmford *et al*., 2002; Millennium Ecosystem Assessment, 2003).

The marine benthic ecosystems are increasingly affected by environmental stress and degradation due to pollution (Halpern *et al*., 2008) and other anthropogenic factors such as overfishing (Jackson, 2008), bottom trawling and dredging (Pauly *et al*., 2005) and human-induced climate change (Bindoff *et al*., 2007). Many of the expected responses to human activities in the marine environment may best be monitored at the seafloor in the benthic communities (Jorgensen *et al*., 2011). This is due to the fact that benthic organisms have limited locomotion; they are long-lived and able to integrate into their system both short-term and long-term environmental processes (Borja, 2000).

Increasing importance of marine biodiversity and fisheries in general have resulted in integrated approach, such as Ecosystem Approach to Management (EAM), which requires sustainable and ecosystem-based assessment. For instance, Ecosystem Approach to Fisheries (EAF) requires that managers take account of the ecosystem effects of fishing in management plans that are intended to achieve sustainable exploitation of target species (Kaiser *et al*., 2002). Ecological Quality Objectives (EcoQO's) is now used to assist in the movement toward an ecosystem approach to management (Frid and Hall, 2001). Skjoldal *et al.* (1999) defined the EcoQ as *an overall expression of the structure and function of the aquatic systems.* It is therefore reasonable to assume that the development of ecosystem approaches to environmental management is to define the 'overall structure and function' desired for the ecosystem being considered. It also calls for integration of commercial marine resources (e.g., fish) and non-commercial communities (Brind'Amour *et al*., 2009) such as epibenthic fauna.

Epifaunal component of the benthos includes organisms of high biomass and potentially of high ecosystem importance as they provide habitat structure, and potentially different functional components of the community (Jørgensen *et al*., 2011). Larger fauna (e.g., epifauna) often represent long-lived and slowly reproducing species that are more prone to decline if mortality is increased due to fishing (Witbaard and Klein, 1994). For the marine benthos, the issues that need to be considered include (i) aspects of the composition and structure of the benthic community – species diversity, species abundance patterns (i.e., how individuals are distributed between the species present), and biomass. Further, the functioning of this assemblage; and (ii) functional attributes such as the productivity of the community and the degree, rate and pathways of nutrient and carbon cycling. In coastal ecosystem, indicators integrating both the structural (i.e., species composition) and functional attributes of the communties are increasingly recognized as useful tools to assess change in these ecosystems (Elliott and Quintino, 2007).

A huge body of knowledge exists on the evidence of fishing effects on the marine macrobenthos (Jennings and Kaiser, 1998; Kaiser and De Groot, 2000; Trush and Dayton, 2002), however a lack of comparable quantitative data of fish and epifauna is still a concern and confounds our understanding of the extent of the fishing effects. Given the growing appreciation of the value of marine biodiversity as critical to the sustainability of commercially valuable ground fish stocks as well as for its own unique heritage (Bengtsson *et al*., 1997; Costanza *et al*., 1997; Freckman *et al*., 1997; Gray, 1997; Schlapfer and Schmidt, 1999), there is now an increasing need to understand and sustain biodiversity as a part of any fisheries management plan.

Trawling is a common method for catching fish and bottom trawling is one kind of fishing practice with heavy nets connected to large trawl doors. The nets drag along the seafloor leaving deep visual marks on the sea bottom (Enticknap, 2002). The design and mode of operation of the trawling gear influences how it interacts with the seafloor and how many species are removed (Thrush and Dayton, 2002). The otter trawl is an example of bottom trawl and is commonly used to catch fish and invertebrate species. The otter trawl can penetrate the sea bed down to 20 cm (Querios *et al*., 2006). The beam trawl is held open by a steel beam fitted with chains and the penetration of the beam trawl and the amount of physical disturbance caused by beam trawl, depend on the weight of the gear, towing speed and bottom type (sediment), and varies between 3 mm and 6 cm (Lindeboom and de Groot, 1998a; Duplisea *et al*., 2002).

Bottom trawling has been documented to cause extensive impacts on benthic communities and habitats, leading to reduced biomass, production and diversity (e.g. Kaiser and De Groot, 2000; Hiddink *et al*., 2006). When heavy trawling gear is dragged along the seabed, some of the complex benthic structure that serves as refugia are damaged (Stone *et al*., 2005). Bottom trawling is harmful to seafloor habitats and this effect has been well studied in marine systems (Kaiser *et al*., 1998; McConnaughey *et al*., 2000; Sparks-McConkey and Watling, 2001; Rosenberg *et al*., 2003; Tillin *et al*., 2006). Modifications of the composition of benthic assemblages may result in changes to the ecological functioning of the system (Bremner, 2006; Tillins *et al*., 2006).

Relatively few studies have investigated the impact of bottom trawling on benthic ecosystem integrating fisheries and epibenthic data/information along bathymetric gradient. Nonetheless, most benthic biodiversity systems are stratified by water depth (Zmarzly *et al*., 1994; Bergen, *et al*., 2001). Study of that nature will unearth the influence of bathymetry on epibenthic fauna distribution and may obviate confounding issues of impact of bottom trawling on the epibenthic bottom dwellers.

Integrated assessment of fisheries requires studies that focus on the whole ecosystem and not only on single species, and that consider fishing activities as key pressures affecting several ecosystem components (Gaertner *et al.*, 2005; Massuti and Reñones, 2005). Therefore, it is highly necessary to develop studies like these, which identify the components, assemblage structure and functioning of ecosystems at a regional scale.

4.2 Study Objectives

The present study is the first attempt in the Gulf of Guinea to compositely describe the spatial distribution patterns of epibenthic fauna (treated as non-targeted species or by-catch from bottom trawl). The main objectives were to characterise epibenthic assemblages (i.e., composition and structure) caught by the beam trawl, establish the bathymetric relationships between demersal fish and epibenthic fauna distribution patterns in terms of abundance and biomass and ascertain the functional attributes (i.e., feeding and mobility) of epibenthic fauna along bathymetric gradients.

The findings of this study will attempt to answer the questions: i) what are the community structural differences in epifauna and fish in a bottom trawled samples?, ii) how do the assemblage patterns of fish trawl samples and epibenthic by-catch differ along bathymetric gradient? and iii) is the epifauna by-catch functionally significant to influence ecosystem functions and processes?

4.3 Materials and Methods

4.3.1 Study Area

The study was conducted in the Gulf of Guinea of the Guinea Current Large Marine Ecosystem along the continental shelves of Ghana, Togo, Benin and western part of Nigeria. The GCLME extends from approximately latitude 12^0N south to about 16^0S latitude, and varies from 20^0 west to about 12^0 east longitude (Fig. 2.3). It extends from Bissagos Island (Guinea Bissau) to Republic of Congo with its boundary extending in a north–south direction from the intense upwelling area of the Guinea Current (GC) south to the northern seasonal limit of the Benguela Current (BC). In an east–west sense, the GCLME includes the drainage basins of the major rivers seaward to the GC front delimiting the GC from open ocean waters (a time- and space-variable boundary).

4.3.2 Field Sampling

Epibenthic fauna samples were collected from beam trawl (Plate 4.1) catches carried out from 3-14 March 2003 aboard the RV Geo-Explorer scientific vessel during the West Africa Pipeline Project basleine studies from Ghana to Nigeria using a randomized stratified survey design (Fig. 4.1 & Table 4.1). Beam trawls are very effective in sampling vagile as well as epibenthic macrofauna and the latter may represent a large proportion (density and biomass) of the catches (Kaiser *et al.*, 1994; Till *et al.*, 2006). It should be noted that no trawl gear ever sample all the individuals present in the path of the net (Jorgensen *et al.*, 2011) and the beam trawl net based on the mesh-size will select certain size classes of the same epibenthic faunal taxa. As such, the actual epifauna abundance may have been grossly under-represented in the sample collection and consequently the analysis likewise the fish data although fishes are relatively larger than epifauna.

Therefore the impressions of the epibenthic community gained from the analysis of the sample data is not that of the actual epifaunal community present at each sampled location, but rather it is a view of the community biased by the differential selectivity of the sampling gear for each species present at each location (Tillin *et al*., 2006).

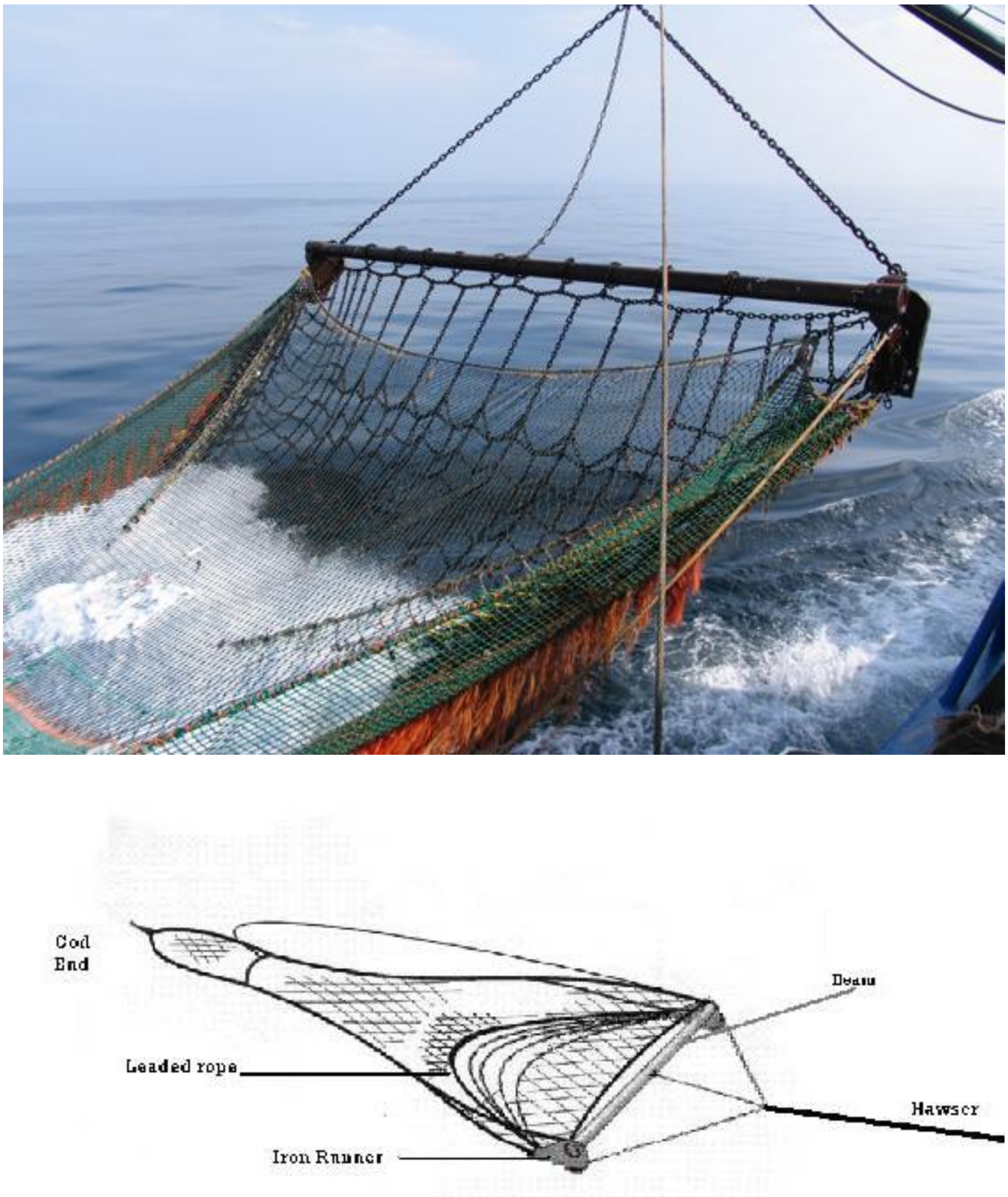


Plate 4.1 Beam trawl gear. (Source: ilvo.vlaanderen & Grantontrawlers)

A total of 18 trawls were made within a depth range of 10–70 m (Table 4.2). Of this, 7 hauls were carried out in the shelf of Ghana, 4 in Togo, 4 in Benin and 3 in the western shelf of Nigeria (Table 4.1). The sample stations were located at approximately 50 km intervals along predetermined defined areas, which were selected based on a prior geotechnical assessment by the West Africa Gas Pipeline Project. Each haul lasted for 30 minutes with a tow speed of 1.5 knots over the ground and covering appropriately a distance of 2.7 km.

Table 4.1: Length of coastline and number of hauls made per sector (WAPCo, 2003)

	Ghana	Togo	Benin	Nigeria
Length of coastline covered (km)	330	50	120	30
Maximum length of) coasline (km)	550	50	120	853
Number of hauls	7	4	4	3

At each station, the trawl was hauled in, emptied and prepared for the next tow. As the catches were chuted to the processing area, the net and deck were examined carefully and all epibenthic fauna collected. The epibenthic samples from each trawl station were separated from the fish catches on a sorting table, put into labeled containers and fixed with 10% borax pre-buffered fomaldehyde solution for later laboratory examination and taxonomic resolution. All the trawl fish samples were identified taxonomically onboard, counted and weighed for each haul.

4.3.3 Laboratory Processing of Samples

The epibenthic fauna were processed (i.e., washing & sorting) in the laboratory. The formaldehyde solution in the epibenthic samples was replaced with 70% ethanol until samples were ready for taxonomic identification. Species identification was carried out to the lowest practicable taxonomic unit using various taxonomic manuals and guides namely Day, (1967ab); LeLœuff and Intes, (1974); Fauchald, (1977); Edmunds, (1978); Intes and Lœuff (1984); Kirkegaard, (1988); Cosel, (2006) and Rakel, (2007). Each species was counted and weighed (blotted wet weight in grams) to determine the biomass.

Table 4.2 Trawl station information and trawl distance covered during the West Africa Pipeline Project baseline studies.

Trawl Station	Country	Latitude	Longitude	Mean Depth (m)	Speed of tow (km/h)	Distance towed (m)
T 02	Nigeria	E2^0 59.1487	N6^0 11.9672	64	5.18	2.59
T 04	Nigeria	E2^0 47.7939	N6^0 11.5422	61	5.55	2.78
T 05	Nigeria	E2^0 26.5627	N6^0 10.9210	45	5.55	2.78
T 07	Benin	E2^0 20.5873	N6^0 14.4042	21	5.74	2.78
T 08	Benin	E2^0 10.5182	N6^0 09.7585	54	5.37	2.87
T 10	Benin	E1^0 42.0839	N6^0 05.6873	49	5.18	2.68
T 11	Benin	E1^0 16.5090	N6^0 04.7729	18	5.37	2.59
T 12	Togo	E1^0 18.9000	N6^0 01.5600	13	5.18	2.59
T 13	Togo	E1^0 21.5790	N5^0 58.3448	60	4.44	2.68
T 14	Togo	E0^0 52.4986	N5^0 41.8603	13	5.55	2.78
T 16	Togo	E0^0 07.2247	N5^0 30.6685	56	5.18	2.59
T 17	Ghana	E0^0 04.5541	N5^0 33.7917	39	5.55	2.78
T 19	Ghana	W0^0 41.1364	N5^0 07.6678	28	5.44	2.59
T 20	Ghana	W0^0 22.3600	N5^0 16.7100	36	5.55	2.78
T 22	Ghana	W1^0 34.8500	N4^0 58.1300’	16	5.55	2.78
T 24	Ghana	W1^0 32.3500	N4^0 51.2900	32	5.92	2.96
T 25	Ghana	W1^0 25.1300	N4^0 34.9800	50	5.55	2.78
T 26	Ghana	W1^0 08.4700	N4^0 59.7600	26	5.37	2.68

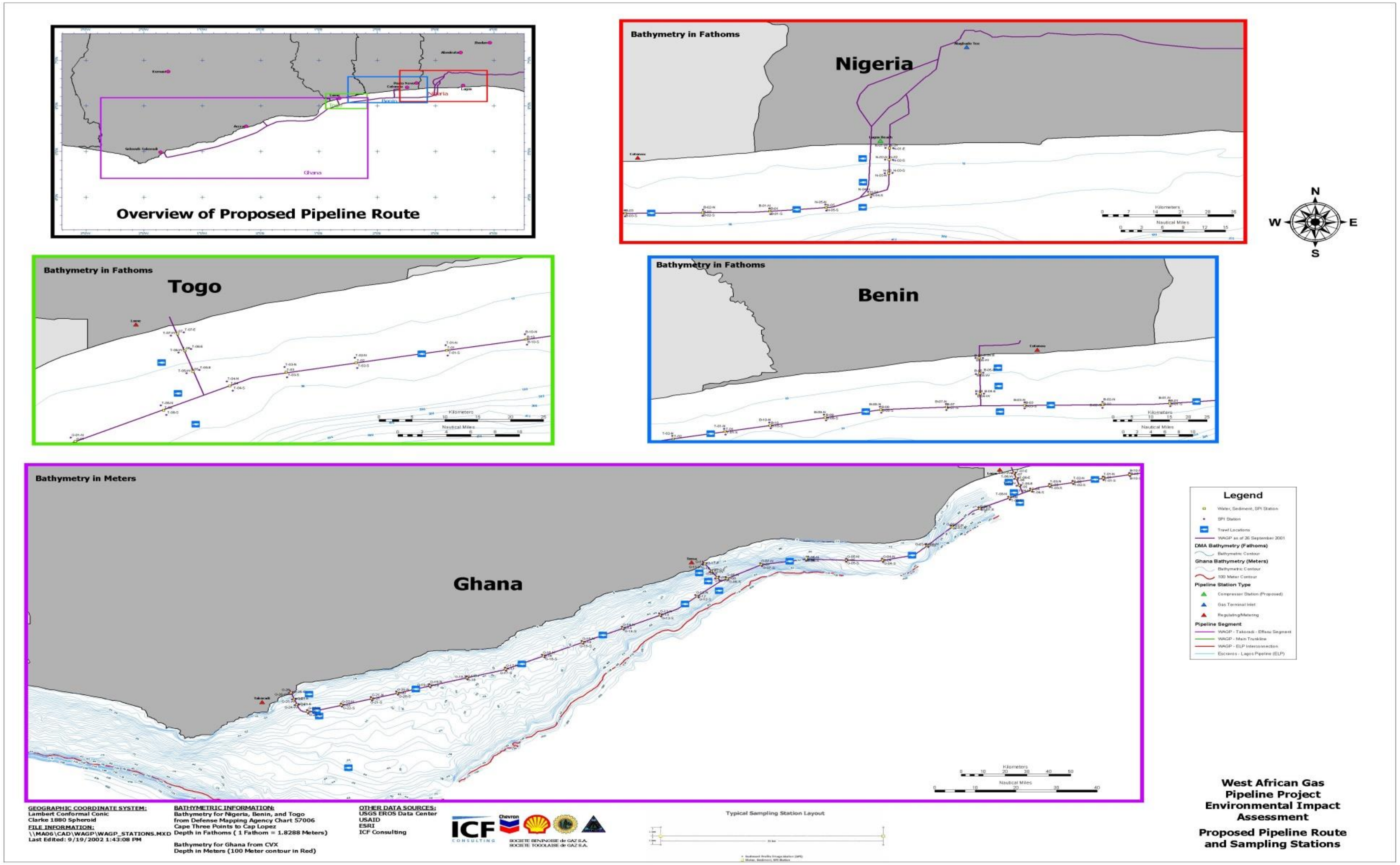


Figure 4.1 Map showing routes along which bottom trawling was carried out (WAPCo, 2003)

4.3.4 Statistical Analysis

All the epibenthic fauna identified and counted were categorized into polychaeta, mollusca, crustacea, echinodermata, and “others”. The ‘others’ category included cnidaria, nematoda, sipunculida, priapulida, brachiopoda and tunicata.

A frequency of occurrence of epifaunal taxa was calculated using the F-index described by Guille (1970): $F=p_a/P \times 100$, where: p_a, is the number of stations where the species occurred and P is the total number of stations. Using this formula the species were classified as: constant ($F>50\%$), common ($10\% < F < 49\%$) and rare species ($F<10\%$). Consequently, all the rare species ($F<10\%$) were eliminated before the community structural analyses using suites of multivariate techniques with the PRIMER v6 package (Clarke and Gorley, 2006). Bray-Curtis similarity index was calculated. Prior to that, the data sets were fourth-root transformed to stabilize the variance. Using a complete linkage, sample classifications were achieved and thereafter samples related to each other identified based on the resulting non-parametric multidimensional scaling (MDS).

Changes of epifauna along bathymetric gradient were assessed with one-way ANOSIM (Clarke and Warwick, 1994). Thereafter, Similarity Percentage (SIMPER) analysis (Clarke and Gorley, 2006) was used to identify characteristic species, which contributed most to the statistical dissimilarity between the different bathymetric gradients among samples. For each sample, the Shannon–Wiener diversity index (H’, Log e) and Margalef’s richness was determined from abundance data.

Functional group classification of the species was carried out using feeding type and mobility. The functional trait of feeding type (predator/scavenger, deposit feeder, filter/suspension feeder) and mobility (sessile/tube-dwelling/motile) according to a variety of references (Fauchald and Jumars, 1979; Barnes, 1987; Beesley *et al*., 2000; Pechenik, 2000; Rouse and Pleijel, 2001; Brusca and Brusca, 2003) were used for the functional group classfication. A functional group is a collection of organisms with similar suites of co-occurring functional attributes and as such has similar responses to external factors and/or effects on ecosystem processes (de Bello *et al*., 2010).

4.4 Results

4.4.1 Epifauna Composition

A total of 3959 individual epibenthic fauna comprising 65 taxa from major taxonomic groups were encountered in the 18 trawl hauls (Table 4.3). The mean epifauna abundance per trawl haul was 792. The highest taxa abundance (3268 individuals) was noted for the mollusca due to the highest contribution of *Chlamys purpurata* (64.17%) and *Pecten jacobaeus* (30.02%) recorded at Stations T26 and T22 respectively. Mollusca contributed 82.55% to the total epifaunal numerical abundance. The other dominant groups were Crustacea and Echinodermata contributing 8.26% and 5.23% respectively to the total numerical abundance. The species placed in the ‘others’ category contributed 2.98%, while polychaetes accounted for 0.99%.These indicate the direct impact of beam trawling on the different epibenthic fauna taxa.

Of the total 65 taxa identified, molluscs, crustaceans and echinoderms recorded 28 (43%), 15 (23.08%) and 10 (15.39%) species respectively (Table 4.3), thus representing the major epibenthic faunal groups of the study area. However, in terms of biomass, the ‘others’ category ranked second with 34.88% after the molluscs with 36.90% (Table 4.3). The two numerical dominant species of the crustaceans were *Scyllarides herklotsii* (24.46%) and *Maja squinado* (13.76%). For the echinoderms, *Echinocardium caudatum* (36.23%) and *Diadema* sp. (29.47%) were the dominant species. The five most distributed species based on the F-index were *Portunus validus* (40%), *Scyllarides herklotsii (40%), Lithodes ferox* (40%), *Pagurus* sp. (40%) and *Stenorynchus lanceolatus* (35%).

From Left: *Strombus* sp., *Conus* sp., *Strombus* sp. *Tonna* sp., *Strombus* sp., & *Murex* sp.

Sea cucumber,

From left *Pagrus* sp. in *Tonna* shell; *Pentaceraster* spp., *Echinus* sp. and Barnacle

Plate 4.2 Photographs of epibenthic fauna from bottom beam trawl samples

The taxa contribution to the total biomass of 3235.4 g was highest for the molluscs (36.90%) and species placed in the ‘others’ category (34.88%). The species *Prianpulus caudatum* contributed substantially (75.88%) to the total biomass of the ‘others’ category. The lowest biomass contribution (<1%) was noted for the Polychaeta (Table 4.3). The mean biomass per haul was ~162 g (wet wt.).

Table 4.3: Number of species , abundance and biomass of epibenthic fauna from 18 trawl hauls of the study area in March 2003. The percentage contribution of each taxa is given in parenthesis.

Taxa	No. Of species	Abundance (No. Of indi.)	Biomass (mass) (wet wt. g)
Mollusca	28 (43.08)	3268 (82.55)	1194 (36.90)
Crustacea	15 (23.08)	327 (8.26)	334.0 (10.32)
Echinodermata	10 (15.38)	207 (5.23)	552.5 (17.08)
Polychaeta	3 (4.62)	39 (0.99)	26.5 (0.82)
‘Others’	9 (13.85)	118 (2.98)	1128.4 (34.88)
Total	**65**	**3959**	**3235**

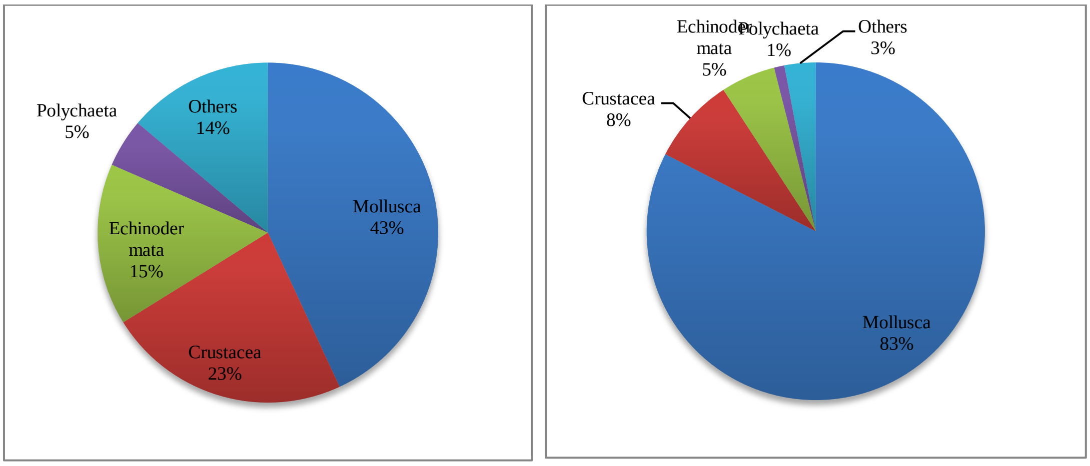


Figure 4.2 Percent distribution of major epibenthic faunal richness (left) and numerical abundance (right).

4.4.1.1 Comparison of Bathymetric Distribution of Epifauna and Fish Assemblage Structure

The distribution of taxa abundance across bathymetric gradient indicated a decrease in numerical abundance of epibenthic fauna with increasing water depth (Fig. 4.3). Abundance of fish on the other hand did not show any discernible bathymetric pattern except that the highest abundance occurred at mid-depth water (i.e., 31-50m). There were no significant differences (p>0.05) in abundance of epifauna and fish at both mid-depth (31-50m) and deeper waters (51-70m), which suggests that for the study area impact of bottom trawling epifauna abundance could be inferred from fish catches, albeit comparatively fish abundances at these depths were relatively higher than the epifauna. The significant difference (p<.05, ANOVA) between abundances of fish and epibenthic fauna at shallow-dept (11-30m) suggests that trawling impact at this depth would be significant on the epibenthic fauna, since numerically epifauna ranked highest (Fig. 4.3).

For taxa biomass, the epifauna ranked highest across all the depth zones in comparison with the fish abundance. The highest biomass (catch by weight) was recorded at mid-depth (31-50m). The degree of variations in taxa biomass for both epifauna and fish assemblage decreased with increasing water depth (Fig. 4.4). This occurrence may suggest prevailing benign conditions at deeper depths or conversely a higher degree of disturbances at shallow depths. This dichotomy may have been due to the creation of different niches that have physiologically and ecologically adapted to the respective zones.

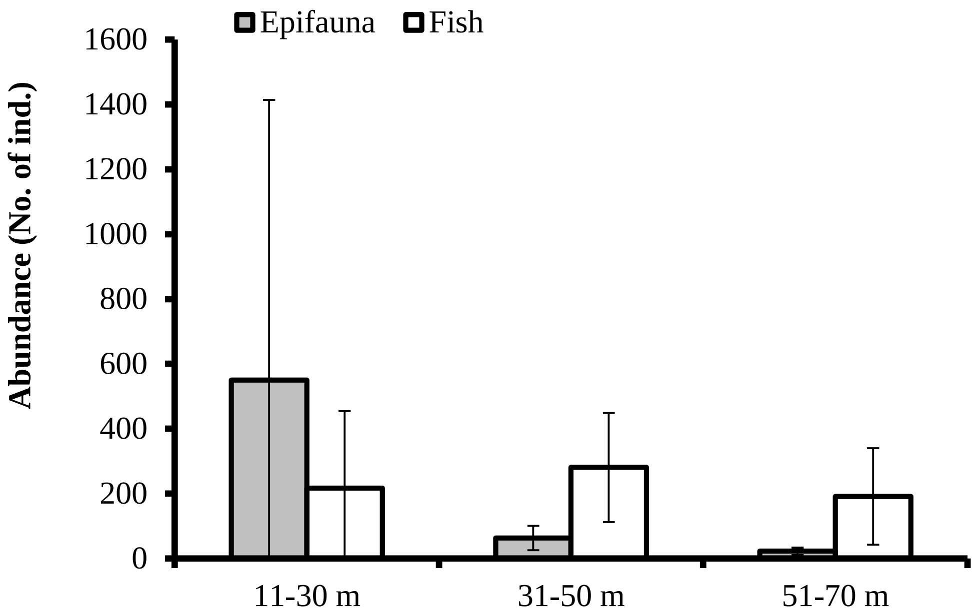


Figure 4.3 Bathymetric pattern of mean abundance (±SE) for epifauna and fish from trawl catches.

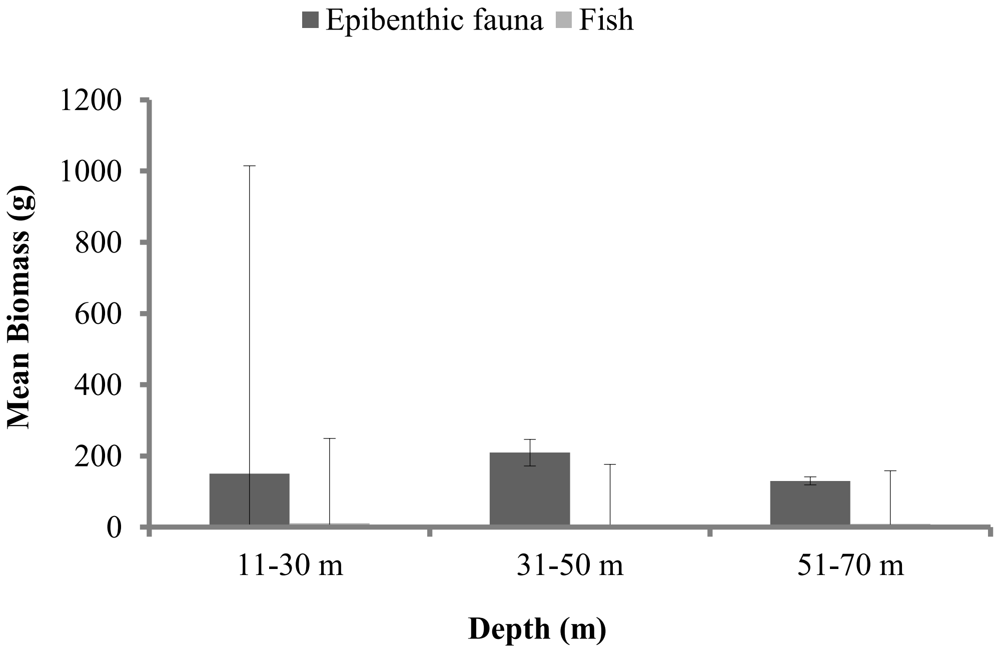


Figure 4.4 Bathymetric pattern of mean biomass (±SE) for epifauna and fish from trawl catches.

The taxa richness of fish species was higher than the epifauna across the bathymetric gradient (Fig. 4.5) although the differences were not statistically significant (p>0.05). The highest richness occurred within the mid-depth water (31-50m) for both fish and epifaunal taxa (Fig. 4.5) suggesting a synergistic trophic relationship.

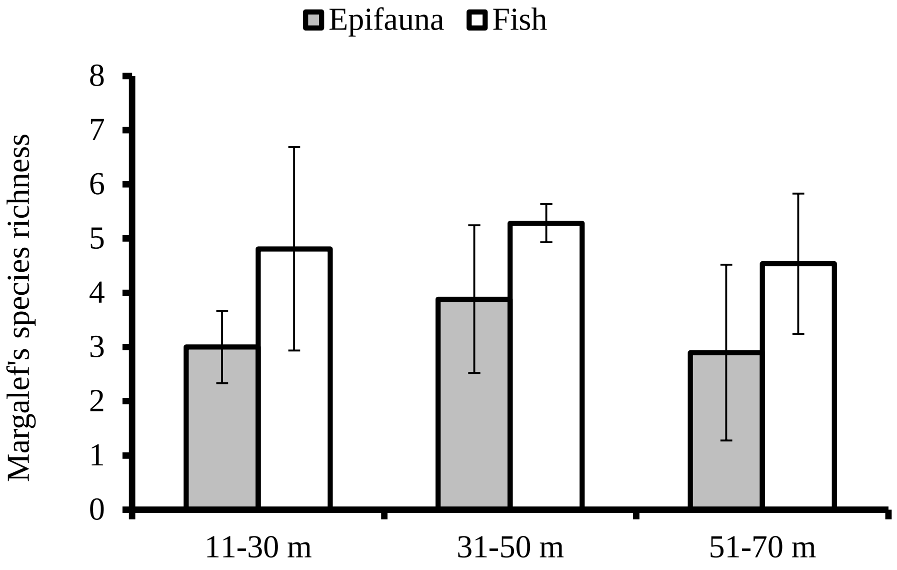


Figure 4.5 Distribution of Margalef's species richness index along depth gradient. The error bars indicate 95% confidence interval.

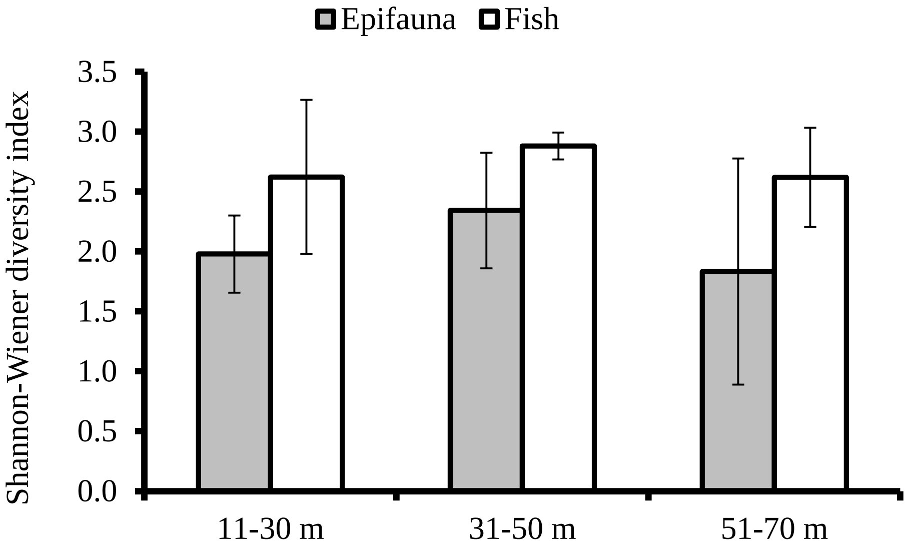
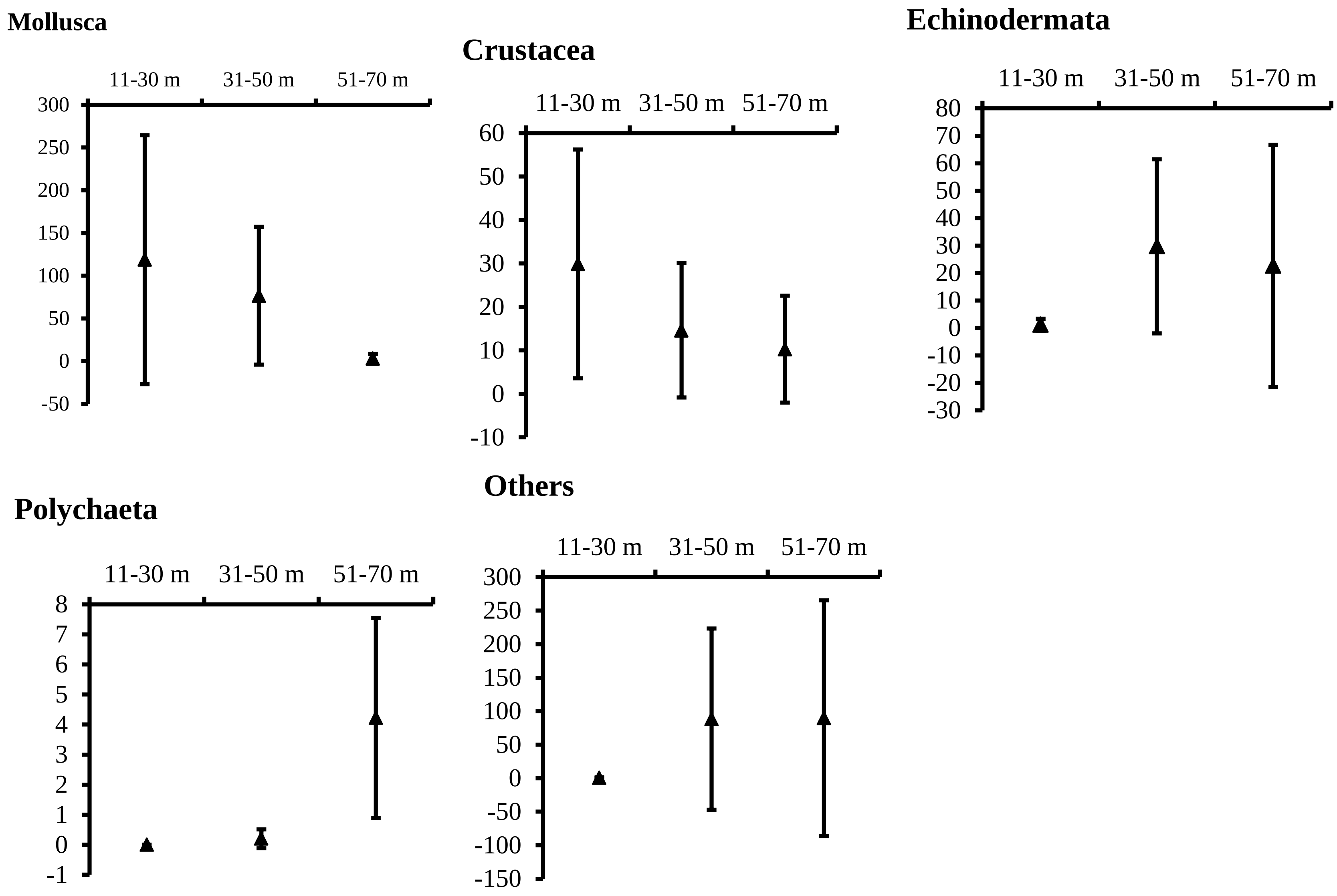


Figure 4.6 Distribution of Shannon-Wiener divesity index along depth gradient. The error bars indicate 95% confidence interval.

4.4.2 Pattern of Major Epifaunal Taxa

The patterns of distribution for the major epifauna groups showed a steady decrease in biomass for molluscs and crustaceans with increasing water depth (Fig. 4.7). Conversely, polychaetes, ‘others’ category and echinoderms revealed increases in biomass with increasing water depth except that the highest biomass for the echinoderms occurred at mid-depth. All but polychaetes did not reveal any discernible bathymetric pattern. The bathymetric pattern for the numerical abundance of the epifauna was different from the pattern depicted by the biomass. The striking observation was the highest numerical abundance at mid-depth (31-50m) for crustaceans, echinoderms and ‘others’ category (Fig. 4.7). The molluscs and polychaetes revealed similar pattern of abundance and biomass, with the abundance decreasing with increasing water depth while biomass increased with depth (Fig. 4.7).



Mollusca

Crustacea

Echinodermata

Polychaeta

Others

Figure 4.7 Mean biomass (±SE) of major epibenthic fauna along bathymetric gradient.

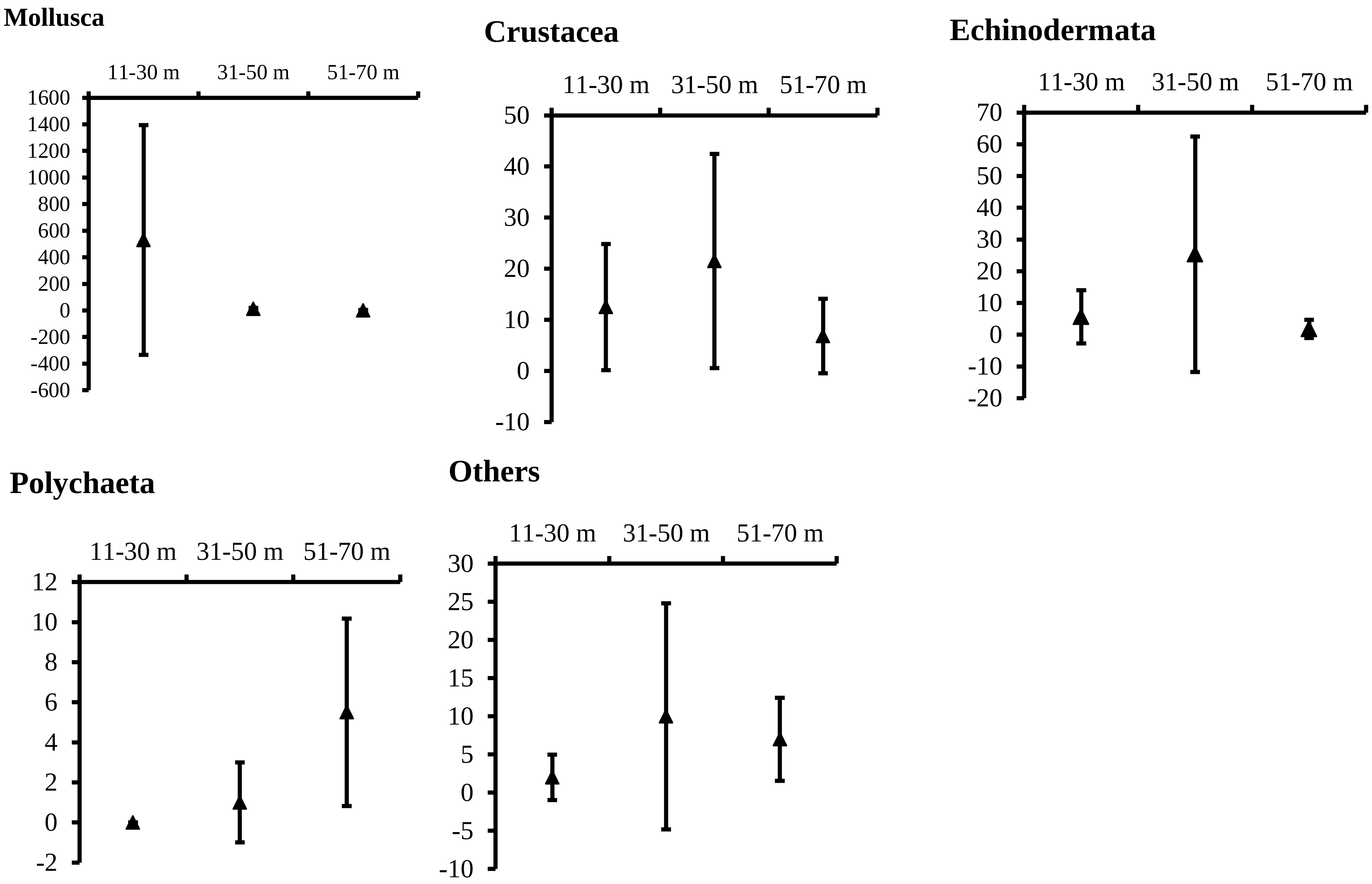


Figure 4.8 Mean abundance (±SE) of major epibenthic fauna along bathymetric gradient.

The abundance and biomass of the epifauna varied significantly with water depth (one-way ANOSIM, $p<0.05$) (Table 4.4). Spatial (bathymetric) differences of the epifaunal abundance and biomass were particularly important (or significant) between 11-30m (Shallow zone) and 51-70m (Deep zone) (one-way ANOSIM, $p=0.002$). Nonetheless, no significant difference existed between shallow and mid-depth zones, and also mid-depth and deep zones (Table 4.4).

Table 4.4: Pairwise ANOSIM test of epifaunal abundance and biomass

Depth (m)	Abundance		Biomass	
	R-statistic	Significance Level (*p*)	R-statistic	Significance Level (*p*)
11-30, 31-50	0.25	0.069	0.144	0.152
11-30, 51-70	0.47	0.002	0.491	0.002
31-50, 51-70	0.093	0.199	0.005	0.457

For taxa abundance; Global R= 0.271, *p*=0.5%; for taxa biomass; Global R= 0.213, *p*=1.9%.

The distribution pattern of the stations in the MDS ordination (Fig. 4.9) showed a clear separation of shallow depth stations (11-30m) and deep depth stations (51-70m). The pattern is consistent with the observation in the pairwise ANOSIM test (Table 4.4). The distribution of the stations shows strong spatial (east-west axis) and bathymetric patterns. The spatial pattern is indicative that stations located in each specific sampled country tend to cluster together (see Table 4.1), which also suggest the influence of surrogate abiotic water conditions.

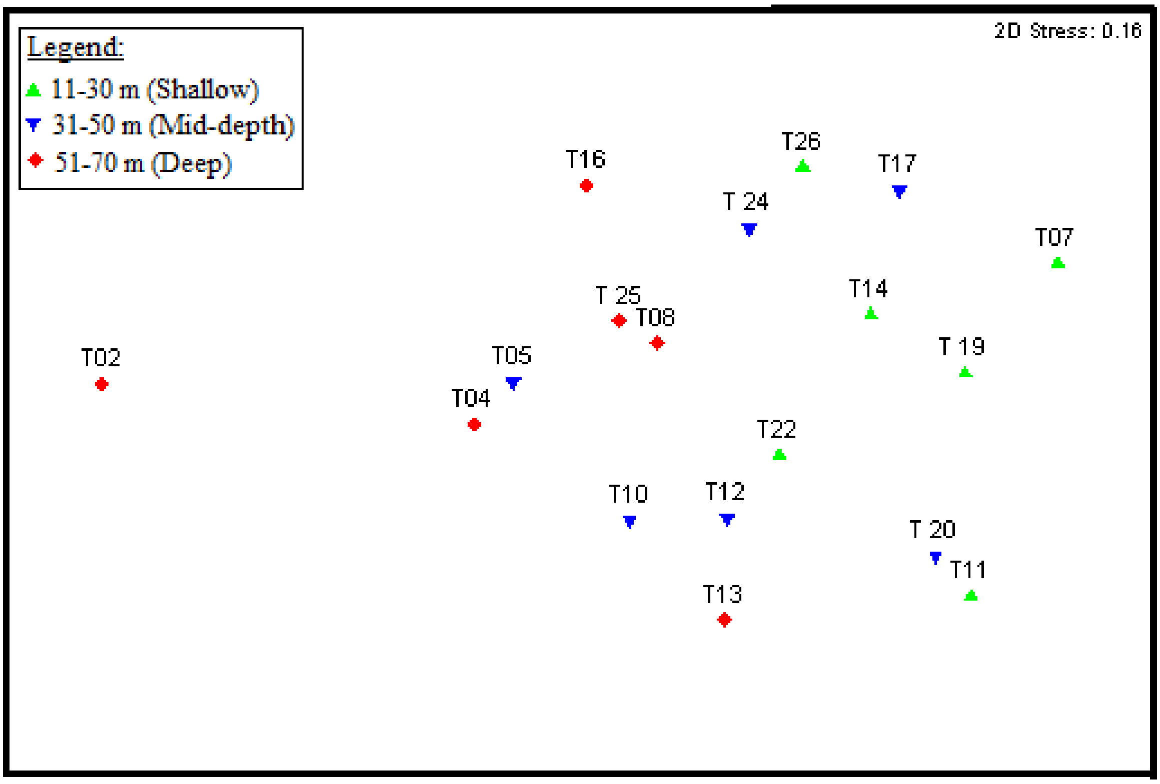


Figure 4.9 Non-parametric multidimensional scaling (MDS) of epibenthic faunal abundance data

SIMPER analysis (Table 4.5) showed that the significant difference between shallow stations (11-30m) and deep station (51-70m) was attributable to differing numerical abundance of 10 discriminating species that contributed 51.73% to the average dissimilarity of 89.04% (Table 4.5).

Table 4.5 SIMPER analysis results: species contributing to the average dissimilarity between shallow stations (11-30m), mid-depth (31-50m) and deep waters (51-70m) based on simultaneous analysis of taxa abundance data. δi: contribution of the i-th faunistic group to the average Bray-Curtis dissimilarity (δ) between depths, also expressed as a cumulative percentage (∑δi%). Diss/SD is the ratio of dissimilarity to standard deviation. For brevity, only species that contributed to ≥ 3.0% and cumulative percentage of ≥50% are listed. The codes in the parenthesis after the species name indicate: 'C' crustacean, 'P' Polychaete, 'M' Mollusc, 'E'Echinoderm

Species	Ave. Abundance **11-30 m**	Ave. Abundance **31-50m**	Av.Diss	Diss/SD	δi	∑δi%
Average dissimilarity 11-30m & 31-50m = 81.22%						
Chlamys purpurata (M)	1.13	0.27	4.88	0.54	6.01	6.01
Astropecten sp. (E)	0.52	0.77	3.88	0.98	4.78	10.79
Pagurus sp. (C)	0.93	0.49	3.80	1.35	4.68	15.47
Lithodes ferox (C)	0.00	1.02	3.79	1.26	4.66	20.13
Strombus latus (M)	0.17	0.70	3.67	0.92	4.52	24.65
Diadema sp. (E)	0.33	0.80	3.66	0.89	4.51	29.16
Scyllarides herklotsii (C)	0.20	0.96	3.54	1.00	4.36	33.51
Portunus validus (C)	0.94	0.65	3.53	1.14	4.35	37.86
Turris sp. (M)	0.66	0.49	3.46	0.99	4.26	42.12
Chlamys sp. (M)	0.76	0.00	3.19	0.64	3.92	46.04
Philine sp. (M)	0.00	0.75	2.82	0.95	3.47	49.52
Stenorynchus lanceolatus (C)	0.33	0.53	2.63	0.93	3.24	52.76

Species	Ave. Abundance **11-30 m**	Ave. Abundance **51-70m**	Av.Diss	Diss/SD	δi	∑δi%
Average dissimilarity between 11-30m & 51-70m = 89.04%						
Portunus validus (C)	0.94	0.25	5.93	1.02	6.66	6.66
Pagurus sp.(C)	0.93	0.20	5.55	1.12	6.23	12.90

Nereis sp. (P)	0.00	1.02	5.26	1.25	5.91	18.81
Chlamys purpurata (M)	1.13	0.00	5.02	0.43	5.63	24.44
Scyllarides herklotsii (C)	0.20	0.93	4.55	1.17	5.11	29.55
Maldanid sp. (P)	0.00	0.63	4.39	0.79	4.93	34.48
Chlamys sp.(M)	0.76	0.00	4.14	0.62	4.65	39.14
Turris sp. (M)	0.66	0.00	4.04	0.86	4.54	43.67
Astropecten sp. (E)	0.52	0.24	3.65	0.73	4.10	47.78
Lithodes ferox (C)	0.00	0.70	3.52	1.26	3.96	51.73

Species	Ave. Abundance **31-50 m**	Ave. Abundance **51-70m**	Av.Diss	Diss/SD	δi	∑δi%
Average dissimilarity between 31-50m & 51-70m= 80.14%						
Scyllarides herklotsii (C)	0.96	0.93	4.27	1.18	5.33	5.33
Strombus latus (M)	0.70	0.00	3.98	0.84	4.97	10.30
Diadema sp. (E)	0.80	0.25	3.97	0.87	4.95	15.25
Nereis sp. (P)	0.33	1.02	3.94	1.21	4.91	20.16
Astropecten sp. (E)	0.77	0.24	3.63	0.86	4.53	24.70
Lithodes ferox (C)	1.02	0.70	3.56	1.23	4.45	29.14
Maldanid sp. (P)	0.24	0.63	3.32	0.84	4.14	33.28
Portunus validus (C)	0.65	0.25	3.20	0.91	4.00	37.28
Priapulus caudatus (O)	0.55	0.27	3.11	0.73	3.88	41.16
Pagurus sp. (C)	0.49	0.20	2.97	0.65	3.71	44.87
Philine sp. (M)	0.75	0.00	2.87	0.93	3.59	48.45
Stenorynchus lanceolatus (C)	0.53	0.53	2.87	1.08	3.58	52.03

4.4.3 Species Dominance and Pollution Status

In order to ascertain the impact and the level of habitat stress possibly from bottom trawling or natural process, species abundance/biomass comparison (ABC) curves were determined as proposed by Warwick (1986). Warwick suggested on theoretical considerations that the distribution of the numbers of individuals among species should differ from the distribution of biomass among species when influenced by pollution-induced disturbance. This difference can be shown by *K-dominance* plots (Lambshead *et al*., 1983; Shaw *et al*., 1983). The curves rank species in order of importance on the x-axis and show the percentage of each species or the total numbers or biomass on a cumulative scale (called percentage dominance) on the y-axis. There are three scenarios of the ABC curves. These are:

i) when the community is approaching equilibrium, the biomass becomes increasingly dominated by one or a few large species, each represented by few individuals. The numerical dominants are generally smaller species. Hence, when plotted as *K-dominance* curves, 'numerical diversity' is greater than 'biomass diversity', so that the line for abundance lies well below the line for biomass, since one species forms a much larger proportion of the total biomass than it does of the total numbers.

ii) Under stress (natural physical and biological or pollution-induced disturbances), large competitive dominants are eliminated and biomass and abundance curves are close together and crossing one or several times.

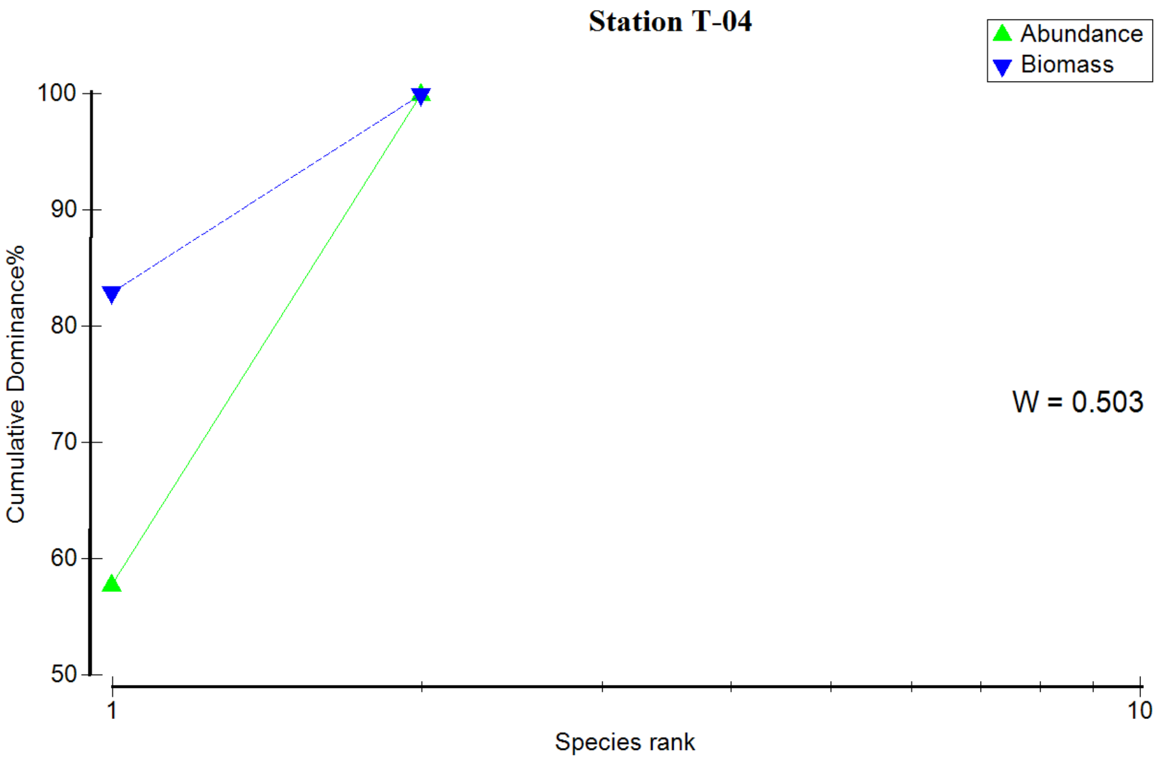
iii) Under severe disturbance, benthic communities become increasingly dominated by one or a few very small species (usually annelids such as *Capitella* spp. or oligochaetes) and few larger species are present. Hence 'numerical diversity' is lower than 'biomass diversity'.

These three cases were termed unpolluted, moderately polluted and grossly polluted by Warwick (1986). This can also be equated to unstressed, moderately stressed and heavily stressed habitats/locations. The representative ABC plots of the ABC analysis are presented in Figures 4.10 to 4.18. Further, Table 4.6 shows the pollution levels of the trawl stations. The results indicate that 50% of stations were moderately stressed, 5.56% stressed, 11% heavily stressed (giving a total stress of 66.56%) with 28% unstressed. The degree of stress from the results is inversely related to increasing water depth such that heavily stressed areas fall within shallow depths and vice versa.

Table 4.6 ABC Analysis results of bottom trawl epibenthic data and pollution status.

Trawl Station	Country	Latitude	Longitude	Mean Depth (m)	W-statistics	Pollution Status
*T 02	Nigeria	E2^0 59.1487	N6^0 11.9672	64	??	Undetermined
T 04	Nigeria	E2^0 47.7939	N6^0 11.5422	61	0.503	unstressed
T 05	Nigeria	E2^0 26.5627	N6^0 10.9210	45	0.166	moderately stressed
T 07	Benin	E2^0 20.5873	N6^0 14.4042	21	0.104	moderately stresses
T 08	Benin	E2^0 10.5182	N6^0 09.7585	54	0.147	moderately stresses
T 10	Benin	E1^0 42.0839	N6^0 05.6873	49	0.173	moderately stressed
T 11	Benin	E1^0 16.5090	N6^0 04.7729	18	0.173	moderately stressed
T 12	Togo	E1^0 18’90’’	N6^0 01’56’’	13	0.138	moderately stressed
T 13	Togo	E1^0 21.5790	N5^0 58.3448	60	0.338	Unstressed
T 14	Togo	E0^0 52.4986	N5^0 41.8603	13	-0.02	heavily stressed
T 16	Togo	E0^0 07.2247	N5^0 30.6685	56	0.145	moderately stressed
T 17	Ghana	E0^0 04.5541	N5^0 33.7917	39	0.248	Unstressed
T 19	Ghana	W0^0 41.1364	N5^0 07.6678	28	0.309	Unstressed
T 20	Ghana	W0^0 22.3600	N5^0 16.7100	36	0.311	Unstressed
T 22	Ghana	W-1^0 34.8500	N4^0 58.1300	16	0.110	moderately stressed
T 24	Ghana	W-1^0 32.3500	N4^0 51.2900	32	0.062	Stressed
T 25	Ghana	W-1^0 25.1300	N4^0 34.9800	50	0.101	moderately stressed
T 26	Ghana	W-1^0 08.4700	N4^0 59.7600	26	-0.189	heavily stressed

**Inadequate data due to high zeroes (97%) for the PRIMER software to analyse for the W-statistics.*



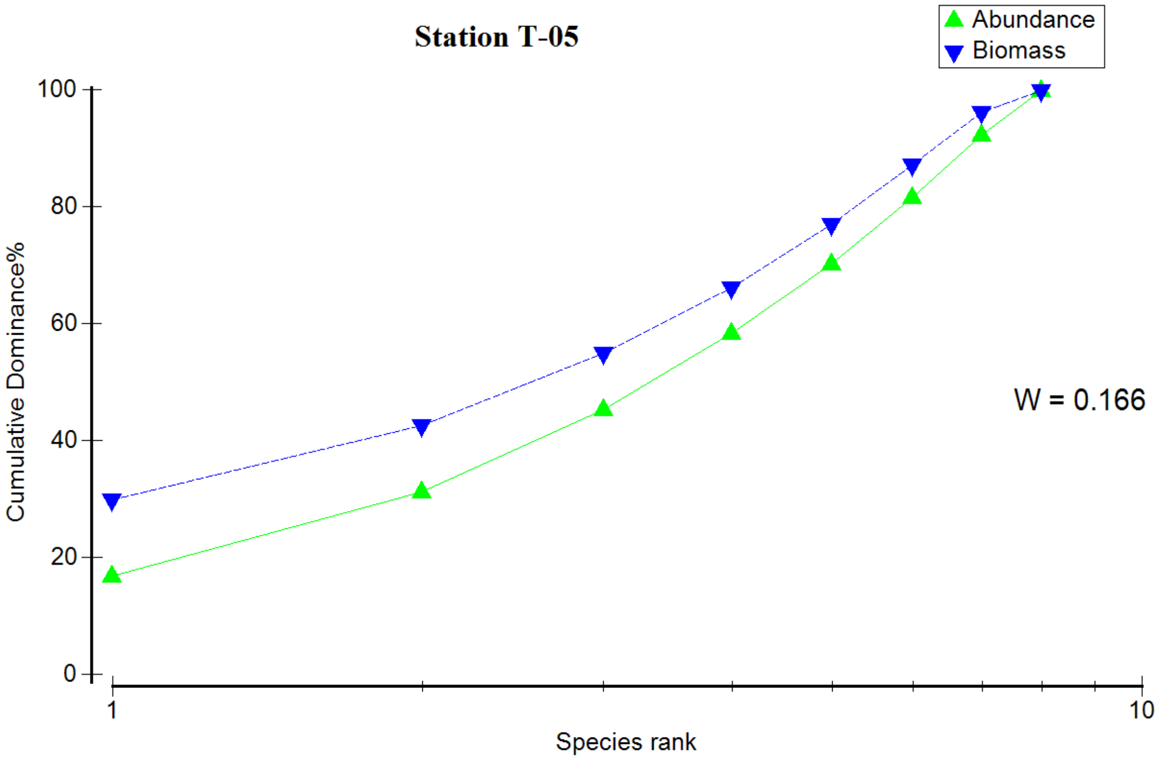


Figure 4.10 ABC plots for stations T-04 (top) and T-05 (bottom) based on epibenthic fauna abundance and biomass data.

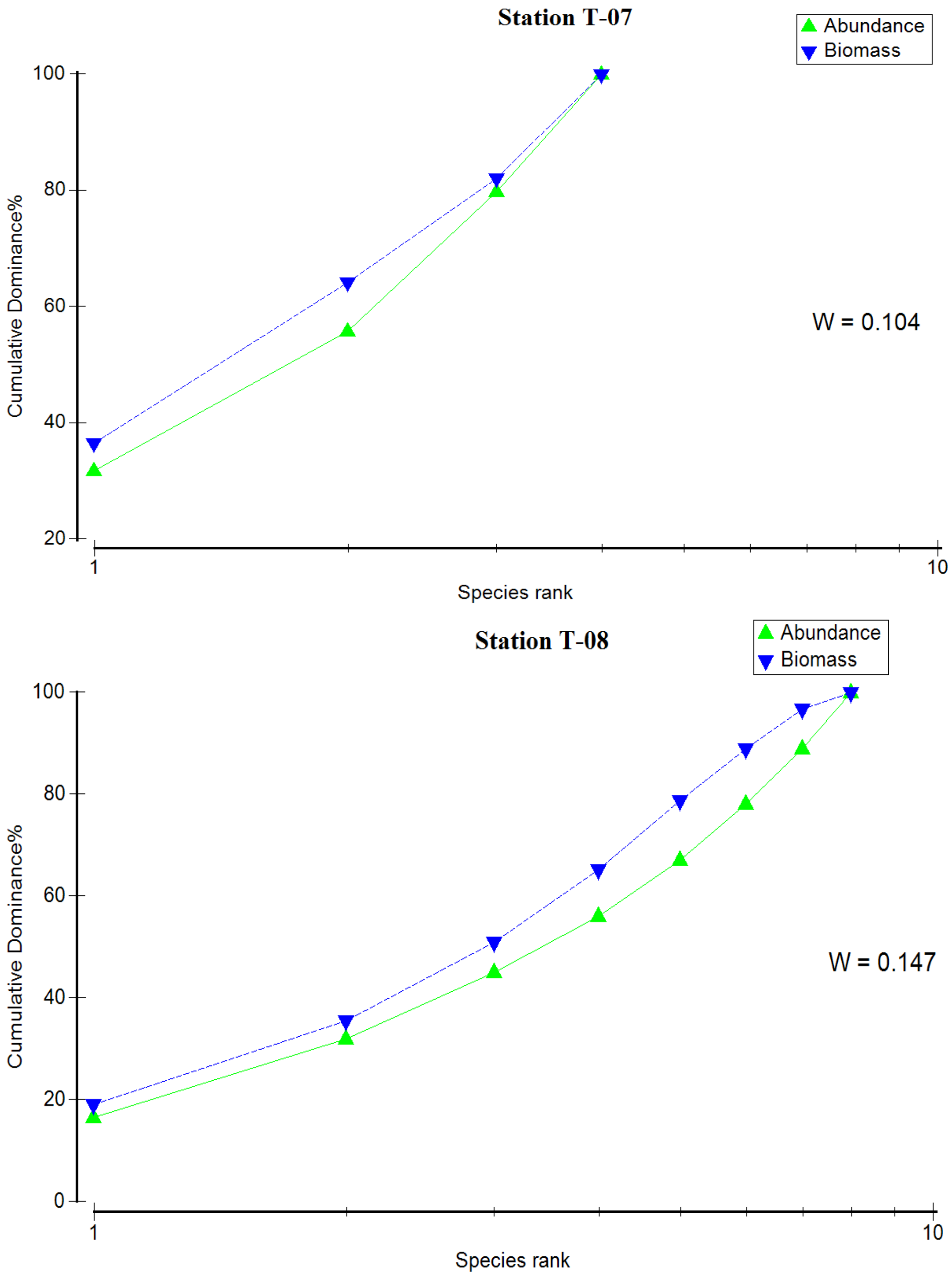
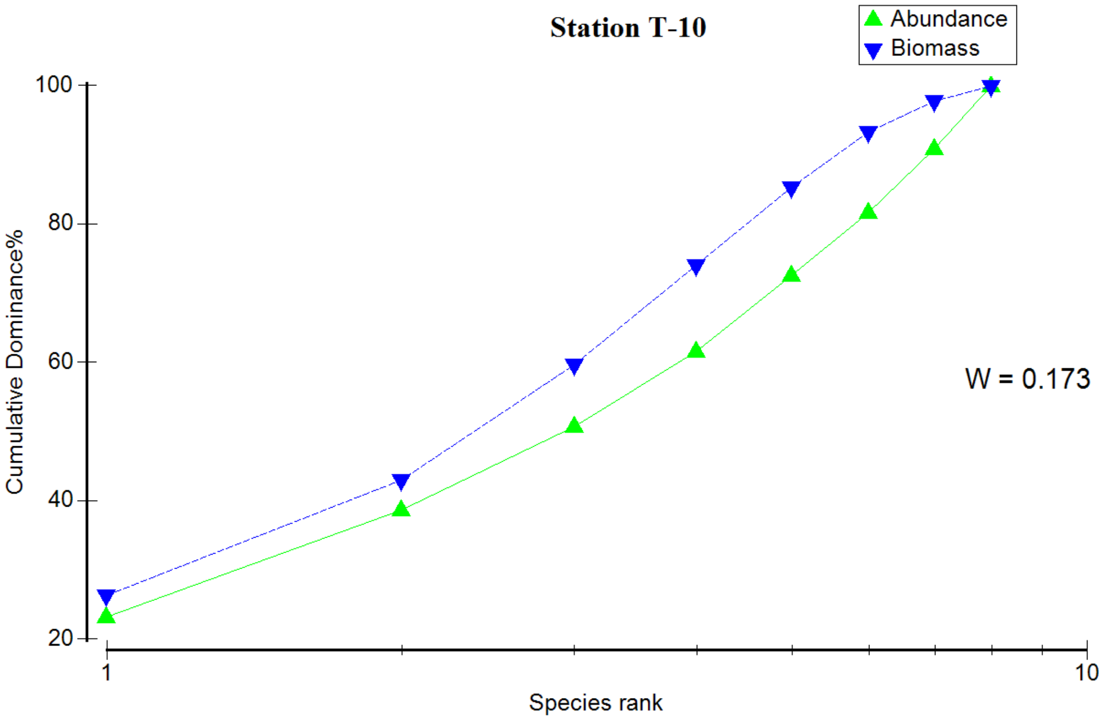


Figure 4.11 ABC plots for stations T-07 (top) and T-08 (bottom) based on epibenthic fauna abundance and biomass data.



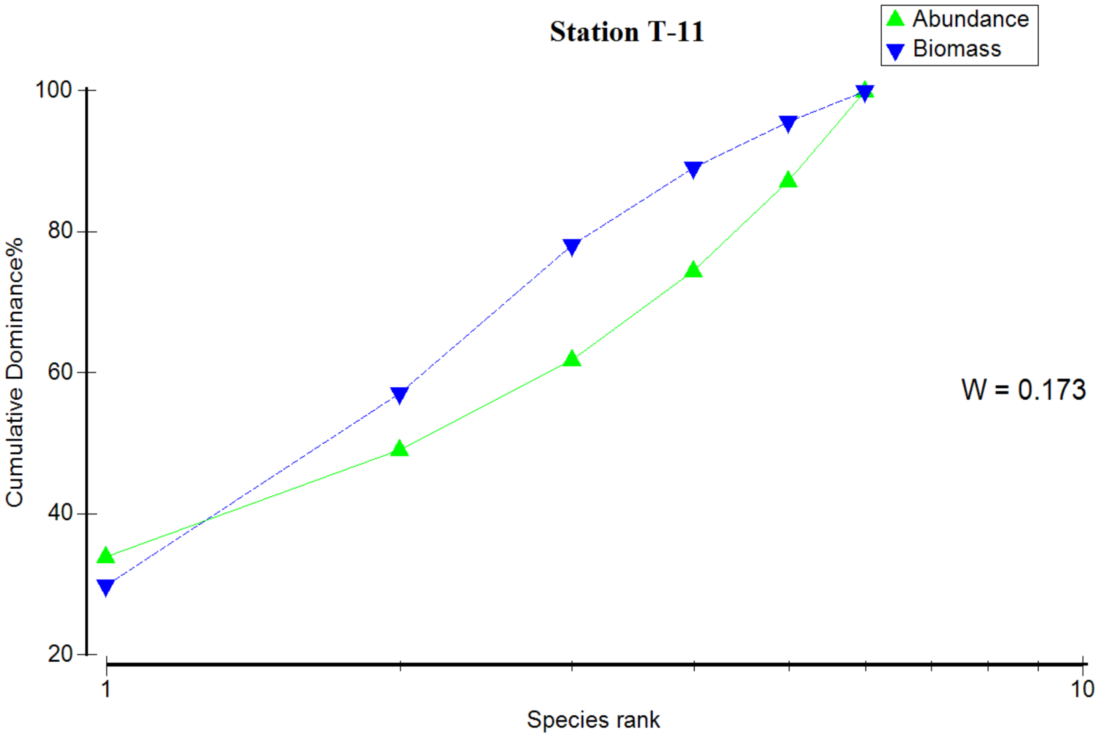
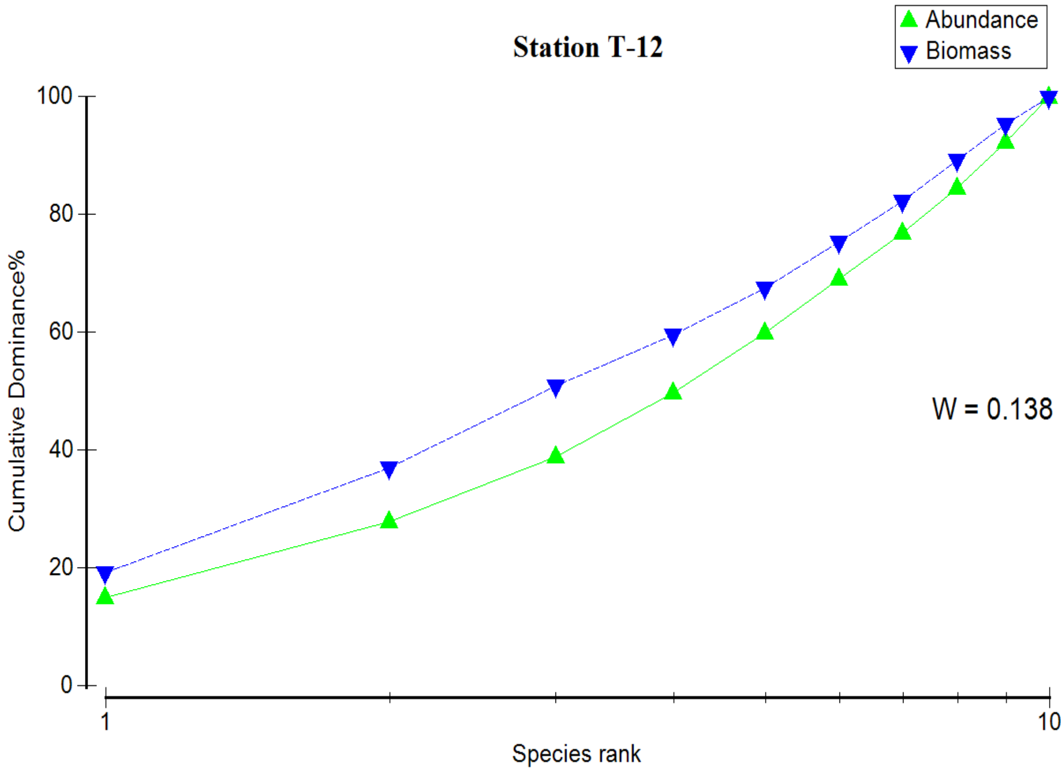


Figure 4.12 ABC plots for stations T-10 (top) and T-11 (bottom) based on epibenthic fauna abundance and biomass data.



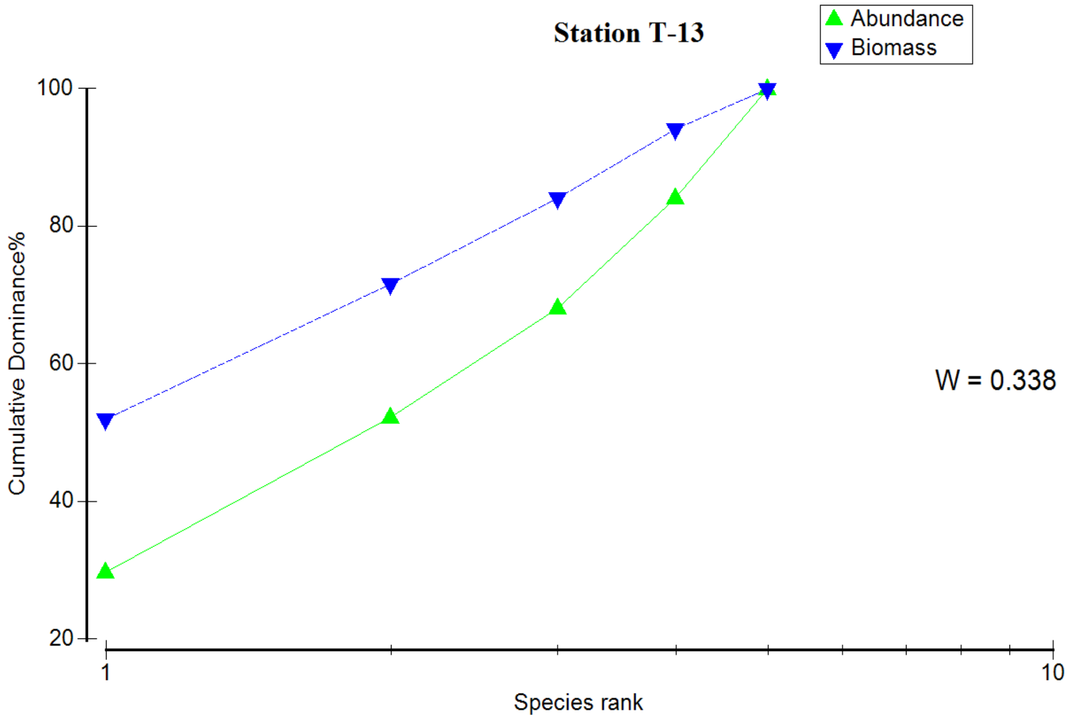
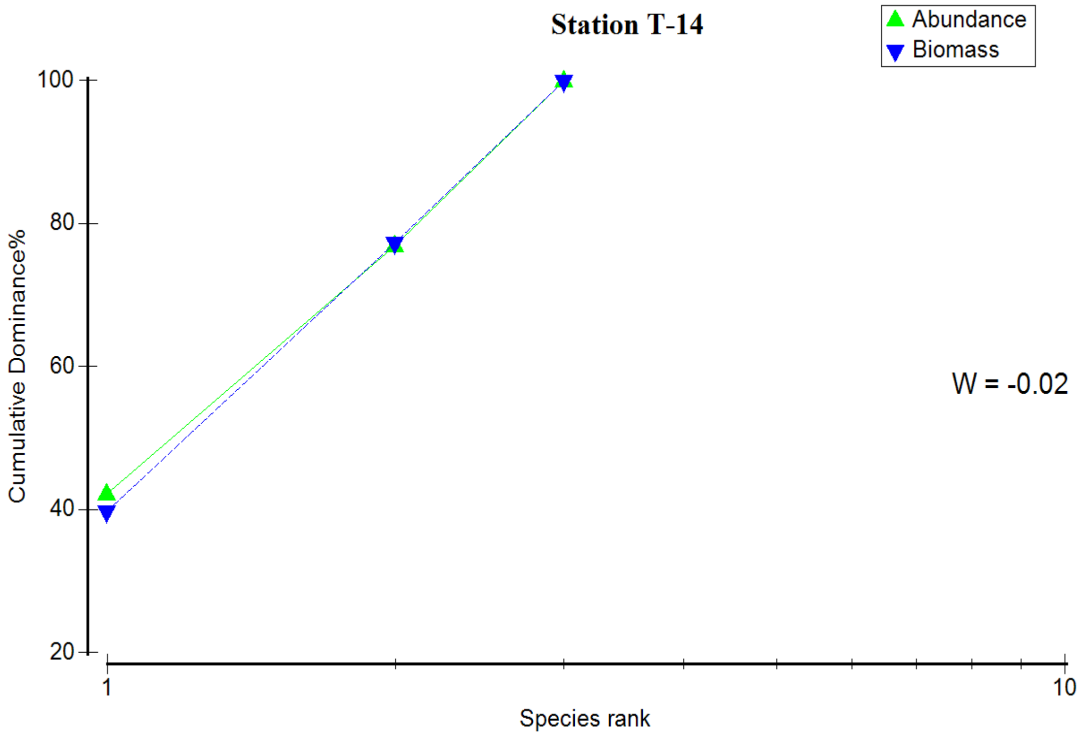


Figure 4.13 ABC plots for stations T-12 (top) and T-13 (bottom) based on epibenthic fauna abundance and biomass data.



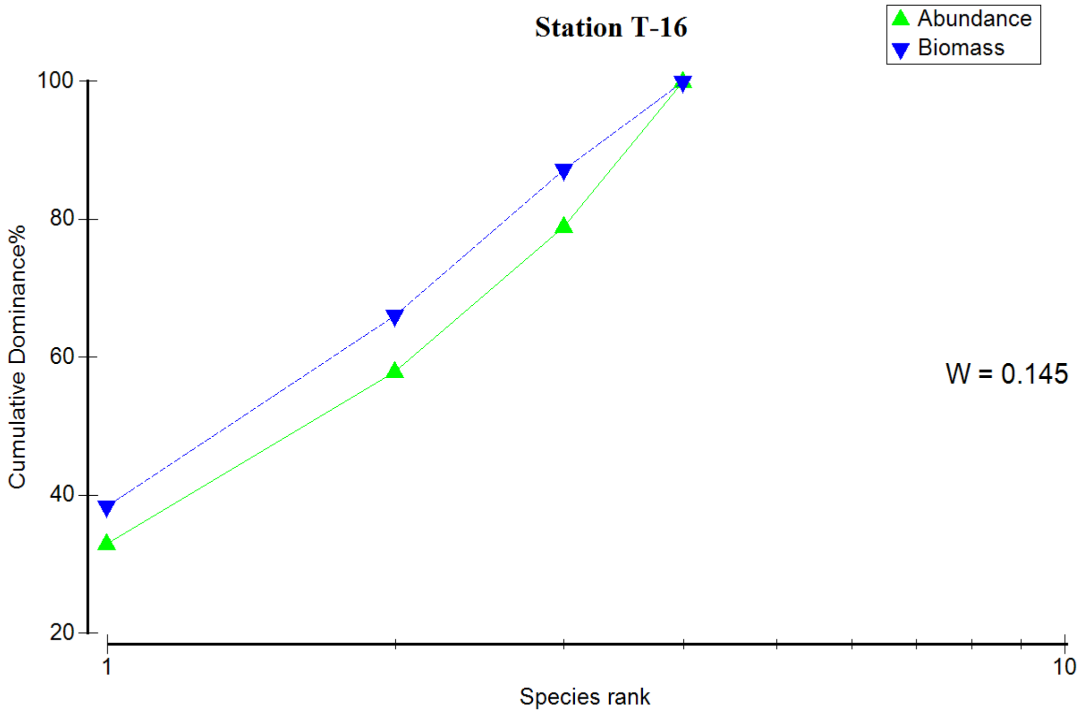
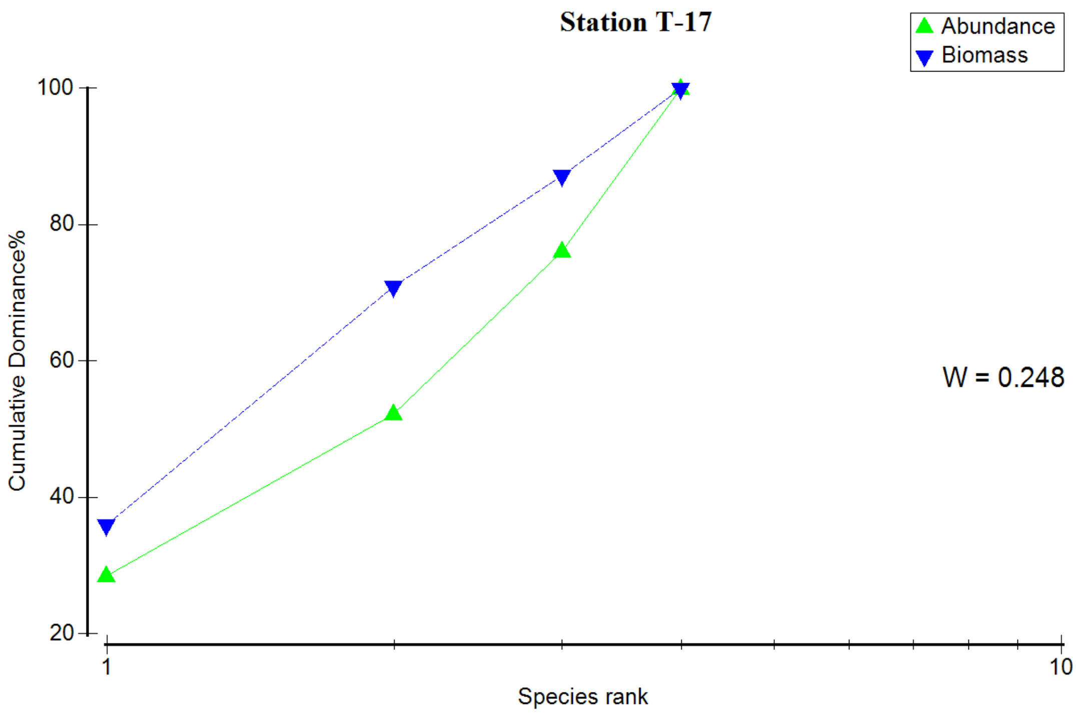


Figure 4.14 ABC plots for stations T-14 (top) and T-16 (bottom) based on epibenthic fauna abundance and biomass data.



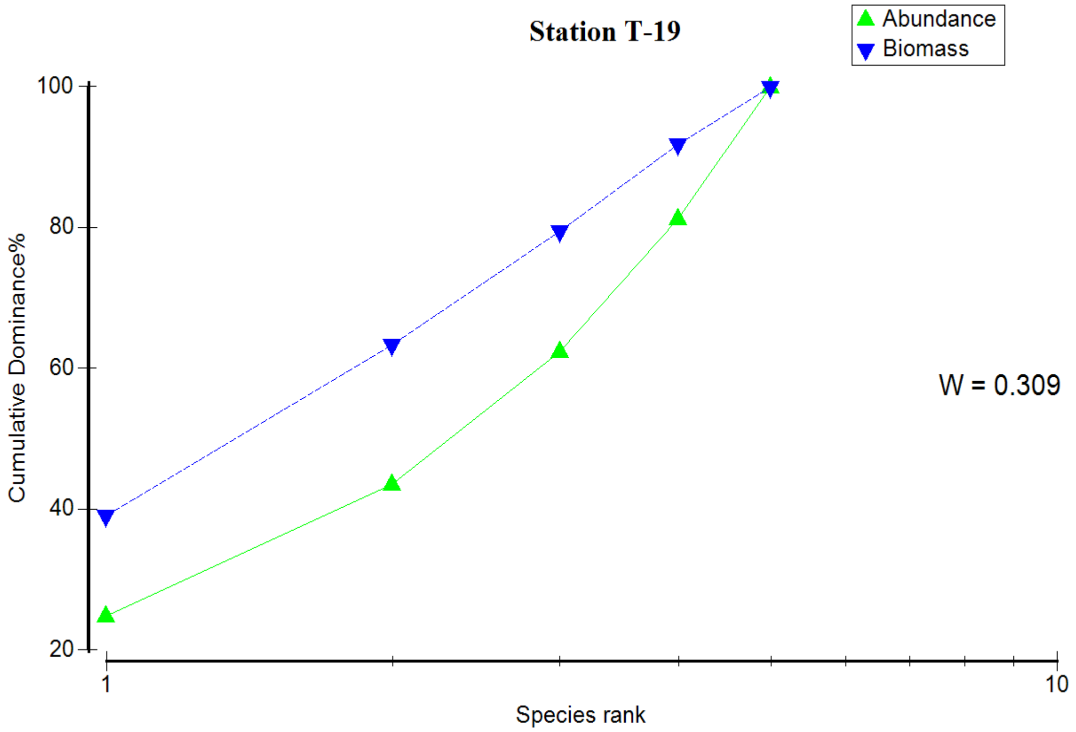


Figure 4.15 ABC plots for stations T-17 (top) and T-19 (bottom) based on epibenthic fauna abundance and biomass data.

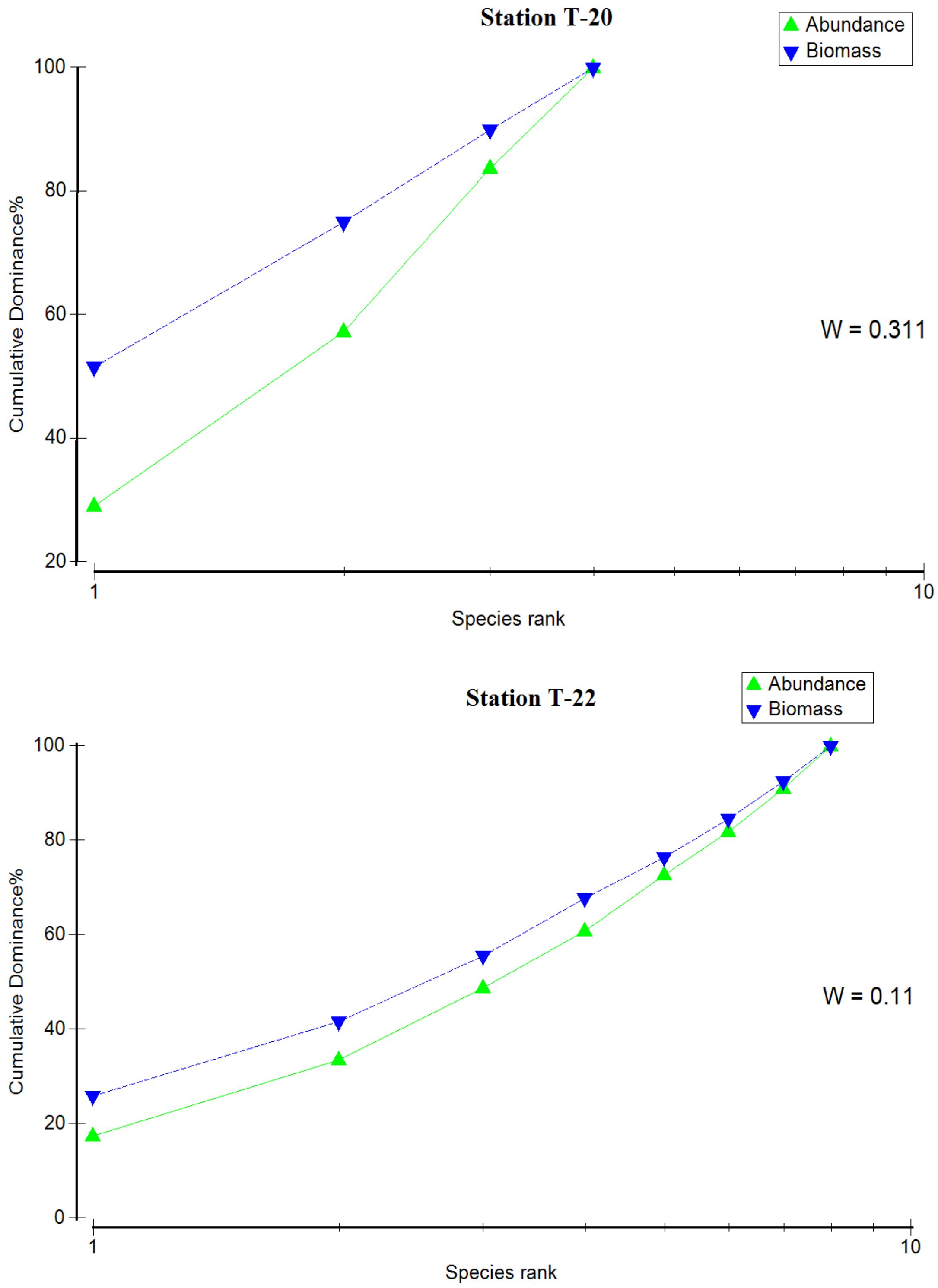
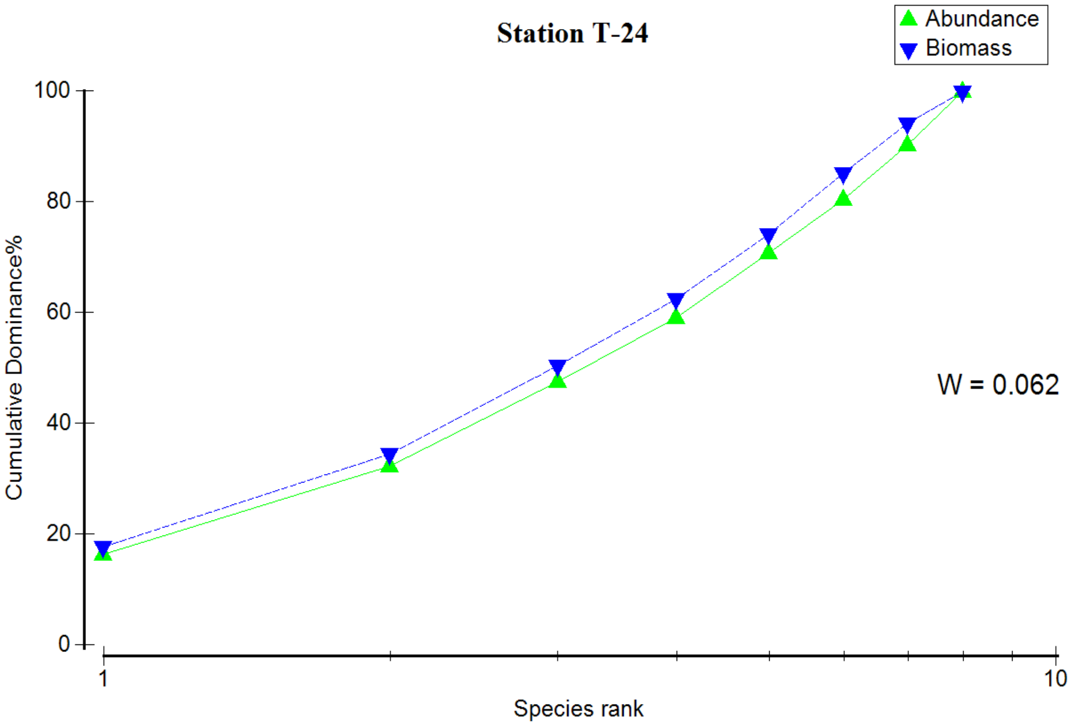


Figure 4.16 ABC plots for stations T-20 (top) and T-22 (bottom) based on epibenthic fauna abundance and biomass data.



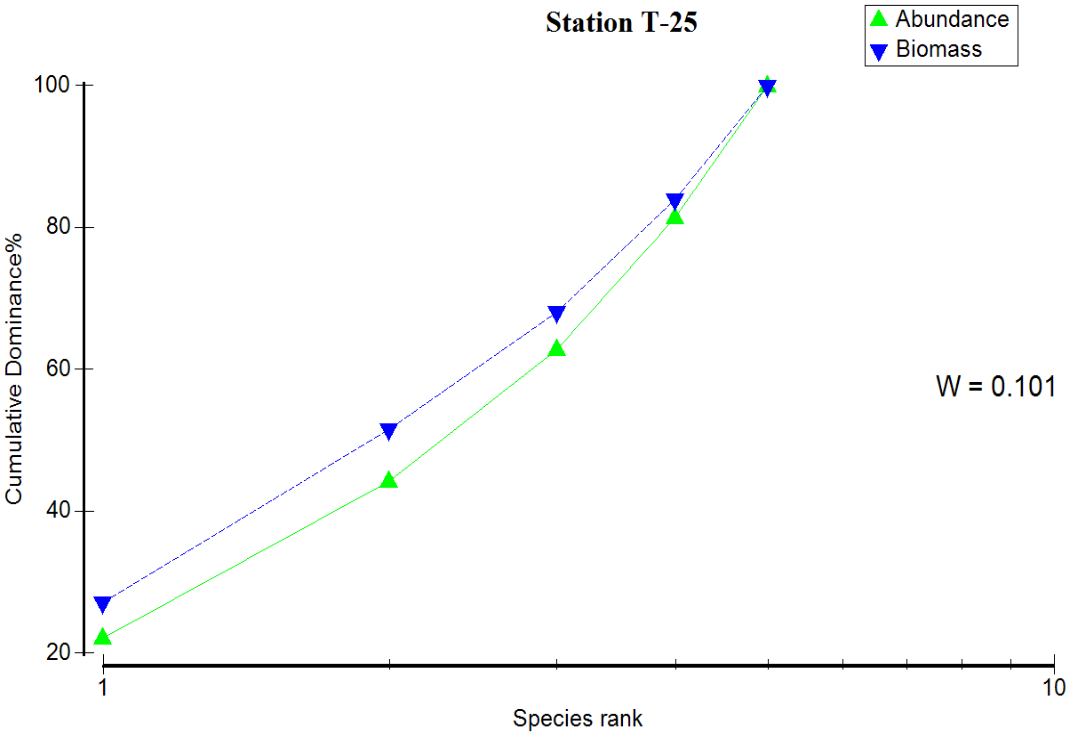


Figure 4.17 ABC plots for stations T-24 (top) and T-25 (bottom) based on epibenthic fauna abundance and biomass data.

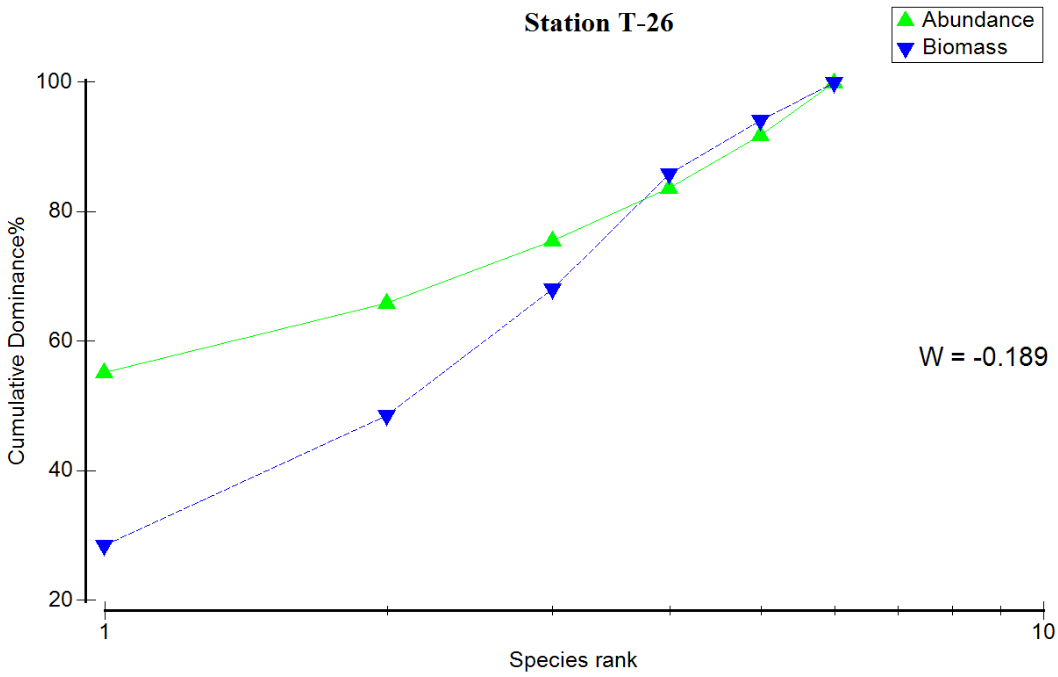


Figure 4.18 ABC plots for station T-26 based on epibenthic fauna abundance and biomass data.

4.4.4 Epifauna Functional Composition

4.4.4.1 Functional Group Diversity

The main benthic feeding types can be divided in two ways: what they feed on and how they feed. Category one can be divided into herbivores, carnivores, and detritivores, and the second into suspension-feeders, filter-feeders, deposit-feeders, scavengers, and predators (Fauchald and Jumars, 1979). Feeding strategy can offer ecologically relevant information on if and how human activities may affect the ecosystem, from the scale of an organism to the community. The Fauchald and Jumars (1979) feeding category was used for the epibenthic functional categorization.

In all, a total of twelve benthic feeding group categories were identified with some organisms sharing more than one feeding group. The result of feeding group composition depicts that carnivores largely contributed to the feeding community with

28% and was followed by filter feeding and predator/scavenging groups with 18% and 12% respectiely (Fig. 4.19). The contributions by omnivores, herbivores and opportunitsts/scavenging were similar. The lowest ranked feeding functional groups were the detritivores, detritivore/carnivore, deposit-feeding, deposit-feeding/herbivores, filter-feeding/omnivores with a contribution of 3% each (Fig. 4.19).

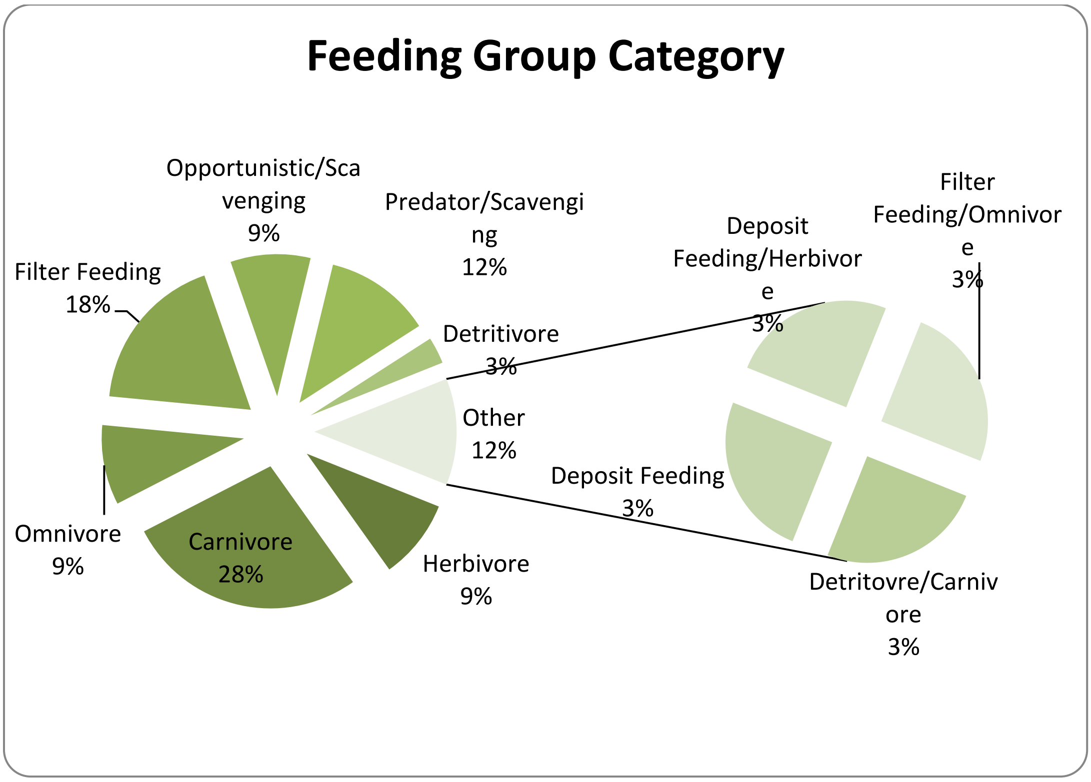


Figure 4.19 Feeding functional group categories for epibenthic fauna from 18 trawl hauls of the Gulf of Guinea.

The bathymetric distribution of the functional feeding groups of the epibenthic fauna indicated significantly higher numbers of carnivores, herbivores, filter feeders and predatory scavengers at mid-depth than both shallow- and deep-depths, and reflecting in their overall dominance across the feeding groups (Fig. 4.20). Omnivore scanvegers and deposit feeders showed signifcantly ranked higher in deep depths than the mid-depth and shallow areas. As regards, the shallow areas, the ooportunistic scavengers and detritivore carnivores signficantly dominated (Fig. 4.20)

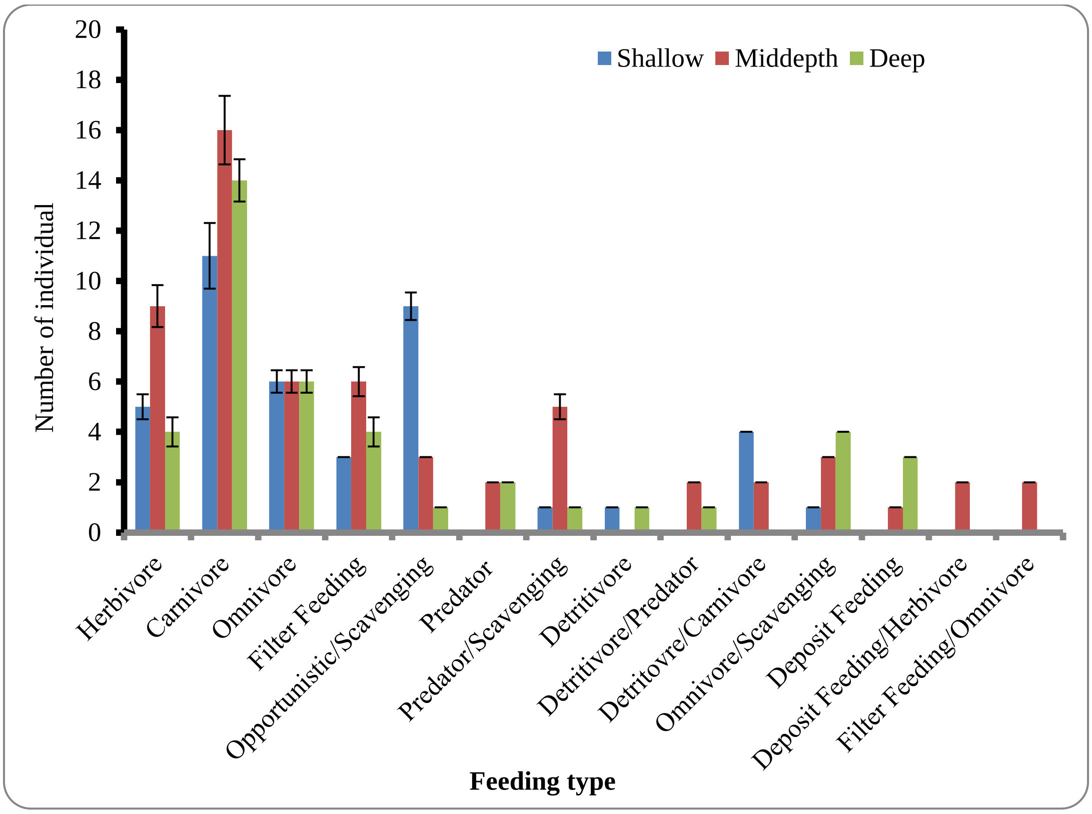


Figure 4.20 Richness of functional feeding groups across bathymetric gradient.

An important component of foraging strategy is motility and motility patterns may be related to feeding. The structure of the feeding apparatus may force the animal to remain sessile while feeding or the use of the feeding apparatus may be independent of, or require locomotion for proper fuction. Further, the mobility pattern may indicate escape response mechanisms of the organisms from disturbance (e.g., bottom trawling, predation) and may influence the community pattern.

The results of the analysis revealed that approximatley 64% of the epibenthic fauna encountered were motile and 12% were sessile with only 3% being sedentary (Fig. 4.21). This high mobility reflects in the dominance of carnivores, herbivores and filter feeders functional groups. These feeding groups require mobility in their foraging strategies. Sessile organisms throughout their life span do not move sufficiently to feed in an area different from that in which they settled as larvae. Discretely motile organisms are capable of moving between bouts of feeding, while motile species move independently of feeding, or in which efficient use of the feeding apparatus requires locomotion.

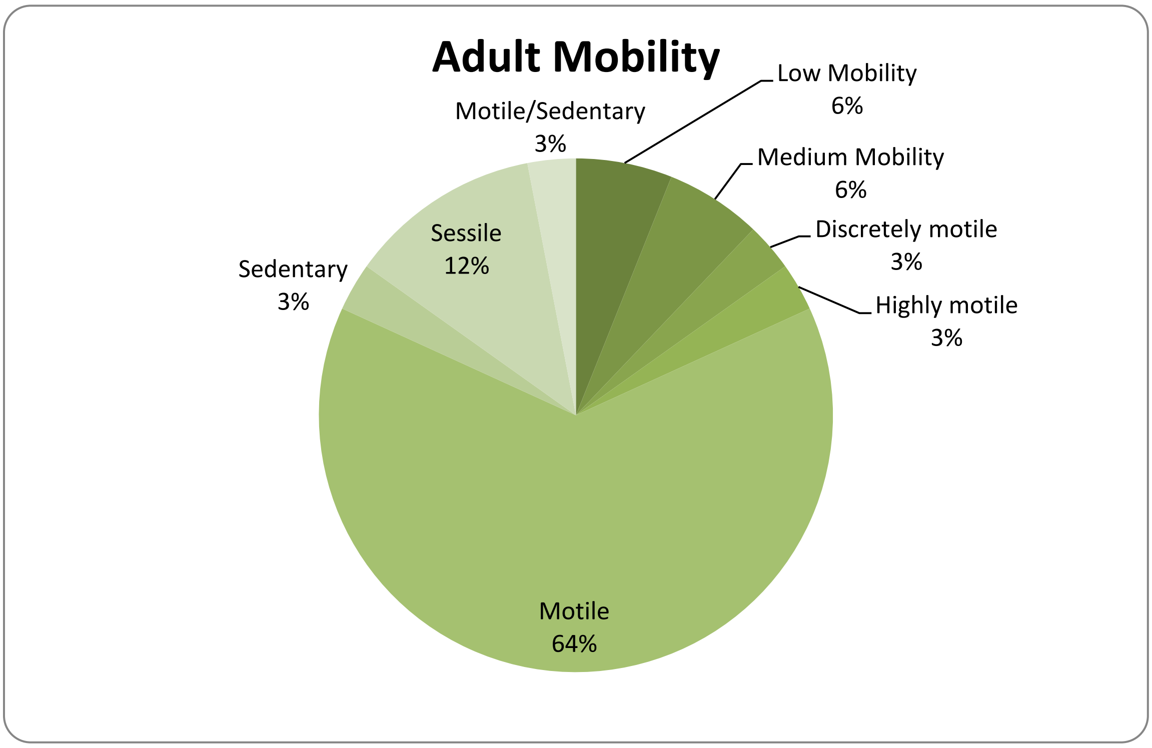


Figure 4.21 The proportion of adult relative mobility of epibenthic fauna from 18 trawl hauls in the Gulf of Guinea.

4.5 Discussion

Typical bottom beam trawling for demersal fishes are very efficient in catching epibenthic invertebrates (Reiss *et al*., 2006). These epibenthic organisms though often treated as by-catch are a dominant component of the trawl catches. According to Clarke (2000), the direct effect of mortality caused by beam trawling varies from species to species, with 10-40% mortality in gastropods, starfish, crustaceans and annelid worms, from 10-50% for sea urchins to 30-80% for bivalves. However, this study showed that epibenthic invertebrate by-catch was primarily made up of molluscs (82.6% richness and 43.1% numerical abundance), crustaceans (23.1% richness) and echinoderms (15.4% richness) (Table 4.3). These percentages are consistent and compared well with estimated percentage of benthic production that is consumed by fish predators (~45%) (Clarke, 2000).

At the community level, the mortality imposed by the trawl fishery will depend on the level of direct mortality, the trawling frequency and the overlap in spatial distribution between the fishery and the benthic organisms. Studies of the annual direct fishing mortality rates on benthic invertebrates, for example, in the southern North Sea were estimated at between 7 and 45% of the individuals (de Groot and Lindeboom, 1994). The epibenthic faunal organisms often contribute considerably to total benthic biomass (Lampitt *et al*., 1986) and carbon cycling (Piepenburg *et al*., 1995) and are supposed to have a strong impact on the micro-scale environment with, for instance, bio-turbation and bio-irrigation (Huettel and Gust, 1992). These important ecosystem services as a result of their functional attributes is potentially eroded by bottom trawling activities, which sweep the seafloor of epibenthic invertebrates that are treated as by-catch. Aside the variation of the severity of impacts from species to species, the impact of the trawling is also spatial dependent as trawling varies from location to location.

The current study revealed significant differences in epibenthic biomass across depth scales. In particular, the biomasses of crustaceans and molluscs decreased with increasing water depth (Fig. 4.8), which confirmed a generally recognized pattern (e.g., Rowe, 1983). Importantly, the epibenthic fauna community of the central sections of the GCLME (Gulf of Guinea) presented a clear defined bathymetric pattern of distribution both in terms of species abundance and functional richness and abundance. The assemblage pattern depicted a significant difference ($p<0.05$) between shallow-depth and deep-depth suggesting the existence of a unique abiotic factors or conditions structuring the epibenthic species assemblages. At the mid-depth however, both the species richness and diversity of fish and epibenthic fauna assemblages were correlatively higher (Figs. 4.6 and 4.7), which i) suggested a trophic dependence or interactions of fish and epibenthic fauna, and ii) the existence of conducive (or tolerable) abiotic conditions supporting the higher diversity.

Dietary studies have confirmed that large fishes prey on decapods (Polunin *et al*., 2001) and this was evident in this study with crustaceans numerically dominant at md-depth (Fig. 4.9). The numerical dominance of echinoderms and species placed in ‘Others’ category at mid-depth (Fig. 4.9) could further lend credence to the trophic interactions or dependence of fishes on epibenthic fauna. It is reasonable to assume that these epibenthic invertebrates are the dominant food items in the diet of the fishes. Stomach content analyses by several authors have indicated dominance of benthic invertebrates in demersal fishes. For instance, amphipods provide an important food resource to many demersal and benthic fishes (e.g. Gon and Heemstra, 1990; Kock, 1992; Olaso *et al.*, 2000), as well as other benthic invertebrates (McClintock *et al.*, 1994).

The observed higher Margalef's species richness and Shannon-Wiener diversity indices at the mid-depth may have been driven by trophic and physiological adaptation of the communities to the prevailing abiotic conditions. This may be as a result of the existence of multiple micro-habitats serving as, i) refugia (the patchy, diverse and multi-stratified sessile benthos offer a high diversity of potential microhabitats to small vagile invertebrates) and ii) the refugia enhancing foraging strategy (hiding and striking at preys). The assignment of a marine species to a given habitat will depend on the time it spends in that habitat. In other words, it depends on the organism's depth distribution and the resource segment that it feeds upon, as well as on where it has the best chance to avoid being taken as prey in its turn or where it faces less competition for food and space (Sarda *et al.*, 2005).

Some species will likely prefer a certain habitat or move between habitats, as well as gather or disperse, depending on other indirect factors such as vertical migrations under the influence of the photoperiod, annual seasonality, hydrographic conditions of the water masses, or inter and intraspecific relationships (e.g. resource competition, recruitment, sexual maturity, mating, biochemical cues etc.) (Sarda *et al*, 2005). These factors may have played considerable structuring role in the observed numerically higher epibenthic fauna abundance and biomass as well as fish assemblages in the mid-depth zone by this study. Understandably, the mid-depth zone represents transitional waters of the turbulent shallow-water zone and benign deep-water zone, and probably presented environmentally tolerable conditions that as a consequence supported rich and diverse epibenthic fauna communities such as crustaceans, echinoderms and species in the 'Others' category (Fig. 4.9).

The selection of a given species to particular habitats is driven by the tolerance of the species to the given environment (Lamptey and Armah, 2008). Newell (1970) pointed out that where the tolerance limits for a particular environmental variable have been determined for an organism, the organism’s realized distribution is much more restricted than its potential distribution. It is reasonable, therefore, to presume that the relatively large significant bathymetric differences in the taxonomic species and functional assemblages were probably the results of existence of extremes of environmental variables restricting the realized distribution of the species across all bathymetric gradients. In other words, the potential differing abiotic environmental factors (condition and resources) in the shallow-depth and deep-depth ensured that species tolerable to these extreme environmental conditions survived. The declension of species abundance of molluscs with increasing water depth and increased polychaete abundance with increasing water depth (Figs. 4.8 and 4.9) gave further support to the assertion of differing abiotic structuring mechanism along bathymetric gradients.

The distribution pattern of polychaete taxa is indicative that the deep-depth is characteristic of fine-grained soft substrate with potentially high organic matter, which probably was influenced by pelagic productivity. This statement is supported by the observation of dominance of deposit-feeding polychaetes in deep-depth (Fig. 4.20) with low suspension/filter-feeding organisms (e.g. molluscs), emphasizing the theory of trophic group ammensalism (Rhoads and Young, 1970). The theory suggested that the physical instability of reworked environment may discourage the settling larvae of suspension feeders, and if settling does occur, early growth stages may be inhibited or killed by the unstable sediment conditions. The inhibitors (deposit-feeders) are unaffected by this relationship, while the amensals (suspension-feeders and sessile epifauna) are either discouraged from settling or are killed during early benthonic stage.

Ostensibly, deep-depth ecosystems have lower energetic turnover than shallow-water or littoral systems and their carrying capacity is expected to be lower (Cartes *et al*., 2002). Conversely, the high numerical abundance and the correspondingly high biomass of molluscs in shallow-water could mean that there is high current energy, which has trophically favored the molluscan assemblage (or have adapted trophically) due in great part to their active and passive suspension-feeding mechanism. Most molluscs prefer to attach to rock stones and shells (Jorcin, 1996) and thus their abundance in the shallow-waters is a reflection of the nature of the substratum influenced possibly by the current energy.

4.5.1 Functional Group Classification

According to Hamerlynck *et al*. (1993) it will make a great biological sense to base functional and process studies on entities which be can distinguished clearly on the basis of their species-abundance composition. Two methods traditional often used in functional diversity in marine benthic ecosystems are: i) relative taxon composition analysis, which interprets changes in the distribution of taxa in terms of the characteristics they exhibit, and ii) trophic group analysis, which investigates differences in feeding mechanisms between assemblages, although biological trait analysis have been employed recently (Bremner *et al*., 2008). A more targeted approach proposed for the study of functional diversity focuses specifically on feeding mechanisms, which are generally thought to be one of the central processes structuring marine ecosystems (Pearson and Rosenberg, 1978; 1987). Essentially, functional feeding strategies have been used to explore the mechanims of the adaptations of communties to the environment in different ecosystem including streams (see Principe *et al*., 2010), estuaries and marine.

The bathymetric analysis of the functional feeding groups showed signficant (*p*=0.017). bathymetric differences between shallow and deep zones, consistent with that of the taxonomic species abundance. This suggests that functional feeding group categorization may give comparable information about community assemblage patterns and possibly the inherent environmental drivers. Bathymetric zonation is reflected in the variations of environmental factors that ensure the selection of species with particular functional trait in which this attribute consequently reflect in the ecosystem functioning of the study locality.

The functional feeding groups contributed differently to the assemblage. For instance, carnivores contributed 28%, filter feeders (18%) and predatory scavengers (12%) and these were dominant at mid-depth. Functional feeding groups is necessary for identification of functional groups partially independent of taxonomic determinations (Cummins, 1974) in order to address important process oriented-ecosytems questions. The concept concerns itself with how a resource or any other ecological component is processed by different species to provide a specific ecosystem service or function (Blondel, 2003). The carnivory was noted as the dominant functional feeding in the epibenthic communities and is a reflection of the nature of the food resources in the habitats level and the morphological and behavioural adaptation that have converged. Feeding strategies are typical traits reflecting the adaptation of species (Statzner *et al*., 2004). The dominance and distribution of the carnivores could be more closely related to the abundance of their potential preys; the densities of these preys were higher in the mid-depth. Predation can enhance coexistence between species of benthic organisms by preventing monopolization of space (Parsons *et al*., 1995). The carnivorous species can facilitate the transport of nutrients retained in the detritivores tissues back in to the mobile pool (Ngai and Srivastava, 2006) and hence renew nutrients for primary producers. The presence of carnivorous species further helped to transfer the nutrients retained in deposit-feeders back into the mobile pool (Sivadas *et al*., 2013). Thus, the functional diverse macrobenthic community rapidly consumed the organic matter and converted it to benthic biomass which forms the food for organisms at the higher trophic level such as the demersal fish.

The filter-feeders processed organic matter from the water column, while deposit-feeders utilized the sedimented detritus. The numerical dominance of deposit-feeders at the deep-depth is suggestive of the influence of the zone by pelagic resources.The deposit-feeders as consumers of newly sedimented food is related to the production in the water column (Gaston, 1987; Gaston *et al.*, 1988; Josefson and Rasmussen, 2000). Although the present study does not present information on the biological productivity in the area, the Gulf of Guinea (GoG) region is characterized by a coastal upwelling that increases the productivity in the water column (Wiafe, 2002), and part of this production settles forming available food for the benthic community. Filter/suspension feeders need high quality food arriving from surface waters and/or via bottom currents, which also may make them some of the first organisms impacted by changes in pelagic production, high sedimentation, or from pollution to the water column.

The potential food for filter/suspension feeders is mainly phytoplankton, which may be produced in waters far away from their locations and transported to them by currents (Pearson and Rosenberg, 1987). The trophic group mutual exclusion hypothesis postulates that current speed controls community composition, through its effects on food supply and sedimentary composition. Predators and scavengers on the other hand need a rich community of potential prey in suitable size classes, and may respond positively to enhanced biodiversity, but also to strong disturbances to the seafloor resulting in mortality or exposure of benthic fauna (Kaiser and Spencer, 1996; Ramsay *et al*., 1998). Food supply is therefore a key factor structuring marine benthic communities (Pearson and Rosenberg, 1978, 1987; Wieking and Kröncke, 2005).

4.5.2 Ecosystem Health and Ecological Status

The ecological status of the marine environment has been assessed using different tools/indices, and these have really focused on the benthos. One of the tools/indices which has successfully been applied to assess the ecological status of the marine benthos is the ABC (Abundance Biomass Curve) proposed by Warwick (1986). The ABC analysis in this study revealed that 11% of the shelf in the Gulf of Guinea (19±9m depth) is heavily stressed due possibly to anthropogenic activities such as fishing and pollution. Five percent (5.56%) (32±8m) of the shelf area is stressed, while 50% (36±18) of the locations were moderately stressed. Adding these areas of stress amounted to a colossal 66.56% of the continental shelf area was stressed although 50% of it is moderately stressed. Nonetheless, this finding presents a worrying picture of the Gulf of Guinea that may exigently necessitate a regional pragmatic effort to arrest the situation. Approximately, 28% (one-third) of the shelf area is unstressed and these areas fall within the average water depth of 45±15m. It is thus evidently striking to note that the degree of stress decrease with increasing water depth. This observation would mean that shallow-depth areas experience intense disturbance possibly from fishing and pollution from land drainages. Many bottom trawlers trawl within shallow-depth due to less advanced technologies and possibly high cost of trawling in deep-depths within the region.

The ecological health of marine ecosystem has been a concern and global efforts are being made to ensure ‘good’ ecological statuses in marine ecosystems. For example, the Marine Strategy Directive Framework (European Commission, 2008), viewed the ecological status as the integration of structure, function and processes of the marine ecosystem with anthropogenic impacts. These require background scientific works to fully understand the dynamics that will ensure that any intervention is not bereft with adequate scientific information. The background works identified by the European Commission to define the good ecological status has been grouped under various task descriptors namely biodiversity (Cochrane *et al*., 2010); non-indigenous species (Olenin *et al*., 2010); exploited fish (Piet *et al*., 2010); food-webs (Rogers *et al*., 2010); human-induced eutrophication (Ferreira *et al*., 2010); seafloor integrity (Rice *et al*., 2010); contaminants (Law *et al*., 2010); litter (Galgani *et al*., 2010); noise (Tasker *et al*., 2010) and hydrographical conditions. This holistic initiative of the European Commission could be harmonized within the Guinea Current Large Marine Ecosystem (GCLME) Programme backed by sound management for implementing the tasks’ findings in order to stem the tide of the ecosystem deterioration, which if continued will lead to the breakdown of its resilience with very devastating consequences.

CHAPTER FIVE

GENERAL CONCLUSION AND RECOMMENDATIONS

5.1 Conclusion

The study has demonstrated that functional traits of soft-bottom macrobenthic assemblage patterns represented a direct and complex response to environmental factors notably sedimentary nitrate, calcium, magnesium, organic carbon and sediment grain-size fraction (silt & clay), which are in turn influenced by the their interactions with other variables to drive functional and species diversity and assemblages. The study revealed that the dominant functional traits (i.e., small adult size, solitary, burrow-dwelling & deposit-feeding) potentially control the assemblage patterns and thus exert the strongest influence on ecosytem processes such as biogeochemical function (nutrient mineralization) contributing immensely to the productivity of the ecosystem. The dominance and distribution of these key eco-fucntional traits are direct responses to tolerance and trophic, morphological, behavioral adaptations to a highly dynamic and unstable ecosystem.

The functional traits analysis, which is first its kind in the GCLME region, has demonstrated that the BTA not only preserve taxonomic information, but also provide important ecological information. These ecological information included the nature of the ecosystem, the ecological status, potential ecosystem processes/functions, and importantly discrimination between habitats/locations, with the latter creating biodiversity zonation in the GCLME. These zones are i) central GCLME, (biodiversity rich), ii) western GCLME (moderately rich biodiversity), and iii) eastern GCLME (poor biodiversity). This habitat zonations may have significant implications not only for resources management but monitoring of ecosystem health for conservation purposes in the GCLME, which is experiencing some degree of ecological stress.

The empirically derived inferences of mechanistic effects of functional biodiversity on ecosystem processes from this study provide important demonstration of relationship between functional diversity and ecosystem functions in natural marine ecosystem. This is against the backdrop of little effort in the scientific literature to demonstrate and substantiate biodiversity-functional relations using data from the real world according to Solan *et al*. (2008).

The key inferential findings of the study were:

- The small body size dominant functional trait provided strongest evidence of habitat instability, high productivity and low-biomass supported ecosystem (i.e.,GCLME)
- The habitat instability may be attributable to anthropogenic activities (i.e., fishing and pollution) creating a stressful condition that affect the ecological health of the GCLME as evidenced by the inverse relations between habitat stress and increasing water depth. Most marine fishing activities are concentrated on shallow waters.
- The ecological disturbances through fishing and/or pollution play interactive and structuring roles in epibenthic fauna distribution patterns especially along bathymetric gradient.
- Benthic species adaptations to the unstable, dynamic, stressful and productive GCLME environment are corroboratively through combined mechanism/strategies notably feeding, lifestyle, anatomical and morphological.

- The identified dominant traits provided an indication of a productive ecosystem primarily influenced by ecosystem process/functions (i.e., nutrient mineralization through biogeochemical functions by burrow dwelling deposit-feeders) and thus providing the strongest empirical evidence of ecosystem function. This is further corroborated by the identification of nitrate and organic carbon as key drivers of functional and species richness.
- The structuring effects of abiotic parameters (e.g., calcium, magnesium) on functional and species diversities suggest climate change factors in the GCLME and thus climate change factors are potential surrogates of abiotic drivers of benthic community and functional structure.
- Results indicated evidence of trophic/feeding dependence (or interactions) of demersal fishes on (between) epibenthic fauna (notably crustaceans, echinoderms and species in ‘others’ category), but this occurred in the most benign conditions or within environmental tolerable areas.

5.2 Recommendations

- The use of functional traits notably adult body size, feeding habit, sociability and mobility for environmental monitoring of the ecosystem health and to understand ecosystem pocesses in the GCLME should be given a highest priority.
- Concurrent investigations of marine benthos and demersal fisheries should be important focus in any GCLME fisheries survey in order to understand the effects of bottom trawling on the benthos with associated ecosystem services, as well as trophic interactions.

- Influence of Benguella and Canary currents on primary productivity or carbon input in the GCLME should be investigated to elucidate the impact they have on benthic community assemblages.
- It is imperative for a long-term monitoring of rate of accumulation or dissolution of $CaCO_3$ and $MgCO_3$ in marine organisms (benthic and planktoninc) and also quantification of shifts in calcification rate in order to understand and delineate the effects of climate change mechanisms in the GCLME.

REFERENCES

American Public Health Association (APHA), American Water Works Association (AWWA), and Water Environment Federation (WEF). (1998). *Standard methods for the examination of water and wastewater*, 20th Edition. United Book Press, Inc., Baltimore, Maryland. pp. 1325.

Aberle, A. and Witte, U. (2003). Deep-sea macrofauna exposed to a simulated sedimentation event in the abyssal NE Atlantic: in situ pulse-chase experiments using ^{13}C-labelled phytodetritus. *Marine Ecology Progress Series* **251**: 37-47.

Adger, W.N., Hughes, T.P., Folke, C., Carpenter, S.R. and Rockstrom, J. (2005). Social-ecological resilience to coastal disasters. *Science* **309**: 1036-1039.

Alldredge. A.L. and Silver, M.W. (1988). Characteristics, dynamics and significance of marine snow. *Progress in Oceanography* **20:** 41-82.

Aller, R.C. and Yingst, Y. (1985). Effects of the marine deposit-feeders Heteromastus filiformis (polychaete), Macoma balthica (bivalve), and Tellina texana (bivalve) on averaged sedimentary solute transport, reaction rates and microbial distributions. *Journal of Marine Research* **43:** 615-645.

Aller, J.Y. and Aller, R.C. (1986). Evidence for localized enhancement of biological activity associated with tube and burrow structures in deep-sea sediments at the HEBBLE site, western North Atlantic. *Deep-Sea Research* **33:** 755-790.

Aller, R.C. and Aller, J.Y. (1998). The effect of biogenic irrigation intensity and solute exchange on diagenetic reaction rates in marine sediments. *Journal of Marine Research* **56:** 905–936.

Alongi, D.M. (1990). The ecology of tropical soft-bottom benthic ecosystems. *Oceanography Marine Biology Annual Review* **28:** 381-496.

Alonso, A. and Camargo, J.A. (2003). Short-term toxicity of ammonia , nitrite, and nitrate to the aquatic snail Potamopyrgus antipodarum (Hydrobiidae, Mollusca). *Bulletin of Environmental Contamination and Toxicology* **70:** 1006-1012.

Alverson, D.L., Freeberg, M.H., Murawski, S.A. and Pope, J.G. (1994). A global assessment of fisheries bycatch and discards. FAO Fisheries Technical Paper 339. FAO, Rome. pp. 233.

Amaro T, Bianchelli S, Billett, DSM, Cunha MR, Pusceddu A. and Danovaro, R. (2010) The trophic biology of the holothurian *Molpadia musculus*: implications for organic matter cycling and ecosystem functioning in a deep submarine canyon. B*iogeosciences* **7:** 2419–2432

Anand, P., Elderfield, H. and Conte, M.H. (2003). Calibration of Mg/Ca thermometry in planktonic foraminifera from a sediment trap time series. *Paleoceanography* **18(15)**: 28.1–28.15.

Andersson, A.J., Mackenzie, F.T. and Bates, N.R. (2008). Life of the margin: implications of ocean acidification on Mg-calcite, high latitude and cold-water marine calcifiers. *Marine Ecological Progress Series* **373:** 265-273.

Anderson, J.G. and Meadows, P.S. (1978). Microenvironments in marine sediments. *Proceedings of the Royal Society of Edinburgh Section B* **76:** 1-16.

Angel, M.V. (1984). Detrital organic fluxes through pelagic ecosystems: In: Fasham, M.R.J. (ed.), *Flows of energy and materials in marine ecosystems: theory and practice*, NATO Conference Series IV, Marine Science, Plenum Press, New York, pp. 475-516.

Arnault, S. (1987). Tropical Atlantic geostrophic currents and ships drifts. *Journal of Physical Oceanography* **18:** 1050-1060.

Arvanitidis, C., Koutsoubas, D., Dounas, C. and Eleftheriou. (1999). Annelid fauna of a Mediterranean lagoon (Gialova lagoon, south- west Greece): community structure in a severely fluctuating environment. *Journal of Marine Biological Association*, U.K **79:** 849-856.

ASTM (2006). Standard guide for collection, storage, characterization and manipulation of sediment for toxicological testing and for selection of samplers used used to collect benthic invertebrates. E 1391-03. In: *Annual book of standards. Vol, 11.05 biological effects and environmental fate; biotechnology; pesticides*. American Society for Testing and Materials, West Conshohocken, PA.

Attril, M.J., Stafford, R. and Rowden, A.A. (2001). Latitudinal diversity patterns in estuarine tidal flats: indications of a global cline. *Ecography* **24:** 318-324.

Austen, M.C. and Widdicombe, S. (1998) Experimental evidence of effects of the heart urchin *Brissopsis lyrifera* on associated subtidal meiobenthic nematode communities. *Journal of Experimental Marine Biology and Ecology* **222:** 219–238.

Auster, P.J. and Langton, R.W. (1999) The effects of fishing on fish habitat. *In:* Benaka, L. (ed) Fish habitat essential fish habitat (EFH) and rehabilitation. American Fisheries Society **22:** 150-187

Austin, M.P. and Smith, T.M. (1989). A new model for the contin-uum concept. *Vegetation* **83:** 35–47.

Austin, M.P., Nicholls, A.O. and Margules, C.R. (1990). Measurement of the realized qualitative niche: environmental niches of five Eucalyptus species. *Ecological Monographs* **60:** 161–177.

Awosika, L.F. and Ibe, A.C. (1998). Geomorphic features of the Gulf of Guinea shelf and littoral drift dynamics. In: Ibe, A.C.. Awosika L.F and Aka, K. (Eds.), *Nearshore dynamics and sedimentology of the Gulf of Guinea*, IOC/UNIDO, CEDA Press, Cotonou, pp. 21–27.

Bady, P., Doledec, S., Fesl, C., Gayraud, S., Bacchi,M., Scholl, F. (2005). Use of invertebrate traits for the biomonitoring of European large rivers: the effects of sampling effort on genus richness and functional diversity. *Freshwater Biology* **50:** 159–173.

Bagnold, R.A. (1963). Mechanics of marine sedimentation *In:* Hill, M.N. (ed.), *The Sea. The Earth Beneath the Sea*, Interscience Publication, pp. 507-582.

Bainbridge, V. (1972). The zooplankton of the Gulf of Guinea. *Bulletin of Marine Ecology* **8:** 61–97

Bakun, A. (1978). Guinea current upwelling. *Nature* **27:** 147-150.

Balmford, A., Bruner, A., Cooper, P., Costanza, R., Farber, S., Green, R.E., Jenkins, M., Jefferiss, P., Jessamy, V., Madden, J., Munro, K., Myers, N., Naeem, S., Paavola, J., Rayment, M., Rosendo, S., Roughgarden, J., Trumper, K. and Turner, R.K. (2002). Ecology – economic reasons for conserving wild nature. *Science* **297:** 950–953.

Balvanera, P., Pfisterer, A.B., Buchmann, N.,He, J.S., Nakashizuka, T., Raffaelli, D. and Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Annual Review of Ecology and Systematics* **9:** 1146–1156.

Bamber, R.N., Evans, N.J. and Robbins, R.S. (2008). The marine soft-sediment benthic communities of Hong Kong: a comparison of submarine cave and open habitats. *Journal of Natural History* **42(9-12):** 953-965.

Barker, S., Kiefer, T., and Elderfield, H. (2004). Temporal changes in North Atlantic circulation constrained by planktonic foraminiferal shell weights. *Paleoceanography* **19:** PA 3008.

Barnes, R. (1987). *Invertebrate Zoology*. Orlando, Florida: Dryden Press.

Barrett, N., Sanderson, J. C., Lawler, M., Halley, V. and Jordan, A. (2001). Mapping of inshore marine habitats in south eastern Tasmania for marine protected area planning and marine management. Technical Report. Tasmanian Aquaculture and Fisheries Institute: Hobart.

Barry, J.P. and Dayton, P.K. (1991). Physical heterogeneity and the organization of marine communities. In: Kolasa, J., Pickett, S.T.A. (Eds.), *Ecological heterogeneity*. Springer- Verlag, New York, pp. 270-320.

Beaman R.J. and Harris P.T. (2005). Bioregionalization of the George V Shelf, East Antarctica. *Continental Shelf Research* **25(14):** 1657-1691.

Beaman, R.J. and Harris, P.T. (2007). Geophysical variables as predictors of megabenthos assemblages from the northern Great Barrier Reef, Australia. *In:* Todd, B.J. and Greene, H.G., *Mapping the Seafloor for Habitat Characterization*, Geological Association of Canada. pp. 247-264.

Beesley, P.L., Ross, G.J. and Glasby, C.J. (2000). Polychaetes and Allies: The Southern synthesis. Fauna of Australia. Vol 4A Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. *CSIRO Publishing*. Melbourne. pp. 465

Begon, M., Harper, J.L., and Townsend, C.R. (1990). *Ecology: individuals, populations, and communities*. Blackwell Scientific Publications, London. pp. 876.

Begon, M., Harper, J.L. and Townsend, C.R. (1996). Ecology, Indiviiduals, Populations and Communities, Blackwell Science Ltd., Australia. pp. 958.

Bell, J.J. (2007). Contrasting patterns of species and functional composition of coral reef sponge assemblages. *Marine Ecology Progress Series* **339:** 73–81.

Bell, S.S and Woodin, S.A. (1984). Community unity: Experimental evidence for meiofauna and macrofauna. *Journal of Marine Research* **42:** 605-632.

Bellwood, D. R., Hughes, T. P., Connolly, S. R., and Tanner, J. (2005). Environmental and geometric constraints on Indo-Pacific coral reef biodiversity. *Ecology Letters* **8(6):** 643-651.

Bellwood, D.R., Hoey, A.S., Choat, H. (2003). Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters* **6:** 281-285.

Belyayev, G.M., Vinogradova, N.G., Levenshteyn, R.Y., Pasternak, F.P., Sokolva, M.N., Filtatova, Z.A., (1973). Distribution patterns of deep-water bottom fauna related to the idea of the biological structure of the ocean. *Oceanography* **13:** 114-121.

Benedetti-Cecchi, L. (2009). Environmental variability: analysis and ecological implications. *In:* Wahl. M. (ed), *Marine hard bottom communities; patterns, dynamics, diversity and changes.* Elsevier, Amsterdam. pp. 281-294.

Benedetti-Cecchi, L. (2001). Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. *Marine Ecology Progress Series* **215:** 79–92.

Bengtsson, J., Jones, H., Setala, H. (1997). The value of biodiversity. *Trends in Ecology and Evolution* **12:** 334-336.

Bergen, M., Weisberg, S., Smith, R., Cadien, D., Dalkey, A., Montagne, D., Stull, J., Velarde, R., Ranasinghe, J. (2001). Relationship between depth, sediment, latitude, and the structure of benthic infaunal assemblages on the mainland shelf of southern California. *Marine Biology* **138:** 637–647.

Biles, C.L., Paterson, D.M., Ford, R.B., Solan, M. and Raffaelli, D.G. (2002). Bioturbation, ecosystem functioning and community structure. *Hydrology and Earth System Sciences* **6(6):** 999-1005.

Bindoff, N., Willebrand, J., Artale, V., Cazenave, A., Gregory, J., Gulev, S., Hanawa, K., Le Quéré, C., Levitus, S., Nojiri, Y., Shum, C., Talley, L. And Unnikrishnan, A. (2007). Observations: Oceanic climate change and sea level. *In:* Solomon, S., Qin, D., Manning, M., Chen, Z.,Marquis, M., Averty, K.B., Tignor, M. and Miller, H.L. (eds.), *Climate Change 2007: The Physical Science Basis.* Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK and New York, NY, USA; Cambridge University Press. pp. 385-431.

Blake, J.A. and Hilbig, B. (1994). Dense infaunal assemblages on the continental slope off Cape Hatteras, North Carolina. *Deep Sea Research II* **41:** 875-900.

Blondel, J. (2003). Guilds or functional groups: does it matter? *Oikos* **100:** 223–231.

Boesch, D.F. (1973). Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. *Marine Biology* **21**: 226-244.

Bolam S.G., Fernandes T.F. and Huxham M. (2002). Diversity, biomass, and ecosystem processes in the marine benthos. *Ecology Monograph* **72:** 599–615.

Bonsdorff, E. and Blomqvist, E.M. (1993). Biotic coupling on shallow water soft-bottom-examples from the northern Baltic Sea. *Journal of Oceanography and Marine Biology* **31:** 153-176.

Bonsdorff, E. and Pearson, T.H. (1999). Variation in the sublittoral macrozoobenthos of the Baltic Sea along environmental gradients: a functional-group approach. *Australlia Journal Ecology* **24:** 312–326.

Bonsdorff, E. and Rosenberg, R. (2007). The impact of benthic macrofauna for nutrient fluxes from Baltic Sea sediment. *Ambio* **36(2):** 161-167.

Bordowskiy, O.K. (1965a). Source of organic matter in marine basins. *Marine Geology* **3**: 5-31.

Bordowskiy, O.K. (1965b). Accumulation of organic matter in bottom sediments. *Marine Geology* **3**: 33-82.

Borja, A., Franco, J., and Perez, V. (2000). A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Marine Pollution Bulletin* **40:** 1100–1114.

Borja, A., Eliot, M., Andersen, J.H., Cardoso, A.C., Carstensen, J., Fereira, J.G., Heiskanen, A.-S., Marques, J.C., Neto, J.M., Teixeira, H., Uusitalo, L., Uyara, M.C. and Zampoukas, N. (2013). Good Environmental Status of marine ecosystems: What is it and how do we know when we have atained it? *Marine Pollution Bulletin* **76:** 928 16-27.

Botta-Dukát, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *Journal of Vegetation Science* **16:** 533–540.

Bouncier, M. (1995). Long-term changes (1954 to 1982) in the benthic macrofauna under the combined effects of anthropogenic and climate action (example of one Mediterranean Bay). *Oceanologia Acta* **19**(1): 67-78.

Boudreau, P.R., Dickie, L.M. and Kerr, S.R. (1991). Body-size spectra of production and biomass as system-level indicators of ecological dynamics. *Journal of Theoretical Biology* **152:** 329–339.

Bouyoucos, G.J. (1934). The hydrometer method for making mechanical analysis of soil. *Soil Science* **38:** 335–343.

Bracken, M.E.S., Friberg, S.E., Gonzalez-Dorantes, C.A., and S.L. Williams. (2008). Functional consequences of realistic biodiversity changes in a marine ecosystem. *PNAS* **105(3):** 924-928.

Bradshaw, C., Veale, L.O. and Brand, A.R. (2002). The role of scallop-dredge disturbance in long-term changes in Irish Sea benthic communities: a re-analysis of an historical dataset. *Journal of Sea Research* **47:** 161-184.

Braeckman, U., Provoost, P., Moens, T., Soetaert, K., Middelburg, J.J., Vincx, M., and Vabaverbeke, J. (2011) Biological vs. Physical Mixing Effects on Benthic Food Web Dynamics. *PLoS ONE* **6(3):** e18078.

Brander, K.M. (2007). Global fish production and climate change. *Proceedings of National Academic Science USA* **104:** 19709-19714.

Bremner. J. (2005). Assessing ecological functioning in marine benthic communities. PhD Thesis. Department of Marine Science and Coastal Management, University of Newcastle upon Tyne. pp. 220.

Bremner J., Frid C.L.J., Rogers S.I. (2003a). Assessing marine ecosystem health: the long-term effects of fishing on functional biodiversity in North Sea benthos. *Aquatic Ecosystem Health Management* **6:** 131–137.

Bremner J., Rogers S.I., Frid C.L.J. (2003b). Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Marine Ecology Progress Series* **254:** 11–25.

Bremner, J., Frid, C. and Rogers, S.I. (2005). Biological traits of the North Sea benthos: does fishing affect benthic ecosystem function? *In:* Barnes, P.T. and Thomas, J.P. (eds), *Benthic habitats and the effects of fishing*. American Fisheries Society, Bethesda, MD, pp. 477–489.

Bremner, J., Rogers, S.I., and Frid, C.L.J. (2006). Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators* **6(3):** 609-622.

Bremner, J. (2008). Species' traits and ecological functioning in marine conservation and management. *Journal of Experimental Marine Biology and Ecology* **366:** 37-47.

Brind'Amour, A., Rouyer, A. and Martin, J. (2009). Functional gains of including non-commercial epibenthic taxa in coastal beam trawl surveys: a Note. *Continental Shelf Research* **29:** 1189-1194.

Broecker, W.S. and Peng, T.-H. (1982). Tracers in the Sea, Eldigio Press ed., Lamont Doherty Geological observatory, Palisades NY, pp. 690.

Bromley, R. (1990). *Trace fossils: Biology and Taphonomy*. London, UK: Unwin Hyman. pp. 280.

Brown, C.J., Hewer, A.J., Meadows, W.J., Limpenny, D.S., Cooper, K.M., Rees, H.L., and Vivian, C.M.G. (2001). Mapping of gravel biotopes and an examination of the factors controlling the distribution, type and diversity of their biological communities. Lowestoft, CEFAS.pp. 43.

Brusca, R. and Brusca, G. (2003). Invertebrates. Sunderland, Massachusetts: Sinauer Association Inc.pp. 936.

Buchanan, J.B., Sheader, M., and Kingston, P.F. (1978). Sources of variability in the benthic macrofauna off the South Northumberland coast, 1971-1976. *Journal of the Marine Biological Association of the UK* **58:** 191-209.

Burrows, M.T., Moore, J.J. and James, B. (2002). Spatial synchrony of population changes in rocky shore communities in Shetland. *Marine Ecology Progress Series* **240:** 39-48.

Butman, C.A. and Grassle, J.P. (1992). Active habitat selection by Capitella sp. I larvae. Two-choice experiments in still water and flume flows. *Journal of Marine Research* **50(4):** 669-715.

Calder, W.A. (1984). *Size, Function and Life History*. Harvard University Press, Cambridge, Massachusetts. pp. 431.

Calder, W.A. (2001). Ecological consequences of body size. *In:* eLS. John Wiley and Sons Ltd., Chichester. http://www.els.net (doi: 10.1038/npg.els.0003208).

Camargo, J.A., Alonso, A. and Salamanca, A. (2005). Nitrate toxicity to aquatic animals: a review with new data for freshwater invertebrates. *Chemosphere* **58:** 1255–1267.

Camargo, J.A., Alonso, A. (2006). Ecological and toxicological effects of inorganic nitrogen pollution in aquatic ecosystems: A global assessment. *Environmental International* **32:** 831–849.

Campbell, N.A. (1990). Biology (2nd edition). The Benjamin/Cummings Publishing Company, Redwood City (CA). pp. 1101.

Carney, R. S. (2005). Zonation of deep biota on continental margins. *Oceanography and Marine Biology- an Annual. Review* **43:** 211–278.

Carriker, M.R. (1967). Ecology of estuarine benthic invertebrates: a perspective. *In:* Lauff, G.H. (ed.), *Estuarine. American Association for Advancement Science Publication*, Washington DC No.83**.** pp. 442-487.

Cartes, J.E., Abello, P., Lloris, D., Carbonell, P.T., Maynou, F., and De Sola, L.G. (2002). Feeding guidles of western Mediterranean demersal fish and crustaceans: an analysis based on spring survey. *Scientia Marina* **66(2):** 209-220.

Convention on Biological Diversity (1992). Convention on Biological Diversity. http://www.cbd.int/.

Convention on Biological Diversity (2009). Scienti- Synthesis of the impacts of ocean acidification on marine biodiversity. Montreal, Technical Series No. 46. pp. 61.

Chapin, F.S., Autumn, K. and Pugnaire, F. (1993). Evolution of suites of traits in response to environmental-stress. *American Naturalist* **142:** S78–S92.

Chapin, F.S., Bret-Harte, M.S., Hobbie, S.E. and Zhong, H.L. (1996). Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science* **7:** 347–358.

Charvet, S., Statzner B., Usseglio-Polatera, P. and Dumont, B. (2000). Traits of benthic macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in Europe. *Freshwater Biology* **43:** 277– 296.

Cheng, S-Y. and Chen, J-C.(2002). Study on the oxyhemocyanin, deoxymocyanin, oxygen affinity and acid-base balance of Marsupenaeus japonicus following exposure yo combined elevated nitrite and nitrate. *Aquatic Toxicology* **61:** 181-193.

Chevenet, F., Doledec, S. and Chessel, D. (1994). A fuzzy coding approach for the analysis of long-term ecological data, *Freshwater Biology* **31:** 295–309.

Chıcharo, L., Chıcharo, M., Gaspar, M., Regala, J., Alves, F. (2002). Reburial time and indirect mortality of *Spisula solida* clams caused by dredging. *Fisheries Research 1379:* 1–11.

Chown S.L, Gaston K.J. and Robinson D. (2004). Macrophysiology: large-scale patterns in physiological traits and their ecological implications. *Functional Ecology* **18:** 159–167.

Clark, R.A. (2000). Long term changes in the North Sea ecosystem. Ph.D. Thesis. Department of Marine Science and Coastal Management, University of Newcastle upon Tyne. Newcastle upon Tyne. pp. 265.

Clarke, K.R. and Green, R.H (1988). Statistical design and analysis for 'biological effects' study. *Marine Ecology Progress Series* **46:** 213-226.

Clarke, K.R. and Ainsworth, M.(1993). A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* **92:** 205-219.

Clarke, K.R. and Warwick, R.M. (1994). Change in marine communities: an approach to statistical analysis and interpretation. *Natural Environmental Research Council*, Plymouth Marine Laboratory, UK. pp. 144.

Clarke, K.R. and Gorley. R.N. (2006). PRIMER v6: User manual/tutorial. PRIMER-E, Plymouth, UK.

Cloney, R.A., Young, C.M., and Svane, I. (2006). Phylum Chordata: Urochordata. *In*: Young, C.M., Atlas of Marine Invertebrate Larvae. *Elsevier*, Barcelona. pp. 565-594.

Clynick, B.G., Blockley, D. and Chapman, M.G. (2009). Anthropogenic changes in patterns of diversity on hard substrata: an overview. *In:* Wahl, M. (ed), *Marine hard bottom communities; patterns, dynamics, diversity and changes*. Elsevier, Amsterdam. pp. 247-256.

Cochrane, S.K.J., Connor, D.W., Nilsson, P., Mitchell, I., Reker, J., Franco, J., Valavanis, V., Moncheva, S., Ekebom, J., Nygaard, K., Serrao Santos, R., Naberhaus, I., Packeiser, T., van de Bund, W. and Cardoso, A.C (2010). Marine Strategy Framework Directive – Task Group 1 Report Biological Diversity. EUR 24337EN – *Joint Research Centre*, Luxembourg: Office for Official Publications of the European Communities: pp. 110.

Coleman, F.C. and Williams, S.L. (2002). Overexploiting marine ecosystem engineers: potential consequences for biodiversity. *Trends in Ecology and Evolution* **17:** 40-44.

Connell, J.H. (1975). Some mechanisms producing structure in natural communities: A model and evidence from field experiments. In: Cody, M.L., and Diamond, J.M. (eds.), *Ecology and evolution of communities. Massachusetts Belknap Press*. Cambridge, pp. 460–490.

Connell, J.H. (1978). Diversity in tropical rain forests and coral reefs. *Science* **199:** 1302-1303.

Cooley, S.R. and Doney, S.C. (2009). "Anticipating ocean acidification's economic consequences for commercial fisheries " *Environmental Research Letters* **4:** 1-8.

Cornwell., W.K. and Ackerly, D.D. (2009). Community assembly and shifts in the distribution of functional trait values across an environmental gradient in coastal California. *Ecological Monographs* **79:** 109-126.

Cosel, R.V. (2006). Taxonomy of tropical West Africa bivalves. VI. Remarks on Lucinidae (Mollusc, Bivalvia), with description of six new genera and eight new species. *ZOOSYSTEMA* **28(4):** 805-851.

Cosson, N., Sibuet, M. and Galeron, J. (1997). Community structure and spatial heterogeneity of the deep-sea macrofauna at three constrasing stations in the tropical northeast Atlantic. *Deep Sea Research* **144:** 247-269.

Costanza, R., d'Arge, R., de Groot, R.S., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R., Paruelo, J., Raskin, R., Sutton, P. and van den Belt, M. (1997). The value of the world's ecosystem services and natural capital. *Nature* **387:** 253-260.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R., Paruelo, J., Raskin, R., Sutton, P. and van den Belt, M. (1998). The value of ecosystem services: putting the issues in perspective. *Ecological Economics* **25(1)**: 67–72.

Costello, M.J. (2000). "The BioMar (Life) project: developing a system for the collection, storage, and dissemination of marine data for coastal management." *In:* Hiscock, K. and Peterborough,U.K, *Classification of benthic marine biotopes of the north-east Atlantic. Proceedings of a BioMar - Life workshop held in Cambridge 16-18 November 1994. Joint Nature Conservation Committee*. pp. 9-17.

Costello, M.J. (2000). A framework for an action plan on marine biodiversity in Ireland. Ecological Consultancy Services Ltd. (EcoServe). pp. 46.

Cox., C.B. and Moore., P.D. (2005). *Biogeography: an ecological and evolutionary approach.* Blackwell Publishing. pp.428.

Craig, R.S., Austen, M.C., Boucher, G., Heip, C., Hutchings, P.A., King, G.M., Koike, I., Lambshead, P.J.D. and Snelgrove, P. (2000). Global change and biodiversity linkages across the sediment water interface: Biodiversity above and below the surface of soils and sediments. *BioScience* **50(12):** 1108-1120.

Crame, J.A. (2000). Evolution of taxonomic diversity gradients in the marine realm: evidence from the composition of recent bivalve faunas. *Paleobiology* **26(2):** 188-214.

Cribb, T.H., Bray, R.A., Barker, S.C., Adlard, R.D., and Anderson, G.R. (1994). Ecology and diversity of digenean trematodes of reef and inshore fishes of Queensland. International *Journal for Parasitology* **24(6):** 851-860.

Crowe, T.P. and Russell, R. (2009). Functional and taxonomic perspectives of marine biodiversity: relevance to ecosystem processes. In: Wahl, M. (ed.), *Marine hard bottom communities: patterns, dynamics, diversity, change.* Elsevier, Amsterdam, pp. 375-390.

Crowe, T.P., Thompson, R.C., Bray, S., Hawkins, S.J. (2000). Impacts of anthropogenic stress on rocky intertidal communities. *Journal of Aquatic Ecosystem Stress and Recovery* **7(4):** 273-297.

Cummins, K.W. (1974). Structures and functions of stream ecosystems. *BioScience* **24:** 631-641.

Cummins, K.W., Merritt, R.W. and Andeade, P.C.N. (2005). The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. *Studies on Neotropical Fauna and Environment* **40(1):** 69–89.

Currie, D.J. (1991). Energy and large scale patterns of animal- and plant-species richness. *American Naturalist* **137:** 27–49.

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegan, J.F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T. Oberdorff, T., O'Brien, E. and Turner, J.R.G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecological Letters* **7:** 1121–1134.

Currie, D.R., and Parry, G.D (1996). Effects of scallop dredging on a soft sediment community: a large scale experimental study. *Marine Ecology Progress Series* **134:** 131-150.

Cury, P. and Roy, C. (2002). Environmental forcing and fisheries resources in Cote d'Ivoire and Ghana: did something happen? *In:* MacGlade J.M., Cury, P., Koranteng, K.A. and Hardman-Mountford, N.J. (eds.). *The Gulf of Guinea large marine ecosystem: environmental forcing and sustainable development of marine resources*. Amsterdam: Elsevier Science, pp. 241-260.

Dampare, S.B., Nyarko, B.J.B., Osae, S., Akaho, E.H.K., Asiedu, D.K., Serfor-Armah, Y. and Nude, P. (2005). Simultaneous determination of tantalum, niobium, thorium and uranium in placer columbite–tantalite deposits from the Akim Oda District of Ghana by epithermal instrumental neutron activation analysis. *Journal of Radioanalytical and Nuclear Chemistry* **265(1):** 53-59.

Danielsen, F, Sorensen, M.K., Olwig, M.F., Selvam, V., Parish, F., Burgess, N.D., Hiralshi, T., Karunagaran, V.M., Rasmussen, M.S., Hansen, L.B., Quarto, A. and Suryadiputra, N. (2005). The Asian Tsunami: a protective role for coastal vegetation. *Science* **310:** 643.

Danovaro, R., Fabiano, M., and Della Croce, N. 1993. Labile organic matter and microbial biomasses in deep-sea sediments (Eastern Mediterranean Sea). *Deep-sea Research I,* **40(5):** 953- 965.

Danovaro, R., Della Croce, N., Eleftheriou, A., Fabiano, M., Papadopoulou, N., Smith, C., Tselepides, A. (1995). Meiofauna of the deep Eastern Mediterranean Sea: distribution and abundance in relation to bacterial biomass, organic matter composition and other environmental factors. *Progress in Oceanography* **36:** 329-341.

Danovaro, R., Dell'Anno, A. and Fabiano, M. (2001). Bioavailability of organic matter in the sediments of the Porcupine Abyssal Plain, northeasetrn Atlantic. *Marine Ecology Progress Series* **220:** 25-32.

Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldes, C., Fraschetti, S., Vanreusel, A., Vincx, M., and Gooday, A. (2008). Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. *Current Biology* **18:** 1-8.

Dauwe, B.J., Middleburg, J.J., Herman, P.M.J. and Heip, C.H.R. (1999). Linking diagenetic alteration of amino acids and bulk organic matter reactivity. *Limnology and Oceanography* **44(7):** 1809-1814.

Davies, K.F., Margules, C.R. and Lawrence, K.F. (2000). Which traits of species predict population declines in experimental forest fragments? *Ecology* **81:** 1450–1461.

Day, J.H. (1967a). A monograph on the Polychaeta of Southern Africa. Part 1 Errantia, Trustees of the British Museum London. pp. 458.

Day, J.H. (1967b). A monograph on the Polychaeta of Southern Africa. Part II Sedentaria, Trustees of the British Museum London. pp. 877.

Day., J.H., Field., J.G and Montgomery., M.P. (1971). The use of numerical methods to determine the distribution of the benthic fauna across the continental shelf of North Carolina. *Journal of Animal Ecology* **40:** 93-126.

Dayton, P.K., Thrush, S.F., Agardy, M.T., Hofman, R.J (1995). Environmental effects of marine fishing. *Aquatic Conservation* **5:** 205–232.

de Bello, F., Lepsˇ, J. and Sebastia, M.T. (2006). Variations in species and functional plant diversity along climatic and grazing gradients. *Ecography* **29:** 801-810.

de Bello, F., Lavergne, S., Meynard, C.N., Lepsˇ, J. and Thuiller,W. (2010). The partitioning of diversity: showing theseus a way out of the labyrinth. *Journal of Vegetation Science* **21:** 992–1000.

de Groot, S. and Lindeboom. H. (1994). Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. Netherlands Institute for Sea Research, Den Burg, Texel, The Netherlands: Netherlands Institute for Sea Research (NIOZ). pp. 257.

de Juan, Thrush, S.F. and Demestre, M. (2007). Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea), *Marine Ecology Progress Series* **334:** 117–129.

de Vaugelas, J. and Buscail, R., (1990). Organic matter distribution in burrows of the thalassinid crustacean Callichirus laurae, Gulf of Aqaba (Red Sea). *Hydrobiologia* **207:** 269 – 277.

Degraer, S., Verfaillie, E., Willems, W., Adriaens, E., Vincx, M., & Van Lancker, V. (2008). Habitat suitability modelling as a mapping tool for macrobenthic communities: An example from the Belgian part of the North Sea. *Continental Shelf Research* **28(3):** 369-379.

Dell'Anno, A., Mei, M.E., Pusceddu, A. and Danovaro, R. (2002). Assessing the trophic state and eutrophication of coastal marine systems: a new approach based on the biochemical composition of sediment organic matter. *Marine Pollution Bulletin* **44:** 611–622.

Denny, M.W. (1993). *Air and water: the biology and physics of life's media*. Princeton University Press, Princeton, N.J. pp. 341.

Derous, S., Agardy, T., Hillewaert, H., Hostens, K., Jamieson, G., Lieberknecht, L., Mees, J., Moulaert, I., Olenin, S., Paelinckx, D., Rabaut, M., Rachor, E., Roff, J., Stienen, E.W. M., van der Wal, J. T., Van Lancker, V., Verfaillie, E., Vincx, M.,Weslawski, J. M., Degraer, S. (2007). A concept for biological valuation in the marine environment, *Oceanologia* **49(1):** 99–128.

Dether, M. N. (1984). "Disturbance and recovery in intertidal pools: maintenance of mosaic patterns" *Ecological Monograph* **54:** 99-118.

Díaz, S., Cabido, M. and Casanoves, F. (1999). Functional implications of trait-environment linkages in plant communities. *In:* Weiher, E. and Keddy, P. (eds.), *Ecological assembly rules, perspective, advances and retreats*. Cambridge University Press. UK. pp. 338-362.

Díaz, S. and Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* **16:** 646–655.

Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., Montserrat-Martí, G., Grime, J.P., Zarrinkamar, F., Asri, Y., Band, S.R., Basconcelo, S., Castro-Diez, P., Funes, G., Hamzehee, B., Khoshnevi, M., Pérez-Harguindeguy, N., Pérez-Rontomé, M.C., Shirvany, F.A.,Vendramini, F.,Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S., Charles, M., Dehghan, M., De Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A., Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martínez, M., Romo-Díez, A., Shaw, S., Siavash, B., Villar-Salvador, P. and Zak, M.R. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* **15:** 295–304.

Dimitriadis, C. and Koutsoubas, D.(2011). "Functional diversity and species turnover of benthic invertebrates along a local environmental gradient induced by an aquaculture unit: the contribution of species dispersal ability and rarity," *Hydrobiological* **670:** 307–315.

Dissard, D., Nehrke, G., Reichart, G.J. and Bijma, J. (2010). Impact of seawater *p*CO2 on calcification and Mg/Ca and Sr/Ca ratios in benthic foraminifera calcite: results from culturing experiments with *Ammonia tepida*. *Biogeoscience* **7:** 81-93.

Dittmann, S. (1995). Benthos structure on tropical tidal flats of Australia. *Helgoländer Meeresunters* **49:** 539-551.

Drabsch, S.L., Tanner, J.E., and Comell, S.D. (2001). Limited infaunal response to experimental trawling in previously untrawled areas. *Journal of Marine Sciences* **58:** 1261-1271.

Duffy, J.E., McDonald, S.K., Rhode J.M. and Parker J.D. (2001). Grazer diversity, functional redundancy, and productivity in seagress beds: an experimental test. *Ecology* **82:** 2417–2434.

Duffy, J.E. and Stachowicz, J.J. (2006). Why biodiversity is important to oceanography: potential roles of genetic, species, and trophic diversity in pelagic ecosystem processes. *Marine Ecology Progress Series* **311:** 179-189.

Dulvy, N.K., Sadovy, Y. and Reynolds, J.D. (2003). Extinction vulnerability in marine populations. *Fish and Fisheries* **4:** 25-64.

Dundas, K. and Przeslawski, R. (2009). Deep-sea Lebensspuren: Biological features on the seafloor of the eastern and western Australian margin. *Geoscience Australia Record* 26. pp. 76.

Duplisea, D.E, Jennings, S., Warr, K.J., Dinmore, T.A. (2002). A size-based model of the impacts of bottom trawling on benthic community structure. *Canadian Journal of Fisheries Aquatic Sciences* **59:** 1785–1795.

Dye, A.H. (2006). Is geomorphic zonation a useful predictor of patterns of benthic infauna in intermittent estuaries in New South Wales, Australia? *Estuaries and Coasts* **29(3):** 455-464.

Edgar, G.J. (2001). *Australian Marine Habitats*. Sydney: Reed New Holland Publishers Australia Pty Ltd. pp. 624.

Edmunds, J. (1978). *Sea shells and other molluscs found on West African shores and estuaries*. Ghana University Press. pp. 144.

Edwards P. and Abivardi, C. (1998). The value of Biodiversity: Where Ecology and Economy Blend. *Biological Conservation* **83:** 238-246.

Eleftheriou, A. and Holme, N.A. (1984). Macrofauna techniques. p. 140-216. *In:* Holm N.A. and McIntyre, A.D. (eds.), *Methods for the study of marine benthos*. Blackwell Scientific Publications, pp. 387.

Ellingsen, K.E., Clarke, K.R., Somerfield, P.J., and Warwick, R.M. (2005). Taxonomic distinctness as a measure of diversity applied over a large scale: the benthos of the Norwegian continental shelf. *Journal of Animal Ecology* **74(6):** 1069-1079.

Elliott, M. and Quintino, V. (2007). The estuarine quality paradox: environmental homeostasis and the difficulty of detecting anthropogenic stress in naturally stressed areas. *Marine Pollution Bulletin* **54:** 640–645.

Emmerson, M.C. and Raffaelli, D.G. (2000). Detecting the effects of diversity on measures of ecosystem functioning: experimental design, null models and empirical observations. *Oikos* **91:**195–203.

Emmerson, M.C., Solan, M., Emes, C., Paterson, D.M., Raffaelli, D.G. (2001). Consistent patterns and the idiosyncratic effects of biodiversity in marine ecosystems. *Nature* **411:** 73–77.

Enticknap,B. (2002). Understanding the effects of bottom trawl fisheries on Alaska's living seafloor. Unpublished Report. *Alaska Marine Conservation Council*. pp. 22.

Estacio, F.J., Garcia-Adiego, E.M., Carballo, J.L., Sanchez-Noyano, J.E., Izquierdo, J.J. and Garcia-Gomez, J.C. (1999). Interpreting temporal disturbances in an estuarine benthic community under combined anthropogenic and climate effects. *Journal of Coastal Research* **15(1):** 155-167.

Etter, R.J. and Mullineaux, L.S. (2001). Deep sea communities. *In*: M. D. Bertness, S. D. Gaines, & M. E. Hay, *Marine Community Ecology*. Sunderland MA: Sinauer. pp. 367-393.

European Commission (2008). Marine Strategy Framework Directive – TG. Directive 2008/56/EC of the European parliament and of the Council.

Fabry, V.J., Seibel, B.A., Freely, R.A. and Orr, J.C. (2008). Impacts of ocean acidification on marine fauna and ecosystem processes, ICES Journal of Marine Science **65:** 414-432.

Faith. D.P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation* **61:** 1-10.

Faith. D.P. (2011). Higher-level targets for ecosystem services and biodiversity should focus on regional capacity for effective trade-offs. *Diversity* **3:** 1-7.

FAO. (2006). *The state of world highly migratory, straddling and other high seas fishery resources and associated species*, by Maguire, J.-J., Sissenwine, M., Csirke, J., Grainger, R. and Garcia, S. FAO Fisheries technical Paper No. 495. pp. 67.

Fauchald, K. 1977. The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series* **28:** 1-188.

Fauchald, K. and Jumars, P. (1979). The diet of worms: a study of polychaete feeding guilds. *Oceanography Marine Biology Annual Review* **17:** 193-284.

Feely, R.A., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J., Fabry, V.J., Millero, F.J. (2004). Impact of anthropogenic CO_2 on the $CaCO_3$ system in the oceans. *Science* **305:** 362-365.

Ferguson, J.E., Henderson, G.M., Kucera, M. and Rickaby, R.E.M. (2008). Systematic change of foraminiferal Mg/Ca ratios across a strong salinity gradient. *Earth and Planetary Science Letters* **265:** 153–166.

Ferreira, J.G., Andersen, J.H., Borja, A., Bricker, S.B., Camp, J., Cardoso da Silva, M., Garcés, E., Heiskanen, A.S., Humborg, C., Ignatiades, L., Lancelot, C., Menesguen, A., Tett, P., Hoepffner, N. and Claussen, U. (2010). Marine Strategy Framework Directive-Task Group 5 Report Eutrophication. EUR 24338 EN Joint Research Centre. Office for Official Publications of the European Communities, Luxembourg. pp. 49.

Field, J.G. (1971). "A numerical analysis of changes in the soft-bottom fauna along a transect across False Bay, South Africa," *Journal of Experimental Marine Biology and Ecology* **7:** 215-253.

Field, C.B., Chapin, F.S., Matson, P.A., Mooney, H.A., (1992). Responses of terrestrial ecosystems to the changing atmosphere – a resource-based approach. *Annual Review of Ecology and Systematics* **23:** 201–235.

Fleddum, A.L. (2010). Effects of human disturbance on bilogical traits and structure of macrobenthic communities. *PhD Thesis*, City University of Hong Kong. pp.451.

Flint, R.W. and Kalke, R.D. (1986). Biological enhancement of estuarine benthic community structure. *Marine Ecology Progress Series* **31:** 23-33.

Floeter, S.R, Ferreira, C.E.L., Dominici-Arosemena, A., Zalmon, I.R. (2004). Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. *Journal Fish Biology* **64:** 1680–1699.

Foote, M. (1997). Sampling, taxonomic description, and our evolving knowledge of morphological diversity. *Paleobiology* **23:** 181–206.

Fortin, M. J., Keitt, T. H., Maurer, B. A., Taper, M. L., Kaufman, D. M., & Blackburn, T. M. (2005). Species' geographic ranges and distributional limits: pattern analysis and statistical issues. *Oikos* **108(1):** 7-17.

Foster, M.S. (2001). Rhodoliths: Between rocks and soft places. *Journal of Phycology* **37(5):** 659-667.

François, F., Poggiale, J-C., Durbec, J-P. and Stora, G. (1997). A new approach for the modelling of sediment reworking induced by a macrobenthic community. *Acta Biotheoritica* **45:** 295-319.

Franklin, J. (1995). Predictive vegetation mapping:Geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography* **19(4):** 474- 499.

Franzen, D. 2004. Plant species coexistence and dispersion of seed traits in a grassland. *Ecography* **27:** 218–224.

Fraschetti, S., Terlizzi, A. and Benedetti-Cecchi, L. (2005). Patterns of distribution of marine assemblages from rocky shores: eveidence of relevant scales of variation. *Marine Ecological Progress Series* **296:** 13-29.

Freckman, D.W., Blackburn, T.H., Bussaard, L., Hutchings, P., Palmer, M.A., Snelgrove, P.V.R., (1997). Linking biodiversity and ecosystem functioning of soils and sediments. *Ambio* **26:** 556-562.

Fretwell, S.D. (1987). Food chain dynamics: The central theory of ecology. *Oikos* ***50*****:** 291–301.

Frid, C. and Hall, S. (2001). Ecological quality objectives for benthic communities: If we protect the habitat do we need to do more? CM 2001/T:06. Theme session: Use and information content of ecosystem metrics and reference points. pp. 15.

Gaertner, J.C., Bertrand, J.A., Gil de Sola, L., Durbec, J.P., Ferrandis, E. and Souplet. A. (2005). Large spatial scale variation of demersal fish assemblage structure on the continental shelf of the NW Mediterranean Sea. *Marine Ecology Progress Series* **297:** 245-257.

Gage, J.D. and Tyler, P.A. (1991). *Deep-sea Biology: A Natural History of Organisms at the Deep-Sea Floor*. Cambridge University Press, Cambridge. pp. 504.

Galgani, F., Fleet, D., van Franeker J., Katsanevakis, S., Maes, T., Mouat, J., Oosterbaan, L., Poitou, I., Hanke, G., Thompson, R., Amato, E., Birkun, A., Janssen, C. (2010). Marine Strategy Framework Directive–Task Group Report Marine litter. EUR 24340 EN –*Joint Research Centre*, Luxembourg: Office for Official Publications of the European Communities. pp. 48.

Galy, V., Bouchez, J. and France-Lanord, C. (2007). Determination of total organic carbon content and delta C-13 in carbonate-rich detrital sediments. *Geostandards and Geoanalytical Research* **31(3):** 199-207.

Garnier, E., Cortez, J., Billès, G., Navas, M-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J-P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology* **85(9):** 2630–2637.

Gaston, G.R. (1987). Benthic polychaete of the middle Atlantic Bight: feeding and distribution. *Marine Ecology Progress Series* **36:** 251-262.

Gaston, G., Lee, D.A. and Nasci, J.C. (1988). Estuarine macrobenthos in Calcasieu Lake, Louisiana: community and trophic structure. *Estuaries* **11:** 192-200.

Gaston, K.J. (2000). Global patterns in biodiversity. *Nature* **405:** 220-227.

GCLME (2006). *Transbounday Diagonistic Analysis*: a programme of the goverments of the GCLME countries. GCLME regional coordinating unit, Accra, Ghana. pp. 175.

Gerino, M., Stora, G., François-Carcaillet, F., Gilbert, F., Poggiale, J.C., Mermillod-Blondin, F., Desrosiers, G. and Vervier, P. (2003). Macro-invertebrate functional groups in freshwater and marine sediments: a common mechanistic classification. *Vie et Milieu* **53(4):** 221–231.

Giller, P.S., Hillebrand, H., Berninger, UG., Gessner, M.O., Hawkins, S., Inchausti, P., Inglis, C., Leslie, H., Malmqvist, B., Monaghan, M.T., Morin, P.J., and O'Mullan, G. (2004). Biodiversity effects on ecosystem functioning: emerging issues and their experimenter test in aquatic environments. *Oikos* **104:** 423-436.

Gitay, H. and Noble, I.R. (1997). What are functional types and how should we seek them? *In:* Smith, T.M., Shugart, H.H. and Woodward, F.I. (eds.), *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*, Cambridge University Press, UK. pp. 3–19.

Gogina, M., Glockzin, M., Zettler, M.L. (2010). Distribution of benchi macrofaunal communities in the western Galtic Sea with regard to near-bottom environmental parameters. Causal analysis. *Journal of Marine Systems* **79:** 112-123.

Golterman, H.L. (1996). Fractionation of sediment phosphate with chelating compounds: a simplification, and comparison with other methods. *Hydrobiologia* **335:** 87-95.

Gon, O. and Heemstra, P.C. (Eds). (1990). *Fishes of the Southern Ocean*. Smith, J.L.B. Institute of Ichthyology, Graham. pp. 462.

Grassle, J.P and Grassle, J.F., (1976). Sibling species in the marine pollution indicator *Capitella* (Polychaeta). *Science* **192:** 567-569.

Grassle, J.F., Grassle, J.P., Brown-Leger, L.S., Petrecca, R.F. and Copley, N.J. (1985). Subtidal macrobenthos of Narragansett bay. Field and mesocosm stuides of the effects of eutrophication and arganic input on benthic populations. *In:* Gray, J.S. and Christiansen, M.E. (eds.), *Marine biology of Polar Regions and effects of stress on marine organisms.* Proceedings of the 18th European Marine Biology Symposium, Chichester, England, John Wiley, pp. 421-434.

Gray, J.S. (1981). *The ecology of marine sediments: an introduction to the structure and function of benthic communities*. Cambridge University Press, Cambridge. pp. 185.

Gray, J.S (1989). Effects of environmental stress on species-rich assemblages. *Biological Journal of Linnaeus Society* **37:** 19–32.

Gray, J.S. (1997). Marine biodiversity: patterns, threats, and conservation needs. *Biodiversity Conservation* **6:** 153-175.

Gray, J.S. (2001). Marine diversity: the paradigms in patterns of species richness examined. *Scientia Marina* **65:** 41-56.

Gray, J.S. (2002). Species richness of marine soft sediments. *Marine Ecology Progress Series* **244:** 285-297.

Gray, J.S., Dayton, P.K., Thrush, S.F. and Kaiser, M.H. (2006). On effects of trawling benthos and sampling design. *Marine Pollution Bulletin* **52:** 840-843.

Grime J.P., Hodgson, J.G. and Hunt, R. (1988). *Comparative plant ecology: a functional approach to common British species.* Unwin Hyman, London.

Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F. Ashenden, T.W., Askew, A.P., Band, S.R., Booth, R.E., Bossard, C.C., Campbel, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, W., Hands, D.W., Hannahs, M.A., Hillier, S.H., Hodkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reiling, K., Ross-Fraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C., Whitehouse. J. (1997). Integrated screening validates primary axes of specialisation in plants. *Oikos* **79:** 259-281.

Grime, J.P. (2001). *Plant strategies, vegetation processes and ecosystem properties.* John Wiley and Sons, Chichester. pp. 417.

Grime J.P. (2006). Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* **17:** 255–260.

Grotkopp, E., Rejmanek, M, and Rost, T.L. (2002). Toward a causal explanation of plant invasiveness: seedling growth and lifehistory strategies of 29 pine (Pinus) species. *American Naturalist* **159:** 396–419.

Guille, A. (1970). Benthic bionomy of continental shelf of the French Catalane Coast.II. Benthic communities of the macrofauna. *Vie et Milieu* **218:** 149–280.

Hagberg, J. and Tunberg, B.G. (2000). Studies on the co-variation between physical factors and the long-term variation of the marine soft-bottom macrofauna in Western Sweden. *Estuarine, Coastal and Shelf Science* **50:** 373-385.

Hall, S.L. (1994). Physical disturbance and marine benthic communities: Life in unconsolidated sediments. *Oceanography and Marine Biology, Annual Reviews* **32:** 179-239.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Argosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fuijita, R., Heinemann, D., Lenihan, H.

S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. and Watson, R. (2008). A global map of human impact on marine ecosystems. *Science* **319:** 948-952.

Hamerlynck, O., Hostens, K., Arellano, R.V., Mees, J. and Van Damme, P.A. (1993). The mobile epibenthic fauna of soft bottoms in the Dutch Delta (south-west Netherlands); spatial structure. *Netherlands Journal of Aquatic Ecology* **27:** 343–358.

Hamilton, M.A., Murray, BR, Cadotte, M.W, Hose, G.C., Baker, A.C., Harris, C.J., Licari, D. (2005). Life-history correlates of plant invasiveness at regional and continental scales. *Ecology Letters* **8:** 1066–1074.

Harper, J.L. and Hawksworth D.L. (1994). Biodiversity: measurement and estimation. Preface. *Philosophical Transactions of the Royal Society, London* **345:** 5–12.

Harris, P.T., Heap, A.D., Whiteway, T. and Post, A. (2008). Application of biophysical information to support Australia's representative marine protected area program. *Ocean and Coastal Management* **51:** 701-711.

Hart, D.E. and Kench, P.S. (2007). Carbonate production of an emergent reef platform, Warraber Island, Torres Strait, Australia. *Coral Reefs* **26:** 53-68.

Hastings, A., Byers, J.E., Crooks, J.A., Cuddington,K., Jones, C.G., Lambrinos,J.G., Tally, T.S., Wilson W.G. (2007). Ecosystem engineering in space and time. *Ecology Letters* **10:** 153-164.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E and Turner, J.R.G. (2003a). Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84:** 3105–3117.

Henin, C., Hisard, P. and Piton, B. (1986). Observations hydrologiques dans I' Ocean Atlantique Equitorial. *ORSTOM FOCAL* **1:** 1-191.

Hessle, R.R. and Sanders, H.L. (1967). Faunal diversity in the deep sea. *Deep Sea Research* **14**: 65-78.

Hewitt, J.E., Thrush, S.F. and Dayton, P.D. (2008). Habitat variation, species diversity and ecological functioning in a marine system, *Journal of Experimental Marine Biology and Ecology* **366:** 116–122.

Hewitt, C.L. and Campbell, M.L (2007). Mechaisms for the prevention of marine bio-invasions for better biosecurity. *Marine Pollution Bulletin* **55:** 395-401.

Hey, J. (2001). The mind of the species problem. *Trends in Ecology and Evolution* **16(7):** 326-329.

Hiddink, J.G., Jennings, S., Kaiser, M.J., Queirós, A.M., Duplisea, D.E. and Piet, G.J. (2006). Cumulative impacts of seabed trawl disturbance on benthic biomass, production and species richness in different habitats. *Canadian Journal of Fisheries and Aquatic Sciences* **63:** 721–736.

Hiddink, J.G., Jennings, S., Kaiser, M.J. (2007). Assessing and predicting the relative ecological impacts of disturbance on habitats with different sensitivities. *Journal of Applied Ecology* **44:** 405-413.

Hiddink, J.G., Davies, T.W., Perkins, M., Machairopoulou, M. and Neill. S.P. (2009). Context dependency of relationships between biodiversity and ecosystem functioning is different for multiple ecosystem functions. *Oikos* **118:** 1892–1900.

Hillebrand, H., Gruner, D.S., Borer, E.T., Bracken, M.E.S., Cleland, E.E., Elser, J.J., Harpole, W.S., Ngai, J.T., Seabloom, E.W. Shurin, J.B. and Smith, J.E. (2007). Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences of the USA* **104:** 10904–10909.

Hodson, R.G., Hackman, J.O. and Bennett, C.R. (1981). Food habits of young spots in nursery areas of the Cape Fear River Estuary, North Carolina. *Transactions of the American Fishery Society* **110:** 495-501.

Hofmann, G.E., O'Donnell, M.J. and Todgham, A.E. (2008). Using functional genomics to explore the effects of ocean acidificiation on calcifying marine organisms. *Marine Ecological Progress Series* **373:** 219-225.

Hölker, F., Dörner, H., Schulze, T., Haertel-Borer, S.S., Peacor, S.D. and Mehner, T. (2007). Species-specific responses of planktivorous fish to the introduction of a new piscivore: implications for prey fitness. *Freshwater Biology* **52:** 1793–1806.

Holme, N.A. and A.D. McIntyre (1971). *Methods for the study of marine benthos*. IBP Handbook No. 16 Blackwell, Oxford, U.K. pp. 334.

Holmes-Farley, R. (2003). Aquarium chemistry: magnesium in reef aquaria. *Advanced Aquarist Online Article. http://www.advancedaquarist.com/2003/10/chemistry.*

Holmes, S.P., Miller, N. and Weber, A. (2002). The respiration and hypoxic tolerance of *Nucula nitidosa* and *N. nucleus*: factors responsible for determining their distribution. *Journal of the Marine Biological Association of the United Kingdom* **82:** 971-981.

Holmlund, C.M. and Hammer, M. (1999). Ecosystem services generated by fish populations. *Ecological Economics* **29:** 253-268.

Holst, G. and Grunwald, B. (2001). Luminescence lifetime imaging with transparent oxygen optodes. *Sensors Actuators B* **74:** 78–90.

Hondorp, W., Breitburg, D.L. and Davias, L.A. (2010). Eutrophication and Fisheries: separating the effects of nitrogen loads and hypoxia on the pelagic-to-demersal ratio and other measures of landing composition. *Marine and Coastal Fisheries: Dynamics, Management and Ecosystem Science* **2:** 339-361.

Hooper, D.U. and Vitousek, P.M. (1998). Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* **68:** 121–149.

Hooper, D.U., Solan, M., Symstad, A., Diaz, S., Gessner, M.O., Buchman, N., Degrange, V., Grime, P., Hulot, F., Mermillod-Blondin, F., Roy, J., Spehn, E., and van Peer, L. (2002). Species diversity, functional diversity, and ecosystem functioning. *In:* Loreau, M., Naeem, S.and Inchausti, P. (eds.), *Biodiversity and Ecosystem Functioning. Synthesis and Perspectives*, Oxford University Press. pp. 95–208.

Hooper, D.U., Chapin, F.S. III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J. and Wardle, D.A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75:** 3-35.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulik, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., and. Connor. M.I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486:** 105–108.

Huettel, M. and Gust, G. (1992). Impact of bioroughness on interfacial solute exchange in permeable sediments. *Marine Ecology Progress Series* **89:** 253–267.

Hughes, J.B., Daily, G.C. and Ehrlich, P.R. (1997). Population diversity: its extent and extinction. *Science* **278:** 689–692.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nyström, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B. and Roughgarden. J. (2003). Climate change, human impacts, and the resilience of coral reefs. *Science* **301:** 929-933.

Hunt, B. and Vincent, A.C.J (2006). Scale and sustainability of marine bioprospecting for pharmaceuticals. *Ambio* **35:** 57-64.

Hurlbert, S.H. (1971). The non-concept of species diversity: a critique and alternative parameters. *Ecology* **52:** 577–586.

Hurlbert, S.H. (1984). Pseudoreplication and the design of ecological field experiments. *Ecological Monograph* **54:** 187-211.

Hutchison, M.J., John, E.A and Wijesinghe, D.K. (2003). Towards understanding the consequences of soil heterogeneity for plant populations and communities. *Ecology* **84:** 2322-2334.

Ieno, E.N., Solan, M., Batty, P. and Pierce. G.J. (2006). How biodiversity affects ecosystem functioning: roles of infaunal species richness, identity and density in the marine benthos. *Marine Ecology Progress Series* **311:** 263–271.

IOC (2013). IOC-IUCN-NOAA consultative committee meeting on Large Marine Ecosystems (LMEs). Intergovernmental Oceanographic Commission report on meetings of experts and equivalent bodies, 15th Annual Session, Paris France. pp. 36.

Inoue, T., Suda, Y., and Sano, M. (2008). Surf zone fishes in an exposed sandy beach at Sanrimatsubara, Japan: does fish assemblage structure differ among microhabitats? *Estuarine and Coastal Shelf Science* **77:** 1-11.

Intes, A. and Lœuff, P. (1984). Polychaeta of Ivory Coast III. Faunstic/Climatic relationship, regional units in the Gulf of Guinea. *Journal of Tropical Oceanography* **19(1):** 3-24.

Iverson, L.R. and Prasad, A.M. (2001). Potential changes in tree species richness and forest community types following climate change. *Ecosystems* **4:** 186–199.

Jackson, A.C. and Chapman, M.G. (2009). Changing biodiversity: introduction. *In:* Wahl. M. (ed), *Marine hard bottom communities; patterns, dynamics, diversity and changes*, Ecological Studies 206. pp. 241-245.

Jackson, J.B.C. (2001) .What was natural in the coastal oceans? *Proc Natl Acad Sci.*, USA **98:** 5411–5418.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W.,Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., PandoLfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J. and Warner, R.R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293:** 629–637.

Jackson J.B.C. (2008). Shifting baselines, local impacts and global change on coral reefs.*PLos Biology*, **6(2):** e54.

Jax, K. (2005), "Function and 'functioning' in ecology: what does it mean?" *Oikos* **111(3):** 641–648.

Jennings, S. and Kaiser, M.J. (1998) .The effects of fishing on marine ecosystems. *Advances in Marine Biology* **34:** 201–352.

Jennings, S., Pinnegar, J.K., Polunin, N.V.C., Warr, K.J. (2001). Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Marine Ecology Progress Series* **213:** 127–142.

Jensen, F.B. (1996). Uptake, elimination and effects of nitrite and nitrate in freshwater crayfish (Astacus astacus). *Aquatic Toxicology* **34:** 95-104

Jiang, L., Zhichao, P.U. and Diana, R. (2008). On the importance of the negative selection effects for the relationship between biodiversity and ecosystem functioning. *Oikos* **117(4):** 488-493.

Jie, H., Zhinan, Z, Zishan, Y. and Widdows, J. (2001). Differences in the benthic-pelagic particle flux (biodeposition and sediment erosion) at intertidal sites with and without clam cultivation in eastern China. *Journal of Experimental Marine Biology and Ecology*. pp. 245-261.

Jones, N.S. (1950). Marine bottom communities. *Biological Reviews of the Cambridge Philosophical Society* **25(3):** 283-313.

Jorcin, A. (1996). Distribucion, abundancia y biomasa de Erodona mactroides DAUDIN (Mollusca, Bivalvia), en la Laguna de Rocha (Dpto. De Rocha, Uruguay). *Revista Brasileiro de Biologia* **56:** 155-162.

Jørgensen, L.L, Renaud, P.E., Sabine K.J. and Cochrane, S.K.J. (2011). Improving benthic monitoring by combining trawl and grab surveys. *Marine Pollution Bulletin* **62(6):** 1183-1190.

Josefson, A.B. and Rasmussen, B. (2000). Nutrient retention by benthic macrofaunal biomass of Danish estuaries: importance of nutrient load and residence time. *Estuaries Coastal Shelf Science* **50:** 205-216.

Jumars, P.A., Mayer, L.M., Deming, J.W., Baross, J.A and Wheatcroft, R.A. (1990). Deep-sea deposit-feeding strategies suggested by environmental and feeding constraints. *Philosophical Transactions of the Royal Society of London*. Series A **331:** 85-101.

Kaiser, M.J., Rogers, S. I. and McCandless, D.T. (1994). Improving quantitative surveys of epibenthic communities using a modified 2 m beam trawl. *Marine Ecology Progress Series* **106:** 131-138.

Kaiser, M.J. and Spencer. B.E. (1996).The effects of beam-trawl disturbance on infaunal comunities in different habitats. *Journal of Animal Ecology* **65:** 348-358.

Kaiser, M.J., Edwards, D.B., Armstrong, P., Radford, K., Lough, N.E.L., Flatt, R.P. and Jones, H.D. (1998). Changes in megafaunal benthic communities in different habitats after trawling disturbance. *ICES Journal of Marine Science* **55:** 353-361.

Kaiser M.J. and de Groot, S.J. (2000). *The effects of fishing on non-target species and habitats: biological, conservation and socio-economic issues*. Blackwell Science, Oxford. pp. 399.

Kaiser, M.J., Collie, J.S., Hall, S.J., Jennings, S. and Poiner, I.R (2002). Modification of marine habitats by trawling activities: prognosis and solutions. *Fish Fish* **3:** 114–136.

Karadzic, B., Marinkovic, S. and Katarinovski, D. (2003). Use of the beta-function to estimate the skewness of species responses. *Journal of Vegetation Science* **14(6):** 799-805.

Katabuchi, M., Kurokawa, H., Davies, S.J., Tan, S. and Nakashizuka, T. (2012). Soil resource availability shapes community trait structure in a species-rich dipterocarp forest. *Journal of Ecology* **100:** 643–651.

Keddy, P.A. (1992). Assembly and response rules: two goals for predictive community ecology. *Journal Vegetation Science* **3:** 157-164.

Kendall, M., Jensen, O., Alexander, C., Field, D., McFall, G., Bohne, R. and Monaco, M. (2005). Benthic mapping using sonar, video transects and an innovative approach to accuracy assessment: a characterization of bottom features in the Georgia Bights. *Journal of Coastal Research* **21:** 1154-1165.

Kerswell, A.P. (2006). Global biodiversity patterns of benthic marine algae. *Ecology* **87(10):** 2479-2488.

Kessler, J.J., Rood, T., Tekelenburg, T. and Bakkenesm M. (2007). Biodiversity and socio-economic impacts of selected agro-commodity production systems. *The Journal of Environment and Development* **16(2):** 131-160.

Kirkegaard, J. B. (1988). The polychaeta of West Africa part II, Errant species, Nephtyidae to Dorvilleidae. *Zoological Museum, University of Copenhagen*, Denmark. pp. 89.

Kjerve, B. (1994). Coastal Lagoons. *In: Coastal lagoon processes*, Kjerve, B. (*ed.*). Elsevier Oceanographic Series. Amsterdam. pp. 1-8.

Kleypas, J.A., Feely, R.A., Fabry, V.J., Langdon, C., Sabine, C.L. and Robbins, L.L. (2006). Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research. Report of a workshop held 18–20 April 2005, St Petersburg, FL, sponsored by NSF, NOAA and the US Geological Survey. pp. 88.

Kock, K.H. (1992). *Antarctic fish and fisheries*. Cambridge Univerity Press, pp. 359.

Koranteng, K.A. (1998). *The impacts of environmental forcing on the dynamics of demersal fishery resources of Ghana*. PhD Thesis, University of Warwick (U.K.). pp. 376.

Krantzberg, G. (1985). The influence of bioturbation on physical, chemical and biological parameters in aquatic environments: a review. *Environmental Pollution* **39:** 99–122.

Kremen, C. (2005). Managing ecosystem services: what do we need to know about their ecology? *Ecology Letters* **8:** 468–479.

Kristensen, E., Jensen, M.H and Andersen, T.K (1985). The impact of polychaete (Nereis virens Sars) burrows on nitrification and nitrate reduction in estuarine sediment. *Journal of Experimental Marine Biology and Ecology* **85:** 75-91.

Kristensen, E., Aller, R.C. and Aller, J.Y. (1991). Oxic and anoxic decomposition of tubes from the burrowing sea anemone *Ceriantheopsis americanus*: Implications for bulk sediment carbon and nitrogen balance. *Journal of Marine Research* **49:** 589-617.

Kröncke, I., Duineveld, G.C.A., Raak, S., Rachor, E. and Daan, R. (1992). Effects of a former discharge of drill cuttings on the macrofauna community. *Marine Ecology Progress Series* **91**: 277-287.

Lambshead, P.J.D., Platt, H.M. and Shaw, K.M. (1983). The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *Journal of Natural History* **17:** 859-874.

Lampitt, R.., Billett, D.S.M.. and Rice, A. L.(1986): Biomass of invertebrate megabenthos from 500 to 4100 m in the northeast Atlantic Ocean, *Marine Biology* **93:** 69–81.

Lamptey, E. and Armah, A.K. (2008). Factors Affecting Macrobenthic fauna in a Tropical Hypersaline Coastal Lagoon in Ghana, West Africa. *Journal of Estuaries and Coasts* **31:** 1006-1019.

Lamptey, E., Armah, A.K. and Allotey, L.C. (2010). *Spatial assemblages of tropical intertidal rocky shore communities in Ghana, West Africa*. Nova Science Publisher Inc., New York. pp.52.

Lancaster, J., Bradley D.C.; Hogan, A. and Waldron, S. (2005). Intraguild omnivory in predatory stream insects. *Journal of Animal Ecology* **74(4):** 619-629.

Lavorel, S., McIntyre, S., Landsberg, J. and Forbes, D. (1997). Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution* **12:** 474-478.

Lavorel, S. and Garnier, E. (2002). Predicting changes in plant community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16:** 545-556.

Lavorel, S., Diaz, S., Dornelissen, H.C., Garnier, E., Harrison, S.P., McIntyre, S., Pausas, J.G., Pérez-Harguindeguy, N., Roumet, C. and Urcelay, C. (2007). *Plant functional types: are we getting any closer to the Holy Grail*? *In*: Canadell, J.G., Pataki, D.E. and. Pitelka, L.F. (eds.). *Terrestrial ecosystems in a changing world*. The IGBP Series. Springer-Verlag, Berlin-Heidelberg. pp. 103-113.

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N.S.G., Garden, D., Dorrough, J., Berman, S., Quetier, F., Thebault, A. and Bonis, A. (2008). Assessing functional diversity in the field methodology matters! *Functional Ecology* **22:** 134-147.

Law, R., Hanke, G., Angelidis, M., Batty, J., Bignert, A., Dachs, J., Davies, I., Denga, Y., Duffek, A., Herut, B., Hylland, K., Lepom, P., Leonards, P., Mehtonen, J., Piha, H., Roose, P., Tronczynski, J., Velikova, V., Vethaak D. (2010). Marine Strategy Framework Directive, Task Group 8 Report, Contaminants and pollution effects. Piha H. (ed). EUR 24335– Scientific and Technical Research series, JRC and ICES. pp. 171.

Lawton, J.H. and Brown. V.K. (1993). Redundancy in ecosystems. *In* Schulze, E. and Mooney, H. (eds.). *Biodiversity and Ecosystem Function*. Springer-Verlag, Berlin, Germany. pp 255–270.

Lehmann, M.F., Sigman, D.M., McCorkle, D.C., Brunelle, B.G., Hoffmann, S., Kienast, M., Cane, G. and Clement, J. (2005). Origin of the deep bering Sea nitrate deficit: constraints from the nitrogen and oxygen isotopic composition of water column nitrate and benthic nitrate fluxes. *Global Biogeochemical Cycles* **19:** 1-15.

Leibold, M.A. (1995). The niche concept revisited: mechanistic models and community context. *Ecology* **76:** 1371–1382.

Le Lœuff, P. and Intes, A. (1974). Les thalassinidea (Crustacea, Decapoda) Du Golfe de Guinée systématique-Écologiè. Vol. XII, No. 1. pp 17-69.

Le Loeuff, P, and von Cosel, R. (1998). Biodiversity patterns of the marine benthic fauna on the Atlantic coast of tropical Africa in relation to hydroclimatic conditions and paleogeographic events. *Acta Oecol* **19:** 309-321.

Lœuff, P and Zabi, G.S.F. (2002). Spatial and temporal variations in benthic fauna and communities of the Tropical Atlantic coast of Africa. *In:* McGlade, J.M., Cury, P. Koranteng, K.A. and Hardman-Mountford N.J.,. *The Gulf of Guinea Large Marine Ecosystem Environmental Forcing and Sustainable Development of Marine Resources***.** pp 147-160.

Lenihan, H.L. and Peterson, C.H. (1998). How habitat degradation through fishery disturbance enhances impacts of hypoxia on oyster reefs. *Ecological Applications* **8:** 128-140.

Lenihan, H. and Micheli, F. (2001). Soft-Sediment Communities. *In*: Bertness, M.D., Gaines, S.D. and Hay, M.E. *Marine Community Ecology*, Sunderland MA: Sinauer. pp. 550.

Lepš J., de Bello, F., Lavorel, S. and Berman, S. (2006). Quantifying and interpreting functional diversity of natural communities: *practical considerations matter*. – Preslia **78:** 481–501.

Levin, L.A. and Gage, J.D. (1998). Relationships between oxygen, organic matter and the diversity of bathyal macrofauna. *Deep Sea Research* **45:** 129-163.

Levin, L.A., Etter, R..J., Rex, M.A., Smith, A.J., Pineda, C.R., Stuart, J., Hessler, R.R. and Pawson, D. (2001). Environmental influences on regional deep sea species diversity. *Annual Reviews of Ecology and Systematics* **32:** 51-93.

Lewis, D.W. and McConchie, D. (1994). *Analytical Sedimentology*. New York: Chapman and Hall. pp. 197.

Li, H. and Reynolds, J.F. (1993). A new contagion index to quantify spatial patterns in landscape. *Landscape Ecology* **8:** 155-162.

Lindeboon, H.J. and de Groot, S.J. (1998a). The effects of different types of fisheries on the North Sea and Irish Sea benthic ecosystems. RIVO-DLO Report C003/98. pp. 404.

Lohrer, A.M., Thrush, S.F. and Gibbs, M.M. (2004). Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature* **431:** 1092–1095.

Longhurst, A.R. (1962). A review of the oceanography of the Gulf of Guinea, *Bull Inst Fr Afr Noire* **14A(3):** 633–663.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. and Wardle, D.A. (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* **294:** 804-808.

Loreau, M., Naeem, S. and Inchausti, P. (2002). *Biodiversity and ecosystem functioning. Synthesis and perspectives*. Oxford University Press, Oxford, UK. pp. 368.

Loreau, M., Mouquet, N. and Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the USA* **100:** 12765-12770.

Lötze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X, Peterson, C.H., Jackson, J.B. (2006). Depletion, degradation, and recovery potential of estuaries and coastal seas worldwide. *Science* **312:** 1806–1809.

MacArthur, R.H. (1955). Fluctuations of animal populations, and a measure of community stability. *Ecology* **36:** 533-536.

MacArthur, R.H., and Levins. R. (1967). The limiting similarity convergence and divergence of coexisting species. *American Naturalist* **101:** 377–385.

MacArthur, R.H. (1972). *Geographical ecology:* patterns in the distribution of species. Harper and Row, New York, U.S.A. pp. 269.

Macdonald, T., Burd, B., van Roodselaar, A. (2012a). Size structure of marine soft-bottom macrobenthic communities across natural habitat gradients: implications for productivity and ecosystem functions. PloS ONE **7(7):** e40071.

Macdonald, T., Burd, B., van Roodselaar, A. (2012b). Facultative feeding and consistency of trophic structure in marine soft-bottom macrobenthic communities. *Marine Ecology Progress Series* **445:** 129–140.

Magurran, A.E. (1988). *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, U.S.A. pp. 179.

Mant, R., Perry, E., Heath, M., Munroe, R., Väänänen, E., Großheim, C., Kümper-Schlake, L. (2014). *Addressing climate change – why biodiversity matters*. UNEP-WCMC, Cambridge, UK. available online at: http://unep-wcmc.org/resources-and-data/biodiversity-criteria-in-iki. pp 1535.

Margalef, R. (1958). Information theory in ecology. *General Systems* **3:** 36–71.

Martinez, N.D. (1996). Defining and measuring functional aspects of biodiversity. *In*: Gaston, K.J. (ed.), *Biodiversity: a biology of numbers and difference*, Blackwell Scientific Publications, Oxford, pp. 115–148.

Mason, N.W.H., MacGillivray, K., Steel, J.B. and Wilson. J.B. (2003). An index of functional diversity. *Journal of Vegetation Science* **14:** 571-578.

Mason, N.W.H., Mouillot, D., Lee, W.G. and Wilson. J.B. (2005). Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* **111:** 112-118.

Massutí, E. and Reñones, O. (2005). Demersal resource assemblages in the trawl fishing grounds off the Balearic Islands (western Mediterranean). *Science Marine* **69:** 167-181.

Mayer, M.S., Schaffner, L. and. Kemp, W.M. (1995). Nitrification potentials of benthic macrofaunal tubes and burrow walls: effects of sediment NH_4^+ and animal irrigation behavior. *Marine Ecology Progress Series* **121:** 157-169.

McArthur, M.A., Brooke, B., Przeslawski, R., Ryan, D.A., Lucieer, V. L., Nichol, S., McCallum, A.W., Mellin, C., Cresswell, I.D. and Radke, L.C. (2009). A review of abiotic surrogates for marine benthic biodiversity. Geoscience Australia Record 2009/42. pp. 61.

McClintock, J.B., Baker, B., Slattery, M,, Hamann, M., Kopitzke, R., Heine, J. (1994). Chemotactic tube-foot responses of the spongivorous sea star Perknaster fuscus to organic extracts from antarctic sponges. *Journal chemical Ecology* **20:** 859- 870.

McConnaughey, R.A, Mier, K.L and Dew, C.B. (2000). An examination of chronic trawling effects on soft-bottom benthos of the eastern Bering Sea. *Journal of Marine Science* **57:** 1377-1388.

McGill, B.J., Enquist B.J., Weiher E., and Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecological Evolution* **21:** 178–185.

McIntyre, S., Lavorel, S, Tremont, R.M. (1995). Plant life-history attributes – their relationship to disturbance responses in herbaceous vegetation. *Journal of Ecology* **83:** 31–44.

Menge, B.A. and Olson, A.M. (1990). Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution* **5:** 52–57.

Menge, B.A., Daley, B.A., Lubchenco, J., Sanford, E., Dahlhoff, E., Halpin, P.M., Hudson, G. and Burnaford, J.L. (1999). Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecological Monographs* **69(3):** 297-330.

Menge, B.A. (2000). Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology Ecology* **250:** 257–289.

Menge, B.A. and Branch, G.M. (2001). Rocky intertidal communities. *In:* Bertness, M. D., Gaines, S.D. Hay, M.E. (Eds.) *Marine community ecology*, Sinauer Associates, Sunderland, pp. 221–252.

Menge, B.A., Olson, A.M. and Dahlhoff, E.P. (2002). Environmental stress, bottom-up effects, and community dynamics: integrating molecular-physiological and ecological approaches. *Integrative and Comparative Biology* **42:** 892-908.

Mensah, M.A. (1995). The occurrence of zooplankton off Tema during the period 1969 – 1992. *In:* Bard, F. X. and. Koranteng K. A (eds.), *Dynamics and Use of Sardinella Resources from Upwelling off Ghana and Ivory Coast.*, ORSTOM Editions, Paris. pp. 279–289.

Meyers, M.B. Di Toto, D.M. and Lowe, S.A. (2000). Coupling suspension feeders to the Chesapeake Bay eutrophication model: *water quality ecosystem modelling* **1:** 123-140.

Meynard, C. N., and Quinn, J.F. (2007). Predicting species distributions: a critical comparison of the most common statistical models using artificial species. *Journal of Biogeography* **34(8):** 1455-1469.

Meysman, F.J., Middelburg, J.J. and Heip, C.H. (2006). Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology and Evolution* **21:** 688–695.

Michaud, E., Desrosiers, G., Mermillod-Blondin, F., Sundby, B., Stora, G., (2006). The functional group approach to bioturbation: II. The effects of the Macoma balthica community on fluxes of nutrients and dissolved organic carbon across the sediment-water interface. *Journal of Experimental Marine Biology and Ecology* **337:** 178–189.

Micheli, F. and Halpern. B.S. (2005). Low functional redundancy in coastal marine assemblages. *Ecological Letters* **8(4):** 391-400.

Millennium Ecosystem Assessment, (2003). *Ecosystem Studies: Ecosystem Science and Management*. Island Press, Washington, DC. pp. 137.

Milliman, J.D. (1994).“Organic matter content in U.S.Atlantic continental slope sediments: decoupling the grain-size factor. *Deep Sea Research* **41:** 797-808.

Mistri, M., Fano, E.A., Rossi, G., Caselli, K. and Rossi, R.(2000). Variability in macrobenthos communiies in the Vali di Comacchio, northern Italy, an hypereutrophized lagoonal ecosystem. *Estuarine, Coastal Shelf Science* **51:** 599-611.

Mistri, M., Rossi, R. and Fano, E.A. (2001). Structure and secondary production of a soft bottom macrobenthic community in a brackish lagoon (Saccadi Goro, North-eastern Italy). *Estuarine, Coastal and Shelf Science* **52:** 605-616.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H. A., McCain, C.M., McCune, A. R., McDade, L. A., McPeek, M.A., Near, T.J., Price, T.D., Ricklefs, R.E., Roy, K., Sax, D. F., Schluter, D., Sobel, J.M. and Turelli, M. (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* **10(4):** 315-331.

Moore, D.M., Lees, B.G., and Davey, S.M. (1991). A new method for predicting vegetation distributions using decision tree analysis in a geographic information system. *Environmental Management* **15(1):** 59-71.

Moroshkin, K.V., Bubnov, V.A. and Bulatov R.P. (1970).Water circulation in the eastern South Atlantic Ocean. Oceanology **10:** 27-34. *Translated from Okeanologiya* **10:** 38-47.

Mouillot, D., Mason, W. H. N., Dumay, O. and Wilson, J. B. (2005). Functional regularity: a neglected aspect of functional diversity. *Oecologia* **142:** 353-359.

Mouillot, D., Spathari S., Reizopoulou, S., Laugier, T., Sabetta, L., Basset, A., and Do Chi, T. (2006). Alternatives to taxonomic-based approaches to assess changes in transitional water communities. Aquatic Conservation: *Marine and Freshwater Ecosystems* **16:** 468-482.

Murphy D.D. and Duffus A.D. (1996). Conservation biology and marine biodiversity, *Conservation Biology* **88:** 155-163.

Murray, J.M.H., Meadows, A. and Meadows, P.S. (2002). Biogeomorphological implications of microscale interractions between sediment geotechnics and marine benthos: a review. *Geomorphology* **47:** 15-30.

Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P., Peterson, C.H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315:** 1846–1850.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. and Woodfin, R.M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature* **368:** 734–737

Naeem, S., Chapin, F.S., Costanza, R., Ehrlich, P.R., Golley, F.B., Hooper, D.U., Lawton, J. H., O'Neill, R.V., Mooney, H.A., Sala, O.E., Symstad, A.J. and Tilman, D. (1999). Biodiversity and Ecosystem Functioning: Maintaining Natural Life Support Processes. Issues in Ecology. *Ecological Society of America*, Washington. pp. 4-11.

Naeem, S. and Wright J.P. (2003). Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* **6:** 567–579.

National Research Council (1995). *Understanding marine biodiversity*. National Academy Press, Washington, D.C. pp. 128.

Needham, H.R, Pilditch, C.A, Lohrer A, Thrush, S.F (2011). Context-specific bioturbation mediates changes to ecosystem functioning. *Ecosystems* **14:** 1096– 1109.

Neira, C., and Hoepner, T. (1994). The role of Heteromastus filiformis (Capitellidae, Polychaeta) in organic carbon cycling. *Ophelia* **39(1):** 55-73.

Newell, R.C. (1970). *Biology of intertidal animals*. New York: Elsevier. pp. 555

Newell, R.C., Sneiderer, L.J. and Hitchcock, D.R. (1998). The impact of dredging works in coastal waters: a review of the sensitivity to disturbance and subsequent recovery of biological resources on the sea bed. Oceanography and Marine Biology: *an Annual Review* **36:** 127-178.

Ngai, J.T. and Srivastava, D.S. (2006). “Predators accelerate nutrient cycling in a bromeliad ecosystem,” Science **314 (5801):** 963-963.

Nichols, F.H. (1970). Benthic polychaetes assemblages and their relationship to the sediment in Port Madison, Washington. *Marine Biology* **6:** 48-57.

Nichols, M.M. and Boon III, J.D. (1994). Sediment transport processes in coastal lagoons. *In:* Kjerfve, B. (ed.), *Coastal lagoon processes*. Elsevier Oceanography Series 60. Amsterdam. pp. 577.

Nicolaidou, A., Bourgoutzani, F., Zenetos, A., Guelorget, O. and Perthuisot, J.P. (1988). Distribution of molluscs and polychaetes in coastal lagoons in Greece. *Estuarine, Coastal and Shelf Science* **26:** 337-350.

Nicolaidou, A. and Papadopoulou, K. N. (1989). Factors affecting the distribution and diversity of polychaetes in Amvrakikos Bay, Greece. *Marine Ecology* (Pubblicazioni Della Stazione Zoologica Di Napoli I) **10(3):** 193-204.

Nilsson, H.C. and Rosenberg, R. (1994). Hypoxic response of two marine benthic communities. *Marine Ecology Progress Series* **115:** 209-217.

Nilsson, H.C. and Rosenberg, R. (2000). Succession in marine benthic habitats and fauna in response to oxygen deficiency: analysed by sediment profile-imaging and by grab samples. *Marine Ecology Progress Series* **197:** 139-149.

Nilsson, H.C. and Rosenberg, R. (2003). Effects on a marine sedimentary habitats of experimental trawling analysed by sediment profile imagery (SPI). *Journal of Experimental Marine Biology and Ecology* **285:** 453-463.

Nixon, S.W. (1995). Coastal marine eutrophication: a definition, social causes and future concerns. *Ophelia* **41:** 199-219.

Noda, T. (2009). Metacommunity-level coexistence mechanisms in rocky intertidal sessile assemblages based on a new empirical synthesis. *Population Ecology* **51:** 41-55.

Norling, K. Rosenberg, R. Hulth, S. Gremare A. and Bonsdorff, E. (2007). Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediments, *Marine Ecology Progress Series* **332:** 11–23.

Nowell, A.R.M. and Jumars, P.A. (1984). Flow environments of aquatic benthos. *Annual Reviews of Ecological Systematics* **15:** 303-328.

Oksanen, L. Fretwell, S.D., Arruda, J. and Niemela, P. (1981). Exploitation ecosystems in gradients of primary productivity. *American Naturalist* **118:** 240–261.

Olabarria, C. (2006). Faunal change and bathymetric diversity gradient in deep-sea prosobranchs from Northeastern Atlantic. *Biodiversity and Conservation* **15(11):** 3685-3702.

Olaso, I., Rauschert, M. and De Broyer, C. (2000). Impact of the family Artetidraconidae (Pisces) on the eastern Weddell Sea benthic communities. *Marine Ecology Progress Series* **194:** 143-158.

Olden, J.D, Poff, N.L, Bestgen, K.R (2006). Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs* **76:** 25–40.

Olenin, S., F. Alemany, A.C. Cardoso, S. Gollasch, P. Goulletquer, M. Lehtiniemi, T. McCollin, D. Minchin, L. Miossec, A. Occhipinti-Ambrogi, H. Ojaveer, K. Rose., Jensen, M. Stankiewicz, I. Wallentinus, B. Aleksandrov, (2010). Marine Strategy Framework Directive–Task Group Report Non -indigenous species. EUR 24342 EN– Joint Research Centre, Luxembourg: *Office for Official Publications of the European Communities*: pp. 44.

Olff, H., Pegtel, D.M., Van Groenendanel, J.M. and Bakker, J.P. (1994). Germination strategies during grassland germination. *Journal of Ecology* **82(1):** 69-77.

Olff, H., Alonso, D., Berg, M.P., Eriksson, B.K. Loreau, M., Piersma, T., & Rooney, N. (2009). Parallel ecological networks in ecosystems. *Philosophical Transactions of Royal Society B* **364:** 1755–1779.

Ormerod, S.J. and Edwards, R.W. (1987). The ordination and classification of macro invertebrate assemblages in the catchments of the River Wye in relation to environmental factors. *Freshwater Biology* **17:** 533-546.

Osmond, B., Ananyev, G., Berry, J., Langdon, C., Kolber, Z., Lin, G., Monson, R., Nichol, C., Rascher, U., Schurr, U., Smith, S., Yakir, D., 2004. Changing the way we think about global climate change research: scaling up in ecosystem experimental science. *Global Change Biology* **10:** 393-407.

Paine, C.E.T., Baraloto, C., Chave, J. and Herault, B. (2011). Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos* **120:** 720– 727.

Palumbi, S.R. (2001). The Ecology of Marine Protected Areas. *In:* Bertness, M.D. Gaines, S.D. and. Hay, M.E. (eds.), *Marine Community Ecology*, Sunderland MA: Sinauer Associates, Inc. pp. 509-532.

Pandolfi, J.M., Jackson, J.B.C., Baron, N., Bradbury, R.H., Guzman, H.M., Hughes, T.P., Kappel, C.V., Micheli, F., Ogden, J.C., Possingham, H.P. and Sala, E. (2005). Are U.S. Coral Reefs on the Slippery Slope to Slime? *Science* **307:** 1725–1726.

Papageorgiou, N., Sigala, K. And Karakassi, I. (2009). Changes of macrofaunal functional composition at sedimentary habitats in the vicinity of fish farms. *Estuarine, Coastal and Shelf Science* **83:** 561-568.

Parmar, R.M., Arora, R.K., Rao, M.V. and Thyagarajan, K. (2006). OCEANSAT-2 mission and its applications - art. no. 64070C. *In:* Conference on GEOSS and Next-Generation Sensors and Missions. Goa, INDIA: Spie-Int Soc Optical Engineering. pp. C4070-C4070.

Parry, D.M., Kendall, M.A., Rowden, A.A and Widdicombe, S. (1999). Species body size distribution patterns of marine benthic macrofauna assemblages from contrasting sediment types. *Journal Marine Biological Association* U.K. **79:** 793-801.

Parsons, T.R., Takahashi, M. and Hargrave, B. (1995). Biological Oceanographic processes. *Butterworth Heinemann Ltd*. Oxford. pp. 330.

Paterson, G.L.J., Lambshead, P.J.D. and Gage, J.D. (1992). Down the slippery slope: A study of polychaete assemblages from bathymetric transects in the Rockall Trough. *Polychaete Research Newsletter* No. 14, Vol 2.

Pauly, D., Watson, R.. and Alder, J. (2005). Global trends in world fisheries: impacts on marine ecosystems and food security. Philosophical Transactions of the Royal Society B-*Biological Sciences* **360:** 5-12.

Pearson, T.H. and Rosenberg. R. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology: an Annual Review* **16:** 229-311.

Pearson, T.H. and Rosenberg. R. (1987). Feast and fanime: structuring factors in marine benthic communities. In: Gee J. and P. Giller (eds), *Organization of communities: past and present*. Oxford. The 27th Symposium of the British Ecological Society Aberystwyth. *Blackwell Scientific Publications* 373-395.

Pearson, T.H. (2001). Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanography and Marine Biology: an Annual Review* **39:** 233-267.

Pechenik, J.A. (2000). *Biology of the invertebrates*, 2nd ed., New York: McGraw-Hill. Pp. 73.

Petch, D.A. (1986). Selective deposit-feeding by *Lumbrineris* cf. *latreilli* (Polychaeta: Lumbrinereidae), with a new method for assessing selectivity by deposit-feeding organisms. *Marine Biology* **93:** 443-448.

Petchey, O.L. and Gaston, K.J. (2002). Functional diversity (FD), species richness and community composition, *Ecology Letters* **5:** 402–411.

Petchey, O.L, Hector, A., Gaston, K.J. (2004). How do different measures of functional diversity perform? *Ecology* **85:** 847–857.

Petchey, O.L. and Gaston, K.J. (2006). Functional diversity: back to basics and looking forward. *Ecology Letters* **9:** 741-758.

Peterson, C.H. and Lubchenco J. (1997). Marine ecosystem services. *In:* Daily, G.C (ed.) *Nature's Services: Societal Dependence on Natural Ecosystems*, Island Press, Washington, DC. pp. 177–194.

Peterson, C.H. and Bishop, M.J. (2005). Assessing the environmental impacts of beach nourishment. *BioScience* **55:** 887-896.

Philander, S.G.H. (1979). Upwelling in the Gulf of Guinea. *Journal of Marine Research* **37**: 23-33.

Pielou, E.C. (1996). The measurement of diversity in different types of biological collections. *Journal of Theoritical Biology* **13:** 131-144.

Piepenburg, D.. Blackburn, T.H., von Dorien, C.F., Gutt, J., Hall, P.O.J., Hulth, A., Kendall, M.A., Opaliński, K.W., Rachor, E. and Schmid. M.K (1995). Partitioning of benthic communities respiration in the Arctic NW Barents Sea. *Marine Ecology Progress Series* **118:** 199–213.

Piet, G.J., Albella, A.J., Aro, E., Farrugio, H., Lleonart, J., Lordan, C., Mesnil, B., Petrakis, G., Pusch, C., Radu, G. and Ratz, H.J. (2010). Marine Strategy Framework Directive – Task Group 3 Report Commercially exploited fish and shellfish. EUR 24316 EN – Joint Research Centre, Luxembourg: Office for Official Publications of the European Communities: pp. 82.

Pilskaln, C.H., Churchill, J.H. and Mayer, L.M. (1998). Resuspension of sediment by bottom trawling in the Gulf of Maine and potential geochemical consequences. *Conservation Biology* **12:** 1223–1229.

Pimm, S.L., Russell, G.J., Gittleman, J.H. and Broks, T.M. (1995). The future of biodiversity. *Science* **269:** 347-350.

Pitcher, C. R., Doherty, P., Arnold, P., Hooper, J., Gribble, N., Bartlett, C., Browne, M., Campbell, N., Cannard, T., Cappo, M., Carini, G., Chalmers, S., Cheers, S., Chetwynd, D., Colefax, A., Coles, R., Cook, S., Davie, P., De'ath, G., Devereux, D., Done, B., Donovan, T., Ehrke, B., Ellis, N., Ericson, G., Jacobsen, I., Johnson, J., Jones, M., Kinninmoth, S., Kistle, S., Last, P., Leite, A., Marks, S., McLeod, I., Oczkowicz, S., Robinson, M., Rose, C., Seabright, D., Sheils, J., Sherlock, M., Skelton, P., Smith, D., Smith, G., Speare, P., Stowar, M., Strickland, C., Van der Geest, C., Venables, W., Walsh, C., Wasssenberg, T., Welna, A., & Yearsley, G. (2007). *Seabed Biodiversity on the Continental Shelf of the Great Barrier Reef World Heritage Area*., AIMS/CSIRO/QM/QDPI CRC Reef Research Task Final Report. pp. 320.

Podani, J. and Schmera, D. (2006). On dendrogram-based measures of functional diversity. *Oikos* **115:** 179–185.

Poff, N.L. (1997). Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* **16:** 391–409.

Polunin, N.V.C., Morales-Nin, B., Pawsey, W.E, Cartes, J.E., Pinnegar, J.K. and Moranta, J. (2001). Feeding relationships in Mediterranean bathyal assemblages elucidated by stable nitrogen and carbon isotope data. *Marine Ecology Progress Series* **220:** 13–23.

Ponder, W., Hutchings, P. and Champman, R. (2002). Overview of the conservation of Australian Marine Invertebrates: A Report for Environment Australia. Sydney, Australian Museum. pp. 588.

Poore, G.C.B., McCallum, A.W. and Taylor, J. (2008). Decapod Crustacea of the continental margin of southwestern Australia and central Western Australia: preliminary identifications of species from FRV Southern Surveyor voyage SS10-2005. Melbourne, Museum Victoria. Reports 11: 1-106.

Post, A.L., Wassenberg, T.J., and Passlow, V. (2006). Physical surrogates for macrofaunal distributions and abundance in a tropical gulf. *Marine and Freshwater Research* **57(5):** 469-483.

Principe, R.E., Gualdoni, C.M., Oberto, A.M., Raffaini, G.B. and Corigliano, M.C. (2010). Spatial-temporal patterns of functional feeding groups in mountain streams of Córdoba, Argentina. *Ecología Australia* **20:** 257–268.

Purvis, A., Gittleman, J.L., Cowlishaw, G. and Mace, G.M. (2000). Predicting extinction risk in declining species. Proceedings of the Royal Society of London Series B-*Biological Sciences* **267:** 1947–1952.

Purvis, A. and Hector, A. (2000). Getting the measure of biodiversity. *Nature* **405:** 212-219.

Quelennec, R.E. (1984). Identification des problemes d'erosion sur le littoral sableux deCote d'Ivoire. Propositions d'actions prioritaires. Rapport du BRGM. pp. 46.

Queirós, A.M., Hiddink, J.G., Hinz, H., Kaiser, M.J. (2006). The effects of chronic bottom trawling disturbance on biomass, production and size spectra of invertebrate infauna communities from different habitats. *Journal of Experimental Marine Biology and Ecology* **335:** 91–103.

Raffaelli, D. and Hawkins, S. (1996). *Intertidal Ecology*. Kluwer Academic Publishers, London. pp. 356.

Raffaelli, D., Emmerson, M., Solan, M., Biles, C., Paterson, D. (2003).Biodiversity and ecosystem functioning in shallow coastal waters: an experimental approach. *Journal of Sea Research* **49:** 133–141.

Rahbek, C. and Graves, G.R. (2001). Multiscale assessment of patterns of avian species richness. *Proceedings of National Academy of Science USA* **98:** 4534–4539.

Rakel, H. O. (2007). A study of West African brittle stars (Ophiuroidea) as a base for further benthic investigations in the Gulf of Guinea. *MS. Thesis*, University of Bergen, Institute of Biology. pp. 96.

Ramsay, K., Kaiser, M.J. and Hughes R.N. (1996). Changes in hermit crab feeding patterns in response to trawling disturbance. *Marine Ecological Progress Series* **144(1-3):** 63–72.

Ramsay, K., Kaiser, M.J. and Hughes, R.N (1998). Responses of ben- thic scavengers to fishing disturbance by towed gears in different habitats. *Journal Experimental Marine Biology and Ecology* **224:** 73–89.

Rao, C.R. (1982). Diversity and dissimilarity coefficients: a unified approach. *Theoretical Population Biology* **21**: 24-43.

Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M., Walters, M.B. (2003). The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences* **164:** S143–S164.

Reichart, G.J., Jorissen, F., Anschutz, P. And Mason, P.R.D. (2003). Single foraminiferal test chemistry records the marine environment. *Geology* **31:** 355-358.

Reid, R.S., Gachimbi, L.N., Worden, J., Wangui, E.E., Mathai, S., Mugatha, S.M., Campbell, D.J., Maitima, J.M., Butt, B., Gichohoi, H., Ogol, E. (2004). Linkages between changes in land use, biodiversity and land degradation in the Loitokitok area of Kenya. LUCID Working Paper 49, Int. Livestock Res. Institute and United Nations Environ. Programme/Division of Global Environ. Facility Coordination, Nairobi, Kenya.

Reineck, H.E. and Singh, I.B. (1980). *Depositional Sedimentary Environments: with Reference to Terrigenous Clastics*. Berlin: Springer - Verlag. pp. 549.

Reise, K. (1985). *Tidal flat ecology: An experimental approach to species interactions*. Ecological studies. Berlin: Springer. pp. 191.

Reiss, H., Kröncke, I. and Ehrich, S. (2006). Estimating the catching efficiency of a 2-m beam trawl for sampling epifauna by removal experiments. *ICES Journal of Marine Science* **63:** 1453-1464.

Reiss, J., Bridle, J.R., Montoya, J.M. and Woodward, G. (2009). Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution* **24(9):** 505-515.

Rex, M.A., Crame, J.A., Stuart, C.T. and Clarke, A. (2005). Large-scale biogeographic patterns in marine molluscs: A confluence of history and productivity? *Ecology* **86(9):** 2288-2297.

Rhoads, D.C. and Young, D.K. (1970). The influences of deposit- feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* **28:** 156-178.

Rhoads, D.C (1974). Organism-sediment relations on the muddy seafloor. *Oceanography and Marine Biology Annual Review* **12:** 263-300.

Rice, J., Arvanitidis, C. Borja, A. Frid C., Hiddink, J. Krause, J. Lorance, P. Ragnarsson, S.A. Skold, M. Trabucco, B. (2010). Marine Strategy Framework Directive –Task Group Report Seafloor integrity. EUR 24334 EN– *Joint Research Centre*, Luxembourg: Office for Official Publications of the European Communities: pp. 73.

Richardson, A.J., Bakun, A. Hays, G.C. and Gibbons, M.J. (2009). The jellyfish joyride: casuses, consequences and mangement response to a more gelatinous future. *Trends in Ecology and Evolution* **24(6):** 312-322.

Richardson, P.L. and Walsh, D. (1986). Mapping climatological seasonal variations of surface currents in the tropical Atlantic using ship drifts. *Journal of Geophysical Research* **19:** 10537-10550.

Ricklefs, R.E. and Schluter. D. (1993). Species diversity: regional and historical influences. *In:* Ricklefs, R.E. and Schluter, D. (eds.). *Species diversity in ecological* communities. *Historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA. pp. 350–363.

Ricklefs, R.E. and Miles. D.B. (1994). Ecological and evolutionary inferences from morphology: an ecological perspective. *In:* Wainwright, P.C. and Reilly, S.M. (eds), *Ecological morphology: integrative organismal biology*. University of Chicago Press, Chicago, Illinois, USA. pp. 13–41.

Ricotta, C. (2005). Through the jungle of biological diversity. *Acta Biotheoretica* **53:** 29-38.

Riisgärd, H.U. and Banta, G.T. (1998). Irrigation and deposit feeding by the lugwoim Arenicola marina, characteristics and secondary effects on the environment. A review of current knowledge. *Vie Milieu* **48:** 243-257.

Ritter, C. and Montagna, P.A. (1999). Seasonal hypoxia and models of benthic response in a Texas Bay. *Estuaries* **22(1):** 7-20.

Rogers, S., M. Casini, P. Cury, M. Heath, X. Irigoien, H. Kuosa, M. Scheidat, H. Skov, K.I. Stergiou, V.M. Trenkel, J. Wikner, O. Yunev, (2010). Marine Strategy Framework Directive– Task Group 4 Report Food Webs. EUR 24343 EN – *Joint Research Centre*, Luxembourg: Office for Official Publications of the European Communities. pp. 55

Rosenberg, R. (1973). Succession in benthic macrofauna in a Swedish fjord subsequent to the closure of a sulphite pulp mill. *Oikos* **24:** 244-258.

Rosenberg, R. Hellman, B., Johansson, B.(1991). Hypoxia tolerance of marine benthic fauna. *Marine Ecology Progress Series* **79:** 127-131.

Rosenberg, R. (1995). Benthic marine fauna structured by hydrodynamic processes and food availability. *Netherlands Journal of Sea Research* **34:** 303-317.

Rosenberg, R., Nilsson, H.C. and Diaz, R.J. (2001). Response of benthic fauna and changing sediment redox profiles over a hypoxic gradient. *Estuaries, Coastal and Shelf Science* **53:** 343-350.

Rosenberg, R, Nilsson, H.C., Gremare, A. and Amouroux, J.M. (2003). Effects of demersal trawling on marine sedimentary habitats analysed by sediment profile imagery. *Journal of Experimental Marine Biology and Ecology* **285:** 465-477.

Rouse, G.W. and Pleijel, F. (2001). *Polychaetes.* Oxford University Press. N.Y. pp. 354.

Rowe, G.T. (1983). Biomass and production of the deep-sea macrobenthos. *In:* Rowe, G.T. (ed.), *The sea*, vol. 8. Wiley-Interscience, New York. pp. 97-121.

Rowe, G.T., Sibuet, M.S., Deming, J., Kripounoff, A., Tietjen, J., Macko, S., Theroux, R. (1991). "Total sediment biomass and preliminary estimates of organic carbon in deep-sea sediments. *Journal of Marine Research* **43:** 925-950.

Roy, K. and Foote, M. (1997). Morphological approaches to measuring biodiversity. *Trends in Ecology and Evolution* **12:** 277-281.

Roy, K., Blalch, D.P. and Helberg, M.E. (2001). Spatial patterns of morphological traits across the Indo-pacific: analyses using strombid gastropod. *Proceedings of the Royal Society B* **268:** 2503-2508.

Roy, K., Jablonski, D. and Valentine. J.W. (2004). Beyond species richness: biogeographic patterns and biodiversity dynamics using other metrics of diversity. in M. V. Lomolino and L. R. Heaney, (eds.). *Frontiers of biogeography: new directions in the geography of nature*. Sinauer, Sunderland, USA. pp. 151–170.

Royal Society. (2005). *Ocean acidification due to increasing atmospheric carbon dioxide*. Policy Document 12/05, The Royal Society, London. pp. 60.

Ruiz, G.M., Carlton, J.T., Grosholz, E.D. and Hines, A.H. (1997). Global invasion of marine and estuarine habitats by indigenous species: mechanisms, extent and consequences. *American Zoology* **37:** 621-632.

Rumohr, H. and Kujawski, T. (2000). The impact of trawl fishery on the epifauna of the southern North Sea. *ICES Journal of Marine Science* **57(5):** 1389-1394.

Ryan, D.A., Brooke, B. P., Collins, L.B., Kendrick, G.A., Baxter, K.J., Bickers, A.N., Siwabessy, P.J.W. and Pattiaratchi, C.B. (2007). The influence of geomorphology and sedimentary processes on shallow water benthic habitat distribution: Esperance Bay, Western Australia. *Estuarine and Coastal Shelf Science* **72:** 379-386.

Schmera, D., Eros, T. and Podani, J. (2009). A measure for assessing functional diversity in ecological communities. *Aquatic Ecology* **43:** 157–167.

Shannon, C.E. and Weaver, W. (1949). *The Mathematical Theory of Communication*. University of Illinois Press, Urbana. pp. 144.

Sivadas, S.K., Ingole, B.S. and Fernandes, C.E.G. (2013). Environmental gradient favours functionally diverse macrobenthic communities in a placer rich tropical bay. *The Scientific World Journal, ID **750580***: 1-12.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A.,Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H.,Walker, M. And Wall, D.H. (2000). Global biodiversity scenarios for the year 2100. *Science* **287:** 1770-1774.

Sanders, H.L. (1968). Marine benthic diversity: a comparative study. *American Naturalist* **102:** 243-282.

Sarda, F., Company, J.B. and Costa, C. (2005). A morphologicalapproach for relating decapod crustacean cephalothorax shape with distribution in the water column. *Marine Biology* **147:** 611-618.

Scanes, P.R., Mann, R.A., Manning, T.M., and Chapman, J.C. (1993). Observations on the biota of an estuarine beach at Hardys Bay (NSW, Australia) following a spillage of aldrin. *Marine Pollution Bulletin* **26(12):** 687-691.

Schemske, D. (2002). *Tropical diversity: patterns and processes*. *In:* Chazdon, R. and Whitmore, T. (eds.), *Ecological and Evolutionary Perspectives on the Origins of Tropical Diversity*: Key Papers and Commentaries. Chicago IL: University of Chicago Press. pp. 163-173.

Schlapfer, F. and Schmid, B., (1999). Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. *Ecological Applications* **9:** 893- 912.

Schubert, C.J., Niggerman, J., Klockgether, G., and Ferdelman, G., (2005). Chlorin Index: A new parameter for organic matter freshness in sediment. *Geochemistry Geophysics and Geosystems* **6(3):** 1-12.

Schwinghamer, P. (1983). Influence of pollution along a natural gradient and in a mesocosm experiment on biomass-size spectra of benthic communities. *Marine Ecology Progress Series* **46:** 199-206.

Sebesvari, Z., Esser, F. and Harder, T. (2006). Sediment-associated cues for larval settlement of the infaunal spionid polychaetes *Polydora cornuta* and *Streblospio benedicti*. *Journal of Experimental Marine Biology and Ecology* **337:** 109–120.

Sneiderer, L.J. and Newell, R.C. (1999). Analysis of the relationship between sediment composition and benthic community structure in coastal deposits: Implications for marine aggregate dredging. *ICES Journal of Marine Series* **56:** 757-765.

Seiter, K., Hensen, C., Schroter, J. and Zabel, M. (2004). Organic carbon content in surface sediments – defining regional provinces. *Deep-Sea Research* **51:** 2001-2026.

Seiter, K., Hensen, C. and Zabel, M. (2005). Benthic carbon mineralisation on a global scale. *Global Biogeochemical Cycles* **19:** 1-26.

Shaw, K.M., Lambshead, P.J.D. and Platt, H.M. (1983). Detection of pollution-induced disturbance in marine benthic assemblageswith special reference to nematodes. *Marine Ecology Progress Series* **11:** 195-202.

Sheppard, C. (2006). The muddle of ‘biodiversity’. *Marine Pollution Bulletin* **52(2):** 123–124.

Sherman, K. (1993). “Large Marine Ecosystems as Global Units for Marine Resources Management- an Ecological Perspective,” Sherman, K.A., Alexander, L.M. and Gold, B.D. (eds.), Large Marine Ecosystems-Stress, Mitigation, and Sustainability. AAAS Selected Symposium, Westview Press Inc., Boulder, CO. pp 3-14.

Sherman, K. And Duda, A.M. (1999). An ecosystem approach to global assessment and management of coastal waters. *Marine Ecology and Progress Series* **190:** 271-287.

Sherman, K. and Anderson, E.D. (2002). A modular approach to monitoring, assessing and managing large marine ecosystems. *In:* McGlade J.M., Cary, P. Koranteng, K.A. and Hardman-Mountford, N. J. (eds.). *The Gulf of Guinea Large Marine Ecosystem*. Elsevier, Amsterdam. pp. 9–26.

Shiel, D.R. (2009). Multiple stressors and disturbance: when changes is not in the nature of thing. *In:* Wahl, M. (ed.), *Marine hard bottom communities; patterns, dynamics, diversity and changes*. Ecological Studies 206. pp. 281-294.

Shimatani, K. (2001). On the measurement of species diversity incorporating species differences. *Oikos* **93:** 135-147.

Shipley, B., Paine, C.E.T. and Baraloto, C. (2012). Quantifying the importance of local niche-based and stochastic processes to tropical tree community assembly. *Ecology* **93:** 760-769.

Shulman, M. J., and Bermingham, E. (1995). Early-life histories, ocean currents, and the population-genetics of Caribbean reef fishes. *Evolution* **49(5):** 897-910.

Simpson, E.H. (1951). "The Interpretation of Interaction in Contingency Tables". *Journal of the Royal Statistical Society, Series B* **13**: 238–241

Skjoldal, H.R., Gool, SV., Offringa, H., Dam, C.V., Water, J., Degré, E., Bastinck, J., Pawlak, J., Lassen, H., Svelle, M., Nilsen, H.-G. and Lorentzen, H. (1999). *Workshop on Ecological Quality Objectives (EcoQOs) for The North Sea*. Scheveningen- the Netherlands. 1-3 September 1999, Tema Nord, The Hague. pp 591.

Smith, C.R., Berelson, W., DeMaster, D.J., Dobbs, F.C., Hammond, D., Hoover, D.J., Popoe, R.H. and Stephen (1997). Latitudinal variation in benthic processes in the abyssal equatorial Pacific: control by biogenic particle flux. *Deep-Sea Research II* **44(9-10):** 2295-2317.

Snelgrove, P.V.R and Butma, C.A., (1994). Animal-sediment relationships revised: cause versus effect. *Oceanography and Marine Biology*. *Annual Review* **32:** 111-177.

Snelgrove, P.V.R., T.H. Blackburn, F.A. Hutchings, D.M. Alongi, J.F. Grassle, H. Hummel, G. King, I. Koike, P.J.D. Lambshead, N.B. Ramsing, and V. Soliweiss. (1997). The importance of marine sediment biodiversity in ecosystem processes. *Ambio* **26(8):** 578-583.

Snelgrove, P.V.R. (1998). The biodiversity of macrofaunal organisms in marine sediments: *Biodiversity and Conservation* **7:** 1123-1132.

Snelgrove, P.V.R. (1999). Getting to the bottom of marine biodiversity: Sedimentary habitats. *ocean bottoms are the most widespread habitat on Earth and support high biodiversity and key ecosystem services. Bioscience* **49:** 129–138.

Snelgrove, P.V.R. (2001). Diversity of Marine Species. Encyclopedia of Ocean Sciences. Oxford: Academic Press. pp. 748-757.

Solan, M., Cardinale, B.J., Downing, A.L., Engelhardt, K.A.M., Ruesink, J.L. and Srivastava, D.S (2004). Extinction and ecosystem function in the marine benthos. *Science* **306:** 1177–1180.

Solan, M., Raffaelli, D.G., Paterson, D.M., White, P.C.L. and Pierce, G.J. (2006). Marine biodiversity and ecosystem function: empirical approaches and future research needs. *Marine Ecology Progress Series* **311:** 175-178.

Solan, M**.,** Batty, P., Bulling, M.T., Godbold, J.A. (2008). How biodiversity affects ecosystem process: implications for ecological revolutions and benthic ecosystem function. *Aquatic Biology* **2:** 289-301.

Solan, M**.,** Godbold, J.A., Symstad, A.,Flynn, D.F.B., Bunker, D. (2009). Biodiversity ecosystem function research and biodiversity futures: early bird catches the worm or a day late and a dollar short?. *In:* Naeem, S., Bunker, D.E., Hector, A., Loreau, M., Perrings, C. (eds.). *Biodiversity and human impacts. Ecological and societal implications*. Oxford University Press. pp.30-45.

Soulé, M.E. (1991). Land use planning and wildlife maintenance, guidelines for conserving wildlife in an urban landscape. *Journal of the American Planning Association* **57(3):** 313-323.

Sousa, W.P. (2001). Natural disturbance and the dynamics of marine benthic communities. *In:* Bertness, M.D., Gaines, S.D and Hay, M.E. *Marine Community Ecology*, Sunderland MA: Sinauer Associates, Inc. pp. 85-132.

Southwood, T.R.E. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology* **46:** 337–365.

Sparks-McConkey, P.J. and Watling, L. (2001). Effects on the ecological integrity of a soft-bottom habitat from trawling disturbance. *Hydrobiologia* **456:** 73-85.

Spehn, E.M., Joshi, J., Schmid, B., Diemer, M. and Koerner, C. (2000). Aboveground resource use increases with plant species richness in experimental grassland ecosystems. *Functional Ecology* **14:** 326–337.

Srivastava, D.S. and Vellend, M. (2005). Biodiervsity-ecosystem function research: is it relevant to conservation? *Annual review of Ecology, Evolution and Systematics* **36:** 267-294.

Stachowicz J.J., H. Fried, R.W. Osman, R.B. Whitllatch. (2002). Biodiversity, invasion resistance, and marine ecosystem function. Reconciling pattern and process. *Ecology* **83:** 2575-2590.

Stachowicz, J.J., Bruno, J.F. and Duffy, J.E. (2007). Understanding the effects of marine biodiversity on communities and ecosystems. *Annual Review of Ecology, Evolution and Systematics* **38:** 739-766.

Stachowicz, J.J., Best, R.J., Bracken, M.E.S. and Graham, M.H. (2008). Complementarity in marine biodiversity manipulations: Reconciling divergent evidence from field and mesocosm experiments. Proceedings of the National Acadamy of Sciences USA **105:** 18842-18847.

Statzner, B. (1987). Characteristics of lotic ecosystems and consequences for future research directions. *In:* Schulze E-D. Ans Zwölfer, H. (eds.), *Potentials and limitations of ecosystem analysis*. Springer Verlag, Berlin. pp. 365-390.

Statzner, B., Resh, V.H. and Roux, A.L. (1994). The synthesis of long-term ecological research in the context of concurrently developed ecological theory: design of a research strategy for the Upper Rhoˆne River and its floodplain. *Freshwater Biology* **31:** 253–263.

Statzner, B., Doledec, S., and Hugueny, B. (2004). Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. *Ecography* **27:** 470–488.

Steffen, W., Sanderson, A., Tyson, P.D., Jäger, J., Matson, P.A., Moore III, B., Oldfield, F., Richardson, K., Schellnhuber, H.J., Turner II, B.L. and Wasson, R.J. (2004). *Global Change and the Earth System: A Planet Under Pressure*. Springer-Verlag, Berlin. pp. 336.

Stevens, T. and Connolly, R.M. (2004). Testing the utility of abiotic surrogates for marine habitat mapping at scales relevant to management. *Biological Conservation* **119(3):** 351-362.

Stone, R.P., Masuda, M.M. and Malecha, P.W. (2005). Effects of bottom trawling on soft-sediment epibenthic communities in the Gulf of Alaska. *Americam Fisheries Society Symposium* **41:** 461–475.

Stramma, L. and Schott, F. (1999). The mean flow field of the tropical Atlantic Ocean, *Deep-Sea Research* **46**: 279–303.

Strathmann, M.F. and Strathmann, R.R. (2007). An extraordinarily long larval duration of 4.5 years from hatching to metamorphosis for teleplanic veligers of *Fusitriton oregonensis*. *Biological Bulletin* ***213*****(2):** 152-159.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H.C., Dı´az S., Garnier, E., Golberg, D., Hooper, D.U., Jackson, S. and Navasm, M-L (2008). Scaling environmental change through the community-level: a trait-based response-and-effect framework for plant. *Global Change Biology* **14:** 1125-1140.

Svensson, J.R., Lindegarth, M., Siccha, M., Lenz, M., Molis, M., Wahl, M. and Pavia, H. (2007). Maximum species richness at intermediate frequencies of disturbance: Consistency among levels of productivity. *Ecology* **88(4):** 830-838.

Taghon, G.L.(1982). Optimal foraging by deposit feeding invertebrates: roles of particle size and organic coating. Oecologia **52:** 295-304.

Tasker, M.L., Amundin, M., Andre, M., Hawkins, A., Lang, W., Merck, T., Scholik-Schlomer, A., Teilmann, J., Thomsen, F., Werner, S. and Zakharia, M. (2010). Marine Strategy Framework Directive Task Group 11 Report - Underwater noise and other forms of energy. Available from http://www.ices.dk/projects/MSFD/TG11final.pdf. pp. 54.

Tenore, K.R. (1972). Macrobenthos of the Pamlico River estuary, North Carolina. *Ecological Monographs* **42**: 51-69.

Ter Braak, C.J.F. (1986). Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67:** 1167-1179.

Ter Braak, C.J.F. and Verdonschot, P.F.M. (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Science* **57**: 255-289.

Ter Braak, C.J.F and Smilauer, P. (1998). CANOCO Reference Manual and user's guide to Canoco for windows: *Software for Canoconical Community Ordination* (version 4). Ithaca, NY: Microcomputer Power. pp. 500.

Ter Braak, C.J. and Smilauer, P. (2002). Canoco reference manual and Canoco Draw for Windows User's guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power (Ithaca, NY, USA). pp. 500.

Terlizzi, A. and Schiel, D.R. (2009). Patterns along environmental gradient. *In:* Wahl, L. (ed.), *Marine hard bottom communities: patterns, dynamics, diversity and change*. Springer. pp. 101-109.

Tett, P., Gowen, R., Mills, D., Fernandes, T., Gilpin, L., Huxham, M., Kennington, K., Read, P., Service, M., Wilkinson, M. and Malcolm, S. (2007). Defining and detecting undesirable disturbance in the context of marine eutrophication. *Marine Pollution Bulletin* **55:** 282-297.

Thompson, J.N., Reichman, O. J., Morin, P.J., Polis, G.A., Power, M.E., Sterner, R.W., Couch, C.A., Gough, L., Holt, R., Hooper, D.U., Keesing, F., Lovell, C.R., Milne, B.T., Molles, M.C., Roberts, D.W. and Strauss, S.Y. (2001). Frontiers of ecology. *BioScience* **51:** 15–24.

Thompson, R. and Starzomski, B.M. (2007). What does biodiversity actually do? A review for managers and policy makers. *Biodiversity Conservation* **16:** 1359–1378.

Thorson, G. (1956). Marine level-bottom animal communities of recent seas. *Journal of Paleontology* **30(4):** 1001-1002.

Thorson, G. (1957). Bottom communities (sublittoral or shallow shelf). *In:* Hedgpeth, G. (ed.). Treatise on Marine Ecology and paleoecology. *Memoir of Geological Society of America* **67:** 461-534.

Thrush, S.F. and Dayton, P.K (2002). Disturbance to marine benthic habitats by trawling and dredging: implications for marine biodiversity. *Annual Review of Ecology and Systemat*ics **33:** 449–473.

Thrush, S.F. and Whitlatch, R.B. (2001). Recovery dynamics in benthic communities: balancing detail with simplification. *Ecological Studies* **151:** 297–316.

Thrush, S.F., Hewitt, J.E., Herman, P.M.J. and Ysebaert, T. (2005). Multi-scale analysis of species environment relationships. *Marine Ecology Progress Series* **302:** 13-26

Tillin, H.M., Hiddink, J.G., Jennings, S., Kaiser, M.J. (2006). Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series* **318:** 31-45.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. and Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science* **277:** 1300–1302.

Tilman, D. (2001). Functional diversity. *In:* Encyclopedia of Biodiversity, Vol. 3 (ed. S.A. Levin), Academic Press, San Diego. pp. 109–120

Tomassetti, P. and Porrello, S. (2005). Polychaetes as indicators of marine fish farm organic enrichment. *Aquaculture International* **13:** 109–128.

Townsend C.R. and Hildrew A.G. (1994). Species traits in relation to a habitat templet for river systems. *Freshwater Biology* **31:** 265–275.

Tsutsumi, H., Fukunga, S., Fujita, N. and Sumida, M., (1990). Relationship between growth of Capitella sp. and organic enrichment of the sediment. *Marine Ecology Progress Series* **63:** 157-162.

Tumbiolo, M.L. and Downing, J.A. (1994). An empirical model for the prediction of secondary production in marine benthic invertebrate populations. *Marine Ecology Progress Series* **114:** 165-174.

Ukwe, C.N. (2003). Implementing innovative best environmental practices and policy approaches for the reduction of nutrient pollution in transboundary waterbodies in Western Africa: contributions of UNIDO technical assistance programmes. *In:* Ibe, A.C. Ukwe C.N. and Nwilo, P.C. (eds.), *Proceedings of an expert group meeting on pollution and sediment sources in the Nigerian Inland waterways and strategies for their management*, Lokoja, Nigeria, pp. 198–224.

Ukwe, C.N., Ibe, C.A., Nwilo, P.C. and Huidobro, P.A. (2006). Contributing to the WSSD Targets on Oceans and Coasts in west and central Africa: The Guinea Current Large Marine Ecosystem Project. *International Journal of Oceans and Oceanography* **1:** 21-44.

Underwood, A.J. and Petraitis, P.S. (1993). Structure of intertidal assemblages in different locations: how can local processes be compared? *In:* Ricklefs, R.E. and Schluter, D. (eds) *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. The University of Chicago Press, London. pp. 39-51.

Usseglio-Polatera P., Bournaud M., Richoux P. and Tachet H. (2000b). Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater Biology* **43:** 175–205.

Van Dalfsen, J.A., Essink, K., Toxvig Madsen, H., Birklund, J., Romero, J. and Manzanera, M. (2000). Differential response of macrozoobenthos to marine sand extraction in the North Sea and Western Mediterranean. ICES *Journal of Marine Science* **57:** 1439-1445.

Vaquer-Sunyer , R. and Duarte, C.M. (2008). Threshold of hypoxia for marine biodiversity. *PNAS* **105(40):** 15452-15457

Vermeij,G.J.(1978). Biogeography and adaptation. Harvard University Press, Cambridge, Massachusetts. pp. 332.

Vetter, E. W. (1995). Detritus-based patches of high secondary production in the nearshore benthos. Marine Ecology Progress Series **120:** 251-262.

Villnäs, A., Perus, J. and Bonsdorff, E. (2011). Structure and functional shifts in zoobenthos induced by organic enrichment- implications for community recovery potential. *Journal of Sea Research* **65:** 8-18.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. and Garnier, E. (2007). Let the concept of trait be functional!. *Oikos* **116:** 882–892.

Walker, P.A and Faith, D.P. (1994). Diversity: Procedures for conservation evaluation based on phylogenetic diversity. Biodiversity. *Letters* **2:** 132–139.

Walker, B., Kinzig, A. and Langridge, J. (1999). Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species, *Ecosystems* **2:** 95–113.

WAPCo. (2003). Environmental impact assessment for the West Africa Gas Pipeline., West Africa Power Company.

Warwick, R.M. (1986). A new method for detecting pollution effects on marine macrobenthic communities. *Marine Biology* **92:** 557-562.

Warwick, R.M and Ruswahyuni (1987). Comparative study of the structure of some tropical and temperate marine soft-bottom macrobenthic communities. *Marine Biology* **95:** 641-649.

Warwick, R.M. (1988). The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. *Marine Pollution Bulletin* **19:** 259-268.

Warwick, R.M. and Clarke, K.R. (1991). A comparison of some methods for analysing changes in benthic community structure. *Journal of the Marine Biological Association of the UK* **71:** 225–244.

Warwick, R.M. and Clarke, K.R. (1993). “Increased variability as a sympton of stress in marine communities”. *Journal of Experimental Marine Biology and Ecology* **172:** 215–226.

Warwick, R.M. and Clarke, K.R. (1994). Relearning the ABC - Taxonomic changes and abundance biomass relationships in disturbed benthic communities. *Marine Biology* **118:** 739–744.

Warwick, R.M. and Clarke, K.R. (1995). New ‘biodiversity’ measures reveal a decrease in taxonomic distinctness with increasing stress. *Marine Ecology Progress Series* **129:** 301–305.

Watling, L and Norse, E.A. (1998). Disturbance of the seabed by mobile fishing gear: a comparison to forest clearcutting. *Conservation Biology* **12:** 1180-1197.

Webb, A.P. and Eyre. B.D. (2004). Effect of natural populations of burrowing Thalassinidean shrimp on sediment irrigation, benthic metabolism, nutrient fluxes and denitrification. *Marine Ecology Progress Series* **268:** 205–220

Weiher E., Clarke, G.D.P. and Keddy, P.A (1998). Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* **81:** 309–322.

Wenzhöfer, F. and Glud, R.N. (2004). Small-scale spatial and temporal variability in coastal benthic O2 dynamics: Effects of faunal activity. *Limnology and Oceanography* **49:** 1471–1481.

Weston, D.P. (1990). Quantitative examination of Macrobenthic community change along an organic enrichment gradient. *Marine Ecology Progress Series* **61:** 233-244.

Whitlatch, R.B. (1977). Seasonal changes in the community structure of the macrobenthos inhabiting the intertidal sand and mud flats of Barn stable Harbour, Massachusetts. *Biological Bulletin* **152**: 275-295.

Whitlatch, R.B. (1980). Pattern of resource utilization and coexistence in marine intertidal deposit-feeding communities. *Journal of Marine Research* **38:** 743-765.

Whitlatch, R.B. (1981). Animal-sediment relationships in intertidal marine benthic habitats: some determinants of deposit-feeding species diversity. *Journal of Experimental Marine Biology and Ecology* **53:** 31-45.

Whitlatch, R.B. and Weinberg, J.R. (1982). Factors influencing particle selection and feeding rate in the polychaete *Cistenides (Pectinaria) gouldii. Marine Biology* **71:** 33-40.

Whittaker, R.H. (1975). *Communities and ecosystems*. 2nd Edition. Macmillan, New York. pp. 352.

Wiafe, G. (2002). *Spatial and temporal dynamics of plankton communities in the Gulf of Guinea ecosystem*. PhD Thesis., University of Ghana, Legon. pp.188.

Wiafe, G., Yaqub, H. B., Mensah, M. A., and Frid, C. L. J. (2008). Impact of climate change on long-term zooplankton biomass in the upwelling region of the Gulf of Guinea. *ICES Journal of Marine Science* **65:** 318–324.

Widdicombe, S., Austen, M. C., Kendall, M. A., Olsgard, F., Schaanning, M. T., Dashfield, S. L. and Needham, H. R. (2004). Importance of bioturbators for biodiversity maintenance: indirect effects of fishing disturbance. *Marine Ecology Progress Series* **275:** 1-10.

Widdows, J., Newell, R.I.E. and Mann, R. (1989). Effects of hypoxia and anoxia on survival, energy metabolism, and feeding of Oyster Larvae (*Crassostrea virginica*, Gmelin). *Biological Bulletin* **177:** 154-166.

Wieking, G. and I. Kröncke. (2005). Is benthic trophic structure affected by food quality? The Dogger Bank example. *Marine Biology* **146:** 387-400.

Wieser. W. (1959). The effect of grain size on the distribution of small invertebrates inhabiting the beaches of Puget Sound. *Limnology and Oceanography* **4:** 181-194.

Williams N.S.G, Morgan J.W, McDonnell M.J, McCarthy M.A (2005). Plant traits and local extinctions in natural grasslands along an urban-rural gradient. *Journal of Ecology* **93:** 1203–1213.

Williams, A. and Bax, N. J. (2001). Delineating fish-habitat associations for spatially based management: an example from the south-eastern Australian continental shelf. *Marine and Freshwater Research* **52(4):** 513-536.

Willig, M.R., Kaufman, D.M., and Stevens, R.D. (2003). Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. *Annual Review of Ecology and Systematics* **34:** 273-309.

Wilson, E.O. (1994). *The Diversity of Life*. London: Penguin. pp. 243.

Witbaard, R. and Klein, R. (1994). Long-term trends on the effects of the southern North Sea beamtrawl fishery on the bivalve mollusc Arctica islandical. (Mollusca, bivalvia). *ICES Journal Marine Science* **51:** 99-105.

Wolanski, E. (2001). *Oceanographic Processes of Coral Reefs: Physical and Biological Links in the Great Barrier Reef*. Boca Raton: CRC Press.

Woodin, S.A. and Jackson, J.B.C (1979). Interphyletic competition among marine benthos. *American Zoologist* **19:** 1029-1043.

Woodin, S.A. (1981). Disturbance and community structure in shallow water sand flat. *Ecology* **62:** 1052-1066.

Woodward, G., Speirs, D.C. and Hildrew, A.G. (2005a). Quantification and resolution of a complex, size-structured food web. *Advances in Ecological Research* **36:** 85–135.

Woodward, G., Thompson, R., Townsend, C.R. and Hildrew, A.G. (2005b). Pattern and process in food webs: evidence from running waters. *In:* Belgrano, A. Scharler, U.M.

Dunne, J. and Ulanowicz, R.E. (eds.), *Aquatic Food Webs: an ecosystem approach*,. Oxford University Press, Oxford, U.K. pp. 51–66.

Woodward, F.I., Thompson, G.B. and McKee, I.F. (1991). The effects of elevated concentrations of carbon-dioxide on individual plants, populations, communities and ecosystems. *Annals of Botany* **67:** 23–38.

Woodward, F.I. and Diament, A.D. (1991). Functional approaches to predicting the ecological effects of global change. *Functional Ecology* **5:** 202-212.

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lötze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J. and Watson, R. (2006). Impacts of biodiversity loss on ocean ecosystem services. *Science* **314:** 787-790.

Wright, J.P., Naeem, S., Hector, A., Lehman, C., Reich, P.B., Schmid, B. and Tilman, D. (2006). Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters* **9:** 111–120.

Wu, R.S.S and Or, Y.Y. (2005). Bioenergetics, growth and reproduction of amphipods are affected by moderately low oxygen regimes. *Marine Ecological Progress Series* **297:** 215-223.

www.coastalwiki.org/wiki/Measurements_of_biodiversity.

Yvon-Durocher, G., Montoya, J.M., Trimmer, M. and Woodward, G. (2011). Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. *Global Change Biology* **17:** 1681–1694.

Zajac, R.N. (2008). Macrobenthic biodiversity and sea floor landscape structure. *Journal of Experimental Marine Biology and Ecology* **366:** 198-203.

Zavaleta, E.S. and Hulvey, K.B. (2004). Realistic species losses disproportionately reduce grassland resistance to biological invasions. *Science* **306:** 1175–1177.

Zmarzly, D.L., Stebbins, T.D., Pasko, D., Duggan, R.M. and Barwick, K.L. (1994). Spatial patterns and temporal succession in soft-bottom macroinvertebrate assemblages surrounding an ocean outfall on the southern San Diego shelf: relation to anthropogenic and natural events. *Marine Biology* **118:** 293-307.

APPENDIX I

Functional trait data base for the benthic macrofauna biodiversity in the GCLME

Species	**Feeding Habit**	**Feeding Structure**	**Adult Mobility**	**Sociability**	**Adult Body Size**	**Adult Body Form**
POLYCHAETA						
Amaeana trilobata	Filter feeder	Tentacles	Peristaltic crawling	Solitary	20mm	Trefoil-shaped
Ampharete acutifrons	Deposit feeder	Tentacles	Burrow/sessile	Solitary	80mm	Cylindrical and tapers towards tail
Ampharete sp	Deposit feeder	Tentacles	Burrow/sessile	Solitary	80mm	Cylindrical and tapers towards tail
Ampharete agulhaensis	Deposit feeder	Tentacles	Burrow/sessile	Solitary	15mm	Cylindrical and tapers towards tail
Amphictes gunneri	Deposit feeder	Buccal tentacles	Burrow	Solitary	60mm	Cylindrical and tapers towards tail
Ampithoie rubricata	Carnivore/detritivore	Maxillipeds	Burrow	Solitary	2.5-7mm	Laterally flattened
Ancistrosyllis rubosta	Carnivore/omnivore	Proboscis/Papillose	Creep	Solitary	54mm	Elongate and flattened
Aphrodita alba	Carnivore	Jaw	Crawl	Solitary	30mm	Oval
Aphrodita sp	Carnivore	Jaw	Crawl	Solitary	30mm	Oval
Arenicola sp.	Deposit feeder	Proboscis/Papillose	Burrow	Solitary	100-400mm	Elongate
Arabella irricolor	Carnivore	Proboscis	Burrow	Solitary	80mm	Vermiform and iridescent
Aricidea capensis	Deposit feeder	Proboscis	Burrow	Solitary	10mm	Vermiform and tapering
Aricidea curvista	Deposit feeder	Proboscis	Burrow	Solitary	20mm	Vermiform and tapering
Aricidea fauveli	Deposit feeder	Proboscis	Burrow	Solitary	20mm	Vermiform and tapering
Aricidea fragilis	Deposit feeder	Proboscis	Burrow	Solitary	20mm	Vermiform and tapering
Aricidea jeffreysi	Deposit feeder	Proboscis	Burrow	Solitary	15mm	Vermiform and tapering
Aricidea longobranchiata	Deposit feeder	Proboscis	Burrow	Solitary	20mm	Vermiform and tapering
Aricidea sp	Deposit feeder	Proboscis	Burrow	Solitary	20mm	Vermiform and tapering
Armandia cf. melanura	Deposit feeder	Proboscis	Burrow	Solitary	30mm	Long and round
Armandia intermidia	Deposit feeder	Proboscis	Burrow	Solitary	12mm	Long and round
Armandia sp.	Deposit feeder	Proboscis	Burrow	Solitary	12-30mm	Long and round
Asychis atlantideus	Deposit feeder	Proboscis/Papillose	Burrow	Solitary	100mm	Cylindrical
Asychis dorsofilis	Deposit feeder	Proboscis/Papillose	Burrow	Solitary	100mm	Cylindrical
Axiothella jarli	Deposit feeder	Proboscis/Papillose	Burrow	Solitary	35mm	Cylindrical
Capitella capitata	Deposit	Papillose	Burrow	Solitary	30mm-40mm	Thread-like

	feeder/detritivore					
Capitellid sp	Deposit feeder/detritivore	Papillose	Burrow	Solitary	30mm-40mm	Thread-like
Caulleriella acicula	Deposit feeder	Feeding palps/tentacular cirri	Burrow	Solitary	20mm	Thread-like
Caulleriella capensis	Deposit feeder	Feeding palps/tentacular cirri	Burrow	Solitary	20mm-30mm	Thread-like
Caulleriella sp	Deposit feeder	Feeding palps/tentacular cirri	Burrow	Solitary	25mm-40mm	Thread-like
Ceratonereis sp.	Omnivore	Mandibles and maxillae/jaws	Burrow	Solitary	30mm	Slender
Chloeia sp.	Carnivore	Pharynx	Burrow	Solitary	20mm-70mm	Depressed and oval
Cirratulus filliformis	Deposit feeder	Tentacles	Burrow/Sessile	Solitary	50mm	Slender
Cirratulus sp	Deposit feeder	Tentacles	Burrow/Sessile	Solitary	25mm-50mm	Slender/thread-like
Cirriformia punctata	Deposit feeder	Pharynx/ feeding palps	Burrow/Sessile	Solitary	40mm	Fairly broad
Cirriformia tentacula	Deposit feeder	Pharynx/ feeding palps	Burrow/Sessile	Solitary	200mm	Fairly broad
Clymene sp	Detritivore	Papillose proboscis	Burrow	Solitary	40mm-138mm	Cylindrical
Clymenura tenuis	Detritivore	Papillose proboscis	Burrow	Solitary	120mm	Cylindrical
Cossura costa	Deposit feeder	Pharynx	Burrow	Solitary	15mm	Thread-like and round
Diopatra cf. monroi	Carnivore	Mandibles and maxillae/jaws	Burrow	Solitary	100mm-150mm	Tube sausage-like
Diopatra cf. musseraensis	Carnivore	Mandibles and maxillae/jaws	Burrow	Solitary	50mm	Tube sausage-like
Diopatra cuprea cuprea	Carnivore	Mandibles and maxillae/jaws	Burrow	Solitary	120mm	Tube sausage-like
Diopatra monroi	Carnivore	Mandibles and maxillae/jaws	Burrow	Solitary	100mm-150mm	Tube sausage-like
Diopatra neopolitana	Carnivore	Mandibles and maxillae/jaws	Burrow	Solitary	300mm	Tube sausage-like
Diopatra neapolitana cuprea	Carnivore	Mandibles and maxillae/jaws	Burrow	Solitary	120mm	Tube sausage-like
Dorvillea rubrovittata	Carnivore	Mandibles and maxillae/jaws	Crawl	Solitary	15mm-30mm	Vermiform and elongate
Dorvillea rudolphi	Carnivore	Mandibles and maxillae/jaws	Crawl	Solitary	15mm	Vermiform and elongate
Dorvillea sp	Carnivore	Mandibles and maxillae/jaws	Crawl	Solitary	10mm-30mm	Vermiform and elongate
Drilonereis falcata	Carnivore	Mandibles and	Burrow	Solitary	100mm	Slender and round

		maxillae/jaws				
Drilonereis monroi	Carnivore	Mandibles and maxillae/jaws	Burrow	Solitary	100mm	Slender and round
Drilonereis sp	Carnivore	Mandibles and maxillae/jaws	Burrow	Solitary	100mm	Slender and round
Epiodiopatra gilchristi	Deposit feeder/carnivore	Tentacles	Burrow	Solitary	60mm	Slender
Epidiopatra hupferiana	Deposit feeder/carnivore	Tentacles	Burrow	Solitary	30mm	Slender
Epiodiopatra hupferiana monroi	Deposit feeder/carnivore	Tentacles	Burrow	Solitary	35mm	Slender
Epidiopatra sp	Deposit feeder/carnivore	Tentacles	Burrow	Solitary	30mm-60mm	Slender
Eteone foliosa	Deposit feeder	Proboscis	Burrow	Solitary	120mm	Tapered
Eteone ornata	Deposit feeder	Proboscis	Burrow	Solitary	120mm	Enlongate and tapered
Eteone (Mysta) siphodonta	Deposit feeder	Proboscis	Burrow	Solitary	200mm	Elongate and flatten
Euclymene luderitziana	Detritivore	Papillose proboscis	Burrow	Solitary	40mm	Long and broad
Euclymene lumbricoides	Detritivore	Papillose proboscis	Burrow	Solitary	150mm	Long and broad
Euclymeme oerstedi	Detritivore	Papillose proboscis	Burrow	Solitary	100mm	Slender
Euclymene sp	Detritivore	Papillose proboscis	Burrow	Solitary	40mm-150mm	Slender
Eunice antennata	Carnivore/predator	Mandibles and maxillae/pharynx	Burrow	Solitary	50mm-100mm	Round top, flattened bottom
Eunice indica	Carnivore/predator	Mandibles and maxillae/pharynx	Burrow	Solitary	50mm	Cylindrical top, flattened bottom
Eunice sp	Carnivore/predator	Mandibles and maxillae/pharynx	Burrow	Solitary	50mm-100mm	Cylindrical top, flattened bottom
Eunice vittata	Carnivore/predator	Mandibles and maxillae/pharynx	Burrow	Solitary	50mm	Cylindrical top, flattened bottom
Eurythoe complanata	Carnivore	Mandibles and maxillae/jaws	Burrow/sessile	Solitary	140mm	Elongate and flattened
Eurythoe sp.	Carnivore	Mandibles and maxillae/jaws	Burrow/sessile	Solitary	140mm-220mm	Elongate and flattened
Glycera convoluta	Carnivore/detritivore	Pharynges/papillose proboscis	Burrow	Solitary	120mm	Elongate, rounded and tapered at ends
Glycera longipinnis	Carnivore/detritivore	Pharynges/papillose proboscis	Burrow	Solitary	100mm	Elongate, rounded and tapered at ends
Glycera sp.	Carnivore/detritivore	Pharynges/papillose	Burrow	Solitary	20mm-100mm	Elongate, rounded and

		proboscis				tapered at ends
Glycera unicornis	Carnivore/detritivore	Pharynges/papillose proboscis	Burrow	Solitary	350mm	Elongate, rounded and tapered at ends
Glycinde sp	Carnivore	Papillose proboscis/macrognath	Burrow	Solitary	30mm-40mm	Elongateand tapered at both ends
Goniada sp	Carnivore	Pharynges	Burrow	Solitary	50mm-150mm	Elongateand tapered at both ends
Gravirella sp.	Carnivore/detritivore	Papillose proboscis	Burrow	Solitary	80mm	Slender and elongate
Harmothoe corralophilla	Carnivore	Pharynx	Burrow/sessile	Commensal/solitary	15mm	Broad
Harmothoe goreensis	Carnivore	Pharynx	Burrow/sessile	Commensal/solitary	10mm	Small, short and flattened
Harmothoe sp	Carnivore	Pharynx	Burrow/sessile	Commensal/solitary	10mm-35mm	Short and flattened
Hyalinoecia sp	Carnivore/omnivore	Mandibles and maxillae/jaws	Crawl	Solitary	60mm-120mm	Quill-like tube
Hyalinoecia tubicola	Carnivore/omnivore	Mandibles and maxillae/jaws	Crawl	Solitary	60mm-120mm	Quill-like tube
Isolda pulchella	Deposit feeder	Tentacles	Tube-dwelling	Solitary	45mm	Tapered
Isolda whydahaensis	Deposit feeder	Tentacles	Tube-dwelling	Solitary	5mm	Tapered
Jasmineira elegans	Filter feeder	Radioles/palps	Creep/tube-dwelling	Solitary	20mm	Small and elongated
Laonice cirrata	Deposit feeder	feedingpalps	Sessile	Solitary	100mm	Vermiform and flattened
Lumbriclymene sp.	Detritivore	Papillose proboscis	Burrow	Solitary	120mm	Long, cylindrical and slender
Lumbreneris gracilis	Carnivore	Mandibles and maxillae/jaws	Burrow	Commensal	20mm	Slender and elongate
Lumbrineris aberrans	Carnivore	Mandibles and maxillae/jaws	Burrow	Commensal	10mm	Slender and elongate
Lumbrineris cf. cavifrons	Carnivore	Mandibles and maxillae/jaws	Burrow	Commensal	25mm-65mm	Slender and elongate
Lumbrineris coccinea	Carnivore	Mandibles and maxillae/jaws	Burrow	Commensal	40mm	Slender and elongate
Lumbrinereis hartimanis	Carnivore	Mandibles and maxillae/jaws	Burrow	Commensal	100mm	Slender and elongate
Lumbrineries cf. *magalhaensis*	Carnivore	Mandibles and maxillae/jaws	Burrow	Commensal	100mm	Slender and elongate
Lumbrineris heteropoda	Carnivore	Mandibles and maxillae/jaws	Burrow	Commensal	120mm	Slender and elongate
Lumbrineris latreilli	Carnivore	Mandibles and maxillae/jaws	Burrow	Commensal	20mm	Slender and elongate

Lumbrinereis paradoxa	Carnivore	Mandibles and maxillae/jaws	Burrow	Commensal	20mm	Slender and elongate
Magelona cincta	Deposit feeder	Feeding palaps/proboscis	Burrow	Solitary	30mm	Slender
Magelona papillicornis	Deposit feeder	Feeding palaps/proboscis	Burrow	Solitary	170mm	Slender
Magelona capensis	Deposit feeder	Feeding palaps/proboscis	Burrow	Solitary	35mm	Slender
Malacoceros indica	Deposit feeder	Tentacles/feeding palps	Burrow	Solitary	60mm	Vermiform and flattened
Malacoceros sp	Deposit feeder	Tentacles/feeding palps	Burrow	Solitary	60mm	Vermiform and flattened
Magelona sp	Deposit feeder	Feeding palps	Burrow	Solitary	20mm-170mm	Slender
Maldane decorata	Detritivore	Pharynx	Burrow	Solitary	100mm	Sausage-like mud tube
Maldane sarsi	Detritivore	Pharynx	Burrow	Solitary	100mm	Sausage-like mud tube
Maldanella sp	Detritivore	Pharynx	Burrow	Solitary	45mm-70mm	Cylindrical and elongate
Marphysa adenensis	Omnivore/detritivore	Mandibles and maxillae/pharynx	Burrow	Solitary	70mm	Slender and rounded
Marphysa cf. mossambica	Omnivore/detritivore	Mandibles and maxillae/pharynx	Burrow	Solitary	350mm	Slender and flattened
Marphysa sanguinea	Omnivore/detritivore	Mandibles and maxillae/pharynx	Burrow	Solitary	250mm	Long and oval
Marphysa sp.	Omnivore/detritivore	Mandibles and maxillae/pharynx	Burrow	Solitary	30mm-250mm	Slender, rounded /flattened
Magelomma vesiculosum	Filter feeder	Tentacular crown	Sessile	Solitary	100mm	Slightly tapered
Megalomma sp	Filter feeder	Tentacular crown	Sessile	Solitary	20mm-100mm	Slightly tapered
Mesochaetopterus minutes	Detritivore	Grooved palps	Burrow	Solitary	15mm	Elongate
Naineris laevigata	Detritivore/carnivore	Proboscis	Burrow	Solitary	40mm	Vermiform and flattened
Nematonereis unicornis	Detritivore/carnivore	Mandibles and maxillae	Burrow	Solitary	150mm-200mm	Slender
Nephtys capensis	Carnivore	Pharynges/papillose proboscis	Burrow	Solitary	60mm	Elongate and depressed
Nephtys (aglaophamus) dibranchis	Carnivore	Pharynges/papillose proboscis	Burrow	Solitary	25mm	Elongate and depressed
Nephtys (aglaophamus) lyrochaeta	Carnivore	Pharynges/papillose proboscis	Burrow	Solitary	30mm	Elongate and depressed
Nephtys hombergi	Carnivore	Pharynges/papillose proboscis	Burrow	Solitary	200mm	Elongate and depressed
Nephtys macrousa	Carnivore	Pharynges/papillose	Burrow	Solitary	150mm	Elongate and depressed

		proboscis				
Nephtys sp	Carnivore	Pharynges/papillose proboscis	Burrow	Solitary	6.5mm-200mm	Elongate and depressed
Nephtys sphaerocirrata	Carnivore	Pharynges/papillose proboscis	Burrow	Solitary	25mm	Elongate and depressed
Neries sp.	Omnivore/filter feeder/deposit feeder	Papillose proboscis	Burrow/creep	Solitary/commensal	15mm-120mm	Elongate
Neridines gilchristi	Deposit feeder	Tentacles/palps	Burrow	Solitary	25mm	Vermiform and flattened
Nicolea sp.	Deposit feeder	Buccal tentacles	Sessile	Solitary	50mm-100mm	Elongate and tapered
Nicomache sp.	Deposit feeder	Jaws/keel	Burrow/sessile	Solitary	160mm-240mm	Cylindrical
Notomastus aberrans	Deposit feeder	Jaws	Burrow	Solitary	60mm	Elongate and round
Notomastus fauvelli	Deposit feeder	Jaws	Burrow	Solitary	90mm	Elongate and round
Notomastus latriceus	Deposit feeder	Jaws	Burrow	Solitary	300mm	Elongate and round
Notomastus sp	Deposit feeder	Jaws	Burrow	Solitary	60mm-300mm	Elongate and round
Onuphis (Nothria) conchylega	Omnivore	Jaws	Sessile	Solitary	40mm-150mm	Elongate and vermiform
Onuphis eremita	Omnivore	Jaws	Sessile	Solitary	80mm-120mm	Elongate and vermiform
Onuphis geophiliformis	Omnivore	Jaws	Sessile	Solitary	30mm	Elongate and vermiform
Onuphis holobranchiata	Omnivore	Jaws	Sessile	Solitary	60mm	depreesed
Onuphis sp.	Omnivore	Jaws	Sessile	Solitary	40mm-350mm	Elongate and vermiform
Ophelina sp	Deposit feeder	Proboscis	Burrow	Solitary	50mm	Vermiform
Ophiodromus cf. berrisfordi	Carnivore	Proboscis	Burrow	Solitary	28mm	Flattened and tapered
Ophiodromus sp	Carnivore	Proboscis	Burrow	Solitary	8mm-28mm	Flattened and tapered
Orbinia curvieri	Deposit feeder	Pharynges	Burrow	Solitary	300mm	Vermiform
Oriopsis neglecta	Suspension feeder	Branchial crown/radioles/palps	Creep	Solitary	3mm-4mm	Fairly stout
Paralacydonia paradoxa	Omnivore/carnivore	Pharynx/papillose	Burrow/swim	Solitary	20mm-30mm	Elongate and rectangular
Paraonides sp.	Deposit feeder/surface feeder	Pharynges	Burrow	Solitary	10mm-20mm	Thread-like
Paraonides lyra capensis	Deposit feeder/surface feeder	Pharynges	Burrow	Solitary	10mm	Thread-like
Pareulepis sp	Deposit feeder/carnivore	Jaws	Burrow	Solitary/commensal	35mm	Oblong
Paronuphis antartica	Carnivore	Mandibles and maxillae/pharynx	Burrow	Solitary	20mm-30mm	Vermiform and elongate
Paronuphis sp.	Carnivore	Mandibles and	Burrow	Solitary	20mm-30mm	Vermiform and elongate

		maxillae/pharynx				
Pectinaria koreni cirrata	Deposit feeder	Tentacles	Burrow/sessile	Solitary	10mm	Tapered
Pherusa sp	Detritivore	Grooved palps/papillose	Burrow	Solitary	30mm	Cylondrical and narrowed posteriorly
Pholoe minuta	Carnivore	Jaws	Creep/crawl	Solitary	10mm	Small and oblong
Phyllocomus sp	Deposit feeder	Buccal tentacles	Burrow	Solitary	50mm	Tapered
Phyllodoce (anatides) madarensis	Carnivore	Pharynx	Burrow	Solitary	100mm	Long and tapered
Phyllodoce malmgreni	Carnivore	Pharynx	Burrow	Solitary	70mm	Long and slender
Phyllodoce scharmadai	Carnivore	Pharynx	Burrow	Solitary	30mm	Long and slender
Phyllodoce sp	Carnivore	Pharynx	Burrow	Solitary	25mm	Long and slender
Phylo foetida linguistica	Deposit feeder	Proboscis	Burrow	Solitary	50mm	Vermiform and flattened
Pistia costata	Filter feeder	Tentacles	Peristaltic crawling	Solitary	25mm	Tapered
Pista cristata	Filter feeder	Tentacles	Peristaltic crawling	Solitary	60mm	Tapered
Pista sp	Filter feeder	Tentacles	Peristaltic crawling	Solitary	10mm	Tapered
Piromis sp	Detritivore	Jaws	Burrow/creep	Solitary	90mm	Tapered posteriorly
Polycirrus sp	Deposit feeder	Buccal tentacles	Burrow	Solitary	15mm	Evenly tapered
Potamilla linguicollris	Filter feeder	Branchial crown	Burrow	Solitary	60mm	Slender
Polyophthalamus sp	Deposit feeders	Proboscis	Burrow	Solitary	25mm	Short and slender
Polyodontes melanontus	Carnivore/omnivore	Pharynx	Burrow	Solitary	300mm	Stout anterior and flattened posterior
Praxillela cf. affinis	Deposit feeder/detritivore	Proboscis	Burrow	Solitary	100mm	Cylindrical
Praxillela sp	Deposit feeder/detritivore	Proboscis	Burrow	Solitary	100mm	Cylindrical
Prionospio cirrifera	Deposit feeder	Proboscis	Burrow	Solitary	30mm	Vermiform and flattened
Prionospio cirrobranchiata	Deposit feeder	Proboscis	Burrow	Solitary	15mm	Small and thread-like
Prionospio elhersi	Deposit feeder	Proboscis	Burrow	Solitary	20mm	Vermiform and flattened
Prionospio malmgreni	Deposit feeder	Proboscis	Burrow	Solitary	25mm	Thread-like
Prionospio pinnata	Deposit feeder	Proboscis	Burrow	Solitary	60mm	Vermiform and flattened
Prionospio saldanha	Deposit feeder	Proboscis	Burrow	Solitary	25mm	Thread-like
Prionospio sexoculata	Deposit feeder	Proboscis	Burrow	Solitary	10mm-20mm	Vermiform and flattened
Prionospio sp	Deposit feeder	Proboscis	Burrow	Solitary	10mm-60mm	Vermiform and flattened
Sabellides octocirrata	Filter feeder	Tentacles	Burrow	Solitary	10mm	Tapered
Scalistosus fragilis	Deposit feeder	Proboscis/jaws	Burrow	Solitary	15mm	Short and depressed
Schroederella sp.	Deposit feeder	Proboscis	Burrow	Solitary	3mm-4mm	Vermiform, flattened and minute

Scolelepis squamata	Deposit feeder	palps	Burrow	Solitary	80mm	Vermiform and flattened
Scolaricia dubia	Detritivore	Proboscis	Burrow	Solitary	35mm	Vermiform and flattened
Scoloplos madagascariensis	Carnivore	Tentacles	Burrow	Solitary	120mm	Vermiform and flattened
Scoloplos sp.	Carnivore	Tentacles	Burrow	Solitary		Vermiform and flattened
Scyphoproctus sp.	Deposit feeder	Probocsis/papillose	Burrow	Solitary	23mm-30mm	Slender and cylindrical
Sigalion spp.	Carnivore	Jaws	Burrow	Solitary	30mm-300mm	Depressed and square in section
Spiohanes sp.	Deposit feeder	Palps	Burrow	Solitary	25mm-60mm	Vermiform and flattened
Spio filicornis	Deposit feeder	Palps	Burrow	Solitary	30mm	Vermiform and flattened
Spiohanes bombyx	Deposit feeder	Palps	Burrow	Solitary	60mm	Vermiform and flattened
Spio multiculata	Deposit feeder	Palps	Burrow	Solitary		Vermiform and flattened
Spio sp.	Deposit feeder	Palps	Burrow	Solitary		Vermiform and flattened
Sternapsis scutata	Deposit feeder/detritivore	Papillose	Burrow	Solitary	20mm-30mm	Dumb-bell shaped and swollen
Sthenelais limicola	Deposit feeder/detritivore	Papillose	Burrow	Solitary	80mm	Elongate and flattened
Sthenolepis tetragona	Deposit feeder/detritivore	Papillose	Burrow	Solitary	80mm	Elongate and flattened
Sthenolepis sp.	Deposit feeder/detritivore	Papillose	Burrow	Solitary	50mm	Elongate and flattened
Strenaspsis persica	Deposit feeder/detritivore	Papillose	Burrow	Solitary	20mm-30mm	Dumb-bell shaped and swollen
Syllis benguellana	Carnivore	Pharyngneal tooth/proventricle	Burrow	Solitary	9mm	Thread-like
Syllis (syllis) gracilis	Carnivore	Pharyngneal tooth/proventricle	Burrow	Solitary	35mm	Slender
Syllis hyalina	Carnivore	Pharyngneal tooth/proventricle	Burrow	Solitary	35mm	Slender
Syllis sp	Carnivore	Pharyngneal tooth/proventricle	Burrow	Solitary	8mm-40mm	Thread-like/slender
Syllis spongida	Carnivore	Pharyngneal tooth/proventricle	Burrow	Solitary	25mm	Thread-like/slender
Terebella pterochaeta	Deposit feeder	Tentacles/ mouth	Burrow	Solitary/colony	100mm	Slender and evenly tapered
Terebellids sp.	Deposit feeder	Tentacles	Burrow	Solitary/colony	70mm	Uniformly tapered
Terebellides stroemi	Deposit feeder	Tentacles	Burrow	Solitary/colony	70mm	Uniformly tapered
Thalenessa oculata	Detritivore	Jaws	Burrow	Solitary	200mm	Elongate and flattened
Tharynx	Deposit feeder	Pharynx/feeding palps	Burrow	Solitary	35mm	Thread-like

dorsobranchialis						
Tharyx filibranchia	Deposit feeder	Pharynx/feeding palps	Burrow	Solitary	20mm	Cylindrical and elongate
Tharyx sp	Deposit feeder	Pharynx/feeding palps	Burrow	Solitary	20mm-100mm	Cylindrical and elongate
CRUSTACEA						
Alpheus sp.	Deposit feeder/detritivore	Rostrum	Burrow/swim	Solitary	50mm	Laterally-compressed
Ampelisca sp.	Detritivore	Mandibular palps	Swim	Solitary	5mm	Laterally-flattened/hunchbacked
Ampithoe sp.	Detritivore/scavengers	Rostrum/gills	Crawl/Burrow	Solitary	15mm	Laterally-flattened/hunchbacked
Anthura sp.	Carnivore/predator	Mandibular palps/maxillipeds	Crawl/Burrow/swim	Solitary	8mm-20mm	Elongate, worm-like body/dorso-ventrally compressed
Aorid sp	Filter feeder	Mandibular palps	Crawl/Burrow/swim	Solitary	2.5mm-6mm	Laterally-flattened/hunchbacked
Apseudes latreille	Filter feeder/detritivore	Mandibular palps/maxillipeds	Creep	Solitary	2mm-12mm	Elongate,cylindrical/dorso-ventrally flattened
Apseudes sp.	Filter feeder/detritivore	Mandibular palps/maxillipeds	Creep	Solitary	2mm-6mm	Elongate,cylindrical/dorso-ventrally flattened
Callianassa sp. A	Detritivore	Maxillipeds	Burrow	Solitary	40mm-50mm	Laterally-compressed
Caridea sp.	Scavenger/detritivore	Rostrum/teeth	Swim	Solitary	12mm-70mm	Laterally-compressed
Cirolana sp.	Omnivore	Mandibles, maxillae and maxillipeds	Runs/Burrow	Solitary	10mm-15mm	Dorso-ventrally compressed
Eurydice	Omnivore	Mandibles, maxillae and maxillipeds	Runs/Burrow	Solitary	10mm	Dorso-ventrally compressed
Excirolana sp.	Scavenger	Mandibular palps/maxillipedes	Swim/Burrow	Solitary	10mm	Dorso-ventrally compressed
Galathea sp..	Omnivore	Rostrum/teeth	Burrow/creep	Solitary	7mm	Lobster-like, hard body with fan shaped tail
Hermit crab	Detritivore/ filter feeding	Claws/third maxillipedes	Crawl	Solitary	20mm-40mm	Occupys hard spiralled gastropod shell
Hyale pontica	Herbivore/omnivore	Mandibular palps/ maxillipeds	Swim/Burrow	Solitary	10mm	Laterally flattened
Iphinoe brevipes	Carnivore	Mandilbes and maxillae	Burrow/swim	Solitary	10mm-20mm	Oval,flattened and compact
Iphinoe sp	Carnivore	Mandilbes and maxillae	Burrow/swim	Solitary	10mm-20mm	Oval,flattened and compact
Ischyrocerus sp	Herbivore/omnivore	Mandibular palps/maxillipeds	Burrow/crawl	Solitary	1.5mm-6mm	Latterally flattened
Leucothoe sp	Filter feeder	Pumped through	Burrow/swim	Commensal	10mm	Latterally flattened

		sponge				
Ligia olfersi	Scavengers	Mandibles,maxillae and maxillipeds	Runs/Burrow	Solitary	15mm-25mm	Broad, flattened and smooth
Liljeborgia sp.	Carnivore	Mandibular palp/maxillipeds	Burrow	Commensal/solitary	1.5mm-5mm	Latterally flattened
Mysid	Omnivore/herbivore	Mandibles, maxillae and maxillipeds	Swim/Burrow	Solitary	40mm-50mm	Latterally compressed
Palinurus sp	Omnivore	Rostrum/teeth	Burrow	Solitary	250mm	Elongate, semi-circular with fan-like telson
Penaeid shrimp	Scavenger/detritivore	Rostrum/teeth	Swim	Solitary	60mm	Cylindrical and latterally compressed
Perioculodes sp.	Omnivore	Rostrum/teeth	Burrow/swim	Solitary	2mm-5mm	Larrerally flattened
Portumnus sp.	Carnivores /detritivore	Maxilliped, mandibular, cheliped	Swim	Solitary	33-170mm width, 23-76mm length	Dorso-ventrally flattened
Tanaids	Filter feeder	Mandibles, maxillipeds and chela	Burrow	Solitary	2mm-6mm	Elongate body, cylindrical/dorsoventrally flattened
Uca tangerii	Detritivore	buccal frame,chelae	Burrow	Solitary	14-30mm width, 8-17mm length	Dorso-ventrally flattened
Upogebia sp.	Filter feeder	Maxillipeds/mandibular palps	Burrow	Solitary	40mm	Elongate,semi-circular withfan-like telson
Urothoe sp.	Detritivore	Maxillipeds/mandibles	Burrow	Solitary	2mm-5mm	Laterally flattened
Xanthid crab	Detritivore	Buccal frame, chelae	Burrow	Solitary/commensal	15mm-25mm	Dorso-ventrally flattened with broad carapace
MOLLUSCS						
Arca subglobosa	Filter feeder	Siphon/gills	Burrow/sessile	Solitary	12mm-25mm	Almost square,rounded anterior, pointed posterior
Asterina sp.	Carnivore	Tube feet/ stomach	Burrow/sessile	Solitary	20mm	Flattened body with short rounded arms
Cardium sp	Filter feeder	Siphon/gills	Burrow/sessile	Solitary	15-100mm	Circular
Corbula sp	Filter feeder	Siphon/gills	Burrow	Solitary	200mm	Oval to triangular
Chiton canariensis	Omnivore	Radula	Creep/sessile	Colony	20mm-35mm	Oval and flattened
Diplodonta sp.	Filter feeder	Siphon/gills	Burrow/ creep	Solitary	15mm-25mm	Circular
Donax oweni	Filter feeder	Siphon/gills	Burrow/sessile	Colony	10mm-20mm	Triangular
Dosinia sp.	Filter feeder	Siphon/gills	Burrow	Colony	15mm-30mm	Circular /triangular
Glycemeris seripta	Filter feeder	Siphon/gills	Burrow	Solitary	50mm	Slightly rounded

Fusus sp.	Herbivore	Radula	Burrow /sessile	Solitary	70mm	Slender shell
Mactra sp.	Filter feeder	Siphon/gills	Burrow	Colony	30-55mm	Triangular
Dentalium coarti	Omnivore	Tentacles/captacula	Burrow/creep	Solitary	40mm	Tusk-shaped
Dentalium maltzani	Omnivore	Tentacles/captacula	Burrow/creep	Solitary	40mm	Tusk-shaped
Mactra stultorum	Filter feeder	Siphon/gills	Burrow	Colony	30-50mm	Triangular
Pitaria cf. tumens	Filter feeder	Siphon/gills	Burrow/sessile	Solitary	20mm-50mm	Triangular and rounded
Dentalium spp.	Filter feeder	Tentacles/feeding chamber	Burrow/creep	Solitary	32mm	Tusk-shaped
Tellina hyalina	Filter feeder	Siphon/gills	Burrow/sessile	Colony	25-40mm	Triangular and rounded
Tellina sp.	Filter feeder	Siphon/gills	Burrow/sessile	Colony	25-40mm	Triangular and rounded
Tivela sp.	Filter feeder	Siphon/gills	Burrow	Solitary	15-30mm	Triangular
ECHINODERMA						
Amphioplus archeri	Suspension feeder/ deposit feeder	Tube feet	Crawl	Solitary	10mm	Flat,circular body with five thin arms
Amphioplus aurensis	Suspension feeder/ deposit feeder	Tube feet	Crawl	Solitary	10mm	Flat,circular body with five thin arms
Amphiura sp	Suspension feeder/ deposit feeder	Tube feet	Crawl	Solitary	25mm	Flat,circular body with five thin arms
Sand dollar	Suspension feeder	Aristotle's lantern	Burrow	Solitary	38mm-40mm	Oval/ circular and flattened
Ophuira africana	Deposit feeder	Aristotle's lantern	Burrow	Solitary	25mm	Star-like and flattened
Ophiotrix sp.	Detritivore	Aristotle's lantern/tube feet	Crawl	Solitary	50mm	Flat,circular body with five thin arms
Diadema sp.	Detritivore/herbivore	Aristotle's lantern/tube feet	Burrow	Solitary	70mm	Oval, heart-shaped, circular and flattened
OTHERS						
Cavolinia sp.	Herbivore/detritivore	Radula	Swim	Solitary	3mm	Bubble-like shell with three stubby horns
Echiura	Deposit feeder/filter feeder	Proboscis	Burrow	Solitary	30mm-40mm	Sausage-shaped trink with flaccid proboscis
Hermit crab	Omnivore/detritivore	Mandibles,maxillae and chela	Creep/burrow	Solitary		Occupys spiralled gastropod shell
Hirudinea sp.	Carnivore/blood sucking	Proboscis/suckers	Wiggle	Solitary	12mm-30mm	Dorso-ventrally flattened
Hydrozoa	Carnivore	Gastrozooid	Sessile	Solitary/colony	10mm-200mm	Tree-like or feather-like
Nemertean worm	Carnivore/scavenger	Proboscis/mouth	Glide/crawl/swim	Solitary	20mm-300mm	Thin and elongate
Sea cucumber	Scavenger/commensal	Tentacles	Crawl	Solitary	30mm-240mm	Elongate or sausage-saped
Sipuncula sp.	Suspension feeder/ deposit feeder	Introvert/tentacles	Burrow	Solitary	2mm-720mm	Cylindrical/sac-like body

Hydroid	Carnivore	Tentacles	Sessile	Colony	10mm-200mm	Tree-like or feather-like
Oligochate sp.	Detritivore/omnivore	Mouth	Burrow	Solitay	10mm	Long, cylindrical,tapered at ends
Ophuiroid sp.	Detritivore/herbivore	Tube feet/toothed jaw	Crawl	Solitary	45mm-100mm	Flat, circular body with five thin arms
Ostracod	Herbivore	Mandibles,maxillae	Burrow	Solitary	1mm-4mm	Short head and oval body
Pagurus sp.	Filter feeder	Mandibles,maxillae and chela	Burrow	Solitary	8mm	Occupys spiralled gastropod shell
Sipunculid sp.	Detritivore	Tentacles	Burrow	Solitary	10mm-50mm	Short bulbous body and elongate tubular introvert
Virgularia sp.	Carnivore	Tentacles, pharynx and siphonoglyph	Sessile	Colony	70mm	Feather-shaped, fan-like body

APPENDIX II

Functional Trait Richness Data Across Sampling Stations

FEEDING HABIT	GB-01	GB-02	GB-03	GB-04	GU-01	GU-02	GU-03	GU-04	SL-01	SL-02	SL-03	SL-04	LI-01	LI-02	LI-03	LI-04
Herbivore	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivore	1	7	1	0	8	4	5	8	1	1	5	5	3	3	1	4
Omnivore	0	0	0	0	1	3	1	0	0	0	1	0	0	0	0	2
Filter Feeding	2	1	3	1	2	0	1	3	3	0	2	0	0	2	2	0
Deposit Feeding	3	9	2	3	7	12	6	9	0	4	10	3	2	5	2	1
Detritivore	0	2	2	2	1	2	2	3	1	1	2	2	2	1	1	1
Scavenging	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0
Suspension Feeding	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivore/Omnivore	0	1	0	0	1	0	1	0	0	0	2	0	1	1	0	1
Herbivore/Omnivore	0	1	1	0	1	2	1	2	0	0	0	0	1	0	0	0
Carnivore/Detritivore	0	1	0	0	2	1	1	2	1	0	1	1	0	0	1	1
Detritivore/Deposit Feeding	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Carnivore/Deposit Feeding	0	1	1	0	2	0	1	0	0	0	0	0	0	0	0	0
Carnivore/Predator	0	2	0	0	1	1	3	3	1	0	0	1	1	0	0	1
Omnivore/Detritivore	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Detritivore/Filter Feeding	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Detritivore/Scavenging	0	0	0	0	0	1	0	3	0	0	0	0	0	0	0	0
Herbivore/Scavenging	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Herbivore/Detrivore	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Carnivore/Scavenging	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Scavenging/Commensal	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Carnivore/Blood Sucking	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deposit Feeding/Filter Feeding	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deposit Feeding/Surface Feeding	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deposit Feeding/Suspension Feeding	0	0	0	0	2	0	0	1	1	1	2	0	0	1	3	2
Autotroph/Carnivore/Filter Feeding	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Omnivore/Filter Feeding/Deposit Feeding	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

FEEDING STRUCTURE	GB-01	GB-02	GB-03	GB-04	GU-01	GU-02	GU-03	GU-04	SL-01	SL-02	SL-03	SL-04	LI-01	LI-02	LI-03	LI-04
Tentacles	0	6	2	0	4	2	2	1	0	0	3	2	3	0	2	0
Buccal tentacles	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maxillipeds	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proboscis/Papillose	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0
Jaws	0	0	0	0	1	2	0	2	0	1	2	1	0	1	0	2
Proboscis	2	4	2	2	7	9	6	6	0	2	4	0	1	1	0	1
Papillose	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feeding palps/Tentacular cirri	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Mandibles/Maxillae/Jaws	0	3	0	0	4	0	3	4	2	0	6	5	3	3	1	4
Pharynx	1	2	0	0	1	1	2	2	0	1	1	0	0	0	1	0
Pharynx/ Feeding palps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pharynges/Papillose	0	2	0	0	3	1	1	2	1	0	0	2	1	1	1	2
Papillose Proboscis/Macrognath	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pharynges	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1
Radioles/palps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feeding palps	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Feeding palps/Branchial crown	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feeding palps/Proboscis	0	1	0	0	0	0	0	0	0	0	2	0	0	1	0	0
Tentacles/Feeding palps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tentacular crown	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grooved Palps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mandibles and Maxillae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Tentacles/palps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jaws/Keel	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Branchial crown/Radioles/palps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pharynx/Papillose	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Pharynges/Papillose	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grooved palps/Papillose	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Branchial Crown	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proboscis/jaws	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Pumped through sponge	0	0	1	0	1	0	0	1	1	0	0	0	0	1	0	0
Palps	0	1	0	1	0	2	1	0	0	0	1	0	0	0	0	0
Pharyngneal tooth/proventricle	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0
Tentacles/ mouth	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rostrum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mandibular palps	0	1	1	1	0	1	1	1	1	0	1	1	1	1	1	1
Rostrum/gills	0	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0
Mandibular palps/Maxillipeds	0	0	2	0	0	5	1	4	1	0	0	0	0	0	0	0
Rostrum/Teeth	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Mandibles/Maxillae/Maxillipeds	0	1	0	0	1	2	2	1	0	0	0	0	1	0	0	0
Mandibles	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mandibles and Maxillipeds	0	1	1	1	0	1	0	1	0	1	0	0	0	0	0	0
Claws/Third maxillipedes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Maxilliped, Mandibular, Cheliped	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mandibles, Maxillipeds/ Chela	0	1	1	1	1	0	0	1	1	0	1	0	0	1	0	0
Buccal Frame/Chelae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Siphon/Gills	2	0	1	0	0	0	1	0	1	0	1	0	0	0	1	0
Tube feet/ Stomach	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Radula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tentacles/Captacula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tentacles/Feeding chamber	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tube feet	0	0	0	0	1	0	0	0	1	1	1	0	0	1	2	1
Aristotle's lantern	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Aristotle's lantern/Tube feet	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Gastrozooid/Tentacles	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proboscis/suckers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gastrozooid	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Proboscis/mouth	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Introvert/tentacles	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1
Ostia/Pinacocytes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beak/radula/tentacles	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mouth	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tube feet/Toothed jaw	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Mandibles/maxillipedes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tentacles/Pharynx/Siphonoglyph	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RELATIVE ADULT MOBILITY	GB-01	GB-02	GB-03	GB-04	GU-01	GU-02	GU-03	GU-04	SL-01	SL-02	SL-03	SL-04	LI-01	LI-02	LI-03	LI-04
Peristaltic crawling	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Burrowing/Sessile	1	2	1	0	1	1	1	2	1	0	1	2	0	0	0	0
Burrowing	5	19	7	5	22	17	16	23	4	6	20	10	7	8	7	8
Creeping	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Crawling	0	1	0	0	2	0	1	0	1	1	3	0	2	1	2	2
Sessile	0	0	0	0	1	3	0	1	0	0	2	0	0	1	0	2
Sessile/Creep	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Burrow/Creep	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tube-dwelling	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Creep/Tube-dwelling	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Burrow/Swim	0	1	3	0	2	2	2	2	2	0	0	0	1	2	0	0
Creep/Crawl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Swim	0	1	1	1	1	1	1	3	1	0	1	1	1	1	1	1
Crawl/Burrow	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0
Crawl/Burrow/Swim	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Run/Burrow	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Wiggle	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glide/Crawl/Swim	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
SOCIABILITY	GB-01	GB-02	GB-03	GB-04	GU-01	GU-02	GU-03	GU-04	SL-01	SL-02	SL-03	SL-04	LI-01	LI-02	LI-03	LI-04
Solitary	5	24	10	6	27	28	22	28	6	7	25	11	9	12	8	11
Commensal	0	1	1	0	2	0	0	3	2	0	1	2	1	2	0	2
Commensal/Solitary	0	1	0	0	0	1	1	2	0	0	0	0	0	0	0	0
Solitary/Colony	0	0	0	0	0	1	0	2	0	0	1	0	1	0	1	0
Colony	1	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0
ADULT BODY SIZE	GB-01	GB-02	GB-03	GB-04	GU-01	GU-02	GU-03	GU-04	SL-01	SL-02	SL-03	SL-04	LI-01	LI-02	LI-03	LI-04
0.5-20mm	1	7	9	4	7	12	6	11	6	4	7	2	3	3	4	5
20.5-40mm	4	4	1	0	3	4	7	6	1	1	4	2	2	6	2	1

40.5-60mm	1	8	1	2	7	5	4	8	2	0	3	2	2	1	1	2
60.5-80mm	0	1	0	0	2	2	3	1	0	0	2	1	1	0	1	0
80.5-100mm	0	2	0	0	4	2	2	4	0	1	6	1	2	1	0	3
100.5-120mm	0	2	1	0	2	3	1	2	0	0	2	2	0	1	0	0
>120mm	0	1	0	0	1	2	0	2	0	1	3	3	1	2	2	2
ADULT BODY FORM	GB-01	GB-02	GB-03	GB-04	GU-01	GU-02	GU-03	GU-04	SL-01	SL-02	SL-03	SL-04	LI-01	LI-02	LI-03	LI-04
Vermiform and Flattened	2	4	1	2	2	6	5	3	0	0	4	1	0	2	0	1
Slender and Elongate	0	1	0	0	1	0	0	2	1	0	1	2	1	1	0	2
Slender	0	2	1	0	3	1	2	1	0	0	3	1	0	1	0	0
Trefoil-shaped	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
oval	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cylindrical & Tapered Posterior	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Elongate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vermiform & Iridescent	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Vermiform and Tapering	0	0	1	1	1	3	1	1	0	0	1	0	1	0	0	0
Long and Round	0	1	1	0	1	0	0	1	0	1	1	0	0	0	0	0
Cylindrical	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0
Thread-like	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
Depressed and Oval	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Broad	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thread-like & Round	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sausage-like	0	1	0	0	1	0	0	0	0	0	2	1	0	1	1	0
Vermiform and Elongate	0	0	0	0	1	2	0	0	0	0	1	0	0	0	0	2
Tapered	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Elongate and Tapered	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Long and Broad	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Round top/Flattened bottom	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cylindrical top/Flattened bottom	0	2	0	0	1	0	2	2	1	0	1	1	1	0	0	1
Elongate/Rounded & Tapered at ends	0	1	0	0	3	1	1	2	1	0	0	1	0	0	1	1
Elongate & Tapered at ends	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1
Small/Short & Flattened	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Quill-like tube	0	1	0	0	1	0	1	0	0	0	2	0	1	0	0	1
Small & Elongated	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Long, Cylindrical & Slender	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cylindrical & Elongate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Slender & Rounded	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Slender &Flattened	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Long & Slender	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Slender & Rectangular	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Long & Oval	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Slender, Rounded & Flattened	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Slightly tapered	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elongate & Depressed	1	1	0	0	1	0	0	0	0	0	0	1	1	1	0	1
Elongate & Flattened	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elongate & Round	0	0	0	0	0	0	0	2	0	1	1	1	0	1	0	0
Depreesed	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vermiform	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Flattened & tapered	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fairly Stout	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elongate & Rectangular	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Oblong	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cylindrical & Narrow Posteriorly	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Small & Oblong	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Long & Slender	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0
Tapered Posteriorly	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Evenly Tapered	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Short & Slender	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0
Stout Anterior & Flattened Posterior	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Small & Thread-like	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Short & Depressed	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Vermiform/flattened & Minute	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0
Slender & Cylindrical	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Depressed & Square in Section	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dumb-bell shaped and Swollen	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thread-like/Slender	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Slender & Evenly tapered	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Uniformly Tapered	0	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0
Laterally-compressed	0	1	0	0	1	1	1	2	0	0	0	0	1	0	0	0
Laterally-flattened	0	1	1	1	1	2	1	2	1	0	1	1	1	1	1	1
Elongate, Worm-like & Dorso-ventrally Compressed	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Elongate, Cylindrical/Dorso-ventrally Flattened	0	1	1	1	1	1	0	2	1	0	1	0	0	1	0	0
Dorso-ventrally compressed	0	0	1	0	0	3	1	0	1	0	0	0	0	0	0	0
Lobster-like, Hard body with Fan shaped tail	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hard spiralled Shell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Latterally Flattened	0	1	3	1	1	3	0	4	1	1	0	0	0	1	0	0
Oval, Flattened & Compact	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Broad, Flattened & Smooth	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elongate, Semi-circular with fan-like telson	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cylindrical & Latterally Compressed	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Dorso-ventrally flattened	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dorso-ventrally flattened with broad carapace	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Square, Rounded anterior, Pointed posterior	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Flattened & Short Rounded Arms	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Circular	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Oval to triangular	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oval & Flattened	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triangular	1	0	1	0	0	0	1	0	1	0	0	0	0	0	0	0
Slightly Rounded	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Slender shell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tusk-shaped	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triangular and Rounded	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Flat, Circular & Five thin arms	0	0	0	0	1	0	0	0	1	1	1	0	0	1	2	1
Oval/ Circular and flattened	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Star-like & Flattened	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oval, Heart-shaped, Circular & Flattened	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Bubble-like shell & Three Stubby Horns	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sausage-shaped trunk & Flaccid Proboscis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree-like or Feather-like	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Thin and Elongate	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0

Elongate/ Sausage-saped	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cylindrical/Sac-like	0	0	0	0	1	0	0	1	0	0	1	0	0	0	1	1
Short Head & Oval Body	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

FEEDING HABIT	CD-01	CD-02	CD-03	CD-04	GH-01	GH-02	GH-03	GH-04	TG-01	TG-02	TG-03	TG-04	BN-01	BN-02	BN-03	BN-04
Herbivore	0	0	0	0	0	0	0	0	1	1	2	0	1	1	1	2
Carnivore	5	3	4	2	5	1	6	3	10	12	13	11	11	16	12	12
Omnivore	0	0	0	0	2	1	0	0	4	0	2	3	3	4	1	1
Filter Feeding	0	0	0	0	6	0	4	1	3	2	4	2	1	6	1	6
Deposit Feeding	3	3	6	4	7	9	5	5	14	13	31	16	7	13	4	13
Detritivore	0	0	0	0	2	1	0	1	6	3	6	5	3	7	6	5
Scavenging	0	0	0	0	2	1	0	1	0	0	0	0	0	0	1	0
Suspension Feeding	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Carnivore/Omnivore	1	1	1	0	1	0	2	1	1	0	0	0	0	0	1	0
Herbivore/Omnivore	0	0	1	0	0	0	1	0	2	1	1	2	0	1	1	0
Carnivore/Detritivore	0	1	0	0	2	1	2	1	5	1	3	0	2	2	1	2
Detritivore/Deposit Feeding	0	0	1	0	2	0	1	2	3	0	3	2	3	3	2	4
Carnivore/Deposit Feeding	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	1
Carnivore/Predator	0	1	0	0	1	0	1	1	1	2	2	1	1	0	1	2
Omnivore/Detritivore	1	2	0	0	0	0	0	1	1	0	0	1	0	1	0	2
Detritivore/Filter Feeding	0	1	0	0	2	0	1	0	1	0	1	0	1	0	0	0
Detritivore/Scavenging	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1
Herbivore/Scavenging	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Herbivore/Detrivore	0	0	0	0	0	0	0	0	2	0	0	2	2	0	0	2
Carnivore/Scavenging	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Scavenging/Commensal	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Carnivore/Blood Sucking	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Deposit Feeding/Filter Feeding	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deposit Feeding/Surface Feeding	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Deposit Feeding/Suspension Feeding	0	1	2	1	3	1	0	2	0	0	0	0	0	0	0	0
Autotroph/Carnivore/Filter Feeding	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Omnivore/Filter Feeding/Deposit Feeding	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0
FEEDING STRUCTURE	CD-01	CD-02	CD-03	CD-04	GH-01	GH-02	GH-03	GH-04	TG-01	TG-02	TG-03	TG-04	BN-01	BN-02	BN-03	BN-04
Tentacles	0	0	0	0	2	3	0	0	3	3	10	6	4	7	2	0

Buccal tentacles	0	0	0	0	1	0	0	0	2	1	3	0	0	0	0	1
Maxillipeds	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0
Proboscis/Papillose	0	0	1	0	0	1	0	0	4	2	3	3	0	6	3	1
Jaws	0	0	1	0	2	1	1	1	6	3	8	4	3	4	2	2
Proboscis	3	3	2	1	4	2	2	3	4	6	8	5	3	5	4	7
Papillose	0	0	0	0	0	0	0	0	3	0	2	0	1	2	1	3
Feeding palps/Tentacular cirri	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0
Mandibles/Maxillae/Jaws	5	5	1	1	3	1	5	4	6	7	3	7	7	7	5	7
Pharynx	1	0	1	1	1	0	1	0	2	2	0	1	2	2	2	0
Pharynx/ Feeding palps	0	0	0	1	0	1	0	1	2	1	3	1	2	1	0	2
Pharynges/Papillose	1	2	1	0	1	1	0	1	3	0	2	3	0	6	2	4
Papillose Proboscis/Macrognath	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pharynges	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1
Radioles/palps	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Feeding palps	0	0	0	0	2	0	0	1	0	1	0	0	0	1	0	0
Feeding palps/Branchial crown	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Feeding palps/Proboscis	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0
Tentacles/Feeding palps	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Tentacular crown	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grooved Palps	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Mandibles and Maxillae	0	0	1	0	0	0	1	0	2	1	1	0	0	1	1	2
Tentacles/palps	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Jaws/Keel	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Branchial crown/Radioles/palps	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Pharynx/Papillose	0	0	1	0	1	0	1	1	0	0	0	0	0	0	0	0
Pharynges/Papillose	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grooved palps/Papillose	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1
Branchial Crown	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Proboscis/jaws	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pumped through sponge	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Palps	0	0	3	1	0	0	1	0	1	0	2	0	0	0	1	0
Pharyngneal tooth/proventricle	0	0	0	0	0	0	0	0	4	1	2	1	0	0	2	0
Tentacles/ mouth	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Rostrum	0	0	0	0	1	0	1	1	0	0	1	1	1	0	0	1
Mandibular palps	0	0	0	0	0	1	0	0	1	1	1	1	1	2	2	1

Rostrum/gills	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1
Mandibular palps/Maxillipeds	0	0	0	0	3	1	3	1	3	0	1	1	2	0	2	1
Rostrum/Teeth	0	0	0	0	0	0	0	0	0	0	1	2	1	2	0	0
Mandibles/Maxillae/Maxillipeds	0	0	1	0	1	1	0	0	1	1	1	1	0	1	1	0
Mandibles	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mandibles and Maxillipeds	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Claws/Third maxillipedes	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Maxilliped, Mandibular, Cheliped	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Mandibles, Maxillipeds/ Chela	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	1
Buccal Frame/Chelae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Siphon/Gills	0	0	0	0	4	0	3	1	2	1	1	2	0	5	0	3
Tube feet/ Stomach	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Radula	0	0	0	0	0	0	0	0	0	0	2	0	2	0	0	2
Tentacles/Captacula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tentacles/Feeding chamber	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tube feet	0	0	1	0	2	0	0	1	0	0	0	0	0	0	0	0
Aristotle's lantern	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aristotle's lantern/Tube feet	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0
Gastrozooid/Tentacles	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proboscis/suckers	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0
Gastrozooid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proboscis/mouth	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Introvert/tentacles	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0
Ostia/Pinacocytes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Beak/radula/tentacles	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Mouth	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Tube feet/Toothed jaw	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	1
Mandibles/maxillipedes	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Tentacles/Pharynx/Siphonoglyph	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
RELATIVE ADULT MOBILITY	CD-01	CD-02	CD-03	CD-04	GH-01	GH-02	GH-03	GH-04	TG-01	TG-02	TG-03	TG-04	BN-01	BN-02	BN-03	BN-04
Peristaltic crawling	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	1
Burrowing/Sessile	0	0	1	2	4	2	3	1	1	2	5	5	3	4	1	4
Burrowing	9	11	9	5	20	7	13	12	40	24	45	30	21	38	26	34
Creeping	0	0	0	0	1	0	1	0	2	0	3	0	1	0	1	0

Crawling	1	1	1	0	3	1	1	1	1	1	2	2	1	1	0	2
Sessile	0	0	0	0	1	0	0	1	5	1	1	1	2	3	1	2
Sessile/Creep	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Burrow/Creep	0	0	0	0	1	0	0	0	1	2	2	1	1	4	0	1
Tube-dwelling	0	0	0	0	0	1	0	0	2	2	2	2	1	2	0	2
Creep/Tube-dwelling	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Burrow/Swim	0	1	3	0	3	1	5	3	1	2	2	3	0	1	2	1
Creep/Crawl	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0
Swim	0	0	0	0	0	1	0	0	1	1	3	1	3	1	1	3
Crawl/Burrow	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1
Crawl/Burrow/Swim	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1
Run/Burrow	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Wiggle	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0
Glide/Crawl/Swim	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
SOCIABILITY	CD-01	CD-02	CD-03	CD-04	GH-01	GH-02	GH-03	GH-04	TG-01	TG-02	TG-03	TG-04	BN-01	BN-02	BN-03	BN-04
Solitary	8	12	13	5	31	15	19	17	50	34	66	42	34	47	28	46
Commensal	2	1	0	1	1	0	1	2	2	3	2	3	2	4	3	3
Commensal/Solitary	0	0	2	1	2	0	0	0	1	2	0	1	0	2	2	0
Solitary/Colony	0	0	0	0	0	0	0	0	1	0	2	0	0	1	0	1
Colony	0	0	0	0	2	0	2	1	2	0	1	1	0	1	0	3
ADULT BODY SIZE	CD-01	CD-02	CD-03	CD-04	GH-01	GH-02	GH-03	GH-04	TG-01	TG-02	TG-03	TG-04	BN-01	BN-02	BN-03	BN-04
0.5-20mm	3	4	4	3	15	6	8	8	12	12	18	8	10	18	12	13
20.5-40mm	2	3	3	0	7	4	4	4	13	7	20	15	7	11	5	13
40.5-60mm	2	1	3	1	4	2	5	3	12	6	13	8	5	3	7	10
60.5-80mm	1	0	0	0	1	1	0	0	6	2	4	3	3	5	1	4
80.5-100mm	1	1	1	0	4	1	3	3	6	8	4	6	5	10	6	3
100.5-120mm	0	1	0	0	1	0	2	0	1	1	4	2	2	3	1	2
>120mm	1	3	2	3	4	1	1	2	6	1	7	4	4	6	1	8
ADULT BODY FORM	CD-01	CD-02	CD-03	CD-04	GH-01	GH-02	GH-03	GH-04	TG-01	TG-02	TG-03	TG-04	BN-01	BN-02	BN-03	BN-04
Vermiform and Flattened	2	2	4	1	2	1	1	3	2	4	7	3	2	5	5	4
Slender and Elongate	2	1	1	1	1	0	1	2	2	2	2	3	2	4	3	3
Slender	0	0	0	0	3	2	1	1	3	2	3	3	1	2	2	3
Trefoil-shaped	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

oval	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0
Cylindrical & Tapered Posterior	0	0	0	0	1	1	0	0	1	2	3	2	2	1	0	1
Elongate	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	0
Vermiform & Iridescent	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Vermiform and Tapering	0	0	0	0	2	1	2	0	0	0	2	0	0	0	0	0
Long and Round	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1
Cylindrical	0	0	2	0	1	1	0	1	1	0	1	2	1	5	3	0
Thread-like	1	0	0	0	0	1	0	1	3	2	3	4	0	1	1	4
Depressed and Oval	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Broad	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	1
Thread-like & Round	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sausage-like	1	1	0	0	1	0	1	0	1	1	2	2	2	1	1	1
Vermiform and Elongate	0	0	0	0	1	0	0	0	4	0	2	1	3	2	0	2
Tapered	0	0	0	0	1	1	0	0	2	2	5	3	1	2	0	3
Elongate and Tapered	0	0	0	0	0	0	0	0	2	1	1	1	1	0	0	1
Long and Broad	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	1
Round top/Flattened bottom	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Cylindrical top/Flattened bottom	0	1	0	0	0	0	1	1	1	2	2	1	0	0	1	1
Elongate/Rounded & Tapered at ends	0	1	0	0	1	1	1	1	2	1	2	0	2	2	1	1
Elongate & Tapered at ends	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Small/Short & Flattened	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0
Quill-like tube	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Small & Elongated	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Long, Cylindrical & Slender	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cylindrical & Elongate	0	0	0	0	0	0	0	0	2	0	1	0	2	1	0	0
Slender & Rounded	0	0	0	0	1	0	0	0	1	3	0	0	1	1	1	1
Slender &Flattened	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Long & Slender	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Slender & Rectangular	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Long & Oval	1	1	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Slender, Rounded & Flattened	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Slightly tapered	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elongate & Depressed	1	1	1	0	0	0	1	0	1	2	0	3	2	4	1	3
Elongate & Flattened	0	0	0	0	0	0	1	0	3	0	0	0	3	0	1	3
Elongate & Round	0	0	1	0	0	1	1	0	1	1	3	2	0	1	0	0

Depreesed	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	1
Vermiform	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Flattened & tapered	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Fairly Stout	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elongate & Rectangular	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0	0
Oblong	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Cylindrical & Narrow Posteriorly	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1
Small & Oblong	0	0	0	0	0	0	0	1	0	1	1	0	0	1	0	0
Long & Slender	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tapered Posteriorly	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Evenly Tapered	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Short & Slender	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stout Anterior & Flattened Posterior	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Small & Thread-like	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Short & Depressed	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vermiform/flattened & Minute	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Slender & Cylindrical	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Depressed & Square in Section	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Dumb-bell shaped and Swollen	0	0	0	0	0	0	0	0	0	0	2	0	0	1	1	0
Thread-like/Slender	0	0	0	0	0	0	0	0	2	0	2	1	0	0	0	0
Slender & Evenly tapered	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Uniformly Tapered	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1
Laterally-compressed	0	0	1	0	2	0	1	1	1	1	2	3	1	1	1	1
Laterally-flattened	0	0	0	0	0	1	0	0	1	2	1	1	2	2	2	2
Elongate, Worm-like & Dorso-ventrally Compressed	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
Elongate, Cylindrical/Dorso-ventrally Flattened	0	0	0	0	2	0	2	0	2	0	1	0	1	0	0	0
Dorso-ventrally compressed	0	0	0	0	1	2	0	1	0	0	0	0	0	0	1	0
Lobster-like, Hard body with Fan shaped tail	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0
Hard spiralled Shell	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Latterally Flattened	0	0	0	0	2	0	1	1	1	1	0	2	0	0	0	0
Oval, Flattened & Compact	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0
Broad, Flattened & Smooth	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Elongate, Semi-circular with fan-like telson	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
Cylindrical & Latterally Compressed	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dorso-ventrally flattened	0	0	0	0	2	0	0	1	0	0	1	1	0	0	0	0

Dorso-ventrally flattened with broad carapace	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Square, Rounded anterior, Pointed posterior	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Flattened & Short Rounded Arms	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Circular	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0
Oval to triangular	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Oval & Flattened	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triangular	0	0	0	0	1	0	2	1	2	0	0	0	0	0	0	1
Slightly Rounded	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Slender shell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tusk-shaped	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triangular and Rounded	0	0	0	0	2	0	0	0	0	0	1	1	0	0	0	1
Flat, Circular & Five thin arms	0	0	1	0	2	0	0	1	1	0	0	1	1	0	0	1
Oval/ Circular and flattened	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Star-like & Flattened	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oval, Heart-shaped, Circular & Flattened	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Bubble-like shell & Three Stubby Horns	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Sausage-shaped trunk & Flaccid Proboscis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tree-like or Feather-like	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thin and Elongate	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Elongate/ Sausage-saped	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cylindrical/Sac-like	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0
Short Head & Oval Body	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1

FEEDING HABIT	NG-01	NG-02	NG-03	NG-04	CR-01	CR-02	CR-03	CR-04	GA-01	GA-02	GA-03	GA-04
Herbivore	1	0	0	0	0	0	0	0	0	0	0	0
Carnivore	6	3	4	1	0	0	2	0	0	2	0	1
Omnivore	1	0	1	0	0	0	0	0	0	1	0	0
Filter Feeding	2	1	2	1	1	1	0	0	0	1	1	0
Deposit Feeding	5	1	6	1	1	0	0	0	0	2	1	1
Detritivore	0	2	0	0	0	0	1	1	0	1	0	1
Scavenging	0	0	0	0	0	0	0	0	0	0	0	0
Suspension Feeding	0	0	0	0	0	0	0	0	0	0	0	0
Carnivore/Omnivore	0	0	0	0	1	0	1	0	0	0	0	0

Herbivore/Omnivore	0	0	0	0	0	0	0	0	0	1	0	0
Carnivore/Detritivore	2	1	0	0	1	0	1	1	0	0	0	0
Detritivore/Deposit Feeding	0	1	1	0	0	0	0	0	0	0	0	1
Carnivore/Deposit Feeding	0	0	0	0	0	0	0	1	0	0	0	0
Carnivore/Predator	0	0	0	0	0	0	0	1	0	0	0	0
Omnivore/Detritivore	1	1	1	0	1	0	0	0	0	0	0	0
Detritivore/Filter Feeding	1	1	1	0	0	0	0	0	0	0	0	0
Detritivore/Scavenging	0	0	0	0	0	1	1	0	0	0	0	0
Herbivore/Scavenging	0	0	0	0	0	0	0	0	0	0	0	0
Herbivore/Detrivore	2	1	1	0	0	0	0	0	0	0	0	0
Carnivore/Scavenging	0	0	0	0	0	0	1	0	0	1	0	0
Scavenging/Commensal	0	0	0	0	0	0	0	0	0	0	0	0
Carnivore/Blood Sucking	0	0	0	0	0	0	0	0	0	0	0	0
Deposit Feeding/Filter Feeding	0	0	0	0	0	0	0	0	0	0	0	0
Deposit Feeding/Surface Feeding	0	0	0	0	0	0	0	0	0	0	0	0
Deposit Feeding/Suspension Feeding	0	0	0	0	0	1	1	1	1	1	0	0
Autotroph/Carnivore/Filter Feeding	1	0	0	0	0	0	0	0	0	0	0	0
Omnivore/Filter Feeding/Deposit Feeding	1	0	0	0	0	0	0	0	0	0	0	0
FEEDING STRUCTURE	NG-01	NG-02	NG-03	NG-04	CR-01	CR-02	CR-03	CR-04	GA-01	GA-02	GA-03	GA-04
Tentacles	1	1	4	0	0	0	0	0	0	0	0	0
Buccal tentacles	0	0	1	0	0	0	0	0	0	0	0	0
Maxillipeds	0	0	0	0	0	0	0	0	0	0	0	0
Proboscis/Papillose	2	1	0	0	0	0	1	0	0	0	0	0
Jaws	0	0	0	0	0	0	0	1	0	0	0	0
Proboscis	0	0	0	0	1	0	0	0	0	1	0	1
Papillose	0	1	1	0	0	0	0	0	0	0	0	1
Feeding palps/Tentacular cirri	0	0	0	0	0	0	0	0	0	0	0	0
Mandibles/Maxillae/Jaws	4	2	2	0	1	0	0	1	0	1	0	0
Pharynx	0	0	0	0	0	0	1	0	0	0	0	0
Pharynx/ Feeding palps	2	0	0	0	0	0	0	0	0	0	1	0
Pharynges/Papillose	4	2	2	1	1	0	2	1	0	0	0	0
Papillose Proboscis/Macrognath	0	0	0	0	0	0	0	0	0	0	0	0

Pharynges	0	0	0	0	0	0	0	0	0	0	0	0
Radioles/palps	0	0	0	0	0	0	0	0	0	0	0	0
Feeding palps	1	0	0	0	0	0	0	0	0	0	0	0
Feeding palps/Branchial crown	0	0	0	0	0	0	0	0	0	0	0	0
Feeding palps/Proboscis	0	0	0	1	0	0	0	0	0	1	0	0
Tentacles/Feeding palps	0	0	1	0	0	0	0	0	0	0	0	0
Tentacular crown	0	0	0	0	0	0	0	0	0	1	0	0
Grooved Palps	0	0	0	0	0	0	0	0	0	0	0	0
Mandibles and Maxillae	0	0	0	0	0	0	0	0	0	1	0	1
Tentacles/palps	0	0	0	0	0	0	0	0	0	0	0	0
Jaws/Keel	0	0	0	0	0	0	0	0	0	0	0	0
Branchial crown/Radioles/palps	0	0	0	0	0	0	0	0	0	0	0	0
Pharynx/Papillose	0	0	0	0	1	0	0	0	0	0	0	0
Pharynges/Papillose	0	0	0	0	0	0	0	0	0	0	0	0
Grooved palps/Papillose	0	0	0	0	0	0	0	0	0	0	0	0
Branchial Crown	0	0	0	0	0	0	0	0	0	0	0	0
Proboscis/jaws	0	0	0	0	0	0	0	0	0	0	0	0
Pumped through sponge	0	0	0	0	0	0	0	0	0	0	0	0
Palps	0	0	1	0	0	0	0	0	0	0	0	0
Pharyngneal tooth/proventricle	0	0	0	0	0	0	0	0	0	0	0	0
Tentacles/ mouth	0	0	0	0	0	0	0	0	0	0	0	0
Rostrum	0	0	0	0	0	0	0	0	0	0	0	0
Mandibular palps	0	0	0	0	0	0	0	1	0	1	0	1
Rostrum/gills	0	0	0	0	0	0	0	0	0	0	0	0
Mandibular palps/Maxillipeds	2	2	1	0	0	0	0	0	0	0	0	0
Rostrum/Teeth	0	0	0	0	0	1	1	0	0	0	0	0
Mandibles/Maxillae/Maxillipeds	0	0	0	0	0	0	0	0	0	2	0	0
Mandibles	0	0	0	0	0	0	0	0	0	0	0	0
Mandibles and Maxillipeds	0	0	0	0	0	0	0	0	0	0	0	0
Claws/Third maxillipedes	0	0	0	0	0	0	0	0	0	0	0	0
Maxilliped, Mandibular, Cheliped	0	0	0	0	0	0	0	0	0	0	0	0
Mandibles, Maxillipeds/ Chela	0	0	0	1	0	0	0	0	0	0	1	0
Buccal Frame/Chelae	0	0	0	0	0	0	0	0	0	0	0	0

Siphon/Gills	1	0	1	0	1	0	0	0	0	0	0	0
Tube feet/ Stomach	0	0	0	0	0	0	0	0	0	0	0	0
Radula	2	1	0	0	0	0	0	0	0	0	0	0
Tentacles/Captacula	1	0	1	0	0	0	0	0	0	0	0	0
Tentacles/Feeding chamber	0	0	0	0	0	1	0	0	0	0	0	0
Tube feet	0	0	0	0	0	0	1	0	0	0	0	0
Aristotle's lantern	0	0	0	0	0	0	0	0	0	0	0	0
Aristotle's lantern/Tube feet	1	0	1	0	0	0	0	0	0	0	0	0
Gastrozooid/Tentacles	0	0	0	0	0	0	0	0	0	0	0	0
Proboscis/suckers	0	0	0	0	0	0	0	0	0	0	0	0
Gastrozooid	0	0	0	0	0	0	1	0	0	0	0	0
Proboscis/mouth	0	0	0	0	0	0	1	0	0	1	0	0
Introvert/tentacles	0	0	0	0	0	1	0	1	1	1	0	0
Ostia/Pinacocytes	1	0	0	0	0	0	0	0	0	0	0	0
Beak/radula/tentacles	0	0	1	0	0	0	0	0	0	0	0	0
Mouth	0	0	0	0	0	0	0	0	0	0	0	0
Tube feet/Toothed jaw	0	0	0	0	0	0	0	0	0	0	0	0
Mandibles/maxillipedes	0	0	0	0	0	0	0	0	0	0	0	0
Tentacles/Pharynx/Siphonoglyph	0	1	0	0	0	0	0	0	0	0	0	0
RELATIVE ADULT MOBILITY	NG-01	NG-02	NG-03	NG-04	CR-01	CR-02	CR-03	CR-04	GA-01	GA-02	GA-03	GA-04
Peristaltic crawling	0	0	1	0	0	0	0	0	0	0	0	0
Burrowing/Sessile	2	0	1	0	0	0	0	0	0	0	0	0
Burrowing	14	8	10	3	5	1	4	4	1	4	2	2
Creeping	1	1	2	0	0	0	0	0	0	0	0	0
Crawling	0	1	0	0	0	0	1	0	0	0	0	0
Sessile	2	1	0	0	0	0	1	0	0	1	0	0
Sessile/Creep	0	0	0	0	0	0	0	0	0	0	0	0
Burrow/Creep	3	0	2	0	0	1	0	0	0	0	0	0
Tube-dwelling	0	0	1	0	0	0	0	0	0	0	0	0
Creep/Tube-dwelling	0	0	0	0	0	0	0	0	0	0	0	0
Burrow/Swim	0	0	0	0	0	0	0	0	0	2	0	1
Creep/Crawl	0	0	0	0	0	0	0	0	0	0	0	0

Swim	1	1	0	0	0	1	1	1	0	1	0	1
Crawl/Burrow	0	0	0	0	0	0	0	0	0	0	0	0
Crawl/Burrow/Swim	0	0	0	0	0	0	0	0	0	0	0	0
Run/Burrow	0	0	0	0	0	0	0	0	0	1	0	0
Wiggle	0	0	0	0	0	0	0	0	0	0	0	0
Glide/Crawl/Swim	0	0	0	0	0	0	1	0	0	1	0	0
SOCIABILITY	NG-01	NG-02	NG-03	NG-04	CR-01	CR-02	CR-03	CR-04	GA-01	GA-02	GA-03	GA-04
Solitary	18	9	15	3	5	3	7	4	1	10	2	4
Commensal	3	1	1	0	0	0	0	0	0	0	0	0
Commensal/Solitary	1	0	0	0	0	0	0	1	0	0	0	0
Solitary/Colony	0	1	1	0	0	0	1	0	0	0	0	0
Colony	1	1	0	0	0	0	0	0	0	0	0	0
ADULT BODY SIZE	NG-01	NG-02	NG-03	NG-04	CR-01	CR-02	CR-03	CR-04	GA-01	GA-02	GA-03	GA-04
0.5-20mm	2	3	3	1	0	0	1	1	0	3	1	3
20.5-40mm	5	1	1	1	1	1	1	1	0	2	0	1
40.5-60mm	2	2	5	0	2	1	2	2	0	2	1	0
60.5-80mm	6	3	3	0	1	0	0	0	0	0	0	0
80.5-100mm	3	1	1	0	0	0	1	0	0	0	0	0
100.5-120mm	1	1	0	1	0	0	1	0	0	1	0	0
>120mm	2	1	3	0	1	1	2	1	1	2	0	0
ADULT BODY FORM	NG-01	NG-02	NG-03	NG-04	CR-01	CR-02	CR-03	CR-04	GA-01	GA-02	GA-03	GA-04
Vermiform and Flattened	1	0	2	0	1	0	0	0	0	0	0	0
Slender and Elongate	4	1	1	0	0	0	0	0	0	0	0	0
Slender	0	0	0	1	0	0	1	0	0	1	0	0
Trefoil-shaped	0	0	0	0	0	0	0	0	0	0	0	0
oval	0	0	0	0	0	0	0	0	0	0	0	0
Cylindrical & Tapered Posterior	1	0	2	0	0	0	0	0	0	0	0	0
Elongate	2	0	0	0	0	0	0	0	0	0	0	0
Vermiform & Iridescent	0	0	0	0	0	0	0	0	0	0	0	0
Vermiform and Tapering	0	0	0	0	0	0	0	0	0	0	0	1
Long and Round	0	0	0	0	0	0	0	0	0	0	0	0
Cylindrical	0	0	0	0	0	0	0	0	0	0	0	0

Thread-like	1	0	0	0	0	0	0	0	0	0	0	1
Depressed and Oval	0	0	0	0	0	0	0	0	0	0	0	0
Broad	0	0	0	0	0	0	0	0	0	0	0	0
Thread-like & Round	0	0	0	0	0	0	0	0	0	0	0	0
Sausage-like	0	0	0	0	0	0	0	0	0	1	0	0
Vermiform and Elongate	0	0	0	0	0	0	0	0	0	0	0	0
Tapered	0	0	1	0	0	0	0	0	0	0	0	0
Elongate and Tapered	0	0	0	0	0	0	0	0	0	0	0	0
Long and Broad	0	0	0	0	0	0	0	0	0	0	0	0
Round top/Flattened bottom	0	0	0	0	0	0	0	0	0	0	0	0
Cylindrical top/Flattened bottom	0	0	0	0	0	0	0	1	0	0	0	0
Elongate/Rounded & Tapered at ends	1	1	0	0	1	0	1	1	0	0	0	0
Elongate & Tapered at ends	0	0	0	0	0	0	0	0	0	0	0	0
Small/Short & Flattened	0	0	0	0	0	0	0	0	0	0	0	0
Quill-like tube	0	0	0	0	0	0	0	0	0	0	0	0
Small & Elongated	0	0	0	0	0	0	0	0	0	0	0	0
Long, Cylindrical & Slender	0	1	0	0	0	0	0	0	0	0	0	0
Cylindrical & Elongate	1	0	0	0	0	0	0	0	0	0	1	0
Slender & Rounded	1	1	0	0	0	0	0	0	0	0	0	0
Slender &Flattened	0	0	0	0	0	0	0	0	0	0	0	0
Long & Slender	0	0	0	0	0	0	0	0	0	0	0	0
Slender & Rectangular	0	0	0	0	0	0	0	0	0	0	0	0
Long & Oval	0	0	0	0	1	0	0	0	0	0	0	0
Slender, Rounded & Flattened	0	0	1	0	0	0	0	0	0	0	0	0
Slightly tapered	0	0	0	0	0	0	0	0	0	1	0	0
Elongate & Depressed	3	1	2	1	0	0	1	0	0	0	0	0
Elongate & Flattened	0	1	1	0	0	0	0	0	0	0	0	0
Elongate & Round	0	0	0	0	0	0	0	0	0	0	0	0
Depreesed	0	0	0	0	0	0	0	0	0	0	0	0
Vermiform	0	0	0	0	0	0	0	0	0	0	0	0
Flattened & tapered	0	0	0	0	0	0	0	0	0	0	0	0
Fairly Stout	0	0	0	0	0	0	0	0	0	0	0	0
Elongate & Rectangular	0	0	0	0	1	0	0	0	0	0	0	0

Oblong	0	0	0	0	0	0	0	1	0	0	0	0
Cylindrical & Narrow Posteriorly	0	0	0	0	0	0	0	0	0	0	0	0
Small & Oblong	0	0	0	0	0	0	0	0	0	0	0	0
Long & Slender	0	0	0	0	0	0	0	0	0	0	0	0
Tapered Posteriorly	0	0	0	0	0	0	0	0	0	0	0	0
Evenly Tapered	0	0	0	0	0	0	0	0	0	0	0	0
Short & Slender	0	0	0	0	0	0	0	0	0	0	0	0
Stout Anterior & Flattened Posterior	0	0	0	0	0	0	1	0	0	0	0	0
Small & Thread-like	0	0	0	0	0	0	0	0	0	0	0	0
Short & Depressed	0	0	0	0	0	0	0	0	0	0	0	0
Vermiform/flattened & Minute	0	0	0	0	0	0	0	0	0	1	0	0
Slender & Cylindrical	0	0	0	0	0	0	0	0	0	0	0	0
Depressed & Square in Section	0	0	0	0	0	0	0	0	0	0	0	0
Dumb-bell shaped and Swollen	0	0	0	0	0	0	0	0	0	0	0	0
Thread-like/Slender	0	0	0	0	0	0	0	0	0	0	0	0
Slender & Evenly tapered	0	0	0	0	0	0	0	0	0	0	0	0
Uniformly Tapered	0	1	1	0	0	0	0	0	0	0	0	0
Laterally-compressed	0	0	0	0	0	1	1	0	0	1	0	0
Laterally-flattened	0	0	0	0	0	0	0	1	0	1	0	1
Elongate, Worm-like & Dorso-ventrally Compressed	0	0	0	0	0	0	0	0	0	0	0	0
Elongate, Cylindrical/Dorso-ventrally Flattened	1	1	1	1	0	0	0	0	0	0	1	0
Dorso-ventrally compressed	0	0	0	0	0	0	0	0	0	1	0	0
Lobster-like, Hard body with Fan shaped tail	0	0	0	0	0	0	0	0	0	0	0	0
Hard spiralled Shell	0	0	0	0	0	0	0	0	0	0	0	0
Latterally Flattened	0	0	0	0	0	0	0	0	0	0	0	0
Oval, Flattened & Compact	0	0	0	0	0	0	0	0	0	1	0	1
Broad, Flattened & Smooth	0	0	0	0	0	0	0	0	0	0	0	0
Elongate, Semi-circular with fan-like telson	1	1	0	0	0	0	0	0	0	0	0	0
Cylindrical & Latterally Compressed	0	0	0	0	0	0	0	0	0	0	0	0
Dorso-ventrally flattened	0	0	0	0	0	0	0	0	0	0	0	0
Dorso-ventrally flattened with broad carapace	0	0	0	0	0	0	0	0	0	0	0	0
Square, Rounded anterior, Pointed posterior	0	0	0	0	0	0	0	0	0	0	0	0
Flattened & Short Rounded Arms	0	0	0	0	0	0	0	0	0	0	0	0

Circular	0	0	0	0	0	0	0	0	0	0	0	0
Oval to triangular	0	0	0	0	0	0	0	0	0	0	0	0
Oval & Flattened	0	0	0	0	0	0	0	0	0	0	0	0
Triangular	0	0	0	0	0	0	0	0	0	0	0	0
Slightly Rounded	0	0	0	0	0	0	0	0	0	0	0	0
Slender shell	1	0	0	0	0	0	0	0	0	0	0	0
Tusk-shaped	1	0	1	0	0	1	0	0	0	0	0	0
Triangular and Rounded	0	0	0	0	0	0	0	0	0	0	0	0
Flat, Circular & Five thin arms	0	1	0	0	0	0	1	0	0	0	0	0
Oval/ Circular and flattened	0	0	0	0	0	0	0	0	0	0	0	0
Star-like & Flattened	0	0	0	0	0	0	0	0	0	0	0	0
Oval, Heart-shaped, Circular & Flattened	1	0	1	0	0	0	0	0	0	0	0	0
Bubble-like shell & Three Stubby Horns	1	1	0	0	0	0	0	0	0	0	0	0
Sausage-shaped trunk & Flaccid Proboscis	0	0	0	0	0	0	0	0	0	0	0	0
Tree-like or Feather-like	0	0	0	0	0	0	1	0	0	0	0	0
Thin and Elongate	0	0	0	0	0	0	1	0	0	1	0	0
Elongate/ Sausage-saped	0	0	0	0	0	0	0	0	0	0	0	0
Cylindrical/Sac-like	0	0	0	0	0	1	0	1	1	1	0	0
Short Head & Oval Body	0	0	0	0	0	0	0	0	0	0	0	0

Appendix III

Carbon-nitrate ratio (nitrate used as a proxy for total nitrogen) indicating sources of organic carbon and corresponding organisms according to Bordowskiy, 1965ab). Phyto=phytoplankton, Zoo=zooplankton, Orga=organisms.

Station Code	C:N	Source	Source Organism
GB-01	0.11	Autochthonous	Phyto/Zoo
GB-02	1.20	Autochthonous	Phyto/Zoo
GB-03	1.04	Autochthonous	Phyto/Zoo
GB-04	1.24	Autochthonous	Phyto/Zoo
GU-01	3.66	Autochthonous	Phyto/Zoo
GU-02	1.72	Autochthonous	Phyto/Zoo
GU-03	4.62	Autochthonous	Phyto/Zoo
GU-04	16.63	Allochthonous	Terrestrial
SL-01	25.80	Allochthonous	Terrestrial
SL-02	14.60	Allochthonous	Terrestrial
SL-03	38.80	Allochthonous	Terrestrial
SL-04	14.54	Allochthonous	Terrestrial
LI-01	12.15	Allochthonous	Terrestrial
LI-02	15.30	Allochthonous	Terrestrial
LI-03	25.12	Allochthonous	Terrestrial
LI-04	12.85	Allochthonous	Terrestrial
CD-01	4.62	Autochthonous	Phyto/Zoo
CD-02	10.40	Autochthonous	Terrestrial
CD-03	4.40	Autochthonous	Phyto/Zoo
CD-04	12.30	Allochthonous	Terrestrial
GH-01	8.85	Autochthonous	Planktonic orga
GH-02	71.06	Allochthonous	Terrestrial

Station Code	C:N	Source	Source Organism
GH-03	22.46	Allochthonous	Terrestrial
GH-04	33.04	Allochthonous	Terrestrial
TG-01	12.78	Allochthonous	Terrestrial
TG-02	15.40	Allochthonous	Terrestrial
TG-03	4.83	Autochthonous	Phyto/Zoo
TG-04	8.11	Autochthonous	Planktonic orga
BN-01	11.60	Autochthonous	Terrestrial
BN-02	14.60	Allochthonous	Terrestrial
BN-03	3.30	Autochthonous	Phyto/Zoo
BN-04	5.68	Autochthonous	Phyto/Zoo
NG-01	1.87	Autochthonous	Phyto/Zoo
NG-02	7.47	Autochthonous	Planktonic orga
NG-03	1.61	Autochthonous	Phyto/Zoo
NG-04	2.86	Autochthonous	Phyto/Zoo
CR-01	1.92	Autochthonous	Phyto/Zoo
CR-02	2.08	Autochthonous	Phyto/Zoo
CR-03	3.63	Autochthonous	Phyto/Zoo
CR-04	3.88	Autochthonous	Phyto/Zoo
GA-01	1.44	Autochthonous	Phyto/Zoo
GA-02	1.57	Autochthonous	Phyto/Zoo
GA-03	1.80	Autochthonous	Phyto/Zoo
GA-04	4.75	Autochthonous	Phyto/Zoo

APPENDIX IV

Sediment physical and chemical analytical results

Parameter	**Guinea Bissau**	**Guinea Conakry**	**Sierra Leone**	**Liberia**	**Cote d'Ivoire**	**Ghana**	**Togo**	**Benin**	**Nigeria**	**Cameroun**	**Gabon**
Sand	92.65	92.53	83.05	61.83	79.07	33.77	56.00	59.25	71.41	29.23	87.74
Silt	3.56	3.53	6.13	20.48	5.63	3.11	16.50	13.25	4.12	21.77	1.38
Clay	3.81	3.87	10.75	17.68	15.30	63.13	27.25	27.50	24.47	48.99	10.88
Phosphate	0.73	0.21	0.41	0.91	0.49	1.51	2.53	1.04	0.43	0.66	0.74
Nitrate	1.23	0.50	0.23	0.25	0.15	0.20	0.14	0.11	0.73	0.83	0.80
Org. Carbon	0.50	2.01	4.73	3.91	1.02	6.12	1.15	1.01	2.48	2.18	1.83
Potassium	2.50	1.04	0.65	2.26	1.80	3.03	2.02	3.16	2.73	2.18	4.20
Sodium	2.53	1.93	1.64	5.33	3.12	7.48	3.64	3.25	1.89	3.08	3.95
Cacium	21.90	24.58	42.09	23.19	15.39	23.50	7.57	7.00	10.81	25.67	29.47
Magnesium	0.04	0.04	0.04	0.03	0.03	0.04	0.02	0.01	0.02	0.03	0.01

APPENDIX V

Water depth of sampling locations

Station Code	Country	Depth (m)
GB-01	Guinea Bissau	53.0
GB-02	Guinea Bissau	125.0
GB-03	Guinea Bissau	153.0
GB-04	Guinea Bissau	28.0
GU-01	Guinea	26.0
GU-02	Guinea	94.0
GU-03	Guinea	43.0
GU-04	Guinea	27.0
SL-01	Sierra Leone	52.0
SL-02	Sierra Leone	34.0
SL-03	Sierra Leone	27.0
SL-04	Sierra Leone	49.0
LI-01	Liberia	34.0
LI-02	Liberia	54.0
LI-03	Liberia	54.0
LI-04	Liberia	24.0
CD-01	Cote d’Ivoire	63.0
CD-02	Cote d’Ivoire	102.0
CD-03	Cote d’Ivoire	49.0
CD-04	Cote d’Ivoire	24.0
GH-01	Ghana	100.0
GH-02	Ghana	76.0
GH-03	Ghana	60.0
GH04	Ghana	29.0
TG-01	Togo	59.0
TG-02	Togo	20.0
TG-03	Togo	35.0
TG-04	Togo	17.0
BN-01	Benin	28.0
BN-02	Benin	18.0
BN-03	Benin	16.0
BN-04	Benin	23.0
NG-01	Nigeria	87.0
NG-02	Nigeria	37.0
NG-03	Nigeria	67.9
NG-04	Nigeria	41.0

CR-01	Cameroon	64.0
CR-02	Cameroon	22.0
CR-03	Cameroon	98.0
CR-04	Cameroon	22.0
GA-01	Gabon	101.0
GA-02	Gabon	111.0
GA-03	Gabon	55.0
GA-04	Gabon	104.0

APPENDIX VI

Results of Statistical Analyses

```
**** Correlation matrix ****

SPEC AX1          1.0000
SPEC AX2          0.0397   1.0000
SPEC AX3         -0.0884  -0.1315   1.0000
SPEC AX4          0.2604   0.3002  -0.3847   1.0000
ENVI AX1          0.7154   0.0000   0.0000   0.0000   1.0000
ENVI AX2          0.0000   0.5430   0.0000   0.0000   0.0000   1.0000
ENVI AX3          0.0000   0.0000   0.3341   0.0000   0.0000   0.0000   1.0000
ENVI AX4          0.0000   0.0000   0.0000   0.3758   0.0000   0.0000   0.0000   1.0000
Sand      -0.1046   0.1404  -0.1130  -0.2462  -0.1463   0.2586  -0.3382  -0.6551
Silt       0.2215  -0.3952   0.0276   0.0038   0.3096  -0.7278   0.0828   0.0100
Clay       0.0907  -0.0843   0.1104   0.2520   0.1267  -0.1553   0.3305   0.6704
Phosphat   0.1583   0.0108   0.0876  -0.0192   0.2213   0.0199   0.2623  -0.0510
Nitrate   -0.4643  -0.0913  -0.1377   0.0646  -0.6490  -0.1682  -0.4121   0.1718
Org. Car  -0.2870   0.0004   0.2060   0.0005  -0.4012   0.0007   0.6164   0.0012
Potassiu  -0.0568  -0.2624   0.1513   0.0886  -0.0793  -0.4832   0.4528   0.2358
Sodium     0.1026  -0.0481   0.1737   0.1528   0.1434  -0.0885   0.5200   0.4066
Cacium    -0.4293   0.1058   0.0310  -0.0773  -0.6001   0.1948   0.0928  -0.2056
Magnesiu          -0.2293   0.1703   0.0588  -0.0478  -0.3205   0.3136   0.1761  -0.1273

          SPEC AX1          SPEC AX2          SPEC AX3          SPEC AX4          ENVI AX1
          ENVI AX2          ENVI AX3          ENVI AX4

Sand       1.0000
Silt      -0.4671   1.0000
Clay      -0.7186   0.3780   1.0000
Phosphat  -0.2046   0.2195   0.1927   1.0000
Nitrate    0.0407  -0.3212  -0.3087  -0.0834   1.0000
Org. Car  -0.2867   0.0628   0.2316   0.0918  -0.1097   1.0000
Potassiu  -0.2505   0.1582   0.3073   0.0652   0.1390  -0.1379   1.0000
Sodium    -0.4369   0.2863   0.2541   0.4441  -0.1296   0.1394   0.4245   1.0000
Cacium     0.0061  -0.0704  -0.1324  -0.0635   0.2256   0.4136  -0.1225  -0.0256
Magnesiu          -0.1364   0.0131  -0.0513  -0.0676  -0.0345   0.0491  -0.0365   0.1565

          Sand     Silt     Clay     Phosphat Nitrate  Org. Car Potassiu Sodium

Calcium           1.0000
Magnesiu          0.5109   1.0000

          Calcium  Magnesiu

 N        name        (weighted) mean    stand. dev.       inflation factor

 1        SPEC AX1                0.0000              1.3977
 2        SPEC AX2                0.0000              1.8415
 3        SPEC AX3                0.0000              2.9931
 4        SPEC AX4                0.0000              2.6610
 5        ENVI AX1                0.0000              1.0000
 6        ENVI AX2                0.0000              1.0000
 7        ENVI AX3                0.0000              1.0000
 8        ENVI AX4                0.0000              1.0000
 1        Sand           4.0720              0.6833              3.7842
```

```
    2     Silt        1.7245      1.1168      1.5808
    3     Clay        2.7123      1.0868      3.2564
    4     Phosphat    0.5261      0.3880      1.3763
    5     Nitrate     0.3393      0.2721      1.9401
    6     Org. Car    1.0889      0.5260      1.7068
    7     Potassiu    1.0741      0.5030      1.7059
    8     Sodium      1.3009      0.6342      2.1259
    9     Cacium      2.8634      0.7507      2.2074
   10     Magnesiu    0.0286      0.0175      1.7838


 **** Summary ****

 Axes                                1       2       3       4      Total variance

 Eigenvalues                :      0.495   0.004   0.002   0.001        1.000
Trait-environment correlations  :  0.715   0.543   0.334   0.376
 Cumulative percentage variance
    of Trait data           :       49.5    49.9    50.0    50.1
    of Trait-environment relation:  98.7    99.5    99.8   100.0

 Sum of all          eigenvalues                                     1.000
 Sum of all canonical    eigenvalues                                 0.501


 All four eigenvalues reported above are canonical and correspond to axes that
 are constrained by the environmental variables.

 *** Unrestricted permutation ***

 Seeds:  23239   945

 **** Summary of Monte Carlo test ****

 Test of significance of first canonical axis: eigenvalue =    0.495
                                    F-ratio    =   32.322
                                    P-value    =    0.0050

 Test of significance of all canonical axes  : Trace      =    0.501
                                    F-ratio    =    3.316
                                    P-value    =    0.0050

 (199 permutations under reduced model)
```

Canonical Correspondence Analysis

```
Program CANOCO Version 4.54 October 2005 - written by Cajo J.F. Ter Braak
 (C) 1988-2005 Biometris - quantitative methods in the life and earth sciences
 Plant Research International, Wageningen University and Research Centre
 Box 100, 6700 AC Wageningen, the Netherlands
 CANOCO performs (partial) (detrended) (canonical) correspondence analysis,
 principal components analysis and redundancy analysis.
 CANOCO is an extension of Cornell Ecology program DECORANA (Hill,1979)

 For explanation of the input/output see the manual or
 Ter Braak, C.J.F. (1995) Ordination. Chapter 5 in:
 Data Analysis in Community and Landscape Ecology
 (Jongman, R.H.G., Ter Braak, C.J.F. and Van Tongeren, O.F.R., Eds)
 Cambridge University Press, Cambridge, UK, 91-173 pp.

 *** Type of analysis ***
  Model            Gradient analysis
             indirect     direct     hybrid
 linear        1=PCA       2= RDA       3
 unimodal       4= CA       5= CCA       6
    ,,          7=DCA       8=DCCA       9
             10=non-standard analysis
 Type analysis number
 Answer =  5


 *** Data files ***
 Species data       : C:\Users\user 1\Desktop\Functional Traits_Infauna\BioAbunDOm
 Covariable data    :
 Environmental data : C:\Users\user 1\Desktop\Functional Traits_Infauna\EnvDataTrasformed
 Initialization file:

 Forward selection of envi. variables =    1
 Scaling of ordination scores         =    2
 Diagnostics                          =    3

 File   : C:\Users\user 1\Desktop\Functional Traits_Infauna\BioAbunDOm
 Title  : WCanoImp produced data file
 Format :  (I5,1X,10F4.0)
 No. of couplets of species number and abundance per line :    0


 No samples omitted
 Number of samples           44
 Number of species           10
 Number of occurrences      150


 File  : C:\Users\user 1\Desktop\Functional Traits_Infauna\EnvDataTrasformed
 Title : WCanoImp produced data file
 Format :  (I5,1X,10F6.2)
 No. of environmental variables :    10


 No interaction terms defined
```

```
No transformation of species data
No species-weights specified
No  sample-weights specified
No downweighting of rare species

No. of active  samples:     43
No. of passive samples:      0
No. of active  species:     10

Total inertia in species data=
Sum of all eigenvalues of CA =    2.62242


****** Check on influence in covariable/environment data ******
The following sample(s) have extreme values
Sample Environmental       Covariable  + Environment space
       variable Influence   influence     influence

   2                 8.5x
   2   1     5.1x
   2   6     8.1x
   2   7     7.8x
   2  10    15.1x
   2                         3.1x
   5                 4.7x
   5   3    13.7x
   5   5    20.2x
   5  10     6.8x
   5                         3.4x
  24   4     5.7x
  24   6     5.6x
  25   1    16.2x
  25   2     8.3x
  26   4    18.4x
  26                         3.1x
  27                 4.2x
  27   7     8.9x
  27   8     6.1x
  27   9     7.2x
  27  10     6.1x
****** End of check ******


**** Start of forward selection of variables ****


*** Unrestricted permutation ***


Seeds:  23239   945

  N    Name   Extra fit

  4 Phosphat    0.0555
  3 Clay       0.0846
  1 Sand       0.1124
  2 Silt      0.1324
  8 Sodium      0.1609
```

```
   5 Nitrate     0.1793
   7 Potassiu    0.1800
   9 Cacium      0.1899
   6 Org. Car    0.3290
  10 Magnesiu    0.3542
Environmental variable    10 tested
Number of permutations=  199

*** Permutation under reduced model ***


P-value 0.0050 (variable  10; F-ratio=  6.40; number of permutations=   199)


Environmental variable    10 added to model
Variance explained by the variables selected:    0.35
   "        "      "      all variables    :    1.33

   N     Name   Extra fit

   7 Potassiu    0.0303
   4 Phosphat    0.0555
   3 Clay        0.0962
   1 Sand        0.1125
   8 Sodium      0.1147
   2 Silt        0.1388
   5 Nitrate     0.1788
   9 Cacium      0.2008
   6 Org. Car    0.3066
Environmental variable     6 tested
Number of permutations=  199

*** Permutation under reduced model ***


P-value 0.0050 (variable   6; F-ratio=  6.25; number of permutations=   199)


Environmental variable     6 added to model
Variance explained by the variables selected:    0.66
   "        "      "      all variables    :    1.33

   N     Name   Extra fit

   7 Potassiu    0.0341
   4 Phosphat    0.0486
   8 Sodium      0.0890
   9 Cacium      0.0912
   3 Clay        0.0963
   2 Silt        0.1080
   1 Sand        0.1216
   5 Nitrate     0.1826
Environmental variable     5 tested
Number of permutations=  199

*** Permutation under reduced model ***
```

```
P-value 0.0050 (variable   5; F-ratio=  4.00; number of permutations=   199)


Environmental variable     5 added to model
Variance explained by the variables selected:    0.84
   "         "       "      all variables    :    1.33

   N     Name   Extra fit

   9 Cacium      0.0231
   4 Phosphat    0.0266
   7 Potassiu    0.0352
   3 Clay        0.0362
   2 Silt        0.0660
   8 Sodium      0.0824
   1 Sand        0.1170
Environmental variable     1 tested
Number of permutations=  199

*** Permutation under reduced model ***


P-value 0.0250 (variable   1; F-ratio=  2.67; number of permutations=   199)


Environmental variable     1 added to model
Variance explained by the variables selected:    0.96
   "         "       "      all variables    :    1.33

   N     Name   Extra fit

   9 Cacium      0.0323
   4 Phosphat    0.0378
   3 Clay        0.0712
   2 Silt        0.0741
   7 Potassiu    0.0951
   8 Sodium      0.1302
Environmental variable     8 tested
Number of permutations=  199

*** Permutation under reduced model ***


P-value 0.0050 (variable   8; F-ratio=  3.15; number of permutations=   199)


Environmental variable     8 added to model
Variance explained by the variables selected:    1.09
   "         "       "      all variables    :    1.33

   N     Name   Extra fit

   9 Cacium      0.0233
   4 Phosphat    0.0283
   7 Potassiu    0.0526
   3 Clay        0.0709
   2 Silt        0.0871
Environmental variable     2 tested
```

```
Number of permutations=  199

*** Permutation under reduced model ***


P-value 0.0150 (variable   2; F-ratio=  2.17; number of permutations=   199)


Environmental variable     2 added to model
Variance explained by the variables selected:    1.18
   "        "      "      all variables    :    1.33

   N     Name   Extra fit

   4 Phosphat    0.0127
   9 Cacium      0.0233
   7 Potassiu    0.0533
   3 Clay        0.0718
Environmental variable     3 tested
Number of permutations=  199

*** Permutation under reduced model ***


P-value 0.0700 (variable   3; F-ratio=  1.83; number of permutations=   199)


Environmental variable     3 added to model
Variance explained by the variables selected:    1.25
   "        "      "      all variables    :    1.33

   N     Name   Extra fit

   4 Phosphat    0.0189
   9 Cacium      0.0252
   7 Potassiu    0.0439
Environmental variable     7 tested
Number of permutations=  199

*** Permutation under reduced model ***


P-value 0.3750 (variable   7; F-ratio=  1.12; number of permutations=   199)


Environmental variable     7 added to model
Variance explained by the variables selected:    1.29
   "        "      "      all variables    :    1.33

   N     Name   Extra fit

   4 Phosphat    0.0148
   9 Cacium      0.0201
Environmental variable     9 tested
Number of permutations=  199

*** Permutation under reduced model ***
```

```
P-value 0.8700 (variable   9; F-ratio=  0.51; number of permutations=   199)


Environmental variable     9 added to model
Variance explained by the variables selected:    1.31
  "        "      "      all variables    :    1.33

  N     Name   Extra fit

  4 Phosphat    0.0165
Environmental variable     4 tested
Number of permutations=  199

*** Permutation under reduced model ***


P-value 0.9450 (variable   4; F-ratio=  0.41; number of permutations=   199)


Environmental variable     4 added to model
Variance explained by the variables selected:    1.33
  "        "      "      all variables    :    1.33

No more variables to improve fit
*** End of selection ***


  N        name         (weighted) mean     stand. dev.         inflation factor

  1        SPEC AX1                0.0000                1.1269
  2        SPEC AX2                0.0000                1.1788
  3        SPEC AX3                0.0000                1.3312
  4        SPEC AX4                0.0000                1.3985
  5        ENVI AX1                0.0000                1.0000
  6        ENVI AX2                0.0000                1.0000
  7        ENVI AX3                0.0000                1.0000
  8        ENVI AX4                0.0000                1.0000
  1        Sand          4.1891              0.6514              5.7573
  2        Silt          1.7114              0.9086              2.2318
  3        Clay          2.2340              1.2095              6.3910
  4        Phosphat      0.5846              0.5301              3.1719
  5        Nitrate       0.2762              0.1965              3.9020
  6        Org. Car      0.9869              0.6192              3.6998
  7        Potassiu      1.0260              0.5739              2.8325
  8        Sodium        1.3836              0.5999              4.3227
  9        Cacium        2.7635              0.6408              6.2848
 10        Magnesiu      0.0292              0.0221              3.9462


**** Summary ****

Axes                              1          2          3          4        Total inertia

Eigenvalues                   :             0.502      0.378      0.202      0.141           2.622
Species-environment correlations  :     0.887      0.848      0.751      0.715
Cumulative percentage variance
  of species data             :          19.2         33.6       41.3       46.7
```

```
   of species-environment relation:      37.8        66.2       81.4       92.0

 Sum of all             eigenvalues                                              2.622
 Sum of all canonical     eigenvalues                                            1.330

 All four eigenvalues reported above are canonical and correspond to axes that
 are constrained by the environmental variables.


Program CANOCO Version 4.54 October 2005 - written by Cajo J.F. Ter Braak
 (C) 1988-2005 Biometris - quantitative methods in the life and earth sciences
 Plant Research International, Wageningen University and Research Centre
 Box 100, 6700 AC Wageningen, the Netherlands
 CANOCO performs (partial) (detrended) (canonical) correspondence analysis,
 principal components analysis and redundancy analysis.
 CANOCO is an extension of Cornell Ecology program DECORANA (Hill,1979)

 For explanation of the input/output see the manual or
 Ter Braak, C.J.F. (1995) Ordination. Chapter 5 in:
 Data Analysis in Community and Landscape Ecology
 (Jongman, R.H.G., Ter Braak, C.J.F. and Van Tongeren, O.F.R., Eds)
 Cambridge University Press, Cambridge, UK, 91-173 pp.

 *** Type of analysis ***
  Model            Gradient analysis
             indirect     direct     hybrid
 linear        1=PCA       2= RDA       3
 unimodal       4= CA       5= CCA       6
   ,,          7=DCA       8=DCCA       9
             10=non-standard analysis
 Type analysis number
 Answer =  5


 *** Data files ***
 Species data       : C:\Users\user 1\Desktop\Functional Traits_Infauna\BioAbunDOm
 Covariable data    :
 Environmental data : C:\Users\user 1\Desktop\Functional Traits_Infauna\EnvDataTrasformed
 Initialization file:

 Forward selection of envi. variables =    0
 Scaling of ordination scores         =    2
 Diagnostics                          =    3

 File   : C:\Users\user 1\Desktop\Functional Traits_Infauna\BioAbunDOm
 Title  : WCanoImp produced data file
 Format :  (I5,1X,10F4.0)
 No. of couplets of species number and abundance per line :    0


 No samples omitted
 Number of samples           44
 Number of species          10
 Number of occurrences       150


 File  : C:\Users\user 1\Desktop\Functional Traits_Infauna\EnvDataTrasformed
 Title : WCanoImp produced data file
```

```
Format :  (I5,1X,10F6.2)
No. of environmental variables :    10


No interaction terms defined


No transformation of species data
No species-weights specified
No  sample-weights specified
No downweighting of rare species

No. of active  samples:     43
No. of passive samples:      0
No. of active  species:     10

Total inertia in species data=
Sum of all eigenvalues of CA =    2.62242


****** Check on influence in covariable/environment data ******
The following sample(s) have extreme values
Sample Environmental       Covariable  + Environment space
      variable Influence   influence     influence

    2                   8.5x
    2    1     5.1x
    2    6     8.1x
    2    7     7.8x
    2   10    15.1x
    2                             3.1x
    5                   4.7x
    5    3    13.7x
    5    5    20.2x
    5   10     6.8x
    5                             3.4x
   24    4     5.7x
   24    6     5.6x
   25    1    16.2x
   25    2     8.3x
   26    4    18.4x
   26                              3.1x
   27                    4.2x
   27    7     8.9x
   27    8     6.1x
   27    9     7.2x
   27   10     6.1x
****** End of check ******

1
**** Weighted correlation matrix (weight = sample total) ****

SPEC AX1          1.0000
SPEC AX2         -0.0724    1.0000
SPEC AX3          0.0013   -0.1029    1.0000
SPEC AX4         -0.0836   -0.0953    0.2112    1.0000
ENVI AX1          0.8874    0.0000    0.0000    0.0000    1.0000
ENVI AX2          0.0000    0.8483    0.0000    0.0000    0.0000    1.0000
```

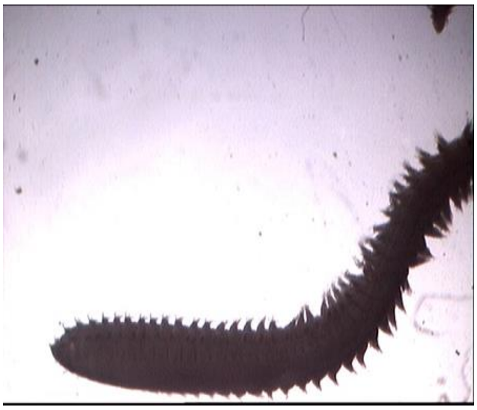
```
ENVI AX3          0.0000   0.0000   0.7512   0.0000   0.0000   0.0000   1.0000
ENVI AX4          0.0000   0.0000   0.0000   0.7151   0.0000   0.0000   0.0000   1.0000
Sand      0.2289  0.1846  -0.0941   0.4429   0.2580   0.2176  -0.1253   0.6194
Silt      0.0386 -0.3665  -0.3735  -0.1228   0.0435  -0.4321  -0.4972  -0.1718
Clay     -0.1690 -0.1322  -0.2686  -0.2799  -0.1905  -0.1559  -0.3576  -0.3914
Phosphat -0.0687  0.1560  -0.2377  -0.2141  -0.0774   0.1839  -0.3164  -0.2994
Nitrate   0.1353  0.1526   0.5922   0.3063   0.1525   0.1799   0.7883   0.4284
Org. Car -0.5006  0.5331   0.1823  -0.0446  -0.5641   0.6284   0.2427  -0.0624
Potassiu  0.4647  0.2475  -0.0949  -0.1157   0.5237   0.2918  -0.1263  -0.1618
Sodium    0.2304  0.3594  -0.0471  -0.4534   0.2597   0.4236  -0.0627  -0.6341
Cacium    0.1658  0.4644   0.3263   0.1389   0.1869   0.5474   0.4343   0.1942
Magnesiu          0.7038   0.2184  -0.0174  -0.0654   0.7931   0.2575  -0.0231  -0.0915

         SPEC AX1         SPEC AX2         SPEC AX3         SPEC AX4         ENVI AX1
         ENVI AX2         ENVI AX3         ENVI AX4

Sand      1.0000
Silt     -0.5015  1.0000
Clay     -0.7623  0.5064   1.0000
Phosphat -0.3234  0.4245   0.4265   1.0000
Nitrate   0.2746 -0.4072  -0.6518  -0.3158   1.0000
Org. Car -0.2197 -0.1818  -0.0173   0.2024   0.1984   1.0000
Potassiu -0.2797  0.3311   0.2699   0.0966   0.0202  -0.1134   1.0000
Sodium   -0.4988  0.3289   0.3958   0.6086  -0.1137   0.2253   0.5769   1.0000
Calcium   0.1433 -0.2895  -0.3131  -0.1014   0.5123   0.5523   0.1636   0.2041
Magnesium -0.0005  0.0846  0.0622  -0.0003   0.0038  -0.0879   0.5539   0.4005

         Sand     Silt     Clay     Phosphat Nitrate  Org. Car Potassiu Sodium

Cacium    1.0000
Magnesiu          0.5281   1.0000

         Calcium  Magnesiu

 N       name        (weighted) mean    stand. dev.       inflation factor

 1       SPEC AX1               0.0000             1.1269
 2       SPEC AX2               0.0000             1.1788
 3       SPEC AX3               0.0000             1.3312
 4       SPEC AX4               0.0000             1.3985
 5       ENVI AX1               0.0000             1.0000
 6       ENVI AX2               0.0000             1.0000
 7       ENVI AX3               0.0000             1.0000
 8       ENVI AX4               0.0000             1.0000
 1       Sand          4.1891             0.6514             5.7573
 2       Silt          1.7114             0.9086             2.2318
 3       Clay          2.2340             1.2095             6.3910
 4       Phosphat      0.5846             0.5301             3.1719
 5       Nitrate       0.2762             0.1965             3.9020
 6       Org. Car      0.9869             0.6192             3.6998
 7       Potassiu      1.0260             0.5739             2.8325
 8       Sodium        1.3836             0.5999             4.3227
 9       Calcium       2.7635             0.6408             6.2848
10       Magnesiu      0.0292             0.0221             3.9462
```

```
**** Summary ****

Axes                               1        2        3        4      Total inertia

Eigenvalues                  :          0.502    0.378    0.202    0.141        2.622
Species-environment correlations  :     0.887    0.848    0.751    0.715
Cumulative percentage variance
   of species data                :      19.2     33.6     41.3     46.7
   of species-environment relation:      37.8     66.2     81.4     92.0

Sum of all              eigenvalues                                          2.622
Sum of all canonical     eigenvalues                                         1.330

All four eigenvalues reported above are canonical and correspond to axes that
 are constrained by the environmental variables.


*** Unrestricted permutation ***

Seeds:  23239   945

**** Summary of Monte Carlo test ****

Test of significance of first canonical axis: eigenvalue =    0.502
                                   F-ratio    =    7.585
                                   P-value    =    0.0100

Test of significance of all canonical axes  : Trace      =    1.330
                                   F-ratio    =    3.293
                                   P-value    =    0.0050

(  199 permutations under reduced model)
```

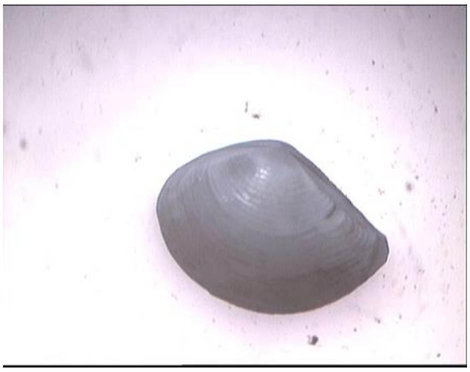
Ampipod

Capitellid sp.

Tanaid sp.



Nepthys sp.



Tellina sp.

Sipuncula sp. (Sipunculidae)

Glycera spp. (Glyceridae)

Marphysa sp. (Eunicidae)

Nepthys sp. (Nepthyidae)

Maldane sp.(Maldanidae)