CITY UNIVERSITY OF HONG KONG
香港城市大學

Effects of Human Disturbance on Biological Traits and Structure of Macrobenthic Communities
人爲擾動對大型底棲動物群落的生物特徵及結構的影響

Submitted to
Department of Biology and Chemistry
生物及化學系
in Partial Fulfilment of the Requirements
for the Degree of Doctor of Philosophy
哲學博士學位

by

Anne Lise Fleddum

July 2010
二零一零年七月

Abstract of thesis entitled

Effects of Human Disturbance on Biological Traits and Structure of Macrobenthic Communities

人爲擾動對大型底棲動物群落生物特徵及結構的影響

Submitted by

Anne Lise Fleddum

For the Degree of Doctor of Philosophy at the City University of Hong Kong

Rapid changes in marine biodiversity are occurring globally due to human disturbances, such as fishing and pollution; yet, the ecological impacts of functional features and diversity loss in ecosystems are poorly understood. The effects of trawling on benthic habitat and community structures have drawn much attention in recent years. Trawling is probably the most significant factor affecting the structure of soft sediment communities globally and may lead to large-scale shifts in the functional composition of the marine benthos, with likely effects on the functioning of the entire coastal ecosystem. However, the use of functional features, in combination with traditional methods of analysis of community patterns, based on biodiversity data to detect the effects of trawling is scarce. Although Biological Traits Analysis (BTA) is considered to be a powerful method for evaluating the ecological functioning of benthic assemblages, only a few studies have been reported in temperate waters. Further, the focus of these studies has generally been on the anthropogenic impact. This thesis discusses the impact of trawling on different coastal systems based on the combined use of traditional biodiversity analysis and BTA methods, taking into account the amount of rare species and their total contribution to ecosystem functioning. There have been no previous studies published using this methodology.

In this study, BTA was used together with traditional biodiversity analysis to investigate how the structure and function of macrobenthic communities are affected by:

1) non- or low- (known) trawling frequency in two different water masses (Arctic and Atlantic);
2) high-trawling frequency with annual hypoxia (hypoxic gradient on infauna and epifauna) and from three coastal systems with different controls (infauna):
    (a) a fjord system in Norway where trawled sites were compared to non-trawled sites,
    (b) an upwelling system in the southern part of Africa (coastal South Africa and Namibia) where heavily trawled sites were compared to lightly trawled sites and
    (c) a subtropic system in Hong Kong where heavily trawled sites were compared to a marine protected area (MPA).
3) recovery from trawling inside the MPA in Hong Kong where past and present data were compared.

All these systems showed changes in structure and functioning to some different degree. As reviewed in literature, the role that rare species play in ecosystem functioning is not well understood. Traditional biodiversity data analysis methods tend to underestimate the importance of rare species. However, the present study showed that rare species are very important when considering the total pool of biological traits (BTs) and, therefore, should not be ignored.

In the study of Norwegian water masses, taxonomic composition, abundance of taxa and BTAs were used to investigate differences in structure and functional diversity. Two distinct marine macrobenthic assemblages were considered: the Arctic (cold water) and the southern part of Norway (relatively warm water). Multivariate analysis techniques were used to examine each assemblage's structure and functioning at 60 sampling stations. The data from seven BTs were divided into 36 categories, for 284 common marine benthic taxa. The two areas showed clear differences in taxonomic composition and relative species abundance. However, when BTs information was taken into account (weighted), the differences between the two areas in the ordination plot were not so apparent. When only the presence or absence of species in the BTs data was considered, there was no significant difference between the assemblages. All of the above suggested that the same BTs are represented in both water masses, but to different degrees, depending on the community dominance of species adapted to each system.

It was also noteworthy that in these two Norwegian water masses, several species within the same genus and family had exactly the same combination of BTs. The results thus indicated that different species possessed the same trait combination, even though they came from different water masses. This finding emphasized a balance in functional traits and indicated that different species contributed equally to the BTs for this analysis. However, the effects that species composition and diversity have on ecosystem functioning

are difficult to distinguish, and this observation is not mutually exclusive of an idiosyncratic pattern.

In the Norwegian (Oslofjord) study, taxonomic and BTs compositions of communities from sampling stations collected in trawled and non-trawled areas were compared. Surprisingly, there were significantly higher numbers of species, individuals and BTs diversity at the trawled locations compared to the non-trawled locations in the Oslofjord. The Intermediate Disturbance Hypothesis may explain this finding since repeated trawling will act as an occasional community disturbance. The hypothesis predicts that a certain degree of disturbance may enhance diversity, provided that the disturbance is not too severe. In cases of severe disturbance, a reduced diversity would result.

The South Africa study explored the use of BTA to assess differences in the ecological functioning of infaunal communities between areas exposed to heavy and light-trawling intensities in the southern Benguela region of the south-east Atlantic. Multivariate analyses of biomass were employed to investigate differences in infaunal community composition between sites and differences in intensities of trawling. Multivariate analyses showed significant differences among sampling sites, as well as between heavily and lightly-trawled areas (ANOSIM, $p < 0.05$). The analysis of infauna biomass weighted by BTs showed significant differences between heavily and lightly trawled areas for 17% of the traits investigated (non-parametric Mann-Whitney U test, $p < 0.05$). BTs were also shown to differ significantly between areas having larger or smaller proportions of sand (12% traits differed significantly) and mud (7% traits differed significantly). This suggested that in the coastal region of southern Africa, the disturbances caused by trawling contributed more to the observed differences in BTs than sediment composition.

In the Hong Kong study, heavily trawled sites inside Tolo Channel were compared to a Marine Protected Area (MPA) in Hoi Ha Wan, which has been closed to trawling for approximately 12 years. There were significant differences in community structure and biological functioning between the wet and dry seasons. However, the BTs results showed that there were no significant differences between the trawled area and the non-trawled area (MPA). It was noteworthy that seasonal changes appeared to play a more important role in determining both the structure and functioning of the two macrobenthic communities (trawled and non-trawled) than that played by the effects of trawling.

Prior to this study, it was assumed that biodiversity would increase after the MPA was established (i.e., after trawling has ceased) and that larger and long-lived species would dominate. However, when the author's benthic data from the MPA was compared to historical data (i.e., prior the closure of the area to trawling), it was found that the opposite was the case, i.e., the biodiversity and abundance had decreased dramatically inside the protected area since trawling had ceased.

Regarding the MPA in Hoi Ha Wan, there are three important factors to consider: the rate of recovery from the cessation of trawling, the hydrodynamics of the protected area and the presence of artificial reefs deployed in the MPA. Given the difficulty of assessing the individual effects of these factors, it is hard to deduce any clear cause for the decreasing trend in biodiversity after the closure of the area for trawling. It is suggested that further, long-term research is carried out on the structural and functional diversity inside the MPA. This research should include changes around the artificial reefs and comparisons of the community structures over time between trawling sites and the MPA.

The second study in Hong Kong was related to heavily trawled sites with annual hypoxia problems. Organic pollution and eutrophication arising from poor water circulation and dispersion is a known problem in the Tolo Harbour area and has caused major changes in the structures of phytoplankton, fish and benthic communities. The differences in the macrobenthic communities between the wet and dry season are significant in Hong Kong waters. Data taken at the end of the wet season showed that there was a clear increase in both the hypoxic gradient and the total organic carbon (TOC) gradient moving inland from coastal areas (i.e., from Mirs Bay towards the Tolo Channel and the inner harbour). In general, the dissolved oxygen increased after trawling for all four of the layers measured (1 cm below the sediment surface, and 1 cm, 50 cm and 1 m above the sediment surface). The biodiversity of the infauna decreased with increasing levels of TOC in the sediment. The epifauna followed a similar pattern.

In the dry season, the level of dissolved oxygen (DO) was high for all the stations, and the differences after trawling were not as clear in the upper layers (50 cm and 1 m above the sediment surface) as for the wet season. High mortality occurred in the summer due to the low oxygen content in the inner part of the Tolo Harbour. However, in the winter (dry season), the community managed to revert to normal due to the higher oxygen content, and rapid re-colonization occurred. There were significant differences in BTs composition for the infauna between the two seasons. A closer examination of the traits showed significant

differences for 14% (five categories) of the 36 categories considered. These five categories were: size < 5 mm: medium mobility; dorsal flat body form; permanent tube habitat and scavenger feeding type. For the epifauna, 58% (21 out of 36) of the categories showed significant differences. It was anticipated that opportunistic and small-body-size species would be abundant under more hypoxic conditions (summer/wet season). However, the significant BT characteristics of the few species which remained under the hypoxic summer conditions (i.e., no mobility, cylindrical body, permanent and sessile attachment) suggested adaptation rather than opportunism to the low DO levels.

In this thesis, the BTs under different environmental stressor conditions (e.g., different levels of trawling and hypoxia) were examined. The differences in BTs which were observed have led to a better understanding of the impact due to changes in some environmental conditions. A similar examination of the differences in BTs may also help with the future assessment of the effects of different environmental changes (stressors) on the soft benthic community. Study of the changes in the relative proportions of BTs considered in this thesis complements traditional methods of biodiversity and community structure analyses. This combined approach may be helpful in identifying impact-driven alterations to ecological functioning and may also offer more information on ecosystem monitoring, management and conservation.

Table of Contents

Declaration i

Abstract ii

Thesis Acceptance ix

Publications, poster, report and award x

Acknowledgements xii

Table of Contents xiv

List of Tables xx

List of Figures xxv

Chapter 1 Introduction 1

1.1 General introduction 1

1.2 Datasets 5

1.3 Objectives 6

1.4 Organisation of thesis 7

Chapter 2 Background of Study 9

2.1 Structure and functioning debate 9

- 2.1.1 The importance of biodiversity 9
- 2.1.2 Hypothesis of biodiversity and ecosystem functioning 10

2.2 Biological Traits (BTs) 16

2.3 Rare species and Species Abundance Distribution (SAD) 18

2.4 r and K-selected species 20

2.5 Intermediate Disturbance Hypothesis (IDH) 23

2.6 Trawling 26

- 2.6.1 Trawling methods 26
- 2.6.2 Trawling effects 29
- 2.6.3 Trawling regulations 35

2.6.4 Recovery from trawling 37
2.7 Eutrophication and hypoxia 39

Chapter 3 Structure and function of infaunal communities in arctic and temperate water masses 43
3.1 Introduction 43
3.2 Materials and methods 45
3.2.1 Data mining 45
3.2.2 Biological traits (BTs) 48
3.2.3 Data analysis 50
3.3 Results 51
3.3.1 Abundance structure 51
3.3.2 Abundance weighted with BT structure 54
3.3.3 BT structure 54
3.3.4 BT combination 58
3.4 Discussion 62
3.4.1 Abundance and BT structure 62
3.4.2 BT combinations 64
3.4.3 Continuing research 67

Chapter 4 Impact of structure and function of infaunal communities in trawled and non-trawled areas in the Oslofjord, Norway 69
4.1 Introduction 69
4.2 Materials and methods 72
4.2.1 Benthic infauna sampling 72
4.2.2 Sediment analysis and TOC determination 73
4.2.3 Biological traits (BTs) 73

4.2.4 Statistical analysis 74

4.3 Results 81

4.3.1 Environmental analysis 81

4.3.2 Biodiversity analysis 84

4.3.3 Biological Traits Analysis (BTA) 88

4.3.4 Species Abundance Distribution (SAD) and BT contribution 92

4.4 Discussion 96

4.4.1 Environmental analysis and trawling effects 96

4.4.2 Biodiversity 97

4.4.3 Biological traits (BTs) 100

4.4.4 Species Abundance Distribution (SAD) and BT contribution 101

Chapter 5 Impact of structure and function of infaunal communities in heavily and lightly trawled areas in Southern Benguela upwelling region 103

5.1 Introduction 103

5.2 Materials and methods 106

5.2.1 Sampling design 106

5.2.2 Environmental components 112

5.2.3 Biological Traits Analysis (BTA) 115

5.2.4 Statistics and analysis 115

5.3 Results 117

5.3.1 Environmental analysis 117

5.3.2 Univariate and multivariate analysis of community structure 122

5.3.3 Species Abundance Distribution (SAD) 127

5.3.4 Biomass 130

5.3.5 Biological Traits Analysis (BTA) 132

5.4 Discussion 139

5.4.1 Environmental characteristics 139

5.4.2 Community structure 139
5.4.3 Rare and opportunistic species 140
5.4.4 Functional structure 141

Chapter 6 Impact of Intense Fishing Disturbance on Infaunal Communities and Recovery from Trawling in a Marine Protected Area (MPA), Hong Kong 144

6.1 Introduction 144
6.2 Materials and methods 147
6.2.1 Sampling design 147
6.2.2 Field sampling 151
6.2.3 Laboratory analyses 151
6.2.4 Biological traits (BTs) 154
6.2.5 Data analysis 155
6.3 Results 157
6.3.1 Environmental analysis 157
6.3.2 Benthic infauna 161
6.3.3 Biological traits (BTs) 176
6.4 Discussion 179
6.4.1 Environmental factors 179
6.4.2 Biodiversity 180
6.4.3 Biological traits (BTs) 186
6.4.4 Recovery from trawling in Marine Protected Areas (MPAs) 187

Chapter 7 Impact of structure and function of infauna and epifauna in heavily trawled areas and under a low level of oxygen in Tolo Harbour, Hong Kong 193

7.1 Introduction 193
7.2 Materials and methods 196
  7.2.1 Benthic infauna sampling 196
  7.2.2 Epifaunal sampling 200
  7.2.3 Sediment analysis and TOC determination 200
  7.2.4 BTs 201
  7.2.5 Species abundance distribution (SAD) 201
  7.2.6 Statistical analysis 201
7.3 Results 202
  7.3.1 Dissolved Oxygen (DO) 202
  7.3.2 Benthic infauna 206
  7.3.3 Species Abundance Distribution (SAD) for the infauna 215
  7.3.4 BTs for the infauna 219
  7.3.5 Benthic epifauna 221
  7.3.6 Species Abundance Distribution (SAD) for the epifauna 227
  7.3.7 BTs the epifauna 229
7.4 Discussion 234
  7.4.1 Impact of the structure of infauna and epifauna to seasonal oxygen changes 234
  7.4.2 Impact of BTs to seasonal oxygen changes 238

Chapter 8 General Discussion and Conclusions 241

8.1 General discussion 241
8.2 Limitations 250
8.3 Suggestions for further work 251
8.4 Contributions to our knowledge and overall conclusions 253

Chapter 9 References 257

9.1 References cited 257

9.2 References for biological traits and taxa 305

  9.2.1 Articles 305

  9.2.2 Books 311

  9.2.3 Software 314

  9.2.4 Web 314

Appendix I Statistics 320

Appendix II BT scores and species lists (CD) 325

List of Tables

Table 2.1 Summary r- and K-selected species in anthropogenic impacted and non-impacted circumstances based on experience from earlier studies 22

Table 2.2 Selected studies and reviews undertaken on impacts of trawling and dredging on benthic habitats worldwide 1971-2009 32

Table 3.1 BT and categories used in the analysis. Each of the categories has affinities ranging from 0-3, where 0 is no affinity and 3 is total affinity 49

Table 3.2 Dominant taxa in each area measured in % of the total abundance within each species, genus and family of the data collected from the database 52

Table 3.3 Top ten taxa in Arctic and South of Norway. B = Bivalvia, E = Echinodermata, O = Others and P = Polychaeta 52

Table 3.4 Significantly different BTs in infauna, as tested by non-parametric Mann-Whitney U, between Arctic (Ar) and Atlantic (At) water masses 56

Table 3.5 Results from Bray Curtis similarity of BT combinations. This table is based only on taxa sharing 100% similarities between groups. Each letter represents one type of combination and is marked with A-V. The letter X is area (30% of the most abundant) with the specific trait combination 59

Table 4.1 Sampling date, depth and positions for the stations in outer Oslofjord, Norway. Four locations (A, B, C, D) with non-trawled controls (C) and trawled areas (T) 77

Table 4.2 Overview of the 13 biological traits and 58 categories chosen for the analysis. Each category was scored according to the affinity of each taxon for each trait category, ranging from 0-3, where 0 is no affinity and 3 is total affinity 79

Table 4.3 Summary of environmental variables for the control (C) and trawled

(T) stations: TOC (%), sand/silt/clay (%) and Md Φ 82
Table 4.4 Summary of univariate diversity indices (pooled) for the control (C) and trawled (T) stations. Total species (S/0.5 m^2), total individuals (N/0.5 m^2), Pielou evenness (J') and loge Shannon diversity (H') 85
Table 4.5 Top ten species for control and trawled stations (pooled data) 85
Table 4.6 Summary of significant species (alphabetic order) based on Mann-Whitney U rank of pooled abundance for trawled and control areas. Higher rank sum for control areas are marked in bold 86
Table 4.7 Top ten categories for control and trawled treatments (weighted with square-root transformed abundance) 90
Table 4.8 Results from Mann-Whitney U test by variable treatments (trawled vs. control). Only significant categories are mentioned in the table. Higher rank sum for control is marked in bold 91
Table 5.1 Details of the four sampling sites in the southern Benguela region 111
Table 5.2 Grain size of all the sampling stations and the relationship between Folk’s triangle (Gravel-Sand-Mud) and Wentworth scale (Sand). Sand (s), muddy sand (ms), sand mud (sm), fine sand (fs) and very fine sand (vsf) 119
Table 5.3 Summary of total biomass (g/m^2), total species (S/m^2), total individuals (N/m^2), Pielou’s evenness (J') and Shannon-Wiener diversity (H' in loge) for lightly trawled (LT) and heavily trawled (HT) stations 124
Table 5.4 Percent of dominant taxa occurring at each site and treatment: Mollusca (M), Polychaeta (P), Echinodermata (E), Crustacea (C) and Others (O) 125
Table 5.5 Top ten species contribution from one-way analysis of SIMPER (Similarity Percentages) for lightly and heavily trawled areas based on abundance (Average dissimilarity = 66.89%) and biomass (Average dissimilarity = 69.38%). Taxa in bold face occurred at higher abundance/biomass in heavily trawled treatments 126

Table 5.6 Significantly different biological traits between heavily and lightly trawled areas as tested for BTs weighted by biomass (square-root transformed) using Mann-Whitney U tests 134

Table 5.7 Significantly different biological traits between small (SS) and large proportions of sand (LS) as tested for BTs weighted by biomass (square-root transformed) using Mann-Whitney U tests. Sand content was classified as large if $> 72\%$ and small if $\leq 72\%$ 135

Table 5.8 Significantly different BTs between small (SM) and large proportions of mud (LM) as tested for biological traits weighted by biomass (square-root transformed) using Mann-Whitney U tests. Mud content was classified as large if $> 20\%$ and small if $\leq 20\%$. 136

Table 6.1 Position of the heavily-trawled stations (T) and the control area (C) inside the Marine Protected Area 150

Table 6.2 Wentworth (Φ) scale (Buchanan 1984) and grade classification ($\Phi = -\log_2$) of the particle diameter in millimeters 153

Table 6.3 Summary of the environmental characteristics and trawling intensity per week of all the sampling stations in both control/trawled treatments and seasons. DO = Dissolved Oxygen, Temp = Temperature, TOC = Total Organic Carbon, TI = Trawling Intensity, MD = Median Diameter of particle size 158

Table 6.4 Eigenvalues, percentage variation (contribution to the variance) and cumulative variance for the environmental factors for both seasons. PC 1-5 represents the axis in the PCA plot. 159

Table 6.5 Dominant taxa measured in percentages for both seasons. Polychaeta (P), Mollusca (M), Crustacea (C), Nemertinea (N), Sipuncula (S), Echinodermata (E) and Echiura (Ec) 163

Table 6.6 Univariate analysis of pooled abundance data (0.5 m^2) is shown for the wet and dry season. The letters that represent in the table are: Species (S/0.5 m^2); total biomass (B) (g/0.5 m^2); number of individuals (N/0.5 m^2); Pielou's eveness (J') and loge Shannon diversity (H') 164

Table 6.7 Test statistics for pair-wise PERMANOVA analysis of infaunal abundance and biomass between control and trawled areas for both seasons. Significant values at $p < 0.05$, based on permutations, are shown in bold 167

Table 6.8 The top five species contribution from SIMPER (Similarity Percentages) for the wet and dry season 169

Table 6.9 The BT categories contribution from one-way analysis of SIMPER (Average dissimilarity = 64.58%) and Mann Whitney U test is calculated between seasons. Cut off for low contribution is 90%. Significant level ($p < 0.05$) is shown in bold 177

Table 6.10 The top ten dominant species ($N/0.5\ m^2$) from grab samples in non-trawled and trawled treatments in outer Oslofjord (from Olsgard 2008) 183

Table 7.1 Position and depth at the grab and trawling stations taken during the wet (September 2007) and the dry season (January 2008). The five stations sampled in this study were the same used by the EPD in their monitoring programme. Stations marked in brackets (107, 112 and 113) are the same stations used in a consultancy study on marine benthic communities in Hong Kong 199

Table 7.2 Dominance taxa at each grab sampling station measured in percentage (%) for both seasons. Crustacea (C), Echinodermata (E), Mollusca (M), Nemertea (N), Polychaeta (P) and Sipunculida (S) 207

Table 7.3 Summary of sediment characteristics: total organic carbon (mean TOC) measured in percentage, total biomass ($g/0.5\ m^2$), total species ($S/0.5\ m^2$), total individuals ($N/0.5\ m^2$), Pielou evenness (J') and loge Shannon diversity (H') for all the grab stations 210

Table 7.4 Significantly different biological traits of the infauna as tested by non-parametric Mann-Whitney U between wet/dry seasons for biological traits weighted with biomass (square-root transformed) 218

Table 7.5 Dominant taxa at each trawling sampling station measured in % for the wet and dry season. Crustacea (C), Echinodermata (E), Mollusca (M) and Others (O) 222

Table 7.6 Summary of mean biomass (g/10^4 m^2), mean species (S/10^4 m^2), mean individuals (N/10^4 m^2), Pielou evenness (J') and loge Shannon diversity (H') for all the trawling stations in both seasons. Data on biomass, species and individual are the mean of six replicates while the Pielou and Shannon diversity is the pooled data of six replicates. Standard deviation (± SD) is marked beside the number 224

Table 7.7 Significantly different biological traits of the epifauna as tested by non-parametric Mann-Whitney U between wet/dry seasons for biological traits weighted with biomass (log (X+1) transformation) 230

List of Figures

Figure 2.1 Elaborations on the Central Hypothesis, explaining the relationships between biodiversity and ecosystem functioning 14

Figure 2.2 A graphical representation of the variation of biodiversity with different levels of disturbance, as predicted by the Intermediate Disturbance Hypothesis (IDH). The hypothesis predicts the highest biodiversity when disturbance level is of an intermediate intensity 25

Figure 2.3 Common trawling gear used for commercial fishing 28

Figure 2.4 Pearson-Rosenberg model (1978) illustrating how species, abundance and biomass change along a gradient of disturbance 42

Figure 3.1 Overview of the two study areas and the 60 sampling stations. 30 grab stations are located at the Pechora Sea, Barents Sea and Franz Josef Land, and 30 grab stations are in the southern Norwegian Sea and North Sea. Each dot represents a sampling station, which is the sum of five 0.1 m^2 van Veen grab samples 47

Figure 3.2 MDS of square root transformed species abundance showing significant dissimilarity (ANOSIM, $p < 0.001$, $R = 0.97$). Black spots represent assemblage in Arctic water masses and grey triangles in warmer waters in the South of Norway 53

Figure 3.3 MDS of transformed species abundance weighted with BT score affinities showing significant dissimilarity (ANOSIM, $p < 0.001$, $R = 0.19$). Black spots represent assemblages in Arctic water masses and grey triangles in warmer waters in the South of Norway 55

Figure 3.4 MDS without abundance showing significant similarity in BT patterns (ANOSIM, $p < 0.001$, $R = 0$). Black spots represent assemblages in Arctic water masses and grey triangles in warmer waters in the South of Norway 57

Figure 4.1 Sampling locations of the four different areas (A-D) in the Oslofjord, Norway. The treatment C after area A-D is control (non-trawled), while T is the trawled sites 78

Figure 4.2 PCA bi-plot of environmental data showing the relationship between trawling (black triangle) and control stations (grey circle). The percent sand, clay, silt and TOC were arcsine transformed before data were normalized and are represented by the lines within the circle 83

Figure 4.3 MDS of the abundance with five replicates (square-root transformed). Black triangle is the control and grey circle represents the trawled treatment. Capital A-D is the area 87

Figure 4.4 MDS of square-root transformation abundance weighted with BTs (five replicates). Black triangle is the control and grey circle represents the trawled treatment. Capital A-D is the area 89

Figure 4.5 Histogram of Species Abundance Distributions (SAD) for the trawled (light grey) and control (dark grey) areas using abundance category of modified $\log_2$ classes. Number 1 (Bin 1) at the x-axis represents one species, number 2, 2-3 species, number 3, 4-7, number 4, 8-15, etc in a logarithmic scale 93

Figure 4.6 BT contributions for rare species from trawling (light grey) and control (dark grey) areas measured as percent of the whole trait pool. The BT is ranked as presence/absence. Dark grey = control areas, light grey = trawled areas 94

Figure 5.1 Study areas in the southern Benguela region. Black circles represent heavily trawled areas and grey circles represent lightly trawled areas 109

Figure 5.2 Diagrammatic representation of abandoned wellhead structure in lightly trawled area in South Africa 110

Figure 5.3 Gravel-Sand-Mud classifications according to composition ratios 114

Figure 5.4 Total organic carbon (%) contributions (above) and comparison by site in pie diagram (below) for HT and LT areas. The two-way nested ANOSIM analysis showed significant differences in sediment composition among sites (Global R = 0.783, p = 0.001) but not between treatments (Global R = - 0.188, p = 1.0) 120

Figure 5.5 Principal Component Analysis plot (correlation-based) of pooled environmental data and depth at lightly trawled (open triangles) and heavily trawled (black circles) sites. NAM: Namibia, Child: Childs Bank; Col: Cape Columbine; POINT: Cape Point (see Fig. 5.1). The eigenvectors are superimposed on the PCA plot. The two-way nested ANOSIM analysis showed significant differences in the environmental variables among sites (Global R = 0.875, p = 0.01) and between treatments (Global R = 0.504, p = 0.0001) 121

Figure 5.6 Species Abundance Distributions (SAD) for heavily- (grey bars) and lightly- (white bars) trawled areas, using abundance category of modified $\log_2$ classes 128

Figure 5.7 BTs' contribution for rare species from LT and HT sites measured as a percent of the whole traits pool. The BT is ranked as presence/absence 129

Figure 5.8 MDS of square-root transformed infaunal biomass (two-way nested ANOSIM, Bray-Curtis similarity with all replicates. Sites: Global R = 0.833, p = 0.01; Treatments: Global R = 0.508, p = 0.001). Black circles represent heavily-trawled areas and grey triangles represent lightly-trawled areas 131

Figure 5.9 MDS of square-root transformed infaunal biomass × biological traits (two-way nested ANOSIM, Bray-Curtis similarity with all replicates. Sites: Global R = 0.258, p = 0.001; Treatments: Global R = 0.277, p = 0.004). Black circles represent heavily-trawled and grey triangles lightly-trawled areas 134

Figure 5.10 PCoA graphs reflecting square-root-transformed infaunal biomass weighted by significant BTs from Table 5.6. Panel a) shows the PCoA of 40 site and area replicates using Euclidean distance on the biomass-weighted BTs matrix. Panels b) to g) show bubble plots superimposed on a) and scaled to represent biomass distribution of each trait of each replicate sample at each site and area. H = heavily trawled, L = lightly trawled 138

Figure 6.1 Map of all the sampling sites, A-D, and the control, C, inside the Hoi Ha Wan Marine Park and trawled T outside the protected area.

The dotted line is the boundary line for the protected area 149

Figure 6.2 Principle Component Analysis (PCA) of normalised environmental factors using Euclidean distance. AT-DT = Trawling stations; AC-DC = control stations. The lines show the direction of the environmental factors relative to the stations. Percentage of TOC was arcsine transformed before data being normalised. The upper figure a) is the result from the wet season and b) from the dry season 160

Figure 6.3 Principal Coordinate Analysis (PCoA) of the transformed pooled biomass (g/0.5 m^2) for both treatments (T = trawled, C = control) and seasons (d = dry, w = wet) 166

Figure 6.4 Species Abundance Distribution (SAD) for each season and each treatment (trawled and control/MPA). The X-axis is a logarithmic scale (modified $\log_2$ classes). Class 1 represents 1 individual, 3 represents between 2-3 individuals, 7 represent 4-7 individuals, etc. 171

Figure 6.5 Biological traits contribution for rare species from the wet and dry season (trawled area and the control/MPA) measured as percent of the whole traits pole. The BT is ranked as presence/absence. See Chapter 3 for category names 172

Figure 6.6 Bubble plot of the PCoA (the same station positions as in Fig. 6.3) of species contributors (g/0.5 m^2) from the SIMPER analysis 174

Figure 6.7 PCoA of weighted traits with square-root transformed biomass for treatments (AC-DC = Control areas; AT-DT = trawled areas) and seasons (w = wet; d = dry) 177

Figure 7.1 Grab and trawling stations in Tolo Harbour (HP1, HP2, HP3), Tolo Channel (HP4, HP5, HP6) and Mirs Bay (control stations, C1, C2) for the wet (September 2007) and dry season (January 2008) 198

Figure 7.2 Dissolved oxygen 1 cm below the sediment, and 1 cm, 50 cm and 1 m above the sediment, measured in percentage, for all the stations before (solid line) and after trawling (dashed line), in wet season in September 2007 204

Figure 7.3 Dissolved oxygen 1 cm below the sediment, and 1 cm, 50 cm and 1 m above the sediment, measured in percentage, for all the stations before (solid line) and after trawling (dashed line), in dry season in January 2008 205

Figure 7.4 Total organic carbon (TOC) measured in percentage as an increasing gradient. SAB: Species (diamond), abundance (square) and biomass (triangle), as points and trend line in logarithmic scale in the wet season 211

Figure 7.5 Total organic carbon (TOC) measured in % as an increasing gradient. SAB: Species (diamond), abundance (square) and biomass (triangle), as points and trend line in logarithmic scale in the dry season 212

Figure 7.6 Hierarchical cluster analysis of the infauna for both seasons (Bray-Curtis similarities, square-root transformation). Branches connected to each solid line showed significance differences (SIMPROF, $p < 0.05$) in community structure 214

Figure 7.7 Species Abundance Distributions (SAD) for the wet (grey bars) and the dry (white bars) season using abundance category of modified $\log_2$ classes 216

Figure 7.8 Histogram of the significant traits (biomass infauna × biological traits occurring in wet and dry seasons) from Table 7.4, based on Mann-Whitney U rank. See Table 7.4 for category names 219

Figure 7.9 Cluster analysis (Bray-Curtis similarity) of all the grab stations based on similarities in biological traits composition (square-root transformed pooled biomass × categories) for the wet and dry seasons. Branches connected to each solid line showed significance differences (SIMPROF, $p < 0.05$) in traits structure 220

Figure 7.10 Hierarchical cluster analysis of the epifauna measured for both seasons (Bray-Curtis similarities, Log (X+1) transformation). Branches connected to each solid line showed significant differences (SIMPROF, $p < 0.05$) in community structure 226

Figure 7.11 SAD for the wet (grey bars) and dry (white bars) season using abundance category of modified $\log_2$ classes 228

Figure 7.12 Histogram of the significant categ ories based on non-parametric Mann-Whitney U rank. The log (X+1) biomass of the epifauna was weighted with biological traits occurred in the wet and dry seasons. See Table 7.7 for category names 231

Figure 7.13 Cluster analysis (Bray-Curtis similarity) of all the trawling stations based on similarities in biological traits composition (log (X+1) transformed, pooled biomass × categories) for the wet and dry season. Branches connected to each solid line showed significant differences (SIMPROF, $p < 0.05$) in biological traits structure 233