Effects of demersal trawling on marine infaunal, epifaunal and fish assemblages: studies in the southern Benguela and Oslofjord

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Declaration

I hereby declare that all the research presented in this thesis is my own, except where otherwise stated and acknowledged in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

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Date

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Abstract

This thesis investigates the impacts of the demersal trawl fishery on infaunal, epifaunal and fish assemblages in the southern Benguela upwelling system for the first time. In the absence of representative areas of similar habitat protected from trawling in the southern Benguela region, infaunal and epifaunal assemblages were compared between heavily and lightly trawled areas to assess the impacts of the otter-trawl fishery. Infauna were sampled at four sites, from southern Namibia to near Cape Town by means of five replicate grab samples at each paired heavily and lightly trawled area. Invertebrate epifauna were sampled at two sites in heavily and lightly trawled areas using a fine-meshed otter trawl. Sites ranged in depth from 350-450 m in unconsolidated sediment habitat. Epifaunal assemblages showed greater differences at heavily trawled areas with significantly reduced species diversity, average number of species and individuals. Several epifaunal species were absent from heavily trawled areas highlighting their vulnerability to impacts of trawling. Multivariate analyses show significant differences in composition of both infaunal and epifaunal assemblages among the sites and between trawling treatments at all sites. The results of this study suggest that intense trawling activities are at least partially responsible for significantly altering benthic community composition, affecting epifauna to a greater measurable extent than infauna.

Biological Traits Analysis (BTA) was used to explore potential changes in ecological functioning of benthic assemblages, comparing areas exposed to heavy and light trawl intensities in the Benguela system. BTA incorporates biological traits (life-history, morphology and behaviour) of infaunal and epifaunal species with biomass, capturing a broad range of information of marine benthic assemblages. Seventeen percent of the infaunal traits analysed showed a significant difference between heavily and lightly trawled areas. Twenty-four percent of epifaunal biological traits investigated were significantly different between areas of heavy and light trawling. This study suggests that more intense trawling modifies some trait constituents of the benthic assemblage in the southern Benguela region, confirming the sensitivity of functional traits analysis in detecting changes induced by trawling disturbance. Biological traits analysis of benthic invertebrates shows promise as a practical technique for incorporation into monitoring programmes and for developing indicators of benthic ecosystem health, needed for implementation of an ecosystem approach to fisheries management in South Africa.

A lack of representative untrawled areas in the trawl grounds of southern Africa precluded investigations comparing trawl impacts with unfished reference sites. A bilateral agreement between South Africa and Norway (NORSA) provided the opportunity to conduct experiments in an untrawled area of Oslofjord, Norway, where a shrimp trawl fishery for *Pandalus borealis* operates nearby. Infauna were sampled at four untrawled sites in Oslofjord with five replicate grabs after which an Agassiz beam sled was dragged across two of the sites (impact sites) four times, simulating a trawl disturbance. Infauna were re-sampled at all four sites immediately after trawling (post-impact), 14 days and 64 days after the impact to monitor recovery of infaunal populations. Multivariate analyses comparing the impact sites with paired control sites for each sampling occasion showed no significant differences in infaunal assemblages at any stage of the experiment. Whilst it is considered possible that the trawl simulation was not a sufficient impact to represent that of a commercial trawl effect, it is considered more likely that trawl activities in Oslofjord do not inflict measurable impacts on infaunal assemblages. However, the impact of trawling on epifaunal assemblages in Oslofjord was not investigated in this study.

Annual research survey data collected over the past 24 years (1986-2009) provide an opportunity to explore long-term demersal fish assemblage composition changes on the west coast of South Africa. Differences in spatial (latitude and depth) and temporal (seasonal and annual) factors were examined using multivariate analyses. Possible long-term changes were investigated using the Sequential T-test Algorithm to detect Regime Shifts (STARS). Results indicate geographic differences in fish assemblage composition from the northern to the southern region on the west coast of South Africa. The fish community composition is also clearly influenced by depth with a distinct change in fish assemblages in the shelf break region between 300 m and 400 m. Multivariate analyses also show two clear temporal changes in assemblage composition, firstly, in the early 1990s and secondly, in the mid-2000s. STARS analyses detect long-term shifts in 27% of demersal species with the majority of species' shifts detected either in the early- to mid-1990s or in the past decade (2002 to 2009). Multivariate analyses among year groups reveal an increase in three fast-growing, early maturing species and decreases in two slow-growing, long-lived species. STARS analysis detected increases in two of the same fast-growing species, decreases in an additional four slow-growing, long-lived species, but four other slow-growing, long-lived species showed the opposite trend (i.e. increases). The hypothesis of an increase in fast-growing, early maturing species and a decline in slow-growing, long-lived species in fished systems is therefore only partially supported by these findings. Shifts in demersal fish assemblages coincide temporally with spatial shifts observed in small pelagic species and west coast rock lobster. The shifts in the demersal fish assemblage composition detected in this study are probably a reflection of long-term indirect effects of fishing in combination with environmental changes.

The response of benthic invertebrate assemblages to two levels of fishing intensity in the southern Benguela region justifies regular monitoring of epifauna during existing annual demersal research surveys and infaunal monitoring through dedicated, periodic sampling initiatives. Demersal fish assemblage data should be regularly assessed for changes in community composition. Representative protected areas can serve as reference areas against which fishing impacts could be assessed and improve our understanding of ecosystem effects of demersal fishing.

Chapter One

Introduction to the impacts of demersal trawling

The world's earliest account of demersal trawling dates back to the year 1376 (Thrush *et al.* 1995, Roberts 2007) when a request was made to the King of England to ban the "*wondyrechaun*" (a fishing instrument described as an early type of beam trawl gear) that "*when fishing it destroys the flowers of the land below the water there, and also the spat of oysters, mussels and other fish upon which the great fish are accustomed to be fed and nourished.*" (Roberts 2007). Upon investigating this complaint, it was agreed by all parties that the use of the "wondyrechaun" would thereafter only be permitted in "deeper waters" and not used in coastal estuaries or bays (Roberts 2007). From the outset, trawl fishing has been controversial and its early history can be tracked through enquiries, complaints and various bans or restrictions of its use. More than 600 years later, in the 21st century, the general controversies regarding the impacts of trawling persist. The ongoing disparity in beliefs can be broadly summarized into two groups of opinions, those that believe the evidence of unequivocal damage to the benthos by trawling is clear and scientifically verifiable (e.g. Rogers 2005, Gray *et al*. 2006, Gray *et al*. 2007a & b) and those that question the appropriateness of some sampling methods and robustness of the scientific evidence detecting extensive damage or significant changes to benthic species or unconsolidated sediment habitats (e.g. Hoydal 2005, Løkkeberg 2005, Løkkeberg 2007). It is, however, widely acknowledged that there are limitations to the conclusions from many studies, largely due to a lack of baseline information prior to fishing, a paucity of unfished representative control sites, difficulties in differentiating between natural variability and the effects of fishing and the practical challenges of investigating deep sea habitats (Jennings & Kaiser 1998). The fundamental argument remains not whether trawling impacts on marine habitats, but whether the extent of impact is unequivocally deleterious to marine resources, ecosystems and biodiversity. The investigations conducted in this study do not aim to provide a panacea for the 600-year debate but aim to improve understanding of the impacts of demersal trawl fishing in the highly dynamic, southern Benguela upwelling ecosystem. This study is the first investigation of the effects of demersal trawling in the region, despite the fact that the 100-year old demersal trawl fishing industry is the largest, most valuable fishery in southern Africa and substantial effort is directed towards monitoring its target resources.

Impacts of demersal fishing

Fishing, by its nature, selectively removes target species of specific sizes from the marine environment, largely to satisfy the needs and desires of humans, and is considered the most widespread exploitative activity in the marine environment (Jennings & Kaiser 1998). The fishing industry fulfills a demand that is created and driven by society. Some types of fishing may be highly selective, targeting only the desired species and having little direct impact on other species or the environment e.g. tuna pole. Other fishing methods are less selective, yielding large quantities of bycatch and wide-scale impacts, both direct and indirect e.g. demersal trawling.

Mobile demersal fishing gears are deployed on every continental shelf in the world (Collie *et al*. 2000a) with nearly 20 million km^2 (75% thereof) subjected to trawl and/or dredge activities (Kaiser *et al*. 2002). Over the past decade, it has become widely acknowledged that such fishing activities have a profound disturbance effect on the ecosystem (Dayton *et al*. 1995, Jennings & Kaiser 1998, Auster & Langton 1999, Watling & Norse 1998, Hall 1999, Kaiser & de Groot 2000) and are described as “one of the greatest sources of anthropogenic disturbance to marine benthic communities” (Kaiser *et al*. 2000, Kaiser *et al.* 2006). Watling and Norse (1998) compare the impacts of demersal trawling to that of forest clearcutting, reporting that the total area trawled each year is approximately 150 times greater than the area of forest lost but that the effects of trawling have been largely overlooked because they manifest in the ocean depths, beyond the view of most. The process of fishing results not only in the removal of target and non-target species, but also causes varying levels of disturbance to the environment that can alter habitat complexity, remove, damage or kill biota thereby reducing overall benthic production, and leading to substantial changes in benthic community composition and habitat (Dayton *et al.* 1995, Auster & Langton 1999, Kaiser *et al.* 2002, Hiddink *et al*. 2006, Kaiser *et al.* 2006).

Many different types of demersal fishing gear are deployed around the world and generally include trawls, dredges and traps, with various modifications, to maximize landings of target species (Jennings & Kaiser 1998). The type of physical impact the fishing gear has on the seafloor and the bycatch depends, *inter alia*, on the mass and design of the gear, degree of contact with the seafloor and the towing speed (Thrush & Dayton 2002). In assessing the impacts of trawling and dredging in different habitats, from a range of studies that used different gears and different sampling designs, Collie *et al.* (2000a) and Kaiser *et al.* (2002) conclude that dredging (intertidal and scallop), rock-hopper otter trawling and beam trawling have the greatest measurable effect on the seabed. Dredges and rock-hopper otter trawls are often used in areas that support highly diverse and sensitive communities, resulting in severe habitat damage (Kaiser *et al.* 2000). Lighter gears, e.g. small otter and prawn trawls, are predicted to have less direct impact on the seabed, except for the trawl doors which create furrows in the soft sediment. Although these gears generally have a lighter impact on the seabed, the ropes and warps are often dragged across the seabed and can dislodge emergent epifauna (Smith *et al.* 2000). Attempts to rank the degree of trawling impact with respect to habitat type based on sediment or biogenic properties, yielded inconsistent results, which Collie *et al.* (2000a) largely attributes to the unbalanced nature of the data (many combinations of gear and habitat were unrepresented in their assessment). Kaiser *et al*. (2003) suggests that habitats should not be classified by the sediment type alone and that depth, physical and oceanographic features and species composition all contribute to defining the habitat type that can be expected.

The degree and longevity of direct impacts caused by fishing gear are influenced by habitat type and the extent of natural disturbances. Large-scale natural disturbances, like seasonal storms and strong currents, form a background against which smaller disturbances occur, e.g. bioturbation effects (Hall *et al.* 1993, Jennings & Kaiser 1998, Kaiser 1998). Several studies have shown that habitats exposed to frequent natural perturbations (e.g. mobile megaripple habitats) are able to recover from the effects of low levels of trawling disturbance in weeks to months (Kaiser & Spencer 1996). Organisms living in habitats with a high degree of natural disturbances are adapted to periodic sediment resuspension and smothering (Collie *et al.* 2000a) and are less likely to undergo long-term changes in composition in response to the disturbance caused by fishing activities (Kaiser 1998). The effects of small-scale fishing activities are frequently masked by high levels of natural disturbance in such habitat types (Thrush & Dayton 2002, Hiddink *et al.* 2006). In any particular habitat, the associated biota are most likely to have some degree of resilience, adaptations or biological traits that enable them to persist alongside the associated natural disturbances (Kaiser *et al.* 2003). However, the spatial scale and frequency of fishing events may increase to a point where lasting ecological effects are observed, even against a background of natural disturbance (Kaiser *et al*. 2002). High levels of trawling disturbance could potentially exceed those of natural disturbances resulting in ecological shifts in community composition (Kaiser *et al.* 1998, Kaiser *et al.* 2002).

More stable, sheltered or complex habitats are usually more profoundly affected by fishing activity, and can result in long-term community changes (Jennings & Kaiser 1998). Stable habitat types (e.g. mud and sand sediments in deeper waters) experience fewer natural disturbances with the associated communities being longer-lived and slower to recolonise following a disturbance event (Kaiser & Spencer 1996, Kaiser *et al.* 1998, Hiddink *et al.* 2006, Queirós et al. 2006). Not only are structurally complex habitat types (e.g. coral reefs, seagrass beds) destroyed by passing trawl gear, but subtly textured sediments (e.g. soft sandy grounds) are smoothed over, reducing the heterogeneity of surficial sediment structures. Organic matter accumulates in and around subtle sediment features (Curry & Parry 1996) and plays an important role in influencing diversity and species composition of benthic communities (Hall 1994). Structural features of marine habitats, even small mounds and indentations, are important in providing surfaces for feeding and sheltering from predators through various life-history phases of many commercially important species (Watling & Norse 1998, Kaiser *et al.* 2002, Thrush & Dayton 2002).

The ecological disturbance theory predicts that short-lived, highly mobile, dispersing species with high fecundity (*r-selected* species) are better adapted to recover from disturbances than species that are long-lived, sessile and have low fecundity (*K-selected* species, Pianka 1970). Several studies have shown this theory applies to areas disturbed by trawling, where a measurable increase in *r-selected* species and a concomitant decrease in *K-selected* species are observed with increasing intensity of trawl activities (Steele *et al.* 2002). The effects of disturbance on communities most frequently affect all trophic levels of benthic biota, from meiobenthos through to demersal fish communities. Community changes in fish populations are likely to manifest over considerably longer time periods (decades) than smaller, more confined species like epifauna and infauna, and may not be readily detected through short-term studies (Frid *et al*. 2000, Ball *et al*. 2000).

The greatest measurable, direct impacts are usually detected in epifaunal communities (Engel & Kvitek 1998, Jennings & Kaiser 1998, Kaiser *et al*. 2000, Hansson *et al.* 2000, McConnaughey *et al.* 2000, Steele *et al*. 2002). Epifauna, defined as those species living on, protruding from, anchored in or attached to benthic substrates, are most vulnerable to the passage of trawl gear due to their life history characteristics (Jennings & Kaiser 1998). Sessile epifauna, like sponges, bryozoans, hydroids, gorgonians and corals that form complex three-dimensional habitat structures, are particularly vulnerable to mechanical disturbance. Decreases in these species provide the first indications of the effects of demersal fishing (Jennings & Kaiser 1998). Reduced epifaunal abundance has been closely coupled with decreases in fish productivity and survival (Sainsbury *et al*. 1997, Auster *et al*. 1997). Juvenile fish are known to seek shelter and food amongst structures created by epifauna (e.g. sponges, bryozoans, gorgonians etc.). Auster *et al*. (1997) reported greater densities of early juvenile (0-year) silver hake (*Merluccius bilinearis*) associated with habitat cover of amphipod tubes. They proposed that juvenile hake avoid visual predators among the tube cover and co-occur with their preferred prey (i.e. amphipods and shrimp). A reduction in habitat complexity, concurrent with that of epifaunal species loss, increases predation risk for juvenile commercial species and reduces the abundance of important prey species for other piscivorous fish (Walters & Juanes 1993, Tupper & Boutilier 1995, Auster *et al*. 1997, Collie *et al*. 2000b).

Infauna (species living within the sediment) are also affected by trawling disturbances, however, many of these species have life history characteristics that facilitate either escape from the disturbance impact or rapid recolonisation following the disturbance (e.g. burrowing urchins, bivalves and some polychaetes). Deeply buried fauna are likely to escape the physical effects of passing trawl gear, although their burrows may collapse, requiring additional energy to rebuild (Jennings & Kaiser 1998). These types of indirect negative effects on benthic communities are unlikely to be readily detected by experiments typically designed to examine direct impacts of trawling. Other infaunal species are more severely impacted by high levels of disturbance (e.g. tube-building polychaetes) and are rapidly eliminated from areas that are frequently subjected to disturbance, being replaced by more opportunistic, *r-selected* species. Opportunistic species can rapidly recolonise disturbed areas and maintain species diversity, abundance and biomass measures, although the composition of the community may have been altered significantly. Changes in infaunal communities as a result of impacts from disturbance may not always be readily detected through measures of species abundance, biomass or diversity (Gibbs *et al*. 1980, Drabsch *et al*. 2001, Kenchington *et al*. 2001). Differences may only become apparent when community changes are investigated on a more holistic level in relation to ecosystem functioning.

Benthic infauna and epifauna are considered good indicator species with which to measure indices of biological ecosystem functioning (Gray *et al.* 1974, Salas *et al.* 2006, Bremner *et al.* 2006a). Benthic organisms living within sediments significantly influence major ecological processes contributing to regulation of carbon, nitrogen and sulphur cycling, transport, burial and metabolism of pollutants, secondary production, bioturbation and stability of sediments (Snelgrove *et al*. 1997, Snelgrove 1998, Hutchings 1998). Species having certain combinations of life history characteristics (biological traits) may be less vulnerable under adverse environmental conditions (Townsend & Hildrew 1994, Usseglio-Polatera *et al.* 2000, Tillin *et al.* 2006). Changes in the biological trait composition of benthic communities, as a result of trawling disturbance, are likely to result in altered ecological functioning of the system (Tillin *et al.* 2006, Bremner *et al.* 2006a). Measures of ecosystem functioning are believed to be more relevant in understanding the broader effects of trawling impacts and forms part of an ecosystem-based management approach. Investigating changes in biological traits incorporates aspects of species presence (abundance or biomass) with a variety of biological characteristics (life history, morphological and behavioural) and in this way is considered more likely to detect changes in ecosystem functioning as a result of a species' vulnerability to disturbance.

Measuring the impact of demersal fishing

Three approaches are generally adopted to quantify impacts of trawling in scientific studies; 1) comparisons at the scale of the fishery, 2) long-term monitoring and 3) manipulative experiments. Chronic impact studies compare conditions between areas fished at different intensities (or fished with unfished) in similar habitat types, or monitor conditions over time in the same fished area to determine the effects of cumulative impact at the scale of the fishery (McConnaughey *et al.* 2000, Gordon *et al*. 2005). Studies that monitor the recovery of the environment, subsequent to closure of a fishery or enforced habitat protection, can provide measures of impacts that may have been as a result of fishing activity (Kaiser *et al*. 1998). These approaches accurately represent trawling disturbance in terms of real effort and spatial dimensions (McConnaughey *et al.* 2000), however, are likely to be confounded by natural variability or fluctuations which may mistakenly be attributed to fishing-induced disturbance (Jennings & Kaiser 1998). Long-term changes in communities are frequently influenced by natural variability and can seldom unequivocally be attributed to the impacts of fishing alone. A third option involves acute impact studies, such as small-scale manipulative experiments or experimental fishing, which can provide direct evidence of immediate impacts, contrasting before and after effects or fished with unfished conditions of a known disturbance in a single habitat type (McConnaughey *et al.* 2000, Gordon *et al*. 2005). Such manipulative experiments provide a more structured study approach but seldom accurately represent the effort and spatial scale of a commercial fishery. All the approaches described above have been implemented in a multitude of studies, either independently or in combination, to investigate the effects of fishing disturbance on marine invertebrate and fish communities in a diverse range of ecosystems throughout the world.

The many studies investigating the impacts of trawling each contribute some level of information unique to the particular suite of circumstances occurring (habitat type, trawl intensity, gear type, natural disturbances etc.) and information more generally applicable to trawling impacts. Nonetheless it remains almost impossible to accurately predict the response of biota in specific habitats without employing dedicated experiments within that particular suite of circumstances (Hall 1994, Kaiser 1998, Collie *et al.* 2000a). Collie *et al*. (2000a) published a meta-analysis of 57 experiments that aimed to investigate the effects of fishing disturbance on benthic fauna and communities around the world. Of these studies, 18% were conducted in either Australia or New Zealand while only one study reported on the effects of intertidal bait collection in muddy sand habitats of South Africa (Wynberg & Branch 1994). The remaining studies in this meta-analysis were conducted in northern Europe (50%) or North America (32%). A mere six years later, Kaiser *et al* (2006) repeated a similar meta-analysis with nearly twice as many fishing impact manipulations (101) investigating the effects of fishing disturbance on benthic fauna and communities, including those reporting on recovery but excluding studies that investigated across different levels of fishing intensity. Again, only one intertidal study (Wynberg & Branch 1994) had been conducted in southern Africa and was included in the analysis, with the majority of studies being conducted in Europe or North America. Such global meta-analyses highlight the paucity of available information on the effects of demersal trawling in Asia and the southern hemisphere, especially South America and Africa. The reasons for such glaring disparity in the number of studies from Asia and the southern hemisphere being reported on may vary, however, in southern Africa, studies investigating the impacts of demersal trawling had simply not yet been conducted. This cannot be attributed to a lack of such fishing activities in this region. On the contrary, southern Africa hosts substantial demersal hake fisheries on the west and south coasts (Payne & Punt 1995, Griffiths *et al.* 2004) and crustacean trawl fisheries on the east coast (De Freitas 1989, Fennessy & Groeneveld 1997) that are of socio-economic importance in the region. Identifying and monitoring the effects of demersal fisheries has been identified as a research gap in southern Africa (Wilkinson & Japp 2005, Nel 2005, Shannon *et al*. 2006, Nel 2007).

Demersal fishing on the west coast of southern Africa

It was through the earliest marine research that demersal trawling became established in South African waters. In 1897, the first research vessel dedicated to exploring the Cape waters was that of the *Pieter Faure*, a trawler brought to South Africa by John D. F. Gilchrist, the government marine biologist at the time (Lees 1969, Brown 1997). The successful research catches lured the first commercial trawler to the Cape in 1899, pioneering the development of the South African fishing industry (Lees 1969). Initially the demersal fishery targeted Agulhas sole *Austroglossus pectoralis* and west coast sole *A. microlepis* (Payne & Badenhorst 1989), but with the discovery of the vast hake resource off the west coast, this soon became the targeted catch of demersal trawlers (Payne & Punt 1995). South Africa's demersal fishery, based on two hake species, *Merluccius capensis* and *M. paradoxus*, soon developed into the most important fishery in the region. Extensive historical reviews of South Africa's demersal fishery have been conducted by Lees (1969), Payne (1989) and Payne & Punt (1995) with more recent summaries provided by Griffiths *et al.* (2004) and Shannon *et al.* (2006). The expansion of the fishery was initially hindered by the Anglo-Boer war (1899-1902) and the two World Wars, after which annual hake landings were approximately 50 000 tons (Payne 1989). Originally centered off Cape Town, improved technology and development of landing ports facilitated the spread of the fishery northwards to Saldanha (Fig. 1.1), at this time still exploited mostly by South African fleets (Payne 1989, Payne & Punt 1995). In the early 1960's foreign fleets, largely from Soviet Union, Japan and Spain, joined the local fleets in trawling for hake off South Africa and Namibia, rapidly escalating the landings of hake with the peak in landings of nearly 300 000 tons being reached in 1972 (Payne 1989, Payne & Punt 1995). The over-exploited hake resource was subjected to additional pressure with illegal practices frequently reported e.g. the use of fine mesh liners. In the same year the International Commission for the Southeast Atlantic Fisheries (ICSEAF) was established and implemented a minimum trawl net mesh size of 110 mm, a system of international inspection and allocated a quota system to member countries (Payne 1989). In 1977 South Africa declared a 200-nautical mile economic exclusion zone (Fig. 1.1), preventing the majority of foreign vessels from fishing within this zone (Payne 1989) and set about rebuilding the hake stocks with conservative annual total catch limits being set (Shannon *et al.* 2006).

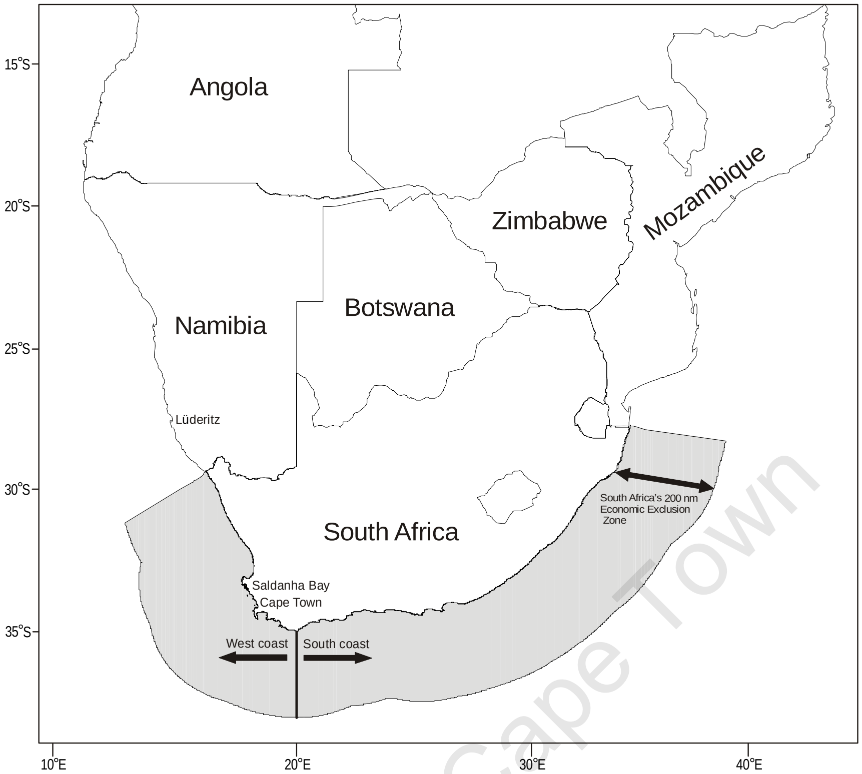


Fig. 1.1. Southern Africa with South Africa's 200-nautical mile economic exclusion zone represented and demarcation of west and south coasts.

The demersal fishery is South Africa's most valuable fishery with offshore and inshore landings accounting for approximately half of the income generated by marine fisheries in the country (Shannon *et al*. 2006) and providing employment for nearly 9000 people (Sauer *et al*. 2003). Present management of the fishery aims to optimize economic and social benefits without compromising long-term biological sustainability of the target and bycatch species (Shannon *et al*. 2006). The fishery is primarily managed under an Operational Management Procedure (OMP) whereby management objectives, risks and constraints are agreed upon and tested using models which underlie management advice for the annual total allowable catch (TAC) limits (Shannon *et al*. 2006). The conservative management strategies currently implemented in South Africa still focus on rebuilding the hake stocks, one of which (*M. paradoxus*) is probably shared with its north-western neighbouring country, Namibia (Payne 1989).

The two target hake species of the demersal fishery are morphologically similar and comprise between 60% to 90% of the total retained catch (Walmsley *et al*. 2007). *Merluccius capensis* (shallow water hake) occur shallower than 450 m while *M. paradoxus* (deep water hake) range from 150m to 800m+

(Payne & Punt 1995). Hake also constitute an important component of the hake longline, handline and inshore demersal fishery which is located on the south coast of South Africa (Payne & Punt 1995). Valuable bycatch species for this fishery on the west coast include kingklip *Genypterus capensis*; monkfish *Lophius vomerinus*; horsemackerel *Trachurus capensis;* ribbonfish *Lepidopus caudatus* (scabbardfish); gurnards *Chelidonichthys capensis* and *C. queketti*; jacopever *Helicolenus dactylopterus*; Cape dory *Zeus capensis* and angelfish *Brama brama* (Walmsley *et al.* 2007). There is growing concern regarding the increasing valuable bycatch of chondrichthyan species like soupfin shark *Galeorhinus galeus* and smoothhound *Mustelus mustelus* in the trawl catch (Shannon *et al*. 2006). Incidental bycatch species commonly occurring in the catch include, *inter alia*, rattails (grenadiers) of the genus *Caelorinchus* sp. and *Malacocephalus* sp., which are mostly discarded (Griffiths *et al*. 2000).

South Africa is signatory to the World Summit on Sustainable Development Plan of Implementation (2002) and is thereby committed to establishing and implementing an ecosystem approach to fisheries (EAF) in the country by 2010. South African legislation provides a governance framework for preserving biodiversity, protecting ecosystems as a whole and implementing ratified international agreements (Marine Living Resources Act No. 18 of 1998, National Environmental Management: Biodiversity Act No. 10 of 2004). In establishing an EAF for South African demersal trawl fisheries, it is crucial to identify and define the effects of trawling on the impacted habitat, fish and benthic communities. In 2004, the Marine Stewardship Council (MSC), a marine eco-labeling certification body, awarded South Africa’s demersal hake fishery MSC certification for a period of four years, implying that the fishery is sustainable and not harmful to the environment. Several conditions were required to be addressed during the four years in order to obtain re-certification after this time, one of which was to investigate the effects of trawling on benthic habitats. Subsequently, a study conducted by Wilkinson and Japp (2005), investigating the hake-directed trawl intensity on benthic habitat in South Africa, stated that “*there have thus far been no specific studies of habitat impacted by hake-directed gear in South Africa*.” Pitcher *et al*. (2008) evaluated the progress of 33 countries in implementing an ecosystem-based fishery management approach and South Africa ranked within the top six on each of the performance ratings measures. While South Africa is making measurable progress in implementing an EAF approach, several ecological components of major fisheries in the region require further consideration. A risk assessment for sustainable fisheries of the South African demersal hake fishery identified the impact of trawling on the benthic habitat and biota to be a high risk to sustainability of the fishery (Nel 2005, Nel 2007). Shannon *et al*. (2006) identified the impact of trawling on benthic habitat and biota as a major ecosystem concern to be addressed as part of South Africa’s commitment to EAF. There is an urgent need to investigate the interactions between demersal fishing activities, fishing pressures, the marine habitats they affect and the impacted fish and benthic communities. The South African deep-sea demersal fishing permit conditions, issued in 2006, for the first time include the requirement to "…take cognizance of sustainable fishing practices and of the impacts of trawling on the ecosystem." Furthermore, bobbins or rock-hopper gear with a diameter in excess of 750 mm or a weight in excess of 200 kgs are not permitted to be deployed with the trawl gear (DEAT 2006 Hake deep-sea trawl permit conditions). These precautionary measures serve as initial steps towards minimizing detrimental impacts on benthic habitats. Studies conducted in this thesis aim to investigate aspects of infaunal, epifaunal and demersal fish communities in response to impacts of the demersal hake fishery on the west coast of southern Africa and in this way contribute towards fulfilling South Africa's commitment to EAF.

Thesis structure

This thesis comprises a series of studies aimed at investigating impacts of the offshore demersal trawl fishery on the benthic assemblages of the west coast of southern Africa for the first time. Three components of the southern African west coast ecosystem are considered namely; infaunal, epifaunal and demersal fish assemblages. There being no representative trawling habitats formally protected from fishing in South Africa (Shannon *et al*. 2006), the bilateral agreement between South Africa and Norway (NORSA), created an opportunity to conduct *in situ* experiments in untrawled areas of Oslofjord, Norway to quantitatively assess impacts of demersal trawl gear on infaunal assemblages.

Chapter Two presents the findings from a study which compares the composition of infauna and epifauna between areas subjected to intense and light levels of trawling at sites within the southern Benguela upwelling region (27°S to 34°S). This study aimed to investigate the hypothesis that intense demersal trawling significantly alters the abundance, biomass, diversity and composition of benthic infaunal and epifaunal assemblages. The influence of environmental variables on benthic faunal assemblages was also examined. Infauna (> 1 mm in size) were collected using a 0.2 m^2 Van veen grab at four sites and epifauna were semi-quantitatively sampled using research demersal otter-trawl gear at two sites. Sediment particle size and total organic carbon content were measured from each grab sample with temperature, salinity, dissolved oxygen and depth also being recorded at each sampling station. Differences in infaunal and epifaunal assemblages, measured with abundance, biomass and diversity, between heavily and lightly trawled areas were investigated using univariate and multivariate analyses.

In Chapter Three biological traits (life-history, morphological and behavioural characteristics) of infaunal and epifaunal species sampled from heavily and lightly trawled areas were compiled and weighted by biomass. This study applies Biological Traits Analysis (BTA) in unconsolidated sediments in southern Africa's offshore marine environment to test the hypothesis of an increased disturbance as a result of intense demersal trawling leads to an increase in opportunistic, small-bodied, fast-growing species, while larger-bodied, longer lived species occur with lighter levels of trawling. Analyses of biological traits weighted by biomass aimed to investigate whether ecological functioning of infaunal or epifaunal biota differed significantly between areas of heavy and light trawling intensities. The use of BTA to provide an index of change of overall ecological function in marine benthic fauna as a result of fishing pressures, has only recently been conducted in the northern hemisphere (Bremner *et al*. 2005, Tillin *et al*. 2006, de Juan *et al*. 2007, Kenchington *et al*. 2007, Cooper *et al*. 2008).

As a result of there being no representative areas formally protected from trawling in southern Africa, an *in situ* experimental study was conducted in an untrawled area of Oslofjord, Norway, forming the subject of Chapter Four. A commercial otter-trawl fishery targets shrimp *Pandalus borealis* in large areas of Oslofjord deeper than 60 m. Legislation prevents trawling shallower than 60 m in the area, effectively providing representative habitat protected from trawling. It was hypothesized that there would be a decrease in larger-bodied, rare infaunal species as a result of the trawl disturbance and that recovery of the benthic infaunal community would be dominated by small-bodied, opportunistic species. A Before-After Control-Impact (BACI) experiment was conducted in an untrawled area to quantitatively assess the impact of an experimental trawl-disturbance on abundance, biomass and diversity of benthic infauna. Infaunal community recovery was monitored for 64 days after the trawl impact.

In Chapter Five, changes in the demersal fish assemblage of South Africa's west coast offshore region are investigated using annual research data collected over 24 (1986-2009) years during dedicated surveys. It was hypothesized that there would be a decrease of late-maturing, slow-growing demersal fish species over time, with either no change or an increase in fast-growing, early-maturing species. Multivariate analyses were used to detect changes in spatial (latitude and depth) and temporal (seasonal and annual) components. A sequential t-test algorithm (STARS) analyses was used to test for long-term shifts in demersal species.

The final chapter synthesizes the results of these studies, distills general conclusions and provides monitoring recommendations based on the impacts of the demersal trawl fishery on infaunal, epifaunal and fish assemblages identified in these studies.

Chapter Two

Comparing areas of heavy *versus* light demersal trawling along the west coast of southern Africa: Multivariate analysis of benthic assemblages

INTRODUCTION

All marine ecosystems, except those of the abyssal sea, are fished to some extent (Jennings & Kaiser 1998). The most dramatic changes in the community composition are likely to occur at the onset of fishing in a pristine area or when the fishing pressure increases dramatically from a very low level (Hiddink *et al*. 2006). Once fishing at a commercial scale has begun, the system enters a "fished" state and any changes as a result of increased fishing intensity are often smaller and more difficult to detect (Jennings & Kaiser 1998). It has been suggested that heavily fished, marine systems become less responsive (showing smaller changes) to the effects of fishing with increasing fishing duration and degradation severity of the system (Shannon *et al*. 2009). Many of the world's demersal trawl grounds were transformed to a "fished" state more than a century ago, well before the scientific value of pristine habitat was understood. Ecologists seldom have access to reference areas where the natural structure and variability of systems can be investigated without the confounding factors of anthropogenic influence. The scarcity of similar habitat areas protected from fishing to serve as suitable control sites is one of many reasons why marine protected areas are needed in many heavily fished ecosystems (Dayton *et al.* 1995, Jennings & Kaiser 1998, Kaiser *et al*. 2002).

Attempts to quantify fishing induced impacts on the environment are frequently confounded by natural perturbations, a history of fishing activities and small-scale patchiness (Gordon *et al.* 2005, Auster & Langton 1999, Dayton *et al.* 1995, Jennings & Kaiser 1998). Ideally, fished areas should be compared to the same areas before fishing commenced. This is frequently not possible when investigating large-scale ecosystems and one is confronted by issues relating to unreplicated sites and pseudoreplication (Hurlbert 1984) in comparing adjacent fished and unfished areas. Hurlbert (1984) defines pseudoreplication as the use of inferential statistics to test for treatment effects where either treatments are not replicated or replicates are not statistically independent. In a recent review of the topic, Oksanen (2001) considers the criticism of pseudoreplication "unwarranted stigmatization of a reasonable way to test predictions referring to large-scale systems". Hurlbert (1984) also acknowledges that replication is often impossible or undesirable when investigating large-scale systems and that when large effects of treatments are expected or when cost of replication is great, experiments involving unreplicated treatment may be the only or best option. Hurlbert (1984), however, further cautions that conclusions derived from unreplicated treatments should not be extrapolated to broader application.

Demersal trawling activities are known to alter the physical nature of the environment with intensely trawled areas having reduced habitat complexity and altered sediment and organic composition (Engel & Kvitek 1998, Jennings & Kaiser 1998). Natural variability and small-scale patchiness also result in gradients of change with respect to environmental variables in marine ecosystems (Hall *et al.* 1994). In attempting to tease apart the effects of natural variability and disturbances from those induced by fishing activities, it is important to reduce the number of factors that could confound results observed, as far as possible. Comparisons between assemblages occurring in fished *vs.* unfished or lightly fished areas will be more robust if environmental variables (e.g. sediment composition, organic content, depth, salinity etc.) at the areas are similar. Minimizing environmental variability strengthens the possibility of any biotic changes observed being as a result of trawling impacts.

Benthic fauna have been shown to play important ecological roles in both structuring the habitat and as prey for commercially valuable species (Gray 1974). Furthermore, benthic assemblages are considered to effectively integrate historical environmental conditions as a result of their comparatively limited mobility and permanence over seasons (Warwick 1993, Salas *et al*. 2006). Benthic assemblages provide useful indices to evaluate the status of marine ecosystems in monitoring for long-term responses and site-specific impacts (Salas *et al*. 2006).

The comparison of abundance and biomass dominance values of benthic assemblages as indicators to detect levels of disturbance was originally described by Warwick (1986) and called the Abundance-Biomass Comparison (ABC) method. The theory of ABC plots is based on evolutionary theory of *K*- and *r-selected* species (MacArthur & Wilson 1967, Pianka 1970) in response to a pollution-induced disturbance effect (Warwick 1986). The terms *K*- and *r-selection* were first presented by MacArthur and Wilson (1967) with *K* referring to carrying capacity and *r* to the maximal intrinsic rate of natural increase (Pianka 1970). *K-selected* species are usually competitively dominant with large body size, long lifespan and a fairly constant population size, but are also slow-growing and have delayed reproduction. At the opposite end of the continuum, *r-selected* species are small in body size, have a short lifespan, highly variable population sizes, rapid development and early reproduction (Pianka 1970). Warwick (1986) proposed that with stable, undisturbed conditions, *K-selected* species are predicted to dominate benthic communities in terms of biomass, but these species are rarely numerically dominant. With a pollution-induced disturbance (organic enrichment), *K-selected* species are less likely to survive, while opportunistic species (*r-selected*) are able to proliferate and can dominate numerically (Warwick 1986).

The ABC method involves plotting separate dominance curves for abundance and biomass on the same graph on a cumulative percentage dominance scale y-axis and species ranked in order of importance on a logarithmic scale x-axis (Warwick 1986). In undisturbed communities, large organisms result in the biomass curve lying above the abundance curve. In highly disturbed communities, a large number of small organisms are likely to dominate and the abundance curve lies above the biomass curve (Warwick & Clarke 1994). Under moderate disturbance conditions the abundance and biomass curves lie close together and may intersect one or more times (Warwick & Clarke 1994). Categorizing the disturbance at only three levels renders the method not particularly sensitive and results can be confounded by erratic occurrence of large numbers of small, mobile species, like amphipods or molluscs (Beukema 1988), or recruitment of spat (Warwick & Clarke 1993). A measure of the area between the abundance and biomass curves is provided with Clarke's *W-statistic* ranging from -1 to +1 where positive values are expected for undisturbed assemblages and negative values for impacted samples (Warwick & Clarke 1994, Clarke & Warwick 2001). ABC plots are considered appropriate to obtain an index of the community status when there is no reference to a true control site as the abundance and biomass curves serve as an "internal control" against each other (Warwick & Clarke 1994). With the absence of representative areas protected from demersal fishing in southern Africa, the ABC method is considered appropriate to investigate the effects of trawling on benthic assemblages.

The South African demersal otter-trawl fishery has existed for over 100 years and spans the Benguela region between depths of 200 to 700 m, on occasion extending to 1000 m (Payne & Punt 1995, Fairweather *et al*. 2006) and is South Africa's most important, valuable fishery (Shannon *et al*. 2006). The Namibian demersal hake fishery started in the late 1950s (Boyer & Hampton 2001) and is similarly Namibia's largest, most lucrative fishery (Bianchi *et al.* 2001). The physical impacts of demersal fisheries and concomitant ecosystem impacts have not previously been studied in southern Africa. This study aims to quantify the effects of demersal trawling on benthic invertebrate assemblages for the first time in the dynamic southern Benguela upwelling region. As with many other similar studies, the lack of suitable, unfished control sites in the region (Shannon *et al*. 2006) limited the scope of this study. Comparison of benthic invertebrates between areas that are intensively fished with those of similar habitat type, but which are lightly fished, is considered the best alternative option currently available. Benthic invertebrate assemblages were sampled at four sites spanning the southern Benguela region and compared between areas with different levels of trawling disturbance (heavy *vs*. light).

In exploring the dynamics of large-scale ecosystems, spatial variability is inevitable. The experimental design implemented in this study recognizes the wide spatial diversity to be expected among sites spanning seven degrees of latitude and for this reason the sites sampled are not considered replicates of each other. The overall aim of the study is to investigate the effects of disturbance (i.e. heavy versus light trawling) at four locations in the southern Benguela region. No two areas studied *in situ* are likely to be exposed to identical variables over time. In comparing site specific heavily and lightly fished areas in this study, it is assumed that the natural variability is approximately equivalent at adjacent areas. Invertebrate assemblages are primarily compared between treatments (trawl intensity) within a site, with the focus being on whether the fauna compositions differ with different treatments. Small-scale variability is accounted for by collecting five random, replicate grab samples (for infauna) and three replicate trawl samples (for epifauna) at each treatment level at each site. This research aims to specifically address the following questions;

- Does intense trawling result in significantly different abundance, biomass, diversity and composition of benthic infaunal and epifaunal assemblages in the southern Benguela region?
- To what extent do the environmental variables measured explain the distribution patterns of benthic assemblages observed?

METHODS

Study Sites

The spatial distribution of commercial fishing activity from 2003 to 2007 in South Africa was plotted using a geographical-information system (GIS) with start- to end-points of actual trawl positions reported in decimal degrees, minutes and seconds from vessel monitoring systems (Wilkinson & Japp 2005, incorporating more recent data for this study). Commercial trawl position data were obtained from Marine and Coastal Management, a branch of the Department of Water and Environmental Affairs (formerly Department of Environmental Affairs and Tourism). Due to a lack of operational vessel monitoring systems in Namibia, demersal trawl catch-per-unit-effort data from 2004 to 2005 were translated into hours fished at specific Namibian areas in question to obtain an indication of spatial fishing intensity (Ministry of Fisheries and Marine Resources demersal trawl database). Based on this information, four sites were identified (Fig. 2.1) as areas of intense commercial trawling (heavily trawled areas, HT, see below) with adjacent areas, in similar habitat types and depths, where trawling was considerably lighter (lightly trawled areas, LT, see below). Every effort was made to minimize differences in depth and sediment type between paired heavily and lightly ("treatment") trawled areas. The four sites sampled are named from north to south, Namibia, Childs Bank, Cape Columbine and Cape Point, for the purposes of this study (Fig. 2.1) and ranged from 346 to 459 m depth (Table 2.1). The northern most site is located approximately 130 km (75 nautical miles) south-west of Lüderitz, Namibia, where intense trawling occurs at depths of approximately 400 m, as the continental shelf begins to narrow and where demersal fish are believed to concentrate (MFMR demersal trawl database). The second site sampled was located near Childs Bank, a submarine mound on the west coast of South Africa in 350-400 m water, where an abandoned petroleum wellhead is reported to obstruct trawl fishing in a small area, with the larger area around the wellhead feature being frequently fished (Wilkinson & Japp 2005, Annual Summary of South African Notice to Mariners 2007). However, prior to sampling at this site numerous passes over the documented wellhead position (South African Notice to Mariners 2007) failed to detect an echo-sounder reading for this wellhead. A third sampling site was identified 115 km (~ 62 nautical miles) west of Cape Columbine, South Africa at a depth between 400 m and 440 m. The southern-most site was selected 57 km (~ 31 nautical miles) west of Hout Bay, Cape Point in 350 m water. The heavily trawled area of this site lies within one of the most intensively trawled areas in South African waters (Wilkinson & Japp 2005).

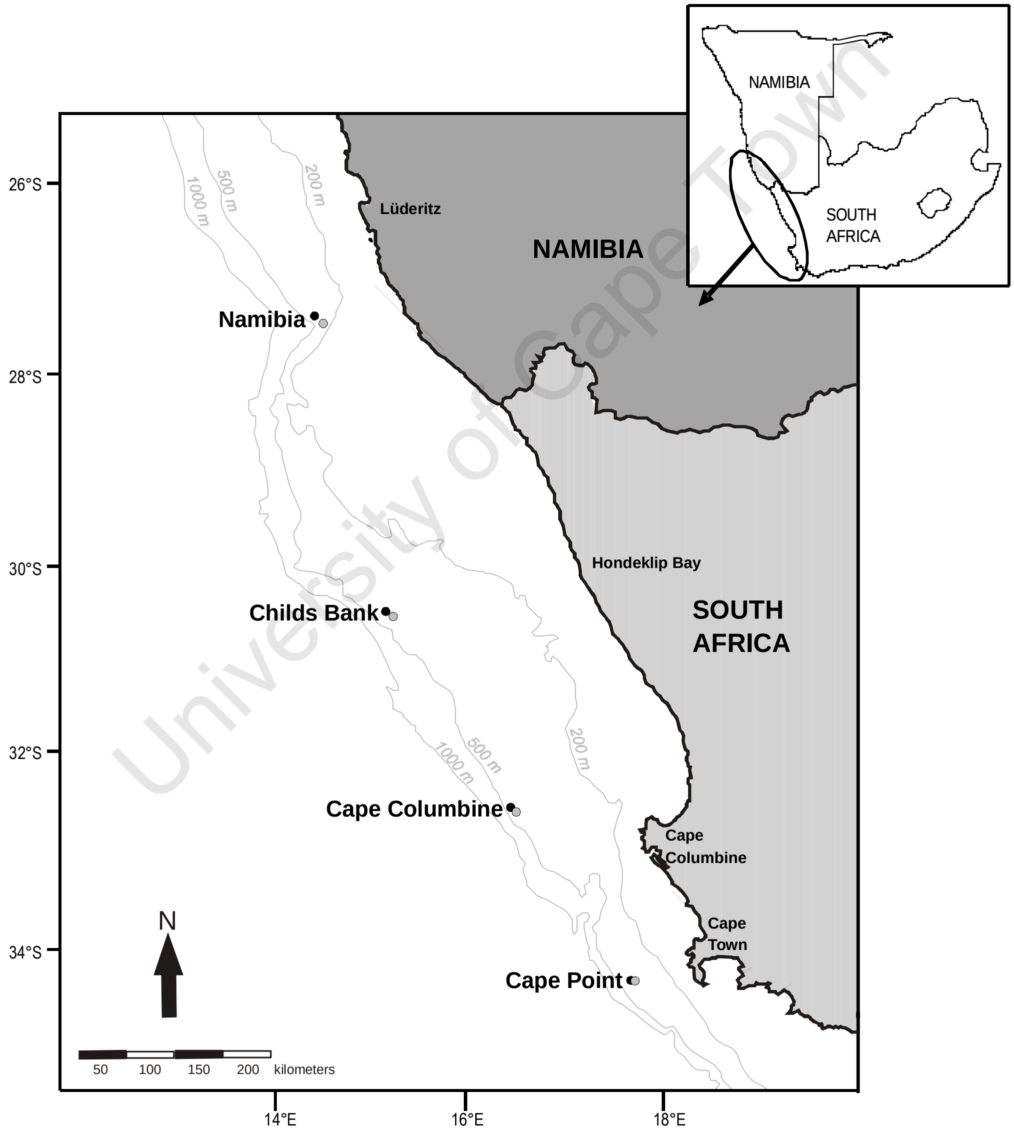


Fig. 2.1. Location of four selected sample sites. Black circles represent heavily trawled areas, grey circles represent lightly trawled areas.

The trawl intensity at each site located in South Africa (i.e. Childs Bank, Cape Columbine and Cape Point) was defined by calculating the number of trawl passes within a half nautical mile (nm) radius of each sample location over a 5 year period (2003 – 2007) using commercial data obtained from the Department of Water and Environmental Affairs: Marine & Coastal Management (MCM). Heavily trawled areas had ≥ 270 trawl passes over the five year period, while lightly trawled areas had between 30-187 trawl passes over the same time period (Table 2.1). The same level of detailed data were not available from Namibian Ministries of Fisheries and Marine Resources (MFMR), however, heavily trawled *vs.* lightly trawled areas sampled at the Namibian site were defined by the total number of hours spent fishing in each area during 2004 and 2005 (data obtained from the MFMR, Namibia). Commercial vessels fished between 18.3 and 27.7 hours in the heavily trawled area, compared to 0.17 and 11 fishing hours in the lightly trawled area over the same time period (Table 2.1). To facilitate comparisons between heavily and lightly trawled areas among sites, trawl tracks from South African sites were converted to estimated hours fished over five years and hours fished at the Namibian site were converted to estimated trawl tracks over a five year period (shown in parentheses in Table 2.1). To account for the fact that not all trawl tracks traverse through the centre of a half nautical mile radius buffer zone around a sample location, the average length of a trawl track was estimated to be 0.5 nm. For the purpose of converting between trawl tracks and hours, the average width of the trawl net opening was considered 30 m and the average towing speed of offshore trawl vessels being 3.5 nm/hr (Wilkinson & Japp 2005). These values provide comparable estimate fishing effort values based on the current best available data.

Five replicate benthic grabs were collected at each trawling treatment area at all four sites from RV *Dr Fridtjof Nansen* in April 2007 and FRS *Ellen Kuzwayo* in February 2008 (Cape Point, Table 2.1). Three replicate trawl samples were collected at heavily and lightly trawled areas of Namibia and Childs Bank sites during April 2007 to obtain large invertebrate epifaunal abundance and biomass. Limited research ship-time prevented further trawl sampling at the remaining two sites (Cape Columbine and Cape Point).

Table 2.1: Co-ordinates of benthic grabs and trawls, depths and trawl intensities at the sites sampled. See text for trawl intensity details.

Site	Benthic grabs					
	Heavily fished			Lightly fished		
	Co-ordinates	Depth	Trawl intensity*	Co-ordinates	Depth	Trawl intensity*
Namibia (south of Lüderitz)	27°46.5'S 14°41.91'E	405 m	18.3-27.7 hrs (320-485 tracks)	27°48.9'S 14°46.43'E	435 m	0.17-11 hrs (3-193 tracks)
Childs Bank	30°42.88'S 15°25.66'E	400 m	285 tracks (~ 41 hrs)	30°42.67'S 15°26.01'E	350 m	30 tracks (~ 4.5 hrs)
Cape Columbine	32°37.4'S 16°38.47'E	436 m	271 tracks (~ 39 hrs)	32°36.9'S 16°41.36'E	412 m	112 tracks (~ 16 hrs)
Cape Point	34°19.40'S 17°49.03'E	349 m	270 tracks (~ 39 hrs)	34°19.31'S 17°49.40'E	348 m	187 tracks (~ 27 hrs)

	Trawls			
	Heavily fished		Lightly fished	
	Co-ordinates	Depth†	Co-ordinates	Depth†
Namibia (south of Lüderitz)	27°45.7'S 14°41.7'E	406-409 m	27°48.8'S 14°46.0'E	446-453 m
Childs Bank	30°43.0'S 15°25.2'E	399-400 m	30°40.4'S 15°25.0'E	346-349 m

* Represents average number hours fished at Namibia site for 2004 and 2005 and actual trawl tracks passing within 0.5 nautical mile radius of South African sample sites from 2003 until 2007. Figures in parentheses represent calculated estimates of either trawl tracks (Namibia) or hours fished (South Africa) standardized to a five year period for both South Africa and Namibia.

† Maximum depths recorded during trawl replicates

Biological Sampling

Infauna

A 0.2 m^2 van Veen grab was used to collect five replicate infaunal samples at each heavily (H1 to H5) and lightly (L1 to L5) trawled area of each site. A trap door at the top of the grab allowed access to collect 250 ml of undisturbed sediment for particle size and organic carbon content analysis. The sediment volume was measured (in litres) and washed over two stacked sieves with mesh sizes of 10 mm (upper sieve) and 1 mm (lower sieve). A 1 mm mesh covering the seawater hose prevented large planktonic organisms from washing into the samples. All infauna >1 mm in size retained by the sieves were placed into sample bottles and preserved in 96% ethanol, replaced 24-48 hours later to ensure adequate preservation. Ethanol was washed from the samples over a 1 mm sieve and the sample material rinsed into a sorting tray. All infauna were picked out and sorted into broad taxonomic groups, labeled and again preserved in 96 % ethanol. Suitably intact specimens were identified to the lowest taxonomic level possible using a dissecting microscope (Leica EZ4 56 x magnification). Abundance, biomass (ethanol wet mass) and average size of all benthic infauna were recorded.

Epifauna

Epifauna were sampled with three replicate trawls in heavily and lightly trawled areas at the Namibian and Childs Bank sites (Fig. 2.1, Table 2.1). The otter-trawl gear consisted of 47 m footrope with 12 cm roller disks, 18-22 m mouth opening, 32 mm cod end mesh, lined with 25 mm mesh (defined as Gesund Super). Trawls were conducted during daylight hours between 07h00 and 18h00 local time (GMT+2) after the benthic grab samples had been collected at each site. Standard research trawl sampling protocols were followed according to Strømme (1992) with the exception that all epibenthic invertebrate fauna retained by the net were sorted by taxon, identified, counted and weighed. All unknown specimens were preserved for further identification. Epifaunal abundance and biomass values were scaled to a uniform trawl duration of 30 minutes. To analyse the semi-quantitative trawl epifaunal data, abundance and biomass measures were categorized on a log-scale for further analyses (Table 2.2). Analyses of demersal fish assemblages sampled during the trawls form a component of a parallel study and are not reported in this thesis.

Table 2.2: Categories allocated to abundance and biomass measures of epifauna collected from demersal trawls scaled to a 30-minute duration.

Category	Abundance (individuals)	Biomass (kilograms)
1	1 - 10	0.001 – 0.0100
2	11 – 100	0.011-0.100
3	101 – 1000	0.101-1.000
4	1001 – 10 000	1.001-10.000
5	10 001 – 100 000	10.001-100.000

Attempts were made to re-sample the trawled areas using the grab, immediately after the passage of the trawl net to provide a before-after comparison of infaunal assemblages. The probability of placing the grab accurately within the trawled path, at depths of 350-400 m in the dynamic, exposed southern Benguela region was considered very low and further sampling of this nature was abandoned.

Environmental variables

At each sampling site, a CTD (Conductivity-Temperature-Depth) meter was lowered to within 5 m of the sea floor, providing a water column profile of depth, salinity, oxygen and temperature.

Sediment particle size

Defrosted sediments from each replicate were dialyzed for approximately 12 hours using cellophane tubing and fresh water to remove salts. The salt-free sediment was washed out of the tubing and wet-sieved through a 63 µm mesh, separating sediments > 63 µm and mud (< 63 µm) fractions. The sand component was visually examined through a dissecting microscope to identify sediment components and then dried at 70°C. Once dry, the sediment was sieved to separate gravel (>2 mm) and sand (< 2 mm > 63 µm) and the sand component sieved for a further 5 minutes through a mechanised stack sieve system of five size categories according to the Wentworth scale (Wentworth 1922). The gravel and sand fractions were weighed to three decimal places. The mud component was left to settle for 24 hours, after which the excess water was poured off and a calibrated Andreasen pipette used to measure off 25 ml of homogenised mud which was dried at 70°C. A pipetting factor of 43.353 was used to determine the mass of the dried mud proportion. The mass of the gravel, sand and mud were converted into percentages and the Gravel-Sand-Mud texture category of each replicate sample determined using Folk's sediment classification triangle (Folk, 1968). Sediment processing and classification was conducted by the Department of Geological Sciences, University of Cape Town, under the guidance of Prof. John Rogers.

Organic carbon

Defrosted sediments from each site replicate were dried at 60°C, homogenised using a pestle and mortar and washed with 50 % hydrochloric acid to remove the inorganic carbon component ($C_{total} = C_{org} + C_{inorg}$). Once dried (at 60°C) the sediments were washed with 1M ammonium formate (removing any acid residue), filtered onto a filter paper and returned to the 60°C oven. Dried sediment, with inorganic carbon removed, were scraped from the filter paper into glass vials. The organic carbon contents of sediments from each site replicate were measured with a Thermo Flash 1112 elemental CHN analyzer using combustion in pure oxygen with helium carrier gas and column separation with assistance from a technician at the Department of Chemistry, University of Cape Town.

Statistical and numerical analyses

Univariate analyses

The average percent abundance and biomass were calculated per treatment (heavily and lightly trawled) at each site for the dominant phyla Mollusca, Annelida, Echinodermata and Crustacea with all remaining species being grouped as "Other" to provide an overview of benthic assemblages occurring at sites and treatments.

Proportions of total organic carbon (TOC) were arcsine transformed (Sokal & Rohlf 1969, Zar 1999) and tested for normality and homoscedacity. Univariate indices (number of species, number of individuals, Pielou's species evenness and Shannon-Wiener diversity) of infauna and epifauna were computed. Differences in the average abundance and biomass values, % TOC and univariate indices were tested by means of paired t-tests (STATISTICA V.8) between heavily and lightly trawled areas at each site.

Multivariate analyses

Proportions of sand and mud were highly positively correlated (Pearson correlation coefficient $r = 0.99$), thus only one of these variables (% sand) was used for further analysis. Gravel contributed very small proportions to the overall sediment composition (< 5%) and was excluded from further statistical analyses. Following arcsine transformation (Sokal & Rohlf 1969, Zar 1999) and normalization, replicate % sand values were compared using Euclidean distance. Statistical differences of % sand among sites and between treatments were analysed using the pair-wise, permutational multivariate analysis of variance, PERMANOVA (Clarke & Gorley 2006, Anderson *et al*. 2008) with the fixed factor "trawling treatment" crossed with the fixed factor "sites".

To test for differences in assemblages between trawl treatments, sample by species matrices were calculated for both abundance and biomass measures of infauna and categorized epifauna at all sites. Abundance-Biomass Comparison plots were constructed for infauna and epifauna, with their associated *W-statistic*, for each treatment (heavily and lightly trawled) at each site. The infaunal abundance and biomass matrices were 4th root transformed to down-weight the excessive contributions of quantitatively dominant species to the similarities calculated between species (Field *et al*. 1982, Clarke & Gorley 2006). The 4th root transformation effectively reduces the weighting of abundant species and is also considered most appropriate when similarity is assessed using the Bray-Curtis measure as the similarity coefficient is not affected by scale differences (Field *et al.* 1982). A 4th root transformation is similar to a log transformation in effect but without the disadvantages in dealing with zero values (Field *et al*. 1982). The epifauna data were effectively transformed by log-scale categorization (Table 2.2). The Bray-Curtis measure of (dis)similarity was used to compare samples on the basis of species abundance or biomass for both infaunal and epifaunal data (Field *et al*. 1982). These were summarized in cluster dendrograms and multi-dimensional scaling (MDS) plots. Permutation based PERMANOVA was used to test for significant differences in infaunal assemblage structure among sites (Namibia, Childs Bank, Cape Columbine and Cape Point) and between trawling treatments (heavily *vs*. lightly trawled, Anderson *et al*. 2008). PERMANOVA was also used to test epifaunal abundance and biomass data between heavily and lightly trawled areas at Namibia and Childs Bank. "Treatment" (fixed factor) was crossed with "sites" (fixed factor). Where differences or interactions were significant, pair-wise permutation tests were used to further explore these differences. PERMANOVA tests the dissimilarity values generated by the resemblance matrix on which permutations are based, generating a test statistic value of pseudo-F (or pseudo-*t,* for pair-wise tests, Anderson *et al*. 2008).

To assess which species contribute most to differences between groups, a similarity of percentages (SIMPER) analysis was conducted, whereby the average (Bray-Curtis) dissimilarities between all pairs of samples (heavily *vs*. lightly trawled) are broken down into separate contributions from each species, divided by the dissimilarity between each area (Clarke & Warwick 2001) after 4th root transformation of the data.

The relationship between biotic data (abundance or biomass) distribution patterns at each site and measured environmental variables were investigated using a distance-based linear model (DISTLM, Anderson *et al.* 2008). Trawl intensity was used to quantify fishing pressure as a measure of likely substrate disturbance and included in the DISTLM analysis as a categorical variable being either "heavy" or "light". The contribution of environmental variation and fishing pressure in influencing the biotic data distribution was simultaneously assessed. DISTLM partitions the variation in data distribution according to a multiple regression model (based on predictor variables), as selected by the user (e.g. forward, stepwise, best fit etc). The "Best" procedure (examines the value of the selection criterion for all possible combinations of predictor variables) and AIC criteria (Akaike's Information Criterion) options (Anderson *et al*. 2008) were selected in this study. The environmental variables selected for the model were % sand and % total organic carbon (arcsine transformed), depth and two categories of trawl intensity. DISTLM analyses were conducted at each site independently due to the large variation among sites. All multivariate and diversity analyses were performed using PRIMER-E v.6 and its add-on package PERMANOVA+ (Clarke & Warwick 2001, Clarke & Gorley 2006, Anderson *et al*. 2008).

RESULTS

Environmental variables

Vertical profiles of temperature, salinity and oxygen over the 300-400 m isobaths alongshore from Lüderitz to Cape Point indicated no marked gradients in water mass properties close to the seabed. Seabed temperatures at 300-450 m ranged from 6-8°C, seabed salinities from 34.6-34.8 PSU and 3.5-4.0 ml/l dissolved oxygen. The entire sampling region was considered to be fairly uniform with respect to seabed temperature, salinity and dissolved oxygen at depths between 300 to 450 m during the sampling period. The areas sampled in this study were deeper than the coastal hypoxic region (0.5-1 ml/l^{-1} Decker 1970, Monteiro & van der Plas 2006) where biota are likely to be impacted by frequently limited oxygen levels.

Sediment particle size

Sediment particle size classifications were conducted at two scales, firstly gravel-sand-mud (and intermediate) ratios were obtained according to Folk’s triangle (Fig. 2.2, Folk 1968) with further separation of the sand component according to the Wentworth scale (Wentworth 1922, Fig. 2.3). The sediments at both heavily and lightly trawled areas at Namibia, Childs Bank and Cape Point sites were classified as “sand” or “muddy sand” according to the Folk Classification triangle (Folk 1968, Table 2.3) with sand comprising between 72-90% (Fig. 2.3). The sediment at Cape Columbine lightly trawled area was classified as “sandy mud”, having a larger proportion of finer grained mud particles (79%) than the heavily trawled area (47% mud), which was classified as “muddy sand” (similar to all other areas).

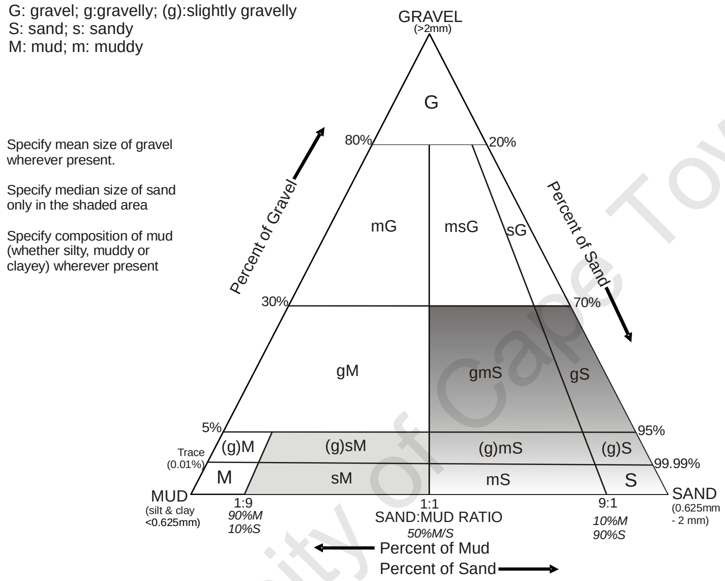


Fig. 2.2. Gravel-Sand-Mud classification according to composition ratios (Folk 1968)

Table 2.3. Sediment type classification according to Folk (1968) and Wentworth (1922) at lightly and heavily trawled areas of each sample site.

Site	Trawl intensity	Gravel-Sand-Mud	Sand
Namibia	Light	Sand – muddySand (S-mS)	fine sand (125-250 µm)
	Heavy	muddySand (mS)	fine sand – very fine sand
Childs Bank	Light	muddySand (mS + slight gravel)	fine sand (125-250 µm)
	Heavy	muddySand (mS)	fine sand (125-250 µm)
Cape Columbine	Light	sandyMud (sM)	very fine sand (63-125µm)
	Heavy	muddySand-sandyMud (mS-sM)	very fine sand (63-125µm)
Cape Point	Light	muddySand (mS + slight gravel)	fine – medium sand (125 – 500µm)
	Heavy	muddySand (mS + slight gravel)	medium sand (250 - 500 µm)

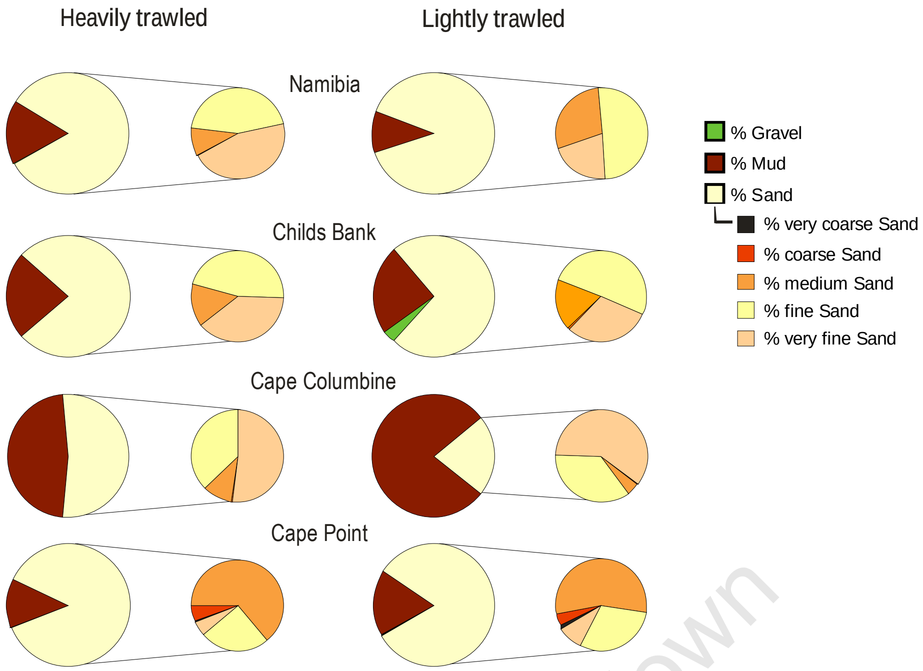


Fig. 2.3. Representative proportions of sediment particle size contributions in lightly and heavily trawled areas of sample sites according to Folk's classification. The sand component is further divided into five categories in accordance with the Wentworth classification scale.

A PERMANOVA test showed significant differences in sediment composition among sites (pseudo-F=264.45, d.f.=3, p=0.001), treatments (pseudo-F=32.72, d.f.=4, p=0.001) and the interaction between sites and treatments (pseudo-F=35.24, d.f.=3, p=0.0001), i.e. treatment affects sediment composition differently at the four sites. Pair-wise tests showed significant sedimentary differences between heavily and lightly trawled areas off Namibia (less sand at the heavily trawled area, t=4.48, p=0.009) and Cape Columbine (more sand at the heavily trawled area, t=11.95, p=0.0081), but no significant sedimentary differences at Childs Bank (t=1.76, p=0.1337) or Cape Point (t=1.94, p=0.115).

Organic carbon

The total organic carbon content (% TOC) measured in the sediment collected from the Childs Bank site was considerably greater than that recorded at any of the other three sites (11 – 14 % *vs*. 0.6 – 5.6 %, Fig. 2.4). Furthermore, the TOC was significantly greater at the heavily trawled Childs Bank area (t=3.83, d.f.=8, p = 0.005) and similarly at the heavily trawled Namibia area (t=3.36, d.f.=8, p=0.0009) than respective lightly trawled areas. Showing the opposite trend, the percent TOC was significantly less at the heavily trawled Cape Columbine area in comparison to the lightly trawled area (t=5.30, d.f.=8, p=0.0007) while there was no significant difference in TOC in heavily and lightly trawled areas at Cape Point (t=1.69, d.f.=8, p=0.13).

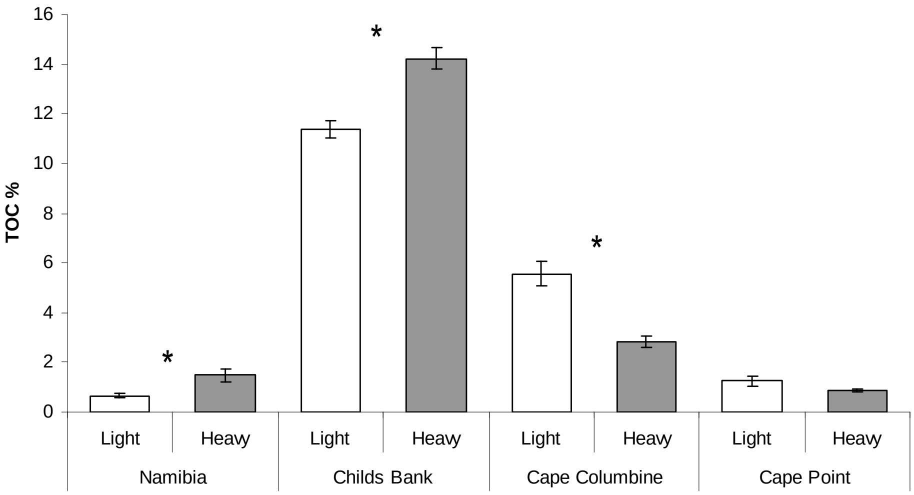


Fig. 2.4. Percent total organic carbon (TOC) measured at heavily and lightly trawled areas of each sample site (± SE). Significant differences (T-test) of TOC between trawl intensities at each site are indicated with an asterix (*).

Infauna

A species accumulation curve of all infaunal samples approaches an asymptote towards the end point, suggesting that the number of species obtained approximates that predicted to occur in the system. Phyla dominant at all sites were annelids (polychaetes) and crustaceans (small-bodied amphipods). Molluscs, annelids and crustaceans each contributed approximately 30% to the benthic assemblage at the lightly trawled area off Namibia while the heavily trawled area was dominated by annelids (48%, Fig. 2.5). Annelids contributed the greatest biomass (66%) at the lightly trawled area of this site, while molluscs contributed the greatest biomass (53%) at the heavily trawled area (Fig. 2.5). Crustaceans, followed by annelids, dominated both treatment areas at Childs Bank with the heavily trawled area having slightly greater molluscs present (8%) than the lightly trawled area (2%, Fig. 2.5). Echinoderms contributed > 50% to the biomass of the benthic assemblage at Childs Bank, followed by annelids (38% at lightly trawled and 23% at heavily trawled areas). The lightly trawled area off Cape Columbine was dominated by annelids (61%) while the heavily trawled area had equal proportions of annelids and echinoderms (34% each, Fig. 2.5). Echinoderms however, contributed as much as 88% to the biomass at the heavily trawled area off Cape Columbine (Fig. 2.5). The heavily and lightly trawled sites off Cape Point had similar species proportions, dominated by annelids and crustaceans with the biomass being dominated by echinoderms (Fig. 2.5). Average infaunal abundances were significantly greater at the heavily trawled area off Namibia (t=-4.36, d.f.=8, p=0.002) and at the lightly trawled area off Cape Columbine (t=4.32, d.f.=8, p=0.002, Fig. 2.5).

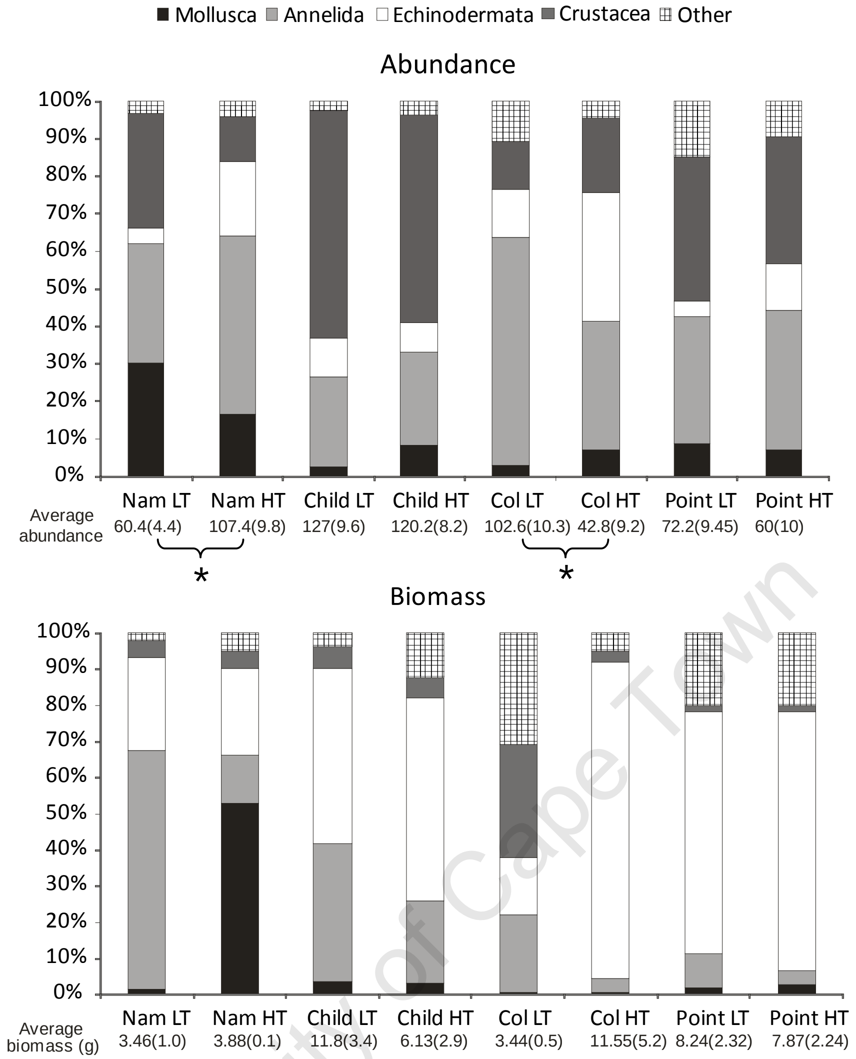


Fig. 2.5. Percent average abundance and biomass of dominant infaunal phyla for lightly trawled (LT) and heavily trawled (HT) areas. Average abundance and biomass values are indicated below site labels, ± SE in brackets. Significant differences (T-test) in infaunal abundance between trawl intensities per site are indicated with an asterix (*). Nam = Namibia, Child = Childs Bank, Col = Cape Columbine, Point = Cape Point, HT = heavily trawled, LT = lightly trawled.

A total of 256 species were identified from all sites, with the most species occurring at the lightly trawled area of Childs Bank (n = 41, Table 2.5) and the fewest at the heavily trawled area of Cape Columbine (n = 15, Table 2.5). The lightly trawled area off Cape Columbine yielded the largest number of individual infauna (n = 355, Table 2.5) but had comparatively few species and low evenness and diversity (Table 2.5). Unexpectedly, the heavily trawled area off Namibia had significantly greater average number of species (t=2.6, d.f.=8, p=0.03), average number of individuals (t=12.3, d.f.=8, p=0.0002) and species evenness (t=4.7, d.f.=8, p=0.001), than the lightly trawled area at this site (Table 2.5).

Table 2.5. Mean infaunal diversity indices for lightly and heavily trawled areas of four study sites (± SE in brackets, significant differences between lightly and heavily trawled areas indicated in bold).

Site	Trawl intensity	Mean no. species	Mean no. individuals	Mean species evenness*	Mean species diversity**
Namibia	Light	21.8 (1.28)	68 (5.6)	0.850 (0.02)	2.614 (0.10)
	Heavy	29.6 (2.56)	156 (4.6)	0.725 (0.01)	2.446 (0.10)
Childs Bank	Light	41.2 (1.98)	267 (89.08)	0.614 (0.09)	2.284 (0.35)
	Heavy	39.2 (2.42)	185 (13.25)	0.717 (0.02)	2.623 (0.06)
Cape Columbine	Light	18.2 (1.32)	355 (19.2)	0.339 (0.02)	0.981 (0.06)
	Heavy	15.2 (2.99)	319 (42.5)	0.267 (0.07)	0.756 (0.239)
Cape Point	Light	38 (4.56)	115 (20.9)	0.771 (0.05)	2.777 (0.17)
	Heavy	31 (3.0)	73 (10.3)	0.876 (0.02)	2.997 (0.09)

*Pielou's evenness index (J'), ** Shannon-Wiener diversity index (H')

Abundance-Biomass comparisons (ABC) of infaunal species at heavily and lightly trawled areas of each site result in all sites being classified as undisturbed (biomass curve lying above abundance curve, Warwick 1986), except Cape Columbine. The lightly trawled area off Cape Columbine was classified as disturbed (abundance curve lies entirely above biomass curve, Warwick 1986) and the heavily trawled area at this site as moderately disturbed (abundance and biomass curves intersect, Warwick 1986, Fig. 2.6). Conducting a partial dominance curve analysis (computing the dominance of the second ranked species over the remainder) to further explore these inconsistent findings, as recommended by Clarke (1990), revealed two taxa (*Euphausia lucens* and foraminifera) being responsible for greater cumulative abundance at Cape Columbine. ABC plots excluding these two taxa resulted in the biomass curve lying above the abundance (i.e. an undisturbed assemblage classification) for both lightly and heavily trawled areas off Cape Columbine (*W-statistic* = 0.226 and 0.4111, plots not shown).

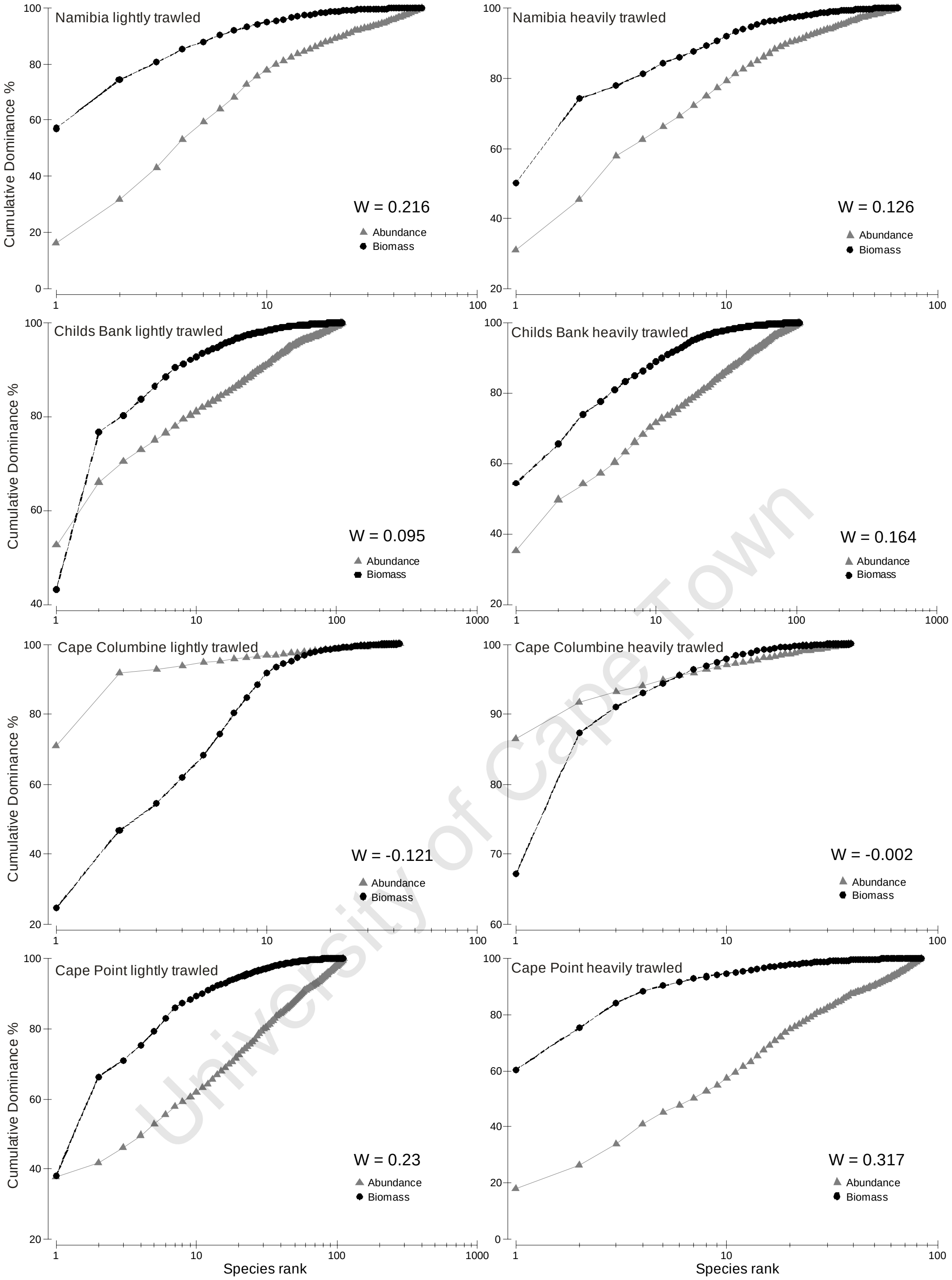


Fig. 2.6. Abundance-Biomass comparison plots of infaunal species for pooled replicates at lightly and heavily trawled areas at four sites spanning the southern Benguela region.

A dendrogram (cluster analysis) of infaunal abundance data from all sites shows grouping of the four sites at a similarity level of 33% (Fig. 2.7a). The corresponding multi-dimensional scaling (MDS) plot shows distinct grouping of sites (Fig. 2.7c) and at Namibia and Childs Bank sites, separation of heavily and lightly trawled areas. PERMANOVA analysis of the abundance data shows significant differences among sites, trawling treatments and the interaction between sites and treatments (Table 2.6). The significant interaction between sites and treatments indicates that infaunal assemblages are affected differently with respect to the treatment (heavily or lightly trawled) at the four sites, e.g. some taxa may be more abundant in heavily trawled areas at some sites and less abundant in heavily trawled areas at others. Analysis of infaunal biomass data from all sites shows a similar dendrogram grouping pattern (Fig. 2.7b), MDS plot (Fig. 2.7d) and similarly significant PERMANOVA results among sites, treatment and the interaction between sites and treatments (Table 2.6). Spatial grouping of station data in the MDS plots indicates greater among-site variability than between heavy or light trawl intensity (Fig. 2.7a & b). A stress value of 0.21 associated with the 2-dimensional MDS plots may be considered to reflect the high variability in benthic assemblages among the sites, treatments and other possible factors. Three-dimensional MDS plots had lower stress values of 0.13 (not presented). Pair-wise *a posteriori* PERMANOVA analyses between heavily and lightly trawled areas at each site for abundance and biomass data showed highly significant differences at all sites, except for biomass at Cape Point (Table 2.7).

Table 2.6. Test statistics for multivariate PERMANOVA analysis of infaunal assemblages among four sites with heavily and lightly trawled treatments. Significant values at $p < 0.01$ are indicated in bold.

Abundance	Degrees of freedom	Sum of Squares	Mean Squares	Pseudo-F	p-value	Unique no. permutations
Site	3	44125	14708	10.72	0.0001	9886
Treatment	1	4071.5	4071.5	2.97	0.0001	9909
Site x Treatment	3	13183	4394.4	3.20	0.0001	9829
Biomass						
Site	3	44503	14834	9.43	0.0001	9890
Treatment	1	4474.8	4474.8	2.85	0.0001	9882
Site x Treatment	3	15164	5054.6	3.21	0.0001	9803

Table 2.7. Test statistics for pair-wise PERMANOVA analysis of infaunal abundance and biomass assemblage data between heavily and lightly trawled areas. Significant values at $p < 0.01$, based on permutations, are indicated in bold, NS = not significant.

Site	Data type	t-value	p-value (perm)
Namibia	Abundance	2.565	0.0001
	Biomass	2.689	0.0073
Childs Bank	Abundance	1.626	0.0001
	Biomass	1.532	0.0069
Cape Columbine	Abundance	1.934	0.0001
	Biomass	1.936	0.0073
Cape Point	Abundance	1.251	0.0065
	Biomass	1.184	0.0634 (NS)

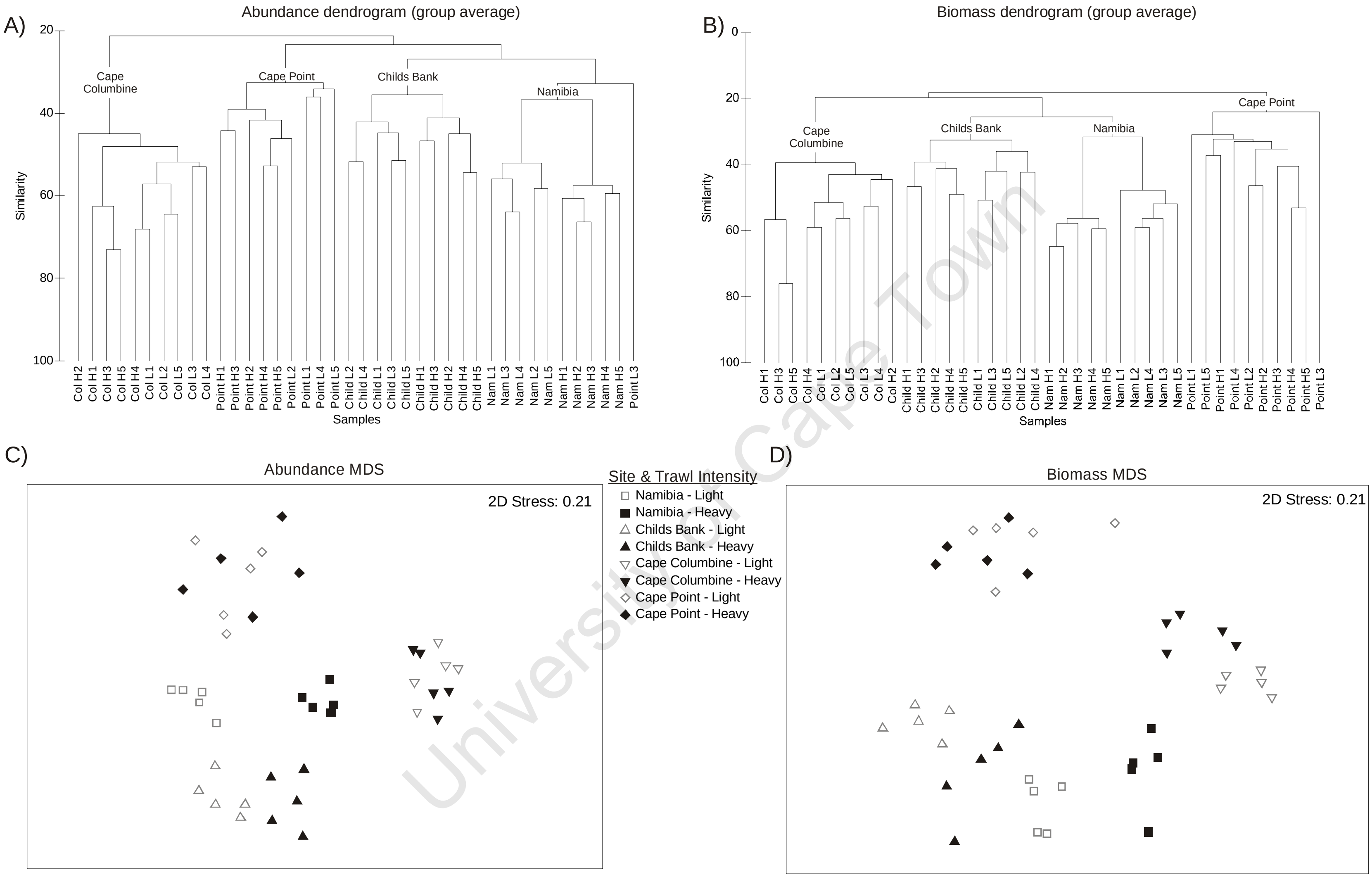


Fig. 2.7. Infauna: Dendrogram and Multi-Dimensional Scaling plot of abundance (A & C) and biomass (B & D) measures from all study sites after 4th root transformation and Bray Curtis resemblance.

The primary species responsible for the Bray-Curtis MDS clusters are revealed by SIMPER analysis (Clarke 1993) comparing trawling treatments (Fig. 2.9a-b). SIMPER analysis computes the percentage contribution of each species towards the Bray-Curtis dissimilarity (after transformation) between two groups of samples (Clarke & Gorley 2006). Several species showed consistent trends among sites, e.g. *Ophiura* sp. (Fig. 2.8F) are more abundant at heavily trawled areas and *Chloeia inermis* had higher biomasses at lightly trawled areas (indicated in bold in Fig. 2.9a-b), while others showed variable abundance among sites and trawling treatments (e.g. *Amphiura* sp. [Fig. 2.8E] and *Brissopsis lyrifera capensis*, underlined in Fig. 2.9a-b). Several species were unique to specific sites and occurred either exclusively, or in greater abundance, at lightly trawled areas. These include the tanaid crustaceans *Apseudes cooperi* off Namibia (Fig. 2.8G) and *Tanais philetaerus* off Cape Columbine, an unidentified ascidian sp., sipunculid *Phascolosoma* sp. (Fig. 2.8H) and chiton *Leptochiton sykesi* off Cape Point.

The distance-based linear model (DISTLM) analyses (Legendre & Anderson 1999, McArdle & Anderson 2001) of infaunal assemblages at each site with environmental variables % sand, % TOC, depth and a categorical trawl intensity variable shows that trawl intensity best explains the data distribution at the Namibian (45.13% of total variation), Childs Bank (24.84% of total variation) and Cape Columbine (31.86% of total variation) sites (Table 2.8). Depth at the Namibian and Childs Bank sites and % sand at the Cape Columbine site explain marginally less variation than trawl intensity (Table 2.8). Trawl intensity and % sand explain almost the same amount of variation at the Cape Point site (16.36% *vs*. 16.38% respectively, Table 2.8), however, the overall best model solution shows that % sand, followed by trawl intensity, provides the best fit of the data at this site.

Table 2.8. Test statistics for Distance-based Linear Model (DISTLM) analyses based on "Best" procedure and AIC criteria of infaunal abundance at each of the four sites sampled. SS = Sum of Squares, RSS = residual Sum of Squares, R^2 = RSS/SS.

Marginal tests:

Site	Variable	SS(trace)	Pseudo-F	p-value	% of total variation
Namibia	Trawl intensity	6354.4	6.5786	0.0085	45.13
	TOC	4665.7	3.964	0.0077	33.13
	Sand	4370.2	3.6	0.0099	31.03
	Depth	6233.2	6.3534	0.0052	44.26
Childs Bank	Trawl intensity	4181.8	2.6443	0.0084	24.84
	TOC	3323.7	1.9681	0.012	19.74
	Sand	2347.4	1.2963	0.1526	13.94
	Depth	4158.1	2.6243	0.0059	24.70
Cape Columbine	Trawl intensity	3636.8	3.7401	0.0084	31.86
	TOC	2875.9	2.6942	0.0121	25.19
	Sand	3590	3.6699	0.0023	31.45
	Depth	2914.5	2.7426	0.0182	25.53
Cape Point	Trawl intensity	3081.6	1.5653	0.0231	16.36
	TOC	2883.5	1.4464	0.0483	15.31
	Sand	3084.6	1.5671	0.0132	16.38
	Depth	2432.9	1.1869	0.1872	12.92

Overall best solution:

Site	AIC	R^2	RSS	No. Variables	Selection
Namibia	70.5	0.45125	7727.4	1	Trawl intensity
Childs Bank	70.5	0.45125	7727.4	1	Trawl intensity
Cape Columbine	70.6	0.31858	7779	1	Trawl intensity
Cape Point	77.6	0.1638	1547	1	Sand

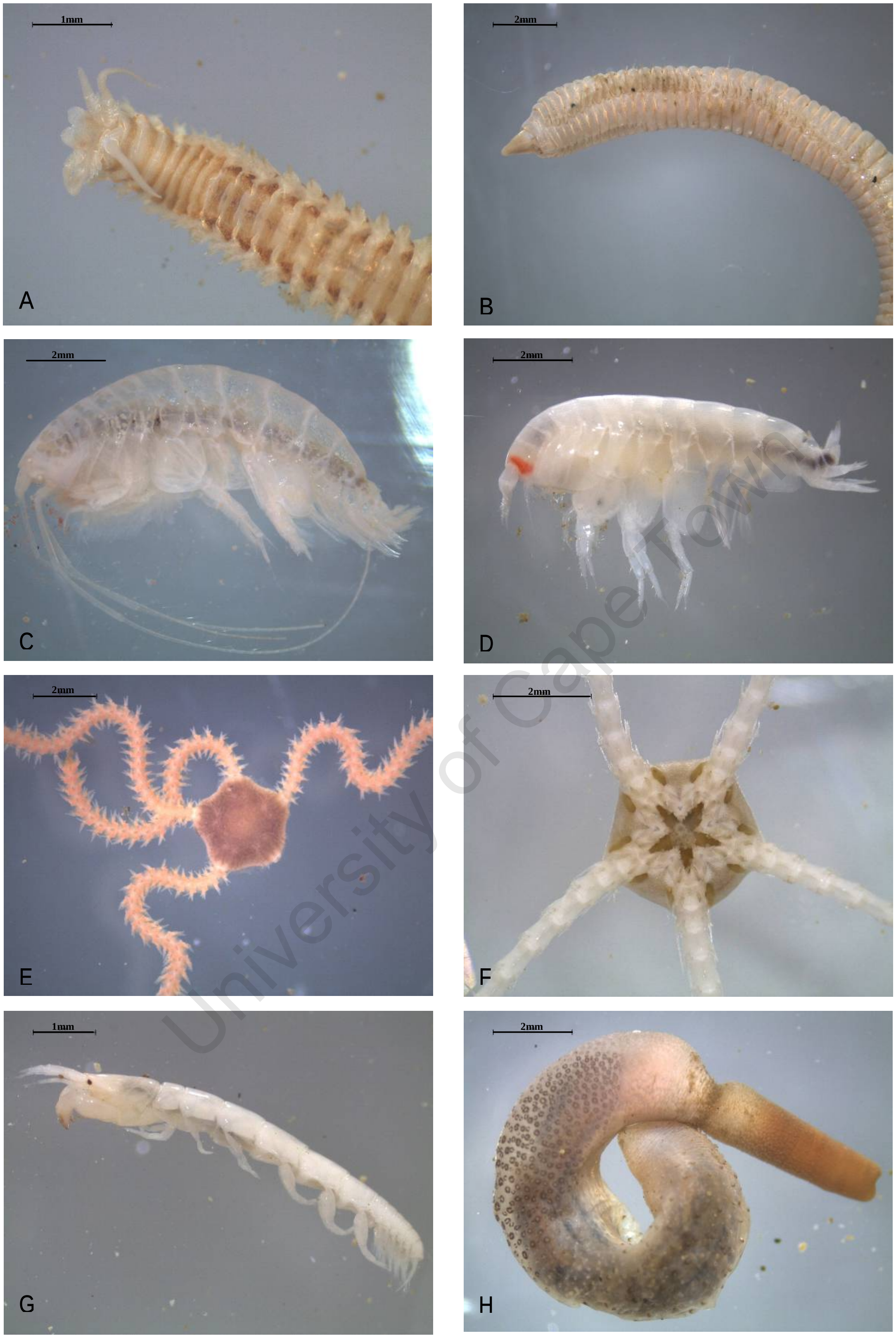


Fig. 2.8 Photographs of some infauna collected by van Veen grab. Polychaetes A) *Diopatra dubia*, B) *Lumbrineris albidentata*; Amphipods C) *Ampelisca brevicornis* D) *Hippomedon onconotus*; Brittle stars E) *Amphiura* sp. F) *Ophiura* sp.; G) Tanaid *Apseudes cooperi* and H) Sipunculid *Phascolosoma* sp.

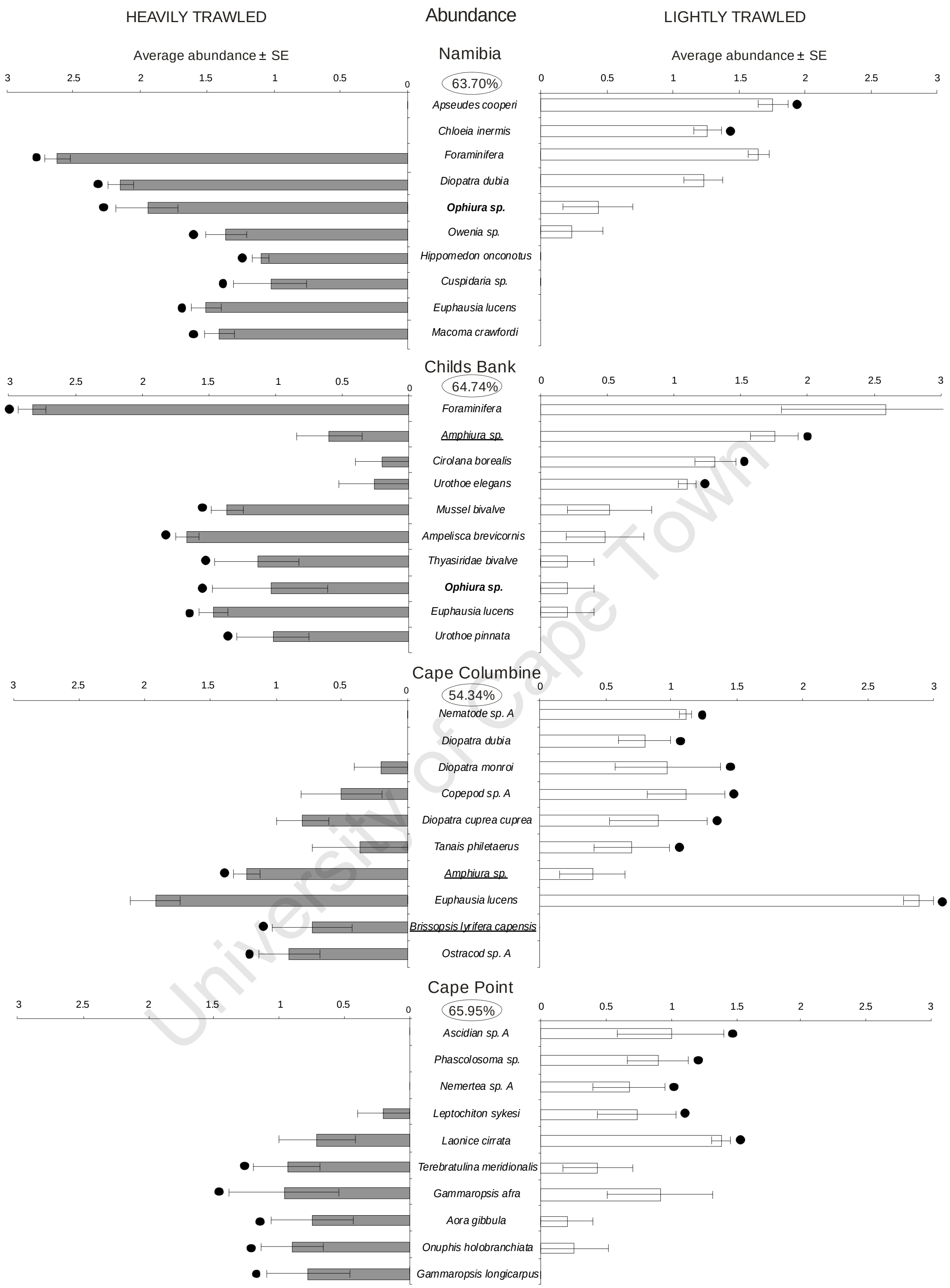


Fig 2.9a. Abundance: Infaunal SIMPER results (top ten species contributing to differences) between lightly and heavily trawled areas at each site (±SE) after 4th root transformation. Species names in bold show consistent trends between sites. Species names underlined show opposite trends between sites. Dissimilarity percentages between treatments at each site are indicated in ellipses. A black circle indicates the area of greater abundance of each taxon.

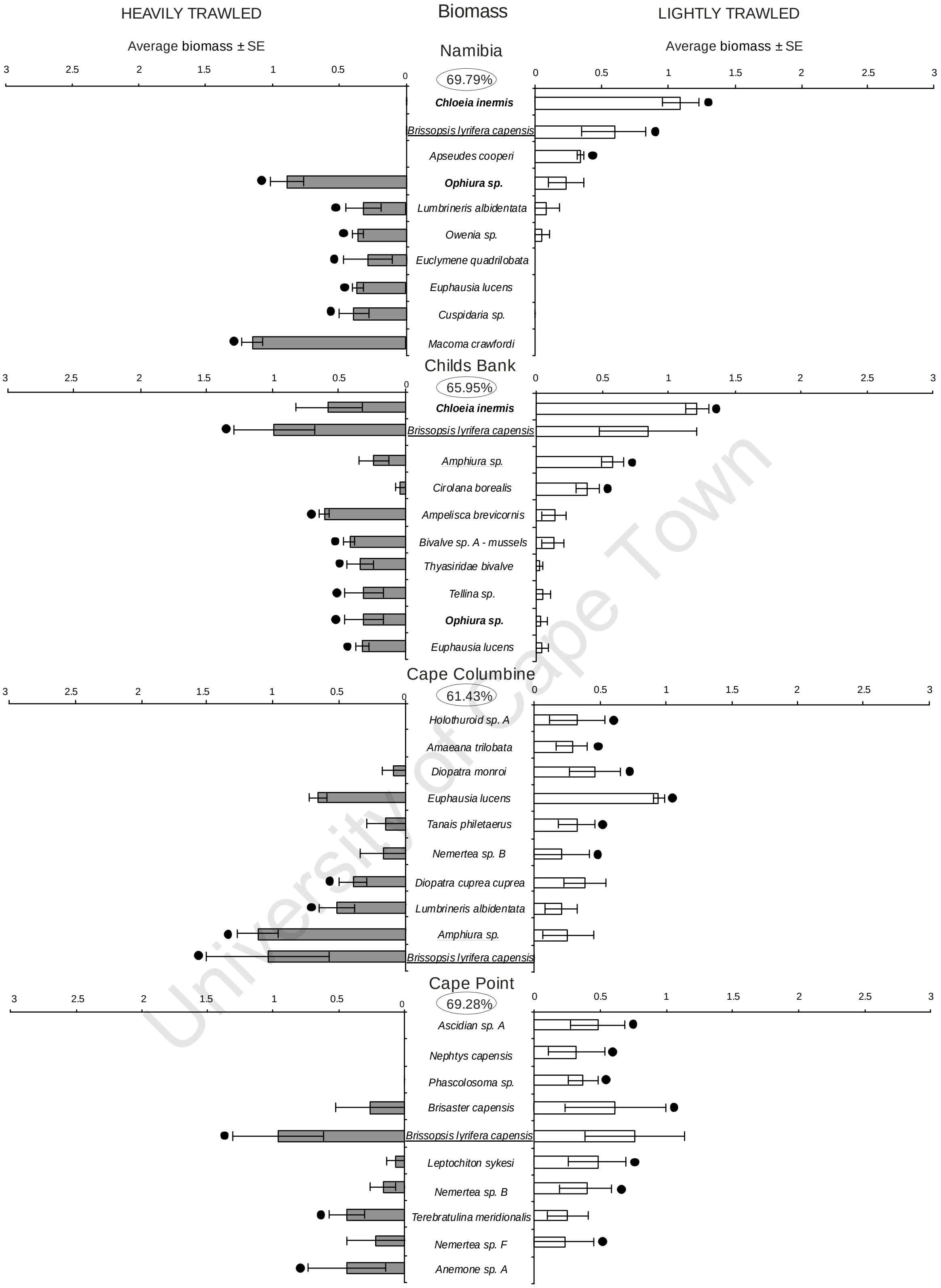


Fig 2.9b. Biomass: Infaunal SIMPER results (top ten species contributing to differences) between lightly and heavily trawled areas at each site (±SE) after 4th root transformation. Species names in bold show consistent trends between sites. Species names underlined show opposite trends between sites. Dissimilarity percentages between treatments at each site are indicated in ellipses. A black circle indicates the area of greater biomass of each taxon.

Epifauna

A total of 81 epifaunal species were sampled at Childs Bank and off Namibia. Sufficient replicate trawls were not possible at the other two sites. Significantly more species (t=4.46), individuals (t=4.45), and higher Shannon-Wiener diversity (t=4.76) were recorded at lightly trawled areas ($p \leq 0.01$ shown in bold, d.f. = 10, Table 2.9) at both sites. The lightly trawled area at Childs Bank also shows significantly more species (n=39 vs. 24) and individuals (n=67 vs. 41, $p \leq 0.01$, Table 2.9) than the lightly trawled area off Namibia. These univariate indices are calculated for epifauna data categorized on a log-based scale. Owing to the logarithmic categorization of the epifauna data, species evenness (Pielou's index) and diversity (Shannon-Wiener) values in Table 2.9 should not be compared with other studies.

Table 2.9. Mean epifaunal diversity indices for heavily and lightly trawled study sites (± SE) Significant differences between heavily and lightly trawled areas are in bold.

Site	Trawl intensity	Mean no. species	Mean no. individuals	Mean species evenness*	Mean species diversity**
Namibia	Light	24.7(1.86)	41.7(3.38)	0.94(0.003)	3.0(0.08)
	Heavy	15(0.58)	24.7(0.67)	0.94(0.001)	2.5(0.04)
Childs Bank	Light	39.7(2.19)	67(3)	0.96(0.001)	3.5(0.05)
	Heavy	16.7(1.2)	29(2.08)	0.96(0.003)	2.7(0.06)

*Pielou's evenness index (J'), ** Shannon-Wiener diversity index (H') based on log-categorized abundances.

Abundance-Biomass comparisons of epifaunal assemblages are classified as disturbed (i.e. abundance curve lies entirely above the biomass curve, Warwick 1986) at lightly and heavily trawled areas off Namibia and at Childs Bank (Fig. 2.10). The *W-statistic* ranges from -0.036 to -0.084, indicating that the abundance and biomass curves lie in fairly close proximity to each other at each location (Fig. 2.10).

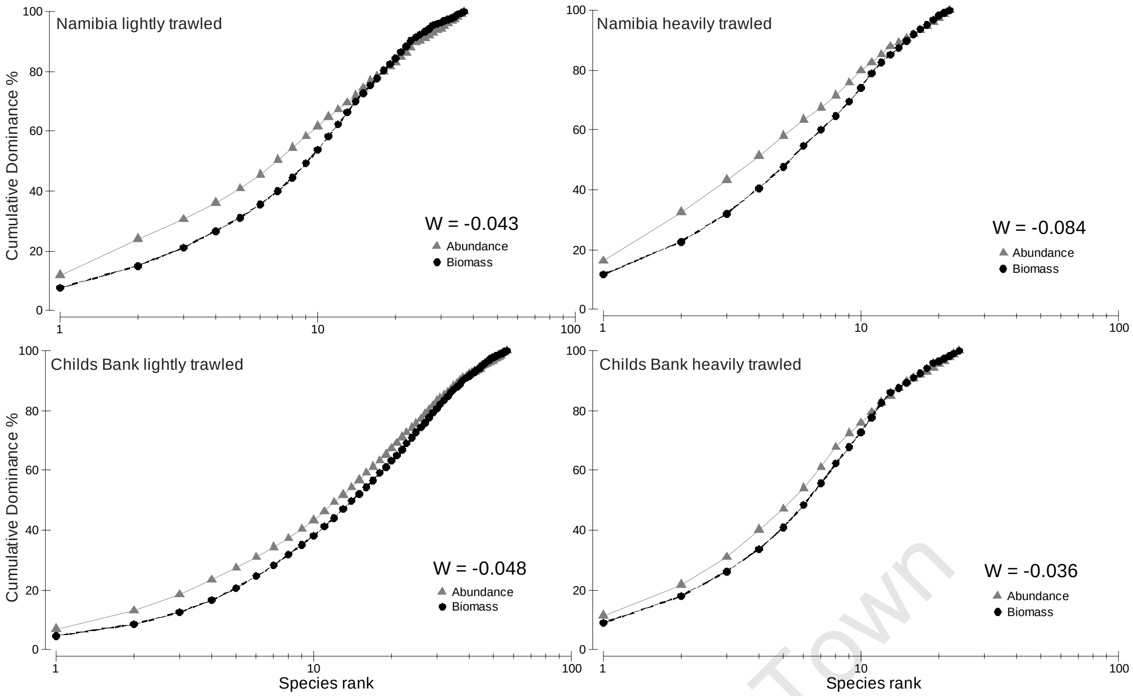


Fig. 2.10. Abundance-Biomass comparison plots of epifaunal species at lightly and heavily trawled areas at Namibia and Childs Bank sites.

Dendrograms (not presented) and MDS plots of categorized epifaunal abundance and biomass data show clear separation of the two sites and different trawling treatments (Fig. 2.11). Biomass results closely resemble those of abundance and are therefore not presented. Main effects PERMANOVA analysis of multivariate epifaunal abundance and biomass data shows significant differences among sites, treatments and interaction of sites and treatments (Table 2.10). The significant interaction between sites and treatments indicates that the treatment effect (trawl intensity) manifests differently at the Namibian and Childs Bank sites. *A posteriori* pair-wise PERMANOVA analysis between treatments (heavy vs. light trawling) at each site were also significant ($p<0.01$) for both abundance and biomass data (Table 2.11). When the number of possible permutations is low (< 999), there is an increased likelihood of a type I error (rejecting the null hypothesis when it is true) at the 95% confidence level (Manly 1997). The likelihood of a type 1 error is increased with a decrease in the number of possible unique permutations (Manly 1997). Anderson *et al*. (2008) recommend that if the number of unique permutations possible in any PERMANOVA routine is less than 100, Monte Carlo p-values (based on asymptotic theory) should be preferred. Due to the few pair-wise permutations possible (10) for this analysis, significance levels were based on Monte Carlo probability values instead of permutation values in this analysis.

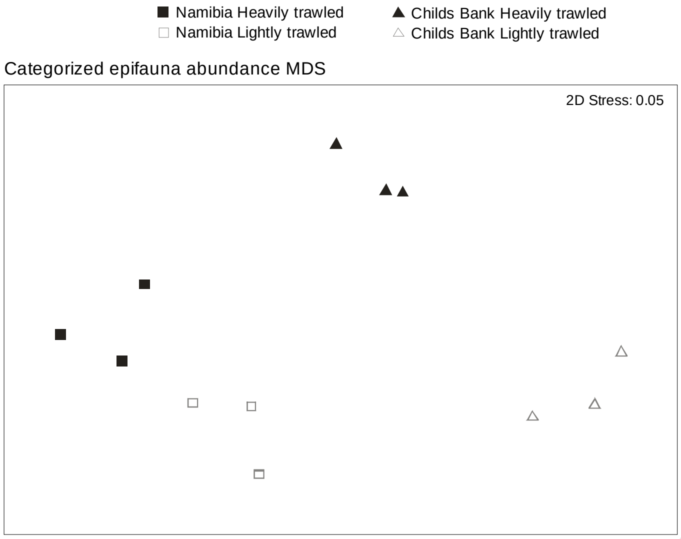


Fig. 2.11. Epifauna: Multi-dimensional scaling plot of categorized abundance data at two sites, representing two levels of trawl intensity. Namibia = squares, Childs Bank = triangles, open shapes = light trawling, closed shapes = heavy trawling (Note: MDS plot of biomass closely mirrors the abundance plot and is not presented).

Table 2.10. Test statistics for multivariate PERMANOVA analysis of epifaunal assemblages among four sites with heavily and lightly trawled treatments. Significant values at $p < 0.01$ are indicated in bold.

Abundance	Degrees of freedom	Sum of Squares	Mean Squares	Pseudo-F	p-value	Unique no. permutations
Site	1	9123.8	9123.8	31.64	0.0026	8917
Treatment	1	5032.3	5032.3	17.45	0.0021	8969
Site x Treatment	1	3920.7	3920.7	13.6	0.0025	8866
Biomass						
Site	1	7888.4	788.4	26.9	0.0023	8898
Treatment	1	5327.1	5327.1	18.16	0.0026	8882
Site x Treatment	1	3114.6	3114.6	10.62	0.0025	8887

Table 2.11. Test statistics of multivariate pair-wise PERMANOVA permutations of epifaunal abundance and biomass between heavily and lightly trawled areas. Significant values at $p < 0.05$, based on Monte Carlo sampling, are indicated in bold.

Site	Data type	t-value	p-value (Monte Carlo)
Namibia	Abundance	3.37	0.0064
	Biomass	2.97	0.0105
Childs Bank	Abundance	4.45	0.0016
	Biomass	4.52	0.0016

SIMPER analyses, based on the categorized epifauna data, show a clear reduction in species abundance and biomass at heavily trawled areas off Namibia and at Childs Bank (Fig. 2.13). Some species occur at lightly trawled areas only e.g. the urchin *Spatangus capensis* (Fig. 2.12 & Fig. 2.13), while other species show considerable variability between trawling treatments at the two sites e.g. the bristle worm *Euphrosine* sp. (Fig. 2.13). The burrowing anemone *Actinauge richardii* consistently occurs in greater abundance and biomass in heavily trawled areas (Fig. 2.12 & 2.13).

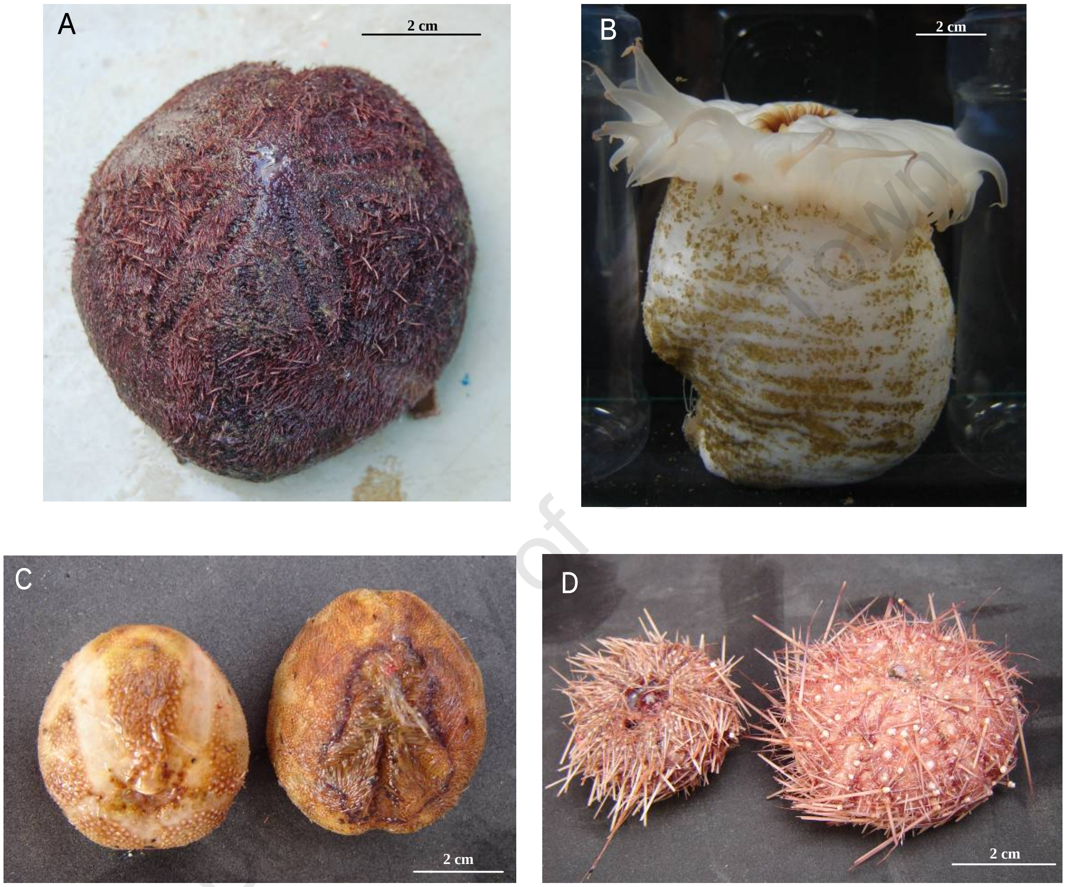


Fig. 2.12 Photographs of four epifaunal species occurring at Namibia and Childs Bank sites. Urchin species occur in greater abundance and biomass in lightly trawled areas while the burrowing anemone occurs in greater abundance and biomass in heavily trawled areas.
A) Urchin *Spatangus capensis*; B) Burrowing anemone *Actinauge richardii;*
C) Urchin *Brissopsis lyrifera capensis;* D) Urchin *Echinus gilchristi*

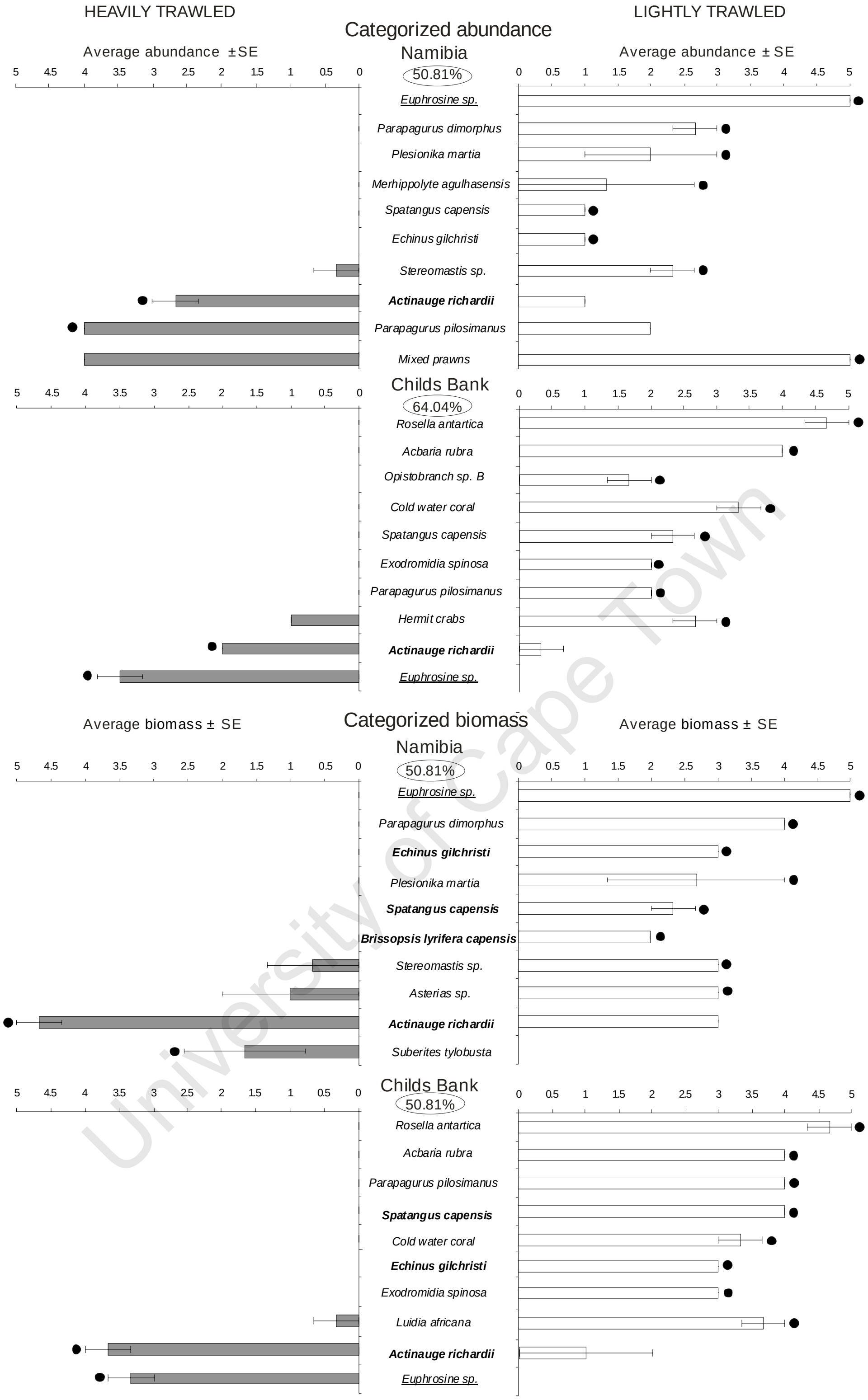


Fig 2.13. Epifaunal SIMPER analysis of categorized abundance and biomass data (top ten species contributing to differences) between lightly and heavily trawled areas at each site (± SE) after 4th root transformation and Bray-Curtis dissimilarity. Species in bold show consistent trends between sites. Species underlined show opposite trends between sites. Dissimilarity percentages between treatments at each site are indicated in ellipses. A black circle indicates the area of greater abundance or biomass per species.

DISCUSSION

Benthic assemblages

Infauna

The total number of infaunal species > 1 mm in size sampled by grab at four sites was 256 from 8.0 m^2 combined sample area. The richness of infaunal species can be considered representative of the Benguela region (a species accumulation plot approaches an asymptote) and is higher than that reported from other similar infaunal studies. Ellingsen (2001) recorded 175 species occurring in the North Sea in 8.0 m^2 combined sample area, Lindegarth *et al*. (2000) recorded 135 species from the Gullmarsfjord in Sweden in 48 m^2 total sample area, while 165 species were recorded in Greece by Smith *et al*. (2000) in 14 m^2 total sample area. This study, being the first trawling-related impacts study to be conducted in the nutrient rich, Benguela upwelling region at depths greater than 200 m, suggests high infaunal species diversity can be expected from this region, compared to studies conducted in semi-enclosed bodies of water, as in other studies mentioned above.

The significantly greater average abundance, number of species and number of individuals occurring at the heavily trawled area off Namibia was an unexpected result. On closer examination of the species contributing to these differences, it becomes apparent that a large number of small-bodied polychaetes, having low biomass but high abundance, were present at this heavily trawled area. There was no significant difference in average biomass between heavily and lightly trawled areas at this site. This can be expected according to *r-* and *K-species* selection theory (Pianka 1970) which states that an increase in small-bodied, low biomass species can be expected with increasing disturbance, thus explaining the unexpected results at this site. The significantly greater average abundance of infauna at the lightly trawled area off Cape Columbine, specifically dominated by *Diopatra* sp. polychaetes (Fig. 2.8), however, does not support this theory, but may reflect an erratic influx or recruitment event for this particular genus. Alternatively, *Diopatra* sp. may only be able to tolerate low disturbance levels (i.e. light trawling) and are thus much reduced at the heavily trawled area of this site.

Abundance-Biomass Comparisons (ABC) of infaunal species indicate undisturbed assemblages (*W-statistic* = 0.095-0.317) for both heavily and lightly trawled areas at all sites, except those off Cape Columbine, which suggest a disturbed assemblage at the lightly trawled area (*W-statistic* = -0.121) and a moderately disturbed assemblage at the heavily trawled area (*W-statistic* = -0.002, Fig. 2.6). Further exploration of Cape Columbine data using partial dominance curves, as recommended by Clarke (1990), reveals that two small-bodied, low biomass taxa (*Euphausia lucens* and foraminifera) numerically dominate at this site, resulting in the moderate to grossly disturbed status attributed using the ABC method. Re-analysis excluding these two species results in ABC plots indicating undisturbed assemblages at both heavily and lightly trawled areas off Cape Columbine (*W-statistic* = 0.411 and 0.226). The undisturbed classification of infaunal assemblages in this study, especially those at heavily fished areas, was nonetheless unexpected. Warwick and Clarke (1994) show that the ABC response is a result of firstly the shift in proportions of different phyla with disturbance as a result of the *r-K* continuum, and secondly, due to a shift in abundance and biomass of the polychaeta, but not within any of the other major phyla (e.g. Mollusca, Crustacea and Echinodermata). A study conducted by Beukema (1988) showed that the presence of a large number of small-bodied amphipods and molluscs, not indicative of disturbed conditions, confounded ABC plots. Warwick and Clarke (1994) caution that the ABC method might not accurately classify community disturbance levels if the small dominant species are not polychaetes. The considerable contribution of amphipods to the infaunal assemblages investigated in this study, clearly confound the results of the ABC plots and the sites should therefore not be classified as undisturbed using this method.

The similarity of univariate indices (number of species, number of individuals, species evenness and diversity) between most heavily and lightly fished areas in this study (with the exception of the Namibian site as discussed above) suggests that these measures may not be sensitive for detecting assemblage changes at this level. Similar results were obtained by Kaiser *et al*. (1998) when studying the impacts of beam trawling on megafaunal assemblages (epifauna > 10 mm) over a period of 6 months. Kaiser *et al*. (1998) concluded that changes in benthic assemblages detected in their study were too subtle to be detected by univariate analyses and were only revealed after multivariate analyses. In identifying changes to a suite of taxa with various life-history characteristics and sensitivities to disturbance, Thrush *et al*. (1998) also considered multivariate analyses to be more sensitive than univariate ones. Multivariate analyses show that infaunal assemblages are significantly different between lightly and heavily trawled areas at all four sites sampled in this study. It is widely reported that multivariate methods, incorporating a far greater amount of community information, are more sensitive at detecting change in communities than univariate measures (Gray *et al.* 1990, Warwick & Clarke 1993). Similarly, this study revealed greater sensitivity of multivariate analyses in detecting benthic assemblage differences under heavy or light fishing pressures.

The species assemblage composition varies considerably among sites in this study (pseudo-F=10.7, d.f.=3, p=0.0001), reflecting the expected high spatial variability across the sampling region. Consistent trends in infaunal species contributing to differences observed between heavily and lightly fished areas at each site were not detected (SIMPER results). This suggests that infaunal assemblages are similar in species composition under different trawl intensities investigated but that their abundance and biomass contributions differ. *Ophiura* sp. (brittle star) consistently occurred in greater densities and biomass in heavily trawled areas. Several other studies have also reported an increase in ophiuroids as a result of trawl disturbance and attribute this to the highly mobile nature of these brittle stars and their ability to regenerate lost arms (Pearsen *et al.* 1985, Bergman & Hup 1992, Engel & Kvitek 1998, Smith *et al.* 2000, Kaiser *et al.* 2000).

Epifauna

A total of 81 epifaunal species were sampled from the Namibian and Childs Bank sites by means of a research trawl net. The mean numbers of epifaunal species, individuals and diversity were significantly greater ($p \leq 0.01$) in lightly fished areas at both sites sampled (Namibia and Childs Bank). Epifaunal assemblages at both sites are classified as "grossly disturbed" (abundance curve lies above biomass curve, Warwick 1986) at both heavily and lightly trawled areas, quantifying the overall disturbance effect of fishing on epifauna, even under lightly trawled conditions. Multivariate analyses of epifaunal abundance and biomass showed highly significant differences in assemblages at different trawl intensities and between sites.

Both univariate and multivariate analyses detected significant differences in epifaunal assemblages sampled in this study, between heavily and lightly trawled areas. There was a marked decrease in species diversity in heavily trawled areas with the majority of species contributing to differences being more abundant at lightly trawled areas. The urchin species (*Spatangus capensis, Brissopsis lyrifera capensis* and *Echinus gilchristi*), believed to be susceptible to damage by passing trawl gear (Jennings *et al.* 2001, Widdicombe *et al.* 2004), only occur in the epifaunal samples at lightly fished areas (Fig. 2.13). The occurrence of *Brissopsis lyrifera capensis* in grab samples at both heavily and lightly trawled areas of Childs Bank and Cape Point (Fig. 2.9 a&b), suggests that this species (and possibly other similar species) can escape damage from trawl gear if they are sufficiently buried beneath the sediment (Bergman & Hup 1992, Thrush *et al.* 1998). Grab sampling in this study penetrated approximately 9 cm into the sediment and will therefore include some buried fauna, like burrowing urchins. The presence of urchins in epifaunal assemblages, predominantly in lightly fished areas, suggests that these species do not readily withstand the disturbance of frequent trawling. A conspecific (*Brissopsis lyrifera*) present prior to experimental trawling conducted in Crete, Greece, remained absent from the trawled area for at least eight months, indicating the susceptibility and slow recovery of these fauna (Smith *et al.* 2000). It has been suggested that vulnerability of such burrowing species to trawling is influenced by their position in the sediment and the type of trawl gear and depends on sediment grain size and size of individuals (Bergman & Hup 1992).

Conversely, the anemone *Actinauge richardii* is more abundant and has greater biomass in heavily trawled areas. This anemone is large, thick-walled and burrows making it more likely to withstand the impact and disturbance of the trawl gear. Collie *et al.* (2000b) similarly concluded that burrowing anemones were not affected by trawl disturbance.

Epifauna show greater differences between heavily and lightly trawled areas than infauna in this study. Other studies have also shown that epifaunal assemblages are more vulnerable to trawling (Engel & Kvitek 1998, Hansson *et al.* 2000, McConnaughey *et al*. 2000, Kaiser *et al*. 2000). Changes in epifaunal assemblages may impact on other ecosystem components. Auster *et al.* (1997) showed that early juvenile silver hake (*Merluccius bilinearis*) occurred in greater densities in areas of complex habitat structure and proposed that these habitats increase the probability of survival of this species. Several studies have shown that reduced epifaunal structure increases the predation risk for juvenile fish (Walters & Juanes 1993, Tupper & Boutilier 1995, Collie *et al*. 2000b).

Environmental differences

Depth differences were never more than 50 m between paired heavily and lightly trawled sampling areas. A difference in depth of this magnitude (50 m) at depths of between 350-400 m is not, in itself, likely to contribute to differences in benthic invertebrate assemblages. Low oxygen water has not been recorded at depths sampled in this study in the southern Benguela system (Decker 1970, Monteiro & van der Plas 2006) and is therefore unlikely to influence benthic invertebrates sampled in this study. The water mass variables of seabed temperature, salinity and dissolved oxygen showed minimal variations between fishing intensities and among sites sampled in this survey. This suggests that these variables do not contribute to differences observed in faunal assemblages at these sites.

Larger proportions of mud in the sediment at the lightly fished Cape Columbine site may be attributable to reduced disturbance levels minimizing re-suspension and removal of finer-grained sediments. Evidence of such re-suspension was observed in video recordings after the passage of a trawler in a study conducted in Crete, Greece (Smith *et al.* 2000). Similarly finer particles (flocculent matter) were reported to be significantly denser in a lightly trawled area in the Monterey Bay National Marine Sanctuary, this being attributed to less trawling disturbance, allowing for accumulation of finer particles (Engel & Kvitek 1998). The inconsistent differences in sediment composition between heavily and lightly trawled areas among the four sites suggest that sediment composition is not a primary factor driving differences observed in the biotic assemblages. However, the percentage sand component was shown to best fit the infaunal data distribution at Cape Point (DISTLM) but only accounts for 16.5 % of the total variation. Overall this site is considered one of the most intensely trawled areas within the region (Wilkinson & Japp 2005) and differences in the actual number of trawl tracks between heavily and lightly trawled areas were few (270 *vs*. 187, Table 2.1). It is feasible that the lightly trawled area at Cape Point more closely represents that of a moderately trawled area.

The significant differences in total organic carbon (% TOC) observed between heavily and lightly trawled areas do not reflect any consistent trend with respect to trawl-induced disturbances. The heavily trawled areas off Namibia and Childs Bank show significantly greater % TOC than lightly trawled areas, while the opposite is evident at Cape Columbine, with no significant difference in % TOC at the Cape Point site. The variability in % TOC observed in this study is interpreted to be a result of inter-site variability and not directly related to trawling activity.

Trawling effects *vs*. environmental effects

Apart from the substantial variability among sites, infaunal assemblages were most strongly influenced by trawl intensity at the Namibian, Childs Bank and Cape Columbine sites (DISTLM analyses, Table 2.7). Cape Point infaunal assemblages were most strongly influenced by sand content, closely followed by trawl intensity, but this may be due to the small difference in trawling intensity between heavily and lightly trawled areas at this site (Table 2.1). Depth (Namibian and Childs Bank sites) and sand content (Cape Columbine site) were also important in influencing infaunal assemblages.

The occurrence of sponge, gorgonian and cold water corals at the lightly trawled Childs Bank area indicates that the trawl gear passed over some patch(es) of hard ground, as these species only occur on solid substrates. Other environmental factors (sediment particle size, depth, salinity, oxygen), however, were not significantly different between heavily and lightly trawled areas at this site and it is possible that other heavily trawled areas nearby once hosted similar patches of hard ground emergent fauna, prior to being fished. The obstructive feature of an abandoned well-head in the vicinity of the lightly trawled area is likely to have provided some *de facto* "protection" from trawling at this site, indicated by the trawl tracks diverting around the well-head coordinate. However, even light trawl intensities are likely to have eliminated sessile slow-growing, long-lived species. Without sampling a control site that has remained unfished for many decades, the measure of change from a true unfished state is not possible. The lack of a representative unfished control site in the region prevents the experimental design in this study from measuring trawl impacts on sessile slow-growing, long-lived species, such as corals, gorgonians and their epifauna.

Wilkinson & Japp (2005) used historic commercial trawl tracks from principal demersal trawl quota holders to calculate trawl intensities per commercial grid block (20' x 20'), along with actual commercial and observer data from 2002 to 2005. The greater trawl intensity values calculated for the Cape Point and Cape Columbine regions classified these areas as "intensely fished" (Wilkinson & Japp 2005). These findings support the observation that fishing effort is frequently concentrated closer to ports or landing sites (Sampson 1991, Rijnsdorp *et al*. 2000), with both Cape Point and Cape Columbine being within 70 nm of commercial landing ports. The Childs Bank area, 190 nm from the nearest port, has a lower trawl intensity value and is classified as only "heavily fished". Unfortunately the Wilkinson and Japp (2005) study did not extend into Namibia, however, the Namibian site is 75 nm from the nearest port of Lüderitz and would probably be considered "heavily fished". The intensely trawled regions around the Cape Point and Cape Columbine sampling sites most likely represent a "fished" environmental state. Once having entered into a "fished" state, it is usually more difficult to detect subtle changes in benthic communities (Jennings & Kaiser 1998). Indeed in comparing ecosystem indicators of fishing impacts across three ecosystems, the most heavily fished system, the South Catalan Sea (Coll *et al*. 2008), showed the smallest changes (Shannon *et al.* 2009). This may similarly explain the less obvious (but still significant) MDS separation of lightly and heavily fished infaunal assemblages at the more intensely fished areas off Cape Columbine and Cape Point, in comparison to those at Childs Bank and off Namibia.

Species contributions

In this study, several infaunal and epifaunal species occurred only, or in greater abundance, at lightly trawled areas and can be considered rare species (e.g. tanaid *Apseudes cooperi*; chiton *Leptochiton sykesi;* sponge *Rosella antartica*; pycnogonid *Pallenopsis capensis*). Chapman (1999) discusses different ways in which rarity can be measured, depending on the particular species under consideration and its ecological attributes. Rare species have been defined either as a result of few individuals overall, those occupying a small geographical range, marginal populations of widespread species or rarely found species (reviewed by Gaston 1994 in Chapman 1999). Schoener (1987) summarized rare species as being those characterized by small populations with low abundances at local and regional scales. Rare species are reported to make important contributions to the functioning of marine systems (Lyons *et al* 2005, Ellingsen *et al*. 2007). In light of these studies, the less common species recorded in this study, largely at lightly trawled areas, are therefore likely to contribute to the overall functioning of benthic ecosystems in these areas. Many previous studies have concluded that trawling-induced disturbances result in a shift in benthic assemblages from large, long-lived or rare, structurally delicate or complex organisms towards small-bodied, highly mobile, scavenging species (Engel & Kvitek 1998, Kaiser *et al.* 2002, Thrush & Dayton 2002, Jennings *et al.* 2001, de Juan *et al.* 2007). The structural and functional roles of different benthic invertebrate life-history traits and their response to trawling disturbances are further explored in Chapter Three of this thesis, using biological traits analysis (BTA).

Conclusion

This first study of the potential impacts of demersal trawling on benthic ecosystems in the southern Benguela region reveals that both infaunal and epifaunal assemblages are significantly different between heavily and lightly trawled areas. As expected, variability among the sites sampled in the region was large, with benthic assemblages reflecting significant among-site differences. This serves to emphasize the considerable spatial diversity of the offshore environment in this region. There is convincing evidence that epifauna are directly impacted by trawling, but the evidence for direct impacts of trawling on infaunal assemblages is less clear. Epifauna, specifically urchins and sponges, showed greater vulnerability to the impacts of trawling than infauna. Furthermore, some epifaunal species (as sampled by trawl net in this study) show a preference for areas that are more intensely fished e.g. burrowing anemone and *Ophiura* sp. brittle stars. These results demonstrate the potential for epifaunal species to be used as indicators of heavily or lightly disturbed benthic habitats. This study shows that benthic faunal assemblages in unconsolidated habitats respond to the disturbance of demersal trawl fishing and that multivariate analyses are an appropriate tool to detect and measure differences as a result of fishing intensity. More rigorous studies to further quantify the impacts of demersal trawling on benthic fauna in the southern Benguela require monitoring the recovery of representative areas closed to fishing.

Regular monitoring of benthic faunal communities, especially epifauna, can provide measurable indicators of community status, which is an important component required for implementation of an ecosystem approach to demersal fisheries management in South Africa. South African legislation provides a framework to support EAF management objectives in preserving marine biodiversity, protecting ecosystems as a whole and to give effect to ratified international agreements e.g. Convention on Biological Diversity and World Summit of Sustainable Development Plan of Implementation (2002). While the results of this study reveal the importance of benthic faunal assemblages for assessing the effects of demersal trawling, further studies, beyond the scope of this thesis, are required to develop practical indicators of the state of the ecosystem.

Chapter Three

Biological traits analysis in comparing benthic assemblages in areas of heavy *versus* light trawling along the west coast of southern Africa

INTRODUCTION

An ecosystem approach to fisheries management requires *inter alia* evaluation of the state of ecosystems. Practical methods are needed to evaluate and monitor ecosystem status (Garcia *et al.* 2003). This has prompted investigation into how benthic community assemblages can be used to indicate the status of ecosystems, especially with respect to anthropogenically induced changes or as the basis to identify conservation priorities (Kaiser 1998, Usseglio-Polatera *et al.* 2000). Benthic invertebrates are considered good candidates with which to measure ecosystem quality and change (Usseglio-Polatera *et al.* 2000). These species occur in a wide variety of forms and habitats and potentially respond rapidly to many types of environmental pressures e.g. pollution, habitat degradation, climate change. Furthermore, benthic invertebrates, having limited mobility, are generally confined to relatively small areas and as a result, effectively integrate historical environmental conditions (Warwick 1993, Salas *et al*. 2006). Under adverse environmental conditions, certain species are excluded by interactions with predators or competitors or their inability to tolerate the physical conditions, with the result that only species having traits that match the altered environment will remain (Townsend & Hildrew 1994). Certain combinations of general biological traits and life history strategies are favoured, depending on the environmental characteristics of the habitats in question. Understanding the link between species traits and environmental variability will facilitate better predictability of ecosystem responses (Usseglio-Polatera *et al.* 2000, Tillin *et al*. 2006).

Demersal trawl fishing activities are considered to be one of the greatest global sources of anthropogenic disturbance to marine benthic communities (Watling & Norse 1998, Jennings & Kaiser 1998, Kaiser *et al.* 2000). Several studies investigating the impacts of demersal trawling on benthic habitats conclude that large-scale trawling results in reduced biomass and diversity of benthic organisms (e.g. Engel & Kvitek 1998, Kaiser *et al*. 1998, McConnaughey *et al*. 2000, Jennings *et al.* 2001, Thrush & Dayton 2002, Kaiser *et al.* 2003, Tanner 2003 and several others). Continual habitat disturbance, as imposed by a large-scale demersal trawl fishery, has been shown to lead to an abundance of small-bodied, opportunistic, short-lived (*r-selected*) species with a concomitant loss of larger-bodied, longer lived, slower growing (*K-selected*) species (Jennings *et al.* 1999, Ball *et al.* 2000, Sparks-McConkey & Watling 2001). Changes in the composition of benthic assemblages may result in altered ecological functioning of the system (Tillin *et al.* 2006, Bremner *et al.* 2006a). To understand the potential effects trawling may have in contributing towards modification of communities (and therefore, functioning of the ecosystem), it is necessary to identify the relationship between the biological functions of species and their vulnerability to trawl disturbance (Tillin *et al.* 2006). An ecosystem approach to fisheries management not only aims to conserve diversity, but also considers functional diversity. The range and contribution of species functional traits in a community will determine its ecosystem functional diversity (Tillin *et al.* 2006). Maintaining functional diversity can provide a buffer against dramatic environmental shifts induced naturally or resulting from anthropogenic factors (Folke *et al*. 2004, Bremner 2008).

Biological Traits Analysis (BTA) aims to describe multiple aspects of ecological functioning based on features of the species present in the ecosystem assemblages e.g. life history, morphological and behavioural characteristics (Bremner *et al.* 2006b, Bremner 2008). Snelgrove (1998) reported that the roles performed by benthic species are important in regulating ecosystem processes and can be portrayed through the biological traits they exhibit. No one individual parameter can provide a measure of ecosystem functioning as a whole, thus simultaneously considering multiple variables is considered a more appropriate means to reflect an index of ecological functioning (Bremner 2008). BTA uses specific species traits to provide an indication of ecological functioning within an ecosystem by incorporating information on both the relative biomass (and abundance) of species and a wide variety of biological characteristics (trait information), in one analysis. Changes in the relative biomass (or abundance) of species assemblages are frequently associated with anthropogenic impacts (e.g. fishing, pollution, Bremner *et al.* 2006a), and are often reflected by an increase in those species able to withstand the impacts. Species having different biological traits are likely to respond differently to different impacts. Larger organisms have lower natural mortality, slower growth, lower annual reproductive output and increased longevity, making them less able to compensate for high mortalities induced by demersal trawling (Kaiser *et al.* 2000). Smaller species frequently have a faster life cycle and higher reproductive output making them able to rapidly recolonise disturbed areas (Kaiser *et al.* 2000, Jennings *et al.* 2001). BTA provides a useful tool to monitor changes in assemblage functioning when ecosystems are exposed to anthropogenic pressures (Bremner 2008).

Management of the marine environment involves identifying, assessing and mitigating the effects of human activities. Traits analysis can provide a useful technique to assess the suitability of management measures that are being implemented (Bremner 2008). Pressures on the marine environment seldom occur in isolation and management strategies designed to mitigate the impacts of specific activities may fail when multiple pressures interact. There is limited understanding of the interactive, cumulative effect of pressures on the system as a whole. Biological traits analysis provides a practical approach to monitor overall functional diversity, providing early warning signals of altered or compromised functional diversity. Comprehensive multi-trait analysis of marine assemblages however, requires substantial amounts of data and research time, resulting in high costs and limited scope for implementation at managerial levels. It has been suggested that analyses focusing on a subset of the available data (e.g. on the most abundant or widespread species) are likely to yield similar findings to that of full data set analyses, but in considerably less time (Bremner 2008). The selection of the subset of species and traits to be analysed is, therefore extremely important as representation across the full possible spectrum must be maintained. This approach requires further investigation and careful consideration prior to implementation.

Applications of BTA in freshwater and terrestrial systems are well established, however, they have thus far seldom been applied in the marine environment (Bremner 2008). Published studies to date employing analysis of benthic faunal functional traits in relation to ecological functioning and changes induced by fishing are few and have only been conducted in European or Canadian waters, these being:

- Bremner *et al.* (2005) - investigated temporal changes in biological traits of benthos of the North Sea as a result of fishing,
- Tillin *et al.* (2006) - examined differences in epifaunal biological traits across a gradient of demersal fishing activity in the North Sea,
- de Juan *et al.* (2007) - compared infaunal and epifaunal biological traits between areas of heavily fished and unfished areas of the northwest Mediterranean Sea,
- Kenchington *et al.* (2007) - detected changes in epifaunal biological traits over 30 years of scallop fishing in the Bay of Fundy, Canada and,
- Cooper *et al.* (2008) - compared the recovery of macrofaunal assemblages after dredging in the English Channel using various methods, one of which was biological traits analysis.

This study is the first application of BTA to examine impacts of demersal trawling on marine benthic fauna in the southern Benguela region. Biological traits of benthic infaunal and epifaunal assemblages are compared between lightly and heavily trawled areas. As there are no representative untrawled areas at similar depths and sediment types in the region (Shannon *et al.* 2006), the investigations of this study are thus limited to a comparison between impacts of heavy and light trawling. Four sites were sampled, each having a paired heavily-lightly trawled area with similar environmental variables (depth, temperature, salinity, oxygen, sediment properties, see Chapter Two of this thesis). It was expected that areas exposed to lower levels of fishing intensity would yield more species reflecting biological traits aligned with that of *K-selected* species (e.g. larger-bodied, specialist feeders, long-lived). Areas subjected to heavier fishing activities were expected to yield species with biological traits characteristics of *r-selected* species (e.g. opportunistic, small-bodied, fast-growing, short life-span).

METHODS

Sampling design

A detailed description of the sampling design and procedure is described in Chapter Two of this thesis.

Biological Traits

Biological trait databases of all infaunal and epifaunal taxa sampled in this study were developed by sourcing information from a range of literature, (e.g. scientific publications, theses, web databases, general field books, technical papers and expert knowledge). Eight biological traits with 42 categories were identified for the infaunal species analysis (Table 3.1) while nine biological traits with 41 categories were selected for the epifaunal analysis (Table 3.2). Each category and trait were allocated unique codes for analytical purposes (see Table 3.1 & 3.2). Each category was scored according to the affinity of each taxon for each trait category, ranging from 0-3, were 0 is no affinity and 3 is total affinity. A taxon may be allocated several scores for the same trait which is referred to as "fuzzy coding" (Chevene *et al.* 1994), e.g. one species with two types of feeding strategies is given the affinity 2 in both feeding categories. In the event that no information of a trait at the species level was available, a search was conducted at the genus level, and if still no information was found, then at the family level. Twelve unidentified epifaunal species were excluded from traits analysis and nine species were merged into higher groupings (i.e. to genus or family level). To investigate any differences in functional body size of infauna between heavily and lightly trawled sites, the average length of each infaunal taxon was measured and scored as affinities. As an indication of the size of epifaunal species, the average biomass of taxa occurring were categorized on a log-based scale and scored as affinities.

The "fuzzy coded" species by traits matrices were weighted by their biomass at each site through matrix multiplication using MS Excel separately for infauna and epifauna. The biomass-weighted trait category scores were summed over all taxa present at the area, providing a measure of frequency of occurrence of trait categories over the whole assemblage (Charvet *et al.* 2000, Bremner *et al.* 2006a). The traits weighted by biomass matrices for infauna and epifauna assemblages were analysed independently.

Table 3.1. Infaunal biological traits and categories used in the analysis. Each category is allocated affinities ranging from 0-3 where 0 is no affinity and 3 is total affinity. Size was analysed for both measured size at capture (NSA) and normal adult size (NSB) obtained from the literature.

Trait	Code	Classification
Size (NSA & NSB):	NS1	< 5 mm
	NS2	5 mm-1 cm
	NS3	> 1-3 cm
	NS4	> 3-6 cm
	NS5	> 6-10 cm
	NS6	> 10 cm
Larval type:	LT1	Planktotroph
	LT2	Lecithotroph
	LT3	Direct development
Mobility:	AM1	None
	AM2	Low
	AM3	Medium
	AM4	High
Body form:	BF1	Short/cylindrical
	BF2	Dorsally flat
	BF3	Laterally flat
	BF4	Spherical
	BF5	Long thin
	BF6	Irregular
Attachment:	DA1	None
	DA2	Temporary
	DA3	Permanent
Adult Habitat:	AH1	Sessile
	AH2	Tube permanent
	AH3	Tube semi-permanent
	AH4	Burrower
	AH5	Surface crawler
Feeding:	FH1	Suspension / filter
	FH2	Scraper / grazer
	FH3	Surface deposit feeder
	FH4	Subsurface deposit feeder
	FH5	Dissolved matter / symbiont
	FH6	Detritus / sandlicker
	FH7	Carnivore / detritivore
	FH8	Scavenger
	FH9	Parasite / commensal

Infaunal traits information was provided by Annelise Fleddum of City University Hong Kong.

Table 3.2. Epifaunal biological traits and categories used in the analysis. Each category is allocated affinities ranging from 0-3 where 0 is no affinity and 3 is total affinity. Maximum adult size (MS) was obtained from literature.

Trait	Code	Classification
Sampled size:	SS1	1 - 10 g
	SS2	11 – 100 g
	SS3	101-1000 g
	SS4	1001 – 10 000 g
	SS5	> 10 000 g
Maximum adult size:	MS1	1 – 3 cm
	MS2	> 3-6 cm
	MS3	> 6 – 10 cm
	MS4	> 10 cm
Adult longevity:	AL1	< 2 years
	AL2	2-5 years
	AL3	> 5 years
Larval type:	LT1	Planktotroph
	LT2	Lecithotroph
	LT3	Direct development
Mobility	AM1	None
	AM2	Low
	AM3	Medium
	AM4	High
Body form	BF1	Cylindrical
	BF2	Dorsally flattened
	BF3	Laterally flattened
	BF4	Spherical
	BF5	Long thin
	BF6	Irregular
Attachment	DA1	None
	DA2	Temporary
	DA3	Permanent
Adult habitat	AH1	Sessile
	AH2	Burrower
	AH3	Surface crawler
	AH4	Swimmer
Feeding:	FH1	Suspension / filter
	FH2	Scraper / grazer
	FH3	Surface deposit feeder
	FH4	Sub-surface deposit feeder
	FH5	Dissolved matter
	FH6	Large detritus
	FH7	Scavenger
	FH8	Carnivore / omnivore
	FH9	Parasite / commensal

The non-parametric Mann-Whitney U test, which ranks data on an ordinal scale and compares between two allocated groups, was used to test for significant differences in each biological trait (infaunal and epifaunal) weighted with biomass between heavily and lightly trawled areas (STATISTICA V.8). Furthermore, the Mann-Whitney U test was also used to test for significant differences in biological traits of infauna occurring between low (≤ 72%) and high (> 72%) proportions of sand and mud (low: < 20% and high: ≥ 20%). The classification of sediment (low or high percent sand or mud) were identical at paired heavily and lightly trawled areas except at Cape Point where the mud content was classified as low in heavily trawled areas and high in lightly trawled areas (Table 3.3, see Chapter Two of this thesis for further sediment classification details).

Table 3.3. Classification of sand and mud sediment components (Folk 1968) at heavily and lightly trawled areas of four sites sampled. Areas containing > 72% sand = high sand, < 72% sand = low sand. Areas containing ≥ 20% mud = high mud, < 20% mud = low mud.

Site	Sediment type	Heavily trawled	Lightly trawled
Namibia	Sand	High	High
	Mud	Low	Low
Childs Bank	Sand	High	High
	Mud	High	High
Cape Columbine	Sand	Low	Low
	Mud	High	High
Cape Point	Sand	High	High
	Mud	Low	High

Bubble plots, scaled to represent the biomass of infaunal species exhibiting significant traits at each site, were overlaid on PCO plots (Principal Coordinate Analysis) of 4th root transformed infaunal biomass. Vectors representing epifaunal species biomass with significant traits were overlaid on a PCO plot of log-scale categorized biomass at each area. Bubble plots show a clearer illustration of the four sites where infaunal biomass was sampled, while vector overlays suitably illustrate the two sites sampled for epifauna. PCO analysis ordinates data onto Euclidean axes, minimizing residual variation defined by the dissimilarities of the selected resemblance measure (Bray-Curtis in this study). Principal coordinate analyses were performed using PRIMER-E v.6 and its add-on package PERMANOVA+ (Clarke & Warwick 2001, Clarke & Gorley 2006, Anderson *et al.* 2008).

RESULTS

Infaunal biological traits analysis

A total of 248 infaunal species were identified and assigned traits scores. Seventeen percent of infaunal biological traits tested were significantly different at the 5% level between areas of heavily and lightly trawled intensities (Table 3.4). Ten and seven percent of infaunal biological traits were significantly different at the 5% level in areas yielding low or high sand or mud contents, respectively (Tables 3.5 & 3.6). The sum of ranks allocated in the Mann-Whitney U test for trait data of the groups being compared are reported (Table 3.4, 3.5 & 3.6), however, comparisons of rank values among traits are not relevant. Comparing the summed rank values for each infaunal trait between heavily and lightly trawled areas (calculated with the Mann-Whitney U test), it is evident that a higher biomass of smaller

(< 5 mm) suspension and surface deposit feeders occurred at heavily trawled areas (Table 3.4). A greater number of surface crawlers with a long thin body form and high mobility occurred at lightly trawled areas. Species between 5 mm and 1 cm in size, sessile, having lecithotrophic larval phases and a detritus/sandlicking feeding strategy occurred at greater biomass in areas with more than 72% sand composition (Table 3.5). Surface crawlers and species having no larval life phases (direct development) occurred at significantly greater biomass in areas with more than 20% mud composition. Sessile species occurred at significantly less biomass in areas with high mud proportions (Table 3.6).

Table 3.4. Heavily vs. Lightly trawled areas: Significantly different infauna biological traits (17% of traits tested) tested by non-parametric Mann-Whitney U between heavily and lightly trawled areas for biological traits weighted by infaunal biomass. LT = lightly trawled, HT = heavily trawled.

Trait	Classification	Code	U-value, p- value	LT Rank Sum	HT Rank Sum
Size (sample size)	< 5 mm	NS1A	U=123, p=0.037	333	487
Size (adult size)	1-3 cm	NS3B	U=105, p=0.01	315	505
Mobility	high	AM4	U=91, p=0.003	519	301
Body form	long thin	BF5	U=123, p=0.037	487	333
Habitat	surface crawler	AH5	U=116, p=0.023	494	326
Feeding	suspension	FH1	U=99, p=0.006	309	511
Feeding	surface deposit feeder	FH3	U=110, p=0.015	320	500

Table 3.5. Sand content: Significantly different infaunal biological traits (10% of traits tested) tested by non-parametric Mann-Whitney U between low and high sand content groups for biological traits weighted by infaunal biomass. Sand contents was classified as high if > 72% and low if ≤ 72%

Trait	Classification	Code	U-value, p-value	High Sand Rank Sum	Low Sand Rank Sum
Size (A)	5mm-1 cm	NS2A	U=111, p=0.03	573	247
Larval type	lecithotroph	LT2	U=118, p=0.04	566	254
Mobility	none	AM1	U=112, p=0.028	571	248
Feeding	detritus/sandlicker	FH6	U=114, p=0.032	414	406

Table 3.6. Mud content: Significantly different infaunal biological traits (7% of traits tested) tested by non-parametric Mann-Whitney U between low and high mud content groups for biological traits weighted by infaunal biomass. Mud content was classified as high if ≥ 20% and low if < 20%

Trait	Classification	Code	U-value, p-value	High Mud Rank Sum	Low Mud Rank Sum
Larval type	direct development	LT3	U=122, p=0.034	488	332
Mobility	none	AM1	U=133, p=0.04	343	476
Habitat	surface crawler	AH5	U=111, p=0.02	499	321

The first two axes of the PCO analysis of infaunal biomass account for only 33.6% of the total variation, suggesting a poor reflection of the structures occurring in the multivariate space in two-dimensions (Fig. 3.1 A). Nonetheless heavily trawled and lightly trawled areas separate within sites. An overlay of circles, scaled to represent the biomass of species occurring with specific traits, was used to retrospectively investigate the relationship of significant traits with heavily and lightly trawled areas. Species having small body size (< 5mm measured and 1-3 mm from literature) occurred in greater biomass at the heavily trawled areas off Namibia and Cape Columbine (Fig. 3.1 B & C). Similarly species that suspension- or surface deposit-feed also occurred in greater biomass at heavily trawled areas (Fig. 3.1 G & H). Species displaying the biological traits of high mobility (AM4), long thin body form (BF5) and surface crawlers (AH5) occurred in larger biomass at lightly trawled areas of Namibia and Childs Bank (Fig. 3.1 D, E & F).

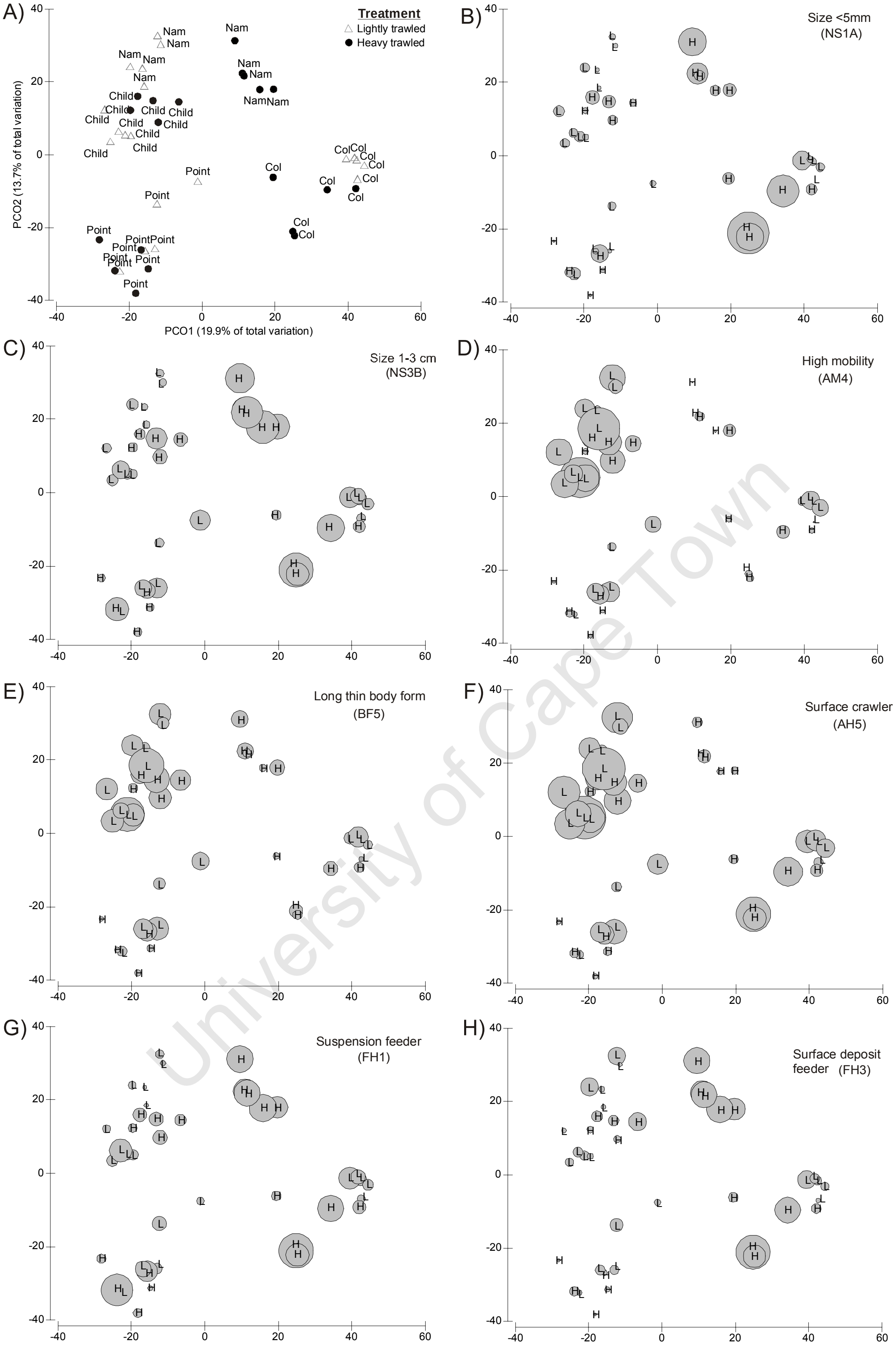


Fig. 3.1. Principal Coordinate Ordination of infaunal biomass data, with bubble overlays scaled to represent infaunal biomass distribution of each significant biological trait (see Table 3.4) between heavily and lightly trawled areas after 4th root transformation, based on Bray-Curtis resemblance measure. H = heavily trawled areas, L = lightly trawled areas.

Epifaunal biological traits analysis

A total of 60 epifaunal species were identified to genus or species level and assigned traits scores. Twenty four percent of traits tested were significantly different at the 5% level between heavily and lightly trawled areas (Table 3.7). Most (80%) of the significant traits occurred at greater biomass in the lightly trawled areas with only traits of temporary attachment and cylindrical body form occurring in higher biomass in the heavily trawled areas (Table 3.7). Species weighing less than 10 g in the samples, but able to reach a body size of 6-10 cm occurred in greater biomass at lightly trawled areas. Similarly species having medium mobility, dorsally flattened, laterally flattened or spherical body form and having feeding strategies of scraper/grazer and sub-surface deposit feeder occurred in significantly greater biomasses at lightly trawled areas in comparison to paired heavily trawled areas (Table 3.7).

Table 3.7. Significantly different epifauna biological traits (24% of traits tested) tested by non-parametric Mann-Whitney U between heavily and lightly trawled areas for biological traits weighted with epifaunal biomass.

Trait	Classification	Code	U-value, p-value	LT Rank Sum	HT Rank Sum
Size (sampled)	1-10g	SS1	U=2, p=0.013	55	23
Size (maximum)	6-10cm	MS3	U=2, p=0.013	55	23
Mobility	medium	AM3	U=0, p=0.005	57	21
Attachment	temporary	DA2	U=0, p=0.005	21	57
Body form	cylindrical	BF1	U=0, p=0.005	21	57
Body form	dorsally flat	BF2	U=1, p=0.008	56	22
Body form	laterally flat	BF3	U=0, p=0.005	57	21
Body form	spherical	BF4	U=0, p=0.005	57	21
Feeding	scraper/grazer	FH2	U=0, p=0.005	57	21
Feeding	subsurface deposit feeder	FH4	U=0, p=0.005	57	21

The first two axes of the PCO plot account for 74% of the total variation indicating a good portrayal of the epifaunal biomass multivariate analysis in two dimensions (Fig. 3.2). Superimposing a vector overlay (Pearson correlation) of significant traits onto the PCO plot it is evident that the traits temporary attachment (DA2) and cylindrical body form (BF1) feature in species having greater biomasses at the Namibian heavily trawled area (Fig. 3.2). The length and direction of each vector indicates the strength and sign of the relationship between that trait and the PCO axes. All other significant traits measured (SS1, MS3, AM3, BF2, BF3, BF4, FH2 and FH4) are as a result of species with these traits occurring in greater biomass at either Childs Bank or Namibian lightly trawled areas.

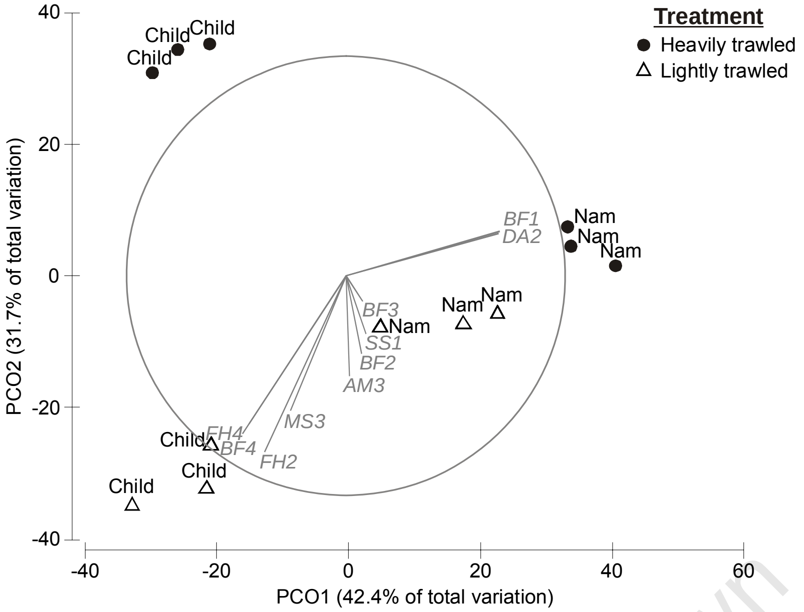


Fig. 3.2. Principal Coordinate Ordination plot with vector overlays scaled to represent epifaunal biomass of each significant trait distribution (see Table 3.7) between heavily and lightly trawled areas after log-scale categorization, based on Bray-Curtis resemblance measure. Nam = Namibia, Child = Childs Bank.

DISCUSSION

Infaunal biological traits analysis

As predicted, infauna with a smaller measured body size (< 5 mm) occur in significantly greater biomass at heavily trawled areas in this study (Table 3.4). Other studies on benthic trawling impacts have also observed a shift from large slow growing fauna to smaller, faster growing organisms (Jennings *et al.* 2001, Ball *et al.* 2000, Kaiser *et al.* 2000, Rumohr & Kujawski 2000, Sparks-McConkey & Watling 2001). Other biological traits also show a positive response to trawling disturbance. Surface deposit feeders and suspension feeders occurred at significantly greater biomass in heavily trawled areas, possibly attracted by increased disturbance leading to increased suspended food supply (Dayton *et al*. 1995, Steele *et al*. 2002). Unpredictably, the long, thin body form, usually attributed to species like polychaetes and expected to proliferate in areas of greater disturbance, occurred in larger biomass in areas of light trawl activity in this study. In this study, *Nephtys* spp. and *Chloeia inermis* accounted for the greatest polychaete biomass in lightly trawled areas. Such species may be vulnerable to physical damage due to intense trawling levels whilst being able to withstand lighter levels of disturbance. This may similarly explain the greater prevalence of surface crawlers and highly mobile species in lightly trawled areas in this study, these traits are also largely represented by *Nephtys* spp and *Chloeia inermis*. Further investigations comparing a true reference site (untrawled) would improve understanding of biological trait selection with respect to trawl disturbance.

Significant differences in biological traits occurring between high and low proportions of mud include surface crawling species and those having direct larval development being more prevalent in areas with more mud. Areas with more fine mud are frequently less disturbed (Steele *et al.* 2002). In this study, areas with greater mud content are also detected to be lightly (rather than heavily) trawled. Trawling disturbs the sediment with fine mud particles likely to be transported in suspension by near-benthic currents, leaving coarser particles to settle out near the area trawled. Surface crawlers generally occurred in greater biomass in the lightly trawled areas of this study indicating their vulnerability to heavier trawl activities in being exposed to the passing gear on the surface of the sediment. Species with direct larval development are also likely to be vulnerable to higher levels of disturbance as the emerging juveniles, usually small in size could easily be swept away or damaged by passing trawl gear.

Epifaunal biological traits analysis

Epifaunal species having biological traits of temporary attachment and cylindrical body form occur in greater biomass in areas of heavier trawling (Table 3.7). In this study, the burrowing anemone, *Actinauge richardi*, is largely responsible for these traits and indeed appears to prevail in areas subjected to heavy trawling (see Chapter Two). All other significant biological traits analysed were represented by greater biomasses occurring in lightly trawled areas (Table 3.7). Species having a dorsally flattened body form were largely starfish and crabs in this study, while laterally flattened body forms were represented by three prawn species known to feed on or near the seabed. Various sponge species were categorized as having a spherical body form and occurred in greater biomass in lightly trawled areas in this study. Similarly three urchin species (*Echinus gilchristi, Brissopsis lyrifera capensis* and *Spatangus capensis*) having feeding strategies of either scraper or subsurface deposit feeder, occurred in greater biomass at lightly trawled areas. These widely diverse species, (starfish, crabs, benthic prawns, sponges and urchins) appear less tolerant of intense levels of trawling.

Changes reflected through biological traits analysis might be expected to differ among different studies, largely as a result of the unique suite of environmental factors present in different habitats. Furthermore, studies conducted to assess changes in benthic communities in response to trawling impacts are unlikely to have identical trawl gear or levels of trawl intensity and are therefore unlikely to be directly comparable. Nonetheless, in comparing biological traits most vulnerable to disturbance, one might expect some similarities among studies. Bremner *et al.* (2005) reported a decrease in infaunal species of large body sizes with increased fishing activity in the North Sea, results which are supported by this study. Predators and scavengers also decreased with an increase in fishing intensity in the Bremner *et al.* (2005) study. Tillin *et al.* (2006) reported significantly more burrowers and scavengers in areas of high fishing impact and more filter feeders and attached fauna in less disturbed areas. de

Juan *et al.* (2007) reported greater abundance of mobile burrowing traits in the trawled area, while the untrawled area had more surface crawlers, highly mobile (similar to results from this study) and filter- and deposit feeding organisms. Kenchington *et al.* (2007) observed increases in mobile species, burrowers and scavengers with a decrease in sessile, filter feeders and species having permanent tubes (e.g. fan worms) with the onset of low intensity trawl fishing in the Bay of Fundy, Canada. Species expressing the biological traits of mobility, burrowing life habit and scavenging feeding mode appear to respond similarly (i.e. increase) to fishing disturbance (Bremner *et al.* 2005, Tillin *et al.* 2006, de Juan *et al*. 2007, Kenchington *et al.* 2007). Sessile species, filter feeders and those with larger body sizes appear to be negatively impacted by fishing disturbance. The results from this study are comparable to previous studies with respect to some traits measured (body size, mobility), however, not with others (e.g. feeding strategies and life habits). Some species with *K-selected* traits appear to be vulnerable to the impacts of trawling, however, others do not, implying that a simple *r-K selected* classification is not necessarily indicative of the species' vulnerability to trawling. The variability in results obtained from BTA illustrates the uncertainty of true quantification of the effects of fishing with respect to functional diversity (Bremner 2008). Furthermore, different studies will have different baseline environmental conditions against which change is measured, necessitating further studies in all fished habitats with appropriate comparisons in similar unfished habitats.

The biological traits of infaunal and epifaunal species analysed in this study are significantly different between areas of heavy and light trawling in the southern Benguela shelf region. A greater proportion of epifaunal (24%) traits measured are significantly different between heavily and lightly trawled areas, than infaunal traits (17 %, Tables 3.4 & 3.7). Significant differences in biological traits (infaunal) also occur with differences in proportions of sand (10% of biological traits) and mud (7% of biological traits) (Table 3.5 & 3.6). Habitat modification and changes in the ratio of sand to mud content can occur when the sea bed is frequently trawled (Steele *et al.* 2002), which in turn can change the habitat suitability for some organisms. A greater percentage of infaunal biological traits differ significantly between heavily and lightly trawled areas (17%) than between sand (10%) or mud (7%) content, suggesting that trawling disturbance alters biological traits to a greater extent than the sediment composition in this study. The results indicate that intense trawling activities modify the functional diversity of benthic assemblages in the southern Benguela region. Epifauna showed a greater percentage of biological traits affected by trawling than infauna (24% *versus* 17% respectively), illustrating their heightened vulnerability to trawl disturbance.

Monitoring implications

The most severe impacts of trawling disturbances in the southern Benguela region are likely to have occurred 100 years ago when trawling was initiated in shallow waters of this area. Species with traits that were able to adapt and survive the initial impacts of trawling now remain and maintain the functioning of the ecosystem. Any species unable to adapt to continual trawl disturbances, are likely to have been displaced from the impacted area. The effects of trawling in terms of assemblage changes, or the reduction/enhancement of specific species traits are unknown, as historical baseline studies from this region did not include benthic invertebrates and no appropriate reference areas are protected from fishing disturbances. Quantifying the effects of fishing disturbance in the southern Benguela is thus severely limited by the lack of appropriate reference areas (Shannon *et al.* 2006), necessitating a comparison between heavily and lightly fished areas. Monitoring the recovery of species in an area protected from fishing is likely to provide some insight into the original benthic assemblage composition and thereby provide more appropriate measures of the impacts of fishing. Areas subjected to severe disturbances can be re-colonised, initially by opportunistic species, gradually increasing the species (and traits) diversity. As a result of patchy recruitment patterns and slow growth to maturity of some structure-forming species (e.g. sponges, corals, gorgonians), Watling and Norse (1998) propose that it is likely to take several years, or perhaps even decades, for benthic systems to recover after heavy demersal fishing activities. It is likely that a substantial period of time, without further intense anthropogenic disturbances, is necessary for benthic communities to recover (if ever) to a similar functional suite of species as that prior to the original disturbance (Watling & Norse 1998).

It is widely recognized that protection of habitats and their ecological functioning is fundamental to ensuring ecological sustainability and thus a key element in applying the ecosystem approach to fisheries management (Shannon *et al.* 2006, Frid *et al.* 2006, 2008). South Africa is committed to establishing an ecosystem approach to fisheries management by 2010 (Nel 2007). The use of biological traits analysis to describe and quantify aspects of ecological functioning is growing in popularity. Frid *et al.* (2008) report that the use of BTA is currently considered to be the best tool available to quantify ecological functioning in marine benthic communities. Using a case study in south west England (the proposed Eddystone Special Area of Conservation), Frid *et al.* (2008) illustrated how BTA can be used as a surrogate to define ecological functioning, set boundaries for marine protected areas and to inform management objectives. However, Bremner (2008) cautions that BTA should not to be considered a universal solution to define ecological functioning, as true whole ecosystem functioning should contain elements combining physical, chemical and biological components. Furthermore, a comprehensive ecosystem assessment would require information of all organism groups i.e. micro-, meio-, macro- and mega-organisms, their interactions and energy flows. BTA clearly only addresses a small component of whole ecosystem functioning and its limitations are acknowledged. Nonetheless, BTA is considered a useful tool to provide benthic faunal information to be further developed into indicators of ecosystem functioning in marine systems and has good potential for application within management frameworks. Future considerations in implementing ecosystem monitoring should include developing a suite of benthic assemblage status indicators using biological traits analysis.

Conclusion

This study has shown that Biological Traits Analysis reflects differences in benthic faunal functional groups in response to intense trawl disturbance. Epifauna show particularly vulnerable traits to the impacts of trawling. Biological Traits Analysis presents a promising approach to improve understanding of benthic ecological functioning and develop a suite of benthic ecosystem health indicators for monitoring the Benguela benthic ecosystem status.

Acknowledgement

Biological traits information for infaunal species was provided by Annelise Fleddum, City University of Hong Kong through a collaborative agreement.

Chapter Four

Assessing the impacts of an experimental trawl-simulated disturbance on infauna in Oslofjord, Norway

INTRODUCTION

Many studies have investigated benthic community shifts as a result of trawling impacts, yielding varied results (reviews by Auster & Langton 1998, Jennings & Kaiser 1998, Collie *et al.* 2000a, Steele *et al.* 2002, Thrush & Dayton 2002, Kaiser *et al.* 2006). Detecting changes in benthic biota that can conclusively be attributed to fishing impacts is not a simple task (Drabsch *et al.* 2001, Gray *et al.* 2006). Changes that are observed through experiments and monitoring studies, frequently occur in conjunction with natural disturbances and a general lack of appropriate control sites hinders the ability to distinguish between fishing and natural disturbances (Auster & Langton 1998, Gray *et al.* 2006). Furthermore the disturbance severity depends on the trawl regime, type of gear used (configuration and weight), the sediment type and the frequency and intensity of natural disturbances (Jennings & Kaiser 1998, Collie *et al.* 2000a, Kaiser *et al*. 2002, Thrush & Dayton 2002, Drabsch *et al.* 2001). Substantial variability of benthic communities themselves, spatially and temporally, can further confound sampling designs that attempt to detect the effects of trawling (Lindegarth *et al.* 2000). For these reasons, direct comparisons across studies are seldom possible and often, comparisons within studies, fail to detect changes that can unequivocally be attributed to trawling (Hall *et al.* 1993, Thrush & Dayton 2002). Studies attempting to account for the difficulties in attributing changes to fishing impacts have frequently conducted spatially replicated Before-After, Control-Impact (BACI) sampling designs (e.g. Curry & Parry 1996, Tuck *et al.* 1998, Ball *et al.* 2000, Lindegarth *et al.* 2000, Kenchington *et al.* 2001 & 2006, Drabsch *et al.* 2001). The BACI sampling approach is often recommended to overcome problems of inferring that changes observed are due to an impact rather than natural variability (Green 1979, Underwood 1991 & 1992, Stewart-Oaten *et al.* 1986 & 2001, Hewitt *et al.* 2001). Using a BACI design, evidence of an impact is shown by a significant interaction between time (Before *vs*. After the impact) and treatment (Control *vs*. Impact) using analysis of variance (parametric data) or analysis of similarities (non-parametric data). Sampling more than one control site, preferably a randomly-selected set of control locations (Underwood 1992), strengthens the experimental design in being able to unambiguously detect changes as a result of an impact.

A lack of representative areas protected from fishing in the offshore environment of southern Africa precluded an experimental assessment of the impacts of trawling with a comparative unfished control site. However, through the bilateral research agreement between South Africa and Norway (NORSA), an opportunity arose to conduct *in situ* experiments to investigate the effects of trawling in an area of

Oslofjord where trawling is prohibited. This facilitated the opportunity to conduct small-scale Before-After, Control-Impact (BACI) experiments in an untrawled area, serving as a control site.

The Norwegian Oslofjord forms a northern branch of the Skagerrak in the North Sea, an area which has been subjected to intensive demersal fishing for several decades (Frid *et al.* 2000) with some of the earliest shrimp trawling records in Oslofjord dating back to 1898 (Seaton & Suomela 1958). Large areas of the Oslofjord, deeper than 60 m, are subjected to commercial trawl fishing, the target species being the edible shrimp, *Pandalus borealis,* with some by-catch of other demersal species (Olsgard *et al.* 2008). Legislation implemented in 1984 (Saltwater Act 3 June 1983 No. 40) prevents trawling shallower than 60 m in the Oslofjord, effectively providing representative habitat protected from trawling for more than 20 years. Otter trawl configurations generally used by shrimp trawlers in the fjord, deploy otter boards weighing an average of 125 kg each with head ropes and ground ropes averaging 10 m and 14 m in length, respectively (Hannson *et al.* 2000, Olsgard *et al.* 2008). The fishing gear used in this shrimp fishery is comparatively smaller and lighter than those deployed offshore. Nonetheless, the otter boards leave behind 10-20 cm deep furrows in the muddy sediment of the fjord, which are visible on sidescan sonar and with remotely operated vehicles (ROVs). Each part of the trawled areas of Oslofjord is swept on average 2-3 times each year (Olsgard *et al.* 2008).

The Oslofjord is 110 km long, extending from the city of Oslo to the open Skagerrak coast. A shallow (19 m) sill located at Drøbak (30 km south of Oslo) is an important feature influencing water exchange between the inner and outer fjord areas (Mirza & Gray 1981, Valderhaug & Gray 1984). The water body of the fjord is relatively stable throughout the year and although Oslofjord is regarded as organically enriched, the benthic macrofauna in the outer fjord area, are considered to be typical of a species-rich undisturbed boreal community of silt-clay sediments (Mirza & Gray 1981, Valderhaug & Gray 1984). Valderhaug & Gray (1984) found the benthic fauna of the Oslofjord remain extremely constant in species composition and numbers over time, dominated by surface and sub-surface feeders. The macrofauna species occurring in the outer Oslofjord are considered similar to those of other Scandinavian and Scottish fjords (Mirza & Gray 1981). Some deeper areas (> 80 m) of the Oslofjord support long-lived, slow-growing species colonizing hard grounds, like the cold-water coral *Lophelia pertusa*, basket star *Gorgonocephalus caputmedusae* and gorgonian *Paramuricea placomus* (Rosenberg *et al*. 2005). Early dredging work conducted in 1865 by Michael Sars in Norway also reports on “coral banks formed by *Lophelia pertusa* in Oslofjord” (Roberts *et al.* 2009).

The aim of this study was to investigate the effects of an experimental trawl-simulation impact on the infaunal assemblage of a previously untrawled area of the Oslofjord. The fact that trawling has not taken place in the study area (due to the legally imposed depth restrictions) provides an excellent opportunity to investigate benthic assemblage changes as a result of trawling disturbance in an untrawled environment. The likelihood of detecting effects of the experimental trawl in a naturally variable system was increased by investigating effects at two paired control *vs*. impact sites, sampling being conducted before and after the impact and monitoring recovery of the benthic assemblages 14-and 64-days after the impact.

The hypotheses tested in this study were that

- There would be significant differences in benthic infaunal assemblages after a trawl-simulation impact disturbance in comparison to nearby unimpacted sites. It was hypothesized that there would be a decrease in large-bodied and/or rare species that are vulnerable to disturbance impacts.
- Some level of infaunal benthic assemblage recovery would be measurable over the subsequent nine weeks (64 days) of monitoring, approaching composition to that prior to the impact and comparable to that of the unimpacted control sites. It was hypothesized that an increase in small-bodied, opportunistic species would be detected in the weeks and months following the trawl-simulation disturbance, with a gradual shift towards the original assemblage composition.

METHODS

Study site

An untrawled, heterogenous area in the outer Oslofjord, representative of typical soft sediment habitat, was identified as a suitable location for this study (Fig. 4.1). The *in situ* experimental area was located westwards of Jeløya, approximately 50 km south of Oslo (59°29.482'N 10°36.948'E) and approximately 2 nautical miles east of commercial trawl grounds (Fig. 4.1). To confirm the untrawled status of the benthos (lack of visible trawl furrows) at the experimental site, a remotely operated vehicle (ROV), equipped with autonomous positioning system, digital video recorder and sonar was deployed to examine the seabed. Two areas, each having a control and an impact site, were identified in which to conduct this study. The area A-B (A = control, B = impact) was approximately 100 m north of the second area C-D (C = impact, D = control) with A being approximately 50 m north of B and C being 50 m north of D (Fig. 4.1). The average depth at all sites was 35 m.

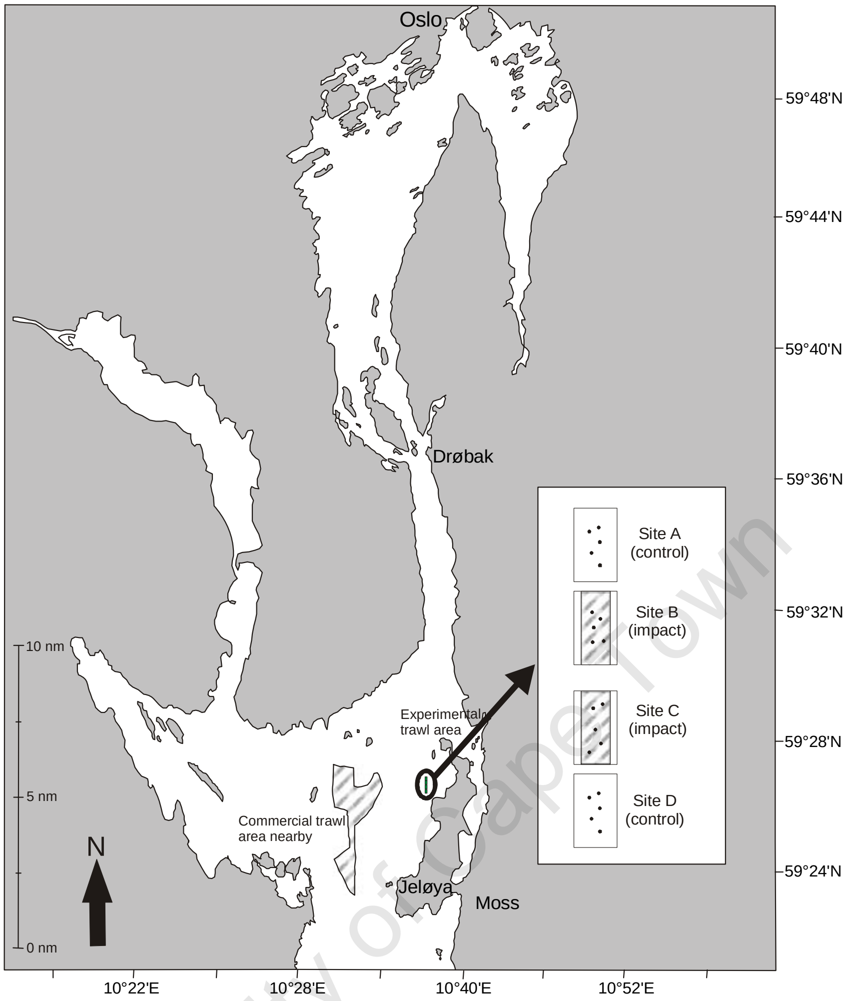


Fig. 4.1. Map of Oslofjord, Norway showing sampling stations.

Biological Sampling

Benthic infauna were sampled at each site (A – D) using a 0.1 m^2 van Veen grab. Five replicate samples were obtained from each site on 15th August 2007 (time zero). Once the van Veen grab was onboard, it was opened, releasing the sediment containing macrofauna into a washing table. A sediment sample was collected, labeled and frozen for further particle size and organic content analysis in the laboratory. The sample was then washed through two mesh sizes, 5 mm and 1 mm (round hole mesh) retaining all macrofauna > 5 mm and > 1 mm separately. The macrofauna were transferred to plastic containers, labeled and preserved with 40% formaldehyde. Rose Bengal dye was added, staining all organic matter pink in colour, facilitating the sorting process and maintaining local practice for comparative purposes. After benthic macrofauna had been sampled, an Agassiz sled was deployed from a single winch cable and towed across each of the two impact sites (B and C) four times. The Agassiz beam sled (a smaller and lighter version of a regular beam trawl) used in this study to provide a trawl-simulation impact, had a beam length of 1.9 m, 75 cm vertical mouth opening, a beam trawl shoe width of 15 cm each and weighed approximately 200 kg out of water (Fig. 4.2). The mesh size of the net was 3.5 cm stretched and 1.5 cm in the cod-end. The disturbance created by the Agassiz beam sled was intended to simulate, at a smaller scale, that of shrimp (*Pandalus borealis*) trawling, as occurs in the region and was the only trawl gear permitted in this experimental circumstance. The impact of ~ 200 kg spread over the two 15 cm beam trawl shoe widths can be considered roughly similar to that of two 125 kg otter boards, as Hannson *et al.* (2000) and Olsgard *et al.* (2008) report are used in the commercial fishery. All epifauna retained in the net after each tow, were identified, counted and weighed. Subsequent to four passes of the Agassiz beam sled, a further five replicate benthic grab samples were obtained from within the tracks of the sled passage at all four sites, providing an immediately post-impact sample. The stable dynamic positioning ability of the vessel and minimal water currents in the fjord facilitated an estimated 90% certainty of re-sampling within the passage of the sled, at the average depth of 35 m.

Fig. 4.2. Agassiz beam sled used to simulate a trawl impact at sites B & C, Oslofjord.

Fourteen days (end August 2007) after the trawl-simulation impact, a further five replicate infauna samples were obtained from each of the four sites using the van Veen grab. Every possible effort was made (estimated 90% certainty) to re-sample within the Agassiz beam sled tracks at sites B and C. Nine weeks (64 days) after the trawl-simulation impact the final five replicate infauna samples were collected from each of the four sites.

In the laboratory, the 80 infaunal samples were thoroughly washed with water to remove formaldehyde, sorted into broad taxonomic groups and transferred to 96% ethanol for preservation. Further identification of all species to the lowest taxonomic resolution (genus or species) was conducted yielding abundance, biomass (wet mass) and average size of all infauna from the four areas over time (zero, post-impact, 14 days and 64 days).

Statistical analyses of univariate indices (number of species, number of individuals, Pielou's species evenness and Shannon-Wiener diversity) of infauna were computed and a *post-hoc* power analysis, based on repeated measures ANOVA between factors on data collected at time zero, was performed to determine the statistical power of the experimental design to detect changes in the univariate indices (Cohen 1988, Faul *et al*. 2007, G*Power 3.1). Univariate indices were then tested for significant differences between paired control-impact sites for each of the four sampling events over the 64-day duration of the experiment (t-tests STATISTICA V.8, Stewart-Oaten *et al.* 1986).

The use of a BACI design with repeated measures over time at the same locations to test for the effects of an impact, raises the issue of non-independence within the fixed factor "time" (i.e. temporal pseudo-replication, Hulbert 1984). To address this issue, a test for sphericity (investigation of the nature of correlations between sample units through time) is recommended when results relevant to the hypothesis being tested are significant (Anderson *et al*. 2008). The abundance and biomass of all infauna sampled at all sites and each sampling event were combined into matrices. Each matrix was 4th root transformed to down-weight the excessive contributions of quantitatively dominant species to the similarities calculated between species (Field *et al*. 1982, Clarke & Gorley 2006). A resemblance matrix was created using the Bray-Curtis measure of (dis)similarity, subsequently being used to generate non-metric multi-dimensional scaling (MDS) plots. The multivariate permutation based PERMANOVA analysis routine (permutational multivariate analysis of variance) was used to test for significant differences in species abundance and biomass over time between paired control and impact sites (Anderson *et al*. 2008). This semi-parametric permutational procedure assumes exchangeability of samples resulting in the correlation structure among samples through time, if any, essentially being irrelevant under permutation (Anderson *et al.* 2008). PERMANOVA allows for further testing of any interaction term for any multi-factorial model with P-values being obtained by permutation techniques and is considered applicable to analyzing assemblages in response to BACI or Beyond BACI experimental designs. Anderson *et al.* (2008) recommend that if statistically significant results are obtained in a repeated measures analysis, a separate test for sphericity (by calculating the dissimilarities between levels of the repeated measures factor across treatments) should be used to further interpret the results. The crossed experimental design comprised two sites (fixed factor) with two treatment effects (control and impact, fixed factor), over four sampling times (fixed factor). The PERMANOVA routine assigns importance to the dissimilarity values generated by the resemblance matrix on which permutations are based, generating a test statistic value of pseudo-F (or pseudo-*t,* Anderson *et al.* 2008). All multivariate and diversity analyses were performed using PRIMER-E v.6 and its add-on package PERMANOVA+ (Clarke & Warwick 2001, Clarke & Gorley 2006, Anderson *et al*. 2008).

Furthermore, all polychaetes (thirty families thereof) sampled were also analysed separately to explore whether all phyla together obscured any patterns that might be reflected by polychaetes only.

Sediment particle size

A detailed description of methods used to determine gravel-sand-mud particle size components is provided in Chapter Two of this thesis. The greater silt and clay content in sediment from Oslofjord necessitated slightly modified methodology. The mud-fractions were pipetted with an Andreasen pipette, to determine the proportions of silt and clay, after 5 g of finely ground sodium hexametaphosphate had been added as a deflocculant. The pipette was calibrated by weighing 20 successive aliquots to determine a mean volume. The 1000 ml graduated cylinder was divided by the mean aliquot volume (22.73 ml) to obtain a pipetting factor of 43.993. The mass of a pipetted subsample was then multiplied by the pipetting factor to obtain the mass of silt plus clay (mud) and then of clay, the mass of silt being obtained by subtraction.

The total mass of sediment for each sample was calculated from the mass of dried gravel, the mass of dried sand and the pipetted mass of mud. The total mass was used to estimate the percentage clay, silt, sand and gravel for each sample. The Gravel-Sand-Mud texture of each sample was determined using a classification triangle (Folk, 1968, see Chapter Two of this thesis). Similarly, the Sand-Silt-Clay texture of each sample was categorized using a relevant classification triangle (Shepard, 1964). A splitter was used to obtain a random split of 2 - 3 g of each sand-fraction and its size distribution (mean particle size) obtained using a computer-linked settling column. Sediment processing and classification was conducted by the Geology Department, University of Cape Town, under the guidance of Prof. John Rogers.

Total Organic Carbon, Nitrogen and Hydrogen

A detailed description of methods used to determine total organic carbon is provided in Chapter Two of this thesis and is identical for determination of total organic nitrogen and hydrogen. Measurements of organic carbon, nitrogen and hydrogen using the CHN analyzer were conducted by a technician at the Department of Chemistry, University of Cape Town.

T-tests for independent samples, grouped by control or impact area, after converting percentages to proportions and arcsine transformation (Zar 1999, Sokal & Rohlf 1969), were used to test for differences in sediment characteristics and total carbon, hydrogen and nitrogen between paired sites (A *vs.* B and C *vs.* D) using STATISTICA V.8.

RESULTS

Sediment particle size & Organics

The sediment samples from all four areas (A – D) comprised predominantly mud (89 – 98 %) on a Gravel-Sand-Mud classification, according to Folk (1968, see Chapter Two). Using the Shepard (1964) Sand-Silt-Clay classification the sediments from all four areas were categorized as clayey-silts (Table 4.1). T-test analyses for independent samples grouped by treatment (control/impact) showed no significant differences in arcsine transformed proportions of gravel, sand, silt or clay or mean sand particle size between paired sites (p > 0.1, d.f.=8, A *vs.* B and C *vs*. D). The sediment from the sample sites were considered to be sedimentologically very uniform and well sorted.

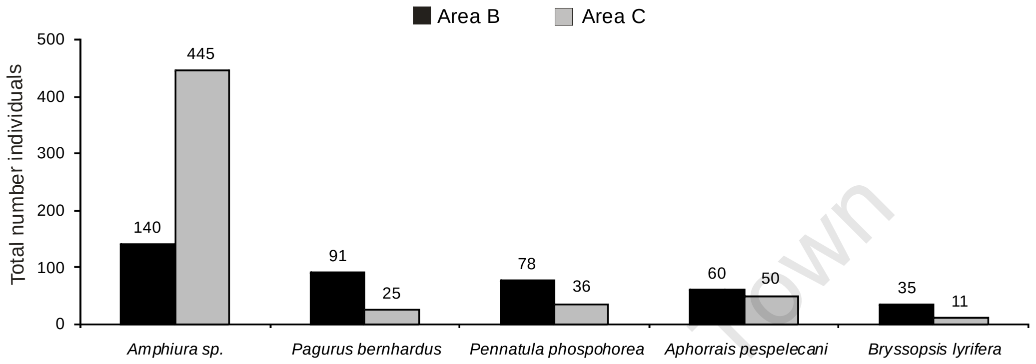
No significant differences were evident among the arcsine transformed proportions of total organic carbon, hydrogen or nitrogen between either of the paired control-impact sites sampled (t-tests, p > 0.1, d.f.=8, A *vs.* B and C *vs*. D). The organic content was considered uniform throughout the four sites sampled in this study.

Table 4.1. Mean environmental variables measured at control and impact areas A, B, C and D prior to experimental trawl impact in Oslofjord. (± SE in brackets). No significant differences were observed between paired control and impact sites using T-tests.

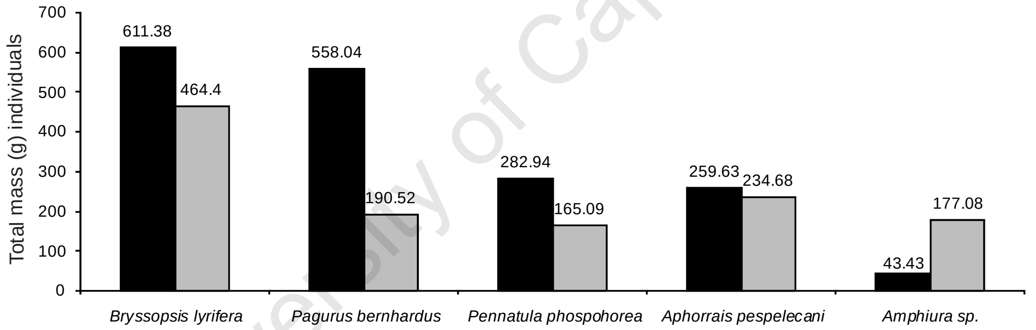
	Area 1		**Area 2**	
Variable	**A (control)**	**B (impact)**	**C (impact)**	**D (control)**
% Gravel	0	0	0.078 (±0.06)	0.39 (±0.3)
% Mud	92.9 (±0.28)	91.6 (±1)	96.1 (±0.52)	96.2 (±0.26)
% Sand	7.05 (±0.28)	8.4 (±1)	3.85 (±0.5)	3.4 (± 0.39)
% Silt	56.7 (±3.6)	56.1 (±3.73)	57.34 (±2.75)	62.25 (±1.38)
% Clay	36.2 (±3.8)	35.5 (±2.95)	38.74 (±3.23)	33.9 (±1.29)
Mean particle size	3.27 (±0.02)	3.21 (±0.06)	3.2 (±0.03)	3.07 (±0.1)
% TOC	0.98 (±0.02)	1.03 (±0.02)	1.17 (±0.02)	1.14 (±0.02)
% TOH	0.74 (±0.04)	0.56 (±0.13)	0.65 (±0.02)	0.65 (±0.02)
% TON	0.23 (±0.03)	0.24 (±0.01)	0.32 (±0.01)	0.31 (±0.02)

Epifauna removed by trawl-simulation

A total of 442 epifaunal organisms were removed by four passes of the Agassiz sled in area B, while at area C a total of 599 individuals were removed. The total biomass of organisms removed by four passes of Agassiz sled in area B was 1944 g while at area C was 4441 g, however, one butter flounder (*Phrynorhombus norvegicus*) made up 3070 g of this mass. Excluding the butter flounder, a more comparable epifaunal mass of 1371 g was removed from area C. More than 90 % of individuals removed from area B and C comprised the same five species (Fig. 4.3) with the brittlestar, *Amphiura* sp. making up the greatest number of individuals. Ninety percent of the biomass removed from area B and C were also made up of the same species (Fig. 4.3) at each site, with the urchin *Brissopsis lyrifera* (Fig. 4.3 & 4.6) contributing the greatest total biomass removed, followed by the hermit crab, *Pagurus bernhardus*. Seapens, *Pennatula phosphorea*, an emergent epifaunal species suspected to be sensitive to the impacts of trawling, also occurred in large abundance and biomass at both impact sites (Fig. 4.3 & 4.4).



Top 5 Species removed (abundance)



Top 5 Species removed (biomass)

Fig. 4.3. Abundance and Biomass of top five epifauna species removed by four passes of an Agassiz trawl-simulation disturbance at area B and C, Oslofjord, Norway.

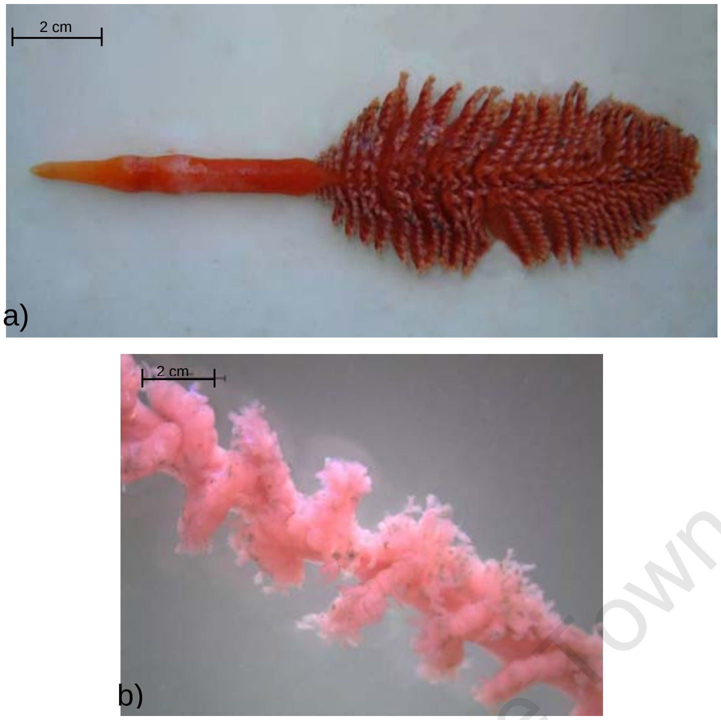


Fig. 4.4. Photographs of seapens a) *Pennatula phosphorea* and b) *Virgularia mirabilis* (magnified) sampled by benthic grab in Oslofjord, Norway.

Benthic infauna

In total, 106 infaunal species were identified from grab samples at all sites combined, with a cumulative 8470 individuals. The infauna were represented by six phyla sampled at all sites with polychaetes being the most diverse group sampled representing 29 families, followed by bivalves represented by 11 families. The most dominant species, with respect to abundance and biomass, at all sites over the 64 days of the experiment were two species of brittle stars, *Amphiura filiformis* and *Amphiura chiajei* (Fig. 4.7). Other species frequently occurring at all sites include the gastropod *Hydrobia ulvae*, the bivalve *Corbula gibba* and polychaetes, *Chaetozone setosa, Lumbrineris fragilis, Diplocirrus glaucus, Nephtys incisa* and *Spiophanes kroeyeri* (Fig. 4.7).

In this study, the power of a statistical test is defined as 1-β (Faul *et al*. 2007) with β being the probability of falsely accepting the null hypothesis when the alternate hypothesis is actually true (Type II error, Manly 1997). The assumption of sphericity (equal variances and correlations among repeated measures) is not applicable to tests between factors (Faul *et al*. 2007) and is therefore not required for this power analysis. Based on the experimental design the *post-hoc* power analysis provides the probability of obtaining a significant result ($p < 0.05$) for an effect size which is calculated from the means and standard deviation of preliminary univariate data collected at time zero (Faul *et al*. 2007, Table 4.2). The power test makes the assumption that the variance among the means does not vary over time. The probability of detecting the observed effect (calculated from the means at time zero) as a result of the trawl treatment in the total number of individuals was low (20 %, Table 4.2). The means of the total number of species at time zero indicate a 55 % probability of detecting the observed effect (0.39) between treatments (Table 4.2). Species evenness showed a 58 % probability of the observed effect while species diversity showed greater power (97 % Table 4.2) to detect the observed treatment effects, as calculated from the means at time zero. This analysis shows that similar differences are likely to be detected mostly in species diversity in subsequent sampling.

Table 4.2. *Post-hoc* power analysis for ANOVA repeated measures between factors experimental design. The effect size is calculated from the means and standard deviations of preliminary univariate data collected at time zero, 1- β represents the probability of detecting a significant difference ($p < 0.05$) in the data observed between control and impact sites. The effect size f ratio is calculated from the standard deviations of the effect and population respectively (Faul *et al.* 2007).

Univariate index	**Effect size f**	**Critical F**	**Power (1- β)**
Total # species	0.39	4.414	0.55
Total # individuals	0.21	4.414	0.20
Species evenness*	0.41	4.414	0.58
Species diversity**	0.73	4.414	0.97

*Pielou's evenness index (J'), ** Shannon-Wiener diversity index (H')

Analyses of univariate indicators (t-tests) showed few significant differences occurring between paired control-impact sites. A significantly greater total number of species (t=3.3, d.f.=8, p=0.01) occurred at Site A (control) compared to Site B (impact), fourteen days after the trawl-simulation impact (Table 4.3). Site C (impact) supported a significantly greater species diversity (t=2.7, d.f.=8, p=0.03, Shannon-Wiener index) prior to the trawl-simulation disturbance than Site D (control, Table 4.3). No further significant differences in univariate indices were observed between paired control-impact sites over the duration of the experiment (Table 4.3).

Table 4.3. Mean diversity indices for control and impact areas A, B, C and D in Oslofjord (± SE in brackets). Significant differences detected by t-tests between paired control and impact sites per sampling occasion, are highlighted in bold at $p < 0.05$.

		Area 1		Area 2	
Univariate index	**Time**	**Site A (control)**	**Site B (impact)**	**Site C (impact)**	**Site D (control)**
Total # species	Zero	15.8 (±1.66)	17.6 (±0.81)	20 (±1.05)	17.2 (±1.64)
	Post-impact	23.6 (±2.94)	19.8 (±0.58)	21.2 (±2.13)	17.4 (±0.51)
	14 days	**22.2 (±0.49)**	**19 (±0.84)**	20.6 (±2.79)	16.6 (±1.54)
	64 days	19.2 (±0.49)	17.2 (±0.86)	18.6 (±1.17)	17 (±0.32)
Total # individuals	Zero	71.4 (±7.49)	91.2 (±4.39)	107.4 (±5.52)	110 (±9.73)
	Post-impact	120.2 (±11.7)	95.8 (±6.57)	118.6 (±2.13)	112.8 (±9.09)
	14 days	122.4 (±6.9)	109.7 (±6.64)	98.8 (±5.62)	114.8 (±10.1)
	64 days	99 (±14.12)	90 (±7.25)	123.8 (±15.8)	108.2 (±4.91)
Species evenness*	Zero	0.7 (±0.01)	0.75 (±0.03)	0.7 (±0.001)	0.7 (±0.02)
	Post-impact	0.7 (±0.01)	0.7 (±0.02)	0.64 (±0.03)	0.66 (±0.01)
	14 days	0.7 (±0.02)	0.7 (±0.02)	0.68 (±0.04)	0.64 (±0.02)
	64 days	0.74 (±0.02)	0.71 (0.03)	0.64 (±0.02)	0.064 (±0.03)
Species diversity**	Zero	1.92 (±0.06)	2.01 (±0.04)	**2.09 (±0.05)**	**1.81 (±0.09)**
	Post-impact	2.34 (±0.14)	2.08 (±0.07)	2.12 (±0.15)	1.89 (±0.03)
	14 days	2.17 (±0.06)	2.05 (±0.04)	2.07 (±0.2)	1.79 (±0.08)
	64 days	2.19 (±0.05)	2.02 (±0.09)	1.88 (±0.01)	1.82 (±0.08)

*Pielou's evenness index (J'), ** Shannon-Wiener diversity index (H')

Multi-Dimensional Scaling plots of 4th root transformed infaunal abundance and biomass data resulting from a Bray-Curtis resemblance matrix show no evidence of replicate samples grouping over time (Fig. 4.5). The high stress values associated with these MDS plots (0.32 for abundance and 0.30 for biomass) are indicative of the lack of any pattern in the data. A main-effects PERMANOVA showed no significant difference between treatments (control and trawl impact) and all treatment interaction terms for both biomass and abundance measures (Table 4.4), eliminating the need for further multivariate analyses to investigate effects of the trawl impact or tests of sphericity. Significant differences were detected between the two areas (abundance and biomass) and among the four sampling events over time (abundance, Table 4.4). Significant differences between areas and over time are not considered relevant to the hypothesis in question and within the confines of the current experimental design, are probably attributable to natural variation.

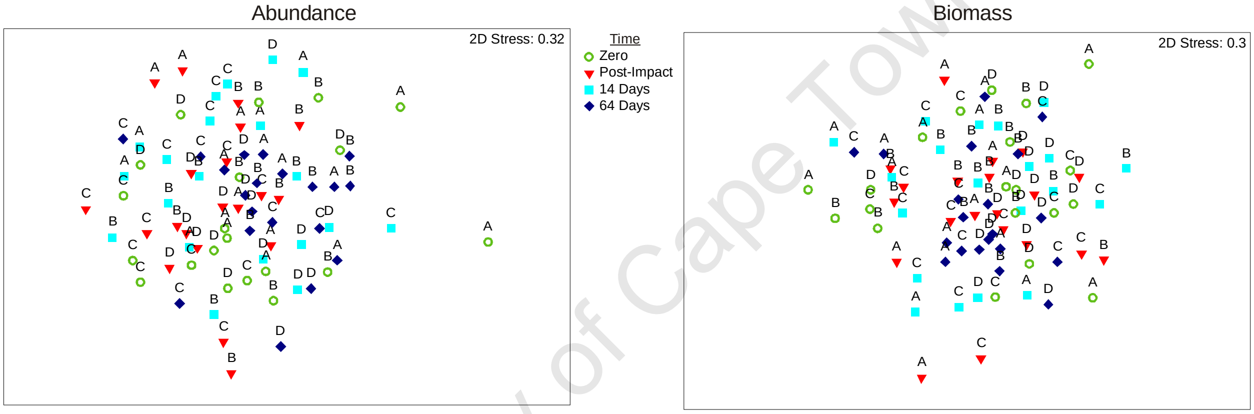


Fig. 4.5. Multi-Dimensional Scaling plot of all infauna abundance and biomass measures from all sample sites (A-D) over the 64-day experimental period, after 4th root transformation and Bray-Curtis similarity measures.

Table 4.4. Test statistics for multivariate main-effects PERMANOVA analysis of infaunal abundance and biomass measures of all species between areas, treatments and over four sampling events. Significant values at $p < 0.01$ are indicated in bold.

ABUNDANCE	**Degrees of freedom**	**Sum of Squares**	**Mean Squares**	**Pseudo-F**	**p-value**	**Unique no. permutations**
Area	1	1869.6	1869.6	2.2064	**0.0025**	9935
Treatment	1	696.79	696.79	0.82232	0.6702	9912
Time	3	3931.9	1310.6	1.5468	**0.0092**	9861
Area x Treatment	1	1333.3	1333.3	1.5735	0.0657	9910
Area x Time	3	3817.4	1272.5	1.5017	0.0124	9876
Treatment x Time	3	2801.1	933.69	1.1019	0.2991	9870
Area x Treatment x Time	3	2774.1	924.7	1.0913	0.3262	9855
BIOMASS	**Degrees of freedom**	**Sum of Squares**	**Mean Squares**	**Pseudo-F**	**p-value**	**Unique no. permutations**
Area	1	2036.4	2036.4	2.2644	**0.0038**	9932
Treatment	1	883.65	883.65	0.98256	0.4758	9922
Time	3	3473.1	1157.7	1.2873	0.0881	9858
Area x Treatment	1	1602.7	1602.7	1.782	0.025	9924
Area x Time	3	3192.3	1064.1	1.1832	0.1747	9846
Treatment x Time	3	2940.4	980.14	1.0899	0.3129	9864
Area x Treatment x Time	3	2316.4	772.14	0.85857	0.7527	9847

Multivariate analyses of polychaete abundance and biomass data conducted independently at the family level resulted in similar MDS plots as depicted in Fig. 4.5 and non-significant PERMANOVA results and are not reported further.

Fig. 4.6. *Brissopsis lyrifera* sampled using Agassiz beam sled and van Veen grab in Oslofjord, Norway.

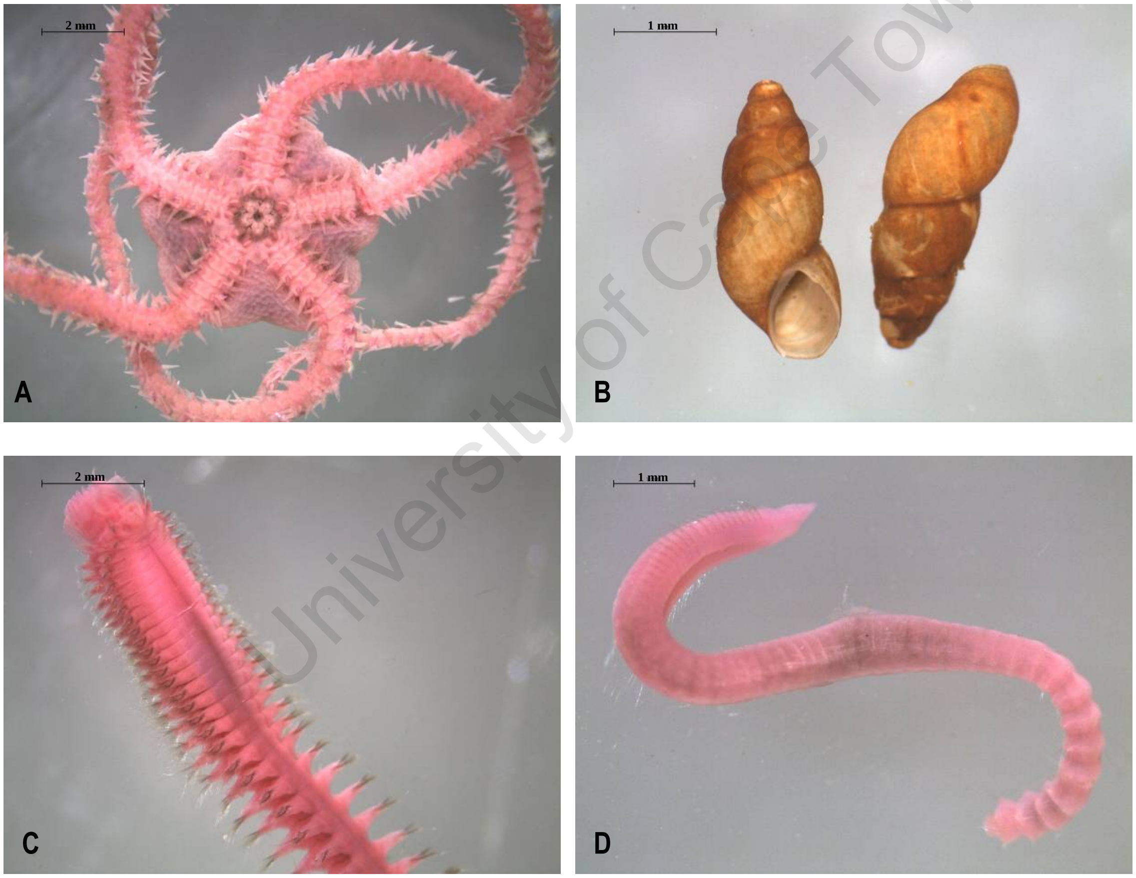


Fig. 4.7. Abundant benthic infauna sampled in Oslofjord, Norway A) *Amphiura chiajei*, B) *Hydrobia ulvae*, C) *Nephtys incisa* and D) *Chaetozone setosa*.

DISCUSSION

The results of this study show no evidence of changes in benthic infaunal assemblages as a result of a trawl-simulation disturbance. Kaiser *et al.* (2002) states that for a fishing disturbance of the seabed to have an ecologically significant impact it should exceed the background levels and frequency of natural disturbance. Furthermore, chronic effects of fishing disturbance are likely to accumulate over long periods of time and isolated, small experimental disturbances are seldom able to mimic the broad-scale effects of fishing disturbances (Thrush *et al.* 1998). The trawl-simulation impact applied in this study appears to have been insufficient to exceed that of natural disturbances, resulting in no significant changes in infaunal assemblages being detected by the sampling techniques used.

The habitat type in which this study was conducted is classified as a shallow, organically enriched fjord system (Mirza & Gray 1981) with muddy sediments (more specifically clayey-silt) at untrawled depths of 35 m. It has been hypothesized that some organisms living in a soft muddy habitat are able to burrow deep (10 – 200 cm) into the sediment and in this way avoid the impact of passing trawl gear (Kaiser *et al.* 2002). This adaptation could result in limited initial impacts of disturbance being detected in such habitats, as was observed in this study. The shallow area studied is also likely to be subjected to the effects of waves and strong currents resulting from tidal fluctuations. The elevated levels of bioturbation (from burrowing organisms) and water movement probably result in increased levels of small-scale natural disturbance in the areas sampled. These levels of disturbance invariably lead to some degree of natural variation in community species composition. Significant differences detected between areas sampled and among sampling events (Table 4.4) are likely to have been caused by natural disturbance. The degree of natural disturbance appears to mask any detectable changes in benthic infauna, as a result of the trawl-simulation disturbance resulting in a non-significant effect of treatment (Table 4.4).

Fauna and flora naturally occurring in a habitat will have adaptations to allow them to persist in that environment. Most communities have an inherent resilience to a certain level of natural physical disturbance, although periodic extreme events can lead to widespread kills of biota (Kaiser *et al.* 2002). Bergman and Hup (1992) observed that it is the position of burrowing urchins in the sediment column that can render them susceptible to trawl damage, rather than their size, as was previously believed. Smaller urchins only burrow a few centimeters into the sediment and are therefore unearthed and damaged or killed by passing trawl gear. With an increase in age and size, however, urchins burrow deeper into the sediment and are thereby afforded protection from the disturbance of passing trawl gear (Jennings & Kaiser 1998). The fourteen burrowing urchins (*Brissopsis lyrifera*) sampled by benthic grab in this study were all greater than 30 mm in diameter, indicating a mature assemblage (Austen *et al.* 1998). Their abundance was equally distributed among sites sampled before and after trawling (seven in each), suggesting that the passing trawl gear did not affect the size or abundance of buried *Brissopsis lyrifera* in this study. However, considerably more *Brissopsis lyrifera* were removed by the Agassiz sled from the impact sites (n=46, Fig. 4.4), substantiating claims that urchin species on the surface of the sediment are negatively affected by trawl gear, while buried individuals can escape such impacts.

Emergent epifauna are predicted to be highly susceptible to removal by trawl gear contacting the seabed (Currie & Parry 1996, Jennings & Kaiser 1998, Collie *et al.* 2000b). Indeed, as many as 114 individual *Pennatula phosphorea* and five *Virgularia mirabilis* were removed by four passes of the Agassiz sled at two impact areas of this study (Fig. 4.3). It was predicted that immediately after the trawl disturbance, no seapens would occur in the grab samples taken from the impacted sites, however, 12 *Virgularia mirabilis* and one *Pennatula phosphorea* were present in grab samples taken immediately after the impact. Eno *et al.* (2001) found that the seapens *Pennatula phosphorea* and *Virgularia mirabilis* bent in response to pressure waves created by descending fish traps and were able to lie flat on the sediment surface. Moreover, when uprooted, the seapens were able to re-establish themselves in the sediment, incurring little damage. Tuck *et al.* (1998) also reported that *Virgularia mirabilis* are able to rapidly withdraw into the mud when vibrations are detected, thereby escaping damage from trawl gear. This type of adaptive behaviour could explain the occurrence of seapens, especially *Virgularia mirabilis* (a fragile species previously considered to be highly susceptible to disturbance impacts), in grab samples after the trawl-simulation impact.

Many empirical studies of fishing disturbance have failed to detect the anticipated reductions in species or changes in community composition (e.g. Gibbs *et al.* 1980, de Wolf & Mulder 1985, Brylinksi *et al.* 1994, Kaiser *et al.* 1998, Drabsch *et al.* 2001). The difficulty of detecting changes in the benthic environment is often considered a reflection of the once-off pulse-disturbance sampling designs used (Thrush *et al.* 1998). The sampling design is, in turn, frequently limited by financial, time and practical constraints associated with most scientific studies (Collie *et al.* 2000b). Long-term studies that examine chronic disturbance, at the scale of the fishery, are considered more representative of commercial fishing practices (Rijnsdorp *et al.* 1998) and more likely to detect changes in marine communities. Changes detected in such long-term studies are, however, frequently confounded by natural fluctuations in the environment (Kenchington *et al.* 2001). Without adequately representative controls (unfished, protected areas), these changes in marine communities cannot be unequivocally attributed to fishing disturbances (Hall *et al.* 1993, Auster & Langton 1999, Jennings & Kaiser 1998, Kaiser 1998). It is thus clear that a combination of study approaches is necessary to make progress in understanding and distinguishing between changes attributed to natural fluctuations and fishing disturbances.

A long-term study (6 months) conducted by Kaiser *et al.* (1998) was unable to detect changes in megafaunal (> 10 mm) benthic communities as a result of a commercial beam trawl disturbance in mobile sediments, while stable sediments yielded a significantly altered assemblage. After a recovery period of six months, natural fluctuations had occurred in both habitats and the effects of the trawling disturbance were no longer evident. Similarly, de Wolf and Mulder (1985) were unable to provide accurate estimates of benthic species abundances in megaripple (highly mobile) environments because of the increased levels of natural disturbance and spatial variability within this type of habitat. Brylinsky *et al.* (1994) were unable to detect adverse effects of otter trawling over intertidal mud flats that are regularly exposed to large-scale disturbances, such as ice-scour, in the Bay of Fundy, Canada. A study conducted by Gibbs *et al.* (1980) in an estuary in south east Australia where commercial prawn trawling takes place, implemented a BACI experimental design to test for trawl induced impacts. Three treatment sites and one control site were sampled before, after one week and at the close of the commercial trawl season to investigate impacts of the otter trawl fishery. Small differences in macrobenthos were detected and attributed to the differences in sediment composition, faunal patchiness and natural seasonal changes. The study concluded that otter prawn trawling occurring in most New South Wales estuaries does not cause detectable alterations in the macrobenthic fauna assemblages (Gibbs *et al.* 1980). More recently, a study conducted by Drabsch *et al.* (2001), also in Australia (Gulf St. Vincent, Adelaide), examined the impact of experimental trawling on infaunal populations, with reference to the commercial prawn otter trawl fishery. Once again, a BACI experimental design was implemented and commercial gear used to trawl in areas that had not been trawled for fifteen years. This study was also unable to detect significant changes in the benthic infaunal assemblage that could unambiguously be attributed to trawling impacts. Drabsch *et al.* (2001) concluded that the light-weight gear used by the prawn commercial fishery and low levels of trawling, combined with the amount of natural temporal and spatial variability resulted in no clear trawling impacts being evident on infaunal assemblages. In conjunction with the study conducted by Drabsch *et al.* (2001), Tanner (2003) examined the impact of the prawn trawl fishery on sessile benthic epifauna in the same location. Tanner (2003) found an overall negative effect on the epifauna, with a 28% decrease in abundance within two weeks after the trawling impact and further declines of up to 8% in the following 2-3 months. The species found to be most affected were ascidians, sponges, bryozoans and the bivalve *Pinna bicolor*.

The lack of available representative areas, protected from the impacts of fishing (either legally or *de facto*), are often considered to hinder appropriate design of scientific experiments aimed at determining the effects of demersal fishing (Hall *et al.* 1993, Auster & Langton 1999, Jennings & Kaiser 1998, Kaiser 1998). Indeed, in the southern Benguela there are no representative areas protected from demersal trawl fishing activities and studies in this region were limited in terms of comparisons with unfished control sites. In the present study, a long-standing prohibition on trawling shallower than 60 m depth in the Oslofjord, in effect, provides untrawled areas of representative habitat in which experimental investigations can be conducted. The presence of unfished control sites in an otherwise fished habitat facilitated investigation of the effects of demersal trawling in a soft sediment habitat using a BACI (Before-After Impact-Control) experimental design. Selecting two areas in close range of each other, each having a control and impact site, strengthened the experimental design to detect changes resulting from a disturbance (Underwood 1991 & 1992). All sites were sampled at 35 m depth with sediment classified as clayey-silt and no significant differences in organic carbon content ($p>0.1$, d.f.=8). Natural disturbances occurring during the study were likely to have been equal in all sites, thereby minimizing the chance of a Type I error (incorrectly rejecting the null hypothesis). Furthermore, infauna were monitored for nine weeks after the impact to assess for any recovery. It is most likely that the significant differences detected by PERMANOVA routines between the areas and among sampling events were as a result of natural variation rather than trawl-induced disturbance.

Initially, the most likely explanation for a failure to detect any significant changes in faunal assemblages as a result of trawling was that the spatial scale, temporal intensity and gear type did not represent the scale of the commercial fishery (see Thrush *et al.* 1998). A study conducted in 2002 in an area adjacent to that sampled in this study, examined infaunal assemblages within the commercial trawl zones in comparison to representative untrawled sites (Fleddum *in prep*). The 2002 study investigated the impacts of trawling at the scale of the fishery but also yields results that indicate no significant changes in the infaunal assemblages that can be attributed to trawling impacts (Fleddum *in prep*.). This leads to the unexpected, but plausible consideration that the Oslofjord shrimp trawl fishery, operating at the current spatial scales and intensity, with the comparatively light-weight otter-trawl configurations used, does not cause sufficient physical disturbance on the seafloor to result in detectable changes in the infaunal assemblages.

Effects of the Oslofjord shrimp trawl fishery on emergent, sessile epifauna, however, remain unquantified. The substantial biomass of epifauna removed with only four passes of the trawl gear in this study (Fig. 4.3), which was small and light-weight compared to commercial gear, indicates that large proportions of epifauna are likely to have been removed at the onset of commercial trawling activities in the fjord as early as 1898 (Seaton & Suomela 1958). Long-lived, sessile, slow-growing species vulnerable to the effects of trawling (e.g. cold-water corals, gorgonians, basketstars) have been recorded both historically and more recently in certain areas of Oslofjord (Rosenberg *et al*. 2005, Roberts *et al*. 2009). Such emergent epifaunal species were however not encountered during sampling conducted at untrawled areas in this study. An alternative hypothesis for the failure to detect significant changes in faunal assemblages in this study may be as a result of the untrawled area not yet having recovered from trawling disturbance inflicted prior to depth restrictions being implemented in 1984. Epifaunal species are known to provide habitat structure for other mobile species, many of which may be prey for important commercial species (Auster *et al*. 1997, Sainsbury *et al.* 1997, Collie *et al*. 2000b). The major effects of fishing on epifaunal assemblages include modification of substrata and removal of biogenic taxa, with a consequent decline of fauna associated with them (Jennings & Kaiser 1998). Slow recovery of epifaunal species at these high latitudes and low temperatures in areas protected from trawling may inhibit the recovery of infaunal assemblages.

Conclusion

The results of this study of benthic infauna show no immediate effects attributable to a once-off trawl induced disturbance at two sites in the outer Oslofjord, Norway. Further monitoring of the sites for up to nine weeks post-impact also revealed no meaningful changes in benthic infaunal assemblages. Whilst it is possible that the small-scale spatial disturbance of this study may not have provided an impact comparable with that of the commercial fishery, it is also possible that the current scale of the fishery does not disturb the habitat more than natural disturbances. However, the impact of commercial trawling on epifauna, which is more likely to be directly affected by the passing trawl net, may hinder recovery of infaunal assemblages that rely upon hard, structure-forming micro-habitats..

Chapter Five

Investigating long-term changes in demersal fish assemblages on the west coast of South Africa: 1986 to 2009

INTRODUCTION

The South African demersal trawl fishery commenced in the early 1900s, targeting two Cape hake species, *Merluccius capensis* (shallow water hake) and *Merluccius paradoxus* (deep water hake). Initially the fishery concentrated close to Cape Town (Lees 1969) with the areas around Dassen Island and Cape Columbine being reported as the "greatest of all known hake fishing grounds" (Irvin and Johnson, 1963). After World War II (1950), annual hake landings were approximately 50 000 tons (Fig. 5.1). In the early 1960s, combined efforts of South African and foreign (Soviet Union, Japanese and Spanish) trawlers escalated the total annual landings of hake to 160 000 tons with a peak in 1972 of nearly 300 000 tons (Fig. 5.1). This represented a substantial over-exploitation of the resource (Payne 1989) and anecdotal information suggests that illegal practices, such as the use of net liners, added to the pressure on the hake stocks. In 1972 the International Commission for the Southeast Atlantic Fisheries (ICSEAF) was established and in 1975 implemented a minimum mesh size of 110 mm, a monitoring system (observer programme) and allocated quotas to member countries (Payne 1989). In 1977 South Africa declared a 200-nautical mile economic exclusion zone (EEZ, Fig. 5.1), preventing the majority of foreign fishing effort within this zone (Payne 1989, Payne & Punt 1995). South Africa began rebuilding its hake resource with the introduction of conservative total allowable catch (TAC) limits in 1978 and formal separation of the fishery on the southeast coast into inshore and offshore sectors at the 110 m contour, targeting *M. capensis* and *M. paradoxus* respectively (Fig. 5.1).

In 1983 an experimental kingklip-directed (*Genypterus capensis*) longline fishery was introduced in South Africa (Griffiths *et al.* 2004) specifically targeting this species on the west and south coasts. By 1986 the kingklip resource began to decline and by 1991 all demersal longline fishing was terminated (Punt & Japp 1994, Griffiths *et al.* 2004). In 1994, a hake-directed experimental longline fishery was introduced with a maximum catch allowance of 4000 tons per annum (R. Leslie, MCM, pers. comm.). In 1999 the experimental longline fishery was replaced by a commercial hake-directed longline fishery, being managed as part of the total hake resource, with 10% of the global hake TAC being shared between hake handline and longline (Fairweather *et al*. 2006). The experimental longline fishery was largely restricted to untrawlable grounds, but with the expansion of the commercial longline fishery and decline in catch rates on untrawlable grounds, the longline fishery moved into traditional trawl grounds (R. Leslie, MCM, pers. comm.). With an increase in fishing area overlap frequent conflict between the trawl and longline fishing sectors in South Africa is reported (Fairweather *et al.* 2006). Longliners are known to target large, adult hake, which are usually females (Payne 1989). Large females are believed to have greater reproductive success than their smaller, younger counterparts (Berkley *et al.* 2004, Field *et al*. 2008). Longliners are able to exploit rough grounds which are proposed to have provided refuge for a proportion of the stock (Fairweather *et al*. 2006, Yemane *et al.* 2008). Conflict between the sectors is escalating with longliners increasingly fishing over soft sediment habitats and deeper waters, such as those targeted by trawlers. Since 2000 the hake resource has started showing signs of depletion and the precautionary management measures of a reduction in the TAC by between 2000 and 4000 tons have been implemented over subsequent years.

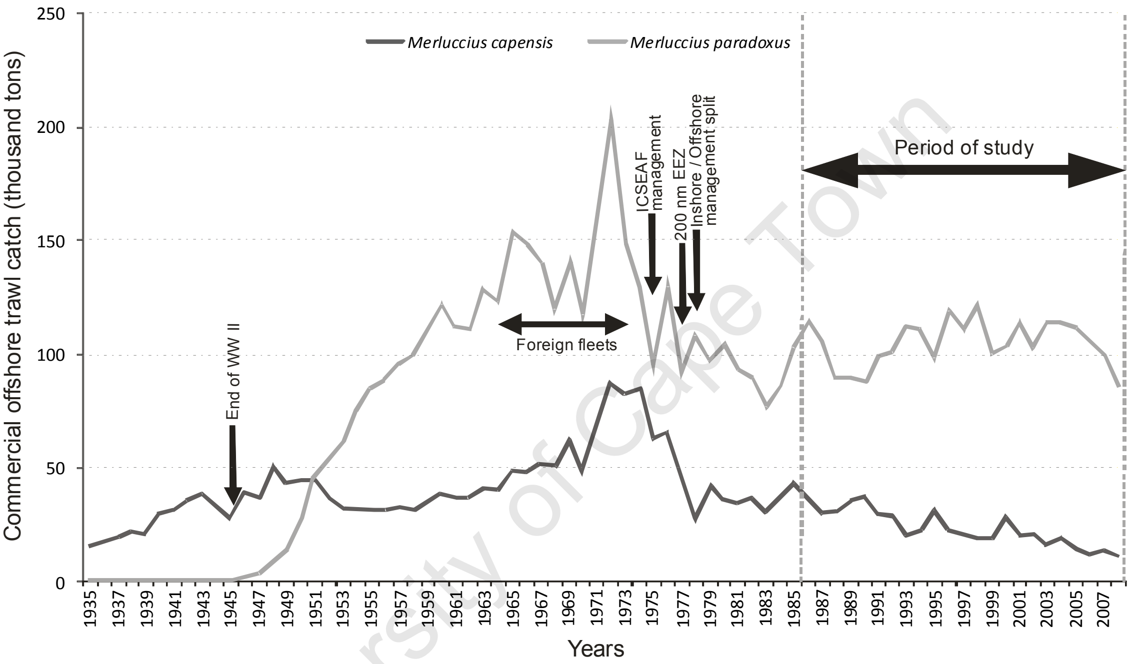


Fig. 5.1. Estimated offshore trawl catches of South African hake from the south and west coasts combined. Arrows indicate time frames mentioned in the text. The period investigated by this study is indicated from the vertical dashed line. Data source: Marine & Coastal Management, branch of Department of Water and Environmental Affairs.

Historically the commercial fishery did not distinguish between the two hake species and they were assessed and managed as a single resource (Shannon *et al*. 2006). Introduction of the longline fishery in 1994, which preferentially targets *M. capensis*, changed the relative contribution of the two hake species in commercial catches. Species-specific assessment models were necessary for effective management, but these required species-specific catch estimates from previous years (Geromont *et al*. 1995). Research survey data were used to define the relationship between depth and species proportion (adult *M. paradoxus* occurring deeper than *M. capensis*, Payne & Punt 1995) to estimate the necessary historical catches of each species separately for inclusion in species-specific assessment models (Geromont *et al*. 1995). More recently, models were refined by incorporating size information and a year effect (Gaylard & Bergh 2004, Rademeyer & Butterworth 2007). Figure 5.1 illustrates the commercial offshore hake trawl catches for west and south coasts of South Africa combined, from 1935 until 2008. Until 1977, the split by species (*M.capensis* vs. *M. paradoxus*) assumes that the proportion of *M. capensis* caught follows a logistic function over this period. From 1978 onwards, the species split has been obtained by applying the size-based species proportion-by-depth relationships for the west and south coasts from research survey data, as developed by Geromont *et al.* 1995, Gaylard and Bergh 2004 and Rademeyer and Butterworth 2007.

Fishing affects the demersal fish community structure both directly and indirectly (Jennings & Kaiser 1998, Bianchi *et al*. 2000). Direct impacts include the selective removal of target species imposing subsequent influences on growth, mortality, production and recruitment (Jennings & Kaiser 1998). Indirectly, fishing removes non-target species through bycatch (Hall 1999) and can, in the case of demersal trawl fishing, modify habitats, resulting in changes in overall biomass, species composition, predator-prey relationships and size structure of the fish community (Dayton *et al*. 1995, Jennings & Kaiser 1998, Bianchi *et al*. 2000). The response of the fish community depends on life-history characteristics of individual species, trophic interactions and the type of habitat changes resulting from fishing activities (Jennings *et al*. 1999b, Bianchi *et al*. 2000).

Most fished marine ecosystems which have been studied for more than a decade show changes in the structure of fish communities over time (Jennings & Kaiser 1998). Several studies, conducted in various marine systems around the world, have detected changes in demersal fish community composition over periods of increasingly intensive fishing activity. Rijnsdorp *et al.* (1996) compared trawl survey data collected in the southern North Sea from the periods 1906-1909 and 1990-1995. Differences in trawl gear between the periods necessitated a swept area correction factor to be applied to allow comparison. Results showed reduced species diversity and evenness in the latter period as well as a shift towards smaller fish. Greenstreet and Hall (1996) compared data between periods 1929-1953 and 1980-1993 in regions of the north-western North Sea and Greenstreet *et al.* (1999) updated the data to include 1925 until 1996. These studies showed significant changes in the relative abundance of species and a reduction in species diversity between time periods and among different areas of the North Sea. Analysing the same data set, Jennings *et al*. (1999) examined life histories of species occurring and observed a relative decrease in the abundance of slower-growing, late-maturing species. Similarly, Suvapepun (1991) reported a substantial decline in the overall catch rates in the Gulf of Thailand trawl fishery, from 300 kg.h^{-1} in 1961 to only 54 kg.h^{-1} in 1983. The abundance of large, long-lived fish (e.g. rays) and several families of smaller fish (e.g. Leiognathidae, Gerreidae and Mullidae) decreased considerably over this time period. Yemane *et al*. (2004) investigated changes in linefish size and catch compositions from historic records in South Africa. This study showed a decline in the number of large size-classes and a change in catch composition over the 100-year period investigated. The severely overfished status of several predatory linefish was believed to influence the tropho-dynamic functioning of the ecosystem.

Roel (1987) investigated demersal fish communities on the west coast of South Africa from data collected during four research cruises conducted between 1984 and 1986, using a presence-absence index and hierarchical classification. The species composition of demersal fish communities was predominantly influenced by depth with two main communities separating at 380 ± 45 m, this depth representing the continental shelf edge (Roel 1987). The shallower shelf communities were variable between summer and winter months whereas the deeper communities were homogenous in species composition throughout the year. The seasonal variability in the shelf communities was considered likely to be as a result of environmental factors (Roel 1987), like low oxygen water that usually spreads inshore during the summer months (Monteiro & van der Plas 2006). The deeper communities also displayed latitudinal effects with some species only occurring in the northern areas of the study.

Many studies have reported significant changes in size composition of fished communities using a variety of size-based indicators (e.g. Rice & Gislason 1996, Haedrich & Barnes 1997, Greenstreet *et al*. 1999, Zwanenburg 2000, Graham *et al.* 2005, Piet & Jennings 2005, Yemane *et al.* 2008). An overall decrease in target species' size has generally been observed in fished communities, the cause of which has partially been attributed to the strong size selectivity of fishing activities. Yemane *et al*. (2008) investigated changes in size-based indicators of demersal fish communities from the south coast of South Africa from 1986 to 2003. Their study showed a decrease in the mean length, mean maximum length and the proportion of large fish over this time. Yemane and Leslie (in prep) also investigated changes in size structure of selected species of the South African west coast demersal fish community over the past 23 years (1985-2008) and detected an increasing dominance of smaller individuals. The mean length of the species investigated on the west coast has also decreased and the abundance of individuals < 20 cm in size increased. An increase in both the abundance of smaller size species and smaller sized individuals of some species is shown to have contributed to the observed shift in the size composition towards a community dominated by smaller sized individuals (Yemane & Leslie in prep).

Species extinctions are unlikely to result from the direct effects of fishing (Beverton 1990). Economic extinction usually occurs first and may discourage further exploitation (Jennings & Kaiser 1998). Reduced species diversity and genetic diversity within species, however, are likely to result from intense, long-term fishing activity (Jennings & Kaiser 1998). The effects of decreased species diversity are likely to become more significant over time scales longer than thus far measured. Species that are functionally similar in one environmental state may fulfil different roles within the environment should conditions change (Jennings & Kaiser 1998). Diverse systems are more likely to contain some species which can thrive during natural or anthropogenically induced perturbations and thus compensate for the loss of species resulting from the disturbance. Several species may be lost from the system with little short-term change in overall ecological function. However, as more and more species are removed, the system approaches a threshold where further removals will eventually lead to a shift in ecosystem structure or function (Jennings & Kaiser 1998). This can be illustrated by urchins proliferating in Kenyan and Caribbean reef systems subsequent to several species of urchin-eating fish being fished out, leading to reef habitat bioerosion (McClanahan & Muthiga 1988, Hughes 1994). Highly diverse systems are considered more likely to adapt and maintain ecosystem functionality with changing environmental conditions e.g. resulting from broad-scale climate change patterns (Jennings & Kaiser 1998, Folke *et al.* 2004, Bremner 2008).

The most severe, quantifiable effects of fishing activity on diversity and community composition occur at the onset of fishing or light fishing intensities (Jennings & Kaiser 1998, Pitcher 2000). Once systems enter a fished state, diversity, ecosystem function and overall production often remain relatively stable despite increasing fishing intensity (e.g. Jennings & Polunin 1996, Shannon *et al*. 2009). Modelling studies conducted in areas where intense fishing activity preceded investigations suggested little or no change in diversity or community structure (Shannon *et al*. 2009). If true measures of baseline conditions were obtainable, it is likely that all fished ecosystems would show significant decreases in, *inter alia*, species diversity. Within a fished community, late-maturing, slow-growing species with low reproductive outputs are considered to be more susceptible to the impacts of fishing than fast-growing species with early maturity (Pianka 1970, Jennings & Kaiser 1998, Stevens *et al*. 2000).

Regime shifts

Long-term ecosystem changes observed in the Benguela region have been classified as species alterations, species dominance shifts or regime shifts (Cury & Shannon 2004, Jarre *et al*. 2006). A regime shift may be defined in several ways, however, generally a regime shift can be considered to be a sudden change from a stable ecosystem state, acting over a large spatial scale, causing trophic restructuring which persists to allow an alternative stable ecosystem state to exist (de Young *et al*. 2004, Jarre *et al*. 2006). There are several agreed criteria that define regime shifts in the ocean. These include the duration of the shift being relatively short in comparison to the length of the actual regimes, and changes being recorded across a wide range of trophic levels and species that reflect the state of the ecosystem (de Young *et al*. 2004). Quantifying the state of an ecosystem is not a simple task and requires a combination of analyses, frequently including models and indicators. An indicator can be defined as a variable, pointer or index, whose position or trend in relation to reference points reflect the present state and dynamics of the system (Jarre *et al*. 2006). Much research has recently been conducted on the applicability and types of quantitative ecosystem indicators that can be used to clearly identify the state of marine ecosystems (Rochet & Trenkel 2003, Daan *et al*. 2005, de Juan *et al*. 2009). It has been shown that community-based indicators, rather than single-species measures, are likely to best reflect ecosystem status (Fulton *et al*. 2005) and that a variety of indicators, used simultaneously, most effectively capture several key functional groups (Jarre *et al*. 2006).

Dramatic shifts in fish community structure have frequently occurred in highly productive clupeoid populations in upwelling ecosystems (Jarre *et al.* 1998, Jennings & Kaiser 1998, de Young *et al*. 2004, van der Lingen *et al.* 2006). External pressures on species, anthropogenic or natural, are likely to be of great significance, particularly over the time at which a regime shift is actually taking place and can magnify and accelerate shifts (Jennings & Kaiser 1998, Rothschild & Shannon 2004, Shannon *et al.* 2004). At the time when species are undergoing a regime shift, they may be more sensitive to pressures, including fishing, and the outcome of the imminent regime shift may be influenced (Rothschild & Shannon 2004). Cury and Shannon (2004) investigated the possibility of regime shifts having occurred in the northern and southern Benguela regions. They concluded that the fluctuations between sardine and anchovy dominance observed in the southern Benguela between the mid-1980s and 2000 did not affect several ecosystem levels and hence these changes were considered species dominance shifts rather than regime shifts. Persistent low levels of exploited fish catches and altered trophic level energy transfers observed in the northern Benguela ecosystem, however, indicate a clear regime shift to have occurred in the late 1980s and early 1990s in this ecosystem (Cury & Shannon 2004). More recently, Howard *et al*. (2007) investigated several biological, environmental and anthropogenic forcing variables in the southern Benguela ecosystem using a Sequential T-test Algorithm for Regime Shift (STARS) detection (Rodionov 2004). This study detected two major long-term regime shifts in the southern Benguela since the 1950s. The first change occurred during the 1960s and was believed to be largely as a result of intense fishing pressure along with some environmental changes. The second change occurred in the early 2000s as a result of environmental forcing (Howard *et al*. 2007). Robust shifts were detected by Howard *et al.* (2007) in 1991 and 2004/2005 in response to the environmental forcing variables of sea surface temperature (SST) and upwelling anomalies. There is little convincing evidence for observed shifts in pelagic fisheries being a result of fishing effects only (Shannon *et al*. 2004). Changes in pelagic species abundance may interact with pelagic stages (larvae or juveniles) of certain demersal species in terms of predation, recruitment success and competition for food (Hislop 1996).

Regime shifts are likely to have profound effects on fisheries targeting those species influenced by the shift. A persistent eastward shift in small pelagic species occurred between 1996 (anchovy) and 2001 (sardine, van der Lingen *et al.* 2006). Reasons for the spatial shift are not clear, but it is hypothesized that increasing fishing pressure on the west coast combined with favourable environmental conditions on the south coast are likely to have driven this eastward shift (Coetzee *et al.* 2008). As a result, the resource, and thus fishery, are now concentrated on the south coast of South Africa (Coetzee *et al*. 2008). Similarly, a major shift in the west coast rock lobster (*Jasus lalandii*) resource from the traditional fishing grounds on the west coast of South Africa to more southern grounds was observed between the late 1980s and early 1990s (Cockcroft *et al.* 2008). Despite studies focused on the variability of the physical environment, and other changes in this valuable resource (reduced somatic growth and increased lobster walkouts), the causes for the eastward shift in rock lobster abundance remain poorly understood. It is currently not known whether there are any common causes between the eastward shift in small pelagic and benthic rock lobster resources observed in the southern Benguela (Cockcroft *et al*. 2008).

South Africa's deep-sea hake fishery primarily targets *M. paradoxus* in waters of 200 m to 600 m depth off the west coast of southern Africa (Wilkinson & Japp 2005) and forms the focus of this study. The South African fishing grounds for this species extends in a continuous band from approximately 300 m depth off Port Nolloth on the west coast to the southern tip of the Agulhas Bank (Fig. 5.2). Technological advances in fishing and vessel equipment since 1950 have allowed the fishery to expand to depths of 1000 m at times (Griffiths *et al.* 2004, Fairweather *et al*. 2006). The deep-sea trawl vessels comprise mostly stern trawlers of approximately 50 m length, making use of otter-trawl configurations with trawl doors weighing an average of 1.8 tons each (Wilkinson & Japp 2005). In addition to the trawl doors (otter boards), the main warps, bridal wires, footrope and occasionally the net, all make contact with the benthic substrate (Wilkinson & Japp 2004).

Annual demersal research surveys have been conducted since 1986 by Marine and Coastal Management (Department of Water and Environmental Affairs), primarily to monitor the hake stock status for management and collect biological information for several other key species. Through interrogation of this long-term (24 years) demersal research database, this study aims to detect changes at the species, community or ecosystem level in fish diversity and community composition in a fished ecosystem. Furthermore, a decrease in the abundance (measured through biomass) of late-maturing, slow-growing species is hypothesized, with either no change or an increase in faster-growing, early-maturing species.

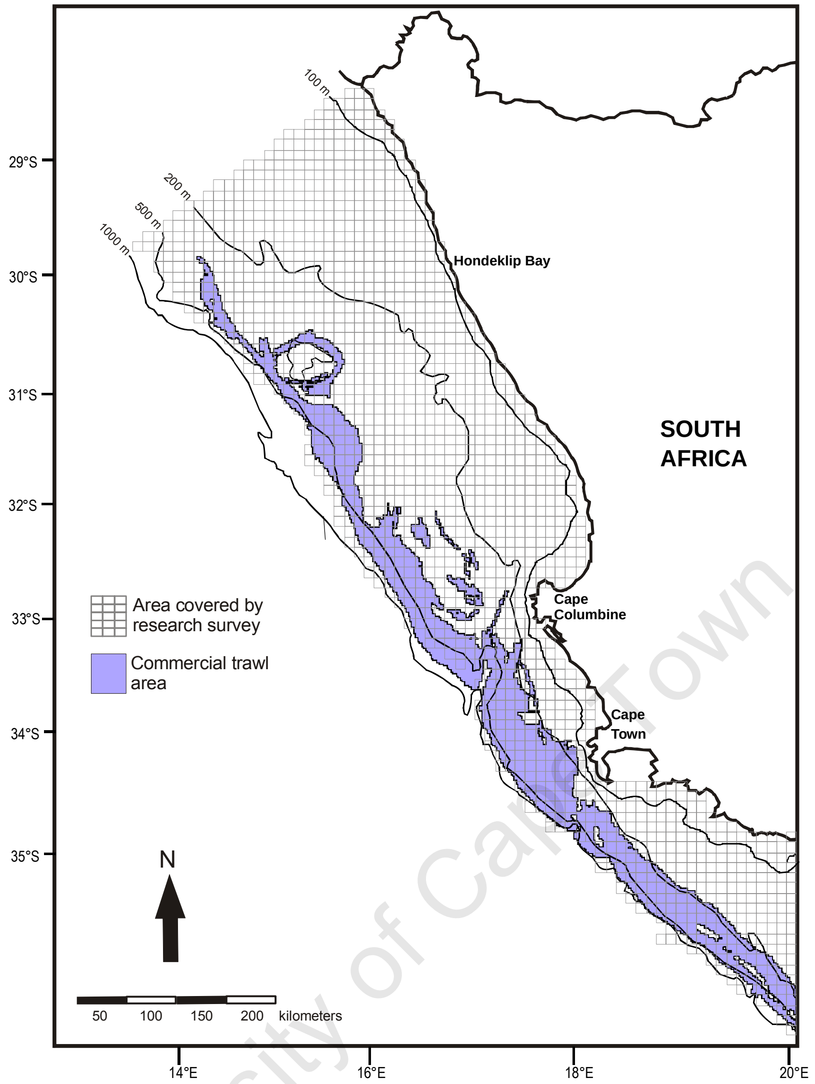


Fig. 5.2. West coast area covered by annual demersal research trawl survey and commercial trawl area. Data source: Marine & Coastal Management, branch of Department of Water and Environmental Affairs and Wilkinson & Japp (2005).

METHODS

Data analysed in this study were collected by Marine and Coastal Management (MCM), a branch of the South African Department of Water and Environmental Affairs, during annual research trawl surveys on the west coast of South Africa (westwards of 20 °E, Fig. 5.2). This study primarily investigated data collected during austral summer (January/February) surveys from 1986 until 2009. Four years of winter (June/July) surveys were also conducted (1986, 1987, 1988 and 1990) providing a subset of data for seasonal analysis (summer-winter). All data analysed in this study were collected using the research vessel FRS *Africana*. The trawl gear configuration of this vessel was altered in May 2003. All west coast demersal research surveys analysed, including that of 2003 (survey conducted in January 2003), used trawl gear consisting of a two panel 180 ft German otter trawl rig having approximately 120 m door spread (2 m vertical and 26 m horizontal mouth opening) with 75 mm mesh codend, 35 mm mesh liner, a rope-wrapped chain footrope and 1.5 ton WV otter boards (Yemane *et al*. 2008). From January 2004 (excluding 2006 when the old gear was used again) a four panel 180 ft German otter trawl rig was used on the west coast surveys, with a 4 m vertical mouth opening, a narrower door spread (~ 60 m) and footrope consisting of rubber rollers (R. Leslie, MCM, pers. comm.). The changes in the trawl gear resulted in a greater portion of the water column being sampled (increased vertical mouth opening), reduced herding (narrower door spread) and reduced flatfish sampling as a result of the modified footrope (R. Leslie, MCM, pers. comm.). The research survey in 1989 was not completed as the vessel encountered technical problems. During 2000 and 2001 the annual demersal research surveys were conducted by the RV *Dr Fridtjof Nansen* and data from these years are excluded from this study due to differences in trawl gear configurations.

All trawl durations were 30 minutes where possible, but were sometimes reduced due to rough grounds. In all cases, catch biomass data (in kilograms) were standardized to 30-minute tows. An assumed constant towing speed of 3.5 knots and mouth width of 26 m are used to calculate the swept area of a 30-minute tow as 0.0246 square nautical miles using the following equation:

Swept area = [speed x duration/60] x [mouth width/1852]

The catch biomass (in kilograms) was standardized by dividing by the swept area to obtain a mean density of fish with units of kilograms per square nautical miles (kg.nm^{-2}). Standardized data in kg.nm^{-2}, referred to hereafter as fish density, were analysed using multivariate techniques, as described below.

The total area of continental shelf forming part of the research surveys up to the 500 m isobath on the west coast of South Africa is ~ 32 000 nm^2 (Fig. 5.2). Since 1986, the annual west coast demersal research surveys have covered 76% of the 5'x5' grid blocks spanning the continental shelf (Leslie & Fairweather 2008). The randomly stratified survey design targets five depths zones; 0-100 m, 101-200 m, 201-300 m, 301-400 m and 401-500 m and aims to obtain the same density of stations within each depth zone (i.e. homogenous sampling across the shelf). On rare occasions a few trawls (0.3%) extended deeper than 500 m (e.g. 2004 to 2008, Table 5.1), however, for the purpose of this study, these data were analysed as part of the 401-500 m depth category. Approximately 100 trawls are conducted during each annual survey. The entire catch of the majority of trawls (99%) was sorted to the lowest practical taxon and weighed. Trawls greater than 4 tons (1%) were considered too large to be fully sorted on deck and a subsample of the catch was processed, with the remainder of the catch being screened for large individuals or rare species. The abundance of major commercial or specific fish species of interest were recorded from each catch, however, abundance measures of the full species composition are not recorded or estimated as part of the annual surveys.

The density of all species retained in the net were collated for each trawl and averaged within each 100 m depth zone category per survey. The density averages were further split along a latitudinal gradient at 33°S (Cape Columbine) yielding averaged density values per 100 m depth zone, per survey within a northern and southern region of the west coast of South Africa (Fig. 5.2). The continental shelf narrows considerably near Cape Columbine (33°S, Fig. 5.2) with the steeper continental shelf being closer to the coastline in the southern region. It has been suggested that the demersal fish communities differ across a latitudinal gradient in this region (Roel 1987). Based on this rationale, differences in fish communities on either side of Cape Columbine were investigated.

The 0-100 m depth zone was consistently poorly sampled in the southern region (Table 5.1) with more than 50% of surveys failing to obtain trawls within this depth zone. The reason for under-representation within this depth zone in the southern region is due to unsuitable trawl habitat (rocky ground) dominating the shallow depths in this region (Dingle *et al.* 1987, R. Leslie, MCM, pers. comm.). Instances where the 0-100 m depth zones were successfully sampled tend to repeatedly target one or two suitable locations within the region, thereby eliminating the random nature of the design. From 2002 the 0-100 m depth zone therefore no longer forms part of the sample design in the southern region. For this reason, the fish densities from the 0-100 m depth zone are eliminated from further analyses in this study, except for spatial representation in the multi-dimensional scaling plot (Fig. 5.3). Commercial trawl activities along the west coast do not occur in waters shallower than 100 m and are unlikely to have direct influence on community composition in this depth zone. It is, however, acknowledged that impacts in deeper waters may indirectly affect shallow water communities (e.g. low oxygen waters, spawning/recruitment, predation). Hamukuaya *et al.* (1998) showed that low oxygen waters inshore on the central and northern Namibian shelf displaced juvenile hake (*Merluccius capensis*) into deeper waters, subjecting them to increased mortality from predation by larger hake and commercial trawling.

Inconsistent expertise in identification can result in different certainty levels of species identification in long term data series. Depending on the scientific expertise aboard the vessel at the time of sampling, the accuracy of species identification for different groups may vary. Where such inconsistencies occurred in this study, the higher common taxonomic order was adopted (i.e. some species were analysed at the genus or family level rather than species level, e.g. *Caelorynchus braueri* was combined with *Caelorynchus* sp.).

Table 5.1. Details of trawl data with respect to number of trawls per region, depth zone and environmental parameters measured. Numbers in parenthesis indicate the number of stations for which environmental parameters were measured. Surveys conducted during winter months are shaded in grey, (N) = new trawl gear configuration.

		Number of stations in each region		Number of stations in northern region each depth range					Number of stations in southern region each depth range									
Date	Number trawls	North of 33 °S	South of 33 °S	0-100	101-200	201-300	301-400	401-500	0-100	101-200	201-300	301-400	401-500	Depth range (m)	Near seabed Temperature °C	Near seabed Salinity (PSU)	Near seabed Oxygen (ml/L)
Jan/Feb-86	92	59	33	5	24	15	9	6	0	14	10	3	6	71-515	4.55-11.66 (122)	34.39-35.05 (122)	-
Jul-86	86	53	33	5	20	10	10	8	0	16	11	4	2	55-495	4.31-11.27 (81)	-	-
Jan-87	91	64	27	7	29	17	5	6	0	13	8	3	3	62-480	5.08-10.38 (98)	34.04-34.87 (98)	-
Jun/Jul-87	75	51	24	3	20	12	9	7	0	11	9	2	2	81-480	5.2-10.75 (78)	34.4-34.93 (78)	-
Feb-88	91	63	28	7	26	18	5	7	1	13	9	2	3	77-520	5.53-9.7 (103)	-	-
Aug-88	81	58	23	6	23	13	12	4	1	10	7	2	4	39-500	-	-	-
Jan-90	86	62	24	7	26	19	5	5	1	11	7	4	1	45-468	3.99-10.99 (84)	34.37-34.79 (84)	-
Jul/Aug-90	89	67	22	10	27	17	7	6	2	8	7	2	3	30-500	4.52-14.35 (66)	-	-
Jan-91	111	80	31	6	39	21	7	7	0	14	9	6	2	80-500	5.05-10.5 (59)	34.37-34.90 (59)	-
Jan-92	105	75	30	7	31	20	12	2	3	15	7	5	3	45-498	3.80-11.53 (126)	34.30-34.86 (126)	-
Jan-93	87	53	34	4	13	18	12	6	3	15	10	2	4	21-490	6.5-10.95 (77)	34.40-34.91 (77)	
Jan-94	102	69	33	6	29	16	11	7	4	16	7	3	3	38-500	4.77-10.68 (98)	34.35-34.88 (98)	-
Jan-95	121	87	34	9	37	23	10	8	4	16	7	4	3	43-500	3.06-10.47 (108)	-	-
Jan-96	96	72	24	7	32	17	9	7	1	11	9	2	1	27-500	5.66-9.79 (95)	-	-
Jan-97	94	62	32	6	24	19	5	8	1	14	8	4	4	30-500	3.16-10.05 (80)	34.38-34.83 (80)	-
Jan-99	89	61	28	5	28	15	8	5	1	12	7	4	4	47-505	4.84-9.85 (73)	34.33-34.78 (73)	-
Jan-02	111	79	32	10	29	20	11	8	0	17	9	1	5	22-500	4.55-12.73 (110)	34.35-34.95 (110)	0.06-5.09 (110)
Jan-03	97	74	23	7	27	21	10	9	0	13	7	2	1	20-486	5.96-10.01 (88)	34.41-34.78 (88)	06-4.17 (88)
Jan-04 (N)	105	75	30	7	15	21	9	6	0	32	8	3	4	24-504	5.96-10.41 (115)	34.4-34.85 (115)	0.04-4.77 (115)
Jan-05 (N)	113	83	30	7	34	21	12	9	0	14	9	3	4	50-539	5.07-10.44 (100)	34.36-34.84 (100)	0.21-5.82 (100)
Jan-06	98	71	27	7	30	18	8	8	0	13	8	3	3	52-528	5.43-10.46 (74)	34.35-34.82 (69)	1.1-4.35 (74)
Jan-07 (N)	102	76	26	9	29	21	10	7	0	13	7	2	4	54-615	5.04-10.36 (96)	34.32-34.8 (96)	-
Jan-08 (N)	105	79	26	8	31	21	11	8	0	12	7	3	4	58-608	4.59-10.47 (88)	34.32-34.82 (88)	-
Jan-09 (N)	108	83	25	7	35	23	9	9	0	11	6	3	5	47-486	6.69-9.87 (96)	34.39-34.88 (96)	0.7-4.73 (96)
Total shelf area nm^2		23958	8040	2087	10095	6440	3113	2223		4048	2088	1107	797				

Demersal trawl sampling gear is not considered appropriate to accurately reflect biomass availability of pelagic species (e.g. sardine, anchovy, red-eye round herring, and mackerel). Mesopelagic fish species having a small adult body size (e.g. lantern fish and light fish) easily pass through the mesh and their abundance is therefore not considered appropriately sampled by means of demersal trawl gear. There is also some uncertainty over the sampling representivity for several demersal species known to rise off the seabed at times (e.g. hake). Analysis of fish community composition as a whole would, however, lose some meaning with each selected species being eliminated on the basis of their proposed availability to the sampling gear. For these reasons, initial analyses conducted in this study included all species recorded in the net and thereafter, data were re-analysed excluding small pelagic species (*Sardinops sagax, Engraulis encrasicolis* and *Etrumeus whiteheadi*), mid-water species (*Trachurus capensis* and *Thyrsites atun*) and mesopelagic species belonging to the families Myctophidae and Photichthyidae. Where results from the two data sets differ in their interpretation, they are discussed. In general, the results presented in this study reflect analyses excluding small pelagic, mid-water and mesopelagic species.

Spatial analysis (depth and latitude)

Differences in species composition between northern and southern regions and among depth zones were tested using the species densities of summer research trawl surveys with a MDS plot spatially representing the data. Data were 4th root transformed to down weight the excessive contribution by dominant species (Field *et al*. 1982) and the Bray-Curtis measure of (dis)similarity used to compare among samples. PERMANOVA analyses (permutational multivariate analysis of variance) were used to test for significant differences in community structure among years, regions and depth zones, excluding the 0-100 m depth zone (as discussed above). Where differences or interactions were significant, pair-wise permutation tests were used to further explore these differences. The crossed sample design contained the factors “years” (random), “regions” (fixed) and “depth zones” (fixed). The factor “years” was treated as random as they were not considered to represent any particular chosen state and the aim of the analysis was to measure the kind of variability across the years without being concerned with differences between individual years (Anderson *et al.* 2008). In addition, to test for significant differences among year groups (fixed factor, as defined by subsequent analyses), between northern and southern regions (fixed factor) and among depth zones, main effects and pair-wise PERMANOVA analyses were conducted. Similarity of percentages (SIMPER) analysis was used to assess which species contribute most to differences observed between regions and among depth zones. The SIMPER analysis decomposes the average Bray-Curtis dissimilarities (after 4th root transformation) into percentage contributions from each species and lists them in decreasing order of contribution (Clarke & Gorley 2006).

Temporal analysis (seasonal and annual)

Seasonal differences in species composition were tested using data from four years of summer and winter surveys (1986-1988 & 1990). A cluster dendrogram and multi-dimensional scaling (MDS) plot were used to spatially assess the data. PERMANOVA was used to test for significant differences in fish assemblages between summer and winter surveys. The sample design was crossed with factors of "years" (random), "seasons" (fixed), "regions" (fixed) and "depth zones" (fixed). Pair-wise permutation tests were used to explore any differences between interactions.

To test for species community composition changes among years from 1986 until 2009, the total average species densities from each year were calculated, grouped using a cluster dendrogram and MDS plot. *A posteriori* pair-wise PERMANOVA analysis was used to test for significant differences among year groups identified by the dendrogram and MDS plot. Similarity of percentages (SIMPER) analysis was used to identify which species contribute most to differences observed among the year groups.

Environmental variables

Water temperatures (°C) were recorded a few meters above the seabed during all surveys. Salinity (PSU) and dissolved oxygen (ml/L) parameters were less consistently recorded with salinity being measured during 74% and oxygen during 30% of the surveys (Table 5.1). The patchiness of environmental data made it difficult to assess the influence of these variables with respect to changes in assemblages observed, however, the influence of temperature (available for all surveys) on community assemblages was included as a covariate in a PERMANOVA analysis. The influence of environmental variables (bottom temperature, salinity and oxygen) on fish community composition were assessed using a subset of data for which all three variables were available (2002-2008, Table 5.1) using a distance-based linear model (DISTLM, selection criteria "AIC" and "Best" procedure). DISTLM partitions the variation in data distribution according to a multiple regression model (based on predictor variables), as selected by the user (e.g. forward, stepwise, best fit etc). The "Best" procedure (examines the value of the selection criterion for all possible combinations of predictor variables) and AIC criteria (Akaike's Information Criterion) options (Anderson *et al*. 2008) were used in this study. Temperature and salinity were strongly correlated (r = 0.98), thus salinity was excluded from the model (Anderson *et al*. 2008).

To investigate the influence of surface oceanographic factors on the demersal fish community composition, sea surface temperature (SST) and upwelling index anomalies were assessed within the southern Benguela region. Oceanographic data were obtained from the Extended Reconstructed Sea Surface Temperatures analysis (ERSST v2, Smith & Reynolds 2004) for two locations, namely 32°S 18°E and 30°S 16°E (courtesy of Dr. C. Roy, Institut de recherche pour le développement , France). Average monthly data from 1985 until 2005 were obtained for December (the month prior to research cruises) and January (the month during which research cruises were usually conducted). The influence of oceanographic variables on annual fish community composition (density kg.nm-2) was investigated using a distance-based linear model (DISTLM, selection criteria "AIC" and "Best" procedure).

All multivariate analyses were conducted using PERMANOVA+ add-on for PRIMER v6 (Clarke & Warwick 2001, Clarke & Gorley 2006, Anderson *et al*. 2008) after mean fish density was 4th root transformed and Bray-Curtis similarity matrices calculated.

Temporal analysis (regime shifts)

Regime shift analyses of the demersal fish community were conducted using Sequential T-test Algorithm for Regime Shifts (STARS) detection (Rodionov 2004). Comparison of results obtained in this study with those of Howard *et al.* (2007) was desirable. For this reason model parameters of STARS used in this study were similar to those used by Howard *et al.* (2007). The STARS algorithm tests each new observation (data point) for a significant difference from the mean of the current regime (as determined by previous observations) under the statistical criteria of a Student's t-test. If the current value is determined to be greater or less than the critical value of the current regime mean, then the value (year) is marked as a possible change point. Subsequent observations are similarly tested to confirm this change point as a new regime or simply an outlier. The testing procedure calculates a Regime Shift Index (RSI) which represents a cumulative sum of normalised anomalies relative to the critical level (Rodionov 2004). A detailed description of the STARS algorithm is provided by Rodionov (2004) and summarised by Howard *et al.* (2007).

The cut off length (l, years) determines the minimum length of regimes for which the magnitude of the shifts remains intact (Rodionov 2004). Regimes that are longer than the cut-off length will be detected, but the probability of detecting regimes shorter than the cut-off length decreases proportionally to their length. Regimes shorter than the cut-off length may still be detected if the shift is sufficient in magnitude (Rodionov 2004). Demersal fish data were only available for a total period of 24 years, this being considerably shorter than most data sets investigated by Howard *et al.* (2007). Cut off lengths of 5 and 7 years (as indicated by cluster analysis and MDS results) were considered appropriate for testing of the demersal fish data in this study.

The significance level is the maximum level at which a new regime is detected from shifts in the mean (Rodionov 2004). The lower the significance level, the larger the magnitude of the shift required in order to be detected. Howard *et al.* (2007) investigated shifts at significance levels of 5% (p=0.05) and 10% (p=0.1) and concluded that the 10% level was more appropriate to compensate for the large interannual variability displayed by the noisy time-series. Similarly, significance levels of 5% and 10% were investigated in this study.

Outliers in the data may prevent the average from representing the mean value of a regime and may significantly affect the results of the regime shift detection (Huber 2005). To account for outliers, a Huber's parameter is applied which controls the weight assigned to outliers and thus the magnitude of the average values of each regime (Rodionov 2004). Howard *et al*. (2007) tested the influence of Huber's parameter values of H = 1, 3 and 6, and concluded that there was negligible difference among results and therefore selected H = 1 throughout their study. The same rationale was applied to this study, with Huber's parameter values of 1, 3 and 6 yielding negligible differences at the cut-off length of 5 years and 10% significance. Results are reported for a Huber's parameter value of 1 only in this study.

Time series data frequently show serial correlation (red noise), however, STARS assumes that there is no auto-correlation (Howard *et al.* 2007). Prior to STARS analyses, serial correlation can be removed using a "prewhitening" method. Following methodology used by Howard *et al*. (2007), a prewhitening method of IP4 (inverse proportionality with four corrections), was used in this study. This prewhitening method involves subsampling and bias correction of the least-squares estimate of the serial correlation (Rodionov 2006). Shifts that are detected in a prewhitened time series are smaller in magnitude than those detected without prewhitening, under "strait" analysis (Rodionov 2006). All variables (species) in this study were analysed straight and prewhitened under all model parameters described above (cut off length, significance level and Huber's parameter), corresponding to methods employed by Howard *et al*. (2007). Prewhitened results can be considered to be more robust.

All demersal fish species (excluding small pelagic, mesopelagic and mid-water species) occurring in more than 10% of years surveyed (i.e. species occurring in more than two annual surveys) were selected for STARS analysis, resulting in 97 (56%) species (variables) being analysed for regime shifts. If STARS analysis detected a shift (either straight or prewhitened) in more than 50% of model settings (cut-off lengths, significance levels, Huber's parameter, straight and prewhitened) for a species, the shift was considered robust and likely to reflect a true long-term shift for the purposes of this study.

RESULTS

Spatial analysis (depth and latitude)

An MDS plot of fish community composition distribution between northern and southern regions and among all five depth zones between 1986 and 2009 shows separation of regions along the vertical axis and depths along the horizontal axis (Fig. 5.3). PERMANOVA analysis of data from summer surveys only (see temporal analysis below) and excluding the 0-100 m depth zone (as discussed above) show significant differences between years, regions, depth zones and the interaction between regions and depth zones (Table 5.2). Pair-wise analysis of the region and depth zones interaction shows significant differences in community assemblages between northern and southern regions within each of the four depth zones (t=2.74 - 5.64, p = 0.0001).

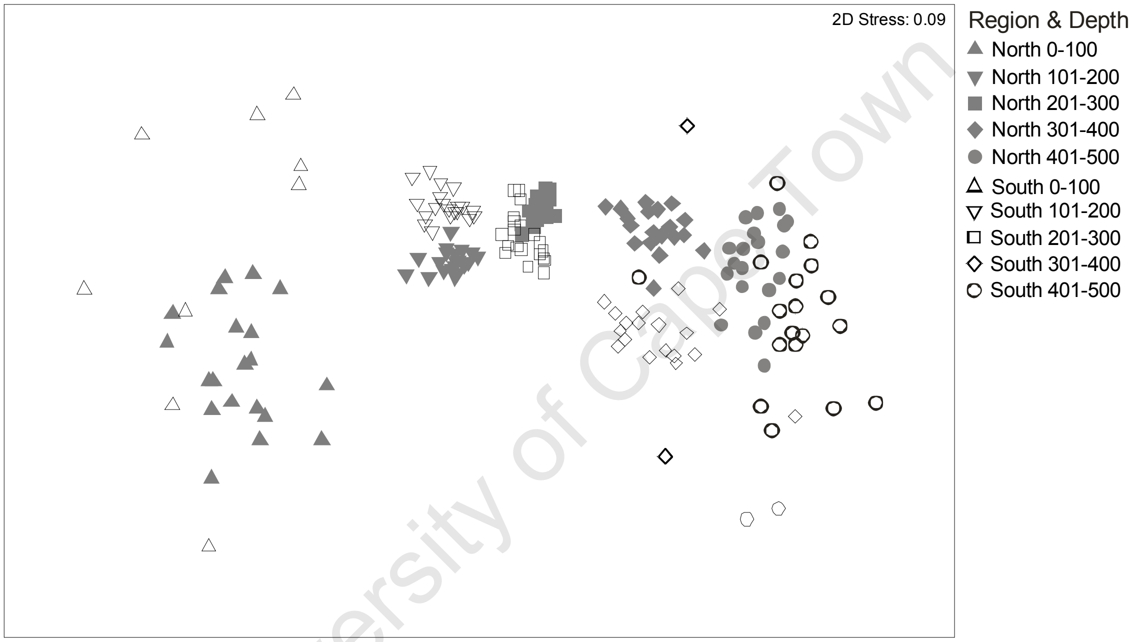


Fig. 5.3. Multi-dimensional scaling plot of summer fish density data from all years, both regions and five depth zones, based on Bray-Curtis resemblance, after 4th root transformation.

Table 5.2. Test statistics for multivariate PERMANOVA analysis of demersal fish assemblages among years, regions, depths and interactions. Significant values at $p < 0.01$ are indicated in bold.

	Degrees of freedom	Sum of Squares	Mean Squares	Pseudo-F	p-value	Unique no. permutations
Year	19	11800	621.05	2.2372	0.0001	9749
Region	1	9616.1	9616.1	30.239	0.0001	9930
Depth	3	81294	27098	88.716	0.0001	9937
Year x Region	19	6042.1	318	1.1456	0.0924	9735
Year x Depth	57	17410	305.44	1.1003	0.0984	9633
Region x Depth	3	8655.1	2885	10.393	0.0001	9887

SIMPER analyses identifying the average density of species contributing most to differences between northern and southern regions are shown in Fig. 5.4. Species dominating the southern region include *Merluccius paradoxus* (deep-water hake), *Chelidonichthys capensis* (Cape gurnard), *Squalus megalops* (bluntnose spiny dogfish) and *Caelorinchus* sp. (rattails). Those species occurring in greater abundance in the northern region include *Merluccius capensis* (shallow-water hake), *Zeus capensis* (Cape dory), *Squalus mitsukurii* (longnose spiny dogfish), *Lepidopus caudatus* (ribbonfish), *Brama brama* (angelfish), *Malacocephalus laevis* (rattail) and *Genypterus capensis* (kingklip).

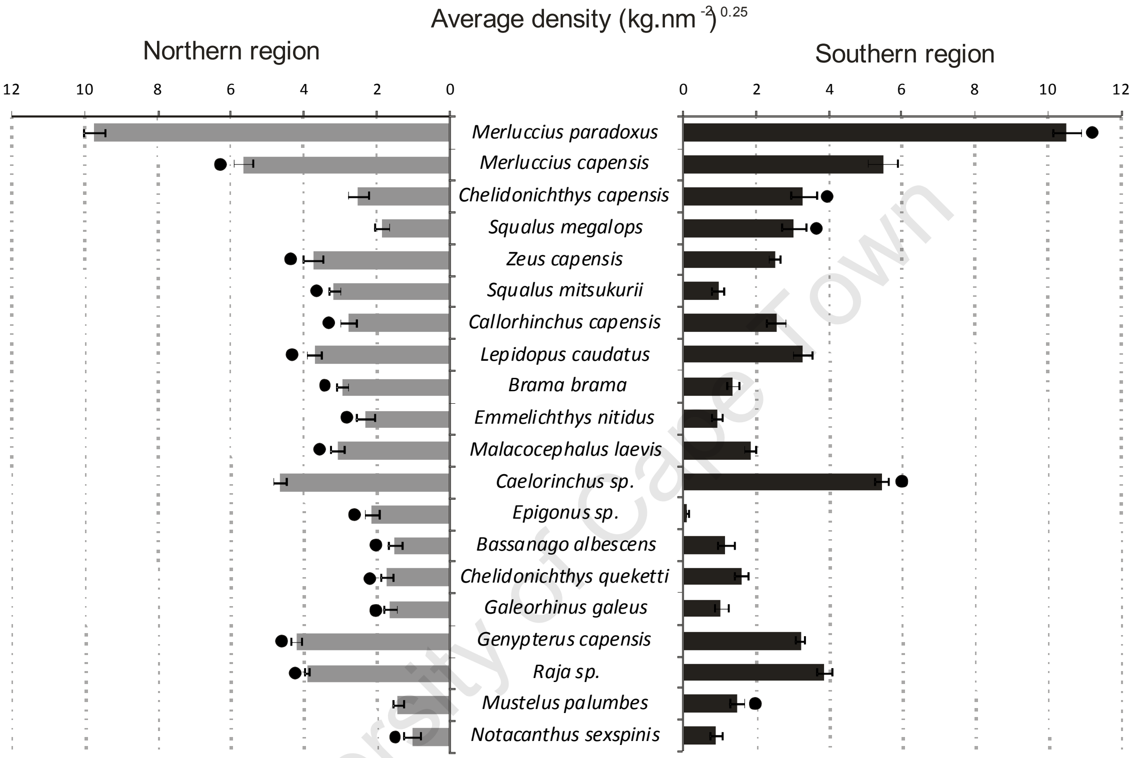


Fig. 5.4. Northern *vs.* southern regions, separated at 33°S: SIMPER results (top 20 species contributing to differences) of fish densities after 4th root transformation, represented by species contributions of average dissimilarity between regions (±SE). Total average dissimilarity = 59.56%. A black circle indicates the area of greater biomass per species.

SIMPER analysis between northern and southern regions, including small pelagic, mid-water and mesopelagic species (not presented) indicated greater abundance of *Trachurus capensis* (horse mackerel) in the southern region contributing most to the differences observed between north and south. *Etrumeus whiteheadi* (red-eye round herring) were also more abundant in the southern region while *Thyrsites atun* (snoek) were more abundant in the northern region.

Figure 5.5 reflects the average similarity within each depth zone of species contributing up to 80% Bray Curtis similarity, northern and southern regions combined (SIMPER analysis). The density data show a clear decrease in species diversity with an increase in depth, while some species are present throughout all depth zones e.g. *Merluccius paradoxus* (deep-water hake), *Lophius vomerinus* (monk), *Raja* sp. (rays), *Helicolenus dactylopterus* (jacopever), *Caelorinchus* sp. (rattails) and *Lepidopus caudatus* (ribbonfish).

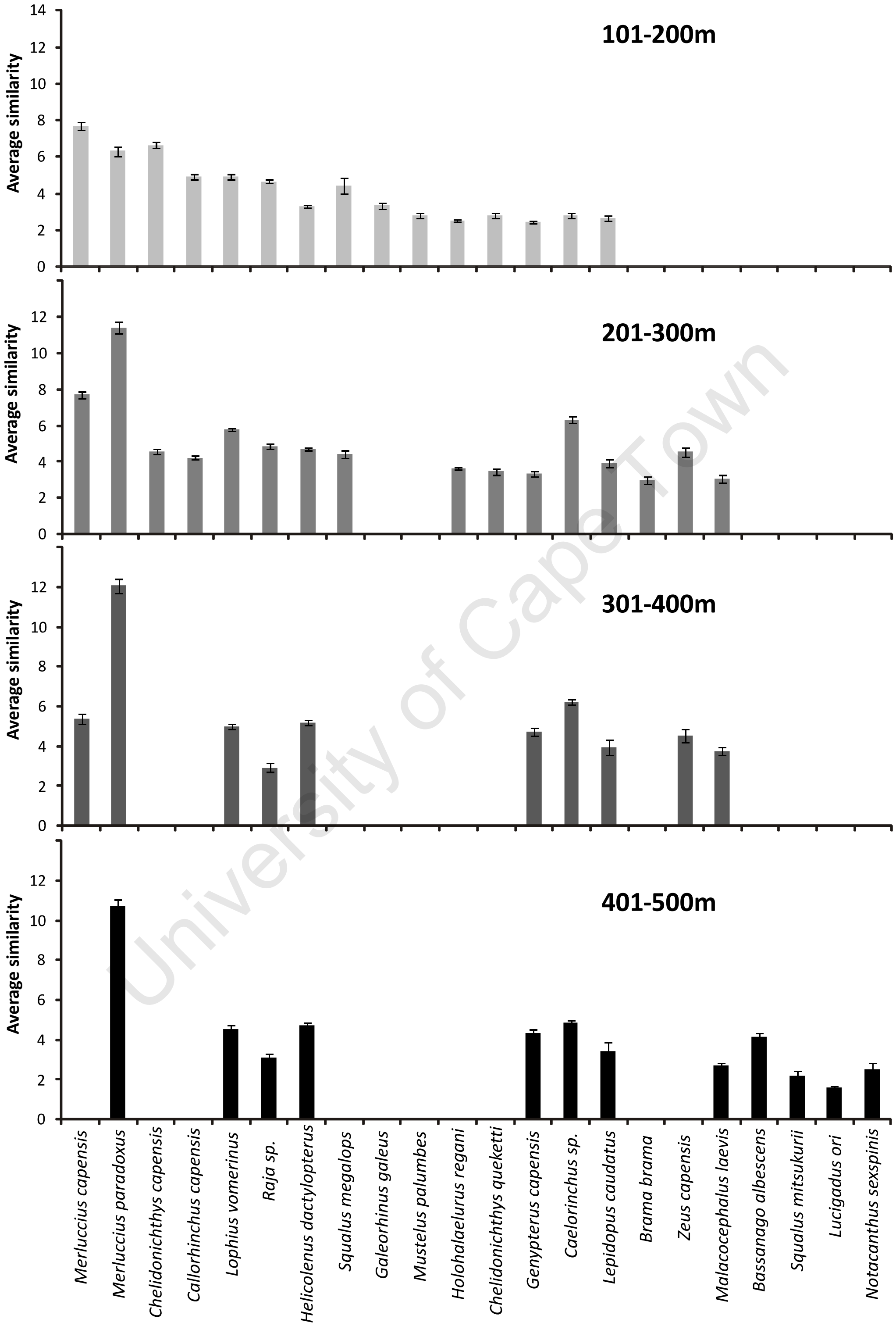


Fig. 5. 5. Depth zones: SIMPER results (species contributing up to 80% Bray-Curtis similarity) within each depth zone (northern and southern regions combined) representing species contributions to average similarity within each depth zone (±SE), based on 4th root transformed density data.

Temporal analysis (seasonal and annual)

PERMANOVA of a subset of four years of data (1986-1988 & 1990) yielded insignificant differences in community densities between summer and winter (pseudo-F=2.43, d.f.=1, p=0.097). Pair-wise tests showed no significant seasonal differences in fish communities in the northern (t=1.51, p=0.1033) or southern (t=1.42, p=0.1365) regions. Similarly, no significant seasonal differences were detected by pair-wise analyses among all 100 m depth zones (101-500 m) between summer and winter data (t=1.61-1.85, p>0.06). Fish community composition densities were not significantly different between summer and the only winter seasons sampled during the years 1986, 1987, 1988 and 1990. Winter survey data were thus eliminated from all further analyses.

A cluster analysis of annual average fish density results in three groups at the 81% similarity level (Fig. 5.6). Group 1 consists of the earliest survey years 1986 to 1992, group 2 consists of survey years 1993 to 2005 (excluding 2004) and the most recent years 2004 to 2009 (excluding 2005) make up the third group. An MDS plot of the same data, with an overlay trajectory and clusters at the 81% similarity level, show years grouped into the same three clear groups (Fig. 5.7).

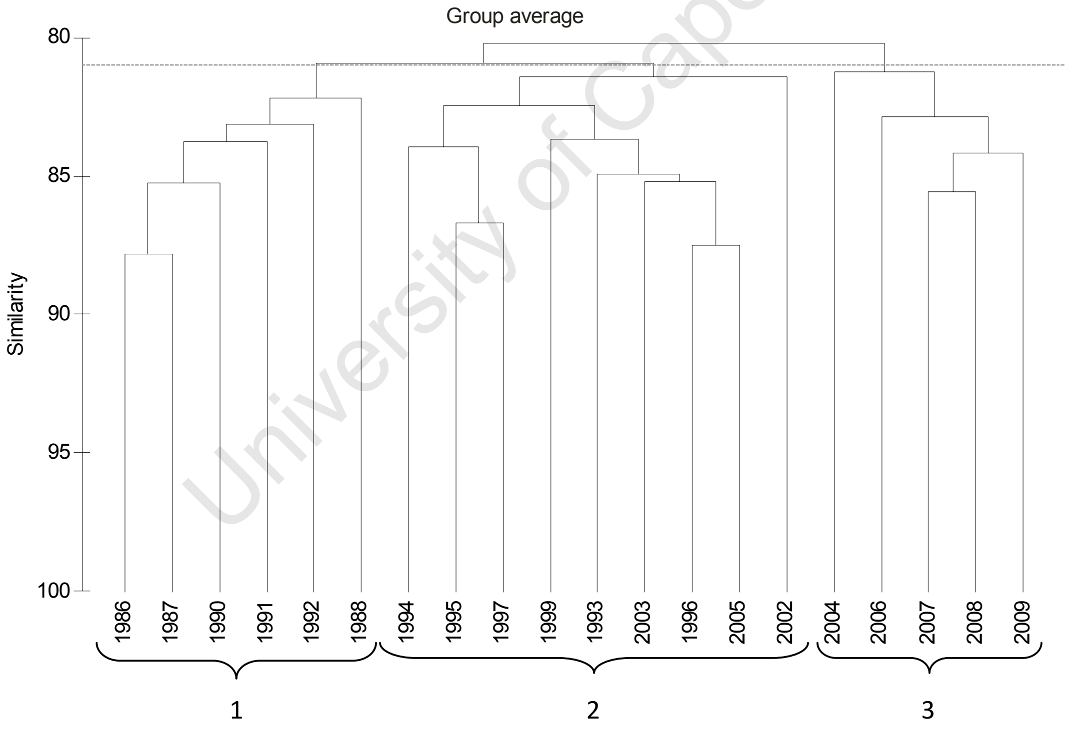


Fig. 5.6. Temporal analysis: Cluster dendrogram of average annual fish mean density based on Bray-Curtis resemblance, after 4th root transformation. Dashed grey line indicates 81% similarity level, year groupings are shown and numbered with parentheses.

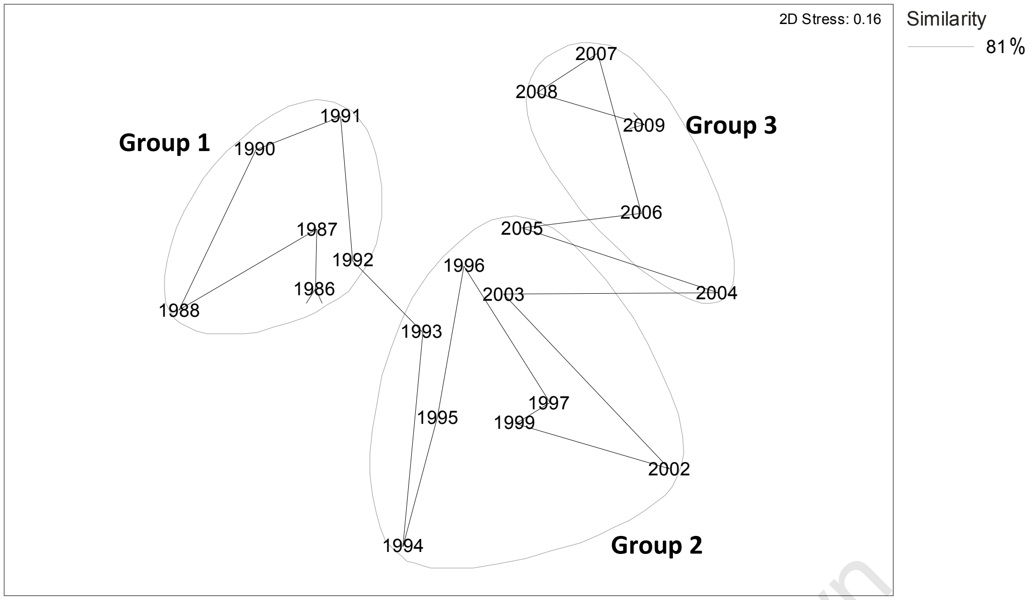


Fig. 5.7. Temporal analysis: Multi-dimensional scaling plot of averaged annual fish density after 4th root transformation based on Bray-Curtis resemblance with groups indicated at 81% similarity.

A posteriori pair-wise multivariate PERMANOVA (fixed factor "year groups") reveals significant differences among all groups as identified by the cluster dendrogram and MDS plot (Table 5.3).

Table 5.3. Multivariate PERMANOVA pair-wise test statistics of demersal fish assemblages between year groups as defined by dendrogram and MDS. Significant p values at $p < 0.05$ indicated in bold text.

Year groups	t-value	P-value (permutation)	Unique perms
1 *vs.* 2	1.7684	0.0003	4296
1 *vs.* 3	1.9154	0.002	462
2 *vs.* 3	1.6545	0.0004	1981

A main effects PERMANOVA with the full data set coded by year groups (as defined by dendrogram and MDS plot Fig. 5.6 and 5.7), regions and depth zones shows significant differences among all year groups (pseudo-F=6.7697, d.f.=2, p=0.0001), regions (pseudo-F=28.954, d.f.=1, p=0.0001) and depth zones (pseudo-F=86.288, d.f.=3, p=0.0001) with significant interaction effects. Pair-wise PERMANOVA between northern and southern regions and among depth zones for each year group combination resulted in significant differences on each account (Table 5.4).

Table 5.4: Regions and depth zones: Multivariate PERMANOVA pair-wise test statistics of demersal fish assemblages among year groups. All tests are significant at $p < 0.05$.

	Year group 1 *vs.* 2		Year group 1 *vs.* 3		Year Group 2 *vs.* 3	
	t-value	p-value	t-value	p-value	t-value	p-value
North	2.5414	0.0001	2.8663	0.0001	2.3604	0.0001
South	1.7871	0.0003	1.8542	0.0001	1.4714	0.009
101-200m	1.8793	0.0002	1.7126	0.0002	1.8712	0.0001
201-300m	1.7994	0.0002	1.8845	0.0001	1.9849	0.0001
301-400m	1.6147	0.004	1.9532	0.0004	1.5738	0.0018
401-500m	1.934	0.0002	2.1733	0.0002	1.4839	0.0058

SIMPER analyses, based on the average density of species occurring within year groups (Fig. 5.8), show an increase in two species of eel, *Notocanthus sexspinis* (spiny eel) and *Congor wilsoni* (conger eel), over the study period. *Lepidopus caudatus* (ribbonfish) initially decreased between year group 1 and 2 but increased during year group 3 resulting in little overall change in abundance. *Merluccius paradoxus* (deep-water hake) also shows an increase from the early years (1986-1992) to more recent years (2004 & 2006-2009). Species that have decreased overall during the sampling period include *Callorhinchus capensis* (St Joseph shark) and *Squalus acanthias* (spiny dogshark).

Analyses conducted including small pelagic, mid-water and mesopelagic species result in similar dendrograms and MDS groupings and significant PERMANOVA results, in all respects. SIMPER analyses (not shown) including these species indicated that small pelagic (*Engraulis encrasicolus*, *Sardinops sagax* and *Etrumeus whiteheadi*) and mid-water species (*Trachurus capensis)* increased in abundance over the study period. Acoustic sampling data would provide more accurate abundance indices for these species.

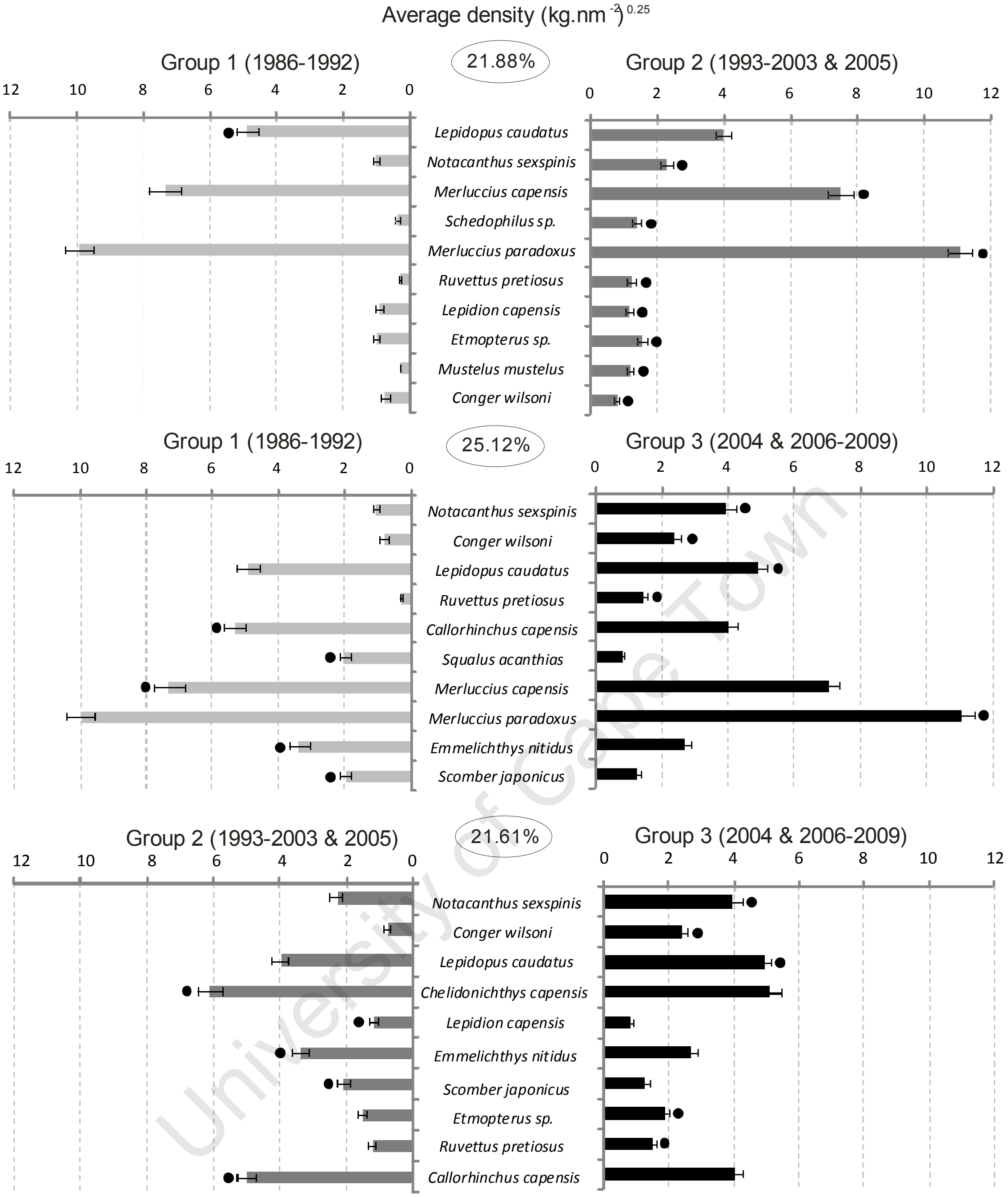


Fig. 5.8. Group years: SIMPER results (top ten species densities contributing to differences) of fish densities (kg.nm^{-2})$^{0.25}$ after 4th root transformation (±SE) between year groups, representing species contributions of average Bray- Curtis dissimilarity between groups. Dissimilarity percentages between groups are indicated in ellipses. A black circle indicates the group of greater biomass per species.

Environmental variables

PERMANOVA analysis with average seabed temperature values incorporated as a covariate, shows that temperature has a significant relationship to the distribution pattern of fish species biomass (pseudo-F=698.3, d.f.=1, p=0.0001). Taking into account the known relationship of temperature to the data distribution through inclusion of this covariate, significant variability is still detected among fish communities between regions (pseudo-F=30.79, d.f.=1, p=0.0001) and among depth zones (pseudo-F=24.86, d.f.=3, p=0.0001). The covariate temperature also had significant interactions with fish distributions between northern and southern regions (pseudo-F=71.34, d.f=1, p=0.0001).

A distance-based linear model using a subset of normalised benthic temperature and benthic dissolved oxygen data (2002-2009) showed that both variables significantly influence the distribution of fish communities (Table 5.5). The overall best solutions presented by the model were primarily temperature influencing the data distribution, followed by temperature combined with dissolved oxygen (Table 5.5). A Principal Coordinate Analysis (PCO) provides a spatial representation of the influence of temperature and oxygen with 51.7% of the variation explained by the PC1 axis, along which temperature (and salinity by correlation) and oxygen factors align (Fig. 5.9). The vector overlay of Pearson correlation illustrated in Fig. 5.9 clearly shows the dominant influence of temperature (longer vector, Anderson *et al*. 2008) in the shallower zones (101 – 300 m) over oxygen, which appears more influential in the deeper zones (301 – 500 m). The PCO plot also clearly illustrates the dominant effect of depth in influencing the distribution of fish, the gradient of which aligns with PC1 axis.

Table 5.5. Test statistics for a Distance-based Linear Model (DISTLM) analysis based on “Best” procedure and AIC criteria of the influence of a subset of average near seabed temperature and dissolved oxygen (2002-2009) on demersal fish assemblage. SS = Sum of Squares, RSS = residual Sum of Squares, R^2 = RSS/SS.

MARGINAL TESTS:

Variable	SS(trace)	Pseudo-F	p-value	Proportion of variation
Ave Temperature	23678	44.365	0.0001	0.4171
Ave Dissolved Oxygen	4962.3	5.9387	0.0008	0.0874

OVERALL BEST SOLUTIONS:

AIC	R^2	RSS	Number of Variables	Selections
403.88	0.4171	33090	1	Ave Temperature
404.14	0.4326	32206	2	Ave Temperature & Dissolved Oxygen

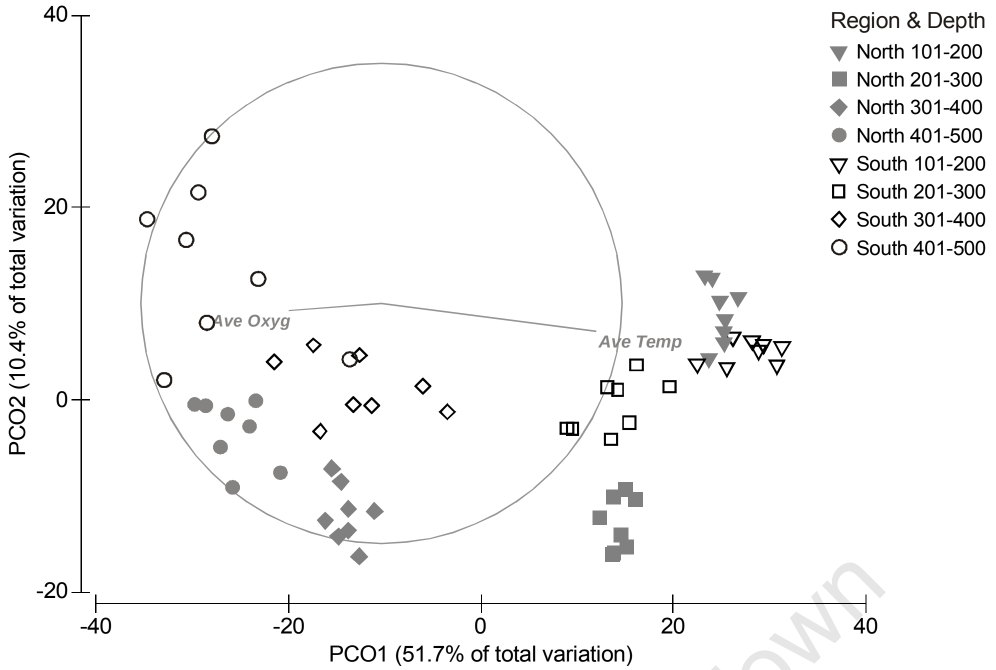


Fig. 5.9. Principal Coordinate Analysis of 4th root transformed Bray Curtis similarity fish density data (2002-2009) at four depth zones with near seabed environmental variables temperature and dissolved oxygen vectors (Pearson correlation) superimposed.

Analysis of the influence of surface oceanographic variables (SST and upwelling indices) on annual fish community composition using a distance-based linear model result in only one variable being significant. The January upwelling index at 30°S 16°E (Hondeklip Bay) showed a significant correlation with fish density (pseudo-F=1.76, p=0.03, Table 5.6). All other variables resulted in non-significant correlations ($p \geq 0.05$). A distance-based redundancy analysis (dbRDA, a constrained ordination of the fitted values from the linear model for visual representation) based on the surface oceanographic variables selected in the DISTLM routine indicates that the total variation explained by the axes is only 11.14% (dbRDA plot not shown).

Table 5.6. Test statistics for a Distance-based Linear Model (DISTLM) analysis based on "Best" procedure and AIC criteria of the influence of surface oceanographic variables on demersal fish assemblages. SS = Sum of Squares, RSS = residual Sum of Squares, R^2 = RSS/SS. Significant values at $p < 0.05$ are indicated in bold.

MARGINAL TESTS:				
Variable	SS(trace)	Pseudo-F	p-value	Proportion of variation
Dec-SST32S	234.46	1.6126	0.05	0.10329
Dec-UpW32S	181.65	1.2178	0.21	0.08002
Dec-SST30S	205.3	1.3921	0.10	0.09044
Dec-UpW30S	96.587	0.62216	0.94	0.04254
Jan-SST32S	175.9	1.1759	0.24	0.07748
Jan-UpW32S	111.26	0.72157	0.83	0.04901
Jan-SST30S	230.2	1.5799	0.05	0.10141
Jan-UpW30S	252.95	1.7557	0.03	0.11143
OVERALL BEST SOLUTIONS:				
AIC	R^2	RSS	Number of Variables	Selections
81.389	0.11143	2017.1	1	Jan-UpW30S

Regime shifts

Species population shifts were detected in a total of 37 (40%) demersal species, of which 25 (27%) occurred in ≥ 50% of model settings and were considered true population shifts in this study (Table 5.7). More than half (52%) of these species show population shifts towards the latter part of the time series (i.e. from 2002 to 2009), however, many of these species' shifts (46%) occur at the very end of the time series (in 2008/9, shaded in grey in Table 5.7). Successive annual data are considered necessary to validate shifts detected at the end of a time series. Ten species (40%) show shifts in both early (1992 to 1997) and later (2002 to 2009) years, while a shift in early years only was detected in just one species (*Lophius vomerinus*, monkfish). One species (*Austroglossus microlepis*, west coast sole) showed population shifts in 1999 and 2009, thus not fitting into any of the previous categories described (Table 5.7). Twenty-four percent of species show population shifts that correlate to an increase in density in the early years (1992 to 1997) followed by a negative shift in more recent years (2002 to 2009). Long-term shifts of representative species from the first two categories (Table 5.7) are illustrated in Figure 5.10 and 5.11.

Table 5.7. Classification of demersal fish species in which true population shifts (≥ 50% of model settings) were detected with STARS analysis in this study. Species shaded in grey show shifts detected at the end of the time series only. Symbols in parentheses indicate positive (+) or negative (-) direction of shift.

Population shifts detected between 2002 and 2009	Population shifts detected in 1992-1997 and 2002-2009	Population shift detected in early years only (1997)	Population shifts detected in 1999 and 2009
Notocanthus sexpinis (+) (-) *Sufflogobius bibarbatus* (+) *Paracallionymus costatus* (+) *Galeorhinus galeus* (-) *Scombrops boops* (+) *Brama brama* (+) *Torpedo nobiliana* (+) *Holplostethus mediterraneus* (+) *Hexanchus griseus* (+) *Tripterophycis gilchristi* (+) *Scomberesox saurus* (+) *Synogrops japonicas* (+) *Metelectrona ventralis* (+)	*Lepidopus caudatus* (-) (+) *Chelidonichthys queketti* (+) (-) *Congipodus spinifer* (+) (-) *Holohalalurus regani* (+) (-) *Squalus megalops* (+) (-) *Raja sp.* (+) (-) *Zeus capensis* (+) (-) (+) *Genypterus capensis* (+) *Scyliorhinus capensis* (+) *Hydrolagus africanus* (+)	*Lophius vomerinus* (+)	*Austroglossus microlepis* (-) (+)

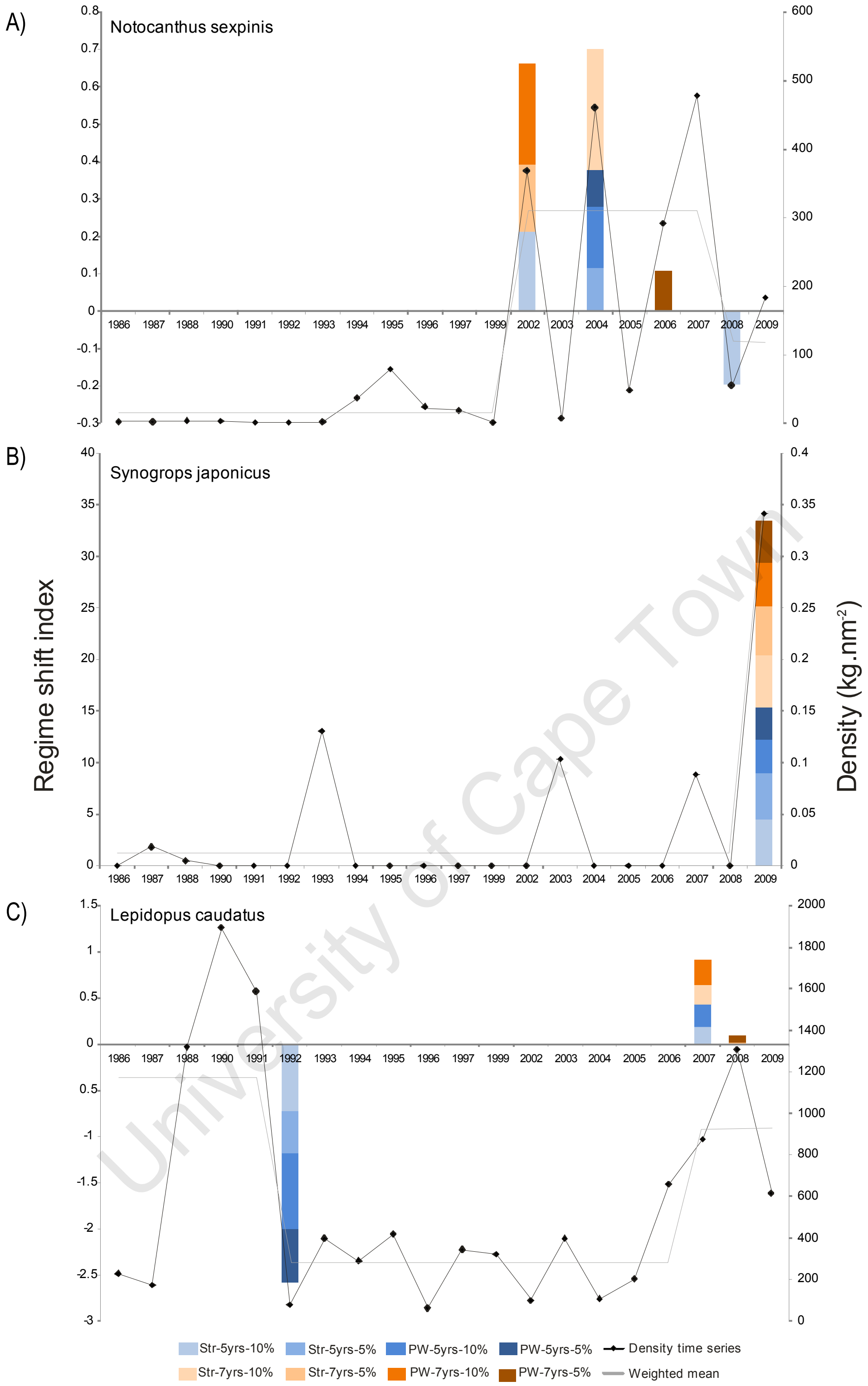


Fig. 5.10. Results of STARS analysis showing magnitudes of regime shift indices (vertical bars, left axis) occurring in representative species A) *Notocanthus sexpinis* (spiny eel) shifts in later years (2002-2009), B) *Synagrops japonicus* (lanternbelly) shifts at the end of the time series and C) *Lepidopus caudatus* (ribbonfish) shifts in early (1992-1997) and later (2002-2009) years. Str = straight, PW = prewhitened, 10% = 0.1 significance, 5% = 0.05 significance, 5 yrs and 7 yrs refer to respective cut-off length model settings. Right axis = fish density and weighted mean

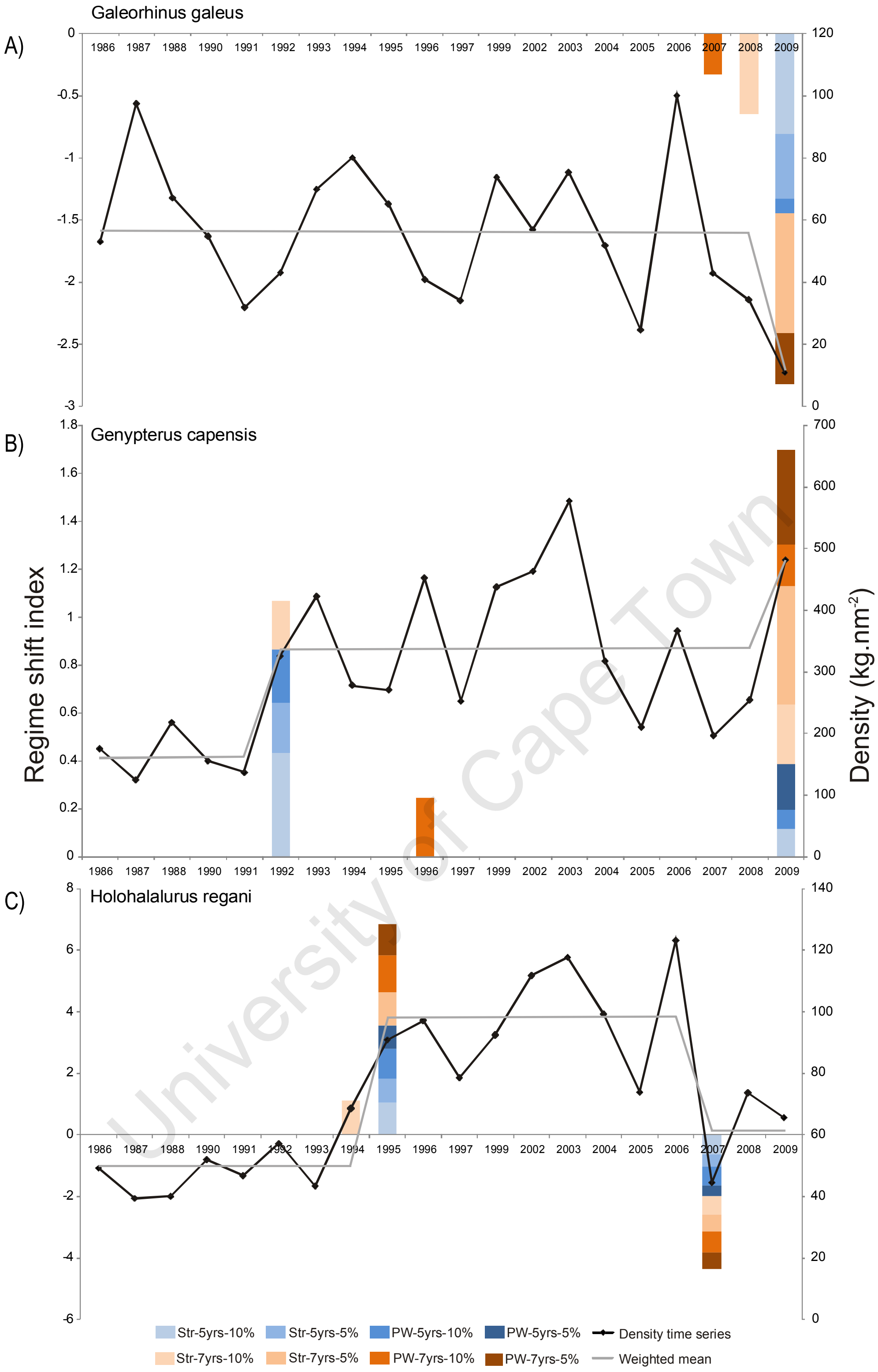


Fig. 5.11. Results of STARS analysis showing magnitudes of regime shift indices (vertical bars, left axis) occurring in representative species A) *Galeorhinus galeus* (soupfin shark) shifts in later years (2007-2009), B) *Genypterus capensis* (kingklip) increasing shifts in 1992, 1996 and 2009 and C) *Holohalalurus regani* (spotted shyshark) shifts in early (1992-1997) and later (2002-2009) years. Str = straight, PW = prewhitened, 10% = 0.1 significance, 5% = 0.05 significance, 5 yrs and 7 yrs refer to respective cut-off length model settings. Right axis = fish density and weighted mean.

DISCUSSION

Spatial differences

The separation of northern and southern regions at 33°S in this study resulted in significantly different fish assemblages being detected either side of Cape Columbine. Whilst the overall densities of various species occurring differed between the regions, there was no clear species loss with latitudinal change (i.e. all species occurred throughout the region). Some species, however, occur in greater density in a particular region. For example, deep-water hake (*Merluccius paradoxus*) occur at greater density in the southern region, while shallow-water hake (*Merluccius capensis*) occur at greater density in the northern region. Subtle differences in species densities throughout the region result in significantly different fish assemblages being detected between the southern and northern regions in this study. It is likely that the fish assemblage changes gradually between the northern and southern reaches of this study and variation in geographic and oceanographic features around 33°S may enhance fish community composition changes in this area.

Fish community changes with increasing depth are well-documented in the Benguela region (Roel 1987, Smale *et al*. 1993, Macpherson & Gordoa 1992, Bianchi *et al*. 2001). Fish assemblages observed at increasing 100 m depth increments in this study clearly show the appearance of deeper water species (e.g. *Lucigadus ori* and *Bassanago albescens*) with the concomitant loss of shallow water species (e.g. *Galeorhinus galeus* and *Mustelus palumbes*) along an increasing depth gradient (Fig. 5.5). There is some degree of species overlap between each subsequent depth zone and some species span all depth zones investigated in this study e.g. *M. paradoxus*, *Lophius vomerinus* and *Helicolenus dactylopterus*. Significant differences were detected between each 100 m depth zone in this study, however, the most substantial change in species composition appears to be between 300 m and 400 m (Fig. 5.3 and 5.5) supporting the distinct change in fish community in the shelf break region (± 385 m), as suggested by Roel (1987).

Temporal changes

The demersal fish community composition did not change significantly between summer and winter seasons during 1986, 1987, 1988 and 1990. The lack of seasonal differences was consistent between northern and southern regions and among all depth zones. No further winter demersal research surveys have been conducted along the South African west coast. Considering the time series available for seasonal analyses, this study concludes that the demersal fish community composition does not display strong seasonal trends. A study conducted by Roel (1987) found some evidence of seasonal differences in fish communities in the shallow (< 380 m), northern region (north of 32° S) of the same area. Roel (1987) however only had access to survey data for two summer (1984 and 1985) and two winter (1985 and 1986) seasons. The increased annual sample size in the current study shows that with a longer time series, no seasonal differences seem apparent in the demersal fish community on the west coast. A sample size of only four years, however, may still be too few to detect broad seasonal differences. This highlights the importance of long-term studies in distinguishing true community changes from natural variability (Kaiser 1998, Thrush *et al*. 1998).

Multivariate analyses showed significant changes in the fish community composition over the 24-year period with three significantly different groups emerging, these being: Group 1) late 1980s and early 1990s, Group 2) mid-1990s to early 2000s and Group 3) mid-2000s until present (2009). Species shown to increase in biomass and contribute to differences among year groups include two eel species (*Notacanthus sexpinis* and *Conger wilsoni*) and ribbonfish (*Lepidopus caudatus*). No studies on the life-history of these species have been conducted, but studies conducted on different species of the same families (Oymak *et al*. 2009, Correia *et al*. 2009, Bingzheng *et al.* 1984, Kwok & Ni 1999), suggest that these species are likely to be relatively fast-growing, early maturing species. The biomass of two of Chondrichthyan species (St Joseph shark, *Callorhinchus capensis* and spiny dogfish, *Squalus acanthias*) decreased significantly among year groups, these species being considered slower-growing, oviparous or ovoviviparous, longer lived and more vulnerable to fishing pressure (Stevens *et al.* 2000). The two species of *Merluccius* show opposite trends over the years with *M. capensis* decreasing over time while *M. paradoxus* increased. This is similarly reflected by trends in the offshore commercial trawl industry over the same period (Fig. 5.1). Some species support the hypothesis of an increase in fast-growing, early maturing species (e.g. *Notacanthus sexpinis, Conger wilsoni* and *Lepidopus caudatus*) and a decline in slow-growing long-lived species (e.g. *Callorhinchus capensis* and *Squalus acanthias* Fig. 5.8). Insufficient information on the life-histories of several species limited further interpretation of results in this respect. The SIMPER analyses including small pelagic, mid-water and mesopelagic species, shows an overall increase in density over time of the three small pelagic species (*Engraulis encrasicolus, Etrumeus whiteheadi* and *Sardinops sagax*). Demersal sampling gear is not considered appropriate to obtain biomass estimates of pelagic species, but more accurate acoustic sampling methods also reveal an increase in abundance of the three small pelagic species since the mid-1990s (van der Lingen *et al*. 2006). These findings support the hypothesis of an increase in *r-selected* species within the southern Benguela system.

Of the environmental variables measured and available in this study (temperature, salinity and dissolved oxygen), temperature, (and by correlation, salinity), appears to influence the fish community most substantially. A decrease in temperature is expected to occur with an increase in depth and these variables are well documented to significantly influence the fish community composition (Roel 1987, Smale *et al.* 1993). Temperature appears to have greater influence in the shallower regions (100-300 m), while the dissolved oxygen content vector is more closely associated with the deeper (300-500 m) stations (Fig. 5.9). Relatively low oxygen water (1 - 2 ml/l^{-1}) is known to seasonally spread in the inshore regions of the southern and central Benguela (Monteiro & van der Plas 2006) and is likely to favour only those demersal species able to tolerate these conditions. Deeper waters (> 300 m) are seldom oxygen poor in the southern Benguela (Monteiro & van der Plas 2006), thus species occurring here are unlikely to tolerate low oxygen conditions. Surface oceanographic environmental conditions (sea surface temperature and upwelling indices), used as indicators of large scale oceanographic processes such as upwelling, do not appear to be directly related to demersal fish community changes in any measurable manner.

Fishing pressure alone is considered unlikely to account for the changes in fish community observed in this study. Substantial changes in community structure caused by fishing pressure are expected to have occurred shortly after the onset of fishing or with a sudden increase in fishing intensity (Jennings & Kaiser 1998). This would probably have manifested in the southern Benguela region during the late 1950s and early 1960s, when there was a rapid increase in demersal fishing activities and an increase in the depth range fished (Griffiths *et al*. 2004, van der Lingen *et al*. 2006). As in many parts of the world, few demersal baseline surveys or information were gathered during these earlier years and changes, as a result of increased fishing pressure, are not accurately documented. Reports compiled by John D. F. Gilchrist (the first government marine biologist in South Africa) between 1897 and 1908 were not sufficiently quantitative or accurate with respect to biomass of species landed by the trawl fishery in particular. Furthermore, no comparable areas in the region have been protected from fishing (Shannon *et al*. 2006) to facilitate scientifically robust, comparative studies. In the absence of accurate baseline data or representative areas protected from fishing impacts for comparisons, it is difficult to tease apart changes induced by fishing pressure from those of a purely environmental nature. The two fish assemblage shifts observed over the past 24 years in this study occurred during a comparatively stable (with respect to catches Fig. 5.1) period of time in the fishery. No dramatic increase in fishing pressure is evident over the period of study that can unequivocally explain the shifts observed. These assemblage shifts are therefore likely to be a reflection of long-term indirect effects of fishing (e.g. species replacements, trophic cascades, habitat modification) in combination with environmental changes, both naturally and human induced.

Dramatic changes in the composition of fish catches over long periods of time have been documented in several marine ecosystems (Rijnsdorp *et al.* 1996, Haedrich & Barnes 1997, Rogers & Ellis 2000, Yemane *et al*. 2004) and have often been associated with the depletion of a target species as a direct result of fishing pressure, facilitating another species to proliferate (Jennings & Kaiser 1998). Species replacements refer to large, absolute changes in the biomass of species and changes that appear to be in compensation for another species e.g. one species proliferates while another declines. Species replacements can manifest as an indirect effect of fishing. Changes in catch composition frequently occur as a fishery develops and does not necessarily equate to species replacements (Jennings & Kaiser 1998).

The implementation of various fishery area closures as management measures aimed at rebuilding overexploited target stocks, have shown that by excluding the impact of fishing, many species populations can recover, but that benefits are not universal (Fogarty & Murawski 2004). The offshore closed areas on Georges Bank, north-eastern United States, showed significant increases in some demersal fish populations and scallops within five years of protection but afforded little protection for migratory phases of Atlantic cod *Gadus morhua* and haddock *Melanogrammus aeglefinus* (Murawski *et al*. 2000). Increases in abundance and diversity of non-target fish species, infauna and epifauna have also been observed (Murawski *et al.* 2000, Collie *et al*. 2000b, Collie *et al*. 2009). A large area closed to fishing on the Scotian Shelf, Nova Scotia, Canada, implemented to protect juvenile haddock, showed increases in haddock and several other finfish species with some evidence of spill-over benefits into adjacent fished areas (Fisher & Frank 2002). The "Plaice box", a gear-restricted area in the North Sea that was established to reduce the bycatch of undersized plaice *Pleuronectes platessa,* has been shown to be ineffective in protecting the target species (Hiddink *et al.* 2008). Juvenile plaice are more abundant outside the protected area and Hiddink *et al.* (2008) propose that the small-bodied benthic fauna on which plaice feed occur in greater abundance in areas disturbed by fishing. The ineffectiveness of the "Plaice box" at protecting juvenile plaice appears to be as a result of the species' feeding preference, highlighting the need for consideration of life-history traits and ecology in selecting appropriate management measures (Hiddink *et al*. 2008).

Long-term changes in demersal fish assemblages

Investigating the research demersal fish database for regime shifts over the past 24 years using STARS analyses indicates the occurrence of population shifts in the early- to mid-1990s and again in the mid-2000s. Six species reflecting population shifts during the early- to mid-1990s and in the mid-2000s are likely to have *K-selected* life-history strategies (based on information available at the genus or family level only), these being yellowspotted catshark *Scyliorhinus capensis,* African chimaera *Hydrolagus africanus,* smooth horsefish *Congipodus spinifer*, spotted shyshark *Holohalalurus regani*, spiny dogshark *Squalus megalops* and skates *Raja* sp., (Jennings *et al*. 1999, Stevens *et al.* 2000). The latter four of these species (Table 5.4) show an initial positive shift, followed by a negative, overall decreasing shift in more recent years. However, there were also four long-lived, slow-growing species (Walmsley *et al*. 2005, Stevens *et al*. 2000) that increased in recent years, these being monkfish *Lophius vomerinus*, Atlantic electric ray *Torpedo nobiliana*, African chimaera *Hydrolagus africanus* and yellowspotted catshark, *Scyliorhinus capensis*.

Genypterus capensis (kingklip) and *Galeorhinus galeus* (soupfin shark), two commercially valuable species, show population shifts that are likely to be influenced to some extent by fishing activities. A kingklip-directed longline fishery was terminated in 1991 as a result of stock collapse and this species is now only landed as bycatch with a controlled maximum quota allocation (Griffiths *et al.* 2004). Furthermore, an area along the south coast, known to be a kingklip aggregating and spawning area, has been seasonally closed to fishing since 2005 to protect spawning stocks (DEAT 2005a). Population biomass shifts for this species show a positive increase in 1992 and again in 2009 which could reflect an increase in stocks as a result of effective management measures having been implemented. Soupfin shark are targeted by the demersal shark longline fishery and declining catch rates have been reported since 2001 (DEAT 2005b). Negative population shifts are detected in 2007, 2008 and 2009 for this species, suggesting a decrease in the population, possibly influenced by fishing pressure. Large, slow-growing, late-maturing sharks and rays are known to be particularly vulnerable to overfishing due to their *K-selected* life-history characteristics (Stevens *et al*. 2000). Stevens *et al*. (2000) suggest that fluctuation in shark populations may indicate community changes induced by fishing pressure and fishery managers should be attentive to such fluctuations.

It is not only the effects of fishing pressure or management measures that may result in detection of a population shift for a particular species using STARS. Population shifts detected in the small dragonet species, *Paracallionymus costatus*, closely correlate with the introduction of the new trawl gear configuration in 2004. This species appears to reflect inflated densities when the new trawl gear configuration is used and reduced densities when the old configuration was used (prior to 2004 and in 2005), suggesting that the shifts detected for this species are simply an effect of gear differences. The pelagic goby, *Sufflogobius bibarbatus*, is reportedly increasing in abundance in southern Namibian waters (central Benguela region) as a result of regime shifts in the late 1980s/early 1990s (Boyer & Hampton 2001). This area lies immediately north of the sampling region investigated in this study and it is possible that the positive population shifts detected for the pelagic goby in 2005 and 2007 with STARS are a reflection of a southward spread in distribution range due to its increasing abundance. The change in trawl gear may also influence the catch rates of this species.

Ecosystem regime shifts have profound implications for marine ecosystems and need to be incorporated into management strategies (e.g. single species stocks managed as part of dynamic ecosystems of interacting species, Rothschild & Shannon 2004). The possibility of regime shifts occurring where important economic marine resources (e.g. small pelagic, rock lobster and demersal species) are affected, implies that management of fishing pressures on these ecosystems should aim towards enhancing stability and resilience in the system and not attempt to prevent natural fluctuations (de Young *et al*. 2008). Resilience of a system implies the capacity to absorb disturbance and reorganize itself while undergoing change so as to retain similar overall functioning and structure (Folke *et al.* 2004). The diversity within species and populations and the diversity of functional groups appear to be critical in maintaining ecosystem resilience (Folke *et al*. 2004). Ecosystem resilience is reduced when key functional groups of species, age groups or trophic levels are removed from the system. Fishing, pollution and habitat destruction can result in species reduction or removal. Reduced resilience of ecosystems renders them more vulnerable to changes that could previously be absorbed, thus increasing the likelihood of anthropogenically-driven regime shifts (Folke *et al.* 2004).

Ecosystem regime shifts present a challenge for fisheries management. Successful management under potential regime shift conditions requires flexibility to rapidly adapt to unexpected events through adaptive management strategies. Maintaining (or rebuilding) resilient ecosystem states in conjunction with adaptive, flexible management protocol are considered to be an effective way of implementing an ecosystem approach to fisheries management (Cury & Shannon 2004, de Young *et al*. 2008). Jarre *et al*. (2006) propose the use of indicators, derived from observations and models, to be synthesized in a rule-based expert system that captures and organises disparate information to interpret and assess the probability or risk of long-term ecosystem change occurring. This study has shown the applicability of multivariate and STARS techniques in identifying changes in fish assemblages and populations, both spatially and temporally, but does not address further development of these techniques into indicators appropriate for management.

Conclusion

The primary objective of this study was to investigate whether the demersal fish community on the west coast of South Africa has changed significantly over the past 24 years. Multivariate analyses indicate two significant community changes occurring, initially in 1992 and again in 2003/2004. Population shifts in a diverse range of demersal fish species from different trophic levels are also detected by STARS analysis in the early 1990s and the mid-2000s, showing coherence between these two analytical methods. Up to 68% of demersal species reflecting population shifts, correspond to at least one of the periods of change in demersal fish community composition detected by multivariate analyses i.e. 1992 or 2004/2005 (Fig. 5.6 & 5.7).

Two fast-growing early maturing species, *Notocanthus sexpinis* and *Lepidopus caudatus*, increased over the period investigated and these changes were evident in both multivariate and STARS analyses in the years 1992 and 2004 (Fig. 5.10). A third fast-growing species (*Conger wilsoni*) also increased; this is identified as a key distinguishing species using SIMPER. Multivariate and STARS analyses revealed an overall decrease in two and four slower-growing, long-lived species, respectively. However, STARS analyses also demonstrated increases in four slow-growing, long-lived species. The hypothesis of an increase in fast-growing, early maturing species and a decline in slow-growing, long-lived species in fished systems is thus only partially supported.

Two long-term community shifts in demersal fish appear to have occurred, the first (early to mid-1990s) is associated with an overall increase in density of many species, while the second shift (mid-2000s), is largely associated with many species decreasing in density. The community shifts observed in the demersal fish populations of the southern Benguela region correspond temporally with regime shifts detected in environmental forcing variables on the west coast (SST and upwelling anomalies) by Howard *et al.* (2007) and with the eastward shifts observed in both small pelagic and rock lobster populations (Coetzee *et al.* 2008, Cockcroft *et al.* 2008). The principal factors catalyzing the shifts observed at similar times in all three of South Africa's most important commercial fisheries, thus far remain poorly understood.

This study has shown that regular (annual) evaluation of the demersal fish community composition and species populations in South Africa provides an appropriate means for detecting signs of long-term shifts. As a step towards implementing an ecosystem approach to managing this fishery, it is recommended that research demersal fish assemblage data should be analysed annually using 1) multivariate techniques to detect changes at the community level and 2) regime shift analysis tools to detect significant fluctuations at the population level. A combination of the two analytical approaches strengthens confidence in detecting changes in the fish community that accurately reflect the state of the community. Further development of these results into a set of meaningful indicators is required. Indicators are needed that will allow assessment of the state of demersal fish assemblages and detect changes in populations that may result from management measures implemented to mitigate the negative effects of trawling.

Chapter Six

Synthesis

Progressing from the single species fisheries management approach towards holistic ecosystem-based fisheries management is an important step for South Africa's largest and most lucrative fishery. Initial steps towards management of demersal fisheries within an ecosystem approach to fisheries (EAF) framework require *inter alia*, the impacts of the fishery on marine habitats, fish and benthic assemblages to be quantified. Studies conducted in this thesis investigate impacts of the demersal trawl fishery on benthic infaunal, epifaunal and fish assemblages in the southern Benguela region for the first time. This initial assessment of impacts of the demersal fishery in southern Africa is needed to guide subsequent development towards EAF implementation (Shannon *et al*. 2006, Nel 2007). South African legislation provides a legal framework to support implementation of EAF in terms of preserving marine biodiversity, protecting ecosystems as a whole and to give effect to ratified international agreements like the Convention on Biological Diversity and the World Summit of Sustainable Development Plan of Implementation (2002) through national legal requirements like the Marine Living Resources Act (No. 18 of 1998) and the National Environmental Management: Biodiversity Act (No. 10 of 2004).

This thesis employs three study approaches, investigates two habitat types and considers three ecosystem components in assessing the impacts of trawling. Firstly, infaunal and epifaunal assemblages are compared at different trawl intensities in unconsolidated sediments within the hake trawl fishing grounds of southern Africa (Chapter Two). This component explored changes in ecological functioning of these assemblages with recently developed analytical techniques integrating biological traits (Chapter Three). Secondly, changes in infaunal assemblages in a shallow, muddy habitat were investigated in a small-scale disturbance experiment implemented in an untrawled area of Oslofjord, Norway (Chapter Four). Finally, long-term changes in demersal fish populations and assemblages on the west coast of South Africa were investigated (Chapter Five).

As with similar studies investigating the impacts of fishing conducted elsewhere, there are no representative untrawled areas of comparable habitat in the southern Benguela region. Investigating the effects of trawling on benthic assemblages at different levels of trawl intensity is considered the next best alternative. This study aimed to investigate the hypothesis that intense demersal trawling significantly alters the abundance, biomass, diversity and composition of benthic infaunal and epifaunal assemblages in comparison to lightly trawled areas in the southern Benguela region. The influence of measured environmental variables on distribution patterns of benthic assemblages was also investigated. Benthic assemblages sampled at heavily and lightly trawled areas were analysed using univariate and multivariate techniques. Benthic assemblages, sediment composition and total organic carbon content varied significantly among the four sites sampled, illustrating changes across a latitudinal gradient. Significant differences in abundance, biomass and diversity of infaunal and epifaunal assemblages in the southern Benguela were detected between paired heavily and lightly trawled areas. Infaunal species specifically indicative of heavily or lightly trawled areas were not evident suggesting that the infaunal species composition remains largely similar, but that measures of abundance and biomass proportions vary under heavy or light trawl intensities. Limited loss of infaunal species diversity at heavily trawled areas suggests that the overall functional role of infauna in this ecosystem is unlikely to be severely altered as a result of trawling.

Some larger, slower growing epifaunal species appear to be more severely impacted by trawling than the generally smaller, faster growing infaunal species. The epifaunal burrowing urchins, *Brissopsis lyrifera capensis* and *Spatangus capensis,* appear to be particularly vulnerable to intense trawling in this study. Using burrowing urchins as indicator species of intense trawling activity, however, should be cautiously applied as their burrowing behaviour is reported to facilitate escape from the impacts of the trawl net (Bergman & Hup 1992, Thrush *et al*. 1998). The large, thick-walled burrowing anemone *Actinauge richardii* and brittle star *Ophiura* sp. occurred in greater biomass and abundance at heavily trawled areas and appear able to survive intense trawl activities. The burrowing anemone can withstand the impact of the passing trawl gear by withdrawing below the sediment surface when disturbed, while the brittle star is considered an opportunistic, highly mobile species, likely to rapidly colonise areas that are frequently disturbed. The overall results show that infaunal species occur at different densities and that different epifaunal assemblages occur in lightly trawled areas in comparison to heavily trawled areas of similar habitat type at the same sites.

The novel approach of Biological Traits Analysis (BTA), incorporating faunal biological traits (life-history, morphology and behaviour) with biomass, was used to explore changes in benthic invertebrate ecological functioning between heavy and light trawl intensities (Chapter Three). This study investigated the hypothesis that infaunal and epifaunal species with small-bodied and fast-growing biological traits would increase with increased disturbance as a result of intense trawling, while species with larger bodied and longer-lived biological traits would decrease. This analytical tool has seldom been applied in marine ecosystems and this study is the first application thereof in a southern African marine environment. Seventeen percent of infaunal traits and 24% of epifaunal traits assessed were significantly different between heavily and lightly trawled areas. Certain trait combinations reflected in some species were shown to occur in greater biomass at lightly trawled areas (e.g. high mobility, long, thin body form, surface crawler, dorsally and laterally flat, spherical body form, scraper/grazer and subsurface deposit feeder). Some species in this study support the proposed hypothesis (e.g. greater small infaunal body size at heavily trawled areas), while others do not (e.g. long, thin body form greater at lightly trawled areas), suggesting that the classification of *r-* or *K- selected* species does not necessarily indicate vulnerability to trawling. Few trait categories are completely lost under heavier trawling conditions, with the result that overall ecological functioning of the system is probably maintained. It is important to acknowledge that measuring ecological functioning of benthic fauna in areas undisturbed by trawling was not possible in this study and results reported therefore only apply to heavy versus light trawling intensities. The functional role of benthic fauna may differ considerably in untrawled areas. This study has shown that BTA of marine benthic invertebrates in the Benguela ecosystem is a promising approach for monitoring ecological functioning and should be further developed with the aim of deriving a suite of benthic ecosystem indicators.

A lack of representative areas protected from trawling on the west coast of southern Africa precluded the possibility of incorporating adequate control sites in experimental trawl studies in this region. However, an established bilateral agreement between South Africa and Norway (NORSA) provided the opportunity to conduct an *in situ* experiment in areas of Oslofjord, Norway that are protected from shrimp (*Pandalus borealus*) trawling by legislation. This provided the necessary untrawled control sites within an otherwise trawled area (Chapter Four). A BACI (Before-After Control-Impact) experimental design was implemented to test the hypothesis that larger-bodied, rare infaunal species would decrease as a result of a trawl disturbance. It was further hypothesized that recovery of infaunal assemblages would be dominated by small-bodied, opportunistic species. Univariate and multivariate analyses did not detect significant effects on infaunal communities attributable to the simulation of trawling disturbance in this study, thereby rejecting the hypothesis. Whilst it is considered possible that the scale of the trawling simulation did not represent that of a commercial shrimp trawling and thus did not measurably affect the infaunal community, it is considered more likely that current trawling activities in Oslofjord do not significantly affect infaunal communities. This is supported by results from a study conducted at the scale of the fishery which failed to detect significant differences among infaunal assemblages in fished and unfished areas (Fleddum *in prep.*). Epifaunal communities were found to be more sensitive to the impacts of trawling than infauna in the southern Benguela region (Chapter Two), but were not investigated in the Oslofjord study. In the absence of representative untrawled habitat in the southern Benguela, it was anticipated that an infaunal impact measure could be quantified by trawling a previously untrawled area in Oslofjord. In reality, the results of this study exemplify findings of several other studies (e.g. Kaiser & Spencer 1996, Kaiser *et al.* 1998, Queirós *et al.* 2006) which show that different habitat types, fishing gear and intensity result in different ecological impact levels.

The availability of representative unfished areas of comparable habitat to fished areas in Oslofjord enabled unequivocal interpretation of results from this study, highlighting the value of areas protected from fishing in this respect.

Annual demersal research survey data have been collected over the past 24 years (1986-2009) providing an opportunity to explore long-term demersal fish assemblage changes in this fished ecosystem on the west coast of South Africa. It was hypothesized that a decrease in late-maturing, slow-growing demersal fish species would be evident with either no change or an increase in fast-growing, early-maturing species. Using multivariate and regime shift analytical methods, changes in demersal fish populations and assemblages were detected in the early- to mid-1990s and in the mid-2000s. Three fast growing, early-maturing species increased in density and six slower-growing, long-lived species declined. However, four slow-growing, late-maturing species increased in density over the study period, thus the proposed hypothesis is only partially supported by the findings of this study. The principal target species of this fishery, *Merluccius capensis* and *M. paradoxus*, do not show distinct changes in density over the past 24 years. Shifts in demersal fish communities detected in this study coincide temporally with shifts observed in small pelagic species (Howard *et al*. 2007, Coetzee *et al.* 2008) and west coast rock lobster populations (Cockcroft *et al.* 2008), these being the target species of two other important fisheries in South Africa. Environmental forcing variables (sea surface temperature and upwelling indices) were also found to undergo shifts at similar periods (Howard *et al*. 2007). Measured and unmeasured environmental perturbations in the system, in conjunction with fishing pressure, are likely to have caused the changes in fish assemblages observed in this study.

Ecological theory predicts that a decrease in species with traits of slow-growth, large body size and late maturity will occur with an increase in disturbance levels (Pianka 1970). Studies conducted in this thesis hypothesized that with intense demersal trawling disturbances, infaunal, epifaunal and fish assemblages would respectively reflect a decrease in species that are slow-growing, have a larger relative body size and late maturity. Few infaunal species showed consistent changes between heavily and lightly trawled areas, but several larger, slow-growing epifaunal species only occurred at lightly trawled areas. The life history, morphology and behaviour of some epifaunal species, predicted to be adversely impacted by disturbance (e.g. burrowing urchins and seapens), facilitate their persistence under heavy trawling conditions (e.g. burrowing or contracting below the surface). Whilst nine demersal fish species support the hypothesis proposed, four slow-growing, late maturing species increased over time, showing the opposite trend to that expected. The categorization of taxa on an *r-K* continuum does not appear to provide an indication of vulnerability to trawling disturbance. This serves to emphasize the importance of analysing assemblages using a multivariate approach and taking cognizance of benthic ecosystems as a whole in assessing the effects of trawling disturbance.

Outlook: Implications for monitoring

Changes in infaunal and epifaunal assemblages as a result of trawling may have consequences for biodiversity and ecosystem processes (Thrush & Dayton 2002, Widdicombe *et al*. 2004, Bremner *et al.* 2006b). Benthic fauna are known to structure their habitat, play a role in nutrient cycling, oxygenation and provide prey for commercially valuable species (Gray 1974, Snelgrove *et al*. 1997, Snelgrove 1998, Hutchings 1998). Reduced epifaunal abundance and habitat complexity have been linked to declines in fish productivity (Sainsbury *et al.* 1997) and may also impact on the recruitment and survival of some fish species (Auster *et al.* 1997, Collie *et al*. 2000b, Lindholm *et al.* 2001). Regular monitoring of benthic fauna has been suggested as a means of quantifying and monitoring impacts of trawl disturbance and other natural and anthropogenic factors (Callaway *et al.* 2002, Collie *et al.* 2004). Development of a regular, structured benthic invertebrate sampling and monitoring programme, encompassing a diverse range of habitat types and environmental conditions in the southern Benguela region, is necessary to build fundamental understanding of natural variability and to assess impacts of fishing activities within this system.

Quantifying infaunal assemblages requires specialised equipment (benthic grabs), dedicated ship time, lengthy processing time and specialised identification expertise. Obtaining regular, meaningful measures of benthic infaunal assemblages are likely to encounter constraints in terms of these requirements. Infaunal assemblages are known to effectively integrate environmental conditions over long periods of time, have relatively low mobility and have permanence over seasons (Warwick 1993, Salas *et al*. 2006). In view of these factors, detailed sampling and analysis of infaunal assemblages every two to three years is considered appropriate to indicate infaunal assemblage status. Replicate benthic grab samples should be obtained at pre-defined sites selected according to depth zones, sediment type and disturbance intensity, ensuring that a diverse range of unconsolidated habitats and conditions are sampled within the Benguela region. Sediment samples from each site should be analysed for grain size and organic carbon content and averaged environmental variable measures (e.g. benthic temperature, salinity, oxygen and chlorophyll) should be assessed for substantial temporal changes that could influence infaunal assemblages. To assist in identifying and qualifying different habitat types, it is recommended that visual images (photographic or video) be obtained from each site prior to sampling, where possible. It has been shown that analyses of infaunal communities with taxonomic identification at higher levels (i.e. genus or family as opposed to species), produce similar results with considerably reduced processing time (Warwick 1988, Olsgard *et al*. 2003, Lampadariou *et* *al*. 2005). For the purpose of long-term monitoring studies, identification of benthic invertebrates, especially infauna, at the genus or family level is considered to be more practical than species identification. Biological Traits Analysis can also be applied at higher taxonomic levels with species grouped according to their biological traits, reducing processing time and expertise required.

Epifaunal assemblages are shown to reflect more dramatic measurable changes than infauna as a result of intense trawl activities in this study and several others (e.g. Engel & Kvitek 1998, Hansson *et al*. 2000, Kaiser *et al*. 2000, McConnaughey *et al.* 2000). With limited training, epifaunal samples can readily be obtained in conjunction with currently well-established annual demersal research surveys conducted along South Africa's west and south coasts. Epifauna retained in the research trawl net should be classified according to pre-defined biological traits that represent the full spectrum of possible traits. Recording epifaunal abundance and biomass from all trawls conducted as part of annual research demersal surveys (approximately 100 trawls per year from each of the west and south coasts) would provide regular sampling of benthic invertebrate communities encompassing a wide spatial coverage across several habitat types (e.g. mud, sand, gravel and combinations thereof), spanning 100 m to 500 m depth. This study has shown that multivariate analysis techniques, combined with biological traits analysis are appropriate tools with which to assess changes in benthic invertebrate assemblages under heavily or lightly trawled conditions in the southern Benguela.

Benthic fauna of the North Sea have been sampled and mapped during dedicated surveys or in combination with existing fisheries surveys. The Benthic Ecology Working Group of ICES conducted a dedicated sampling effort of infaunal assemblages throughout the North Sea during 1986 (Künitzer *et al.* 1992, Heip *et al.* 1992). This concentrated sampling effort provided comparable measures of benthic biomass, abundance and diversity, clearly defining community types in different habitats in the North Sea. Callaway *et al.* (2002) report on a large-scale, collaborative survey conducted in 2000 in which five nations sampled epifauna and demersal fish assemblages using standardized methodology throughout the North Sea, in conjunction with standard annual fish surveys (International Bottom Trawl Survey, IBTS). Their study demonstrated that, effective monitoring of benthic invertebrate assemblages can indeed be conducted in combination with existing fisheries surveys without a substantial increase in time at sea. One replicate beam trawl sample per habitat type was shown to sufficiently identify communities into broad areas (Neumann *et al*. 2008). Increasing the sample size to 9 replicate trawls per habitat type provided additional information to quantify the large spatial variability of benthic fauna in the North Sea (Neumann *et al*. 2008). Identifying the appropriate replication required for a specific study is necessary for adequate data quality and interpretation in highly variable systems. Callaway *et al*. (2002) conclude that with annual collection of benthic fauna within different habitat types, the effects of trawling can begin to be disentangled from those of habitat type and natural disturbance at unprecedented temporal and spatial scales. The success of these studies in obtaining thorough spatial coverage of epifauna of the North Sea with limited additional resources highlights the feasibility of conducting similar coordinated, cooperative sampling in the southern Benguela to obtain valuable information applicable to an ecosystem approach to fisheries management in this region.

Studies conducted in this thesis have demonstrated the applicability of multivariate and regime shift analyses in detecting long-term changes in fish assemblages and populations. Regular multivariate and regime shift analyses of demersal fish research data, currently collected annually in the southern Benguela region, specifically aimed at detecting significant assemblage or population shifts, are recommended using methods detailed in this thesis. Regular monitoring of benthic infaunal, epifaunal and fish assemblages spanning a wide spatial and temporal coverage in the southern Benguela region could provide data needed for further development of meaningful indicators for implementation in an EAF.

Outlook: Recovery measures

Kaiser *et al.* (2002) propose that future research priorities should aim to investigate large scale “press and relaxation” experiments, with one half of the experiment already in place in terms of fishing activity having provided the “press” for many years. The “relaxation” component of the experiment is required in terms of areas being closed to fishing activity such that recovery of fish and benthic communities can be measured at the spatial scale and intensity level of the fishery, previously active in the area. Several studies have successfully capitalised on such fishery area closures that were implemented largely for fishery management purposes (Collie *et al.* 1997 & 2000b, McConnaughey *et al.* 2000, Lindholm *et al*. 2004) but inadvertently also enabled recovery monitoring of benthic habitats and communities, with comparisons to adjacent areas that remained fished (Hermsen *et al*. 2003, Collie *et al.* 2004 & 2009).

Comparisons of benthic fauna in unconsolidated sediments between the unfished “Crab and Halibut Protection Zone” and an adjacent heavily trawled area of the eastern Bering Sea showed a greater abundance and diversity of sedentary epifauna in the areas protected from fishing (McConnaughey *et al.* 2000). Hermsen *et al*. (2003) and Collie *et al.* (1997, 2000b, 2004 & 2009) monitored the effect of fishery closures on epifaunal assemblages in three gravel areas of Georges Bank, north-eastern United States. A greater number of epifaunal organisms, biomass and diversity were recorded in unfished areas of Georges Bank where colonial, emergent epifauna also provided increased habitat structure (Collie *et al.* 1997, 2000b & 2004). Hermsen *et al* (2003) reported a significant increase in benthic epifaunal production in areas closed to fishing activities. Whilst fishery area closures have been implemented in several continental shelves (e.g. the "Plaice Box" in the North Sea, Georges Bank and along the Scotian shelf off Canada), few have been specifically for protection of benthic habitat (with the exception of the Benthic Protection Zone of the Great Australian Bight, see below). Studies to monitor the effectiveness of the fishery closures have largely focussed on changes in target fish densities (Piet & Rijnsdorp 1998, Pastoors *et al*. 2000, Murawski *et al*. 2000, Fisher & Frank 2002, Jaworski *et al.* 2006 and others) with the result that the recovery of benthic habitat and fauna in these protected areas has received relatively limited focus. Studies conducted by Hermsen *et al.* (2003) and Collie *et al.* (1997, 2000b, 2004 & 2009) report on benthic epifaunal assemblages sampled prior to implementation of fishery closed areas on Georges Bank and on annual recovery monitoring, subsequent to closure. Few other published studies have been able to sample areas prior to protection from fishing activities with the purpose of monitoring recovery or applied systematic sampling designs to monitor recovery of benthic communities subsequent to excluding fishing activities.

The ecological importance of benthic communities of the Great Australian Bight (GAB) was formally recognised with the proclamation of the Benthic Protection Zone (BPZ) within the GAB Marine Park in 1998 (Ward *et al*. 2006, Currie *et al.* 2009). The BPZ was implemented with the objective to protect a representative sample of the region's benthic assemblages from anthropogenic impacts including trawling, which had been conducted in the GAB since the early 1900s (Currie *et al.* 2009). The BPZ has been shown to effectively represent the diversity of benthic infaunal and epifaunal assemblages and provide protection to communities occurring in seven sedimentary habitat types in the eastern Great Australian Bight region (Ward *et al.* 2006, Currie *et al.* 2009).

Once-off sampling events conducted several years after protection from fishing (e.g. Ward *et al*. 2006, Currie *et al*. 2009) can provide measures of benthic biodiversity and natural variation, however, monitoring the change in species composition over the recovery phase would provide better understanding of the effects of fishing disturbance. Long-term, regular monitoring studies of benthic fauna in areas protected from fishing activities, compared with adjacent fished areas (e.g. Hermsen *et al.* 2003, Collie *et al*. 1997, 2000b, 2004 & 2009) have shown the greatest gain in understanding changes attributable to fishing effects.

Studies conducted in this thesis have shown that trawling affects benthic invertebrate assemblages in unconsolidated sediments in the southern Benguela region, but in order to understand the extent of fishing impacts separately from that of habitat type and natural disturbances, unfished areas of similar habitat are required to provide control sites against which comparisons can be made. Implementing protection of representative areas from fishing in the southern Benguela offshore region would allow monitoring changes in benthic assemblages in response to the exclusion of fishing activities, more rigorous comparisons of ecological processes in impacted versus unimpacted environments and preservation of a representative portion of continental shelf benthic biodiversity. A systematically designed long-term monitoring plan, including thorough benthic sampling prior to closure of an area to fishing, would be an important component of investigating the effectiveness of a closed area for protecting the habitat, benthic invertebrate and fish assemblages.

Conclusion

This thesis provides the first quantitative assessment of impacts of the demersal trawl fishery in southern Africa. Benthic infauna, sediment properties and total organic carbon vary significantly among four sites at similar depths over a distance of 800 km in the southern Benguela. Both epifaunal and infaunal assemblages differ significantly between lightly and heavily trawled areas, with epifauna measurably more affected than infauna and therefore showing the most promise to be developed into indicators of the status of trawled ecosystems. Demersal fish community composition has changed significantly over the past 24 years, but fishing pressure alone is unlikely to be responsible for these changes. The lack of representative untrawled areas of similar habitat to trawl grounds in the Benguela region limited this study to comparisons between heavily and lightly fished areas. Representative areas protected from fishing can provide reference areas against which impacts of trawling can be more robustly assessed, taking into account changes attributed to habitat type and natural variability. Furthermore, protected areas can preserve marine benthic biodiversity and ecosystems thereby fulfilling requirements of national legislation and ratified international agreements. The results of these investigations support proposals for protection of representative habitats from trawling pressures within the southern Benguela region and the implementation of a structured long-term benthic invertebrate monitoring programme.

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