Interannual changes in abundance and distribution of jellyfish along the west coast of South Africa

By

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A thesis submitted in fulfillment of the requirements for the degree of Magister Scientiae, in the Department of Biodiversity and Conservation Biology, University of the Western Cape.

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Abundance, Distribution, Diversity, Hydromedusae, Siphonophora, Southern Benguela, Spawner Biomass Survey, Upwelling

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Abstract

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Hydromedusae are mostly carnivorous planktivores that under ideal conditions can reproduce and accumulate to form dense masses of jellyfish, known as blooms. These jellyfish blooms may have various impacts on their surrounding biota and in severe cases have the potential to result in ecosystem-wide changes. This study investigated assemblages of hydromedusae within the southern Benguela ecosystem, between the years 2000 and 2006. The samples analyzed were collected as part of routine Spawner Biomass Surveys conducted by the Department of Environmental Affairs: Ocean and Coasts (previously Marine and Coastal Management) using Bongo nets. Two hundred and forty two of the samples collected during the spring months, October and November, were analyzed. Environmental variables including (amongst others) sea surface temperature (SST), sea surface salinity (SSS), sea surface oxygen (SSO) and fluorescence (as a proxy for Chlorophyll *a* concentration) were measured to observe their influence on medusoid assemblages, distribution, abundance and diversity.

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Assemblages of hydromedusae were represented by 69 species and were dominated by Siphonophora and Leptomedusae. Mean abundance of hydromedusae were highest in 2005 (3.15 ind.m^{-3}, SD 3.21) and lowest in 2002 (0.50 ind.m^{-3}, SD 0.70). Trends in abundance displayed a general bell-shaped curve relationship with SST. The random-effects meta-analysis model revealed, across all years and all medusaoid classes that SSS (R=0.469), latitude (R=0.223), bottom fluorescence (R=0.533), mean fluorescence (R=0.338) and volume filtered (R=-0.408) were all significant factors in driving medusoid abundance at $p<0.05$. Medusoid diversity displayed a positive correlation to both temperature and salinity. A BIOENV analysis was used to explore the environmental factors that best described the variation observed in the biological assemblages. The results from this analysis suggest that SSS and bottom oxygen (BO) are the environmental factors that most influence the composition of medusoid assemblages.

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DECLARATION

I declare that: ***Interannual changes in abundance and distribution of jellyfish along the west coast of South Africa*** is my own work, that it has not been submitted before for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged as complete references.

Nausheena Parker

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Chapter 1: Introduction

1.1. Physical characteristics of the Benguela

The west coast of southern Africa is dominated by a broad northward flowing current: the Benguela Current, which represents the eastern arm of the South Atlantic Gyre. The Benguela Current extends along the west coast of southern Africa from Cape Agulhas in the south to southern Angola in the north, before it is deflected westward into the South Atlantic Ocean (Shannon, 1985).

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The Benguela Current ecosystem is characterised by seasonal upwelling. This is a wind driven physical process whereby south-easterly coastal winds results in the Ekman transportation of surface waters offshore (Shannon, 1985). This displacement of surface waters allows for sub-surface waters to replace it. As long as the wind blows, this is a continuous process causing sediment and nutrients to be "churned" up to the surface, resulting in an isothermic, nutrient-rich water column (Shannon, 1985).

The Benguela ecosystem is sub-divided into two regions, the northern Benguela and the southern Benguela upwelling ecosystems. The northern Benguela extends from the Orange River in the south (28°S, 16°E) to the Benguela-Angola Front (18^{o}S) in the north, whilst the southern Benguela extends from the Orange River in the north to the Benguela-Agulhas (35^{o}S) front in the south. The two systems are separated on arbitrary grounds at the political border between Namibia and South Africa, although the major internal boundary

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to the two systems is actually at Lüderitiz (27^{o}S). However, the two systems do differ from each other in a number of ways. The shelf off Namibia is generally broader than it is off South Africa, which means that the topographically steered upwelling currents are more pronounced in the latter than the former (Shannon, 1985). This is reflected in a greater residence time of water over the shelf in the north and a less dynamic hydrography, which in turn is reflected by differences in production and biomass. There are also differences in the seasonality of the winds, and hence upwelling. For the southern region, peak upwelling is intensely pulsed and occurs during October and March whilst in the northern Benguela, peak upwelling takes place between July and November: upwelling at Lüderitz is perennial owing to the narrow nature of the continental shelf in that region and the extensive deserts to be found inland (Shannon, 1985). The intense warming of the land during the day serves as a thermal barrier for the prevailing winds, guiding them in a SE direction along the coast and favouring upwelling.

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1.2. Biological structure of southern Benguela

The biological and trophic dynamics of the Benguela ecosystem are complex. Diversity on the west coast is much lower than that of the tropic-originating waters of the east coast of southern Africa, but the abundance of species on the west coast is substantially greater (Gibbons and Hutchings, 1996). This is as a result of the Benguela's nutrient-rich properties and upwelling process where the high concentration of nutrients promotes phytoplankton blooms and increases productivity (Verheye *et al.*, 1992). The high productivity experienced on the west coast of South Africa is able to sustain larger sized zooplankton and this allows for shorter food chains to be established. While on the east

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coast where productivity is generally much lower, the zooplankton particles are much smaller and hence supports longer food chains (Hayward, 1980). Shorter food chains tend to support higher abundances but lower diversity while longer food chains display higher assemblage diversity but low abundances (Gibbons and Hutchings, 1996; Fréon *et al*., 2009).

Phytoplankton blooms are initially dominated by large diatoms (Pitcher *et al.*, 1992) and as the upwelled water matures and moves NW under the influence of Ekman transport, the biomass of phytoplankton increases but then starts to decline owing to nutrient limitation and self-shading (Pitcher *et al.*, 1992). As the biomass declines so the composition of the phytoplankton communities also change – from diatoms through to dinoflagellates to small, naked flagellates in the warmer, more stratified and nutrient-poor waters (Pitcher *et al.*, 1992). The biomass of phytoplankton is generally higher in the northern than southern Benguela (Brown *et al*., 1991) owing to the greater residence time observed there, although production is generally lower because of increased self-shading (Brown *et al*., 1991). In the southern Benguela areas of high primary production are largely restricted to the shelf. North of Cape Columbine, where the shelf is relatively broad, there is a wide plankton-rich zone, whilst around Cape Point, where the coastal shelf narrows the plankton-rich zone narrows as well (Pitcher *et al.*, 1992). This change in primary production reflects the influence of upwelling, as areas of active upwelling (narrow shelf) support a lower concentration of phytoplankton than downstream regions (Pitcher *et al.*, 1992).

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Zooplankton communities in the southern Benguela are dominated by copepods, euphausiids and thaliaceans (Hutchings *et al*., 1995). Standing stocks of zooplankton in the southern Benguela increase from south to north, with standing stocks south of Cape Columbine ~0.5-1.0 $gC \cdot m^{-2}$, while north of Cape Columbine standing stocks are estimated at ~0.5-2.5$gC \cdot m^{-2}$ (Verheye *et al*., 1992). Copepod biomass varies seasonally in response to primary production (Verheye *et al*., 1992), being greatest in December when upwelling is most prevalent (Verheye *et al*., 1991)

Upwelling areas around the globe tend to support industrial fisheries (Jarre-Teichmann and Christensen, 1998) with often enormous yields of small pelagic fishes (anchovies and sardines). Such high fisheries yields can be supported because of the very short nature of the food-chains that lead to small pelagic fishes (Hayward, 1980). Sardines (*Sardinops sagax*) can consume phytoplankton directly if in high concentrations (Van der Lingen, 1994), whilst both sardines and anchovies (*Engraulis capensis*) can eat zooplankton, such as copepods (Van der Lingen, 1994; James and Findlay, 1989), which mainly eat phytoplankton.

1.3. Cnidarians and jellyfish biological structure

Cnidarians are globally distributed, with the majority confined to marine habitats and a small number reported in freshwater environments (Jankowski *et al*., 2005; Smith and Alexander Jr., 2008). This phylum contains over 10 000 species (World Register of Marine Species, 2014) and displays great diversity in life history strategies (Fautin, 1992).

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Cnidarians are characterized by their possession of nematocytes. These are cells containing organelles, known as cnidae, that are unique to this group and perform a locomotive, defensive and predatory function (Tardent and Holstein, 1982). They cell operates using high osmotic pressure to discharge the hook-containing organelle into its prey upon contact (Szczepanek *et al.*, 2002). The cnida structure can be described as being a coiled up hollow tube with a 'hook-like' structure attached at the end. Once the cell is triggered, the hook end is discharged with the 'hook' penetrating the prey organism. Venom is then released and injected into the prey via the hollow thread component of the cnida. With hundreds of these nematocytes being triggered (Tardent and Holstein, 1982), the prey is immobilized and guided towards the mouth by means of its tentacles.

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Cnidarians are "primitive" animals that have simple body forms and basic system functioning: they lack true organs, a brain or a central nervous system (Arai, 1997). Their basic body structure consists of two epithelial tissue layers, an endodermis and ectodermis layer, separated by gelatinous connective tissue known as a mesoglea. This "jelly-like" substance is secreted by the epidermal cells and functions as a form of structural support and buoyancy (Arai, 1997). The two tissue layers form a sac-like structure, with a single opening, used for both ingestion and egestion. The mouth opening leads to the enclosed cavity which forms the organism's stomach. Numerous tentacles surround the mouth region and these are densely equipped with nematocysts.

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With no true organs, cnidarians operate at tissue level; with groups of cells having become specialized to perform various functions: the cells that surround the stomach are known as the gastrodermis and are responsible for secreting gastric acids for digestion. Similarly cells have become specialized to perform the functions of nerves and muscles. Contractile cells along with myofibrils function as muscles and in the case of medusae are seen as darkened bands. These can be longitudinal bands (radial canals) that run length-wise down the medusae as well as a circular band (ring canal), which is found along the base opening of the medusae (Arai, 1997). On the epidermal surface along the radial canals are receptor cells, detecting various stimuli from its environment, such as light. These cells communicate with the contractile cells causing the medusa to response (Arai, 1997).

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Cnidarians have two structural forms, a sessile polyp and a free-swimming medusa; species can experience either one or both forms within their life cycle. Polyps are sedentary, sac-shaped organisms that normally occupy a benthic habitat. They may be either solitary, colonial or in clonal groups. The polyp stage tends to be the stage in which asexual reproduction occurs (Arai, 1997; Fautin, 1992), resulting in the budding off of either additional polyps or medusoids (Fautin, 1992; Collins, 2002). In the medusoid stage, individuals are solitary and bell-shaped, occupying mostly the pelagic waters where conditions are favourable. Medusae reproduce sexually; the fertilized eggs develop into a planula larva that settles on the sea-floor and moves by means of cilia-induced gliding. Once the planula has settled on the seabed it will develop into a polyp (Arai, 1997; Fautin, 1992). The free-swimming medusa stage is commonly known as a jellyfish. This term also includes other free-swimming gelatinous organisms such as ctenophores.

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There are five classes of cnidarians, each grouped according to their life cycle strategies and morphology. The class Anthozoa forms a sister group to the sub-phylum Medusozoa, which contains the remaining four classes-Staurozoa, Cubozoa, Schyphozoa and Hydrozoa, as described by Marques and Collins (2004). Anthozoans lack a medusoid phase in this life cycle expressing only a polipoid body-form. These include organisms such as corals and sea anemones. They are also structurally different when compared the remaining cnidarian groups, with anthozoans possessing a pharynx as well as distinctive cnidae (Arai, 1997).

Medusozoans are characterized by the presence of a free-swimming medusoid stage at some point in their life cycle. Staurozoans, "stalked jellyfish", were originally thought to be part of the class Schyphozoa. However, their genetic relationship with other medusiods suggests they are most likely a sister group to Cubozoa or the other medusozoans and could not have originated from one of the other classes (Collins, 2002). Staurozoa contains two orders, Stauromedusae and the extinct group, Conulatae (Marques and Collins, 2004).

In the class Cubozoa, the medusae are more commonly known as the box jellyfish - so named and characterized by their tetramerous shape and the fact that the tentacles are arranged at each of the four ventral corners. Cubozoa are more closely related to the Scyphozoa than Hydrozoa in both behavioural and structural characteristics, as discussed by Arai (1997). Of all the medusozoans, cubozoans tend to possess toxins most lethal to humans (Arai, 1997).

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Medusae, of the class Scyphozoa are generally much larger than those of Hydrozoa but, like the latter, feed on a variety of prey including copepods, other medusae, ctenophores, and fish larvae to name but a few. There has been research into the impacts of medusae feeding by Purcell (1992) and its effects on commercially important fish stocks (Purcell *et al*., 2007). The class, characterized by strobilation and ephyrae within its life cycle, consists of three orders, Coronatae, Semaeostomeae and Rhizostomeae (Marques and Collins, 2004).Within this class we generally know more about the medusoid than polypoid stage, as they are much more conspicuous (Arai, 1997). They also tend to have a more direct impact on human, such as stings to beach-goers and negative effects on fisheries (Purcell *et al*., 2007; Richardson *et al*., 2009). Whilst the nematocysts of scyphomedusae are known to have toxins, these are generally not lethal to humans (Arai, 1997).

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Members of the Class Hydrozoa tend to be much smaller than the other medusoid classes, as a rule, and they can form an important part of the plankton. Like other Cnidaria, they are predominantly carnivores with a few feeding on bacteria, protozoans, phytoplankton, algae and occasionally dissolved organic matter (Bouillon, 1999). Hydrozoa consists of two sub-classes, Trachylina and Hydroidolina. The former sub-class contains the orders Actinulida, Trachymedusae and Narcomedusae, and the latter sub-class contains orders Leptothecata, Siphonophorae and Anthoathecata (Marques and Collins, 2004).The order Limnomedusae is an order within the class Hydrozoa and does not fall within either of the two sub-classes mentioned (Marques and Collins, 2004). See Figure 1 for the illustration of the taxonomic tree of orders within Cnidaria extracted from Marques and Collins' (2004) study.

Hydrozoans may possess both polyp and medusoid stages in their life cycles, though in

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various groups one or the other stage may be absent: species in the order Trachymedusae have lost their polypoid stage whilst species in the family Plumulariidae (Leptothecata) have lost their medusoid stage (Collins, 2002). In those hydrozoan taxa that have a polyp stage, the polyps tend to occur in colonies (clones) with their coelenteron interconnected with one another (Bouillon, 1999). This allows for various polyps to be functional specialists (feeding, defence, reproduction). There are over 3500 species of hydromedusae known globally (World Register of Marine Species, 2014).

1.4. Ecological importance and our understanding of jellyfish

Jellyfish are known to aggregate in localised areas at high densities; this is referred to as a jellyfish "bloom" (Brierley *et al*., 2001). With the correct set of conditions which include warm sea surface temperatures and nutrient availability, medusae may thrive and aggregate together, resulting in sporadic blooms. It is usually a seasonal phenomenon owing to favourable conditions, but the intensity may vary between both regions and years (Purcell, 2005). There are numerous reports, from various regions around the globe, that indicate these jelly-blooms are occurring a lot more frequently and at a greater intensity (Attrill *et al*., 2007; Hay, 2006; Mills, 1995; Brotz *et al*., 2012). Ecologically, this could lead to alterations in the food-web structure. They are an opportunistic group of species with a broad diet range and fast growth rate, allowing them to quickly thrive in favourable conditions and are strong competitors with pelagic fish (Bakun and Weeks, 2006). The increasing fishing pressure on pelagic fish provides jellyfish with an even further advantage to bloom (Lynam *et al*., 2006). Jellyfish blooms can have a number of negative impacts on humans and their use of the sea, including the closing of beaches (negative effect on

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tourism), damage to commercial fishing nets and a contamination of commercial fish catches, blocking of coastal plant pipes and harm to aquaculture farms (Richardson *et al*., 2009; Båmstedt *et al*., 1998, Purcell *et al*., 2007). A number of theories have been proposed to explain the increase in jellyfish blooms witnessed in recent times. Much of the evidence points towards a variety of environmental (Attrill *et al.*, 2007) and biological (Arai, 2001; Lynam *et al*., 2006) factors that may influence their abundances, but what seems apparent is that many of the responses are a result of anthropogenic causes (Richardson *et al*., 2009; Purcell *et al*., 2012).

Global climate change (GCC) has been suggested as one such cause (Purcell, 2005). Increased atmospheric temperature results in higher sea surface temperature and an increased stratification of the water column. Phytoplankton will thrive in these conditions until nutrients are exhausted even though sea surface temperatures remain high (Pitcher *et al.*, 1992). A stratified water column gives microflagellates the advantage over larger diatoms (Pitcher *et al.*, 1992), because their mobility allows them to move deeper into the water column and thereby access nutrients otherwise denied to non-motile phytoplankton taxa. Microflagellates are significantly smaller in size than diatoms and this increases the food chain across the affected system (Richardson *et al.,* 2009). However, jellyfish are able to consume microflagellates (fish are not) and it has been suggested that this allows them to thrive in these altered systems.

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Global climate change (GCC) will also alter the pH of sea surface waters (Hays *et al*., 2005). Ocean carbonate concentrations are altered by the increase in atmospheric carbon dioxide, resulting in an increase in hydrogen ions in the ocean and thus decreasing its pH. The decrease in pH and increase in water acidity may curb calcification of organisms with calcified outer casings such as echinoderms, molluscs and various crustaceans. A study in the North Sea found a relationship between jellyfish abundance and pH in one small area: there was an increase in jellyfish as pH decreased (Attrill *et al.*, 2007). Attrill *et al.* (2007) suggested that the lower pH has a negative impact on calcifying organisms that may promote non-calcifying organisms such as jellyfish. Attrill *et al.*'s (2007) findings were queried by Richardson and Gibbons (2008) and the data reinvestigated across the entire North Sea as well as the North Eastern Atlantic. The latter authors found that there was no direct relationship between pH and jellyfish abundance in any of the regions investigated and cautioned wider generalisations of Attrill *et al*.'s (2007) results.

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Eutrophication in the marine environment has also been invoked to explain the increase in jellyfish blooms over recent time (Arai, 2001). Higher nutrient concentrations (based on skewed nitrogen, phosphorous and silicate ratios), encourages blooms of non-diatomaceous phytoplankton. Although primary production increases (leading to increased turbidity), new biomass is not utilised by consumers at a fast enough rate (Arai, 2001). As a consequence, the excess phytoplankton sinks to the benthos and undergoes bacterial degradation that leads to reduced oxygen concentrations. Such conditions favour polyp and jellyfish propagation rather than fish thriving, this was noted in the study by Richardson *et al*. (2009).

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Zooplanktivorous fish are both commercially and ecologically important. Fish, such as anchovies and sardines, have been subject to high fishing pressure over the last few decades and in various areas such as the Benguela, stock numbers have reduced drastically (Lynam *et al*., 2006). Small pelagic zooplanktivorous fish and jellyfish share the same dietary requirements and a decline in pelagic fish numbers lowers the competition pressure with jellyfish allowing them to take advantage of the opportunity (Lynam *et al*., 2006; Purcell *et al.*, 2007). The combined effects of fishing pressure and climate change may promote jellyfish to thrive (Boero *et al*., 2008). This coupled with a decrease in nutrients, may restrain high energy food chains, such as with fish and whale, and may regress the pelagic environment, promoting medusae as the top predators (Boero *et al*., 2008).

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1.5. Jellyfish within the Benguela ecosystem

The Benguela system is highly productive, with upwelling stimulating plankton blooms. This plankton biomass is then able to support an abundance of fish. This characteristic of highly productive regions, like the Benguela, makes it a key location for commercial fisheries. Namibia, in the northern Benguela upwelling system, was renowned for its prosperous fishing industry (Heymans *et al.*, 2004). Reports have shown a global decrease in fish stock due to over-fishing (Pauly *et al.*, 1998). Pauly *et al.* (1998) describes how removal of top predatory fish from the system promotes invertebrates and smaller planktivorous fish. In the northern Benguela system this did not seem to be the case. During the 1980s and 1990s observations in an increase in jellyfish abundance were noted (Brierley *et al*., 2001; Heymans *et al.*, 2004). It is suggested that they were able to dominate due to the excess food that was available as competition with fish had decreased

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(Mills, 1995; Lynam *et al.*, 2006). Jellyfish also tend to reduce fish propagation by feeding on their eggs and larvae (Arai, 1997). A combination of factors such as opened ecological space and the ability to expand their populations much faster than fish (Arai, 1997), makes jellyfish an opportunistic top predator in ecosystems. The southern Benguela is also characterized by upwelled nutrients and high productivity. Zooplankton in the southern Benguela appears to have increased over the past few decades as opposed to a general decrease along other eastern boundary current systems (Hugget *et al.*, 2009; Verheye, 2000). One of the reasons for this increase is thought to be a decline in small planktivorous fish (Verheye, 2000; Roux *et al*., 2013).

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Interannual variations in gelatinous zooplankton were studied by Buecher and Gibbons (2000). The study analysed 10 years of samples in the St Helena Bay region and found that species assemblages could be divided into two groups each year, those found in cool shallow water were dominated by meroplanktonic species and those found in warm deeper waters were dominated by holoplanktonic species. Species richness of meroplanktonic medusa was found to have a negative correlation to temperature and depth and a positive correlation to total chlorophyll *a*. Also, the abundance of meroplanktonic meduasae showed to be significantly negatively correlated with depth (Buecher and Gibbons, 2000). On the other hand species richness of holoplanktonic medusae displayed a positive correlation between temperature as well as depth, but a negative correlation to total chlorophyll *a*. The abundance of holoplanktonic medusae displayed a positive correlation with temperature but showed no correlations with depth or chlorophyll *a* (Buecher and Gibbons, 2000).

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Elsewhere, studies have discussed interannual variation in jellyfish abundance and factors closely linked to it. In the Ligurian Sea it was noted that prolonged environmental changes resulting in increased sea surface temperature promoted frequent jellyfish blooms at greater intensities (Molinero *et al*., 2008). Also, in the North Atlantic, the abundance of oceanic jellyfish was related to the abundance in zooplankton as well as increased temperature (Gibbons and Richardson, 2009).

There are numerous theories and speculations for patterns in gelatinous zooplankton abundance, distribution and species assemblages. Most of the findings seem specific to location and particular environmental conditions. The aim of this study is to explore interannual patterns in community assemblages of hydromedusae along the west coast of South Africa subsequent to the year 2000 as well as link community responses to environmental fluctuations. .

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Chapter 2: Materials and Methods

Samples collected along the west coast of South Africa, between Cape Town and Hondeklip Bay were examined. These samples were collected by the former Marine and Coastal Management during their routine surveys. Two hundred and forty two samples were examined for copepods and hydromedusae and environmental measures were also collected at each station. The data were variously analyzed using Spearmans Rank correlations (explore relationships between environmental measures), and Multiple Regression analysis, Meta-analysis and BIOENV analysis (to explore relationships between the biota and environment).

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2.1. Field sampling

The samples used in this study were collected between Cape Town (~34.3^{o}S) and Hondeklip Bay (~30.4^{o}S) on the south-west coast of South Africa during routine spawner biomass surveys conducted during October/November each year for the period between 2000 and 2006, inclusive. These surveys were conducted by former Marine and Coastal Management (now divided between Department of Agriculture, Forestry and Fisheries (DAFF) and Department of Environmental Affairs (DEA)) and were annual acoustic surveys of pelagic fish during which zooplankton samples were collected within the upper 200 m of the water column. The purpose of this, as a government mandate, is to understand the annual zooplankton and more particularly, copepod, assemblages that relate to food production for planktivorous fish, such as anchovy (*Engraulis encrasicolus*) and sardines

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(*Sardinops sagax*) (Huggett *et al*., 2009). The full survey extends from Hondeklip Bay on the west coast and continues along the south of South Africa to about Port Elizabeth (Figure 2). This survey forms the "summer" portion of the zooplankton stock assessment that has been running since 1988 (Huggett *et al*., 2009). The exact set of stations sampled each year varies, but stations are generally 10 nautical miles apart from each other along transects orientated perpendicular to the coastline (Figure 2).

Zooplankton samples were collected from each station using paired vertical bongo nets that were fished from 5 m above the seabed to the surface, to a maximum depth 200 m. The nets had a diameter of 0.57 m, were fitted with a 200 μm mesh (Huggett *et al*., 2009) and were equipped with a General Oceanics flow-meter (Huggett *et al*., 2009). The nets were hauled vertically at a rate of 1 m per second. Upon collection, the zooplankton samples were immediately preserved in a 5% buffered sea-water formalin for later examination in the laboratory. The volume of water filtered by each net was calculated using equation 1.

Volume Filtered (m^3) = Average Flow Rate (m/s) **x** Tow Duration (s) **x** Net Mouth Area (m)

Equation 1

At each station sampled, a Seabird model SBE 9 conductivity-temperature-depth (CTD) instrument was used to profile the water column, following standard techniques (e.g.

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Buecher and Gibbons, 2000). The CTD was additionally equipped with an oxygen sensor and a fluorometer, so that vertical profiles of dissolved oxygen and fluorescence could be obtained. Water samples were collected for the determination of chlorophyll *a* concentration using Niskin bottles, that were triggered just below the surface, at 5 m above the bottom (or at a maximum of 200 m in deeper water), as well as at the fluorescence maximum.

The CTD measured physical parameters throughout the water column: depth (m), sea temperature (^{o}C), sea salinity (psu), sea oxygen (ml/l) and fluorescence (ug/l). Bottom depth (m), latitude and longitude were also recorded at each station. From the CTD the data were then transmitted to the SeaBird software computing console aboard the research vessel. Values for sea surface and bottom variables (temperature, salinity, oxygen and fluorescence) were obtained from the CTD reading closest to the surface and closest to the bottom respectively. The mean fluorescence and integrated fluorescence were both calculated from the fluorescence values obtained throughout the water column depth. Fluorescence was used as a proxy for chlorophyll *a* concentration (as e.g. Jesus *et al.*, 2006).

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2.2. Laboratory analysis

The copepods from each zooplankton sample were analyzed by colleagues at DEA following standard procedures (Verheye *et al*., 1998). In short, the zooplankton sample was re-suspended in a known volume of seawater (generally 10 x the settled volume), and three

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subsamples of 2 ml each were removed using a Stempel Pipette (Hugget *et al*., 2009). All copepods were identified and counted from each sub-sample in a Bogorov Tray (Corner *et al.,* 1976) under a stereo-microscope at various magnifications. Identification included species and stages, to the lowest possible taxonomic level. The data from each subsample were then pooled, and densities then calculated using knowledge of the volume filtered by each net, and the fraction of the sample represented by the subsamples counted.

Following the estimation of copepod density, samples were stained with Rose Bengal for 24 hrs. The medusae and siphonophores were then counted from each sample under a stereomicroscope between 10x and 40x magnification. Specimens were identified to the lowest taxonomic level where possible using Pagès *et al*. (1992), Bouillon (1999) and Bouillon *et al.* (2006).

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When medusae could not be identified to species they were described using a combination of morphological features (including bell and manubrium shape and size; number and shape of radial canals; bell consistency; number and form of tentacles, tentacular bulbs, statolyths and ocelli; mouth and lip shape; position of gonads as in Bouillon *et al.* (2006)), and unique morpho-types were assigned an identifier: voucher specimens were retained. In the case of siphonophores, specimens of Calycophorae were identified (and counted) on the basis of their anterior nectophores only (polygastric and eudoxid stages were counted separately). Physonect siphonophores were identified on the basis of nectophore morphology, and were counted based on the numbers of pneumatocysts: samples without

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pneumaotcysts but with nectophores were assumed to contain a single individual. All counts of medusae per sample were converted to density by dividing the counts by the volume filtered. Species data were additionally categorized by Order (Leptothecata, Anthoathecata, and Trachy-, Narco- and Limno-medusae).

2.3. Data handling and statistical analyses

To visualize spatial patterns in the distribution of all measured variables each year, contour plots were generated using Surfer 9 software (as in e.g. Huggett *et al.*, 2009). Average measures (+/- standard deviation) of each variable were also generated for each year and tabulated. The species richness and diversity measures of medusae were calculated for each sample based on the Shannon Index (Magurran and May, 1999) using PRIMER 6 (Clarke and Gorley, 2006). Further, the data for each year were pooled and the diversity of assemblages calculated for the entire study period (2000-2006).

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To explore the relationship between environmental variables, a matrix of Spearman Rank correlations was generated each year. The bottom fluorescence (BFL), integrated fluorescence and mean fluorescence variables were omitted from the analyses for 2000 (only) owing to the paucity of data. The multiple testing nature of this analysis increases the chances of a Type I error (increases the likelihood of obtaining a false significant result), and so the Bonferroni Correction was applied to adjust the critical p-value (as Richardson and Verheye, 1998), following Quinn and Keough (2002). Scatter-plots were also generated between bottom depth and sea surface temperature (SST), sea surface

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salinity (SSS), sea surface oxygen (SSO) and sea surface fluorescence (SSF) and between fluorescence and temperature as well as fluorescence with salinity. These were the only variables used in the scatter plots as they had a tendency to generally display strong relationships.

In order to explore pattern in the multivariate environment, data were first $\log_{10}$ transformed and normalized, and a resemblance matrix generated (Euclidean Distance) between samples (Clarke and Gorley, 2006). The matrices were subsequently used to construct dendrograms of percent similarity between the multivariate sample environments each year. The bottom depth of each sample was used *a priori* as a grouping factor in the dendrograms to provide a visual aid of how samples were clustered in relation to depth.

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To explore patterns in the structure of medusoid assemblages, jellyfish data for each year were square-root transformed to reduce the bias of dominant and rare species (Clarke and Gorley, 2006). This was followed by the production of a Bray Curtis resemblance matrix between samples, as this is an appropriate index for determining similarity between biological samples (Clarke and Gorley, 2006). The similarity matrix was subsequently used to construct dendrograms of percentage dissimilarity between samples each year. The bottom depth of each sample was used *a priori* as a grouping factor in the dendrograms, providing a visual aid of how samples were clustered in relation to depth.

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To understand the diversity of medusoid assemblages at each station and for each year, the Shannon diversity index (H') was calculated, using PRIMER 6 (Clarke and Gorley, 2006). The calculation also returned a measure for species eveness (J'), which corrects diversity for dominating species, and the number of species present in the sample (S') (Magurran and May, 1999).

In order to explore the relationships between the structure of medusoid assemblages and the multivariate environment, a BIOENV analysis was conducted in Primer 6 (Clarke and Gorley, 2006). This analysis indicates the environmental variables that most influences medusoid assemblages. The BIOENV analysis was conducted on assemblages each year and used the medusae resemblance matrix and the corresponding normalized environmental dataset. The model applied a Spearman correlation method and generated 99 permutations to produce the test statistic. This test is more robust for unbalanced datasets and makes no assumptions about the dataset's normality (Clarke and Gorley, 2006).

In order to explore drivers of abundance (dependent variable) for each of the major medusoid orders across the time series, a backwards step-wise multiple regression analysis was first conducted with all environmental variables (log_{10} transformed) each year, using STATISTICA v7. A meta-analysis using partial correlations was then constructed following Worm and Myers (2003) and Worm et al. (2003). The model combines individual partial correlations between each order and each variable within each year to generate an overall correlation across all years. A random-effects model was used as

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opposed to the fixed-effects model as it makes no assumptions that the effect size for each year's correlation coefficient was identical. The random-effects model is also more conservative than the fixed-effects model (as in e.g. Gibbons *et al*., 2005).

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Chapter 3: Results

3.1. Environmental characteristics

Caveat

Although all measured environmental variables were used in all of the analyses, only those that displayed some significance were highlighted and discussed further. This was also done to avoid repetition, particularly in the case of the correlation matrix results.

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3.1.1.Sea Surface Temperature (SST)

Generally SST tended to increase in an offshore direction (Figure 3), though localized minima were observed NW of Cape Columbine and between Lamberts Bay and Hondeklip Bay (Figure 3). SST was highest (on average) in 2001 (mean 15.82 ^{o}C, SD 0.88), and lowest in 2004 (13.37 ^{o}C, SD 1.75) (Figure 3b and 3e respectively, Table 1). In most years SST displayed a significant positive relationship with bottom depth and sea surface salinity (SSS) as well as with bottom oxygen (BO) (0.80) in 2006 (Table 2). By contrast, there was a significant negative correlation with bottom fluorescence (BFl) in 2003 (-0.87) and bottom temperature (BT) (-0.84) in 2005 (-0.80) and with bottom salinity (BS) (-0.87) in 2004 (Table 2).

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Across all years SST ranged between 10.08 ^{o}C and 19.23 ^{o}C. The scatter plots between SST and bottom depth revealed a general trend across all the years where temperature increased steeply until about 200 m. Thereafter it remained mostly constant as the depth increased (Figure 4a). This trend was displayed each year and at very similar gradients, with only the year 2001 portraying slightly higher SST values inshore.

3.1.2. Sea Surface Salinity (SSS)

Like SST, SSS also tended to increase in an offshore direction (Figure 5a-g) and with a mean of 35.10 was highest during 2001 (SD 0.23), 2002 (SD 0.30), 2003 (SD 0.20) and 2005 (SD 0.24) and lowest during 2004 (34.82, SD 0.17) (Figure 5b and 5e, Table 1). Besides the positive relationship between SSS and SST and depth (Table 2), there was a strong negative correlation with BFl during 2002 (-0.83) (Table 2c), while in 2004 (Table 2e) there was a strong negative correlation with BT (-0.88) and BS (-0.84).

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Across all years SSS ranged between 34.53 and 35.64. The positive relationship between SSS and depth was also observed in the scatter plots, where salinity initially increased gradually within the first 100 m then increased more steadily between 100 m and 300 m (Figure 4b). The salinity remained approximately constant at depths greater than 300 m. Unlike SST, there was some interannual variability where salinity was generally lower in the year 2000 and slightly higher in the year 2005. The inshore values also displayed less variability than the offshore values.

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3.1.3.Sea Surface Oxygen (SSO)

SSO displayed a relatively constant relationship with depth, fluctuating around 6 ml/l (Figure 4c). This stability was observed throughout most of the water column, except for the upper 50m where the variability was greatest. Surface oxygen concentration was highest in 2000 (mean 6.60 ml/l, SD 1.28); the variance was also greatest during this year (Table 1). Surface oxygen concentration was lowest in 2005 (5.30 ml/l, SD 0.53) (Table 1). Across all years SSO ranged between 2.72 ml/l and 10.76 ml/l.

3.1.4.Sea surface fluorescence (SSF)

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In general, fluorescence was higher inshore than offshore and localised maxima were observed either downstream from the upwelling centres at Cape Point or Cape Columbine (2000, 2002, 2004) or near-shore in St Helena Bay (2003, 2005-6) (Figures 6). Highest surface fluorescence was observed in the year 2000 (mean 1.59 ug/l, SD 1.89), and it was lowest in 2001 (0.34 ug/l, SD 0.37) (Figure 7a, Table 1). In general, SSF did not display consistently strong correlations with any of the other environmental variables (Table 2 a-g). It was only in 2004 that there was a strong positive correlation between SSF and sea surface oxygen (0.81) (Table 2e). Slightly weaker negative correlations were observed in some of the years between SSF and bottom depth, SST and SSS, but these were less than -0.80.

Across all years SSF ranged between 0.07 ug/l and 11.96 ug/l. The scatter plots between SSF and SST indicated a dome-shaped relationship, where the relationship was positive

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until it reached a peak thereafter exhibiting a negative relationship. At temperatures below 13 ^{o}C, fluorescence was relatively low, then peaked between 14 ^{o}C – 16 ^{o}C and reduced again at temperatures beyond 16 ^{o}C (Figure 7b). This trend was generally observed for all years, but in the years 2001 and 2005 the fluorescence peaked at much lower concentrations. The relationship between SSF and SSS also displayed a dome-shaped curve, but with a very steep increase to 34.8 where salinity fluorescence peaked then gradually declining thereafter (Figure 7c). Interannually, the years 2000 and 2002 generally displayed slightly higher fluorescence concentrations.

3.1.5.Copepod abundance

With the exception of 2004, copepod abundance was generally higher inshore than offshore and it had a tendency to be highest in the core of St Helena Bay (Figure 8). Average abundance was highest in 2004 (mean 12763 ind.m^{-3}, SD 23597) (Table 1), and lowest during 2005 (1485 ind.m^{-3}, SD 2018) (Table 1). Across all years copepod abundance ranged between 0 and 233 9226.67 ind.m^{-3}. In general, copepod densities had a tendency to be greatest at temperatures between 11 ^{o}C and 16 ^{o}C (Figure 9a), and at salinities between 34.5 and 35 (Figure 9b). While a weak dome-shaped relation was observed between fluorescence and abundance (Figure 9c), abundance tended to decline exponentially with depth (Figure 9d).

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3.2. Hydromedusoid patterns

3.2.1.Abundance

Unlike the patterns observed for the various environmental measures or for copepods, there was no consistent interannual pattern in the distribution of jellyfish in the region (Figure 10). In some years, densities were highest inshore e.g. 2000 (Figure 10a), whilst in others they were most common offshore e.g. 2002 (Figure 10c). Jellyfish were most abundant in 2005 (Table 1) when average densities of 3.15 ind.m^{-3} (SD 3.21) were recorded, and they were least abundant in 2002 when only 0.50 ind.m^{-3} (SD 0.70) were observed. Across all years hydromedusan abundance ranged between 0 and 62.87 ind.m^{-3}.

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The results of the meta-analysis (Table 3) indicates significant positive correlations between overall medusae abundance and latitude, salinity, bottom fluorescence as well as mean fluorescence. There was also a significant negative correlation between overall medusae abundance and the volume of water filtered by the nets (Table 3). Across all years a weak dome-shaped relationship was observed between abundance and both SST and SSF (Figure 11). There was also a general decrease in abundance with increasing depth, although densities levelled off at depths greater than 200 m (Figure 11d). As supplemental data, the partial correlations that the meta-analysis was based on can be found in Table 4.

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3.2.2.Diversity

A total of 69 species of medusae were identified across the area over the study period (Table 5). With the exception of the year 2000, species richness was generally higher offshore than inshore (Figures 12).While the greatest number of species (40) was recorded in the year 2006, the year with the highest average diversity was 2002 (H' = 0.82, Table 1). Both species richness and diversity were lowest in 2003, when only 18 species were recovered from the sampling region.

There was a general positive relationship between jellyfish species richness and surface temperature as well as with surface salinity (Figure 13a and 13b), indicating that the number of species increased with temperature and salinity. Hydrozoan richness did not display any obvious relationship with sea surface fluorescence, but was generally higher when surface fluorescence was less than 1.5 ug/l (Figure 13c). Generally a positive relationship was observed between depth and richness. Most of the samples were collected within the 200 m water column, but those that were collected within a water column greater than 300 m generally displayed higher diversity (Figure 13d).

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3.2.3. Analysis by order

The abundance of medusae in each order was mapped out individually for each year. In general, communities were dominated by siphonophores, although there were occasions (e.g. 2000 and 2004) when leptothecate medusae were most abundant (Table 1)). Narcomedusae were the least common group. In general, the orders Anthoathecata,

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Leptothecata and Limnomedusae were distributed near the coast, whilst Narcomedusae, Trachymedusae and Siphonophorae were (with some exceptions) distributed further offshore (Figure 14).

3.2.3.i. Anthoathecata

In the years 2000 (Figure 15a) and 2005 (Figure 15f) medusae displayed similar distribution patterns: highest concentrations were found around Lamberts Bay. In the years 2001 (Figure 15b), 2002 (Figure 15c) and 2006 (Figure 15g), peak numbers were found near St Helena Bay, whilst in 2003 (Figure 15d) they were concentrated around Yzerfontein. Across all years Anthoathecata medusan abundance ranged between 0 and 8.45 ind.m^{-3}. The results of the meta-analysis indicated that the only predictor influencing abundance across the time series was the volume of water filtered by the nets with a positive relationship (Table 3).

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3.2.3.ii. Leptothecata

Medusae from this order appeared to be well represented along the coast in the region north of 32^{o}S (Figure 16) each year, although in some years they extended further (north and south). During the years 2001 and 2003 (figure 16b and 16d respectively) low densities were observed along most of the coast, although in 2001 an offshore distribution was observed as well. Also, in the year 2001, medusae displayed a slightly different pattern, and high concentrations were found south of 32^{o}S (off St Helena Bay). In the years 2000 (Figure 16a), 2002 (Figure 16c) and 2006 (Figure 16g) high concentrations of these

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Hydrozoa were found near Hondeklip Bay. In 2003 and 2005 (Figure 16f) peak concentrations were observed near Doring Bay. Across all years Leptothecata medusan abundance ranged between 0 and 62.23 ind.m^{-3}with maximum abundances observed in 2004. Results of the meta-analysis revealed that there was a significant positive correlation with bottom fluorescence and a negative correlation with integrated fluorescence (Table 3).

3.2.3.iii. Limnomedusae

This order displayed a fairly constant distribution pattern across all years. The main regions where the abundance of Limnomedusae peaked each year were along the coast in the St Helena Bay region (approximately between 32^{o}S and 33^{o}S) and near Hondeklip Bay (north of 31^{o}S) (Figure 17). In the years 2000 (Figure 17a), 2004 (Figure 17e) and 2005 (Figure 17f) distributions were only observed in the St Helena Bay region, while in the years 2001 (Figure 17b), 2002 (Figure 17c), 2003 (Figure 17d) and 2006 (Figure 17g) they were also common close to Hondeklip Bay. Across all years Limnomedusan abundance ranged between 0 and 3.33 ind.m^{-3}.The only environmental variable that was significantly related (negative) to the abundance was bottom oxygen (Table 3).

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3.2.3.iv. Trachymedusae

Trachymedusae displayed an offshore distribution across all years, with highest concentrations of medusae found in the water column with depth greater than 200 m (Figure 18). Their latitudinal range was also widespread as they were observed all along the study area (30^{o}S-34.5^{o}S). These patterns were consistent for all years except 2003

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(Figure 18d) where peak abundances of Trachymedusae were found along the coast north of Doring Bay (31°S-32°S) and near Cape Town. Across all years Trachymedusan abundance ranged between 0 and 3.40 ind.m^{-3}. There was a significant positive correlation with volume filtered and with sea surface salinity variables (Table 3).

3.2.3.v. Narcomedusae

This order of hydrozoa was absent in two of the years under study, namely 2000 and 2003. In the years where they were present their distributions were mostly offshore and widespread across the survey area (Figure 19). Although in 2004 (Figure 19c) and 2005 (Figure 19d) their distributions were isolated to smaller ranges. Distribution patterns in 2001 (Figure 19a) and 2006 (Figure 19e) were similar, and the abundance of medusae increased from north to south and decreased closer to the coast. In 2002 (Figure 19b) the densities of Narcomedusae were generally evenly distributed across the latitudinal range and had also decreased along the coast. Across all years Narcomedusan abundance ranged between 0 and 2 ind.m^{-3}. From the data that was analyzed there was an overall positive significant correlation with sea surface oxygen and a significant negative correlation with longitude and with total copepods (Table 3).

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3.2.3.vi. Siphonophorae

Distribution patterns for Siphonophorae were diverse, some years displayed peak coastal abundances while other years had higher densities offshore (Figure 20). During 2001 (Figure 20b), 2003 (Figure 20d), 2005 (Figure 20f) and 2006 (Figure 20g) siphonophores

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were concentrated along the coast, where densities were greatest between Saldanha Bay and Cape Town, and occurred at much lower densities offshore. In the years 2000 (Figure 20a), 2002 (Figure 20c) and 2004 (Figure 20e) siphonophores were predominantly concentrated offshore. Across all years Siphonophorae abundance ranged between 0 and 15.57 ind.m^{-3}. The only environmental variable that displayed a significant relationship with Siphonophorae was sea surface salinity, with a positive correlation (Table 3).

3.3. Cluster Analysis

3.3.1.Environmental data

In most years there was a general clustering according to sample depth and these could be divided into three groups (Figure 21). Inshore samples collected within 100 m were grouped together; offshore samples collected at depths deeper than 200 m displayed a high level of similarity and clustered together. Samples collected over the shelf area (between 100 m and 200 m) were not clearly separate and rather tended to cluster variously with the inshore or offshore samples. In some years a few samples were taken at greater depths (>300 m), and although these did not cluster together, they were clustered with the balance of deeper-water samples, as seen in the years 2000 (Figure 21a) and 2006 (Figure 21g).

3.3.2.Hydrozoan assemblages

Just as observed with the environmental data, hydrozoan assemblages also displayed clustering according to the depths they were collected at. Overall, distinct assemblages

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could be identified each year by inshore (< 100 m) and offshore (>200 m) sample groups (Figure 22), with mid-shelf samples (100 – 200 m) tending to be part of either former group. In 2000 (Figure 22a), 2001 (Figure 22b) and 2002 (Figure 22c) assemblage were grouped at a similarity level of approximately 30%. In each of these years most of the inshore samples were grouped together, while a few samples displayed greater similarity to either shelf or offshore groupings.

In the years 2003 (Figure 22d) and 2004 (Figure 22e), a higher level of similarity was observed between inshore and offshore samples (60-70%) than in the previous years. In the case of the year 2003 (Figure 22d) a number of outlying samples were noted, but most of the offshore and shelf samples formed distinct clusters. In the year 2004 (Figure 22e), two main clusters were seen, one that contained only offshore and shelf samples and the other contained two shelf samples, an inshore and an offshore sample. The other inshore samples were outliers.

In the year 2005 (Figure 22f) most of the samples formed offshore and shelf clusters. The inshore samples either displayed greater similarity to the offshore or shelf clusters or they formed outlying groups. In the year 2006 (Figure 22g), the shelf and offshore samples display greater similarity to one another, while inshore samples generally clustered close to the shelf samples.

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3.4. BIOENV analysis

The results from the BIOENV analyses between environmental variables and hydromedusae assemblages (Table 6) suggest that sea surface salinity (SSS) and bottom oxygen (BO) play a strong role in influencing the multi-species structure of assemblages. SSS was found to be significant in the years 2001, 2002, 2005 and 2006, while BO was important in the years 2001, 2002, 2004 and 2005. The strongest correlation was noted in the year 2001 (0.716) linking SSS, BO and mean fluorescence as significant environmental variables. The weakest correlation factor was observed in the year 2003 (0.478) linking latitude, surface temperature (SST), bottom salinity (BS) and bottom fluorescence (BFl). BFl was noted to be significant in three years (2002, 2003 and 2005).

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Chapter 4: Discussion

4.1. Environmental trends

4.1.1. Physico-chemical

The individual environmental and chemical factors that structure the habitat for biotic communities play an important role in influencing organism abundance and distribution by either promoting or inhibiting a species success (Huggett *et al.*, 2009; Overland *et al*., 2010; Palma *et al*., 2011). Usually, the environmental factors vary together (positively or negatively) to create a general set of conditions within particular regions (Shannon, 1985): for example the relationship between SST and depth. The results from the cluster analysis indicated that the environment could be separated into inshore, shelf and offshore areas, displaying similar environmental attributes according to their depth range (Figure 21). This was most likely due to the wind driven process of upwelling, as during the process an isothermic water column becomes established. As a result, the inshore area was characterised by low surface temperatures and low surface salinities (Shannon, 1985) as well as other environmental characteristics that are influenced by these two properties.

Within the study region SST generally increased with increasing bottom depth to about 300 m, whereafter it started to level off (Figure 4a). The cooler coastal waters is an indication of coastal upwelling, with the cold sub-surface upwelled water warming up as it is moved offshore by Ekman transport (Shannon, 1985). The upwelling intensity is reflected by the extent of cooler coastal water (Shannon, 1985). For example, in 2002 (Figure 3c) the extent

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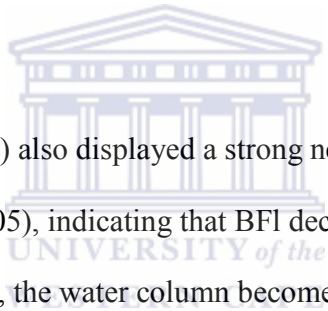
of the cooler water covered most of the region shallower than 100 m, whereas in 2005 (Figure 3f) the cooler region was much reduced. This suggests that recent upwelling may have occurred at the time of the 2002 sampling cruise. Throughout the years observed, the regions south of Hondeklip Bay consistently had cooler temperatures along the coast than the other regions. The coastal regions near Lamberts Bay also frequently displayed cooler temperatures. These persistently cooler regions indicate areas that tend to experience consistent coastal upwelling each year (Shannon 1985). Regions such as Cape Columbine, which is an upwelling centre exhibit highly variable temperatures, particularly in the summer months, which is mainly wind-driven (Blanke *et al*., 2002).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Sea surface temperature (SST) also displayed a strong negative correlation with bottom fluorescence (in 2003 and 2005), indicating that BFl decreases offshoreward. As SST and depth both increased offshore, the water column becomes stratified and at greater depths less light is able to penetrate reducing solar heating and bottom temperature (Shannon, 1985).The low chlorophyll content of source water reflects the reduced bottom fluorescence due to limited light and as well as bottom salinity (Shannon, 1985). These conditions were reflected in the correlations between SST and bottom temperature (BT) and bottom salinity (BS) in the year 2004 and a positive correlation with bottom oxygen (BO) in 2006. The increase in BO may be due to the improved solubility of oxygen at lower temperatures and higher oxygen content of source water (Shannon and Nelson, 1996).

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For most of the years, sea surface salinity (SSS) displayed a strong positive correlation to both depth and SST, exhibiting low salinities in cool, nearshore waters. This reflects the process of upwelling (Shannon, 1985) as the source water has a comparatively low salinity (Chapman and Shannon, 1985). As the surface water layer is displaced offshore it is subject to solar heating and evaporation and the SSS increases (Shannon, 1985; Verheye *et al*., 1991). Due to the positive relationship between SSS and SST and bottom depth, the correlations with other variables were similar to those observed with SST. Hence BFl, BT and BS were observed to decrease at higher SSS, while BO increased.

Sea surface oxygen (SSO) did not display any strong correlations with the other environmental variables. There was a moderate negative correlation between SSO and depth: warmer, offshore waters generally have lower concentrations of dissolved oxygen than cooler upwelled waters as solubility decreases with increasing temperature (Shannon and Nelson, 1996). This was true for all years expect during 2004, where a very weak positive correlation was observed (Table 2e), which may be explained by the strong positive correlation with sea surface fluorescence (SSF) then, as an increase in primary production may result in elevated levels of oxygen (during the day) (Chapman and Shannon, 1987).

4.1.2. Fluorescence

Fluorescence was highest along the coast, where upwelling occurred and lowest offshore where the water column begins to stratify and nutrients become depleted in the surface

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layers (Pitcher *et al.*, 1992). Sea surface fluorescence (SSF) shows a general trend to peak between temperatures 14 ^{o}C and 16 ^{o}C with lower concentrations on either side of this range. Actively upwelled water, where SST ranges between 10 ^{o}C and 12 ^{o}C (Verheye *et al.*, 1992) is nutrient rich, is moved offshore and this surface layer of water is exposed to solar heating, allowing phytoplankton to flourish. As the water moves further offshore the nutrients become exhausted and phytoplankton concentrations cannot be sustained and are eventually reduced (Pitcher *et al.*, 1992). The only strong correlation between SSF and any of the other measured environmental variables was with mean fluorescence (positive), indicating that mean fluorescence increases as SSF increases, which is expected.

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Various regions along the coast displayed a higher tendency to concentrate phytoplankton (Figures 6a, 6c and 6e). These areas were generally near Saldanha Bay, St. Helena Bay and Hondeklip Bay. According to Shannon and Nelson (1996) Cape Columbine and Cape Point are all regions that demonstrate a greater upwelling intensity. The constant influx of nutrients within these regions was able to sustain the phytoplankton biomass noted downstream (Pitcher *et al.*, 1992). Further, St. Helena Bay is also influenced by cyclonic eddies that promote a semi-closed circulation system (Holden, 1985), which results in enhanced chlorophyll biomass following retention (Hutchings *et al.*, 2009).

4.1.3. Copepod abundance

Copepods were more abundant inshore, rapidly declining with offshore distance. In most years the densities start to decrease beyond the shelf region (depth greater than 200 m)

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(Figure 8 and Figure 9d). Copepod numbers are known to increase with elevated levels of phytoplankton biomass, which in turn is a response to upwelling. Therefore during the peak upwelling season when phytoplankton biomass is higher, between October and March, the abundance of copepods is expected to be higher than during the seasons with little or no upwelling (Verheye *et al*., 1991). In most years copepod abundances were higher downstream of active upwelling, in areas such as Lamberts Bay, Hondeklip Bay and St Helena Bay, wherein they may have been trapped by cyclonic eddies and coastal gyres (Holden, 1985). The increase in primary production, as a result of the entrapped phytoplankton within the enclosed circulation enhances the developmental rates of copepods, which are mostly herbivorous planktivores (Verheye *et al*., 1992). Verheye *et al*. (1991) also explain that larger copepods are more commonly found near the coast, while the smaller juvenile stages tend to be offshore. The juvenile stages occupy the upper layers of the water column (Verheye *et al*., 1991) and possess limited vertical mobility making them prone to offshore Ekman transportation during active upwelling (Verheye *et al*., 1991; Shannon, 1985). As the adult copepods accumulated inshore, resulting in greater densities inshore rather than offshore and this was also reflected in the results.

Copepod abundance displayed high interannual variability, ranging from an annual mean of 12 763 ind.m^{-3} in 2004 to 1 485 ind.m^{-3} in 2005 and a dome-shaped relationship with temperature, salinity and fluorescence was observed. The abundance peaked between 12 ^{o}C and 14 ^{o}C (Figure 9a) and at 1.5 ug/l for fluorescence, while salinity displayed a steep peak in abundances around 34.5 with a sharp decline with higher SSS (Figure 9b). These relationships partly reflect the variables (SST, SSS and SSF) correlation with bottom depth

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(Table 2). Hence in coastal waters, where temperature and salinity were lower, copepod abundances peaked, while offshoreward where temperatures and salinities increased, copepod abundances decreased. This also indicates the link to upwelling and primary production that is present along the coast, as certain species of copepod, such as *Calanoides carinatus,* are upwelling specialists and may dominate assemblages (Verheye, 2000).

4.2. Medusae

4.2.1. Abundance and assemblage structure

Hydromedusae generally occur at much lower abundances than copepods, which have been observed in this study. When comparing the two biota, the highest annual mean for medusae was <3.5 ind.m^{-3} in 2005 (Table 1), while copepods had a maximum annual mean of 12 763 ind.m^{-3} in 2004 (Table 1). This difference in abundance was expected as they occupy different trophic levels. Copepods are generally herbivorous or omnivorous planktivores that occupy a lower level down on the food chain and occur at higher abundances than medusoids, which are carnivorous. Generally, the lower trophic levels are found in greater abundances as they supply food and energy to the trophic level above it (Shannon *et al*., 2003).

The abundance of medusae generally peaked near or downstream of upwelling centres and densities were higher along the coast than offshore (Figure 10). This was also observed in the scatter plot between the abundance of medusae and depth, where there was a peak very

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close to the coast, within the 100 m bottom depth (Figure 11d). Although the coastal assemblages were more abundant, previous studies note that hydromedusae form two types of assemblages, either coastal or offshore (Pagès and Gili, 1992; Gibbons *et al*., 2010) and offshore assemblages of trachymedusae and narcomedusae were present as well. This assemblage structure was also supported by the cluster analysis where samples displayed a similarity in their species composition and abundance based on their distance from the coast (Figure 22) forming inshore, shelf and offshore assemblages. The higher coastal abundances were mostly due to the dominating siphonophore species, which occurred at high densities during most years. In the years 2002 (Figure 10c) and 2005 (Figure 10f) a general offshore dominated assemblage was observed and although siphonophores still dominated during those years their distribution displayed greater offshore dispersal than in other years. Siphonophores occupy the surface waters and posses limited mobility, this subjects them to offshore Ekman transport after upwelling once the upwelled water had matured (Pagès et al., 1991). It is possible that in those two years samples were collected post an upwelling event, resulting in the dominant siphonophores being part of the offshore medusae assemblages.

In the study by Beucher and Gibbons (2000) it was noted that the Leptothecata medusa *Mitrocomella millardae* occurred every year and was also the most abundant species observed at St Helena Bay. In comparison, this study only noted the species at a total of three stations during 2002 and 2005 (Table 5). Some of the more common species observed every year were *Leuckartiara octon, Obelia sp., Proboscidactyla menoni, Persa incolorata, Dimophyes arctica and Muggiaea atlantica,* which were also observed every year in the study by Beucher and Gibbons (2000). The samples collected by Beucher and Gibbons (2000) were winter samples while the ones collected in this study were spring samples and

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not limited to St Helena Bay alone. These factors may explain the differences notes in species assemblages.

There was a dome-shaped relationship between the abundance of medusae and temperature, indicating that there was an optimal thermal window between 12 – 16 ^{o}C (Figure 11a). With higher temperatures certain species have been reported to respond favourably, such as *Liriope tetraphylla*, which displayed an increase in abundance at higher temperature in the Mediterranean Sea (Buecher *et al*., 1997). Similar positive responses of the same species were noted for salinity increases (Pagès and Gili, 1992; Buecher *et al*., 1997). The results collected here indicate that although hydromedusae were found in approximately the same salinity range as copepods they occurred at relatively higher abundances towards the higher end of the salinity range (figure 11b).

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In the years 2000, 2004 and 2005 the abundance of hydromedusae all displayed similarly high annual means. This mostly mirrors the trend observed in copepod abundance, which peaked in 2000, 2004 and 2006 (the latter being the only inconsistent year). While 2005 had the highest annual mean for medusae it was also the lowest annual mean for copepods. 2005 was also the year where assemblages were dominated by siphonophores. The assemblages in 2000 and 2004 had, in contrast, been dominated by Leptomedusae. These two orders of medusae did not exist at equal abundances, the one always dominated over the other. Siphonophores, such as *Muggiaea atlantica*, which was also the most common siphonophore observed, prefer to feed on smaller crustaceans such as copepods (Purcell,

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1982). This suggesting that they may have had an impact on copepod densities as the years with siphonophore dominance displayed much lower copepod densities, with the exception in 2006. *Muggiaea atlantica* is considered a cold-water species that thrives in upwelling areas (Pagès et al., 1991; Thibault-Botha *et al.*, 2004), and may dominate assemblages along the south east coast of South Africa, where waters can occasionally be cool and productive (Thibault-Botha *et al.*, 2004). Further north along the east coast, where waters are more characteristic of the Agulhas Current, higher temperatures and low productivity, siphonophores if present were in low numbers (Thibault-Botha *et al.*, 2004).

There was also an evident trend where siphonophores generally dominated the gelatinous assemblages when salinity was higher. This was seen in 2001-2003 and 2005 (Table 1), all years with higher salinities. The only exception was in 2006 and although salinity levels were low, siphonopores still dominated the assemblage (Table 1). In general, medusae displayed a peak in abundance around 15-16 ^{o}C and decreased moving away from this temperature. Although many studies have concluded that gelatinous zooplankton increase in abundance with the rise in temperature, Buecher and Gibbons (2000) explain that holoplankton (typically offshore species such as *Liriope tetraphylla*) increase during warmer years, while meroplankton (typically coastal species such as *Leuckartiara octona*) decrease during warmer years.

Narcomedusae, part of the offshore assemblages and occurring at very low densities displayed a negative relationship with copepods, longitude and surface oxygen (Table 3).

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The negative relationship with copepods indicates that as the abundance of narcomedusae increased offshoreward, copepod abundance decreased. This relationship was expected as copepod densities were higher along the coast. The negative relation with longitude and positive relationship with surface oxygen were a bit unclear, but this may be due to the low number and patchiness of narcomedusae collected. Leptothecata displayed a positive relationship with bottom fluorescence, indicating that abundances are higher with higher concentrations of bottom fluorescence. Bottom fluorescence would be higher inshore in the shallower nutrient –rich waters as opposed to offshore where the water column is nutrient-poor and light penetration in weaker at greater depths. Hence the relationship indicates that the abundance of Leptothecata medusae were higher inshore, which corresponds to them being an inshore group. There was a positive relationship between Anthoathecata medusae and the volume filtered by the nets, indicating that the greater the volume of water filtered by the nets the higher the number of medusae collected. This may suggest an aggregation of Anthoathecata medusae at the time samples were collected.

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General trends across all years and orders displayed that the abundance of medusae shared significant correlations with latitude, volume of water filtered by the nets, mean fluorescence, bottom fluorescence and sea surface salinity (Table 3). While surface temperature did not display an overall significance in the meta-anaysis, even though a one was expected, this may have been due to the conflicting relationships between SST and the difference medusae orders. The inshore orders resulted in a negative relationship with SST while offshore orders were positive; this may possibly have resulting in an overall non significant result.

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4.2.2. Diversity

A total of 35 hydromedusae and 33 siphonophorae species were found. Beucher and Gibbons (2000) reported 50 hydromedusae species near St Helena Bay and Pagés *et al.,* (1992) found 54 hydromedusae and 52 siphonophorae species within the south eastern Atlantic. This indicates that there were still quite a few species that were not observed, for example *Ectopleura dumortieri* and *Mitrocomella grandis* (Beucher and Gibbons, 2002). Assemblages of hydromedusae displayed a general trend where species diversity increased in an offshore direction and scatter plots indicated a positive relationship between temperature and diversity (Figure 13a). This indicated that medusae diversity was higher in warmer offshore waters rather than cooler waters in the shelf region. Similar trends in general zooplankton diversity were also observed by Gibbons and Hutchings (1996), where the zooplankton included species of hydromedusae. Buecher and Gibbons (2000) also observed these trends and attributed them to the addition of offshore species of Trachy- and Narco- medusa. Diversity would also be lower inshore as upwelling allows for a higher biomass of organisms resulting in certain specialists species, like Anthoathecata and Leptothecata, to dominate the assemblages (Pagès et al., 1991; Thibault-Botha *et al.*, 2004).

Unlike the abundance of medusae there was a general positive association between diversity and temperature, instead of a domed-shamed one. However, diversity displayed a decline with increasing fluorescence concentration. These results were in agreement with Buecher and Gibbons (2000), where they found that offshore holoplanktonic species

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became more diverse with the increase in temperature and decrease in fluorescence concentration. The relationship between diversity and fluorescence is in contrast with Gibbons and Hutchings (1996), where it is described that there is no particular connection between variables; although that study looked at a variety of zooplankton and was not limited to medusae.

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Chapter 5: Conclusion

The west coast off South Africa is environmentally highly variable, with influences from the Benguela Current, upwelling processes and the Agulhas Current all impacting the physical, chemical and biological status of the region (Shannon, 1985). In this unstable, but productive environment certain species are able to dominate, for example the siphonopore *M. atlantica*. Diversity on the other hand tends to be low compared to other coastal systems such as the South Africa's east coast (De Decker, 1984; Gibbons *et al*., 2010). With 69 species of medusa observed over the study, the diversity of hydromedusae tended to increase offshore and also at higher temperatures.

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As the environmental conditions influence each other, samples tend to form similar groups. These groups were based on the sample's depth range, so that inshore, shelf and offshore samples shared resemblances. The study region can be described as having nutrient –rich productive waters with low temperatures, low salinities and moderate fluorescence along the coast. Surface temperature and salinities increase offshoreward; fluorescence also increases but as the stratified water column becomes nutrient depleted the chlorophyll concentration decreases.

Copepod abundance was closely linked to upwelling, with a dome-shaped relationship to temperature and negative relation to salinity. Although these results were seen overall after collating each year's data, the relationship between these variables and copepods

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abundance were less conspicuous when comparing the data of each year to each other. For example, inter-annually, temperature did not display as strong a correlation between temperature and abundance; so that the warmest temperature did not necessarily have the highest abundance in copepods.

Hydromedusae have recently become the focus of much research with the reported increases in blooms and their intensity, although much earlier work done on this group remains limited (Hosia and Bamstedt, 2008). This also means that long term abundance data are rare and understanding their long term trends remains inconsistent. The abundance of medusa reflected similar clustering to the environmental variables, where samples formed inshore, shelf and offshore groups, indicating the inshore assemblages composed of Anthoathecata, Leptothecata, Limnomedusae and Siphonophores and offshore assemblages composed of Trachy- and Narco- medusae orders. In general abundance displayed a significantly positive correlation with surface salinity and although temperature was expected to reflect some significance (Buecher and Gibbons, 2000), this was not observed. The reason for this may be the conflicting positive and negative correlations that offshore and inshore assemblages had with temperature, respectively, resulting in an overall insignificant correlation.

In general the diversity and abundance of hydromedusae displayed strong links to their environmental conditions, for example inshore conditions favour certain medusa orders while offshore conditions favour others. As a group they are dynamic with quick responses

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to changes within their environment, it is therefore beneficial to understand their environmental cues and observe regular monitoring.

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Appendix 1: List of Tables

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Appendix 2: List of Figures

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Summary Table

	2000	2001	2002	2003	2004	2005	2006
N #of samples	44	24	38	30	29	26	43
Mean Sea Surface Temperature (^oC)	14.50	15.80	14.30	15.20	13.40	14.70	14.90
SD	1.93	0.88	2.30	1.63	1.75	1.65	1.60
Mean Sea Surface Salinity (psu)	35.00	35.10	35.10	35.10	34.80	35.10	35.00
SD	0.31	0.23	0.30	0.20	0.17	0.24	0.21
Mean Sea Ssurface Oxygen (ml/l)	6.60	6.30	5.60	5.90	5.70	5.30	6.40
SD	1.28	0.84	1.08	0.83	1.06	0.53	1.06
Mean Sea Surface Fluorescence (ug/l)	1.59	0.34	1.08	1.26	1.17	0.47	1.03
SD	1.89	0.37	1.10	1.21	0.69	0.43	0.74
Mean Bottom Temperature (^oC)	9.17	10.07	8.35	8.61	8.07	9.29	8.71
SD	1.66	2.45	1.39	0.89	1.01	0.87	1.25
Mean Bottom Salinity (psu)	34.70	34.80	34.62	34.63	34.56	34.71	34.62
SD	0.17	0.25	0.11	0.09	0.10	0.09	0.13
Mean Bottom Oxygen (ml/l)	3.81	3.67	3.65	3.49	3.27	3.77	3.62
SD	1.05	1.50	1.23	0.85	1.51	1.04	1.27
Mean Bottom Fluorescence (ug/l)	-	0.08	0.03	0.05	0.04	0.07	0.03
SD	-	0.03	0.02	0.06	0.03	0.07	0.03
Intergrated Fluorescence	37.47	13.89	37.54	37.57	32.43	18.83	32.55
SD	39.07	5.04	22.83	23.37	15.30	10.54	17.14
Mean Fluorescence (ug/l)	1.35	0.17	0.31	0.34	0.32	0.20	0.27
SD	0.94	0.19	0.28	0.31	0.37	0.18	0.28
Mean Copepod abundance (ind.m^{-3})	5390	3302	2109	1701	12763	1485	5458
SD	6783	3716	2835	1816	23597	2018	9575
Mean Anthomedusae abundance (ind.m^{-3})	0.39	0.18	0.05	0.02	0.01	0.15	0.13
SD	1.43	0.45	0.12	0.06	0.02	0.46	0.40
Mean Leptomedusae abundance (ind.m^{-3})	1.13	0.13	0.01	0.01	1.89	0.15	0.22
SD	6.70	0.24	0.03	0.0	10.83	0.46	1.31
Mean Limnomedusae abundance (ind.m^{-3})	0.19	0.14	0.02	0.03	0.04	0.01	0.01
SD	0.62	0.31	0.04	0.07	0.19	0.05	0.02
Mean Trachymedusae abundance (ind.m^{-3})	0.07	0.16	0.04	0.02	0.03	0.57	0.08
SD	0.17	0.32	0.10	0.04	0.14	0.94	0.16
Mean Narcomedusae abundance (ind.m^{-3})	0.00	0.01	0.00	0.00	0.00	0.01	0.00
SD	0.00	0.04	0.01	0.00	0.00	0.03	0.01
Mean Siphonophores abundance (ind.m^{-3})	0.03	1.24	0.39	0.61	0.15	2.26	0.74
SD	0.08	2.54	0.62	2.84	0.30	2.93	1.32
Mean Hydromedusae abundance (ind.m^{-3})	1.81	1.86	0.50	0.69	2.14	3.15	1.18
SD	7.21	2.67	0.70	2.92	10.92	3.21	1.84

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Table 1 continue

Jellyfish species richness (S')	29	32	31	18	25	38	40
Jellyfish Diversity (H')	0.80	0.69	0.82	0.29	0.30	0.73	0.78
Jellyfish Evenness (J')	0.24	0.20	0.24	0.10	0.09	0.20	0.21

Table 1: A summary table providing annual means and standard deviations for measured variables collected during the period 2000 to 2006: details regarding medusoid diversity and orders were also included.

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a)

2000	Sounding	SST	SSS	SSO	SSF	BT	BS	BO
Sounding								
SST	**0.86**							
SSS	0.71	**0.84**						
SSO	-0.12	0.03	0.01					
SSF	-0.29	-0.14	-0.18	0.07				
BT	-0.57	-0.40	-0.31	-0.23	0.14			
BS	-0.57	-0.36	-0.19	-0.19	0.11	**0.96**		
BO	0.55	0.65	0.58	0.01	0.06	-0.09	-0.13	

b)

2001	Sounding	SST	SSS	SSO	SSF	BT	BS	BO	BFl	Integrated Fluoresc.	Mean Fluoresc.
Sounding											
SST	0.50										
SSS	**0.83**	0.55									
SSO	-0.71	-0.40	-0.56								
SSF	-0.54	-0.46	-0.36	0.68							
BT	-0.19	-0.02	0.06	0.11	0.48						
BS	-0.11	0.04	0.15	0.03	0.41	**0.98**					
BO	0.58	0.07	0.73	-0.27	0.01	0.35	0.35				
BFl	-0.62	-0.25	-0.29	0.60	0.57	0.37	0.29	-0.15			
Integrated Fluoresc.	0.40	0.02	0.27	0.08	-0.05	-0.50	-0.54	0.36	-0.26		
Mean Fluoresc.	-0.73	-0.33	-0.46	0.78	**0.85**	0.47	0.38	-0.17	0.67	-0.15	

c)

2002	Sounding	SST	SSS	SSO	SSF	BT	BS	BO	BFl	Integrated Fluoresc.	Mean Fluoresc.
Sounding											
SST	**0.92**										
SSS	**0.96**	**0.94**									
SSO	0.36	0.44	0.33								
SSF	-0.51	-0.41	-0.49	0.25							
BT	-0.15	-0.06	-0.19	-0.16	0.14						
BS	-0.14	-0.05	-0.18	-0.15	0.14	**1.00**					
BO	0.76	0.68	0.75	0.18	-0.47	-0.32	-0.32				
BFl	**-0.87**	-0.75	**-0.83**	-0.19	0.55	0.32	0.31	-0.93			
Integrated Fluoresc.	-0.01	0.01	0.00	0.50	0.76	-0.02	-0.02	-0.11	0.11		
Mean Fluoresc.	-0.66	-0.54	-0.64	0.00	**0.90**	0.27	0.27	-0.53	0.63	0.65	

Table 2: Spearman Rank correlations between the measured environmental variables each year: a) 2000, b) 2001, c) 2002, d) 2003, e) 2004, f) 2005 and g) 2006. Significant correlations are indicated in bold.

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d)

2003	Sounding	SST	SSS	SSO	SSF	BT	BS	BO	BFl	Integrated Fluoresc.	Mean Fluoresc.
Sounding											
SST	**0.89**										
SSS	0.64	0.71									
SSO	-0.63	-0.50	-0.38								
SSF	-0.72	-0.78	-0.77	0.57							
BT	**-0.82**	-0.66	-0.54	0.56	0.62						
BS	**-0.86**	-0.69	-0.53	0.57	0.64	**0.99**					
BO	0.62	0.62	0.76	-0.23	-0.59	-0.36	-0.41				
BFl	**-0.94**	**-0.87**	-0.70	0.55	0.73	0.73	0.77	-0.67			
Integrated Fluoresc.	-0.55	-0.56	-0.53	0.61	0.87	0.38	0.40	-0.43	0.55		
Mean Fluoresc.	**-0.92**	**-0.82**	-0.68	0.75	**0.84**	**0.81**	**0.83**	-0.61	**0.90**	0.75	

e)

2004	Sounding	SST	SSS	SSO	SSF	BT	BS	BO	BFl	Integrated Fluoresc.	Mean Fluoresc.
Sounding											
SST	**0,87**										
SSS	**0,87**	**0,86**									
SSO	0,11	0,09	0,06								
SSF	-0,25	-0,32	-0,37	**0,81**							
BT	**-0,87**	**-0,84**	**-0,88**	-0,07	0,37						
BS	**-0,88**	**-0,87**	**-0,84**	-0,07	0,35	**0,98**					
BO	0,76	0,79	0,74	0,14	-0,36	**-0,88**	**-0,88**				
BFl	-0,66	-0,77	-0,66	-0,17	0,26	0,74	0,73	**-0,89**			
Integrated Fluoresc.	0,33	0,12	0,12	0,45	0,53	-0,16	-0,17	-0,06	0,09		
Mean Fluoresc.	-0,41	-0,45	-0,53	0,42	0,79	0,53	0,48	-0,55	0,47	0,57	

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Table 2: Spearman Rank correlations between the measured environmental variables each year: a) 2000, b) 2001, c) 2002, d) 2003, e) 2004, f) 2005 and g) 2006. Significant correlations are indicated in bold.

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f)

2005	Sounding	SST	SSS	SSO	SSF	BT	BS	BO	BFl	Integrated Fluoresc.	Mean Fluoresc.
Sounding											
SST	**0,82**										
SSS	**0,83**	**0,93**									
SSO	-0,22	-0,14	-0,26								
SSF	-0,67	-0,69	-0,78	0,41							
BT	-0,05	-0,03	0,17	-0,37	-0,22						
BS	-0,05	-0,02	0,18	-0,37	-0,19	**1,00**					
BO	0,72	0,69	0,79	-0,01	-0,64	0,24	0,25				
BFl	**-0,88**	**-0,80**	-0,79	0,19	0,59	0,01	0,00	-0,58			
Integrated Fluoresc.	0,08	0,00	-0,05	0,46	0,41	-0,26	-0,20	-0,05	-0,07		
Mean Fluoresc.	-0,76	-0,70	-0,70	0,36	0,78	0,17	0,19	-0,64	0,65	0,42	

g)

2006	Sounding	SST	SSS	SSO	SSF	BT	BS	BO	BFl	Integrated Fluoresc.	Mean Fluoresc.
Sounding											
SST	**0,84**										
SSS	**0,93**	**0,91**									
SSO	-0,21	-0,22	-0,27								
SSF	-0,58	-0,65	-0,61	0,48							
BT	-0,02	0,13	-0,03	-0,34	-0,15						
BS	-0,03	0,12	-0,04	-0,34	-0,14	**1,00**					
BO	**0,85**	**0,80**	0,87	-0,14	-0,58	0,04	0,02				
BFl	**-0,84**	-0,67	-0,76	0,14	0,52	0,01	0,03	**-0,80**			
Integrated Fluoresc.	-0,14	-0,23	-0,18	0,62	0,63	-0,45	-0,45	-0,23	0,08		
Mean Fluoresc.	-0,69	-0,62	-0,69	0,45	**0,80**	-0,05	-0,04	-0,63	0,55	0,64	

Table 2: Spearman Rank correlations between the measured environmental variables each year: a) 2000, b) 2001, c) 2002, d) 2003, e) 2004, f) 2005 and g) 2006. Significant correlations are indicated in bold.

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Variable	Overall R	Anthoathecata	Leptothecata	Limno-medusae	Trachy-medusae	Narco-medusae	Siphonophorae	All medusae
Volume Filtered	Lower CI	0.018	-0.433	-0.375	-0.385	-0.274	-0.396	-0.615
	R^{bar}	0.111	-0.212	-0.128	-0.202	-0.060	-0.165	-0.408
	Upper CI	0.202	0.033	0.136	-0.004	0.160	0.085	-0.147
Total copepods	Lower CI	-0.052	-0.224	-0.224	-0.084	-0.190	-0.121	-0.274
	R^{bar}	0.137	-0.080	-0.068	0.090	-0.102	0.039	0.116
	Upper CI	0.317	0.068	0.091	0.258	-0.011	0.198	0.474
Bottom depth	Lower CI	-0.274	-0.204	-0.306	-0.030	-0.244	-0.289	-0.284
	R^{bar}	-0.053	-0.011	-0.058	0.360	-0.027	-0.046	0.043
	Upper CI	0.173	0.181	0.198	0.654	0.192	0.204	0.361
Latitude	Lower CI	-0.200	-0.393	-0.064	-0.176	-0.386	-0.113	0.045
	R^{bar}	0.148	-0.189	0.181	0.053	0.083	0.245	0.223
	Upper CI	0.462	0.032	0.406	0.277	0.519	0.546	0.388
Longitude	Lower CI	-0.440	-0.238	-0.296	-0.275	-0.527	-0.282	-0.180
	R^{bar}	-0.197	0.002	-0.092	-0.056	-0.290	-0.088	0.025
	Upper CI	0.074	0.242	0.121	0.167	-0.012	0.112	0.228
SST	Lower CI	-0.021	-0.426	-0.322	-0.093	-0.159	-0.273	-0.057
	R^{bar}	0.217	-0.159	-0.006	0.019	0.070	0.101	0.105
	Upper CI	0.431	0.133	0.311	0.131	0.291	0.449	0.262
SSS	Lower CI	-0.196	-0.115	-0.132	0.200	-0.162	0.288	0.107
	R^{bar}	0.026	0.156	0.071	0.454	0.162	0.506	0.469
	Upper CI	0.245	0.405	0.268	0.651	0.456	0.674	0.722
SSO	Lower CI	-0.710	-0.269	-0.624	-0.100	0.118	-0.265	-0.234
	R^{bar}	-0.353	-0.131	-0.312	0.023	0.223	0.045	0.113
	Upper CI	0.147	0.012	0.086	0.145	0.323	0.347	0.434
SSF	Lower CI	-0.096	-0.154	-0.122	-0.118	-0.225	-0.296	-0.086
	R^{bar}	0.233	-0.053	0.177	-0.015	-0.024	-0.073	-0.007
	Upper CI	0.516	0.050	0.446	0.089	0.179	0.158	0.072
BT	Lower CI	-0.238	-0.172	-0.112	-0.461	-0.971	-0.117	-0.231
	R^{bar}	0.105	-0.044	0.019	-0.191	-0.581	0.014	0.060
	Upper CI	0.424	0.085	0.150	0.112	0.649	0.145	0.340
BS	Lower CI	-0.425	-0.169	-0.109	-0.003	-0.540	-0.027	-0.380
	R^{bar}	-0.153	-0.026	0.023	0.330	0.537	0.081	-0.067
	Upper CI	0.144	0.117	0.154	0.597	0.947	0.186	0.259
BO	Lower CI	-0.642	-0.269	-0.582	-0.049	-0.228	-0.236	-0.277
	R^{bar}	-0.351	-0.087	-0.371	0.070	-0.069	0.085	0.089
	Upper CI	0.029	0.101	-0.114	0.187	0.094	0.389	0.432
BFl	Lower CI	-0.301	0.226	-0.332	-0.176	-0.127	-0.287	0.041
	R^{bar}	0.359	0.545	0.072	-0.003	0.055	0.311	0.533
	Upper CI	0.787	0.758	0.455	0.169	0.234	0.734	0.817

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Table 3 continue

Mean Fluorescence	**Lower CI**	-0.355	-0.259	-0.034	-0.195	-0.210	-0.155	0.021
	R bar	0.197	-0.006	0.258	0.164	-0.047	0.088	0.338
	Upper CI	0.647	0.248	0.510	0.485	0.119	0.322	0.593
Integrated Fluorescence	**Lower CI**	-0.490	-0.439	-0.168	-0.536	-0.203	-0.137	-0.661
	R bar	-0.118	-0.285	0.002	-0.186	-0.064	-0.015	-0.363
	Upper CI	0.290	-0.115	0.172	0.218	0.078	0.107	0.033

Table 3: Results of the random-effects meta-analysis conducted on partial correlations between environmental predictors and the abundance of different pelagic Hydrozoa. Upper and lower confidence intervals around R also shown: data highlighted in grey significant at the 0.05 level.

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Anthoathecata							
Variables	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Bottom Fluorescence		0.089	-0.010	0.937	0.301	0.685	-0.583
Bottom Oxygen	0.253	-0.872	-0.311	-0.104	-0.330	0.070	-0.673
Bottom Salinity	-0.681	0.358	0.021	-0.229	-0.117	0.149	-0.329
Bottom Temperature	0.726	0.289	-0.031	-0.186	-0.137	0.147	-0.287
Integrated Fluorescence		-0.098	0.070	0.660	-0.452	-0.374	-0.535
Latitude	0.081	0.379	-0.161	-0.304	-0.224	0.284	0.741
Longitude	-0.050	-0.009	-0.153	-0.235	-0.269	0.261	-0.697
Mean Fluorescence		0.031	0.617	-0.677	-0.401	0.735	0.622
Sounding	0.120	0.139	0.202	0.192	-0.554	-0.109	-0.318
Sea S surface Fluorescence	0.167	0.109	0.134	0.124	-0.493	0.789	0.522
Sea Surface Oxygen	0.324	-0.019	-0.656	-0.066	-0.487	-0.940	0.180
Sea Surface Salinity	0.259	0.327	0.124	-0.120	0.298	-0.326	-0.348
Sea Surface Temperature	0.319	-0.055	0.203	0.276	0.104	0.707	-0.169
Total copepods	-0.018	0.106	0.005	0.234	0.039	-0.078	0.538
Volume Filtered	0.131	-0.022	0.192	0.281	0.073	-0.161	0.096

b)

Leptothecata							
Variables	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Bottom Fluorescence		0.370	0.259	0.827	0.626	0.797	0.055
Bottom Oxygen	0.074	-0.563	-0.161	0.272	-0.058	-0.067	-0.124
Bottom Salinity	0.021	0.097	0.170	-0.158	-0.363	0.185	-0.140
Bottom Temperature	-0.051	0.193	0.017	-0.122	-0.341	0.208	-0.127
Integrated Fluorescence		-0.162	-0.168	-0.227	-0.058	-0.382	-0.555
Latitude	-0.162	0.148	-0.638	-0.129	0.124	-0.255	-0.201
Longitude	-0.303	0.127	0.517	-0.140	0.068	-0.328	0.027
Mean Fluorescence		0.436	-0.063	-0.279	-0.025	-0.403	0.278
Sounding	0.265	-0.376	-0.042	0.069	0.042	0.265	-0.307
Sea S surface Fluorescence	-0.144	0.131	-0.043	-0.178	-0.071	-0.245	0.131
Sea Surface Oxygen	-0.276	0.133	-0.248	-0.022	-0.087	-0.401	0.058
Sea Surface Salinity	0.182	0.057	0.661	0.041	0.176	0.155	-0.310
Sea Surface Temperature	-0.012	0.154	-0.718	-0.094	0.168	0.045	-0.378
Total copepods	-0.337	0.176	-0.025	-0.122	-0.275	0.158	0.005
Volume Filtered	-0.619	-0.482	-0.248	0.006	0.147	0.138	-0.217

Table 4: Partial correlations between each order and environmental variables for each year- a) Anthoathecata, b) Leptothecata, c) Limnomedusae, d) Trachymedusae, e) Narcomedusae, f) Siphonophorae and g) All orders.

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c)

Limnomedusae							
Variables	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Bottom Fluorescence		0.172	0.610	-0.202	-0.089	0.426	-0.532
Bottom Oxygen	-0.176	-0.809	-0.199	-0.262	-0.611	0.154	-0.436
Bottom Salinity	0.037	0.294	0.077	-0.091	-0.325	0.184	0.002
Bottom Temperature	0.027	0.307	0.041	-0.067	-0.317	0.200	-0.012
Integrated Fluorescence		-0.399	-0.026	-0.008	0.311	0.048	0.054
Latitude	0.159	0.360	-0.259	-0.243	0.349	0.371	0.493
Longitude	-0.002	0.005	-0.184	-0.260	0.258	0.205	-0.498
Mean Fluorescence		0.756	-0.071	0.101	0.464	0.106	0.051
Sounding	0.077	0.076	0.101	0.111	0.007	0.028	-0.631
Sea S surface Fluorescence	0.057	-0.399	-0.003	0.004	0.356	0.785	0.198
Sea Surface Oxygen	0.060	-0.407	-0.718	-0.040	0.270	-0.853	0.024
Sea Surface Salinity	0.035	0.507	0.007	0.024	0.205	0.189	-0.349
Sea Surface Temperature	0.304	0.358	0.027	-0.743	0.180	0.187	-0.151
Total copepods	0.155	-0.384	-0.089	-0.020	-0.255	-0.253	0.158
Volume Filtered	-0.649	-0.297	0.091	0.117	-0.017	0.020	0.010

d)

Trachymedusae							
Variables	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Bottom Fluorescence		-0.087	-0.226	0.008	0.412	-0.077	0.001
Bottom Oxygen	-0.014	-0.068	0.359	-0.006	0.116	-0.089	0.065
Bottom Salinity	-0.009	-0.130	0.497	0.186	-0.042	0.641	0.779
Bottom Temperature	0.010	-0.052	-0.139	0.194	-0.098	-0.248	-0.748
Integrated Fluorescence		0.074	-0.234	0.126	-0.854	0.044	0.112
Lattitude	0.172	-0.161	0.449	0.104	0.307	-0.392	-0.186
Longitude	-0.143	-0.238	0.298	0.231	0.214	-0.446	-0.296
Mean Fluorescence		-0.013	-0.153	0.179	0.810	-0.091	-0.019
Sounding	0.118	0.002	0.753	-0.207	0.877	0.229	0.150
Sea S surface Fluorescence	-0.169	0.039	-0.184	0.110	0.046	0.052	0.153
Sea Ssurface Oxygen	-0.231	-0.035	-0.001	0.114	0.262	0.052	0.141
Sea Surface Salinity	0.585	0.593	0.088	-0.073	0.290	0.774	0.634
Sea Surface Temperature	0.170	0.160	-0.131	-0.142	0.228	0.012	-0.080
Total copepods	-0.072	0.178	0.424	0.139	-0.056	0.223	-0.179
Volume Filtered	-0.020	-0.109	-0.599	-0.194	-0.370	-0.006	-0.019

Table 4: Partial correlations between each order and environmental variables for each year- a) Anthoathecata, b) Leptothecata, c) Limnomedusae, d) Trachymedusae, e) Narcomedusae, f) Siphonophorae and g) All orders.

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e)

Narcomedusae						
Variables	**2000**	**2001**	**2002**	**2004**	**2005**	**2006**
Bottom Fluorescence			0.250	-0.052	-0.190	0.090
Bottom Oxygen			-0.240	0.131	0.075	-0.099
Bottom Salinity			0.982	-0.197	-0.024	0.257
Bottom Temperature			-0.991	-0.178	-0.028	0.239
Integrated Fluorescence			0.077	0.045	-0.069	-0.223
Latitude			-0.348	0.157	-0.153	0.590
Longitude			-0.101	-0.013	-0.403	-0.548
Mean Fluorescence			0.167	-0.148	-0.217	-0.086
Sounding			-0.278	0.180	0.186	-0.087
Sea Surface Fluorescence			0.175	-0.232	-0.233	0.075
Sea Surface Oxygen			-0.030	-0.025	-0.131	-0.179
Sea Surface Salinity			-0.271	0.445	0.341	0.159
Sea Surface Temperature			-0.144	0.304	0.286	-0.068
Total copepods			-0.137	-0.052	0.047	-0.141
Volume Filtered			-0.153	0.148	0.171	-0.276

f)

Siphonophorae							
Variables	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Bottom Fluorescence		-0.502	0.059	0.948	0.303	0.223	0.063
Bottom Oxygen	0.018	-0.197	-0.041	0.748	-0.506	0.256	0.124
Bottom Salinity	-0.049	-0.218	0.183	0.125	0.052	0.235	0.172
Bottom Temperature	-0.106	-0.307	-0.064	0.100	0.029	0.244	0.180
Integrated Fluorescence		-0.090	-0.138	0.208	-0.063	0.205	-0.087
Latitude	-0.383	0.079	0.593	0.162	0.009	0.294	0.712
Longitude	-0.413	-0.061	-0.336	0.080	0.271	0.175	-0.142
Mean Fluorescence		-0.399	-0.153	0.224	0.400	0.377	0.076
Sounding	0.128	0.068	0.288	0.096	-0.249	-0.662	0.047
Sea S surface Fluorescence	-0.085	-0.668	-0.037	0.130	0.234	0.210	-0.179
Sea Surface Oxygen	-0.217	0.680	-0.533	0.296	-0.014	0.151	-0.043
Sea Surface Salinity	0.244	0.760	0.369	0.294	0.637	0.803	0.241
Sea Surface Temperature	0.147	-0.657	0.743	0.343	-0.234	-0.006	0.200
Total copepods	-0.245	0.328	0.099	0.178	0.232	0.036	-0.154
Volume Filtered	0.144	-0.703	-0.048	0.028	-0.478	-0.051	0.019

Table 4: Partial correlations between each order and environmental variables for each year- a) Anthoathecata, b) Leptothecata, c) Limnomedusae, d) Trachymedusae, e) Narcomedusae, f) Siphonophorae and g) All orders.

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All medusae							
Variables	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Bottom Fluorescence		0.232	0.013	0.947	0.733	0.449	0.110
Bottom Oxygen	0.235	0.425	0.013	0.635	-0.732	0.305	-0.208
Bottom Salinity	0.048	-0.405	0.260	0.198	-0.765	0.040	0.318
Bottom Temperature	0.032	-0.730	0.308	0.172	0.324	0.077	0.318
Integrated Fluorescence		-0.801	-0.060	0.197	0.065	-0.759	-0.404
Latitude	-0.025	0.201	0.470	0.100	0.105	0.073	0.496
Longitude	-0.349	0.030	0.442	0.116	-0.049	-0.022	0.007
Mean Fluorescence		0.401	0.022	0.305	0.135	0.829	0.088
Sounding	0.354	-0.514	0.667	-0.090	-0.004	-0.048	-0.232
Sea Surface Fluorescence	-0.013	0.119	0.012	0.183	0.024	0.139	-0.161
Sea Ssurface Oxygen	-0.121	0.729	-0.491	0.275	0.209	0.409	-0.289
Sea Surface Salinity	0.346	0.843	0.457	0.142	-0.031	0.892	-0.009
Sea Surface Temperature	0.382	-0.189	0.258	0.117	0.102	0.056	-0.127
Total copepods	-0.318	0.770	0.461	0.252	-0.638	0.260	-0.108
g) Volume Filtered	-0.787	-0.588	-0.507	-0.145	-0.020	-0.245	-0.252

Table 4: Partial correlations between each order and environmental variables for each year- a) Anthoathecata, b) Leptothecata, c) Limnomedusae, d) Trachymedusae, e) Narcomedusae, f) Siphonophorae and g) All orders.

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Order	Species	2000	2001	2002	2003	2004	2005	2006
N		**44**	**24**	**38**	**30**	**29**	**26**	**43**
Anthoathecata	***Bougainvillia macloviana***	3	1	1	0	1	2	1
	Euphysa aurata	5	3	4	3	1	0	0
	Euphysa spA	1	0	0	0	0	0	0
	Leuckartiara octona	26	9	10	4	2	5	26
	Pandae spA	0	1	0	0	1	0	2
	Specimen O	0	0	0	1	0	0	2
	Velella velella	0	0	0	0	0	0	1
Leptothecata	***Clytia hemisphaerica***	2	2	0	0	0	2	2
	Clytia simplex	8	3	0	0	0	2	0
	Mitrocomella millardae	0	0	2	0	0	1	0
	Obelia sp.	5	6	1	2	1	3	4
	Specimen I	0	1	0	0	0	0	0
	Specimen A	1	1	0	0	1	0	0
	Specimen B	1	0	0	0	0	0	0
	Specimen D	1	1	0	0	0	4	3
	Specimen G	0	2	0	0	0	1	1
	Specimen H	0	9	0	0	0	0	1
	Specimen L	0	0	1	0	1	1	0
	Specimen M	0	0	0	0	0	0	1
	Specimen N	0	0	0	0	0	0	1
	Specimen Q	0	0	0	0	0	1	0
Limnomedusae	***Aglauropsis edwardsii***	2	1	0	0	2	0	0
	Proboscidactyla menoni	21	10	9	8	4	3	6
	Proboscidactyla stellata	0	0	0	1	0	0	0
Trachymedusae	***Acrtapodema ampla***	0	0	0	0	0	0	1
	Aglaura hemistoma	9	6	8	4	6	10	12
	Liriope tetraphylla	4	0	6	0	0	13	8
	Persa incolorata	12	11	5	4	5	10	23
	Rhopalonema velatum	6	3	1	0	1	2	3
	Rhopalonematidae spA	0	0	1	1	0	0	0
	Specimen C	3	2	4	0	3	2	5
Narcomedusae	***Cunina globosa***	0	0	1	0	0	0	0
	Solmissus marshalli	0	0	0	0	0	0	1
	Solmundella bitenticulata	0	1	1	0	1	4	9
	Tetraplatia volitans	2	0	0	0	0	0	0
Siphonophorae	***Abylopsis eschscholtzi***	1	0	0	0	0	0	0
	Agalma elegans	0	0	0	0	0	1	0
	Agalma okeni	0	0	0	0	0	1	0
	Aphicaryon acule	0	0	0	0	0	0	0

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Table 5 continue

Order	Species	2000	2001	2002	2003	2004	2005	2006
N		**44**	**24**	**38**	**30**	**29**	**26**	**43**
	Chelophyes appendiculata	0	0	0	0	0	1	1
	Chelophyes contorta	0	0	1	0	0	0	0
	Cordagalma cordiformis	0	0	0	0	0	1	0
	Dimophyes arctica	4	7	17	4	10	13	21
	Diphyes bojani	0	0	1	0	0	0	1
	Diphyes dispar	0	0	0	0	0	0	1
	Eudoxoides mitra	0	3	3	1	0	1	1
	Eudoxoides spiralis	1	3	6	5	1	8	6
	Forskalia leuckarti	0	0	0	0	2	1	3
	Halistem marubrum	1	1	4	0	0	2	0
	Hippopodius hippopus	0	0	0	0	0	0	0
	Lensia companella	0	0	1	0	0	0	0
	Lensia conoidea	0	1	0	0	0	2	1
	Lensia hardy	3	2	8	2	2	8	11
	Lensia hotspur	0	5	9	2	6	9	8
	Lensia meteori	0	0	3	0	1	3	3
	Lensia multicristata	2	3	6	1	3	2	10
	Lensia subtilis	0	4	6	0	1	5	9
	Muggiaea atlantica	5	23	24	13	9	17	29
	Nanomia bijuga	2	6	6	1	0	7	4
	Praya reticulata	1	0	1	0	0	0	0
	Rhizophysaeysen hardtii	0	0	0	0	1	0	0
	Rosacea sp	0	0	0	1	0	0	2
	Sphaerontectes gracilis	0	2	0	0	0	1	1
	Sulculeolaria chuni	0	0	2	0	0	0	1
	Vogtia glabra	0	0	0	0	0	2	0
	Specimen F	1	1	0	0	0	0	0
	Specimen K	0	0	0	0	0	2	0
	Specimen P	0	0	0	0	0	0	1
Semaeostomeae	***Chrysaora fulgida***	12	0	0	0	4	1	0

Table 5: Number of stations occupied by pelagic Hydrozoa each year over the period 2000-2006. Total number of samples collected (N) also shown.

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BIOENV correlations between environmental variables and hydromedusae assemblages							
Variable	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Latitude				*			*
Longitude							
Sounding	*						
Sea surface temperature (SST)				*			
Sea surface salinity (SSS)		*	*			*	*
Sea surface oxygen (SSO)							*
Sea surface fluorescence (SSF)						*	
Bottom temperature (BT)						*	
Bottom salinity (BS)				*			
Bottom oxygen (BO)		*	*		*	*	
Bottom fluorescence (BFl)			*	*		*	
Mean fluorescence		*					
Global R	**0.589**	**0.716**	**0.623**	**0.478**	**0.65**	**0.549**	**0.555**

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Table 6: Harmonic correlations between environmental parameters which, either singularly or in combination, were significantly correlated ($p<0.05$) with the structure of medusae assemblages identified by the cluster analysis for each year (2000-2006). The analysis was conducted using BIOENV procedure in PRIMER.

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Phylum Cnidaria
- Class Anthozoa
- Subphylum Medusozoa
  - Class Staurozoa nov.
    - Order Stauromedusae
    - Order Conulatae (extinct)
  - Class Cubozoa
  - Class Scyphozoa
    - Order Coronatae
    - Subclass Discomedusae
      - Order Semaeostomeae
      - Order Rhizostomeae
  - Class Hydrozoa
    - Order Limnomedusae
    - Subclass Trachylina
      - Order Actinulida
      - Order Trachymedusae
      - Order Narcomedusae
      - Order Laingiomedusae
    - Subclass Hydroidolina
      - Order Leptothecata
      - Order Siphonophorae
      - Order Anthoathecata

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Figure 1: Cnidarian classification as presented by Marques and Collins (2004) that were also consistent with phylogenetic hypotheses.

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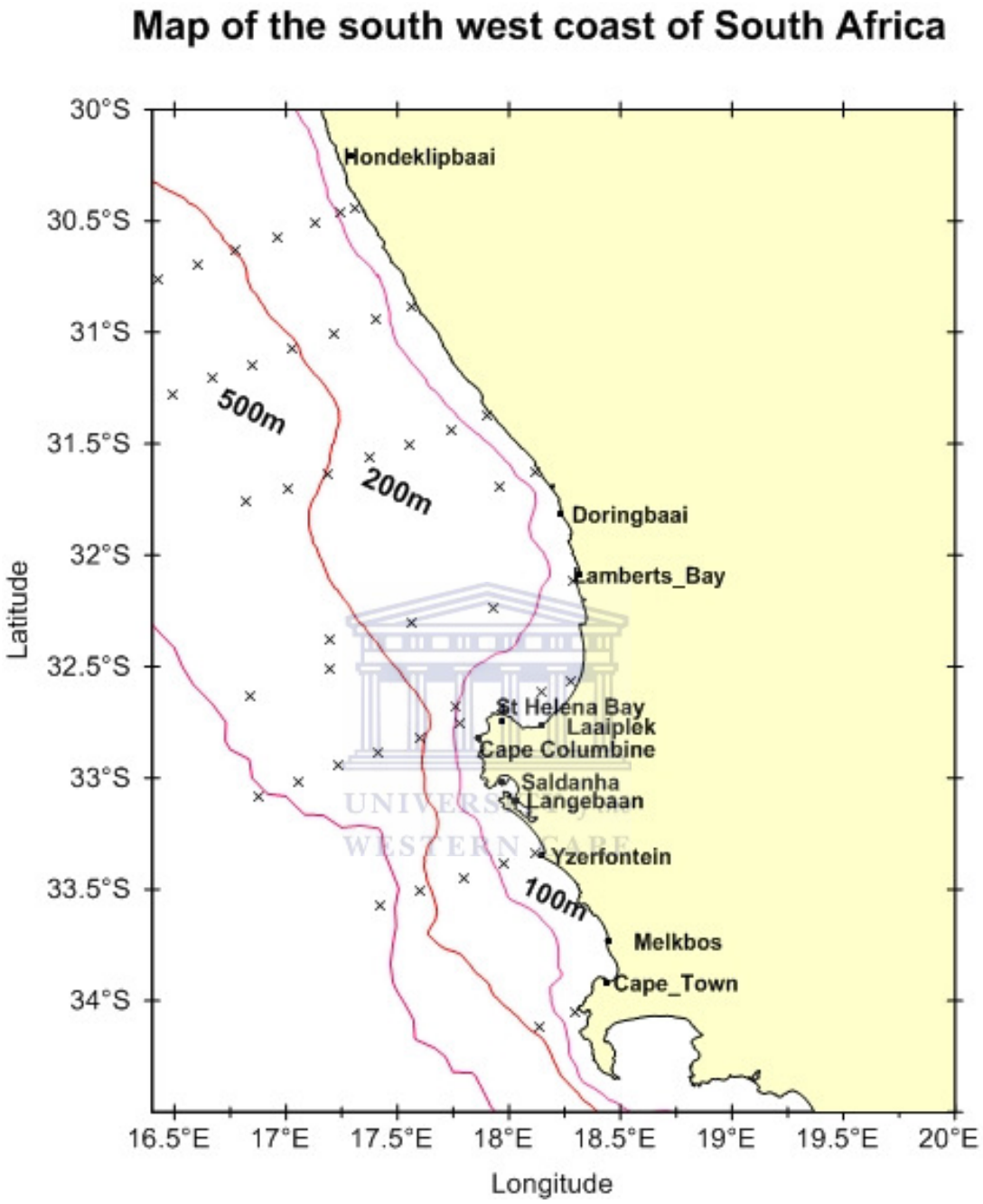

Figure 2: The map above shows the sampling regions with coastal city landmarks and an example of how the stations were positioned.

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Sea Surface Temperature

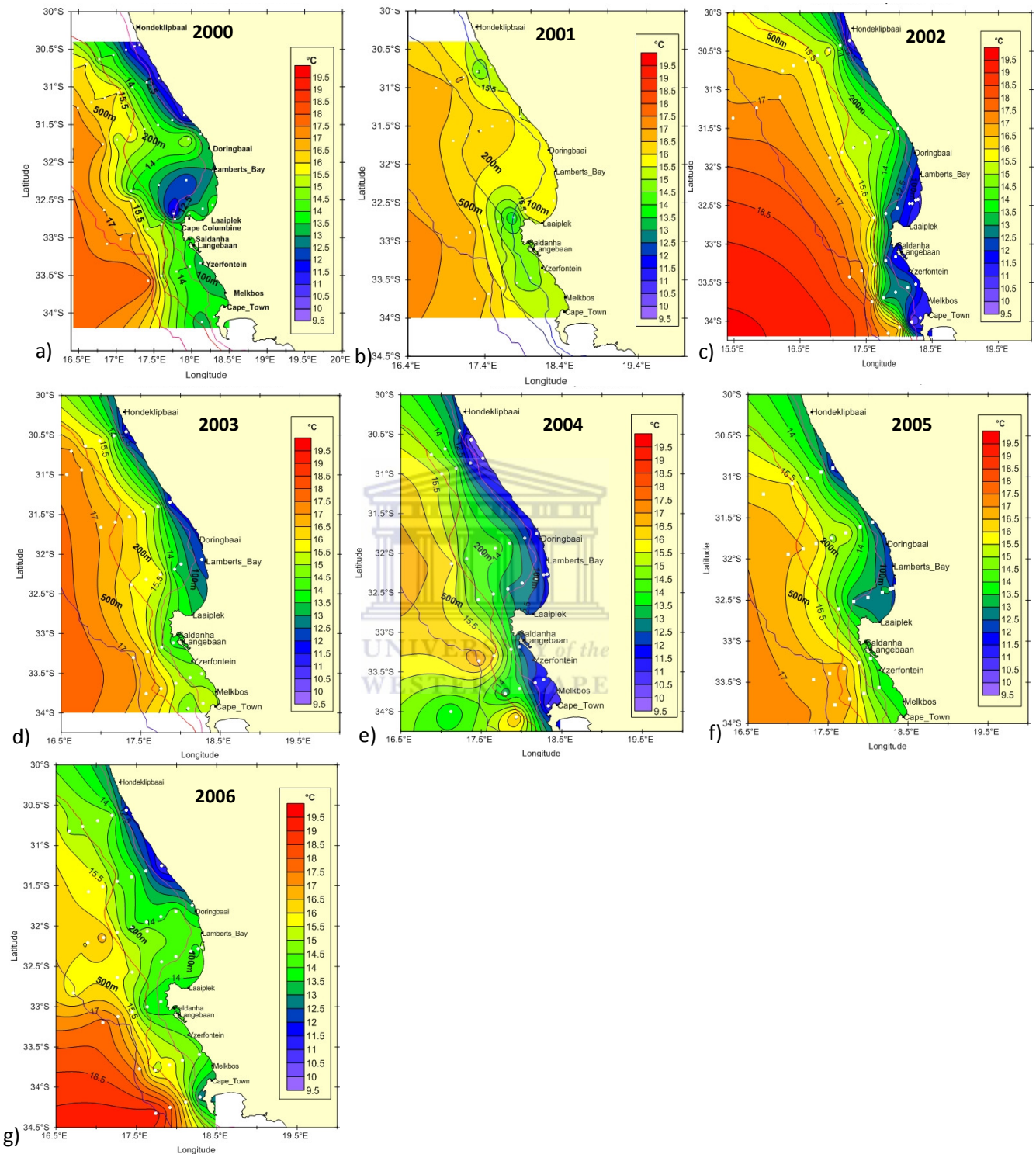

Figure 3: Contour plots showing sea surface temperature across the study area for each year, from 2000 to 2006 (a-g). The plots are mapped along the west coast of South Africa, between Cape Town and Hondeklip Bay.

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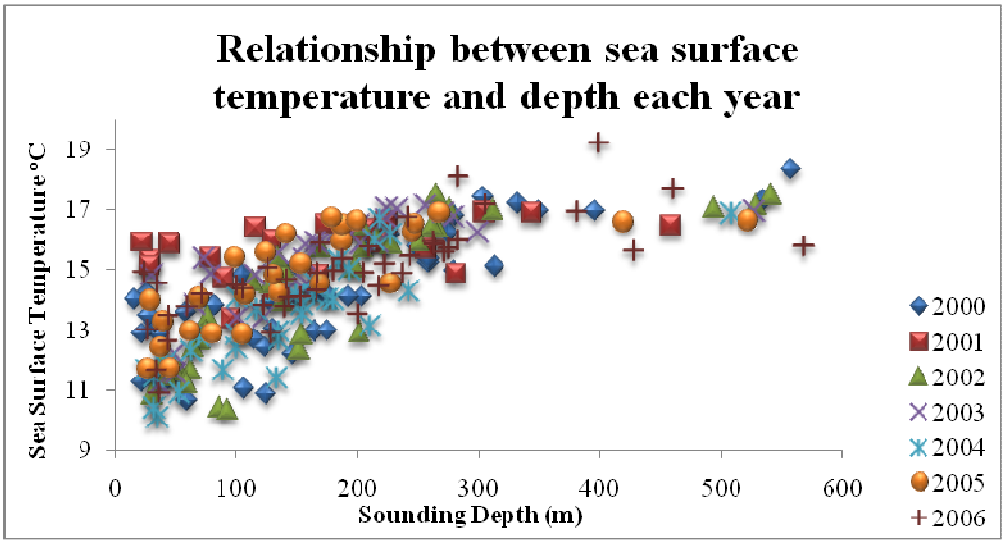
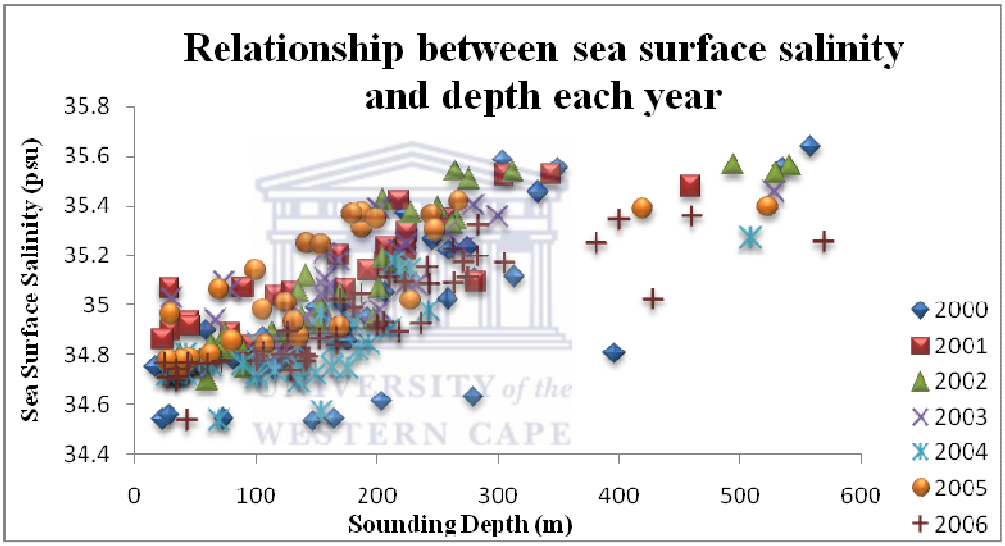
a)



b)



c)

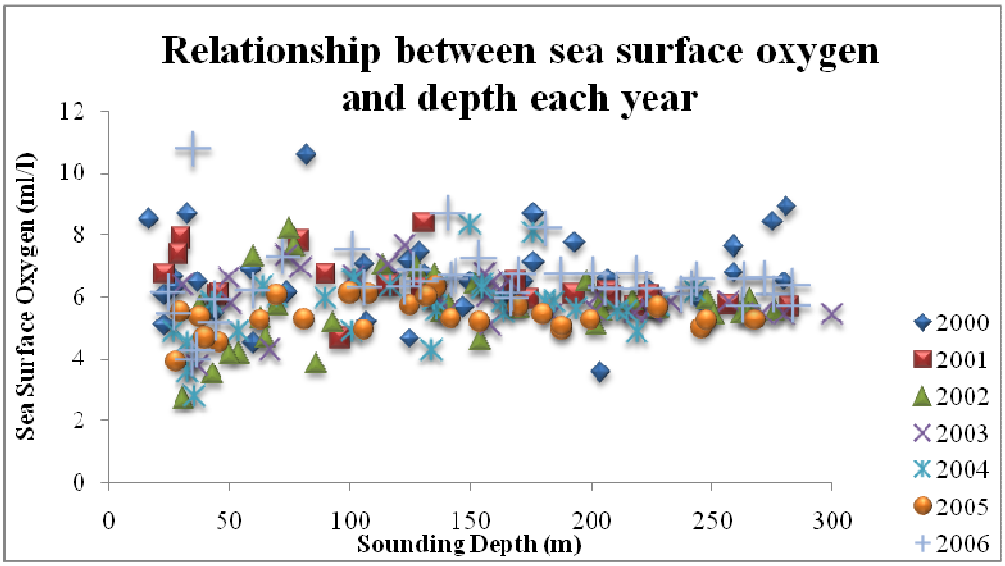


Figure 4: Scatter plots illustrating the relationship between bottom depth and (a) sea surface temperature, (b) sea surface salinity and (c) sea surface oxygen for each year.

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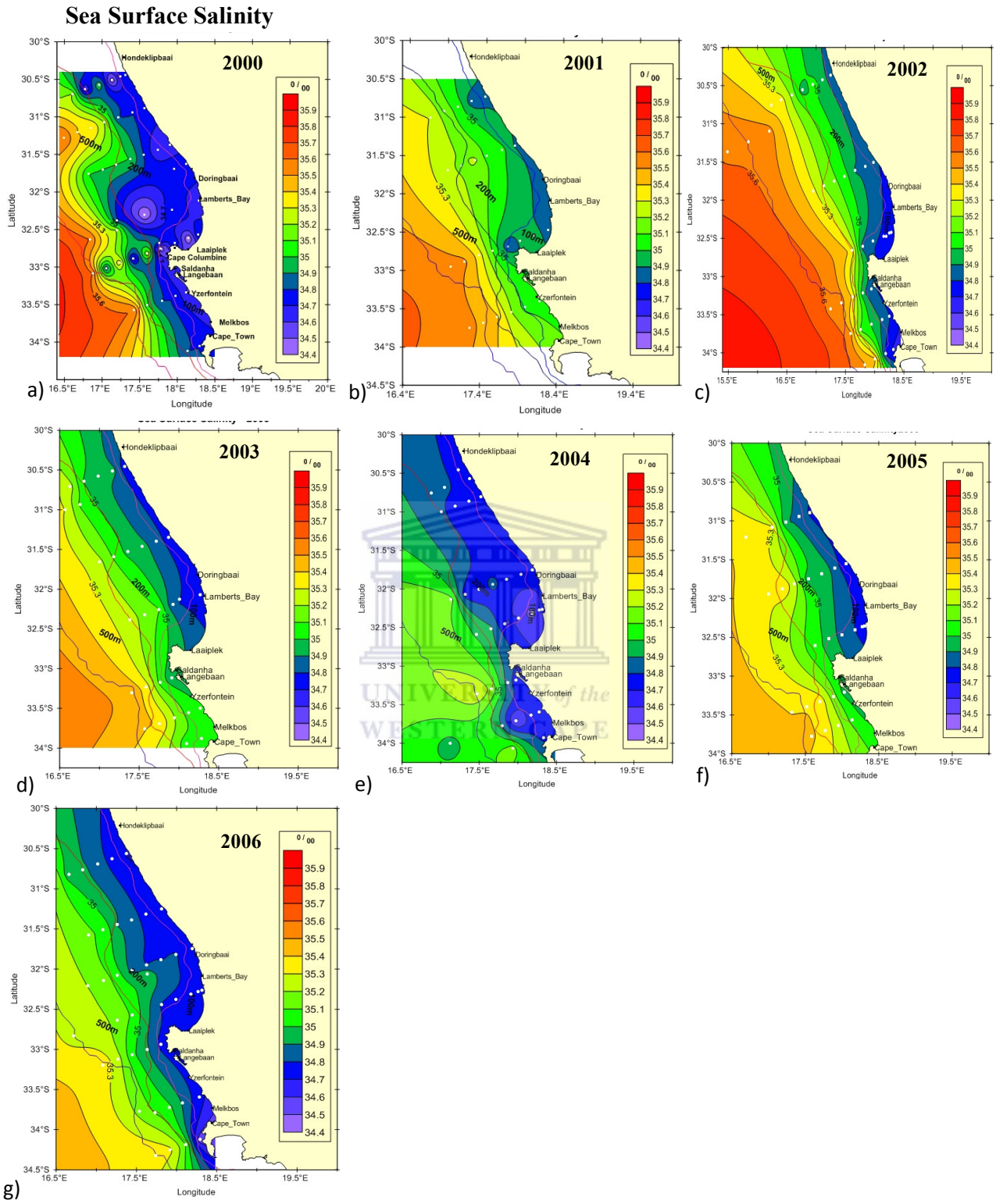

Figure 5: Contour plots illustrating sea surface salinity across the study area for each year, from 2000 to 2006 (a-g). The plots are mapped along the west coast of South Africa, between Cape Town and Hondeklip Bay.

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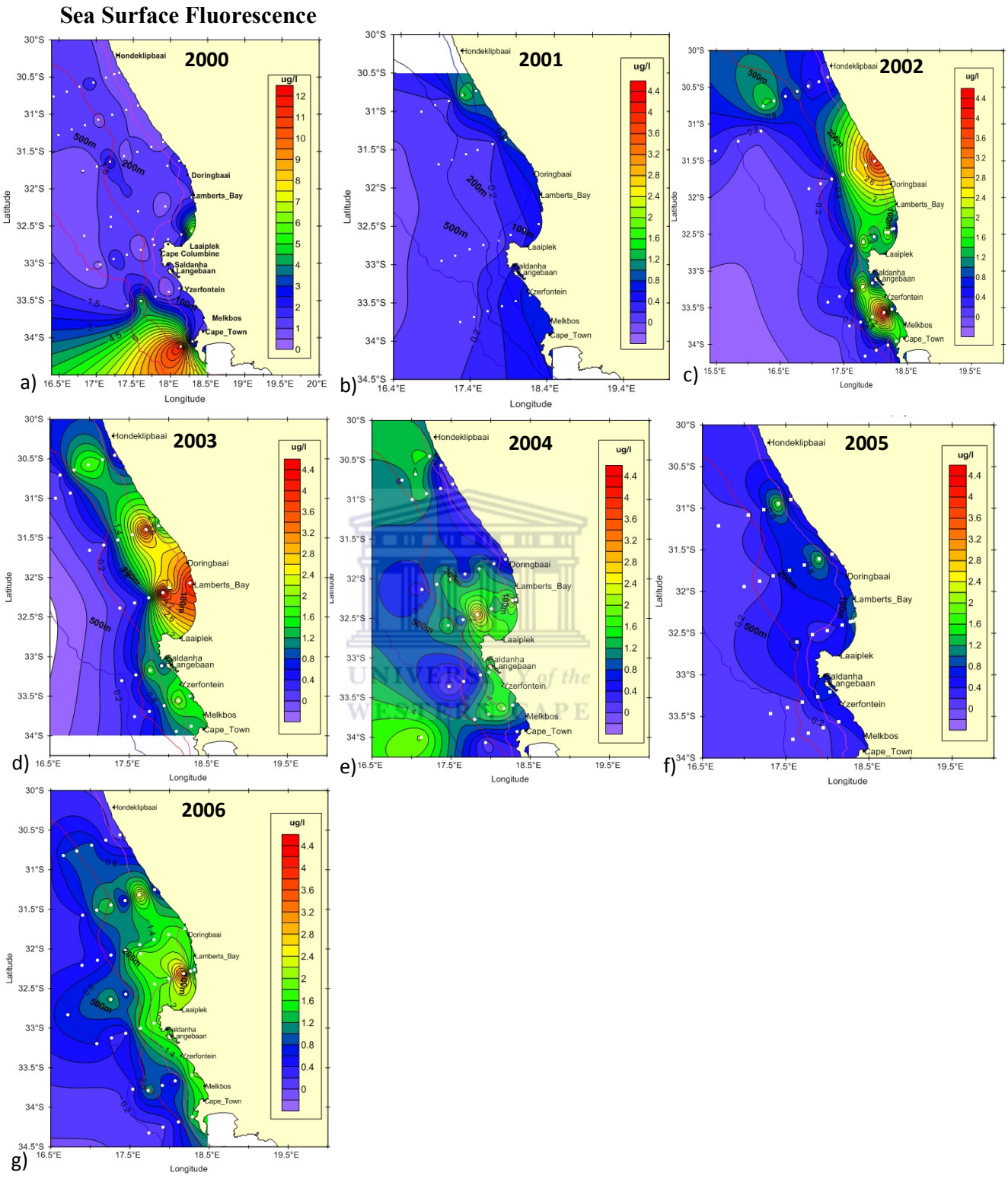

Figure 6: Contour plots illustrating sea surface fluorescence across the study area for each year, from 2000 to 2006 (a-g). The plots are mapped along the west coast of South Africa, between Cape Town and Hondeklip Bay. Note that the scale for the year 2000 is different.

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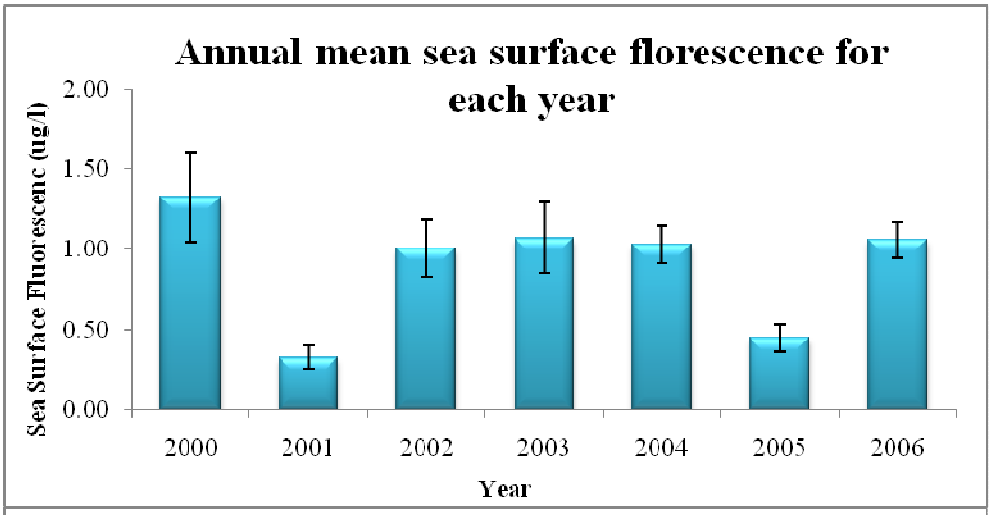
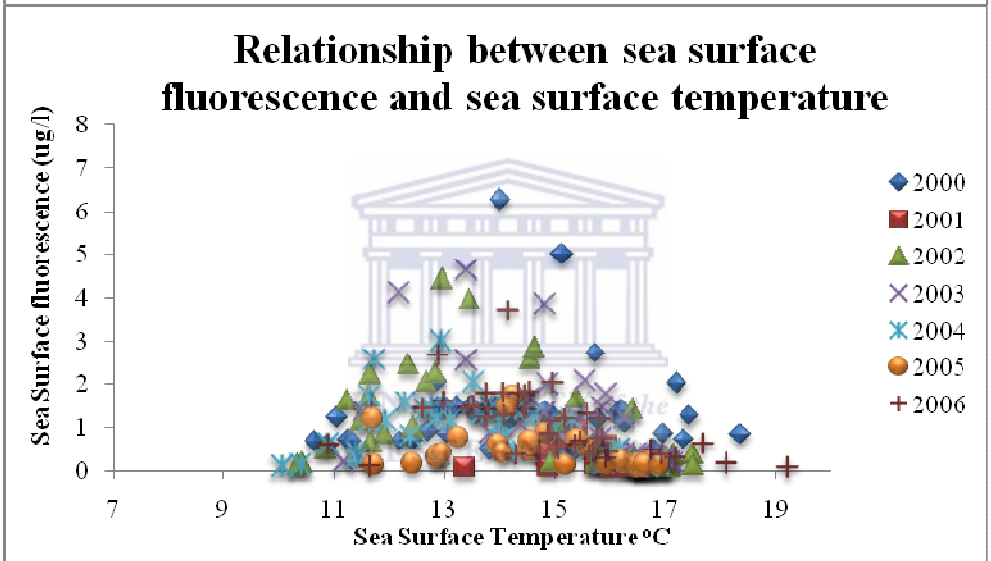
a)



b)



c)

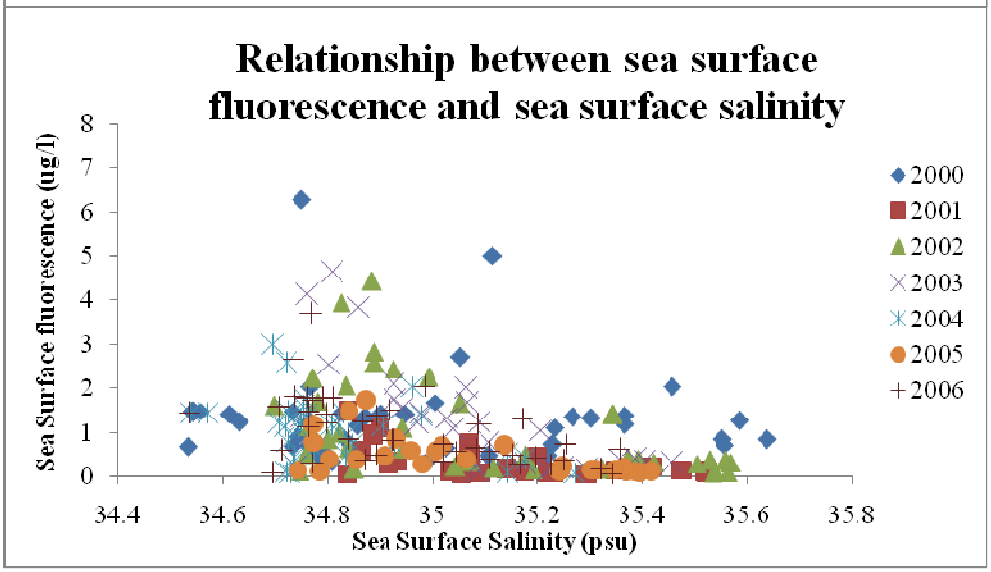


Figure 7: Graphs illustrate (a) annual means for sea surface fluorescence and relationship scatter plots between surface fluorescence and (b) temperature and (c) salinity.

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Copepod Abundance

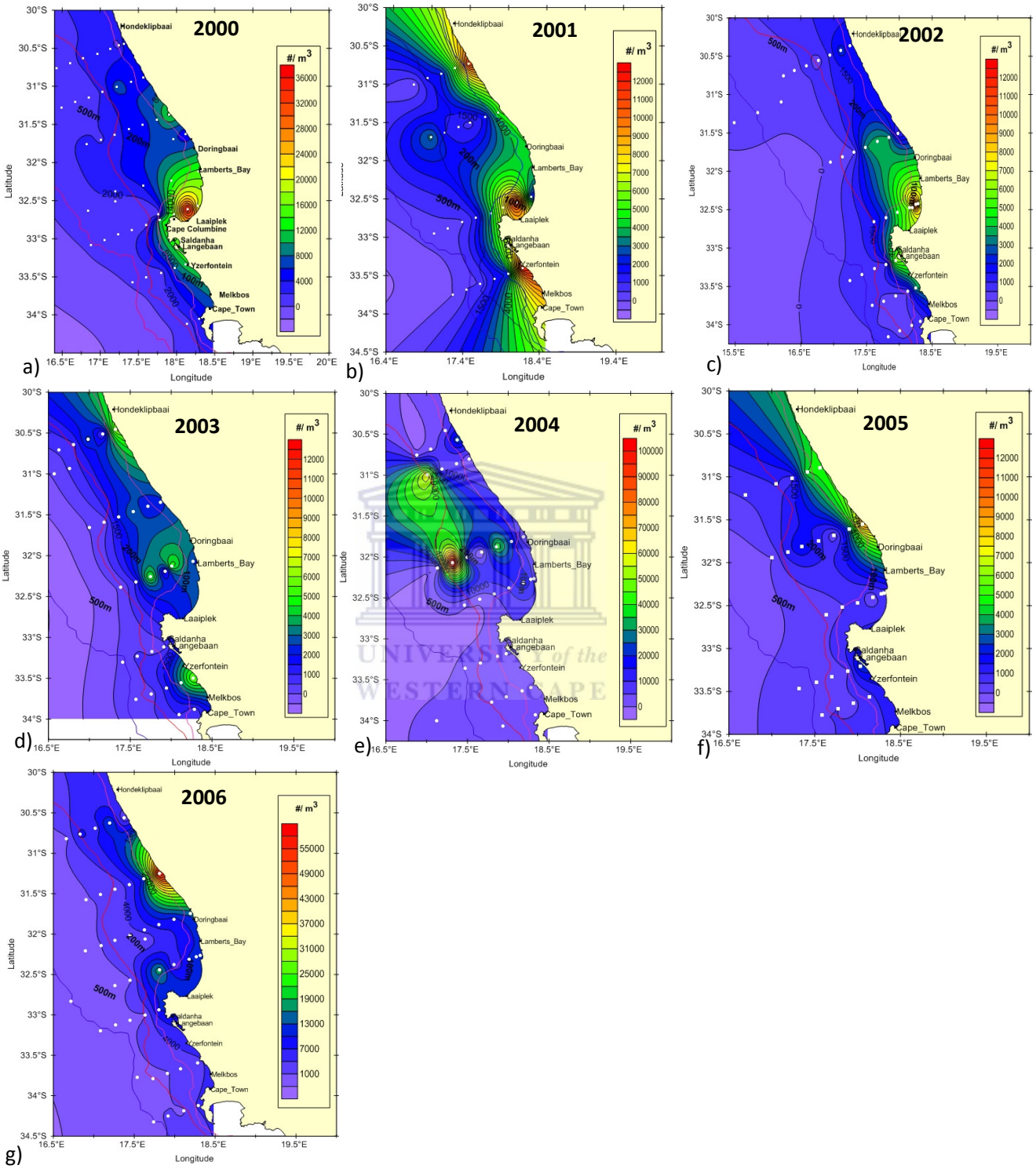

Figure 8: Contour plots illustrating copepod abundance across the study area for each year, from 2000 to 2006 (a-g). The plots are mapped along the west coast of South Africa, between Cape Town and Hondeklip Bay. Note that the scales are different for years 2000, 2004 and 2006.

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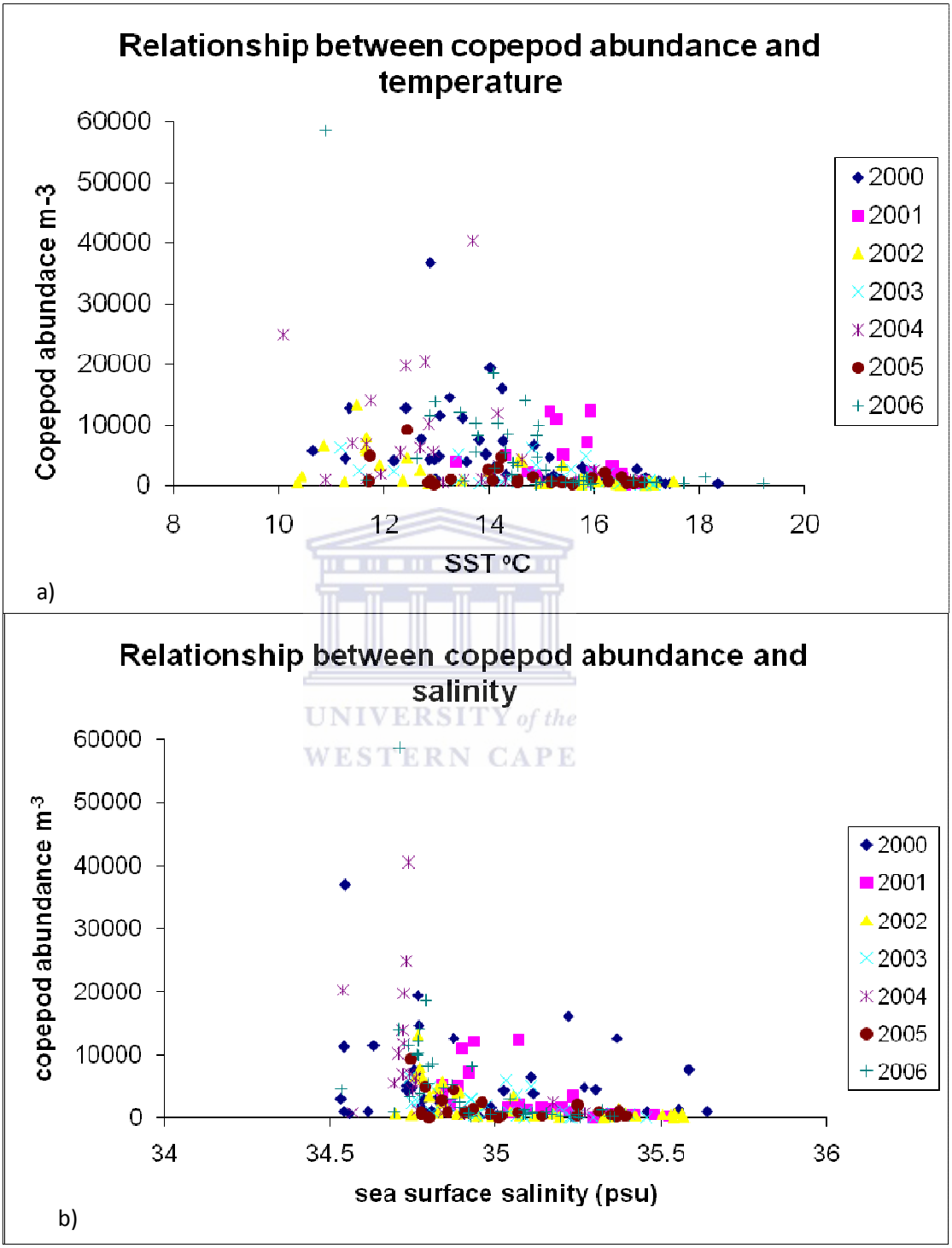

Figure 9: Scatter plot graphs illustrating the relationship between copepod abundance and environmental factors a) sea surface temperature, b) sea surface salinity, c) sea surface fluorescence and d) depth.

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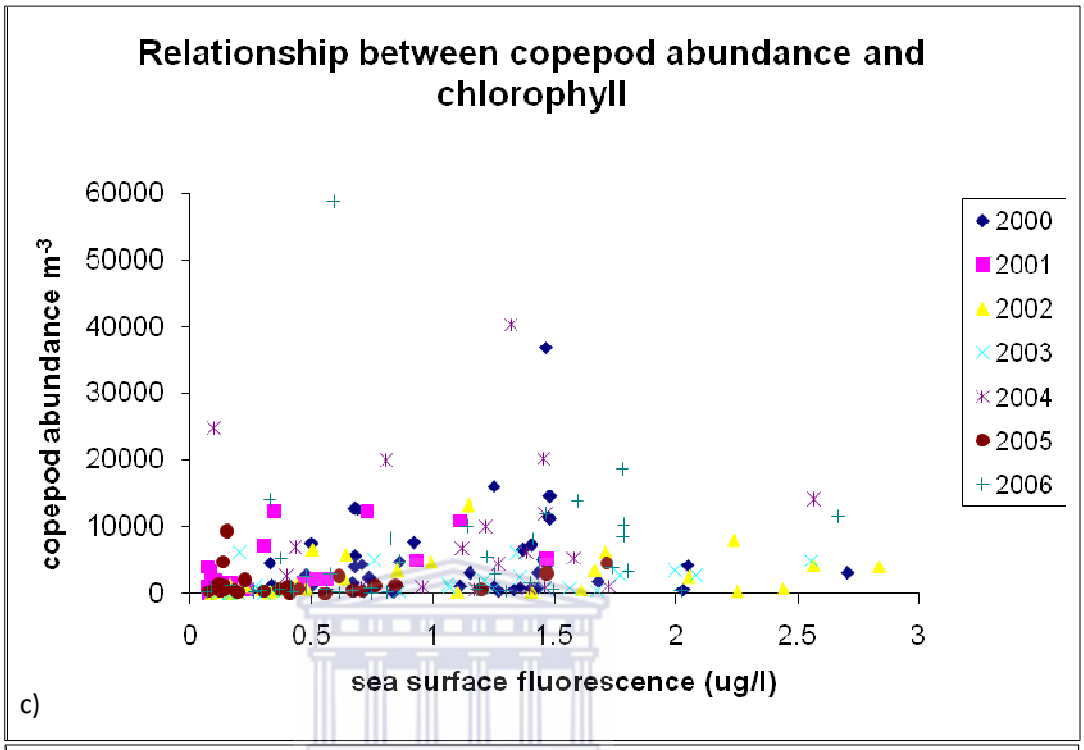

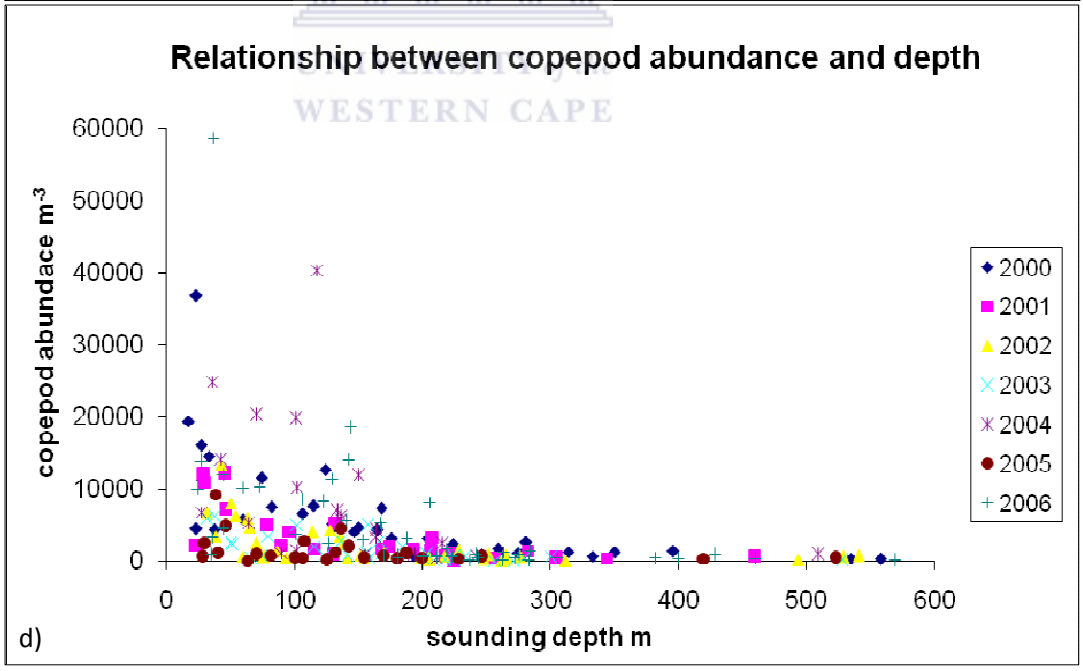

Figure 9: Scatter plot graphs illustrating the relationship between copepod abundance and environmental factors a) sea surface temperature, b) sea surface salinity, c) sea surface fluorescence and d) depth.

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Jellyfish Abundance

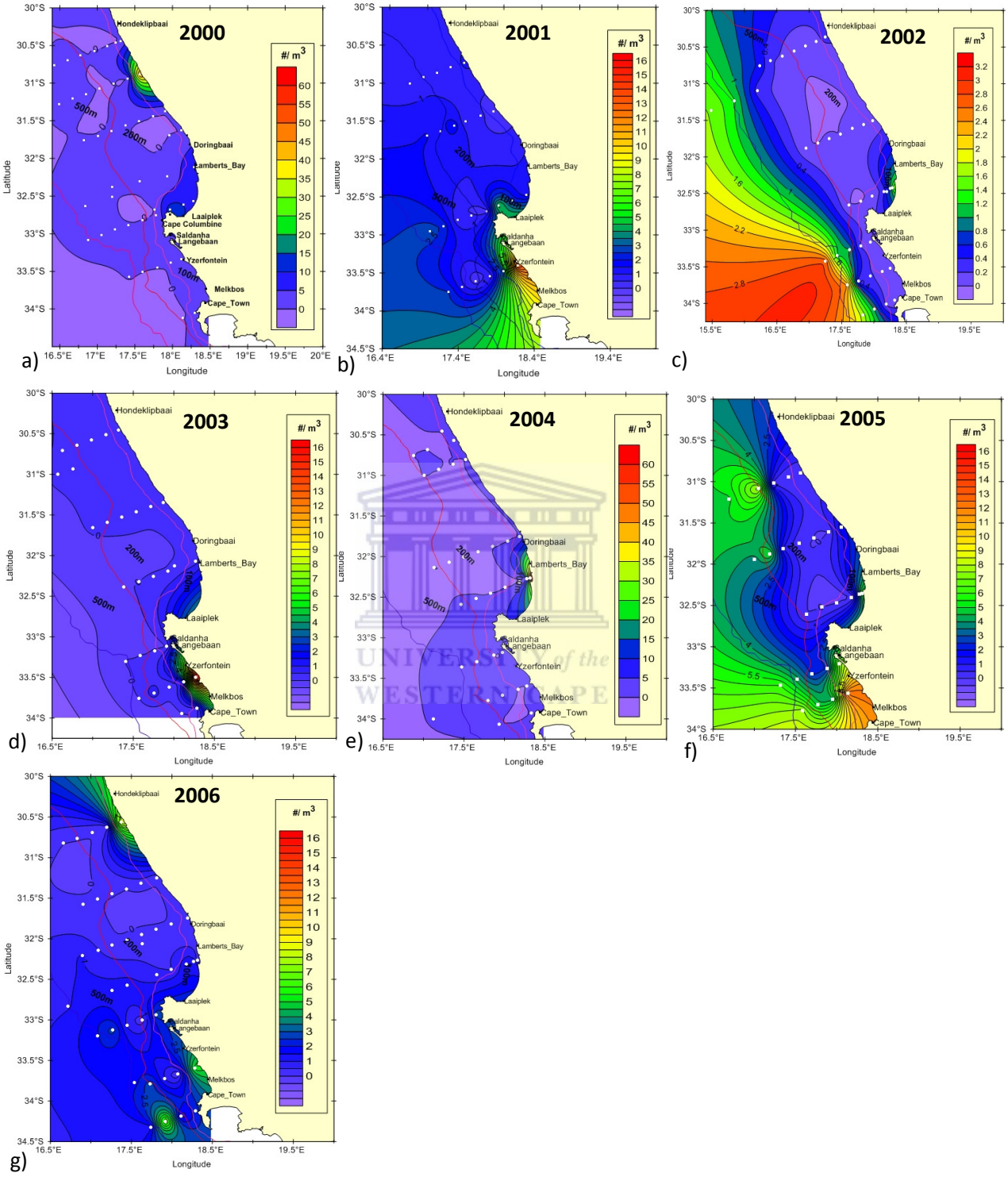

Figure 10: Contour plots illustrating jellyfish abundance across the study area for each year, from 2000 to 2006 (a-g). The plots are mapped along the west coast of South Africa, between Cape Town and Hondeklip Bay. Note that the scales are different for years 2000, 2002 and 2004.

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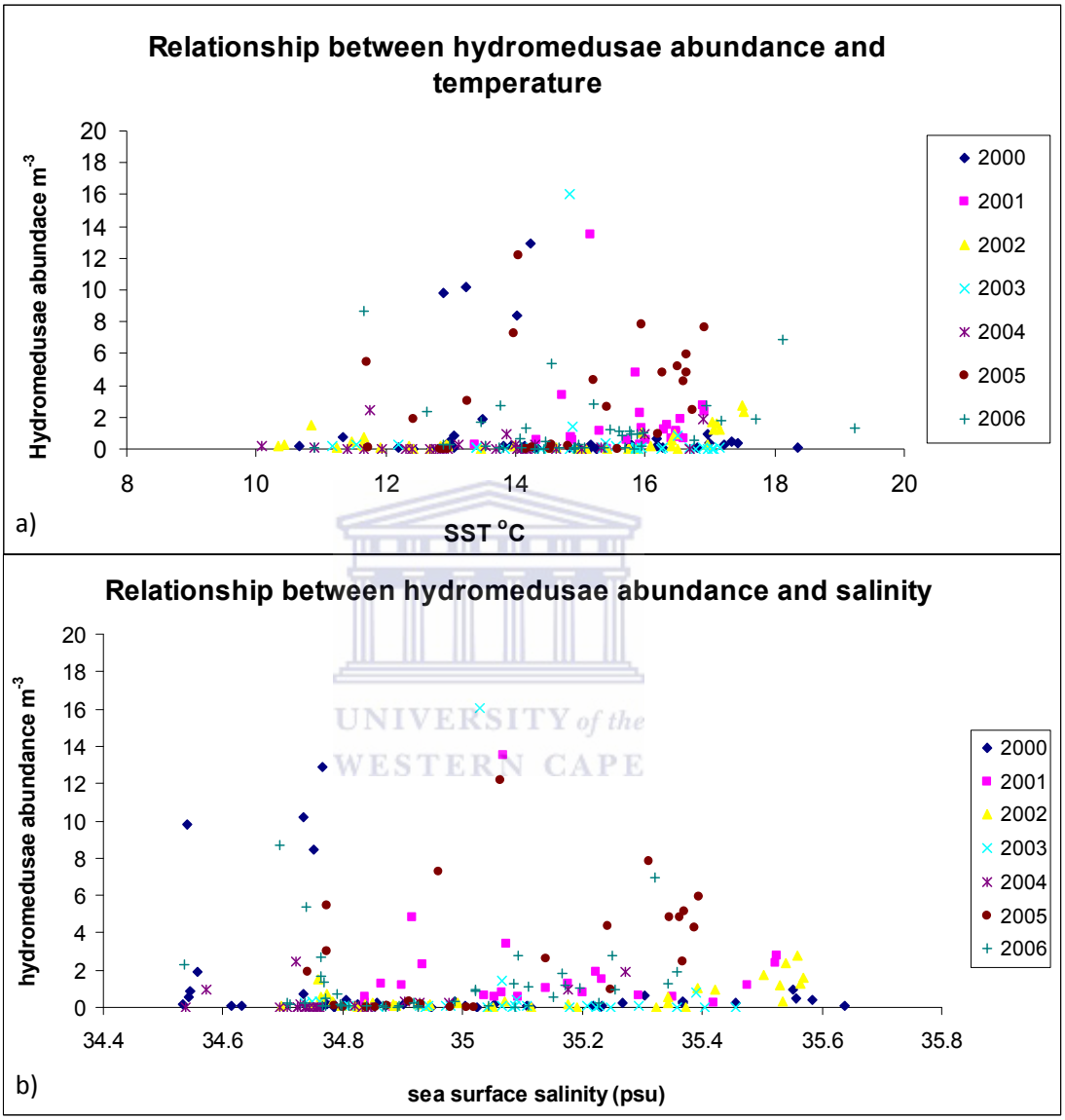

Figure 11: Scatter plot graphs illustrating the relationship between hydromedusae abundance and environmental factors a) sea surface temperature, b) sea surface salinity, c) sea surface fluorescence and d) depth.

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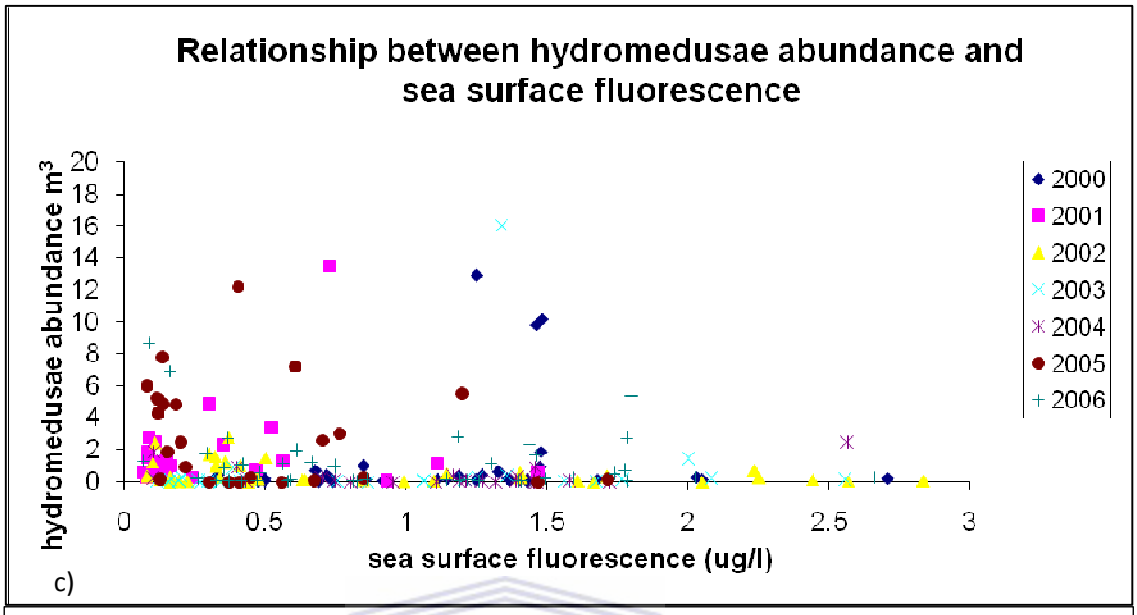

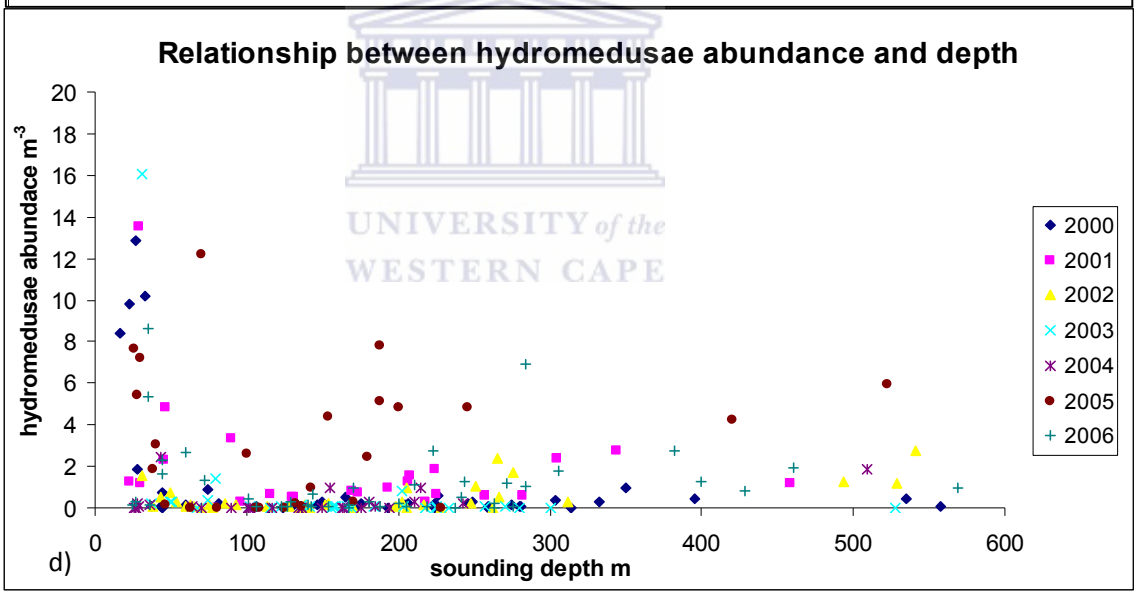

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Figure 11: Scatter plot graphs illustrating the relationship between hydromedusae abundance and environmental factors a) sea surface temperature, b) sea surface salinity, c) sea surface fluorescence and d) depth.

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Jellyfish Species Richness

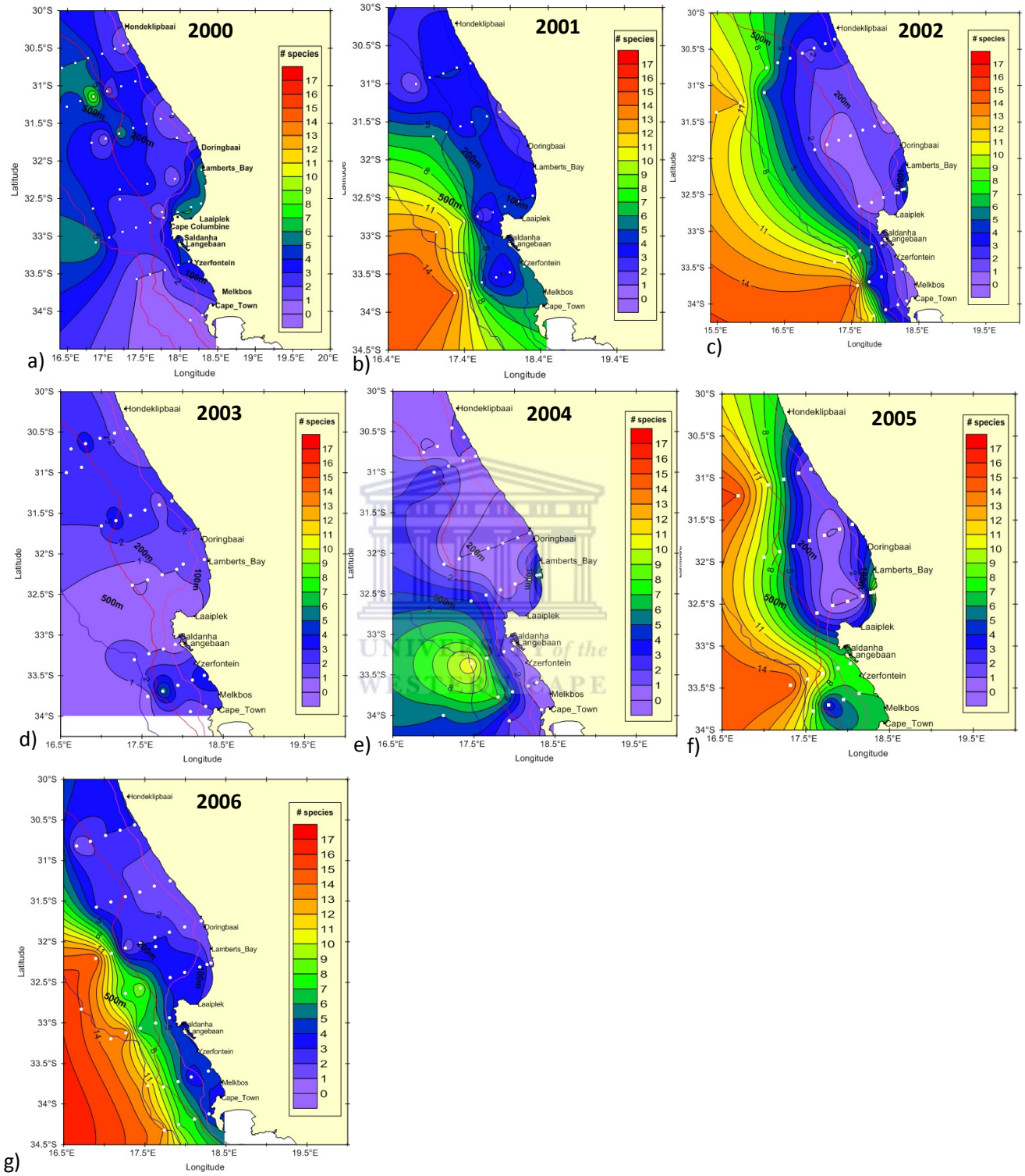

Figure 12: Contour plots illustrating species richness of jellyfish across the study area for each year, from 2000 to 2006 (a-g). The plots are mapped along the west coast of South Africa, between Cape Town and Hondeklip Bay.

http://etd.uwc.ac.za/

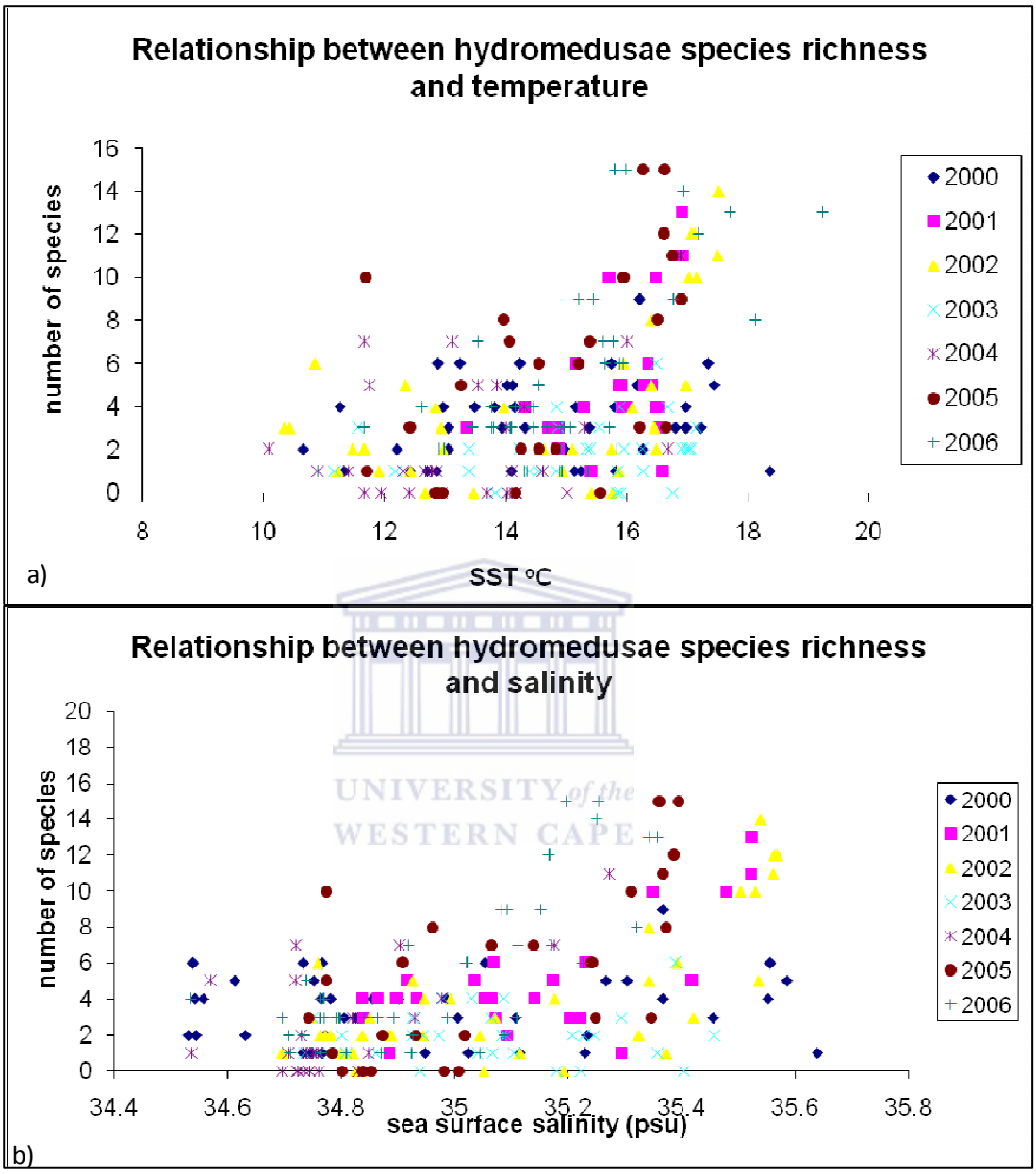

Figure 13: Scatter plot graphs illustrating the relationship between hydromedusae species richness a) sea surface temperature and b) sea surface salinity, c) sea surface fluorescence and d) depth.

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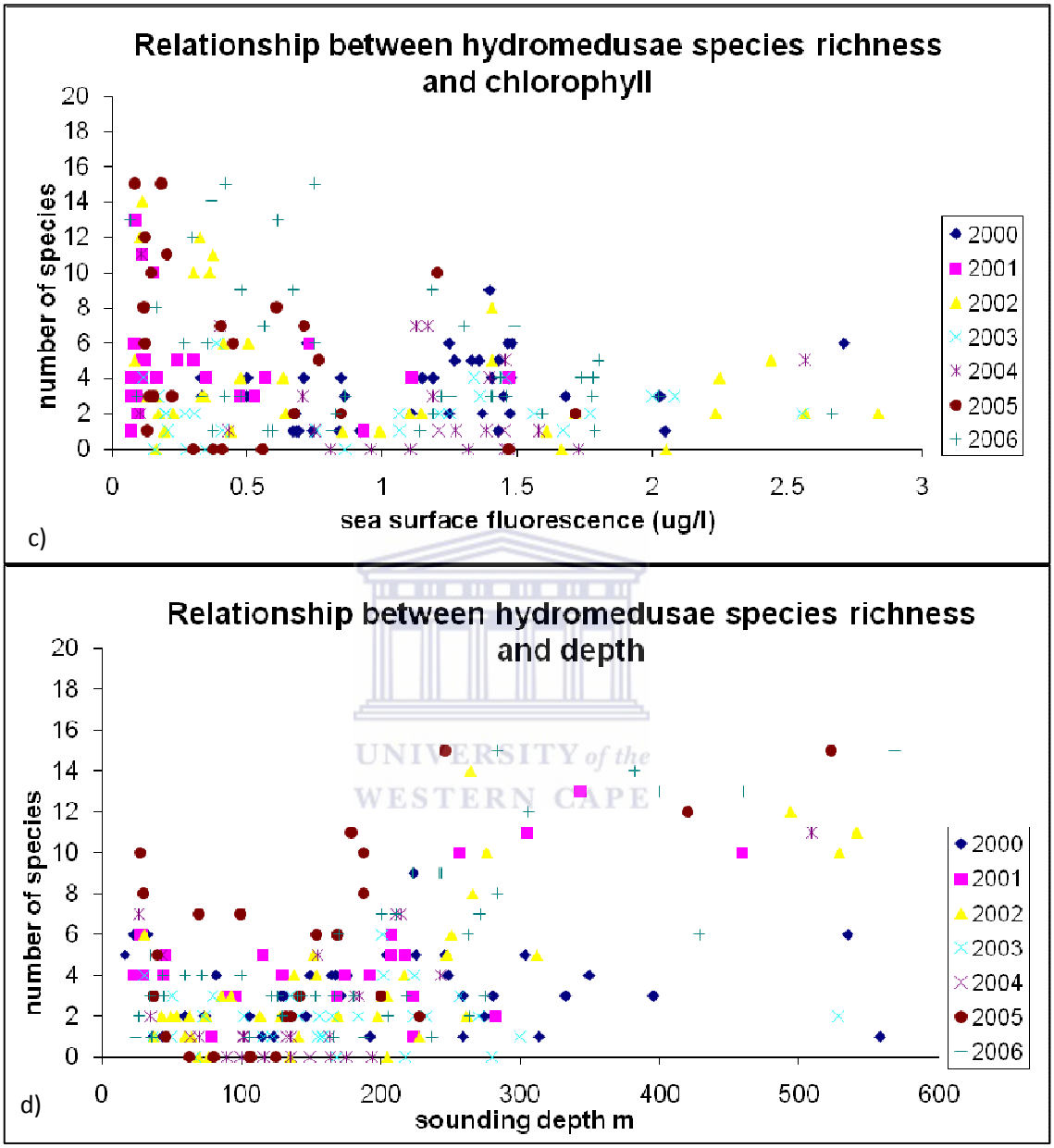

Figure 13: Scatter plot graphs illustrating the relationship between hydromedusae species richness and a) sea surface temperature and b) sea surface salinity, c) sea surface fluorescence and d) depth.

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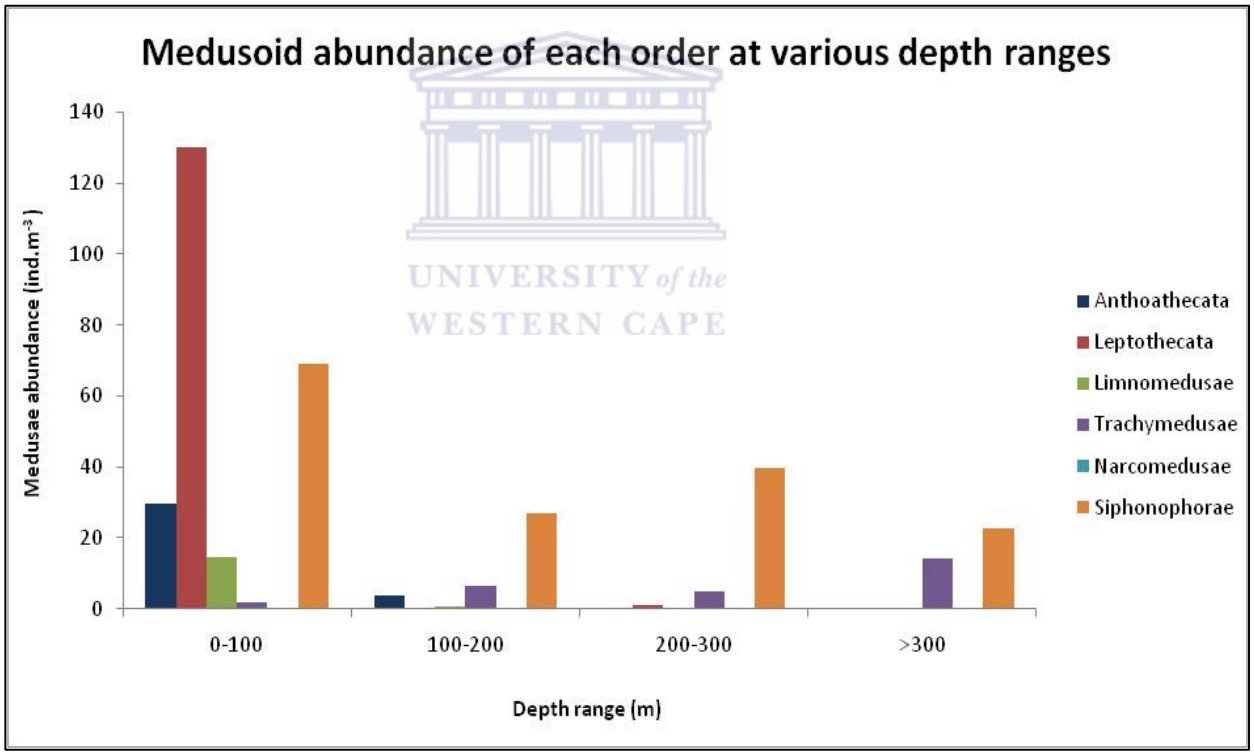

Figure 14: Bar graph illustrating accumulative hydromedusae abundance within each order across the time series and the depth range at which they were found.

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Anthoathecata

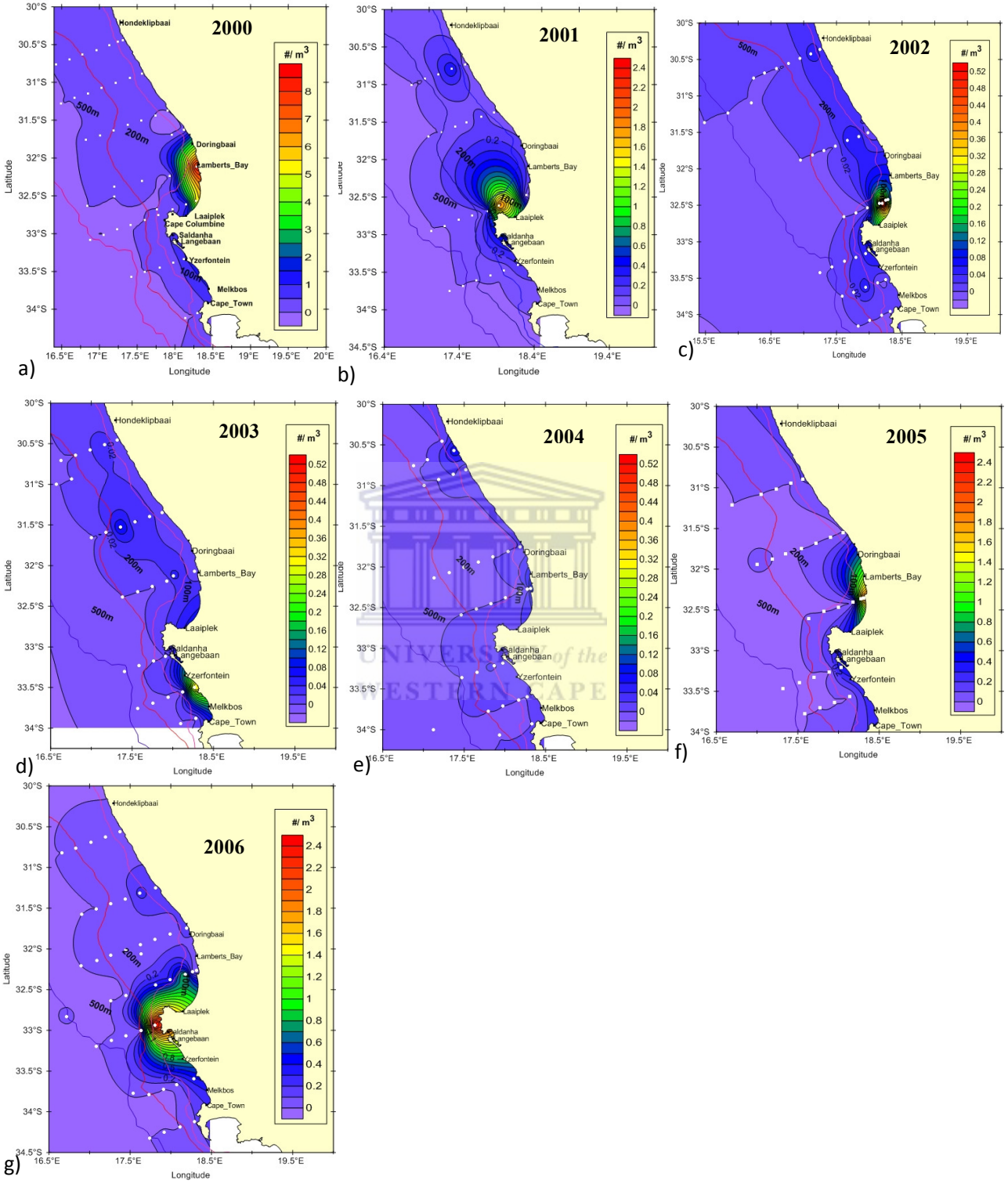

Figure 15: Contour plots illustrating Anthoathecata medusae across the study area for each year, from 2000 to 2006 (a-g). The plots are mapped along the west coast of South Africa, between Cape Town and Hondeklip Bay. Note that the scales are different.

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Leptothecata

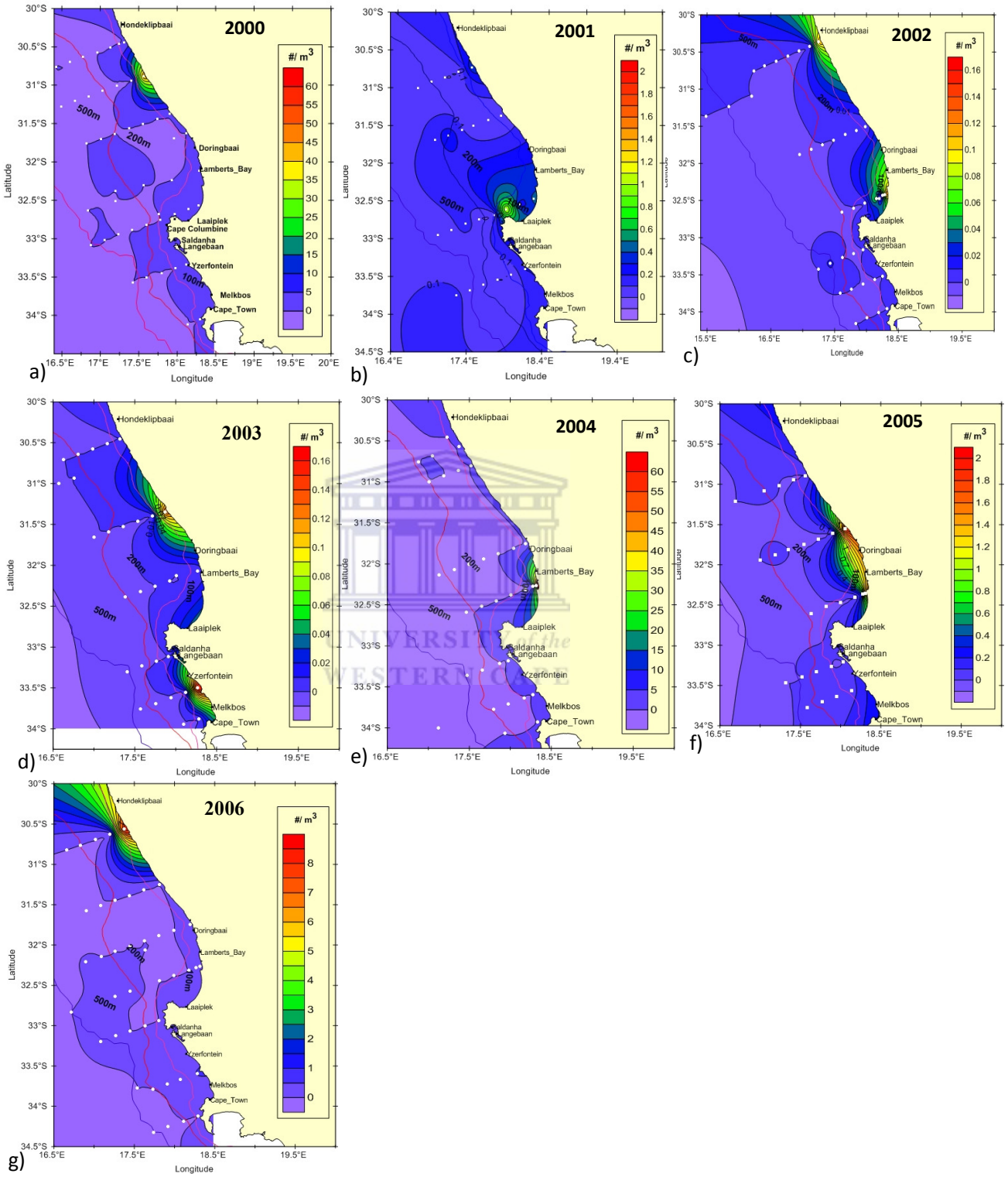

Figure 16: Contour plots illustrating Leptothecata medusae abundance across the study area for each year, from 2000 to 2006 (a-g). The plots are mapped along the west coast of South Africa, between Cape Town and Hondeklip Bay. Note that the scales are different.

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Limnomedusae

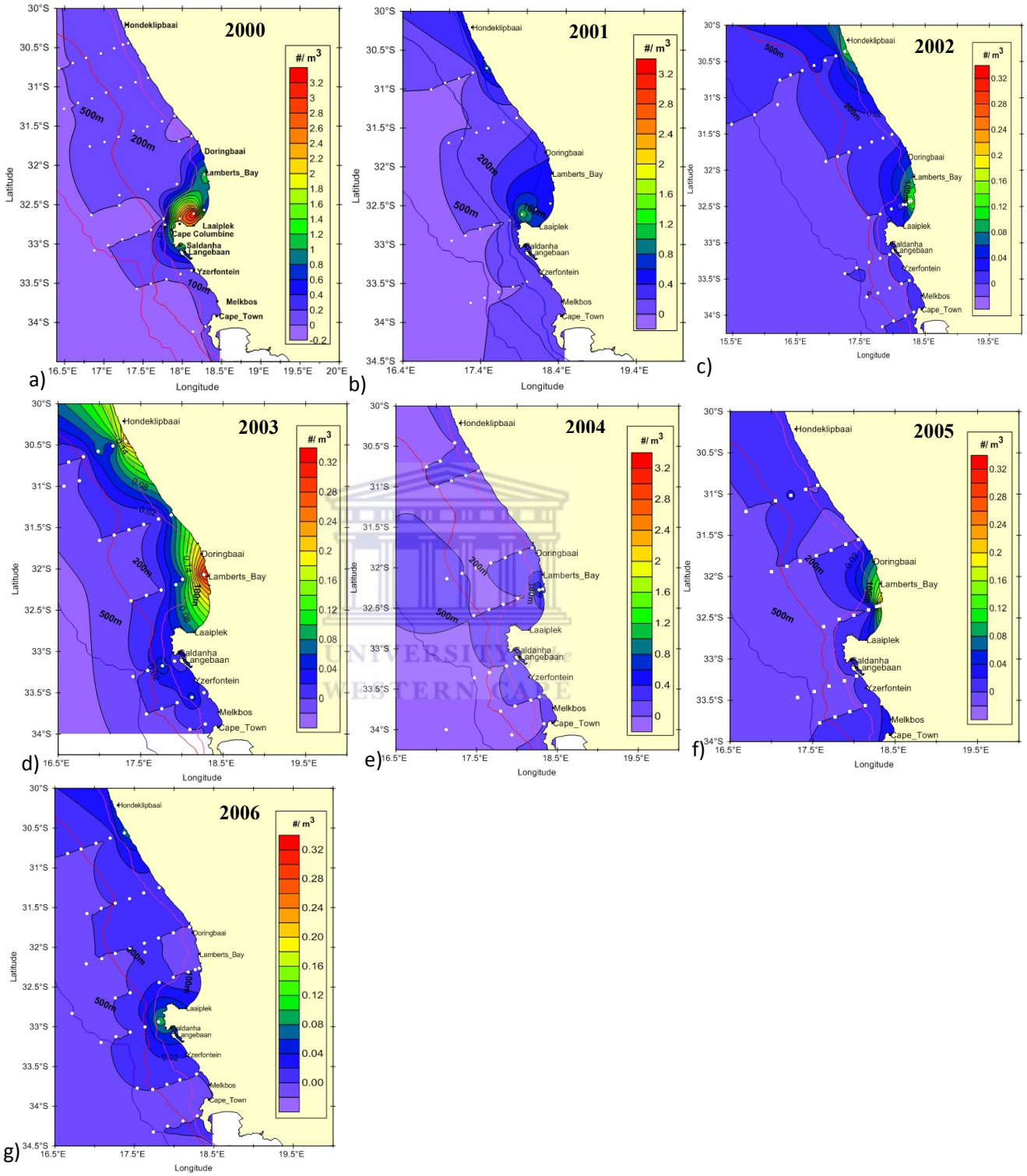

Figure 17: Contour plots illustrating Limnomedusae abundance across the study area for each year, from 2000 to 2006 (a-g). The plots are mapped along the west coast of South Africa, between Cape Town and Hondeklip Bay. Note that the scales are different.

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Trachymedusae

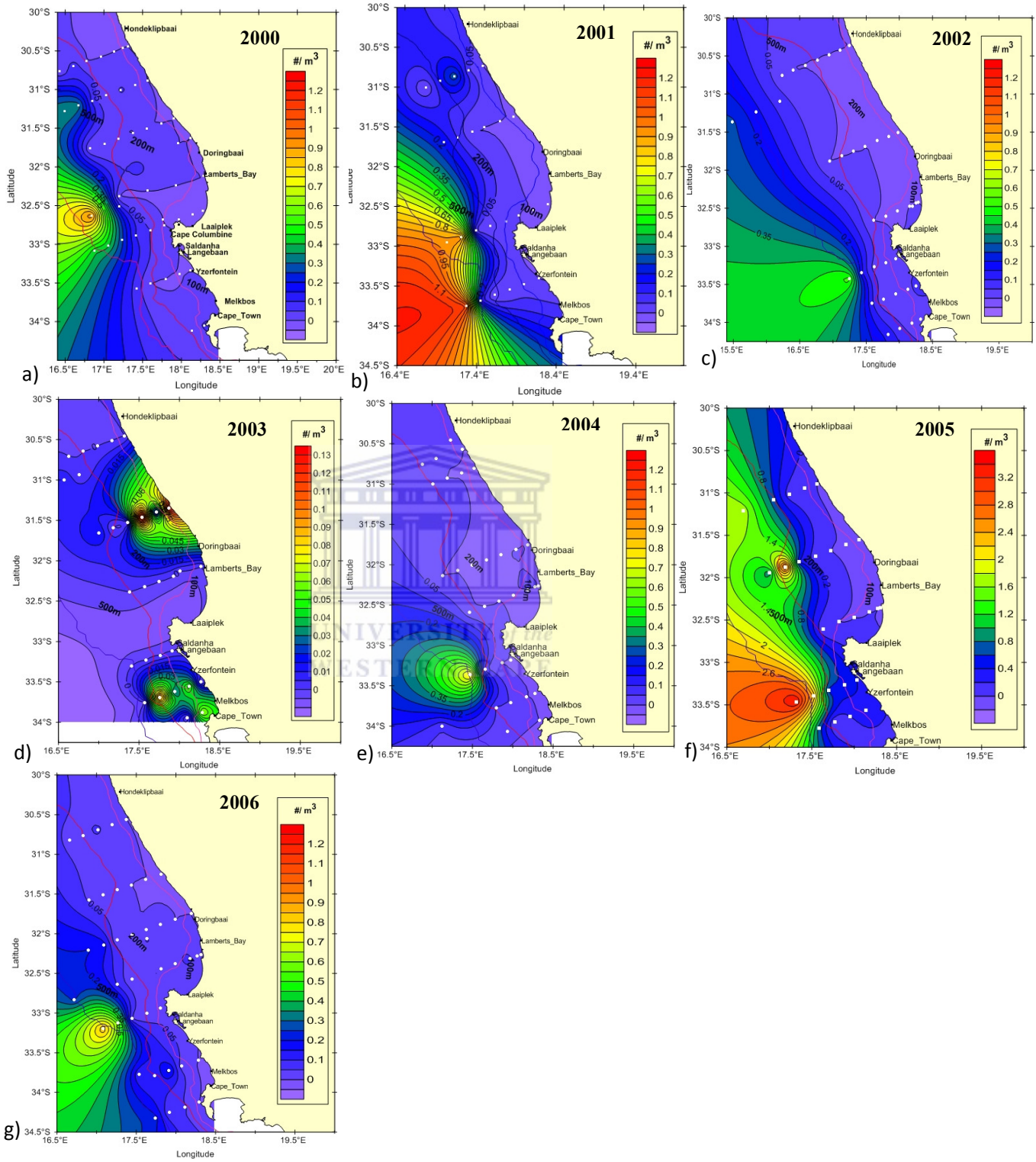

Figure 18: Contour plots illustrating Trachymedusae abundance across the study area for each year, from 2000 to 2006 (a-g). The plots are mapped along the west coast of South Africa, between Cape Town and Hondeklip Bay. Note that the scales are different for the years 2003 and 2005.

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Narcomedusae

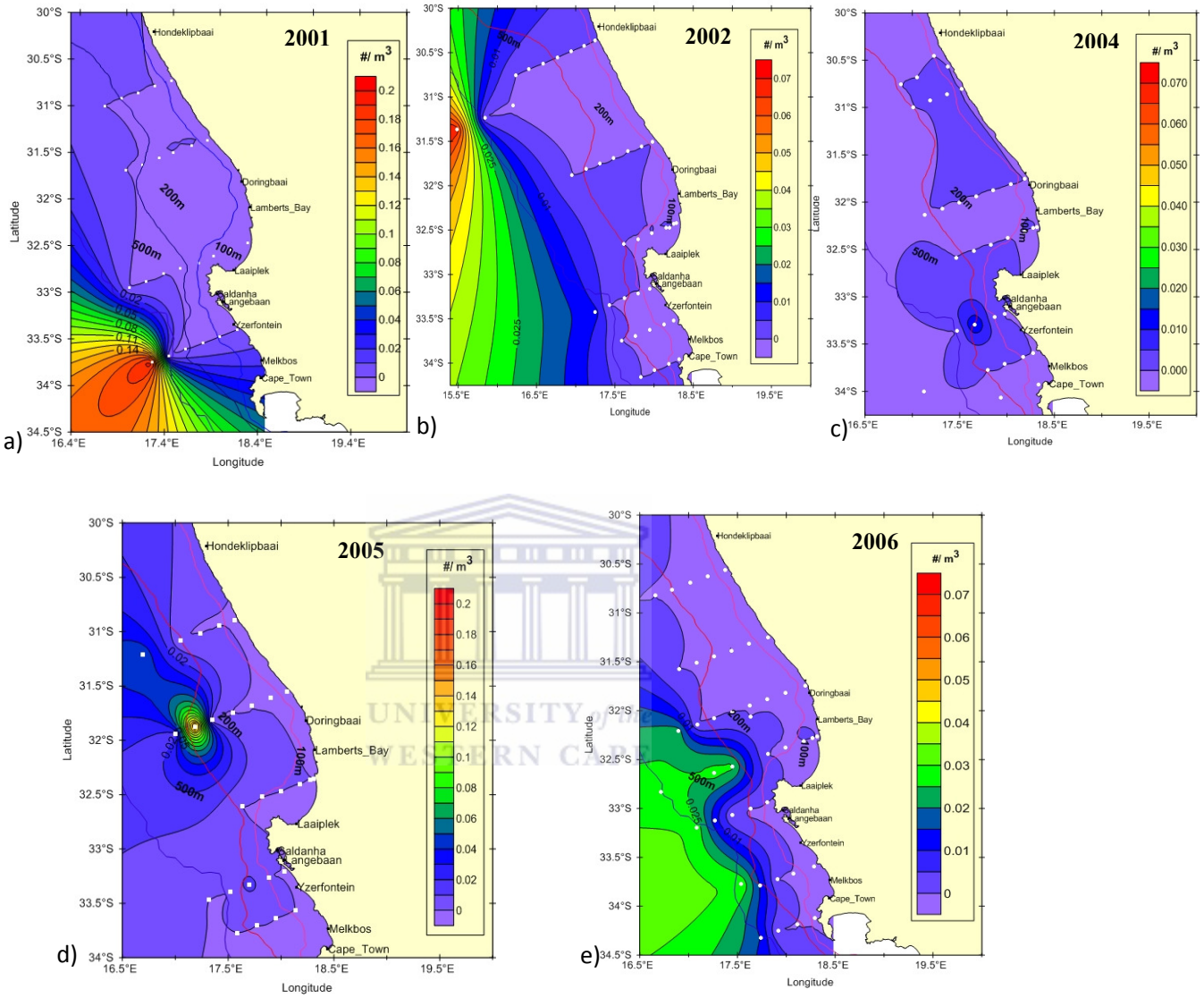

Figure 19: Contour plots illustrating Narcomedusae abundance across the study area for each year, from 2000 to 2006 (a-e). The plots are mapped along the west coast of South Africa, between Cape Town and Hondeklip Bay. Note that the scales for years 2001 and 2005 are different.

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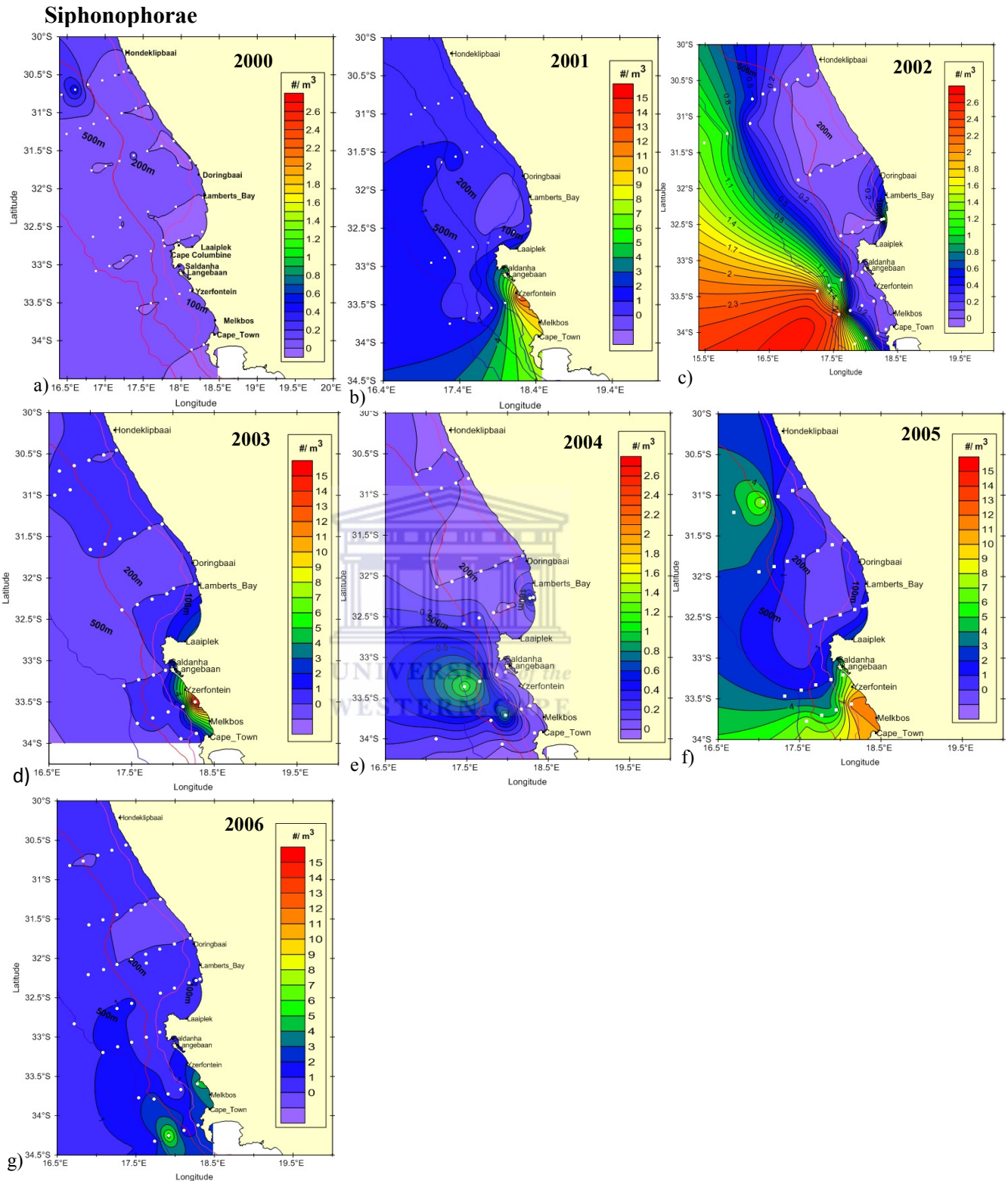

Figure 20: Contour plots illustrating Siphonophorae abundance across the study area for each year, from 2000 to 2006 (a-g). The plots are mapped along the west coast of South Africa, between Cape Town and Hondeklip Bay. Note that the scales are different.

http://etd.uwc.ac.za/

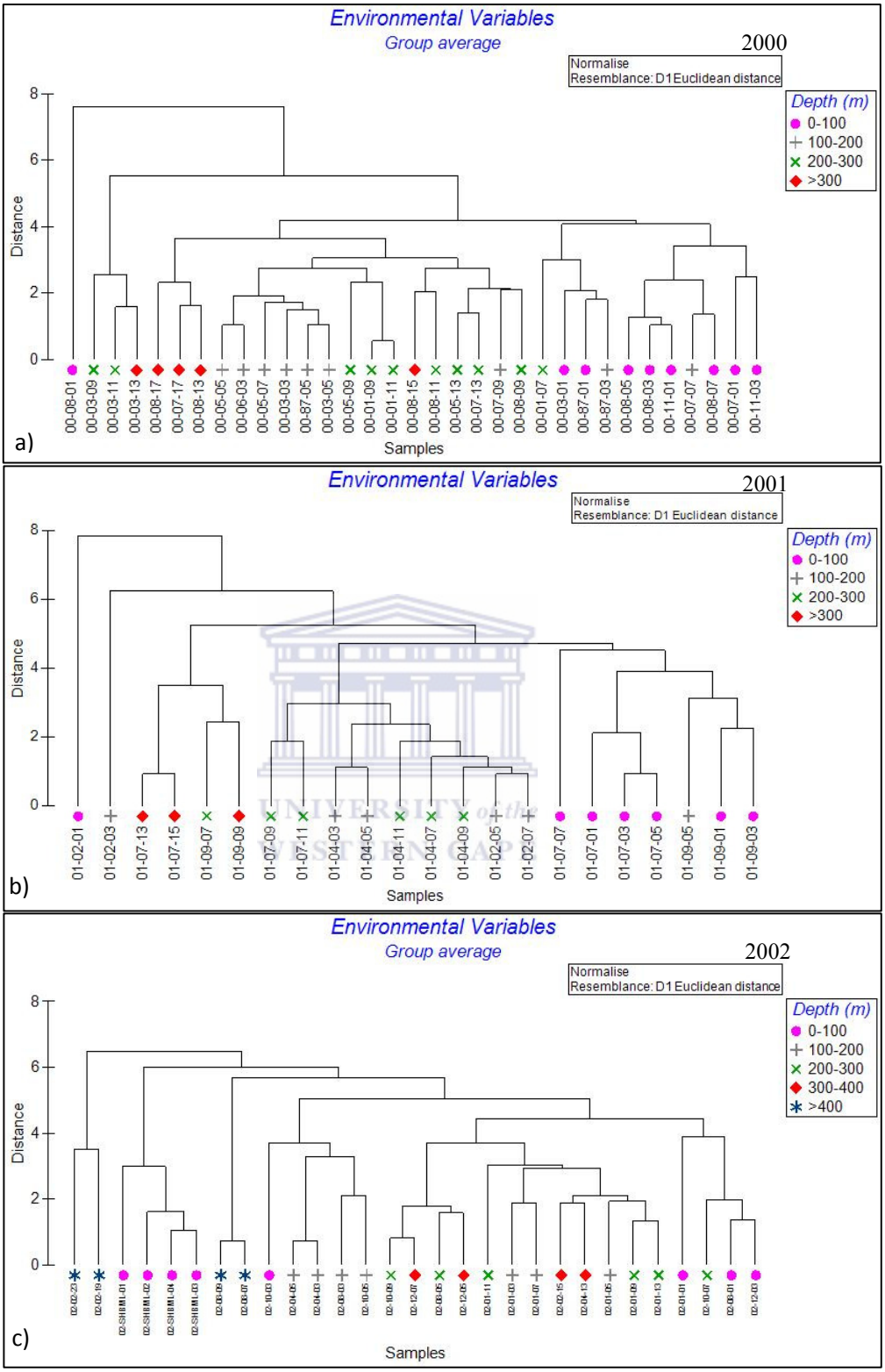

Figure 21: The cluster diagram for the year 2000 -2006 (a-g) presented the similarity between samples with regards to environmental variables. The diagram also displayed how samples were grouped according to depth.

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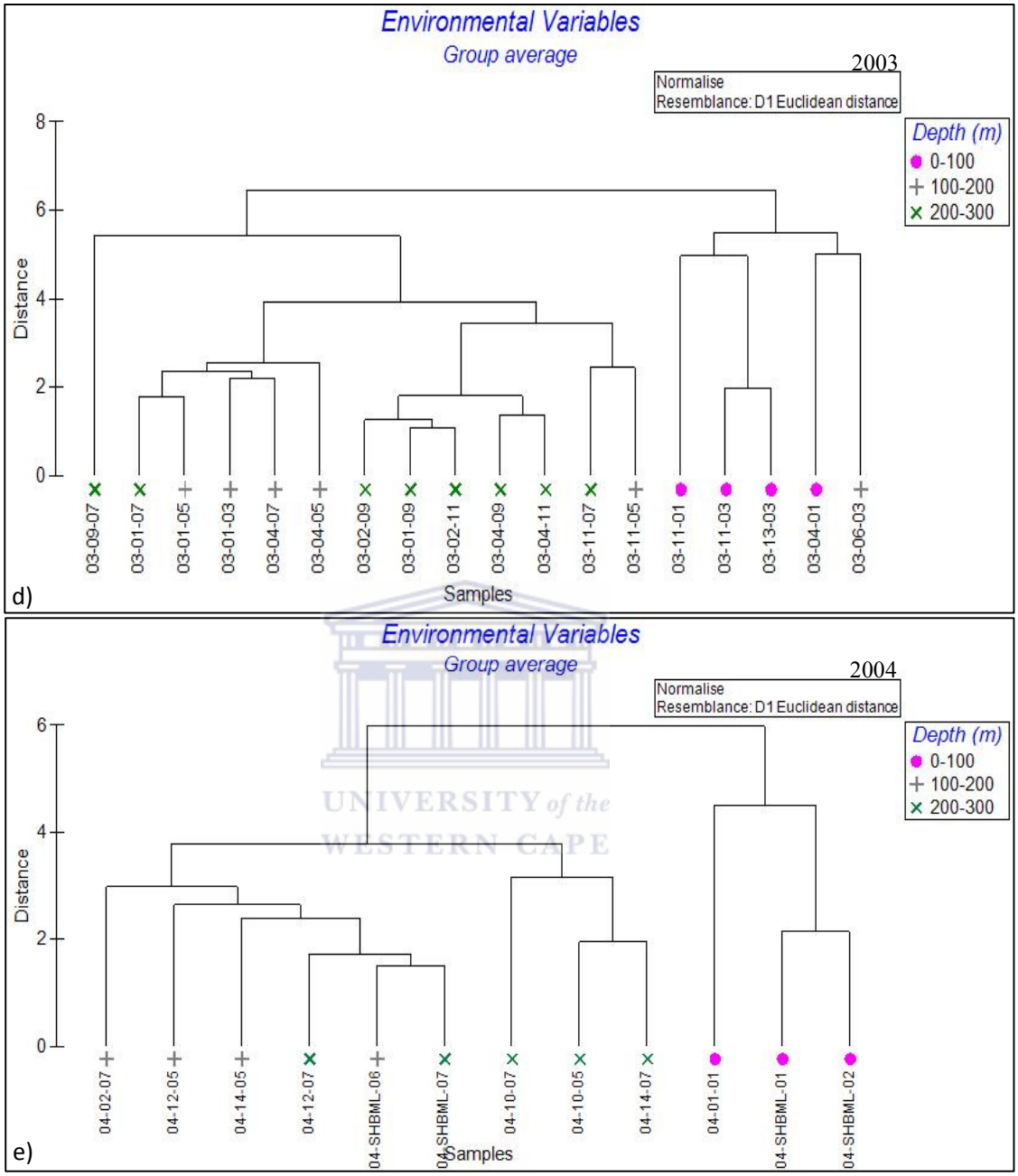

Figure 21: The cluster diagram for the year 2000 -2006 (a-g) presented the similarity between samples with regard to environmental variables. The diagram also displayed how samples were grouped according to depth.

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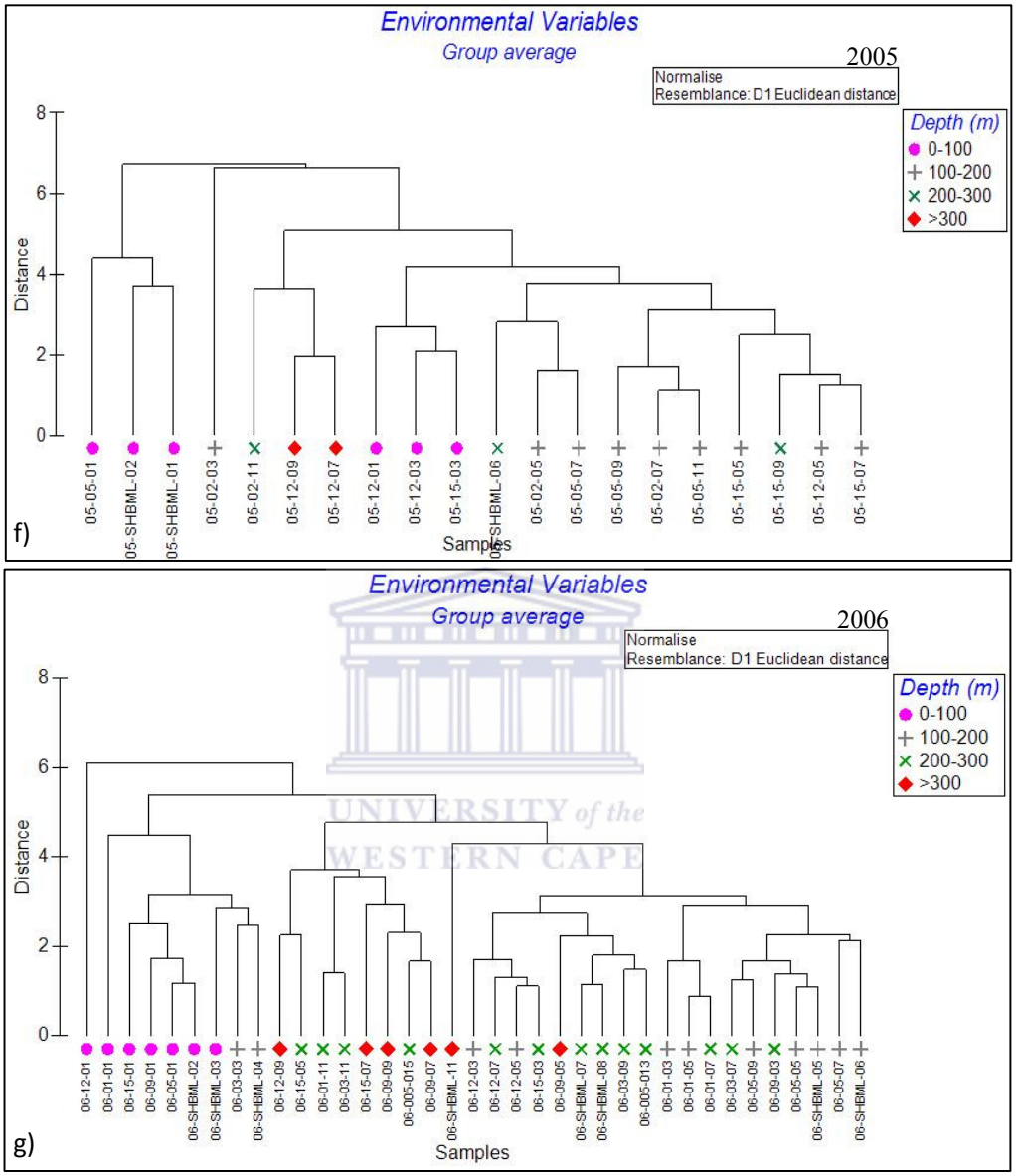

Figure 21: The cluster diagram for the year 2000 -2006 (a-g) presented the similarity between samples with regard to environmental variables. The diagram also displayed how samples were grouped according to depth.

http://etd.uwc.ac.za/

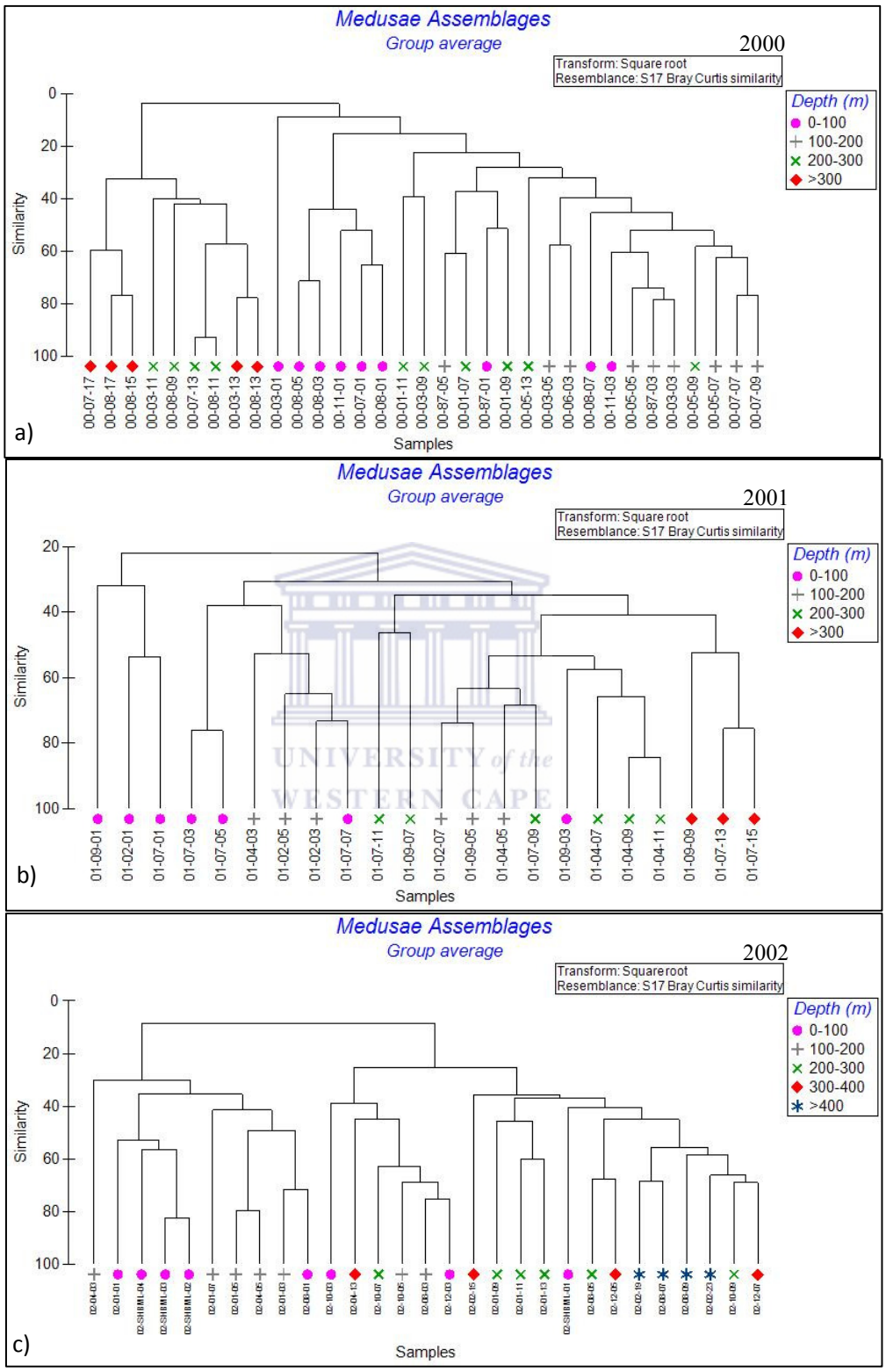

Figure 22: The cluster diagram for the year 2000-2006 (a-g) presented the similarity between samples with regard to medusa assemblages. The diagram also displayed how samples were grouped according to depth.

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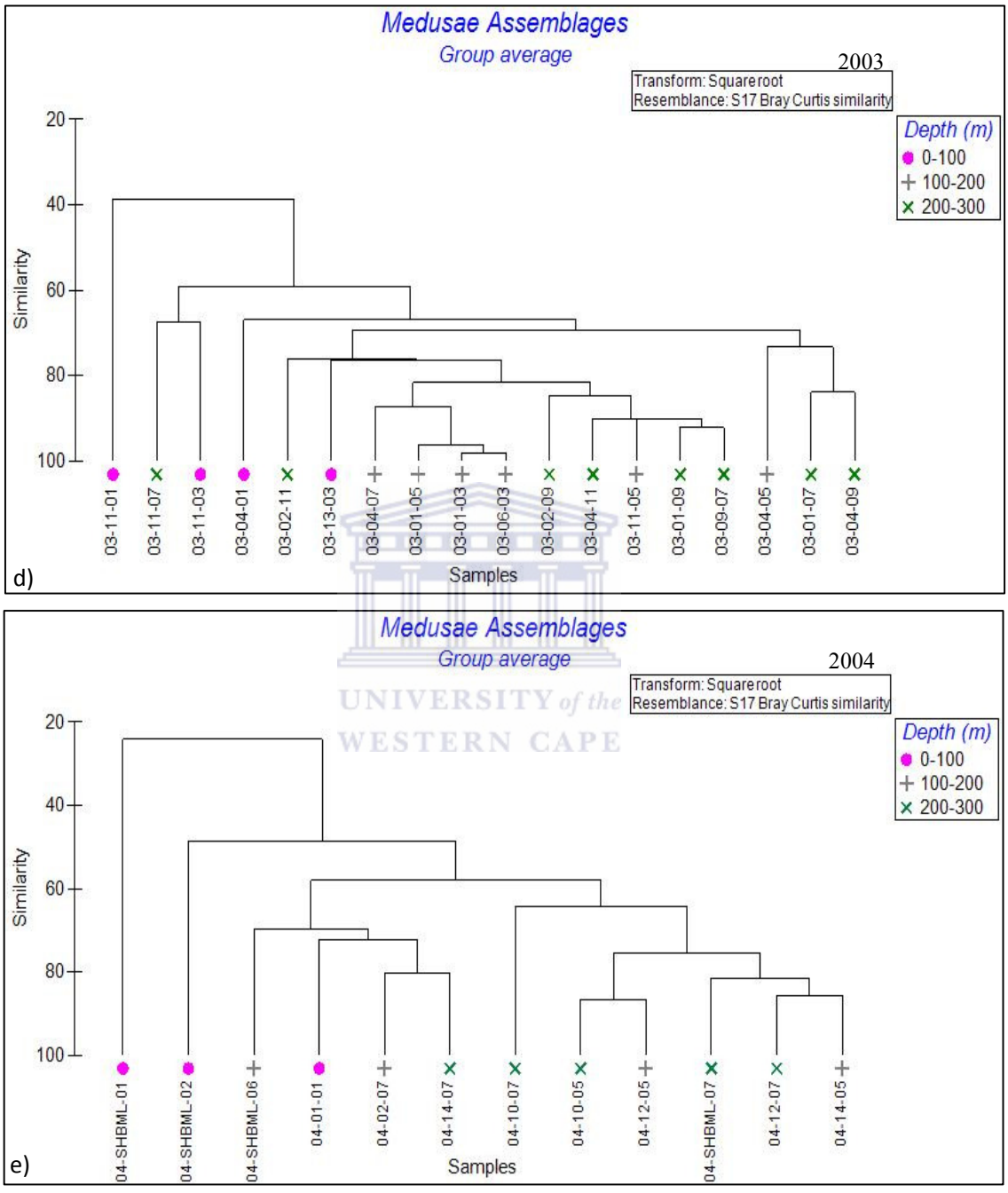

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Figure 22: The cluster diagram for the year 2000-2006 (a-g) presented the similarity between samples with regard to medusa assemblages. The diagram also displayed how samples were grouped according to depth.

http://etd.uwc.ac.za/

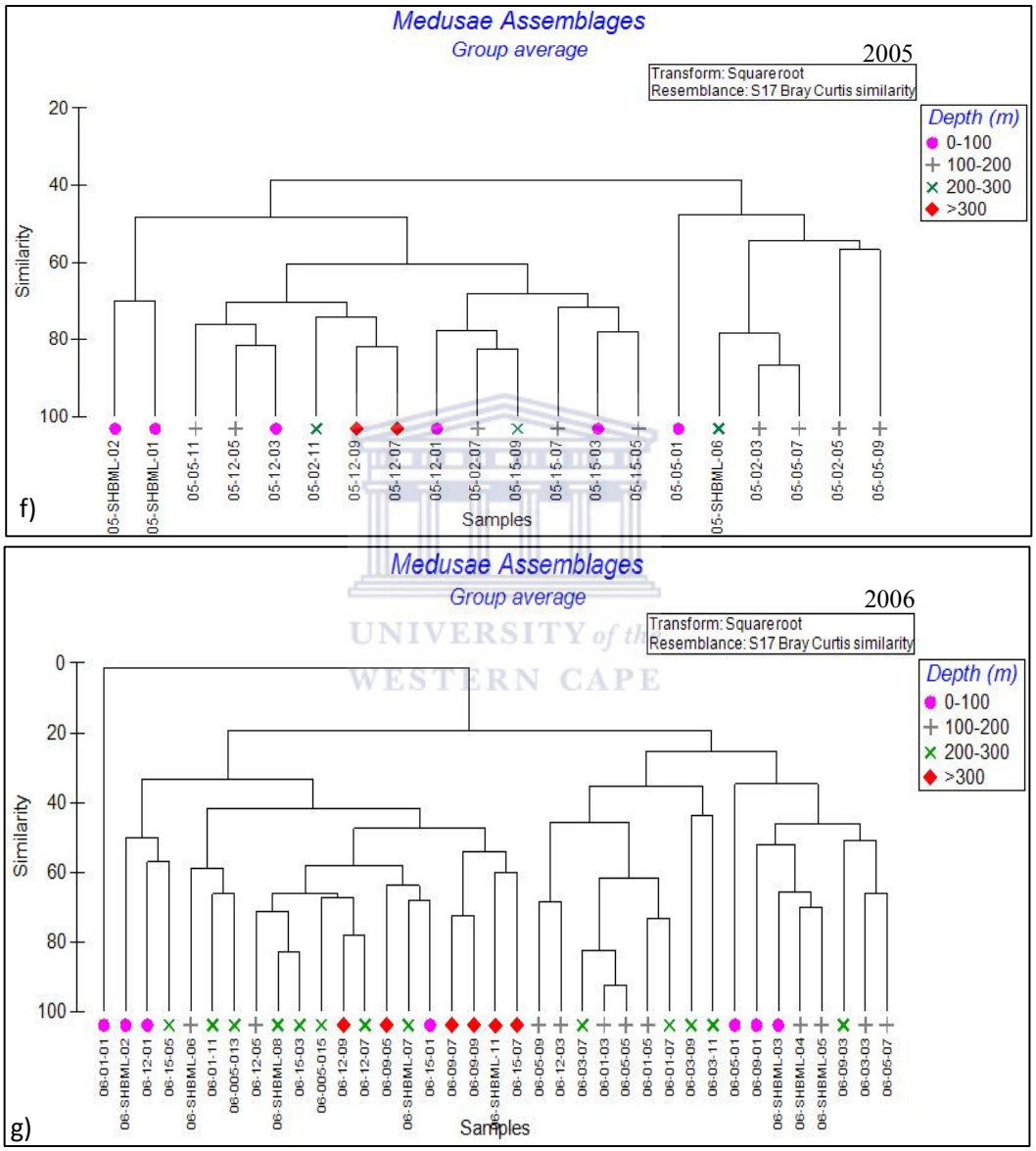

Figure 22: The cluster diagram for the year 2000-2006 (a-g) presented the similarity between samples with regard to medusa assemblages. The diagram also displayed how samples were grouped according to depth.

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