Modelling the distribution and abundance of several demersal fish species on the Agulhas Bank, South Africa

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by

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The world is your exercise-book, the pages in which you do your sums.

It is not reality, although you can express reality there if you wish.

You are also free to write nonsense, or lies, or tear the pages."

(R. Bach)

Dedicated to my Mother

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Abstract

The Agulhas Bank supports a speciose fish community, many of which are commercially important. Despite substantial research being conducted on aspects of their biology spatial aspects of their distribution and abundance in relation to environment parameters has been ignored. This study, therefore, addressed aspects related to the distribution and abundance of representative species on the Agulhas Bank within a Geographic Information System (GIS). Four candidate species were chosen due to their importance either in numbers or unit mass to the South African demersal trawl fishery. The species also shared morphological and taxonomic similarities. The candidate species chosen were the two Cape hake species, shallow-water hake *Meluccius capensis,* and deep-water hake *Merluccius paradoxus,* and the two pleuronectiform species being Agulhas sole *Austroglossus pectoralis* and redspotted tonguesole *Cynoglossus zanzibarensis*. The use of a GIS was appropriate and allowed for hidden spatial patterns be exposed and illustrated visually, while also facilitating the quantification of the relationships between distribution/abundance and certain environmental predictors using statistical methods

The Department of Marine and Coastal Management, Cape Town, supplied biological data in the form of length frequency and biomass information from spring (April/May) and autumn (September/October) cruises conducted between 1986 and 1993 on the *R. V. Africana*. The Council for National Geoscience, Cape Town, supplied sediment data for the entire southern African coastline. Initial exploratory data analysis highlighted potential relationships between environmental variables and abundance for each specie's life-history stanzas. Variations in spatial distribution were found to be significantly different between each life-history stanzas within species. Fish density as a function of the additive effects of the various environmental parameters, including temperature, depth and sediment type, was assessed using a Poisson Generalized Additive Model (GAM), while distribution was analysed with a logistic GAM. A predictive logistic model was then created, taking into consideration the importance of the predictor variables for each species, allowing for predictive estimates to be made for each species by inputting environmental information within the study area. The importance of certain environmental variables influencing distribution and abundance were noted. General patterns indicated that sediment was the most important to both the distribution and abundance of the two pleuronectiform species and juvenile life-history stanzas, while the adult gadoids' distribution and abundance appeared to be depth dependent.

Chapter 1 – General introduction

Introduction

Fish populations, and the communities of which they are part, have specific distributions that are structured in space and time. These patterns are more noticeable in aquatic than terrestrial systems as spatial structure has an additional third vertical dimension (Kracker 1999). Spatial investigation of physiological parameters, particularly those that are critical at the extreme ranges of tolerance assist in understanding how spatial structure is determined and therefore mirrored in life-history patterns. This structure describes underlying processes within the environment that regulate the biological and population dynamics of aquatic resources. Recently greater emphasis has been placed on the importance of spatial pattern, scale and variation as a component in ecological processes (Petitgas 1993, Syrjala 1995, Kracker 1999). Given the intrinsic interactions between organisms and their habitat, the role of the environment cannot, therefore, be ignored (Maravelias 1999).

Numerous studies suggest that fluctuations in abundance and/or distribution are due to the influence of biotic factors that include prey distribution and abundance, and favourable abiotic factors such as temperature, salinity, sediment type, suitable depth strata and habitat availability. For example, temperature and depth have been shown to influence bimodal distribution in fish schools in the Bering Sea (Swartzman *et al.* 1994), and temperature has been established as a factor influencing cod schools in the northern eastern Gulf of St. Lawrence (Rose and Leggett 1989). The effect of the environment has also been noticed in catch rates. Correlations have been found between fish catches and local sea temperatures (Sutcliffe *et al.* 1977), the distribution of herring catches being a consistent pattern related to localised environmental changes (Corten 2001) and environmental factors with seasonal variability like wind field, bottom temperature, oxygen concentration, together with sediment type, accounting for significant proportions of the variability in catch rate of Agulhas sole (Le Clus and Roberts 1995).

Ichthyology related to commercial fisheries, has traditionally focused on behaviour, age and growth, and reproduction. Biological research has dominated literature, and it is only recently that distribution and abundance information is being analysed quantitatively. The value of previous biological studies will also be fully realised when linked to distribution and abundance information as predictive models can be developed because they will now be supported by a thorough understanding of environmental processes.

Biological distribution can be defined as that spatial location geographically that is influenced by biotic and physical factors. Similarly, distribution can be defined as a spatial trend - the change in the average value of a response variable such as abundance (Kaluzny 1987). Distribution can be directly influenced by favourable environmental variables, and is most noticeable and influential at the extremes of specific variables for an organism of interest (Syrjala 1995). Within a species' distribution range there are differing abundances that are influenced by optimal environmental conditions such as food, habitat availability and suitability, as well as differences in harvesting pressure. An area will only be able to sustain a certain number of species in specific numbers based on availability of food and substrate required for breeding and establishment of territories.

The more abundant a certain key resource is, the more abundant the stocks can become in the area. However, there is evidence that fish density is not completely dependent on the availability of habitat (Richardson 1999), as abundance can also be influenced by recruitment, which in turn depends on different environmental variables.

The strategy of a species within different life-history stanzas will allow certain environmental variables to affect them more than others, thus giving them a specific range of environmental parameters or a 'spatial signature' (Maravelias 1999). The 'spatial signature', once determined for each species, will be advantageous for better understanding and management, as optimal environmental ranges can be used as indicators of species distribution and possibly density. A need, therefore, exists to scientifically determine optimal fish habitats to support decision making for management of essential fish habitats, which are those waters and substrate necessary for spawning, breeding, feeding, or growth to maturity (Rubec *et al.* 1998). Retaining social information regarding the organisation of habitats and species within the water column, the relationships between predator and prey, and the variation in habitat characteristics will contribute to the understanding of ecosystem processes and the sustainability of fish populations (Kracker 1999).

A South African case study

The ichthyofaunal community on the Agulhas Bank is diverse (Smale *et al.* 1993). Research cruises since 1986 have caught 219 species (Japp *et al.* 1994), many of which are commercially important and are harvested by the pelagic, mid-water and demersal fishing sectors (Japp *et al.* 1994). The Agulhas Bank also acts as an important nursery area for numerous teleosts and elasmobranches (Smale *et al.* 1993).

The uniqueness of the area and its high diversity are due to various factors. The warm Agulhas and cold Benguela currents converge in the area and import nutrients and fish larvae (Shannon 1989), fluctuating weather patterns, a highly variable substratum and bottom topography, and the broad extent of the area all provide a greater availability of habitat (Japp *et al.* 1994). The habitat complexity and a relatively stable oceanography allows for development of unique and diverse fish communities (Japp 1989).

Despite this diversity there has, however, been a lack of hypothesis-driven fish research (Smale *et al.* 1993) as past research initiatives have been predominantly biological and descriptive (Japp *et al.* 1994). Shannon (1989) noted that scientists are fortunate to conduct research in areas that are complex and unpredictable, as it provides an ideal area for investigating the influence of environmental variables on the structuring of populations and communities.

Identification of candidate species

Four commercially important candidate species were identified for the purposes of this study. Candidate species were chosen, because they displayed varying similarities in morphology, phylogeny and sympatry.

Two important pleuronectiform fish species inhabit the Agulhas Bank. These are Agulhas sole *Austroglossus pectoralis* and redspotted tonguesole *Cynoglossus zanzibarensis*. Both species are harvested by commercial trawl fisheries, either directly as in the case of *A. pectoralis,* or as bycatch for *C. zanzibarensis*.

A. pectoralis is the most valuable fish species by mass harvested along the South African coastline (Payne and Badenhorst 1989, Japp *et al.* 1994). It is a slow growing species, with males growing slower than females, with fish reaching a maximum age of *ca.* 12 years (Zoutendyk 1974). Sexual maturity is attained at four to five years of age for females at *ca.* 33 cm TL, whilst males mature at two years at *ca.* 18cm TL (Zoutendyk 1974). Reproduction is occurs throughout the year and it has been suggested that locality has a strong influence on breeding. Preferred habitat of *A. pectoralis* appears to be small areas dominated by clay and silt (Le Clus *et al.* 1996), with feeding directed at invertebrates such as polychaetes, crustaceans and molluscs as in other sole species like the common sole *Solea solea* (Molinero and Flos 1991).

C. zanzibarensis is the most abundant pleuronectiform and cynoglossid species on the Agulhas Bank (Japp *et al.* 1994). It exhibits fast growth and attains a maximum age in excess of 8 years (Booth and Walmsley-Hart 2000). Sexual maturity occurs at 1.3 years of age (ca. 32 cm TL), and is similar to *A. pectoralis* in that spawning occurs throughout the year. Dietary items include polychaetes, isopods, amphipods and crabs (Meyer and Smale, 1991). Preferred habitat is assumed to consist of coarse unconsolidated sediments, such as sand at depths greater than 100 metres (Meyer and Smale 1991, Smale *et al.*

1993, Japp *et al.* 1994). Commercial catch rates for *C. zanzibarensis* vary intra- and inter-annually suggesting that environmental factors may influence abundance (Badenhorst and Smale 1991).

The Cape hakes, comprising shallow water hake *Merluccius capensis,* and deep water hake *Merluccius paradoxus*, form the basis of the demersal trawl industry in southern Africa (Payne 1989), and are targeted by nearly all sectors of the fishing industry (Japp *et al.* 1994). Over the Agulhas Bank *M. capensis* is the dominant species constituting *ca.* 70% of the ichthyobiomass, while *M. paradoxus* has a 90% dominance on the west coast (Payne 1989). Reasons for these differences are not fully understood although it has been suggested that the change in width and steepness of the continental shelf reduces available habitat for *M. capensis* on the west coast (Punt and Leslie 1991).

Both hake species are mid-water spawners and spawn all year round, however, increased spawning occurs over spring and early summer (Payne 1989). One of the biggest differences between the species is their preferred depth range, with *M. capensis* generally not occurring deeper than 400 metres and *M. paradoxus* occurring up to 800 metres (Botha 1985). Males in both species tend to be slower growers with females reaching a larger size. *M. capensis* also grows slightly faster than *M. paradoxus* (Payne 1989). *M. capensis* reaches sexual maturity at 3.4 years (41 cm TL), and 95 % are sexually mature by 6.15 years (64 cm TL) (Punt and Leslie 1991). *M. paradoxus* are 3.5 years old (42 cm TL) at sexual maturity and 6.3 years old (64 cm TL) at 95 % sexual maturity (Punt and Leslie 1991).

Hake are generally considered to be opportunistic feeders with a diet changing ontogenetically as well as seasonally. Feeding occurs mainly at night in mid-water and prey items range from crustaceans and squid to various fish species, including inter- and intra-specific cannibalism (Payne 1989). On the south coast *M. capensis* feeds mainly on other fish, followed by crustaceans and then cephalopods (Pillar and Wilkinson 1995). Hake have highly variable recruitment, which may be linked to fluctuations in the environment (Payne 1989).

Application of Geographic Information Systems

Geographical Information System (GIS) technology has been used for 25 years but more recently, in the last 15 years, its true efficiency as an analysis tool has being recognised (Longley and Batty 1996). The ability of a GIS system to hold a vast amount of data, separate it into different categories, analyse it, represent it spatially through maps and then visualise the different relationships between analysed information, makes it a powerful tool. The importance of GIS is further emphasised by the global move towards computerised digital information that can be analysed and stored for future use (Longley and Batty, 1996).

The primary use of a GIS is to process spatial, or geographically referenced, information which can range from geological, hydrological and any ecological information, and in this case, fisheries information (Chou 1997). The sources of information are generally from Governmental census', land use surveys, satellite imagery and aerial photographs, and paper maps (Chou 1997). In terms of fisheries science the utilisation of GIS's is firmly established, with their importance being shown in literature ranging from deep ocean science (Wright and Goodchild 1997), monitoring fisheries effort and catch (Meaden and Kemp 2000), remote sensing (Kracker 1999), establishing essential fish habitat (Rubec *et al.* 1998), and the analysis of fish distribution and abundance (Booth 1998).

Thesis objectives and structure

Considering the paucity of information pertaining to those biotic and abiotic parameters responsible for structuring the distribution and abundance of fish species on the Agulhas Bank, this study provides the first quantitative investigation within a GIS framework. Several parameters have been identified to be important, based on *a priori* evidence from other species and from initial exploratory data analysis. Individual parameters were investigated before a statistical model was developed to describe their combined influence and interactions.

The thesis has been structured to follow the logical analytical steps that were undertaken. Chapter 2 describes the study area and explains the materials and methods that were used for analysis. Exploratory Data Analysis was conducted in Chapter 3 to gain insight into the distribution and abundance of species and to gauge which environmental parameters could act as structural agents. Chapters 4 and 5 outline the development of suitable generalised models, incorporating important environmental parameters. Overall trends and results are discussed and concluded in Chapter 6.

Chapter 2 - Materials and methods

Study area

The Agulhas Bank (Figure 2.1) is a triangular extension of the South African continental shelf lying within the 200 metre isobath between 18°E and 25 ° E, and occupies an area of *ca.* 100 000 km^2 (Boyd and Shillington 1994). The central portion of the Bank is the widest, extending 300 km southwards from the African continent, while the eastern section is not more than 150 km wide (Shannon 1989).

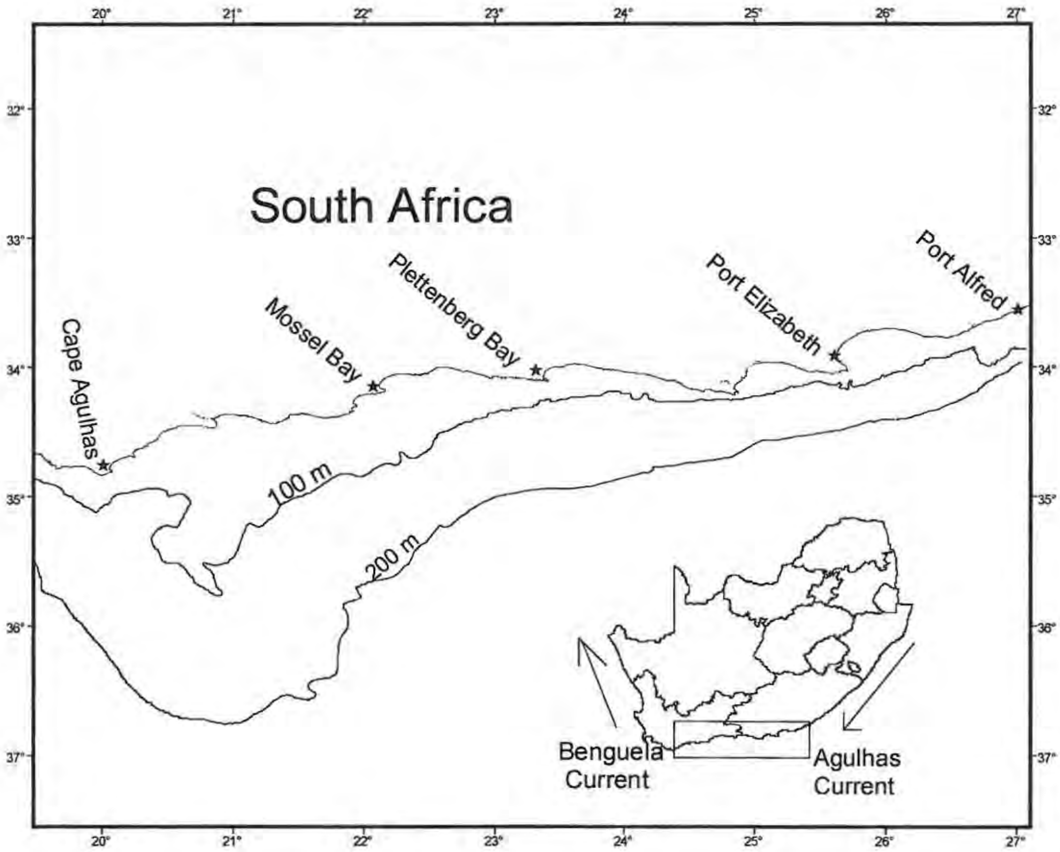


Figure 2.1: Map of the Agulhas Bank, South Africa, showing the 100 and 200 metre isobaths. The Agulhas and Benguela Currents are illustrated in the insert.

The Agulhas Bank is oceanographically unstable because of the convergence of two currents; the westwards warm Agulhas current, and the northerly cold Benguela current (Shannon 1989). Oceanographic complexity is enhanced by a steep continental shelf breaking towards the South Western Indian ocean ridge (Shannon 1989, Badenhorst and Smale 1991). Variation in the physical and chemical nature of these currents provides a variety of micro-environments affecting the diversity in both fauna and flora (Shannon 1989). The system is nutrient poor, especially in nitrates which reduces chlorophyll levels (Largier *et al.* 1992). Overall the system is considerably less productive than the upwelling Benguela system off South Africa's west coast (Largier *et al.* 1992).

Flow patterns of the Bank are complex (Boyd and Shillington 1994), and rotate in an anti-cyclonic direction (Shannon 1989). The eastern Agulhas Bank is dominated by wind forcing together with the position and orientation of the Agulhas current. While the central region has a cold water ridge separating the inner and outer Bank (Boyd and Shillington 1994), thermoclinal layers dominate the central Agulhas Bank in summer (Shannon 1989), which are mixed and negated by storms, resulting in uniformly well mixed waters in winter (Schumann and Beekman 1984). The eastern Agulhas Bank is strongly influenced by the Agulhas Current, generally being nutrient poor with the exception of the far-eastern Agulhas Bank upwelling cell, that provides localised productivity (Booth 1997). Counter flows on the edge of the current occur above the 200m isobath (Lutjeharms *et al.* 1989).

Bottom sediments on the Agulhas Bank can be divided into a number of main substrate types, each interspersed with rocky outcrops (Japp *et al.* 1994). A large proportion of the Bank is covered with sandy sediments, with muds common in the west. Sediments tend to be coarser towards the shelf-break, possibly due to higher bottom currents than in inshore areas (Shannon 1989).

Data acquisition

Three sources of data were available for this study; biological, physical and sedimentary.

Biological and physical data

The Department of Marine and Coastal Management, Cape Town, supplied biological data in the form of length frequency and biomass information from spring (April/May) and autumn (September/October) cruises conducted between 1986 and 1993 on the *R. V. Africana*. Surveys covered the area between Cape Agulhas (34°50′S, 20°00′E) and slightly north of Port Alfred (33°26′S, 26°54′E). Physical data including depth, bottom temperature, salinity and dissolved oxygen were collected at the end of each trawl using a conductivity, temperature and depth (CTD) rosette sampler to within 10m of the bottom (Figure 2.2).

Survey trawling was confined to flat areas due to the study area being interspersed with rocky outcrops (Badenhorst and Smale 1991). Trawls were selected from a semi-randomised depth stratified sampling grid (Figure 2.2) with each block covering an area of *ca.* 25nm^2 (5′ × 5′ nm). For the sake of a scale reference, one nautical mile is approximately one minute. Trawls took place during the day, for a 30minute period, using a 55m German otter trawl with a mouth opening of 26 metres. The speed of the vessel was *ca.* 3nm.hr^{-1}, with the trawl time standardised if a trawl had to be shortened. Each trawl, therefore, surveyed an area of *ca.* 0.0026nm^2, which allowed for density to be standardised according to number of fish per nautical mile trawled.

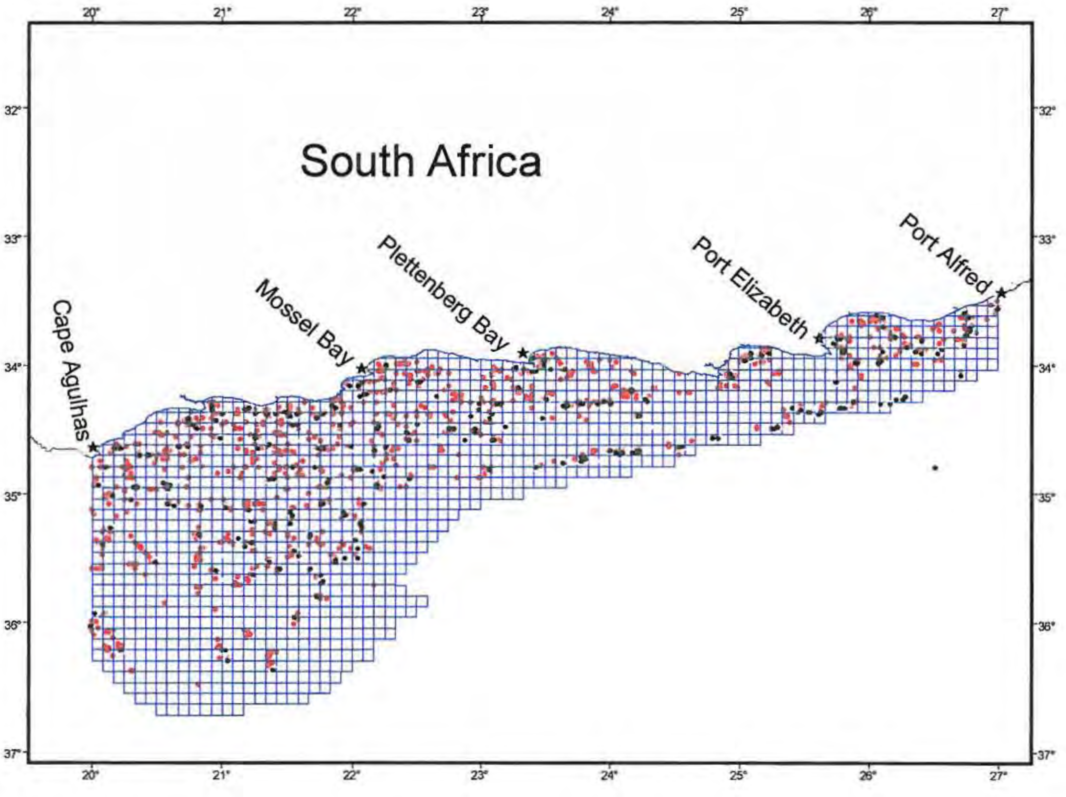


Figure 2.2: Map illustrating the Agulhas Bank, South Africa, with the position of trawl stations and where CTD information was acquired (red) or is absent (black). The research survey grid is represented in blue.

The catch at each trawl station was sorted, identified and weighed on board. Length frequencies in centimetre size classes were collected for all commercial species. Published literature concerning the biology of each species was used to ascertain the size categories for juveniles, sub-adults and adults' life-history strategies (Table 2.1).

Table 2.1: Life-history stanza size categories for each species investigated.

Species	Juvenile (cm TL)	Sub-adult (cm TL)	Adult (cm TL)	Reference
A. pectoralis	< 24		> 25	Le Clus *et al.* (1994)
C. zanzibarensis	< 23	24 - 31	> 32	Booth and Walmsley-Hart (2000)
M. capensis	< 32	33 - 48	> 49	Botha (1985), Punt and Leslie (1991)
M. paradoxus	< 33	34 - 49	> 50	Botha (1985), Punt and Leslie (1991)

Fish density in each size category for each species was calculated according to the number of fish caught in each size category and the area covered by the net. This information was then natural-log transformed (plus an offset of one) to stabilize variance and to reduce the influence of zero catches in the dataset.

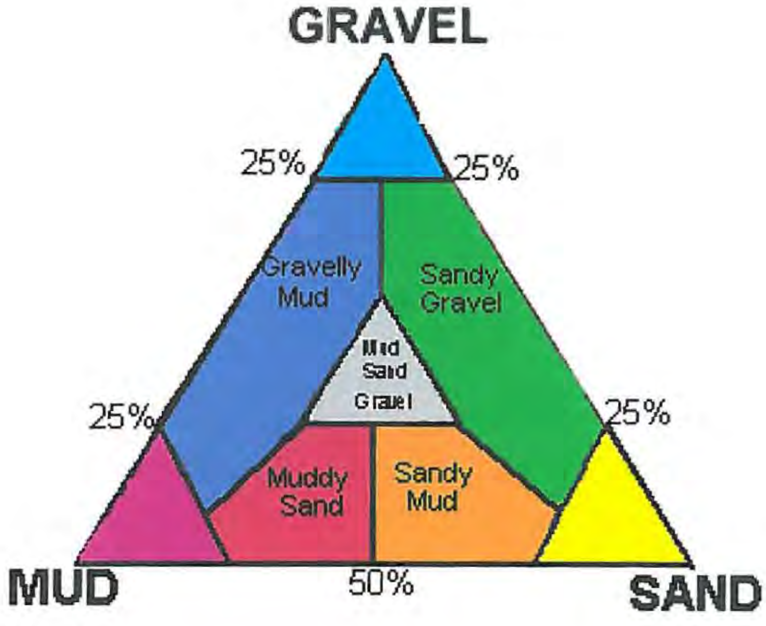


Figure 2.3: Texture breakdown of sediment along the Southern African coastline. (From Council for National Geoscience Cape Town)

Sediment data

The Council for National Geoscience, Cape Town, supplied sediment data for the entire southern African coastline. Sediment information was divided by texture and composition. Texture information was further divided into eight categories: Muddy Sand, Sand, Sandy Gravel, Mud, Gravelly Mud, Sandy Mud, Gravel, and Mud Sand Gravel (Figure 2.2). Definitions of these substrate types are summarised below:

Mud	–silt and clay with sediment particles less than 63 microns in diameter,
Sand	–mineral particles with a size between 0.6 and 2.0 millimetres in diameter,
Gravel	–unconsolidated sediments composed of rock fragments greater than 2mm,
Rock	–compact and consolidated mass of mineral matter; three types are recognised: igneous, sedimentary and metamorphic and,
Minerals	–naturally occurring inorganic solids with a crystalline structure and specific chemical composition.

Composition information pertaining to the sediment was biologically based. This can be divided into Authigenic, Biogenic and Terrigenous. Authenigenic material is defined as material created *in situ* and is the product of chemical and biochemical activity. Biogenic material arises from the physiological activities of organisms and can be divided into two more categories: Foraminiferal sediments from unicellular animals of the subclass Sarcodina and biogenic derived from molluscan debris. The third category, terrigenous material, is derived from the earth. This substrate is derived mainly from fluvial origin and is deposited by the main rivers along the South

African coastline; like the Breede, Gamtoos, Swartkops, Great Fish and Sundays Rivers (Payne 1989). Only six of the eight sediment types were tabulated as no trawls took place over Gravel and Mud Sand Gravel did not occur in the study area.

Data manipulation

GIS is suited form this project for a number of reasons: Firstly, the fact that all the catch data has latitude and longitude information attached to every point allows for a spatial index for the data. Secondly, the information pertaining to each point can then be attached or linked to this point through the use of a primary key. Finally once the layers are created for each species size category, the GIS can be used to extract information for each of the species according to any of the inputted environmental variables.

Length frequency information per life-history stanza was linked to the trawl station number. Additional information available for each trawl included station number, latitude, longitude, depth, temperature and dissolved oxygen. Data were, therefore, considered multivariate. The area trawled was also added, calculated by taking the size of the net, distance travelled and duration of the trawl. Density information for each life-history stanza was then calculated. Tables for all trawls were imported into *MS-Access* and then joined to create one large table for each species.

Each species table was imported into a GIS, *ArcView* 3.2 via the *SPLUS-ArcView* link. In *ArcView,* sediment information at each geo-referenced trawl station was extracted by overlaying the station data onto the sediment data. This information was re-imported into *SPLUS* and then added to the other tabulated information in *MS-*

Access. The final validated master table contained all environmental variables - sediment type, latitude, longitude, station number and the related density information from each life-history stanza. The master table allowed for any information pertinent to each species to be extracted, using standard SQL queries. Querying facilitated the extraction of manageable tables for each species and specific environmental variables. These tables were then exported dynamically into *SPLUS*, via the *SPLUS-ArcView* link for further analysis.

Chapter 3 – Exploratory Data Analysis

Introduction

Graphics are essential in expressing relationships and trends for different statistical methods in a simplified and informal manner (Du Toit *et al.* 1986). Graphic methods are, therefore, crucial when detecting clues in data that are used in inferential statistics with the possibility of making certain justifiable pronouncements (Tukey 1977). The strength of illustrating data visually is that humans have limited ability to visualise or digest numerically presented data. Hence, presenting and exploring the data graphically allows for better interpretation and understanding. The process involved simply transforms numbers into insight. In addition, maps of numbers (data/processes) must be transformed into images by means of some algorithmic technique, with trends in the maps uncovered by means of perception and analysis.

Exploratory data analysis (EDA) encompasses a set of techniques that allows for the visual exploration of data either at the initiation, or throughout the duration of a statistical analysis. The techniques included in the process are to maximise insight into the data set, uncover underlying structures, extract important variables, detect outliers and anomalies, test underlying assumptions, develop parsimonious models and determine optimal factor settings (Engineering Statistics Handbook 2002).

The philosophy behind exploratory data analysis is that few *a priori* assumptions are made about the data and what statistical models are suitable. The data are initially approached to show any underlying structures, thus allowing the user to evaluate and decide on the best model applicable to the data. Contributing to this is the fact that in fisheries related data, mathematical models describing the relationships between habitat type and abundance do not generally exist (Rubec *et al.* 1998).

This chapter describes an exploratory analysis of the data to expose possible trends between the densities of different life-history stanzas of various species with respect to environmental variables. The creation of scatterplots and maps allows for the effective visualisation of possible patterns thus allowing for decisions to be made on the use of appropriate statistical analyse discussed in later chapters. This chapter therefore endeavours to create the foundation for the development of a suitable model for each species.

Materials and methods

Species specific tables, created by querying the *MS-Access* master table, were imported into *Splus* via the *ArcView* link. Each table included information pertaining to four environmental variables: temperature, depth, sediment type and dissolved oxygen, and log-transformed density of each life-history stanza.

Scatterplot matrix graphs were plotted to investigate potential relationships between density of each life-history stanza and the selected environmental variables. Additional visualisation was achieved by fitting a local regression smoother (loess) to each pairwise combination of variables. The density of each species' life-history stanza was then plotted in *ArcView* to illustrate distribution and relative abundance.

To test the spatial distribution of the various life-history stanzas from within each species a Syrjala (1995) test was conducted. The hypothesis being tested was that density for each life-history stanza was randomly distributed in space across the study area. The test is based on the generalisation of the two-sampled Cramér-von Mises test, which tests for a difference between two univariate probability distributions (Syrjala 1995). The test is designed to be sensitive to the differences in the way that the populations are distributed across the study area, but at the same time insensitive to differences in abundance between the populations.

The percentage area that each sediment type comprised of the total study area was calculated from extracting each sediment type as polygons from the sediment coverage in *ArcView*. A pie chart visualised these data (Figure 3.2). Box plots were created, each derived from the calculations of the average density of each species size category (Figures 3.5, 3.8, 3.11 and 3.14) columns in these figure with common number show these sediment types to have a statistically different average density between them. This was conducted by averaging the specific density of each trawl to each sediment type. These results, therefore, provided an indication as to the general preference that each species life-history stanza had for each sediment type.

Statistical analyses were conducted to test for differences in abundance of each species over the various sediment types. The first test was to address the first null hypothesis that species density was equal across all of the sediment types. A Kruskall-Wallace test was employed to test sediment type differences. If differences were noted, a Bonferroni procedure was then conducted to assess which sediment types were significantly different from one another. The Bonferroni procedure compares *n*-pairwise combinations of sediment types with a Mann-Whitney U test (non-parametric z-test equivalent) with a modified rejection criteria.

Results and discussion

The observed relationships between the four selected environmental variables in the scatterplots were consistent with the physical nature of each variable (Figures 3.1, 3.3, 3.5 and 3.7) . A decreasing trend between depth and temperature was noticed, with temperature decreasing with increased depth. This trend was expected as water cools at greater depths. A similar trend, although not as clear and possibly with a weaker relationship as that between depth and temperature, was noticed between depth and dissolved oxygen. A slight decrease in dissolved oxygen was noticeable with increased depth, possibly a result of the interaction between oxygen saturation at lower temperatures and water pressure. Dissolved oxygen showed an initial negative trend changing to a positive one with an increase in temperature. Figure 3.2 shows that a high percentage of the substrate in the study area comprised of sand (70.3%) followed by muddy sand (15.4%).

A. pectoralis

The highest density of *A. pectoralis* in both life-history stanzas occurred at shallow depths between 50m and 100m (Figure 3.3). Few fish were recorded beyond these depth strata. The effect of temperature was interesting as density in both life-history stanzas increased with increasing temperature. Even at the highest recorded temperatures of 19°C, fish were recorded. Dissolved oxygen had a weakly positive effect on density in both life-history stanzas. This trend was more than likely correlated to positive temperature and dissolved oxygen trends.

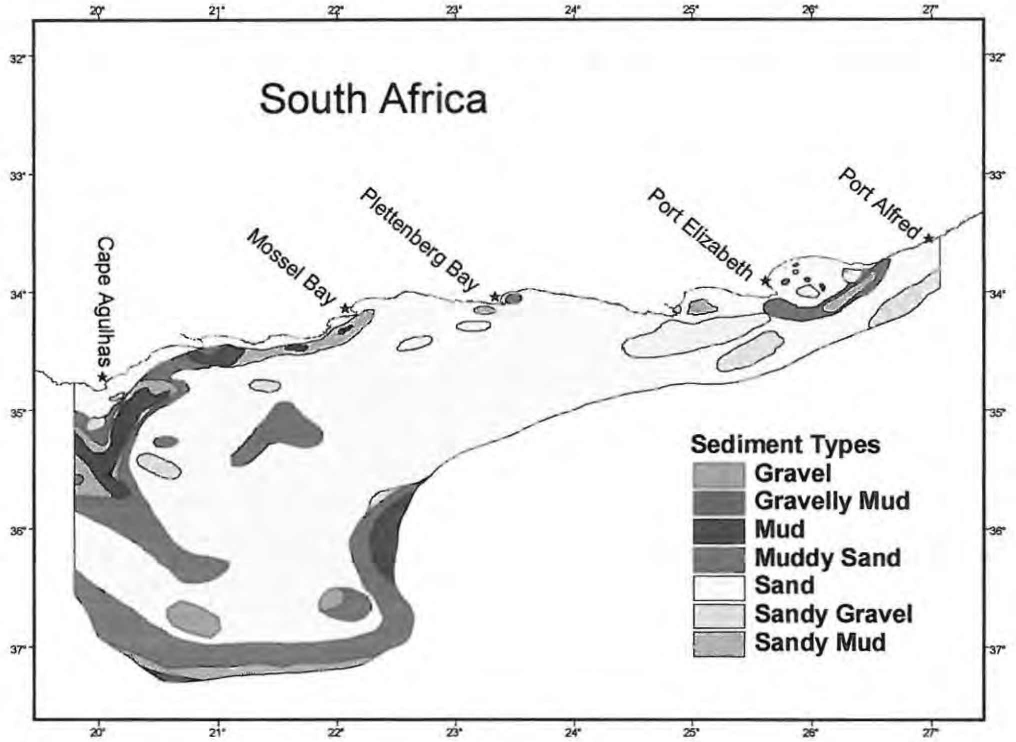


Figure 3.1: Map of study area showing the extent of each of the sediment types over the Agulhas Bank.

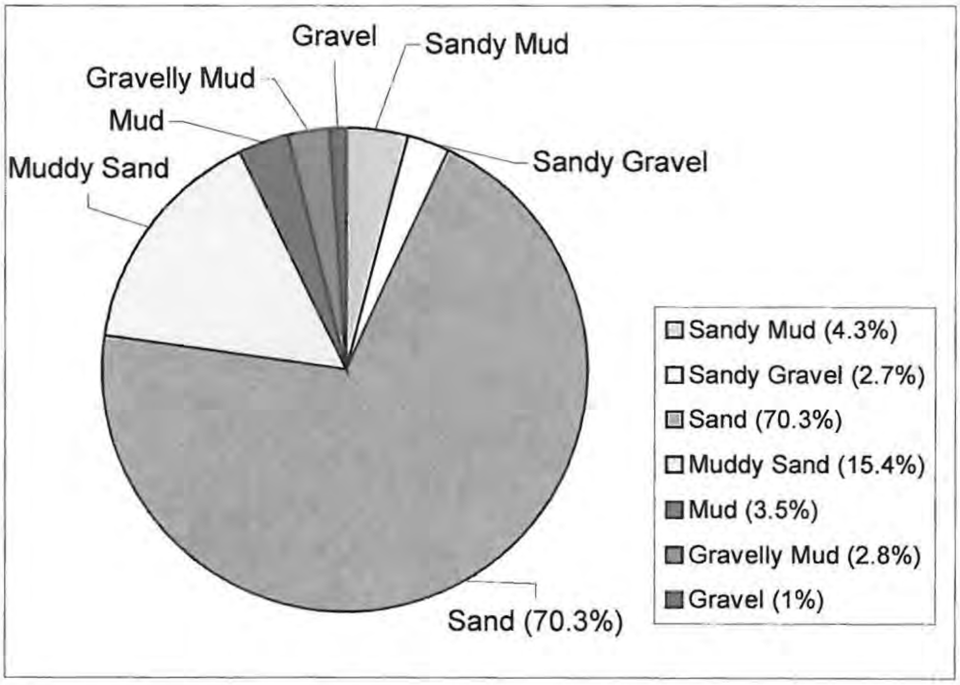


Figure 3.2: Percentage of different sediment types that occur over the Agulhas Bank between 20°E and 27° E.

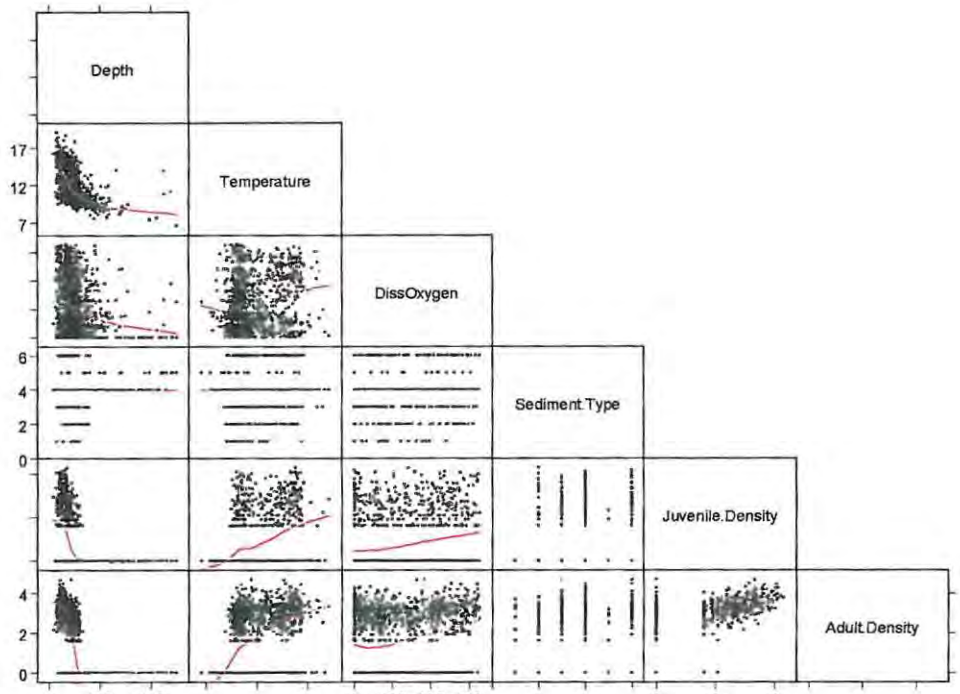


Figure 3.3: Scatterplots illustrating the relationships between density of each life-*history* stanza for *A. pectoralis* and depth (meters), temperature (Degrees Celsius), dissolved oxygen (Parts per million) and sediment type. Trend lines are local regression smoothers between pairs of variables.

The relative abundance maps for *A. pectoralis* (Figure 3.4) showed a clear distribution pattern. The highest juvenile densities were found adjacent to the coast on the central Agulhas Bank between Cape Agulhas and 23°E. Another important area occurred adjacent to the coast from Mossel Bay to Cape Agulhas. Few fish occurred below 100m. Adults showed a similar trend with more fish occurring up to and slightly deeper than 100m, indicating a possible movement of mature fish to deeper waters offshore.

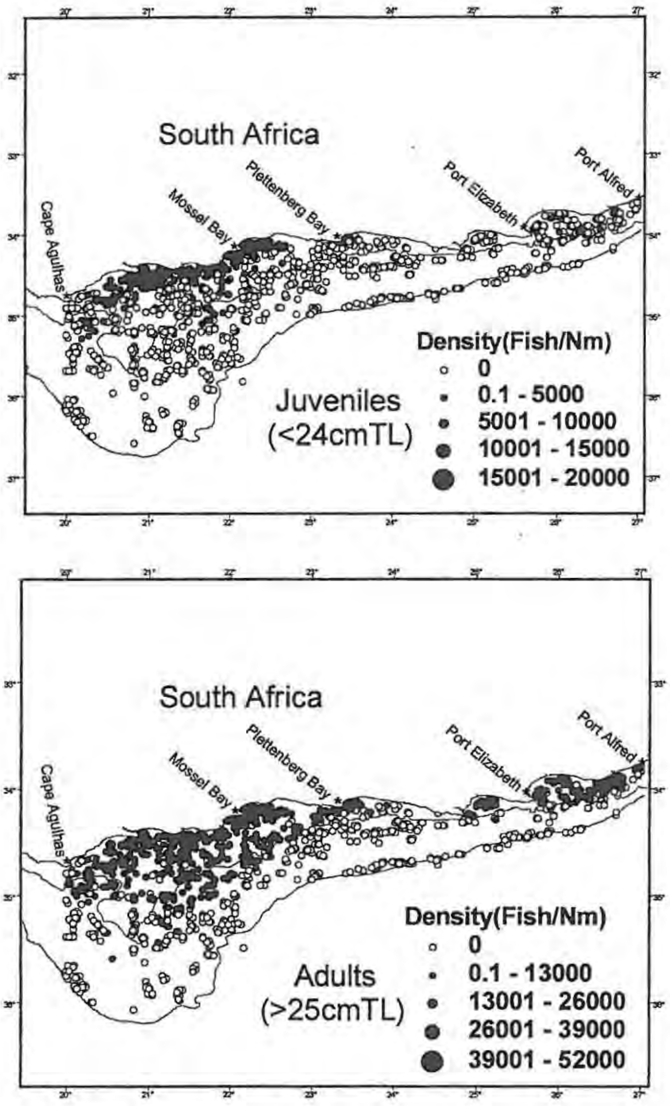


Figure 3.4: Distribution and abundance of two life-history stanzas of *A. pectoralis* on the Agulhas Bank, South Africa.

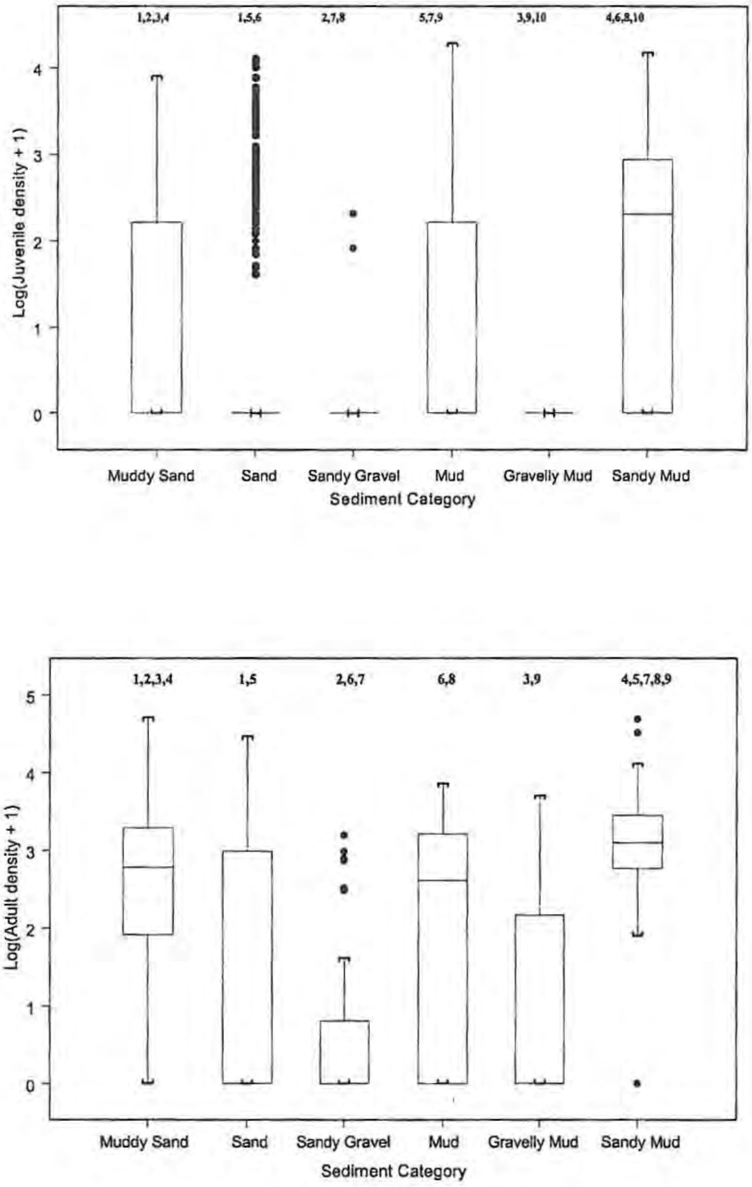


Figure 3.5: Density of *A. pectoralis* juveniles (top panel) and adults (bottom panel) across the different sediment categories. Columns showing a common number are significantly different from each other. Black dots represent outliers.

A. pectoralis juveniles had the highest average density over the Sandy Mud sediment with lower densities over the other sediment types (Figure 3.5)(Table 4.1). Similarly median density of adult fish was also highest over Sandy Mud (Figure 3.5). High adult densities also occurred over the Muddy Sand and Mud, indicating a general preference for a Mud dominated sediment.

Juvenile pair-wise comparison results indicated a preference for Muddy Sand and Sandy Mud, both having the significant differences (Figure 3.5). Adults had similar results with Sandy Mud and Muddy Sand dominating the number of significant differences. It therefore appears that *A. pectoralis* juveniles and adults select substrates with a high percentage of mud.

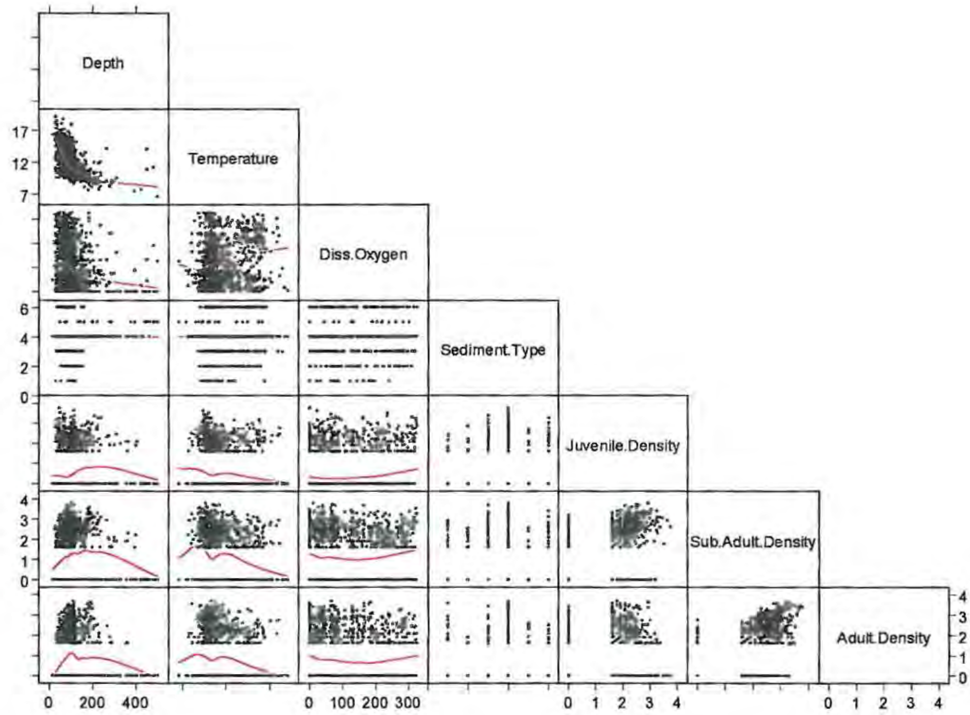


Figure 3.6: Scatterplots illustrating the relationships between density of each life-history stanza for *C. zanzibarensis* and depth (meters), temperature (Degree Celsius), dissolved oxygen (Parts per million) and sediment type. Trend lines are local regression smoothers between pairs of variables.

C. zanzibarensis

Trends for *C. zanzibarensis* (Figure 3.6), although noticeable, were not as exaggerated as for the other species (Figures 3.3, 3.9, 3.12). This may be a result of a high number of zero catches from many of the trawls. The relationship to depth was similar for all life-history stanzas. An initial positive trend occurred between the 100 and 200m depth strata with a general decrease in density occurring thereafter. Few fish were caught deeper than 350m.

An interesting pattern arose between densities in relation to temperature. In all three stanzas the trend had an initial increase in density to a pair of bimodal maximum points at 8.5 and 12°C, decreasing thereafter (Figure 3.6). Dissolved oxygen trends were minimal, with density showing marginal increases with increased dissolved oxygen. Patterns with respect to sediment were almost identical for all three stanzas. Juveniles and sub-adults selected for two of the sediment types, Sand and Muddy Sand, with sand having the highest abundance (Figure 3.6).

Relative abundances for *C. zanzibarensis* illustrated similar trends to *A. pectoralis* but with fish being more widely distributed and occurring in deeper water (Figure 3.7). Juveniles had higher abundance in the same areas, Port Alfred to Port Elizabeth, and in the Mossel Bay area. However, a distinct increase of abundance into deeper waters was noticeable. Sub-adults were similar with fewer zero catches and an increase in abundance of fish in deeper water. An interesting phenomenon was apparent in adults as very few fish were caught west of 21° and high abundance was noticeable in the Plettenberg Bay area.

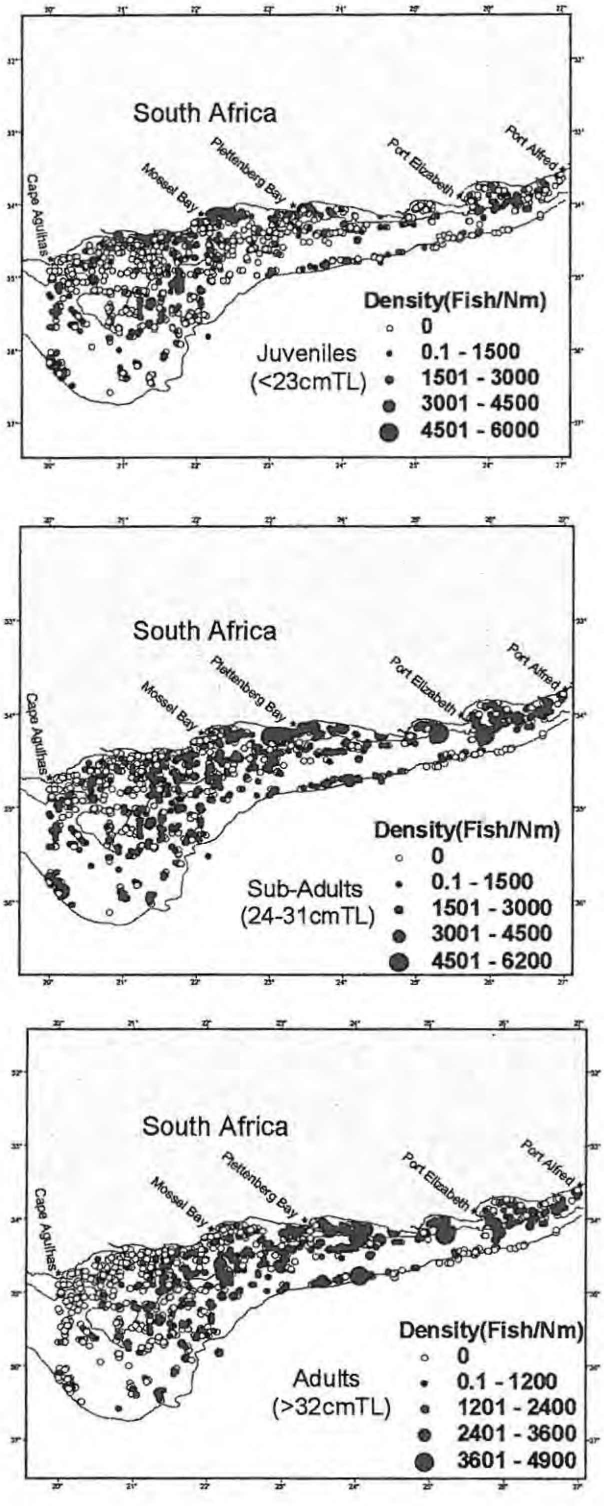


Figure 3.7: Distribution and abundance of three life-history stanzas of *C. zanzibarensis* on the Agulhas Bank, South Africa.

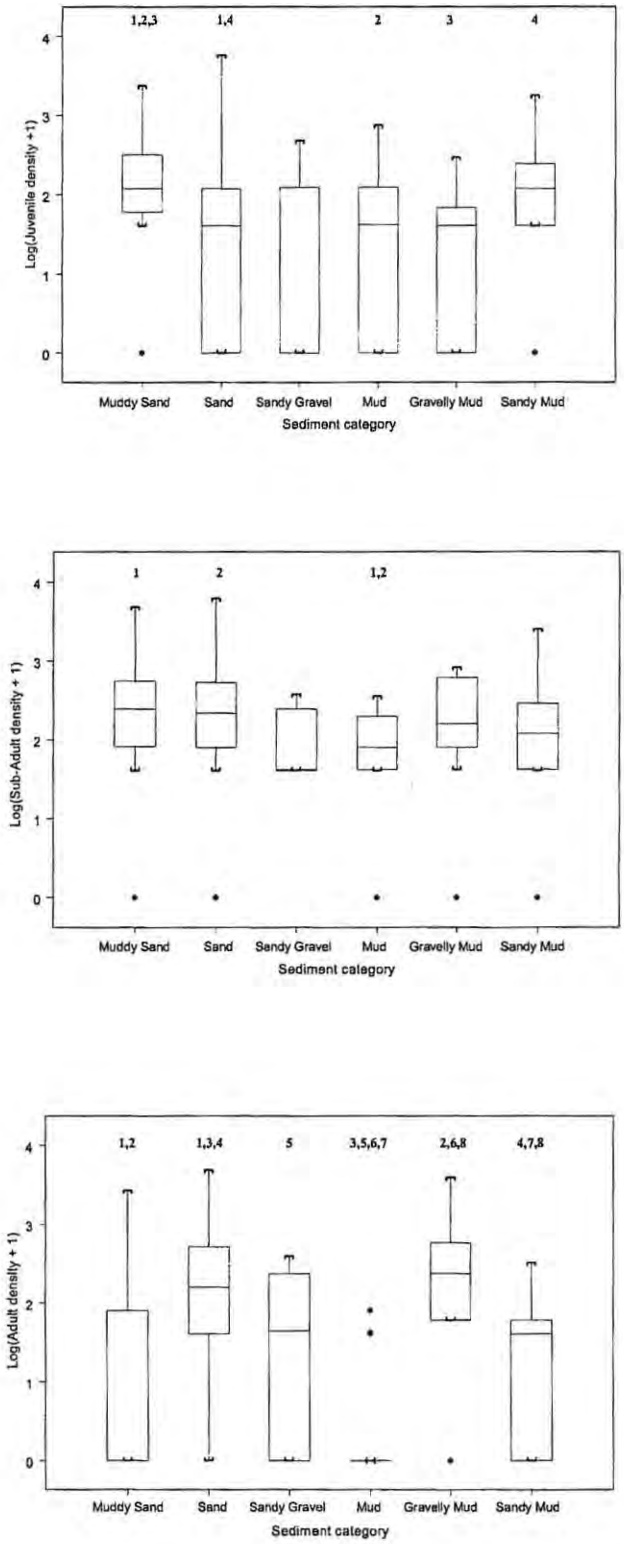


Figure 3.8: Density of *C. zanzibarensis* juveniles (top panel), sub-adults (middle panel) and adults (bottom panel) across the different sediment categories. Columns showing a common number are significantly different from each other. Black dots represent outliers.

Box plots for *C. zanzibarensis* showed the highest median density occurred over Sandy Mud for juveniles, closely followed by Muddy Sand, with Gravelly Mud, Mud and Sand also having high densities (Figure 3.8). Similarly, sub-adults showed all six sediment categories to have similar medians, peaking with Muddy Sand and Sand. Box plots for adults showed Gravelly Mud with the highest density, Sand, Sandy Gravel and Sandy Mud were slightly less (Figure 3.8).

M. capensis

The different life-history stanzas of *M. capensis* showed similar trends with respect to both depth and temperature (Figure 3.9). Poor trends were, however, noticeable with respect to dissolved oxygen and depth. A strong negative relationship with depth was noticeable in juvenile fish, with abundance declining steeply as depth increased (Figure 3.9). The negative trend noted in sub-adult fish, although similar to juveniles, was not as pronounced. From initial inspection it appears that immature fish are found at shallower depths. Adults by contrast had an initial strong positive trend reaching a maximum at about 100 metres, declining thereafter. This indicates that predominantly mature fish are found at highest densities, between 100 and 200m.

All life-history stanzas showed a similar pattern when related to temperature. In all life-history stanzas an initial positive trend reached a maximum at approximately 10°C. At temperatures lower than 10°C the density of all life-history stanzas decreased. A specific temperature range, therefore, appears to be an important variable in structuring abundance in this species with fish density increasing at lower temperatures with increasing fish length.

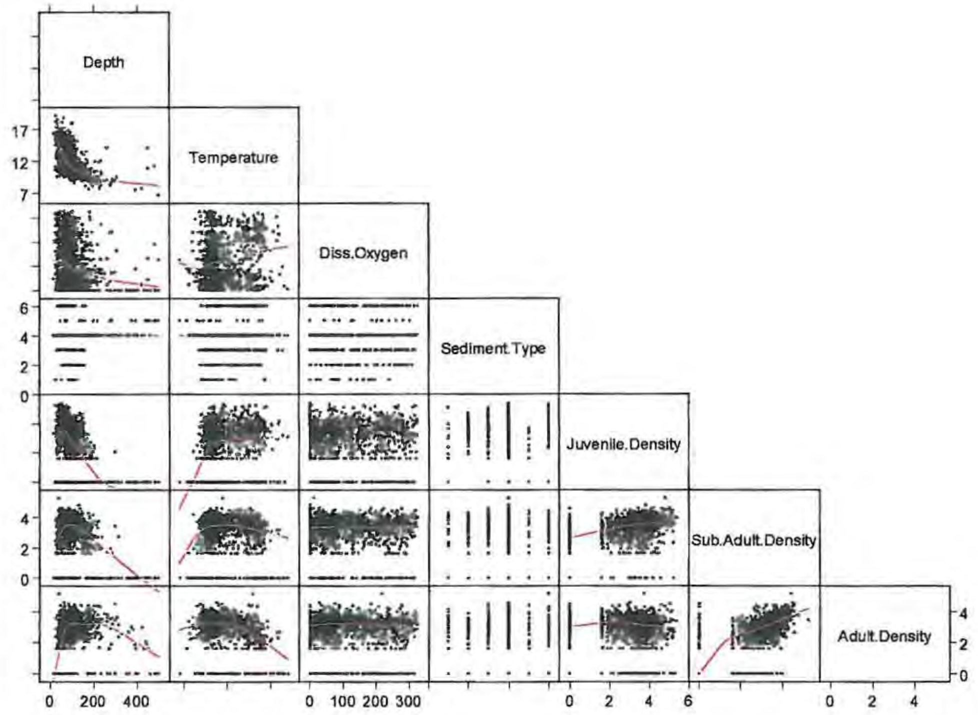


Figure 3.9: Scatterplots illustrating the relationships between density of each life-history stanza for *M. capensis* and depth (meters), temperature (Degree Celsius), dissolved oxygen (Parts per million) and sediment type. Trend lines are local regression smoothers between pairs of variables.

The relationship between abundance and dissolved oxygen was weak, with a negligible trend noticeable in all three life-history stanzas. Figure 3.10 illustrates the distribution of life-history stanzas *M. capensis* along the coastline of the study area with fish from all life-history stanzas being widely distributed. Juvenile density was noticed to occur in a number of areas between Port Alfred and Port Elizabeth within 100m, and adjacent to the coast either east or west of Mossel Bay. Similarly, sub-adult and adult abundance was also highest in those areas with high juvenile density, but further off shore. This pattern is a possible indication of movement to deeper water with maturity. This is indicative of the depth information for this species, with few specimens being found beyond 200m in depth.

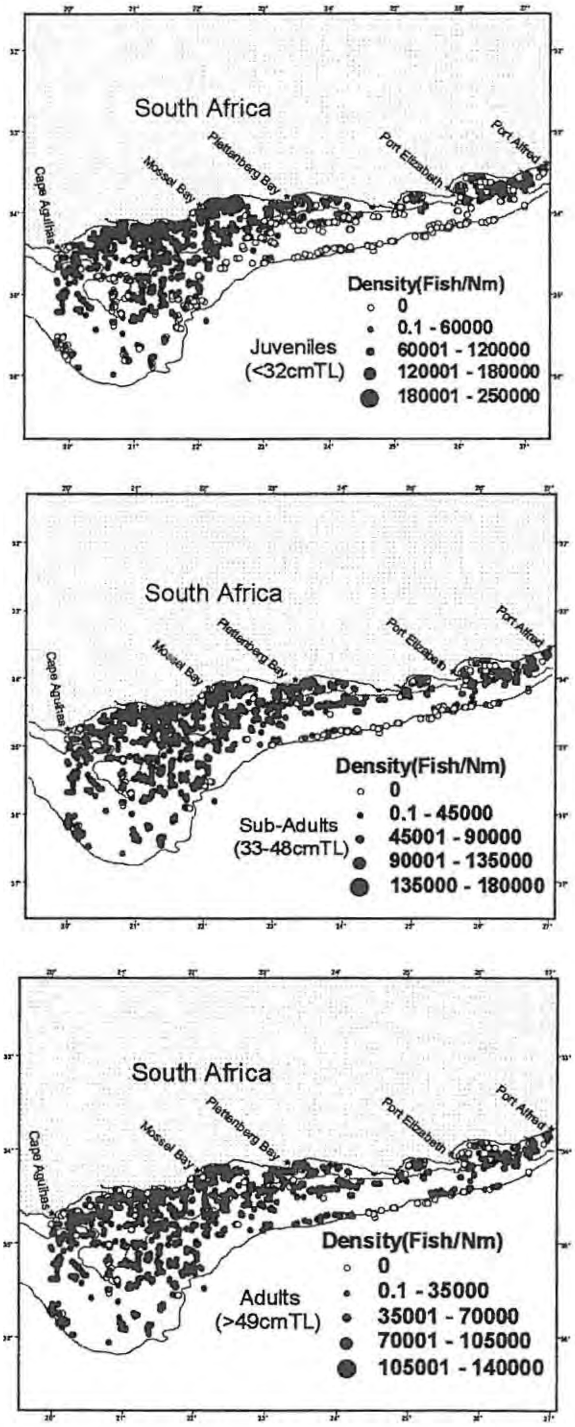


Figure 3.10: Distribution and abundance of three life-history stanzas of *M. capensis* on the Agulhas Bank, South Africa.

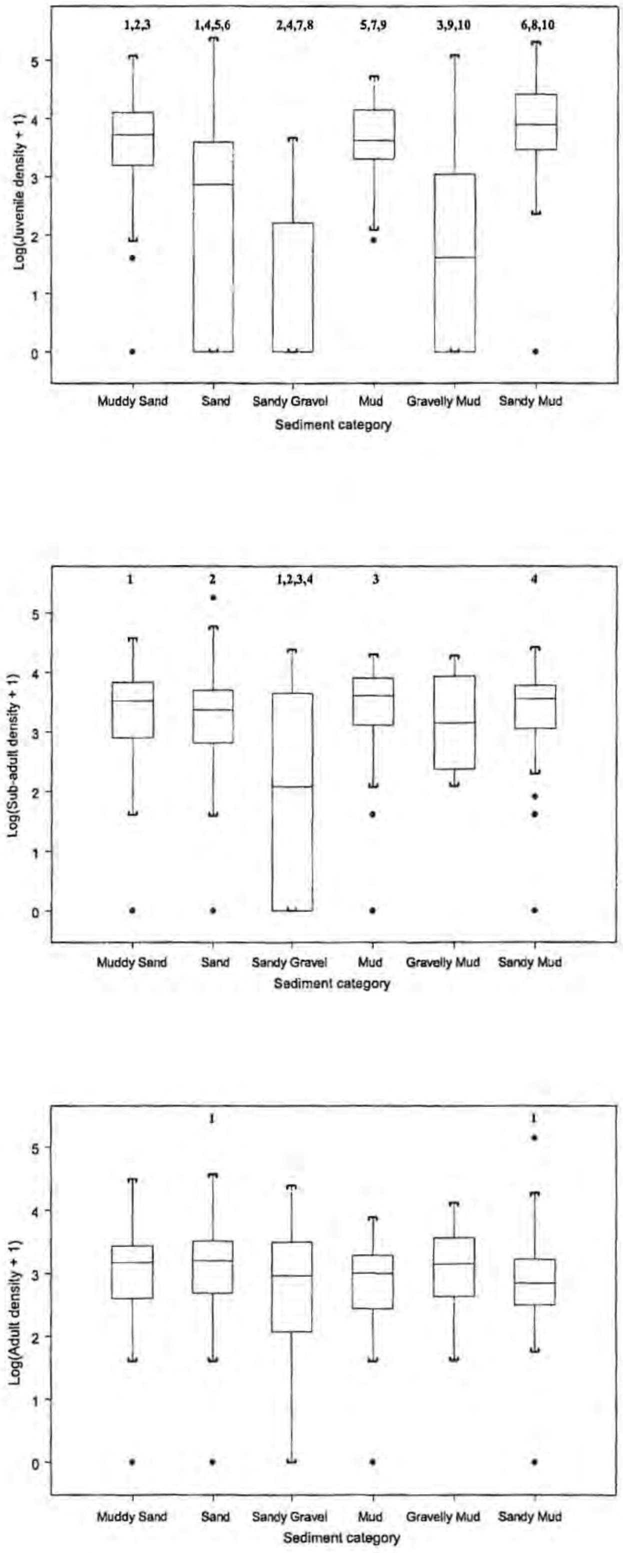


Figure 3.11: Density of *M. capensis* juveniles (top panel), sub-adults (middle panel) and adults (bottom panel) across the different sediment categories. Columns showing a common number are significantly different from each other. Black dots represent outliers.

Results for the box plots showed that the highest median density for juveniles occurred over Sandy Mud and Muddy Sand (Figure 3.11). Sub-adult fish had the highest densities over Mud with similar medians occurring for Muddy Sand, Sandy Mud and Sand (Figure 3.11). Gravelly Mud, Muddy Sand and Sand had almost identical median averages for adults.

M. paradoxus

Trends for this species were conspicuous with respect to both depth and temperature (Figure 3.12). Juvenile and sub-adult abundance increased steeply between 150m and 350m. From 350m density decreased slowly, although not considerably, to 500m. Adults had a gradual increase from 150m to 500m. However, this occurred not as rapidly as the other two life-history stanzas.

There was a negligible difference in abundance between all life-history stanzas and temperature. For all three stanzas a steep negative trend was present between 7°C to 10°C. Few fish were recorded at temperatures greater than 10°C (Figure 3.12).

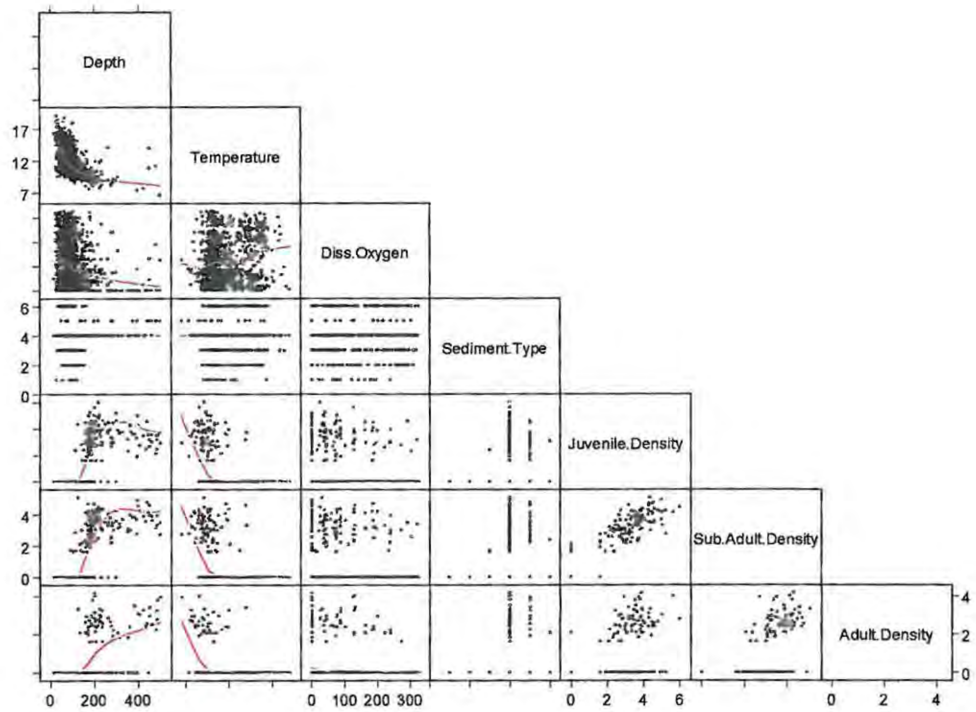


Figure 3.12: Scatterplots illustrating the relationships between density of each life-history stanza for *M. paradoxus* and depth (meters), temperature (Degrees Celsius), dissolved oxygen (Parts per million) and sediment type. Trend lines are local regression smoothers between pairs of variables.

Dissolved oxygen showed no trend with respect to density in all stanzas examined. Abundance over different sediment types was dominated by Sand for all of the stanzas, weakly followed by Sandy Gravel (Figure 3.12). Other sediments had no more than a few observed catches. There was a distinct absence of fish close inshore for all three life-history stanzas (Figure 3.13) with distribution confined to the 200m isobath and deeper. Unfortunately few trawls were conducted over 500m due to trawl gear restrictions.

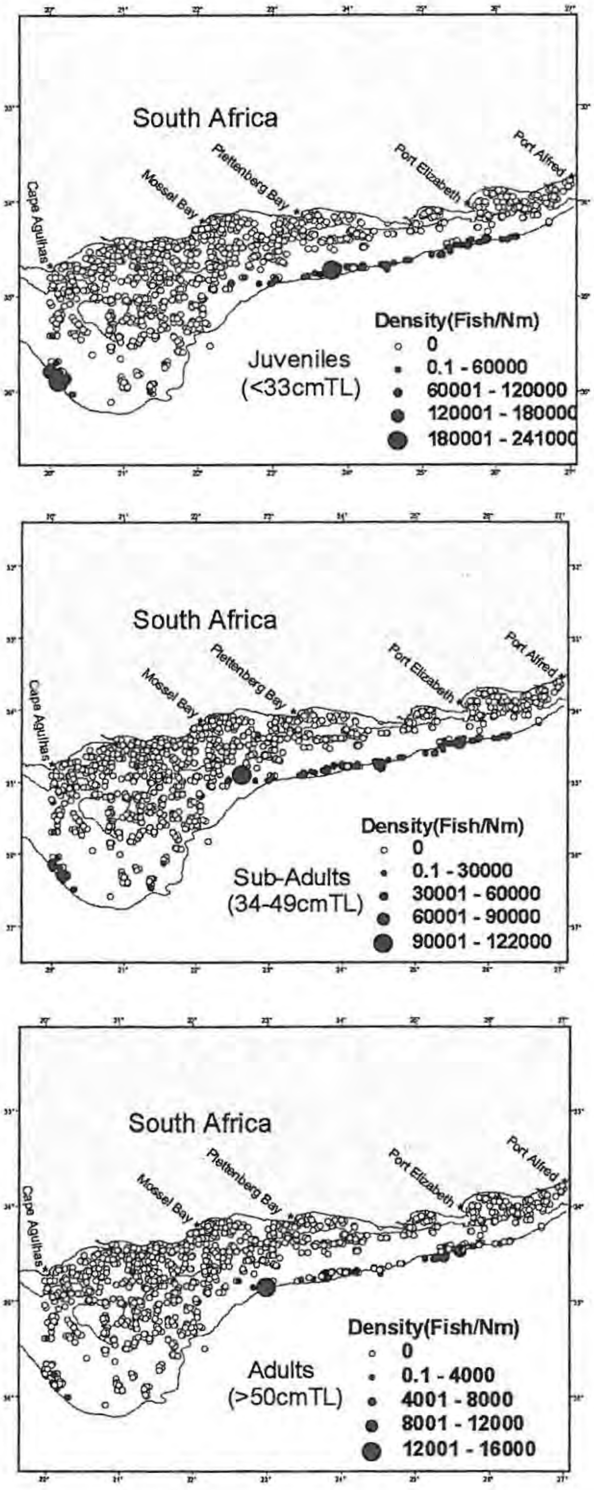


Figure 3.13: Distribution and abundance of three life-history stanzas of *M. paradoxus* on the Agulhas Bank, South Africa.

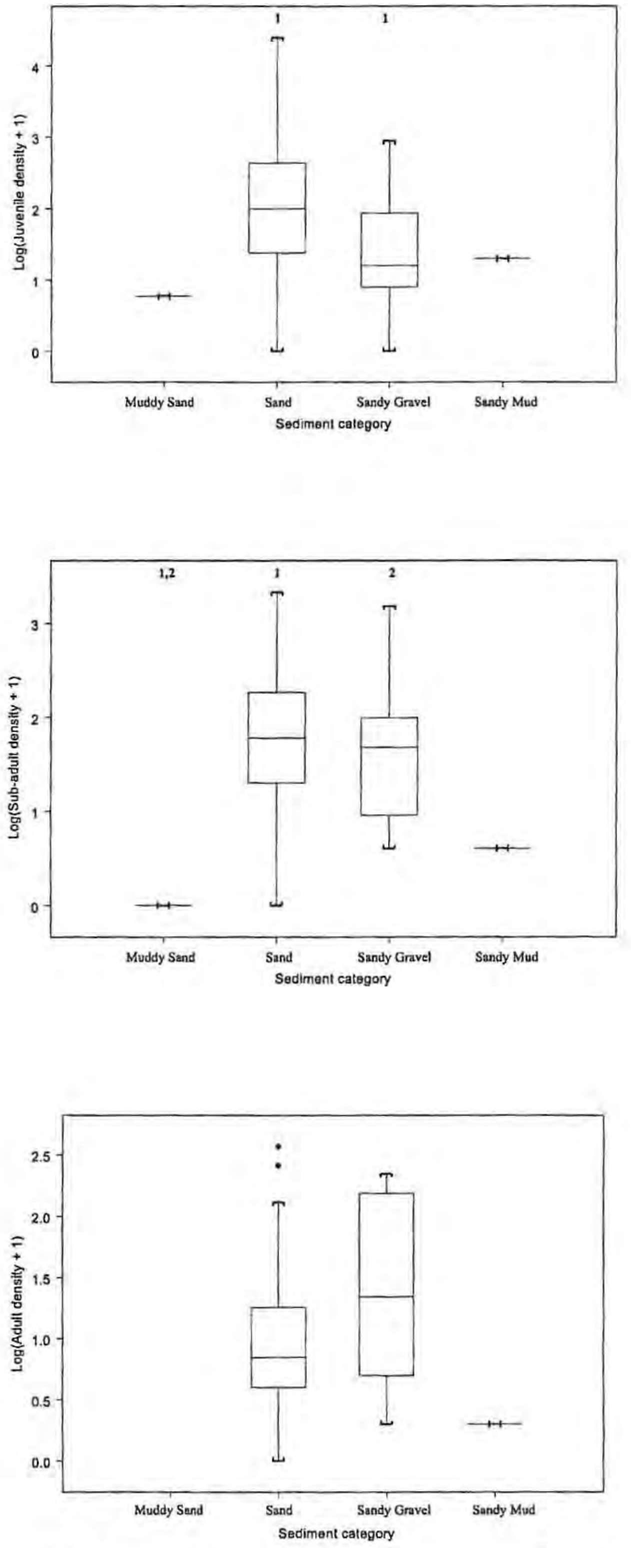


Figure 3.14: Density of *M. paradoxus* juveniles (top panel), sub-adults (middle panel) and adults (bottom panel) across the different sediment categories. Columns showing a common number are significantly different from each other. Black dots represent outliers.

Sediment box-and-whisper plots for *M. paradoxus* may well be biased due to few trawls recording positive catches, with only 145 trawls recording fish from a possible 1585 (Figure 3.14). Juvenile and sub-adult fish had their highest median densities over Sand and then Sandy Gravel. Adult fish density was highest over Sandy Gravel and then Sand (Figure 3.14).

Table 3.1: Results from the Syrjala test comparing the spatial distribution of each species' life-history stanzas across the study area.

Species	Life-history stanzas compared	Ψ	P-value
A. pectoralis	Juveniles vs Adults	4.19	0.001
C. zanzibarensis	Juveniles vs Adults	7.23	0.001
	Juveniles vs Sub-adults	1.36	0.001
	Sub-adults vs Adults	3.53	0.001
M. capensis	Juveniles vs Adults	3.54	0.001
	Juveniles vs Sub-adults	1.46	0.001
	Sub-adults vs Adults	0.61	0.001
M. paradoxus	Juveniles vs Adults	26.78	0.001
	Juveniles vs Sub-adults	0.78	0.001
	Sub-adults vs Adults	19.11	0.001

Results from the Syrjala tests showed that the spatial distribution of all the life-history stanzas for each species were significantly different from each other (p values ≤ 0.001)(Table 3.1).

General conclusion

This chapter presents an initial analysis of the interaction between the environmental variables and density in the four candidate species. The objective was to assess which variables were significant and possibly influential on the abundance of species, and forms the basis of the development of predictive models covered in Chapters 4 and 5.

The strong influence of temperature and depth on all species was apparent, suggesting that they are important in determining both distribution and abundance. Furthermore, an interaction between the two became apparent, which surely would have been overlooked in a non-visual analysis. Density generally decreased with depth but increased with temperature. The general relationship is that temperature generally decreases with increasing depth. Dissolved oxygen did not have a major impact on any of the species densities and will not be considered further. Specific sediment types appeared to be selected for and emerged to be particularly important for certain species, most noticeably the pleuronectiformes. Results from the Syrjala tests showed that spatial distribution was significantly different between each life-history stanza within all the species, indicating that each life-history stanza has its own spatial signature within the study area.

Chapter 4 – Modelling the effect of environmental variables on abundance

Introduction

Numerous methods have been used to quantify and visualise the relationships between fish species distribution and abundance and their environment. Some of these methods include the creation of Habitat Suitability Indexes based on frequency occurrence, mean catch rates within ranges and smooth-mean catch rates determined by polynomial regression aided by a GIS for certain fish species in Florida (Rubec *et al.* 1998). Linear regression has also been used for analysing fisheries data response to various ecological variables (Chen and Jackson 2000).

Regression analysis can be used for exploring relationships between variables, and has been used extensively in ecological and fisheries based studies to explain the variation in a response variable to one or more explanatory variables (Chen and Jackson 2000). This technique has been extended by the addition of robust methods and generalizations. Generalizations allow for categorical, bounded response and non-linear data analysis such as Poisson and logistic regression to be included and area thus termed as generalized linear models (GLM). A further generalization using non-linear, non-parametric smoothers to replace the linear predictors gives rise to the generalized additive model (GAM). According to Hastie and Tibshirani (1986), a GAM has less restrictive statistical assumptions than traditional regression methods, as it can use scatterplot smoothers. Furthermore, a GAM avoids the problems of increased dimensionality as it uses an univariate smoother, with estimates of each individual term explaining how the dependent variable changes with the corresponding independent variables.

The use of these generalized models is becoming established in fisheries related work. Swartzman *et al.* (1992) used a GAM for detecting spatial trends in groundfish distribution and improved abundance estimates by including estimated trends. Maravelias (1999) use a GAM for the interpretation of the distribution and abundance of Atlantica herring *Clupea harengus*. Similarly, Kaluzny (1987) use a GAM for detecting trends in the spatial distribution of several flatfish related to temperature and depth on the eastern Bering Sea shelf, as did Booth (1997) for *Pterogymnus laniarius* on the Agulhas Bank. The advantage of using a GAM in this context is that it is easily understood, as with general linear regression, but does not have to fulfil the assumptions of normality or linearity that relate response variables to their predictors.

Understanding the population dynamics and abundance of a species is important for management in that these trends can be used for updating existing biomass estimates that are crucial as input into various stock assessment models (Booth 1997). Linking abundance and distribution information to various environmental variables may also be used for more versatile and predictive assessment models in the future. The importance of accurately estimating the abundance of fish species is, therefore, derived from the fundamental need for better resource management.

A generalised modelling approach was deemed most suitable and was conducted within this chapter to assess the effect of several environmental and physical parameters on the density of the four candidate species.

Materials and methods

Background to Generalized models

The general linear model specifies that the mean response of the dependant variable μ is identical to a linear function η of the independent predictor variables x_j such that

$$E(Y) = \mu = \eta = \beta_0 + \sum_{j=1}^{p} \beta_j x_j$$

with the unknown parameter vector $\boldsymbol{\beta}$ estimated by minimizing the residual sum of squares, the maximum likelihood estimator for normally distributed data. Generalized linear models encompass the class general linear models and enlarge the class by assuming that the distribution of Y for fixed x is merely from the exponential distribution family and that the relationship between $E(Y) = \mu$ and η is specified by a non-linear link function $\eta = g(\mu)$ that is monotonic and differentiable (McCullagh and Nelder 1989). The link function serves to link the random or stochastic component of the model (the probability distribution of the response variable) to the systematic component of the model (the linear predictors) such that

$$E = g(\mu) = \beta_0 + \beta_1 x_1 + \ldots + \beta_j x_j$$

Analogous to the residual sum of squares in linear regression, the goodness of fit of a generalized linear model can be measured by the scaled deviance

$$D(y_i;\hat{\mu}_i) = 2\sum_{i=1}^{n} \left[\ln(y_i;y_i) - \ln(y_i;\hat{\mu}_i)\right]$$

where the $l(y;y)$ is the maximum likelihood achievable for an exact fit in which the fitted values are equal to the observed values, and $l(y;\hat{\mu})$ the log-likelihood function calculated at the estimated parameter vector β. Generalised Additive Models further generalizes the linear model by modelling the expected value of Y as a linear function of some additive independent, or predictor, variables such that

$$E(Y) = f(x_1,\ldots x_p) = \eta = S_0 + \sum_{j=1}^{p} S_i(x_i)$$

where $s_j(x)$, $i = 1,\ldots, p$ are functions that are estimated in either a non-parametric or parametric fashion (Hastie and Tibshirani 1986),. The relationship between the mean μ of the response and η is defined, as with all generalized models by a link function $g(\mu) = \eta$.

The coefficient of determination, as with general linear models, was calculated as

$$R^2 = 1 - \frac{Residual\ deviance}{Null\ deviance}$$

Model used in this study

It was assumed that fish density data, as with other count data, are governed by an underlying non-homogeneous Poisson process, and related through linear or non-linear functions to several additive environmental predictors. The intensity of the response is a function of the additive effects of the environmental predictors. The function form of this relationship can therefore be expressed as

$$Density = Intercept + f(Temp) + f(Depth) + f(Sediment\ Type)$$

where $f(.)$ is the linear/non-linear relationship. The link function of Poisson distributed data is $\eta = ln\mu$. Due to the presence of zero density values, densities were natural logarithm transformed with an offset of one.

From the EDA presented in Chapter 3 it was noted that there was a strong negative correlation between temperature and depth together with the possibility of an interaction, as density increased with temperature but decreased with depth. This relationship was included into the model as an additional interaction term. The calculated model for each life-history stanza was therefore expressed as

$$\ln(Density + 1) = Intercept + f(Temperature) + f(Depth) + f(Sediment\ Type) + f(Temp \times Depth)$$

The parameter estimates of $f(.)$ were calculated by minimising the Poisson scaled deviance

$$D(y;\mu) = 2\sum_{i=1}^{n}\left[y_i \ln\left(\frac{y_i}{\mu_i}\right) - (y_i - \mu_i)\right]$$

Trends, or predictor effects, in the data were visualized through the plotting of partial residuals for the data point i, with a partial residual for observed data x_i calculated as

$$r_i = Y_i - s_0 - \sum_{i \neq j}^{n} s_j(x_j)$$

Furthermore, in multiple linear regression the correlations among predictors are often difficult to visualize. Through partial residual analysis the relationship between the response variable and the explanatory variables can be shown as it removes effects of all other predictors.

Choice of a suitable model

The most appropriate and robust statistical model can be chosen by assessing the fit of the model to any combination of predictors in a stepwise fashion. Akaike's Information Criterion (AIC), which is a penalized version of the of the log-likelihood function, was used to determine the best fitting model as it assesses the trade-offs between deviance explained by the model and the number of predictors used.

Results

Preliminary analysis of deviances (McCullagh and Nelder 1989) noted that, for all life-history stanzas for all species, the saturated model incorporating cubic spline smoothers were significantly better than those predictors expressed as linear functions (p-values < 0.001). A stepwise procedure was then applied to the saturated GAM ,using smoothers for each predictor to determine which were statistically significant and if they warranted inclusion into the final model. Partial residual plots and model statistics are presented in Figure 4.1 to 4.4 and summarised in Tables 4.1 to 4.4. In half the species analysed the saturated model was found to be statistically superior to the various combined sub-models. In several instances the inclusion of covariates explained significant portions of the overall model deviance but were not statistically significant, i.e. the effect of temperature on juvenile and sub-adult *M. capensis* and *M. paradoxus* abundance.

A. pectoralis

The partial residual plots illustrated in Figure 4.1 show a slightly negative yet statistically significant trend (p-value < 0.001) in juvenile abundance with an increase in depth. At depths greater than 100m a strong decline in abundance occurred. Similar results were also noted in the adult life-history stanza with both depth and sediment type having significant effects (p-value < 0.001)(Table 4.1). Both life-history stanzas were significantly affected by sediment (p-value < 0.001)(Table 4.1) with highest abundances noted for Mud, closely followed by Muddy Sand and Sandy Mud. The coefficients of determination were reasonably high ($0.49 \leq R^2 \leq 0.56$)(Table 4.1), with the variation explained by the model increasing with size and age of fish analysed.

C. zanzibarensis

Similar to *A. pectoralis*, water temperature was not statistically significant, and was omitted from juveniles. As illustrated in all life-history stanzas in Figure 3.6, a similar bimodal trend for adults was noted in the GAMs that used cubic splines smoothers (p-value < 0.001)(Figure 4.2). Depth was statistically significant in juvenile and adult fish (p-value ≤ 0.012)(Table 4.2), with a preferred depth range occurring between 100 and 200m (Figure 4.2). Sediment was statistically significant in all life-history stanzas analysed (p-values < 0.001)(Table 4.2). The coefficients of determination were low for all life-history stanzas analysed ($0.04 \leq R^2 \leq 0.14$)(Table 4.2) indicating a relatively poor fitting model.

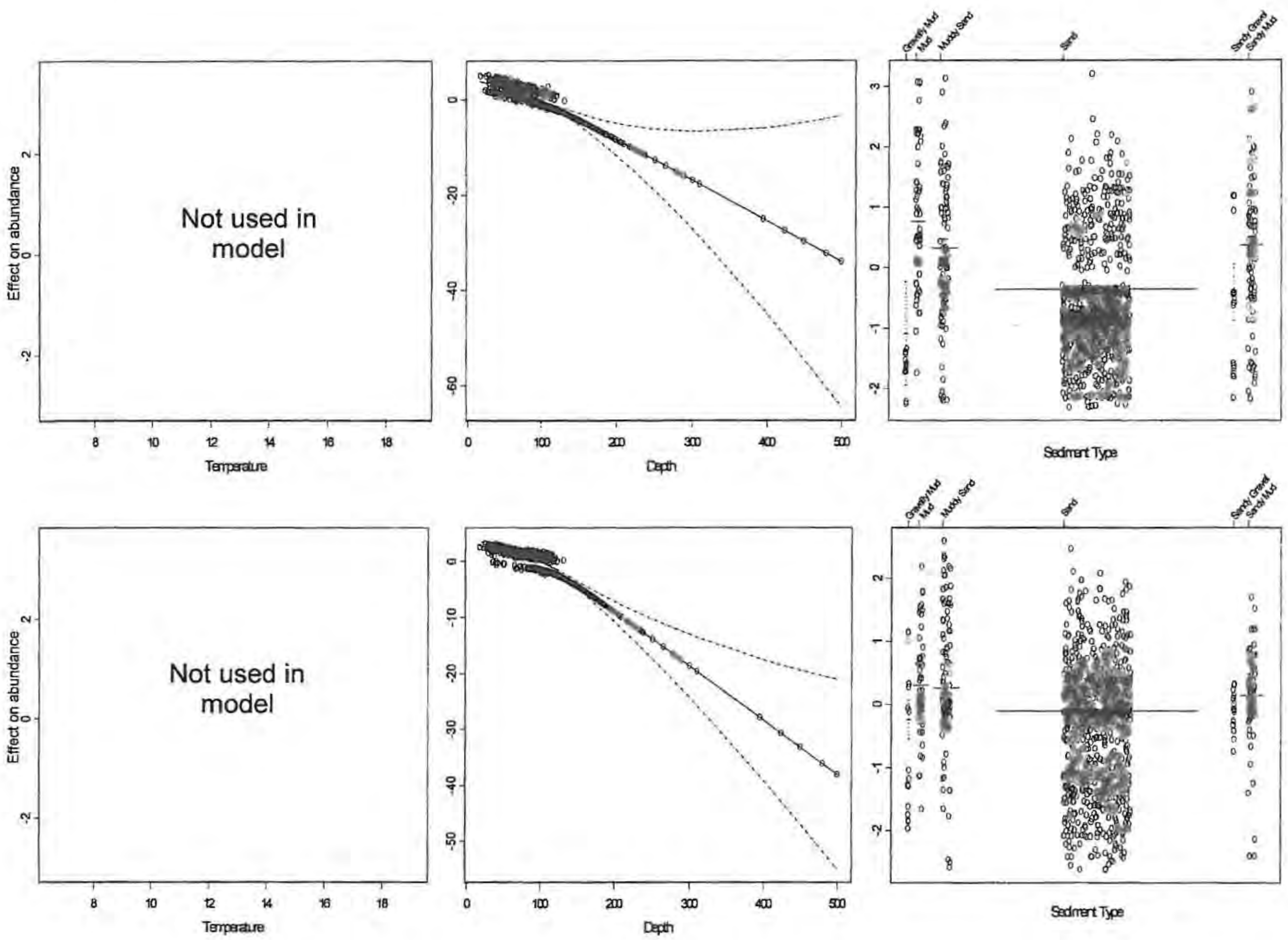


Figure 4.1: Partial residual plots describing the effect of three environmental variables on the abundance of juvenile (upper panels) and adult (lower panels) *A. pectoralis*. Dashed lines represent the upper and lower twice-standard error bands.

M. capensis

The partial residual plots for this species illustrated a slight decrease in abundance with an increase in temperature. Only in adult fish was this trend significant (p-value < 0.027)(Table 4.3)(Figures 4.3). All life-history stanzas had significantly decreasing trends in abundance with increasing depth ($0.001 \leq$ p-values ≤ 0.018). A movement to deeper water by mature fish was apparent with increased abundance approximately occurring at 150m. Sediment was only incorporated into the GAM for juvenile fish (p-value < 0.001) with highest abundances occurring over mud-based sediments. The coefficients of determination were reasonable, ranging between 0.26 and 0.30 (Table 4.3).

Table 4.1: Results from the GAM for all *A. pectoralis* life-history stanzas.

	Juveniles		
	df	Deviance	
Null	1331	2515.49	
Residual	1319.13	1293.13	
R^2	0.49		
	df	χ^2	$P(\chi^2)$
Depth	4	91.33	< 0.001
Temperature × Depth	4	23.95	< 0.001
Sediment type	4	185.13	< 0.001
	Adults		
	df	Deviance	
Null	1331	2687.71	
Residual	1319.22	1193.72	
R^2	0.56		
	df	χ^2	$P(\chi^2)$
Depth	3.8	208.30	< 0.001
Temperature × Depth	4	12.39	0.006
Sediment type	4	60.85	< 0.001

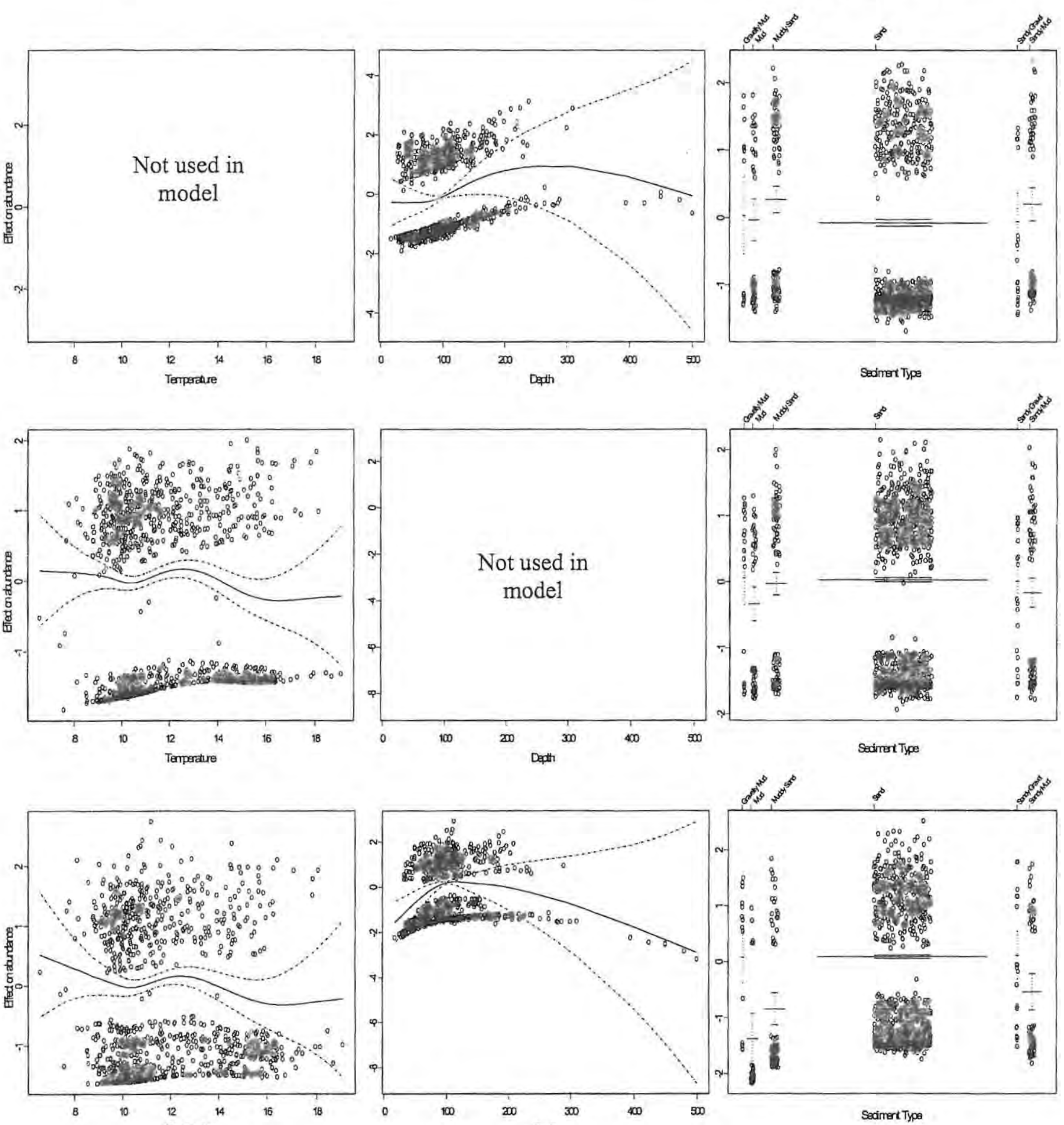


Figure 4.2: Partial residual plots describing the effect of three environmental variables on the abundance of juvenile (upper panels), sub-adult (middle panels) and adult (lower panels) *C. zanzibarensis*. Dashed lines represent the upper and lower twice-standard error bands.

Table 4.2: Results from the GAM for all *C. zanzibarensis* life-history stanzas.

	Juveniles		
	df	Deviance	
Null	1331	2129.21	
Residual	1319.48	2051.37	
R^2	0.04		
	df	χ^2	P(χ^2)
Depth	3.8	16.53	< 0.001
Sediment type	3.9	20.66	< 0.001
Temperature × Depth	3.8	18.64	< 0.001
	Sub-adults		
	df	Deviance	
Null	1331	2303.04	
Residual	1319.33	2176.33	
R^2	0.06		
	df	χ^2	P(χ^2)
Temperature	3.9	26.51	< 0.001
Temperature × Depth	3.8	21.56	< 0.001
Sediment type	4.0	15.52	< 0.001
	Adults		
	df	Deviance	
Null	1331	2361.71	
Residual	1315.54	2020.35	
R^2	0.14		
	df	χ^2	P(χ^2)
Temperature	3.9	21.45	< 0.001
Depth	3.8	65.18	< 0.012
Temperature × Depth	3.9	42.75	< 0.001
Sediment type	3.9	105.42	< 0.001

M. paradoxus

Temperature was incorporated into the GAM for all life-history stanzas, and showed a strong negative trend. The trend was, however, only significant in adult fish (p-value < 0.005)(Table 4.4). Depth as in *M. capensis* was important in all life-history stanzas (p-values < 0.001)(Table 4.4). Sub-adult and adult fish showed declining trends with most fish occurring before 200m. Adults increased in density up to 200m. Thereafter, a sharp decline occurred (Figure 4.4). Sediment, although used in all life-history stanzas, was only significant for adults (p-value < 0.019)(Figure 4.4). The sand-based sediments had the highest abundance for all life-history stanzas (Figure 4.4). Coefficients of determination for the GAMs were reasonably high ($0.72 \leq R^2 \leq 0.85$) (Table 4.4).

Interactions

The ability of the model to cope with interaction allows for the natural negative correlation that occurs between temperature and depth to be represented in the results (Figure 4.5). The interaction response surfaces between temperature and depth illustrate important trends. In three species, *A. pectoralis*, *M. capensis* and *M. paradoxus,* the interaction was strongest at increasing depth and temperatures. In contrast, the surface for *C. zanzibarensis* was reversed, with a strong interaction response at low temperatures and shallow depths.

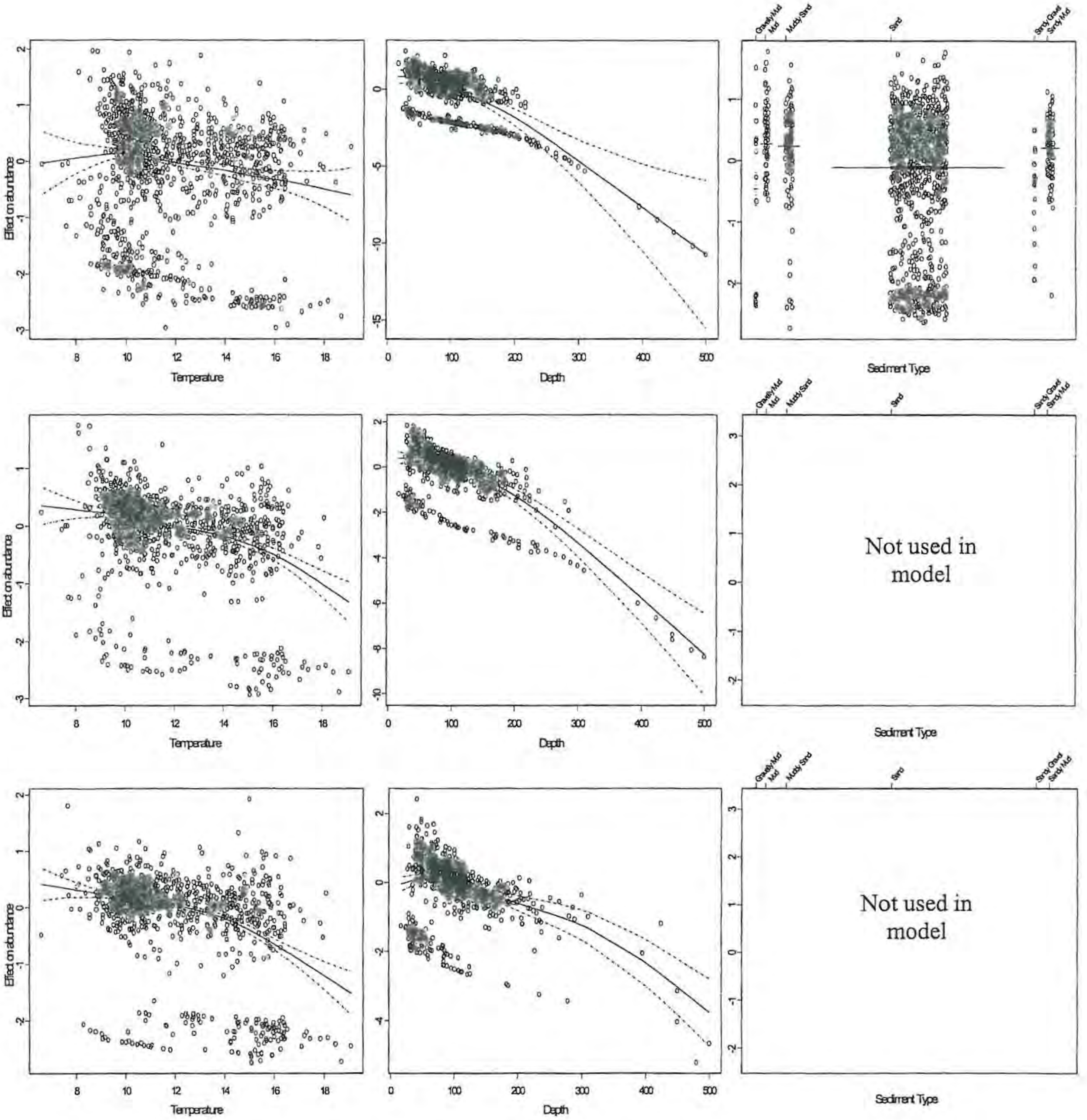


Figure 4.3: Partial residual plots describing the effect of three environmental variables on the abundance of juvenile (upper panels), sub-adult (middle panels) and adult (lower panels) *M. capensis*. Dashed lines represent the upper and lower twice-standard error bands.

Table 4.3: Results from the GAM for all *M. capensis* life-history stanzas.

Juveniles			
	df	Deviance	
Null	1331	1990.2	
Residual	1315.15	1468.74	
R^2	0.26		
	df	χ^2	$P(\chi^2)$
Temperature	4	5.56	0.130
Depth	3.9	10.72	< 0.013
Temperature × Depth	3.9	20.59	< 0.001
Sediment type	4	106.39	< 0.001

Sub-adults			
	df	Deviance	
Null	1331	917.05	
Residual	1319.07	659.67	
R^2	0.28		
	df	χ^2	$P(\chi^2)$
Temperature	4	6.44	0.090
Depth	4	10.06	< 0.018
Temperature × Depth	4	37.57	< 0.001

Adults			
	df	Deviance	
Null	1331	940.89	
Residual	1322.01	659.37	
R^2	0.30		
	df	χ^2	$P(\chi^2)$
Temperature	4	9.16	< 0.027
Depth	4	29.01	< 0.001
Temperature × Depth	4	61.75	< 0.001

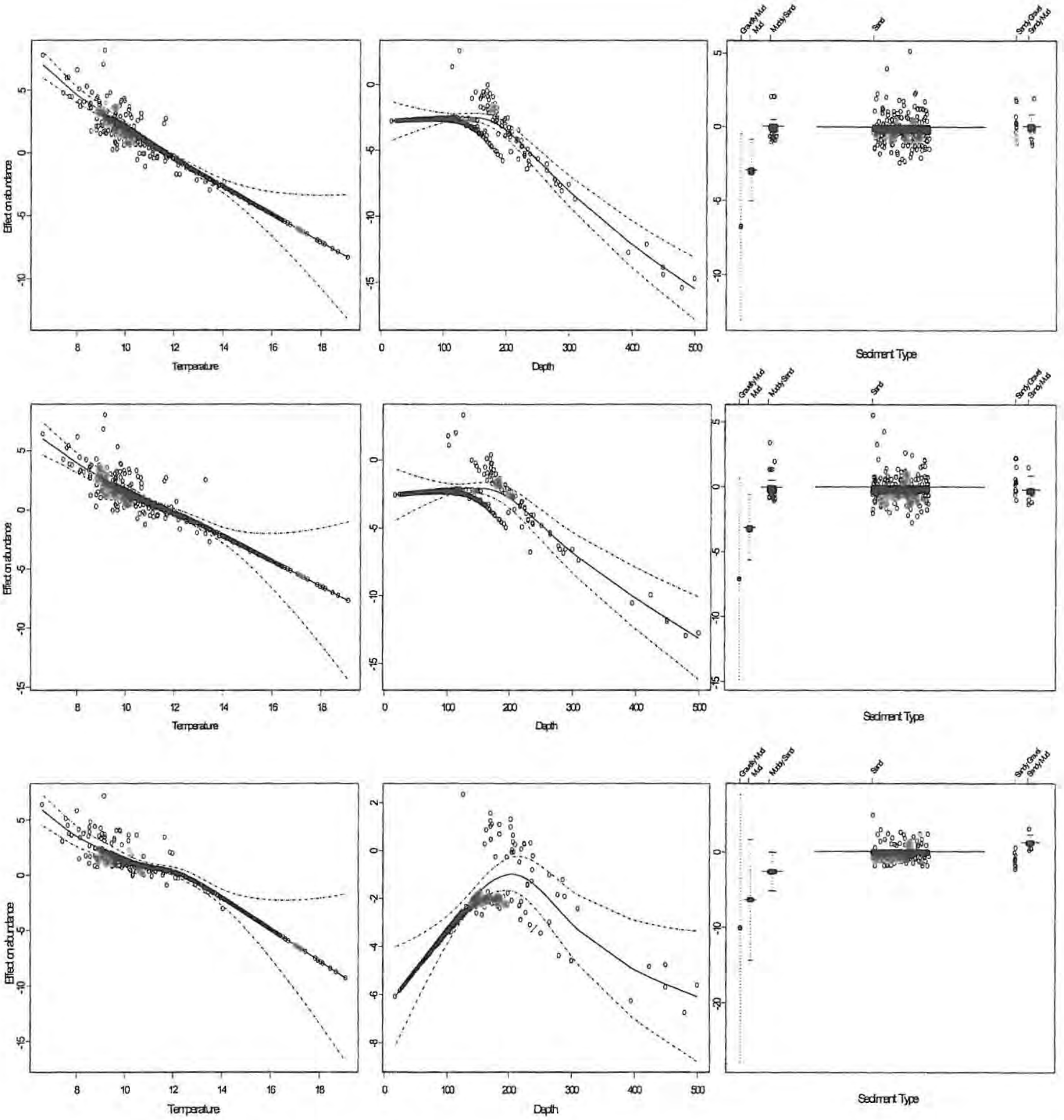


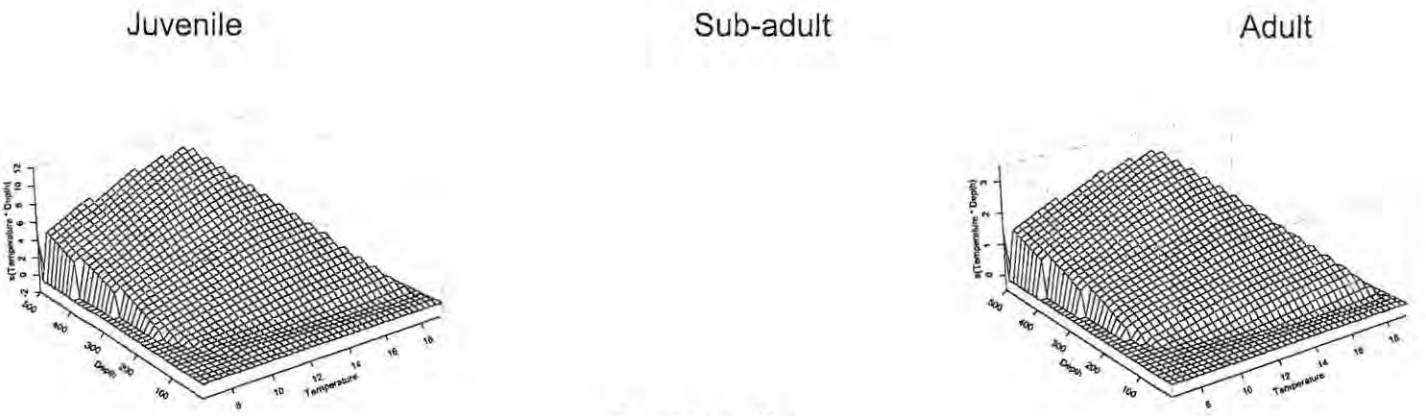
Figure 4.4: Partial residual plots describing the effect of three environmental variables on the abundance of juvenile (upper panels), sub-adult (middle panels) and adult (lower panels) *M. paradoxus*. Dashed lines represent the upper and lower twice-standard error bands.

Table 4.4: Results from the GAM for all *M paradoxus* life-history stanzas.

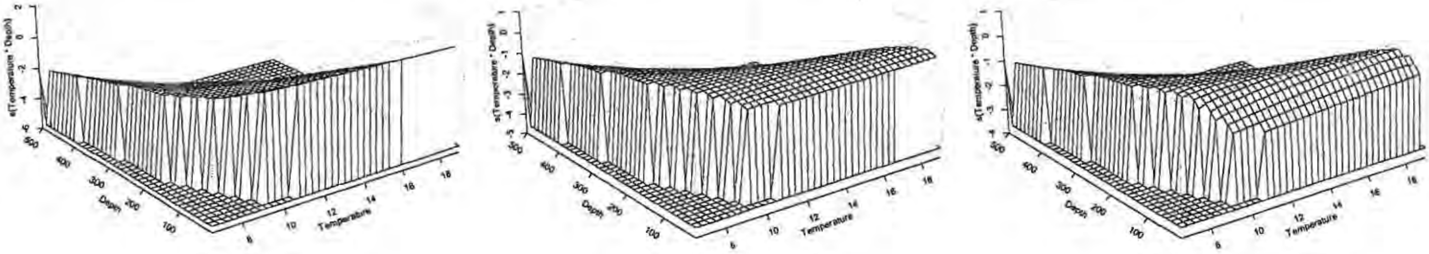
Juveniles			
	Df	Deviance	
Null	1331	1910.57	
Residual	1315.42	278.39	
R^2	0.85		
	Df	χ^2	$P(\chi^2)$
Temperature	4	5.11	0.164
Depth	4	119.41	< 0.001
Temperature × Depth	3.9	111.70	< 0.001
Sediment type	3.7	5.59	0.11

Sub-adults			
	df	Deviance	
Null	1331	1747.23	
Residual	1315.39	310.0	
R^2	0.82		
	df	χ^2	$P(\chi^2)$
Temperature	4	3.904	0.272
Depth	4	116.48	< 0.001
Temperature × Depth	3.9	95.19	< 0.001
Sediment type	3.7	6.63	0.066

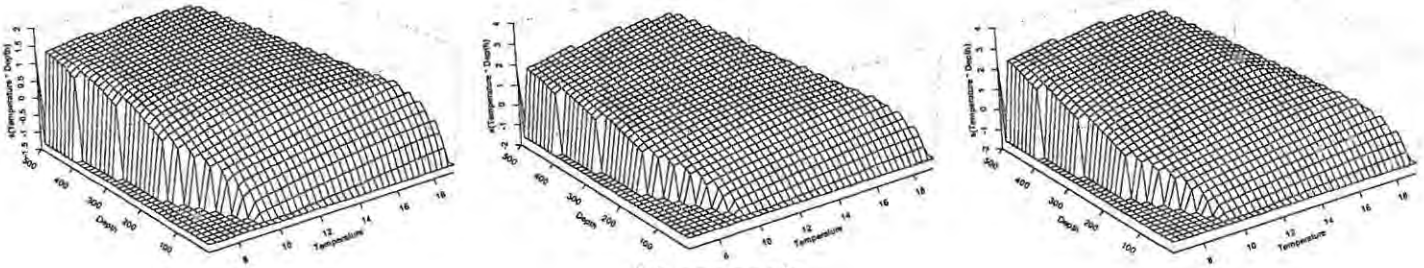
Adults			
	df	Deviance	
Null	1331	769.95	
Residual	1316.33	211.37	
R^2	0.73		
	df	χ^2	$P(\chi^2)$
Temperature	4	12.95	0.005
Depth	3.9	45.01	< 0.001
Temperature × Depth	4	38.43	< 0.001
Sediment type	2.8	7.62	0.019



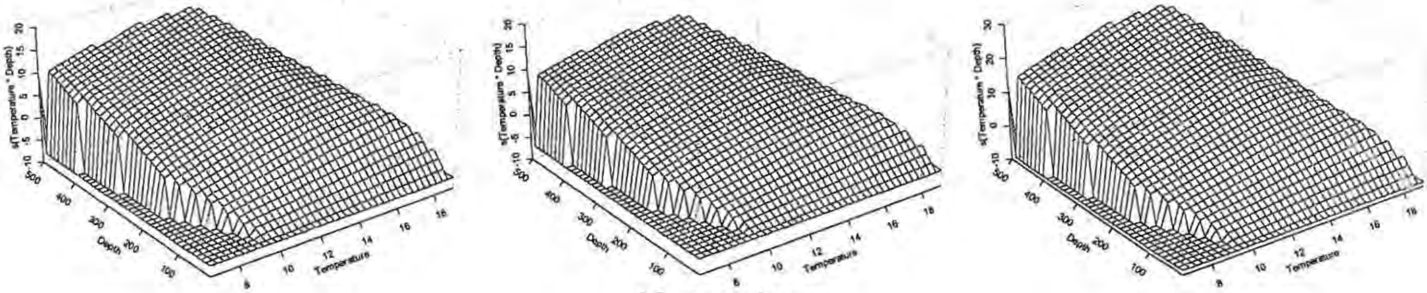
A. pectoralis



C. zanzibarensis



M. capensis



M. paradoxus

Figure 4.5: Illustration of the GAM interaction response surface between depth and temperature for all species examined.

Discussion

Species life-history stanzas followed similar trends with regards to the effect of which environmental variable was the most influential on abundance. Sediment for juvenile *A. pectoralis*, *C. zanzibarensis* and *M. capensis* was the most important variable. The temperature and depth interaction was the most influential for sub-adult *M. capensis*, while depth was most important for *M. paradoxus*. In adult fish, depth was the most important for all species with the exception of *C. zanzibarensis*.

A. pectoralis

The influence of temperature on the abundance of Agulhas sole appeared to be negligible in contrast to depth and sediment, which were both found to be statistically significant. Both life-history stanzas showed sharp declines in density with increases in depth. Abundance was highest within 100m of the shore, thus showing either this species' selectivity for this specific depth range or the inability to physiologically sustain deeper waters. This is biologically plausible as fish are known to adapt physiologically to specific environmental parameters, and have specific physiological restrictions imposed by the environment (Blaxter 1980).

Sediment was noted to be important for both life-history stanzas and explained most of the model deviance for juvenile fish. Possible reasons can be attributed to the absence or presence of prey, or in the case of juveniles which select for muddy based sediments for the added opportunity of protection in turbid water. The interaction between temperature and depth was similar for juvenile and adult fish with depth being more important than the influence of the interaction between them.

Catch rates of *A. pectoralis* are noted to vary seasonally as well as with depth and over various sediment types (Badenhorst and Smale 1991, Le Clus and Roberts 1995, Le Clus *et al.* 1996). Adults and juveniles both had higher densities over the Mud and Sandy Mud sediment types, following a similar trend with studies conducted by Le Clus *et al.* (1994, 1996). Indications are that *A. pectoralis* is highly selective towards muddy substrates (Payne and Badenhorst 1989, Le Clus *et al.* 1994, Le Clus *et al.* 1996). This trend is best explained by the fact that mud has a higher proportion of polychaetes, which makes up a high proportion of *A. pectoralis'* diet (Payne and Badenhorst 1989, Le Clus *et al,* 1994). The other correlation with the findings of Le Clus *et al.* (1995) was that lowest catch rates occurred over sediments containing gravel, such as Gravelly Mud and Sandy Gravel, which was noticeable for both juveniles and adults in this study.

It is generally accepted that sole distribution is greatly influenced by the presence of food like polychaetes, due to its dominance in their diet (Payne and Badenhorst 1989). Studies by Flemming *et al.* (1983) found that endobenthic macrofauna is more abundant in the mud belts than in the sand samples. Furthermore the distribution of these invertebrates appears to also be influenced by depth (Le Clus *et al.* 1994). These data indicate that a high number of *A. pectoralis* should occur in softer sediments containing mud. This observation holds true as over 60% of the abundance for both stanzas occurred over Mud and Sandy Mud.

Payne and Badenhorst (1989) stated that the distribution of *A. pectoralis* was patchy and limited by the extent of muddy sediment, and further narrowed distribution down to the patches with rocky outcrops on the landward side and sand on the offshore side.

The results from the study are unfortunately not as predictive, but do suggest that both juveniles and adults appear to select for Sandy Mud and Mud. Another factor that is beyond the scope of this study is that of the influence of turbidity. It has been speculated in Zoutendyk (1974) that juveniles may well use areas such as mud-based sediments of higher turbidity for cover from potential predators.

C. zanzibarensis

All life-history stanzas were significantly affected by the three environmental variables examined. Despite the significant effects, the model illustrated poor predictive abilities. Temperature, with its bimodal trend, did not have a clear positive or negative trend. Fish did, however, select for two specific temperatures, reasons for which are unknown. Depth had a significantly positive effect on this species indicating selectivity for deeper water, up to 300m. The importance of sediment type highlighted a movement of mature fish from mud-based sediments to sediments dominated by sand. As in *A. pectoralis,* this could be due to changes in diet or juvenile fish seeking refuge in turbid waters. Interaction results were very interesting and showed very different patterns to those of the other species (Figure 4.5). Although significant in all life-history stanzas where compared to the other variables examined, the interaction term was the second most important variable for juvenile and sub-adult fish, and third most important for adults.

Juvenile redspotted tonguesole had their highest median abundance over Muddy Sand and Sandy Mud, while sub-adults had similar abundances over all of the sediment types. Booth and Walmsley-Hart (2000) noted that *C. zanzibarensis* appeared to have a preference for coarse unconsolidated sediment, as food sources occurring in these sediment types like polychaetes, isopods, amphipods and crabs are more numerous (Badenhorst and Smale 1991). Badenhorst and Smale (1991) also suggested that *C. zanzibarensis* is a more widely distributed species than *A. pectoralis*. This is substantiated by more of the sediment types contributing to the percentage abundance results, rather than one or two of the sediments dominating as in *A. pectoralis*.

M. capensis

A change in the relative importance of the various environmental variables through the life-history stanzas was noticeable for *M. capensis*. In juvenile fish, sediment and depth were both significant with the juveniles being restricted to shallower waters. The importance of sediment is not fully understood, as juvenile fish are generally piscivorous and sediment type should not necessarily affect their diet (Pillar and Wilkinson 1995). Depth, which showed a negative trend for abundance with increasing depth was statistically significant for both sub-adult and adult fish. It also explained the most model deviance, with the exception of juveniles, indicating the importance of this variable to determining abundance. Temperature was also an important variable in the two older life-history stanzas, with abundance decreasing with increasing temperatures. This can be attributed to the relationship between temperature and depth and this species selecting for deeper, cooler water. The interaction between temperature and depth was the second most important variable for all life-history stanzas.

Various studies have shown the diet of *M. capensis* to be dominantly piscivorous (Pillar and Wilkinson 1995), with 92% of the diet by mass comprising of fish. Of these results 50% of the prey was pelagic (Pillar and Wilkinson 1995). These results may indicate that *M. capensis* would not be as dependent on the sediment type as the pleuronectiformes that feed predominantly on invertebrates. However, it is possible that *M. capensis* could be indirectly influenced by substrate due to their prey items selecting for certain areas due to their food source. *M. capensis* exhibit an ontogenetic shift in diet with adults moving towards larger prey items like demersal fish, as opposed to juveniles which feed mainly on crustaceans (Pillar and Barange 1993). This species is also noted to have a different feeding regime on the west and south coast, with anchovy dominating the diet on the south coast (Pillar and Wilkinson 1995).

M. paradoxus

Temperature was only significant for adult fish, showing a negative trend with increasing temperatures. Depth, which was significant for all life-history stanzas, and being the dominant explanatory variable, illustrated sharp increases in abundance with increasing depth up to 200m. For deepwater species, such as *M. paradoxus* the importance of sediment in the model is not understood. Fish selected for the coarser sand-based sediments, which generally occur in the deeper waters due to stronger currents.

As for *M. capensis* the abundance of *M. paradoxus* was dominated by two sediment types. Sand was the dominant sediment type for juveniles and sub-adults, followed by Sandy Gravel. In adults, median abundance was dominated by Gravelly Mud and then Sand. Therefore, for all life-history stanzas of this species, sand-based sediments had the strongest effects on abundance.

General patterns

Preferences by certain fish species towards certain temperature or depth conditions can be attributed to various factors such as the distribution patterns of prey, upper and lower levels of tolerable or critical temperatures, and seasonal movements in relation to spawning and juvenile dispersion (Murawski and Finn, 1998). In the case of prey distribution and abundance, temperature may not directly influence predators but rather their prey. Noted trends are, therefore, ultimately influenced by prey distribution and abundance (Sutcliffe *et al.* 1977). Studies have also noted the influence of temperature on breeding, growth rates, migration patterns and abundance (Maravelias and Reid 1994, Helle and Pennington 1999). Temperature is also regarded to be one of the most important physiological determinants influencing a fish's or any other organism's survival (Rose and Leggett 1989). Moreover, the importance of temperature arises because most species have optimal and critical temperature ranges (Shannon 1989). This was noted by Shannon *et al.* (1988) with sea surface temperature accounting for up to 50% of the recruitment variability in Cape hake. Shannon *et al.* (1988) concluded that larger year classes in certain species, particularly those that are pelagic, were influenced by sea surface temperature.

Overholtz and Tyler (1985) noted that depth, in combination with other environmental variables, described the distribution and abundance of demersal fish assemblages of Georges Bank. Perry and Smith (1994) similarly showed that four ground fish species are dependent on certain temperature and depth ranges, as did Polacheck and Volstad (1993), Swartzman *et al* (1994) and Swartzman (1995). On the Agulhas Bank Smale *et al.* (1993) noted that depth strongly influenced the ichthyofauna, as it grouped species within specific depth ranges.

Depth and its related pressure change are responsible for biochemical and physiological changes in fish, because fish are influenced directly by the increase of pressure as depth increases (Blaxter 1980). Various life-history stages of *M. capensis* and *M. paradoxus* on the west coast of South Africa have been found to exhibit selectivity towards specific depth strata (Millar 2000). In addition, recruitment and stronger year classes have also been attributed to warmer temperature (Maravelias and Reid 1994, Shannon *et al.* 1988, Helle and Pennington 1999).

Related to depth is water mass – a factor of temperature and salinity. The interactions between these variables all influence oxygen concentration and prey distribution, and in turn, affect fish distribution and abundance (Perry and Smith 1993). It is, therefore, necessary to discriminate between the effects of temperature and depth on specific species. Perry and Smith (1993) noted that species like haddock and silver hake were "temperature keepers" as they were more reliant and, therefore, more influenced by temperature. Consequently "temperature keepers" have a preferred temperature range. Conversely they also found that other species were "depth-keepers", like yellowtail flounder, showing little seasonal variation of the depth strata at which they occurred. Murawski and Finn (1988) had similar findings for silver hake, which occurred over a narrow temperature range, while haddock distribution was more related to depth than temperature.

Inagake and Hirano (1983) concluded that specific fish species depended on the thermocline layer rather than the value of the temperature, indicating a stronger influence by the depth than a specific temperature. The Agulhas Bank has a strong thermocline layer, experiencing an abrupt decline in temperature with depth (Shannon

1989). The interaction of the thermocline with depth and its influence on fish distribution cannot be ignored. It must be noted that the temperature cannot necessarily account for all variability in distribution and abundance. It is rather the causative influence that it has on other environmental variables (Swartzman *et al.* 1995). Temperature, while not necessarily being the most important influence, often has the longest continuous datasets and is critical when used as an indicator of local oceanographic climate changes (Sutcliffe *et al.* 1977).

The negative interaction between depth and temperature in this study is interesting, because it can be more important than either temperature or depth independently. This result is not surprising and is explained by Shannon *et al.* (1988) as the decrease in temperature that occurs with increasing depth. This interaction may become significant if a species has to make a trade-off between preferred depth and temperature, depending on which is more important. If the combined effects are found to be more important than the singular effects of either variable, the interaction needs explicit incorporation into the model. Furthermore, in the GAM context, it highlights that the predictors are not strictly additive.

Sediment may have many of its physical properties linked with other factors like depth or disturbance by wave action and current strength (Seider and Newell 1999). However, sediment through proximate effects, independently influences benthic communities and therefore fish communities (Künitzer *et al.* 1992). The influence of sediment is also thought to be controlled by complex interactions between physical and biological factors at the sediment water interface, rather than the granulometric properties of the sediment (Snelgove and Butman, 1994).

Fish have been found to select for different sediment types for both food and camouflage (Meyer and Smale 1991). The influence of sediment type was also initially thought to be more important on the *A. pectoralis* and *C. zanzibarensis* as they are not known to undergo vertical diurnal migrations and tend to spend more time in contact with the sediment. *A. pectoralis* is even acknowledged to select for certain sediment types, which may be to target certain food sources (Payne and Badenhorst 1989, Le Clus *et al.* 1996). Certain invertebrates are publicised to select for specific sediment types, like the tube-dwelling worm, *Sabellaria spinulosa* (Seider and Newell 1999). The selection of specific sediment types by benthic communities can in turn directly influence fish species that feed on them. Results, therefore, may indicate that fish species are selecting for certain sediment types when they are actually targeting a food source. The sediment results therefore, which indicate a species preference for a specific sediment may be as a result of a food item selecting for that sediment type. Polychaetes are the most abundant invertebrate in mud substrates on the Agulhas Bank with densities recorded up to 400 individuals.m^{-1} (Flemming 1983). This possibly explains the high density of *A. pectoralis* over mud-based sediments. Sediment types are also selected for as camouflage by some species, as noted for *C. zanzibarensis* that selects for soft substrata (Meyer and Smale 1991).

Le Clus *et al.* (1996) noted that the majority of juveniles are at or below 50 meters with few research trawls being conducted at depths of 25m, and commercial trawling prohibited in most bays at depths <50m to protect juvenile fish, thus certain species distribution patterns are incomplete confirming a gap in the data. This problem is further complicated by the lack of knowledge of the rocky areas that could not be trawled by the *R. V. Africana*. Data concerning *M. paradoxus* are also be under-represented because of its preference for greater depths, therefore introducing possible bias into this study.

Chapter 5 – Modelling the effect of environmental variables on distribution

Introduction

Successful predictions of organisms and distribution patterns (be they terrestrial or aquatic) arise from the need for better management and conservation. Knowledge of an organism's biology is not sufficient. It is rather an understanding of the organism's proximate environment, and its influence on fish distribution that is paramount (Ord 1979). Distribution patterns reflect survival, hence the ability to survive may be as much a function of location as it is of the individual's innate biological attributes (Ord 1979). Furthermore, distribution among foragers has been noted to be density dependent as at low abundances the best habitats will be occupied. However, as competition increases poorer habitats are inhabited (Swain and Morin 1996).

Presence or absence data can be used to determine the geographic range, or distribution of fish species. Relating this information to certain environmental variables allows the investigator to understand the species of interest and what influence the environment has on it. Distribution data is most commonly analysed using some form of multiple logistic regression model.

Analysing the distribution of various animals using a logistic GAM is not new to the scientific community and has been noted in terrestrial (Walker 1990, Parker 1999) and aquatic contexts (Stefansson 1996, Maravelias 1999, Garrison *et al.* 2000). Maravelias (1999) used a logistic GAM to calculate distribution, and motivated that its advantages over conventional regressive models were the fewer restrictions in its assumptions about the underlying statistical distribution of the data. Garrison *et al.*

(2000) used logistic regression to determine distribution of larval Atlantic cod *Gadus morhua*, addressing similar problems as in this project, with recorded zero catches. Logistic regression was used to predict presence of longfin eels *Anguilla dieffenbachia* in the Taieri river, New Zealand (Broad *et al.* 2001) and a numerical habitat model was used to predict distribution of juvenile Atlantic salmon *Salmo salar* (Guay *et al.* 2000). Stefansson (1996) used a logistic GLM incorporating zero and non-zero values, concluding that this method alleviated many prior problems related to data incorporating zeros. Furthermore, these approaches could accommodate spatial and temporal variability into an explicit statistical model.

The objective of this chapter is to develop a predictive logistic generalized model that uses binomial (presence or absence) data to represent distribution, while taking into account the various predictive environmental variables. The output from this model could be used for creating species maps across the study area. Linked with the GIS, this information will also be a powerful tool for identifying a spatial signature for each of the species and to delineate essential fish habitats (Rubec *et al.* 1998).

Materials and methods

The methodology followed in this chapter is similar to that outlined in Chapter 4, whereby a generalized model that uses either linear or non-linear predictors was constructed to explain the variation in distribution of the candidate species. It was assumed that distribution, denoted by presence or absence at specific spatial locations, was governed by a binomial response. The logistic link function can therefore be expressed as

$$y = \ln\left(\frac{\mu}{1-\mu}\right)$$

and the deviance to be minimised being

$$D(y;\mu) = 2\sum_{i=1}^{n} y_i \ln\left(\frac{\mu_i}{1-\mu_i}\right) + \ln(1-\mu_i)$$

The data was converted into a binary format, based on presence or absence of fish at each trawl location. If the trawl had a zero catch it was given a zero value. Anything above zero was given a value of one. A stepwise procedure was then applied to determine the most robust model that included the least number of the most influential predictors.

Presence and absence predictions

The binary data was further analysed to assess the predictability of the model by comparing observed and expected values. The model expectation was assigned a value of one, or present, if there was at least a 50% chance of fish occurring in the area, or a value of zero denoting absence. This was calculated for each species' life-history stanza. The total number of correct predictions was divided by the total predictions to produce a predictive ratio. Although not strictly statistically based the predictive ratio still provides an index of the model's accuracy.

Results

Partial residual plots and model statistics are presented in Figures 5.1 to 5.4 and summarized in Tables 5.1 to 5.4. In only one life-history stanza, that of juvenile *M. capensis,* was the saturated logistic model more robust than the other sub-models.

In all other models for the different species and their respective life-history stanzas, only a few predictors were included in the GAM.

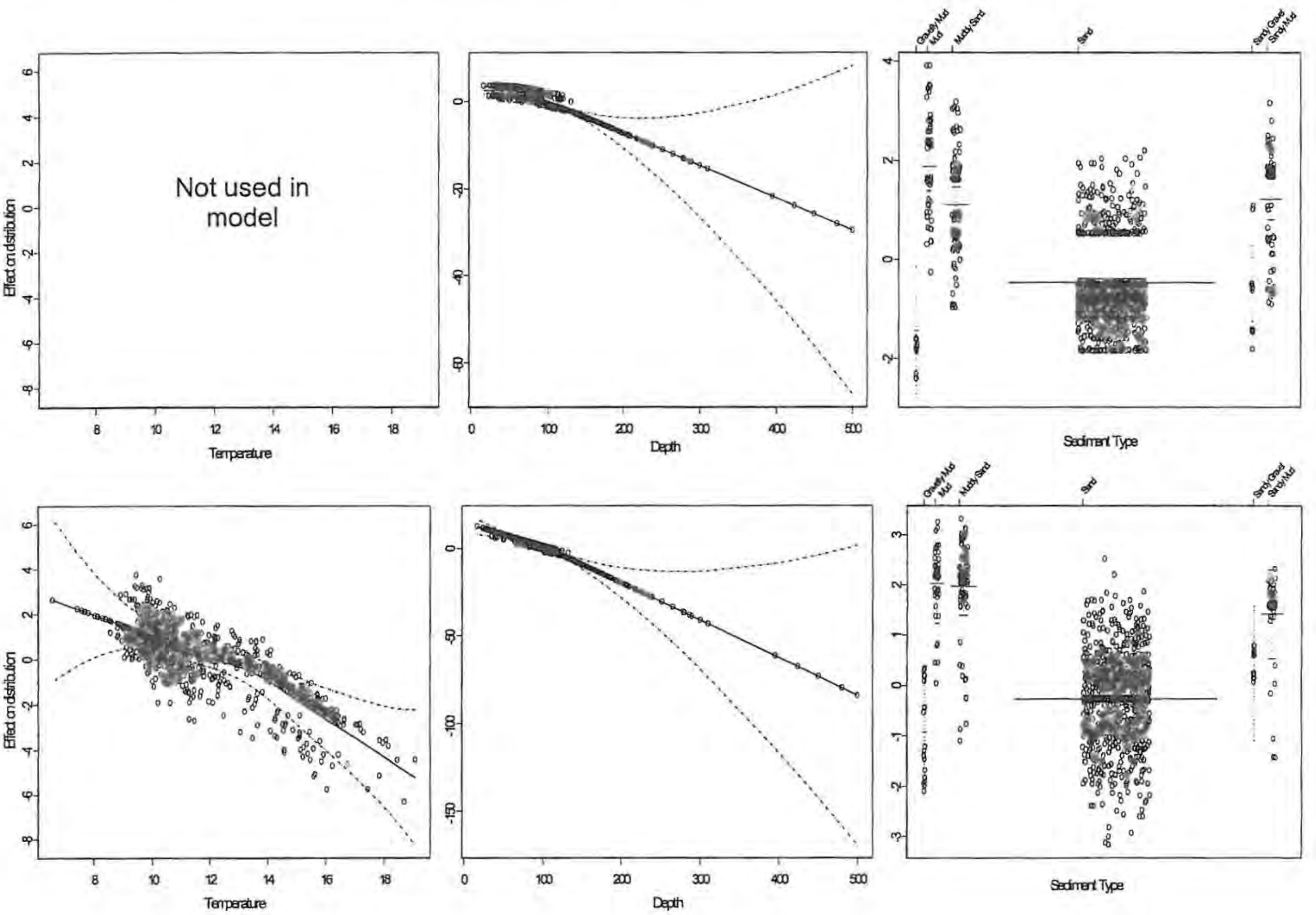


Figure 5.1: Partial residual plots describing the effect of three environmental variables on the density of juvenile (upper panels) and adult (lower panels) *A. pectoralis*. Dashed lines represent the upper and lower twice-standard error bands.

A. pectoralis

Although omitted for juveniles, temperature in adult fish showed a statistically significant decrease with respect to distribution with increasing temperatures (p-value = 0.06)(Table 5.1). Depth constrained distribution as all fish occurred within 150m.

Sediment type was also significant in both life-history stanzas examined (p-value < 0.001)(Figure 5.1), with mud-based sediments being the most influential. The interaction between temperature and depth was statistically significant in juvenile fish (p-value < 0.001). The coefficient of determination was reasonably high ($0.37 \leq R^2 \leq 0.53$).

Table 5.1: Results from the GAM for all *A. pectoralis* life-history stanzas.

Juveniles			
	df	Deviance	
Null	1331	1583.46	
Residual	1319.8	980.58	
R^2	0.38		
	df	χ^2	$P(\chi^2)$
Depth	3.6	27.30	< 0.001
Temperature × Depth	3.7	15.41	< 0.001
Sediment type	3.9	114.39	< 0.001

Adults			
	df	Deviance	
Null	1331	1830.94	
Residual	1319.14	860.74	
R^2	0.53		
	df	χ^2	$P(\chi^2)$
Temperature	4	16.22	< 0.001
Depth	3.9	23.17	< 0.001
Sediment type	3.9	84.30	< 0.001

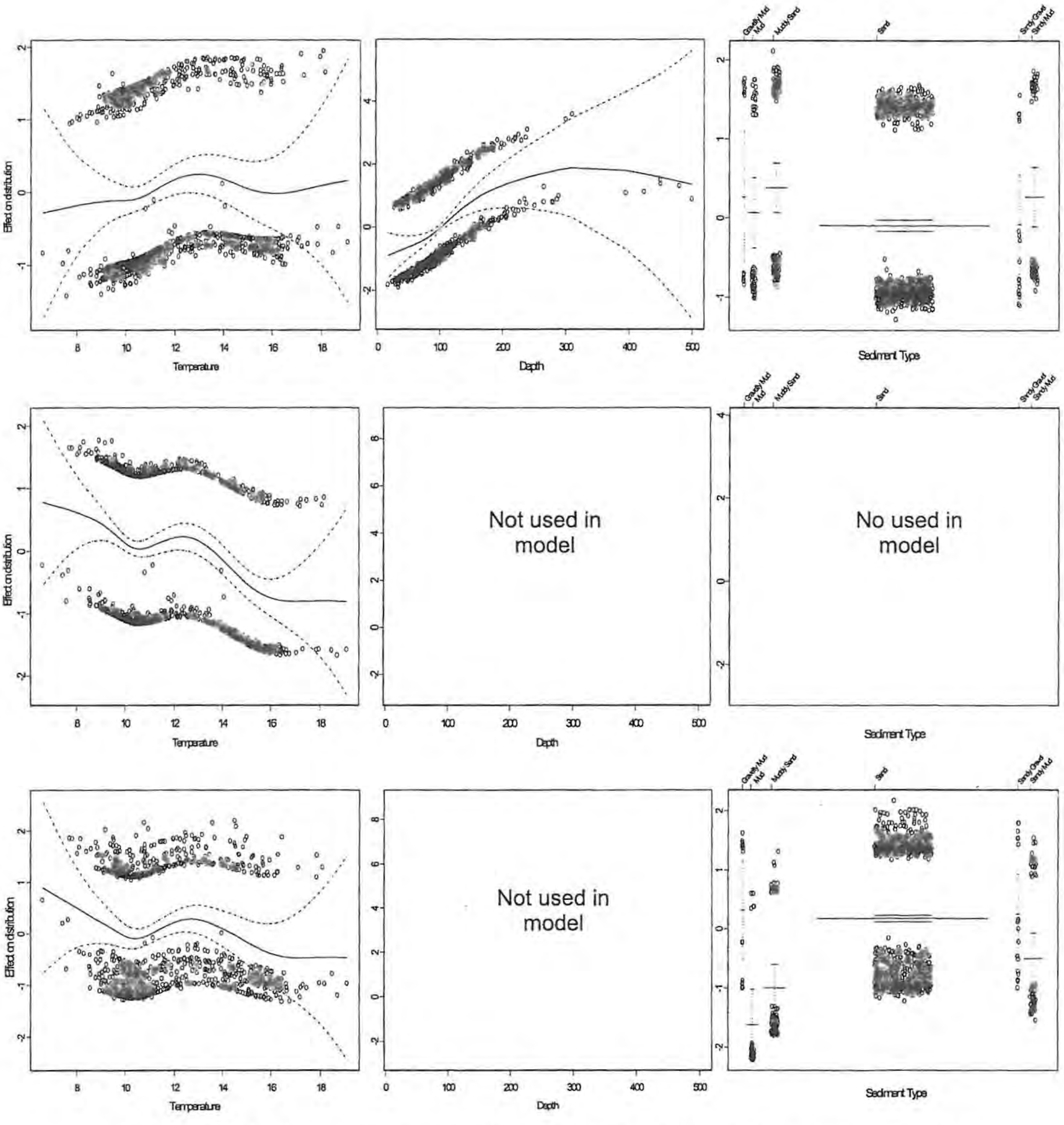


Figure 5.2: Partial residual plots describing the effect of three environmental variables on the density of juvenile (upper panels), sub-adult (middle panels) and adult (lower panels) *C. zanzibarensis*. Dashed lines represent the upper and lower twice-standard error bands.

Table 5.2: Results from the GAM for *C. zanzibarensis* life-history stanzas.

	Juveniles		
	df	Deviance	
Null	1331	1684.36	
Residual	131.34	1644.92	
R^2	0.02		
	df	χ^2	$P(\chi^2)$
Depth	4.0	12.17	0.006
Temperature	3.8	5.41	0.12
Sediment type	3.9	10.81	0.01
	Sub-adults		
	df	Deviance	
Null	1331	1843.07	
Residual	1323.27	1782.46	
R^2	0.03		
	df	χ^2	$P(\chi^2)$
Temperature	3.9	21.64	< 0.001
Temperature × Depth	3.8	11.01	0.009
	Adults		
	df	Deviance	
Null	1331	1746.91	
Residual	1319.35	1584.16	
R^2	0.09		
	df	χ^2	$P(\chi^2)$
Temperature	4	15.97	0.001
Temperature × Depth	3.7	51.07	< 0.001
Sediment type	4	57.87	< 0.001

C. zanzibarensis

Partial residual plots showed temperature, as with abundance (Figure 4.2), to have a bimodal trend for all life-history stanzas. The effect of this variable was statistically significant for both sub-adult and adult fish (p-value < 0.001)(Table 5.2), with most fish confined between 9° and 17°C. Depth, which was only included in juvenile GAM, showed a positive and statistically significant trend with fish occurring up to a depth of 250m (p-value = 0.006)(Figure 5.2). Sediment, which was only included in the juvenile and adult GAMs, was statistically significant (p-value < 0.01)(Table 5.2), with the mud-based sediments having the greatest influence on distribution (Table 5.2). The interaction between depth and temperature was also statistically significant for sub-adult and adult fish (p-value = 0.009)(Table 5.2). The coefficients of determination were low for this species ($0.02 \leq R^2 \leq 0.09$).

M. capensis

The partial residual plots were noticeably similar for all life-history stanzas and environmental variables (Figure 5.3). Temperature, which was significant for juvenile and sub-adult fish (p-value < 0.05)(Table 5.3) showed that distribution occurred up to 10°C, declining thereafter (Figure 5.3). Depth was significant for all life-history stanzas (p-value < 0.001)(Table 5.3) and showed distribution to slowly decline with increased depth. The majority of fish occurred within 250m of the shore. The interaction between temperature and depth was only used for juvenile fish and was statistically significant (p-value < 0.001)(Table 5.3). The sediment type for all life-history stanzas was statistically significant (p-value = 0.025)(Table 5.3), with mud-based sediments having the most influence on this species' distribution. The coefficients of determination was reasonable ranging from 0.25 to 0.36.

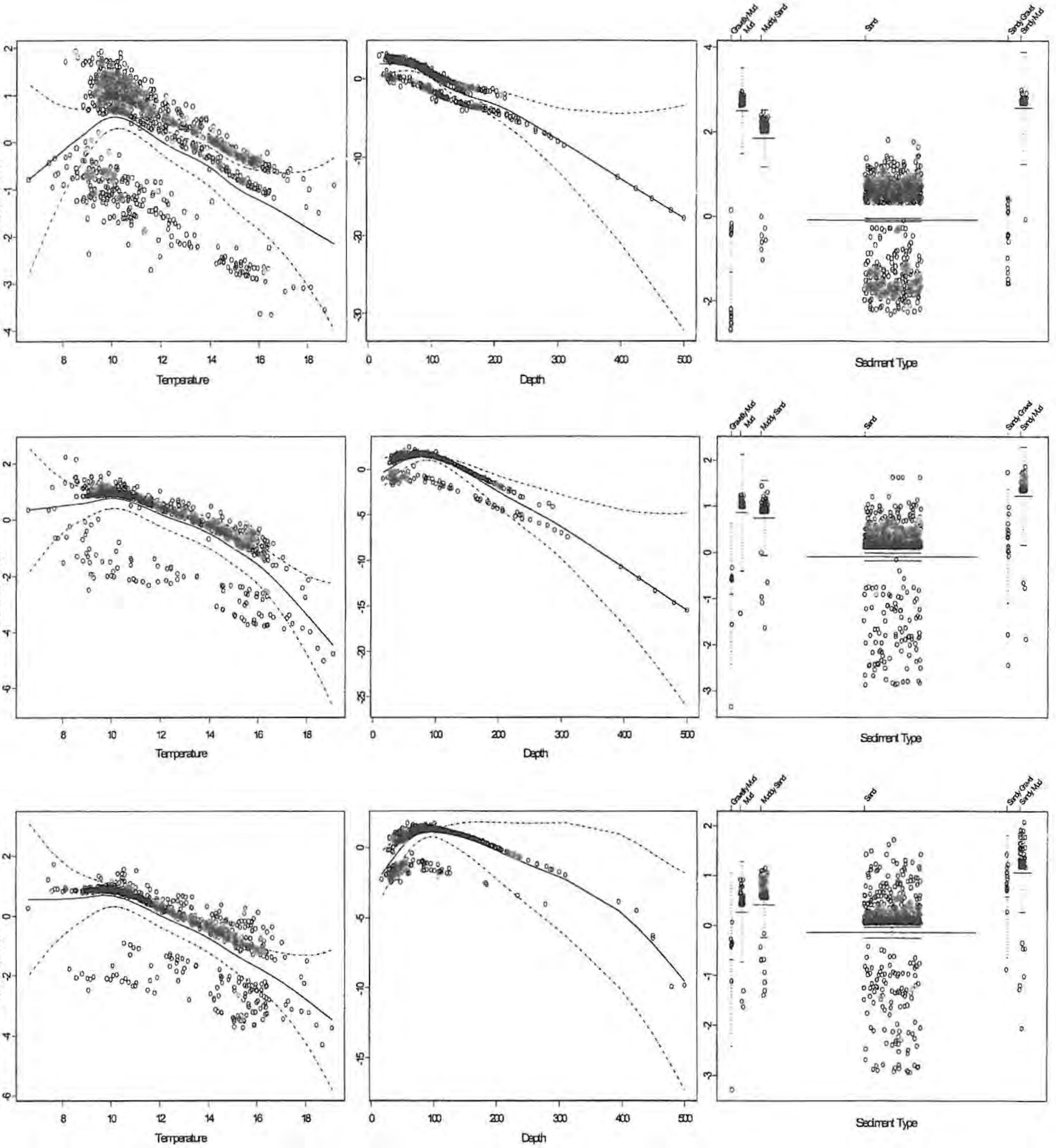


Figure 5.3: Partial residual plots describing the effect of three environmental variables on the density of juvenile (upper panels), sub-adult (middle panels) and adult (lower panels) *M. capensis*. Dashed lines represent the upper and lower twice-standard error bands.

Table 5.3: Results from the GAM for all *M. capensis* life-history stanzas.

Juveniles			
	df	Deviance	
Null	1331	1430.9	
Residual	1315.35	1075.72	
R^2	0.25		
	df	χ^2	$P(\chi^2)$
Temperature	3.9	11.98	0.006
Depth	3.9	32.56	< 0.001
Temperature × Depth	4	25.23	< 0.001
Sediment type	4	69.09	< 0.001

Sub-adults			
	df	Deviance	
Null	1331	801.88	
Residual	1319.13	538.65	
R^2	0.33		
	df	χ^2	$P(\chi^2)$
Temperature	4	15.65	0.001
Depth	3.9	93.96	< 0.001
Sediment type	4	9.71	0.02

Adults			
	df	Deviance	
Null	1331	878.26	
Residual	1319.05	559.29	
R^2	0.36		
	df	χ^2	$P(\chi^2)$
Temperature	4	8.32	0.038
Depth	4	111.63	< 0.001
Sediment type	4	9.36	0.025

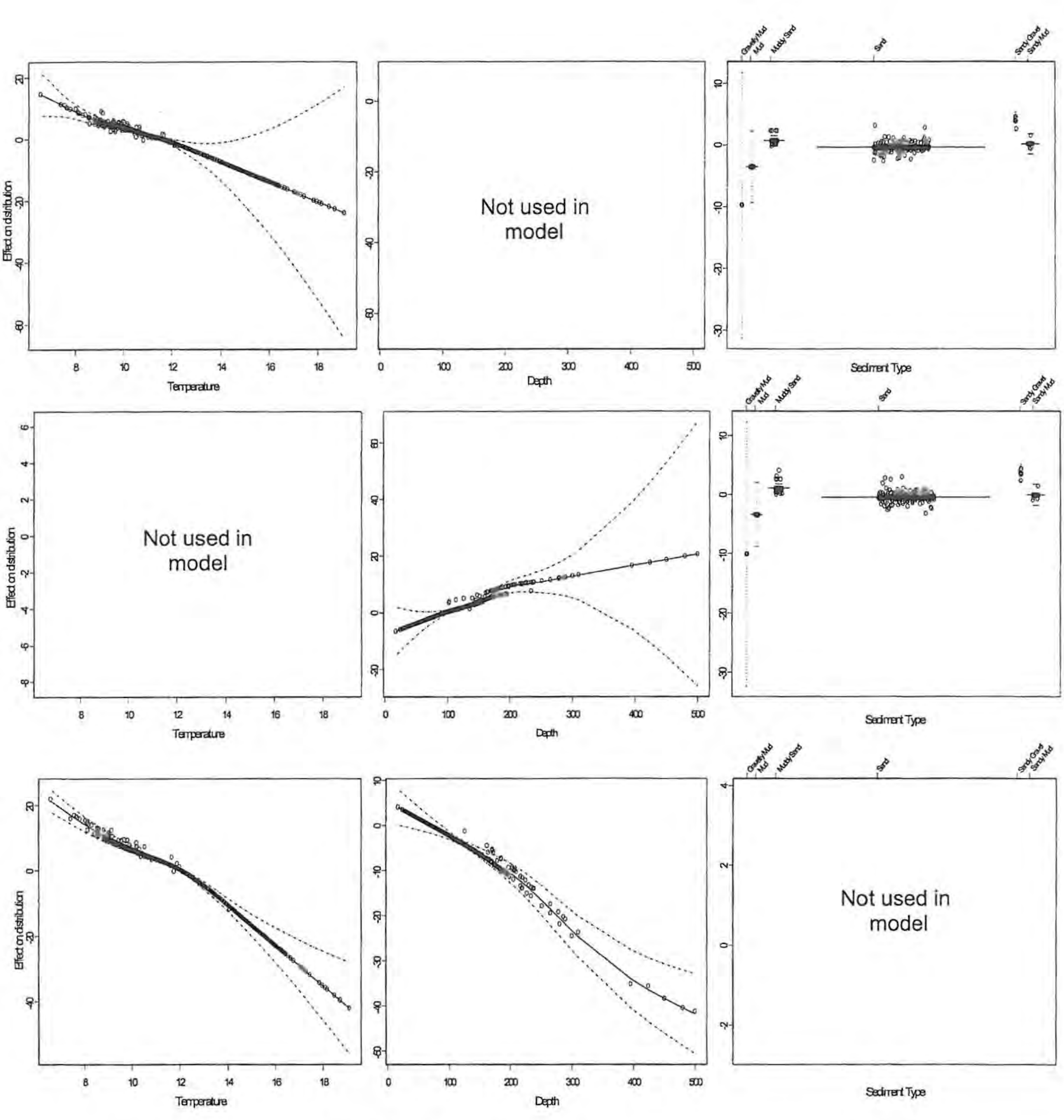


Figure 5.4: Partial residual plots describing the effect of three environmental variables on the density of juvenile (upper panels), sub-adult (middle panels) and adult (lower panels). *M. paradoxus*. Dashed lines represent the upper and lower twice-standard error bands.

Table 5.4: Results from GAM for distribution of *M. paradoxus*.

Juveniles			
	df	Deviance	
Null	1331	759.32	
Residual	1322.41	129.09	
R^2	0.84		
	df	χ^2	$P(\chi^2)$
Temperature	3.7	5.010	0.139
Temperature × Depth	3.9	7.02	0.068
Sediment type	3.8	16.25	< 0.001

Sub-adults			
	df	Deviance	
Null	1331	773.68	
Residual	1323.03	174.42	
R^2	0.77		
	df	χ^2	$P(\chi^2)$
Depth	4.1	9.68	0.024
Sediment type	3.9	25.43	< 0.001

Adults			
	df	Deviance	
Null	1331	379.85	
Residual	1319.05	139.13	
R^2	0.63		
	df	χ^2	$P(\chi^2)$
Temperature	3.9	6.47	0.087
Depth	4	12.77	0.005
Temperature × Depth	4	3.64	0.304

M. paradoxus

Distribution declined with increasing temperature for both juvenile and adult fish. Despite being included in the GAM it was not statistically significant (p-value = 0.087)(Table 5.4), with most fish occurring between 9°C to 16°C (Figure 5.4). Depth, which was used in both the sub-adult and adult GAM, showed a positive trend in sub-adults with increasing depth. This trend was reversed in the adult fish (Figure 5.4). Depth was statistically significant for both life-history stanzas (p-value = 0.024) (Figure 5.4). The interaction between temperature and depth was included in both the juvenile and adult GAMs but was not significant in either (p-value ≥ 0.068)(Table 5.4). The coefficients of determination were high, ranging between 0.82 and 0.63.

Presence and absence results

Figures 5.5 to 5.8 illustrate the correct distribution predictions of all life-history stanzas for each species on the Agulhas Bank. Predictive ratios were reasonably high for some species, with all results being over 33%. High predictability was noticeable for *A. pectoralis* along the shoreline and also along the 200m isobath (Figure 5.5). The lowest predictive ratios occurred for *C. zanzibarensis* with the lowest value being 33% and the highest at 48% (Figure 5.6). For both hake species the model had predictive ratios above 78% (Figure 5.7, 5.8). Overall, the predictive ratios were dependant on the significance of certain predictors such as sediment type in juvenile fish and depth in adults. Results are summarized in Table 5.5.

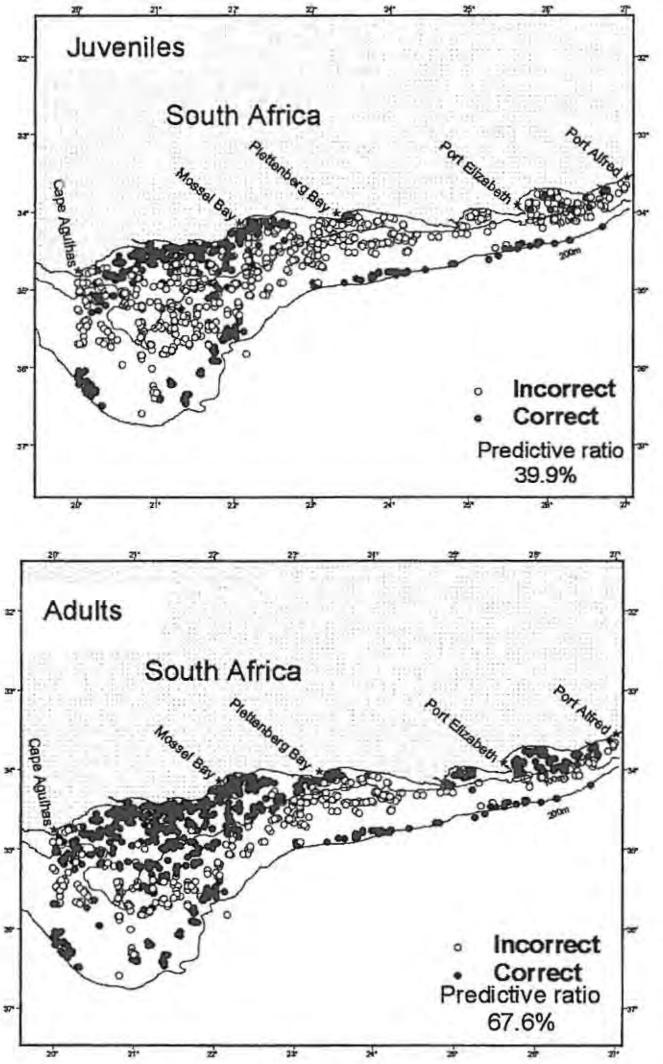


Figure 5.5: Maps for *A. pectoralis* showing the correct predictions from the observed and expected, presence and absence data.

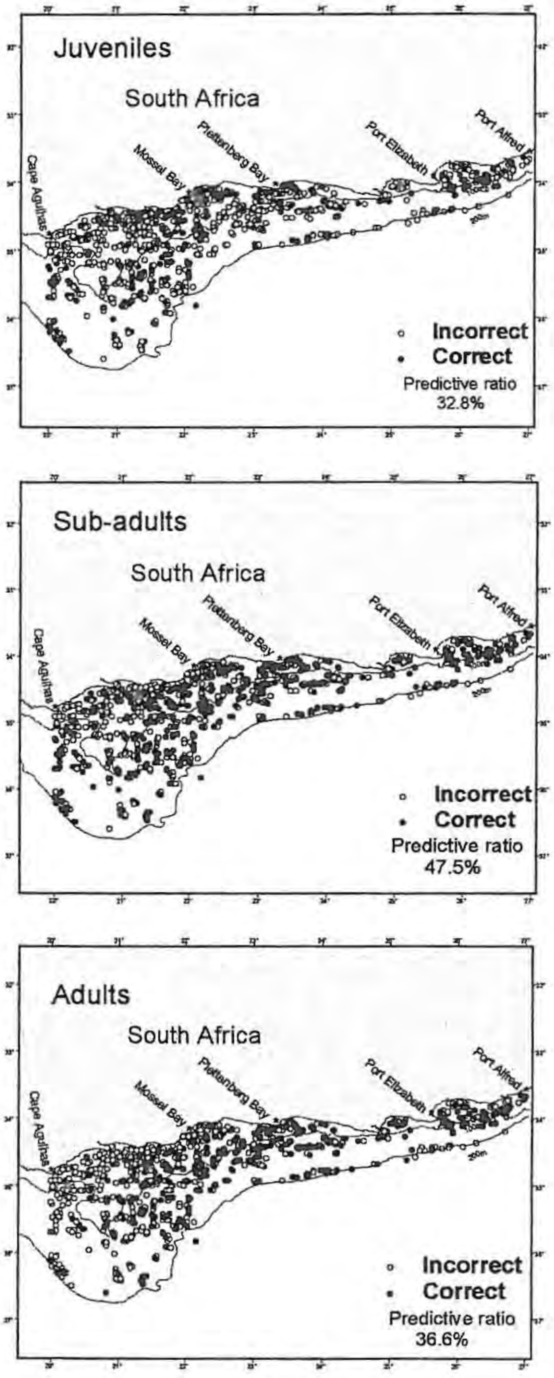


Figure 5.6: Maps for *C. zanzibarensis* showing the correct predictions from the observed and expected, presence and absence data.

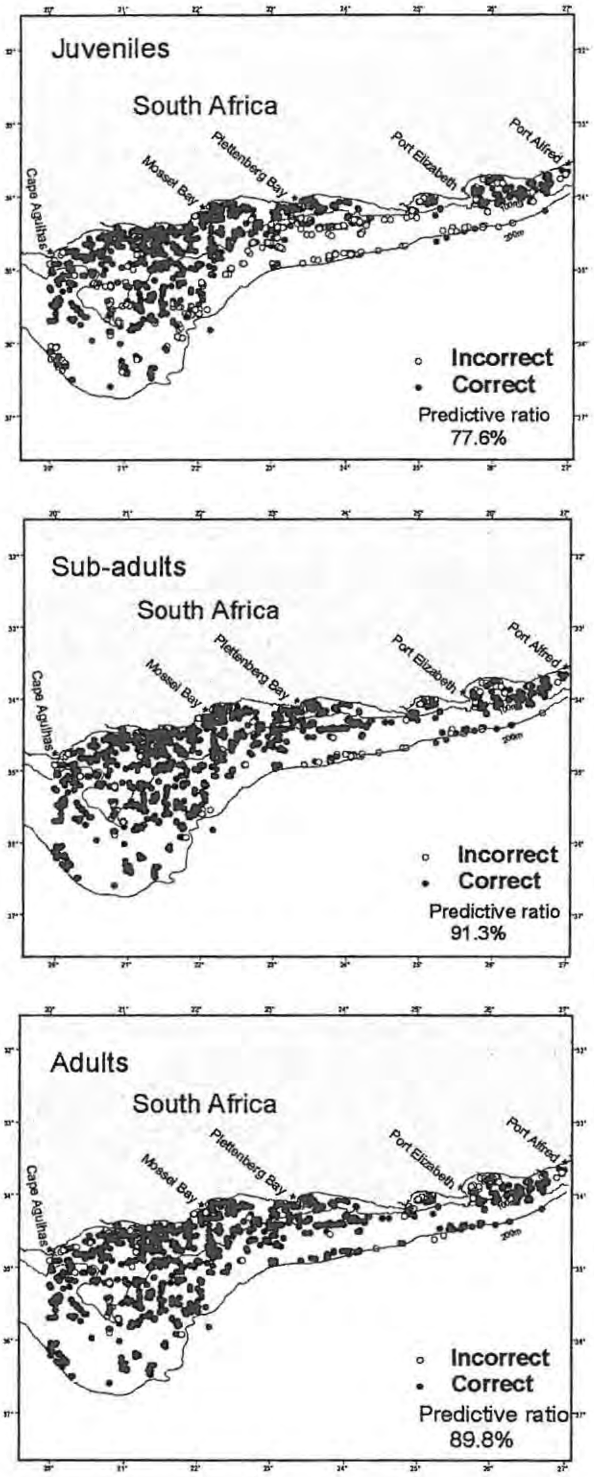


Figure 5.7: Maps for *M. capensis* showing the correct predictions from the observed and expected, presence and absence data.

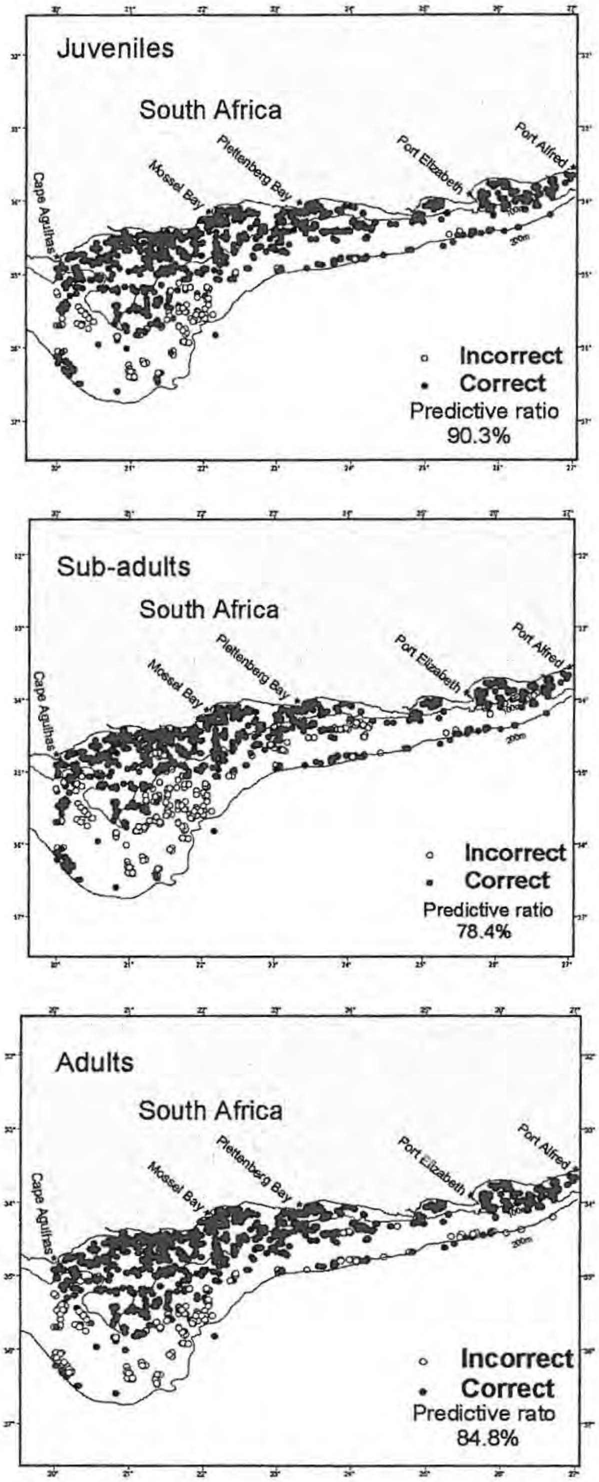


Figure 5.8: Maps for *M. paradoxus* showing the correct predictions from the observed and expected, presence and absence data.

Table 5.5: Summary of results from the predictions from the observed and expected, presence and absence data.

Species	Life-history stanza	Predictive ratio (%)
A. pectoralis	Juveniles	39.9
	Adults	67.6
C. zanzibarensis	Juveniles	32.8
	Sub-adults	47.5
	Adults	36.6
M. capensis	Juveniles	77.6
	Sub-adults	91.3
	Adults	89.8
M. paradoxus	Juveniles	90.3
	Sub-adults	78.4
	Adults	84.8

Discussion

The strength of predictive environment modelling lies in the possibility of accurately predicting responses to future changes that the environment may undergo, like sediment changes due to current deposits and increasing temperature due to global warming. A model that can reliably describe a considerable proportion of the deviance of each variable can be utilised by inputting possible scenarios that could occur in a changing environment, and outputting the impact this has on the fish populations. This information can then be utilised for a variety of management purposes.

Most variability was described by sediment type in both the life-history stanzas of *A. pectoralis*. As a consequence, both life-history stanzas were correctly predicted in those areas inshore along the coast and deeper around the 200m isobath. It was these areas where fish were always present or absent. Poor predictability occurred in intermediate areas, between these two areas. *C. zanzibarensis* had most deviance explained by depth for juvenile fish, temperature in sub-adults, and sediment type in the adult life-history stanzas. *C. zanzibarensis* showed an area of poor predictability in the north-west corner of the study area. The strongest predictor was for sediment type in juvenile fish, and depth in sub-adult and adult fish in *M. capensis*. *M. paradoxus* juvenile and sub-adult fish were mainly influenced by sediment type, with importance shifting to depth in adult fish. *M. paradoxus* in the centre portion of the Agulhas Bank are in deeper water, just inside the 200m depth mark.

In all species the main areas of non-correct predictions were generally in deeper water, where the maturing fish should occur, and very few fish were interspersed within the area. This may be resultant of varying maturation rates within the population stanza, which would inevitably reduce the predictability of the results. Although not as high as the result for the Cape hakes, *A. pectoralis* and *C. zanzibarensis* results would still be useful in their predictive abilities. Distribution predictions have taken into account all of the environmental variables, and also exposed which variable was more important for each species. This varied from species to species, mainly due to different life-history strategies.

The general trend for all species was that sediment was important in the pleuronectiforms and the juvenile gadoids. The significance of mud-based sediment on the distribution of *A. pectoralis* has already been noted in literature by Le Clus *et al.* (1994), and is due to the major food sources of this species occurring in mud-based sediments. Sediment also strongly influenced distribution in juvenile and adult *C. zanzibarensis*, with mud-based sediments being the most important for juveniles, changing to sand-based sediments for mature fish. These results are probably due to a dietary change and their food source of polychaetes, isopods, amphipods and crabs occurring in specific sediment types (Booth and Walmsley-Hart 2000). The general distribution of this species across all sediment types across the entire Agulhas Bank is indicative of them having non-selective breeding areas (Booth and Walmsley-Hart 2000).

The trend of sediment being important in juvenile *M. capensis* is understandable as younger fish occur in shallower water and are not as dependent on depth. Maturing fish move into deeper water and the importance of depth becomes apparent, reflected in their statistical significance. Furthermore the change in diet from crustaceans in juveniles, to meso-pelagic fish in sub-adult fish and then larger fish species in the adult *M. capensis,* can be held recognisable for the decrease in importance of sediment type to distribution patterns being influenced by depth (Payne 1989). Similar to *M. capensis,* juvenile and sub-adult *M. paradoxus* distribution was more influenced by sediment, becoming less important as the fish moved into deeper water.

Life-history stanzas of certain species are physiologically suited to survive at certain depths, thus directly influencing their horizontal and vertical distribution (Blaxter 1980). A number of studies have noted significant correlations between fish distribution and depth (Gabriel and Tyler, 1980, Mahon 1985, Overholtz and Tyler 1985). Depth was found to be a key variable, amongst a suite of variables, influencing the distribution and dynamics of pollock schools in the Bering Sea (Swartzman *et al.* 1994).

A noticeable characteristic of depth is the restriction it places on distribution. *A. pectoralis* was restricted to 150m, while in *C. zanzibarensis* depth was only significantly important for juvenile fish. Depth was important to all life-history stanzas for *M. capensis,* while it was only statistically significant for adult fish. The change of importance from sediment to depth in the gadoids can be attributed to a change in diet causing the movement of maturing fish into deeper water (Payne 1989). The relationship of depth with temperature and the interaction of the two also proved to be important to certain species' life-history stanzas. Sutcliffe Jr *et al.* (1977) noted that ten of the seventeen species under investigation had significant correlations with sea temperatures, one of which was the silver hake *Merluccius bilinearis*. Similarly the distribution of walleye pollock (*Theragra chalcogramma*), another gadoid, was related to both temperature and depth. Their prey distribution was, however, also found to be related to similar factors making it unclear which are accountable for distribution (Swartzman *et al.* 1995).

Temperature, as a structural agent, also fits the "patch, corridor, matrix, hypothesis", which suggests that the thermal structure of different water masses can act as specific habitats, since fish have certain temperature preferences (Rose and Leggett 1989). These water masses can therefore act as significant physical structures with movement occurring between optimal thermal corridors (Magnuson *et al.* 1979).

Temperature and its interaction with depth was significant in juvenile *A. pectoralis*. Temperature in *C. zanzibarensis* was more important than in *A. pectoralis*, attributable to this species occurring in deeper waters. Temperature was significant in sub-adults and adult *C. zanzibarensis*, with most deviance being described in sub-adults. In adult fish the interaction was important. Temperature influences on the gadoids were variable. It was more important in sub-adult and adult *M. capensis,* which could be related to their life-history stanzas, due to them moving into deeper water. The interaction of temperature and depth was statistically significant in juvenile fish. Temperature was not important in *M. paradoxus*, which was more influenced by sediment or depth, depending on the life-history stanzas.

General conclusion

In essence a "bell-shaped" or Gaussian curve can best describe the difference between distribution and abundance. Distribution is most important at the extremities of the continuum, where survival is the priority. Fish can occur in this area due to the environmental variables, but only when certain biological requirements are satisfied. The mode of distribution can be ascribed as the preferred area, which will explain abundance, like sufficient food and favourable conditions conducive to breeding and growth. The results for the prediction calculations can be considered correct enough for all the species. If the environmental variable information is available for a specific area, a successful model could be created for the hake species that would be able to predict distribution patterns.

The literature notes the influence of the various environmental variables on the distribution of species (Rose and Leggett 1988, Maravelias 1999, Corten 2001, Zheng *et al* 2001). Interactions of the variables and the fact that they may not necessarily influence the species directly, but their food items, magnifies the problems of trying to isolate the importance of each variable separately and interactively. There is, however, no doubt that the distribution of the four candidate species is influenced by these variables. A few general trends were noticeable: Juvenile fish for all species were most significantly influenced by sediment, while sub-adults in each species were influenced by various variables. Sediment type dominate adult pleuronectiformes and while gadoids are influenced by depth. These findings can be related to the fact that the two pleuronectiformes are not known to move to deeper water at maturity. Therefore depth is not as influential as sediment type. However, in the hakes the significance of depth was exposed as the fish matured and it was responsible for the highest variance in the model.

Knowledge of the distribution patterns and structuring variables relating to South African fish species are sorely lacking. In a worst case scenario this problem becomes that of severe mismanagement. Strategies like delineating essential fish habitat (Magnuson *et al.* 1979) and habitat suitability indexes need this information, allowing for up to date effective management of the resource.

Chapter 6 – General discussion

Introduction

The South African demersal trawl fishery is the largest hake-based fishery in the world (Botha 1985), harvesting two species each distributed between southern Angola on the west coast to East London on the east coast (Payne 1989). Variation in abundance is common knowledge, occurring spatially with *M. paradoxus* dominating on the west coast and *M. capensis* on the South coast (Payne 1989). Agulhas sole, by contrast, is only harvested on the south coast by a directed fishing fleet. Sole catches range between 500-1000 tons annually, and comprise of 5% of the inshore demersal trawl landings (Japp *et al.* 1994, Le Clus *et al.* 1998). Agulhas sole fishery is nevertheless important, as it is the highest valued fish species per mass harvested in South Africa (Japp *et al.* 1994). *C. zanzibarensis*, which is gaining in popularity as a table fish, is the most abundant pleuronectiform and cynoglossid species by mass and number on the south coast and is caught in appreciable numbers in either the hake or sole directed trawlfisheries (Japp *et al.* 1994, Booth and Hecht 1998).

Fisheries collected data be it biological, geological or socio-economic has an explicit spatial component that is often ignored. Past distribution and abundance analyses that have been conducted on various demersal fish species on the Agulhas Bank have unfortunately been confined to estimating the mean or relative abundance, together with their associated variances (Badenhorst and Smale 1991, Smale *et al.* 1993). Unfortunately all analyses have only been conducted on a temporal scale. These temporal trends can now be incorporated into spatial analyses, and can be linked to existing biological information relating to the four candidate species (Zoutendyk

1974, Botha 1977, Botha 1985, Japp 1989, Payne 1989, Payne and Badenhorst 1989, Badenhorst and Smale 1991, Gordoa and Macpherson 1991, Macpherson *et al.* 1991, Meyer and Smale 1991, Punt and Leslie 1991, Smale and Badenhorst 1991, Pillar and Barange 1993, Smale *et al.* 1993, Japp *et al.* 1994, Le Clus *et al.* 1994, Punt 1994, Le Clus and Roberts 1995, Pillar and Wilkinson 1995, Le Clus *et al.* 1996, Pillar and Barange 1996, Le Clus *et al.* 1998, Booth and Walmsley-Hart 2000, Millar 2000).

Various spatial analytical methods have been used for analysing ichthyological data. These methods include; time sequence cluster analysis (Overholtz and Tyler 1985) used to assess the possible changes of Georges Bank fish assemblages on a seasonal basis; a statistical ellipse technique, as used by Atkinson *et al.* (1997), to assess distribution changes and abundance of northern cod (*Gadus morhua*); Principal Component Analysis and cluster analysis to assess spatial patterns of whiting in Scottish waters (Zheng *et al.* 2001); the use of generalised models (Hastie and Tibshirani 1986, McCullagh and Nelder 1989, Booth 1997); and geostatistics (Journel and Huijbregts 1978, Sullivan 1991, Petitgas 1993). Geostatistics is the most commonly used form of spatial analysis and uses models to analyse spatial autocorrelation, considering the correlations between variables over space as a function of the distance between them, and then linearly interpolating a surface via kriging. Geostatistics can also be used in conjunction with other methods for analyses. This was illustrated by Garisson *et al.* (2000) who used variographic analyses and kriging to estimate spatial overlap of larval gadids associated with hydrographic features on Georges Bank. Geostatistics can, therefore, be used to analyse the influence of environmental variables on species distribution and abundance be it on a seasonal or annual time scale.

Various studies on demersal fish assemblages have found that diversity varies seasonally and spatially because of environmentally induced migrations, with temperature usually being the dominant driving force (Overholtz and Tyler 1985). Hence, if environmental variables are responsible for seasonal variability it is possible that they can also be responsible for structuring diversity in general. Given the high ichthyofaunal diversity and the mixture of environmental variables converging over the Agulhas Bank, unique management problems are presented that require creative and possible spatially referenced solutions.

General findings

This study endeavoured to utilise available methods to investigate the distribution and abundance of several demersal species. The exploratory data analysis presented in Chapter 3 exposed some general patterns, and provided a solid basis for more complicated statistical analyses. Several environment parameters were identified as possible predictor variables, and when included into a modelling framework, were found to explain observed distribution and abundance patterns.

The influence of the identified predictors on distribution and abundance were analysed in Chapters 4 and 5 using Generalized Additive Models, each with different error structures. Distribution and abundance of both pleuronectiform species, and all juvenile fish in general was determined by sediment type. These results confer with the findings for *A. pectoralis* of Badenhorst and Smale (1991), where depth was found to be unimportant, and minor fluctuations occurred in distribution patterns seasonally. Distribution and abundance of most sub-adult fish showed no pattern, as the main influence coming from various single environmental variables. Similar to the juvenile fishes, adult gadoids were mainly influenced a single predictor variable - the temperature/depth interaction in the case of *M. capensis*, and depth in the case of *M. paradoxus*, with distribution being strongly depth dependent. These results were similar to those of Payne (1989) who concluded that the two hake species abundance was influenced by temperature at preferred depths, i.e., certain depths that are favoured and they will occur there if temperature is favourable. Furthermore it is accepted that the hake are more influenced by, and possibly dependent on, depth (Botha 1985). In both hake species it has been noted that distribution can expand or contract or shift in response to environmental factors (Payne 1989). Distribution and abundance of the hakes was further distorted as wide fluctuations tend to occur in recruitment, the result of erratic spawning success in a dynamic environment.

Implications of findings to management

This project is unique in that it has linked a suite of powerful methods. They include relating abundance to environment covariates using GAMs (Swartzman *et al.* 1992, 1994, 1995), the development of predictive distribution models (Walker 1990, Parker 1999) and a comparison of the spatial distribution of populations (Syrjala 1995). The thesis also used GIS as a visualisation tool. Working within a GIS environment, and the added use of generalised modelling, allowed for detailed spatial and temporal relationships to be understood between fish distribution and abundance and a variety of environment parameters.

The spatial component of the study could, therefore, be considered as an adaptive framework, as it allows all the data and results to be synthesised and analysed within a spatial context. For example, the representation of the data within a GIS allows for hidden patterns be exposed and to be illustrated visually, while further additional hidden relationships can be revealed using statistical methods. In addition, various management strategies could be developed within this GIS (Giles *et al.* 1992, Isaak and Hubert 1997, Rubec *et al.* 1998, Meaden 2000a,b). Better management practices, as noted by Giles *et al.* (1992), can be developed to produce optimised management that is site, and therefore spatially, specific to the conditions of the area.

The establishment of areas falling under the context of 'Essential Fish Habitat' - those waters and substrate necessary for spawning, feeding, or growth to maturity - can be discovered spatially and mapped (Rubec *et al.* 1998). In this study, areas of high juvenile and adult abundance have been found. Statistical analysis used to determine importance of structuring variables exposed those areas that had the correct combination of the environmental variables that are preferred by each species - essentially unique "spatial signatures". Management action could, therefore, be the isolation of nursery areas with high juvenile density and areas of high adult density suitable for harvesting.

It has been recognised that fish stocks of the Agulhas Bank cannot be managed in isolation (Booth and Hecht 1998). Furthermore, the multi-species nature of trawl catches is problematic for effective management because of high bycatch ratios (Badenhorst and Smale 1991). Additional complications arise because of a need for better stock assessment methods that include multi-species models, or single species models that are biologically based. Improved understanding of the basic patterns of abundance fluctuations, imposed in part by the environment, would clearly assist in the formulation of management policies and the imposition of quotas. Environmental parameters should also be considered as negative effects of incorrect management decisions include economic ramifications and possible breakdown in ecological linkages.

Furthering the study and where to from here?

The data, and therefore part of the analyses, although collected over a period of eight years, has several weaknesses. Data were collected over the spring and autumn biomass surveys and not throughout the year. Unfortunately due to the excessive cost associated with surveys, and South Africa's current financial position, additional surveys that account for seasonal variation will not be feasible. Understanding spatial patterns requires additional data collection. This is due to the increase in dimensionality, geometrically increasing the size of the dataset.

Samples that are collected temporally and spatially add another aspect of variation over time that requires mentioning. Le Clus and Roberts (1995) postulated that environmental factors with variable seasonal and spatial signals, such as wind field and its influence on water temperature or oxygen concentration account for some of the inter-annual variability in catches and catch rates. Considering that sediment dynamics vary on decadal scales and temperature fluctuations occur a daily to weekly scales, dataset compatibility needs attention. While the influence of sediment type and fish life-histories is not completely understood, the occurrence of different sediment types may be directly related to depth, as the Agulhas Bank has stronger currents in deeper waters at the shelf break. As a result there appears to be a correlation between coarser sediment and stronger currents. This problem may be further exacerbated by biotic factors, in particular the distribution and abundance of prey which could cause variations in species distribution over space and time (Rose and Leggett 1988, Rose and Leggett 1989). Furthermore *M. paradoxus* occurs to depths up to 800m (Payne 1989) and Agulhas sole at depths of 50m. In this analysis trawls were restricted to 500m and few trawls were conducted at depths less than 50m. This sampling protocol therefore omits data crucial to certain species, and introduces bias into further analyses.

Fisheries dependent data is another option when collecting information on distribution and abundance. Fisheries data, including commercial fishing patterns and catch rates, is unfortunately known to be unreliable and largely dependent on market conditions, management regulations, and weather patterns. Surveys are generally not affected by these factors are, therefore, considered to be a more reliable source of data (Fox and Star 1996). Additional biological work is required regarding aspects related to reproduction of the candidate species and their feeding biology. Feeding biology information has to be linked to various sediment types and the prey distribution and abundance.

To conclude, it is suggested that this thesis provides a potential modelling framework for the future calculation of improved relative biomass estimates. The GAMs developed to detrend the density estimates could be coupled with geostatistical methods. For example, and described by Sullivan (1991) for acoustic data, the observed temporal series of abundance estimates reflect three processes; variation due to harvesting and population growth, variation spatially and variation due to environmental conditions. The GAMs can account for the latter, and as such, the spatial structure can be removed with variographic analysis. The final result obtained from kriging will, therefore, describe net changes in abundance due to harvesting pressure and the intrinsic rate of increase in the population.

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