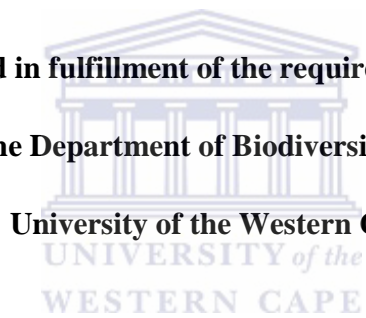


**The diet and feeding ecology of the pelagic goby, *Sufflogobius  
bibarbatus*, off Namibia**

**By**

**Riaan Brinley Cedras**

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



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## ABSTRACT

The general diet of *Sufflogobius bibarbatus* in the northern Benguela upwelling ecosystem was investigated from gut content analysis in two separate studies. The first study was conducted over two 48 h diel sampling stations onboard the *RV Dr. Fridtjof Nansen* during a dedicated cruise conducted in January 2006, whilst the second was conducted on cruises of opportunity aboard the *RV Welwitschia* during 2001 and 2002. The results of both studies indicate that *S. bibarbatus* has a fairly generalised diet, feeding on benthic and pelagic animals for the most part: phytoplankton was uncommonly reported from the 3739 fish examined. Larger fish ate primarily benthic organisms, whereas smaller individuals include substantial number of pelagic organisms in their diet. There would appear to be a clear relationship between the environment occupied by individuals and their diet: large fish are predominantly demersal and display limited vertical migration, whilst small fish are thought to be more pelagic. Results strongly indicate that this species is opportunistic. The present study sheds new light on the ecology of the species, which is becoming increasingly important in the region.

## DECLARATION

I declare that: *The diet and feeding ecology of the pelagic goby, Sufflogobius bibarbatus, off Namibia* is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

Riaan Brinley Cedras

October 2009

Signed.....



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## CHAPTER ONE: INTRODUCTION

### 1.1. Oceanography

Southern Africa is bathed by the cold, northward flowing Benguela Current in the west and by the warm, southward flowing Agulhas Current in the east and south. The Benguela upwelling region along the west coast extends from the Agulhas Bank off South Africa in the South, to southern Angola in the North (Shannon, 1985). Unlike other eastern boundary current systems, the Benguela Current system is bounded in the North and the South by warm water systems: the Angola and Agulhas currents respectively. The region is traditionally separated into northern and southern sub-regions at the Lüderitz upwelling cell (26°S). The system is dominated by wind-driven coastal upwelling that becomes perennial in the vicinity of Lüderitz (between latitudes 23-26°S) and more seasonal towards the northern (18°S) and southern limits (35°S) (Shannon, 1985). Maximum upwelling occurs from October to March in the southern Benguela and from July to November in Namibian waters (Shannon, 1985).

In the southern Benguela, the shelf-break occurs close inshore between Cape Point and Cape Columbine and upwelling is particularly strong in these areas (Figure 1). A subsurface equatorward jet develops near the shelf break (Shannon, 1985), which bifurcates at Cape Columbine, in the vicinity of the Cape Canyon. One branch of the jet follows the shelf edge northwards, whilst the other tracks the eastward curving isobaths inshore. A poleward undercurrent is found close inshore (Shannon, 1985). This undercurrent is an extension of that which develops in the northern Benguela, and it flows southwards along the continental shelf, mixing oxygen depleted shelf waters from the Walvis and Lüderitz upwelling areas (Dingle and Nelson, 1993), and flows as far south as the Cape of Good Hope (Boyer *et al.*,

2000). During summer, strong offshore winds advance the development of cyclonic curvature around Cape Columbine into St Helena Bay, allowing both prolonged water retention and animals to be trapped inshore (Shannon, 1985; Gibbons and Hutchings, 1996). Nearshore during winter little or no upwelling occurs off Cape Columbine. The main shelf edge jet may provide a mechanism for the northward transport of animals into the northern Benguela (Shannon, 1985) from regions to the SE.

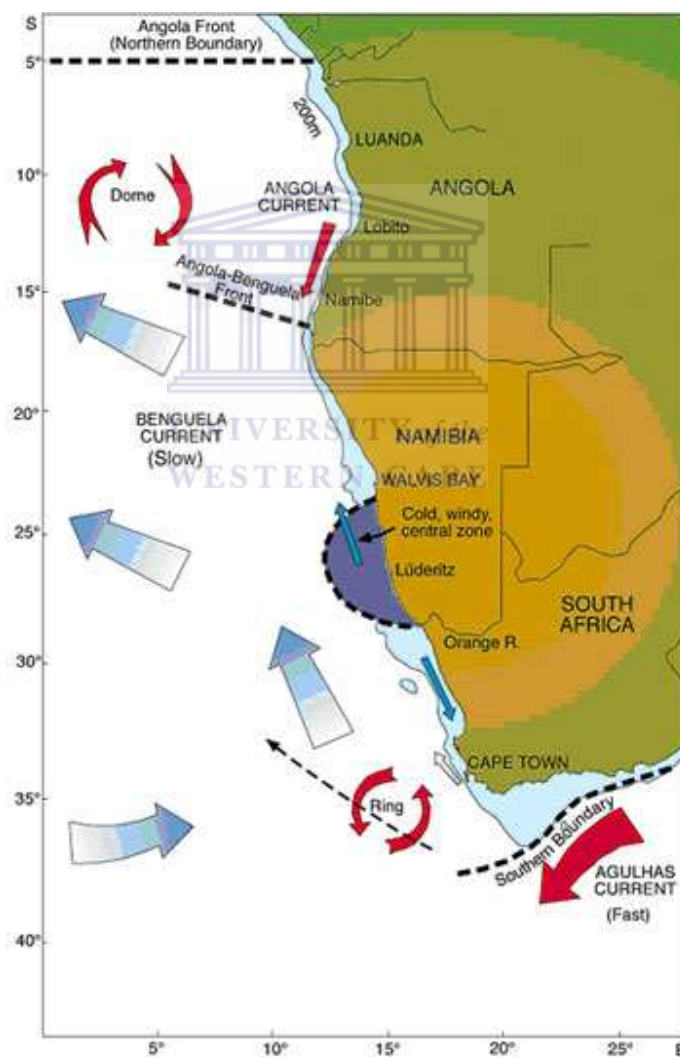
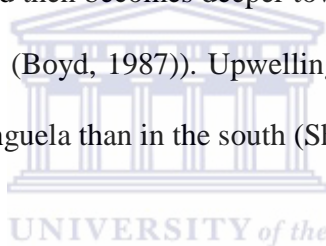


Figure 1. Map showing the major bathymetric features and surface currents of the Benguela Current with internal and external boundaries (taken from O'Toole, 2001).

The northern Benguela ecosystem is characterised by wind-induced upwelling of cold nutrient rich waters, as in the south (Nelson and Hutchings, 1983; Shannon, 1985), though the areal extent of the northern region is much larger and covers between ~150-170 000 km<sup>2</sup> (Hewitson and Cruickshank, 1993, Boyer *et al.*, 2000). The narrow (37-56 km) and steep continental shelf that extends from the Cunene River at the border between Namibia and Angola to Cape Frio (18°26'S) in the north of Namibia widens rapidly towards the south, extending 110-150 km from the coast between 19-23°S (Boyd *et al.*, 1987). From 24° to 26°30'S the width of the shelf varies from 180-239 km, being narrowest where it is shallowest (26°S) and broadest where it is the deepest (26°30'). It is particularly steep south of Lüderitz (27° to 27°30'S) and then becomes deeper towards the south at the Orange River Cone and Banks (28°S to 29°S (Boyd, 1987)). Upwelling is less temporally variable and is more stable in the northern Benguela than in the south (Shannon, 1985).



The northern region of the Namibian upwelling ecosystem (15-19°S) is bounded in the north by the warm tropical waters of the Angolan Current (Shannon, 1985). Nearshore, between 15-16°S a dynamic front known as the Angola Benguela Front develops (Shannon *et al.*, 1987) between the two current systems that shifts its position inter- and intra-annually (Boyer *et al.*, 2000, Shillington *et al.*, 2006). The considerable westward flow of the surface current in the northern Benguela (23-15°S) produces a large cyclonic gyre between the main branch of the Benguela Current and the eastward flowing South Equatorial Counter Current at the Walvis Ridge of the Angola dome (Shannon, 1985).

Central Namibia (19-24°S) (Boyd, 1987) is characterised by favourable longshore winds, with less intense upwelling that initiates at depths above 150-200 m over the wide

Swakop shelf (Boyer *et al.*, 2000). Moderate and shallow thermoclines, as well as onshore and longshore flow of warmer waters are common oceanographic features within this region during summer and early autumn (Boyd, 1987, Boyer *et al.*, 2000). However, during periods of relaxed upwelling, Angolan water from the north and oceanic waters from the west and northwest may seasonally intrude into the region (Boyer *et al.*, 2000). The region north of Lüderitz is characterised by a double-celled cross-shelf circulation, where secondary upwelling occurs at the shelf break (Barange and Pillar, 1992).

The southern region of the northern Benguela system (24-29°S) is dominated by the strong, Lüderitz upwelling cell that persists throughout the year. This is considered to be southern Africa's (indeed the world's) most intense upwelling cell (Shannon, 1985; Lutjeharms and Meeuwis, 1987), with others off Cape Frio, Palgrave Point and Conception Bay (Shannon, 1985). The Lüderitz upwelling cell is thought to function as an environmental barrier between the northern and southern Benguela communities (Agenbag and Shannon, 1988; Barange and Stuart, 1991; Barange *et al.*, 1992; Pillar *et al.*, 1992; but see Lett *et al.*, 2007). The perennial nature of the Lüderitz upwelling cell is determined by the wind stress that persists there throughout the year, the narrow width of the continental shelf and the surrounding orography (Shannon, 1985). This is dictated by the South Atlantic high-pressure system over the continent and by the east-moving cyclones in the south (Shannon, 1985). The Lüderitz upwelling cell stretches generally 380 km offshore, decreasing in extent towards the north and south (Lutjeharms and Meeuwis, 1987): it is strongest during autumn, though it can extend its longshore range into the Walvis region during winter and spring (Lutjeharms and Meeuwis, 1987).

## 1.2. Plankton

Like other eastern boundary current systems, the Benguela is characterised by high primary productivity and it supports a low species diversity (Gibbons and Hutchings, 1996). The inshore areas are generally dominated by diatoms, but this may change in the offshore direction, during periods of onshore water flow or during periods of calm following upwelling, when dinoflagellates and other smaller taxa may dominate in the stratified waters that develop (Armstrong *et al.*, 1987; Moloney *et al.*, 1991; Pitcher *et al.*, 1992).

Brown *et al.*, (1991) described phytoplankton and bacterial abundance and production in the Benguela ecosystem using a carbon flow model. They reported that phytoplankton carbon biomass from chlorophyll *a* in the northern Benguela (~2 558 300 tons) was far higher than in the southern Benguela, which was estimated at 1 187 820 tons (671 420 tons and 516 400 tons for the west and south coast respectively). These differences have been attributed to lower loss rates of phytoplankton in the North, either through reduced offshore transport and turbulence or a reduction in biological grazing (Brown *et al.*, 1991). Interestingly, however, overall annual production estimates were thought to be similar for the southern and northern Benguela. This reflects the fact that the mean P:B ratio for the northern Benguela was lower than that for the southern Benguela, which is thought to reflect density-dependent limitations on primary production, such as shelf shading within phytoplankton communities (Brown *et al.*, 1991). In the northern Benguela zooplankton display little seasonality in biomass and highest biomass occurs slightly offshore than that of the phytoplankton: further south, zooplankton biomass is highest during summer and lowest during winter (Hutchings *et al.*, 1991). The mesozooplankton community in the Benguela ecosystem is mainly

dominated by copepods and the macrozooplankton community mainly by euphausiids (Hutchings *et al.*, 1991).

Copepods dominate the zooplankton of the Benguela ecosystem both numerically and in terms of biomass (Verheye *et al.*, 1992). As the majority of the species are herbivorous or at least omnivorous, copepods provide an important link between the primary producers and higher trophic levels (Verheye *et al.*, 1992). Copepods are the preferred prey of a wide variety of invertebrate and vertebrate predators including commercially exploited pelagic fish (James, 1987; van der Lingen, 2002; Louw *et al.*, 1998). The dominant herbivorous copepods in the northern Benguela ecosystem are *Calanoides carinatus* and *Rhincalanus nasutus* (Verheye *et al.*, 1992; Timonin, 1992). The adaptation of copepod developmental stages together with ontogenetic vertical migration in the Benguela upwelling system, allow them to maintain high population densities and exploit the longshore current regimes and cross-shelf advective processes (Verheye *et al.*, 1991; Verheye *et al.*, 1992)

In the Benguela ecosystem, three euphausiid species dominate the fauna; *Euphausia lucens* in the shelf region of the southern Benguela, *Nyctiphanes capensis* in the southeast (20°E, Pillar *et al.*, 1992) and in the northern coastal areas (26°S), the latter along with *Euphausia hanseni* in the outer shelf region there (Barange and Stuart, 1991; Barange and Pillar, 1992). The dominance of *E. lucens* in the southern Benguela suggests that this species has adaptations to the complex physical-chemical conditions existing there (Barange *et al.*, 1992). The distribution of *N. capensis*, more common in the northern Benguela but less so in the southern Benguela, perhaps reflects the fact that environmental conditions are more stable and productive in the north (Barange *et al.* 1992; Pillar *et al.*, 1992), and in the



southeast. *N. capensis* occurs close inshore in the northern Benguela, the upwelling front significantly affects the distribution and maintenance of the species in this region. Near the shelf-break of the Benguela, reduced concentrations of *E. lucens* and *N. capensis* occur, where they are replaced by a different community of euphausiids (Barange and Stuart 1991; Pillar *et al.*, 1992). *E. hanseni* is the dominant and most abundant euphausiid species over the Namibian shelf-break (29°S, Barange and Stuart, 1991).

The biomass of euphausiids in the northern Benguela is estimated to be about double that of the southern Benguela and is consistent with geographical differences in phytoplankton abundance (Pillar *et al.*, 1992), as suggested in Brown *et al.* (1991). Euphausiids seem to take advantage of the double-cell circulation present off central Namibia (Barange and Pillar, 1992), which may reduce advective losses and retain plankton patches (Barange and Stuart, 1991; Brown *et al.*, 1991). Grazing by euphausiids in the Benguela system plays a minor role in phytoplankton and mesozooplankton loss and therefore only a small proportion of the primary production is likely to be transferred to euphausiids through mesozooplankton (Pillar *et al.*, 1992). However, indications are that euphausiids compete directly with zooplanktivorous fish in particular pelagic fish recruits, which occupy similar habitats to those euphausiids occurring in the nearshore zone of the West Coast (Pillar *et al.*, 1992).

Despite their low species diversity, “common” carnivorous zooplankton species attain high densities, and frequently exceed those of herbivores zooplankton (Gibbons *et al.*, 1992). Their greater abundance in the northern than southern region of the Benguela ecosystem most likely reflects differences in the relative stability and productivity of the two systems (Gibbons *et al.*, 1992).

### 1.3. Fish and fishing

The northern Benguela ecosystem supports several important and industrial scale fisheries: Cape hakes (*Merluccius paradoxus* and *M. capensis*) are mainly targeted by bottom trawling and long-line operations, horse mackerel (*Trachurus trachurus capensis*) are fished particularly by mid-water trawls and epipelagic shoaling fishes, mainly sardines (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*) are largely caught using purse-seine nets.

Commercial fisheries started around the mid 1940s in the Benguela system, and large trawler fleets targeted three main pelagic species primarily sardines, horse mackerel and in the late 1960s anchovies (van der Lingen *et al.*, 2006b). The area of greatest fishing activity in the 1960s was located near Walvis Bay (Bakun and Weeks, 2006). At this time, sardines were abundant off Namibia and they served as an important diet item for many other commercially valuable pelagic and demersal fish species, as well as diverse mammals and seabirds (Moorsom, 1984; Cury and Shannon, 2004).

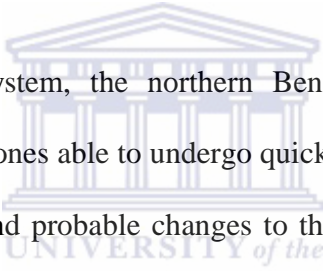
However, in the early 1970's fishing pressure increased, which in combination with a series of recruitment failures led to a reduction in the size of the pelagic fish stocks (especially those of sardine) to a portion of their former size (Butterworth (1980) as cited in Hewitson and Cruickshank (1993)). The sardine biomass during the 1960s was believed to be around 10 million tons, with peak sardine catches (~1.5 million tonnes) during boom years, with annual landings later on stabilizing at between 50-60 thousand tons (Hewitson and Cruickshank, 1993; Bakun and Weeks, 2006; van der Lingen *et al.*, 2006b). The sardine fishery was considered to have been overexploited and has shown no clear signs of recovery (Fairweather *et al.*, 2006).

Bakun and Weeks (2006) have postulated that during years of high sardine biomass, in the area of the upwelling cells (e.g. at Lüderitz), these fish would have efficiently consumed phytoplankton before it was taken offshore to the convergent frontal zones. They further suggested that intense grazing by sardines could then cause the collapse of primary production in zones near an intense upwelling core resulting in the escape of local upwelled nutrients. These nutrients could then be transported out of the highly divergent zone to further nourish trophic chains in a broader ecosystem. Otherwise, they suggested this production would be accessible to aggregations of weakly swimming herbivorous zooplankton (e.g. copepods, Bakun and Weeks, 2006).

Subsequent to the sardine collapse in the 1970s (reduced sardine grazing pressure), available phytoplankton near the core of the Lüderitz upwelling cell has been allowed to grow exponentially, which has resulted in a substantial settling of cells onto the sea floor followed by their subsequent decomposition (Bakun and Weeks, 2006). Furthermore, this has in turn allowed an increased inflow of phytoplankton to the convergence zones downstream of the Lüderitz upwelling cell which in time accelerated zooplankton growth and possibly allowed breakouts of zooplankton to occur at the downstream fronts, subsequently fuelling the production and growth rates of zooplanktivores such as medusae, allowing them to replace in the absence of a suitable fin fish replacement, the previously dominant sardines (Bakun and Weeks, 2006).

The build-up of unoxidised organic matter on the continental shelf creates areas characterised by continuous hypoxia and anoxia (Weeks *at al.*, 2004). Natural hypoxia is

linked to either the local decay of organic matter or to more widespread reductions in oxygen supply to water (Monteiro *et al.*, 2006). Hydrogen sulphide, which is particularly toxic to marine organisms (Bakun and Weeks, 2006) may be released from the sea floor into the water column via both periodic eruption of methane gas pockets and small spatially extended bubble fluxes (van der Plas *et al.*, 2007). It has been suggested that hydrogen sulphide eruptions in the northern Benguela might have contributed to the recruitment failure of Namibian hake in 1992-1994 (Woodhead *et al.*, 1997). Furthermore, these sporadic natural anoxic events may have contributed to the mass mortalities of rock lobsters in South Africa (Cockcroft *et al.*, 2000).



As a rapidly changing ecosystem, the northern Benguela may support unspecialised generalist species, particularly ones able to undergo quick population responses, as observed with recent jellyfish blooms and probable changes to the structure and functioning of that ecosystem (Bakun and Weeks, 2006; Lynam *et al.*, 2006; Richardson *et al.*, 2009). The overexploitation of marine fisheries may unwittingly have led to the increasingly abundant jellyfish *Chrysaora hysoscella* and *Aequorea forskalea* in the northern Benguela, causing serious problems to fishery-management at present (Lynam *et al.*, 2006).

With a decline in sardine stocks, other plankton-eating fish have become more common. These include anchovy, horse mackerel and the bearded, or pelagic, goby *Sufflogobius bibarbatatus* (Cury and Shannon, 2004). These changes in the fish community have been reflected by changes in the diets of several predators such as African penguins (*Spheniscus demersus*), cape cormorants (*Phalacrocorax capensis*), bank cormorants (*Phalacrocorax neglectus*), horse mackerel and fur seals (*Arctocephalus pusillus*). Historically, the diets of

these predators were dominated primarily by sardines, however subsequent to the sardine collapse their diets have shifted to other resources, including the bearded goby (Crawford *et al.*, 1985; Cury and Shannon, 2004).

#### **1.4. *Sufflogobius bibarbatus***

The bearded goby was first described from South African waters in 1923 by von Bonde, as *Gobius bibarbatus*, but was later re-described as a member of a new genus *Sufflogobius* by Smith in 1956. This re-description was based on the existence of two skin flaps beneath the lower jaw and by its ability to inflate its body cavity. The family Gobiidae is considered to be the largest family of marine fishes in the world and contains more than 2000 species (Froese and Pauly, 2005). Gobies can be found in freshwater, brackish and marine environments, and although most occur in very shallow water and intertidal waters, some can occur in waters greater than 1000 m (Simonović *et al.*, 2001; Kostrzewa and Grabowski, 2003; Grabowska and Grabowski, 2005; Kovačić, 2007). Although some gobies can play an important part in local communities, few have a system-wide role. Amongst the more ecologically important species are *Gobiusculus flavescens* along the Norwegian coast, and *Pomatoschistus minutus* and *P. pictus* alongside the Norwegian (and Spanish) coast, which serve as important prey items for cod *Gadus morhua* (Salvanes *et al.*, 1992).

Little information is available on the current biomass of *S. bibarbatus* off Namibia, although two published biomass estimates exist. The first of these estimated a biomass of 600 000 tons, and was based on Bongo net hauls collected during SWAPEL (South West African Pelagic Egg and Larval) surveys in 1978-79 (Hewitson and Cruickshank, 1993). The other estimated a biomass of 1.45 million tons, and was based on an ECOPATH model for the

northern Benguela in the 1980's (Shannon and Jarre-Teichmann, 1999). More recent estimates from swept area bottom trawl surveys (1990-2005) collected by the *RV Dr Fridtjof Nansen*, have shown that the biomass of pelagic gobies could range between 10 000 - 100 000 tons, which suggests that the species is less abundant than previously thought (Staby and Krakstad, 2006).

The distributional range of *S. bibarbatus* extends from south of Tiger Bay in southern Angola, along the Namibian shelf, to the SE coast of South Africa, with its largest concentrations in central Namibia (Staby and Krakstad, 2006). *S. bibarbatus* appears to be most abundant and most broadly distributed between Hollams Bird Island (24°38'S) and Mõwe Point (19°23'S) up to 85 km offshore and to depths of approximately 350 m (Staby and Krakstad, 2006). Its distribution off central Namibia corresponds with that of the diatomaceous mud belt in the region, which is characterised by periodic sulphur eruptions and anoxic waters (Staby and Krakstad, 2006).

Adult gobies are considered to be more demersal and are generally found further offshore than juveniles and sub-adults (O'Toole, 1978). Juveniles and sub-adults are found in the meso-pelagic zone and commonly inhabit the inshore region off Namibia (D'Arcangues, 1977; O'Toole, 1978). Since juveniles generally occur inshore of the 200 m isobath, O'Toole (1978) suggested that spawning by the pelagic goby occurs mainly inshore between spring and early summer.

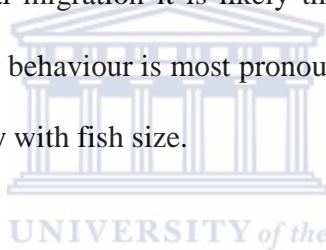
The maximum size recorded for the pelagic goby is 13 cm in total length with an estimated longevity of 6 years (Melo and Le Clus, 2005). Melo and Le Clus (2005) have

suggested that *S. bibarbatus* is a late maturing (2 – 3 years of age), long lived nektonic gobioid with a long reproductive life: males mature later and at a larger size than females (Melo and Le Clus, 2005). The pre-reproductive mortality of juveniles, suggests that *S. bibarbatus* is not well suited for sustained targeting by commercial fisheries in Namibian waters (Melo and Le Clus, 2005).

The bearded goby has long been recognised as an important component of the sound scattering layers in neritic waters off Namibia (D’Arcangues, 1977). From hydroacoustic observations, D’Arcangues (1977) recorded the migratory behaviour of *S. bibarbatus*: adults (50-83 mm) remain deeper in the water column than most juveniles (D’Arcangues, 1977). Juveniles show a clear migratory pattern, moving towards the surface at sunset, forming a dense layer at between 13-15 m in the middle of the night, and then migrating downwards again at sunrise (D’Arcangues, 1977). Catch data of *S. bibarbatus* support the general observations that gobies stay in the pelagic zone during the night and near the sea floor during the day (Staby and Krakstad, 2006). Videotape observations taken from the research submersible *Jago* operating over the mid-shelf benthic environment off the Orange River mouth in 1996 and 1997 showed that gobies live over soft bottom sediments, and form an important component of the demersal nekton communities there (Gibbons *et al.*, 2000). *S. bibarbatus* is a common member of the fish community off Namibia and coincides with other common shelf species such as *Austroglossus microlepis* (west coast sole), *Chlorophthalmus atlanticus* (Atlantic greeneye), *Lepidopus caudatus* (silver scabbardfish, also known as the beltfish), *Merluccius capensis* (shallow-water Cape hake) and *Pterothrissus belloci* (longfin bonefish) (Macpherson and Gordo, 1992). Further South, it is associated with shallow water communities off the west coast of South Africa, including

*Austroglossus microlepis*, *Pasiphaea semispinosa*, *Pterygosquilla armata capensis* and *Lolliguncula mercatoris* (Roel, 1987).

Despite its likely importance in the northern Benguela ecosystem, our understanding of the species' biology and the role it might play in terms of energy flow in the Namibian ecosystem is limited. The literature has conflicting information about the diet of this species: early accounts suggest that it feeds primarily on phytoplankton (Barber and Haedrich, 1969; O' Toole, 1978; Crawford *et al.*, 1985), whilst others suggest that it feeds mostly on zooplankton (D'Arcangues, 1977; Macpherson and Roel, 1987). Given that the species shows pronounced diel vertical migration it is likely that the diet changes throughout the day. Furthermore, as migratory behaviour is most pronounced in small fishes (D'Arcangues, 1977); diet is also likely to vary with fish size.



The objective of the study is to look at the general diet of *S. bibarbatus* in the northern Benguela upwelling ecosystem with an emphasis on size related and diel changes in feeding.



## CHAPTER TWO: MATERIALS AND METHODS

This study is divided into two major investigations. The first (Study 1) comprises a study conducted over two 48 h diel stations off central Namibia during January 2006 aboard the *RV Dr. Fridtjof Nansen*: a goby-dedicated survey. The second (Study 2) is a more general study on the feeding ecology of *S. bibarbatus* off the Namibian coast and was conducted on cruises of opportunity using the *RV Welwitschia* during 2001 and 2002. The materials and methods (and results) for Study 1 and Study 2 are presented separately.

### 2.1.1. Study 1: Survey area

A survey was conducted using the *RV Dr. Fridtjof Nansen*, during January 2006. It consisted of two diel stations (Figure 2), the first of which was conducted at a depth of 120 m close inshore (23°21'S 14°12'E, 16-18 January 2006), whilst the second was further offshore, at a depth of 180 m (23°32'S 13°44'E, 18-20 January 2006). A 48 h intense sampling regime was initiated at each station in order to identify the acoustic layers in the water column and to collect relevant environmental and biological data concerning gobies, including their predators and prey (Table 1). The first seven stations (1654 – 1666) listed in Table 1 are stations where gobies were collected for length frequencies, male to female ratios, and length-weight distributions, however, these gobies were excluded from the diel cycle diet analysis. Sound-scattering layers of fish shoals were continuously monitored by two Simrad EK 500 echo sounders (with operating frequencies of 18 kHz, 38 kHz, 120 kHz (split beam) and 200 kHz (single beam) during the survey.

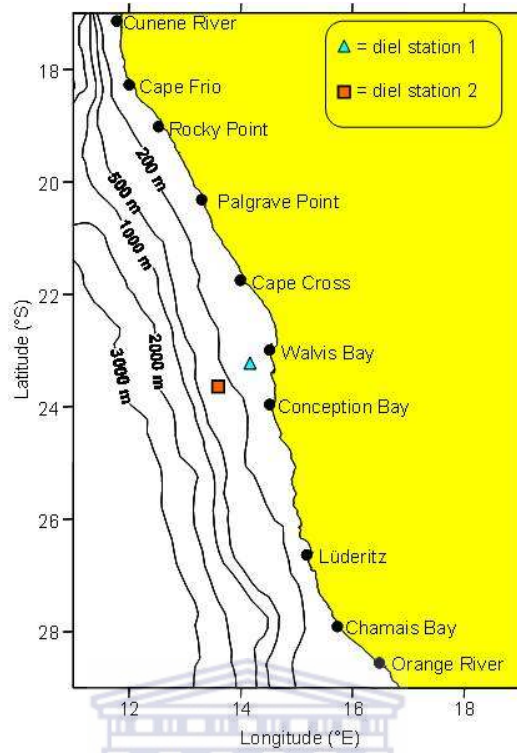


Figure 2. Map of the study area off Namibia during 16-20 January 2006, showing the positions of the two diel stations occupied.

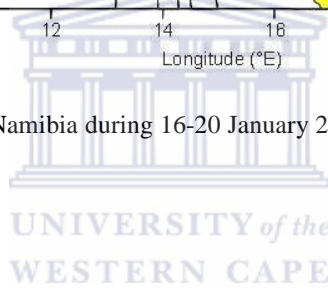


Table 1. Summary of the sampling stations occupied for 48 h during January 2006, showing details of the fish catches made: D, day; N, night.

Station	Region	Date	Time of day	Time	Diel station	Tow Duration (min)	Latitude (°S)	Longitude (°E)	Bottom depth	Fishing depth
1654		2006/01/12	D	12:02		2	23.23	14.14	117	117
1655		2006/01/12	D	14:07		10	23.28	14.24	47	47
1656		2006/01/12	D	16:21		18	23.37	14.16	110	110
1659		2006/01/12	N	23:23		30	23.53	14.02	195	195
1663		2006/01/14	N	4:48		21	24.51	13.52	228	228
1665		2006/01/14	D	12:13		30	23.54	14.04	183	183
1666		2006/01/14	D	15:20		21	23.38	14.07	150	150
1668	Inshore	2006/01/16	D	12:28	1	7	23.21	14.11	123	123
1669	Inshore	2006/01/16	D	13:19	1	8	23.20	14.11	122	122
1671	Inshore	2006/01/16	D	17:59	1	15	23.24	14.14	116	98
1672	Inshore	2006/01/16	D	18:30	1	15	23.25	14.15	113	98
1676	Inshore	2006/01/16	N	23:01	1	15	23.22	14.11	123	100
1679	Inshore	2006/01/17	N	3:50	1	15	23.21	14.11	124	95
1680	Inshore	2006/01/17	N	4:14	1	15	23.22	14.11	125	95
1688	Inshore	2006/01/17	D	17:36	1	15	23.23	14.13	121	95
1689	Inshore	2006/01/17	D	17:56	1	15	23.22	14.12	121	95
1693	Inshore	2006/01/17	N	22:05	1	15	23.21	14.09	129	100
1694	Inshore	2006/01/18	N	1:54	1	5	23.20	14.08	128	128
1695	Inshore	2006/01/18	N	3:50	1	15	23.20	14.09	126	105
1696	Inshore	2006/01/18	N	4:10	1	15	23.20	14.1	124	102
1700	Offshore	2006/01/18	N	20:13	2	29	23.32	13.45	179	156
1701	Offshore	2006/01/19	N	0:10	2	15	23.32	13.45	178	150
1704	Offshore	2006/01/19	N	2:18	2	11	23.33	13.45	181	160
1705	Offshore	2006/01/19	N	3:50	2	15	23.33	13.45	180	165
1706	Offshore	2006/01/19	N	4:10	2	15	23.32	13.45	177	160
1717	Offshore	2006/01/19	D	15:28	2	30	23.34	13.45	182	182
1718	Offshore	2006/01/19	D	17:37	2	16	23.33	13.46	180	154
1721	Offshore	2006/01/19	D	19:48	2	30	23.35	13.46	180	180
1725	Offshore	2006/01/20	N	1:15	2	30	23.34	13.45	180	180
1729	Offshore	2006/01/20	N	5:40	2	29	23.34	13.44	183	183

### 2.1.2. Fish sampling methods

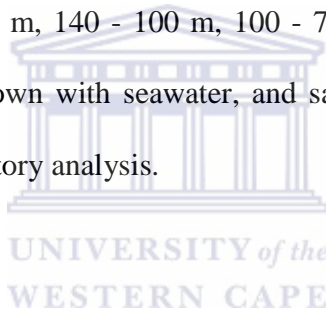
Two trawls were used to collect gobies throughout the water column for this and other studies, and to validate acoustic recordings. A standard Gisund Super Bottom trawl (BT) was used to sample demersal fish and this had a wing distance of 18 m and a vertical net opening of 4.5-6 m: it was fitted with a 20 mm mesh and the cod-end was lined with a mesh of 10 mm. The BT was typically towed for 15-30 minutes at  $6 \text{ m}\cdot\text{s}^{-1}$  and was slowly hauled at  $59 \text{ m}\cdot\text{min}^{-1}$  to the surface. An Åkrahamn pelagic trawl (PT) was used to sample the water column, this had a vertical net opening of 18 m with a wing-to-wing distance of 35 m. The pelagic trawl was connected to a multisampler with three cod-ends, which could be opened and closed at selected depths, in order to collect three discrete samples. The PT was towed at  $6 \text{ m}\cdot\text{s}^{-1}$ , and each of the multinetts was typically open for 10-15 minutes.

On retrieval of the nets, the entire catch was placed into a series of fish buckets and weighed using standard techniques (del Norte-Campos and Temming, 1994). A sample of the catch was sorted to species from a random number of buckets, and all species were weighed (to the nearest 100 g) in order to obtain an estimate of the contribution by each to the total catch. A maximum of 100 randomly selected specimens of each species were then measured (to the nearest mm: total length (TL)) in order to get size-frequency data, and the gobies were then frozen for subsequent gut contents analysis in the laboratory.

A total of 13 trawl stations (10 PT and 3 BT) were conducted during the first diel station and 10 trawl stations (6 PT and 4 BT) during the second.

### **2.1.3. Zooplankton sampling**

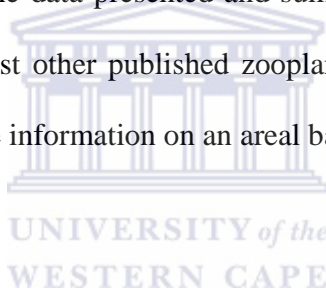
Zooplankton samples were collected at irregular time intervals during the survey using a MultiNet MiDi plankton sampler (Hydro-Bios Apparatebau GmbH). The zooplankton sampler had five nets with an opening of 0.5 x 0.5 m, fitted with 200  $\mu\text{m}$  mesh. A Scanmar depth recorder was mounted on the frame of the net, and depth information was transferred acoustically to the vessel. The net was towed obliquely at a speed of 2 - 2.5 knots at five depth strata, from just above the bottom to the surface, and was retrieved at a speed of 0.5 - 1.0  $\text{m}\cdot\text{s}^{-1}$ . At the first diel station, the depth strata sampled were approximately 120 - 100 m, 100 - 70 m, 70 - 40 m, 40 - 20 m and 20 - 0 m, whilst at the deeper offshore station they were approximately 180 - 140 m, 140 - 100 m, 100 - 70 m, 70 - 30 m and 30 - 0 m. On retrieval, nets were washed down with seawater, and samples were fixed in 5% seawater formalin for subsequent laboratory analysis.



### **2.1.4. Zooplankton analysis**

Zooplankton samples were first decanted into a graduated measuring cylinder and the volume was topped up to 100 ml. Zooplankton were then retained in suspension by bubbling air through the measuring cylinder and three 2 ml sub-samples were taken using a wide-bore Stempel pipette (Gibbons, 1999). Copepods and other numerous small meso-zooplankton (e.g. cladocerans, larvaceans etc.) were counted from sub-samples in a Bogorov tray, under a dissecting stereomicroscope at varying magnifications between 10-40 x. Mean abundances per sub-sample were calculated and an estimate of total abundance per sample was determined from a knowledge of sample and sub-sample volumes.

The remainder of each sample was poured into a Folsom Plankton Splitter, split into two equal halves by rotating the splitter and poured into labelled containers (Gibbons, 1999). The procedure was repeated until suitable (less dense sample) sub-sample sizes had been obtained (Gibbons, 1999). A minimum of 50 individuals of each macro-zooplankton taxon were counted under a dissecting stereomicroscope at magnifications ranging between 10-40 x, following standard protocols (Gibbons, 1999). Because the flow-meter was not operational at the time of the study, zooplankton data were standardised to densities using information on the vertical extent of a sampled layer. This assumes that towing speed, winch speed and tow angle were maintained at a constant throughout the survey, and that nets did not clog. As a consequence, the data presented and summarised here are relative data and should not be compared against other published zooplankton data. Data from all sampled layers were summed to provide information on an areal basis.



#### **2.1.5. Hydrographic data**

Vertical profiles of temperature, salinity and oxygen were obtained at irregular time intervals during the diel stations using a Sea-Bird (Electronics Incorporation) model 911 plus CTD, fitted with a rosette of 8 L Niskin bottles. Real time logging was carried out using the PC based Seabird Seasave software. CTD casts were stopped a few meters above the bottom, to a maximum of 200 m depth.

### **2.2.1. Study 2: Survey area**

A colleague participated in some of these surveys conducted on the research vessel *RV Welwitschia* in 2001 and 2002 and these data form the focus of this study. The Namibian Ministry of Fisheries and Marine Resources undertake routine survey cruises along the Namibian coast each year. Specimens of *S. bibarbatus* were collected as by-catch on hake surveys off the Namibian coast, (20°-28° S and 13°-15°E) in early 2001 at depths ranging between 130 and 265 m. The second survey was conducted during a pilchard survey in Namibian waters (23°08'S 14°23'E) in early 2002 at a maximum depth of 20 m.

### **2.2.2. Fish sampling methods**

Two trawls were used to catch gobies from shallow and deep waters. A Hampidjan Gloria 448 m<sup>2</sup> mid-water trawl was used to sample pelagic fish. This had a vertical opening of 15-16 m and was fitted with an anchovy net mesh, with a cod-end lined with a mesh of 11 mm. The door-spread of the trawl was approximately 50 m, and trawls during this survey used near-surface buoys to effectively lift the head rope. The trawl had 100 m of warp and was generally towed for 15 – 30 minutes at speeds of around 5 knots.

A One CARMEN 103.2 m bottom trawl was used to sample demersal fish. The vertical opening of the trawl was approximately 7 m, with a headline of 32.8 m. The trawl had Poly-Ice El Casador 4.2 m<sup>2</sup> combination doors that weighed about 1 000 kg. The cod-end was lined with 12 mm mesh and nets were towed for 15-30 minutes at around 5 knots.

From each haul, catches were taken onboard, placed into buckets, sorted and total catch per species was subsequently recorded and weighed to the nearest 0.1 kg in order to

obtain an estimate of the contribution by each to the total catch. Gobies were subsequently collected from each haul and total length (TL) of each goby was measured to the nearest mm and frozen on board for further diet analysis. A total of 10 bottom trawl stations and 1 pelagic trawl station were conducted during Study 2.

### **2.3.1. Laboratory analysis**

On return to the laboratory, pelagic gobies from both sets of surveys were first defrosted and then individually blotted dry using tissue paper prior to measurements of total (TL) and precaudal length (PCL), both to the nearest mm. Fish were sexed and weighed to the nearest 0.001 g. The sex of *S. bibarbatus* was assessed externally by their urogenital papilla: females have a much shorter, broader and blunt urogenital papilla, whereas males have a conical, elongated, pointed and flexible urogenital papilla (Melo and Le Clus, 2005).

The alimentary canal was dissected out from the oesophagus to the rectum, because gobies do not have a well-defined stomach (del Norte-Campos and Temming, 1994). The alimentary canal was removed and weighed to the nearest 0.001 g. The gut was then split open using a scalpel in a petri-dish containing water under a dissecting stereomicroscope, and the contents were flushed out. The stomach contents were then fixed in 5% formalin stained with rose Bengal and preserved for further analysis. The empty gut was then blotted dry and re-weighed to the nearest 0.001 g in order to determine contents' weight.

The stomach contents were identified and counted to major taxonomic group using a dissecting stereomicroscope at various magnifications ranging from 10-40 x. When prey items were badly fragmented or partly digested the numbers of specimens was estimated



from the number of individual-specific body parts. For example, if there were three euphausiid eyes, then two euphausiids were scored as present. If one polychaete head was observed, a single polychaete was scored as present. In the event that no readily identifiable number of individuals could be determined from fragments, one individual of that taxon was scored as present. This technique has the potential to underestimate the number of prey items actually eaten but is relatively unambiguous in practice.

When individual prey items were intact, a suite of body measures were recorded from each. These are listed in Table 2 (illustrated, where appropriate, in Figure 3), and were used to calculate the volume of individual prey items, moreover volumes were only estimated for the dominant prey groups and not the remaining prey groups. A knowledge of body mass is normally required in order to calculate index of relative importance (IRI) for each prey type (see below). As it was not possible to determine individual prey mass, a proxy for same had to be sought, and prey volume was considered to represent a useful measure in these circumstances. It is assumed that the volume of each prey type is directly comparable. For our purposes here polychaetes, copepods and euphausiids are considered to be cylinders, whilst hyperiid amphipods are considered to be semi-spheres. Amphipod volume was estimated directly from whole specimens and mean measures were taken from the head to the urosoma of amphipods, following illustrations of Vinogradov *et al.* (1996). Euphausiid volume was determined from a knowledge of the relationship between eye diameter and volume using information for all species of *Euphausia* and *Nyctiphanes* (the dominant species in the northern Benguela ecosystem (Pillar *et al.*, 1992)) from Baker *et al.*, (1990); copepod volume was determined from prosome length using the equations of Mauchline (1998). Polychaete volume was estimated directly from whole specimens (i.e. individuals

with both head and tail: diameter was determined as the mean of posterior and anterior measures).

The equations used to determine specimen volume are shown in Table 2. When prey items could not be measured owing to their fragmented nature, volumes was determined from the relationship between fish length and the average volume per prey type (constructed using known data).



Table 2. Equations used to convert body (or body part) size to volume for dominant prey of gobies (upper panel), and equations used to estimate prey volume from fish size in cases where prey measurements were not possible (lower panel).

X-axis	Y-intercept	m	c	N	r <sup>2</sup>	r	P-value
Euphausiid eye width (mm)	log euphausiid volume (mm <sup>3</sup> )	1.3992	0.1995	28	0.8812	0.9387	0.05
Log Copepod prosome length (µm)	copepod volume (mm <sup>3</sup> )	3.164	-10.69	38	0.94478	0.9720	0.05
Polychaete Anterior width (mm)	polychaete posterior width (mm)	0.2983	26.563	20	0.7252	0.8516	
Polychaete length (µm)	polychaete width (mm)	0.0381	252.08	28	0.1891	0.4349	0.05
Polychaete length (µm)	polychaete volume (mm <sup>3</sup> )	0.0006	-2.1057	28	0.6329	0.7956	0.05
Amphipod length (µm)	amphipod Volume (mm <sup>3</sup> )	0.1212	-226.26	5	0.9961	0.9980	0.05
Fish size (mm)	copepod prosome length (µm)	19.808	-35.123	5	0.7878	0.8876	0.05
Fish size (mm)	copepod volume (mm <sup>3</sup> )	0.0078	-0.3306	5	0.6922	0.8320	0.1
Fish Size (mm)	euphausiid eye width (µm)	3.4963	717.28	5	0.4433	0.6658	not significant
Fish Size (mm)	euphausiid volume (mm <sup>3</sup> )	0.3512	11.826	5	0.4588	0.6773	not significant
Fish Size (mm)	log polychaete length (mm)	0.034	-1.3251	3	0.9846	0.9923	0.1
Fish Size (mm)	polychaete volume (mm <sup>3</sup> )	1.5982	-92.324	3	0.7121	0.8439	not significant
Fish Size (mm)	amphipod length (µm)	54.5	-49.55	5	0.6381	0.7988	not significant
Fish Size (mm)	amphipod volume (mm <sup>3</sup> )	6.4924	-225.65	5	0.6137	0.7834	not significant

Key: x, x-axis; y, y-axis; m, slope; c, y-intercept; r<sup>2</sup>, correlation coefficient ;r, linear regression.

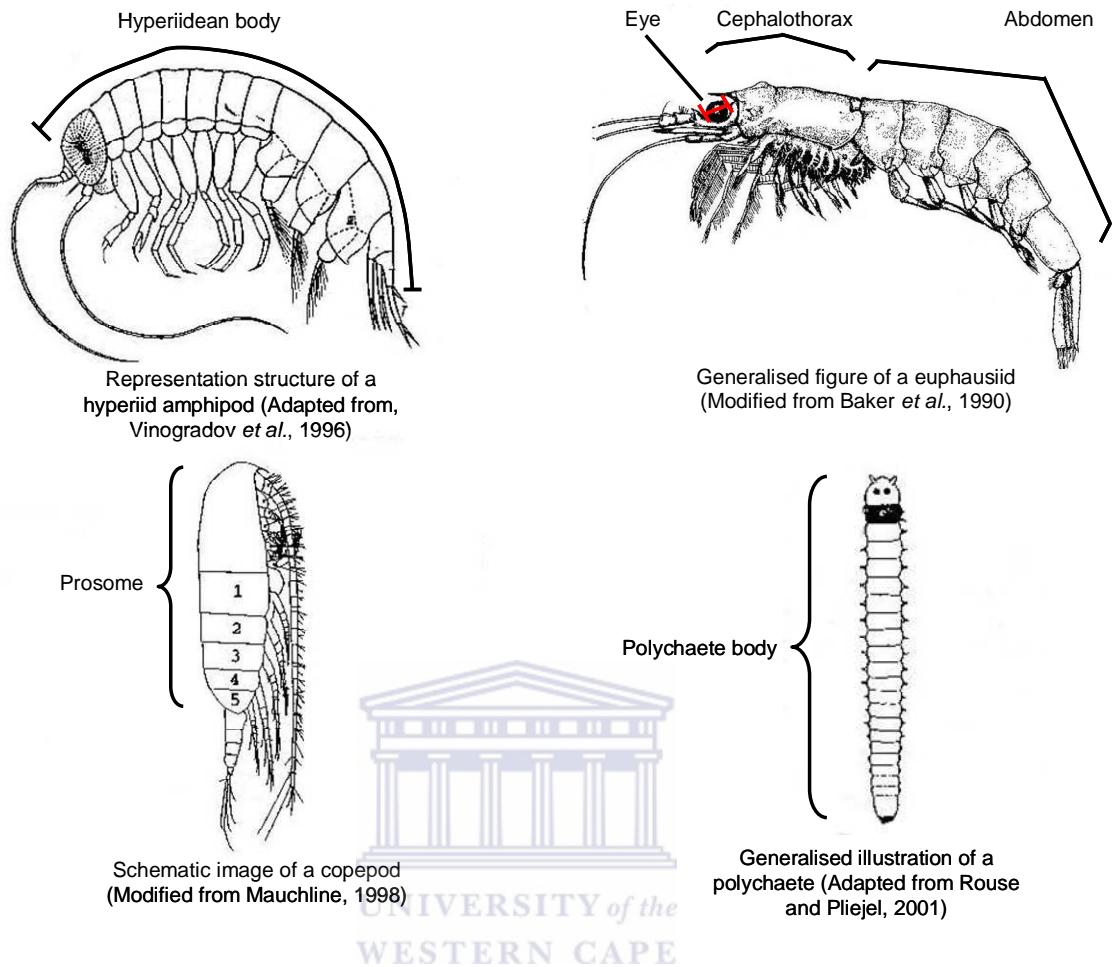


Figure 3. The body measures taken from dominant prey items ( $\mu\text{m}$ ) found in the gut of *S. bibarbatus* collected in Namibian waters during the period 12-20 January 2006.

A number of different methods have been used to summarize the diet of *S. bibarbatus* and to examine how diet changes with fish size. These generally follow the standard procedures outlined by Hyslop (1980).

Frequency of Occurrence (%F): defined as percentage of fish containing a given prey category. This was calculated as number of stomachs in which each prey item had occurred and expressed as a percentage of the total number of stomachs examined.

$$\%F = 100 \frac{n_i}{n} \quad \text{equation 1}$$

where  $\%F$  = percentage frequency of occurrence of food item  $i$  in the sample;  $n_i$  = number of stomachs in which the food item  $i$  was found;  $n$  = total number of stomachs containing food in the sample.

Numerical abundance (%N): defined as the numerical abundance of individuals of a given prey category. This was calculated as the number of individuals of each prey category expressed as a percentage of the total number in all food categories.

$$\%N = 100 \frac{N_{ALL}}{n} \quad \text{equation 2}$$

where  $\%N$  = the number of food item  $i$  in the sample;  $N_{ALL}$  = the total number of food item  $i$  in all stomachs in sample;  $n$  = total number of stomachs in sample containing food.

Food Containing Ratio (%FCR): defined as the percentage of fish containing food.



$$\%FCR = 100 \frac{n_i}{n} \quad \text{equation 3}$$

where  $\%FCR$  = proportion of stomachs containing food;  $n_i$  = number of stomachs containing food in sample;  $n$  = total number of stomachs examined.

The relative stomach content weight (%SCW): defined as the wet weight of stomach contents of a given specimen and expressed as a percentage of fish weight. The weight of an eviscerated stomach was first calculated by subtracting the weight before and weight after gut content removal (content weight). The %SCW was then calculated using the following formula:

$$\%SCW = 100 \frac{W}{W_i} \quad \text{equation 4}$$

where %SCW = the mean weight of stomach contents of a given specimen;  $W$  = the total stomach content weight of an eviscerated stomach;  $W_t$  = total weight of the given specimen.

Volume method (%V): defined as the volume of individuals of a given prey type and expressed as a percentage of the total volume of food items measured in all stomachs (Hyslop, 1980). For equations on volume of prey types see Table 2.

The Index of Relative Importance (IRI): defined as the importance of each food item relative to other food items by taking into account both the volume and number of each food item, and the frequency at which it occurs in diet of fish (Pinkas *et al.*, 1971). The %V, %N and %F values was used to calculate the IRI for each major food item.

$$IRI = (\%N + \%V) \times \%F \quad \text{equation 5}$$

The IRI values for each prey type was then expressed as percentage index (%IRI, Pinkas *et al.*, 1971) and calculated using the following formula:

$$\%IRI = 100 \frac{IRI_i}{\sum_{i=1-n} IRI} \quad \text{equation 6}$$

## CHAPTER THREE: RESULTS

### 3.1.1. Study 1: Hydrography

At diel station 1, a pronounced thermocline existed between 9 and 28 m, with cool water masses around 13°C below this (Figure 4a). Although salinity decreased between 9 and 17 m and then increased between 17 and 50 m before gradually decreasing thereafter (Figure 4a), overall differences were small. Dissolved oxygen concentrations were highest in the upper 34 m and declined strongly thereafter, with concentrations of < 0.3 ml/l below 80 m depth (Figure 4a).

At diel station 2 (Figure 4b), by contrast, a less pronounced thermocline was observed, and water of 13°C was observed from 80 m depth to the bottom. There was little or no change in salinity with depth (Figure 4b). A gradual decline in oxygen was observed with depth and again low oxygen water masses with concentrations of < 0.3 ml/l occurred below 140 m.

### 3.1.2. Zooplankton

Information on the abundance of all zooplankton identified are shown in Table 3, from which it can be seen that there was much intra- and inter-site variability in composition. The inner station (Diel Station 1) was dominated by copepods, the juvenile stages of euphausiids and polychaetes, whilst the outermost station (Diel Station 2) was more diverse. Typically oceanic taxa (pteropods, thaliaceans) were absent at the inner station. As most of the zooplankton taxa collected did not feature in the diet of *Sufflogobius bibarbatus* (see below), attention here will focus only on those that were important.

Copepods were found throughout the water column at both study stations (Figures 5 and 6). At Diel Station 1 they were generally found closer to the surface than in deep water – despite the fact that all samples were collected during the daytime. At Diel Station 2, by contrast, there was no clear diel pattern in vertical distribution, though individuals were generally more dispersed at night than by day. Copepods were much more common at Diel Station 1 than Diel Station 2 (Table 3).

Polychaetes and polychaete larvae were more common at depth at both stations (Figures 5 and 6); although at Diel Station 2 there was no clear pattern to their vertical distribution. Polychaetes and polychaete larvae were slightly more common at Diel Station 1 than Diel Station 2 (Table 3).

Amphipods were found throughout the water column at both study stations (Figures 5 and 6). At Diel Station 1 they generally appeared to be more common in the upper part of the water column. By contrast, at Diel Station 2, there was no clear diel pattern in their vertical distribution, though individuals were generally more or less evenly distributed at night than by day. Amphipods were much more common at Diel Station 1 than Diel Station 2 (Table 3).

Euphausiids were patchily distributed throughout the water column at both study stations (Figures 5 and 6). At Diel Station 1 they were generally found closer to the surface than at depth. At Diel Station 2 there was no clear diel migration pattern. Euphausiids were slightly more common at Diel Station 1 than Diel Station 2 (Table 3).



### 3.1.3. Fish Size

There were strongly significant relationships between TL and PCL of *S. bibarbatu*s (Figure 7), and between TL and mass (Figure 8), the latter relationship being best described by a power curve of the form  $TL = 0.000003x^{3.1475}$  ( $r^2 = 0.9277$ ). There was a strong significant relationship between slopes of TL and mass by gender (Figure 9) and males attained a greater length (128 mm-TL, and 122 mm-TL, respectively) and a heavier body mass than females (17.989 g, and 16.014 g, respectively) (Figure 9).

Length frequency plots of *Sufflogobius bibarbatu*s caught and sampled (for gut-contents) during January 2006 are shown in Figure 10A, whilst those of the two stations are shown separately in Figure 10B and C. The 2 743 specimens of *S. bibarbatu*s measured onboard ship ranged in size from 20-140 mm in TL (Figure 10A), and displayed a unimodal length-frequency distribution peaking at 70 mm (Figure 10A, line graph *a*). This is broadly similar to the data obtained from the 1 485 individuals actually analysed for gut-contents, suggesting that the latter was indeed a random sample of the former.

Although the length-frequency distributions obtained from both the Diel Stations were similarly unimodal, there were some differences between the two (Figures 10B, C). Fish at the inner of the two stations ranged in length from 25-110 mm in TL (Figure 10B), and showed a pronounced modal peak at 60-75 mm TL, while those from Diel Station 2 ranged in length from 40-140 mm in TL (Figure 10C) and the modal peak was slightly larger (60-90 mm-TL). Not only did fish from the outer station attain a longer length, but the shape of the length-frequency curve was much broader.

There were pronounced differences in the length-frequency distributions of males and females (Figure 11). Of the 1485 specimens analysed for stomach contents, 801 were males and 633 were females: 146 individuals could not be sexed (Figure 11). Males were generally larger (30-130 mm TL) than females (25-125 mm-TL), and were represented in the population by different modal size classes. The individuals for whom gender could not be determined also displayed an approximately modal size distribution, the peak of which was mid-way between that of the males and females and suggests that the individuals were not juveniles. The sex ratio of the sampled population at both stations was ~1:1.

The mean TL of sampled fish increased with both bottom depth and with capture depth (Figures 12a, b), but did not change with time of day (Figure 12c). This reflects the fact that although *Sufflogobius bibarbatu*s were caught in the PT, most individuals were either caught in the BT or in the bottom-most net of the PT. In other words, we were unable to sample individuals high up in the water column and consistently collected animals from close to the seabed because high numbers of jellyfish were continuously caught close to the surface.

#### **3.1.4. Feeding Rhythms**

To describe diel feeding patterns of *S. bibarbatu*s %FCR was plotted against time of day and grouped into 4-hourly classes (Figure 13), using all the data. These results indicate that some *Sufflogobius bibarbatu*s had food in their guts throughout the day/night period and that there was no clear diel feeding rhythm. The overall %FCR was 23.6%.

### 3.1.5. Feeding and Fish Length

Generally, the bigger the fish, the more likely it was to have food in its guts (Figure 14), and %FCR gradually increased in fish size from 30-65 mm TL and peaked in individuals greater than 70 mm TL. This pattern was reflected in plots of stomach content weight against TL (Figure 15), which indicates that large fish were both more likely to be caught feeding and they were eating more when they were caught. The relationship between %SCW and fish length was strongly negative (Figure 16):  $TL = 1064x^{-1.5943}$  ( $r^2 = 0.9502$ ).

### 3.1.6. Overall Diet Composition

To assess diet and dietary importance of key components, as well as changes in diet with ontogeny and time of day all the samples were pooled. A summary of these data is shown in Table 4. Material such as fish scales, sand grains and foraminifera have been considered here either as an indication of cod-end feeding (fish scales) or of incidental ingestion with benthic prey. They have been ignored from detailed analyses. Unidentifiable fragments of material, such as detritus were considered here as “other”.

The most frequently occurring prey items in the diet of *Sufflogobius bibarbatus* were polychaetes and crustaceans (euphausiids being the second most frequent followed by copepods and amphipods, Table 4), though a number of other taxa were occasionally recorded. Juvenile gobies were observed in a number of instances, as were fish eggs and bivalves. Nematodes observed in stomach contents were likely parasites. Note that diatoms were relatively uncommon. The most numerous food items were polychaetes, copepods and euphausiids (Table 4). Although amphipods were numerically less important, because of their high %V values this taxon contributed substantially to the %IRI. Indeed, the three most

important prey taxa for *S. bibarbatus* during this study were large crustaceans (euphausiids and amphipods) and benthic polychaetes (Table 4), and the contribution made by copepods was relatively insignificant.

### 3.1.7. Diet versus Time of Day

It is clear from the data summarised in Table 5A and B that diet varied with station, and with time of day. However, there was no consistent pattern to this variation. For example, the daytime values of %F and %N for amphipods at Diel Station 1 were low on day 1 and high on day 2 (Table 5A), while the same values for euphausiids were considerably lower on day 2 than day 1 (Table 5A). Although amphipods were more numerically observed in the diet at night than by day at Station 1, the reverse pattern was observed at Station 2. Similar observations can be made for most prey taxa at both stations.

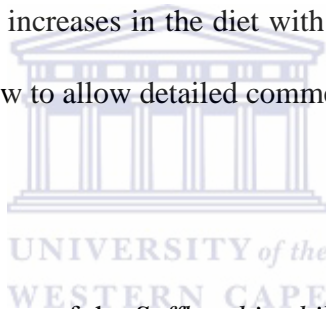
The few consistent patterns that emerge from the data were: polychaetes were the dominant prey at both stations: polychaetes were present in the guts throughout the day and night cycle but seemed to be slightly more prevalent during the day: copepods and euphausiids were more commonly eaten at Diel Station 1 than 2, which is in agreement with their greater abundances in the water column at Diel Station 1 than 2 (Table 3): and both latter prey taxa were more commonly seen in the guts of fish collected at night at both stations.

These observations are supported in the frequency of occurrence plots for the key prey groups over time (Figures 17a, b). Polychaetes were consumed by *S. bibarbatus* throughout the diel cycle (Figure 17a). *S. bibarbatus* appeared to feed on small zooplankton (copepods)

mostly by the early part of the night (Figure 17b), whilst larger zooplankton (euphausiids) was consumed throughout the diel cycle (Figure 17b).

### 3.1.8. Ontogenetic changes in Diet

Plots of frequency of occurrence for the key prey groups against fish size are shown in Figure 18. These data suggest that copepods were much more common in the diet of small fish albeit this is based on a single high (%F = 100) value for fish of 40 mm-TL, whilst euphausiids and polychaetes were more frequently recorded in the diet of larger fish. Indeed, in the case of polychaetes, the relationship between fish size and %F was near linear, suggesting that this prey taxon increases in the diet with increasing fish size. The data with respect to amphipods are too few to allow detailed comment.



### 3.2.1. Study 2: Fish Size

The length-frequency distributions of the *Sufflogobius bibarbatus* collected and analysed for gut-content analysis by the combined BT and from the single PT are shown in Figure 19. In the demersal study, 1 955 specimens of *S. bibarbatus* were caught during 2001 and these ranged from 50-130 mm in TL (Figure 19). By contrast, 204 specimens were caught in the PT and these ranged from 50-70 mm in TL (Figure 19). A unimodal length-frequency distribution was observed for gobies during both studies, though it is clear that there were big differences in the size of fishes from the two environments. Unfortunately, fish in this study were not sexed, so it is not possible to differentiate patterns by gender. The mean TL of sampled fish showed an increased with capture depth (Figure 20a), but did not change with time of day (Figure 20b).

### 3.2.2. Feeding Rhythms

Unfortunately, fish capture times in this study were all done during daylight hours only, however, to describe diel feeding patterns of *S. bibarbatatus* the relationship between %FCR was plotted against available times (Figure 21), using all demersal data. As noted in Study 1 (Figure 13) results indicate that some *Sufflogobius bibarbatatus* had food in their guts throughout the day and that %FCR showed a decline during daylight hours. The overall %FCR was 17.9%.

### 3.2.3. Feeding and Fish Length

As noted in the previous study (Figures 14-16), the relationship between fish size and feeding activity (Figure 22) and fish size and stomach content weight (Figure 23) were positive. In the former case, there was a very good agreement between the results of the two studies, and the length at which %FCR became independent of size was approximately 80 mm in TL. Note however that in comparison with the results of Study 1, the results in Study 2 indicate a lesser amount of feeding. The plot of %SCW against fish length was negative (Figure 24), as it was in Study 1 (Figure 16), and was best described by the equation:  $TL = 67.991x^{-1.0371}$  ( $r^2 = 0.4336$ ). The %SCW data for Study 2 (range 0.5 – 1.5%) also indicate reduced feeding compared to Study 1 (range 0.5 – 4.0%), supporting the inference from comparing %FCRs.

### 3.2.4. Overall Diet Composition

The data in Table 6 represent the results from the pooled demersal samples, whilst those in Table 7, are the same from the single pelagic sample. Sand grains have been omitted from further calculations, but were clearly common in samples collected from the seabed. Unfortunately, no measurements of prey items were made and so it is not possible to

calculate the %IRI from these data. As noted in Study 1 (Table 4), the diet of demersal caught fish was dominated by polychaetes and crustaceans (Table 6). Euphausiids were common, but amphipods were not (cf Study 1, Table 6). No copepods were recovered. These results are in stark contrast to those observed for pelagic caught fish, whose diet was dominated by pelagic crustaceans (principally copepods), and polychaetes were uncommon (Table 7).

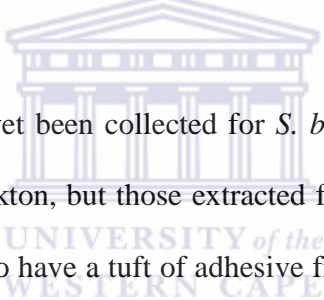
### **3.2.5. Ontogenetic changes in Diet**

The dominant recognisable prey items were euphausiids and polychaetes: amphipods and copepods were uncommon in most material examined and so consequently it is only possible to make comments about the former two taxa. In the case of polychaetes, it is clear that these become increasingly common in the diet of *Sufflogobius bibarbatatus* as the fish increases in length (as noted in Study 1, Figure 25). For gobies collected from demersal trawls a similar pattern of larger fish eating more euphausiids was observed euphausiids are similarly suggestive; though it should be realised that the sample size for smaller fish was small.

## CHAPTER FOUR: DISCUSSION

### 4.1. Fish Size

The maximum size recorded for *S. bibarbatus* in this study was 13 cm, which is similar to that recorded by Hoese (1986), and Melo and Le Clus (2005). This is shorter than that reported by Staby and Krakstad (2006), who found gobies up to 20 and 21 cm in length. Larger gobies (>13 cm) were not observed in this study and are generally distributed further offshore (Staby and Krakstad, 2006). *S. bibarbatus* is a fairly big goby, though there are others with a similar size, e.g. *Gobius cobitis* (27 cm; Gibson, 1970), *G. niger* (15 cm; Vaas *et al.*, 1975), *G. gastevini* (12 cm; Miller, 1986) and *G. auratus* (10 cm; Miller, 1986).



No pelagic eggs have yet been collected for *S. bibarbatus* (O'Toole, 1978) despite extensive sampling of the plankton, but those extracted from mature females (Melo and Le Clus, 2005) have been shown to have a tuft of adhesive filaments that develops between the follicle granulosa (Giulianini and Ferrero, 2001). Such features of the egg capsule are typically associated with eggs that are spawned in a benthic habitat, and it has consequently been suggested that this species lays its eggs in soft bottom environments (Melo and Le Clus, 2005). It is likely (though there is as yet no hard evidence) that the breeding biology of *S. bibarbatus* is similar to that of gobies elsewhere (Lindström, 1988; Forsgren *et al.*, 1996; Malavasi, 2001; Scaggiante *et al.*, 2005). Male gobies typically build a nest on the seabed, and they spawn with one or more females in that nest and then protect and defend the developing eggs prior to their hatching and subsequent planktonic development (Lindström, 1988). This would also explain why males are bigger than females in this species, an observation also recorded by Melo and Le Clus (2005) and noted for *Gobius roulei*



(Kovačić, 2001), *G. buccichi* (Sasal *et al.*, 1996) and *Pomatoschistus minutus* (Lindström, 1988). In the sand goby (*P. minutus*) as well in the common goby, *P. microps*; large territorial males defend and protect nest sites aggressively from predators as well as from intermediate and smaller males known as sneaker males (Magnhagen, 1995; Malavasi, 2001). Male size is thus important in influencing the outcomes of male-male competition (Lindström, 1988).

The smaller, sneaker males differ from territorial males in their body size, age, testes investment, and seminal vesicle and ejaculate characteristics (Scaggiante *et al.*, 2005). In the grass goby *Zosterisessor ophiocephalus*, a sneaker male approaches a spawning pair and releases a large ejaculate in the nest or around it (Mazzoldi *et al.*, 2000). While sneaker males are chased away from nest sites by aggressive territorial male, they will likely have succeeded in fertilising some eggs (Mazzoldi *et al.*, 2000; Scaggiante *et al.*, 2005), and so dominance by males does not necessarily mean mating success with females, but rather egg parental care by larger males (Forsgren, 1997). It is possible, given that some of the sampled population here could be neither identified as male nor as female (Figure 11), that sneaker males might exist within populations of *S. bibarbatu*s off Namibia, but research on this is clearly needed.

The results from Study 1 indicated that gobies collected at the innermost station (Station 1) were smaller on average than those caught further offshore, regardless of gender. These results are similar to those obtained by O'Toole (1978); Crawford *et al.* (1985); Melo and Le Clus (2005) and Staby and Krakstad (2006), and are observed for a variety of different fishes in the northern Benguela (Gordoa *et al.*, 1995). If the egg masses are benthic

then on hatching the larvae will be released into water that is tending to move onshore (Stenevik *et al.*, 2001) regardless of where spawned, their shoreward transfer occurs presumably when upwelling is more pronounced (Staby and Krakstad, 2006). Such would explain the tendency for smaller fish to be found nearshore, though it should be noted that small fish were also found offshore most likely during a period of low upwelling (Staby and Krakstad, 2006).

#### **4.2. Diet**

There was some indication of cod-end feeding, as evidenced by the high incidence of fish scales in guts. I have interpreted the presence of juvenile gobies in the guts of some specimens similarly (they were intact) following D'Arcangues (1977), who suggested that gobies might have experienced a stressed condition inside the net, though juveniles are often reported to be eaten by other species of goby naturally. For example, the racer goby, *Neogobius gymnotrachelus* (Grabowska and Grabowski, 2005), and the round goby, *N. melanostomus* (Miller, 1986) from the Black Sea, and the black goby, *Gobius niger* in the eastern North Atlantic (Vaas *et al.*, 1975) have all been shown to eat small gobies on occasions.

The general dietary results obtained here can be summarised thus: *S. bibarbatu*s fed primarily on benthic polychaetes and amphipods, euphausiids and copepods; phytoplankton was uncommon.

Previous studies on the feeding of this species have produced some fairly contradictory findings (Barber and Haedrich, 1969; D'Arcangues, 1977; O'Toole, 1978; Crawford *et al.*,

1985; Macpherson and Roel, 1987). Barber and Haedrich (1969) examined the guts of three juvenile gobies and noted mostly phytoplankton of the genus *Delphineis* (= *Fragilaria*) *karstenii* and *Coscinodiscus* spp in the contents. By contrast, D'Arcangues (1977), who examined the guts of (no indication of the number of specimens examined was provided by D'Arcangues) adult and juvenile gobies, found predominately copepods and euphausiids in the diet of *S. bibarbatus* – results that are very similar to those reported here. Then again, O'Toole (1978) observed that the diet of 210 adults, juveniles and larvae consisted largely of diatoms (*Delphineis* spp. and *Chaetoceros* spp.), with some fragments of copepods and euphausiids. Similar observations were also reported by Crawford *et al.* (1985), who noted from 10 specimens (of different size) collected over the period 1979-1981, that gobies stomach contents contained (numerically) more than 90% phytoplankton and less than 10% zooplankton. These results again contrast with those recorded by Macpherson and Roel (1987), who reported (from approximately 120 specimens) that the diet of *S. bibarbatus* consisted mainly of polychaetes and copepods.

The data presented here represent the most comprehensive collected to date (3739 specimens in total) and indicate that *S. bibarbatus* is a generalised carnivore. Although it could be argued that the absence of phytoplankton in the sampled animals reflects the fact that specimens were collected close to or on the seabed, it is important to realise that *S. bibarbatus* is unlikely to have been feeding on phytoplankton in the water column during the studies conducted by Barber and Haedrich (1969), O'Toole (1978) or Crawford *et al.* (1985). Anchovies and sardines possess narrowly spaced gill rakers on the inside edges of their gill arches which act as filtering meshes as the fish swims (James, 1987, van der Lingen, 1994); features that gobies lack in general. That said, more information on this is

needed, in part because the previous studies were conducted at inshore locations (maximum sampling depths of <60 m). Phytoplankton concentrations are often significantly greater closer to the shore off Namibia (Hart and Currie, 1960; Crawford *et al.*, 1985; Brown *et al.*, 1991), which could account for why phytoplankton was the dominant food item in their results (Barber and Haedrich, 1969; O'Toole, 1978; Crawford *et al.*, 1985). That notwithstanding, it is more likely that the phytoplankton eaten by *S. bibarbatus* in the previous studies was consumed directly from the seabed as detritus.

If the high primary productivity associated with the northern Benguela does not get consumed directly, it gets either broken down into detritus in the water column and remains there as suspended particulate organic carbon (POC), or it settles onto bottom sediments and decomposes (Heymans and Baird, 2000). Fish that predominantly ingest detritus are considered as detritivores and this source of food can be enough to facilitate growth (Wilson *et al.*, 2003). Many studies on non-detritivorous fish often overlook the presence of detritus in stomach contents, or attribute its presence to sediments (Wilson *et al.*, 2003). Even when detritus is present, its volume may be poorly quantified (Wilson *et al.*, 2003), which can lead to an underestimation of the relative importance of this food source. Many gobies have been shown to eat detritus when it is common: *Gobius bucchichii* and *G. cobitis* in the western Mediterranean (Gibson, 1968), *Gobionellus sagittula* from the Gulf of California and Peru (Todd, 1976), and *Gobioides broussoneti* in the estuarine system of Tecolutla (Mata-Cortés *et al.*, 2004), Mexico and *Neogobius gymnotrachelus* from the Black and the Caspian Seas (Grabowska and Grabowski, 2005).

The very high level of variability in the results generated here, and elsewhere, indicates that *S. bibarbatus* has a generalised feeding habit, and that it feeds on both benthic

and pelagic organisms, depending on where it is and what is available. Similar conclusions have been reached from feeding studies of other species of goby elsewhere, though as most gobies are benthic, their gut contents are dominated by infaunal prey (Grossman *et al.*, 1980). The importance of benthic prey items is underscored by the presence of sand grains and foraminifera in their diet, which are generally considered to represent an accidental intake while feeding on benthic invertebrates (Kamukuru and Mgyaya, 2004; Kovačić, 2007).

### **4.3. Ontogenetic changes in Diet**

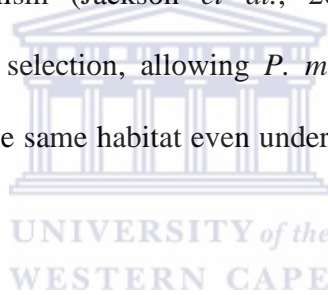
In the present study, the relative feed intake of small gobies was higher than that of big gobies (Figures 16 and 24) and similar observations have been noted for most fishes (Jobling, 1983; Hölker, 2003; Tran-Duy *et al.*, 2008). Generally, the standard metabolic rate of fish is the oxygen consumed while the fish is at rest (Brett and Groves, 1979), and Tran-Duy *et al.* (2008) have shown that greatest oxygen consumption relative to body weight occurs in smaller fish than bigger fish. In other words the metabolic demands of smaller fish are greater than those of big fish, which is reflected by their greater need for more food. Similar observations have been made for most organisms (Schmidt-Nielsen, 1979).

The present results suggest that although gobies of all size classes feed on much the same basic prey, shifts in diet with ontogeny do occur (Figures 18 and 25). Both studies suggest that as fish increase in size, so too does the size of the items in their diet: small individuals are found more frequently with copepods in their diet, whilst benthic polychaetes and large zooplankton are found more commonly in the diet of large individuals.

Ontogenetic changes in diet have been noted for other species of goby elsewhere in the world. *Pomatoschistus microps* in the northern Wadden Sea (del Norte-Campos and Temming, 1994) feed on meiofauna when they are small, but tend to feed more on macrofauna when they are large. Similar results have also been noted for a variety of Mediterranean gobies, including *Gobius cobitis* (Gibson, 1970), *G. paganellus* (Mazé, 2004) and *G. vittatus* (Kovačić, 2007). Indeed, ontogenetic changes in the size-spectrum of the diet are common in all fishes, and reflect changes in metabolic demands (Post and Lee, 1996; Levy 1990) and morphology (Grossman, 1980; Timmerman *et al.*, 2000), as well as changes in habitat (Schmitt and Holbrook, 1984; Grossman, 1980), behaviour (Grossman *et al.*, 1980), prey availability (Grossman, 1980) and predation risk (Werner and Gilliam, 1984; Miller *et al.*, 1988; Post and McQueen, 1988).

Grossman *et al.* (1980) suggested that ontogenetic dietary differences between small and large bay gobies (*Lepidogobius lepidus*) were more related to their foraging times and the ability of large fish to capture prey unobtainable to smaller individuals. Saeki *et al.* (2005) investigated the diet of two *Trimma* gobioid species (*T. caudomaculata* and *T. caesiura*) on coral reefs in Okinawa, Japan and found that ontogenetic diet shift was not significantly related to changes in the animal's dentition and they suggested that differences were a reflection of differences in foraging behaviours and microhabitat use (and served to reduce inter-specific competition between the two sister species). Prey size generally changes as fish grow. These changes have been positively correlated with morphological changes (i.e. mouth parts) and dietary shifts can also be attributed to age-specific use of habitat at spatial or temporal scales (Grossman, 1980; Schmitt and Holbrook, 1984; Timmerman *et al.*, 2000). Generally, species mass is considered as the ontogeny parameter

when determining prey selection (Post and Lee, 1996), and the latter authors have suggested that early life history stages of teleost fishes have mass-independent metabolic rates whilst later life-history stages have mass-dependent metabolic rates. Ontogenetic changes in the diet of teleost fishes can then be seen as a result of related changes in metabolism. Jackson *et al.* (2004) explored the dietary shift of *Pomatoschistus microps* (common goby), by means of a foraging model, in relation to laboratory and field study records. The data obtained through their model corresponded with previous studies (e.g. del Norte-Campos and Temming, 1994) and indicated that the prey group (copepods) selected by smaller size classes allowed *P. microps* to increase its net energy intake by a genetically controlled mechanism such as metabolism (Jackson *et al.*, 2004). The change in body size consequently influenced prey selection, allowing *P. microps* to switch from feeding on meiofauna to macrofauna in the same habitat even under predation pressure (Jackson *et al.*, 2004).



The gobies found at the inner of the two diel anchor stations in Study 1 (Diel Station 1) were smaller than those found offshore (Figure 12), and copepods were recovered from the diet of individuals more frequently than they were at Diel Station 2 (Table 5). It is noteworthy that the abundance of copepods was higher at this station than at Diel Station 2 (Table 3) (as also observed by Hutchings *et al.* (1991), Verheye *et al.* (1992)), which indicates perhaps that ambient prey abundance may play some role in diet as is likely.

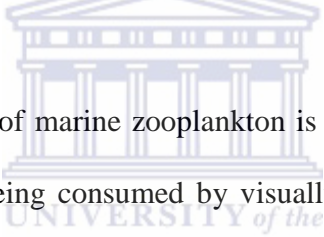
As noted above, it is important to realise that the ontogenetic changes in diet very strongly reflect ontogenetic changes in the habitat or environment occupied by different size classes, and how these change (in this case through diel cycle). Adult gobies are thought to

be largely demersal throughout the day-night period (D'Arcangues, 1977), whilst small individuals are thought to be more pelagic, especially at night (D'Arcangues, 1977). Thus, large fish would be expected to prey primarily on benthic organisms throughout the diel cycle, whilst smaller individuals might consume benthic organisms during the day whilst demersal, but then feed on more planktic prey items at night when they are in the water column. Unfortunately, sampling in the upper layers of the water column during the two diel stations here (Study 1) was not possible because of high numbers of jellyfish clogging the net. Nevertheless, the single haul obtained in Study 2 from the pelagos (at night) indicates very strongly that small individuals in the water column were eating primarily pelagic animals (Table 7): cumaceans, whilst primarily benthic will nevertheless move up into water column at times (Gibbons *et al.*, 1999). Furthermore, consistently sampling of demersal individuals at night should have revealed the presence of any prey caught and eaten in the water column as fish then returned to the seabed. Such could be argued to account for the presence of euphausiids in the diet of fish (Table 5), although because these prey items can display very strong patterns of diel vertical migration in the region (Barange, 1990; Pillar *et al.*, 1992), it is not improbable that they were consumed by gobies whilst in deep water, especially during the day.

The data presented here then indicate that *S. bibarbatus* feeds (or at least has food in its guts) throughout the diel cycle, and that distinct diel feeding rhythms are weak though there was perhaps a slight tendency for animals to be more likely to have food in their guts at night (Figure 13), especially early in the night. D'Arcangues (1977) too noted that the gut fullness of adult gobies was greatest at the start of night, with a decrease in stomach fullness in early morning. The sand goby *Pomatoschistus minutus* has also been shown to feed



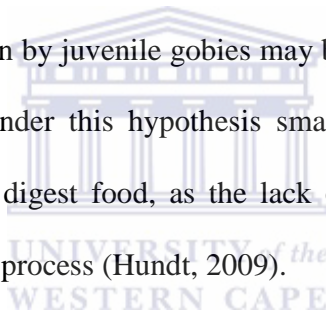
primarily at night in order to reduce its predation risk at a time when prey are most vulnerable (Thetmeyer, 1997). Unlike most gobies which feed during the day, however, such as *Gobius niger* (de Casabianca and Kiener, 1969 cited in Vaas *et al.*, 1975) and *Gobiusculus flavescens* (Thetmeyer, 1997), *P. minutus* has big eyes in relation to its body size, which allows it to detect prey under very dim light conditions. Unlike the other essentially shallow-water gobies cited above, *S. bibarbatus* can change its vertical position through the day. Unlike most gobies, *S. bibarbatus* has retained its swim bladder and D'Arcangues (1977) suggested that the ascent for the pelagic goby was light controlled while the descent began when some individuals were fully fed after pelagic feeding. By contrast, O'Toole (1978) suggested that *S. bibarbatus* was a diurnal feeder.



Diel vertical migration of marine zooplankton is thought to have evolved primarily as a response to the risk of being consumed by visually feeding predators in the surface waters during the day (Ohman *et al.*, 1983; Bollens *et al.*, 1994; Koulouri *et al.*, 2009): individuals need to migrate to close to the surface at some time, as that is where their food is most abundant. In the case of *S. bibarbatus*, however, the rationale for vertical migration must be slightly different. Large individuals remain on the bottom throughout the day:night period, where they are clearly able to obtain the food they need and avoid predators. Given that small fish are able to feed on benthic invertebrates too, why then should they migrate into the water column? The fact that they migrate into the water column at night (rather than by day) obviously reflects a need to avoid visually feeding predators in the surface waters, and once in the surface waters they then feed on available prey. Clearly though the rationale for migration cannot be predation by demersal predators (including larger conspecifics), as small fish must be more vulnerable to predation by day than night, even on the bottom. It

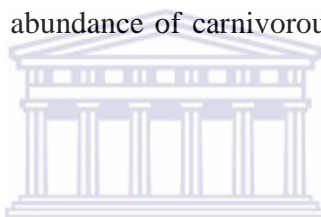
could be stimulated by temperature-related metabolic benefits that facilitate their digestion and which serve to increase their feeding and growth rates (Levy, 1990). The feeble swimming abilities and low net avoidance of juveniles (O'Toole, 1976; O'Toole, 1978) could limit their escape abilities from predators and consequently increase their vulnerability to predators (Werner and Gilliam, 1984; Miller *et al.*, 1988; Post and McQueen, 1988). The low levels of light at night would serve as an antipredation window for nocturnal migration of juveniles; sequentially lower their predation risk, allowing juveniles of *S. bibrabatus* to successfully migrate to the pelagic environment above the thermocline, where temperature ranges (13-18°C, Figure 4) would optimise their metabolic efficiency (Levy, 1990).

Alternatively, vertical migration by juvenile gobies may be related to the low oxygen waters in which the species lives. Under this hypothesis small gobies migrate into the pelagic habitat in order to efficiently digest food, as the lack of oxygen associated with bottom waters constrains the digestion process (Hundt, 2009).



## CHAPTER FIVE: CONCLUSION

It is clear from the results presented in this study and those of others that *Sufflogobius bibarbatus* is an opportunist and a generalist feeder. Although the majority of the prey items consumed by *S. bibarbatus* here were animals (phytoplankton was uncommon), the results of other studies have unambiguously demonstrated the diet to be dominated by phytoplankton. These differences must reflect differences in the sampling locations and times, and the prey fields available. It is argued that phytoplankton is not consumed by filtration from the water column but rather it must be eaten directly (or incidentally) from the seabed - perhaps when the abundance of carnivorous prey is low (as Grossman *et al.*, 1980).



Although gobies of all size classes feed on much the same basic prey, shifts in relative proportions of diet items do occur with ontogeny and these shifts must reflect changes in the habitats occupied through the diel cycle. Benthic prey items predominate, but these are supplemented with pelagic components, especially in smaller, migratory fish.

James (1987) found that the diet of anchovy in the Benguela ecosystem consisted primarily of copepods and euphausiids, and King and Macleod (1976), van der Lingen (2002), Louw *et al.*, (1998) and van der Lingen *et al.* (2006a) have noted that sardines consume both phytoplankton and zooplankton (mostly copepods), depending on relative prey abundances (van der Lingen, 1994). Round herring (*Etrumeus whiteheadi*) eat mostly zooplankton (Wallace-Fincham, 1987) and juvenile horse mackerel eat mainly copepods (Crawford *et al.*, 1987). Although *S. bibarbatus* eats zooplankton, it would be an

overstatement to suggest that it directly competes with major pelagic fishes off Namibia, despite the fact that its biomass is thought to have increased since the collapse of the major pelagic fisheries (J.P. Roux, Ministry of Fisheries and Marine Resources, Lüderitz Namibia-pers. comm.). Not only does it feed on zooplankton at a different time of day (night for small individuals), or in a different part of the water column (near bottom for large individuals) to most of the aforementioned pelagic fishes, but zooplankton are only really important in the diet of a portion of the population, with polychaetes dominating the diet of larger, more benthic fish.

Although this study represents one of the largest studies on the diet of *S. bibarbatu*s, there is considerable room for future work. Perhaps one of the biggest problems with the data set collected here was the lack of information on individual prey mass and this should be corrected in future studies as this sort of information is needed for trophic modeling (Shannon and Jarre-Teichmann, 1999; Heymans and Baird 2000; Jennings *et al.*, 2002). It was not possible to sample the population throughout the diel cycle throughout the water column, because of problems associated with catching “too many” jellyfish in the pelagos and this needs to be remedied. Given that the species is clearly opportunistic it is also necessary to conduct a number of studies in different geographic locations and at different times of year, in order to get an understanding of how changes in the ambient prey field influence dietary intake. And of course ideally it is necessary to undertake laboratory experiments in order to look in more detail at some the physiological and rate processes associated with feeding in this species (as van der Lingen, 1994).

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### 3.1.1. Study 1: Hydrography

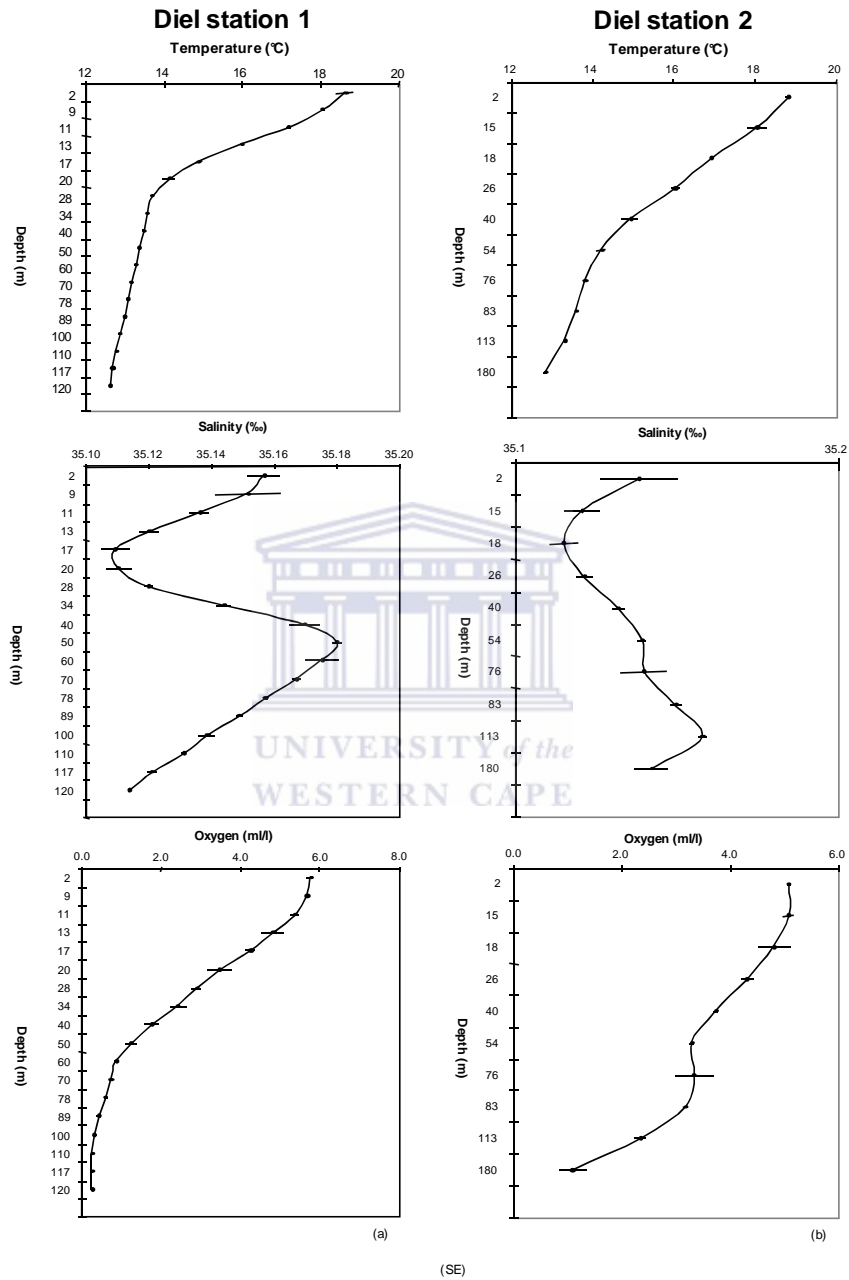


Figure 4. Temperature, oxygen and salinity profiles sampled across the sampling grid off the Namibian coast in January 2006. Diel station 1 indicates the hydrography of the inshore station (16-18 January 2006) and diel station 2 indicate the hydrography of the offshore station (18-20 January 2006). Error bars are SE.

### 3.1.2. Zooplankton

Table 3. Total numbers (per standardized unit volume (m<sup>2</sup>)) for each zooplankton taxon in the water column, at each sampling station for both diel stations at different time intervals in Namibian waters, over the study period 16-20 January 2006.

Station number	Diel 1				Diel 2							
	4	8	11		15	17	22	23				
Maximum depth (m)	115	120	118		168	180	165	165				
Time (00h00)	10.4	6.7	19.7		22.8	8.5	22.8	11.4				
Time of day	Day	Day	Day		Night	Day	Night	Day				
Date (dd/mm/yr)	16/01/06	17/01/06	17/01/06	Overall	18/01/06	19/01/06	19/01/06	20/01/06	Night	Day	Overall	
Copepods	841.11	1389.72	685.74	972.19	564.52	181.02	537.88	388.38	551.20	284.70	693.55	
Euphausiids	0.28	11.57	1.70	4.52	0.83	0.31	0.15	0.15	0.49	0.23	0.60	
Calyptopes	45.32	1.68	62.84	36.61	1.91	0.19	2.94	1.39	2.43	0.79	2.82	
Larvaceans	0.28	1.00	0	0.43	3.81	8.33	15.12	10.42	9.47	9.38	14.16	
Chaetognaths	0.70	2.53	2.84	2.03	11.54	7.61	16.24	11.94	13.89	9.78	18.78	
Medusae	2.85	0.50	0.15	1.17	10.94	4.44	12.82	5.06	11.88	4.75	14.26	
Siphonophores	0.72	0.48	0.46	0.55	0.83	4.56	0.73	2.70	0.78	3.63	2.59	
Hyperiid amphipods	3.15	3.42	6.97	4.51	1.58	1.33	1.85	0.36	1.71	0.85	2.14	
Polychaetes	21.03	0.35	9.82	10.40	6.74	0.94	2.88	3.82	4.81	2.38	6.00	
Polychaete larvae	1.83	0.15	0.75	0.91	1.40	3.86	1.15	3.42	1.28	3.64	3.10	
Cyphonauts	0	0.15	0	0.05	0.21	0	0.06	0	0.13	0	0.13	
Gastropod larvae	0.45	0.32	0.89	0.55	3.03	1.14	0.42	1.39	1.73	1.27	2.36	
Mysids	0	0	0	0	1.07	0.61	1.09	0.09	1.08	0.35	1.26	
Echinoderm larvae	0.70	0	0.03	0.24	1.73	0.25	0.21	0.39	0.97	0.32	1.13	
Thaliaceans	0	0.07	0	0.02	7.69	2.17	12.94	3.09	10.32	2.63	11.63	
Decapods	0.68	0	0.27	0.32	1.90	0.31	0.15	0.39	1.03	0.35	1.20	
Fish eggs	0.12	0.30	0.13	0.18	22.46	5.25	22.06	4.64	22.26	4.94	24.73	
Fish larvae	0.0	0.07	0	0.02	0.03	0.67	0.03	0.76	0.03	0.71	0.39	
Cumaceans	0.12	0.05	0.33	0.16	0.06	0.06	0.06	0	0.06	0.03	0.07	
Ctenophores	0	0.13	0	0.04	0.51	1.03	0.39	0.67	0.45	0.85	0.88	
Pteropods	0	0.05	0	0.02	0.06	0.03	0.55	0.24	0.30	0.14	0.37	
Cladocerans	0	0.05	0	0.02	0.03	0.19	0.03	0.03	0.03	0.11	0.09	
Bivalve larvae	0	0	0	0	0	0	0	0	0	0	0	
Brachiopod larvae	0	0	0.10	0.03	0	0	0.06	0	0.03	0	0.03	
Alima	0	0	0	0	0	0	0	0.03	0	0.02	0.01	
Ostracods	0	0	0	0	0.03	0	0.03	0	0.03	0	0.03	
Zoea	0	0	0.05	0.02	0.09	0	0.03	0.06	0.06	0.03	0.07	
Foraminifera	0	0.20	0	0.07	0	14.39	0	2.48	0	8.44	4.22	
Totals				1035.07					636.44	340.31	806.59	

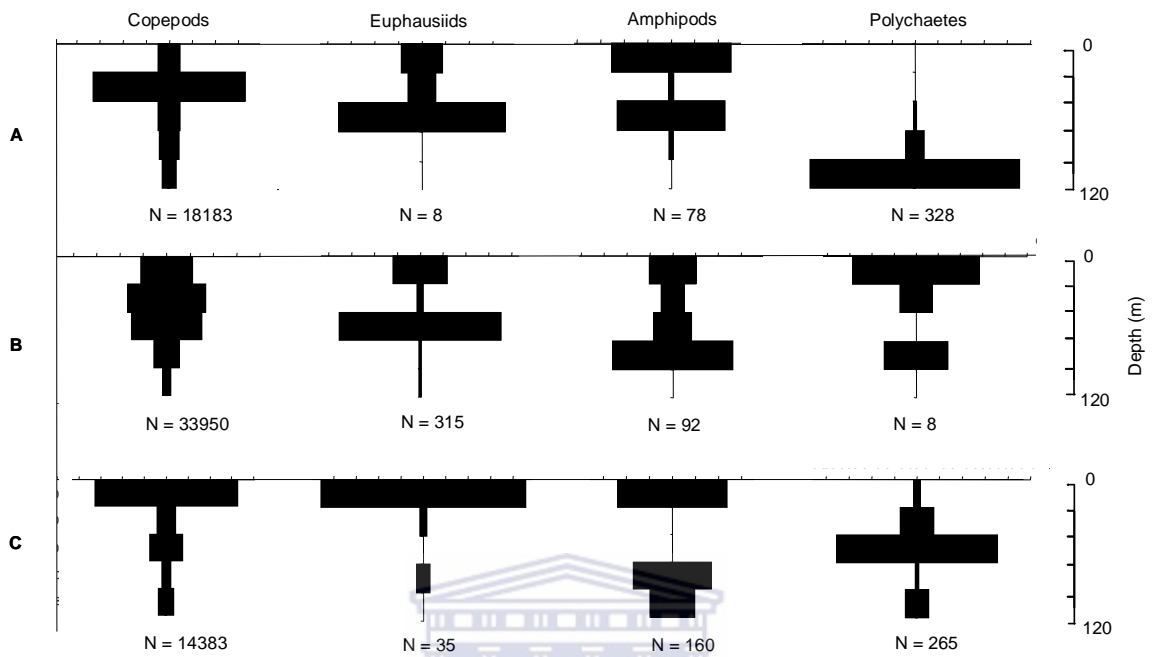


Figure 5. Vertical distribution of the dominant zooplankton taxa (numbers per standardised unit volume (see methods)) eaten by *S. bibarbatus* at each sampling station for diel station 1, over the study period 16-17 January 2006. Numbers at bottom of plots indicates numbers per standardised unit area. All stations were sampled in daylight: A = station 4, B = station 8 and C = station 11.

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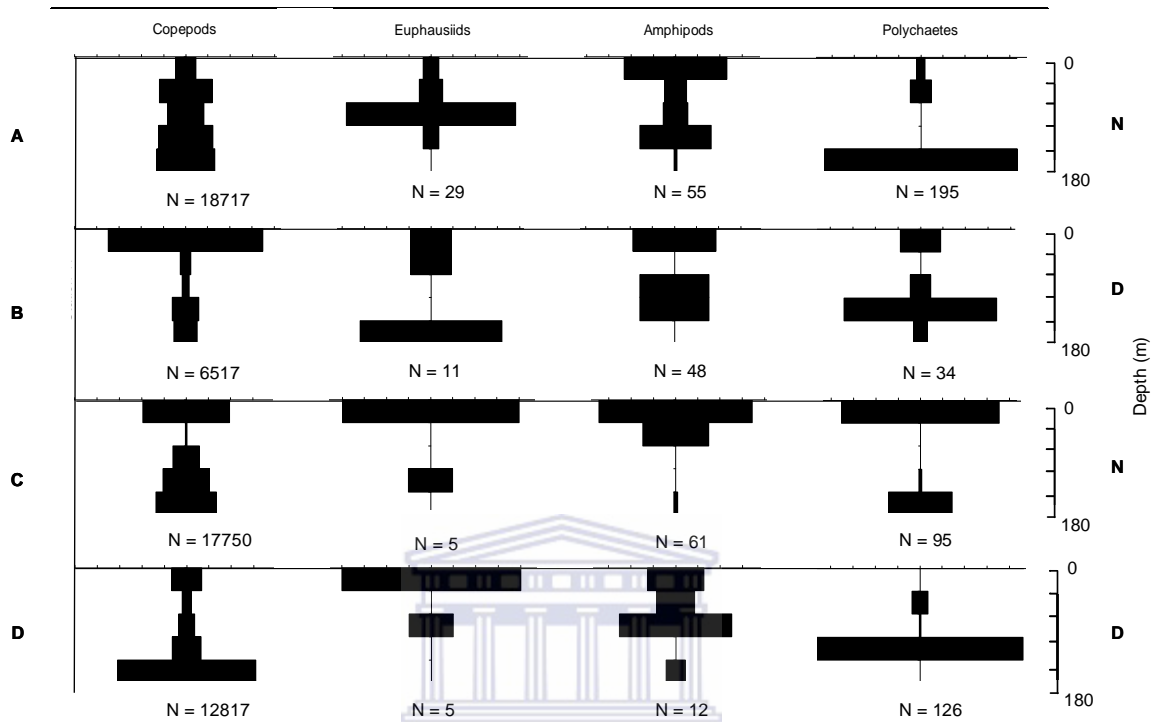


Figure 6. Vertical distribution of the dominant zooplankton taxa (numbers per standardised unit volume (see methods)) eaten by *S. bibarbatus* each sampling station for diel station 2, over the study period 18-20 January 2006. Numbers at bottom of plots indicates numbers per standardised unit area. A = station 15, B = station 17, C = station 22 and D = station 23. Day is designated as “D” and night as “N” along the right hand side of figure.

### 3.1.3. Observations on Fish Size

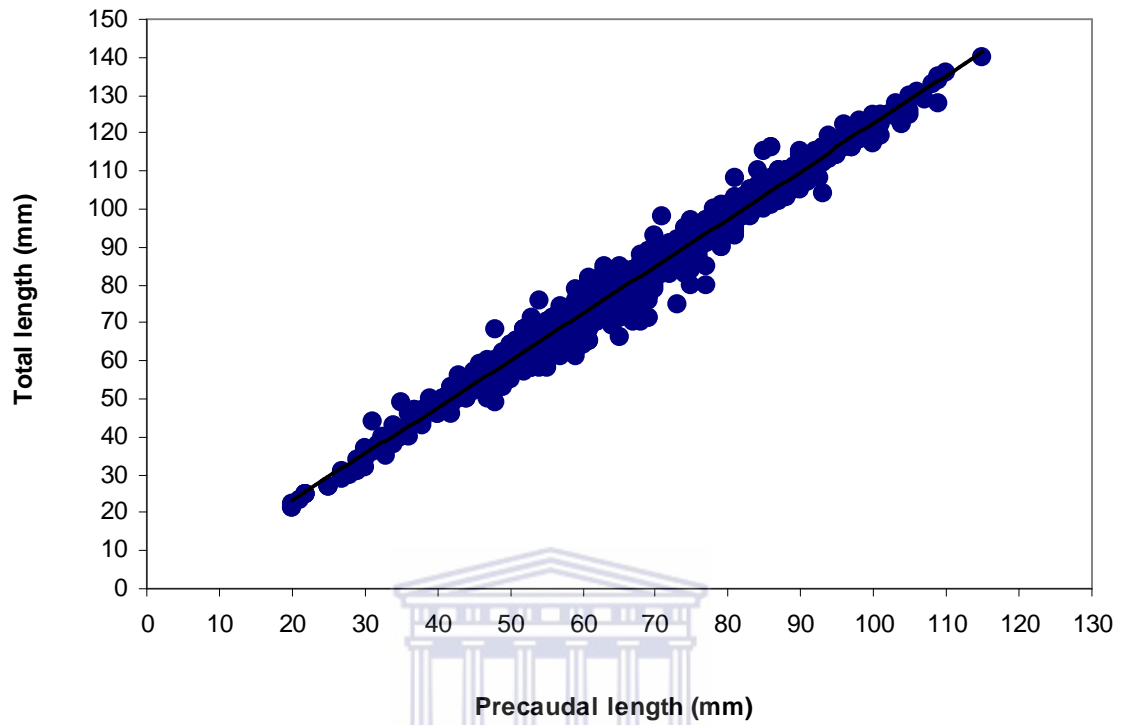


Figure 7. The relationship between total and precaudal length (mm) measures of the pelagic goby, caught in Namibian waters during both studies ( $n = 3739$ ). All fish combined. Linear function for the relationship between TL and PCL:  $TL = 1.0692x^{1.0297}$ ,  $r^2 = 0.984$ .

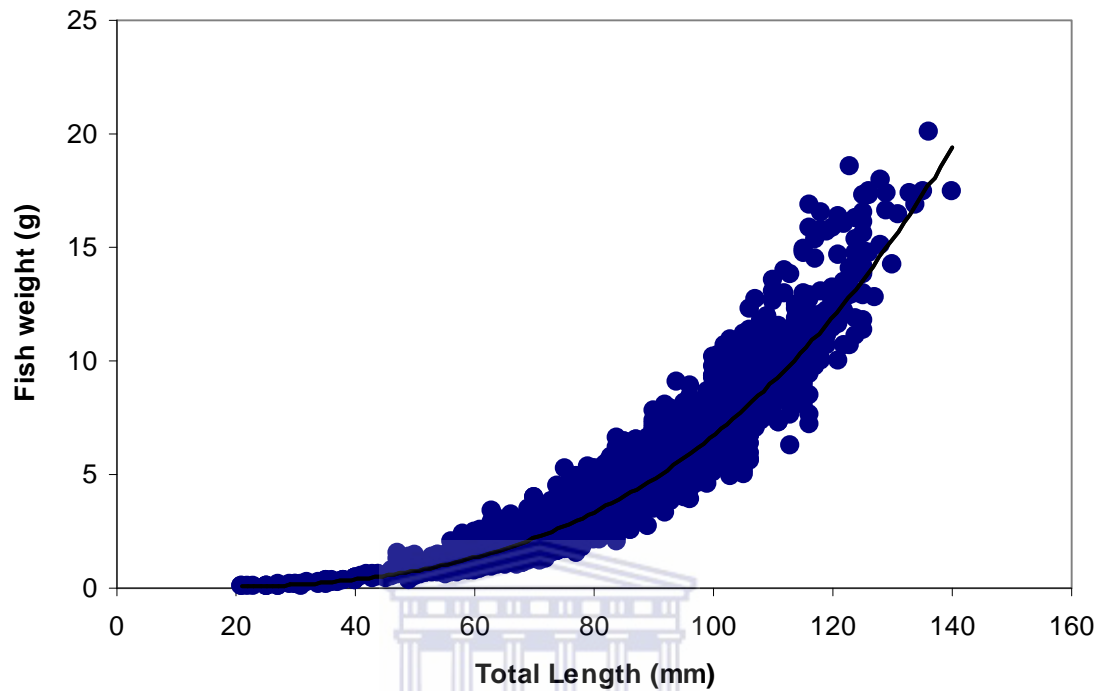


Figure 8. The relationship between total fish length (TL) and fish weight of *S. bibarbatus*, collected off the Namibian coast during both studies ( $n = 3739$ ). Power function for the correlation between TL and fish weight:  $TL = 0.000003x^{3.1475}$ ,  $r^2 = 0.9277$ .

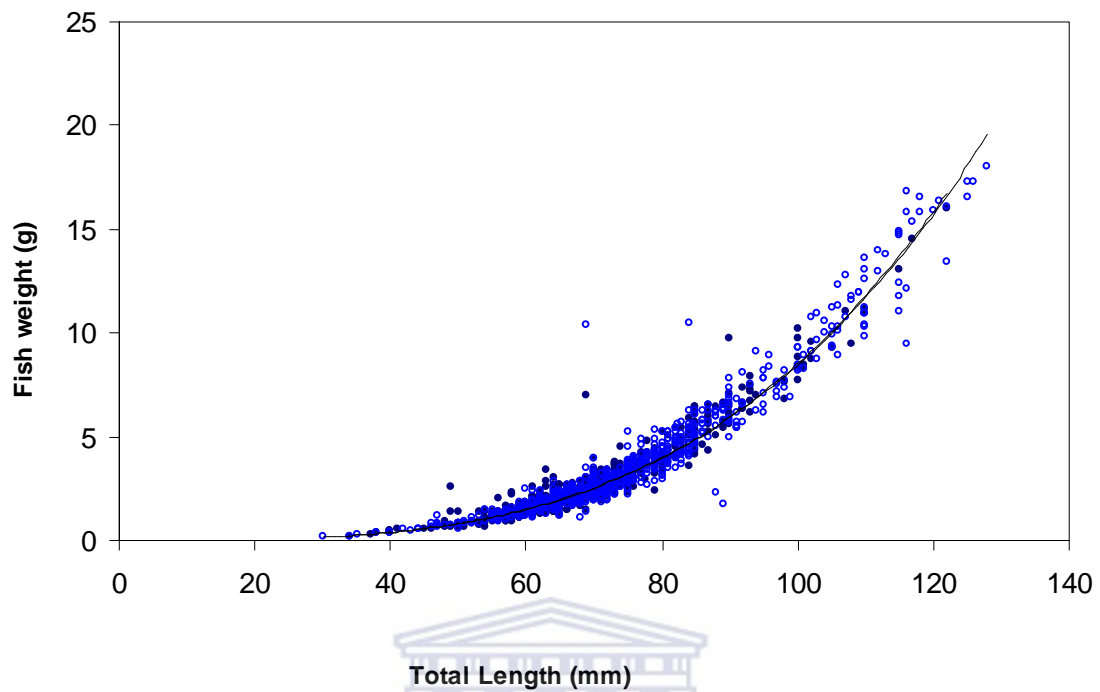


Figure 9. Length-weight distribution for male (o) and female (●) of *S. bibarbatus* caught during the period of 12-20 January 2006 off the Namibian coast. Power functions for the relationship between gender lengths and weights: males:  $TL = 0.000001x^{3.3898}$ ,  $r^2 = 0.946$ ; females:  $TL = 0.000001x^{3.3939}$ ,  $r^2 = 0.9146$ .

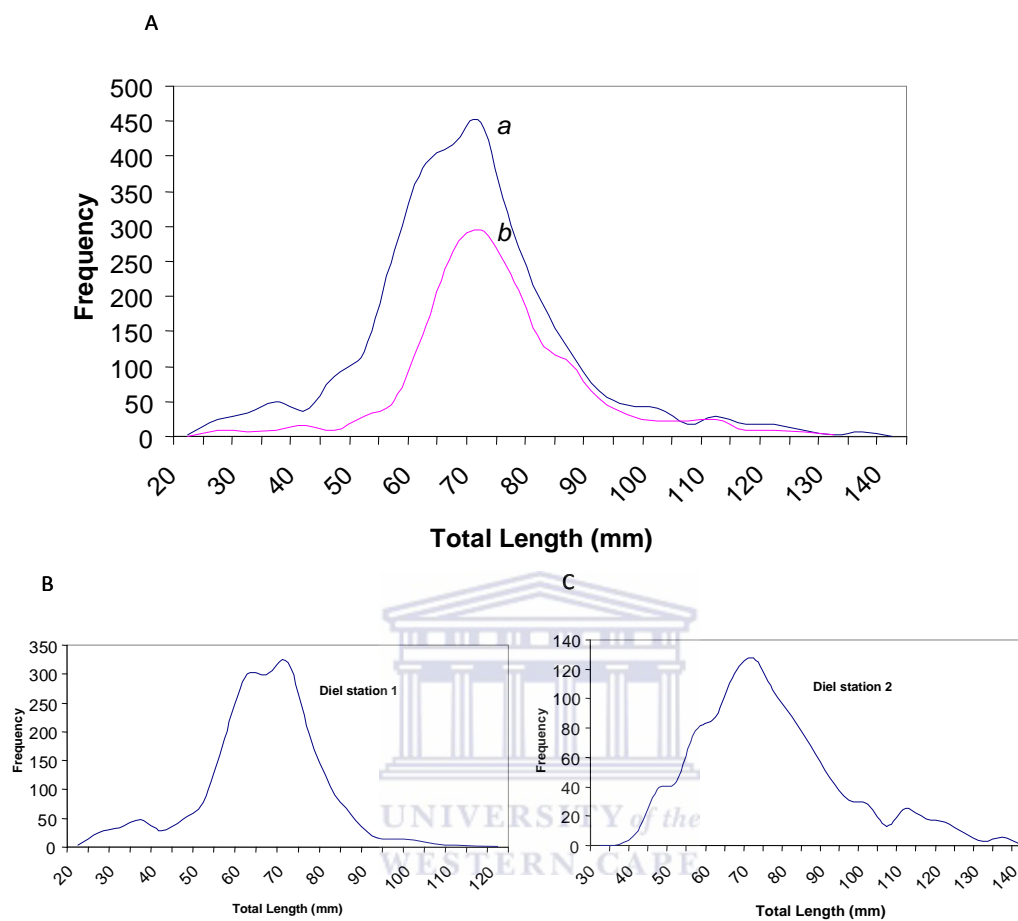


Figure 10. Length-frequency distribution of pelagic goby, *S. bibarbatus*, collected in Namibian waters over the study period of 16-20 January 2006, a) specimens measured onboard during the survey,  $n = 2743$ ; b) specimens measured in laboratory,  $n = 1485$  and summarised for diel station 1 (B) and 2 (C).



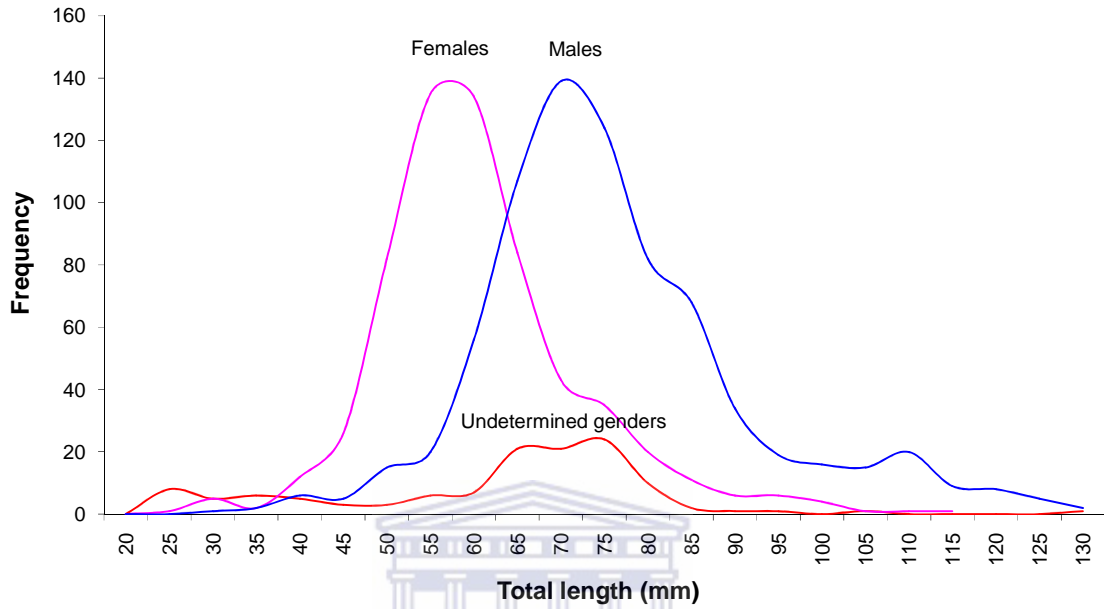


Figure 11. Length-frequency distribution of males, females and undetermined genders of *S. bibarbatus*, caught off the Namibian coast for the period of 12-20 January 2006.

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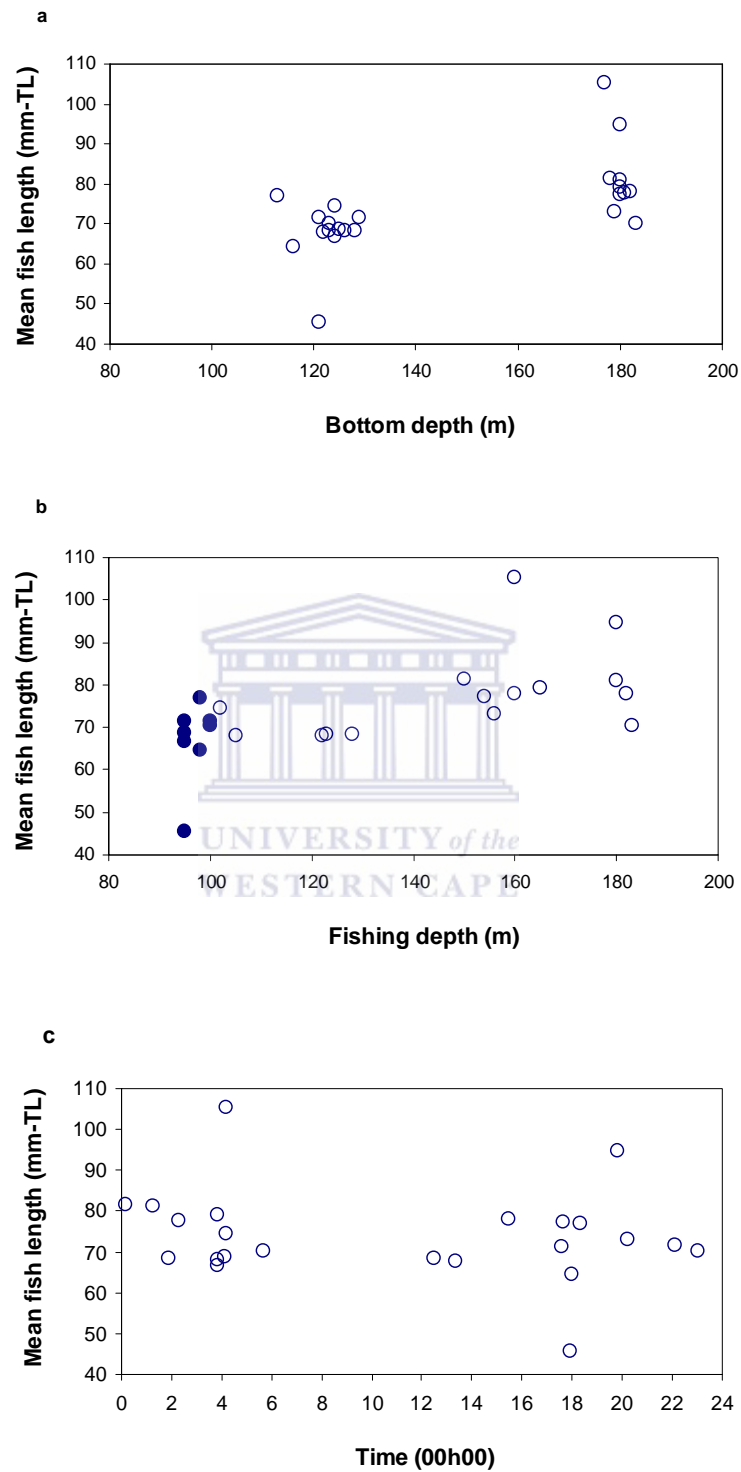


Figure 12. Mean fish length distribution plotted against bottom depth (a); fishing depth (b) and time (c) across the sampling grid in Namibian waters over the study period 12-20 January 2006. In Figure 11b closed circles (●) indicate depths less than 100 m and open circles (○) greater than 100 m.

### 3.1.4. Food versus Time of Day

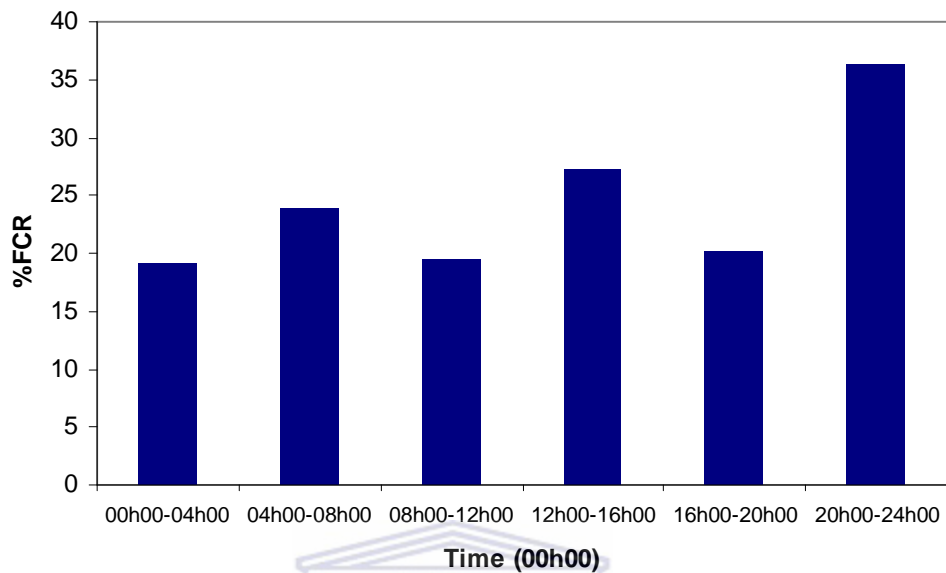
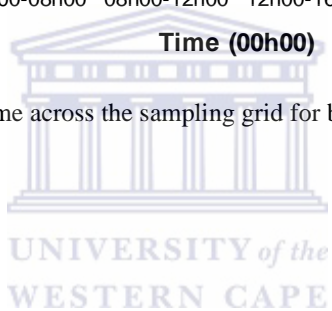


Figure 13. Changes in %FCR over time across the sampling grid for both diel stations in Namibian waters over the study period 16-20 January 2006.



### 3.1.5. Food versus Fish Lengths

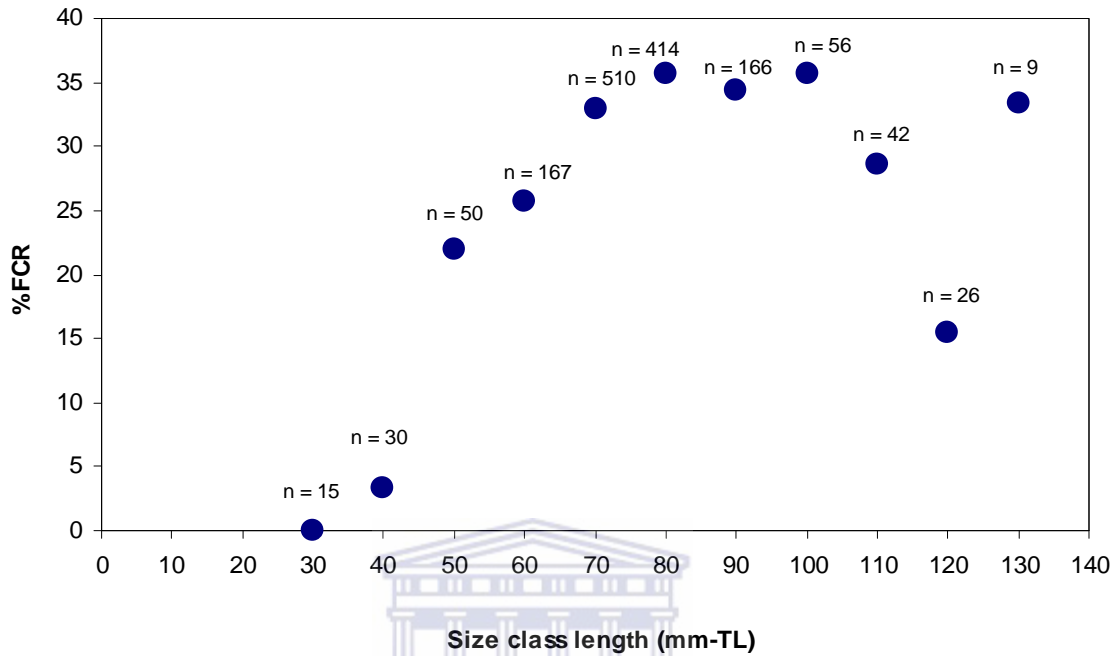


Figure 14. Changes in %FCR with size class of *S. bibarbatius* across the sampling grid in Namibian waters during the study period of 12-20 January 2006 (n = 1485).

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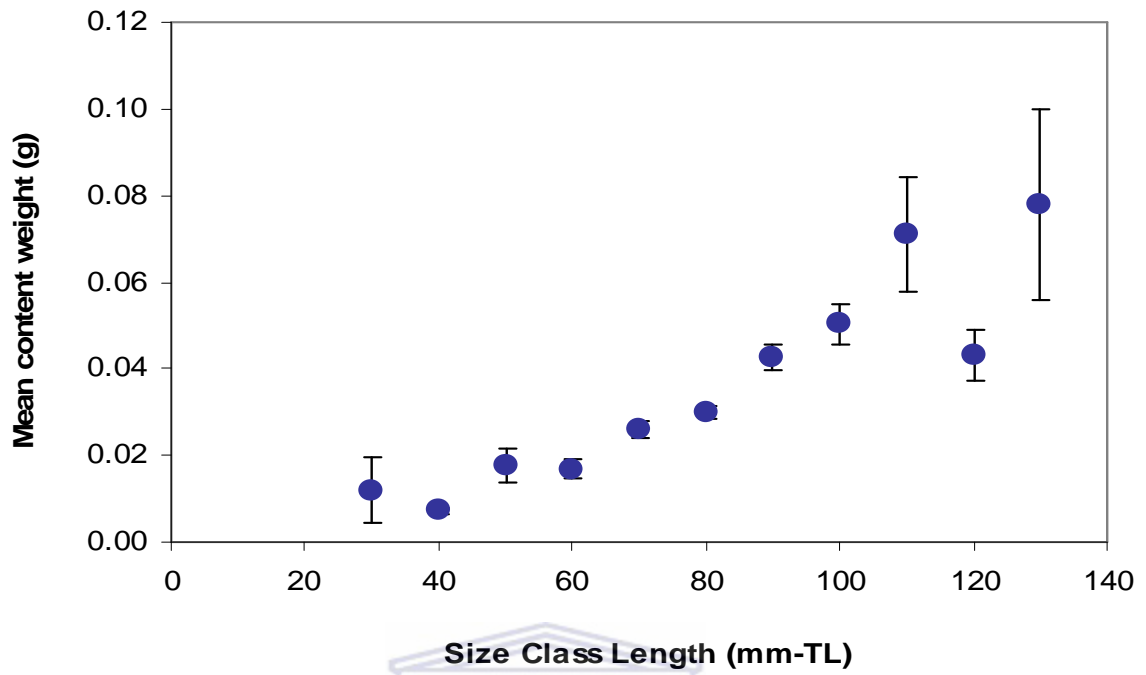
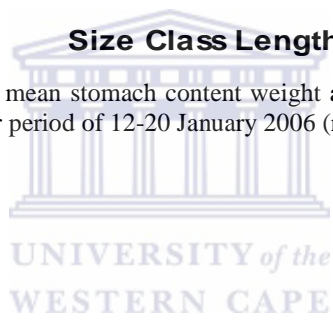


Figure 15. The relationship between mean stomach content weight and size class of *S. bibarbatius* across the sampling grid in Namibian waters for period of 12-20 January 2006 (n = 467). Error bars SE.



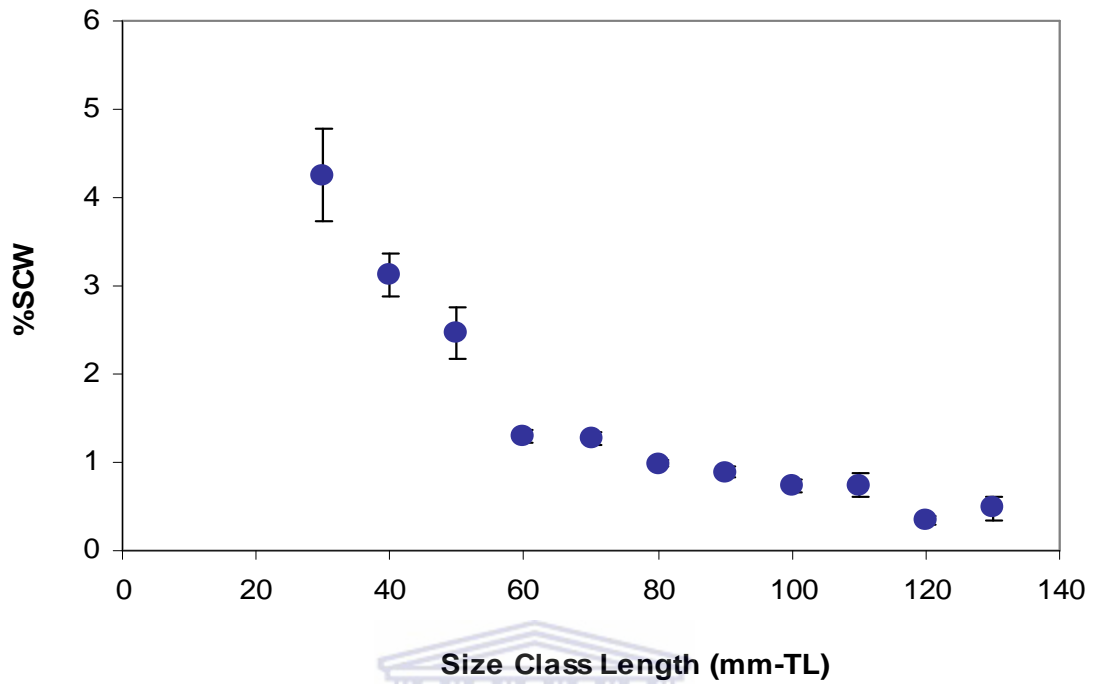
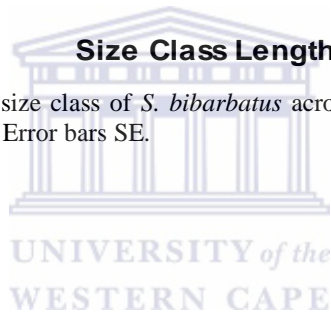


Figure 16. Changes in %SCW with size class of *S. bibarbatus* across the sampling grid in Namibian waters during 12-20 January 2006 (n = 467). Error bars SE.



### 3.1.6. Diet Composition

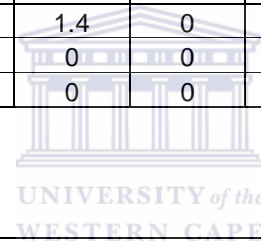
Table 4. Diet items recovered from *S. bibarbatu*s across the sampling grid in Namibian waters for period of 16-20 January 2006. %F = percentage frequency of occurrence of diet items; %N = percentage of total prey items; %V = percentage volume of main prey items; %IRI = percentage cumulative index of relative importance of main prey items.

	%F	%N	%V	%IRI
<b>Sand grains</b>	6.6			
<b>Fish scales</b>	150.7			
<b>Amphipods</b>	12.2			
<b>Amphipod fragments</b>	4.7			
<b>Amphipods + fragments</b>	14.3	8.1	61.6	30.7
<b>Copepods</b>	16.3			
<b>Copepod fragments</b>	7.1			
<b>Copepods + fragments</b>	18.6	18.0	0.1	10.4
<b>Euphausiids</b>	16.9			
<b>Euphausiid fragments</b>	13.3			
<b>Euphausiids + fragments</b>	22.9	15.4	29.2	31.4
<b>Polychaetes</b>	12.0			
<b>Polychaete fragments</b>	26.1			
<b>Polychaetes + fragments</b>	30.2	20.6	9.0	27.5
<b>Crustacean fragments</b>	23.6	12.7		
<b>Crab larvae</b>	0.2	0.1		
<b>Decapod shrimp larvae</b>	0.9	0.4		
<b>Diatoms</b>	6.0	7.3		
<b>Fish eggs</b>	1.9	3.0		
<b>Bivalves</b>	2.1	1.1		
<b>Foraminiferans</b>	1.7	1.2		
<b>Nematodes</b>	3.0	1.9		
<b>Juvenile gobies</b>	1.1	0.4		
<b>Other</b>	21.8	9.7		

### 3.1.7. Diet versus Time of Day

Table 5. Diet of pelagic goby *S. bibarbatus*, at diel stations 1 (A) and 2 (B) in Namibian waters over a 48 h study period. F% = average frequency of prey occurrence in diet; N% = average percent of total prey abundance; Time indicated along the top of the table (D1 = Day1, N1 = Night1 etc.). Data summarised by day (D) and night (N) separately, and overall.

A	Diel Station 1													
	(1668-1672)		(1676-1680)		(1688-1689)		(1693-1696)		Frequency			Numbers		
	D1 (n = 220)		N1 (n = 167)		D2 (n = 93)		N2 (n = 179)		D	N	Overall	D	N	Overall
	%F	%N	%F	%N	%F	%N	%F	%N						
Amphipods	0.8	1.5	0	0	10.0	1.4	50.3	36.1	5.4	25.1	15.3	1.5	18.1	9.8
Copepods	6.3	16.4	10.4	7.1	28.3	15.6	7.5	29.2	17.3	9.0	13.1	16.0	18.1	17.1
Euphausiids	33.1	14.9	5.4	2.8	0	0	2.2	2.8	16.6	3.8	10.2	7.4	2.8	5.1
Polychaetes	21.6	31.3	2.1	4.3	78.3	33.7	10.6	5.6	50.0	6.3	28.1	32.5	4.9	18.7
Diatoms	6.3	6.0	0	0	0	17.0	0.8	1.4	3.1	0.4	1.8	11.5	0.7	6.1
Other	21.2	22.3	32.9	67.2	20.0	23.8	25.8	25.0	20.6	29.4	25.0	23.1	46.1	34.6
Fish eggs	1.6	3.0	2.1	17.1	1.7	7.1	0	0	1.6	1.0	1.3	5.0	8.5	6.8
Bivalves	0	0	0	0	10.0	1.4	0	0	5.0	0	2.5	0.7	0	0.4
Foraminifera	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Juvenile gobies	2.3	4.8	2.1	1.4	0	0	0	0	1.2	1.0	1.1	2.4	0.7	1.5
														100



B	Diel Station 2													
	(N/A)		(1700-1708)		(1717-1721)		(1725-1729)		Frequency			Numbers		
	D1 (n = 0)		N1 (n = 236)		D2 (n = 68)		N2 (n = 111)		D	N	Overall	D	N	Overall
	%F	%N	%F	%N	%F	%N	%F	%N						
Amphipods	-	-	20.0	2.3	6.7	7.7	0	0	6.7	10.0	8.3	7.7	1.2	4.4
Copepods	-	-	0	0	0	0	2.8	1.4	0	1.4	0.7	0	0.7	0.3
Euphausiids	-	-	10.0	7.0	0	0	2.8	1.4	0	6.4	3.2	0	4.2	2.1
Polychaetes	-	-	43.3	62.8	70.0	92.3	76.0	73.0	70.0	59.7	64.8	92.3	67.9	80.1
Diatoms	-	-	0	0	0	0	0	0	0	0	0	0	0	0
Other	-	-	21.7	27.9	0	0	18.0	14.9	0	19.8	9.9	0	21.4	10.7
Fish eggs	-	-	0	0	0	0	0	0	0	0	0	0	0	0
Bivalves	-	-	0	0	0	0	0	0	0	0	0	0	0	0
Foraminifera	-	-	0	0	0	0	6.5	9.5	0	3.2	1.6	0.0	4.7	2.4
Juvenile gobies	-	-	0	0	0	0	0	0	0	0	0	0	0	0
														100



### 3.1.8. Ontogenetic changes in Diet

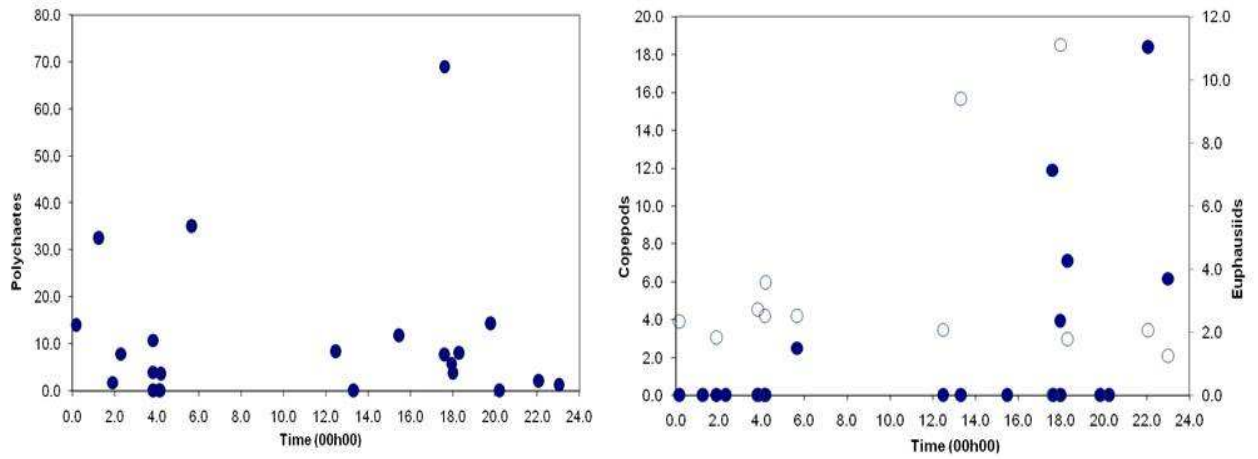


Figure 17. The percent frequency of occurrence of polychaetes (a), copepods (●) and euphausiids (○) (b) over time across the sampling grid in Namibian waters over the study period 16-20 January 2006.



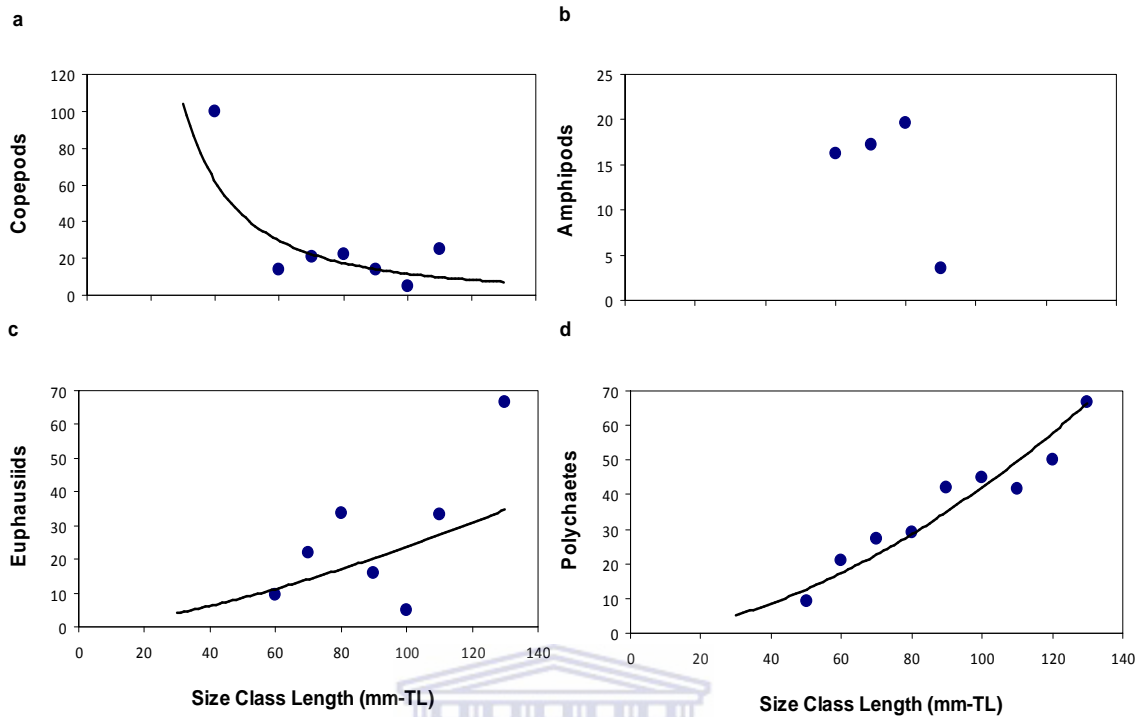


Figure 18. The percent frequency of occurrence of the key groups in diet of *S. bibarbatus* by size class for copepods (a), amphipods (b), euphausiids (c), and polychaetes (d) across the sampling grid, in Namibian waters during the period of 16-20 January 2006. Power function for the correlation between TL and copepods:  $TL = 51124x^{-1.8214}$ ,  $r^2 = 0.4923$ , euphausiids:  $TL = 0.0284x^{1.46}$ ,  $r^2 = 0.1995$  and polychaetes:  $TL = 0.0142x^{1.7355}$ ,  $r^2 = 0.9035$ .

### 3.2.1. Study 2: Observations on Fish Size

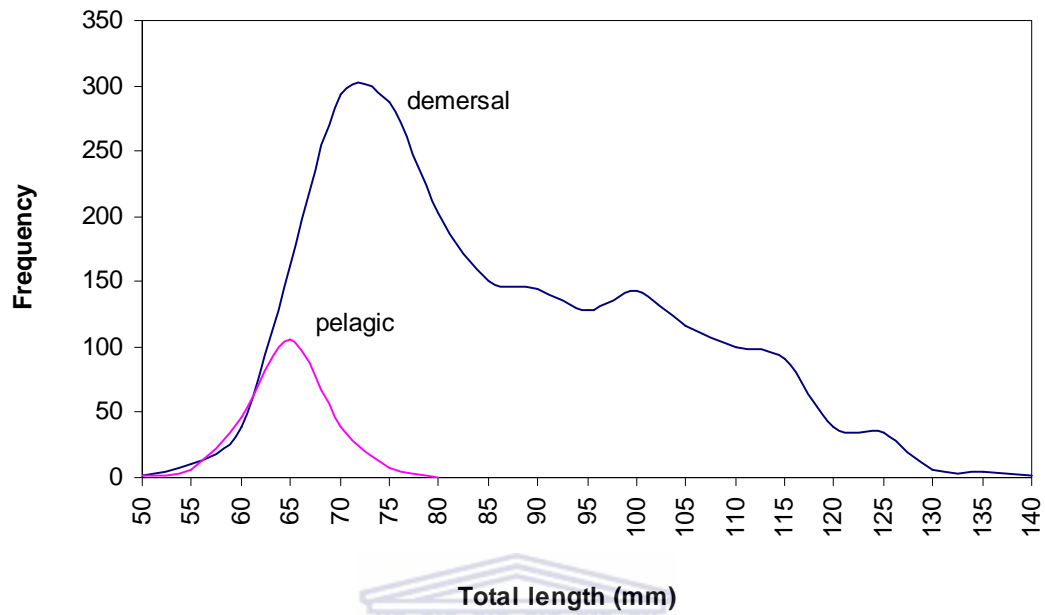
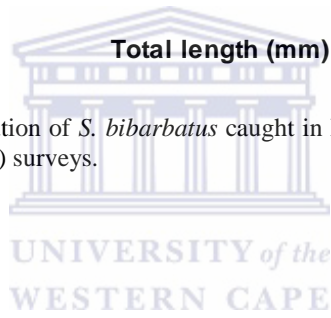


Figure 19. Length-frequency distribution of *S. bibarbatus* caught in Namibian waters, for the pelagic (2002, n = 204) and demersal (2001, n = 1955) surveys.



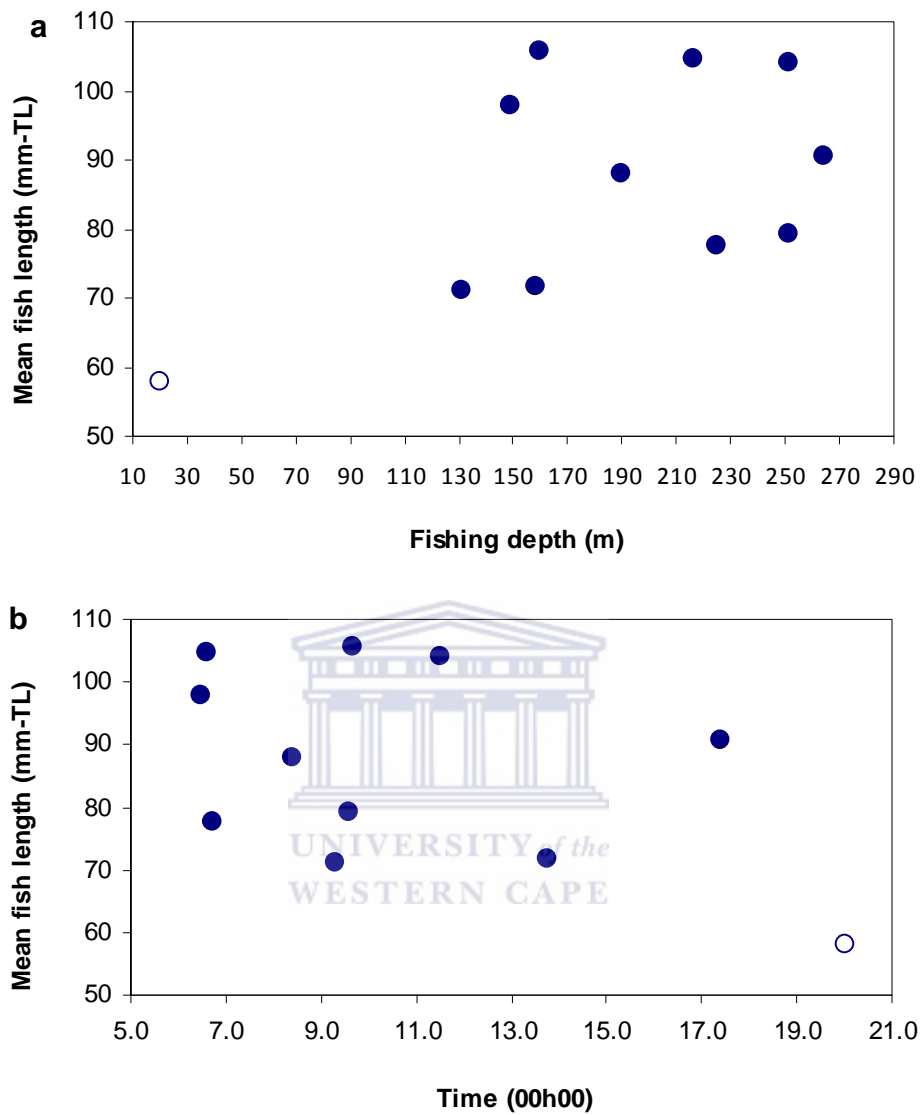


Figure 20. Mean fish length distribution of the pelagic goby plotted against fishing depth (a) and time (b) for the period of the pelagic (2002, (○)) and demersal (2001, (●)) surveys in Namibian waters.

### 3.2.2. Food versus Time of Day

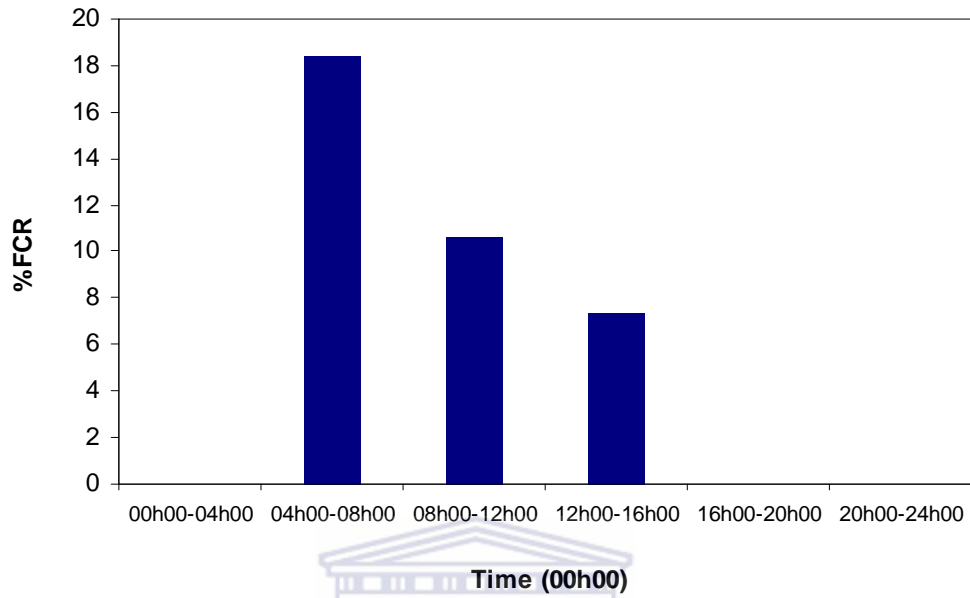
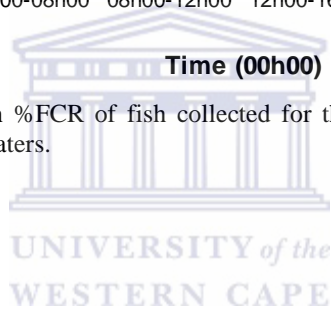


Figure 21. The comparison between %FCR of fish collected for the period of the demersal survey (2001) during daytime hours in Namibian waters.



### 3.2.3. Food versus Fish Lengths

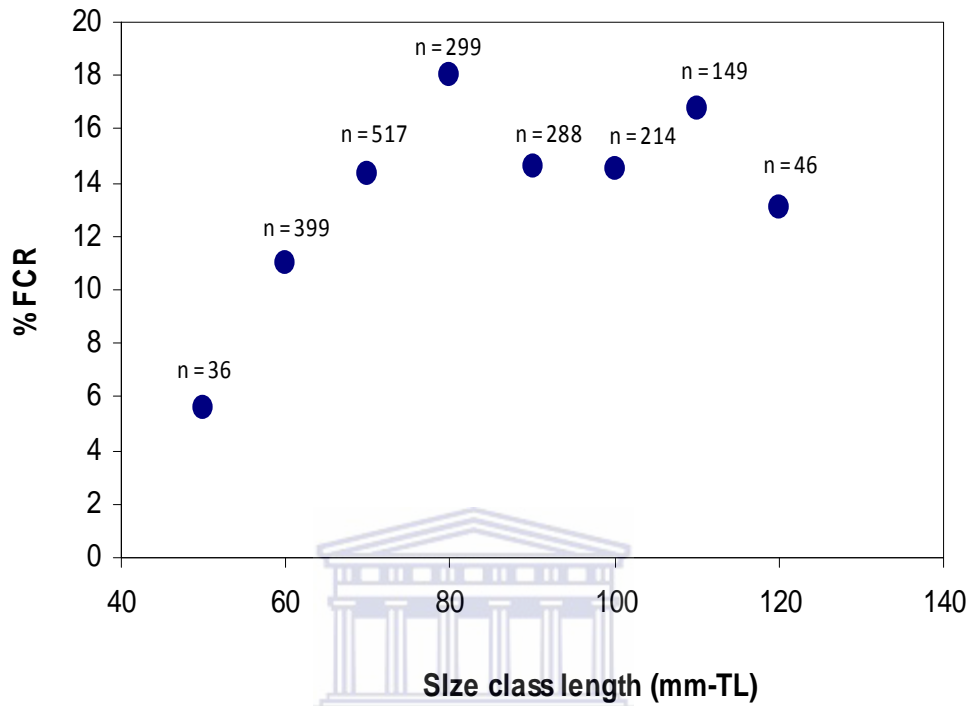


Figure 22. The changes in %FCR of *S. bibarbatus* collected off the Namibian coast in 2001 for the duration of the demersal survey (n = 1955).

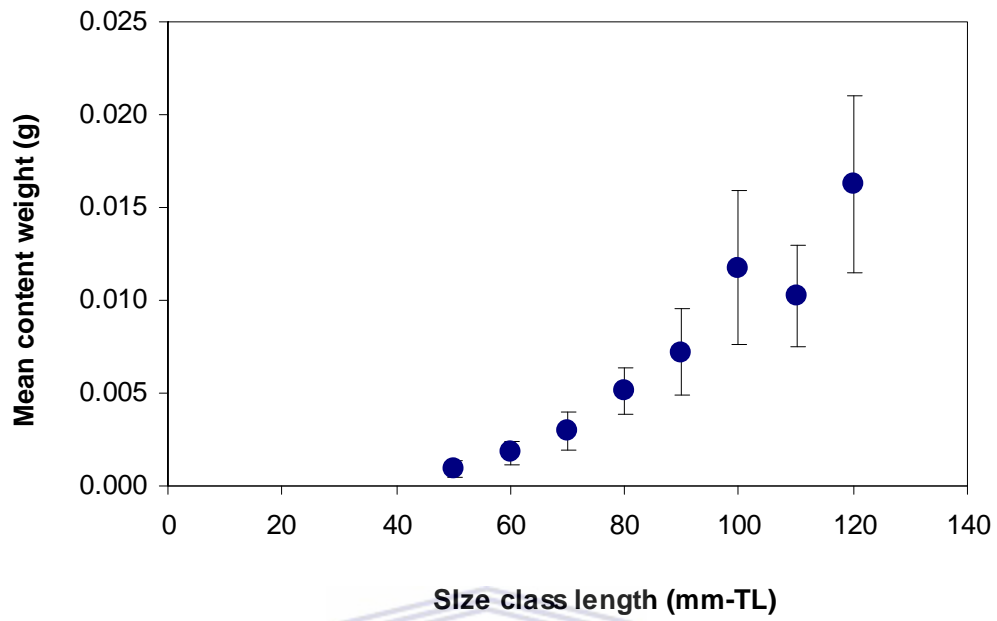
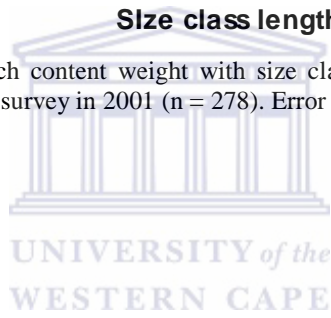


Figure 23. Changes in mean stomach content weight with size class of *S. bibarbatius* caught in Namibian waters for the period of the demersal survey in 2001 (n = 278). Error bars SE.



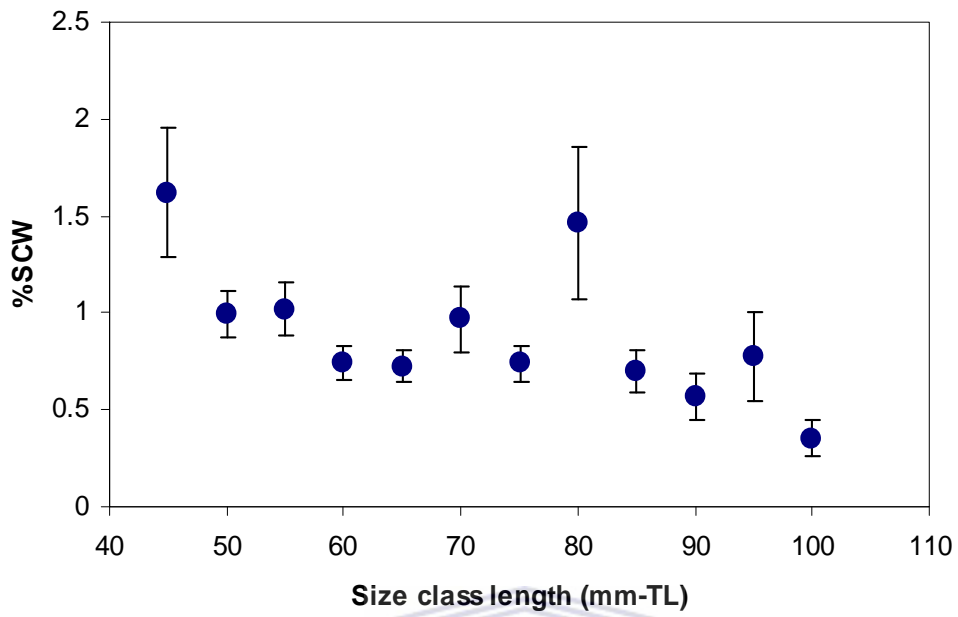
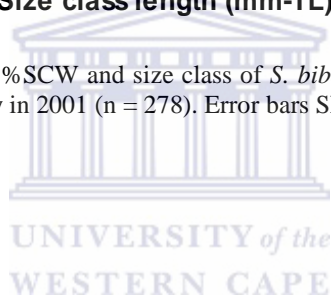


Figure 24. The comparison between %SCW and size class of *S. bibarbatus*, collected off the Namibian coast for the duration of the demersal study in 2001 (n = 278). Error bars SE.





### 3.2.4. Diet Composition

Table 6. Diet items recovered from *S. bibarbatus* collected off the Namibian coast for the period of the demersal survey in 2001. %F = percentage frequency of occurrence of diet items; %N = percentage of total prey items.

	<b>%F</b>	<b>%N</b>
<b>Sand Grains</b>	30.8	
<b>Amphipods</b>	1.1	1.9
<b>Euphausiids</b>	13.1	18.2
<b>Polychaetes</b>	15.0	
<b>Polychaete fragments</b>	13.1	
<b>Polychaetes + fragments</b>	24.4	37.4
<b>Crustacean Fragments</b>	25.8	29.7
<b>Bivalves</b>	2.2	3.5
<b>Juvenile gobies</b>	1.1	1.3
<b>Other</b>	6.9	8.0



Table 7. The diet items recovered from *S. bibarbatus* during the pelagic survey off the Namibian coast in 2002. %F = percentage frequency of occurrence of diet items; %N = percentage of total prey items.

	<b>%F</b>	<b>%N</b>
<b>Copepods</b>	73.6	93.1
<b>Cumaceans</b>	38.7	5.6
<b>Amphipods</b>	7.5	0.3
<b>Polychaetes</b>	1.9	0.0
<b>Euphausiids</b>	0.9	0.0
<b>Crustacean Fragments</b>	26.4	0.5
<b>Juvenile gobies</b>	15.1	0.3
<b>Other</b>	2.8	0.1



### 3.2.5. Ontogenetic changes in Diet

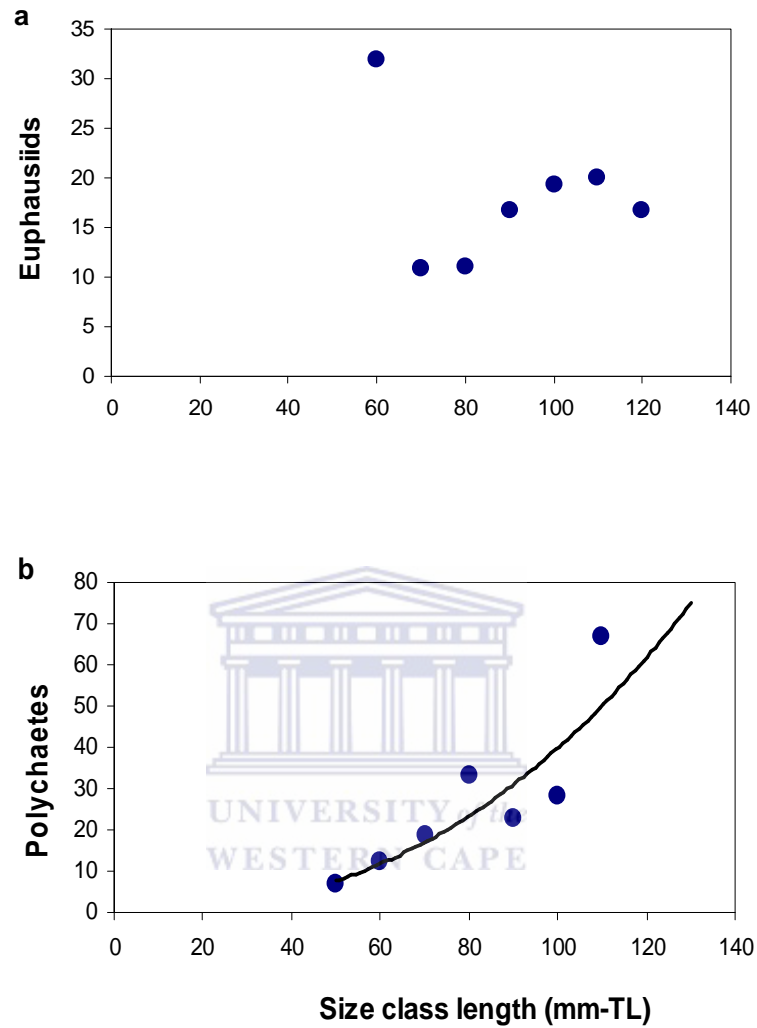


Figure 25. The percent frequency of occurrence of key groups: euphausiids (a) and polychaetes (b) found in the gut of *S. bibarbatus*, caught off the coast of Namibian during the demersal survey (2001). Power function for the correlation between TL and polychaetes:  $TL = 0.0006x^{2.3998}$ ,  $r^2 = 0.8589$ .