DIURNAL AND NOCTURNAL ACTIVITY PATTERNS AND HABITAT USE OF ALGOA BAY'S ROCKY REEF FISH COMMUNITY

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ABSTRACT

Distinct day-night changes in ambient light are recognised as an important driver of animal activity patterns, with predictable changes to the structure and composition of animal communities between day and night. While day-night variation in the structure of animal communities has been well researched for terrestrial organisms and shallow marine fish communities around the world, there has been limited research of this type conducted on South Africa's rocky reef fish communities. Consequently, we have a poor understanding of how nocturnal reef fish communities are structured and the day-night activity patterns of species inhabiting both shallow (10-30m) and deep-aphotic (55-100m) reefs.

This research was conducted at two warm-temperate South African rocky reefs situated in Algoa Bay. The importance of natural ambient light in shaping the distribution of reef fish communities at shallow and deep-aphotic reef sites was demonstrated using baited remote underwater stereo-video systems (stereo-BRUVs). Distinct day and night fish communities were sampled at shallow and deep-aphotic reef sites. These differences were driven by significant changes in species richness ($p < 0.001$), species abundance ($p < 0.001$) and community composition ($p < 0.001$). These shifts appeared to be driven by day-night activity patterns that were the result of increased detectability of certain species at either day or night. The majority of species belonging to the family Sparidae showed evidence of strict diurnal activity, with their activity being further restricted to shallow reefs. These species showed evidence that they may enter micro-habitats within the reef at night. Similar activity patterns were shown for other top predatory teleost species and low level consumers, with substantial reductions in abundances, or no recordings at night throughout this study. Shallow reefs at day harboured the most diverse fish community. It is therefore hypothesised that this habitat was associated with conditions that offered improved access to resources for many visual species. In addition, the diverse community inhabiting shallow reefs at day is associated with a high risk of negative interspecies interactions, such as competition and predation. It is hypothesised that the biotic conditions associated with shallow reefs at day drove three movement patterns identified in this study; *Pagellus bellottii natalensis* showed evidence of movement onto shallow reefs at night from adjacent sandy flats, while *Pterogymnus laniarius* and *Squalus* sp. 1 showed evidence of movement onto shallow reefs at night from the deep-aphotic reefs that remain dark throughout the diel cycle. It is further hypothesised that other species which showed evidence for nocturnal activity, i.e. *Galeichthys ater, Eptatretus* *hexatrema* and *Haploblepharus edwardsii,* may enter sheltered micro-habitats within the reef during day light hours. These findings have highlighted the complex patterns that have evolved within marine fish to allow multiple species to coexist and exploit productive reef ecosystems by partitioning resource use and activity patterns at day or night, between depth zones and habitat types.

Keywords: Marine ecology, stereo-BRUVs, rocky reef fish, diurnal, nocturnal, movement, remote video

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DECLARATION

The following thesis has not been submitted to a university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of the author unless otherwise stated.

1 GENERAL INTRODUCTION

1.1 PROBLEM IDENTIFICATION

Research focused on how diurnal and nocturnal marine fish communities compare typically lags behind that on terrestrial vertebrates (Fox & Bellwood, 2011). This is because, globally, ecological studies investigating marine fish communities have predominantly focused on diurnal communities (Sale, 1991; Hammerschalg *et al.*, 2017). As a result, much of what we know about marine species in response to the diel cycle is based on the extensive literature available for diel patterns of terrestrial vertebrates (Kronfeld-Schor & Dayan, 1999; Kronfeld-Schor & Dayan, 2003; Birt *et al.*, 2012; Ferreras *et al.*, 2013; Marti *et al.*, 2016; Grácio *et al.*, 2017). The disproportionate amount of research conducted on terrestrial versus aquatic vertebrates (Turpie *et al.*, 2000) is largely attributed to the logistical, safety and technological challenges of sampling aquatic habitats in darkness (Ross, 1986; Hammerschlag *et al.*, 2017). In addition to this, there are a number of challenges associated with observing fish in darkness in an unobtrusive manner (Axenrot *et al.*, 2004; Fitzpatrick *et al.*, 2013). For these reasons, nocturnal fish communities and those inhabiting deep-aphotic marine habitats are considered to be relatively poorly understood despite there being a general consensus that observations in the day are likely to differ markedly from those made at night (Hammerschlag *et al.*, 2017). Deep-aphotic marine habitats are defined here as benthic habitats that are characterised by continuous, or semi-continuous, aphotic conditions irrespective of the diel cycle.

Research of South Africa's fish communities follows this same global trend. Our current understanding of these marine fish assemblages is predominantly based on the findings of studies that have been limited to diurnal sampling. From the few studies that have conducted diel research in a range of marine habitats elsewhere, the importance of including nocturnal sampling in fish surveys and monitoring programmes has been highlighted (Helfman, 1978; Azzuro *et al.*, 2007; Harvey *et al.*, 2012a; Fitzpatrick *et al.*, 2013). Nocturnal species are proposed to make up one third of all fish communities (Helfman, 1978), and are therefore important components of ecosystems warranting focussed research. The paucity of nocturnal research on reef fish has led to concerns being raised regarding the progression of our ecological understanding of these communities (Jadot *et al.*, 2002). It has been suggested that neglecting the night may produce misleading results, if ecological patterns and processes of these nocturnal fish communities do not reflect those observed at day (Carpentieri *et al.*, 2005; Fitzpatrick *et al.*, 2013). Furthermore, our knowledge gap may have important implications for the protection of fish communities (Lewis *et al.*, 1996) and the provision of ecological baselines for future management efforts. There are further associated implications for the sustainability of livelihoods and food provision from a fisheries management perspective. It is likely that including night time sampling in fish community studies will provide a more comprehensive ecological understanding of the dynamics of these communities, and may facilitate management and conservation efforts.

1.2 ANIMAL COMMUNITIES AND THEIR RESPONSE TO THE DIEL CYCLE

Day-night variation in animal communities is a widespread phenomenon (Okun *et al.*, 2005). Studies conducted across a vast geographic range have demonstrated that contrasting aquatic and terrestrial habitats support distinct day and night animal communities (Rooker & Dennis, 1991; Rooker *et al.*, 1997; Nagelkerken *et al.*, 2000; Harvey *et al.*, 2012b). These day-night shifts are generally described in terms of species diversity (Molles & Cahill, 1999). This is conducted by measuring attributes that make up the community structure, such as the types of species present (*species composition*), the number of species present (*species richness*) and the number of individuals present per species (*species abundance*; Molles & Cahill, 1999).

Studies investigating animal responses to the diel cycle have demonstrated that observed day-night changes in community structure are caused by species-specific behavioural responses to the diel cycle (Helfman, 1986). These responses generally involve changes in the timing of species' activities according to the 24-hour diel cycle (Helfman, 1986). The way species distribute their activities throughout the diel cycle is described as a diel activity pattern (Hammerschlag *et al.,* 2017). In reef fish communities, the majority of species are visual foragers and adopt a diurnal lifestyle, meaning they are primarily active at day (Hobson, 1974; Schmitz & Wainwright, 2011). The recent increase in day-night research focused on marine fish communities has demonstrated that many reef fish species are primarily active at night (nocturnal; Hammerschlag *et al.,* 2017). These nocturnal species are rarely investigated and this may leave us with an incomplete ecological understanding, with their movement patterns and community dynamics being largely unknown (Hammerschlag *et al.,* 2017). Hammerschlag *et al.* (2017) has revealed the importance of including nocturnal assemblages in studies as this gap in the knowledge may have implications for effective conservation and management.

The day-night activity pattern of a species is determined by its endogenous circadian rhythm (Kronfeld-Schor & Dayan, 2003). This rhythm, otherwise referred to as the biological clock, is an internal, typically hormone regulated mechanism that controls the behaviour and biological processes of an organism according to a 24-hour rhythm (Fox & Bellwood, 2011). Biological clocks are entrained by certain environmental conditions that act as cues (Fox & Bellwood, 2011). Of these environmental cues, the predictable day-night change in ambient light is considered to be the ultimate factor responsible for establishing biological clocks and is thus important in determining animal activity patterns (Kronfeld-Schor & Dayan, 2003). It is important to note that investigations into the concept of biological clocks of organisms are outside the scope of this thesis. This thesis is rather concerned with uncovering the role of ambient light in determining species activity patterns and structuring of fish communities (Kronfeld-Schor & Dayan, 2003).

Distinct day-night changes in ambient light affect the ability of species to access their required resources and carry out their basic activities (Helfman, 1978). The way ambient light influences species' activities and their access to resources, varies according to their visual capacity, ecological position (i.e. trophic level, resource strategy, life history trait) and their physiological and morphological adaptations to differences in ambient light (Pankhurst, 1989; McFarland, 1991; Warrant, 2004; Annese & Kingsford, 2005; Azzuro *et al.*, 2007; Becker *et al.*, 2011; Birt *et al.*, 2012; Harvey *et al.*, 2012a). For example, a visual feeder may have a reduced foraging efficiency at night. These biological attributes that vary across species, may act as constraints and thus limit an organisms' ability to carry out their activities at certain times of the diel cycle (Kronfeld-Schor & Dayan, 2003).

Day-night activity patterns are further influenced by other environmental factors. For example, temperature or ecological characteristics such as the availability of a resource (KronfeldSchor & Dayan, 2003), otherwise referred to as masking factors, vary across space and are unique according to local settings (Fox & Bellwood, 2011). It is therefore unlikely that the timing at which species carry out their activities is consistent between different habitats or geographic locations. As a result, species' activity patterns are often complex, and require ecosystem and species-specific investigation.

The activities that make up a species' day may include all those necessary for survival. While some activities ensure energy gains (feeding) and preservation (resting), others are carried out to reduce the risk of mortality (i.e. interference and exploitative species' interactions; Fernandez-Duque, 2003). There are a number of other important activities that a species conducts to ensure survival. These include seeking mates, reproducing, spawning and guarding territories (Fernandez-Duque, 2003). Feeding and avoiding negative interspecies interactions, however, are considered to be the most important activities when describing and explaining diel activity patterns of animals (Arrington & Winemiller, 2003).

The ecological concept of trade-offs between maximising energy gains and minimising mortality risk is well accepted as the driver of species' diel activity patterns and other behavioural strategies (Stephens & Krebs, 1986). For example, species may change the timing of certain activities to ensure optimal feeding (Rooker & Dennis, 1991; Piet & Guruge, 1997) and minimise the risk of predation (Wright, 1989). Hobson (1974) showed that the majority of diurnal species on a coral reef forage by day and avoid predation at night by becoming inactive and entering sheltered reef sites. Similarly, nocturnally active species seek refuge in reef caves during day-light hours, or adopt schooling behaviours (Hobson, 1974). Seeking refuge in physical shelter provided by the habitat that a species occupies or seeking 'safety in numbers' are common predator avoidance strategies in animal communities (Molles & Cahill, 1999). Alternatively, some species conduct inter-habitat movements, referred to as commuting (Dingle *et al.*, 1996), and this has been described for many reef fish species including the white trevally (*Pseudocaranx dentex*; Afonso *et al.*, 2009). In this, species move between habitats that differ in terms of resources, and selection of habitat depends on ambient light and a species' ability to maximise energy gains and minimise mortality under those conditions. These movements are therefore frequently described to be a result of ecological trade-offs between optimal foraging and reducing negative species interactions (Hitt *et al.*, 2011; Harvey *et al.*, 2012b; Grácio *et al.*, 2017).

These changes in species' activities throughout the day may also be thought of as changes in their resource use. Species of a community separate their resource use according to three dimensions, either according to spatial, trophic and temporal scales (Schoener, 1974). For example, spatial resource partitioning may occur when species with overlapping diets separate their foraging activities by occupying different habitats (Bangley & Rulifson, 2017). Trophic partitioning may occur when species that share a habitat avoid competition by feeding on different food items (Bangley & Rulifson, 2017). In partitioning resources between periods of the diel cycle, species may avoid interference competition or exploitative competition for limited resources (Kroner-Schor & Dayan, 2009; Reebs, 2003). While this study is largely concerned with diel partitioning of resources, it is also concerned with the spatial dimension. This type of resource partitioning is described as spatio-temporal partitioning (Guidetti & Boero, 2009; Bangley & Rulifson, 2017) and commuting would be an example of this. Investigating resource use by species provides important insight into the coexistence of multiple species in communities (Molles & Cahill, 1999). This is because resource partitioning allows predator and prey species to coexist (Schoener, 1974), and reduces interference competition between species that require similar resources (i.e. species that have similar ecological niches; Piet & Guruge, 1997; Connell, 1980). This basic ecological information can therefore provide a more comprehensive understanding of the functioning of the community.

1.3 AIMS

This thesis aimed to investigate the importance of natural ambient light in shaping the distribution of warm-temperate rocky reef fish communities at shallow and deep-aphotic reef sites in Algoa Bay, South Africa. Other environmental and biotic factors influencing observed reef fish assemblages are also explored. Particular emphasis is placed on diel activity patterns and whether these patterns result in observable differences in fish assemblages. The possibility of day-night movement patterns between shallow and deep-aphotic reef sites, due to species-specific patterns of detectability are also investigated.

1.4 RESEARCH APPROACH

The relatively slow progression of day-night research on marine compared to freshwater and terrestrial animals is attributed to the particular challenges associated with sampling marine habitats (Harvey *et al.*, 2012a; Fitzpatrick *et al.*, 2013). Technological advances and the realisation of the importance of including nocturnal sampling has resulted in a number of methods for studying fish in aphotic conditions, including the use of underwater cameras fitted with an artificial light source (Hammerschlag *et al.*, 2017).

Baited remote underwater stereo-video systems are a relatively novel sampling technique that improve access to marine species, especially those inhabiting reefs, by reducing the reliance on observers underwater. As such, stereo-BRUVs have provided an opportunity to investigate the relationship between the diel cycle and shallow and deep rocky reef fish communities within South Africa (Whitmarsh *et al.*, 2017). This is the first study to use stereo-BRUVs as a nocturnal sampling technique in South Africa. Furthermore, to our knowledge, the application of stereo-BRUVs to indirectly investigate fish movement by sampling along a depth gradient has not been conducted elsewhere.

1.4.1 TRADITIONAL SAMPLING TECHNIQUES VERSUS STEREO-BRUVS

Underwater video techniques are relatively new and have gained considerable support over recent years as a method for sampling demersal fish assemblages in South Africa (Bernard & Götz, 2012; Bernard *et al.*, 2014; Parker *et al.*, 2016) and elsewhere (Gladstone *et al.*, 2012; Harvey *et al.*, 2012a, 2012b; Langlois *et al.*, 2010; Unsworth *et al.*, 2014). This is because they overcome some of the limitations and potential biases associated with traditional sampling methods (Cappo *et al.*, 2003).

Fishery dependent techniques, such as demersal trawls, angling and fish traps are common nocturnal sampling methods, particularly for pelagic species and those inhabiting soft bottom habitats (Mallet & Pelletier, 2014). There is, however, some concern about the data collected by these methods when comparing diurnal and nocturnal assemblages. For example, day-night variation in the distribution and abundance of species has been shown to affect the efficiency of capture techniques such as trawls and seines (Sissenwine & Bowman, 1978; Walsh, 1989; Casey & Meyers, 1998; Petrakis *et al.*, 2001). From a research point of view, this has important implications when fishery dependent techniques are used as sampling methods to investigate fish species and communities due to differential catchability (Fabi & Sala, 2002).

Day-night changes in behaviour and distribution of fish and how this affects their susceptibility to fishing gear has been demonstrated for many demersal species (Sissenwine & Bowman, 1978; Casey & Myers, 1998; Petrakis *et al.*, 2001). In addition to changes in distribution, ambient light plays a role in affecting the catchability of a species as their ability to detect and avoid fishing gear changes between day and night, depending on species-specific visual capacities (Carpentieri *et al.*, 2005). These changes were found to produce misleading results and provide a flawed perception of fish stocks (Rooker & Dennis, 1991; Azzuro *et al.*, 2007). For these reasons, and the inherent selectivity of these capture techniques (Harvey *et al.*, 2012b), fishery dependent techniques were considered to be unsuitable for this study that aims to investigate the day-night responses for multiple reef fish species separately.

Of the fishery-independent techniques, diver conducted underwater visual censuses (UVCs) are commonly used to investigate fish communities at shallow marine habitats (Mallet &

Pelletier, 2014), particularly at reefs with a high habitat complexity (Thresher & Gunn, 1986). Data collected by this method may be biased by the presence of a diver in the water as this has been shown to alter fish behaviour (Kulbicki, 1998; Lindfield *et al.,* 2014; Gray *et al.,* 2016). Another important source of bias may result from variability in observations among multiple divers and errors due to limited observer experience (Kulbicki *et al.*, 2010). In terms of this study, the most important limitation of UVCs was that they are restricted to depths that are safe for SCUBA activity (usually < 30m; Murphy & Jenkins, 2011). This particular limitation makes the UVC method inappropriate for this research project that also investigates depth effects on fish communities.

1.4.2 BAITED REMOTE UNDERWATER STEREO-VIDEO SYSTEMS

The general principle underlying stereo-BRUVs involves the use of bait to attract fish into the overlapping field of view of two stereo-video cameras, where they can be identified, counted and measured (Cappo *et al.*, 2003). Counts of species and individuals provides information on composition, species richness and relative abundance (Mallet & Pelletier, 2014). An important advantage of this method is the application of bait as it generally increases the number of species and individuals in the cameras fields of view (Watson *et al.*, 2010). Attraction of fish to the cameras ensures increased abundances are consistently recorded among samples (Mallet & Pelletier, 2014). This is associated with reduced variability in the data resulting in higher diagnostic power (Mallet & Pelletier, 2014). As a result, using bait reduces the sampling effort required without jeopardising the diagnostic power of the data set (Mallet & Pelletier, 2014).

Baited remote underwater stereo-video systems have been acknowledged as a particularly effective method for sampling large mobile predators and generalist carnivores (Willis & Babcock, 2000; Watson *et al.*, 2005; Harvey *et al.*, 2007). The wide area surrounding the bait canister provided by a horizontally oriented stereo-BRUVs provides an opportunity to observe species that are attracted to the bait, as well as those that don't directly approach the bait canister (Mallet & Pelletier, 2014). The method is therefore also efficient at recording herbivorous and omnivorous species as they tend to be attracted to the activity around the bait in a process called 'the sheep effect' (Watson *et al.*, 2005; Harvey *et al.*, 2007; Watson *et al.*, 2010). Baited remote underwater stereo-video systems have been considered a viable method to investigate a wide range of fish species making up marine communities (Cappo *et al.*, 2004, 2007; King *et al.*, 2006; Harvey *et al.*, 2007; Shortis *et al.*, 2009; Murphy & Jenkins, 2010).

Studies that have used this method in South Africa, have shown that stereo-BRUVs effectively sample all components of warm temperate rocky reef fish communities (Bernard & Götz, 2012; Bernard *et al.*, 2014; Parker *et al.*, 2016; Heyns-Veale *et al.*, 2016).

The ability of stereo-BRUVs to sample multiple components of the fish community is a major advantage of this method over fishery dependent techniques. Furthermore, underwater video techniques may overcome the potential biases associated with traditional sampling techniques. Baited remote underwater stereo-video systems provide a means to investigate fish in their natural habitat in a less intrusive way than diver conducted UVCs or extractive fishing techniques (Mallet & Pelletier, 2014). There is no need for a human observer underwater while sampling is being conducted (Mallet & Pelletier, 2014). Furthermore, the video sample provides a permanent record which may be referred to if there is a possibility that observer bias entered the analysis while at the same time facilitating the implementation of quality control procedures (Bernard, 2012). The housings in which the cameras are held, may be designed to withstand extreme pressure changes associated with deep deployments.
As a result, stereo-BRUVs are able to overcome the depth limitations experienced by UVC.

1.4.2.1 LIMITATIONS ASSOCIATED WITH STEREO-BRUVS

A number of limitations are associated with stereo-BRUVs. For example, cryptic and small species are poorly sampled by this method compared to UVCs (Watson *et al.*, 2010). While this was a limitation for this study, warm-temperate rocky reefs harbour few cryptic species and their omission from the dataset was not considered to be overly influential. Water visibility also poses a potential limitation to all visual techniques including stereo-BRUVs and UVC compared to capture techniques (Mallet & Pelletier, 2014). Bait imposes a number of disadvantages too, including the potential influence of bait on fish behaviour (Bernard, 2012). Furthermore, difficulties in quantifying the size and direction of the bait plume in shallow coastal environments is an important limitation of stereo-BRUVs as the area sampled is usually unknown or difficult to quantify (Mallet & Pelletier, 2014). As a result, count data collected from stereo-BRUVs is difficult to standardise by the area sampled (Bernard, 2012). The extensive post sampling analysis time associated with this technique can also be considered a disadvantage (Mallet & Pelletier, 2014), however, time in the field is considered more expensive than that in the laboratory (Bernard & Götz, 2014). Since all sampling techniques are associated with biases and limitations (Mallet & Pelletier, 2014), it is acknowledged that no single technique is able to provide information on all fish species (Willis & Babcock, 2000). Certain methods are however more appropriate for particular research objectives (Mallet & Pelletier, 2014). Motivation for the use of stereo-BRUVs as the research approach was determined by relating key advantages associated with this method to the objectives of this study.

1.4.2.2 EVALUATION OF THE APPLICABILITY OF STEREO-BRUVS

Baited remote underwater stereo-video systems have recently been refined as a sampling method to investigate fish communities inhabiting aphotic environments. Researchers using stereo-BRUVs have successfully sampled deep water fish assemblages (Bailey *et al.*, 2007; Heyns-Veale *et al.*, 2016), and the last two decades have seen BRUVs being used at night (Whitmarsh *et al.*, 2016). In studies by Svane *et al.* (2008) and Svane & Barnett (2008), nocturnal BRUVs have proven to effectively sample nocturnal fish assemblages, and are particularly effective at distinguishing between diurnal and nocturnal assemblages. Similarly, a more recent publication that compared diurnal and nocturnal assemblages across six contrasting shallow coastal habitats also revealed that BRUVs are effective at discerning day-night variation in these communities (Harvey *et al.*, 2012b)

Cappo *et al.* (2004) conducted the first nocturnal fish survey using BRUVs along the Great Barrier Reef on the east coast of Australia by fitting the systems with a light source. The research aimed at comparing the latter technique with prawn trawls, and showed that remote underwater video techniques are more accurate at surveying the nocturnal fish community, with larger mobile species from a wider size range (Cappo *et al.*, 2004). The large, mobile species that tend to avoid SCUBA divers and fishery-dependent techniques are a key component to the present study. These results suggest that stereo-BRUVs are better suited to assess fish assemblage changes in relation to the diel cycle than traditional sampling techniques.

The majority of nocturnal fish species that have been investigated have shown that they possess light sensitive cells within their retina, called cones and rods with a spectral sensitivity range of 525-620nm (Von der Emde *et al.*, 2004). Infrared (>700nm) light is considered the ideal artificial light source for sampling animal communities (Widder *et al.*, 2005). It is predicted to have the lowest potential impact on species' behaviour as its wavelength is well beyond the visual spectrum of most animals. Infrared is, however, unsuitable for marine sampling as it attenuates rapidly in water and thus significantly limits the range of view (Fitzpatrick *et al.*, 2013). Harvey *et al.* (2012a) compared red light (620630nm) and white light (550-560nm) with stereo-BRUVs across six shallow warm-temperate habitats, including rocky reefs. The sampling area was standardised to the minimum sampling area provided by red light, by only counting those individuals that were recorded within the average range of view that red light penetrated (Harvey *et al.*, 2012a). While both light sources recorded similar assemblages in the majority of the habitats, white light surveyed a greater number of individuals and species on reef and sandy habitats. This was attributed to the white light attracting more bait fish which in turn attracted predatory fish (Harvey *et al.*, 2012a). Similar results were shown by Fitzpatrick *et al.* (2013). Using stereo-BRUVs to sample nocturnal communities on subtropical reefs at Houtman Abrolhos Islands, blue (450-465nm) and white lights recorded greater fish abundances than red light due to the attraction of zooplankton in the white and blue light samples. Based on these studies, red light has been described to have the least impact on fish behaviour and was therefore chosen in this study.

Diel activity patterns of mammals and other terrestrial vertebrates are typically either diurnal (active at day), nocturnal (active at night) or crepuscular (active at the twilight periods, dusk and dawn; Helfman, 1973), with a few exceptions (Ashby, 1972; Reebs, 2002). Fish follow a similar pattern, where the majority of species are diurnal and nocturnal, and fewer crepuscular (Hobson, 1965; Starck & Davis, 1966), however, fish activity is said to be plastic (Ali, 1992).

Day-night activity in fish is therefore complicated by the ability of an individual or population to change their activity patterns in response to a variety of external factors (Reebs, 2002). This plasticity of activity patterns in fish results in intra-species differences (Reebs, 2002; Colmenero *et al.*, 2010), thus making it difficult to apply general theories to the diel effect across systems (Ali, 1992).

1.5 THESIS OVERVIEW

The present thesis has been divided into five chapters (Figure 1.1). Following the general introduction (Chapter 1), Chapter 2 provides a detailed description of the South African warm-temperate bioregion, the study area and sampling sites, and the general methods and materials that were applied to achieve the objectives of this study. The two main objectives were divided into two chapters, Chapters 3 and 4. Chapter 3 investigates day-night variation in assemblage structure of Algoa Bay's shallow and deep-aphotic rocky reef fish communities. Chapter 4 investigates possible fish movement patterns as a driver of the assemblage patterns observed in Chapter 3. Finally, a synthesis of the findings of Chapters 3 and 4 is provided in the general conclusions (Chapter 5).

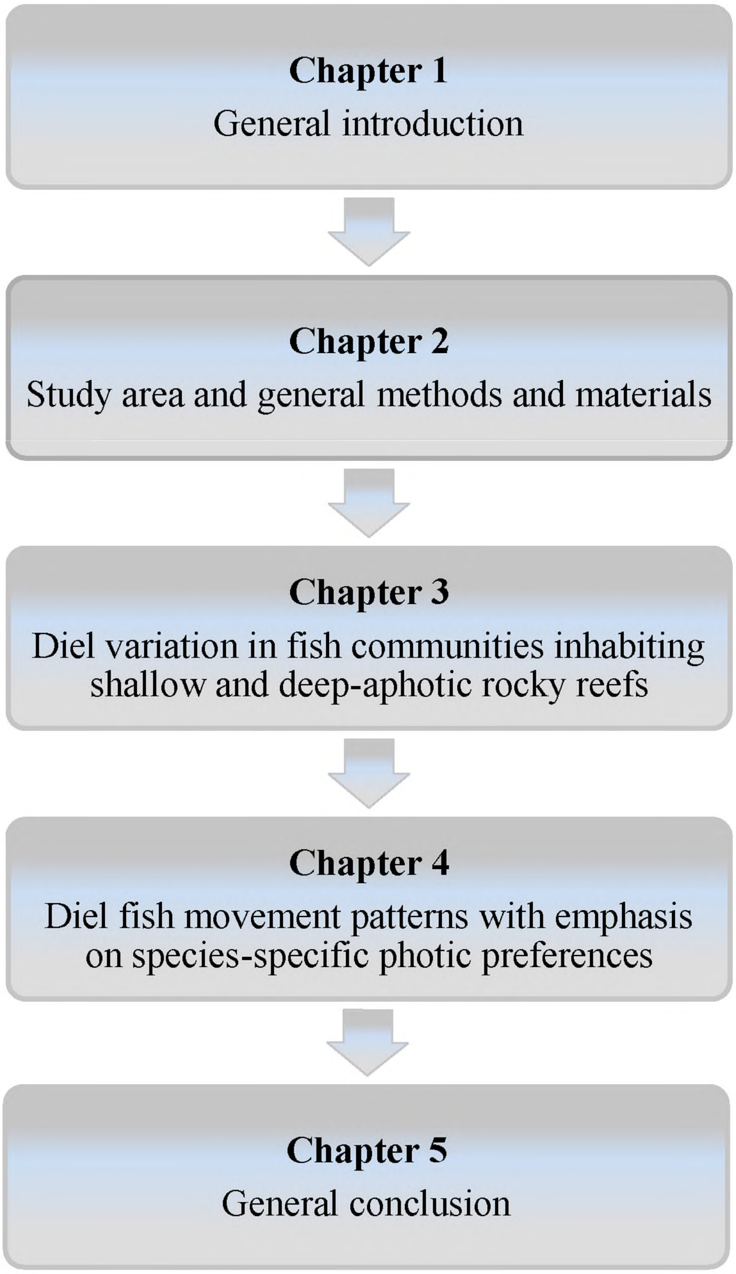

Figure 1.1. Outline of this thesis.

2 STUDY REGION & GENERAL METHODOLOGY

2.1 STUDY REGION, AREA AND SITES

2.1.1 WARM-TEMPERATE AGULHAS ECOREGION

Biogeographic regions, hereon referred to as ecoregions, are defined according to organism's distributional ranges (Turpie *et al.*, 2000). Organisms' distributional ranges are determined by species-specific tolerance levels to a number of biological and physical environmental factors (Turpie *et al.*, 2000). Temperature is one of the main physical factors that limit an organism's distribution, and is therefore important in characterising marine ecoregions (Porter *et al.*, 2013).

Two thermally contrasting currents that flow along the western and eastern coastlines of southern Africa have given rise to three broad inshore ecoregions around the southern tip of the continent (Figure 2.1; Sink *et al.*, 2010). These include the cool-temperate West Coast (also referred to as the Namaqua Ecoregion), subtropical East Coast (Delagoa and Natal ecoregions) and the warm-temperate South Coast (also called the Agulhas Ecoregion) (Gibbons, 1999; Turpie *et al.*, 2000; Lutjeharms, 2006; Sink *et al.*, 2010).

The cool-temperate ecoregion stretches from Luderitz to Cape Point along South Africa's western coastline (Figure 2.1; Lombard *et al.*, 2004). Along this coastline, the Benguela Current carries cold, nutrient rich water from the Atlantic Ocean in a northward direction (Figure 2; Hutchings *et al.*, 2011). This region is characterised by sudden drops in water temperature and high biological productivity due to the occurrence of dynamic wind-driven upwelling events (Griffiths *et al.*, 2010). These cold-water features have a major influence on the biota of this region (Griffiths *et al.*, 2010).

Southern Africa's eastern marine inshore region that stretches from Cape Vidal to Mbashe River is defined as the subtropical Natal Ecoregion (Figure 2.1; Sink *et al.*, 2010). This region is influenced by the Agulhas Current that carries warm equatorial Indian Ocean water in a southward direction along the eastern continental shelf (Figure 2.2; Griffiths *et al.*, 2010). The subtropical ecoregion is characterised by relatively low productivity with clear blue waters (Lombard *et al.*, 2004). To the north of the subtropical Natal Ecoregion lies the Delagoa Ecoregion that is host to a diverse array of tropical marine habitats, such as coral reefs that are restricted to St Lucia and Mozambique coastlines. The southern extremities of the subtropical ecoregion support rocky reefs (Celliers *et al.*, 2010).

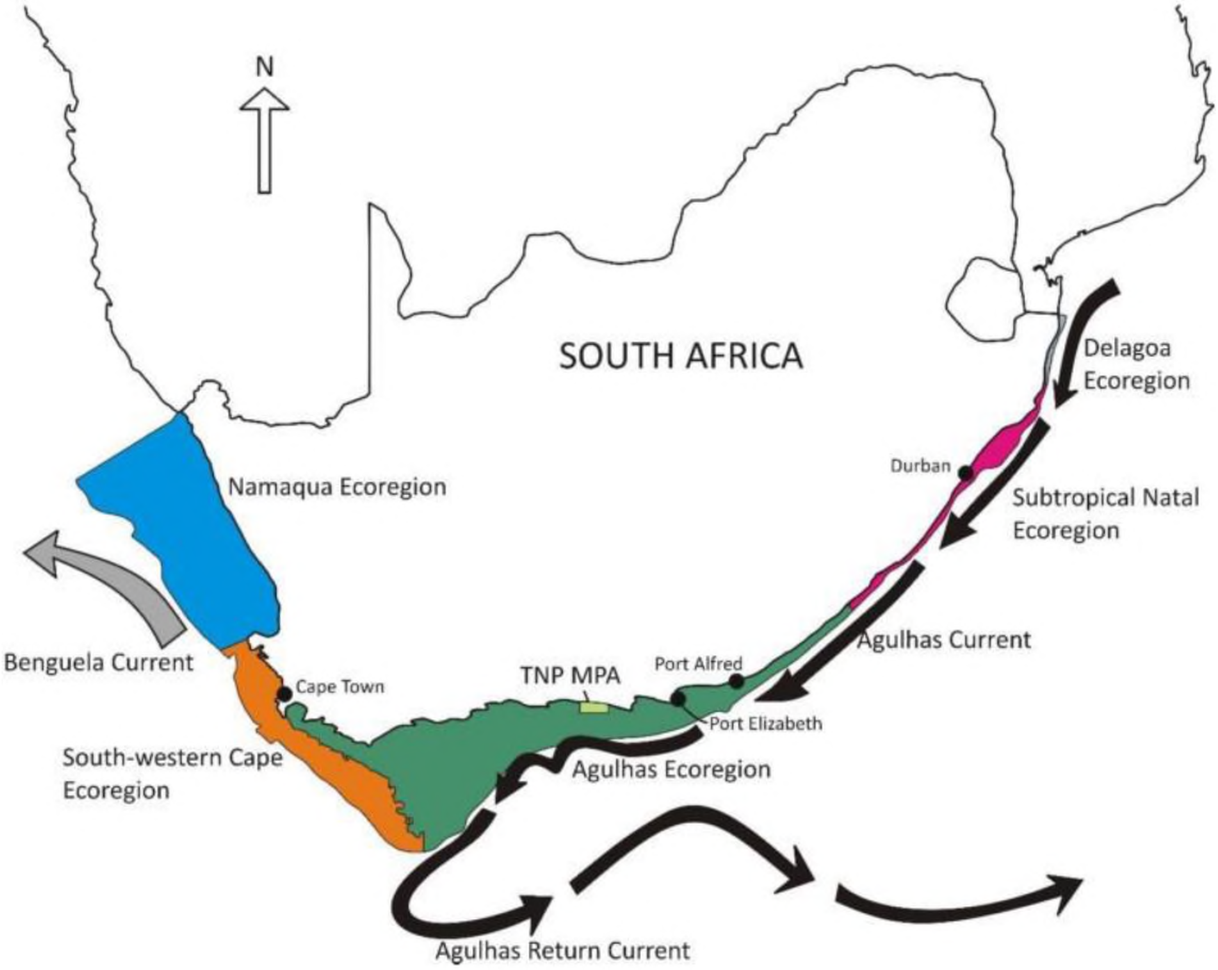

Figure 2.1. A map of South Africa indicating the five broad marine inshore ecoregions. South Africa's West Coast is defined as the cool-temperate Namaqua Ecoregion. This ecoregion and the south-western Cape Ecoregion are influenced by the cold Benguela Current that is represented by the grey arrow. The Delagoa and subtropical Natal ecoregions stretch along the eastern coastline, represented in grey and pink respectively. The black arrow represents the flow of the warm Agulhas Current that influences the water temperatures along the southern coastline, which is described as the warm-temperate Agulhas Ecoregion (taken from: Heyns-Veale *et al.*, 2016); modified from Lutjeharms (2006)).

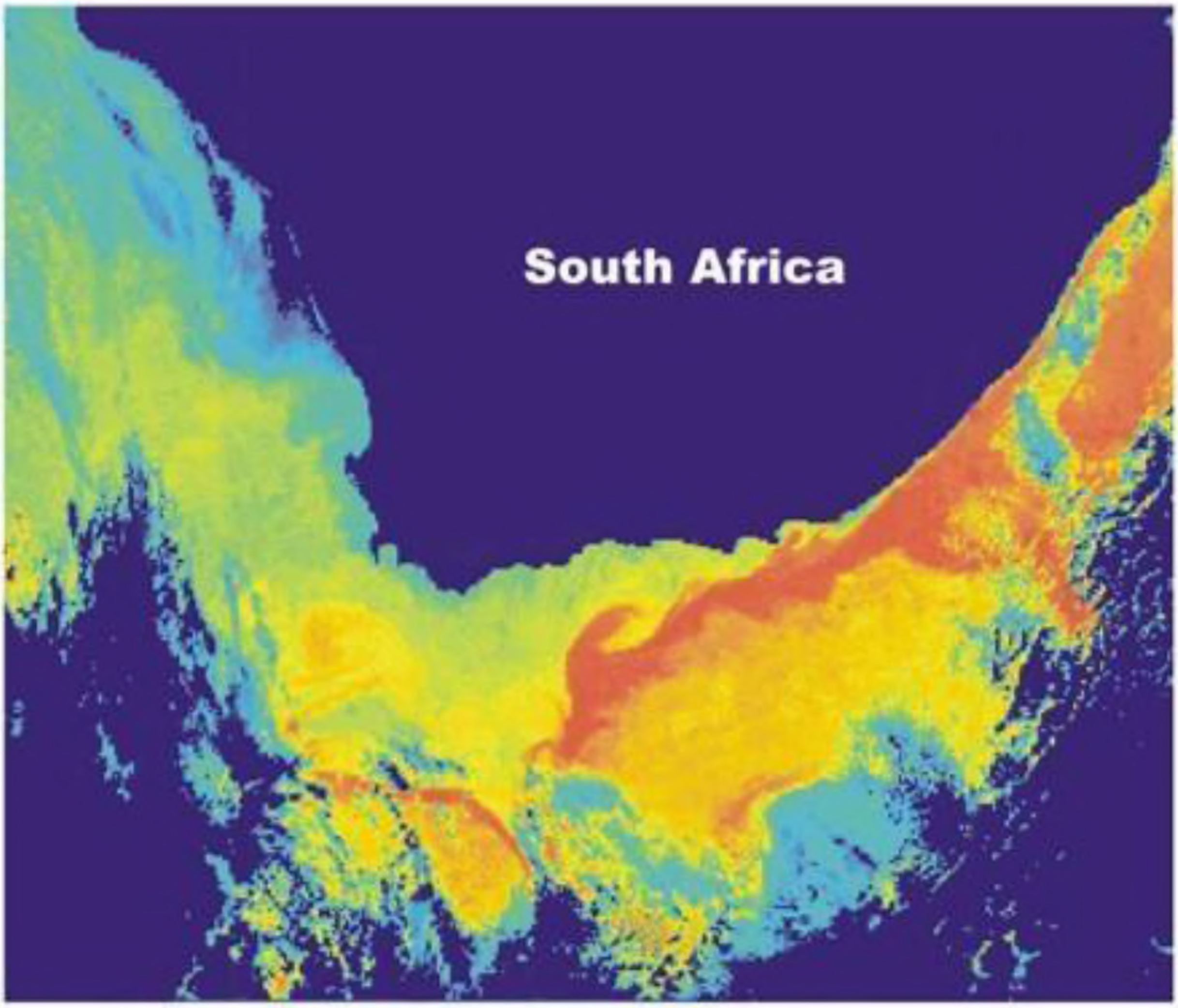

Figure 2.2. Satellite image displaying the oceanic characteristics around southern Africa. Southern Africa's eastern coastline is dominated by the southward flowing warm Agulhas current that is represented by the colour red. The West Coast is characterised by cooler water, which is represented by pale blue. South Africa's West Coast is influenced by the cold northward flowing Benguela Current and frequent upwelling events. The warm and cool water masses mix along the southern coastline, forming a transition zone (Lombard *et al.*, 2004; figure from Lombard *et al.*, 2004 courtesy of Sue Lane and Robin Carter).

The mixing of subtropical and cool-temperate waters along South Africa's southern coastline forms a transition zone that is described as the warm-temperate Agulhas Ecoregion (Figure 2.3). This ecoregion extends from Cape Point, in the west, to Mbashe River, in the east (Lombard *et al.*, 2004), and is characterised by intermediate average sea temperatures of 17–22 °C (Goschen & Schumann, 1998) and low seasonal rainfall with peaks in spring and autumn (Griffiths *et al.*, 2010; Whitfield, 1998).

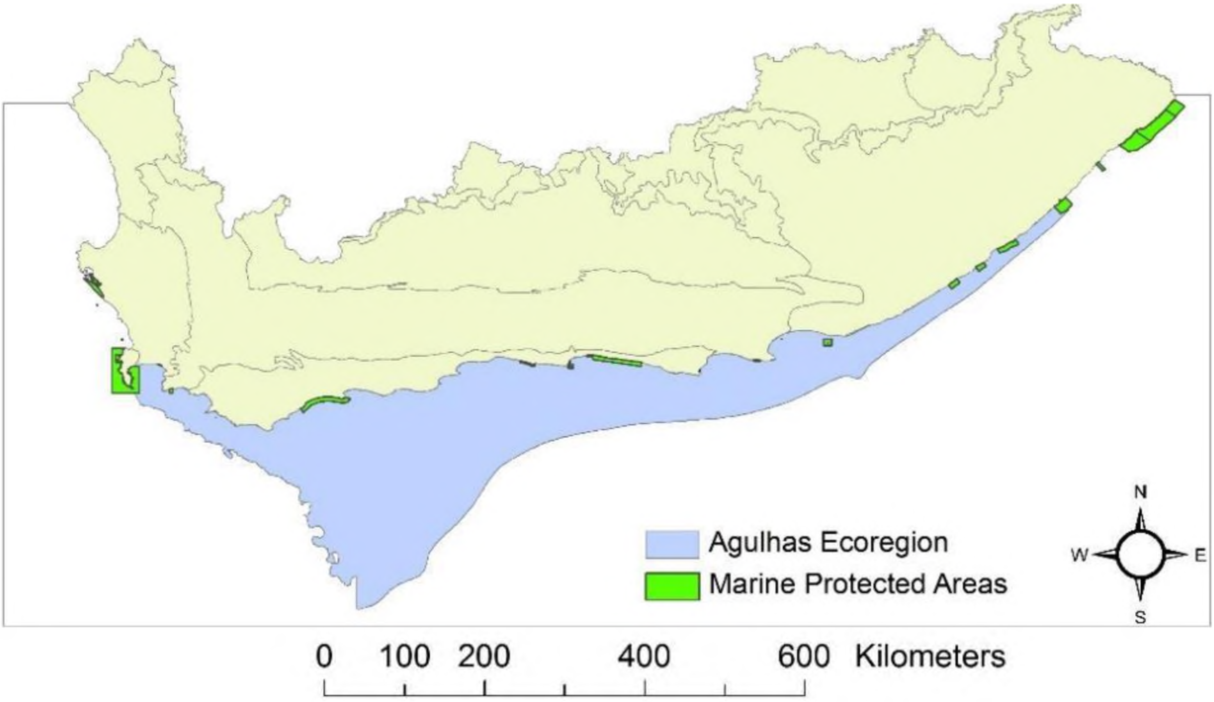

Figure 2.3. Map of South Africa's southern coastline, indicating the position of the warmtemperate ecoregion, also referred to as the Agulhas Ecoregion, represented by the colour pale blue (Bernard, 2012).

The warm-temperate Agulhas Ecoregion is unique as it possesses physical and biological features that are typical of both the eastern and western coastlines (Turpie *et al.*, 2000). Rocky reefs represent important subtidal marine habitats that are dispersed all over the continental shelf, including the inshore zone of the cool-temperate, the subtropical and the warm-temperate ecoregions (van der Elst, 1990). These reefs form rocky flats or steep pinnacles and provide their fish communities with all the necessary resources such as shelter and food (van der Elst, 1990). Warm-temperate rocky reef fish communities are described to be associated with higher species richness than rocky reef fish communities of the cooltemperate ecoregion (Penrith 1976; Smale & Buxton, 1989; Smale, 1992). The division between warm-temperate and subtropical ecoregions is less distinct, but there is a gradual reduction of tropical species with the southward progression (Turpie *et al.*, 2000).

Ichthyofaunal surveys within the warm-temperate ecoregion agree that the seabream family, Sparidae (sparids), dominates shallow rocky reef communities. Small shoaling species such as frans madam (*Boopsoidea inornata*) and steentjie (*Spondyliosoma emarginatum*) are the most abundant (Buxton & Smale, 1984; Burger, 1990; Smale, 1992; Götz *et al.*, 2009; Solano-Fernandez *et al.*, 2012; Heyns-Veale, 2016). Although deep rocky reef fish communities are poorly understood, there is general consensus that they are less diverse than shallow communities with fewer herbivorous species (van der Elst, 1990; Heyns-Veale *et al.*, 2016). Furthermore, deep rocky reef fish communities have been shown to be dominated by different species, including two species of sparids, panga (*Pterogymnus laniarius*) and carpenter (*Argyrozona argyrozona*; Smale, 1992; Brouwer *et al.*, 2002; Heyns-Veale, 2016). The high abundances of sparids, which is a family recognised in South Africa for its high levels of endemism, contribute to the high diversity recorded in the warm-temperate ecoregion.

Endemic species are restricted to a particular place (Crother & Murray, 2011), and their presence represents the unique characteristics and niches offered by the region that they occupy (Patil *et al.*, 2015). Endemic species are therefore frequently used to define biogeographic boundaries (Crother & Murray, 2011). Faunal assemblages that are strongly associated with these unique regions are particularly vulnerable to environmental impacts, such as habitat destruction and climate change (Malcolm *et al.*, 2006). Monitoring these regions and investigating endemic species is therefore crucial from a conservation point of view (Patil *et al.*, 2015). Using existing biogeographical data on 1 239 southern African shelf and coastal species (Smith & Heemstra, 1986), Turpie *et al.* (2000) revealed an increase in fish diversity from South Africa's western coastline to the east. This trend was attributed to the increase in subtropical species richness with the eastward progression (Turpie *et al.*, 2000; Griffiths *et al.*, 2010). It was further demonstrated that a significant proportion of southern and South African endemic fish and invertebrates were recorded along the middle sections of the warm-temperate ecoregion (Turpie *et al.*, 2000), with numbers peaking near Algoa Bay (Turpie *et al.*, 2000; Griffiths *et al.*, 2010). Investigating Algoa Bay and its associated faunal assemblages may provide insight into the ecological significance of communities and environmental conditions in the region.

2.1.2 ALGOA BAY

The present study was conducted in Algoa Bay. Algoa Bay forms a bight on the coastline of South Africa's Eastern Cape Province (Figure 2.4). The city of Port Elizabeth is situated along the western coastline of Algoa Bay (Figure 2.4). Algoa Bay is the largest (3 100 km^2) of the lunate bays found along the South Cape coast (Schumann & Goschen, 2011) and stretches along 135 km of coastline between two headlands, Cape Padrone and Cape Recife.

Cape Padrone (33°46'S 26°28'E) is situated on the east side of the bay and the more prominent Cape Recife (34°02'S 25°42'E) on the west side (Goschen & Schumann, 2011; Melly, 2011).

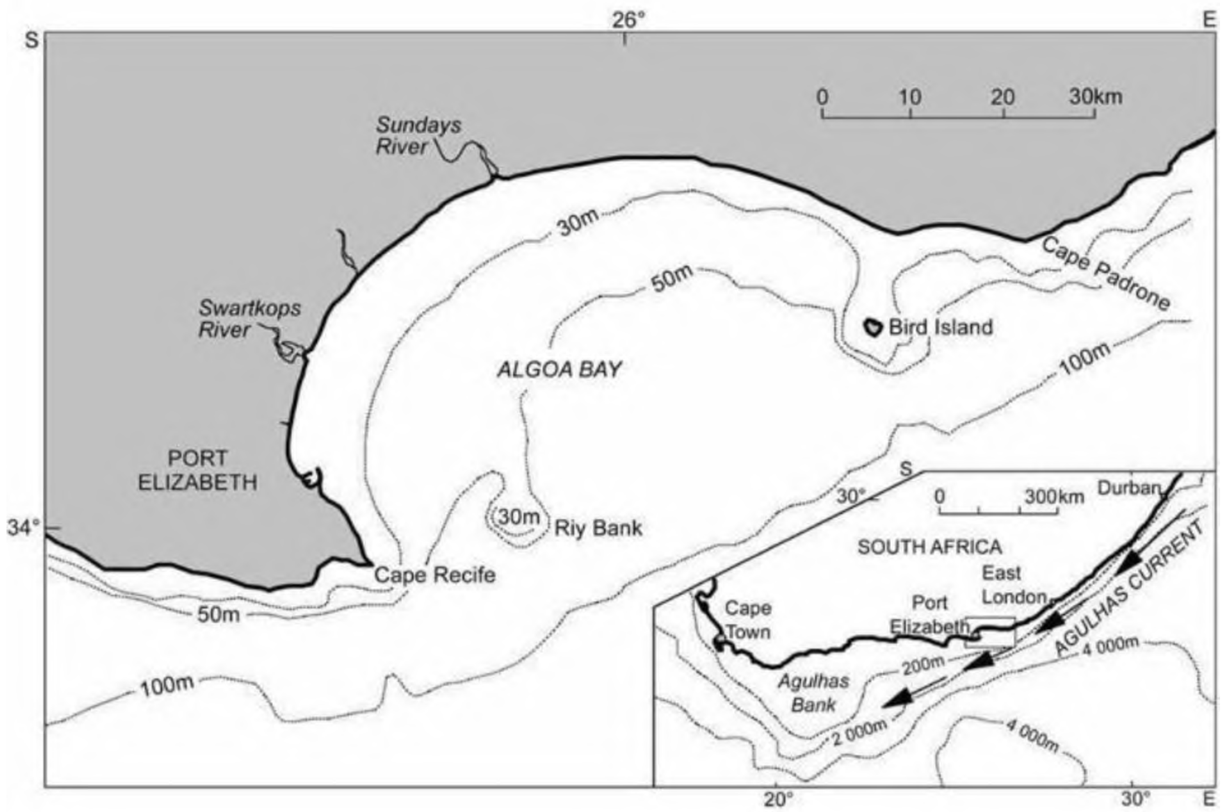

Figure 2.4. The location of the two study sites, Cape Recife and Riy Banks, is shown within Algoa Bay (Schumann *et al.*, 2005).

Algoa Bay was considered a suitable area to conduct nocturnal sampling due to the shelter provided by the Cape Recife headland. Open ocean swell predominantly travels toward Algoa Bay from a southwest direction (Lombard *et al.*, 2004). Waves therefore penetrate the bay after a major reduction in energy from the interaction with the Cape Recife headland (Schumann & Goschen, 2011). As a result, Algoa Bay is relatively sheltered compared to the exposed, high energy coastline of South Africa (Griffiths *et al.*, 2010). Furthermore, Algoa Bay is characterised by a number of large, expansive reef habitats which are easily accessible through the harbour of Port Elizabeth. Port Elizabeth is situated in the southwestern sector of Algoa Bay and is in close proximity to the Cape Recife and Riy Banks reef complexes, which, together with the Addo Marine Protected Area (MPA), include higher profile bathymetry than reef complexes elsewhere in the bay (Hutchings *et al.*, 2013).

2.1.2.1 HYDROLOGICAL FEATURES

The two prominent capes that border Algoa Bay disrupt the general direction of the prevailing winds. These winds tend to follow the contour of the southern coastline, in either west south-westerly or east north-easterly directions (Goschen & Schumann, 2011). The westerly wind component dominates throughout the year at Algoa Bay, with intermittent easterlies. The latter generally increase in strength and duration during the summer months (Goschen & Schumann, 2011). The western rocky headland, Cape Recife, is a quartzite outcrop that protects the bay from the predominant prevailing westerlies (Goschen & Schumann, 2011). Although the bay is afforded a degree of protection against wind and waves, the interaction between the winds and the two headlands results in a dynamic ocean around Algoa Bay that influences the temperature structures of the region (Goschen & Schumann, 2011).

The Agulhas Current is the dominant oceanographic feature in the eastern region of South Africa, tightly following the edge of the continental shelf (Figure 2.5; Grundlingh, 1983; Goschen & Schumann, 2011). The northerly part of the eastern section of the continental shelf is very narrow permitting the current to flow close inshore. As the continental shelf widens around East London (Figure 2.5), the Agulhas Current begins to separate from South Africa's eastern coastline to flow in a more southward direction (Dingle *et al.*, 1987). The sharp difference in temperatures between the warm Agulhas Current and the waters of the adjacent continental shelf in this region causes thermal and oceanographic instability (Goschen & Schumann, 2011). As a result, warm Agulhas Current water periodically penetrates onto the continental shelf and into Algoa Bay as filaments and plumes (Goschen & Schumann, 2011). This impact of the Agulhas Current is an important source of variability in water temperatures along the Eastern Cape coastline, as well as within Algoa Bay (Hutchings *et al.*, 2011).

Shelf edge upwelling also contributes to the variability in water temperature along South Africa's Eastern Cape coastline (Beckley, 1983). Upwelling events between Algoa Bay and East London are common and are caused by the widening of the continental shelf (Goschen & Schumann, 2011). Surface layers are forced in an offshore direction due to a combination of the southward flowing Agulhas Current and the Coriolis Effect. As a result, cold dense bottom water upwells along the coastline (Goschen & Schumann, 2011). Easterly winds spread cold upwelled water across Algoa Bay, and influence the horizontal surface water temperature structure by cooling the eastern sector of the bay (Figure 2.5).

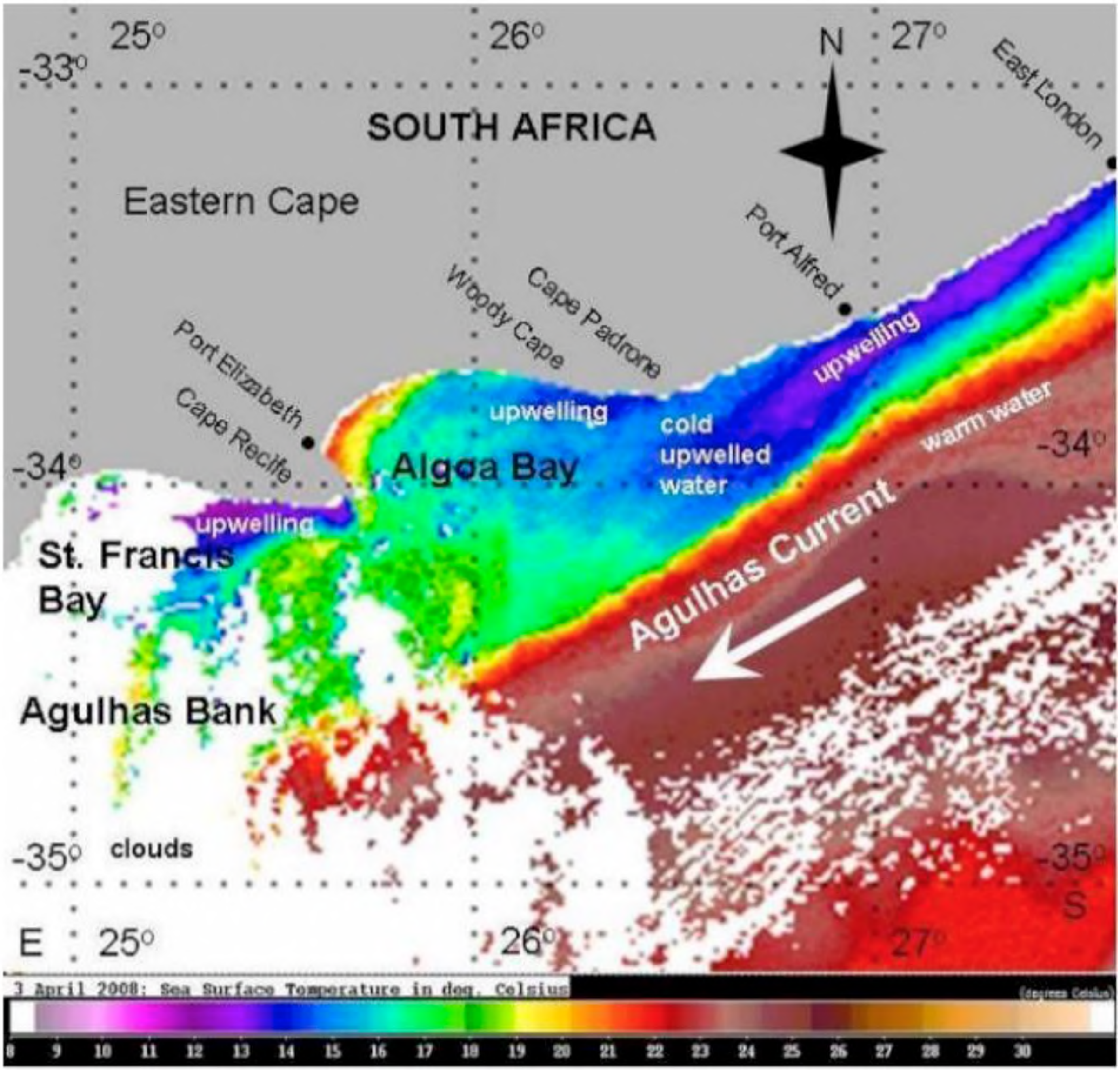

Figure 2.5. Satellite thermal image displaying sea surface temperatures around Algoa Bay, with the colour blue representing cold water and red representing warm water (Goschen & Schumann, 2011).

Wind driven upwelling events that occur downwind of Cape Padrone and Cape Recife play a similar role in influencing the water temperatures of Algoa Bay (Goschen & Schumann, 2011). Upwelling associated with the capes causes rapid temperature drops in Algoa Bay, with temperature recordings as low as 6 °C (Ross, 1988). This is a result of the steep slope of the headlands and Ekman transport (Roberts, 2005). North-easterly winds drive surface layers offshore at the capes thus allowing cold bottom water to be brought up to the surface (Goschen & Schumann, 2011). These winds then push the cold, upwelled water further westward around Cape Padrone, in a similar way as shelf edge upwelling waters penetrate Algoa Bay (Goschen & Schumann, 2011). Cold upwelled water at Cape Recife penetrates Algoa Bay if the direction of the wind shifts to a westerly or if the easterly winds suddenly relax following the upwelling event (Schumann *et al.*, 1988). Since the frequency and speed of both prevailing winds tend to reach their maximums in October and November (minimums between May and July), such events predominantly occur in summer (Goschen & Schumann, 2011). Despite the short duration and relative weakness of the upwelling events at the capes, they may have profound effects on the biota and have been associated with fish kills (Hutchings *et al.*, 2012).

The vertical temperature structure of the deeper sections of Algoa Bay off Cape Recife is characterised by seasonally varying thermoclines. Thermoclines form as a result of direct heating of the water's surface by solar radiation (Goschen & Schumann, 2011). Sharp increases in solar radiation at Algoa Bay between winter and summer (Goschen, 1991) cause average summer water temperatures to reach maximums of 20–22 °C (Beckley, 1983), with intense temperature gradients of 3 °C m^{-1} in waters deeper than 15 m (Schumann *et al.*, 2005). The intensity of the summer thermocline is thought to be exacerbated by warm surface water intrusions from the Agulhas Current (Swart & Largier, 1987). Vertical movement of the summer thermocline has been shown by recording temperature fluctuations of as much as 7 °C in a 12-hour period between depths of 9 and 21 m (Hutchings *et al.*, 2013). In contrast, average winter water temperatures reach a minimum of 11 °C (Beckley, 1983), and the water column remains isothermal with minimal water column temperature fluctuations of less than 2 °C (Goschen & Schumann, 2011). Similarly, the shallower sections of Algoa Bay remain well mixed throughout the year (Goschen & Schumann, 2011).

2.1.2.2 ROCKY REEF FISH ASSEMBLAGES

The diverse ichthyofaunal assemblage of Algoa Bay's subtidal rocky reefs is typical of warm-temperate reefs along South Africa's coastline, with sparids dominating the communities. Sparids have been described as an important family in South African marine habitats due to their high abundances, endemicity and their economic value. Many sparids are important components of South Africa's hook-and-line fishery (Branch *et al.*, 2010). Their life history characteristics such as slow growth, late maturation and sex-change make them particularly vulnerable to overexploitation and, on the International Union for Conservation of Nature (IUCN) red list of threatened species, many stocks are currently listed as near threatened (red roman, *Chrysoblephus laticeps*), endangered (red steenbras, *Petrus rupestris*, white steenbras, *Lithognathus lithognathus*, and red stumpnose, *Chrysoblephus gibbiceps*) or critically endangered (seventy four, *Polysteganus undulosus*, and dageraad, *Chrysoblephus cristiceps*).

Furthermore, like many other reef fish, sparids are resident, meaning they typically remain on a reef all year-round (van der Elst, 1990) and are unlikely to exhibit large scale movements (Griffiths & Wilke, 2002; Kerwath *et al.*, 2007; Cowley *et al.*, 2002). Only few sparids exhibit continual large scale movements that are associated with life-stage events (Penny & Wilke, 1993; Brouwer, 2002). These characteristics and the high levels of endemism of this family make them particularly vulnerable to overexploitation (Buxton, 1993; Chale-Matsau *et al.*, 2001). The importance of studying these species lies not only in the risk of losing endemics and exploitable fish stocks, but also in their ecological significance. Many sparids targeted in the commercial and recreational fisheries are top predators of rocky reefs, and their removal may have significant effects on these fish communities (Brouwer, 2002). This research is particularly important at Algoa Bay, where many of the reefs, such as Cape Recife and Riy Banks, are exposed to high levels of commercial and recreational fishing pressure (Melly, 2011). The area is also subject to marine ecotourism activities such as yacht sailing, whale watching, spearfishing and recreational SCUBA diving. The high levels of anthropogenic activities in Algoa Bay may put these reefs and the faunal assemblages at risk. They are therefore important to understand and monitor, so that any potential changes due to anthropogenic impacts can be recognised early and mitigated against.

2.1.3 CAPE RECIFE AND RIY BANKS

Cape Recife and Riy Banks are two near-shore reef complexes situated in the western sector of Algoa Bay (Figure 2.6). The two rocky reefs were selected as study sites to ensure a representative assessment of Algoa Bay's rocky reef fish communities. They were considered logistically feasible to sample at night as they are both relatively close to Port Elizabeth harbour. Riy Banks lies 25 km east-southeast of Port Elizabeth harbour (Bremner, 1979a), while Cape Recife reef is 21 km away and lies just south of the Cape Recife headland (Figure 2.6). The steep bathymetry of these reefs was also considered suitable as this study aimed at indirectly determining if reef fish movement was occurring between *Depth zone*s of Algoa Bay's rocky reefs.

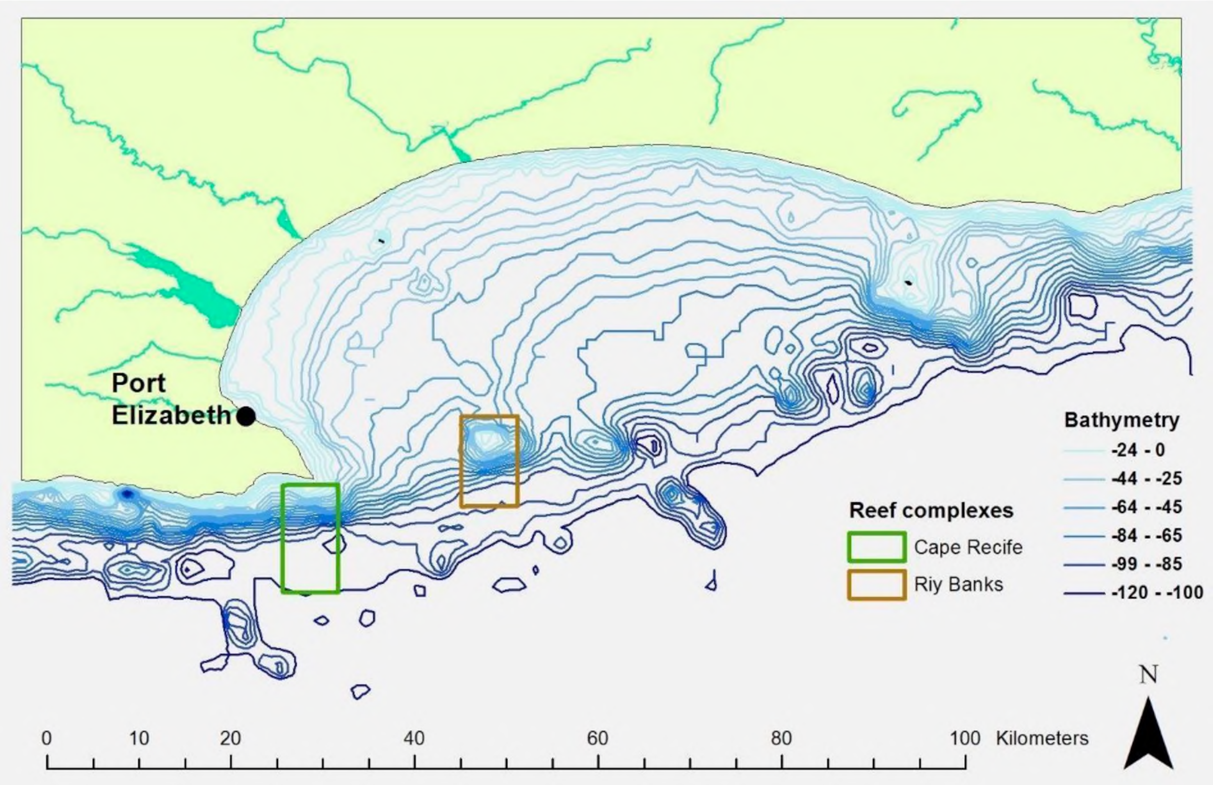

Figure 2.6. Bathymetry map of Algoa Bay indicating the study sites, Riy Banks and Cape Recife.

Two conditions had to be met by the study sites. Firstly, to avoid pseudoreplication due to fish moving between study sites, the chosen study sites had to represent isolated complexes. The majority of Algoa Bay is characterised by sandy flats, with Cape Recife, Riy Banks and the Addo MPA reefs being the most complex habitats in Algoa Bay (Goschen & Schumann, 2011). The open sandy flats that surround the reefs are characterised by very low habitat complexity, and have been described as unsuitable habitat for the majority of reef fish species (Hobson, 1973; Doherty, 1983). These flats may therefore act as natural barriers to the movement of most reef fish species (Chapman & Kramer, 2000), and this ensured minimal reef fish exchange between the two study sites during the sampling periods. Secondly, both Cape Recife and Riy Banks represent continuous rocky reef habitat that extends along a depth gradient from the shallow zone (10–30 m) to the deep-aphotic zone (55–100 m; Figure 2.6). This structure allowed for potential day-night intra-reef movement between *Depth zone*s to be investigated.

In this study, samples taken from the shallow zone of Riy Banks ranged between 13 and 32 m. These samples were collected along the shallow plateau that spans 24 km^2 (Bremner, 1979a). Deep-aphotic samples were collected at depths of 51–81 m along the steep northern and western slopes of the plateau, and along the gentler slopes of the eastern and southern sides (Bremner *et al.*, 1991). Samples collected in the shallow zone of Cape Recife ranged between 13 and 34 m and between 51 and 99 m for the deep zone. To remove any influence that low levels of ambient light may have had on the fish assemblage, all deep-aphotic samples collected during the day time that showed the presence of ambient light were excluded from the analysis.

2.1.3.1 DETERMINING THE RANGE OF THE DEEP-APHOTIC ZONE

This study was concerned with the distinct day-night differences in ambient light from photic to aphotic conditions, between shallow and deep rocky reef sites. To determine the depth of the aphotic rocky reef zone, underwater ambient light was recorded. Before sampling commenced for each sampling trip, a LI-COR LI-251A Light Meter was deployed off the side of the boat to record ambient light conditions at two metres within the water column, and at reef depths of 20 m and 60 m at both day and night. Light recordings taken during the day at 60 m were highly variable throughout this study and ranged between 0 and 12.52 µmol. This was expected since light penetration is dependent on a number of environmental conditions such as cloud cover, rainfall and *Time of day* (Kotwicki *et al.*, 2009). Light penetration to the seafloor is also affected by water conditions such as turbidity, suspended load and organic matter in the water column (Kotwicki *et al.*, 2009). In this study, the majority of light recordings taken at approximately 60 m during the day revealed aphotic conditions and those that showed the presence of ambient light were excluded from the analysis. Based on the assessment of light recordings, the *deep-aphotic* zone for this study was defined as greater than 51 m. Light recordings taken during this study showed that no light penetrated deeper than two metres during all nocturnal sampling trips for this study.

2.2 GENERAL METHODOLOGY

2.2.1 DEPLOYMENT SITE SELECTION

Depth and *habitat*, the latter of which is defined in terms of complexity and substrate, have been described as important determinants of the composition and structure of South Africa's warm-temperate rocky reef fish assemblages (Götz *et al.*, 2009; Heyns-Veale *et al.*, 2016). At the Tsitsikamma National Park MPA, shallow rocky reef fish communities (11–25 m) were described as more diverse, with a higher proportion of low trophic level consumers, than deep reef communities (45–75 m) that were characterised by higher abundances of predators and larger species (Heyns-Veale, 2016). Furthermore, *habitat* complexity has a profound influence on the community structure of observed fish assemblages (Smith *et al.*, 2014; Sala *et al.*, 1998; Heyns-Veale, 2016). This is because *habitat*s with a higher structural complexity, such as *high profile reef*s, provide more niches and therefore allow more species to coexist than do *habitat*s with low structural complexity, such as sandy flats (Smith *et al.*, 2014). To control for the effects of depth and *habitat* on fish assemblage structure, Cape Recife and Riy Banks were stratified according to these local *habitat*s, from now on referred to as *habitat* criteria.

Stratification involved *habitat* mapping of Cape Recife and Riy Banks using ArcMap 10 (Environmental Systems Research Institute, Redlands, CA, U.S.A.). An equally spaced (300 x 300 m) point-grid was overlaid onto the known locations of the two reefs. From this, each point represented a potential sampling site. Bathymetric mapping surveys were then conducted using a GPS linked echo-sounder. The surveys consisted of line-transects going across the depth gradient from shallow to deep, with each line-transect passing directly over a row of points in the grid. Using ArcMap 10, geographic coordinates and depth data were interpolated to create a three-dimensional bathymetric contour map for each study site (Götz, 2005).

Depth and variation in depth data, together with the associated geographic coordinates, were then obtained from 50 m either side of each point (or potential sampling site). This allowed each potential sampling site to be classified as one of six *habitat* criteria based on the depth, substrate and reef profile of the grid cell. The depth of each grid cell was determined from the map as either shallow (10–35 m) or deep (55–100 m). *Habitat*, which comprised reef profile and substrate, was inferred by calculating the change in depth over 50 m either side of the centre of each grid cell. *High profile reef* was defined as a change in depth of more than five metres, and *low profile reef* was classified as a change in depth between 2 and 5 m. Grid cells that showed low variation in bathymetry, where depth varied by less than two metres, were described as intermittent *sandy reef patch*es. Grid cells that were predominantly characterised as sand were excluded as potential deployment sites as this study was only concerned with rocky reef *habitats*. Deployment site selection then followed a stratified random sampling procedure based on Bernard (2012), while ensuring an even allocation of sampling effort among the six *habitat* criteria:

1. *shallow-high profile reef*
2. *shallow-low profile reef*

3. *shallow-sandy patch*
4. *deep-high profile reef*
5. *deep-low profile reef*
6. *deep-sandy patch*

Pseudoreplication may be caused by overlapping bait plumes of separate baited deployments which may potentially cause an individual to be counted more than once (Harvey *et al.*, 2007). To avoid this, most studies separate baited deployments by a minimum of 500m (Harvey *et al.*, 2007). For the present study, however, the continuity of that habitat was important to infer movement between shallow and deep reef sites, and to ensure reefs were comparable. Baited deployments were therefore separated by a minimum of 300m, as this was the minimum recommended distance (Langlois *et al.*, 2012b). According to Parker (2015), separation of BRUVs by 300m at Tsitsikamma National Park was sufficient to exclude autocorrelation, which itself proves independence of data points, and therefore no discernible effect of the bait plume.

2.2.2 EXPERIMENTAL DESIGN

To test the effects of the diel cycle and *Depth zone* on Algoa Bay's rocky reef fish communities, a crossed design was employed:

site (random; c=2 levels: Cape Recife (CR) vs Riy Banks (RB))

survey (random; d=2 levels: *2015* vs *2016*)

Depth zone (fixed; b=2 levels: *shallow* (S) vs *deep* (Dp))

Time of day (fixed; a=2 levels: *day* (Dy) vs *night* (N))

2.2.2.1 RANDOM EFFECTS – SIZE AND SURVEY

In addition to *site* being included as a random effect, *survey* was also included as a random effect to account for interannual variability in sampling. At Cape Recife and Riy Banks, sampling was conducted over two field *surveys* in an attempt to control for the potential effects of seasonal variation in environmental conditions and species' behaviour (spawning, recruitments; Williams & Sale, 1981). Although the aim was to minimise temporal (between day) variability in environmental conditions by minimising the duration of each field trip, this was not possible due to poor weather conditions. This field work was largely dependent on suitable weather conditions, particularly for nocturnal sampling. A total of 49 samples were collected during field *survey* one, which took place in 2015 over five days in June and two consecutive days in October. Thirty-nine samples were collected during field *survey* two, which was conducted in 2016 over two days in April and four days in May. Where possible, the data collection plan ensured that samples were collected from the *Time of day* and *Depth zone* treatments within a site either on the same day or consecutive days to account for between-day differences in environmental conditions.

2.2.2.2 MAIN EFFECTS – *DEPTH ZONE* AND *TIME OF DAY*

In addition to *Depth zone*, *Time of day* was included as a second main effect to the experimental design to investigate the effect of day and night on Algoa Bay's rocky reef fish communities. Samples were collected at *shallow* (13–34 m) and *deep-aphotic* zones (51– 99 m) of Cape Recife and Riy Banks at both times of day. *Day* time sampling was carried out between 07h45 and 15h39, and always commenced at least an hour after sunrise which ranged between 05h31 and 7h20 during this study. *Night* time sampling was carried out between 19h41 and 00h27, and commenced at least two hours after sunset which ranged between 17h16 and 18h35. Since the majority of fish species are strictly diurnal or nocturnal and are described to exhibit a shift in their activities during the twilight periods (Helfman, 1978), it was assumed that the majority of species were already in their respective diurnal and nocturnal habitats once sampling had commenced.

A total of 88 samples were collected throughout this study. The sampling design was balanced with n=11 replicate stereo-BRUVs deployments in each of the combinations of levels for the treatment variables, *Time of day* and *Depth zone*, and the random variable, Site (Table 2.1).

Table 2.1. Number of baited remote underwater stereo-video systems deployed in each of the eight combinations for the levels of *Time of day* (day vs night), *Depth zone* (shallow vs deep-aphotic) and site. (Shallow = Sh; Deep-aphotic = Dp).

	Cape Recife				Riy Banks			
	day		night		day		night	
Survey	Sh	Dp	Sh	Dp	Sh	Dp	Sh	Dp
2015	3	6	9	2	8	7	7	7
2016	8	5	2	9	3	4	4	4

2.2.3 SAMPLING APPROACH

Sampling was carried out using four custom designed baited remote underwater stereo-video systems (Figure 2.8), based on the design of Harvey & Shortis (1995). The systems were independent of the boat, thereby improving sampling efficiency as multiple (n = 4) stereoBRUVs could be deployed simultaneously. Each system was weighted up to 60 kg and connected to surface marker buoys by means of a rope. For *night* time sampling, buoys were fitted with red flashing torpedo lights that are used by commercial seine netting fishermen to indicate their location. The stereo-BRUVs consisted of a stainless-steel frame where a pair of identical video cameras (two SONY PJ430E or two CANON HFM5x), protected in waterproof housings, were mounted 70 cm apart with an inwards convergence angle of 8°. The cameras' fields of view overlapped and allowed stereo vision and measurements to be extracted during video analysis (Harvey & Shortis, 1995). Calibration procedures were conducted using the programme CAL SeaGIS Pty. Ltd. Calibration of the cameras was conducted before and after each sampling trip to enable length and distance measurements, and to also ensure that the relative orientation of the two cameras remained the same during the sampling. A 1.5 m stainless steel bait arm was fitted to each system to extend horizontally within both cameras' fields of view. At the end of the bait arm, a perforated PVC container was connected. For each deployment, the container was filled with 0.8–1 kg of crushed pilchards (*Sardinops sagax*).

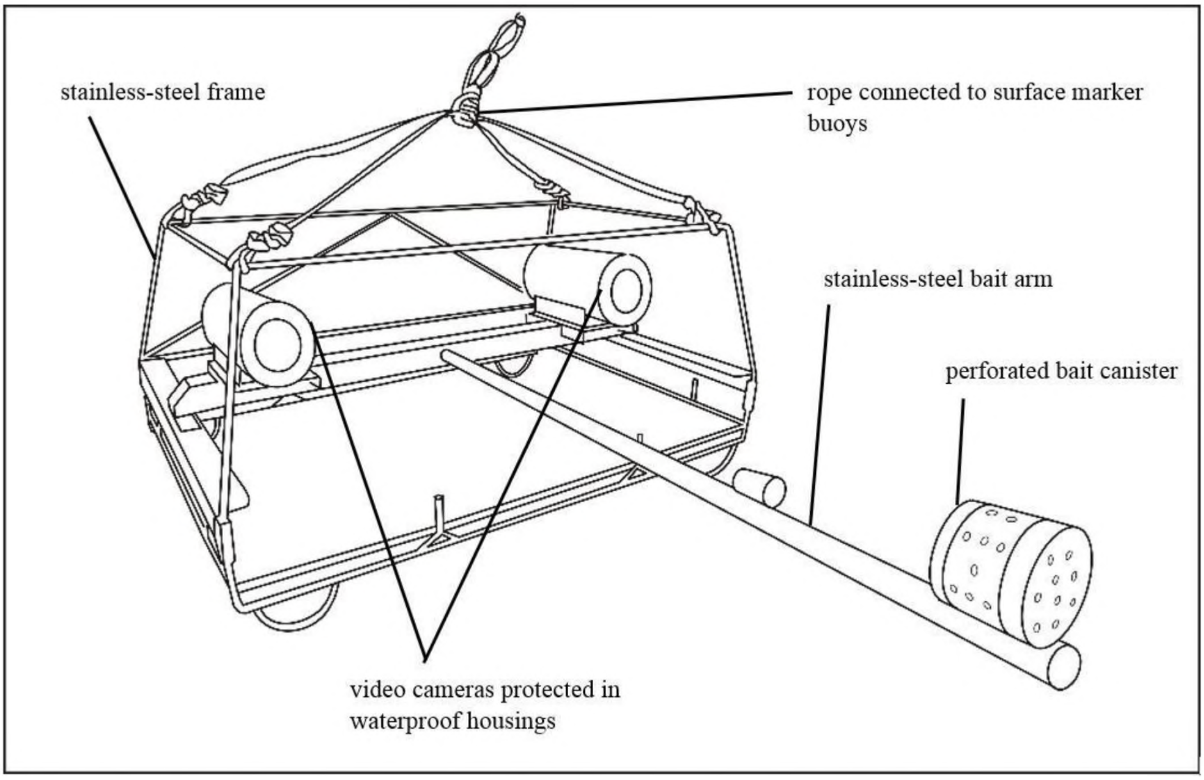

Figure 2.8. Baited remote underwater stereo-video system based on the design of Harvey & Shortis (1996; Image courtesy of E Heyns-Veale).

2.2.3.1 NOCTURNAL AND DEEP-APHOTIC STEREO-BRUVS DEPLOYMENTS

For nocturnal and deep aphotic deployments, each stereo-BRUVs was equipped with a redlight mounted between the two stereo-video cameras (Fitzpatrick *et al.*, 2013), while no light was used for day shallow deployments. An LED panel with eight Cree X Lamp diodes with wavelengths between 620 and 630 nm was used. The choice of a red-light source over blue or white was based on the findings of Harvey *et al.* (2012a) and Fitzpatrick *et al.* (2013), where red light appeared to have the least impact on the behaviour of reef fish sampled using BRUVs. More information regarding this is provided in the research approach section of Chapter 1.

Stereo-BRUVs were retrieved only after a standard one-hour period starting once the system had settled on the seafloor. Upon settling on the seafloor, the time and exact depth obtained from a GPS linked-echosounder, were recorded for each deployment. One-hour bottom time has been shown to ensure sufficient numbers of species and individuals are recorded while rendering the sampling cost-effective from a time-effort perspective (Watson *et al.*, 2009; Colton & Swearer, 2010; Langlois *et al.*, 2010; Bernard & Götz, 2012).

2.2.3.2 VIDEO ANALYSIS

Eighty-eight videos were analysed using EventMeasure (Stereo) software (SeaGIS Pty. Ltd., 2011). All videos were analysed by a single observer to avoid inter-observer variability to the data (Mallet & Pelletier, 2014), and a standardised analysing approach was followed for each video.

2.2.3.2.1 SPECIES RICHNESS AND SPECIES ABUNDANCE

All fish observed from the time the stereo-BRUVs settled on the seafloor until 60 minutes later, were identified to species level when possible using a range of identification guides (Smith & Heemstra, 1986; Branch *et al.*, 2010) and an online stereo-BRUVs photoreference library. Individuals were identified to genus or family if they could not be identified to species level from the stereo-BRUVs footage. Eight species, one from each of the genuses *Argyrosomus, Carangid, Carcharhinus, Jasus, Lagocephalus, Sarda, Sphyrna* and *Squalus*, were not identified to species level due to difficulties in discerning morphological characteristics from the stereo-BRUVs footage. This proved to be particularly difficult under red artificial lighting, which provided a relatively poor image quality compared to other light sources, such as blue and white light (Harvey *et al.*, 2012a).

Species richness for each sample was determined as the total number of species recorded during a 60-minute video.

Estimating the abundance for each species was then conducted using the MaxN approach, which is commonly used in studies using stereo-BRUVs (Willis & Babcock, 2000; Cappo *et al.*, 2006). The MaxN is determined by identifying a single frame out of the full 60-minute video in which the maximum number of individuals per species are present and counting them (Cappo *et al.*, 2003; Shortis *et al.*, 2009). Thus, for each video, there was a single MaxN frame for each species. The MaxN value is considered to be a conservative measure of relative abundance as it is likely to underestimate the actual abundance (Willis & Babcock, 2004). For example, individuals that are attracted to the bait, but are not visible in the MaxN frame are not counted. The benefit of the MaxN approach is that pseudoreplication is avoided by ensuring that no individual is counted twice (Willis *et al.*, 2003).

2.2.3.2.2 EXPLANATORY VARIABLES

In addition to *habitat*, other explanatory variables (covariates) that may influence the observed reef fish assemblages were recorded to aid in explaining some the variation in the data (i.e.

water temperature and a suite of variables that are known to affect the visible area of the camera's fields of view (i.e. sampling area)). Underwater visibility, percentage obstruction and percentage water column were considered the suite of variables affecting the camera's fields of view and were determined during video analysis following a standardised method for each video.

WATER TEMPERATURE

Variation in water *temperature* has been shown to result in variability in fish assemblage structure and fish activity patterns (Fernandez-Duque, 2003; Kotwicki *et al.*, 2009). While sampling design could not directly control for this, the water *temperature* at each sampling site was recorded with an underwater temperature logger (Onset HOBO Pro Version 2). The logger was attached to the top of the stereo-BRUVs, which sits approximately one metre off the seafloor. The logger recorded the water *temperature* every five minutes throughout the deployment, and from this an average water *temperature* from the middle thirty minutes of each deployment was calculated for each sample.

PERCENTAGE WATER COLUMN

Percentage *water column* was determined for each sample during video analysis using the software package Vidana (Version 1.0.1be; Hedley, 2003). This allowed the differences in species composition due to differences in percentage of reef in view to be accounted for. For example, there is likely to be a decreased probability of detecting cryptic reef-attached species in samples with an increased percentage of *water column*. To account for this, the area of visible *water column* in view, as opposed to visible reef, was calculated.

PERCENTAGE OBSTRUCTION

The percentage of reef structures causing *obstruction* in the camera's fields of view was also determined for each sample. *Obstruction* was determined in a similar way as for water column. Samples with a calculated obstruction of over 50% were excluded from analyses. This was based on the assumption that a reduced field of view is likely to result in lower estimates obtained from that sample.

UNDERWATER *VISIBILITY*

Underwater *visibility* was determined for each sample during video analysis. *Visibility* was determined using the stereo-component of the BRUVs method. This was carried out by calculating the distance (m) from the cameras to the furthest visible fish that could be accurately identified, at a single frame during the 60-minute video.

3

DAY-NIGHT VARIATION IN THE FISH COMMUNITY STRUCTURE OF SHALLOW AND DEEP-APHOTIC ROCKY REEFS

3.1 INTRODUCTION

The marine environment is considered relatively challenging to sample (Axenrot *et al.*, 2004). As a result, shallow coastal habitats that are easily accessible and logistically feasible to sample at night have received the most scientific attention in terms of day-night research. The majority of this research has been conducted in sheltered environments such as estuaries (Lubbers *et al.*, 1990; Maes *et al.*, 1999; Becker *et al.*, 2011), soft-bottom bays (Nash *et al.*, 1994; Nash & Santos, 1998; Carpentieri *et al.*, 2005), seagrass beds (Kopp *et al.*, 2007), tropical mangrove forests (Rooker & Dennis, 1991) and other shallow macrophyte habitats (Harvey *et al.*, 2012a). For studies conducted in soft-bottom habitats, fishery dependent techniques, such as trawl and seine surveys, have dominated diurnal and nocturnal sampling (Smale, 1992; Petrakis *et al.*, 2001; Arrington & Winemiller, 2003, Guest *et al.*, 2003). In contrast, SCUBA UVCs (Underwater Visual Census) was commonly used in shallow marine habitats with higher seafloor rugosity and complexity, such as reefs (Thresher & Gunn, 1986; Cappo *et al.*, 2003; Holmes *et al.*, 2013; Mallet & Pelletier, 2014).

Studies investigating day-night variation in reef habitats have demonstrated distinct day and night fish assemblages at warm-temperate rocky reefs (Azzuro *et al.*, 2007), tropical coral reefs (Rooker *et al.*, 1997; Gilbert *et al.*, 2005) and artificial reefs (Santos *et al.*, 2002). These day-night shifts in fish community structure, which involve changes in community composition, species richness and species abundance, are relatively well understood. Furthermore, it is well understood that day-night variation in fish community structure and composition is owed to inter- and intra-specific differences in diel activity patterns of fishes (Hammerschlag *et al.*, 2017). This is because a species' ability to access resources and carry out basic activities is affected by changes in ambient light (Helfman, 1986; Rooker & Dennis, 1991; Piet & Guruge, 1997; Kronfeld-Schor & Dayan, 2003; Fox *et al.*, 2011). It is therefore expected that day-night variation in fish communities exists at contrasting shallow marine habitats where distinct day-night changes in ambient light occur.

Just as nocturnal fish communities are relatively poorly understood, communities inhabiting aphotic depths have also received little scientific attention (Hammerschlag *et al.*, 2017). With regards to reef habitats, the majority of research has predominantly focused on shallow depths (10–30 m) that are within the safe decompression limits for SCUBA UVC (Ebeling & Bray, 1976; Howard, 1989; Santos *et al.*, 2002; Annese & Kingsford, 2005; Azzuro *et al.*, 2007; Azzuro *et al.*, 2013). To overcome observer biases and depth limitations associated with SCUBA UVCs (see Chapter 1 for details), and to investigate deep-aphotic reef fish communities, baited remote underwater stereo-video systems (stereo-BRUVs) have been increasingly applied as a depth-independent sampling method in a number of day-night studies investigating marine reef systems (Cappo *et al.*, 2004; Basset & Montgomery, 2011; Harvey *et al.*, 2012a; Harvey *et al.*, 2012b). The technological advances and research developments have demonstrated the importance of these deep marine habitats (Hammerschlag *et al.*, 2017).

At South African rocky reefs, Heyns-Veale *et al.* (2016) were among the first to investigate deep (45–75 m) reef fish assemblages with stereo-BRUVs. They showed distinct shallow (11–25 m) and deep reef fish assemblages at Tsitsikamma National Park (TNP) marine protected area (MPA), which lies in the centre of the warm-temperate Agulhas Ecoregion (Heyns *et al.*, 2012; Figure 2.4). They concluded that the inclusion of deep reef fish assemblages in ecological studies may improve our understanding of resource requirements for reef fish species (Heyns-Veale *et al.*, 2016). Similarly, it is expected that the inclusion of day-night effects on fish assemblages may further help to improve our ecological understanding of South African fishery management and conservation targets.

Day-night variation in South Africa's warm-temperate rocky reef fish communities has not been previously investigated, and our nocturnal fish communities have received little attention. As a result, our ecological understanding of reef fish communities in South Africa is based almost entirely on studies that have been limited to day time sampling – a situation similar in the rest of the world (Harvey *et al.*, 2012a; Fitzpatrick *et al.*, 2013). Neglecting nocturnal fish communities has important implications. Nocturnal species have been described to represent approximately one third of fish communities (Helfman, 1978). It is therefore crucial to investigate these components of the community in order to determine whether communities observed during the day reflect those at night, and whether the management strategies in place remain applicable. Such considerations are also important in the study area for this thesis, Algoa Bay. This is because the reefs that were selected as study sites are unprotected and subjected to intense fishing pressure (Hutchings *et al.*, 2011). Furthermore, the reefs harbour a rich biodiversity and a high number of endemic species, in particular those belonging to the sparids (Buxton, 1993; Götz *et al.*, 2009; Solano-Fernández *et al.*, 2012).

Based on studies conducted at other warm-temperate shallow rocky reefs (Annese & Kingsford, 2004; Azzuro *et al.*, 2007; Bassett & Montgomery, 2011; Harvey *et al.*, 2012a), it was hypothesised that distinct diurnal and nocturnal fish assemblages exist at Algoa Bay's shallow (10–30 m) rocky reefs in response to the changes in ambient light between day and night. The importance of the diel cycle and the role of ambient light was then further explored by investigating whether day-night variation in fish assemblages occurs at deep (55-100 m) rocky reefs where aphotic conditions persist throughout the diel cycle.

The findings of this study may contribute significantly to our knowledge of warm temperate fish ecology, and may provide an opportunity to postulate generalisations about patterns in day-night variation that can be applied to South Africa's Agulhas Ecoregion, which is considered a conservation hotspot (Turpie *et al.*, 2000).

3.1.1 STUDY AIM

The aim of this study was to investigate the relationship between the diel cycle and Algoa Bay's shallow and deep-aphotic rocky reef fish communities. This was conducted by comparing the Algoa Bay reef fish assemblage, in terms of community composition, species richness and species abundance, between day and night, at both shallow and deep-aphotic rocky reef sites.

3.2 MATERIALS & METHODS

3.2.1 STATISTICAL ANALYSES

3.2.1.1 EXPLANATORY VARIABLES

CONTROLLED VARIABLES

To control for the effects of localised rocky reef *habitat* on reef fish communities, a stratified random sampling approach was followed. This aimed at ensuring that each study *site*, i.e. Cape Recife and Riy Banks, was stratified according to six *habitat* criteria based on reef profile and bottom substrate. For more information and maps of the study area, study *site* and deployment *site* selection procedure, refer to Chapter 2.

UNCONTROLLED VARIABLES

Other explanatory variables that were impossible to control for, but were accounted for, included water temperature and those affecting the camera's field of view (i.e. sampling area). The latter explanatory variables included *visibility*, percentage *water column* and percentage *obstruction*. The way in which these variables may influence the observed reef fish assemblages and the general materials and methods of how these variables were measured are described in Chapter 2.

3.2.1.2 FISH RESPONSES TO *TIME OF DAY* AND *DEPTH ZONE*

To test the null hypothesis of no day-night differences in community structure (*species richness, species abundance or community composition*), diurnal and nocturnal fish communities inhabiting *shallow* (13–34 m) and *deep-aphotic* (51–99 m) reefs in Algoa Bay were compared. *Time of day* (T) and *Depth zone* (DZ) were fixed effects in this experimental design. To provide inter-reef and inter-annual variability in fish communities recorded in this study, *Site* (ST) and *Survey* (SV) were added as random effects. The experimental design therefore consisted of the following variables:

Factor *Site* (ST; random with st = 2 levels: Cape Recife versus Riy Banks)

Factor *Survey* (SV; random with sv = 2 levels: 2015 versus 2016).

Factor *Time of day* (T; fixed with t=2 levels: day versus night)

Factor *Depth zone* (DZ; fixed dz= 2 levels: shallow versus deep)

An unequal number of replicate samples between the two levels of the factor *Survey* were collected. Forty-nine samples were collected in 2015 and 39 samples were collected in 2016. The design was, however, balanced with 11 replicate stereo-BRUVs (n) deployed in each of the eight combinations of the treatment variables, *Time of day* and *Depth zone*, and the random variable, *Site* (T x DZ x ST). This resulted in a total of 88 stereo-BRUVs deployments (N = t x dz x st x n; see Table 2.7 in Chapter 2).

SPECIES RICHNESS

Univariate statistical analyses were conducted using the base packages in R software (R Core Team, 2013) to analyse fish assemblages with the use of a biodiversity index, species richness. This was conducted by applying generalised linear models (GLMs) to investigate the variability in *species richness* as a function of the explanatory variables (*temperature, habitat, visibility, water column*), *Site* and *Survey*, and the biologically meaningful interaction between the treatment variables, *Time of day* and *Depth zone* (T x DZ). Generalised linear models are suitable for investigating non-normal response data in relation to multiple continuous and categorical covariates (Zuur *et al.*, 2010). A detailed data exploration procedure following the protocol of Zuur *et al.* (2010) was conducted prior to applying GLMs. This involved producing Cleveland dotplots to inspect the response and explanatory variables for outliers in the data (Cleveland, 1994). Pairplots were then produced and were used in combination with variance inflation factor (VIF) values to assess collinearity between the continuous covariates. Similarly, boxplots were used to detect collinearity between the continuous and categorical covariates (Zuur *et al.*, 2010). Finally, multi-panel scatterplots were produced to visualise relationships between the explanatory variables and species richness data. The saturated model, i.e. that containing all of the potential explanatory variables, was shown to be suitable to analyse species richness in response to *Time of day* and *Depth zone*, and was given by:

$$f\,(species\ richness) = \beta 1 + \beta 2\ (visibility) + \beta 3\ (temperature) + \beta 4\ (water\ column) + \beta 5\ (habitat) + \beta 6\ (Site) + \beta 7\ (T \times DZ) + \varepsilon$$

This model was then subjected to validation and optimisation processes to ensure reliability of the outputs (Zuur *et al.*, 2010). Model validation involved the investigation for homogeneity of variance by analysing patterns in the residuals plotted against the fitted values and all other explanatory covariates in the dataset. Model selection was then conducted following an Akaike Information Criterion (AIC) based approach by sequentially removing parameters from the saturated model and selecting the simplest model, with the lowest AIC score.

SPECIES ABUNDANCE AND COMMUNITY COMPOSITION

All multivariate graphical presentations and statistical analyses were conducted using the PERMANOVA+ (permutational analysis of variance) add-on package (Anderson *et al.*, 2008) in PRIMER-E v6 (Plymouth Routines in Multivariate Ecological Research) statistical software package (Clarke & Gorley, 2015). Multiple graphical presentations and statistical routines were applied in combination to identify and explore patterns in community composition and species abundance of rocky reef fish assemblages.

Relative abundances were appropriately transformed to account for the high variability in the MaxN data, which is typical of community abundance data (Clarke & Warwick, 2001). Relative abundances were square root transformed to analyse as *species abundance* data. This ensured that the effect of highly abundant species was reduced, and the effect of rare species was increased (Clarke & Warwick, 2001). In this study, rare species were considered to be those where only a single individual was recorded (i.e. greater amberjack (*Seriola dumerili*), unidentified requiem shark Carcharhinus sp. 1), diamond ray (*Gymnura natalensis*), diamond stingray (*Dasyatis dipterura*), geometric moray (*Gymnothorax griseus*), cape knifejaw (*Oplegnathus conwayi*), blackbelly rosefish (*Helicolenus dactylopterus*), dane (*Porcostoma dentata*), unidentified hammerhead shark (*Sphyrna* sp. 1), cape gurnard (*Chelidonichthys capensis*) and john dory (*Zeus faber*; see Appendix A, Table A). In contrast, highly abundant species were considered to be schooling species (i.e. *Sarpa salpa*; see Appendix A, Table A). All species recorded in the stereo-BRUVs footage, including rare and highly abundant species, were included in the multivariate analyses.

The distributions of the continuous explanatory variables that were measured for each sample, such as *temperature* and those influencing the sampling area (i.e. *visibility, percentage water column and percentage obstruction*) were investigated prior to running any multivariate analyses. This was conducted using Draftsman plots, which produce multiple scatter plots for pairs of explanatory variables. Where variables showed outliers, skewed or bimodal distributions, the variables were log-transformed to ensure approximately symmetric distributions that make the data more appropriate for use as Euclidean distance measure (Clarke & Warwick, 2001). The continuous explanatory variables were then normalised to ensure all variables were placed on a comparable scale (Clarke & Warwick, 2001). The choice of Euclidean distance resemblance matrices to analyse environmental variables was based on recommendations by Anderson (2006). *Habitat* was added to the experimental design as a factor to control for the effects of profile and bottom substrate on fish assemblages (see General methods and materials in Chapter 2 for more detail).

The resemblance measure chosen to analyse abundance data was a Bray–Curtis similarity matrix and included the similarities between every pair of samples. Based on Anderson *et al.* (2008), the Bray–Curtis similarity measure is considered appropriate to investigate data that are heavily zero inflated, such as community abundance data (Anderson *et al.*, 2008). Permutation routines analysing species abundance were based on a Bray–Curtis resemblance matrix from square root transformed MaxN data.

Overall patterns in the multivariate data, and within-treatment variability, were visualised using unconstrained non-metric multi-dimensional scaling (MDS) plots (Kruskal, 1964; Clarke, 1993). The distances among the points in the MDS plot represent the same rank order as the Bray–Curtis dissimilarities among samples, and can be used to make inferences about the community composition of samples (Anderson, 2007).

A test for homogeneity of multivariate dispersions using the PERMDISP routine was conducted prior to performing the PERMANOVA (Clarke, 1993), since the latter test is sensitive to differences in dispersions among treatments. This test was used to examine the differences in dispersion among groups, which was done in combination with an unconstrained ordination plot to reveal the nature of the differences that may be detected by PERMANOVA. The PERMDISP was based on a Bray–Curtis similarity measure and conducted for random variables, *site* and *survey*, and treatment variables, *Time of day* and *Depth zone*,

Permutational analysis of multivariate variance routines were then conducted to test the response of species abundance data to the aforementioned variables and the interaction between the main effects (Clarke, 1993). Based on recommendations by Anderson *et al.* (2008), PERMANOVAs involved permutation of residuals under a reduced model. Since it is suggested that the power and precision of the PERMANOVA routine increases with an increase in the number of permutations used, 9999 random permutations of the residuals to obtain p significance values were chosen for this study. The number of unique permutations is the number of unique values of the test statistic that were under permutation. The number of ‘unique perms’ were always almost equal to the chosen number of random permutations (9999), thus indicating that the use of Monto Carlo p values was not necessary and the resultant p values were sufficient to interpret the results (Anderson *et al.*, 2008).

The known relationships between *species abundance* and *temperature, habitat* and sampling area (*visibility, percentage water column* and *percentage obstruction*) were taken into account. For the categorical variables, this was done by using a sequential PERMANOVA, otherwise called a type 1 sum of squares, for the partitioning (Anderson *et al.*, 2008). All explanatory variables that were impossible to control for, i.e. *visibility, percentage obstruction, percentage water column* and *water temperature*, were added as the first, second, third and fourth covariates in the PERMANOVA analysis. *Habitat,* which was the only categorical explanatory variable, was added as the fifth covariate followed by *site*, *survey*, *Depth zone* and *Time of day*, in that order.

The PERMANOVA routine produces estimates of variation for each component (explanatory, random and treatment variables) that is added to the experimental design (Anderson *et al.*, 2008). These were investigated to compare the sizes of each component of variation (Anderson *et al.*, 2008), and to further investigate if the overall variability in *species abundance* and *community composition* is explained by the explanatory and random variables.

Pair-wise comparisons among levels of the treatment variables, *Time of day* and *Depth zone*, were conducted where the main PERMANOVA test revealed significant effects ($p < 0.05$) for the main effects and their interactions. These were conducted to explore differences between the treatment groups (Anderson *et al.*, 2008).

Characterisation of species responsible for the observed multivariate patterns were analysed using the similarity percentage (SIMPER) of contributing species analysis in PRIMER-E statistical package (Clarke, 1993). The SIMPER routine covered a two-factor design (*Depth zone* and *Time of day*) to identify the dominant species contributing to the Bray–Curtis similarities and dissimilarities among sample groups (Clarke, 1993).

SPARID RESPONSES TO *TIME OF DAY* AND *DEPTH ZONE*

Since sparids were the dominant family inhabiting warm-temperate rocky reefs in South Africa (see Chapter 2), species belonging to this family were given particular attention. In R software, GLMs were applied in a similar manner as described for *species richness* with similar data exploration and model validation procedures being carried out. These GLMs aimed at testing the variability in the grouped abundance of all sparids, sparids, as a function of the explanatory variables, and the interaction between the two main effects (T x DZ).

INDICATOR SPECIES ANALYSIS

An indicator species analysis was conducted using the IndVal method (De Caceres *et al.*, 2010) in the indicspecies package version 17.1 (De Cáceres & Legendre, 2009) in R software (R Core Team, 2013). This analysis produces an indicator value index, which provides a representation of the strength of the relationship between a species' abundance (MaxN data) and the type of '*site*s' it was observed in (Legendre *et al.*, 2013). For this, '*site*s' were classified into 'groups' according to the four combinations of levels for *Time of day* and *Depth zone*. The four '*site* groups', otherwise referred to as treatments, were therefore: *day/shallow*, *day/deep-aphotic*, *night/shallow* and *night/deep-aphotic*. Using the indicator value indices, species that could be used as ecological indicators for each of the four treatments were identified. This was done by considering a species with an indicator value index of greater than 0.25 as a good indicator species (Legendre *et al.*, 2013). This value consists of two components referred to as 'A', which is the specificity value, and 'B,' which is the fidelity value (Dûfrene & Legendre, 1997). The specificity value is also described as the mean abundance of a species in a given '*site* group' divided by the sum of the mean abundances of all species over all *site* groups (Dûfrene & Legendre, 1997). The fidelity value is described as the relative frequency of occurrence of a species in a given '*site* group'; Dûfrene & Legendre, 1997). The null hypothesis of no association between '*site* groups' and species was then formally tested by permutation analysis (Dûfrene & Legendre, 1997).

Since this study was also concerned with habitat use and activity in relation to diurnal and nocturnal conditions, the four treatments were combined into two groups according to similarities in their photic conditions, and correlation indices were produced to identify the differences in detectability of species observed in this study (De Cáceres & Legendre, 2009). Photic group consisted only of the *day/shallow* treatment, and the aphotic group consisted of a combination of *day/deep-aphotic, night/deep-aphotic* and *night/shallow* treatments. The association of species to the aphotic group was determined using a Pearson's phi coefficient of association between species presence/absence data and the three dark treatments.

3.3 RESULTS

3.3.1 EXPLANATORY VARIABLES

3.3.1.1 CONTROLLED EXPLANATORY VARIABLES

A randomly stratified sampling approach was employed in order to sample only *high profile reef* and *low profile reefs* (see General methods and materials in Chapter 2). Despite this, 20.5% of the total number of stereo-BRUVs that were deployed landed on intermittent *sandy reef patch*es (Table 3.1). A total of nine intermittent *sandy reef patches* were sampled at each *site*, with a fairly even distribution of these samples collected among the treatments at Cape Recife. No *sandy reef patches* were, however, sampled at the shallow zone of Riy Banks (Table 3.1). Despite this, there was a near even allocation of sampling effort for *high profile reefs* and *low profile reefs* among the treatments at both *site*s (Table 3.1).

Table 3.1. Distribution of sampling effort among three within-reef habitats for each treatment combination of the levels of *Time of day*, *Depth zone* and *Site* for different reef *site*s in Algoa Bay, South Africa. Sampling aimed at an even allocation of effort among *high profile reef* (High), *low profile reef* (Low) and intermittent *sandy reef patch* (Sand) *habitat* criteria.

	Cape Recife		
Treatments	*high profile reef*	*low profile reef*	*sandy reef patch*
day/shallow	5	4	2
day/deep-aphotic	3	5	3
night/shallow	3	5	3
night/deep-aphotic	3	7	1

	Riy Banks		
	high profile reef	*low profile reef*	*sandy reef patch*
day/shallow	7	4	0
day/deep-aphotic	2	5	4
night/shallow	4	7	0
night/deep-aphotic	4	2	5

3.3.1.2 UNCONTROLLED EXPLANATORY VARIABLES

Table 3.2. Average water *temperature* (° C ± SD) and underwater *visibility* (mm ± SD) for each treatment combination for the levels of *Time of day*, *Depth zone* and *Site*. Temperature range is displayed in brackets.

	Cape Recife	Riy Banks	Cape Recife	Riy Banks
Day/shallow	15.1 ± 2.6 (9.8 - 19.3)	16.3 ± 0.9 (15.3 - 18.3)	2,324.3 ± 1,738. 3	4,359. 5 ± 2,358.5
Day/deep-aphotic	13.4 ± 2.8 (9.9 - 18.5)	15.1 ± 1.5 (12.4 - 16.8)	1,681.3 ± 0,500.0	1,670.5 ± 0,362.8
	Temperature		Visibility	
Night/shallow	15.6 ± 2.0 (12.0 - 17.3)	16.5 ± 0.9 (15.2 - 18.0)	1,810.0 ± 0,402. 5	2,542. 2 ± 0,750.1
Night/deep-aphotic	15.9 ± 2.1 (11.0 - 17.8)	14.0 ± 1.6 (11.9 - 17.2)	1,502.7 ± 0,221. 3	1,982. 6 ± 0,431.3

Average water *temperatures* were similar across all treatments and between both *site*s (Table 3.2). A broader *temperature* range was recorded at Cape Recife compared to Riy Banks (Table 3.2). This was due to very low *temperatures* being recorded for diurnal samples, likely reflecting localised upwelling events at Cape Recife during the sampling (Table 3.2). For these treatments (*day/shallow* and *day/deep-aphotic*), minimum *temperatures* of 9.8 °C and 9.9 °C were recorded, respectively (Table 3.2). Maximum *temperatures*, however, were similar for all treatments at both Cape Recife and Riy Banks (Table 3.2).

Lower average *visibilities* were recorded for nocturnal and deep-aphotic treatments (*night/shallow, night/deep-aphotic* and *day/deep-aphotic*) compared to the *day/shallow* treatment (Table 3.2). With the exception of similar average *visibilities* being recorded for *day/deep-aphotic* treatments at Cape Recife (1 681.3 mm ± 0,500.0) and Riy Banks (1 670.5 mm ± 0 362.8), the average *visibilities* for *day/shallow, night/shallow* and *night/deep-aphotic* treatments were greater at Riy Banks (Table 3.2).

3.3.2 FISH RESPONSES TO *TIME OF DAY* AND *DEPTH ZONE*

3.3.2.1 *SPECIES RICHNESS*

Data exploration was initially performed using the Poisson distribution family, however, this indicated that the species richness data were underdispersed with a dispersion statistic of less than one (Zuur *et al.*, 2010). A Gaussian model was therefore applied (Zuur *et al.*, 2010), and the model selection process suggested that dropping *site* and temperature from the saturated model (AIC = 431.2) would produce the optimal model (AIC = 427.7), given as:

$$f\ (\textit{species richness}) = \text{ß}1 + \text{ß}2\ (\textit{visibility}) + \text{ß}5\ (\textit{water column}) + \text{ß}4\ (\textit{habitat}) + \text{ß}5\ (\mathrm{T \times DZ}) + \varepsilon$$

A total of 64 species from 28 families were recorded in this study (Appendix A, Table A). Out of a total of 56 species from 24 families that were recorded on *shallow* reefs, 52 species from 23 families were recorded at *day* and 31 species from 16 families were recorded at *night* (Appendix A, Table A). At *deep-aphotic* reefs, a total of 42 species from 20 families were recorded; 37 species from 17 families at *day* and 28 species from 16 families at *night* (Appendix A, Table A).

The results from the sequential analysis of variance run on the Gaussian GLM are displayed in Table 3.3; the reductions in the residual deviance as each variable is added in turn are displayed, as well the residual deviances themselves. Indications are that a portion of the variability in the number of species recorded in this study (i.e. *species richness*) was significantly determined by the covariates, *visibility* ($p < 0.001$), *water column* ($p < 0.001$) and *habitat* ($p < 0.019$; Table 3.3). Furthermore, the results revealed that *Time of day* (p <

0.001), *Depth zone* (p < 0.001) and their interaction, *Time of day* x *Depth zone* (p < 0.013), also significantly explained the observed patterns in *species richness* recorded in this study (Table 3.3).

Table 3.3. Sequential analysis of deviance table for the Gaussian GLM used to explain the variation in species richness of Algoa Bay's rocky reef fish communities and explanatory variables, *visibility*, *temperature*, *water column* and *habitat*, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

	df	Deviance	Residual *df*	Residual deviance	Pr (> Chi)
Null			87	1439.77	
Visibility	1	329.07	86	1110.71	< 0.001
Water column	1	145.45	85	965.26	< 0.001
Habitat	2	53.76	83	911.51	< 0.019
Time of day	1	105.56	82	805.95	< 0.001
Depth zone	1	221.91	81	584.04	< 0.001
T: DZ	1	41.93	80	542.12	< 0.013

The GLM model summary further indicated that a greater *visibility* was predicted to record a higher *species richness*, although this estimate was not significantly different from zero (estimate = 1e-05; p = 0.475; Table 3.4). An increase in *water column*, however, was associated with a lower *species richness*, with a significant coefficient estimate (-3e-05, p < 0.001; Table 3.4). It was further revealed that, although insignificantly different from zero, *sandy reef patches* (estimate = -0.07, p = 0.400) were predicted to be associated with a lower *species richness* (Table 3.4). The coefficient estimates for *low profile reef* (estimate = 0.10, p < 0.015) and high *profile reef* were significant, with both reef types predicted to have a positive effect on *species richness* (estimate = 0.20; p < 0.001; Table 3.4).

Table 3.4. Summary of the model fit for the Gaussian GLM summary providing information on the nature of the relationships between species richness of Algoa Bay's rocky reef fish communities and explanatory variables, *visibility*, water column and *habitat* and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

Coefficients:	Estimate	Std. Error	t value	Pr (> |t|)
Intercept	0.20	9e-02	26,699	< 0.001
Visibility	1e-05	2e-05	0,718	0.475
Water column	-3e-05	8e-04	-3,694	< 0.001
Low profile reef	0.10	5e-02	2,488	< 0.015
Sandy reef patch	-0.07	8e-02	-0,846	0.400
Night	-0.09	9e-02	-1,040	0.302
Shallow	0.50	8e-02	5,862	< 0.001
Night: Shallow	-0.30	1e-01	-2,503	< 0.014

The GLM plot of the predicted values implied that *species richness* was not predicted to differ significantly across the four treatments (Figure 3.1); however, the sequential analysis of deviance on the GLM indicated that there were indeed significant effects (Table 3.3). The overlapping of the confidence intervals displayed in the plot is due to the use of the overall mean *visibility* and *water column* values as opposed to the mean value for each treatment (Figure 3.1). Since the average *visibility* recorded for *day/shallow* treatment was substantially greater than for the aphotic treatments (Table 3.2), the predicted data would have resulted in a lower *species richness* estimate for the *day/shallow* treatment and higher species richness estimates for the remaining aphotic treatments (Figure 3.1). This suggests that the differences in species richness between the photic and aphotic samples may not have been as great if *visibility* was standardised between the different treatments. Since the sequential analysis of deviance identified significant effects for *Time of day* and *Depth zone*, as well as their interaction (after the effects of visibility, and the other covariates, had been taken into account), it is concluded that both *Time of day* and *Depth zone* had a significant effect on *species richness*.

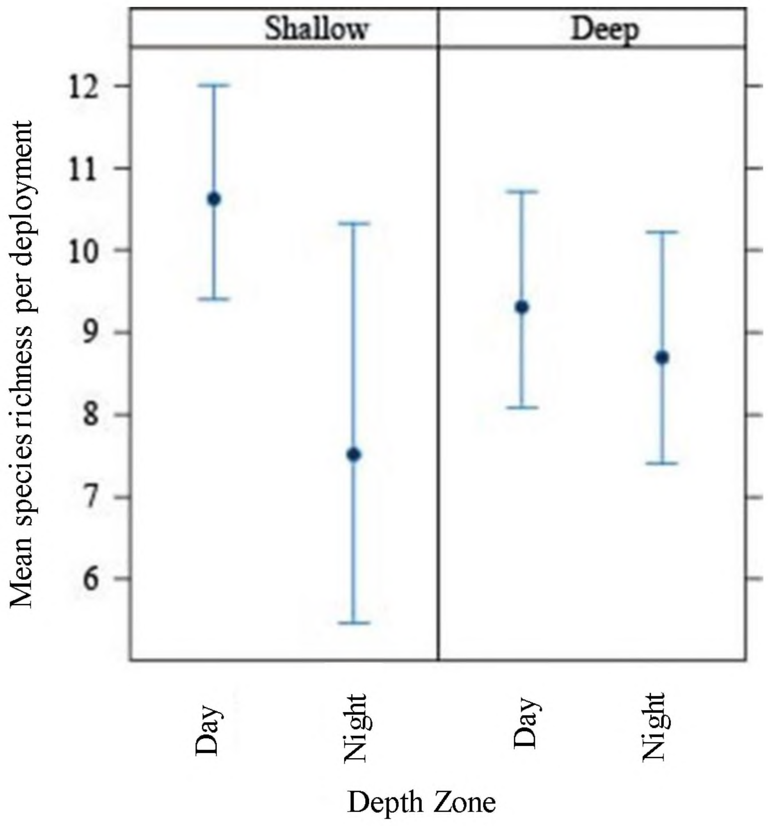

Figure 3.1. Effect of *Depth zone* (shallow versus deep-aphotic) and *Time of day* (day versus night) on species richness. The values for species richness were predicted from the GLM using standardised values for *visibility* (2264.92 mm ± 1200.14) and water column (70.71 ± 27.83). The error bars represent the approximate 95% confidence intervals.

3.3.2.2 SPECIES ABUNDANCE AND COMMUNITY COMPOSITION

The MDS ordination plot revealed that diurnal assemblages (*day/shallow* and *day/deepaphotic* treatments) were highly variable compared to nocturnal assemblages (*night/shallow* and *night/deep-aphotic*), which showed more tightly clustered points particularly for the *night/shallow* treatment (Figure 3.2). A PERMDISP test for homogeneity of multivariate dispersions on *Time of day* showed a greater *variability* in the diurnal treatments than the nocturnal treatment groups (F = 36.67; p < 0.001; Table 3.5). When tested on the interaction between *Time of day* x *Depth zone*, significant differences in dispersions from the centroid were identified (p < 0.001). The *day/deep-aphotic* treatment was the most dispersive (36.8 ± 1.9), thus indicating higher variability in the data for this treatment, followed by samples of *day/shallow* (34.0 ± 2.3), *night/deep-aphotic* (31.9 ± 1.9) and *night/shallow* (24.4 ± 1.4).

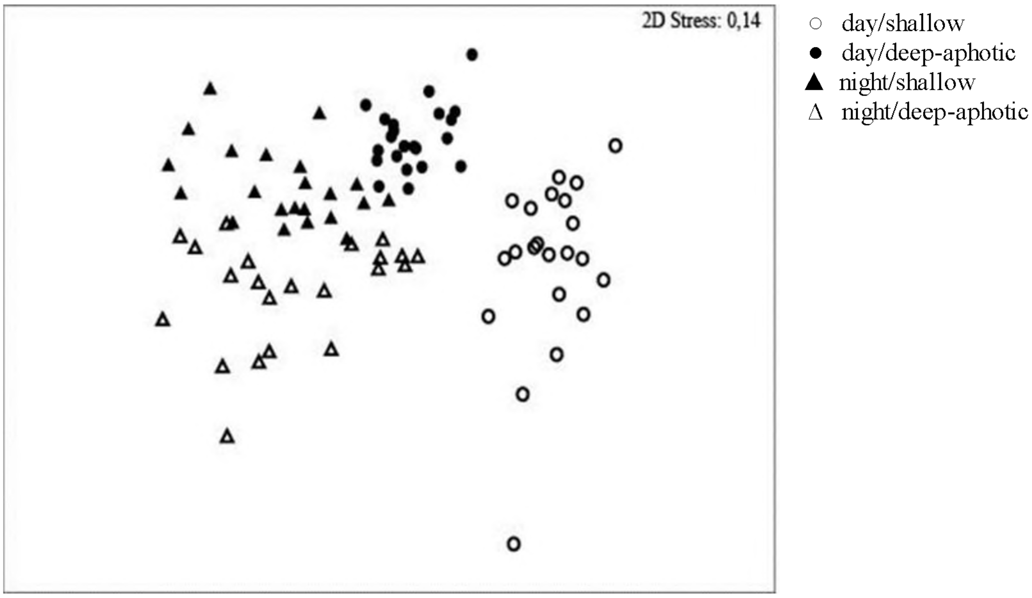

Figure 3.2. Non-metric multi-dimensional scaling plot illustrating square root transformed species MaxN data on the basis of a Bray–Curtis resemblance matrix, with treatment variables, *Time of day* and *Depth zone*.

Table 3.5. Distance-based test for homogeneity of multivariate dispersions using the PERMDISP routine based on a Bray–Curtis resemblance on square root transformed species MaxN data, with the main effects, *Depth zone* and *Time of day*.

	F	*df* 1	*df* 2	*p* (perm)
Survey	8.42	1	86	<0.02
Site	0.64	1	86	0.476
Depth zone	1.39	1	86	0.304
Time of day	36.67	1	86	< 0.001

The PERMDISP on *survey* showed a significantly increased variability in communities recorded during 2016 (47.70 ± 1.56) compared to 2015 (40.81 ± 1.71; $F = 8.42$; $p < 0.020$; Table 3.5). Since the PERMDISP is likely to detect significant differences in dispersions that may not inflate the error rates of the PERMANOVA analysis (Anderson *et al.*, 2008), it was considered acceptable to continue with the PERMANOVA routine.

PATTERNS IN SPECIES ABUNDANCE AND COMMUNITY COMPOSITION

As indicated by the MDS ordination plot (Figure 3.2), there was a clear pattern of relatively distinct fish communities among the four treatments tested in this study. The *day/shallow* community had the most distinct composition recorded in this study. This was demonstrated in the MDS ordination plot (Figure 3.2), by the clear separation of *day/shallow* points from other points belonging to the three aphotic treatments (*night/shallow*, *day/deep-aphotic* and *night/deep-aphotic*; Figure 3.2). Although not as clear, there was also a degree of separation among the three aphotic treatments, particularly between the *day/deep-aphotic* and *night/shallow* communities (Figure 3.2).

When investigating species abundance data in response to the four treatments, a PERMANOVA revealed that *Time of day* ($p < 0.0001$), *Depth zone* ($p < 0.0001$) and their interaction *Time of day* x *Depth zone* ($p < 0.0001$) significantly affected the species abundance of the fish assemblages recorded in this study (Table 3.6). Pair-wise comparisons also showed that all treatments recorded significantly different species abundances from one another ($p < 0.0001$; Table 3.7).

Table 3.6. Results from the sequential PERMANOVA based on Bray-Curtis similarities of square-root transformed species abundance (MaxN) data for rocky reef fish investigated in response to explanatory variables, *visibility*, temperature, water column, obstruction and *habitat*, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

Source	*df*	MS	Pseudo-F	*p* (perm)	Unique perms
Visibility	1	24,800.0	20,141	< 0.0001	9932
Obstruction	1	2,823.2	2,104	< 0.02	9931
Water column	1	3,085.9	2,305	< 0.02	9913
Temperature	1	7,790.5	6,102	< 0.0001	9943
Habitat	1	4,629.3	4,574	< 0.0001	9923
Site	1	2,900.7	2,315	< 0.02	9926
Survey	1	6,562.8	6,593	< 0.0001	9938
Depth zone	1	25,334.0	25,448	< 0.0001	9939
Time of day	1	21,129.0	21,224	< 0.0001	9936
T x DZ	1	7,715.8	7,751	< 0.0001	9939
Residual	76	0,995.5			
Total	87				

Table 3.7. Pair-wise comparisons among all pairs of levels of treatment variables, *Time of day* and *Depth zone*, based on a Bray–Curtis resemblance measure on square root transformed species abundance data.

	t	*p* (perm)	Unique perms
Shallow *versus* deep/aphotic			
day	3. 86	< 0.0001	9950
night	3. 64	< 0.0001	9937
Day *versus* night			
shallow	4. 20	< 0.0001	9945
deep-aphotic	2. 51	< 0.0001	9932

A strong and significant relationship was also revealed between *species abundances* and *temperature* (p < 0.02), *habitat* (p < 0.001) and those variables affecting the sampling area, *visibility* (p < 0.001) and *water column* (p < 0.02), as measured by the Bray–Curtis resemblance measure (Table 3.6). Furthermore, the random variables, *Site* (p < 0.001) and *Survey* (p < 0.02), also had significant effects on the observed *species abundances* (Table 3.6). While *Site* (42.39), obstruction (17.28), *water column* (20.79) and t*emperature* (79.49) were not major contributors to the overall variability in the *species abundance* data, *visibility* (268.13), *Survey* (142.79) and *habitat* (139.96) explained a larger portion of the observed variability (Table 38). Given this, *Time of day* (505.94), *Depth zone* (900.55) and their interaction (377.38) had the highest contribution to the overall variability in the species abundance data (Table 3.8).

Table 3.8. Results of the sequential PERMANOVA for the estimates of components of variation attributed to explanatory variables, *visibility*, temperature, water column, obstruction and *habitat*, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

Source	Estimate	Square root
S (Visibility)	268.13	16.4
S (Obstruction)	17.28	4.2
S (Water column)	20.79	4.6
S (Temperature)	79.49	8.9
S (Habitat)	139.96	11.8
V (Site)	42.39	6.5
V (Survey)	142.79	12.0
S (Depth zone)	900.55	30.0
S (Time of day)	505.94	22.5
S (T x DZ)	377.38	19.4
V (residual)	995.50	31.6

S: source; V: variation

Since significant heterogeneity was detected by the PERMDISP for the treatment variable, *Time of day*, and the random variable, *Survey* (Table 3.5), and the PERMANOVA revealed significant differences among these treatments (Table 3.6). By analysing these results in combination with the MDS plot (Figure 3.2), it is suggested that the differences detected between day and night treatments are largely due to a combination of differences in location and dispersions. The differences detected between *2015* and *2016* treatments in the PERMANOVA (Table 3.6), however, are likely driven by differences in dispersions more so than differences in locations, as shown in the MDS ordination plot (Figure 3.3).

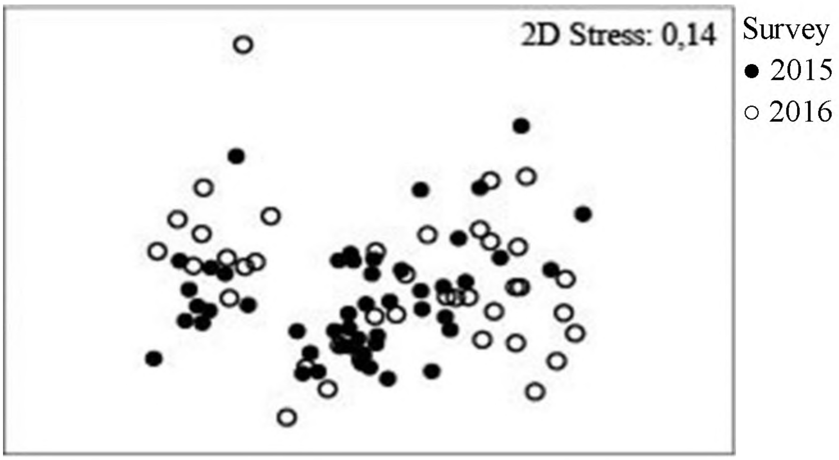

Figure 3.3. Non-metric multidimensional scaling plot displaying the differences in

dispersions of Algoa Bay's rocky reef fish species abundance data collected using baited remote underwater stereo-video systems during two *surveys*, 2015 and 2016.

DISTINCT *DAY/SHALLOW* FISH COMMUNITY

Twenty-one species were responsible for the distinct *day/shallow* community observed in the MDS ordination plot (Figure 3.2). Of these species, seven were described as rare species, four species were described as largely restricted to the *day/shallow* treatment and ten species were exclusively sampled in this treatment (Appendix A, Table B). Here, rare species were described as those where only a single individual was recorded or the species was only recorded in a single sample throughout the study (i.e. *Seriola dumerili, Cheilodactylus fasciatus, Notorhynchus cepedianus, Dasyatis dipterura, Oplegnathus conwayi, Sphyrna* sp. 1 and *Zeus faber*; Appendix A, Table B).

Species that were considered to be largely restricted to the *day/shallow* treatment were those where only a single individual was recorded outside this treatment. These species were four sparids, namely *Cheimerius nufar*, *C. gibbiceps*, *Diplodus capensis* and *Rhabdosargus holubi* (Appendix A, Table B).

Similarly, seven sparids were exclusively sampled in the *day/shallow* treatment throughout this study. These included dageraad, (*C. cristiceps*), zebra (*Diplodus hottentotus*), janbruin (*Gymnocrotaphus curvidens*), red steenbras (*P. rupestris*), scotsman (*Polysteganus praeorbitralis*), dane (*Porcostoma dentata*) and *S. salpa*; Appendix A, Table B). In addition, three non-sparids were also exclusive to the *day/shallow* treatment. These species were the yellowbelly rockcod (*Epinephelus marginatus*), and an unidentified Scombrid and a Tetraodontid (Appendix A, Table B).

3.3.2.3 SPARID RESPONSE TO *TIME OF DAY* AND *DEPTH ZONE*

The data exploration process indicated that the data were overdispersed, with a dispersion statistic that was greater than one. A negative binomial GLM was therefore applied (Zuur *et al.*, 2010), and the model selection process indicated that the saturated model was suitable to analyse sparid responses to *Time of day* and *Depth zone*.

The saturated model took the form of:

$$f\,(sparids) = \beta 1 + \beta 2\ (visibility) + \beta 3\ (temperature) + \beta 4\ (water\ column) + \beta 5\ (habitat) + \beta 6\ (Site) + \beta 7\ (T \times DZ) + \varepsilon$$

The responses of sparids to *Time of day* and *Depth zone* were further investigated using a negative binomial GLM on the grouped abundance of all sparids recorded in this study. The sequential analysis of deviance run on the GLM indicated that *visibility* ($p < 0.001$), *temperature* ($p < 0.001$), *habitat* ($p < 0.001$) and *Site* ($p < 0.001$) significantly explained a portion of the variation observed in the *sparid abundance* data (Table 3.9). While *visibility* (estimate = 5e-05), temperature (estimate = 0.030) and Riy Banks (estimate = 0.470) had positive significant effects on *sparid abundance*, *low profile reef* (estimate = -0.080) and *sandy reef patch* (estimate = -0.530) had significant negative effects (Table 3.10).

The main effects, *Time of day* ($p < 0.0001$) and *Depth zone* ($p < 0.0001$) had significant effects on *sparid abundance*, but their interaction was not significant ($p > 0.07$; Table 3.9). The sequential analysis of deviance on the GLM showed that night had a significant negative effect on *sparid abundance* (estimate = -1.040) and shallow had a significant positive effect (estimate = 1.450; Table 3.10).

Table 3.9. Sequential analysis of deviance table for the negative binomial GLM run on the sparid MaxN data and explanatory variables, *visibility*, temperature, water column and *habitat*, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ). T = *Time of day*; DZ = *Depth zone*.

	df	Deviance	Residual *df*	Residual deviance	Pr(>Chi)
Null			86	416. 70	
Visibility	1	112. 830	85	303. 87	< 0.0001
Temperature	1	15. 080	84	288. 80	< 0.0001
Water column	1	0. 220	83	288. 58	0.64
Habitat	2	37. 100	81	251. 47	< 0.0001
Site	1	4. 850	80	246. 63	< 0.03
Time of day	1	84. 300	79	162. 33	< 0.0001
Depth zone	1	60. 180	78	102. 15	< 0.0001
T: DZ	1	3. 250	77	98. 90	0.07

Table 3.10. Summary of the model fit for the negative binomial GLM revealing the nature of the relationships observed between Algoa Bay's sparid abundance and explanatory variables, *visibility*, temperature, water column and *habitat*, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

Coefficients:	Estimate	Std. Error	t value	Pr (>|t|)
Intercept	2.090	0.480	4.36	< 0.0001
Visibility	5e-05	6e-05	0.80	0.421
Temperature	0.030	0.030	0.95	0.343
Water column	-8e-04	0.002	-0.33	0.744
Low profile reef	-0.080	0.140	-0.61	0.544
Sandy reef patch	-0.530	0.190	-2.74	< 0.006
RB	0.470	0.130	3.36	< 0.0004
Night	-1.040	0.190	-5.31	< 0.0001
Shallow	1.450	0.210	6.76	< 0.0001
T x DZ	-0.500	0.280	-1.81	0.071

The plot of the predicted estimates of sparid abundance, given standardised values for *visibility* and the other covariates, revealed a similar pattern at Cape Recife and Riy Banks (Figure 3.4). *Sparid abundance* was positively and significantly higher in the *day/shallow* treatment compared to all other treatments. The *night/deep-aphotic* had a negative and significant effect on *sparid abundance*, while the *day/deep-aphotic* and *night/shallow* treatments were similar and characterised by low *sparid abundance* (Figure 3.4).

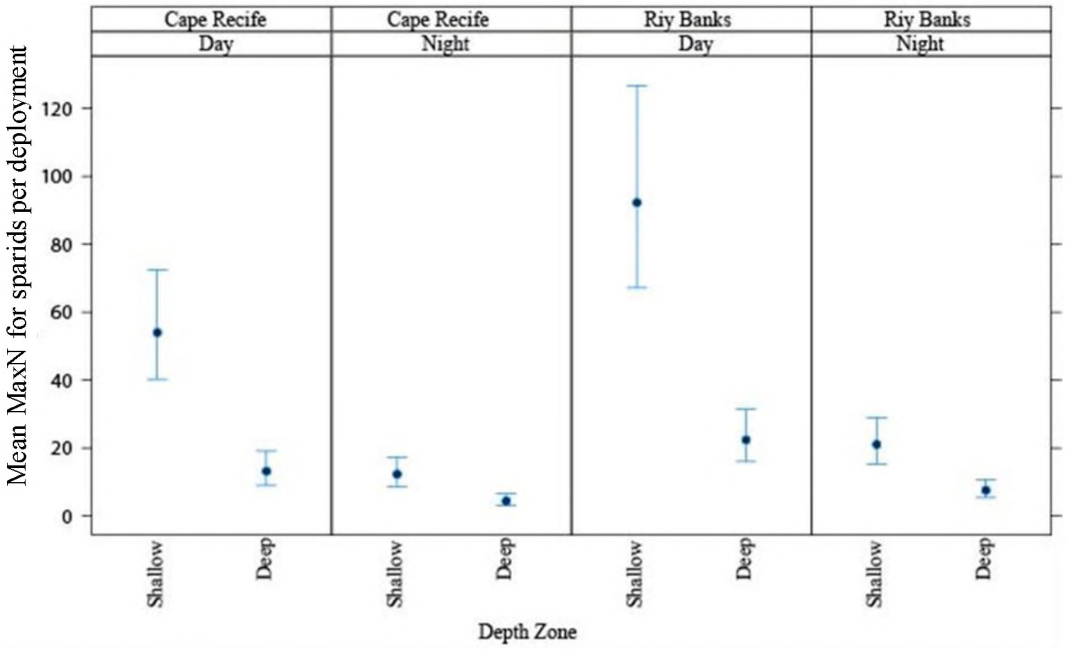

Figure 3.4. Effect of *Depth zone* (shallow versus deep-aphotic) and *Time of day* (day versus night) on grouped abundances of all sparids recorded in this study. The values for sparid abundance were predicted from the GLM using standardised values for *visibility* (2264 mm ± 1200.14) and water column (70.71% ± 27.83). The error bars represent the approximate 95% confidence intervals.

DEPTH EFFECTS AT DAY AND AT NIGHT

As described, a very distinct *day/shallow* community was revealed by the MDS ordination plot (Figure 3.2). Investigations into the differences in community composition and species abundance between *day/shallow* and *day/deep-aphotic* revealed that eight species (*B. inornata, S. emarginatum, D. capensis, C. laticeps, C. nufar, Pachymetopon aeneum, S. salpa* and *Poroderma africanum*) were recorded in greater abundances in the shallow zone compared to the *deep-aphotic* zone (Table 3.12). Seven of the eight species were sparids. In contrast, four species, (i.e. two sparids, *P. laniarius* and *A. argyrozona*, and two non-sparids, *Squalus* sp. and *G. ater*), were recorded in higher abundances in the *day/deep-aphotic* treatment compared to the *day/shallow* treatment (Table 3.12).

Table 3.12. Results of SIMPER analysis showing the dominant fish species contributing to the dissimilarity between *day/shallow* and *day/deep-aphotic* communities recorded in this study. Average species abundances are displayed under the heading for treatments *day/shallow* and *day/deep-aphotic*. The dissimilarity is displayed as a percentage (Dissim contrib %).

Species	*Day/shallow*		*Day/deep-aphotic*	Dissim contrib %
Boopsoidea inornata	5.2	>	0.6	13.7
Pterogymnus laniarius	0.1	<	2.4	6.9
Spondyliosoma emarginatum	2.7	>	0.4	6.7
Squalus sp. 1	0.1	<	1.8	5.4
Diplodus capensis	1.6	>	0,0	4.9
Chrysoblephus laticeps	2.1	>	0.7	4.6
Cheimerius nufar	1.6	>	0.1	4.6
Pachymetopon aeneum	1.6	>	0.3	4.2
Argyrozona argyrozona	0.1	<	1.5	4.1
Sarpa salpa	1.3	>	0,0	3.3
Poroderma africanum	1.5	>	0.9	2.7
Galeichthys ater	0.9	<	1.1	2.6

The MDS ordination plot suggested that the community composition was similar for the two night treatments (*night/shallow* and *night/deep-aphotic*; Figure 3.2). This was demonstrated as there was some overlap of points between *night/shallow* and *night/deep-aphotic* communities. Similarities in community composition between *night/shallow* and *night/deepaphotic* treatments were further investigated using a SIMPER analysis (Appendix A, Table C). This routine revealed that within each treatment, eight species had a cumulative contribution percentage of 90.9% and 91.8% to the average similarity of samples belonging to *night/shallow* and *night/deep-aphotic* samples, respectively. Of these dominant species, five species (*G. ater, B, inornata, P, africanum, H, edwardsii* and *Squalus* sp. 1) were considered important components of both *night/shallow* and *night/deep-aphotic* treatments due to their high abundances in both treatments. This was particularly true for *G. ater*, which was the most dominant species of nocturnal communities at both shallow and deep-aphotic reefs (Appendix A, Table C). Differences between *night/shallow* and *night/deep-aphotic* communities were largely driven by higher abundances of sparids, catsharks, shysharks and large shark species (*Mustelus mustelus* and *Triakis megalopterus*) on *shallow* reefs, while *Squalus* sp. 1 and the two sparids, *P. laniarius* and *A. argyrozona* were more abundant on deep-aphotic reefs (Table 3.13).

Table 3.13. Results of SIMPER analysis showing the dominant fish species contributing to the dissimilarity between *night/shallow* and *night/deep-aphotic* communities recorded in this study. Average species abundances (avg abund) are displayed under the headings for each treatment, *night/shallow* and *night/deep-aphotic*. The dissimilarity is displayed as a percentage (Dissim contrib %).

Species	Night/shallow		Night/deep-aphotic	Contrib%
Boopsoidea inornata	2.66	>	0.71	12.32
Spondyliosoma emarginatum	1.56	>	0.12	8.93
Pagellus bellottii natalensis	1.26	>	0.00	7.5
Squalus sp. 1	0.71	<	1.78	7.21
Galeichthys ater	2.81	>	2.14	6.63
Pterogymnus laniarius	0.53	<	1.35	6.23
Poroderma pantherinum	1.19	>	0.47	5.06
Poroderma africanum	1.46	>	0.83	4.99
Galeichthys feliceps	0.60	<	0.36	4.1
Eptatretus hexatrema	0.43	<	0.71	4.02
Haploblepharus edwardsii	0.86	<	1.23	3.4
Argyrozona argyrozona	0.09	<	0.58	3.33
Haploblepharus fuscus	0.47	>	0.14	2.92
Rostroraja alba	0.09	<	0.34	2.31
Chrysoblephus laticeps	0.2	<	0.28	2.19
Carangid sp. 1	0.36	>	0.00	2.1
Mustelus mustelus	0.27	>	0.18	2.1
Triakis megalopterus	0.27	>	0.05	1.76
Acanthistius sebastoides	0.18	>	0.16	1.61
Argyrosomus sp. 1	0.00	<	0.25	1.5

DEPTH EFFECTS AT DAY AND AT NIGHT

Differences in community composition and species abundance between day and night at *shallow* reefs were also investigated using a SIMPER analysis (Table 3.14). The results revealed that four sparids, (*B. inornata, C. laticeps, S. emarginatum* and *C. nufar*), were primarily responsible for the similarity of *day/shallow* samples, as together these species had a cumulative contribution of 53.6% (Appendix A, Table D). A total of 14 species amounted to a cumulative contribution of 90.4% (Appendix A, Table D). These included nine sparids, two species belonging to the catshark genus *Poroderma* (pyjama catshark, *P. africanum* and leopard catshark, *P. pantherinum*), the black seacatfish (*G. ater*), one species of ray, the shorttailed stingray (*Dasyatis brevicaudata*), and the two-tone fingerfin (*Chirodactylus brachydactylus*; Appendix A, Table C).

Shallow reefs at *night,* however, were dominated by *G. ater* along with the sparid, *B. inornata* (Appendix A, Table C). Together, these species had a cumulative contribution of 44.3% to the average similarity for samples belonging to this treatment (Appendix A, Table C). Eight species primarily made up the *night/shallow* community, with a cumulative contribution of 90.9% (Appendix A, Table C). These species were *G. ater*, three sparids (*B. inornata, S. emarginatum* and *P. bellottii natalensis*), two catsharks (*P. africanum* and *P. pantherinum*), puffadder shyshark (*Haploblepharus edwardsii*) and *Squalus* sp. 1 (Appendix A, Table C). The sand soldier (*Pagellus bellottii natalensis*) was the only sparid to be largely restricted to the *night/shallow* treatment throughout this study, with only a single individual being recorded in the *day/shallow* treatment (Appendix A, Table C).

Ten species were responsible for the differences in community composition and species abundance between *day/shallow* and *night/shallow* treatments. These species individually contributed with more than 2.5% to the average dissimilarity of 66.1% between *day/shallow* and *night/shallow* communities (Table 3.14). Seven sparids (*B. inornata, C. laticeps, S. emarginatum, C. nufar, P. aeneum, D. capensis* and *S. salpa*) were clearly more abundant at day, while only three species (*G. ater, P. bellottii natalensis* and *Squalus* sp. 1) were more abundant at night (Table 3.14).

Table 3.14. Results of SIMPER analysis showing the dominant fish species contributing to the dissimilarity between *day/shallow* and *night/shallow* communities recorded in this study. Average species abundances are displayed under the headings for each treatment, *day/shallow* and *night/shallow*. The dissimilarity is displayed as a percentage (Dissim contrib %).

Species	Day/shallow		Night/shallow	Dissim contrib %
Boopsoidea inornata	5.2	>	2.7	10.5
Galeichthys ater	0.9	<	2.8	6.7
Chrysoblephus laticeps	2.1	>	0.2	6.4
Spondyliosoma emarginatum	2.7	>	1.6	5.5
Cheimerius nufar	1.6	>	0,0	5,0
Pachymetopon aeneum	1.6	>	0.1	5,0
Diplodus capensis	1.6	>	0.2	4.9
Pagellus bellottii natalensis	0.1	<	1.3	4.2
Sarpa salpa	1.3	>	0,0	3.8
Squalus sp. 1	0.1	<	0.7	2.4

DAY-NIGHT VARIATION IN COMMUNITY COMPOSITION AND SPECIES ABUNDANCE AT DEEP-APHOTIC REEFS

A degree of overlap of points was detected between *day/deep-aphotic* and *night/deep-aphotic* treatments in the MDS ordination plot (Figure 3.2). A SIMPER analysis was used to investigate the similarity in community composition between *day/deep-aphotic* and *night/deep-aphotic* treatments. The results revealed that these treatments shared many species; however, their abundances differed substantially between *day* and *night* (Appendix A, Table C).

The ten species that primarily made up the *day/deep-aphotic* community were four sparids (*P. laniarius, A. argyrozona, B. inornata* and *C. laticeps*), *Squalus* sp. 1, *G. ater*, two catsharks (*P. africanum* and *P. pantherinum*), *H. edwardsii* and an unidentified species of kob (*Argyrosomus* sp. 1; Appendix A, Table C). *Squalus* sp. 1 remained the second most dominant species of the deep-aphotic reef fish community throughout the diel cycle (Appendix A, Table E). At *day*, *P. laniarius* dominated the *deep-aphotic* reef fish community, and at *night, G. ater* became the most dominant community member (Appendix A, Table C).

Fifteen species individually contributed by more than 2.5% to the average dissimilarity of 55.0% between deep-aphotic communities recorded at day and night (Table 3.15). Of these, six species (*P. laniarius, A. argyrozona, C. laticeps, Argyrosomus* sp., *S. emarginatum* and *M. mustelus*) were recorded in greater abundances at day (Table 3.15). Five species (*Squalus* sp., *B. inornata, P. africanum, P. pantherinum* and spearnose skate, *Rostroraja alba*) were recorded in similar abundances at day and night in the deep-aphotic zone (Table 3.15). Four species (*G. ater, E. hexatrema, H. edwardsii* and the white seacatfish, *G. feliceps*) were recorded in greater abundances in the *deep-aphotic* zone at *night* compared to *day* (Table 3.15).

Table 3.15. Results of SIMPER analysis showing the dominant fish species contributing to the dissimilarity between *day/deep-aphotic* and *night/deep-aphotic* communities recorded in this study. Average species abundances are displayed under the headings for each treatment, *day/deep-aphotic* and *night/deep-aphotic*. The dissimilarity is displayed as a percentage (Dissim contrib %).

Species	Day/deep-aphotic		Night/deep-aphotic	Dissim contrib %
Pterogymnus laniarius	2.4	>	1.4	9.0
Galeichthys ater	1.1	<	2.1	8.8
Argyrozona argyrozona	1.5	>	0.6	7.5
Squalus sp. 1	1.8	=	1.8	6.8
Boopsoidea inornata	0.6	<	0.7	6
Eptatretus hexatrema	0,0	<	0.7	5.1
Poroderma africanum	0.9	>	0.8	5.0
Haploblepharus edwardsii	0.8	<	1.2	4.7
Chrysoblephus laticeps	0.7	>	0.3	4.6
Argyrosomus sp. 1	0.4	>	0.3	3.7
Poroderma pantherinum	0.5	=	0.5	3.7
Galeichthys feliceps	0.2	<	0.4	3.3
Rostroraja alba	0.3	=	0.3	3.1
Spondyliosoma emarginatum	0.4	>	0.1	2.9
Mustelus mustelus	0.4	>	0.2	2.8

3.3.2.4 INDICATOR SPECIES ANALYSIS

The indicator species analysis revealed that no species were significantly associated with the groups, *day/deep-aphotic* or *night/shallow*. Biscuit skate (*Raja straeleni*), however, was significantly associated with the *night/deep-aphotic* group (IndVal > 0.25; Table 3.16). Although this species was exclusively recorded in *night/deep-aphotic* samples, with a specificity value of A = 1, it was only recorded in few samples belonging to the *night/deepaphotic* group with a fidelity value of B = 0.2 (Table 3.16). When the indicator species analysis was run on aphotic (*day/deep-aphotic, night/deep-aphotic* and *night/shallow*) versus photic groups (*day/shallow*), no species were significantly associated with the aphotic group (IndVal > 0.25; Table 3.16). This was likely to be a result of the high overlap in species composition that was found between nocturnal and deep-aphotic treatments in the MDS plot (Figure 3.2) and SIMPER analysis (Appendix A, Table C).

Four sparids (*C. nufar, C. cristiceps, R. holubi and P. rupestris*), the two-tone fingerfins (*C. brachydactylus*), shallow water hake (*Merluccius capensis*) and yellow-belly rockcod (*E. marginatus*) were strongly and significantly associated with the *day/shallow* group (Table 3.16). Of these species, *C. cristiceps* (A = 0.9), *M. capensis* (A = 0.9), *E. marginatus* (A = 1.0) and *P. rupestris* (A= 0.8) were all largely restricted to the *day/shallow* treatment, however, the latter three species were only recorded in a few *day/shallow* samples (B < 0.32; Table 3.16). *Cheimerius nufar, C. cristiceps, C. brachydactylus* and *R. holubi* were strongly and significantly associated with the *day/shallow* treatment (IndVal > 0.5). In confirmation, the indicator species analysis revealed a combination of high specificity values (A > 0.75) and fidelity values (B > 0.3) for these species and the *day/shallow* group. Based on these values, these species were therefore considered to be good indicators of this group (Table 3.16).

Table 3.16. Species identified as indicators for the *night/deep-aphotic* and *day/shallow* reefs by the IndVal method, where A is the specificity value and B is the fidelity value. The IndVal statistic is a measure of the extent to which the species is indicative of the treatment.

Night/deep-aphotic	A	B	*IndVal*	*p*
Raja straeleni	1.000	0.182	0.426	< 0.02
Day/shallow				
Cheimerius nufar	0.645	0.546	0.593	< 0.002
Chrysoblephus cristiceps	0.938	0.318	0.546	< 0.001
Chirodactylus brachydactylus	0.783	0.318	0.499	< 0.007
Rhabdosargus holubi	0.769	0.318	0.495	< 0.001
Merluccius capensis	0.889	0.273	0.492	< 0.002
Epinephelus marginatus	1.000	0.182	0.426	< 0.01
Petrus rupestris	0.833	0.182	0.389	< 0.04

The results of the phi coefficient of association suggest that four species have a significant association with the aphotic group (Table 3.17). These species were *H. edwardsii, E.*

hexatrema, P. bellottii natalensis and *P. laniarius*. Species that tended to avoid the photic group were an unidentified species of kabeljou (*Argyrosomus* sp.) and *A. argyrozona*.

Table 3.17. Results of the indicator species analysis on MaxN data of rocky reef fish recorded in this study at photic and aphotic *site*s.

	statistic	*p* value
4 species associated with the aphotic group		
Haploblepharus edwardsii	0.35	< 0.01
Eptatretus hexatrema	0.28	< 0.04
Pagellus bellottii natalensis	0.28	< 0.05
Pterogymnus laniarius	0.27	< 0.05

3.4 DISCUSSION

The central hypothesis of this study, that distinct diurnal and nocturnal fish assemblages would exist at Algoa Bay's shallow (10–30 m) and deep-aphotic (55–100 m) rocky reefs was supported by the data. The observed day-night shifts in Algoa Bay's rocky reef fish assemblages were generally characterised by a reduction in species abundances and number of species at night, particularly for sparids. This trend was strongest at shallow reefs where distinct day-night changes in ambient light occurred.

3.4.1 DAY-NIGHT VARIATION IN REEF FISH COMMUNITIES OF ALGOA BAY

3.4.1.1 REDUCED DIVERSITY AT NIGHT

At the shallow and deep-aphotic rocky reefs of Algoa Bay, day-night variation was largely driven by a reduction in species diversity at night. Of the 56-species recorded at shallow rocky reefs, 93% were recorded during the day and 55% were recorded at night. Similarly, out of the 42-species recorded on deep-aphotic reefs, 88% were recorded at day and 67% were recorded at night. This trend, in which nocturnal fish communities were characterised by reduced species richness and abundance, has also been observed in other shallow marine fish communities (Rooker *et al.*, 1996; Santos *et al.*, 2002; Gilbert *et al.*, 2005; Azzuro *et al.*, 2007) from southern Portugal, Italy, and southern-western and eastern Australia (Santos *et al.*, 2002; Annese & Kingsford, 2005; Azzuro *et al.*, 2007; Birt *et al.*, 2012; Harvey *et al.*, 2012a).

A reduction in species richness at night implies that there are fewer nocturnally active species than diurnally active species at Algoa Bay's reefs. Helfman (1978) described that different fish assemblages, including those in freshwater systems (Piet & Guruge, 1997), generally share the same 'temporal ratios'. Fish communities typically consisted of 50–67% diurnal species, 25–33% nocturnal species and approximately 10% crepuscular species (Helfman, 1978). More recent publications investigating shallow coastal *habitat*s in temperate Australia (Harvey *et al.*, 2012a) and Mediterranean rocky reefs (Azzuro *et al.*, 2007) showed that 95% and 83% respectively of the total species making up a community were diurnally active, and only 32–42% and 57% were nocturnally active. The results of this study are therefore in agreement with findings elsewhere around the world.

3.4.1.2 REDUCED DIVERSITY OF SPARIDS AT NIGHT

A reduction in diversity and abundance of sparids also drove the observed day-night variation in shallow and deep reef fish communities of Algoa Bay. At shallow reefs, the diurnal assemblage was made up of a diverse array of sparids that covered a wide range of trophic guilds (Smale, 1992). This assemblage included herbivores (*S. salpa*), omnivores (*P. aeneum* and G. *curvidens*), micro-invertebrate carnivores (*B. inornata* and *S. emarginatum*), macro-invertebrate carnivores (*C. cristiceps, C. gibbiceps, C. laticeps, D. capensis, D. hottentotus, P. dentata* and *R. holubi*), generalised macroinvertebrate carnivores, and piscivores (*C. nufar, P. rupestris* and *P. praeorbitalis*; Heyns-Veale *et al.*, 2016). At deep reefs, different sparids, dominated the diurnal community. These included *P. laniarius* and *A. argyrozona*, which are commonly recorded inhabiting deep sandy *habitat*s adjacent to reef drop-offs along South Africa's southern coastline (Hatanaka *et al.*, 1983; Smith & Heemstra, 1986; Badenhorst & Smale, 1991; Smale, 1992; Brouwer *et al.*, 2002; HeynsVeale *et al.*, 2016).

3.4.2 DAY-NIGHT ACTIVITY PATTERNS

3.4.2.1 DIURNAL SPECIES

The observed diurnal species were either recorded in substantially reduced abundances at night or not at all. Out of a total of 20 sparids that were recorded on shallow reefs at day, 11 species were not recorded at night. Similarly, *E. marginatus* and all herbivores were restricted to *day/shallow* samples. On tropical reefs, species of the same diel activity pattern generally carry out similar behaviours (Hobson, 1965). Diurnal species are often observed resting in night time refuge sites, such as large caves, crevices and overhangs within the reef, before emerging to forage during the day (Hobson, 1965; Mazeroll *et al.*, 1995; Friedlander & Parrish, 1998; Rickel & Genin, 2005; Clarke *et al.*, 2003; Howard *et al.*, 2013). This behaviour has been observed for multiple diurnal reef fish species including scarids, labrids, pomacentrids and a serranid (Hobson, 1965; Dubin & Baker, 1982; Rickel & Genin, 2005). Entering sheltered micro-habitats at night been described as a mechanism that species adopt to avoid competition (McCoy & Bell, 1991), predation (Lima, 1988) or unfavourable environmental conditions (Crowder & Cooper, 1982).

The majority of teleosts inhabiting reefs are visual foragers (Schmitz & Wainwright, 2011). Since these species predominantly rely on vision for detecting food, the reduced ambient light at night may be associated with a number of challenges for foraging (Schmitz & Wainwright, 2011). Furthermore, predator detection and avoidance is also likely to be more challenging at night for these species (Hobson, 1965). It is hypothesised that the majority of diurnal species observed in this study adopted a similar night time behaviour to those diurnal species observed elsewhere. The majority of sparids, large top predatory teleosts and herbivores may have therefore entered sheltered sites in the form of reef caves, crevices and overhangs, as a means of avoiding the reduced levels of light and associated challenges. This behaviour would have made these species unavailable to detection by the stereo-BRUVs. Although there is a possibility that these diurnal species moved off reef at night, as opposed to hiding, sparid movement has been well researched and there is general agreement that this family exhibits a high degree of localised residency on South African reefs (Stander & Nepgen, 1968; Nepgen, 1977; Cowley *et al.*, 2002; Griffiths *et al.*, 2002; Brouwer *et al.*, 2002; Attwood & Cowley, 2005; Kerwath *et al.*, 2007; Kerwath *et al.*, 2009; Watt-Pringle *et al.*, 2013) and in other warm-temperate regions in the world (Paul, 1967; Tong, 1978; Crossland, 1982; Manooch & Huntsman, 1982). Furthermore, the diets of these sparids and the rockcod are predominantly reef associated (Smale, 1992), and it is therefore unlikely that these species forage in other habitats such as sandy flats or the pelagic zone. This, however, is based on speculation, and investigating the day-night use of sheltered rocky reef habitat by diurnal warm-temperate reef fishes would require a more direct sampling approach, such as telemetry.

Cave use by sparids has, however, been previously described at a Mediterranean rocky reef (Harmelin, 1987) and at a warm-temperate South African rocky reef (Kerwath *et al.*, 2007). In the latter study, variations in estimates of average densities during upwelling events were owed to cave use by *C. laticeps* (Kerwath *et al.*, 2007). It was proposed that the sudden drops in temperature associated with upwelling, place physiological limitations on coastal fish species (Kerwath *et al.*, 2007). Substantial decreases in temperature reduce the metabolic rate of animals, and force them to be less mobile and more vulnerable to predation (Buxton & Smale, 1989). It is suggested that *C. laticeps* may have entered caves in response to upwelling events, as a mechanism of reducing the risk of predation due to the physiological limitations imposed by cold water (Kerwath *et al.*, 2007). It is hypothesised that in this study, darkness may place similar physiological limitations on species that are adapted to diurnal activity. These species may therefore enter sheltered habitats within the reef to escape these unfavourable conditions.

The use of shelter to escape adverse conditions is common in terrestrial and marine animals (Ebeling & Hixon, 1991; Sims *et al.*, 2001; Sims *et al.*, 2006). For diurnally adapted species, the reduction in ambient light reduces their ability to detect and avoid predators, and has a negative impact on their foraging efficiency (Schoener, 1974). It can therefore be postulated that these species should prefer photic conditions, and avoid night time since it is associated with conditions that put these species at greater risks of predation and unfavourable competition.

For small fish (<15cm) inhabiting coral reefs, night time refuging has been described as a mechanism for avoiding the high risk of predation by large, predatory piscivores at night (Hobson, 1965). This may explain the mechanism behind this behaviour for small herbivorous and omnivorous species recorded in this study (i.e. *S. salpa*, *D. hottentotus* and *C. brachydactylus*). Herbivores and omnivores are typically diurnally active across terrestrial and marine systems (Hobson, 1965; Harvey *et al.*, 2012b). This is because day-night partitioning results in a trade-off between optimal foraging and bioenergetic efficiency, and the avoidance of biotic interactions, such as predation and competition (Clarke & Levy, 1988). It is therefore generally accepted that, because of this trade-off, a species will only omit a phase of the diel cycle if the risk of predation during that phase outweighs the potential gains (Schoener, 1974). Since the food of herbivores and omnivores is readily available throughout the diel cycle, and since low trophic level consumers typically fall prey to many other species (Schoener, 1974), predation risk is likely to be the predominant driver of their activity patterns (Schoener, 1974). These species may therefore trade foraging at night for safety.

Seeking refuge at night by large diurnal predatory species, however, is unlikely to be directly driven by predation. From an evolutionary point of view, diurnal reef fish are generally more advanced forms (Hobson, 1965). As a result, diurnal reef fish communities typically comprise species with specialised morphological and behavioural adaptations (Hobson, 1965).

Specialists are frequently described as more efficient at extracting energy from resources compared to species that adopt more generalised foraging behaviours (Munroe *et al.*, 2014). For these diurnal species, it therefore makes sense to omit the phase of the diel cycle when foraging is not as efficient. *Petrus rupestris*, *C. nufar* and *E. marginatus* are visual predators (Smale, 1992), and feeding efficiency is therefore reduced at night when light levels are low. Furthermore, the reduced availability of diverse prey species at night may cause night-time feeding for these species not to be worth the energy expenditure. For large diurnal species, omitting a phase of the diel cycle is unlikely to be as directly driven by the risk of predation as it is for lower level consumers. There is evidence that this behaviour, which has also been observed in large sharks and coral reef predators, is rather adopted as an energy conservation strategy that facilitates thermoregulation (Ebeling & Hixon, 1991; Sims *et al.*, 2001; Sims *et al.*, 2006). Nevertheless, entering sheltered habitats while resting further ensures that predation and competition are avoided during these vulnerable resting phases (Ebeling & Hixon, 1991; Sims *et al.*, 2001; Sims *et al.*, 2006). These large species may therefore maximise foraging during day light hours, and trade foraging at night for rest, when visual acuity and prey availability is reduced under low light conditions. Their specialised adaptations therefore not only allow for a period of rest, but also enable these species to coexist in a highly competitive environment through effective trophic partitioning among species (Smale, 1992). While the present study did not directly identify day and night differences in the use of sheltered rocky reef habitats by diurnal warm-temperate rocky reef fishes, the findings have produced a hypothesis for future investigations.

3.4.2.2 NOCTURNAL SPECIES

The present study demonstrated that, at night, marine reef fish communities are typically comprised nocturnal predators. Nocturnal species at both shallow and deep reefs included demersal bottom-feeding sharks belonging to the family Scyliorhinidae, as well as *Squalus* sp. 1, *E. hexatrema* and two species of catfish, *G. ater* and *G. feliceps*. These findings were in agreement with Hobson (1965) who demonstrated that nocturnal species of tropical reefs were generally less specialised in their morphological, behavioural and foraging adaptations compared to diurnal species. Species with more generalised lifestyles are associated with adaptive plasticity, which enables them to occupy a greater range of environmental conditions and exploit wider ecological niches (Reebs, 2003). This may explain the more flexible diel activity patterns observed for nocturnal species in this study. *Galeichthys ater* and scyliorhinids were frequently recorded during the day; however, their abundances were substantially higher at night. Similarly, on tropical reefs, nocturnal species generally reduce their activity at day (Hobson, 1965; Starck & Davis, 1966), and carry out the bulk of their foraging activity at night and at crepuscular periods when the reduced light offers them better hunting conditions (Currie *et al.*, 2012). It is also possible that the use of bait to attract fish to the cameras may have enticed fish that were in close proximity to the sample site to emerge from their refuges during periods in which they would normally be inactive. This suggests that while some fish species may have a day-night preference for foraging, they are prepared to opportunistically feed during unfavourable times.

Carrying out activities at night is associated with a number of challenges due to the low levels of ambient light (Schmitz & Wainwright, 2011). Nocturnal activity requires different morphological and behavioural adaptations to those required for diurnal activity (KronfeldSchor & Dayan, 2003). Nocturnal species require adaptations that ensure adequate performance under the reduced light conditions, and common adaptations in nocturnal reef fish species include large relative eye size (Schmitz & Wainwright, 2011). *Squalus* sp. 1 possesses large eyes and it is likely that this feature enables efficient predation on motile prey items in near darkness (Hobson, 1965).

Typically, nocturnally active species rely predominantly on hearing, smell and tactile sensory adaptations (Kronfeld-Schor & Dayan, 2003). In this study, species showing nocturnal activity on shallow and deep rocky reefs belonged to the families Scyliorhinidae, Arriidae, Squalidae and Myxinidae. These species possess morphological adaptations that have enabled them to forage in aphotic conditions. Some nocturnal predators, however, possess other adaptations that enable them to detect inactive prey that are hidden in reef structures (Hobson, 1965). For example, nocturnal goatfish possess sensory barbels that reveal prey hidden in the substrate (Hobson, 1965). Similarly, *G. ater* and *G. feliceps* possess sensory barbels on their lower jaw that are used for tactile probing (Smith & Heemstra, 1986), and may therefore enable these species to carry out their activities when light levels are low and visual acuity is reduced. *Eptatretus hexatrema* possess similar barbels to those species belonging to the genus *Galeichthys*. All sharks, including scyliorhinids, possess a unique electrosensory system, called the Ampullae of Lorenzini, that acts as an additional sense to detect prey (Kalmijn, 1982). These morphological adaptations have therefore enabled these species to forage in darkness and to adopt a nocturnal lifestyle. In doing so, this has enabled temporal resource partitioning and has facilitated species coexistence in rocky reef habitats.

There are multiple examples in both terrestrial and aquatic animal communities where specialist species outcompete generalist species (Futuyma & Moreno, 1988). The observed temporal partitioning among invertebrate carnivores and piscivores at Algoa Bay's shallow rocky reefs may also be the result of competition avoidance between these two groups that have adopted different resource strategies. The many diurnally active invertebrate carnivores and piscivores that were inactive at night in the present study occupy the same large carnivore guild as the nocturnal rocky reef predators. It is likely that their inactivity at night provides a less competitive environment with an availability of niches, that nocturnal predators may exploit. Temporal partitioning among species of the same guild is commonly observed in animal communities in both marine and terrestrial systems (Fedriani *et al.*, 1999; Linnell & Strand, 2000). It is likely that the ability of the diurnal carnivores and predators to use shallow reef resources more efficiently than the more generalist species has resulted in their nocturnal activity patterns. The differences in species activity patterns of the rocky reef predatory guild may facilitate species coexistence through avoidance of competition (Fedriani *et al.*, 1999; Linnell & Strand, 2000).

3.4.3 IMPORTANCE OF AMBIENT LIGHT IN DRIVING DAY-NIGHT VARIATION AT REEFS IN ALGOA BAY

The results of this study showed that the trend of a reduced diversity and sparid abundance at night was strongest at shallow reefs where distinct day-night changes in ambient light occurred. At day, shallow reefs harboured a diverse fish assemblage characterised by a distinct community. Many sparids, herbivores and other large top predatory teleosts were mainly responsible for the distinct *day/shallow* community observed in this study. The indicator species analysis revealed that three top predatory teleosts (*C. nufar*, *P. rupestris* and *E. marginatus*), two mid-level consumers (*R. holubi* and *C. cristiceps*) and a herbivore (*C. brachydactylus*) were good indicators of the *day/shallow* community. The absence or substantial reductions in abundances of these species on shallow reefs at night resulted in a significantly different community composition and abundance at night.

Although less prominent, day-night variation at deep reefs remained significant. At deep reefs, *P. laniarius* and *A. argyrozona* were the dominant higher trophic guild sparids. There were, however, fewer low-level consumers present on deep reefs compared to shallow reefs throughout the diel cycle. This depth trend has also been shown at another South African rocky reef (Heyns-Veale *et al.*, 2016) and can be attributed to the low light levels associated with deep reefs. This is because primary-productivity derived food is limited, and this is likely to restrict low level consumers to shallower reefs (Heyns-Veale *et al.*, 2016). At shallow reefs, diel activity patterns of low-trophic level consumers played an important role in the observed day-night shifts in community structure. At deep reefs, day-night variation was largely driven by differences in species abundances and to a lesser extent by community composition. Of the 42 species recorded on deep reefs, 55% were common to both day and night assemblages. Marked variations in the abundances of these species were demonstrated between day and night. These day-night shifts in abundances suggest that day-night fish movement patterns may be occurring. Furthermore, these patterns may be driving the observed day-night shifts in Algoa Bay's rocky reef fish communities.

While differences between Cape Recife and Riy Banks were revealed, these differences were generally in the form of variation in species abundance. This was particularly evident for the grouped abundance of all sparids. Higher abundances of sparids were recorded at Riy Banks compared to Cape Recife. Since the majority of sparids recorded in this study were observed in higher abundances on shallow reefs, the higher abundances recorded at Riy Banks may be the result of an increased availability of reef habitat at the shallow zone of Riy Banks. In this study, 45.5% of shallow stereo-BRUVs deployed at Cape Recife landed on *sandy reef patch*es. At the shallow zone of Riy Banks, no stereo-BRUVs landed on *sandy reef patch*es despite following the same randomly stratified sampling approach at both sites. The increased availability of reef habitat at the shallow zone of Riy Banks can be explained by the structure of this reef complex. Riy Banks forms a shallow plateau that spans 24 km^2, with steep slopes along either side that drop to adjacent sandy flats at a depth of 81 m (Bremner, 1979a). It is therefore likely that the shallow zone of Riy Banks is predominantly made up of high and *low profile reef* habitat, rather than sand. Based on the species-area relationship, which states that increased species richness is associated with increased habitat complexity (Arrhenius, 1921; Connor & McCoy, 1979), it is surprising that the observed species richness was not different between the two sites. This study did, however, show that higher species richness was associated with high profile and *low profile reef*s compared to *sandy reef patch*es. It is likely that the increased profile, which is associated with the shallow reefs of Riy Banks compared to Cape Recife, may offer more resources such as shelter and habitat to accommodate higher abundances of species. This finding demonstrates the importance of environmental factors in determining species distributional and abundance patterns. Furthermore, it suggests that patterns observed at Algoa Bay are unlikely to be identical to other regions due to the influence of environmental conditions that are unique to this location.

3.5 CONCLUSION

The finding of this study that sparids dominate these communities is in agreement with other ichthyofaunal surveys conducted at South African warm-temperate rocky reefs (Buxton & Smale, 1984; Beckley & Buxton, 1989; Burger 1990; Heyns-Veale *et al.*, 2016). This study, however, further demonstrated that observations in the day do not necessarily reflect those at night, as day-night variation was largely driven by reduced abundances, or no sparids recorded at night. Ambient light differences between day and night play a crucial role in driving observed day-night shifts in these reef fish communities, and the presence of a species in a habitat largely depends on its trophic guild and adaptations. This study has therefore highlighted the importance of considering spatial (depth) and temporal (day-night) scales when observing or monitoring fish communities.

4

DAY-NIGHT FISH MOVEMENT PATTERNS:

WITH EMPHASIS ON SPECIES-SPECIFIC CHANGES IN DETECTABILITY AT SHALLOW AND DEEP REEFS

4.1 INTRODUCTION

Investigating the movement of individuals among habitats provides important insight into day-night changes in habitat use and activity patterns species (Gratwicke *et al.*, 2006). Many fish species have shown movement between diurnal and nocturnal habitats during the twilight periods in response to the diel cycling (Starck & Davis, 1966; Hobson, 1973; Hobson & Chess, 1973; Gladfelter, 1979; Helfman, 1993). Such habitat selection through movement is described as a systematic process rather than a random one (Crook *et al.*, 2001). A primary concern of habitat selection by a species is to satisfy their resource requirements (Crook *et al.*, 2001). A habitat that provides the necessary resources may therefore be associated with an increased detectability of a species in a particular habitat compared to another. Based on this, ecologists may be able to predict species movement patterns in response to potential environmental changes (Morris, 2003).

Species-specific changes in detectability in a habitat are determined by a range of abiotic (ambient light, food availability, temperature, habitat type and time of day) and biotic factors, such as interactions among species and individuals (Hall *et al.*, 1970; Diehl, 1988; Boujard, 2001; Carpentieri *et al.*, 2005). Species interactions may include competition, predation and mutualism (Molles & Cahill, 1999). Both abiotic factors and species interactions affect species differently according to their attributes, such as visual capacity, life history, trophic level and resource utilisation strategy (Rooker *et al.*, 1991). Since all species differ in these attributes, and thus differ in terms of their day-night patterns of habitat use and activity, habitat selection and associated movement patterns also differ among species (Gratwicke *et al.*, 2006).

Movements are therefore species-specific and complex as they are driven by a number of physical and biological factors (Bangley & Rulifson, 2017). Furthermore, the demands of carrying out basic activities under the changing ambient light conditions result in day-night changes in species resource requirements, which in turn affect activity patterns. Species may therefore move to a different habitat that provides them with the necessary resources for maximising energy gains or minimising mortality through reduced species interactions. These movements are described as the cause of observed day-night shifts in species composition and structure of fish communities (Werner *et al.*, 1983; Jones, 1991; Gliwicz & Jachner, 1992; Helfman, 1993; Samoilys, 2006; Becker *et al.*, 2011).

Diel patterns of fish distribution and habitat use is gaining considerable scientific attention (Hammerschlag *et al.*, 2017). The majority of research that has focused on day-night movements of reef fish has been conducted at tropical coral reef habitats (Hobson, 1965; Starck & Davis, 1966). The focus of these studies has predominantly been on the effectiveness of marine protected areas (MPAs) at conserving mobile species (Santana-Garcon *et al.*, 2014). From these studies, most reef fish species are considered to be rather resident (Samoilys, 1996; Chapman & Kramer, 2000). A recent study demonstrated that home ranges of coral reef fishes are positively related to body size (Nash *et al.*, 2015). From this, it was demonstrated that predatory species that are more mobile undertake larger day-to-day movements than smaller species (Nash *et al.*, 2015). Similarly, predatory species conduct larger movements than herbivorous species due to the lower availability of food resources for carnivorous species (Nash *et al.*, 2015). From their study, Nash *et al.* (2015) suggested that large scale within reef movements occur and that MPAs should encompass whole reefs rather than segments to ensure the protection of small and large, predatory reef fishes.

The best described day-night movement pattern conducted by marine organisms is diel vertical migration (DVM), and, as a result, much of what we know about fish movement in the marine environment is based on this pattern (Loose & Dawidowicz, 1994; Clark & Levy, 1988; Stockwell *et al.*, 2010). Diel vertical migration involves the ascent of organisms into the shallow waters at dusk, which are described as warm, food rich and productive habitats compared to deeper waters that lie below the thermocline or where sunlight doesn’t penetrate (Pérès & Picard, 1964). Here, organisms forage throughout the night, and then descend into deeper waters at dawn, where they remain throughout the day (Hobson, 1973). Diel vertical migration is described as the result of ecological trade-offs between energy gains and mortality risk (Moe *et al.*, 2007). This forms the basis of three hypotheses that have been proposed regarding the adaptive significance of DVM (Sims *et al.*, 2006). Species may undertake DVMs as a strategy primarily for optimising feeding, avoiding predation or optimising bioenergetics (Sims *et al.*, 2006). While benthic species, particularly reef fish (Harvey *et al.*, 2012a), have received less attention in terms of day-night research, certain species have also shown evidence for DVM (Sims *et al.*, 2006; Gorman *et al.*, 2012). In a study by Sims *et al.* (2006), adult male lesser spotted dogfish, *Scyliorhinus canicula*, were described to be undertaking DVM as a bioenergetic strategy. The movements included ascents into the warm shallow zone for night time feeding and descents below the thermocline for digesting, but did not coincide with the distribution of their prey (Sims *et al.*, 2006). Since predation risk decreases with an increase in body size (Okun *et al.*, 2005), it is likely that many large benthic predatory species with few natural predators, such as dogfish and sharks, adopt DVMs as a 'hunt warm, rest cool' strategy to conserve energy rather than to avoid predation (Sims *et al.*, 2006).

The DVM hypotheses have also been applied to explain the function of other types of day-night movements, such as horizontal inter- and intra-habitat movements that are conducted by many benthic species during twilight periods (De Stasio, 1993; Hammerschlag & Serafy, 2010; Harvey *et al.*, 2012a; Webb & Wooldridge, 2015). Day-night movements occurring between shallow mangrove and seagrass habitats have received considerable attention (Parrish, 1989; Robertson & Blaber, 1992; Laegdsgaard & Johnson, 1995; Hammerschlag & Serafy, 2010). Here, nocturnal species have been described to seek day time shelter against visual predators in the prop roots of mangrove habitats. These species then move into the adjacent seagrass habitats that represent important nocturnal feeding sites (Hammerschlag & Serafy, 2010). These findings have shown how a species' resource requirements, which differ according to trophic level and other characteristics, change between day and night. Furthermore, the importance of feeding in driving day-night movements was made obvious (Hrabik *et al.*, 2006).

From research on DVM, it is understood that the pattern where fish move into shallow marine habitats at night is a widespread phenomenon (Johannes, 1981; Thompson & Mapstone, 2002). Movements at benthic habitats along a depth gradient, however, are less comprehensively understood. Factors such as depth and habitat substrate are important physical factors that affect fish distribution (McGehee, 1994). This is because species distributions are determined by a tolerance range of certain environmental conditions (McGehee, 1994). The majority of species are tolerant to only a narrow range of conditions along a gradient, as their ability to occupy a wider range is limited by their biological and physiological traits and is sometimes further limited by other biotic interactions, such as competition and predation (McGehee, 1994). Investigating fish movements may therefore provide insight into species-specific tolerance ranges of certain environmental gradients, such as depth.

At South African warm-temperate rocky reefs, an increase in depth is associated with changes in assemblage structure and a decrease in the diversity of benthic organisms (Heyns-Veale *et al.*, 2016). Benthos acts as important habitat for reef fish and requires light, certain minimum water temperatures and nutrients for growth and sustainability (Garrabou *et al.*, 2002; Heyns-Veale *et al.*, 2016). Since these variables are negatively correlated with depth (Bongaerts *et al.*, 2010), shallow rocky reefs, where light typically penetrates through the water column to the seafloor, are more productive than deep-aphotic reefs (Peres & Picard, 1964). Evidence for this has been demonstrated in this study by the increased diversity of faunal assemblages found on shallow reefs compared to deep reefs at

Algoa Bay (Chapter 3). Since most reef fish predators inhabiting South Africa's warm-temperate rocky reefs are visual feeders (Smale, 1992), it is hypothesised that in Algoa Bay, reef fish may migrate into the food rich and productive shallow zone at night when the risk of predation by visual predators is reduced (Hobson, 1974). It is therefore expected that patterns in habitat use may change over the diel cycle.

4.1.1 STUDY AIM

Baited remote underwater stereo-video systems (stereo-BRUVs) were applied in a novel way to describe the distribution and movements of rocky reef fishes at two Algoa Bay reef sites. This was carried out by comparing depth related patterns of species abundance between day and night, and from these inferring possible patterns of movement into the shallow zone. As such, this study aimed at exploring the potential role of the distinct day-night changes in ambient light in influencing species' movements.

4.2 MATERIALS & METHODS

4.2.1 STUDY AREA AND SITES

The study sites, Cape Recife and Riy Banks, form two isolated rocky reef complexes that are surrounded and separated by open sandy flats. The reefs were chosen as study sites based on their structure that extends as continuous rocky reef habitat from the shallow photic zone (10–30 m) to the deep-aphotic zone (55–100 m). This allowed fish movement that may be occurring between the two *Depth zone*s to be indirectly determined by comparing the observed diurnal and nocturnal assemblages at shallow and deep-aphotic zones. Descriptions of the study area, Algoa Bay, and the study sites are provided in Chapter 2.

4.2.2 SAMPLING STRATEGY AND VIDEO ANALYSIS

Since rocky reefs are heterogenous environments and the within-habitat differences may influence the observed reef fish assemblages, sampling followed a stratified random sampling approach with an even allocation of sampling effort among six different *habitat* criteria (*habitat*). This procedure and the different *habitat* criteria are described in Chapter 2.

Other sampling and environmental variables that were expected to influence the observed reef fish assemblages were measured using various methods that are described in Chapter 2. These factors included those that were not controlled for, namely water temperature (temperature) and those factors affecting the camera's range of view (i.e. sampling area). These included *visibility*, percent water column (water column) and percent obstruction (obstruction).

Over two field surveys (Survey 2015: June and October 2015 and Survey 2016: April and May 2016), diurnal and nocturnal sampling were carried out at randomly selected shallow (13–34 m) and deep-aphotic (51–99 m) deployment sites at both reefs, using stereoBRUVs. During video analysis, *community composition*, *species abundance* and *richness* were determined for each sample. A description of the stereo-BRUVs design, the deployment process and video analysis is provided in Chapter 2. For the sake of this chapter that deals with an unidentified species of dogfish (*Squalus* sp. 1), it was important to note that this species was only observed in nocturnal and deep water stereo-BRUVs recordings using red lighting. This wavelength attenuates rapidly in water and results in a poor image quality, with a limited range of view (Harvey *et al.*, 2012a; Fitzpatrick *et al.*, 2013). This made it difficult to identify the defining morphological characteristics of this species. In the warm-temperate waters of southern Africa, four species of dogfish occur and are described as similar in appearance (Heemstra & Heemstra, 2004). These are *Squalus megalops, Squalus mitsukurii, Squalus acanthias* and *Cirrhigaleus asper.*

4.2.3 STATISTICAL ANALYSES

To test the null hypothesis of no day-night differences in community structure (*species richness, species abundance* or *community composition*), diurnal and nocturnal fish communities inhabiting shallow and deep-aphotic reefs in Algoa Bay were compared. *Time of day* (T) and *Depth zone* (DZ) were fixed effects in this experimental design. To provide inter-reef and inter-annual variability in fish communities recorded in this study, *Site* (ST) and *Survey* (SV) were added as random effects, respectively. The experimental design therefore consisted of the following variables:

Factor *Time of day* (T; fixed with t=2 levels: day versus night)

Factor *Depth zone* (DZ; fixed dz= 2 levels: shallow versus deep)

Factor *Site* (ST; random with st = 2 levels: Cape Recife versus Riy Banks)

Factor *Survey* (SV; random with sv = 2 levels: 2015 versus 2016).

An unequal number of replicate samples between the two levels of the factor *Survey* were collected, with 49 samples collected in 2015 and 39 in 2016. The design was however balanced with 11 replicate stereo-BRUVs (n) deployed in each of the eight combinations of the treatment variables, *Time of day* and *Depth zone*, and the random variable, *Site* (T x DZ x ST). This resulted in a total of 88 stereo-BRUVs deployments (N = t x dz x st x n; see Table 2.7 in Chapter 2).

4.2.3.1 IDENTIFICATION OF CANDIDATE SPECIES

This chapter used the multivariate analyses results from Chapter 3 to identify certain species that may conduct day-night movements between different *Depth zone*s. A Similarity Percentages Routine (SIMPER) conducted in Chapter 3 revealed the species with a cumulative contribution percentage of 100% to the average dissimilarity between the day shallow and night shallow samples. Species that showed substantial increases in abundances in the shallows at night were identified and further investigated using univariate statistical analyses.

The SIMPER results produced in the previous chapter indicated that two catfish species (*G. ater* and *G. feliceps*), two sparids (*P. bellottii natalensis* and *P. laniarius*), dogfish (*Squalus* sp. 1), hagfish (*E. hexatrema*), two species of shyshark (*H. edwardsii* and *H. fuscus*) and a catshark (*P. pantherinum*) were recorded in higher abundances in the shallow zone at night compared to day (Table 4.1).

Table 4.1. SIMPER analysis showing the species with a cumulative contribution percentage of 89.5% to the average dissimilarity of 66.1% between day shallow and night shallow samples. Those species in bold indicate the species that were recorded in substantially higher abundances at night.

Family	Species	Day/shallow		Night/shallow	Contrib %	Cum contrib %
Sparidae	*Boopsoidea inornata*	5.2		2.7	10.5	10.5
Ariidae	*Galeichthys ater*	0.9	<	2.8	6.7	17.2
Sparidae	*Chrysoblephus laticeps*	2.1		0.2	6.4	23.6
Sparidae	*Spondyliosoma emarginatum*	2.7		1.6	5.5	29.1
Sparidae	*Cheimerius nufar*	1.6		0	5.3	34.4
Sparidae	*Pachymetopon aeneum*	1.6		0.1	5	39.4
Sparidae	*Diplodus capensis*	1.6		0.2	4.9	44.3
Sparidae	*Pagellus bellottii natalensis*	0.1	<	1.3	4.2	48.5
Sparidae	*Sarpa salpa*	1.3		0	3.8	52.2
Squalidae	*Squalus sp. 1*	0.1	<	0.7	2.4	54.6
Scyliorhinidae	*Haploblepharus edwardsii*	0.3	<	0.9	2.3	56.9
Ariidae	*Galeichthys feliceps*	0.1	<	0.6	2	59
Scyliorhinidae	*Poroderma africanum*	1.5		1.5	2	601
Scyliorhinidae	*Poroderma pantherinum*	0.9	<	1.2	2	63
Sparidae	*Pterogymnus laniarius*	0.1	<	0.5	2	64.9
Cheilodactylidae	*Chirodactylus brachydactylus*	0.6		0.1	2	66.9
Sparidae	*Chrysoblephus gibbiceps*	0.6		0	1.8	68.7
Sparidae	*Polysteganus praeorbitalis*	0.5		0	1.8	70.5
Scyliorhinidae	*Haploblepharus fuscus*	0.1	<	0.5	1.7	72.1
Sparidae	*Chrysoblephus cristiceps*	0.5		0	1.6	73.8
Sparidae	*Diplodus hottentotus*	0.5		0	1.6	75.4
Dasyatidae	*Dasyatis brevicaudata*	0.5		0.1	1.6	77
Triakidae	*Triakis megalopterus*	0.4		0.3	1.6	78.6
Serranidae	*Acanthistius sebastoides*	0.4		0.2	1.6	80.1
Triakidae	*Mustelus mustelus*	0.4		0.3	1.5	81.6

Sparidae	*Rhabdosargus holubi*	0.5		0	1.5	83.1
Myxinidae	*Eptatretus hexatrema*	0.1	<	0.4	1.5	84.6
Carangidae	*Seriola lalandi*	0.4		0	1.4	86
Cheilodactylidae	*Cheilodactylus pixi*	0.4		0.1	1.4	87.4
Odontaspididae	*Carcharias taurus*	0.3		0.1	1.1	88.5
Sparidae	*Rhabdosargus globiceps*	0.3		0	2	89.5

Only a single individual each for sand soldier (*P. bellotti natalensis*), dogfish (*Squalus* sp., *G. feliceps*) and sixgill hagfish (*E. hexatrema*) was recorded in the day shallow treatment throughout this study. Similarly, panga (*P. laniarius*) was only recorded in a single sample of the day shallow treatment. Black seacatfish (*G. ater*), puffadder shyshark (*H. edwardsii*), leopard catshark (*P. pantherinum*) and brown shyshark (*H. fuscus*) were recorded in substantially higher abundances at night compared to day. Distribution patterns of an unidentified jack (Carangid sp. 1) were not further investigated as this taxon was only recorded in three samples throughout this study, and was not identified down to species level. It was therefore considered inappropriate to draw conclusions about this taxon. Although recorded in higher abundances at night, the shift in abundances for *P. pantherinum* were not as pronounced as for the other mentioned species.

4.2.3.2 Investigating Possible Day-Night Movement Patterns of Candidate Species

Univariate statistical analyses were conducted by applying generalised linear models (GLMs) using the base packages in R software (R Core Team, 2013). This allowed us to investigate the variability in the abundances of those species identified in the SIMPER analysis, as a function of the covariates and the interaction between the treatment variables, *Time of day* and *Depth zone*.

4.3 Results

4.3.1 Investigating Possible Day-Night Movement Patterns of Candidate Species

Data exploration following the protocol of Zuur *et al.* (2010) was conducted prior to applying GLMs. The data exploration process involved producing Cleveland dotplots to inspect the response and explanatory variables for outliers (Cleveland, 1993). Pairplots were then produced and were used in combination with variance inflation factor (VIF) values to assess collinearity between two continuous explanatory variables. Variance inflation factors were all below two and the collinearity was assumed to be acceptable (Zuur *et al.*, 2010). Boxplots were employed when detecting collinearity between a continuous and a categorical explanatory variable. Finally, multi-panel scatterplots were produced to visualise relationships. As the analyses were run on count data, the first GLMs were specific with the Poisson error structure.

The saturated model was given as:

$$f(\text{response variable}) = \beta 1 + \beta 2\,(T \times DZ) + \beta 3\,(\text{visibility}) + \beta 4\,(\text{temperature}) + \beta 5\,(\text{water column}) + \beta 6\,(\text{habitat}) + \beta 7\,(\text{Site}) + \varepsilon$$

Model validation then involved testing for over-dispersion of the model residuals and testing for patterns in the residuals plotted against the fitted values and all other explanatory variables in the dataset. Model selection was conducted following an Akaike Information Criterion (AIC) based approach by sequentially removing parameters from the full model and selecting the simplest model with the lowest AIC score.

GALEICHTHYS ATER

For analyses on *G. ater* abundance, the data exploration indicated a few outliers in the response variable. A negative binomial GLM was applied as the model validation process indicated that the data were overdispersed (dispersion statistic = 1.9). The model summary showed that dropping *Site* (AIC = 398.73) and *habitat* (AIC = 395.43) from the full model (AIC = 400.57) produced the simplest model with the lowest AIC score. The best-fit model therefore took the form of:

$$f(G.\ ater) = \beta 1 + \beta 2\,(\text{visibility}) + \beta 3\,(\text{temperature}) + \beta 4\,(\text{water column}) + \beta 5\,(T \times DZ) + \varepsilon$$

The mean abundance *G. ater* at the shallow zone during the day was 2.38 ± 1.60 individuals, while at night it increased to 8.27 ± 3.14 individuals (Appendix A). Similarly, at the deep-aphotic zone, the mean abundance of this species during the day was 2.24 ± 1.11 individuals and increased to 5.76 ± 4.13 individuals at night (Appendix A).

The results from the sequential analysis of variance run on the negative binomial GLM are displayed in Table 4.2; the reductions in the residual deviance as each variable is added in turn are displayed, as well the residual deviances themselves. It was revealed that the MaxN of *G. ater* was significantly higher at night (Figure 4.1). There was no difference in MaxN between shallow and deep-aphotic reefs during the day; however, the MaxN at night was highest on shallow reefs compared to deep-aphotic reefs (Figure 4.1). This effect, however, appears to be insignificant (p = 0.993; Table 4.2 & 4.3).

Table 4.2. Analysis of deviance table for the negative binomial GLM run on *G. ater* data and explanatory variables, *visibility* and temperature and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

	df	Deviance	Residual *df*	Residual deviance	Pr(>Chi)
NULL	1		87	209.95	
Visibility	1	12.39	86	197.57	< 0.0001
Temperature	1	13.89	85	183.68	< 0.0001
Water column	1	2.60	84	181.08	0.107
DZ	1	9.34	83	171.74	< 0.002
T	1	68.73	82	103.01	< 0.0001
DZ x T	1	2.00	81	101.01	0.157

Table 4.3. Negative binomial GLM summary displaying the nature of the relationships between *G. ater* data and explanatory variables, *visibility* and temperature and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

Coefficients:	Estimate	Std. Error	z value	Pr (>|z|)
Intercept	0.70	0.60	1.27	0.203
Visibility	-2e-04	1e-04	-2.09	< 0.04
Temperature	0.04	0.04	1.00	0.317
Water column	-5e-03	3e-03	-2.13	< 0.04
DZ: shallow (day)	-3e-03	0.30	-0.01	0.993
T: night (deep-aphotic)	1.00	0.20	4.95	< 0.0001
Night: shallow	0.50	0.30	1.40	0.163

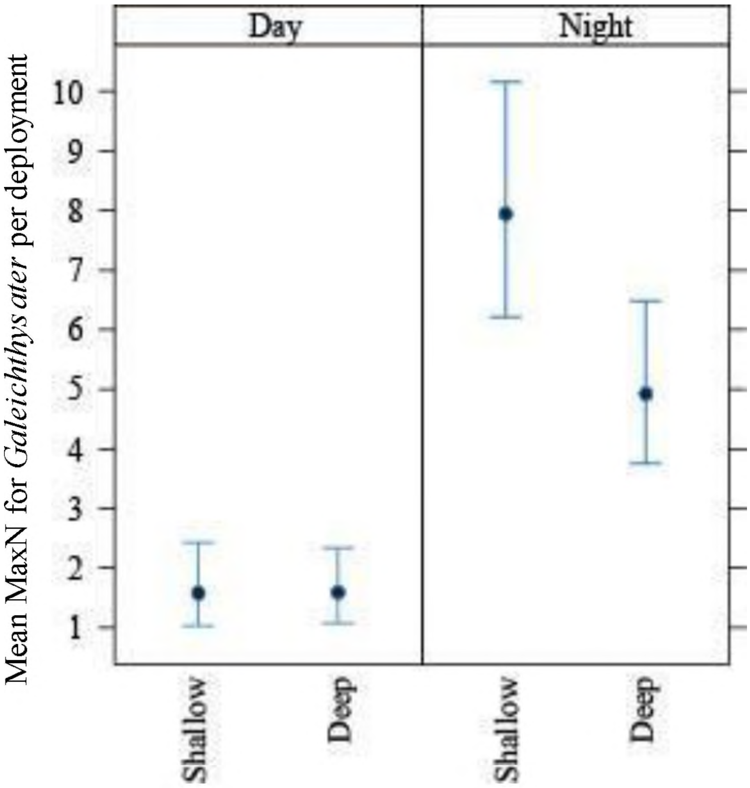

Figure 4.1. Effect of *Depth zone* (shallow versus deep-aphotic) and *Time of day* (day versus night) on *Galeichthys ater* abundance. The abundance values were predicted from the binomial GLM (Table 4.3) using standardised values for *visibility* (2264.92 ± 1200.14), water column (70.71 ± 27.83) and temperature (15.17 ± 2.25). The error bars represent the approximate 95% confidence intervals.

PAGELLUS BELLOTTII NATALENSIS

Data exploration indicated that the abundance data were heavily zero inflated (80%), so the data were transformed to presence/absence and a binomial GLM was applied. Model selection suggested that *visibility* (AIC = 41.3), water column (AIC = 41.1) and *habitat* (AIC = 38.2) be dropped from the full model (AIC = 42.6).

The optimal model was given as:

$$f\,(P.\ bellottii\ natalensis) = \beta 1 + \beta 2\ (T \times DZ) + \beta 3\ (temperature) + \beta 4\ (Site) + \varepsilon$$

With the exception of one individual being recorded in the *day/shallow* treatment throughout this study, *P. bellottii natalensis* was only recorded in the *night/shallow* treatment with a mean abundance of 4.19 ± 5.65 (Appendix A, Table A). While the effect of *Site* was insignificant ($p > 0.4$; Table 4.4), a slightly lower probability of detecting *P. bellottii* *natalensis* at Riy Banks was revealed (Table 4.5 & Figure 4.2). The patterns observed in the presence of *P. bellottii natalensis* were similar at both *site*s (Figure 4.2).

The sequential analysis of deviance table indicated that *Time of day* ($p < 0.05$) and *Depth zone* ($p < 0.08$) had significant effects on the observed variability in the *P. bellottii natalensis* data (Table 4.4). The detection probability of *P. bellottii natalensis* was significantly higher for the *night/shallow* treatment than all other treatments (Figure 4.2). While the probability of detecting *P. bellottii natalensis* during the day on both shallow and deep-aphotic reefs was zero, there was a slightly higher probability of detecting this species at deep-aphotic reefs at night, although this effect was insignificant (Figure 4.1). Temperature significantly contributed to the variability in the *P. bellottii natalensis* data ($p < 0.0002$), with a positive effect on the detectability of *P. bellottii natalensis* (Table 4.5).

Table 4.4. Analysis of deviance table for the binomial GLM displaying the significance in explaining the observed variation in *Pagellus bellottii natalensis* by the explanatory variable, temperature, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

	df	Deviance	Residual *df*	Residual deviance	Pr(>Chi)
NULL			87	86.38	
Temperature	1	9.59	86	76.80	< 0.002
Site	1	0.66	85	76.13	0.416
T	1	18.07	84	58.07	< 0.05
DZ	1	31.90	83	26.17	< 0.08
T: DZ	1	0.00	82	26.17	1.000

Table 4.5. Summary of the model fit for the Binomial GLM revealing the nature of the relationships observed between Algoa Bay's *Pagellus bellottii natalensis* population and explanatory variable, temperature, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

Coefficients:	Estimate	Std. Error	z value	Pr (>|z|)
Intercept	-31.31	3,075.72	-0.01	0.992
Temperature	0.73	0.34	2.16	< 0.040
Site: RB	-2.53	1.44	-1.76	0.079
T: night (deep-aphotic)	-0.47	4,459.97	0.00	1.000
DZ: shallow (day)	16.83	3,075.72	0.01	0.996
Night: shallow	5.87	4,460.0	0.00	0.999

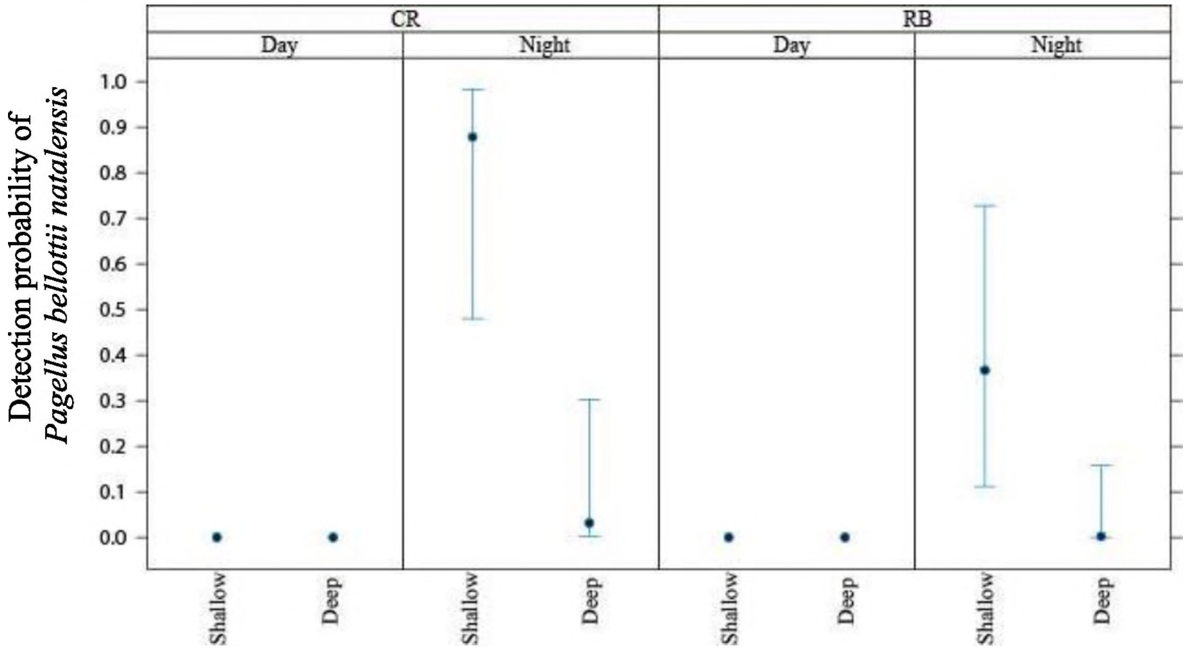

Figure 4.2. Effect of *Depth zone* (shallow versus deep-aphotic) and *Time of day* (day versus night) on *Pagellus bellottii natalensis* abundance. The abundance values were predicted from the binomial GLM (Table 4.3) using standardised values for *visibility* (2264.92 ± 1200.14) and water column (70.71 ± 27.83). The error bars represent the approximate 95% confidence intervals.

SQUALUS SP. 1

Data exploration indicated that the *Squalus* sp. abundance data was heavily zero inflated (34%) and the preliminary Poisson model was overdispersed (dispersion statistic = 1.4). A dispersion statistic that is greater than one indicates that the residuals are overdispersed and the assumption within the Poisson distribution, that the variance is equal to the mean, does not hold. A negative binomial GLM was therefore applied as it is suggested that it is more suitable to overdispersed data (Zuur *et al.*, 2010). The model summary indicated that dropping *Site* (AIC = 279.02) from the full negative binomial model (AIC = 279.05) wasn't necessary, therefore the full model was used:

$$f\,(\textit{Squalus}\text{ sp. }1) = \beta 1 + \beta 2\,(\textit{visibility}) + \beta 3\,(\textit{temperature}) + \beta 4\,(\textit{water column}) + \beta 5\,(\textit{habitat}) + \beta 6\,(\textit{site}) + \beta 7\,(T \times DZ) + \varepsilon$$

Only a single individual of *Squalus* sp. 1 was recorded in the *day/shallow* treatment, while a mean abundance of 1.54 ± 0.84 individuals of *Squalus* sp. were recorded on shallow reefs at night (Appendix A). Higher mean abundances of this species were recorded on deep-aphotic reefs, with 5.22 ± 2.55 individuals recorded in the day and 3.59 ± 2.57 individuals recorded at night (Appendix A).

Although the effect of *Site* was insignificant ($p < 0.7$; Table 4.6), slightly lower abundances were predicted for Riy Banks compared to Cape Recife (Table 4.6). Despite this, the patterns observed in response to the main effects were similar for both *site*s (Figure 4.3). The main effect, *Depth zone* ($p < 0.0001$) and the interaction between *Time of day* x *Depth zone* ($p < 0.0001$) had significant effects on the observed variability in the abundance data of *Squalus* sp. (Table 4.6). Significantly lower abundances of *Squalus* sp. were predicted for shallow reefs compared to deep-aphotic reefs (Figure 4.3). At deepaphotic reefs, the abundances of this species were predicted to be relatively constant throughout the diel cycle (Figure 4.3). In contrast, at shallow reefs, no individuals of *Squalus* sp. were predicted to be recorded at day while significantly higher abundances were predicted at night (Figure 4.3).

Visibility ($p < 0.0001$) and water column ($p < 0.0001$) had significant and positive effects on the observed variability in the *Squalus* sp. abundance data, while temperature ($p < 0.0001$) had a significant negative effect (Tables 4.6 & 4.7). The effect of *habitat* was significant ($p < 0.01$) with higher abundances of *Squalus* sp. 1 occurring on *low profile reef* and *sandy reef patch*es, relative to *high profile reef* (Table 4.6 & 4.7).

Table 4.6. Sequential analysis of deviance table for the negative binomial GLM displaying the significance in explaining the observed variation in *Squalus* sp. 1 data and explanatory variables, *visibility*, temperature, water column and *habitat*, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

	df	Deviance	Residual *df*	Residual deviance	Pr(>Chi)
NULL	1		87	248.75	
Visibility	1	39.58	86	209.17	< 0.0001
Temperature	1	26.44	85	182.74	< 0.0001
Water column	1	14.10	84	168.63	< 0.0001
Habitat	2	14.13	82	154.51	< 0.001
Site	1	0.14	81	154.36	0.705
T	1	0.16	80	154.21	0.692
DZ	1	51.33	79	102.88	< 0.0001
T: DZ	1	16.01	78	86.87	< 0.0001

Table 4.7. Summary of the model fit for the Negative binomial GLM revealing the nature of the relationships observed between Algoa Bay's *Squalus* sp. MaxN and explanatory variables, *visibility*, temperature, water column and *habitat*, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

Coefficients:	Estimate	Std. Error	z value	Pr (>|z|)
Intercept	1.72	0.75	2.28	< 0.020
Visibility	0.00	0.00	0.57	0.569
Temperature	-0.08	0.04	-2.05	< 0.04
Water column	0.01	0.00	1.77	0.077
Low profile reef	0.20	0.23	0.85	0.393
Sandy reef patch	0.56	0.24	2.28	< 0.020
RB	-0.26	0.18	-1.43	0.154
Night (deep-aphotic: RB)	-0.04	0.18	-0.23	0.819
Shallow (day: RB)	-4.36	1.09	-4.01	< 0.0001
Night: shallow (RB)	3.08	1.09	2.83	< 0.001

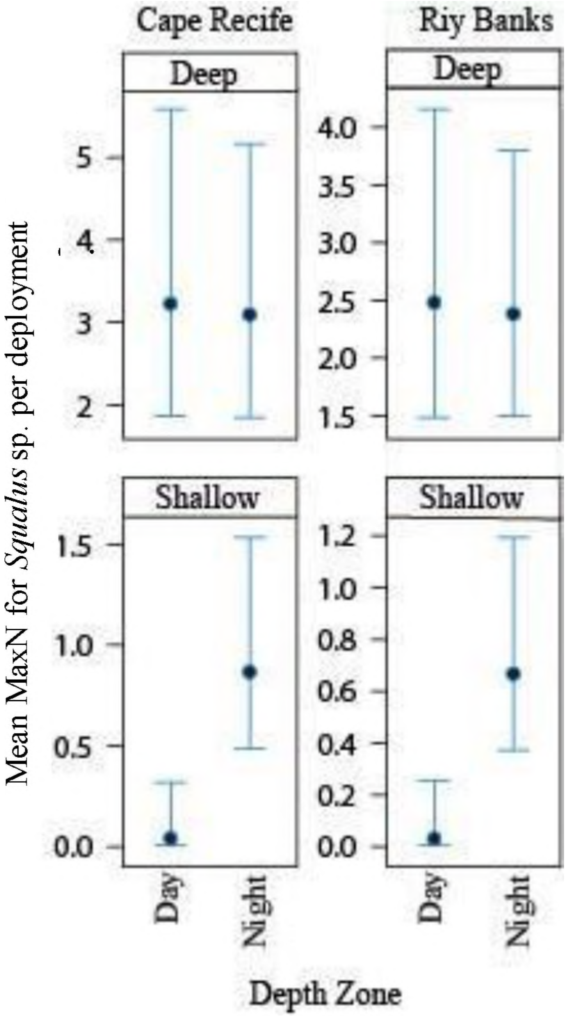

Figure 4.3. Effect of *Depth zone* (shallow versus deep-aphotic) and *Time of day* (day versus night) on *Squalus* sp. abundance. The abundance values were predicted from the negative binomial GLM (Table 4.3) using standardised values for *high profile reef*, temperature (15.17 ± 2.25), *visibility* (2264.92 ± 1200.14) and water column (70.71 ± 27.83). The error bars represent the approximate 95% confidence intervals.

HAPLOBLEPHARUS EDWARDSII

Data exploration indicated that the abundance data for *H. edwardsii* was zero inflated (33%) and thus a binomial GLM was applied. The model summary suggested that temperature (AIC = 85.1) and *habitat* (AIC = 82.3) could be dropped from the full model (AIC = 87.1), thus resulting in the optimal model:

$$f(H.\ edwardsii) = \beta 1 + \beta 2\ (T \times DZ) + \beta 3\ (visibility) + \beta 4\ (water\ column) + \beta 5\ (Site) + \varepsilon$$

The *day/shallow* treatment recorded only a single individual of *H. edwardsii*, while relatively higher abundances were recorded in the three aphotic treatments (*day/deepaphotic*: 1.50 ± 0.50, *night/shallow*: 1.29 ± 0.67 and *night/deep-aphotic*: 1.76 ± 0.92; Appendix A). *Site* had a significant effect ($p < 0.05$; Table 4.8), with a slightly higher probability of detecting *H. edwardsii* at Riy Banks (Table 4.8). Despite this, similar patterns were observed at both *site*s (Figure 4.4).

The detectability of *H. edwardsii* was predicted to be significantly greater in the deepaphotic during the day, and both the shallow and deep-aphotic at night (Table 4.8 & 4.9; Figure 4.4). In contrast, the *day/shallow* had a significant and negative effect on the probability of detecting *H. edwardsii*. At night, *Depth zone* did not significantly affect the detection probability of *H. edwardsii* (Figure 4.4), while there was no significant difference in the detection probability of *H. edwardsii* at night compared to the deepaphotic during the day (Figure 4.4). Water column had a significant ($p < 0.02$; Table 4.8) and negative effect on the probability of detecting *H. edwardsii* (Table 4.9).

Table 4.8. Sequential analysis of deviance table for the binomial GLM displaying the significance in explaining the observed variation in *H. edwardsii* data and explanatory variables, *visibility* and water column, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

	df	Deviance	Residual *df*	Residual deviance	Pr(>Chi)
NULL			87	111.56	
Visibility	1	0.39	86	111.17	0.533
Water column	1	5.08	85	106.08	< 0.02
Site	1	3.98	84	102.10	< 0.05
T	1	19.26	83	82.84	< 0.0001
DZ	1	14.21	82	68.62	< 0.0001
T x DZ	1	0.35	81	68.27	0.555

Table 4.9. Summary of the model fit for the Binomial GLM revealing the nature of the relationships observed between Algoa Bay's *H. edwardsii* population and explanatory variables, *visibility*, temperature and water column, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

Coefficients:	Estimate	Std. Error	z value	Pr (>|z|)
Intercept	2.57	1.25	2.06	< 0.039
Visibility	0.00	0.00	1.80	0.072
Water column	-0.05	0.02	-3.10	< 0.002
Site: RB	1.12	0.68	1.66	0.098
T: night (deep-aphotic)	3.06	1.20	2.56	< 0.010
DZ: shallow (day)	-3.19	1.13	-2.83	< 0.005
Night: shallow	0.95	1.58	0.60	0.547

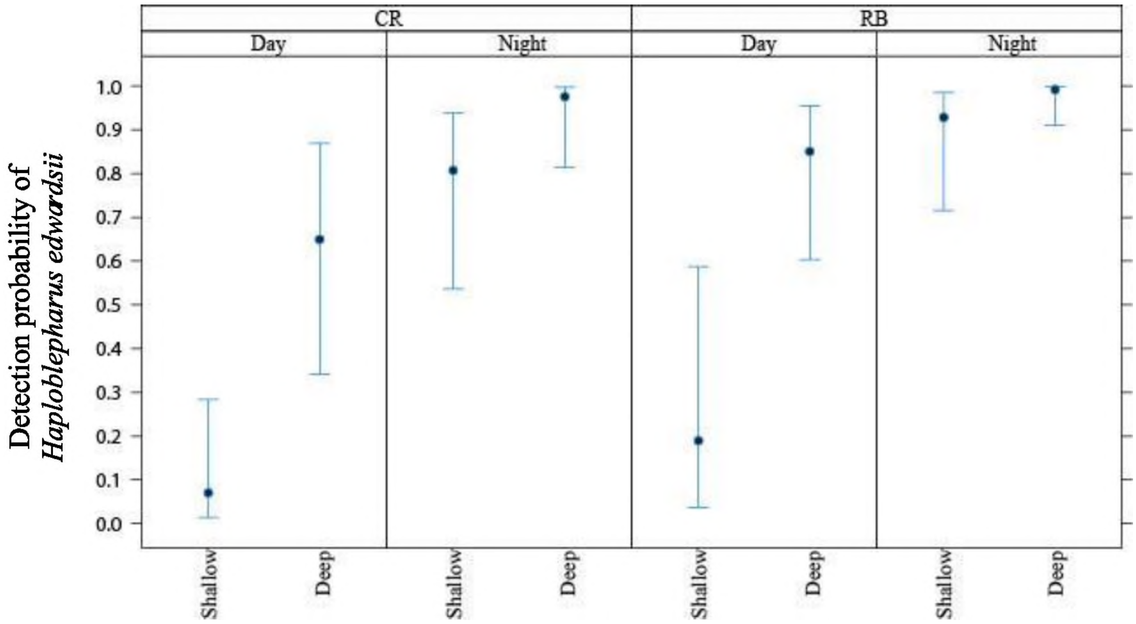

Figure 4.4. Effect of *Depth zone* (shallow versus deep-aphotic) and *Time of day* (day versus night) on *Haploblepharus edwardsii* abundance. The abundance values were predicted from the binomial GLM (Table 4.3) using standardised values for *visibility* (2264.92 ± 1200.14) and water column (70.71 ± 27.83). The error bars represent the approximate 95% confidence intervals.

GALEICHTHYS FELICEPS

Data exploration indicated that the abundance data was heavily zero inflated (77.3%), so the data was transformed to presence/absence and a binomial GLM was applied. Model selection suggested that only temperature (AIC = 70.1) be dropped from the full model (AIC = 71.4) thus resulting in the optimal model:

$$f(G.\ feliceps) = \beta 1 + \beta 2\ (visibility) + \beta 3\ (water\ column) + \beta 4\ (habitat) + \beta 5\ (Site) + \beta 6\ (T \times DZ) + \varepsilon$$

Low abundances of *G. feliceps* were recorded in this study (Appendix A). This is likely because *G. feliceps* is considered to be sand associated (Mann, 2013). The nocturnal treatments recorded higher mean abundances (shallow: 1.90 MaxN ± 1.22 and deepaphotic: 1.83 MaxN ± 0.69) than their diurnal counterparts, where only a single individual was recorded on shallow reefs and slightly lower abundances were recorded on deepaphotic reefs (1.67 MaxN ± 0.94).

Site had a significant effect on the presence of *G. feliceps* in the data ($p < 0.003$; Table 4.10). While the patterns in the detection probability of *G. feliceps* were similar at both *site*s, a significantly lower detection probability was detected at Riy Banks (Table 4.11). *Day/deep-aphotic* had a negative effect on the detection probability of *G. feliceps*, although this effect was insignificant (Tables 4.10 & 4.11; Figure 4.5). Relative to the intercept (*day/deep-aphotic*), *night/deep-aphotic* had a positive effect on the detection probability, but this effect was also insignificant. *Night/shallow* was predicted to have higher detection probability for *G. feliceps*; however, this effect was insignificant (Table 4.11). A similar but weaker effect was observed for *day/shallow*. For the factor *habitat*, *low profile reef* and *sandy reef patch* were predicted to be associated with significantly higher detection probabilities of this species compared to *high profile reef*s.

Table 4.10. Sequential analysis of deviance table for the binomial GLM displaying the significance in explaining the observed variation in the *G. feliceps* data by the explanatory variables, *visibility* and water column and *habitat*, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

	df	Deviance	Residual *df*	Residual deviance	Pr(>Chi)
NULL			87	94.33	
Visibility	1	8.50	86	85.83	< 0.004
Water column	1	5.53	85	80.30	< 0.02
Habitat	2	6.89	83	73.41	< 0.03
Site	1	8.63	82	64.79	< 0.003
T	1	7.84	81	56.95	< 0.005
DZ	1	4.25	80	52.71	< 0.04
T: DZ	1	0.62	79	52.08	0.430

Table 4.11. Summary of the model fit for the Binomial GLM summary revealing the nature of the relationships observed between Algoa Bay's *G. feliceps* population and explanatory variables, *visibility*, temperature, water column and *habitat*, random factor, *Site*, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

Coefficients:	Estimate	Std. Error	z value	Pr (>|z|)
Intercept	-3.81	2.26	-1.69	0.091
Visibility	-0.00	0.00	-1.54	0.124
Water column	0.03	0.02	1.38	0.168
Habitat: low profile reef	2.31	1.12	2.07	< 0.03
Habitat: sandy reef patch	2.72	1.30	2.09	< 0.04
Site: RB	-2.00	0.88	-2.27	< 0.02
T: night (deep-aphotic)	1.27	0.96	1.32	0.186
DZ: shallow (day)	0.84	1.53	0.55	0.584
Night: shallow	1.27	1.65	0.77	0.442

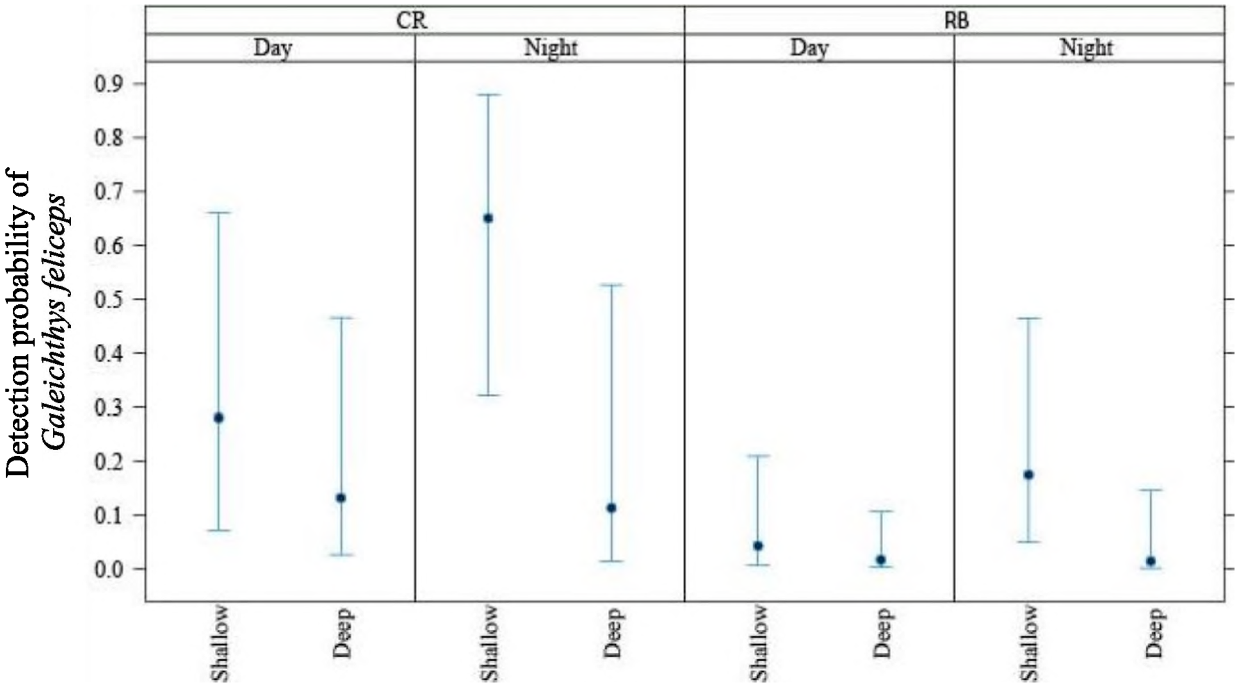

Figure 4.5. Effect of *Depth zone* (shallow versus deep-aphotic) and *Time of day* (day versus night) on *Galeichthys feliceps* abundance. The abundance values were predicted from the binomial GLM (Table 4.3) using standardised values for *high profile reef*, *visibility* (2264.92 mm ± 1200.14) and water column (70.71% ± 27.83). The error bars represent the approximate 95% confidence intervals.

PTEROGYMNUS LANIARIUS

Data exploration indicated that there were outliers in the *P. laniarius* abundance data and the data was heavily zero inflated (43%). Abundance data was therefore transformed to presence absence and a binomial GLM was applied (Zuur *et al.*, 2010). The model summary indicated that *habitat* (AIC = 75.89), *Site* (AIC = 75.68), water column (AIC = 74.71) and temperature (AIC =73.17) may be dropped from the full model (AIC = 80.0), thus resulting in the best model:

$$f\,(P.\ laniarius) = ß1 + ß2\ (visibility) + ß3\ (T \times DZ) + \varepsilon$$

Only a single sample recorded *P. laniarius* in the *day/shallow* community (Appendix A). On deep-aphotic reefs, high abundances were recorded at day (7.24 ± 6.06) and at night (2.68 ± 1.62), while lower abundances were recorded in the *night/shallow* treatment (1.40 ± 0.66; Appendix A).

The explanatory variable, *visibility*, had a significant effect on the presence of *P. laniarius* in the data ($p < 0.001$; Table 4.12), and this effect was positive (Table 4.13). *Depth zone* and the interaction between *Time of day* x *Depth zone* also significantly affected the detection probability of *P. laniarius* (Table 4.13). There was a significantly lower probability of detecting *P. laniarius* on shallow reefs compared to deep-aphotic reefs throughout the diel cycle (Figure 4.6). At shallow reefs, there was a significantly higher probability of detecting *P. laniarius* at night compared to day (Figure 4.6). In contrast, although insignificant, there was a higher probability of detecting this species on deepaphotic reefs at day compared to night (Figure 4.6).

Table 4.12. Sequential analysis of deviance run on a Binomial GLM analysis for *Pterogymnus laniarius* MaxN data. This table displays the significance of the contribution of the explanatory variables explanatory variable, *visibility* and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

	df	Deviance	Residual *df*	Residual deviance	Pr(>Chi)
NULL			87	119.76	
Visibility	1	13.63	86	106.12	0.001
DZ	1	30.58	85	75.55	< 0.008
T	1	3.53	84	72.02	0.060
DZ: T	1	8.85	83	63.17	< 0.003

Table 4.13. Summary of the model fit for the binomial GLM revealing the nature of the relationships observed between Algoa Bay's *P. laniarius* population and the explanatory variable *visibility* and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

Coefficients:	Estimate	Std. Error	z value	Pr (>|z|)
Intercept	2.37	1.24	1.91	0.056
visibility	0.00	0.00	0.95	0.345
DZ: shallow (day)	-7.05	1.92	-3.67	< 0.001
T: night (deep-aphotic)	-1.23	1.20	-1.03	0.305
shallow: night	4.84	1.94	2.49	< 0.010

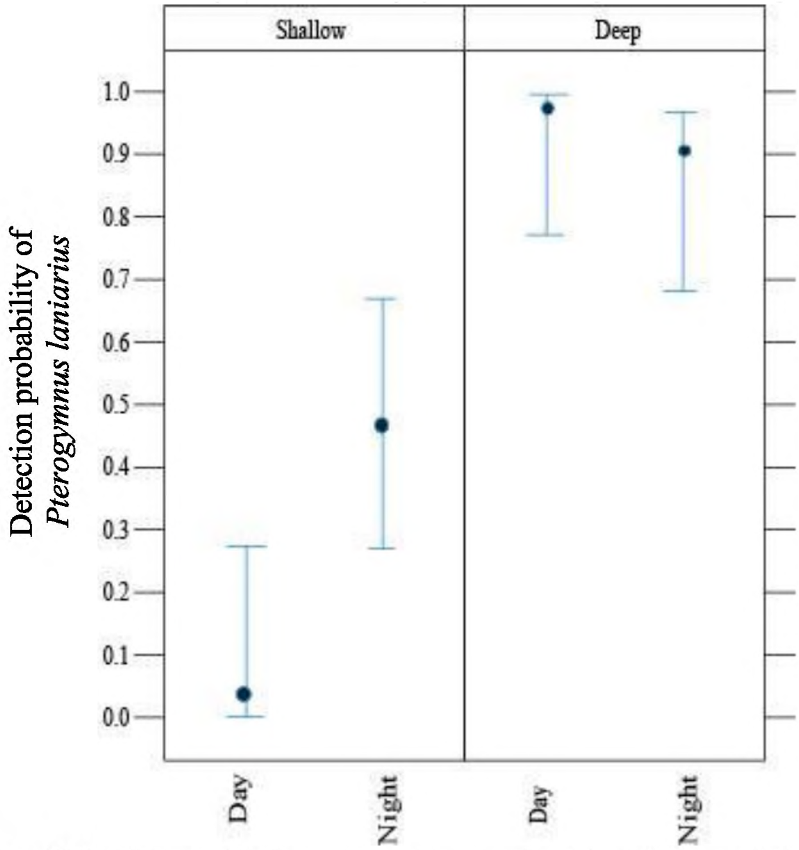

Figure 4.6. Effect of *Depth zone* (shallow versus deep-aphotic) and *Time of day* (day versus night) on *Pterogymnus laniarius* abundance. The abundance values were predicted from the binomial GLM (Table 4.3) using standardised values for *visibility* (2264.92 ± 1200.14). The error bars represent the approximate 95% confidence intervals.

HAPLOBLEPHARUS FUSCUS

Data exploration indicated that the data was heavily zero inflated (81.8%) and it was therefore transformed to presence/absence data and a binomial GLM was applied. Model selection suggested that *visibility* (AIC = 80.0), water column (AIC = 79.6), *habitat* (AIC = 76.3) and *Site* (AIC = 74.8) can be dropped from the full model (AIC = 81.5).

The optimal model was given by:

$$f(H.\ edwardsii) = \beta 1 + \beta 2\ (temperature) + \beta 3\ (T \times DZ) + \varepsilon$$

No individuals were recorded in *day/deep-aphotic* treatment and only a single individual was recorded in each of the *day/shallow* and *night/deep-aphotic* treatments (Appendix A). There were, however, higher abundances recorded in the *night/shallow* treatment (1.1 ± 0.3; Appendix A). The analysis of deviance table for the binomial GLM indicated that *Time of day* ($p < 0.007$) and *Depth zone* ($p < 0.01$) had significant influence on the presence of *H. fuscus* in the data (Table 4.14). There was a slightly higher probability of detecting *H. fuscus* on shallow reefs at night; however, this probability was not significantly greater than that predicted for *day/shallow* and *night/deep-aphotic* treatments (Figure 4.7 & Table 4.15).

Table 4.14. Sequential analysis of deviance table for the binomial GLM for analysing *H. fuscus* MaxN data. This table displays the explanatory variable temperature, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

	df	Deviance	Residual *df*	Residual deviance	Pr(>Chi)
NULL			87	83.45	
Temperature	1	3.78	86	79.67	0.051
T	1	7.26	85	72.41	< 0.007
DZ	1	6.63	84	65.78	< 0.010
T: DZ	1	1.00	83	64.79	0.318

Table 4.15. Summary of the model fit for the Binomial GLM revealing the nature of the relationships observed between Algoa Bay's *H. fuscus* population and the explanatory variable temperature, and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

Coefficients:	Estimate	Std. Error	z value	Pr (>|z|)
Intercept	-21.41	2275.27	-0.009	0.992
Temperature	0.13	0.173	0.746	0.456
Night	17.63	2275.26	0.008	0.994
Shallow	17.51	2275.26	0.008	0.994
Night: shallow	-16.00	2275.26	-0.007	0.994

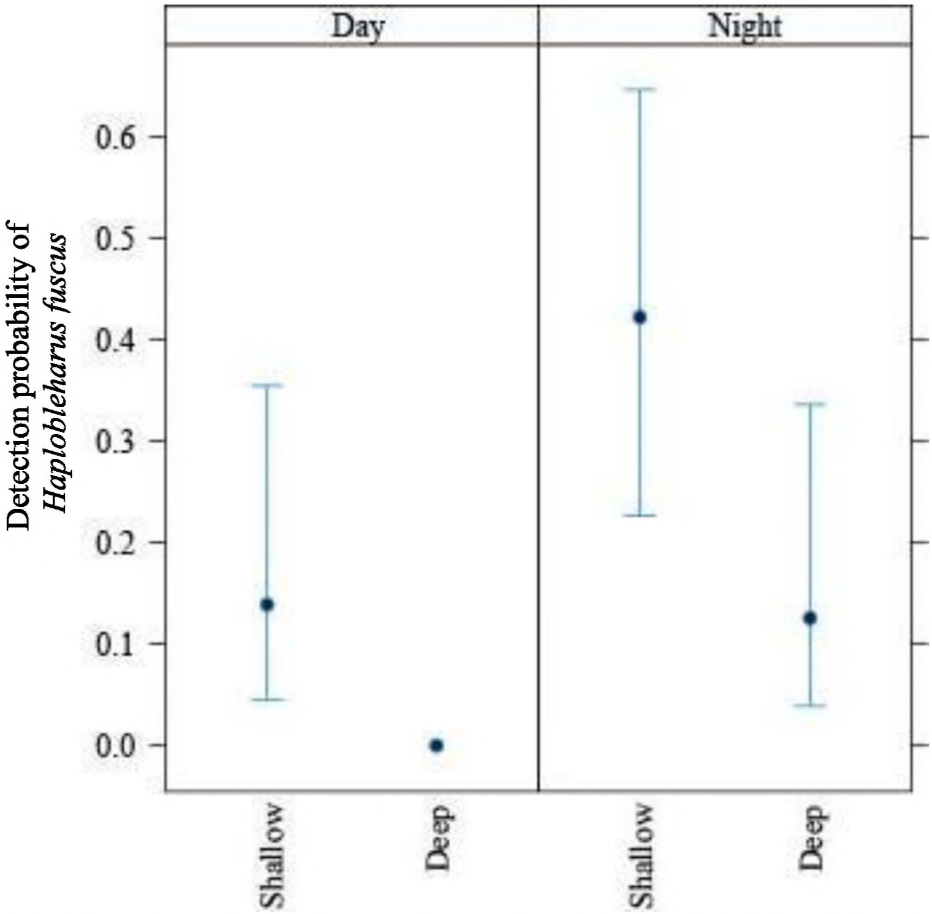

Figure 4.7. Effect of *Depth zone* (shallow versus deep-aphotic) and *Time of day* (day versus night) on *Haploblepharus fuscus* abundance. The abundance values were predicted from the binomial GLM (Table 4.3) using standardised values for temperature (15.17 ± 2.25). The error bars represent the approximate 95% confidence intervals.

EPTATRETUS HEXATREMA

Data exploration indicated that the data was heavily zero inflated (77%) and it was thus transformed to presence absence, and a binomial GLM was applied. Model selection suggested that temperature (AIC = 78.9), water column (AIC = 76.8) and *Site* (AIC = 75.3) could be dropped from the full model (AIC = 80.8).

The optimal model took the form of:

$$f\,(E.\ hexatrema) = \beta 1 + \beta 2\ (visibility) + \beta 3\ (habitat) + \beta 4\ (T \times DZ) + \varepsilon$$

The effect of *visibility* ($p < 0.05$) and *Time of day* ($p < 0.0001$) on the detection probability of *E. hexatrema* were significant, and the interaction between *Time of day* x *Depth zone* was not significant ($p < 0.06$; Table 4.16). The effect of *visibility* was negative (Table 4.17). At day, the detection probability of *E. hexatrema* was greater for shallow reefs compared to deep-aphotic reefs (Figure 4.8). The probability of detecting *E. hexatrema* on shallow and deep-aphotic reefs during the day was very low (Figure 4.8). Alternatively, *E. hexatrema* were significantly more detectable at night, but slightly more so on deepaphotic reefs than on shallow reefs (Figure 4.8; Table 4.17).

Table 4.16. Sequential analysis of deviance table for the binomial GLM analysing *E. hexatrema* MaxN data. This table displays the explanatory variables, *visibility* and *habitat* and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

	df	Deviance	Residual *df*	Residual deviance	Pr(>Chi)
NULL			87	111.56	
Visibility	1	0.39	86	111.17	0.533
Water column	1	5.08	85	106.08	< 0.02
Site	1	3.98	84	102.10	< 0.05
T	1	19.26	83	82.84	< 0.0001
DZ	1	14.21	82	68.62	< 0.0001
T x DZ	1	0.35	81	68.27	0.555

Table 4.17. Summary of the model fit for the Binomial GLM revealing the nature of the relationships observed between Algoa Bay's *E. hexatrema* population and explanatory variables, *visibility* and *habitat* and main effects, *Time of day* (T) and *Depth zone* (DZ), with their interaction *Time of day* x *Depth zone* (T x DZ).

Coefficients:	Estimate	Std. Error	z value	Pr (>|z|)
Intercept	9.60	2.19	-0.01	0.9929
Visibility	-6e-04	5e-04	-1.30	0.1928
Low profile reef	1.58	0.75	2.11	< 0.04
Sandy reef patch	0.39	0.88	0.45	0.6559
Night	20.40	2.19	0.01	0.9926
Shallow	17.60	2.19	0.01	0.9936
Night: shallow	8.30	2.19	-0.01	0.9933

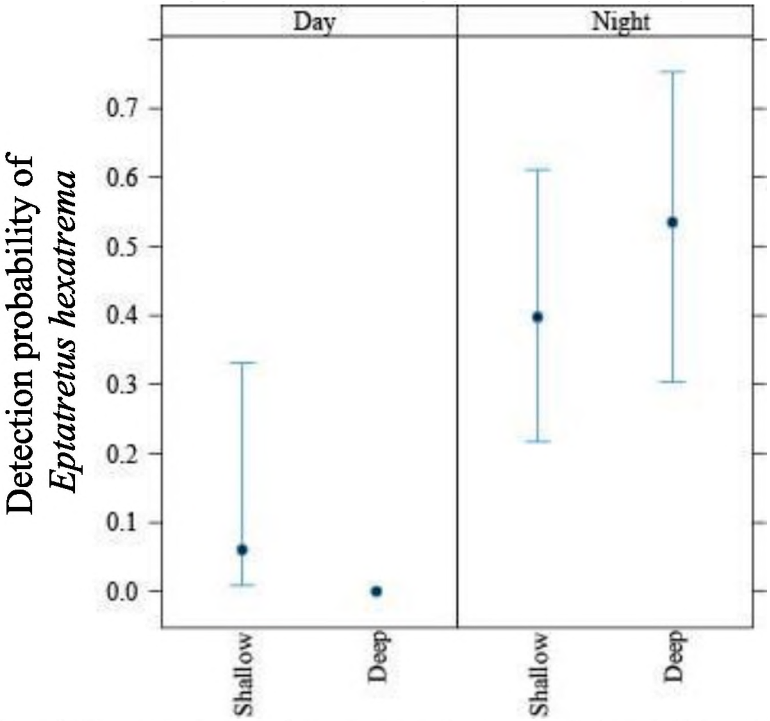

Figure 4.8. Effect of *Depth zone* (shallow versus deep-aphotic) and *Time of day* (day versus night) on *Eptatretus hexatrema* abundance. The abundance values were predicted from the binomial GLM (Table 4.3) using standardised values for *high profile reef* and *visibility* (2264.92 ± 1200.14). The error bars represent the approximate 95% confidence intervals.

4.4 DISCUSSION

The analyses presented in this chapter confirmed that certain fish species inhabiting rocky reefs in Algoa Bay demonstrated species-specific day-night patterns of reef use. *Eptatretus hexatrema*, *G. ater* and *H. fuscus* were recorded in significantly higher night time abundances on shallow and deep reefs compared to day. These patterns reflect nocturnal activity on reefs for these three species, with little dependence on particular *Depth zone*s. All species investigated in this chapter (i.e. *Squalus* sp., *G. ater*, *G. feliceps*, *E. hexatrema*, *P. laniarius*, *P. bellottii natalensis*, *H. edwardsii* and *H. fuscus*) were recorded in significantly higher abundances on shallow reefs at night, with species-specific differences in their responses to the day-night changes in ambient light. From this, three major processes were identified. It is hypothesised that these species that appeared to concentrate the bulk of their shallow reef activity to night time either spent their days hiding in sheltered reef *habitat*s or in an adjacent contrasting habitat, such as the sandy flats or different *Depth zone*s along the rocky reef.

4.4.1 IMPORTANCE OF SHALLOW REEFS TO ROCKY REEF FISH COMMUNITY OF ALGOA BAY

The use of shallow habitats at night by fish is frequently described using three hypotheses. It is suggested that this behavioural strategy is employed to (1) optimise feeding, (2) avoid negative interspecific interactions and to (3) conserve energy (Sims *et al.*, 2006). The latter hypothesis, where fish occupy deep, cooler waters during the day and use warmer, shallow waters for foraging at night as a bioenergetic strategy (Sims *et al.*, 2006), cannot be applied to the results of this study.

Day-night movements have been described for a species of dogfish, *Scyliorhinus canicula*, inhabiting the Lough Hyne, Ireland (Sims *et al.*, 2006). This population was observed conducting diel vertical migrations. Movements into the productive, warm shallow waters to forage at night, and movements into the cooler deeper waters at day were described as a 'hunt warm-rest cool' strategy that increases bioenergetic efficiency in this benthic marine predator (Sims *et al.*, 2006). Dogfish are described to have a high degree of temperature specialisation, at both global and local scales, and are frequently described to be associated with cool water temperatures (Sims *et al.*, 2006; Bangley & Rulifson, 2017). Spiny dogfish have a preference for water temperatures ranging between 7 °C and 13 °C (Jensen, 1966; Shepherd *et al.*, 2002). The results of this study, however, suggested that temperature was not important in driving *Squalus* sp. distribution along the rocky reefs. Average water temperatures were similar across all treatments despite expecting higher average water temperatures to be recorded at shallow reefs, particularly during the day. From this, no evidence for higher diurnal water temperatures or a thermocline was detected at Cape Recife or Riy Banks over the days that sampling was conducted. It is therefore likely that the use of shallow reefs at night was not driven by temperature, but rather driven by a feeding optimising strategy, or a means of avoiding negative interspecific interactions, or a combination.

It is likely that the use of shallow reefs at night is the result of the higher availability of food resources that is typically associated with shallow waters in both freshwater and marine *habitat*s (Pérès & Picard, 1964). Limiting the use of shallow reefs to only night time, however, is likely to be a strategy adopted to avoid species-specific interactions, such as competition or predation by visual and diurnal predators. Alternatively, species could be following patterns of mobile reef invertebrates that might be more active at night. This would imply that reefs at night not only offer a less competitive environment, but also potentially provide more favourable prey. A less diverse and abundant nocturnal assemblage was shown to occupy Algoa Bay's shallow rocky reefs (see Chapter 3). This may provide a less competitive environment with more available resources to offer, in terms of space, food and shelter. These species may therefore trade foraging on productive shallow reefs during the day, when the risk of interspecies interactions is highest, for resting in caves or commuting. These species may then take advantage of the available resources that shallow rocky reefs have to offer at night, when the majority of diurnal species adopt a more inactive state.

4.4.2 DAY-NIGHT MOVEMENT PATTERNS

Three major processes were identified as the drivers of the observed increased use of shallow rocky reefs at night. These included seeking refuge, or commuting either between different *Depth zone*s along the rocky reef, or between shallow reefs and adjacent sandy flats.

Movement of individuals between contrasting habitats, where different activities may be carried out at different times of the day is coined commuting (Dingle, 1996). This movement pattern is common in reef fishes (Hobson, 1972; Sale, 1991; Holland *et al.*, 1996; Meyer & Honebrink, 2005; Currie *et al.*, 2012) including haemulids (Appeldoorn *et al.*, 2009) and reef-associated carangids (Holland *et al.*, 1996). Reef fish species that undertake inter-*habitat* movements are typically large, mobile piscivores (Currie *et al.*, 2012). Covering large distances over contrasting habitat types is likely to improve foraging efficiency, as this increases the chance of encountering prey items (Hitt *et al.*, 2011). In this study, the substantial increases in abundances, of *Squalus* sp., *P. laniarius* and *P. bellottii natalensis* on shallow reefs at night compared to day, were considered to be strong evidence for the movement of these species onto shallow rocky reefs at night from their adjacent day time *habitat*s.

Day-night changes in abundances of *P. laniarius* and *Squalus* sp. were considered strong evidence that these species move between shallow and deep reefs in response to the day-night changes in ambient light. Evidence was provided that a portion of the population of each species moved onto shallow reefs at night from deep-aphotic reefs which they occupied during daylight hours. Since only slight decreases in abundances were recorded on deepaphotic reefs at night, it is suggested that a portion of the population may also be moving onto shallow reefs at night from adjacent non-reef habitats. Similar movement patterns have been described for species of dogfish, *S. canicula,* inhabiting the Lough Hyne, Ireland (Sims *et al.*, 2006). Day-night movement patterns for *P. laniarius*, however, appear to be unknown. *Pterogymnus laniarius* is frequently recorded on deep reef and sandy habitats, with recordings as deep as 200 m (Smith & Heemstra, 1986; Badenhorst & Smale, 1991; Smale, 1992; Heyns-Veale *et al.*, 2016). This study has, however, revealed that in Algoa Bay, this species makes use of shallow rocky reefs at night. It is suggested that the prevalence of *P. laniarius* on deep reefs may not be due to an environmental preference, but may be the result of competitive exclusion from shallow reefs at day by the more dominant diurnal sparids. This may also explain the day-night patterns in abundance of *P. bellottii natalensis* on rocky reefs. This species showed a different pattern of commuting, where the species was absent on reefs during the days and only detected at night. This sparid is commonly recorded inhabiting sandy habitats at depths of up to 30 m during the day (Buxton *et al.*, 1984). It is therefore likely that the adjacent sandy flats, which were not sampled in this study, are where this species remained during the day. Buxton *et al.* (1984) showed using gut content analyses that this species has a relatively unspecialised feeding strategy. There was evidence for feeding on both sand and rocky reefs, with evidence for temporal partitioning of feeding (Buxton *et al.*, 1984). In their study, many individuals that were collected during the day had empty stomachs, thus suggesting that this species may feed primarily at night (Buxton *et al.*, 1984). The findings of the present study have therefore confirmed that, at least within Algoa Bay, *P. bellottii natalensis* commutes between shallow rocky reefs as nocturnal habitat for foraging, and adjacent sandy flats as diurnal habitat where less feeding takes place. It is likely that *P. bellottii natalensis* trades optimal foraging at shallow reefs during the day to avoid the highly competitive environment for foraging on the less food rich adjacent sandy flats. It is likely that commuting benefits a species, as habitats which are better suited to carrying out particular activities at different times of the day can be selected (Currie *et al.*, 2012).

Responses of nocturnal species to the day-night changes in ambient light appeared to be speciesspecific and dependent on morphological adaptations. Conducting inter-habitat movements requires the ability to conduct sustained swimming for long periods of time (Dingle, 1996). The morphology of commuting species was similar in their relatively fusiform bodies, with forked or lunate caudal fins. These features are typical of pelagic and migratory species, and are often associated with sustained swimming (Hobson, 1965). Since swimming efficiency is largely dependent on morphological adaptations, those species that lack the required morphology adopt different behavioural responses to the day-night change in ambient light.

Some nocturnal fish species did not appear to undertake inter-habitat movements, but rather the results suggest that they would have entered sheltered micro-habitats within reef structures in response to the diel cycle. In a similar behaviour to those refuging diurnal species, day time use of sheltered micro-habitats has been observed for nocturnal squirrelfishes, scorpionfishes, cheilodactlyids (Lowry & Suthers, 1998) and apogonids (Fitzpatrick *et al.*, 2013). In this study, *G. ater*, *G. feliceps*, *H. edwardsii*, *H. fuscus* and *E. hexatrema* showed evidence for this behaviour. These species were recorded on shallow reefs during the day; however, there was a clear increase in their detectability in this habitat at night. This was particularly true for *G. ater* as this species remained largely unseen during the day, despite its night-time abundance indicating that it was the fourth most abundant species recorded during this study, with only the daytime abundances of *B. inornata*, *S. salpa* and *S. emarginatum* being greater (Appendix A, Table A). It can therefore be assumed that these species may display more nocturnal behaviour on these rocky reefs than previously expected.

Nocturnally active species on coral reefs frequently enter sheltered *site*s within the reef, where they are less conspicuous during day light hours (Hobson, 1965). These nocturnal species are frequently recorded near their sheltered habitats at day, often near the opening of their cave (Hobson, 1965). Based on this, it is hypothesised that the majority of these populations occupy sheltered habitat on shallow reefs during the day, where they are unavailable for detection by the stereo-BRUVs. Species belonging to the family Ariidae (*G. ater* and *G. feliceps*) are frequently recorded in large caves and crevices within rocky reefs around southern and western South Africa (Prochazka, 1998). The colouration of these species belonging to the Ariidae is not camouflaged within reef habitats as it is for species with mottled colouration, such as those belonging to the family Cheilodactylidae (Prochazka, 1998). The Arriidae species may therefore use caves during the day as a means of affording them protection against predation (Prochazka, 1998). This behaviour may not reflect day-night preferences, but may rather be a result of competition or predator avoidance since these species increase their abundances when all diurnal species hide (Kerwath *et al.*, 2007).

Nocturnal species that showed evidence for seeking refuge at night possess elongated body shapes which appear to be adapted to enter micro-habitats within the reef. Furthermore, the elongated bodies of these species are better suited to unsteady movements, such as rapid starts and increased manoeuvrability (Sfakiotakis & Davies, 1998). These morphological features are therefore more suited to this refuging behaviour, as it allows them to enter narrow crevices, caves and reef overhangs.

Different morphological adaptations among species making up the rocky reef fish community have therefore allowed these species to avoid competitive interactions by adopting different behaviours, of either entering sheltered micro-habitats or moving to an adjacent, less competitive habitat. While commuting allows species to take advantage of the full diel cycle rather than trading a certain phase for safety by entering a state of inactivity (Schoener, 1971), hiding may have associated bioenergetic advantages as described for large sharks and coral reef predators in other studies (Ebeling & Hixon, 1991; Sims *et al.*, 2001).

It is unfortunate that too few individuals of large shark species were recorded in this study to draw inferences about their movement patterns. Since it is known that predators have an important ecological effect on prey species (Bangley & Rulifson, 2017), their changes in distribution that are largely affected by environmental conditions may have important implications on the communities. Day-night movements and preferences of large, shark species at Algoa Bay should be investigated in the future to determine if they have an effect on the movement patterns of the mesopredators recorded in this study. Furthermore, cheilodactylids are frequently recorded to be among the most abundant family on South Africa's southern (Burger, 1990) and western (Prochazka, 1998) rocky reefs. These cryptic species are known to spend the majority of the diel cycle in sheltered reef *site*s such as caves (Prohazka, 1998), and may have been undersampled by stereo-BRUVs in this study.

Cryptic fish assemblages inhabiting South Africa's rocky reefs have demonstrated a high degree of resource partitioning along depth gradients, and the cryptic species recorded in this study showed interesting diel activity patterns. Future studies using a sampling method that is more suited to sample reef caves and crevices might produce interesting results concerning depth and diel partitioning among cryptic rocky reef fish species. Furthermore, such a study might shed some light on the proposed cryptic behaviours that may be carried out by certain sparids, such as *C. laticeps*.

4.5 CONCLUSION

This research, conducted over small spatial (tens of kilometres) and temporal (24 hours) scales, has provided insights into the extent of space use by fish while carrying out their daily activities. Investigating the differences in space use among species making up Algoa Bay's rocky reef fish community has enhanced our understanding of the dynamics of these communities. Interspecific competition between the diurnal and nocturnal species of the carnivorous trophic guild is likely to be the predominant factor driving the observed day-night movements into the shallow zone for nocturnal foraging. This study has revealed the importance of shallow rocky reefs in providing necessary resources for all activities to diurnal species that were shown to be largely restricted to this zone. Furthermore, it has highlighted the importance of shallow reefs as foraging habitat for other species that exhibit less reef-associated activity, i.e. *P. bellottii natalensis*. The results suggest that fishhabitat associations may not always be consistent between day and night, or across different depth ranges. This information on species-specific movements has provided previously unknown basic ecological information which has shed light on the day-night changes in detectability on shallow and deep reefs of these species. While differences in species abundances were detected between Cape Recife and Riy Banks, movement patterns of all species were consistent between the *site*s.

5

GENERAL DISCUSSION

5.1 DAY-NIGHT PATTERNS THAT DRIVE ROCKY REEF FISH COMMUNITY STRUCTURE OBSERVED IN ALGOA BAY

At rocky reefs in Algoa Bay, fish species demonstrated differences in the timing of their activities (Figure 5.1). As observed in multiple tropical reef fish communities (Hobson, 1974), observations of this study suggested that the majority of species recorded on Algoa Bay's rocky reefs are either diurnal or nocturnal. It is possible, however, that certain species within the study area demonstrated crepuscular activity patterns that were not observed since sampling was restricted to day and night hours. This bimodal activity pattern where species carry out their activities during both transitional periods, namely dusk and dawn, has been observed in prawns (Dall *et al.*, 1990), mammals (Fernandez Duque, 2003), and rocky reef fish species (Azzurro *et al.*, 2013). Furthermore, observations at other marine habitats have shown that day-night variation in habitat use by fish species is owed to inter-habitat movements that occur during these crepuscular periods (Lowry & Suthers, 1998; Andrews *et al.*, 2009; Meyer *et al.*, 2010). The experimental design employed here, however, was not designed to detect crepuscular activity, as the primary focus of this study was rather to determine if day-night variation in fish community structure is occurring at Algoa Bay. This was shown as distinct diurnal and nocturnal communities, in terms of species richness, abundance and community composition, which were recorded at both shallow and deep reef sites.

It is suggested that the activity pattern of a species depends largely on their ability to carry out activities and access resources under the different ambient light conditions between day and night, as well their trophic guild and to a degree, their resource use strategy. Temporal and spatial partitioning among different sized individuals within species of vertebrates is common (Marti *et al.*, 1993). In mustelids, smaller individuals have been observed to be nocturnal as a result of the reduced risk of predation at night, while larger individuals have a flexible diel activity pattern (Fernandez-Duque, 2003). The role of size in temporal partitioning at Algoa Bay's rocky reefs has not been investigated in this study. This is, however, a potential avenue for future investigations using this current dataset as stereo-BRUVs provide length data.

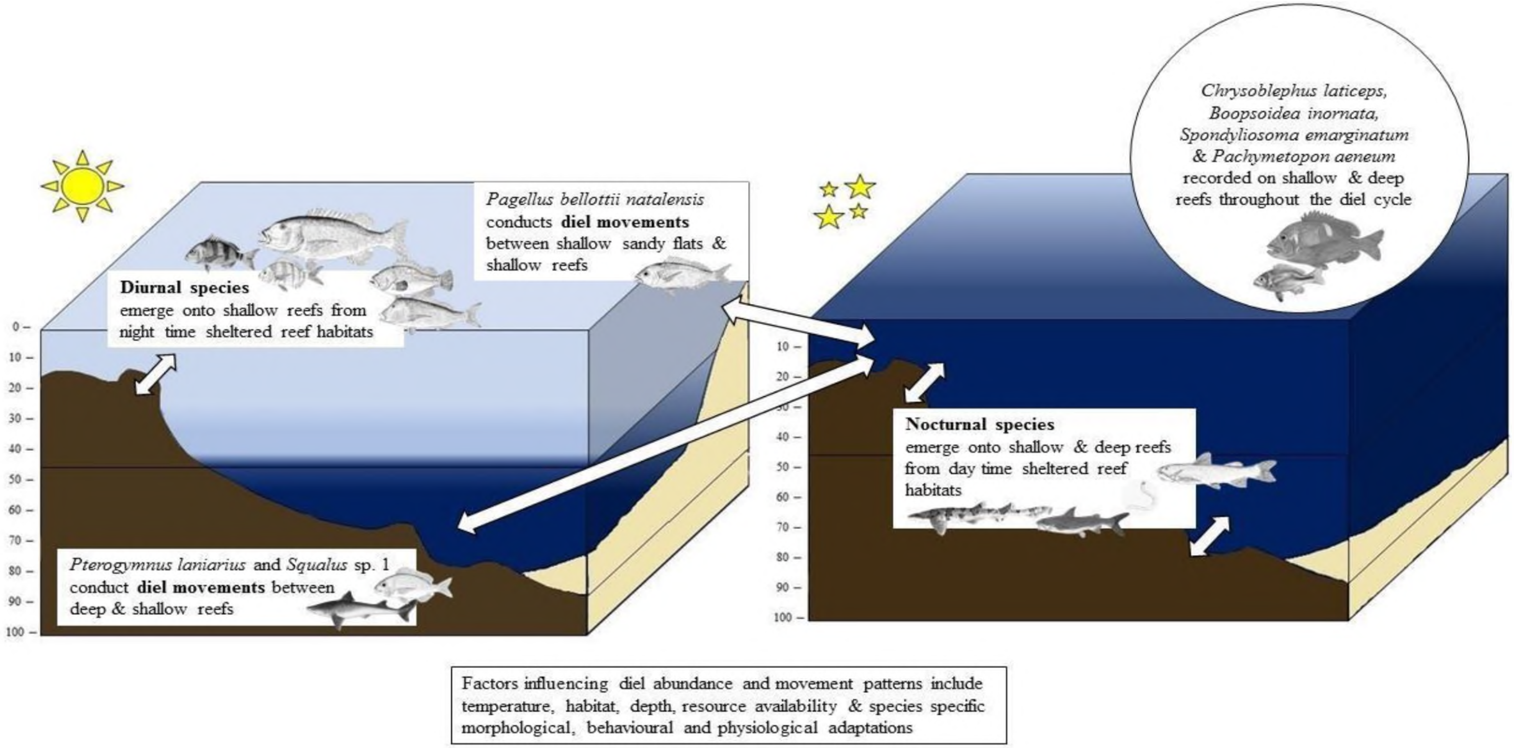

Figure 5.1. Hypothetical diagram illustrating the species-specific responses to the day-night cycle, which are occurring at Algoa Bay's shallow (10– 30 m) and deep-aphotic (55–100 m) rocky reefs (Images of fish from Heemstra & Heemstra, 2004).

In this study, a number of species were exclusively recorded in diurnal samples and played a major role in driving day-night variation at shallow reefs. These species were described as strictly diurnal, and included the majority of sparids recorded in this study as well as other non-sparid predatory teleosts (*E. marginatus*). These sparids covered a wide range of trophic levels (*S. salpa*, *C. cristiceps*, *C. gibbiceps*, *D. capensis*, *D. hottentotus*, *P. dentata*, *R. holubi*, *C. nufar*, *P. rupestris* and *P. praeorbitalis*). For many of these species, their distribution was further restricted to shallow reefs and from this, it is suggested that these species are more likely to be associated with photic conditions compared to aphotic conditions. Since none of these species were recorded by our baited remote underwater stereo-video systems (stereo-BRUVs) at night, it is hypothesised that these species may adopt a similar behavioural response to the day-night change in ambient light as observed for diurnal reef fish species elsewhere. Diurnal reef fish species are often observed resting in sheltered sites within the reef at night, as a means of avoiding the aphotic conditions (Hobson, 1965; Dubin *et al.*, 1982; Mazeroll *et al.*, 1995; Rickel & Genin, 2005).

Few sparids (i.e. *C. laticeps*, *S. emarginatum*, *B. inornata* and *P. aeneum*) demonstrated less rigid diel activity patterns. Despite being recorded in substantially higher abundances at day compared to night, these species were recorded on shallow and deep-aphotic reefs throughout the diel cycle. Environmental conditions that were not recorded in this study, such as resource availability, may have influenced the activity patterns of these species. External environmental conditions, such as food availability, are frequently described to influence the timing of animal activities (Fernandez-Duque, 2003). It is therefore suggested that the use of bait as an attractant to the stereo-BRUVs may have influenced the diel activity pattern typically employed by these species. The presence of bait may have enticed individuals to emerge from their refuges and approach the stereo-BRUVs during periods in which they would normally not be active. This would reflect opportunistic feeding behaviour, which is common in fish species (Reebs, 2003). Furthermore, opportunistic feeding has been frequently described to result in the breakdown of typical diel activity patterns (Reebs, 2003). While this effect of bait may be viewed as a potential bias, this behaviour is likely to occur naturally if the opportunity had to present itself. The diel activity patterns of these species and the influence of environmental factors, such as food availability, require future investigation.

Species-specific differences in diel activity patterns are common to all animal communities (Kronfeld-Schor & Dayan, 2003). The ecological significance of species-specific diel activity patterns has been highlighted in their ability to facilitate species coexistence (Schoener, 1974a; Kronfeld-Schor & Dayan, 2003). Species coexistence is facilitated by reducing negative interspecific interactions, such as resource and interference competition (Carothers & Jaksic, 1984) and predation (Lima & Dill, 1990). This is done by partitioning resources according to the diel cycle. This means that species will concentrate the timing of their activities to a particular phase of the diel cycle, and omit another phase. In omitting a phase of the diel cycle, it is likely that that particular phase is associated with high risks of competition (Carothers & Jaksic, 1984) or predation (Lima & Dill, 1990) and these outweigh the potential gains of foraging. A species is therefore likely to select a diel activity pattern that minimises the risk of negative biotic interactions, and simultaneously maximises gains through foraging (Kronfeld-Schor & Dayan, 2003).

Nocturnal reef fish communities are generally associated with a lower trophic diversity than diurnal communities (Schmitz & Wainwright, 2011). In this study, a similar trend was observed as shallow rocky reefs harboured a diverse diurnal community that was dominated by species representing a wide range of trophic guilds. With the exception of herbivores and some omnivores, the majority of diurnal species were replaced by nocturnal counterparts of the same trophic guild. Diurnal assemblages consisted of species that were micro-invertebrate and macro-invertebrate carnivores, as well as generalist carnivores preying on large invertebrates and fish (*C. cristiceps*, *D. hottentotus*, *P. dentata*, *R. holubi*, *C. nufar*, *P. rupestris* and *P. praeorbitralis*, *E. marginatus*). At night, these guilds were replaced by different nocturnal species of macro-invertebrate carnivores (*G. ater* and *P. bellottii natalensis*) and generalist carnivores (*Squalus* sp. 1, *P. pantherinum* and *H. edwardsii*). This concept is called the 'diel replacement set' and according to Hobson (1965), it is considered to be applicable to fish communities across contrasting systems. This is because similarities in diel replacement patterns of trophic guilds have been shown in markedly different environments, including temperate lakes and tropical marine reefs (Hobson, 1973; Ebeling & Bray, 1976; Hobson & Chess, 1978; Bohl, 1980; Helfman, 1993). It is likely that rocky reef fishes of higher trophic guilds are potential competitors with substantial resource overlap. Based on ecological concepts developed from observations of terrestrial animal communities (Kronfeld-Schor & Dayan, 2003), these species may therefore reduce competition by differing in their diel activity patterns.

It is proposed that catfish, hagfish and species of scyliorhinids are largely constrained to nocturnal activities by competition with the diurnal activities of the dominant rocky reef fish family, Sparidae. Sparids are frequently described as highly territorial species and often engage in aggressive behaviours (Smale, 1992; Kerwath *et al.*, 2007). These traits are considered to be characteristic of the more dominant components of a community (Munroe *et al.*, 2014). Hayward & Slotow (2009) investigated the dynamics of a carnivorous guild of the terrestrial African savanna. In their study, it was demonstrated that subordinate species adapted diel activity patterns that minimised direct encounters with more dominant species of the guild (Hayward & Slotow, 2009). A similar pattern has been observed for a freshwater fish species, *Salmo trutta* (Alanara *et al.*, 2001). Within *S. trutta*, dominant individuals were observed carrying out their activities during times of the day that offered more efficient foraging. In doing so, subordinate individuals were constrained by these superior competitors to be active at times of poorer foraging conditions (Alanara *et al.*, 2001). While the mentioned studies have demonstrated temporal partitioning among different sized individuals within a single species, it may be interesting to investigate this across multiple species within a community. If these principles are applied to the observations of the present study, subordinate rocky reef fish species restrict their shallowreef activities to night time. In doing so, interference competition with the more dominant sparids and other diurnal species at day is avoided. In this case, subordinate species include those that have adopted a nocturnal lifestyle (i.e. *G. ater*, *G. feliceps*, *Squalus* sp. 1, *E. hexatrema* and *P. laniarius*). Many of these supposedly subordinate species have been observed in daylight hours at other locations. This implies that these species are therefore capable of carrying out their activities in both photic and aphotic conditions. It is therefore likely that these subordinate species are being restricted to their realised niches, despite having the capacity to inhabit a greater range of environmental conditions (fundamental niche; Hayward & Slotow, 2009). Investigating temporal partitioning among size classes of species may provide insight into whether this observed partitioning at Algoa Bay's rocky reefs is indeed the result of aggressive interference. Analysing length data from the present dataset is therefore the next step of this research project.

For these nocturnal species, two major processes for avoiding negative biotic interactions were identified in this study. In animal communities, avoiding competition or predation generally involves species either reducing the level of activity in a certain environment at a particular time, or by becoming completely inactive in a refuge (Lima, 1998). The reduced abundances and sometimes complete absence of nocturnal species on shallow reefs recorded at day in this study supports this. It is hypothesised that those nocturnal species that are more cryptic in nature and form (i.e. *G. ater*, *E. hexatrema* and *H. edwardsii*), may avoid the highly competitive shallow diurnal fish community by seeking refuge in sheltered rocky reef micro-habitats. Due to the inability of stereo-BRUVs to effectively sample caves and crevices, this hiding behaviour remains largely unknown and would require a more direct sampling approach to further investigate this. In contrast, those species with morphological adaptations suited for efficient swimming, (i.e. *P. laniarius*, *P. bellottii natalensis* and *Squalus* sp. 1) showed evidence for commuting. In doing so, these species reduce the level of activity in the environment that is associated with a high risk of negative interspecific encounters. Two patterns of commuting were revealed in this study. *Pterogymnus laniarius* and *Squalus* sp. 1 moved onto shallow reefs at night, from deepaphotic reefs that they occupied during the day. *Pagellus bellottii natalensis* moved onto shallow reefs at night from adjacent sandy flats that they occupied during the day. These movements allow species to find habitats that offer the preferred ecological conditions to carry out particular activities, as opposed to omitting a phase of the diel cycle due to competition. The process to avoid adverse biotic conditions is clearly dependent on morphological adaptations. For this reason, those species that are not equipped for efficient swimming have evolved behavioural adaptations that have enabled them to rest during times of unfavourable conditions, rather than move. Differences in morphological and behavioural adaptations among species have therefore given rise to different responses to ambient light conditions.

The observed behavioural responses of rocky reef fishes are the result of the day-night change in ambient light acting on species' endogenous circadian rhythms (Kronfeld-Schor & Dayan, 2003). Other masking factors, including temperature, local reef habitat and depth, also played a role in determining species responses.

A physical factor that is frequently described to be an important predictor of fish distribution patterns is temperature (Burger, 1990; Kerwath *et al.*, 2009). Average water temperatures were similar across all treatments, despite expecting higher average temperatures to be recorded on shallow reefs. Furthermore, higher average water temperatures were expected to be recorded at shallow reefs compared to deep reefs, due to the reduced penetration of sunlight onto deep reefs. No evidence could be provided for higher diurnal temperatures or the presence of a thermocline over sampling trips at either Cape Recife or Riy Banks. It is therefore unlikely that intra-reef movements of species between the investigated *Depth* *zone*s were a result of bioenergetic strategies. Cape Recife did, however, show broader temperature ranges due to substantial drops in temperatures recorded from diurnal samples collected during April 2016. These drops suggested that upwelling may have occurred at Cape Recife while sampling was being conducted. Upwelling events are likely to have a significant effect on the behaviours of reef fish, as cave use during these cold-water events has been demonstrated for *C. laticeps* inhabiting other South African warm-temperate rocky reefs (Kerwath, 2007b). As expected, temperature significantly affected the composition and abundance of species recorded, and this effect was positive for the abundances of sparids.

Food availability is also described as an important predictor of reef fish distribution patterns (Sale & Dybdahl 1978, Smith 1978, Talbot *et al.* 1978). This was shown by herbivorous and omnivorous species, which were largely restricted to shallow reefs where light penetrates the seafloor and an abundance of primary producers are available. Similarly, the majority of sparids that were restricted to shallow reefs in this study are macroinvertebrate feeders. Reefs at this depth are described to be rich in terms of sessile invertebrates, which may be the reason these sparids were limited in their depth range. Similarly, diel activity patterns have been described to be similar for species belonging to a single family (Helfman, 1989). The results of the present study, however, have clearly demonstrated how complex the diel activity patterns in fish communities can be, with many interspecific differences. Few sparids that were present in the shallow zone were also recorded in aphotic conditions (*C. laticeps*, *P. aeneum*, *B. inornata* and *S. emarginatum*). While abundances of *C. laticeps* were highest in the shallow diurnal community, this species was also observed in substantially reduced abundances at night and at deep-aphotic reefs at day. Heyns-Veale *et al.* (2016) used stereo-BRUVs at TNP to demonstrate that the distribution of adult *C. laticeps* does not change with depth. It was shown that *C. laticeps* rather reacts in response to food availability (Heyns-Veale *et al.*, 2016). The presence of *C. laticeps* on deep reefs and at night may have therefore been driven by opportunistic feeding behaviour. This opportunistic feeding behaviour, which is common in fish, has been described to result in breakdowns of typical behaviours (Reebs, 2003). This demonstrates the complexity of diel fish activity patterns, with multiple interacting biotic and abiotic factors. Incorporating size data will shed further light on the observed fish activity patterns.

This thesis has demonstrated that diel fish activity patterns and space use is complex, and there are a number of potential drivers that affect diel activity patterns. These masking factors can vary across geographic locations and are generally unique according to local settings (Bellwood & Fox, 2011). It is therefore important to conduct system specific investigations because it is unlikely that the observed diel activity and movement patterns observed in this study will be consistent across different habitats and locations. In this study, the observed differences between reefs were mostly in the form of variations in abundance but not the underlying ecological patterns. It is therefore suggested that the patterns are representative of all rocky reef fish communities inhabiting Algoa Bay. It is, however, important to note that day-night patterns are known to be affected by biotic conditions, such as conspecific densities (Kronfeld-Schor & Dayan, 2003). The observed local variation in abundances provides reason to believe that patterns observed at Algoa Bay may not represent those of other warm-temperate rocky reefs along South Africa's southern coastline.

5.2 EVALUATION OF THE APPLICABILITY OF STEREO-BRUVS

Baited remote underwater stereo-video systems have been shown to effectively sample all components of warm-temperate rocky reef fish communities along South Africa's coastline (Bernard & Götz, 2012; Bernard *et al.*, 2014; Parker *et al.*, 2016; Heyns *et al.*, 2016). The present study is in agreement, as a total of 64 species from 28 families were recorded during only 88 deployments. These numbers are similar to the recordings of previous ichthyofaunal surveys conducted at South Africa's warm-temperate reefs. Fortynine rocky reef fish species were recorded using diver conducted surveys in Algoa Bay (Beckley & Buxton, 1989) and 65 species from 29 families were recorded using visual transects elsewhere (Buxton & Smale, 1984). In this study also, this method effectively sampled the nocturnal fish community and proved to be suitable at discerning day-night variation in shallow and deep fish communities.

The use of stereo-BRUVs at night has received considerable attention in other locations around the world, particularly around Australia (Cappo *et al.*, 2004; Harvey *et al.*, 2012a, 2012b, 2012c; Fitzpatrick *et al.*, 2013; Whitmarsh *et al.*, 2016). This, however, was the first study to use night-time stereo-BRUVs on South African rocky reefs. Based on the findings of previous studies, that red light effectively samples aphotic communities in an unobtrusive manner, the present study used red light despite this light source producing a poorer image quality compared to blue and white artificial light sources (Harvey *et al.*, 2012b; Fitzpatrick *et al.*, 2013). The wavelength of red light also attenuates most rapidly in the water column and thus provides a limited range of view ((Harvey *et al.*, 2012b; Fitzpatrick *et al.*, 2013). In this study, the use of red light was considered to be a limitation, particularly for deep and nocturnal samples collected at Cape Recife where water turbidity was often high.

Visibility was a major limitation to sampling at Cape Recife (Table 3.3). Cape Recife reef complex is afforded relatively little protection against the prevailing south-westerly winds and open ocean swell, compared to Riy Banks. This is largely due to the position of Cape Recife reef, as it lies south of the Cape Recife headland and is therefore largely exposed. Cape Recife buoy data from the Council for Scientific and Industrial Research (CSIR, 1987) has recorded wave heights between 0.5 and 5.0 m in summer and between 1.0 and 6.5 m in winter. It is therefore likely that turning of the seafloor due to high wave exposure may cause the suspension of sediments in the water column, thus increasing turbidity and reducing visibility (Schumann & Goschen, 2011). Turbidity at Cape Recife may also be exacerbated by the close proximity of Cape Recife reef to the shoreline. As a result, visibility at Cape Recife reef was poorer than that recorded at Riy Banks, which lies further offshore with less interaction with the shoreline. The results of this study showed that visibility significantly affected the composition and abundance of species recorded, with a significantly positive effect on sparid abundances. This may explain why more sparids were recorded at Riy Banks where waters were less turbid. Water clarity has been described as a major limitation to the use of stereo-BRUVs, and this is particularly true for aphotic sampling (Cappo *et al.*, 2004). When selecting an artificial light source, characteristics of the sampling region and water quality should be taken into account.

The potential for visibility to have confounded the data in the present study was noted. The present study used red light to illuminate the field of view surrounding the bait canister for deep-aphotic and night time deployments (i.e. aphotic treatments). The use of red light was based on the assumption that this light source has no effect on the behaviour of the reef fish species investigated in this study since its wavelength of 620-630nm is above the range that the eyes of most coastal species are sensitive to (Whitmarsh *et al.*, 2017). Subjective observations during video analysis suggested that the behaviour of fish observed in the stereo-BRUVs footage did not seem to differ between treatments that used an artificial light source (i.e. deep-aphotic and night time deployments) compared to those that did not use an artificial light source (*day/shallow* deployments). From this, it was assumed that the choice to use a red-light source to investigate the natural behaviours and assemblage structures of nocturnal and deep-aphotic fish communities in an unbiased way was effective.

Concerns are, however, raised regarding the comparison of *day/shallow* and aphotic assemblages since the *day/shallow* treatment, where visibility did not depend on an artificial light source, recorded a substantially higher average visibility. While red light is likely to have the least effect on reef fish behaviour compared to other artificial light sources that have been investigated, such as white and blue light, the wavelength also attenuates more rapidly in the water column and therefore results in a reduced visibility and poorer image quality compared to the mentioned sources (Fitzpatrick *et al.*, 2013). The use of a blue light (450-465nm) source provides a greater range of view, and may have therefore been more suitable in comparing aphotic and *day/shallow* samples. The differences observed in the fish community composition and structure between the *day/shallow* treatment and the aphotic treatments may have therefore been exacerbated due to the differences in visible range of view. With this in mind, however, the results of the present study are in agreement with previous day-night comparative studies where significantly more diverse fish assemblages are sampled at day compared to night (Hobson, 1973; Ebeling & Bray, 1976; Helfman, 1978; Rooker & Dennis, 1991; Rooker *et al.*, 1997; Naglekerken *et al.*, 2001; Santos *et al.*, 2002; Azzuro *et al.*, 2007; Harvey *et al.*, 2012a, b; Myers *et al.*, 2015), and on shallow reefs compared to deep reefs in diurnal surveys conducted in warm-temperate South Africa (45-75m; Heyns-Veale *et al.*, 2016).

The application of stereo-BRUVs to indirectly investigate fish movement by sampling along a depth gradient is considered to be a relatively novel approach. While information on the exact movements could not be provided by this method, stereo-BRUVs provided a holistic review of diel activity patterns, day-night changes in detectability and potential movement patterns for multiple species making up the rocky reef fish communities. This study demonstrated that when stereo-BRUVs are used in a carefully designed sampling approach, the method may provide fundamental information on diel activity patterns, day-night changes in detectability and fish movement patterns for multiple species. Since Algoa Bay's deep and nocturnal communities were considered to be poorly understood prior to this study, it was essential to gain a holistic review of these communities in a cost-efficient manner. Findings of this study may therefore represent a foundation from which future research can be conducted, to shed some light on the observed patterns using a more direct tracking method, such as telemetry. The use of stereo-BRUVs also provided information on fish length, which will be analysed for subsequent research aimed at investigating the effects of fish size and life-stage on day-night changes in habitat use and activity patterns.

5.3 CONCLUSION

This thesis, that was the first dedicated study of its kind within South Africa, has provided a greater understanding of Algoa Bay's rocky reef fish communities in relation to the diel cycle. This was achieved by corroborating existing knowledge and revealing previously unknown information on species-specific day-night changes in detectability which ultimately drive day-night movement patterns. Species-specific responses to the diel cycle are complex, and appear to be influenced by a number of physical and biological environmental factors, as well as a species' morphological and behavioural adaptations. The predictable diel cycle, which is associated with changes in ambient light, is an important driver of the variety of behavioural adaptations observed at rocky reefs of Algoa Bay.

REFERENCES

Afonso, P., Fontes, J., Holland, K.N., Santos, R. S. 2008. Social status determines behaviour and habitat usage in a temperate parrotfish: Implications for marine reserve and design. Marine Ecology Progress Series. 359, 215-227.

Afonso, P., Fontes,J., Holland, K.N., Santos, R.S. 2009. Multi-scale patterns of habitat use in a highly mobile reef fish, the white trevally Pseudocaranx dentex, and their implications for marine reserve design. Marine Ecology Progress Series. 381, 273-286.

Alanara, A. Burns, M.D., Metcalfe, N.B. 2001. Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. Journal of Animal Ecology. 70, 980-986.

Ali, M.A. 1992. Rhythms in fishes. Plenum Press., New York.

Anderson, M.J., Ellingsen, K.E., McArdle, B.H. 2006. Multivariate dispersion as a measure of beta diversity. Ecology Letters. 9, 683-693.

Anderson, M.J., Gorley, R.N., Clarke, K.R. 2008. PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E ltd., Plymouth.

Annese, D.M., Kingsford, M.J. 2005. Distribution, movements and diet of nocturnal fishes on temperate reefs. Environmental Biology of Fishes. 72, 161-174.

Appeldoorn, R.S., Aguilar-Perera, A., Bouwmeester, BL. K., Dennis, G.D., Hill, R.L., Merten,W., Recksiek, C.W., Williams, S. J. 2009. Movement of fishes (Grunts: Haemulidae) across the coral reef seascape: A review of scales, patterns and processes. Caribbean Journal of Science. 45(2), 304-316.

Arrhenius, O. 1921. Species and area. Journal of Ecology. 9, 95-99.

Arrington, D.A., Winemiller, K. O. 2003. Diel changeover in sandbank fish assemblages in a neotropical floodplain river. Journal of Fish Biology. 63, 442-459.

Ashby, K. 1972. Patterns of daily activity in mammals. Mammal Review. 1, 171-185.

Axenrot, T., Didrikas, T., Danielsson, C., Hansson, S. 2004. Diel patterns in pelagic fish behaviour and distribution observed from a stationary, bottom-mounted, and upwardfacing transducer. Journal of Marine Science. 61, 1100-1104.

Azzuro, E., Pais, A., Consoli, P., Andaloro, F. 2007. Evaluating day-night changes in shallow Mediterranean rocky reef fish assemblages by visual census. Marine Biology. 151, 2245-2253.

Azzuro, E., Aguzzi, J., Maynou, F., Chiesa, J.J., Savini, D. 2012. Diel rhythms in a shallow Meditteranean rocky-reef fishes: a chronobiological approach with the help of trained volunteers. Journal of the Marine Biological Association of the United Kingdom. 93(2), 461-470.

Badenhorst, A., Smale, M. J. 2010. The distribution and abundance of linefish and secondary trawlfish on the Cape south coast of South Africa, 1986-1990. South African Journal of Marine Science. 11, 395-407.

Bailey, D.M., Wagner, H.J., Jamieson, A.J., Ross, M.F., Priede, I.G. 2007. A taste of the deep-sea: the roles of the gustatory and tactile searching behaviour in the grenadier fish *Coryphaenoides armatus*. Deep Sea Research Part I. 54, 99-108.

Bangley, C. W., Rulifson, R. A. 2017. Habitat partitioning and diurnal-nocturnal transition in the elasmobranch community of a North Carolina estuary. Bulletin of Marine Science, https://doi.org/10.5343/bms.2016.1038.

Bassett, D. K., Montgomery, J. C. 2011. Investigating nocturnal fish populations *in situ* using baited underwater video: with special reference to their olfactory capabilities. Journal of Experimental Marine Biology. 409, 194-199.

Becker, A., Cowley, P. D., Whitfield, A. K., Järnegren, J., Næsje, T. F. 2011. Diel fish movements in the littoral zone of a temporarily closed South African estuary. Journal of Experimental Marine Biology and Ecology. 406, 63-70.

Beckley, L. E. 1983. Sea-surface temperature variability around Cape Recife, South Africa. South African Journal of Science. 79, 436-438.

Benedetti-Cecchi, L., Bulleri, F., Cinelli, F. 2000. The interplay of physical and biological factors in maintaining mid-shore and low-shore assemblage on rocky coasts in the northwest Mediterrranean. Oceaolgia. 123, 406-417.

Bernard, A. 2012. Monitoring protocol for subtidal reef fish in the Agulhas Ecoregion of South Africa. Ph.D. dissertation, Rhodes University, South Africa.

Bernard, A., Götz, A., Parker, D. 2014. New possibilities for research on reef fish across the continental shelf of South Africa. South African Journal of Science. 110, 1-5.

Birt, M. J., Harvey, E. S., Langlois, T. J. 2012. Within and between day variability in temperate reef fish assemblages: Learned response to baited video. Journal of Experimental Marine Biology and Ecology. 416, 92-100.

Bohl, E. 1980. Diel pattern of pelagic distribution and feeding in planktivorous fish. Oceaologia. 4, 368–375.

Bongaerts, P., Ridgway, T., Sampayo, E. M., Hoegh-Guldberg, O. 2010. Assessing the ‘deep reef refugia’ hypothesis: focus on Caribbean reefs. Coral Reefs. 29, 309-327.

Boujard, T. 2001. Daily rhythms and fish physiology. Vie Milieu. 51, 237-245.

Branch, G. M., Griffiths, C. L., Beckley, L. E. 2010. Two Oceans: A guide to the marine life of Southern Africa. Struik Nature, Cape Town.

Bray, J R., Curtis, J. T. 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs. 27, 325-349.

Bremner, J.M., 1979a. The Bathymetry of Algoa Bay. Report No. 1980-0007, Geological Survey, Department of Mines. 13 pp.

Brouwer, S. 2002. Movement patterns of red Steenbras *Petrus rupestris* tagged and released in the Tsitsikamma National Park, South Africa. South African Journal of Marine Science. 24, 375-378.

Burger, L.T. 1990. The distribution patterns and community structure of the Tsitsikamma rocky littoral ichthyofauna. MSc dissertation, Rhodes University, South Africa. 121pp.

Buxton, C.D., Allen, J.C. 1989. Mark and recapture studies of two reef sparids in the Tsitsikamma Coastal National Park. Koedoe. 32, 39-45.

Buxton, C.D., Smale, M.J. 1984. A preliminary investigation of the marine ichthyofauna in the Tsitsikamma Coastal National Park. Koedoe. 27, 13-24.

Buxton, C.D. 1993. Life-history changes in exploited reef fishes on the east coast of South Africa. Environmental Biology of Fishes. 36, 47-63.

Cappo, M., Harvey, E., Malcolm, H., Speare, P. 2003. Potential of video techniques to monitor diversity, abundance and size of fish in studies of marine protected areas, in: Beumer, J.P., Grant, A., Smith, D.C. (Eds)., World Congress on Aquatic Protected Areas Proceedings., Cairns, pp. 455-464.

Cappo, M., Speare, P., De'ath, G. 2004. Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in interreefal areas of the Great Barrier Reef marine park. Journal of Marine Biology and Ecology. 302, 123-152.

Cappo, M., Harvey, E. S., Shortis, M. 2006. Counting and measuring fish with baited video techniques-an overview. Australian Society for Fish Biology. pp. 101-114.

Cappo, M., Harvey, E., Shortis, M. 2007b. Counting and measuring fish with baited video techniques – an overview, in: Lyle J. M., Furlani, D. M., Buxton, C. D. (Eds.), Proceedings of the 2006 Australian Society of Fish Biological Conference and Workshop Cuttingedge Technologies in Fish and Fisheries Science, Hobart, pp. 101-114.

Carothers, J. H., Jaksic, F. M. 1984. Time as a niche difference: the role of interference competition. Oikos. 42, 403–406.

Carpentieri, P. Colloca, F., Cardinale, M., Belluscio, A., Ardizzone, G.D. 2005. Feeding habits of European hake (*Merluccius merluccius*) in the central Mediterranean Sea. Fishery Bulletin**.** 103, 411-416.

Casey, J. M., Myers, R. 1998. Diel variation in trawl catchability: it is as clear as day and night? Canadian Journal of Fisheries and Aquatic Sciences. 55, 2329-2340.

Celliers, L., Breetzke, T., Moore, L. 2010. A toolkit for implementing the Integrated Coastal Management Act. SSI Engineers and Environmental Consultants. pp. 108.

Chale-Matsau, J. R., Govender, A. Beckley, L. E. 2001. Age, growth and retrospective stock assessment of an economically extinct sparid fish, *Polysteganus undulosus,* from South Africa. *Fisheries Research* **51**: 87-92.

Chapman, M.R., Kramer, D.L. 2000. Movements of fishes within and among fringing coral reefs in Barbados. Environmental Biology of Fishes. 57, 11-24.

Clark, C.W., Levy, D.A. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. American Naturalist. 131, 271–290.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology. 18, 117-143.

Clarke, K.R., Gorley, R.N. 2006. PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth.

Clarke, K.R., Gorley, R.N. 2015. PRIMER v7: User manual/Tutorial. PRIMER-E, Plymouth.

Clarke, K.R., Warwick, R.M. 2001. Change in marine communities: An approach to statistical analysis and interpretation, second ed. PRIMER-E, Plymouth.

Cleveland, W.S. 1993. Visualising Data. Hobart Press, New Jersey.

Collette, B.B., Talbot, F.H. 1972. Activity patterns of coral reef fishes with emphasis on nocturnal-diurnal changeover. Bulletin of the Natural History Museum of Los Angeles County. 14, 98–124.

Colmenero, A.I., Aguzzi, J., Lombarte, A., Bozzano, A. 2010. Sensory constraints in temporal segregation in two species of anglerfish, *Lophius budegassa* and *L. piscatorius*. Marine Ecology Progress Series. 416, 255-265.

Colton, M.A., Swearer, S.E. 2010. A comparison of two survey methods: differences between underwater visual census and baited remote underwater video. Marine Ecology Progress Series. 400, 19-36.

Connell, J.H. 1980. Diversity and the co-evolution of competitors, or the ghost of competition past. Oikos. 35, 131-138.

Cowley, P.D., Brouwer, S.L., Tilney, R.L. 2002. The role of the Tsitsikamma National Park in the management of four shore-angling fish along the south-eastern Cape coast of South Africa. South African Journal of Marine Science**.** 24, 27-35.

Crook, D.A., Robertson, A.I., King, A.J. 2001. The influence of spatial scale and habitat arrangement on diel patterns of habitat use by two lowland river fishes. Oecologia. 129, 525-533.

Crossland, J. 1982. Tagging of marine fishes in New Zealand. Fisheries Research Division Occassional Publication. 33, 1-19.

Crother, B.I., Murray, C.M. 2011. Ontology of areas of endemism. Journal of Biogeoraphy. 38, 1009-1015.

Crowder, L.B., Cooper, W.E. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology. 63, 1802-1813.

Currie, J.C., Sink, K.J., Le Noury, P., Branch, G.M. 2012. Comparing fish communities in sanctuaries, partly protected areas and open-access reefs in South-East Africa. African Journal of Marine Science. 34(2), 269-281.

Dahlgren, C.P., Eggleston, D.B. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology. 81, 2227-2240.

Dall, W., Hill, B.J., Rothlisberg, P.C., Sharples, D.J. 1990. The biology of the Penaeidae. Advances in Marine Biology. 27, 1-489.

Danilowicz, B.S., Sale, P.F. 1999. Relative intensity of predation on the French grunt, *Haemulon flavolineatum,* during diurnal, dusk, and nocturnal periods on a coral reef. Marine Biology. 133, 337-343.

De Cáceres, M., Lengendre, P. 2009. Associations between species and groups of *site*s: indices and statistical inference. Ecology. 90, 3566-3574.

De Stasio, B.T. 1993. Diel vertical and horizontal migration by zooplankton: population budgets and the diurnal deficit. Bulletin of Marine Science**.** 53, 44-64.

De Vos, L., Gotz, A., Winker, H., Attwood, C.G. 2014. Optimal BRUVs (baited remote underwater video system) survey design for reef monitoring in the Stilbaai Marine Protected Area. African Journal of Marine Science. 36, 1-10.

Diehl, S. 1988. Foraging efficiency of three freshwater fishes: effects of structural complexity and light. Oikos. 53, 207–214.

Dingle, R.V., Birch, G.F., Bremner, J.M., de Decker, R.H., du Plessis, A., Engelbrecht, J.C., Fincham, MJ., Fitton, T., Flemming, B.W., Gentle, R.I., Goodlad, S.W., Martin, A.K., Mills, E.G., Moir, G.J., Parker, R.J., Robson, R.H., Simpson, E.E.W., Summerhaves, C.P., Westall, F., Winter, A., Woodborne, M.W. 1987. Deep-sea sedimentary environments around Southern Africa (South-east Atlantic and South-west Indian Ocean). Annals of the South African Museum. 98, 1-27.

Dingle, H. 1996. Migration: the biology of life on the move. Oxford University Press, New York.

Doherty, P.J. 1983. Diel, lunar, and seasonal rhythms in the reproduction of two tropical damselfishes: *Pomacentrus flavicauda* and *P. wardi.* Marine Biology. 75, 215-224.

Dubin, R.E., Baker, J.D. 1982. Two types of cover-seeking behaviour at sunset by the princess parrotfish, *Scarus taeniopterus,* at Barbados, West Indies. Bulletin of Marine Science. 32, 2155-2166.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs. 67, 345-366.

Dunson, W.A., Travis, J. 1991. The role of abiotic factors in community organisation. American Naturalist. 138, 1067-1091.

Ebeling, A.W., Bray, R.N. 1976. Day versus night activity of reef fishes in a kelp forest off Santa Barbara. California Fisheries Bulletin of the United States. 74, 703-717.

Ebeling, A. W., Hixon, M. A. 1991. Tropical and temperate reef fishes: Comparison of community structures, in: Sale, P.F (Ed.) The ecology of fishes on coral reefs. Academic Press., San Diego, pp. 509-563.

Fabi, G., Sala, A. 2002. An assessment of biomass a diel activity of fish at an artificial reef (Adriatic sea) using stationary hydroacoustic technique. Journal of Marine Science. 59, 411-420.

Fedriani, J.M., Palomares, F., Delibes, M. 1999. Niche relations among three sympatric Mediterranean carnivores. Oecologia. 121, 138-148.

Fernandez-Duque, E. 2003. Influences of moonlight, ambient temperature, and food availability on the diurnal and nocturnal activity of owl monkeys (*Aotus azarai*). *Behavioural* Ecology and Sociobiology. 54, 431-440.

Ferreras, P. Monterrosos, P., Paulo, C. 2013. Catch me if you can: Diel activity patterns of mammalian prey and predators. Ethology. 119, 1044-1056.

Fisher, S.G. 1994. Pattern, process and scale in freshwater systems: some unifying thoughts, in: Giller, P.S., Hildrew, A.G., Raffaelli, D.G. (Eds). Aquatic ecology: scale, pattern and process, 34th Symposium of the British Ecological Society., Blackwell, Oxford, pp. 575-591.

Fitzpatrick, C., McLean, D., Harvey, E. S. 2013. Using artificial illumination to survey nocturnal reef fish. Fisheries Research. 146, 41-50.

Fox, J.R., Bellwood, D.R. 2011. Unconstrained by the clock? Plasticity of diel activity rhythm in a tropical reef fish, *Siganus lineatus.* Functional Ecology. 25, 1096-1105.

Futuyma, D.J., Moreno, G. 1988. The evolution of ecological specialisation. Annual Review of Ecology, Evolution, and Systematics. 19, 207-233.

Garrabou, J., Ballesteros, E., Zabala, M. 2002. Structure and dynamics of North-western Mediterranean rocky benthic communtiies along a depth gradient. Estuarine, Coastal and Shelf Science. 55, 493-508.

Garrat, P.A. 1990. Spawning behaviour of *Cheimerius nufar* in captivity. Environmental Biology of Fishes. 31, 345-353.

Gibbons, M.J., Gugushe, N., Boyd, A.J., Shannon, L.J., Mitchell-Innes, B.A. 1999. Changes in the composition of the non-copepod zooplankton assemblage in St Helena Bay (southern Benguela ecosystem) during a six day drogue study. Marine Ecology Progress Series. 180, 111-120.

Gilbert, M., Rasmussen, J.B., Kramer, D.L. 2005. Estimating the density and biomass of moray eels (Muraenidae) using a modified visual census method for hole-dwelling reef fauna. Environmental Biology of Fishes. 73, 415-426.

Gladfelter, W.B. 1979. Twilight migrations and foraging activities of the copper sweeper Pernpheris schornburgki (Teleostei: Pempheridae). Marine Biology. 50, 109-119.

Gladstone, W., Lindfield, S., Coleman, M., Kelaher, B. 2012. Optimisation of baited remote underwater video sampling designs for estuarine fish assemblages. Journal of Experimental Marine Biology and Ecology. 429, 28-35.

Gliwicz, Z.M., Jachner, A. 1992. Diel migrations of juvenile fish: a ghost of predation past or present? Archiv fu¨r Hydrobiologie. 124, 385–410.

Goschen, W.S. 1991. Ocean dynamics associated with prominent capes and bays off the south coast of South Africa. Ph.D. dissertation, University of Port Elizabeth, South Africa, pp. 313.

Goschen, W. S., & Schumann, E. H. 2011. The physical oceanographic processes of Algoa Bay, with emphasis on the western coastal region: A synopsis of the main result of physical oceanographic research in and around Algoa Bay up until 2010. SAEON and IMT.

Götz, A. 2005. Assessment of the effect of Goukamma marine protected area on community structure and fishery dynamics. Ph.D. dissertation, Rhodes University, South Africa.

Götz, A., S.E. Kerwath, C.G. Attwood, and W.H.H. Sauer. 2009. Effects of Fishing on a Temperate Reef Community in South Africa I: Ichthyofauna. African Journal of Marine Science. 31, 241–51.

Gorman, O.T., Yule, D.L., Stockwell, J.D. 2012. Habitat use by fishes of Lake Superior. II. Consequences of diel habitat use for habitat linkages and habitat coupling in nearshore and offshore waters. Aquatic Ecosystem Health Management. 15, 355–368.

Gratwicke, B., Petrovic, C., Speight, M.R. 2006. Fish distribution and ontogenetic habitat preferences in non-estuarine lagoons and adjacent reefs. Environmental Biology of Fishes. 76, 191-210.

Gray, A.E., Williams, I.D., Stamoulis, K.A., Boland, R.C., Lino, K.C., Hauk, B.B., Leonard, J.C., Rooney, J.J., Asher, J.M., Lopes, K.H., Kosaki, R.K. 2016. Comparison of reef fish survey data gathered by open and closed circuit SCUBA divers reveals differences in areas with higher fishing pressure. PLoS ONE. 11(12), e0167724. doi:10.1371/journal.pone.0167724.

Griffiths, M.H., Wilke, C. 2002. Long-term movement patterns of five temperate-reef fishes (Pisces: Sparidae): implications for marine reserves. Marine and Freshwater Research. 53, 233-244.

Griffiths, C.L., Robinson, T.B., Lange, L., Mead, A. 2010. Marine Biodiversity in South Africa: An Evaluation of Current States of Knowledge. PLoS ONE. 5(8), 1-13.

Grundlingh, M.L. 1983. On the course of the Agulhas Current. South African Geographical Journal. 65, 49-57.

Guest, M.A., Connolly, R.M., Loneraga, N.R. 2003. Seine nets and beam trawls compared by day and night for sampling fish and crustaceans in shallow seagrass habitat. Fisheries Research. 64, 185-196.

Guidetti, P., Boero, F. 2009. Spatio-temporal variability in abundance of the parrotfish, *Sparisoma cretense,* in SE Apulia (SE Italy, Mediterranean Sea). Italian Journal of Zoology. 69(3), 229-232.

Hall, D.J., Cooper, W.E., Werner, E.E. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnology and Oceanography**.** 15, 839-928.

Hammerschlag, N., Serafy, J.E. 2009. Nocturnal fish utilization of a subtropical mangroveseagrass ecotone. Marine Ecology. 31, 364-374.

Hammerschlag, N., Meyer, C.G., Grace, M.S., Kessel, S.T., Sutton, T.T., Harvey, E.S., Paris-Limouzy, C.B., Kerstetter, D.W., Cooke, S.J. 2017. Shining a light on fish at night: an overview of fish and fisheries in the dark of night, and in deep and polar seas. Bulletin of Marine Science. 93(0): 000-000.

Harmelin, J.G. 1987. Structure and variability of the ichthyofauna in a Mediterranean protected rocky area (National Park of Port-Cros (Parc national, France). P. S. Z. N. I: Marine Ecology. 8, 263-284.

Harvey, E.S., Shortis, M. 1995. A system for stereo-video measurement of sub-tidal organisms. Marine Technology Society Journal. 29, 10-22.

Harvey, E.S., Shortis, M.R. 1998. Calibration stability of an underwater stereo-video system: implications for measurement accuracy and precision. Marine Technology Society Journal. 32, 3-17.

Harvey, E., Fletcher, D., Shortis, M. 2001b. Improving the statistical power of visual length estimates of reef fish: a comparison of divers and stereo-video. Fishery Bulletin. 99, 72-80.

Harvey, E., Fletcher, D., Shortis, M., 2002a. Estimation of reef fish length by divers and by stereo-video. A first comparison of the accuracy and precision in the field on living fish under operational conditions. Fisheries Research. 57, 255–265.

Harvey, E., Fletcher, D., Shortis, M.R., Kendrick, G.A., 2004. A comparison of underwater visual distance estimates made by scuba divers and a stereo-video system: implications for underwater visual census of reef fish abundance. Marine and Freshwater Research. 55, 573-580.

Harvey, E.S., Cappo, M., Butler, J., Hall, N., Kendrick, G.A. 2007. Bait attraction effects the performance of remote underwater video stations in an assessment of demersal fish community structure. Marine Ecological Progress Series. 350, 245-254.

Harvey, E.S., Butler, J.J., McLean, D.L., Shand, J. 2012a. Contrasting habitat use of diurnal and nocturnal fish assemblages in temperate Western Australia. Journal of Experimental Marine Biology and Ecology. 427, 78-86.

Harvey, E.S., Newman, S.J., McLean, D.L., Cappo, M., Meeuwig, J., Skepper, C.L. 2012b. Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shel demersal fishes. Fisheries Research. 125, 108-120.

Hatanaka, H., Sato, T., Augustyn, C.J., Payne, A.I.L., Leslie, R.W. 1983. Report on the Japan/South Africa joint trawling survey on the Agulhas Bank in November/December 1980. SpecPubl. mar. Fish. Resource Cent. pp. 73.

Hayward, M.W., Slotow, R. 2009. Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. African Journal of Wildlife Research. 39(2), 109125.

Heemstra, P., Heemstra, E. 2004. Coastal fishes of southern Africa. National Inquiry Service Centre (NISC) and South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown, South Africa. 488pp

Helfman, G.S. 1978. Patterns of community structure in fishes: summary and overview. Environmental Biology of Fishes. 3, 129-148.

Helfman, G.S. 1986. Fish Behaviour by day, night and twilight, in: Behaviour of Teleost Fishes (Ed. By T. J. Pitcher), pp. 479-512. London: Chapman & Hall.

Helfman, G.S. 1993. Fish behaviour by day, night and twilight, in: Pitcher, T.J. (Eds.), The behaviour of teleost fishes, second ed. Chapman & Hall., London, pp. 479-512.

Heyns-Veale, E.R., Bernard, A.T.F., Richoux, N.B., Parker, D., Langlois, T.J., Harvey, E.S., Götz, A. 2016. Depth and habitat determine assemblage structure of South Africa's warm-temperate reef fish. Marine Biology. 163, 158.

Hitt, S., Pittman, S.J., Nemeth, R.S. 2011. Diel movements of fishes linked to benthic seascape structure in a Caribbean coral reef ecosystem. Marine Ecology Progress Series. 42, 275-291.

Hobson, E.S. 1972. Activity of Hawaiian reef fishes during the evening and during transition between daylight and darkness. Fishery Bulletin. 70, 715-740.

Hobson, E.S. 1973. Diel feeding migrations in tropical reef fishes. Helgoland Marine Research. 24, 361-370.

Hobson, E.S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. Fisheries Bulletin**.** 720, 915–1031.

Hobson, E.S., Chess, J.R. 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. Fisheries Bulletin. 74, 567-598.

Holbrook, S.J., Schmitt, R.J. 2002. Competition for shelter space causes density-dependent predation mortality in damselfishes. Ecology. 83, 2855-2868.

Holland, K.N., Lowe, C.G., Wetherbee, B.M. 1996. Movement and dispersal patterns of the blue trevally (*Caranx melampygus*) in a fisheries conservation zone. Fisheries Research. 25, 279-292.

Holmes, T.H., Wilson, S.K., Travers, M.J. Langlois, T.J., Evans, R.D. Glenn, I.M., Douglas, R.A., Shedrawi, G., Harvey, E.S., Hickey, K. 2013. A comparison of visual- and stereo-video based fish community assessment methods in tropical and temperate marine waters of Western Australia. Limnology and Oceanography: Methods. 11, 337-350.

Howard, R.K. 1989. The structure of a nearshore fish community of Western Australia: diel patterns and the habitat role of limestone reefs. Environmental Biology of Fishes. 24, 94-104.

Hrabik, T.R.., Jensen, O.P., Martell, S.J.D.,Walters, C.J ., Kitchell, J.F. 2006. Diel vertical migration the Lake Superior pelagic community. I. Changes in vertical migration of coregonids in response to varying predation risk. Canadian Journal of Fisheries and Aquatic Science. 63, 2286–2295.

Hutchings, K., Porter, S., Clark, Sink, K. 2011. Strategic environmental assessment: Identification of potential marine aquaculture development zones for fin fish cage culture. Draft October 2011. Available at: http://www.anchorenvironmental.co.za/index.php?option=com_content&view=article&id=27&Itemid= 29

Jadot, C., Ovidio, M., Voss, J. 2002. Diel activity of *Sarpa salpa* (Sparidae) by ultrasonic telemetry in a *Posidonia oceanica* meadow of Corsica (Mediterranean Sea). Aquatic Living Resources. 15, 343-350.

Jensen, A.C. 1966. Life history of the spiny dogfish. Fishery Bulletin of Washington. 65, 527-554.

Johannes, R.E. 1981. Words of the lagoon. University of California Press, Berkeley, pp. 245.

Jones, G.P. 1988. Ecology of rocky reef fish of north-eastern New Zealand: A review. New Zealand Journal of Marine and Freshwater Research. 22, 445-462.

Kerwath, S.E., Götz, A., Attwood, C.G., Cowley, P.D., Sauer, W.H.H. 2007. Movement pattern and home range of Roman *Chrysoblephus laticeps*. African Journal of Marine Science. 29, 93-103.

Kerwath S.E., Götz, A., Attwood, C.G., Sauer, W.H.H., Wilke, C.G. 2007b. Area utilisation and activity patterns of roman Chrysoblephus laticeps (Sparidae) in a small marine protected area. African Journal of Marine Science. 29, 259–270.

King, N.J., Bagley, P.M., Priede, I.G. 2006. Depth zonation and latitudinal distribution of deep-sea scavenging demersal fishes of the Mid-Atlantic Ridge, 42 to 53°N. Marine Ecology Progress Series. 319, 263-274.

Götz, A., Kerwath, S.E., Attwood, C.G., Sauer, W.H.H. 2009. Effects of fishing on a temperate reef community in South Africa 1: ichthyofauna. African Journal of Marine Science. 31(2), 241-151.

King, N.J., Bagley, P.M., Priede, I.G. 2006. Depth zonation and latitudinal distribution of deep-sea scavenging demersal fishes of the Mid-Atlantic Ridge, 42-53°N. Marine Ecology Progress Series. 319, 263-274.

Kopp, D., Bouchon-Navaro, Y., Louis, M., Bouchon, C. 2007. Diel differences in the seagrass fish assemblages of a Caribbean island in relation to adjacent habitat types. Aquatic Botany. 87, 31-37.

Kotwicki, S., De Robertis, A., Von Szalay, P., Towler, R. 2009. The effect of light intensity on the availability of walleye pollock (*Theragra chalcogramma*) to bottom trawl and acoustic surveys. Canadian Journal of Fisheries and Aquatic Sciences. 66, 983-994.

Kronfeld-Schor, N., Dayan, T. 1999. The dietary basis for temporal partitioning: food habits of coexisting *Acomys* species. Oecologia. 121, 123-128.

Kronfeld-Schor, N., Dayan, T. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution and Systematics. 34, 153-181.

Kruskal, J.B. 1964. Multidimensional scaling by optimizing a goodness of fit to a nonmetric hypothesis. Psychometrika. 29, 1-28.

Kulbicki, M. 1998. How the acquired behaviour of commercial reef fishes may influence the results obtained from visual censuses. Journal of Experimental Biology and Ecology. 222, 11-30.

Kulbicki, M., Cornuet, N., Vigliola, L., Wantiez, L., Moutham, G., Chabanet, P., 2010. Counting coral reef fishes: Interaction between fish life-history traits and tran-sect design. J. Experimental Marine Biology and Ecology. 387, 15–23.

Laegdsgaard P., Johnson C.R. 1995. Mangrove habitats as nurseries – unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. Marine Ecology Progress Series. 126, 67–81

Langlois, T.J., Harvey, E.S., Meeuwig, J.J. 2012a. Strong direct and inconsistest indirect effects of fishing found using stereo-video: testing indicators from fisheries closures. Ecological Indicators. 23, 524-534.

Langlois, T.J., Fitzpatrick, B.R., Fairclough, D.V., Wakefield, C.B., Hesp, S.A., McLean, D. L., Harvey, E.S., Meeuwig, J.J. 2012b. Similarities between line fishing and baited stereo-video estimations of length frequency: novel application of kernel density estiamtes. PLoS ONE. 7, 1-9.

Laroche, J., Baran, E., Rasoanandrasana, N.B. 1997. Temporal patterns in a fish assemblage of a semiarid mangrove zone in Madagascar. Journal of Fish Biology 51, 3-20. Legendre, P., Legendre, L. 1998. Numerical Ecology, second English edition, Amsterdam.

Legendre, P. 2013. Indicator species: computation. Encyclopedia of Biodiversity. 4, 264268.

Levin, S.A. 1992. The problem of patterns and scale in ecology. Ecology. 73, 1943-1967.

Lewis, C.A., Lester, N.P., Bradshaw, A.D., Fitzgibbon, J.E., Fuller, K., Hakanson, L., Richards, C. 1996. Consideration of scale in habitat conservation and restoration. Canadian Journal of Fisheries and Aquatic Sciences. 53, 440-445.

Lima, S.L. 1988. Nonlethal effects in the ecology of predator-prey interactions. BioScience. 48, 25-34.

Lima, S.L., Dill, L.M. 1990. Behavioural decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology. 69, 619–640.

Lindfield, S.J., Harvey, E.S., McIlwain, J. L., Halford, A.R. 2014. Silent fish surveys: bubble free diving highlights inaccuracies assoiated with SCUBA based surveys in heavily fished areas. Methods in Ecology and Evolution. 5(10), 1061-1069.

Linnell, J.D.C., Strand, O. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Diversity and Distributions. 6, 169-176.

Lombard, A.T., Strauss, T., Harris, J., Sink., Attwood, C., Hutchings, L. 2004: South African National Spatial Biodiversity Assessment 2004: Technical Report. Volume 4: Marine Component. Pretoria: South African National Biodiversity Institute.

Loose, C.J., Dawidowicz, P. 1994. Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. Ecology. 75, 2255– 2263.

Lubbers, L., Boytno, W.R., Kemp, W.M. 1990. Variation in structure of estuarine fish communities in relation to abundance of submersed vascular plants. Marine Ecological Progress Series. 65, 1-14.

Lutjeharms, J.R.E. 2006. The Agulhas Current, Springer, Berlin.

Mallet, D., Pelletier, D. 2014. Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952-2012). Fisheries Research. 154, 44-62.

Maes, J., Pas, J., Talilieu, A., Van Damme, P.A., Ollevier, F. 1999. Diel changes in the vertical distribution of juvenile fish in the Zeeschelde Estuary. Journal of Experimental Biology. 54, 1329-1333.

Manooch, III, C, S., Huntsman, G.R. 1977. Age, growth, and mortality of the red porgy, *Pagrus pagrus*. Transactions of the American Fisheries Society. 106, 26-33.

Marti, C.D., Steenhof, K., Kochert, M.N., Marks, J.S. 1993. The roles of diet, body size and activity time in vertebrate predators. Oikos. 67, 6-18.

Mazeroll, A.I., Montgomery, W.L. 1998. Daily migrations of a coral reef fish in the Red Sea (Gulf of Aqaba, Israel): initiation and orientation. Copeia. 893-905.

McCleave, J.D., Fried, S.M. 1975. Night-time catches of fishes in a tidal cove in Montsweag Bay near Wiscasset, Maine. Transactions of the American Fishery Society. 104, 30-34.

McCoy, E.D., Bell, S.S. 1991. Habitat structure: The evolution and diversification of a complex topic, in: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), Habitat Structure, the Physical Arrangement of Objects in Space. Chapman and Hall., New York, pp. 3-27.

McFarland, W.N. 1991. The Ecology of Fishes on Coral Reefs, Academic Press, New York.

McGehee, A. 1994. Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. Marine Ecology Progress Series. 105, 243-255.

Melly, B.L. 2011. The zoogeography of the cetaceans in Algoa Bay. MSc dissertation, Rhodes University, South Africa.

Menge, B.A., Sutherland, J.P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to gradients of environmental stress and recruitment. American Naturalist. 130, 730-757.

Metcalfe, N.B., Fraser, N.H.C., Burns, M.D. 1999. Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. Journal of Animal Ecology. 68, 371-381.

Meyer, C.G., Honebrink, R. 2005. Retention of surgically implanted transmitters by Bluefin trevally (*Caranx melampygus*). Implications for long-term movement studies. Transactions of American Fisheries Society. 134, 602-606.

Molles, M.C., Cahill, J.F. 1999. Ecology: concepts and applications, McGraw Hill.

Morris, D.W. 2003. Toward an ecological synthesis: a case for habitat selection. Oecologia. 136, 1-13.

Munroe, S.E.M., Simpfendorfer, C.A., Heupel, M.R. 2014. Defining shark ecological specialisation: concepts context and examples. Reviews in Fish Biology and Fisheries. 24, 317-331.

Murphy, H.M., Jenkins, G.P. 2010. Observational methods in marine spatial monitoring of fishes and associated habitats: a review. Marine and Freshwater Research. 61, 236-252. Nagelkerken, B.G., Van der Veldea, D.M.W., Gorissena, G.J., Meeijera, T. Van't Hof, C., Den Hartoga, C. 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for coral reef fishes, using a visual census technique. Estuarine, Coastal and Shelf Science. 51, 31-44.

Myer, E.M.V., Harvey, E.S., Saunders, B.J., Travers, M.J. 2016. Fine-scale patterns in the day, night and crepuscular composition of a temperate reef fish assemblage. Marine Ecology. 37, 668-678.

Nash, R.D.M., Santos, R.S., Geffen, A.J., Hughes, G., Ellis, T. R. 1994. Diel variability in catch rate of juvenile flatfish on two small nursery grounds (Port Erin Bay, Isla of Man and Porto Pim Bay, Faial, Azores). Journal of Fisheries Biology. 44, 35-45.

Nash, R.D.M., Santos, R.S. 1998. Seasonality in diel catch rate of small fishes in a shallow-water fish assemblage at Porto Pim Bay, Faial, Azores. Estuarine, Coastal and Shelf Science. 47, 319-328.

Nash, K.L., Welsh, J.Q., Graham, N.A.J., Bellwood, D.R. 2015. Home-range allometry in coral reef fishes: comparison to other vertebrates, methodological issues and management implications. Oecologia. 177, 73-83.

Neilson, J.D., Perry, R.I. 1990. Diel vertical migrations of marine fish: an obligate or facultative process? Advances in Marine Biology. 26, 115-167.

Nepgen, C.S., DE V. 1977. The biology of the hottentot *Pachymetopon blochii* (Val.) and the silver fish *Argyrozona argyrozona* (Val.) along the Cape south-west coast. Investl Rep. Sea Fish. Brch S. Afr. 105, 1-35.

Newman, S.J., Williams, D.M. 1995. Mesh size selection and diel variability in catch of fish traps on the central Great Barrier Reef, Australia: a preliminary investigation. Fisheries Research. 23, 237-253.

Ogden, J.C., Ehrlich, P.R. 1977. The behaviour of heterotypic resting schools of juvenile grunts (Pomadasyidae). Marine Biology. 42, 273-280.

Ogden, J.G., Zieman, J.C. 1977. Ecological aspects of coral reef-seagrass bed contacts in the Carribbean. Proceedings of the Third International Coral Reef Symposium, Miami, pp. 377-381.

Okun, N., Mendonca, R., Mehner, T. 2005. Diel shifts in a community composition and feeding of juvenile fishes in the pelagic area of a large shallow lake. Limnologica. 35, 7077.

Pankhurst, N.W. 1989. The relationship of ocular morphology to feeding modes and activity periods in shallow marine teleosts from New Zealand. Environmental Biology of Fishes. 26, 201-211.

Parker, D. An evaluation of sampling and statistical methods for long-term monitoring of subtidal reef fishes: a case study of the Tstitsikamma National Park marine protected area. Ph. D. thesis, Rhodes University, South Africa.

Parrish, J.D. 1989. Fish communities of interacting shallow water habitats in tropical oceanic regions. Marine Ecology Progress Series. 58, 143–160.

Patil, T.S., Bhosale, A.R., Yadav, R.B., Khandekar, R.S., Muley, D.V. 2015. Study oof endemic and threatened fish species diversity and its assemblage structure from northern western Ghats, Maharashtra, India. International Journal of Zoological Research. 11(3), 116-126.

Pattrick, P., Strydom, N.A. 2008. Composition, abundance, distribution and seasonality of larval fishes in the Greater Addo Marine Reserve, Algoa Bay, South Africa. Estuarine, Coastal and Shelf Science. 79, 251-262.

Paul, L.J. 1967. An evaluation of tagging experiments on the New Zealand snapper, *Chrysophrys auratus* (Forster), during the period 1952-1963. New Zealand Journal of Marine and Freshwater Research. 1, 455-463.

Penrith, M.J. 1976. Distribution of shallow marine fishes around southern Africa. Cimbebasia. 4(7), 138-154.

Pérès, J.M., Picard, J. 1964. Nouveau manuel de bionomie benthique de la Méditerranée. Recueil des Travaux de la Station Marine d'Endoume. 31(47), 1-37.

Petrakis, G., MacLennan, D.N., Newton, A.W. 2001. Day-night and depth effects on catch rates during trawl surveys in the North Sea. Journal of Marine Science. 58, 50-60.

Piet, G.J., Guruge, W.A.H.P. 1997. Diel variation in feeding and vertical distribution of ten co-occurring fish species: consequences for resource partitioning. Environmental Biology of Fishes. 50, 293-307.

Pittman, S.J., McAlpine, C.A. 2001. Movements of marine fish and decapod crustaceans: Process, Theory and Application. Advances in Marine Biology. 44, 206-272.

Porter, N.S., Branch, G.M., Sink, K.J. 2013. Biogeographic patterns on shallow subtidal reefs in the western Indian Ocean. Marine Biology. 160, 1271-1283.

Prochazka, K. 1998. Spatial and trophic partitioning in cryptic fish communities in shallow subtidal reefs in False Bay, South Africa. Environmental Biology of Fishes. 51, 201-220.

Reebs, S.G. 2002. Plasticity of diel and circadian activity rhythms in fishes. Reviews in Fish Biology and Fisheries. 12, 349-371.

R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-70-0. URL: http//www.R-project.org/

Rickel, S., Genin, A. 2005. Twilight transitions in coral reef fish: the input of light-induced changes in foraging behaviour. Animal Behaviour. 70, 133-144.

Grácio, A.R., Mira, A., Beja, P., Pita, R. 2017. Diel variation in movement patterns and habitat use by the Iberian endemic Cabrera vole: Implications for conservation and monitoring. Mammalian Biology. 83, 21-26.

Robertson, A.I., Blaber, S.J.M. 1992. Plankton, epibenthos and fish communities, in: Robertson A.I., Alongi D.M. (Eds.), Tropical Mangrove Ecosystems. American Geophysical Union., Washington, pp. 173–224.

Rooker, J.R., Dennis, G.D. 1991. Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. Bulletin of Marine Science. 3, 684-698.

Rooker, J.R., Dokken, Q.R., Pattengill, C.V., Holt, G.J. 1997. Fish assemblages on artificial and natural reefs in the Flower Garden Banks National Marine Sanctuary, USA. Coral Reefs. 16, 83-92.

Ross, S.T. 1986. Resource Partitioning in Fish Assemblages: A Review of Field Studies. Copia. 2, 352-388.

Ryer, C., Olla, B. 1999. Light-induced changes in the prey consumption and behaviour of two juvenile planktivorous fish. Marine Ecological Progress Series. 181, 41-51.

Sala, E., Boudoursque, C.F., Harmelin-Vivien, M. 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. Oikos. 82, 425439.

Sale, P.F. 1991. Reef fish communities: Open nonequilibrial systems, in: Sale, P. F. (Eds.), The Ecology of Fishes on Coral Reefs. Academic Press., San Diego, pp. 564-600.

Samoilys, M.A. 1996. Movement in a large predatory fish: coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on Heron Reef, Australia. Coral Reefs. 16, 151-158.

Santana-Garcon, J., Newman, S.J., Langlois, T.J., Harvey, E.S. 2014. Effects of a spatial closure on highly mobile fish species: an assessment using pelagic stereo-BRUVs. Journal of Experimental Marine Biology and Ecology. 460, 153-161.

Santos, R.S., Nash, R.D. 1995. Seasonal changes in a sandy beach fish assemblage at Porto Pim, Faial, Azores. Estuarine, Coastal and Shelf Science. 41, 579-591.

Schmitz, L., Wainwright, P.C. 2011. Nocturnality constrains morphological and functional diversity in the eyes of reef fishes. BMC Evolutionary Biology. 11, 338.

Santos, M.N., Monteiro, C.C., Gaspar, M.B. 2002. Diurnal variations in the fish assemblage at an artificial reef. Journal of Marine Science. 59, 32-35.

Deepayan, S. 2008. Lattice: Multivariate Data Visualization with R, Springer, New York.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science. 185, 27-38.

Schumann, E.H., Ross, G.J.B., Goschen, W.S. 1988. Cold water events in Algoa Bay and along the south coast of the cape Province, South Africa. South African Journal of Science. 84(7), 579-584.

Schumann, E.H., Martin, J.A. 1991. Climatological aspects of the coastal wind field at Cape Town, Port Elizabeth and Durban. South African Geographical Journal. 73, 48-51.

Schumann, E.H., Churchhill, J.R.S., Zaayman, H.J. 2005. Oceanic variability in the western sector of Algoa Bay South Africa. African Journal of Marine Science. 27, 65-80.

SeaGIS. 2008. Eventmeasure Software.

Sfakiotakis, M., Davies, J.B.C. 1998. Review of fish swimming modes for aquatic locomotion. *IEEE Journal of Oceanic Engineering*

Shepherd, T., Page, F., Macdonald, B. 2002. Length and sex-specific associations between spiny dogfsh (*Squalus acanthias*) and hydrographic variables in the Bay of Fundy and Scotian Shelf. Fisheries Oceanography. 11, 78-89.

Shortis, M.R., Harvey, E.S., Abdo, D.A. 2009. A review of underwater stereo-image measurement for marine biology and ecology applications. Oceanography and Marine Biology. 47, 257-292.

Sink K.J, Atkinson L.J, Kerwath, S., Samaai, T. 2010. Assessment of offshore benthic biodiversity on the Agulhas Bank and the potential role of petroleum infrastructure in offshore spatial management. Report prepared for WWF South Africa and PetroSA through a SANBI initiative pp. 77

Sims, D.W., Nash, J.P., Morritt, D. 2001. Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. Marine Biology. 139, 1165–1175.

Sims, D.W., Wearmouth, V. J. Southall, E.J., Hill, J.M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G.C., Righton, D., Metcalfe, J.D., Nash, J.P., Morritt, D. 2006. Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. Journal of Animal Ecology. 75, 176-190.

Sissenwine, M.P., Bowman, E.W. 1978. An analysis of some factors affecting the catchability of fish by bottom trawls. ICNAF Fisheries Research Bulletin. 13, 81-87.

Smale, M.J. 1986b. The feeding biology of four predatory reef fishes off the south-eastern Cape coast, South Africa. South African Journal of Zoology. 21, 111-130.

Smale, M.J. 1992. Predatory fish and their prey-an overview of trophic interactions in the fish communities of the west and south coasts of South Africa. South African Journal of Marine Science. 12, 803-821.

Smith, M.M., Heemstra, P.C. (Eds.), 1986. Smith's Sea Fishes. Macmillan., Johannesburg.

Smith, R.S., Johnston, E.L., Clark, G.F. 2014. The role of habitat complexity in community development is mediated by resource availability. PLoS ONE. 9(7).

Solano-Fernández, S. 2012. Assessment of the Effectiveness of South Africa's Marine Protected Areas at Representing Icthyofaunal Communities. Environmental Conservation. 39, 259–70.

Sulikowski, J.A., Galuardi, B., Bubley, W., Furey, N.B., Driggers III, W.B., Walter, G., Ingram, J., Tsang, P.C. W. 2010. Use of satellite tags to reveal the movements of spiny dogfish *Squalus acanthias* in the western North Atlantic Ocean. Marine Ecology Progress Series. 418, 249-254.

Stamps, J.A. 1999. Dominance and territoriality, in: Adams, N.J., Slotow, R.H. (Eds.), Proceedings of the 22nd International Ornithology Congress, Durban, pp. 1592-1605.

Stander, G.H., Nepgen, C.S. 1968. Some facts about linefish-with special reference to False Bay. South African Shipping News and Fishing Industry Review. 33, 108-111.

Starck, W.A. II., Davis, W.P. 1966. Night habits of fishes of Alligator Reef, Florida. Ichthyologia. 38, 313-356.

Stephens, D.W., Krebs, J.R. 1986. Foraging theory. Princeton, Princeton University Press., USA.

Stockwell, J.D., Hrabik, T.R. Jensen, O.P., Yule, D.L., Balge, M. 2010. Empirical evaluation of predator-driven diel vertical migration in Lake Superior. Canadian Journal of Fisheries and Aquatic Science. 67, 473-485.

Svane, I., Barnett, J. 2008. The occurrence of benthic scavengers and their consumption at tuna farms off Port Lincoln, South Australia. Journal of Experimental Marine Biology and Ecology. 363, 110-117.

Svane, I., Roberts, S., Saunders, T. 2008. Fate and consumption of discarded by-catch in the Spencer Gulf prawn fishery, South Australia. Fisheries Research. 90, 158-169.

Swart V.P. and Largier J.L. 1987. Thermal structure of Agulhas Bank water, in: Payne A.I.L., Gulland J.A., Brink K.H. (Eds.), The Benguela and Comparable Ecosystems. South African Journal of Marine Science, pp. 243-253.

Thompson, A.A., Mapstone, B.D. 1997. Observer effects and training in underwater visual surveys of reef fishes. Marine Ecology Progress Series. 154, 53-63.

Thresher, R.E., Gunn, J.S. 1986. Comparative analysis of visual census techniques for highly mobile, reef associated piscivores (carangidae). Environmental Biology of Fishes. 17, 93-116.

Tong, L.J. 1978. Tagging snapper (*Pagrus auratus*) by scuba divers. New Zealand Journal of Marine and Freshwater Research. 12, 73-76.

Topping, D.T., Lowe, C.G., Caselle, J.E. 2005. Home range and habitat utilization of adult California sheephead, *Semicossyphus pulcher* (Labridae), in a temperate no-take marine reserve. Marine Biology. 147, 301-311.

Trenkel, V.M., Cotter, J. 2009. Choosing survey time series for populations as part of an ecosystem approach to fishery management. Aquatique Living Resources. 22, 121-126.

Turpie, J.K., Beckley, L.E., Katua, S.M. 2000. Biogeography and the selection of priority areas for conservation of South African coastal fishes. Biological Conservation. 92, 59-72.

Unsworth, R.K.F., Peters, J.R., McCloskey, R.M., Hinder, S.L. 2014. Optimising stereobaited underwater video for sampling fish and invertebrates in temperate coastal habitats. Estuarine, Coastal and Shelf Science. 1-7.

Van der Elst, R.P. 1990. Marine fish tagging in South Africa. American Fisheries Society Symposium Series. 7, 854-862.

Von der Emde, G., Mogdans, J., Kapoor, B.G. 2004. The Senses of Fish: Adaptations for the Reception of Natural Stimuli. Narosa Publishers, Boston.

Waldner, R.E., Robertson, D.R. 1980. Patterns of habitat partitioning by eight species of territorial Carribbean damselfishes (Pisces: Pomacentridae). Bulletin of Marine Science. 30, 171-186.

Warrant, E. 2004. Vision in the dimmest habitats on earth. Journal of comparative physiology. 190(10), 765-789.

Walsh, S.J. 1989. Diel influence on fish escapement beneath a ground fish survey trawl. ICES Council Meeting papers, pp. 22.

Watson, D.L., Harvey, E.S., Anderson, M.J., Kendrick, G.A. 2005. A comparison of temperate reef fish assemblages recorded by three underwater stereo-video techniques. Marine Biology. 148, 415-425.

Watson, D.L., Anderson, M.J., Kendrick, G.A., Nardi, K., Harvey, E.S. 2009. Effects of protection from fishing on the lengths of targeted and non-targeted fish species at Houtman Abrolhos Islands, Western Australia. Marine Ecology Progress Series. 384, 241-249.

Watson, D.L., Harvey, E.S., Fitzpatrick, B.M., Langlois, T.J., Shedrawi, G. 2010. Assessing reef fish assemblage structure: how do different stereo-video techniques compare? Marine Biology. 157, 1237-1250.

Watt-Pringle, P.A., Cowley, P.D., Götz, A. 2013. Residency and small-scale movement behaviour of three endemic sparid fishes in their shallow rocky subtidal nursery habitat, South Africa. African Zoology. 48, 30-38.

Webb, P., Wooldridge, T.H. 1990. Diel horizontal migration of Mesopodopsis slabberi (Crustacea: Mysidacea) in Algoa Bay, southern Africa. Marine Ecology Progress Series. 62, 73-77.

Werner, E.E., Mittelbach, G.G., Hall, D.J., Gilliam, J.F. 1983. Experimental tests of optimal habitat use in fish – the role of relative habitat profitability. Ecology. 64, 15251539.

Werner, K.I. 1993. Variations of sediment dynamics in Algoa Bay during the Holocene. Suid-Afrikaanse Tydskrif vir Wetenskop. 89, 187-196.

Whitfield, A.K. 1998. Biology and Ecology of Fishes in South African Estuaries. Ichthyological Monographs of Smith Institute of Ichthyology. 2, 223.

Whitmarsh, S.K., Fairweather, P.G., Huveneers, C. 2016. What is Big BRUVver up to? Methods and uses of baited underwater video. Reviews in Fish Biology and Fisheries. 1-21.

Wickham, D.A., Russel, G.M. 1974. An evaluation of mid-water artificial structures for attracting coastal pelagic fishes. Fishery Bulletin. 72, 181-191.

Widder, E.A., Robison, B.H., Reisenbichler, K.R., Haddock, S.H.D. 2005. Using red light for in situ observations of deep-sea fishes. Deep Sea Research Part I. 52, 2077-2085.

Williams, D.M.B., Sale, P.F. 1981. Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within One Tree lagoon, Great Barrier Reef. Marine Biology. 65, 245-253.

Willis, T.J, Millar, R.B., Babcock, R.C. 2003. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pargus auratus* (Sparidae) in northern New Zealand marine reserves. Journal of Applied Ecology. 40, 214-227.

Willis, T.J., Babcock, R.C. 2000. A baited underwater video system for the detection of relative density of carnivorous reef fish. Marine and Freshwater Research. 51, 755-763.

Wright, J.M. 1989. Diel variation and seasonal consistency in the fish assemblage of the non-estuarine Sulaibikhat Bay, Kuwait. Marine Biology. 102, 135-142.

Zuur, A.F., Leno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M. 2009. Mixed effects models and extensions in ecology with R. Springer, New York. ISBN 978-0-387-87458-6. URL: http://www. Link.springer.com/

Zuur, A.F., Leno, E.N., Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. Method Ecology and Evolution. 1, 3-14.

APPENDIX

Table A. Average MaxN (±SD) for each species recorded in this study.

		Shallow		Deep aphotic	
		Day	Night	Day	Night
Ariidae	*Galeichthys ater*	2.4 ± 1.7	8.3 ± 3.2	2.2 ± 1.1	5.8 ± 4.2
	Galeichthys feliceps	1	1.9 ± 1.3	1.7 ± 1.2	1.8 ± 0.8
Carangidae	*Carangid sp. 1*		8.3 ± 7.5	1	
	Seriola dumerili	1			
	Seriola lalandi	7 ± 10			1
Carcharhinidae	*Carcharhinus obscurus*		1	1 ± 0	
	Carcharhinus sp. 1			1	
Cheilodactylidae	*Cheilodactylus fasciatus*	1			
	Cheilodactylus pixi	1.9 ± 1.9	1 ± 0	1	1 ± 0
	Chirodactylus brachydactylus	2.2 ± 2.2	1		
Dasyatidae	*Dasyatis brevicaudata*	1 ± 0	1	1	1
	Dasyatis chrysonota			1 ± 0	
	Gymnura natalensis			1	
Hexanchidae	*Notorynchus cepedianus*	1			
Lamnidae	*Carcharodon carcharias*	2 ± 0.1	1 ± 0		
Merlucciidae	*Merluccius capensis*			1.5 ± 0.6	1 ± 0
Muraenidae	*Gymnothorax griseus*				1
	Gymnothorax nudivomer	1			
Myliobatidae	*Pteromylaeus bovinus*	1.3 ± 0.6			
Myxinidae	*Eptatretus hexatrema*	1	1.1 ± 0.3		1.5 ± 0.9
Octopodidae	*Octopus vulgaris*	1 ± 0	1		
Odontaspididae	*Carcharias taurus*	1 ± 0	1		1
Oplegnathidae	*Oplegnathus conwayi*	1 ± 0			
Palinuridae	*Jasus sp. 1*			4 ± 0.1	1
Rajidae	*Raja straeleni*			1	1
	Rostroraja alba	1	1	1	1.1 ± 0.4
Sciaenidae	*Argyrosomus sp. 1*	1		2 ± 1.4	1.2 ± 0.4
	Atractoscion aequidens		1	1	
Scombridae	*Sarda sp. 1*	4 ± 0.1			
Scorpaenidae	*Helicolenus dactylopterus*			1	
Scyliorhinidae	*Haploblepharus edwardsii*	1	1.3 ± 0.7	1.5 ± 0.5	1.8 ± 0.9
	Haploblepharus fuscus	1	1.1 ± 0.3		1
	Poroderma africanum	3 ± 1.3	2.4 ± 0.9	1.7 ± 0.7	1.8 ± 0.8
	Poroderma pantherinum	1.5 ± 0.7	1.8 ± 0.8	1.2 ± 0.4	1.1 ± 0.3
Serranidae	*Acanthistius sebastoides*	1.3 ± 0.5			1.3 ± 0.6
	Epinephelus marginatus	2 ± 0.8			
Sparidae	*Argyrozona argyrozona*	2.5 ± 2.1		3.7 ± 3.5	1.2 ± 0.4
	Boopsoidea inornata	43.7 ± 64.1	7.4 ± 3.1	3.9 ± 1.5	3.3 ± 1.9
	Cheimerius nufar	2.8 ± 2.4		1	
	Chrysoblephus cristiceps	2 ± 0.9			
	Chrysoblephus gibbiceps	1.2 ± 0.4		1	
	Chrysoblephus laticeps	5 ± 2.5	1.3 ± 0.5	2.9 ± 1.3	1.6 ± 0.9
	Diplodus capensis	3.4 ± 2.6	1		
	Diplodus hottentotus	1.4 ± 0.7			
	Gymnocrotaphus curvidens	1.6 ± 1.3			
	Pachymetopon aeneum	5.3 ± 4.4	1	1.2 ± 0.4	1
	Pachymetopon blochii		1	1.5 ± 1	1.5 ± 0.7
	Pagellus bellottii natalensis	1	4.2 ± 5.8		
	Petrus rupestris	1.2 ± 0.4			
	Polysteganus praeorbitalis	1.2 ± 0.4			
	Polysteganus undulosus	1	2 ± 0.1	1	
	Porcostoma dentata	1			
	Pterogymnus laniarius	10 ± 0.1	1.4 ± 0.7	7.2 ± 6.2	2.7 ± 1.7
	Rhabdosargus globiceps	1		1.3 ± 0.6	
	Rhabdosargus holubi	1.3 ± 0.7		1	
	Sarpa salpa	29.2 ± 26.7			
	Spondyliosoma emarginatum	14.4 22.8	2.6 ± 1.4	1.3 ± 0.5	2 ± 1.4
Sphyrnidae	*Sphyrna sp. 1*	1			
Squalidae	*Squalus sp. 1*	1	1.5 ± 0.9	5.2 ± 2.6	3.6 ± 2.6
Tetraodontidae	*Amblyrhynchotes honckenii*	1.7 ± 0.6		1	
	Lagocephalus sp. 1	3 ± 0.1			
Triakidae	*Mustelus mustelus*	1.1 ± 0.4	1	1	1
	Triakis megalopterus	1.4 ± 0.5	1	1	1
Triglidae	*Chelidonichthys capensis*			1	
Zeidae	*Zeus faber*	1			

Table B. Average MaxN (± SD) of the species that were responsible for the distinct assemblage sampled at *day/shallow* reefs in Algoa Bay.

		Shallow		Deep aphotic	
		Day	Night	Day	Night
Rare taxa recorded in *day/shallow* treatments					
Carangidae	*Seriola dumerili*	1			
Cheilodactylidae	*Cheilodactylus fasciatus*	1			
Hexanchidae	*Notorynchus cepedianus*	1			
Muraenidae	*Gymnothorax nudivomer*	1			
Oplegnathidae	*Oplegnathus conwayi*	1			
Sphyrnidae	*Sphyrna sp. 1*	1			
Zeidae	*Zeus faber*	1			
Largely restricted to *day/shallow*					
Sparidae	*Cheimerius nufar*	2.8 ± 2.4		1	
	Chrysoblephus gibbiceps	1.2 ± 0.4		1	
	Diplodus capensis	3.4 ± 2.6		1	
	Rhabdosargus holubi	1.3 ± 0.7	1		
Exclusively recorded in *day/shallow*					
Sparidae	*Chrysoblephus cristiceps*	2 ± 0.9			
	Diplodus hottentotus	1.4 ± 0.7			
	Gymnocrotaphus curvidens	1.6 ± 1.3			
	Petrus rupestris	1.2 ± 0.4			
	Polysteganus praeorbitalis	1.2 ± 0.4			
	Porcostoma dentata	1			
	Sarpa salpa	29.2 ± 26.7			
Scombridae	*Sarda sp. 1*	4 ± 0.7			
Serranidae	*Epinephelus marginatus*	2 ± 0.8			
Tetraodontidae	*Lagocephalus sp. 1*	3 ± 2.2			

Table C. SIMPER analysis results revealing the species responsible for characterising the rocky reef fish communities sampled for each treatment in this study. Average species abundance (Avg abund); individual contribution percentage (Contrib %); cumulative contribution percentage (Cum %) of 90-95% to the average similarity for each treatment.

		Avg abund	Contrib %	Cum contrib %
Day/shallow (avg sim: 50.51%)				
Sparidae	*Boopsoidea inornata*	5.24	23.12	23.12
Sparidae	*Chrysoblephus laticeps*	2.08	11.72	34.84
Sparidae	*Spondyliosoma emarginatum*	2.74	10.07	44.9
Sparidae	*Cheimerius nufar*	1.56	8.67	53.58
Sparidae	*Diplodus capensis*	1.63	8.48	62.06
Scyliorhinidae	*Poroderma africanum*	1.52	7.96	70.02
Sparidae	*Pachymetopon aeneum*	1.64	6.1	76.12
Scyliorhinidae	*Poroderma pantherinum*	0.91	4.23	80.35
Ariidae	*Galeichthys ater*	0.87	2.65	83
Sparidae	*Chrysoblephus gibbiceps*	0.58	1.83	84.83
Sparidae	*Polysteganus praeorbitalis*	0.54	1.61	86.44
Dasyatidae	*Dasyatis brevicaudata*	0.45	1.4	87.84
Cheilodactylidae	*Chirodactylus brachydactylus*	0.62	1.3	89.14
Sparidae	*Diplodus hottentotus*	0.53	1.24	90.38
Day/deep-aphotic (avg sim: 47.26%)				
Sparidae	*Pterogymnus laniarius*	2.4	26.82	26.82
Squalidae	*Squalus sp. 1*	1.8	20.2	47.02
Sparidae	*Argyrozona argyrozona*	1.45	13.04	60.06
Ariidae	*Galeichthys ater*	1.12	10.43	70.49
Scyliorhinidae	*Poroderma africanum*	0.86	7.19	77.67
Scyliorhinidae	*Haploblepharus edwardsii*	0.77	5.86	83.53
Sparidae	*Chrysoblephus laticeps*	0.68	2.6	86.13
Scyliorhinidae	*Poroderma pantherinum*	0.45	1.97	88.11
Sparidae	*Boopsoidea inornata*	0.61	1.83	89.94
Sciaenidae	*Argyrosomus sp. 1*	0.43	1.8	91.73
Night/shallow (avg sim: 64.45%)				
Ariidae	*Galeichthys ater*	2.81	22.45	22.45
Sparidae	*Boopsoidea inornata*	2.66	21.86	44.31
Sparidae	*Spondyliosoma emarginatum*	1.56	12.35	56.65
Scyliorhinidae	*Poroderma africanum*	1.46	11.33	67.98
Scyliorhinidae	*Poroderma pantherinum*	1.19	8.69	76.67
Sparidae	*Pagellus bellottii natalensis*	1.26	5.76	82.43
Scyliorhinidae	*Haploblepharus edwardsii*	0.86	5.29	87.72
Squalidae	*Squalus sp. 1*	0.71	3.2	90.92
Night/deep-aphotic (avg sim: 54.20%)				
Ariidae	*Galeichthys ater*	2.14	22.92	22.92
Squalidae	*Squalus sp. 1*	1.78	21.54	44.46
Scyliorhinidae	*Haploblepharus edwardsii*	1.23	15.36	59.82
Sparidae	*Pterogymnus laniarius*	1.35	13.66	73.49
Scyliorhinidae	*Poroderma africanum*	0.83	6.07	79.55
Myxinidae	*Eptatretus hexatrema*	0.71	5.59	85.14
Sparidae	*Argyrozona argyrozona*	0.58	3.83	88.97

Sparidae	*Boopsoidea inornata*	0.71	2.85	91.82