EARLY STAGE ICHTHYOFAUNA FROM SHALLOW WATER HABITATS OF THE ANGOLA-BENGUELA FRONTAL ZONE

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Matthew William Farthing

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ABSTRACT

Early stage fishes (larvae and early juveniles) were collected from an array of shallow water (±1.5m) habitats on the warm-temperate southern Angolan coastline between June 2014 and June 2015. This study, the first assessment of the early stages of coastal fishes in Angola, provides important new understanding of non-estuarine shallow water nursery habitat use by coastal fishes from the region. In total, 51 species from 18 teleost families were observed. The exposed surf zone was dominated by postflexion larvae, while the moderately exposed beach and sheltered bay were dominated by early juveniles. Both fish density and diversity peaked in the wet season (Feb – Apr 2015) for all habitats, attributed to the influx of summer spawning species. *Diplodus sargus* dominated catches from the exposed surf zone, and the timing of observations supports the growing consensus that sparid spawning is dictated by temperature, not season. The similitude of the observed species to those observed in warm temperate South Africa highlights the historical connection of the warm-temperate study area with warm-temperate South Africa, prior to the formation of the Benguela Current as a vicariant barrier. The classification of the study assemblage into established estuarine utilization categories showed that the surf zone hosted more exclusively marine species than comparable surf zones in South Africa, attributed to the absence of estuaries in southern Angola. However, the observation of the marine estuarine dependent *Mugil cephalus* in this study area devoid of estuaries suggests that estuarine dependency may be regionally specific for some taxa. It appears that the warm, sheltered, nutrient rich waters of Tombua Bay provide typically estuarine associated taxa with a suitable alternative, non-estuarine nursery habitat. This study provides evidence that the importance of estuaries as critical nursery habitats has been overemphasized for some warm-temperate coastal fishes. However, the absence of other marine estuarine dependent species from the study area suggests that some warm-temperate taxa do intrinsically rely on estuarine function for survival.

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ABFZ	Angola Benguela Frontal Zone.
ANOSIM	Analysis of Similarity.
ATC	Automatic Temperature Compensation.
BL	Body Length.
CPUE	Catch Per Unit Effort.
EJH	Effective Juvenile Habitat.
EMS	Exclusively Marine Species.
HOBO	Brand of data logger, not an abbreviation.
IFAD	International Fund for Agricultural Development.
KWANOVA	Kruskal Wallis Analysis of Variance.
MED	Marine Estuarine Dependent.
MEO	Marine Estuarine Opportunist.
MES	Marine Estuarine Stragglers.
MLR	Maximum Likelihood Ratio.
MWU	Mann-Whitney U test.
NL	Notochord Length.
OB	Outside Bay.
PC	Principal Component.
PCA	Principal Component Analysis.
PRIMER	Statistical software package, not an abbreviation.
RSA	Republic of South Africa.
SAFER	Southern Angolan Fisheries and Ecological Research.
SB	Sheltered Bay.
SIMPER	Similarity Percentage.
SL	Standard Length.
SPRO	Spearman Rank Order Correlation.
SWA	South-Western Australia.
SZ	Surf Zone.
TL	Total Length.

Chapter 1

General introduction

The complex and dynamic nature of early stage fishes has received considerable international attention (e.g. Ruple 1984, Boehlert and Mundy 1988, Olivar and Shelton 1993, Godefroid et al. 1999, Leis et al. 2002, Sato et al. 2007, Whitfield 2016), accompanied by the acknowledgement that the egg, larval and early juvenile phases deserve equal scrutiny to that of adults. Not only do these early stages differ markedly both physically and behaviourally (Leis and Rennis 1983), they also have considerably different habitat and feeding requirements (Leis and Carson-Ewart 2000). As such, the essential habitats required for their success change considerably throughout ontogeny, and therefore to effectively conserve and manage fish stocks, a succinct understanding of their entire ecology and life history is required (Leis 2006). It is therefore unsurprising that habitat use by early stage fishes has been a principal focus of ichthyoplankton research for decades (Neira and Potter 1994, Ramos et al. 2006, Aceves-Medina et al. 2008).

The identification of essential fish habitats is a priority for effective conservation (Rosenberg et al. 2000). For the early stage fishes, nursery areas constitute essential habitats, and these habitats usually differ markedly from the essential habitats of adults. The term nursery has been misappropriated through ambiguity in many studies (Beck et al. 2001). Beck et al. (2001) proposed a clarification of a true nursery, defined as a habitat that facilitates a greater than average per unit area contribution of individuals to the adult population through a combination of four factors: density, growth, survival and eventual recruitment into adult populations. Dahlgren et al. (2006) criticized the nursery role hypothesis (Beck et al. 2001), suggesting that it may overlook important habitats with low per unit area contributions to adult populations which in fact contribute more recruits overall to the adult population. Dahlgren et al. (2006) proposed the Effective Juvenile Habitat (EJH) concept be used alongside the nursery role hypothesis, to evaluate habitats that may be essential for sustaining adult populations despite low per unit area contributions. Despite the controversy over spatial scale, there appears to be consensus between both concepts over the importance of connectivity to adult populations.

The evaluation of the connectivity between juvenile and adult habitat is essential before assigning a habitat nursery importance (Beck et al. 2001, Dahlgren et al. 2006). In their review, Gillanders et al. (2003) highlighted that few studies provide actual evidence of connectivity between juvenile and adult populations, and that this should be a focus of future studies of nursery habitat. In contrast, Sheaves et al. (2006) suggest that connectivity and numbers of recruits is insufficient for measuring nursery habitat value, as number of recruits does not equate reproductive output. The quality of a habitat may affect the size and growth of individuals, and thereby affect their reproductive output in a given lifetime (Chigbu & Sibley 1994, Sedinger et al. 1995). Both the nursery role hypothesis (Beck et al. 2001) and the EJH concept (Dahlgren et al. 2006) have been criticized for the oversimplification of nursery habitat evaluation (Sheaves et al. 2006), ignoring the finer scale ecosystem processes and complexities which support early stage fishes. While there appears to be discord over the resolution at which nursery habitat evaluations should took place, there appears to be concurrence that evidence of high density, growth, feeding, survival and eventual recruitment of the early life stages indicates nursery importance.

Several habitats have been identified as nurseries for coastal fishes, including the shallow nearshore (<15m) (Beckley 1986, Pattrick and Strydom 2008, Pattrick and Strydom 2014), sub tidal bays associated with rocky shores (Strydom 2008, Strydom et al. 2014), tidal pools (Dias 2013), salt marshes (Rogers et al. 1984, Whitfield 2016), mangrove forests

(Sheridan and Hays 2003, Whitfield 2016), sea grass meadows (Heck et al. 2003), large coastal embayments (Harris and Cyrus 1997), primary surf zones (Whitfield 1989, Harris and Cyrus 1996, Strydom 2003) and of course estuaries (Kruger and Strydom 2010, Wasserman and Strydom 2011). While estuaries have enjoyed much attention, non-estuarine shallow water (±1.5m) coastal fish nurseries are poorly understood (Pattrick and Strydom 2008). Recent scrutiny of shallow water habitats has revealed that non-estuarine habitats have a higher nursery value than previously assumed (Strydom 2008, Strydom et al. 2014, Pattrick and Strydom 2014). As such, it has been suggested that non-estuarine shallow water nursery habitats have been largely overlooked and that estuaries have likely been overemphasized as critical nursery habitats as a result (Strydom 2008).

The role of estuaries as nursery habitats for marine coastal fishes around the globe is well known (Day et al. 1981, Dando 1984, Wallace et al. 1984). The shelter, favourable temperatures and high nutrient availability typical of estuaries have been highlighted as advantageous to the early development of marine ichthyofauna (Wallace et al. 1984). It is unsurprising that much effort has been made to assess the importance of this habitat to various fishes, especially considering that estuarine functionality is particularly susceptible to anthropogenic disturbance by urbanization, pollution, water abstraction and climate change (Wallace et al. 1984, Whitfield 1996, Becker et al. 2013). Seminal works have classified the dependence of various fishes on the estuarine environment into categories (Whitfield 1999) and subsequently guilds (Elliott et al. 2007, Potter et al. 2015).

Besides estuarine habitats, several global studies have recently examined the potential nursery role of surf zone environments (Godefroid et al. 1999, Beyst et al. 2001, Cowley et al. 2001, Strydom 2003, Watt-Pringle and Strydom 2003, Strydom and d'Hotman 2005, Sato et al. 2007, Able et al. 2009, Marin et al. 2009, Able et al. 2013). Surf zone ichthyoplankton communities are typically dominated by marine estuarine associated taxa, recognized in this study as either opportunistic (Marine Estuarine Opportunists: MEO) or obligate (Marine Estuarine Dependent: MED) users of estuaries (Elliott et al. 2007, Potter et al. 2015). The predominance of these taxa in surf zones is attributed to their use of the habitat as a transient route into estuaries, and thereby their accumulation while awaiting recruitment opportunities (Cowley et al. 2001, Strydom 2003, Watt-Pringle and Strydom 2003). However, a more recent study at Cape Padrone, a non-estuarine associated surf zone in warm-temperate South Africa, showed high similarity between surf zone ichthyoplankton communities, regardless of proximity to an estuary mouth. This indicates a continuity between surf zone assemblages and further highlights the potential for the surf zone to serve as a nursery habitat for estuarine associated species, even if only for an interim period (Strydom and d'Hotman 2005).

Traditionally, surf zones have only been considered to serve as a transient route between offshore/nearshore spawning grounds and estuarine nursery areas, based on the earlier assumption that the turbulent nature of this habitat is unsuitable for prolonged use by sensitive early stage fishes. However, the observation of larvae awaiting recruitment opportunity in the primary surf zone adjacent to estuary mouths suggests that this habitat may not be as unsuitable for ichthyoplankton as previously assumed (Whitfield 1989). Some workers suggest that the turbulence of this zone and the associated suspension of sediment may actually afford early stage fishes protection from piscivores (Lasiak 1986). Furthermore, the higher abundance of postflexion larvae in surf zone troughs rather than in adjacent open surf water suggests that these larvae are maintaining position and actively selecting habitats with a degree of shelter from higher current velocity (Strydom 2003, Watt-Pringle and Strydom 2003, Strydom and d'Hotman 2005). This further highlights the premise that arrival of larvae at estuaries, particularly those in the postflexion phase, is not a passive process, and that these developmental stages are capable of active habitat selection (Sale 1969, 1970, Doherty and McIlwain 1996, Stobutzki and Bellwood 1997, Dudley et al. 2000).

Coastal embayments have long been known as important nursery areas for early stage coastal fishes (Herman 1963, Beckley 1986, Jenkins 1986, Tzeng et al. 1997, Harris and Cyrus 1997, 1999, Thayer et al. 1999, Pattrick and Strydom 2008), with many species spawn in or near coastal embayments to provide the early stages with advantageous conditions for success and survival (Chute and Turner 2001). Coastal embayments, defined as large, semi-enclosed bays sheltered from prevailing wave energy, provide refuge, shelter from exposure, high food density and favourable temperatures (Bourne and Govoni 1988, Olney and Boehlert 1988, Chute and Turner 2001), similar to those of estuaries. It is therefore no surprise that they are typically dominated by estuarine associated early stage fishes (e.g. Harris and Cyrus 1997, 1999). In arid South Western Australia where estuaries are scarce, the large area of sheltered, coastal embayments has been identified as an alternative, non-estuarine nursery for taxa that are typically estuarine associated (Potter at al. 1990). It therefore appears that coastal embayments may serve as an alternative, non-estuarine nursery for fishes that are typically estuarine associated in other arid regions of the world.

The arid southern Angolan coast is one of two warm-temperate marine ecoregions in southern Africa, the other of which is on South Africa’s east coast. The historic connection of these two warm-temperate regions prior to the formation of the cold water Benguela Current as a vicariant barrier (van Zinderen Bakker 1975) has resulted in a suite of common and similar species present in both habitats. These regions have been isolated for approximately two million years, and subsequent speciation is evident in several historically connected populations (Henriques et al. 2014, Potts et al. 2014). The formation of the Benguela Current significantly altered the southern Angola coastline during the formation of the Namib Desert approximately two million years ago (van Zinderen Bakker 1975).

As a result, these two coastal regions show significantly different physical and topographic features. In South Africa, the temperate coastline is characterized by a high energy, rugged coast endowed with 133 functional estuaries. The low energy coast of southern Angola is characterized by several large coastal embayments (Baia dos Tigres, Tombua Bay, Namibe Bay), devoid of all but one functional estuary (Cunene River). The presence of similar and common species from marine estuarine associated guilds in southern Angola begs the questions: what habitats serve as nursery areas for coastal fishes in southern Angola; and are there alternative, non-estuarine nurseries for marine estuarine associated taxa? In South Western Australia (SWA), the large expanse of sheltered coastal embayments has been identified as an alternative nursery area for typically estuarine dependent taxa, as they provide similar advantageous conditions such as shelter, high temperatures and high nutrient availability (Potter et al. 1990). In South Africa, the high energy, exposed eastern coastline is not endowed with such large inshore habitats, but instead has numerous sheltered estuaries. While Strydom (2008) suggests that South Africa does have alternative, non-estuarine nursery habitats on the exposed coast (e.g. sub tidal bays on rocky shores), investigations of their use by early stage fishes is lacking.

While there are many studies of early stage coastal fishes in regions with many estuaries (e.g. Harris and Cyrus 1996, Cowley et al. 2001, Strydom 2003, Sato et al. 2007, Able et al. 2010), there is a lack of work in arid regions such as southern Angola where estuaries are limited. It is critical to understand which non-estuarine habitats serve as nurseries for warm-temperate fishes if effective conservation and management of important fishery species is to be possible. Furthermore, the biogeography of the two warm-temperate ecoregions in southern Africa has provided us with a unique opportunity to investigate the development of estuarine residency in warm-temperate coastal fishes, and to theorize the adaptability of southern African marine estuary associated species to the forecasted loss of estuarine function due to anthropogenic climate change and habitat degradation (James et al. 2007).

Thesis outline

The principle aim of this thesis is to provide the essential first assessment of the coastal early stage fish community present in shallow water (±1.5m) habitats along the southern Angolan coast. Furthermore, this study endeavours to identify the nursery habitats of species that are considered to be estuary dependent. This study will provide essential baseline information on the early development and habitat utilization of important fishery species, and could provide information on the potential adaptability of other warm-temperate ichthyofaunal assemblages to the loss of estuarine habitat.

To achieve these aims, this study is divided into two data orientated chapters. Warm-temperate surf zones in South Africa are dominated by estuarine dependent ichthyoplankton, even in surf zones independent of estuaries. This suggests that this habitat is more suitable as a nursery habitat for this group than currently recognized. Based on this, Chapter 2 is an assessment of the southern Angolan surf zone early stage fish assemblage, conducted to determine habitat utilization and the overall estuarine dependency of similar taxa in the community. The relative estuarine dependency of the early stage fish community is compared with similar studies from warm-temperate South Africa to infer the response of the assemblage to the loss of functional estuaries. The reproductive seasonality of Sparidae is discussed, as are the concepts of estuarine dependency and habitat suitability.

Chapter 3 is a similar larval and early juvenile assessment of a nearby coastal embayment, in conjunction with a comparison of the three contrasting shallow water habitats in the region. Shelter from exposure is known as a principal component of nursery areas for coastal early stage fishes (Strydom 2008, Pattrick and Strydom 2014, Strydom et al. 2014), so habitats were selected across an exposure gradient. The use of different habitats by early stage fishes is discussed in the context of physical environment and ontogenetic shifts in diet, as is the use of alternative non-estuarine nursery habitats by species whose early life stages are typically associated with estuarine habitats.

Chapter 4 concludes the thesis, synthesizing the findings of both data orientated chapters. The practical implications of this new understanding of Angola's ichthyofauna are discussed. The use of the southern Angolan coastline as a natural laboratory for the investigation of biogeographic and climate change topics is discussed, and future research priorities are suggested.

Study area

The study area was confined to the shallow water habitats (wading depths ± 1.5 m) of the primary surf zone along the southern Angola coastline in the vicinity of Flamingo Lodge (S 15.57005° E 12.01875°), located between the coastal port towns of Tombua and Namibe (Figure 1.1). The inshore littoral zone is characterized by sandy beach with intermittent smooth sandstone reef. The relative proportion of sandy beach and primary reef changes seasonally, with the dry season's rough surf conditions scouring sandy beds and exposing reef (Richardson 2010, Winkler 2013). In contrast, the wet season's calm surf conditions generally inundate reef with sand, reducing the availability of this habitat (Richardson 2010, Winkler 2013). These seasonal changes are attributed to the seasonal shifts of the Angola Benguela Frontal Zone (ABFZ). During the dry season, the increased velocity of the Benguela Current pushes the ABFZ north of the study area (Meeuwis and Lutjeharms 1990), allowing the Benguela Current to dominate. During the wet season, the Angola current increases in velocity, pushing the ABFZ south of the study area (Meeuwis and Lutjeharms 1990), resulting in the Angola Current dominating the study area.

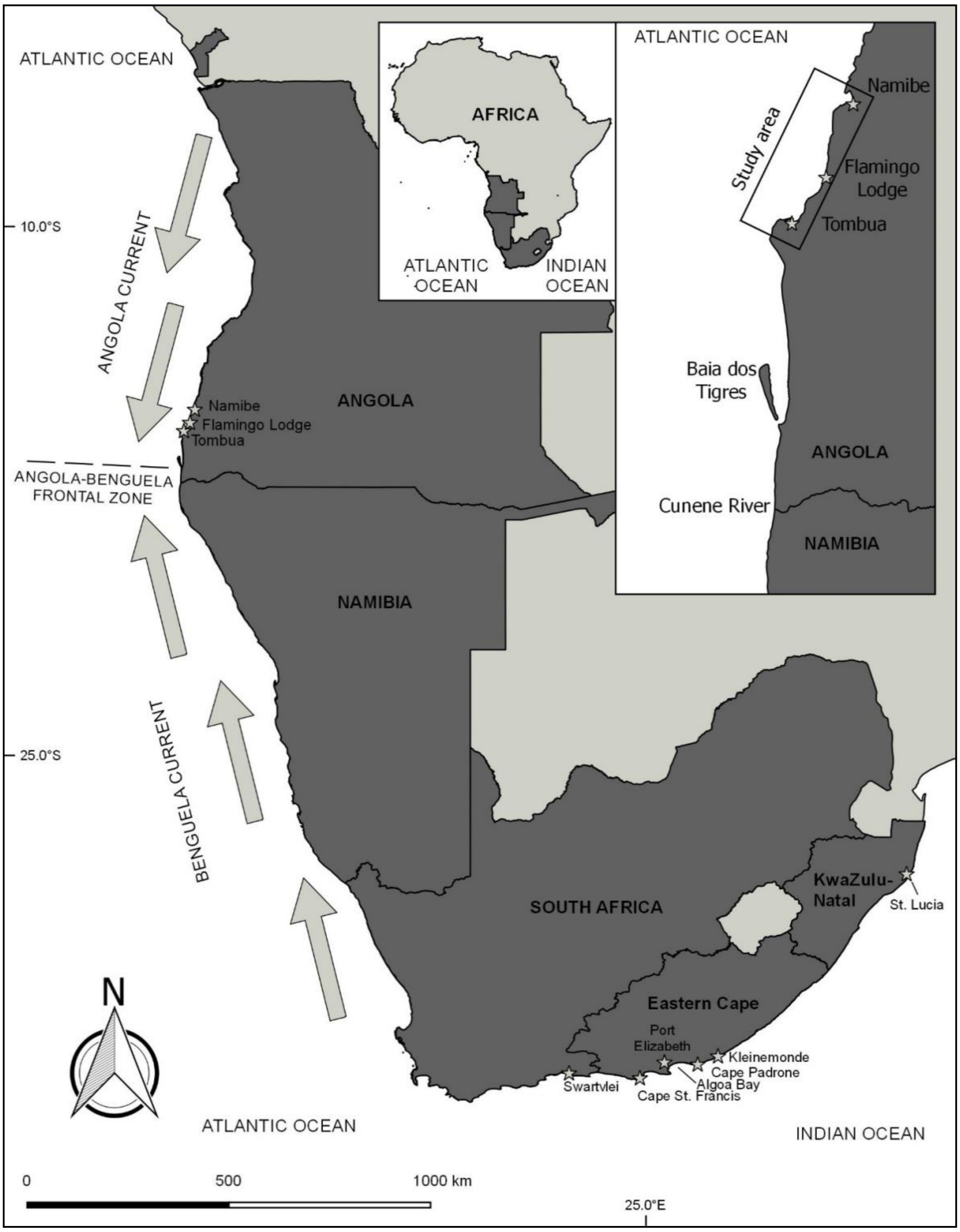

Figure 1.1: Map of southern Africa showing important oceanography and relative position of regions discussed throughout this thesis.

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Chapter 2

The composition and seasonality of the larval and early juvenile fishes of a southern Angolan surf zone

Introduction

The utilization of the primary surf zone by early stage fishes has been documented globally by several workers (e.g. Senta and Kinoshita 1985, Lasiak 1986, Harris and Cyrus 1996, Beyst et al. 1999, Godefroid et al. 2001, Nanami and Endo 2007, Sato et al. 2007, Jarrin et al. 2009). The subsequent paradigm shift in the traditional assumption that this turbulent environment is unsuitable for sensitive developmental stages has prompted many assessments of the early stage fishes associated with this habitat (Ruple 1984, Senta and Kinoshita 1985, Lasiak 1986, Whitfield 1989, Yang and Senta 1993, Harris and Cyrus 1996, Godefroid et al. 1999, Beyst et al. 2001, Cowley et al. 2001, Watt-Pringle and Strydom 2003, Marin et al. 2009, Able et al. 2010) and investigations into the true nursery role of this habitat (Lasiak 1986, Whitfield 1989, Strydom 2008, De Raedemaecker et al. 2012). Beck et al. (2001) proposed that the habitats utilized by early stage ichthyoplankton contribute disproportionately per unit area to adult populations through varying combinations of four factors: density, survival, growth and recruitment into adult populations. Dahlgren et al. (2006) later proposed the Effective Juvenile Habitat concept, which focussed on overall recruitment from a given habitat, and not recruitment per unit area. Both works were later criticized for oversimplifying the evaluation process (Sheaves et al. 2006) on the basis that complex, fine scale ecosystem processes which supported early stage fishes were overlooked. While there has been debate over the scale and resolution at which nursery habitats are to be evaluated, there appears to be general consensus that they must support high density, feeding, growth and make an above average recruitment contribution to the adult population (Beck et al. 2001, Dahlgren et al. 2003, Sheaves et al. 2006).

As the surf zone habitat has long been known to serve as an essential pathway for the recruitment of marine ichthyoplankton into estuarine nursery habitats (Boehlert and Mundy 1988), most studies have focused on surf zones immediately adjacent to estuaries (e.g. Cowley et al. 2001, Strydom 2003, Watt-Pringle and Strydom 2003), and have revealed a distinct larval and early juvenile fish community utilizing this environment as a nursery prior to recruitment into estuaries, composed principally of marine estuarine associated taxa (Strydom 2003). Marine estuarine dependent species (MED *per* Potter et al. 2015; Category IIa *per* Whitfield 1994) such as *Rhabdosargus holubi* accumulate in surf zones adjacent to closed estuaries in an endeavour to recruit during over wash events (Cowley et al. 2001), but also accumulate in the shallow waters (±1.5m) of non-estuary associated surf zones (Strydom and d'Hotman 2005). Recent work in warm-temperate South Africa observed a distinct, estuarine dependent early stage fish community utilizing surf zones in both estuary associated and non-estuary associated surf zones, with similar community structure regardless of proximity to estuaries (Watt-Pringle and Strydom 2003). While this certainly suggests a high level of continuity throughout surf zones, it raises the question of just how reliant estuarine dependent species are on the estuarine environment. The presence of *R. holubi* and *Mugil cephalus*, both considered to be strictly estuarine dependent (Potter et al. 2015; Whitfield 1994), in non-estuarine associated surf zones (Strydom and d'Hotman 2005) suggests that these species may be able to utilize alternative, non-estuarine nursery areas. When compared to South Africa, the low number of species strictly dependent on estuaries in South Western Australia (SWA) has been attributed to availability of alternative nursery habitats, such as coastal embayments and sheltered inshore waters (Potter et al. 1990). *Mugil cephalus* is the only SWA species to be classified as strictly dependent on estuaries, whereas South Africa has several strictly estuarine dependent species

(Potter et al. 1990, Whitfield 1994). This is attributed to South Africa's high energy surf zone and relatively low number of large embayments and inshore areas (Potter et al. 1990). In South Africa, the current degradation of estuaries by pollution and water abstraction (Whitfield, 1999), coupled with the forecasted loss of estuarine function due to anthropogenic climate change may severely limit the availability of this important nursery habitat to important coastal species in the future (James et al. 2007). Understanding the adaptability and potential change to faunal assemblages in response to the loss of estuaries is therefore critical for conservation efforts.

In southern Africa, there are two major warm-temperate marine ecoregions, one on the east coast of South Africa (RSA), the other on the southern Angolan coast. The similarity of the warm-temperate ichthyofauna in these regions is a consequence of their historical connection, prior to the formation of the cold Benguela Current. Not only did the Benguela Current form a vicariant barrier between these two warm-temperate populations, it also had a major influence on the terrestrial climate along the west coast of RSA. Benguela Current associated aridification drastically reduced rainfall, and thereby affected the functionality of estuaries in what is now the Namib Desert. Consequently, the major difference between these two warm-temperate ecoregions is the availability of estuaries. The warm-temperate east coast of RSA has 117 functional estuaries, while southern Angola only has one, namely the Cunene Estuary. While the Cunene Estuary is larger than any estuary in South Africa, its distance from the study area (150 km; Figure 2.1) suggests that it is unlikely to affect the early stage fish assemblage observed in this study.

Southern Angola is characterized by a lower energy surf zone than RSA. Satellite derived wave height data show a general increasing trend in significant wave height along a southerly satellite track down the west coast of southern Africa (Gründlinch 1994). Southern Angola is endowed with two large and several smaller coastal embayments, while RSA typically lacks these environments. This area lies within the ABFZ, an area of both climate change (Hobday and Pecl 2014) and biodiversity importance (Scales et al. 2014). There has been no effort to investigate the early stages of coastal fishes in Angola; the little ichthyoplankton research from the region is limited to investigations of offshore pelagic larvae (Afonso 2000, Ekau et al. 2001, Verheye and Ekau 2005a, b). As such, this chapter serves to address the dearth of information on early stage fishes from this climate change and biodiversity hotspot, to contribute to the understanding of warm-temperate ichthyoplankton in general and to gain insight into the possible response of coastal fish assemblages to the loss of permanent estuary habitats.

Aims

1. To describe the seasonal composition and habitat use of the early stage fish assemblage in a surf zone in southern Angola.
2. To assess the nursery value of the southern Angolan surf zone to early stage fishes found in this habitat.

It is hypothesized that the absence of estuaries in the study area would preclude taxa that are typically classified as marine estuarine dependent, and that the ichthyoplankton community in southern Angolan surf zones has evolved to be more marine centric than that of warm-temperate RSA. It is further hypothesized that taxa classified as marine estuarine stragglers and marine estuarine opportunists may have adapted to utilize alternative, non-estuarine nursery habitats.

Methods and Materials

Study area

Larval and early juvenile fishes were collected from the surf zone of a 30 km stretch of coastline centred at Flamingo Lodge in southern Angola (Figure 2.1). This study area lies approximately in the middle between the coastal port towns of Namibe (S 15.192361° E 12.147714°) and Tombua (S 15.802265° E 11.848411°). The study area coastline is characterized by long exposed beaches with intermittent sandstone reef, with shallow water trough habitats present along sandy beaches for much of the year (Richardson 2010, Winkler 2013). Wave action is continuous, but surf energy varies seasonally, as does the relative proportion of primary reef habitat, which is periodically inundated by sand (Winkler 2013).

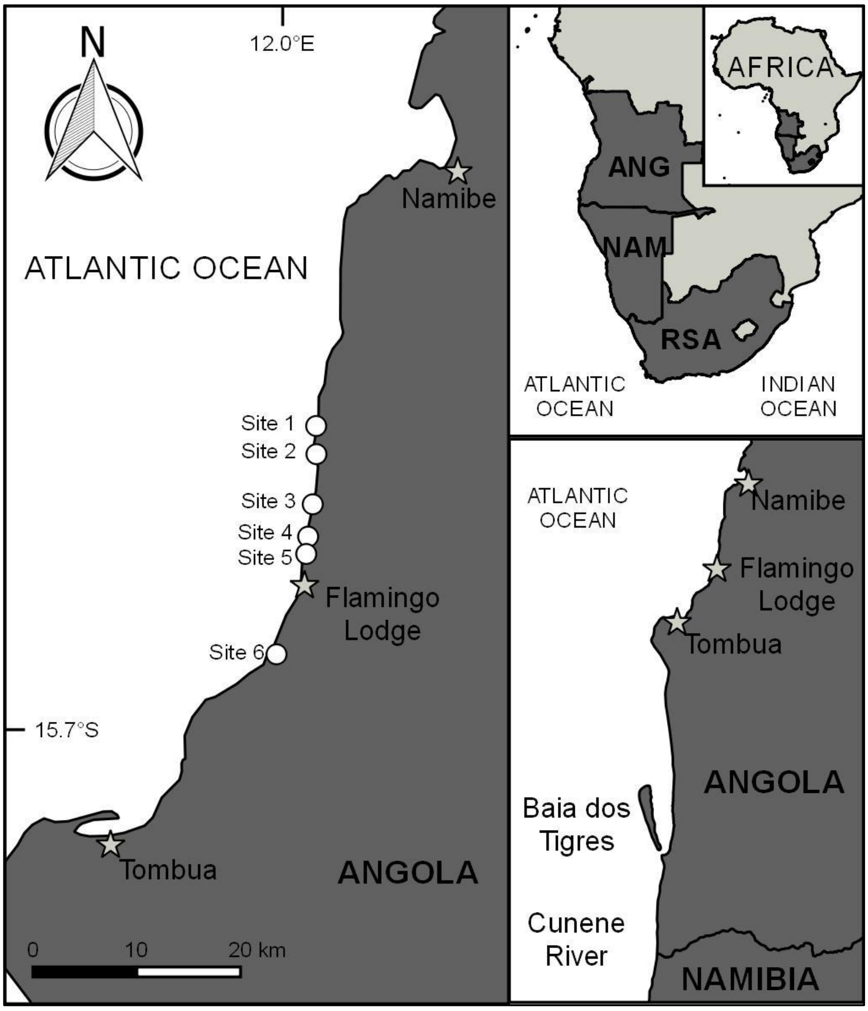

Figure 2.1: Map showing the relative position of the study area and sampling sites along the Angolan coastline.

Field sampling and laboratory analyses

Six sampling sites were chosen during the first month of the study, and monthly samples were conducted at these sites for 13 months. Sampling was restricted to daylight hours within a two-day window either side of spring low tide to allow for selection of best weather and surf energy conditions. Sampling began two hours before low tide, and was generally completed within four hours. When the surf zone was particularly difficult to sample, remaining sites were completed on the same tidal cycle on the following day. Three sites were chosen for each habitat type, namely sandy, defined as exclusively sandy troughs, and mixed shore, defined as sand stone reef interspersed with sandy pockets. As this study was conducted over an entire year, it was occasionally necessary to deviate sampling from the exact GPS location of previous samples due to habitat change. However, sampling was never conducted further than 1 km from the originally selected site.

The field sampling methodology duplicates that used by Strydom (2003) for the sake of comparability between the two warm-temperate ecoregions in southern Africa. Samples were collected sequentially from selected sites spaced approximately equidistant along the study area using a 4.5 x 1.5 m modified beach seine net (500 µm) operated by two people. The seine was pulled into the current for 25 m alongshore, in water that approximated the height of the net (1.5 m) depending on wave action. Operators endeavoured to keep the seine submerged at all times for standardization. Early stage fishes were concentrated into a cod-end (500 µm) using a wash bottle and 25 l bucket, which facilitated easy removal. Samples were fixed using a 10% formalin and seawater solution. Seine net pulls were triplicated at each site, which resulted in a total of 75 m sampled per site per month. A total of 216 individual replicate pulls were performed during the study.

Temperature was recorded at each site using a standard mercury thermometer, turbidity was measured using a Hanna (HI93703) portable turbidity meter, and salinity was recorded using a handheld ATC refractometer. Water samples for turbidity and salinity were taken from the middle of the water column at the same wading depth (± 1.5m) as the seine net was pulled. During the course of the study, uncertainty around instrument accuracy potentially affected the integrity of several months of temperature data. To address this, temperature logger data from the SAFER project monitoring array (Figure 2.2) was substituted for the entire study. When comparing the unaffected in situ hand-held thermometer readings with those from HOBO loggers from the inshore zone (± 7 m depth), temperatures were accurately reflected. The data from several inshore HOBO loggers within the 30 km study area was available and the temperature at the exact time of sampling from the nearest logger to each site was utilized.

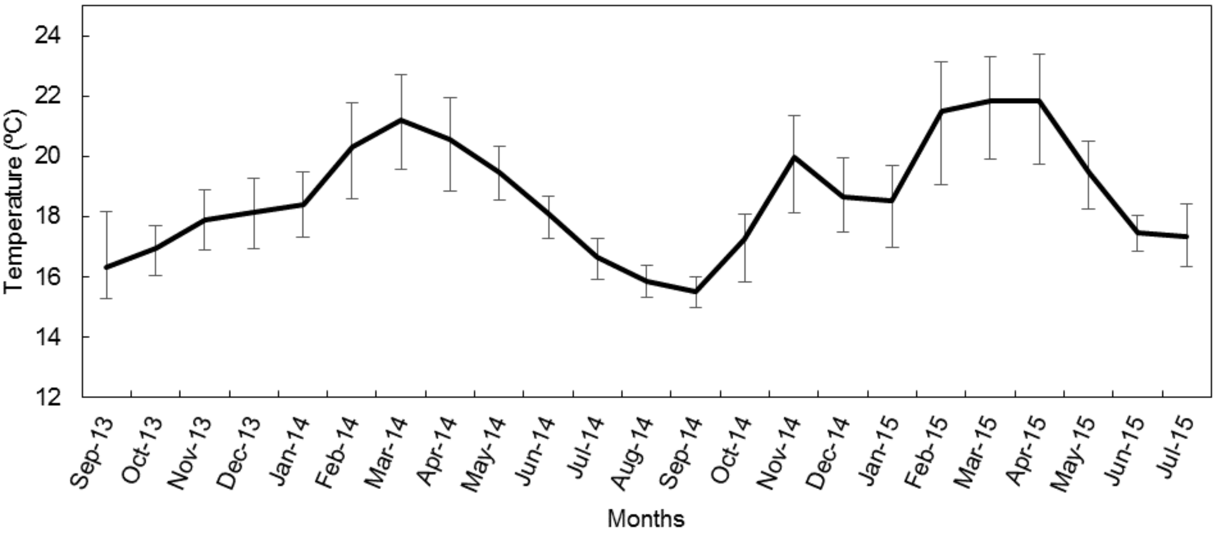

Figure 2.2: Mean monthly temperature from all loggers within the Southern Angolan Fisheries and Ecological Research (SAFER) project monitoring array for each month of the project duration.

Samples were sorted in a laboratory and identified to the lowest possible taxon using available information (Olivar and Fortuño 1991, Neira et al. 1998, Leis and Carson-Ewart 2000, Heemstra and Heemstra 2004, Richards 2006). The lack of available ichthyological information from Angola was particularly troublesome, and many species encountered in this study remain only classified to family level. There is a dearth of information on the meristic and morphometric characteristics of even adult fishes from Angola, limited to a single FAO (1986) identification guide. Many identifications were made using information available from online repositories, including FishBase (Froese and Pauly 2016) and Marine Fish Eggs and Larvae (Connell 2012). Taxa identified to species were classified into guilds based on estuarine association, in concordance with Potter et al. (2015), to assess the overall estuarine association of the community. Species lists from comparable warm-temperate studies were also classified into the same guilds to provide comparative reference, and the percentage contribution of each guild was compared between studies. All terminology pertaining to developmental stages follows Neira et al. (1998). Fish length was recorded as Body Length (BL), which comprised the Notochord Length (NL) for preflexion and flexion larvae, and Standard Length (SL) for post flexion larvae and early juveniles (Neira et al. 1998). The term “larvae/larva” includes preflexion, flexion and postflexion stages, while the term “early stage fishes” refers to both larval and early juvenile fishes. Body length of preflexion, flexion and postflexion larvae was recorded using an eyepiece micrometer, while the BL of early juveniles was measured using hand callipers.

Data analyses

As the entire 13-month sample set does not represent an ecologically meaningful unit, distinction must be made between the entire data set and the seasonal data subset. When referring to seasonal data, only samples from July, August and September (2014) and February, March and April (2015) were utilized. These months represent the dry and wet seasons respectively, and all seasonal comparisons and multivariate community analyses will refer to this subset of data exclusively. Habitat comparisons and basic CPUE/environmental correlations will utilize the full 13-month data set.

Data were tested for normality using Levene’s test and a Kolmogorov–Smirnoff test. All data failed to meet the assumptions of parametric tests, so non-parametric statistics were utilized. Differences in mean temperature and turbidity among sampling sites were tested using a Kruskal–Wallis Analysis of Variance (KWANOVA). Differences in mean temperature and turbidity between habitat types were assessed using a Mann–Whitney U (MWU) test. Seasonal differences in the environmental variables were also tested using a MWU test. Species were considered dominant if they represented more than 1% of the total catch, and only these species are consistently reported on throughout this study. A MWU test was used to test for differences in mean body length between habitat types. Dominant species were only considered for this test if more than 10 individuals were recorded in each habitat type, and if the total catch of that species was greater than 30. Differences in the mean Catch Per Unit Effort (CPUE) of all species from each sampling site were tested using a KWANOVA, while differences between the mean CPUE (all species) of each habitat type were assessed using a MWU test. Differences in the monthly mean CPUE (all species) were assessed using a KWANOVA, while the differences between mean CPUE (all species) of each season were tested using a MWU test. Species diversity was calculated using the Shannon–Wiener Diversity Index, while species richness was calculated using Margalef's Species Richness Index. Indices were calculated, for the entire 13-month sampling period, each month and each season.

Relationships between the environmental variables and CPUE were determined using a Spearman Rank Order (SPRO) correlation and a Multiple Linear Regression (MLR) analysis. Both the SPRO and MLR were utilized to assess both the entire and seasonal datasets. The relationship between the environmental variables and total CPUE of each season was further explored using a Principal Component Analysis (PCA), which included temperature, turbidity and total CPUE from the seasonal data set. A community analysis approach (Clarke 1993) was employed to assess communities across both seasons and habitats. Multivariate analyses were performed using PRIMER V6 statistical software package (Clarke and Warwick 2001). Bray–Curtis similarity matrices were generated for biological data, while a Euclidean distance similarity matrix was utilized for environmental data. The biological data set was log-transformed or transformed to binomial presence/absence. Environmental data were square-root transformed and then normalized prior to analysis. Group average hierarchical clustering was used to assess groups in dendrogram format, while ANOSIM was used to test for differences between groups. Relative contributions to similarity or dissimilarity between groups were determined using SIMPER. Multivariate environmental matching was employed to assess the relatedness of change in the environmental and biological datasets. The relationship between environmental and biological similarity matrices was assessed using RELATE. BIO-ENV was used to determine which environmental variable best explained this relationship.

Results

Environmental variability

Temperature ranged from 15.6 °C (September 2014) to 23.6 °C (February and March 2015), with the lowest and highest mean monthly temperatures recorded in June 2014 ($\bar{x}$ = 16.9 °C; Range = 16.5 – 17.6 °C) and March 2015 ($\bar{x}$ = 23.3 °C; Range = 23 – 26 °C) respectively (Table 2.1). Turbidity ranged from 0.2 NTU (June 2014) to 39.6 NTU (May 2015), with the lowest and highest mean monthly turbidities recorded in September 2014 and May 2015 respectively. Note the missing environmental data for site 5 in October 2014, sites 4 and 5 in November 2014, site 6 in December 2014 and sites 2 and 3 in January 2015 (Table 2.1). These omissions represent unsuccessful biological sampling attempts due to adverse environmental conditions.

There was no significant difference ($P<0.05$) in mean temperature ($H = 1.61$; $P = 0.9$) or turbidity ($H = 6.51$; $P = 0.26$) at any of the six sampling sites during the 13-month sampling period. There was no significant difference in mean temperature ($P = 0.68$) or turbidity ($P = 0.23$) between the two habitat types during the 13-month sampling period. When extracting seasonal data, the mean temperature (P<0.01) and turbidity (P<0.01) was significantly higher during the wet season (February, March and April 2015) (Table 2.1).

Table 2.1*:* Environmental parameters recorded at each sampling site during each monthly sampling trip from June 2014 to July 2015.

			Monthly sampling trip												
Parameter	Habitat	Site	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Temperature (°C)	Mixed	1	16.6	17.5	16.0	15.6	20.0	20.5	18.7	19.4	23.6	23.0	22.0	19.6	18.4
		2	16.5	17.3	15.9	15.8	19.7	19.8	18.2	-	23.0	23.0	22.3	19.7	17.9
		4	17.2	16.8	16.0	15.6	19.6	-	18.1	17.8	22.7	23.6	21.8	19.2	19.3
	Sandy	3	16.5	17.3	15.9	15.8	19.7	19.8	18.2	-	23.0	23.0	22.3	19.7	17.9
		5	17.2	16.8	16.0	15.6	-	-	18.1	17.8	22.7	23.6	21.8	19.2	19.3
		6	17.6	16.8	15.7	15.7	19.4	19.3	-	18.1	22.6	23.5	22.2	18.8	19.3
		Mean	**16.9**	**17.1**	**15.9**	**15.7**	**19.7**	**19.8**	**18.3**	**18.3**	**22.9**	**23.3**	**22.1**	**19.3**	**18.7**
Turbidity (NTU)	Mixed	1	1.8	1.4	7.7	0.3	5.8	5.4	3.7	5.4	10.5	8.6	5.7	6.8	5.9
		2	1.0	1.6	3.3	0.4	5.0	2.6	1.8	-	4.5	6.8	5.7	7.3	11.2
		4	2.1	3.2	6.3	2.0	1.2	-	2.2	13.4	5.2	6.9	30.3	39.6	3.6
	Sandy	3	2.0	2.4	4.2	0.2	1.6	2.9	2.3	-	7.9	6.1	5.0	16.3	3.2
		5	1.3	3.7	1.0	1.1	-	-	1.9	13.3	5.4	6.3	21.0	10.4	4.4
		6	3.4	4.0	0.4	0.8	0.9	2.3	-	7.4	10.6	8.9	14.6	8.6	4.5
		Mean	**1.9**	**2.7**	**3.8**	**0.8**	**2.9**	**3.3**	**2.4**	**9.9**	**7.3**	**7.3**	**13.7**	**14.8**	**5.5**
Salinity	Mixed	1	35.0	35.0	36.0	34.0	34.0	34.0	34.0	35.0	35.0	34.0	34.0	35.0	34.0
		2	35.0	35.0	36.0	34.0	34.0	34.3	34.0	-	35.0	34.0	34.0	35.0	34.0
		4	35.0	35.0	34.0	34.0	34.0	-	34.0	35.0	35.0	34.0	34.0	35.0	34.0
	Sandy	3	34.3	35.0	35.0	34.0	34.0	34.5	34.5	-	35.0	34.0	34.0	35.0	34.0
		5	35.0	35.0	34.0	34.0	-	-	34.0	35.0	35.0	34.0	34.0	35.0	34.0
		6	35.0	35.0	35.0	34.0	34.0	34.5	-	35.0	35.0	34.0	34.0	35.0	34.0
		Mean	**34.9**	**35.0**	**35.0**	**34.0**	**34.0**	**34.3**	**34.1**	**35.0**	**35.0**	**34.0**	**34.0**	**35.0**	**34.0**

Species composition

A total catch of 1875 larval and early juvenile fishes was recorded, composed of 13 families, 24 species and one unclassified specimen (Table 2.2). The catch was dominated (>1%) by six species from five families, namely the Sparidae (76.9%), Clupeidae (13.3%), Tripterygiidae (3.3%), Haemulidae (1.9%) and Mugilidae (1.0%). All other families contributed less than 1% of the total catch. Although the Sparidae were dominant, 76% of the total catch (all species) was attributed to *Diplodus sargus* (MEO) alone, with the remaining Sparidae contributing less than 1%. The other taxa were less common; *Sardinops sagax* (MS) and *Sardinella aurita* (MS) contributed 7.5% and 5.8% respectively, followed by Tripterygiidae 1 (3.3%; M), *Pomadasys rogerii* (1.9%; MEO), and lastly *Liza* spp. (1%; MEO). Species composition differed between habitats. Mixed shore habitats (N = 1780) were dominated (>1%) by 5 species: *D. sargus* (79.6%), *S. sagax* (7.1%), *S. aurita* (5.1%), Tripterygiidae 1 (34%) and *P. rogerii* (1.9%). Each of the 17 species observed at the sandy sites (N = 95) represented greater than 1% of the catch, but catches were notably dominated by *S. aurita* (20%), *S. sagax* (13.7%), *Gobius* spp. 1 (13.7%) and *D. sargus* (11.6%) (Table 2.2). The majority of taxa observed in this study could be classified as Marine Estuarine Opportunists (MEO), with one species, namely *Mugil cephalus*, classified as Marine Estuarine Dependent (MED) (Potter et al. 2015; Table 2.3).

Table 2.2: Total catch (TC) composition by habitat, proportion of TC, mean Catch Per Unit Effort (CPUE), mean Body Length (BL), developmental stages and estuarine association guilds (Potter et al. 2015) (N = 1875). Preflexion (Pr), flexion (F), postflexion (Pf) and early juvenile (Ej). Dominant stage presented in bold.

		Habitat (N)						
Family	Species	Mixed shore	Sandy	Catch	Mean CPUE (range)	Mean BL (range)(mm)	Dev. stage	Guild
Blennidae	*Parablennius pilicornis*	4	2	<1	0 (0-1.3)	15.1 (14.6-16)	**Po**, Ej	M
	Scartella emarginata	2	0	<1	0 (0-0.3)	17.9 (11.1-25.5)	**Ej**	M
Carangidae	*Trachinotus ovatus*	1	6	<1	0 (0-1.7)	19.2 (16-21.6)	**Ej**	MS
Clupeidae	*Sardinella aurita*	90	19	5.8	0.5 (0-21.7)	14.3 (7.7-17.1)	F, **Po**	MS
	Sardinops sagax	127	13	7.5	0.7 (0-39)	17.7 (10.8-25.7)	**Po**	MS
Elopidae	*Elops lacerta*	1	0	<1	0 (0-0.3)	32.8 (32.8-32.8)	**Po**	MEO
Engraulidae	*Engraulis encrasicolus*	1	1	<1	0 (0-0.3)	6.5 (6.5-6.5)	**Po**	MEO
Gerreidae	*Eucinostomus melanopterus*	14	2	<1	0.1 (0-3.7)	10.7 (9-14.9)	**Po**, Ej	MEO
Gobiidae	*Gobius sp. 1*	4	13	<1	0.1 (0-3.7)	12.2 (10.1-18.3)	Po, **Ej**	
	Gobiidae 1	1	2	<1	0 (0-0.7)	11.4 (8.4-13)	**Po**	
Haemulidae	*Pomadasys rogerii*	34	2	1.9	0.2 (0-10.7)	10.3 (7.7-11.7)	**Po**, Ej	MEO
Mugilidae	*Liza species*	11	7	1.0	0.1 (0-2.3)	21.7 (7.7-36.5)	Po, **Ej**	MEO
	Mugil cephalus	3	1	<1	0 (0-0.3)	19 (15.8-22.3)	**Ej**	MED
	Mugilidae 1	0	4	<1	0 (0-1.3)	31.4 (28.2-34.9)	**Ej**	MEO
Sciaenidae	*Umbrina canariensis*	1	0	<1	0 (0-0.3)	5 (5-5)	**Po**	M
Soleidae	*Dicologlossus cuneata*	6	0	<1	0 (0-2)	5.9 (4.3-8.2)	**Po**	MS
Sparidae	*Diplodus sargus*	1416	11	76.1	6.7 (0-451.7)	8.4 (6.1-19)	F, **Po**, Ej	MEO
	Sarpa salpa	0	1	<1	0 (0-0.3)	13.9 (13.9-13.9)	**Po**	MEO
	Spondyliosoma emarginatum	1	1	<1	0 (0-0.3)	10.4 (4.2-20.9)	**Po**	MS
	Sparidae 1	1	0	<1	0 (0-0.3)	3.8 (3.8-3.8)	**Po**	
	Sparidae 2	1	0	<1	0 (0-0.3)	13 (13-13)	**Po**	
	Sparidae 3	0	9	<1	0 (0-2)	6.8 (4.2-8.2)	**Po**	
Tripterygiida	Tripterygiidae 1	61	0	3.3	0.3 (0-20.3)	14.6 (10.5-15.9)	**Po**	M
Unidentified	Species 1	0	1	<1	0 (0-0.3)	2.7 (2.7-2.7)	**Pr**	
	Total Catch	1780	95					

Table 2.3: Relative proportion (%) of marine species observed in this study, and four surf zone studies from warm-temperate South Africa, divided into estuarine utilization categories according to (Potter et al. 2015). Note that this study, and the studies by Strydom and d'Hotman (2005) and Watt-Pringle and Strydom (2003) were in surf zones not immediately associated with estuaries, unlike the other two studies. This table only includes the relative proportion of exclusively marine and marine estuarine associated taxa. Other guilds, such as estuarine taxa, were ignored.

	Proportion of taxa (%)				
	Non-estuarine associated			Estuarine associated	
Estuarine utilization category (Potter et al. 2015)	This study	Strydom & d'Hotman (2005)	Watt-Pringle & Strydom (2003)	Whitfield (1998)	Strydom (2003)
Exclusively marine species	22.2	5.9	10.7	17.6	8.7
Marine estuarine straggler	27.8	11.8	32.1	11.8	26.1
Marine estuarine opportunist	44.4	64.7	50.0	47.1	52.2
Marine estuarine dependant	5.6	17.6	7.1	23.5	13.0

Body length and developmental stage

The catch was dominated by postflexion stage larvae (97.1%), followed by early juveniles (1.3%) (Table 2.2). Flexion stage larvae were less abundant (0.1%), and only one individual preflexion stage larva was recorded (<0.1%). Of the six dominant species recorded, only *D. sargus, S. sagax* and *S. aurita* were found in sufficient numbers (n≥30) and in each habitat type to allow a comparison of mean body length from each habitat type. There was no significant difference (P<0.05) in the mean body length of *D. sargus* (P = 0.58) or *S. aurita* (P = 0.07) between habitat types, however the body length of *S. sagax* from sandy habitat was significantly greater (P = 0.02) than those found in the mixed shore sites.

Spatial and temporal trends in CPUE

There was no significant difference (P<0.05) in mean CPUE (all species) observed among the six sampling sites (H = 2.7; P = 0.75). The apparent difference in the range of total CPUE at site 1 was principally due to high catches of *D. sargus* (N = 1385), during February 2015 (Figure 2.3). Although not significant, the highest maximum range and mean CPUE (all species) were recorded at sites 1, 2 and 4, all of which are mixed shore habitats (Figure 2.3). Despite this, there was no significant difference in mean CPUE (all species: P = 0.45) or mean CPUE for any individual species (P = 0.14 – 0.97) between habitat types.

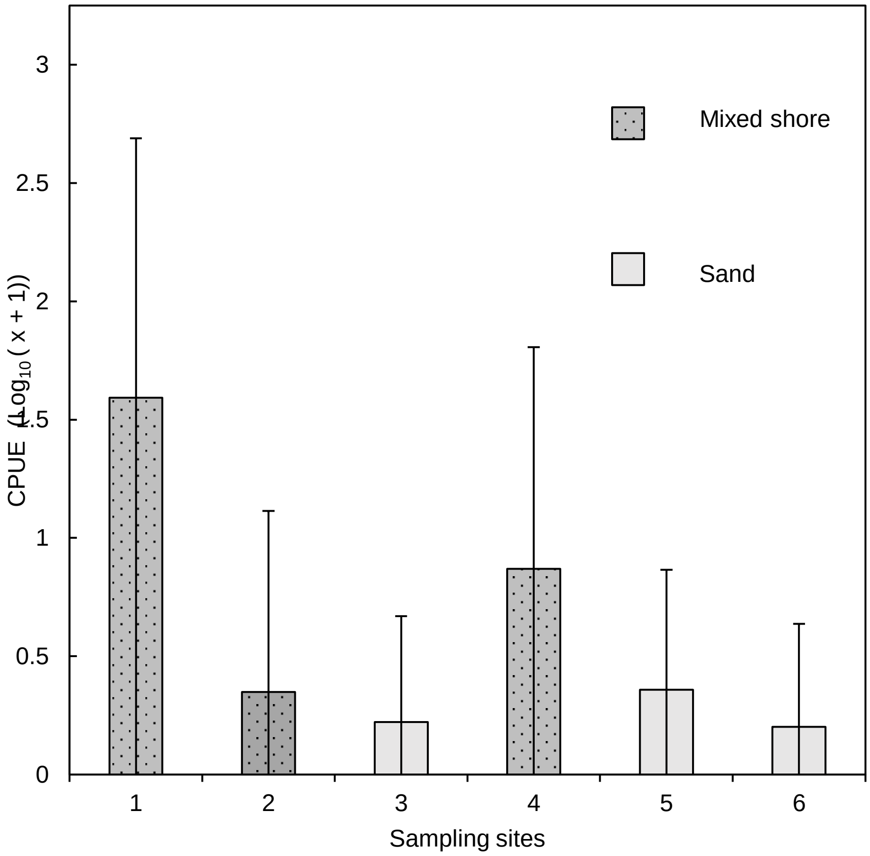

Figure 2.3: Mean Catch Per Unit Effort (CPUE) of all species from each sampling site from the 13-month sampling period, with bars indicated range, represented on a log scale ($\log_{10}(x+1)$).

There was a significant difference in mean monthly CPUE (all species; H = 34.8; P<0.01), with a peak in February 2015, and no catch was recorded in four separate monthly sampling trips: September 2014 and January, April and May 2015 (Figure 2.4). *Diplodus* *sargus* was observed in the catches during June and August 2014 and February 2015 (Figure 2.5). *Sardinops sagax* was observed in the catches during December 2014, February and March 2015 (Figure 2.5). *Sardinella aurita* was observed most often in October, November and December 2014, and February, March and July 2015 (Figure 2.5*)*. Tripterygiidae 1 was only recorded in February 2015 (Figure 2.5). *Pomadasys rogerii* was recorded in December 2014 and February and March 2015 (Figure 2.5). Lastly, *Liza* spp. was recorded in the catch in June, July, August and December 2014, and March 2015 (Figure 2.5). There were no significant differences in the seasonal mean CPUE (all species; P = 0.14), or the mean CPUE of any individual species, except for *S. sagax* – which was significantly more abundant ($P<0.01$) during the wet season (Feb – Apr).

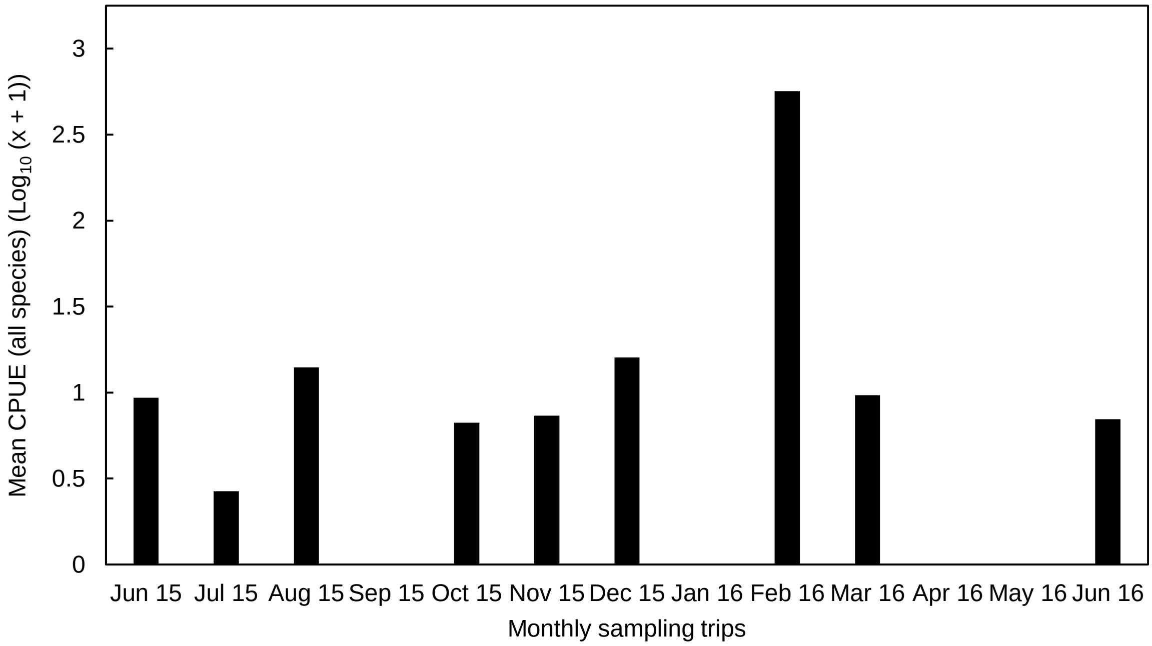

Figure 2.4: Total Catch Per Unit Effort (CPUE) for all sampling sites from each monthly sampling trip ($\log_{10}(x+1)$).

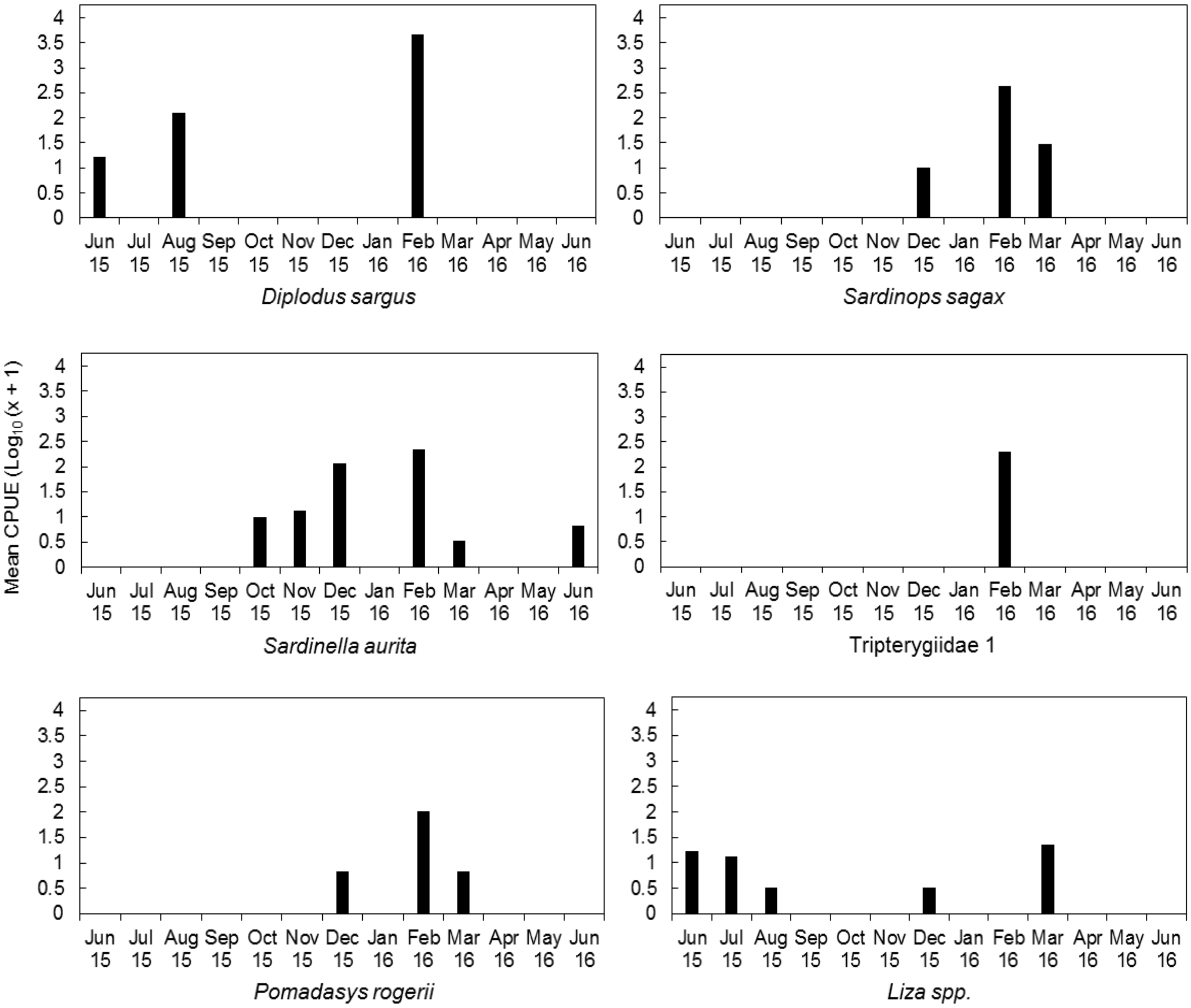

Figure 2.5: Catch Per Unit Effort of each dominant species (> 1 %) for all sampling sites from monthly sampling trip from June 2014 to July 2015, represented on a log scale ($\log_{10}(x+1)$).

Spatial and temporal trends in diversity

The overall Shannon–Wiener species diversity (*H'*) and Margalef's species richness (*d*) indices were *H'* = 1.05 and *d* = 3.05, respectively. Sandy sites had higher species diversity (*H'* = 2.4) and species richness (*d* = 3.51) when compared with the mixed shore sites (*H'* = 0.88; *d* = 2.54). However, the mean CPUE (all species), total catch and species count was higher in the mixed shore sites, (Figure 2.3, Table 2.2). When comparing monthly trends, the highest diversity and richness indices were recorded in June 2014 (*H'* = 1.87; *d* = 2.18) while the lowest species diversity and richness indices were recorded in August 2014 (*H'* = 0.24) and October 2014 (*d* = 0.35) respectively (Figure 2.6). Both species diversity and species richness differed seasonally, with both indices higher in the wet season (*H'* = 0.83; *d* = 1.88) than the dry season (*H'* = 0.56; *d* = 0.79).

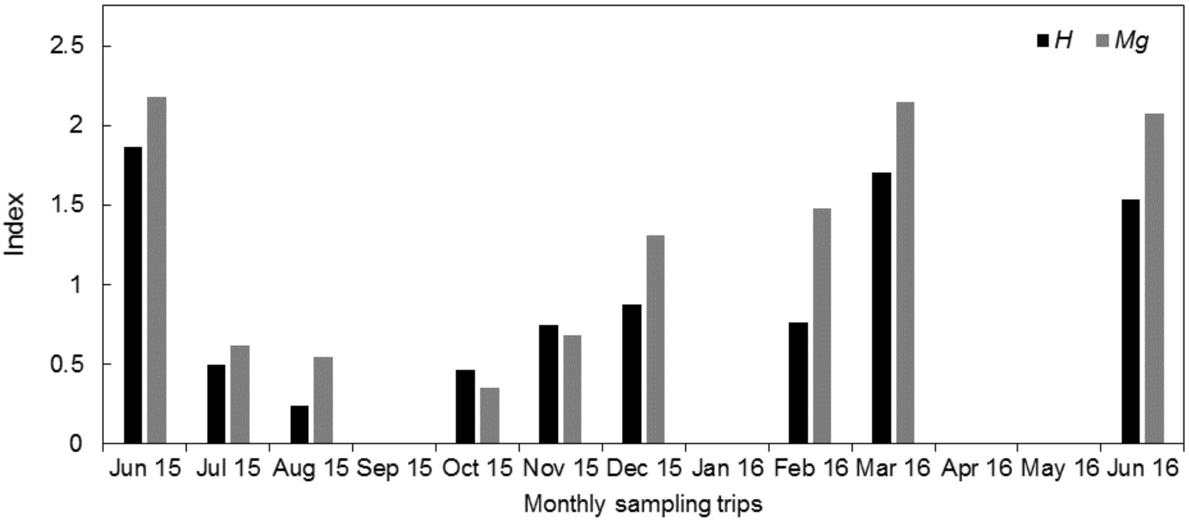

Figure 2.6: Shannon Wiener diversity (*H'*) and Margalef's Species Richness (*d*) indices for each monthly sample from the 13-month sampling effort.

Environmental correlation

The Spearman Rank Order (SPRO) correlations between the environmental parameters and total CPUE were weak. Only the CPUE of *S. sagax* showed a significant ($P<0.05$) correlation (r_s) with temperature ($r_s = 0.42$). A Multiple Linear Regression (MLR) yielded similar results, with no significant relationship present between the two environmental parameters and total CPUE, or between the two environmental parameters and the CPUE of any individual species. Although it was not significant, temperature showed the best regression relationship (R = 0.24) with mean CPUE (all species; P = 0.06).

When seasonal data was examined, there were significant SPRO correlations between temperature and total CPUE (r_s = 0.88), and between temperature and the CPUE of *S. sagax* (r_s = 0.85), *P. rogerii* (r_s = 0.85) and *D. sargus* (r_s = 0.77). A significant correlation was also observed between turbidity and mean CPUE (all species: r_s = 0.65), and between turbidity and the CPUE of *P. rogerii* (r_s = 0.83) and *S. sagax* (r_s = 0.69). A MLR showed no significant relationships between the two environmental parameters and the mean CPUE (all species), or between the environmental parameters and the CPUE of any individual species (P = 0.16 – 0.99).

Community analysis and environmental matching

The PCA extracted two components that explained 91% interaction between biological and environmental variables (Table 2.4). PCA indicated that 61% of the variation in total CPUE could be explained by the first eigenvector (PC 1) (Table 2.4). PC 1 was characterized by a positive correlation with temperature and turbidity (Table 2.4). The second eigenvector (PC 2) explains a further 30% of the variation within the dataset, and is associated with a negative correlation with turbidity and temperature. Cumulatively, these two factorial axes explain 91% of the variation within the dataset. The distribution of samples in the space defined by PC1 and PC 2 failed to yield a distinct pattern when categorized by habitat (Figure 2.7). The two notable outliers (red ellipsoid) represent two mixed shore samples dominated by high catch of *D. sargus, S. sagax* and *S. aurita*. Apart from these two samples, there appears to be no distinct grouping by habitat, which suggests that the community is equally distributed across the study area. When the samples were categorized by season (Figure 2.8), there was strong seasonal separation. Most of the seasonal separation of samples in the PCA space occurred along the temperature and turbidity vectors, with the wet season having higher temperatures and turbidity. The wet season appeared to be associated with higher CPUE (all species), but the high turbidity associated with the four wet season samples within the red ellipsoid (Figure 2.8) was negatively correlated with total CPUE.

Table 2.4: Eigenvectors determined by a Principal Component Analysis (PCA) including temperature, turbidity and total Catch Per Unit Effort (CPUE) from the seasonal data set.

Variable	PC 1	PC 2	PC 3
Temperature	0.68	-0.11	0.73
Turbidity	0.62	-0.45	-0.64
Total CPUE	0.40	0.89	-0.24
Variance explained (%)	61	29.5	9.5
Eigenvalue	1.83	0.88	0.29

The cluster analysis (PRIMER) of samples yielded no useful grouping by habitat type, and ANOSIM indicated no significant separation between habitat types based on species CPUE (R = -0.07; P = 0.75) or species presence/absence (R = -0.08; P = 0.79). There was, however, a significant seasonal separation (ANOSIM) based on species CPUE (R = 0.29; P = 0.01) and species presence/absence (R = 0.28; P = 0.01). The SIMPER for species CPUE identified a 92% dissimilarity between seasons. This was ascribed principally to *S. sagax* (26.3%), *D. sargus* (23.8%), *Liza* spp. (13.4%), *S. aurita* (6.5%), *P. pilicornis* (5.4%) and *P. rogerii* (5.3%). The SIMPER for species presence/absence identified an 86% dissimilarity between seasons. This was attributed mainly to *S. sagax* (19.6%), *D. sargus* (13.5%), *Liza* spp. (12.7%), *P. rogerii* (7.3%), *S. aurita* (5.8%) and *E. encrasicolus* (5.1%). Multivariate environmental matching (PRIMER) indicated that there was a significant correlation (RELATE) between the environmental variables and samples based on species CPUE (R = 0.27; P = 0.01) and species presence/absence (R = 0.26; P = 0.02). Of the two environmental variables, temperature showed the highest correlation with changes in the community structure. Despite this, a combination of temperature and turbidity best explained (BIO-ENV) the changes in the community based on species CPUE (r_s = 0.27) and species presence/absence (r_s = 0.26).

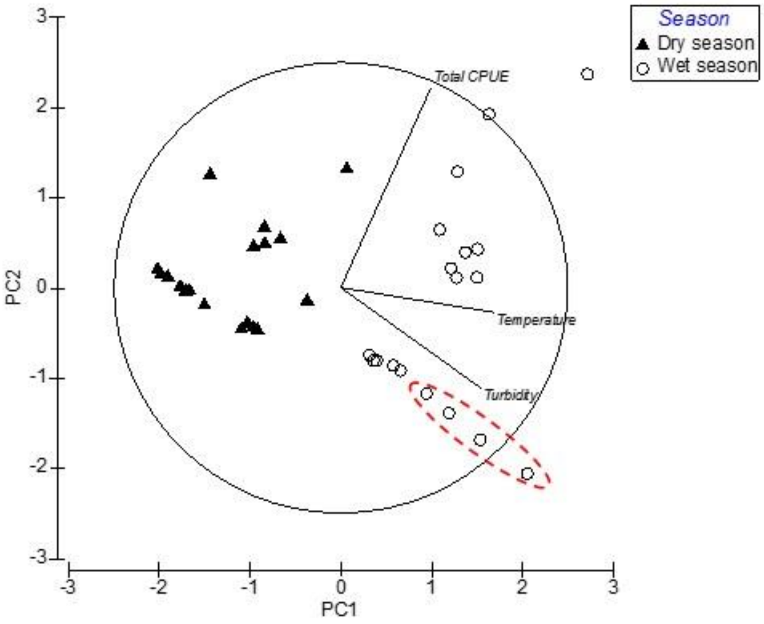

Figure 2.7: Principal Component Analysis (PCA) of seasonal samples labelled by season (dry and wet season) including the variables: temperature, turbidity and total CPUE (shown by vector diagram). This ordination represents 90% of the variation.

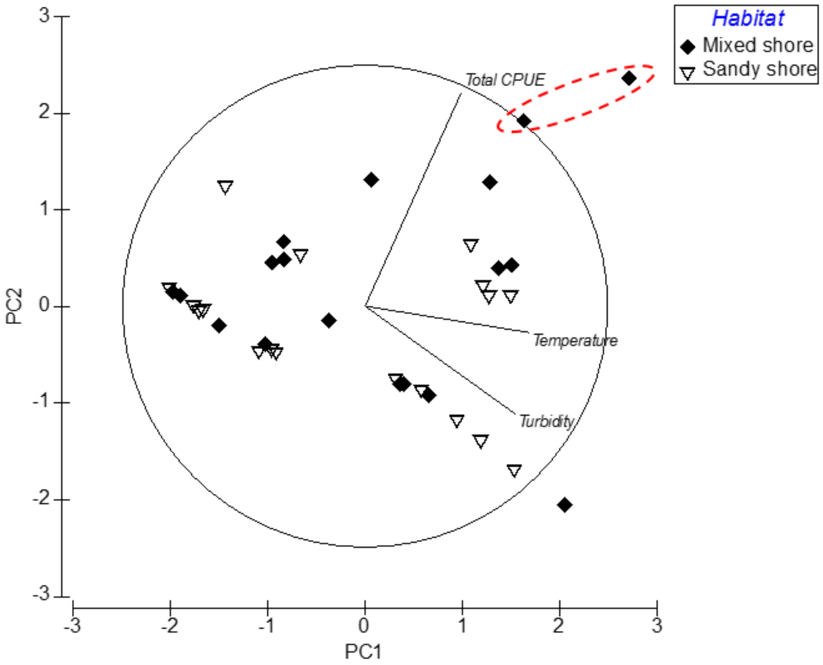

Figure 2.8: Principal Component Analysis (PCA) of seasonal samples labelled by habitat types (mixed shore or sandy shore) including the variables: temperature, turbidity and total CPUE (shown by vector diagram). This ordination represents 90% of the variation.

Discussion

The southern Angolan surf zone, located in the eastern Atlantic, hosts a multifarious early stage fish community, with 24 taxa from 13 families observed in catches. When compared to global patterns, the number of taxa observed was relatively lower than that of Japan: 18 to 100 taxa (Senta and Kinoshita 1985, Suda et al. 2002); and Taiwan: 47 taxa (Yang and Senta 1993), in the Indo-West Pacific. The relatively low species richness of Atlantic biota when compared to the Indo-West Pacific (Paulay 1996; Bellwood and Wainwright 2002) has been ascribed to a smaller geographic area and high frequency of historic mass disturbances resulting in episodic extinctions (Vermeij 2001, Vermeij 2005). A large loss of genera (20-30%) occurred during the Pliocene extinctions (Vermeij 2001, Vermeij 2005), and as a result the Atlantic presently hosts a less diverse reef fish community than it did in the Miocene (Budd 2000).

Similarly, the number of taxa observed in this study was considerably lower than that in Mauritius: 112 taxa (Sato 2007) in the Indian Ocean. Temperature is known as one of the principal drivers of ichthyofaunal distribution (Stebbing et al. 2002, Perry et al. 2005, Last et al. 2011), and the tropical waters of the Indian Ocean are known for high diversity and endemism (Turpie et al. 2000, Floeter et al. 2008, Joyeux et al. 2008). The comparably low species richness in the study area is likely due to the loss of Tropical Indo-Pacific species during the formation of the cold water Benguela Current (Turpie et al. 2000). The cool, nutrient rich Benguela system is known for high productivity but low diversity (Sakko 1998, Nelson and Hutchings 1983, Turpie et al. 2000). The high complexity and availability of inshore habitats likely contributes to the high diversity and speciation in the Indian Ocean. The low availability of inshore habitat and the absence of functional estuaries in the study area results in lower habitat complexity, thereby reducing available niches for speciation.

When compared to other warm-temperate regions, the number of taxa observed in this study was considerably lower than that from New Jersey: 47 taxa (Able 2010); and the Gulf of

Mexico: 69 taxa (Ruple 1984), in the North Western Atlantic. The North Western Atlantic is known for relatively high diversity in the Atlantic context, owing to the historic connection of the region with the Tropical West Pacific prior to the formation of the Isthmus of Panama during the Miocene (Floeter et al. 2008). The North West region of the Atlantic is theoretically “older” than the South East, with colonization occurring prior to the formation of the Isthmus (3.5 mya) by Pacific taxa (Floeter et al. 2008). The major biogeographic events structuring the present South East Atlantic fauna were more recent, with the formation of the Benguela Current and Namib Desert approximately two million years ago (van Zinderen Bakker 1975). The subsequent isolation of the East Atlantic from the Indian Ocean by the Benguela Current soft barrier is far more recent (2 mya) than that of the land bridge separating the Pacific and Atlantic oceans in Panama (3.5 mya). It is likely that the longer period of isolation, tropical climate and more complex habitat better facilitate allopatric speciation (Friedlander and Parrish 1998, Gratwicke and Speight 2005, Joyeux et al. 2008), resulting in a more diverse ichthyofaunal community in the North West Atlantic. The number of taxa observed was most similar to that from Brazil: 29 taxa (Godefroid et al. 1999) in the South Western Atlantic; and several studies from warm-temperate South Africa: 19-52 taxa (Whitfield 1989, Strydom 2003, Watt-Pringle and Strydom 2003, Strydom and D’Hotman 2005, Pattrick and Strydom 2014).

When compared to the other southern African warm temperate zone, the number of taxa observed in the study area (30 km) was greater than that observed in Swartvlei Bay (2.5 km): 16 taxa (Whitfield 1989); Cape Padrone (10 km): 19 taxa (Strydom and d’Hotman, 2005); St Francis Bay (4 km): 13 taxa (Strydom, 2003); and East Kleinemonde: 21 taxa (Cowley et al. 2001). The number of taxa observed was considerably lower than that observed in Kwaaihoek (5 km): 37 taxa (Watt-Pringle and Strydom 2003); Algoa Bay (100 km): 52 taxa (Pattrick and Strydom 2014); and sub-tropical St Lucia (5 km): 88 taxa (Harris and Cyrus 1996). High diversity was expected, as frontal zones (e.g. ABFZ) usually represent areas of biodiversity importance due to the species accumulation effect (e.g. John et al. 2001). In the pelagic trawl survey by John et al. (2001), the latitudes within the ABFZ exhibited higher ichthyoplankton diversity than those within the Benguela or Angola currents individually, which highlights the biodiversity importance of these interface zones (John et al. 2001). While there were 24 species observed in the current study, the diversity index was relatively low due to low evenness among species. This is illustrated by the high species richness index, but relatively low diversity index, attributed to the predominance of six species in the study. The higher diversity of the Kwaaihoek surf zone in South Africa than preceding surf zone studies from the same region was attributed to the influence of the warm-water Agulhas eddies, which likely transported several marine species into the region during the study. Similarly, the higher number of taxa observed in the current study than other studies from the comparable warm-temperate coastline of RSA is attributed to the influence of the tropical Angola current, which shifts seasonally into the southern Angola study area promoting entry of taxa with tropical affinity (e.g. *Trachinotus ovatus, P. rogerii*).

It was hypothesized that the wet season, when the tropical Angola current dominates the region, would exhibit higher diversity than the dry season, which is dominated by the cold Benguela Current. The diversity of fishes is known to decrease with an increase in latitude, associated with a shift from tropical to more temperate marine ecoregions (Hobson 1994, Ebeling and Hixon 1991). In southern Africa, species richness tends to decrease as one moves further south along the east coast. The sub-tropical coast of RSA hosts a high number of taxa, illustrated by the high number of species observed in the work by Harris and Cyrus (1996) (n = 88). The study by Watt-Pringle and Strydom (2003b) in warm temperate RSA recorded 37 taxa, considerably lower than that observed by Harris and Cyrus (1996). The number of taxa observed by Watt-Pringle and Strydom (2003) was considerably higher than most other studies from the same province, attributed to the influence of eddies in the Agulhas Current, which intermittently transports tropical or offshore species into the region. A preceding study by Whitfield (1989) in the cool-temperate Western Cape yielded significantly fewer taxa (n=26), likely attributed to the region's independence from the Agulhas Current. This general trend is evident in most surf zone studies along the east coast of RSA, with species richness decreasing as study areas shift further south and away from the influence of the warm Agulhas current (e.g. Harris and Cyrus 1996, Cowley et al. 2001, Strydom 2003, Watt-Pringle and Strydom 2003, Strydom and d'Hotman 2005). This phenomenon is termed the "subtropical subtraction effect" (Turpie et al. 2000), whereby the number of Indo-pacific and Western Indian Ocean species declines southwards, attributed to their intolerance for cooling water temperatures. This trend continues around the South African coast, with consistently low species richness along the west coast, characterized by the cold Benguela current.

Indeed, the study area diversity was considerably higher during the warmer wet season. This is likely due to the influx of spring/summer spawning coastal species, and the presence of several eastern tropical Atlantic species such as *P. rogerii* and *Trachinotus ovatus*. This is attributed to the seasonal shift of the ABFZ, resulting in a "subtropical addition effect" during the wet season, which facilitates the entry and spawning of species with a tropical affinity in an area normally dominated by the cold Benguela Current. This seasonal change in gross number of taxa is unlike that observed in the nearshore by John et al. (2001), who observed little change in the gross number of taxa across the ABFZ. Assuming that the dry and wet season approximate the Benguela and Angola current systems respectively, it was surprising to observe so few species in the dry season, despite the knowledge that the Benguela current is characterized by low diversity (Turpie et al. 2000). This is likely a result of a complex interaction between behavioural and oceanographic drivers. It is difficult to understand the drivers of the seasonal changes in larval community composition. This is because it is not possible to uncouple the potential influences of behavioural drivers such as spawning seasonality, from the environmental drivers such as temperature and turbidity. This raises the question of whether the exclusive occurrence of several species in the wet season is simply the consequence of spawning periodicity, or a complex interaction between that and the availability of suitable environmental conditions for larvae.

CPUE was highest in the wet season and corresponded with the arrival of several species to the surf zone. In Angola, the wet season sea temperatures approximate South African spring and summer sea temperatures, and it is likely that the peak in larval CPUE during the wet season is linked to the late dry and early wet season spawning of coastal, nearshore and pelagic species in warmer waters. Typical summertime peaks in larval CPUE have been observed in both the South African shallow nearshore (<15m) (Pattrick and Strydom 2008) and surf zone environments (Strydom 2003, Watt-Pringle and Strydom 2003), and in the South Western Australian nearshore (Muhling et al. 2007), Japanese surf zones (Senta and Kinoshita 1985) and Mexican Gulf surf zones (Ruple 1984). In South Africa, this is attributed to the summer spawning of several MEO coastal species that dominate surf zone catches during this time (Strydom, 2003). This is likely an evolved tactic to coincide the recruitment of larvae and juveniles with favourable temperatures and high nutrient availability coupled to coastal productivity (Strydom 2015), ensuring optimal feeding and growth conditions.

The overall surf zone catch comprised taxa typical of warm-temperate ecoregions from around the globe. Sparidae, Clupeidae, Tripterygiidae, Haemulidae and Mugilidae dominated the catch, and were also typical components of surf zone and nearshore ichthyoplankton communities in South Africa (Lasiak 1986, Whitfield 1989, Harris and Cyrus 1996, Cowley et al. 2001, Strydom 2003, Watt-Pringle and Strydom 2003, Strydom and d'Hotman 2005, Pattrick and Strydom 2014), Australia (Muhling et al. 2007), Japan (Senta and Kinoshita 1985, Suda et al. 2002) and the Mediterranean (Sabatés et al. 2007, Sabatés et al. 2004). Not only does this indicate that surf zones are utilized by a specialist group of fishes, it also highlights the continuity of surf zones globally (Pattrick and Strydom 2014). The composition of the catch was most similar to that of studies from warm-temperate South Africa (Whitfield 1989, Strydom 2003, Strydom and d'Hotman 2005) and the warm-temperate Mediterranean (Sabatés et al. 2004, 2007), in both number of taxa and similarity of families (e.g. Sparidae, Mugilidae, Soleidae), genera (e.g. *Diplodus, Mugil, Liza*, *Trachurus*) and species (e.g. *Diplodus sargus*, *Diplodus cervinus*, *Mugil cephalus*). This is unsurprising, as these three regions represent Africa's three warm temperate marine ecoregions. The two warm-temperate marine ecoregions in southern Africa were historically a single population prior to isolation by the Benguela Current, and therefore share many common taxa. Similarly, the Mediterranean ichthyofauna comprises large Atlantic and Indian Ocean groups, many of which are cosmopolitan or occur throughout the Eastern Atlantic seaboard, from South Africa to the Mediterranean (Tortonese, 1964).

While the taxa observed in this study resemble those observed in South African studies, the composition and relative proportions are considerably different. Warm-temperate South African surf zones are typically dominated by Mugilidae (e.g. Whitfield 1989, Cowley at al. 2001, Strydom 2003, Watt-Pringle and Strydom 2003), representing as much as 66% of the catch (Strydom and d'Hotman 2005). In this study, only a small portion of total catch was contributed by Mugilidae (1%), composed primarily of *Liza* spp. Larvae of Sparidae are a typical component of warm-temperate surf zone communities, often representing 16–26% of the total catch (Strydom and d'Hotman 2005, Strydom 2003). Catches of Sparidae were considerably higher in the current study, contributing 77% of total catch. Within the Sparidae, *D. sargus* dominated the catch (99%), as did its sister species (*D. capensis*) in the study by Strydom and d'Hotman (2005). The *Diplodus sargus* sub-species complex is ubiquitous in southern African warm-temperate marine ecoregions, and is extremely abundant in the southern-Angolan surf zone as larvae, juveniles and adults (*D. sargus*: Richardson et al. 2011a, c). The study area in particular hosts a large, unexploited population of *D. sargus*, which may well explain the high numbers of larvae in this area (Richardson et al. 2011a).

It was hypothesized that marine species would dominate southern Angolan surf zone catches, as the absence of estuarine habitat in the region would preclude species that exhibited high estuarine dependence. Indeed, the proportion of exclusively marine species observed in the current study was considerably higher than that of comparable surf zone studies from South Africa (Table 2.3). However, 50% of the taxa observed showed a degree of estuarine dependence, with one species, namely *Mugil cephalus*, classified as marine estuarine dependent. Most previous surf zone studies from South Africa were associated with estuary mouths (e.g. Whitfield 1989, Cowley et al. 2001, Strydom 2003), and as such, catches are often dominated by marine estuarine dependent species such as *Rhabdosargus holubi* and *Rhabdosargus globiceps*, which are known to accumulate in the surf zones adjacent to estuarine habitats (e.g. Whitfield 1989, Cowley et al. 2001, Strydom 2003). However, studies of non-estuarine associated surf zones in South Africa found that marine estuarine dependent species are still present in the surf zone as much as 40 km away from the nearest estuary, and that community structure is near identical regardless of proximity to estuarine habitats (Strydom and d'Hotman 2005). This indicates continuity between surf zone assemblages and highlights the presence of a discrete ichthyofaunal community adapted to utilizing this habitat (Watt-Pringle and Strydom 2003, Strydom and d'Hotman 2005).

While it is impossible to know if observed individuals are in fact recruiting into adult populations, it appears that some species were able to make use of alternative, non-estuarine nursery areas, and *Mugil cephalus*, traditionally considered completely dependent on estuaries, will reach settlement despite the lack of functional estuaries in southern Angola. It is likely that the taxa exhibiting a degree of estuarine dependence have adapted to utilize the relatively low energy surf zone and nearby coastal embayments as a nursery area. In their comparison of the roles estuaries play in the life cycles of fishes from South Africa and South Western Australia, Potter et al. (1990) suggested that the reason for low numbers of species truly restricted to estuaries in South Western Australia was the presence of sufficient alternative, non-estuarine nursery habitats provided by inshore coastal embayments. These sheltered embayments fulfil the necessary habitat requirements, with lowered current velocity, high nutrient availability and increased temperatures being favourable for the early development of many coastal species. The ability of the MED *Mugil cephalus* and other MEOs to reach the settlement stage in an area devoid of estuaries is attributed to the low energy surf and the proximity of two large, sheltered coastal embayments, which likely provide suitable alternative nursery habitats akin to those normally provided by estuaries. This highlights that the estuarine dependence of a cosmopolitan species such as *Mugil cephalus* is not universal, and is likely more a factor of the availability of suitable alternative habitat rather than an intrinsic dependence on estuarine function. This supports the growing consensus that estuarine dependence has been overemphasized for some species (Able and Fahay 1998, Able 2005), particularly in the absence of assessments of other shallow water nursery habitats (Able 2005), such as those associated with rocky shores (Strydom 2008). It is therefore even more critical to understand which alternative, non-estuarine habitat types can serve the critical ecosystem functions that estuarine dependent species would typically use when available.

Catches from mixed shore habitats were dominated (>1%) by *D. sargus*, *S. sagax*, *S. aurita*, Tripterygiidae 1 and *P. rogerii*, while catches from sandy habitats were similarly low for all 17 species recorded. The even distribution of the catch amongst species in sandy sites is likely due to consistently low catch, unlike sites from the mixed shore, which exhibited infrequent high catch events. Sporadic catches of *D. sargus*, *S. sagax* and *S. aurita* in very large shoals from sites 1, 2 and 4 (mixed shore) account for most of the difference in total catch composition among habitats. High catches of *D. sargus* from mixed shore sites were expected, as larvae and juveniles are known to utilize rocky shores as nursery areas (Strydom 2008).

The study area was dominated by postflexion larvae, with only very small proportions of other developmental stages observed. Postflexion larvae are significantly more capable of maintaining their position in the marine environment than earlier stages, and as such are able to select favourable environments (Dudley et al.2000, Kingsford et al. 2002). Reduced current velocity is highlighted as favourable for nursery habitats, as it facilitates feeding and demands less energy to maintain position (Lasiak 1986, Layman 2000, Watt-Pringle and Strydom 2003). As such, it is common for trough habitats within surf zones to yield higher proportions of postflexion larvae than immediately adjacent open surf water (Watt-Pringle and Strydom 2003). This study focused on sandy trough and mixed shore habitats, both of which are characterized by reduced current velocity and presence of suitable micro-habitats, so it is therefore understandable that postflexion larvae capable of selecting these habitats dominated the catches. Sparidae are particularly capable swimmers, with 8-9 mm SL *D. capensis* capable of swimming at 18 cm.s^{-1} for up to 9 km (Pattrick and Strydom 2009), suggesting a high level of endurance. It is therefore unsurprising that postflexion *D. sargus* dominated catches from the exposed surf zone in the current study.

Evidence of growth, feeding, survival and eventual recruitment to adult populations is essential before suggesting a habitat is an important nursery (Beck et al. 2001). Tracking the development of fishes in an open system is troublesome, and the difficulty is exacerbated in species with protracted spawning periods (i.e. *D. sargus*). While cohort analysis is ideal for showing growth within a habitat, the patchy nature of larval fish sampling in the surf zone often renders this indicator largely unsuitable. The presence of more than one developmental stage within a habitat is a coarse indicator of “grow-out”, and when coupled with length frequency information, may tentatively indicate nursery importance. “Grow-out” from flexion to settlement was observed in *D. sargus,* and from postflexion to settlement in *E. melanopterus*, *Gobius sp. 1*, *Pomadasys rogerii* and *Liza* spp. *Sardinella aurita* was observed in both the flexion and postflexion stages. Unfortunately, no meaningful length frequency progression was observed in this study, and therefore the "grow-out" of these dominant species is uncorroborated by more robust indicators such a cohort analysis or modal growth progression. While the presence of various developmental stages of several dominant species was observed, this only tentatively indicates nursery use; but without evidence of feeding or growth within this environment, one cannot accurately suggest its true nursery importance (Beck et al.2001). Further effort must be made to assess the prey field and feeding ecology of species in this environment, before one can safely assess the true value of the surf zone as a nursery, and not simply as a transient route between other areas.

While there was no significant difference in CPUE between sampling sites or habitat types, the extreme difference in total catch between habitats suggests that mixed shore sites may yield higher CPUE for some species. The study area shoreline is characterized by mixed shore and sandy habitats, which are usually in close proximity to each other. While sampling was always restricted to either habitat type, sandy sites were often neighbouring mixed shores, and vice versa. Therefore, it is proposed that habitats within the study area are not as isolated as first hypothesized. While I conclude that species composition appears equally distributed throughout the study area, there is potentially a difference in species composition and CPUE between micro-habitat types. However, it is likely that this is disguised by their close proximity.

Diplodus sargus spawns pelagic eggs in the shallow nearshore (±6m; Richardson et al. 2011c), after which larvae as early as the flexion stage recruit into shallow waters, particularly those associated with rocky substrate (Strydom 2008). While present in sandy troughs in both southern Angola and RSA (Strydom 2003, Watt-Pringle and Strydom 2003), the high catch of *D. capensis* in mixed shore sites suggests that this species actively selects this habitat as a nursery area. It is likely that the high availability of epifaunal prey items associated with algal accumulations (M. Farthing pers. obs.) is the reason for this habitat selection. Ontogenetic shifts in the diet of the genus *Diplodus* are common (Coetzee 1986, Sánchez-Velasco and Norbis 1997, Figueiredo et al. 2005, Richardson et al. 2011b, Winkler et al. 2014), and it is likely that migration of individuals from the shallow nearshore during flexion, to mixed shore surf zones for settlement follows this shift. The change in diet from zooplankton during the pelagic early larval phase, to epifaunal prey items during settlement, to Chlorophyta and Rhodophyta as juveniles, and eventually to Cirripedia and Bivalvia during adulthood likely explains this transition, as algae, mussels and barnacles associated with the mixed shore surf zones are the most important components of juvenile, sub-adult and adult *D. sargus* diets in southern Angola respectively (Richardson et al. 2011b).

The observation of *D. sargus* during the dry season was expected, however the presence of larval *D. sargus* in the surf zone during February, the warmest month of the study period (mean = 23.6 °C), is unusual. While previous studies of the adult histology have shown ripe adults throughout each month of the year (Richardson et al. 2011c), it is uncharacteristic for a sparid to spawn in waters above 21 °C (Sheaves 2006), and the reproduction of the southern Angolan *D. sargus* in particular is restricted to 15–20 °C (Potts et al. 2014). Sparidae from higher latitudes have been shown to spawn throughout the year, with *Pachymetopon blochii* capable of spawning year-round in Cape Town (Sheaves 2006). However, lower latitudes generally show higher mean sea surface temperature (SST), and as such spawning becomes more confined to colder months, likely attributed to a particular early life history phase being intolerant of warmers waters (Sheaves 2006). The presence of *D. sargus* larvae in the warmest month (February; mean = 23.6 °C) is attributed to an uncharacteristically cool water body that has routinely moved into the study area during December and January (Figure 2.2). This cool water body is thought to be driven by an upwelling event that appears to occur on an annual basis in this region (M. Rouault, pers. comm.). Previous studies focused on *D. sargus* and *D. cervinus cervinus* have attributed the presence of ripe, ripe running and spent adults during February to this phenomenon (Richardson et al. 2011c, Winkler 2013, Potts et al. 2014). The mean (7.4 mm SL) and modal (7.7 mm SL) size of *D. sargus* larvae observed during February 2015 correspond to an age of approximately 30 days (Brownell 1979). Assuming a short delay between the onset of suitable temperatures and actual spawning, the age of larvae observed on February 19th 2015 suggests spawning occurred on approximately January 19th 2015. Based on the pattern of early development of this species (Brownell 1979, Connell 2012, Papandroulakis et al. 2004), eggs spawned in January 2015 would be approximately between 8 (Brownell 1979: 15 ºC) and 10 mm SL (Connell 2012: 22-23 ºC) 32 days later, during the sampling of February 2015. The mean and modal size of *D. sargus* captured in February was less than this, however the reference growth rates were observed using enriched feeds (e.g. Brownell 1979, Connell 2012) under intensive mesocosm rearing conditions (e.g. Papandroulakis et al. 2004). It is therefore safe to assume that the larvae of wild *D. sargus* caught in this study would not achieve these same growth rates, as unenriched food sources would not facilitate this rapid growth. This assumption backdates spawning to approximately January 17th 2015, which approximates the central time frame of the cold water anomaly. Similarly, *D. sargus* with a mean (9.9 mm SL) and modal (10 mm SL) size, which approximates 29 days (Connell 2012: 22-23 ºC) to 40 days old (Brownell 1979: 15 ºC), were observed in catches during early July 2015. The observation of approximately 29-40 day old individuals on July 4th 2015 suggests spawning occurred on approximately June 1st 2015. This again coincides approximately with the decrease in temperatures below the 21°C threshold (Figure 2.2, Table 2.1). This corroborates the observation of spent adults in the study area during these periods (Richardson et al. 2011c, Potts et al.2014). Although *Diplodus cervinus cervinus* was not observed in the surf zone study, similar size larvae were observed in a nearby coastal embayment during the same time periods.

This provides tentative evidence that suggests that this species has similar spawning seasonality to *D. sargus*. This further highlights that the spawning of Sparidae, particularly *D. sargus,* is delimited by temperature, and not intrinsically linked to photoperiod as previously assumed. This tactic likely evolved to promote the success and survival of their early developmental stages.

Diplodus sargus is known to spawn in cooler temperatures (Richardson et al. 2011c, Potts et al.2014), so it is unusual that *D. sargus* CPUE and temperature showed a positive relationship. Richardson et al. (2011c) concluded that the December/January cold water anomaly provides an optimal window for concentrated reproductive activity of *D. sargus*. It is likely that the timing of this shift from cool temperatures suitable for spawning to warm temperatures ideal for larval development promotes maximum success of offspring. This is illustrated by the highest density of *D. sargus* being observed in February, which was the warmest month. This explains why temperature and CPUE show a positive relationship, despite *D. sargus* being known to spawn in cooler temperatures.

Assuming *S. sagax* and *S. aurita* are spawned in the nearshore environment, it appears that individuals enter and utilize southern Angolan primary surf zones at a smaller size than in South Africa. The average size of *S. sagax* observed in the study area was considerably smaller ($\bar{x}$ = 17.7 mm) than those observed in the South African surf zone study by Strydom (2003) ($\bar{x}$ = 41.5 mm), and considerably larger than those found by Pattrick and Strydom (2008) in the shallow nearshore (<15m) ($\bar{x}$ = 5.4 - 7.1 mm). This is likely attributed to the relatively low surf energy in southern Angola, which may not preclude the smaller, weak swimming Clupeidae from the surf zone. This is highlighted where *S. sagax* from sandy shores were significantly larger than those from the mixed shore, which offers more protection and refuge than less complex sandy habitats. *S. aurita* showed a similar but non-significant trend, most likely attributed to the lack of shelter at sandy sites, which naturally precludes smaller individuals.

This further illustrates the physical differences between the two warm-temperate marine ecoregions in southern Africa.

Due to the ubiquity of *S. sagax*, spawning seasonality differs greatly throughout its distribution (Fletcher and Sumner 1999, van der Lingen et al. 2001, Ward and Staunton-Smith 2002, Fairweather et al. 2006). In South Africa, *S. sagax* spawns repeatedly in spring and summer months (Beckley and van der Lingen 1999). In the southern Benguela Upwelling system, *S. sagax* shows a preference for spawning in water ranging from 17.4 to 21.1°C (van der Lingen et al. 2001). Within the study area, *S. sagax* larvae were observed in the late dry season and wet season. The presence of larvae in the surf zone appears to be linked to spawning periods when sea temperatures fell within the aforementioned range, namely October to January. The positive correlation between *S. sagax* density and temperature may be evidence of a behavioural tactic to coincide larval recruitment with the high plankton density that is generally observed during the warmer months (Wasmund et al. 2005). The recruitment and success of *S. sagax* depend heavily on planktonic density, and as such spawning is generally associated with upwelling areas (Beckley and van der Lingen 1999). The band of coastal upwelling identified in the ABFZ by Wasmund et al. (2005) likely reaches a maximum between August and October, as do upwelling areas in the northern Benguela region (Hart and Currie 1960). The relatively high chlorophyll *a* and primary production levels recorded in the nearshore zone of the study area during August and September 2000 provide further evidence for this hypothesis (Wasmund et al. 2005).

Sardinella aurita was the most frequently encountered dominant species on a month to month basis. Larvae were observed in the surf zone in both the dry and wet season, particularly between October and March. The spawning of this species is complex, and two distinct spawning seasons often occur, linked to upwelling events in West Africa (Whitehead 1985). The high frequency of larval occurrence in the surf zone during the late dry season and early wet season and the presence of flexion stage larvae can be attributed to high levels of localized adult reproduction, corroborated by personal observations (MW Farthing pers. obs.) and anecdotal evidence of large shoals of migratory adults in the shallow nearshore (<15m) zone during this period. *Sardinella aurita* is highly migratory (Whitehead 1985), but it is difficult to discern whether movement into the study area during the warmer months is a tactic to spawn during high nutrient availability events, or simply due to the southward shift of the ABFZ and suitable isotherms.

Pomadasys rogerii was observed during the late dry season and early wet season, like many other coastal species that arrived in the study area during the warmer months. There is no information on the spawning seasonality of *P. rogerii,* but, based on the seasonality of the closely related *Pomadasys jubelini,* it is likely that this species spawns during the early wet season and has an affinity for tropical waters typical of the Angola current (Marcelle et al. 2013). Adults have been infrequently observed in the surf zone of the study area (De Sousa, unpublished data) and frequently in a high energy surf zone approximately 60 km south of the study area (WM Potts pers. comm.), and it is likely that spawning occurs relatively nearby in the wet season, based on the size of the smallest larvae encountered (Table 2.2). The study area represents the southernmost boundary for the distribution of this marine estuarine opportunist (Lévêque et al. 1990), and as such, the core areas of spawning and nursery importance may be further north in Angola, where estuaries and warmer temperatures are found.

Pomadasys rogerii has a tropical affinity (Carpenter 1992), so it is not surprising that the density of this species increased with temperature. Information on the spawning seasonality is limited, but evidence from the genus suggests that spawning is not protracted like that of Sparidae and is likely timed to coincide with the early wet season and warmer temperatures. As the study area likely represents the southernmost distribution, it is hypothesized that the arrival of larval *P. rogerii* in the surf zone in the early wet season is the result of a combination of limiting isotherms and innate seasonal spawning, although adults have been infrequently observed during the dry season (WM Potts pers. comm., De Sousa unpublished data).

Members of the genus *Liza* are typically common in South African surf zone studies, especially those associated directly with estuary mouths (Strydom 2003, Watt-Pringle and Strydom 2003). Members of the genus *Liza* from warm-temperate South Africa have been observed in surf zones throughout the year, namely *Liza richardsonii* and *Liza dumerili* (Strydom 2003, Watt-Pringle and Strydom 2003). In South Africa, early juveniles of both aforementioned species recruit from the surf zone into estuaries throughout the year (Whitfield 1989). However, peak estuarine recruitment along the east coast occurs in April/May for *L. dumerili* and December/January for *L. richardsonii*, which follows their respective spawning periods (Whitfield 1989). It is hypothesized that *Liza richardsonii* is the most likely candidate species in the *Liza* spp. grouping in this study, based on the records of adults from the study area. However, without positive identification of earlier larval stages, this remains speculative. It is however safe to suggest that the *Liza* spp. group is likely composed of *L. richardsonii* or *L. dumerili*, as the occurrence of *Liza* spp. in both seasons throughout the year in the study area corresponds approximately with the known spawning seasonality of these species from warm-temperate South Africa (van der Horst and Erasmus 1978, de Villiers 1987). *Liza falcipinnis* is the only other *Liza* species known from Angola, but has not been considered as it has a tropical distribution (Thomson 1990). This species is known from Angola, but records are principally from the Cabinda province, which is an exclave and province of Angola located north of the Congo River (Anon. 1997). As such, this species has a tropical affinity and is unlikely to occur in the ABFZ.

Fluctuations in CPUE throughout the 13-month sampling period were expected, but there were four instances in which no catch was recorded at any of the six sampling sites. The surf zone represents an extremely challenging environment for sampling, and surf conditions regularly dictate success. No catch was recorded in September 2014 and January, April and May 2015. The zero catch in April and May was due to extremely high energy surf conditions typical of the dry season that rendered the primary surf zone unsuitable for the employed sampling methodology. High current velocity and swell energy made it impossible to complete the prescribed seine net pulls in a timely manner, and the large amount of suspended solids meant that the net regularly became inundated with sediment in such volumes that it was impossible to operate. Attempts were made to store samples inundated with large volumes of sand for later sorting and separation from nekton, but only invertebrates were observed.

The lack of catch during September and January is attributed to the physical changes in the primary surf zone habitat associated with lower surf energy during the wet season. During the wet season, surf energy is considerably lower than the dry season. Generally, this results in the deposition of sandy sediment over mixed shore and sandy trough habitats, significantly reducing the depth of troughs and area of primary reef, thereby reducing habitat complexity, as observed by several other workers in the area (Richardson 2010, Winkler et al. 2014). This is particularly evident after extended periods of low surf and wind energy. This occurred in September and January, and the low catches are ascribed to the subsequent reduction in the rocky substrate in the mixed shore habitat and the shallow troughs in the sandy habitat. The primary surf zone complexity was reduced to a single depth contour, changing from depths too great for seine net operation to a long shallow bank at wading depth (±1.5m). This bank comprised smooth mixed reef or exclusively sandy bottom. Sandy sites were particularly affected, with sites 3 and 5 devoid of sandy troughs deeper than 45 cm during September and January. The depth of troughs is known to significantly affect the CPUE of larvae in the surf zone, attributed to the associated reduction in current velocity (Watt-Pringle and Strydom 2003).

The community analysis showed that different seasonal water bodies appeared to support different ichthyofaunal communities. There was high dissimilarity (92%) between seasonal communities, further highlighted by the extreme differences in the number of taxa and CPUE between seasons. This was higher (88%) than that observed by John et al. (2001) in the nearshore ichthyoplankton communities across the ABFZ. While nearshore and surf zone early stage fish communities are not directly comparable, the presence of typically pelagic/nearshore species such as *S. aurita* and *S. sagax* in the surf zone may be attributed to the reduced energy in the surf zone during this period, which allows these taxa to feed in this habitat. These species are not typically associated with warm-temperate surf zones in southern Africa, especially not at the body length observed in this study. When assessing the seasonal community based on presence/absence, the absence of pelagic/nearshore species (*S. sagax* and *S. aurita*) from the surf zone in the dry season accounts for approximately 25% of the dissimilarity between seasonal communities. In warm-temperate South Africa, the larvae of *S. sagax* are not common in surf zones, likely attributed to higher surf energy and their relatively poor swimming ability compared to typical surf zone users, like the coastal *D. sargus*.

Environmental matching indicated that both temperature and turbidity may have been responsible for driving changes in the ichthyofaunal community. While temperature is a principal driver of fish community structure (Cochrane et al. 2009, Byrne 2011), the relationship between temperature and turbidity further highlights that seasonal community change in the southern Angolan surf zone is not simply a result of innate spawning seasonality and limiting isotherms, but also a consequence of the seasonal change in oceanographic conditions within this environment. The change in turbidity across seasons highlights the change in surf energy and physical environment (i.e. wave energy, current velocity, reef area and sandy trough depth), which are likely to affect the suitability of the primary surf zone for different species (Watt-Pringle and Strydom 2003, Pattrick and Strydom 2014). The low wave energy associated with the wet season is hypothesized to render the surf zone more habitable by a larger suite of non-specialist species (e.g. *S. sagax*) during this time, while the more turbulent dry season is dominated principally by strong swimming coastal taxa (e.g. *D. sargus*).

In conclusion, this is the first early stage fish investigation in the coastal waters of Angola, and addresses the scarcity of knowledge in this important climate change (Monteiro et al. 2008, Hobday & Pecl 2014, Potts et al. 2014) and biodiversity (John et al. 2001, Scales et al. 2014) hotspot. The southern Angolan surf zone is utilized by the early developmental stages of marine, marine straggler, marine estuarine opportunist and one marine estuarine dependent species, namely *Mugil cephalus*. Contrary to initial hypotheses, marine estuarine opportunist taxa dominate the surf zone, although the relative proportion of solely marine taxa was higher than that found in most other warm-temperate studies from South Africa. Taxa with a lesser degree of estuarine dependency appear to have adapted to utilize low energy surf zones and coastal embayments as nursery areas, and the presence of *Mugil cephalus*, traditionally considered to be strictly estuarine dependent, in a region devoid of estuaries challenges its estuarine dependent classification. It is suggested that the apparent dependence of some taxa on estuaries is regionally specific, and perhaps not due to an intrinsic reliance on estuarine function, but rather the lack of alternative habitats that serve necessary ecosystem functions. This supports the growing consensus that estuaries have been overemphasized as critical nursery habitats in the absence of rigorous qualitative and quantitative assessments of other shallow water nursery habitats, such as rocky bays (Strydom 2008). The early stage fish assemblage undergoes significant seasonal change, with the dry season dominated by *D. sargus* and *Liza* spp., which inhabit the immediate surf zone year around. The wet season is dominated by a much more diverse suite of pelagic, cryptic and coastal species, including *S. sagax*, which is not common in southern African surf zones, and two coastal species with tropical affinity (*P. rogerii* and *T. ovatus*). *Diplodus sargus* exhibited spawning behaviour, which highlights that sparid spawning is not intrinsically linked to photoperiod, but is rather a function of sea temperature. There was no apparent difference in the community associated with each habitat, but future efforts must be made to investigate the potential for different communities to use microhabitats within this heterogeneous surf zone environment. Tentative evidence for the nursery value of the surf zone is presented, but further efforts must be made to assess the true nursery value of these habitats to these species, as it not possible to unequivocally declare this without evidence of growth or feeding in this environment.

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Chapter 3

Evaluation of contrasting shallow water habitats used as nursery areas for the larval and early juvenile fishes in the absence of estuaries in southern Angola

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Introduction

The southern Angolan coastline is one of two warm-temperate marine ecoregions in southern Africa. This region, located within the Angola-Benguela Frontal Zone (ABFZ), is a complex of biogeographic, climatic and oceanographic phenomena. Prior to the formation of the Benguela Current, the fauna of this warm-temperate region was connected to the warm-temperate region on South Africa's east coast (Henriques et al. 2014, Henriques et al. 2015), forming what then was one homogenous warm-temperate assemblage along South Africa's coastline (van Zinderen Bakker 1975). The formation of the cold Benguela Current (2 mya) split this population, forming a vicariant thermal barrier between the two warm-temperate ichthyofaunal assemblages we know today (Floeter et al. 2008, Henriques et al. 2014). Consequently, these two regions share many common fauna, some of which are important fishery species (e.g. *Lichia amia* and *Pomatomus saltatrix*). Allopatric speciation since isolation by the Benguela Current is evident, with several complexes observed, particularly within the family Sparidae (e.g. *Diplodus sargus* and *Diplodus cervinus*) (Richardson 2010, Winkler 2013) and Sciaenidae (e.g. *Atractoscion aequidens* and *Argyrosomus coronus*) (Henriques et al. 2014, Henriques et al. 2015).

These two regions are characterized by markedly different environmental conditions, both marine and terrestrial. Southern Angola has been termed a climate change hotspot, attributed to above average decadal increases in ocean temperatures (Monteiro et al. 2008, Hobday and Pecl 2014, Potts et al.2015). The formation of the Benguela Current caused a mass terrestrial aridification along southern Africa's west coast, forming the Namib Desert. The associated reduction in rainfall reduced estuarine function, leaving only one estuary, the Cunene, on the southern Angolan coast. Warm-temperate South Africa is endowed with 117 functional estuaries (Whitfield 1998), and their use by early stages of warm-temperate coastal fishes is well documented (Beckley 1984, Clarke et al.1994, Wallace et al. 1984, Strydom 2003, Kruger and Strydom 2010, Wasserman et al. 2010, Strydom 2015). Some species are classified as strictly dependent on this environment to complete their life cycle (e.g. *Mugil cephalus*). Assuming these two regions once shared an identical ichthyofaunal assemblage, the response of warm-temperate estuarine dependent species to the loss of functional estuaries in southern Angola is brought into question. Estuarine associated species would have to adapt to utilize alternative nursery habitats, or be extirpated by the loss of this important habitat.

The isolation of these regions presents a unique opportunity to investigate several questions regarding the fate of estuarine residency and the adaptability of warm-temperate ichthyofauna. This natural laboratory presents a unique opportunity to infer the adaptability of South Africa's warm-temperate ichthyofaunal assemblage to anthropogenic climate change and the associated forecasted loss of estuarine function. In Chapter 2, it was hypothesized that the loss of functional estuaries would have extirpated some estuarine associated taxa, particularly those classified as dependent on estuaries. The results from Chapter 2 suggest that the loss of functional estuaries did alter the structure of the larval and early juvenile ichthyofaunal community present in the surf zone, although some taxa appear to persist despite this loss. The predominance of estuarine associated taxa in the southern Angolan surf zone, and the observation of an estuarine dependent species (*Mugil cephalus*), in a region devoid of estuaries suggests that some taxa have adapted to utilize alternative nursery habitats. This raises the question, 'What alternative habitats are these adaptable taxa using as an estuarine substitute?' In other arid areas, for instance in South Western Australia (SWA), estuarine associated taxa have adapted to utilize alternative inshore nurseries such as large coastal embayments (Potter et al. 1990). In their review, Potter et al. (1990) suggest that the reason for the low overall estuarine dependency of the SWA coastal fish community is the high availability of large, sheltered coastal embayments. South Africa's exposed, high energy coastline is not endowed with such embayments, and it was presumed that South African estuaries are the most sheltered habitat available, resulting in a highly estuarine dependent ichthyofaunal community. Conversely, Strydom (2008) suggested that there are in fact alternative, non-estuarine habitats available to early stage fishes, such as shallow sub-tidal bays associated with rocky shores. There appears to be growing consensus that the importance of estuaries as nurseries has been overemphasized for some taxa, a trend exacerbated by insufficient investigations of alternative shallow water nursery habitats (Able and Fahay 1998, Able 2005). This understanding coupled with the results from Chapter 2 suggests that estuarine dependency is regionally specific. For some taxa, their estuarine dependency may rather be a product of suitable alternative habitat availability than an intrinsic dependence on estuarine function (Potter at al. 1990, Able 2005).

Considering the apparent adaptability of some estuarine associated taxa to the absence of functional estuaries in southern Angola, is there potential for some species not found in the surf zone (Chapter 2) to be present in alternative nursery habitats, such as coastal embayments? The aim of this chapter was to assess the community of larval and early juvenile ichthyofauna utilizing Tombua Bay, and to evaluate the utilization of the three contrasting shallow water (±1.5m) habitats that characterize this area of the coastline.

Aims

1. To assess the seasonality and composition of the early stage fishes present in Tombua Bay.

2. To evaluate the nursery potential and utilization of three contrasting shallow water habitats in southern Angola, namely: sheltered bay, moderately exposed beach and exposed surf zone.

Materials and methods

Study site

Larval and early juvenile fishes were collected from three surf zone sampling areas composed of four sampling sites each. The first area is located within the shelter of Tombua Bay (Sheltered Bay – SB), while the second was located immediately outside the shelter of the embayment (Outside Bay – OB). The third sampling area was located in a nearby exposed surf zone (Surf Zone – SZ), approximately midway between Tombua Bay and the town of Namibe (S 15.192361° E 12.147714°). Tombua Bay is a coastal embayment in southern Angola, which serves as a natural deep water port for the fishing town of Tombua (S 15.802265° E 11.848411°) (Figure 3.1). Tombua Bay has a long sandy shoreline with a short bank of approximately 1-2 m deep, which descends rapidly to depths in excess of 31 m. Wave action immediately outside the shelter of the bay is continuous, and varies seasonally, while there is little to no wave action within the bay. The shoreline immediately adjacent to the town of Tombua was avoided, as this area has been developed by the fishing industry and is unsuitable for this sampling methodology due to depth and hazardous infrastructure. The nearby exposed surf zone sampling area is characterized by long sandy beaches interspersed with smooth sandstone reef. Sampling sites from this area were selected to provide an accurate representation of species composition across habitat types. Two sampling sites were restricted to mixed shores, and two sampling sites were confined exclusively to sandy troughs. Overall, the sampling areas and sites were chosen because they provide ready access to four-wheel drive vehicles, and because they represent a spectrum of habitat types and a gradient of exposure to surf zone energy.

Field sampling and larval identification

Twelve sampling sites were chosen (Figure 3.1), and seasonal samples were conducted at these sites for two consecutive months in both the wet and dry season. Sampling was restricted to a two-day window either side of spring low tide to allow for selection of best weather and surf energy conditions. Sampling began two hours before low tide, and was generally completed within four hours. Four sites were chosen inside the sheltered bay (SB), outside the bay (OB) and along the exposed surf zone (SZ). The SB and OB habitats did not change seasonally, and therefore sampling took place at the exact same locations every trip. However, in the SZ study area, seasonal changes in the relative proportions of primary reef and sandy habitat and the depth of sandy troughs meant that individual sites were occasionally shifted several hundred meters (<1 km) to optimize sampling success.

The field sampling methodology duplicates that employed by Strydom (2003) for the sake of comparability between the two warm-temperate ecoregions in southern Africa. Samples were collected sequentially from selected sites spaced approximately equidistant along each study area using a 4.5 x 1.5 m modified beach seine net (500 µm) operated by two people. Fishes were concentrated into a cone shaped cod-end, from which the catch was flushed into a 25 l bucket using smaller containers and further sieved (500 µm) and contracted into sample containers. Samples were fixed using a 10% formalin and seawater solution. The seine was pulled into the current for 25 m alongshore, in water that approximated the height of the net (1.5 m) depending on wave action. Operators endeavoured to keep the seine submerged at all times for standardization. Seine net pulls were triplicated at each site, which resulted in a total 75 m pull of each sampling site per month. A total of 144 individual replicate pulls were performed during the study.

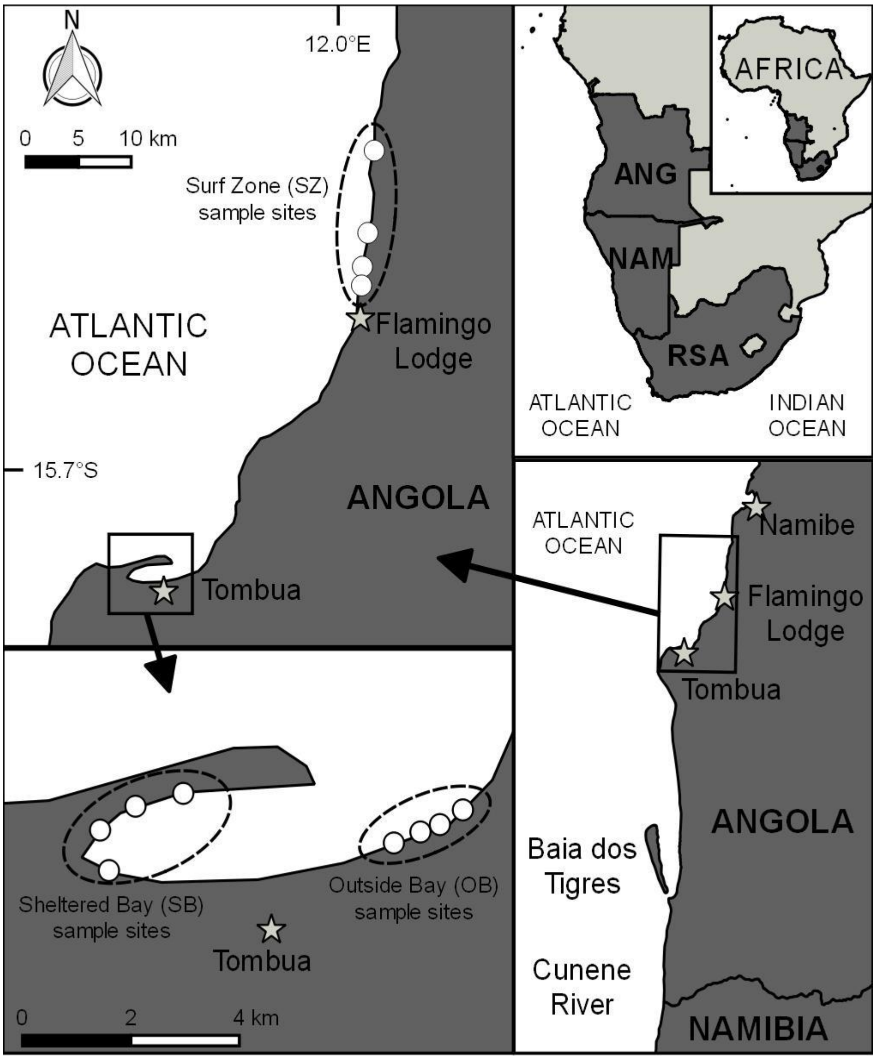

Figure 3.1: Map showing the coastal embayment study area and the relative position of the nearby surf zone.

Temperature was recorded at each site using a standard mercury thermometer, and turbidity was measured using a Hannah turbidity meter. Salinity was recorded using a refractometer, but little variation in salinity and the lack of freshwater influence precluded the usefulness of this variable in this study. All terminology pertaining to developmental stages follows that by Neira et al. (1998). The term "larva/larvae" refers to preflexion, flexion and postflexion developmental stages, while the term "early stage fishes" refers to both larvae and early juveniles. Ichthyoplankton samples were sorted in the laboratory, and identified to the lowest possible taxon. Taxa identified to species were classified into guilds based on estuarine association, in concordance with Potter et al. (2015), to assess the overall estuarine association of the community. The lack of available ichthyological information from Angola was particularly troublesome, and many species encountered remain only classified to family level, despite being in the postflexion phase making them easier to identify with defined characteristics. Many identifications utilized information available from FishBase and the related species from South Africa. Up to 30 individuals per site were randomly measured for each species. Fish length was recorded as Body Length (BL), which comprised the Notochord Length (NL) for preflexion and flexion larvae, and Standard Length (SL) for post flexion larvae and early juveniles (Neira et al. 1998).

Data analyses

Data were tested for normality using a Levene's test and Kolmogorov–Smirnoff test. All data failed to meet the assumptions of parametric tests, so non-parametric statistics were utilized. Differences in mean temperature and turbidity between sampling areas were tested using a Kruskal-Wallis Analysis of Variance (KWANOVA), and between seasons using a Mann–Whitney U (MWU) test. Species were considered dominant if they represented more than 1% of the total catch, and only these species are consistently reported on throughout this study. A KWANOVA was used to assess differences in mean CPUE (all species) of each habitat, and pairwise MWU tests were performed to determine which means differed from others. Species diversity was calculated using the Shannon–Wiener Diversity Index, while species richness was calculated using Margalef's Species Richness Index. Indices were calculated, for the entire 13-month sampling period, each month and each season. A KWANOVA was used to assess differences in mean body length between habitat types, and pairwise MWU tests were used to assess which habitats differed from others. Dominant species were only considered for this test if more than 10 individuals were recorded in each habitat type, and if the total catch was greater than 30.

A community analysis approach (Clarke 1993) was employed to assess communities across both seasons and habitats. Multivariate analyses were performed using PRIMER V6 statistical software package (Clarke and Warwick 2001). Bray–Curtis similarity matrices were generated for biological data, while a Euclidean distance similarity matrix was utilized for the environmental data. The biological data set was log-transformed or transformed to binomial presence/absence. Environmental data were square-root transformed and then normalized prior to analysis. Group average hierarchical clustering was used to assess groups in dendrogram format, while ANOSIM was used to test for differences between groups. Relative contributions to similarity or dissimilarity between groups were determined using SIMPER. Multivariate environmental matching was employed to assess the relatedness of change in the environmental and biological datasets. The relationship between environmental and biological similarity matrices was assessed using RELATE. BIO-ENV was used to determine which environmental variable best explained this relationship.

Results

Habitat variability

There was a significant difference in the mean temperature (H = 9.3; P = 0.01) and turbidity (H = 18.8; P<0.01) among habitats, with mean temperatures in the OB significantly (P<0.01) lower (18.0℃ ± 4.6 SD) than other habitats (SB: $\bar{x}$ = 21.1℃ ± 3.5 SD; SZ: $\bar{x}$ = 21.1℃ ± 2.2 SD). Mean turbidity was significantly higher (P<0.01) in the SZ ($\bar{x}$ = 9.2 NTU ± 8.7 SD) when compared with the OB ($\bar{x}$ = 4.9 NTU ± 1.9 SD) and SB ($\bar{x}$ = 4.1 NTU ± 1.2 SD) (Figure 3.2). There was a significant difference in mean temperature between seasons (H = 16.0; P<0.01), with temperature significantly higher in the wet ($\bar{x}$ = 22.1℃ ± 4.2 SD) than the dry ($\bar{x}$ = 18.0℃ ± 1.7 SD) season. There was no significant difference in temperature (P = 0.10) or turbidity (P = 0.79) within the SB between seasons. Turbidity in the OB was significantly higher (P = 0.02) in the dry season (Figure 3.2). There was no seasonal difference in turbidity (P = 0.98) in the

SZ, however temperature was significantly higher in the wet season ($P<0.01$) (Figure 3.2). The variation in temperature was large for the SB and OB sites, while there was little variation between sites in the SZ (Figure 3.2). The range in temperature decreased from the SB to the SZ. In contrast, the mean and range of turbidity increased from the SB to the SZ.

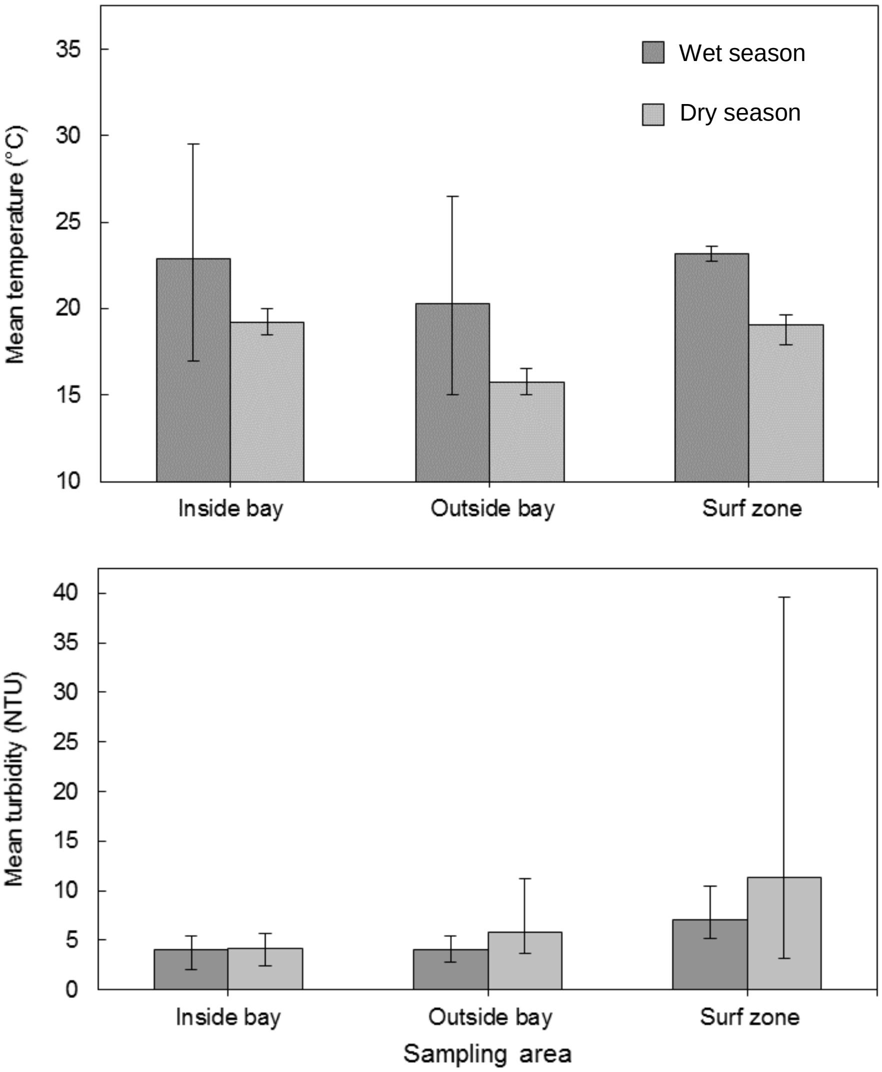

Figure 3.2: Mean temperature and turbidity for the three sampling areas during each season, with range indicated by bars.

Catch composition, developmental stages and estuary association

A total of 14 588 larval and early juvenile fishes were captured, belonging to 18 families and 51 species (Table 3.1). The total catch was dominated by nine species from eight families, namely *Gymnammodytes capensis* (27.3%, Ammodytidae), *Liza* spp. (30.5%; Mugilidae), *Diplodus sargus* (12.2%; Sparidae), *Sardinops sagax* (10.3%; Clupeidae), *Pomadasys rogerii* (5.8%; Haemulidae), *Gobius* spp.1 (3.6%; Gobiidae), *Mugil cephalus* (2.8%; Mugilidae), *Oblada melanura* (1.5%; Sparidae), Carangidae 2 (1.3%; Carangidae) and *Eucinostomus melanopterus* (1%; Gerreidae). *Liza* spp. was the most dominant species in the SB (62.6%), while *Gymnammodytes capensis* (67.7%) dominated catch in the OB. Catches from the SZ were dominated by *Diplodus sargus* (80.4%). While not a dominant species, four individual *Argyrosomus coronus* were captured in the SB, and this represents the first larval record of this species. Nine of the 51 species observed were common to all three habitats, namely *Parablennius pilicornis* (Blennidae), *Sardinops sagax, Sardinella aurita* (Clupeidae), *Eucinostomus melanopterus, Gobius* spp. *1, Pomadasys rogerii, Liza* spp.*, Umbrina canariensis* (Sciaenidae), *Dicologlossa cuneata* (Soleidae), *Diplodus sargus* and Sparidae 5.

Overall, early juveniles dominated the catch (57%), followed by postflexion larvae (35%). Early juveniles dominated the catch from the SB (62%) and OB (59%), while the SZ was dominated by postflexion larvae (99%). Overall, most taxa observed were classified as Marine Estuarine Opportunists (MEO) (44%), which collectively contributed 53% of the total catch by number (Figure 3.3, Table 3.2). Based on number of taxa, MEOs dominated the species composition in the SB (55%) and SZ (43%), while Exclusively Marine Species (EMS) dominated (41%) in the OB. The proportion of Marine Estuarine Dependent (MED) and Marine Estuarine Straggler (MES) taxa was similar across habitats (Figure 3.3). Marine estuarine opportunists dominated the catch (in terms of number) in the SB (83%) and the SZ (84%), while MESs dominated the catch from the OB (68%) (Figure 3.3). Marine estuarine dependent species were not important (<1%) in the catch composition of the SZ or OB. However, they were more important (7%) in the SB. The relative contribution of the MED guild was low in the SZ (<1%) and OB (<1%), but higher in the SB (7%) (Figure 3.3). The catch from the OB showed the highest proportions of Exclusively Marine Species (EMS) (68%) and MES guilds (21%), while SB and SZ showed similarly low proportions of these guilds (4–12%). *Liza* species and *P. rogerii* were the dominant MEO species in the SB, while *D. sargus* was the dominant MEO species in the SZ (Table 3.1; Figure 3.3). *Gymnammodytes capensis* and *S. sagax* were the dominant MES in the OB. *Mugil cephalus* was the most important MED in the SB.

Table 3.1: Total catch and Catch Per Unit Effort of all species observed inside the embayment, outside the embayment and the nearby surf zone.

		Total Catch (n)						Catch Per Unit Effort					
		Inside bay		Outside bay		Surf zone		Inside bay		Outside bay		Surf zone	
Family	Species	N	%	N	%	N	%	Mean	Range (mm)	Mean	Range (mm)	Mean	Range (mm)
Ammodytidae	*Gymnammodytes capensis*	42	<1	3947	**67.7**	-	-	0.9	(0 - 12.7)	82.2	(0 - 1169)	-	-
Blennidae	*Parablennius pilicornis*	1	<1	1	<1	5	<1	0.0	(0 - 0.3)	0.0	(0 - 0.3)	0.2	(0 - 1.3)
	Scartella emarginata	-	-	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)
Carangidae	*Decapterus punctatus*	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-	-	-
	Trachurus spp. *1*	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-
	Trachinotus ovatus	2	<1	-	-	-	-	0.0	(0 - 0.3)	-	-	-	-
	Carangidae 1	31	<1	2	<1	-	-	0.6	(0 - 10)	0.0	(0 - 0.7)	-	-
	Carangidae 2	183	**2.6**	2	<1	-	-	3.8	(0 - 56.7)	0.0	(0 - 0.7)	-	-
Clupeidae	*Sardinella aurita*	24	<1	7	<1	67	**4.0**	0.5	(0 - 5.7)	0.1	(0 - 2.3)	2.0	(0 - 21.7)
	Sardinops sagax	252	**3.6**	1118	**19.2**	129	**7.6**	5.3	(0 - 62.7)	23.3	(0 - 171.7)	3.9	(0 - 39)
Elopidae	*Elops lacerta*	-	-	-	-	1	<1	-	-	-	-	-	-
Engraulidae	*Engraulis encrasicolus*	16	<1	-	-	1	<1	0.3	(0 - 4)	-	-	0.0	(0 - 0.3)
Gerreidae	*Eucinostomus melanopterus*	9	<1	123	**2.1**	11	<1	0.2	(0 - 2.3)	2.6	(0 - 17)	0.3	(0 - 3.7)
Gobiidae	*Gobius* spp. *1*	529	**7.5**	1	<1	1	<1	11.0	(0 - 164)	0.0	(0 - 0.3)	0.0	(0 - 0.3)
	Gobius spp. *2*	3	<1	-	-	-	-	0.1	(0 - 1)	-	-	-	-
	Gobius spp. *3*	-	-	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)
Haemulidae	*Pomadasys rogerii*	691	**9.8**	118	**2.0**	34	**2.0**	14.4	(0 - 129)	2.5	(0 - 16.3)	1.0	(0 - 10.7)
Kyphosidae	*Kyphosus sectatrix*	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-
Mugilidae	*Liza* spp.	4426	**62.6**	20	<1	7	<1	92.2	(0 - 1163.3)	0.4	(0 - 6)	0.2	(0 - 2.3)
	Mugil cephalus	410	**5.8**	-	-	2	<1	8.5	(0 - 124.3)	-	-	0.1	(0 - 0.3)
	Mugilidae 1	10	<1	-	-	-	-	0.2	(0 - 1.7)	-	-	-	-
Percophidae	Percophidae 1	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-
Sciaenidae	*Argyrosomus coronus*	4	<1	0	<1	-	-	0.1	(0 - 1.3)	-	-	-	-
	Umbrina canariensis	2	<1	9	<1	1	<1	0.0	(0 - 0.7)	0.2	(0 - 2)	0.0	(0 - 0.3)
Soleidae	*Dicologlossa cuneata*	93	**1.3**	12	<1	6	<1	1.9	(0 - 31)	0.3	(0 - 4)	0.2	(0 - 2)
	Heteromycteris capensis	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-	-	-

Table 3.1 *continued*: Total catch and Catch Per Unit Effort of all species observed inside the embayment, outside the embayment and the nearby surf zone.

		Total catch (n)						Catch Per Unit Effort					
		Inside bay		Outside bay		Surf zone		Inside bay		Outside bay		Surf zone	
Family	Species	N	%	N	%	N	%	Mean	Range (mm)	Mean	Range (mm)	Mean	Range (mm)
	Monochirus ocellatus	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-
	Pegusa lascaris	1	<1	3	<1	-	-	0.0	(0 - 0.3)	0.1	(0 - 0.7)	-	-
Sparidae	*Diplodus cervinus*	-	-	89	**1.5**	-	-	-	-	1.9	(0 - 18.3)	-	-
	Diplodus sargus	74	**1.0**	339	**5.8**	1359	**80.4**	1.5	(0 - 7.7)	7.1	(0 - 40.3)	41.2	(0 - 451.7)
	Oblada melanura	220	**3.1**	-	-	-	-	4.6	(0 - 66)	-	-	-	-
	Sarpa salpa	6	<1	1	<1	-	-	0.1	(0 - 1)	0.0	(0 - 0.3)	-	-
	Spondyliosoma	3	<1	3	<1	-	-	0.1	(0 - 0.7)	0.1	(0 - 0.3)	-	-
	Sparidae 1	-	-	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)
	Sparidae 2	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-
	Sparidae 3	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-
	Sparidae 4	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-
	Sparidae 5	5	<1	8	<1	3	<1	0.1	(0 - 1.7)	0.2	(0 - 2.7)	0.1	(0 - 1)
	Sparidae 6	3	<1	2	<1	-	-	0.1	(0 - 0.7)	0.0	(0 - 0.7)	-	-
Syngnathidae	*Microphis aculeatus*	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-
Tetraodontidae	*Lagocephalus laevigatus*	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-
Tripterygiidae	Tripterygiidae 1	-	-	1	<1	60	**3.5**	-	-	0.0	(0 - 0.3)	1.8	(0 - 20.3)
Unidentified	Species 1	1	<1	3	<1	-	-	0.0	(0 - 0.3)	0.1	(0 - 0.7)	-	-
	Species 2	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-
	Species 3	1	<1	-	-	-	-	0.0	(0 - 0.3)	-	-	-	-
	Species 4	22	<1	-	-	-	-	0.5	(0 - 7)	-	-	-	-
	Species 5	-	-	-	-	1	<1	-	-	-	-	0.0	(0 - 0.3)
	Species 6	-	-	2	<1	-	-	-	-	0.0	(0 - 0.3)	-	-
	Species 7	-	-	2	<1	-	-	-	-	0.0	(0 - 0.7)	-	-
	Species 8	-	-	2	<1	-	-	-	-	0.0	(0 - 0.7)	-	-
	Species 9	5	<1	1	<1	-	-	0.1	(0 - 1.7)	0.0	(0 - 0.3)	-	-
	Total Catch	7071		582		1691	CPUE	121.4		147.3		17.62	

Table 3.2: Mean body length, developmental stages and estuarine association guilds (Potter et al. 2015) of all species observed inside the embayment, outside the embayment and the nearby surf zone.

		Body length (BL) (mm)									
		Inside bay		Outside bay		Surf zone		Developmental stage			
Family	Species	Mean	Range	Mean	Range	Mean	Range	SB	OB	SZ	Guild
Ammodytidae	*Gymnammodytes capensis*	41.3	(38.2 - 44.8)	36	(18.6 - 74.7)	-	-	Po, **Ej**	Po, **Ej**	-	EMS
Blennidae	*Parablennius pilicornis*	18.4	(18.4 - 18.4)	5	(5 - 5)	15.1	(14.6 - 16)	**Ej**	**Po**	**Po**, Ej	EMS
	Scartella emarginata	-	-	-	-	11.1	(11.1 - 11.1)	-	-	**Ej**	EMS
Carangidae	*Decapterus punctatus*	32.5	(32.5 - 32.5)	-	-	-	-	**Ej**	-	-	EMS
	Trachurus spp. *1*	-	-	12.2	(12 - 12.3)	-	-	-	**Ej**	-	EMS
	Trachinotus ovatus	11	(11 - 11)	-	-	-	-	**Ej**	-	-	MEO
	Carangidae 1	2.6	(2.2 - 2.9)	2.3	(2.3 - 2.3)	-	-	**Pr**	**Pr**	-	
	Carangidae 2	2.4	(1.9 - 3.1)	2.3	(2.3 - 2.3)	-	-	**Pr**	**Pr**	-	
Clupeidae	*Sardinella aurita*	17.9	(14.4 - 24.9)	19	(18.6 - 19.4)	10.8	(8.8 - 12.8)	**Po**, Ej	Po, Ej	F, **Po**	MES
	Sardinops sagax	19	(12 - 25.7)	19.6	(14.7 - 24.6)	17.7	(10.8 - 25.7)	**Po**, Ej	**Po**, Ej	**Po**	MES
Elopidae	*Elops lacerta*	-	-	-	-	32.8	(32.8-32.8)	-	-	**Po**	MEO
Engraulidae	*Engraulis encrasicolus*	38.9	(33.5 - 45.5)	-	-	6.5	(6.5 - 6.5)	**Ej**	-	**Po**	MEO
Gerreidae	*Eucinostomus melanopterus*	14.4	(10 - 20.9)	10.6	(7.4 - 13.4)	10.7	(9 - 14.9)	**Po,** Ej	**Po**, Ej	**Po**, Ej	MEO
Gobiidae	*Gobius* spp. *1*	17	(9.7 - 22)	7.3	(7.3 - 7.3)	15.8	(13.3 - 18.3)	Po, **Ej**	**Po**	Po, **Ej**	
	Gobius spp. *2*	11.3	(10.7 - 11.9)	-	-	-	-	-	Po	-	
	Gobius spp. *3*	-	-	-	-	10.7	(8.4 - 13)	**Po**	-	**Po**	
Haemulidae	*Pomadasys rogerii*	15.3	(7.8 - 24)	11.3	(8.1 - 15.1)	10.6	(9 - 11.7)	**Po**, Ej	**Po**	**Po**	MEO
Kyphosidae	*Kyphosus sectatrix*	-	-	10.1	(10.1 - 10.1)	-	-	-	**Po**	-	EMS
Mugilidae	*Liza* spp.	13.5	(8 - 43.2)	23.3	(12.4 - 31)	28	(16.6 - 36.5)	Po, **Ej**	Po, **Ej**	Po, **Ej**	MEO
	Mugil cephalus	30	(23.5 - 39.5)	-	-	22.3	(22.3 - 22.3)	**Ej**	-	**Ej**	MED
	Mugilidae 1	52	(49.5 - 54.8)	-	-	28.2	(28.2 - 28.2)	**Ej**	-	**Ej**	MEO
Percophidae	Percophidae 1	-	-	8.5	(8.5 - 8.5)	-	-	-	**Po**	-	EMS
Sciaenidae	*Argyrosomus coronus*	8.4	(7.2 - 9.4)	-	-	-	-	-	**Po**	-	MEO
	Umbrina canariensis	9.3	(9.3 - 9.3)	5.9	(5.4 - 7)	5	(5 - 5)	**Po**	**Po**	**Po**	EMS
Soleidae	*Dicologlossa cuneata*	11.1	(7.5 - 13.3)	8.7	(8.1 - 9.4)	5.9	(4.3 - 8.2)	Pr, F, **Po**, Ej	**Po**	F, **Po**	MES
	Heteromycteris capensis	8.4	(8.4 - 8.4)	-	-	-	-	**Ej**	-	-	MEO

Table 3.2: *c*ontinued: Mean body length, developmental stages and estuarine association guilds (Potter et al. 2015) of all species observed inside the embayment, outside the embayment and the nearby surf zone.

		Body length (BL) (mm)									
		Inside bay		Outside bay		Surf zone		Developmental stage			
Family	Species	Mean	Range	Mean	Range	Mean	Range	SB	OB	SZ	Guild
	Monochirus ocellatus	-	-	8.9	(8.9 - 8.9)	-	-	-	**Ej**	-	EMS
	Pegusa lascaris	26	(26 - 26)	15.6	(11.5 - 20.6)	-	-	**Ej**	**Po**, Ej	-	MEO
Sparidae	*Diplodus cervinus*	-	-	10.1	(6.1 - 17.8)	-	-	-	**Po**	-	MES
	Diplodus sargus	17.6	(8.8 - 49)	11.3	(6.8 - 23.2)	8.6	(6.1 - 19)	**Po**, Ej	**Po**, Ej	F, **Po**, Ej	MEO
	Oblada melanura	16.6	(12.8 - 21.3)	-	-	-	-	Po, **Ej**	-	-	EMS
	Sarpa salpa	14.3	(13.4 - 15.5)	12.5	(9.2 - 15.8)	-	-	**Po**	**Po**	-	MEO
	Spondyliosoma emarginatum	8.7	(8 - 9.2)	9.7	(8.2 - 10.8)	-	-	**Po**	**Po**	-	MEO
	Sparidae 1	-	-	-	-	13	(13 - 13)	-	-	**Po**	
	Sparidae 2	-	-	11.9	(11.5 - 12.3)	-	-	-	**Po**	-	
	Sparidae 3	-	-	11.4	(11.4 - 11.4)	-	-	-	**Po**	-	
	Sparidae 4	-	-	9.9	(9.9 - 9.9)	-	-	-	**Po**	-	
	Sparidae 5	-	-	10	(9.5 - 10.7)	8	(7.9 - 8.1)	-	**Po**	**Po**	
	Sparidae 6	10	(9 - 11.5)	13.3	(11.7 - 14.6)	-	-	**P**	**Po,** Ej	-	
Syngnathidae	*Microphis aculeatus*	-	-	37.8	(37.8 - 37.8)	-	-	-	**Ej**	-	MEO
Tetraodontidae	*Lagocephalus laevigatus*	-	-	10.1	(10.1 - 10.1)	-	-	-	**Ej**	-	MEO
Tripterygiidae	Tripterygiidae 1	-	-	8.8	(8.8 - 8.8)	14.8	(13.2 - 15.9)	-	**Po**	**Po**	EMS
Unidentified	Species 1	4.5	(4.5 - 4.5)	2.9	(2.6 - 3.1)	-	-	**F**	**F**	-	
	Species 2	-	-	9.4	(9.4 - 9.4)	-	-	-	**F**	-	
	Species 3	2	(2 - 2)	-	-	-	-	**Pr**	-	-	
	Species 4	2.9	(2.6 - 3.2)	-	-	-	-	**F**	-	-	
	Species 5	-	-	-	-	2.7	(2.7 - 2.7)	-	-	**Pr**	
	Species 6	-	-	2	(2 - 2)	-	-	-	**Pr**	-	
	Species 7	-	-	3.3	(3.2 - 3.3)	-	-	-	**Pr**	-	
	Species 8	-	-	3.8	(2.7 - 4.9)	-	-	-	**Po**	-	
	Species 9	9.8	(9.7 - 9.9)	6.8	(6.8 - 6.8)	-	-	**Po**	**Pr**	-	
						Dominant dev. stage		Ej	Po	Po	

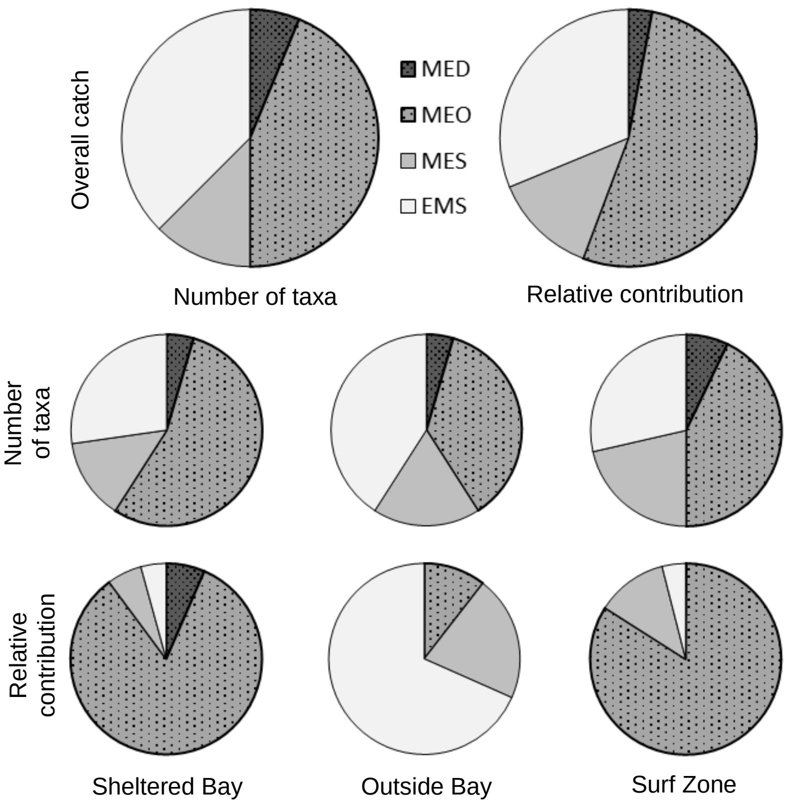

Figure 3.3: Proportion of taxa and relative contribution of taxa classified into guilds of estuarine dependence: Marine Estuarine Dependant (MED), Marine Estuarine Opportunist (MEO), Marine Estuarine Straggler (MES) and exclusively Marine (EMS).

Spatial trends in CPUE and Diversity

More taxa were observed in the SB (n = 31) and OB (n = 30) than the surf zone (n = 20) (Table 3.1; Figure 3.4). The highest diversity was recorded in the SB (H = 1.47; Mg = 3.39), while the lowest diversity was recorded in the SZ (H = 0.84; Mg = 2.29) (Figure 3.4). The catch in the OB had the highest species richness (H = 1.08; Mg = 3.92), while catch in the SZ had the lowest (Mg = 2.29).

There was a significant difference in the mean CPUE between habitat types (*H* = 21.9; P<0.01) (Figure 3.4). The mean CPUE from the SZ was significantly lower than that of sites from the SB (P<0.01) and OB (P<0.01), while mean CPUE did not differ between SB and OB (P = 0.18). There was a significant difference in mean CPUE between habitats for *Liza* species (*H* = 30.9; P<0.001) and *D. sargus* (*H* = 14.78; P<0.01), and a near significant difference for

P. rogerii ($H = 5.94$; $P = 0.05$) (Figure 3.5). The mean CPUE of *Liza* species was significantly higher inside the embayment than outside the embayment ($P<0.01$) or the surf zone ($P<0.01$). Similarly, the mean CPUE of *P. rogerii* was significantly higher inside the embayment than the surf zone ($P = 0.02$). Both *Liza* species and *P. rogerii* showed a decreasing trend in mean CPUE as habitats moved from inside the embayment towards to surf zone (Figure 3.5). There was a significant difference in the mean CPUE of *D. sargus* ($H = 14.78$; $P<0.01$) across habitats, with mean CPUE significantly higher outside the embayment than inside the embayment ($P = 0.04$) or the surf zone ($P<0.01$) (Figure 3.5). There was no significant difference in mean CPUE across habitat for the other dominant species ($P>0.05$).

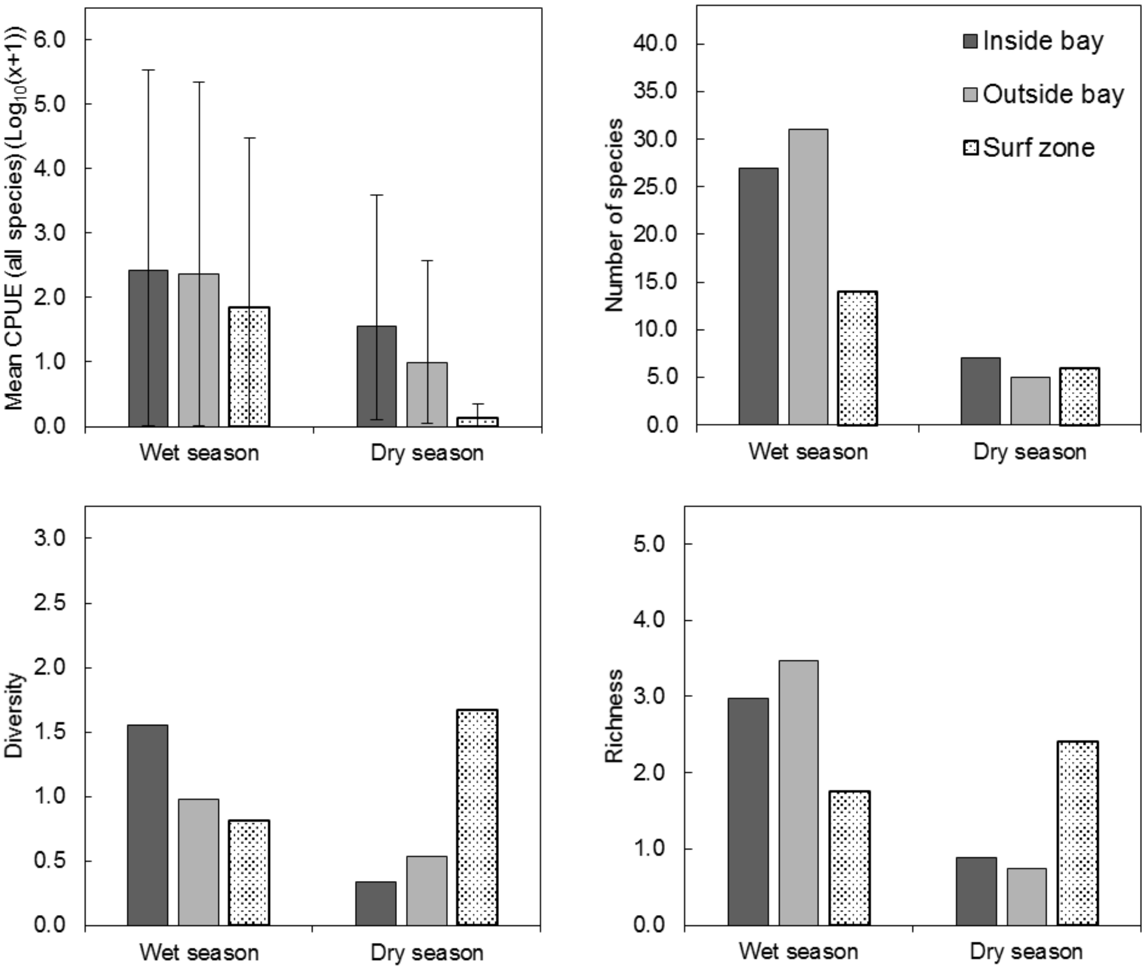

Figure 3.4*:* Mean CPUE (all species) ($Log_{10}(x+1)$), number of species, diversity and species richness of each habitat during each season.

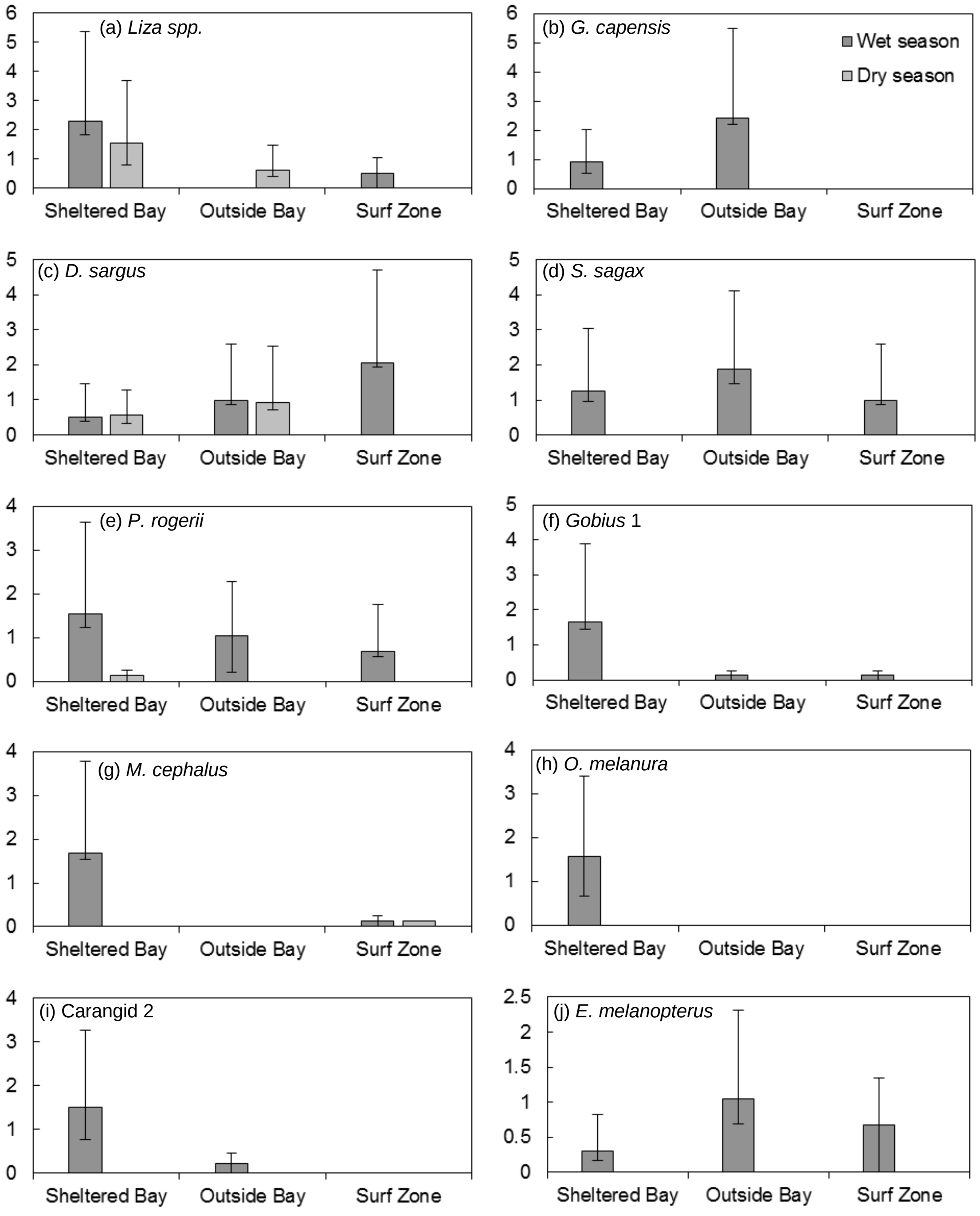

Figure 3.5: Mean Catch Per Unit Effort ($Log_{10}(x+1)$) of the 10 dominant (>1%) species across habitat and season. (a) *Liza* species; (b) *Gymnammodytes capensis*; (c) *Diplodus sargus*; (d) *Sardinops sagax*; (e) *Pomadasys rogerii*; (f) *Gobius* 1; (g) *Mugil cephalus*; (h) *Oblada melanura*; (i) Carangid 2; (j) *Eucinostomus melanopterus*.

Seasonal trends in CPUE and Diversity

During the wet season, the highest diversity was observed inside the embayment (No. of taxa = 27; *H'* = 1.55; *d* = 2.98), while the lowest was observed in the surf zone (No. of taxa = 14; *H'* = 0.81; *d* = 1.75). During the dry season, the inverse occurred, with diversity highest in the surf zone (No. of taxa = 6; *H'* = 1.67; *d* = 2.41), and lowest inside the embayment (No. of taxa = 7; *H'* = 0.34; *d* = 0.89). During the wet season, the highest species richness was observed in the OB (No. of taxa = 31; *H'* = 0.98; *d* = 3.47), while the lowest was observed in the SZ (No. of taxa = 14; *H'* = 0.81; *d* = 1.75). During the dry season, the inverse occurred, with the highest species richness observed in the SZ (No. of taxa = 6; *H'* = 1.67; *d* = 2.41), and the lowest observed in the OB (No. of taxa = 5; *H'* = 0.53; *d* = 0.75). More taxa were observed in catches from all three habitats during the wet season, while all three habitats showed similarly low numbers of taxa during the dry season. Overall, the mean CPUE was significantly higher in the wet season (H = 5.8; P = 0.02) (Figure 3.4). There were no significant differences in the mean seasonal CPUE in the SB (P = 0.32) or OB (P = 0.05). However, the mean CPUE in the SZ was significantly higher during the wet season (P = 0.02).

Community analysis and environmental matching

The cluster analysis yielded no useful groupings by habitat type using fish abundance, but ANOSIM indicated a significant separation between habitats based on species presence/absence (R = 0.24; P>0.01) and species CPUE (R = 0.35; P>0.01). Overall, each habitat showed a relatively low within-group similarity: SB (31.3%), OB (24.8%) and the SZ (6.3%) (SIMPER). In the SB, 94% of the within-group similarity was ascribed to *Liza* spp. (73.7%), *D. sargus* (10.5%) and *P. rogerii* (10%). In the OB, 93% of the within-group similarity was ascribed to *D. sargus* (83.3%), *S. sagax* (5.16%) and *G. capensis* (4.3%). In the SZ, 95% of the within-group similarity was ascribed to *S. sagax* (60%), *D. sargus* (12.7%), *S. aurita* (9.7%), *P. rogerii* (7%) and *M. cephalus* (5.9%). Pairwise ANOSIM indicated a significant separation between the communities from each habitat based on species CPUE (Table 3.3). Four species namely *Liza* spp., *D. sargus, P. rogerii* and *S. sagax* were consistently and principally responsible for dissimilarity (SIMPER) between habitats.

Table 3.3: ANOSIM and SIMPER results from pairwise comparison of habitat specific ichthyofaunal communities. (SB = Sheltered Bay; OB = Outside Bay; SZ = Surf Zone).

	ANOSIM		SIMPER
Habitat	Global R	P	Species (Dissimilarity %)
SB vs OB	0.364	< 0.01	*Liza* spp. (27.4), *Diplodus sargus* (14.1), *Pomadasys rogerii* (10.7), *Sardinops sagax* (8.3), *Gymnammodytes capensis* (8.0).
SB vs SZ	0.386	< 0.01	*Liza* spp. (32.2), *Pomadasys rogerii* (11.7), *Diplodus sargus* (11.1), *Sardinops sagax* (9.0).
OB vs SZ	0.312	< 0.01	*Diplodus sargus* (29.1), *Sardinops sagax* (14.0), *Gymnammodytes capensis* (10.6), *Liza* spp. (6.0), *Pomadasys rogerii* (5.6), *Sardinella aurita* (5.2).

The cluster analysis yielded no useful groupings in abundance by season, but ANOSIM indicated a significant seasonal separation based on species presence/absence ($R = 0.25$; $P<0.01$) and species CPUE ($R = 0.239$; $P = 0.001$). The SIMPER based on species presence/absence indicated relatively low within group similarity between samples from the wet (23.5%) and dry season (30.8%). Within the wet season, 74% of the similarity between samples was ascribed to *D. sargus* (24.6%), *S. sagax* (23.7%), *P. rogerii* (20.3%) and *G. capensis* (5.4). Within the dry season, 98% of the similarity between samples was ascribed to *D. sargus* (64.7%), *Liza* spp. (29.9%) and *S. salpa* (3%). SIMPER indicated an 84% dissimilarity between seasonal communities. More than 55% of this dissimilarity was ascribed to eight dominant species, namely *D. sargus* (10.3%), *Liza* spp. (9.5%), *S. sagax* (8.9%), *P.*

rogerii (8.5%), *G. capensis* (5.3%), *E. melanopterus* (4.4%), *Mugil cephalus* (3.5%), and Gobius spp. 1 (2.8%). Apart from *Liza* spp., all aforementioned dominant species were more abundant during the wet season (Figure 3.5), as were a large number of non-dominant taxa only observed during this period.

Multivariate environmental matching (PRIMER) indicated a significant correlation (RELATE) between environmental variables and samples based on species presence/absence (R = 0.148; P = 0.02) and species CPUE (R = 0.161; P = 0.02). Temperature best explained the presence/absence of species (r = 0.156), while a function of both temperature and turbidity best explained changes in species CPUE (r = 0.161).

Body length

The mean body length of the 10 most dominant species was analysed by season and habitat (Figure 3.6). The most dominant species, *Liza* spp. was observed in all three habitats, and a significant difference was observed in mean body length among habitat types (H = 58.5; P<0.01). *Liza* spp. showed an increasing trend in mean size as habitat moved from the SB ($\bar{x}$ = 13.5 mm BL), to OB ($\bar{x}$ = 23.4 mm SL) and the SZ ($\bar{x}$ = 28 mm SL). A significant difference in mean body length was also observed for *D. capensis* (H = 102.8; P<0.001) and *P. rogerii* (115.7; P<0.001) across habitats. The mean body length of *D. capensis* decreases significantly along the habitat gradient from the SB ($\bar{x}$ = 17.7 mm BL ± 10.9 SD), to the OB ($\bar{x}$ = 11.3 mm BL ± 1.35 SD) and the SZ ($\bar{x}$ = 8.6 mm BL ± 3.2 SD). Similarly, the mean body length of *P. rogerii* decreased from the SB ($\bar{x}$ = 15.3 mm BL ± 3.3 SD) to the OB ($\bar{x}$ = 11.3 mm BL ± 1.4 SD) and the SZ ($\bar{x}$ = 10.5 mm BL ± 0.8 SD). The mean length of *E. melanopterus* ($\bar{x}$ = 14.4 mm; H = 17.8; P<0.01) was significantly higher in the SB. Although not significant, the mean body length was higher inside the embayment for *G. capensis* ($\bar{x}$ = 41.3 mm; P = 0.38) and *M. cephalus* ($\bar{x}$ = 30 mm). Of the three dominant species observed in both seasons, only *Liza* spp. and *D. capensis* were captured in sufficient quantities for a seasonal comparison of body length.

Overall, there was a significant seasonal difference in the mean body length of *Liza* species ($P<0.01$) and *D. capensis* ($P<0.01$). The mean body length of *Liza* species was significantly higher in the wet season ($\bar{x}$ = 18.4 mm BL ± 8.2 SD) than the dry season ($\bar{x}$ = 11.8 mm BL ± 4.2 SD). In contrast, the mean body length of *D. capensis* was higher in the dry season ($\bar{x}$ = 13.4 mm BL ± 3.9 SD) than the wet season ($\bar{x}$ = 10.9 mm BL ± 8.0 SD).

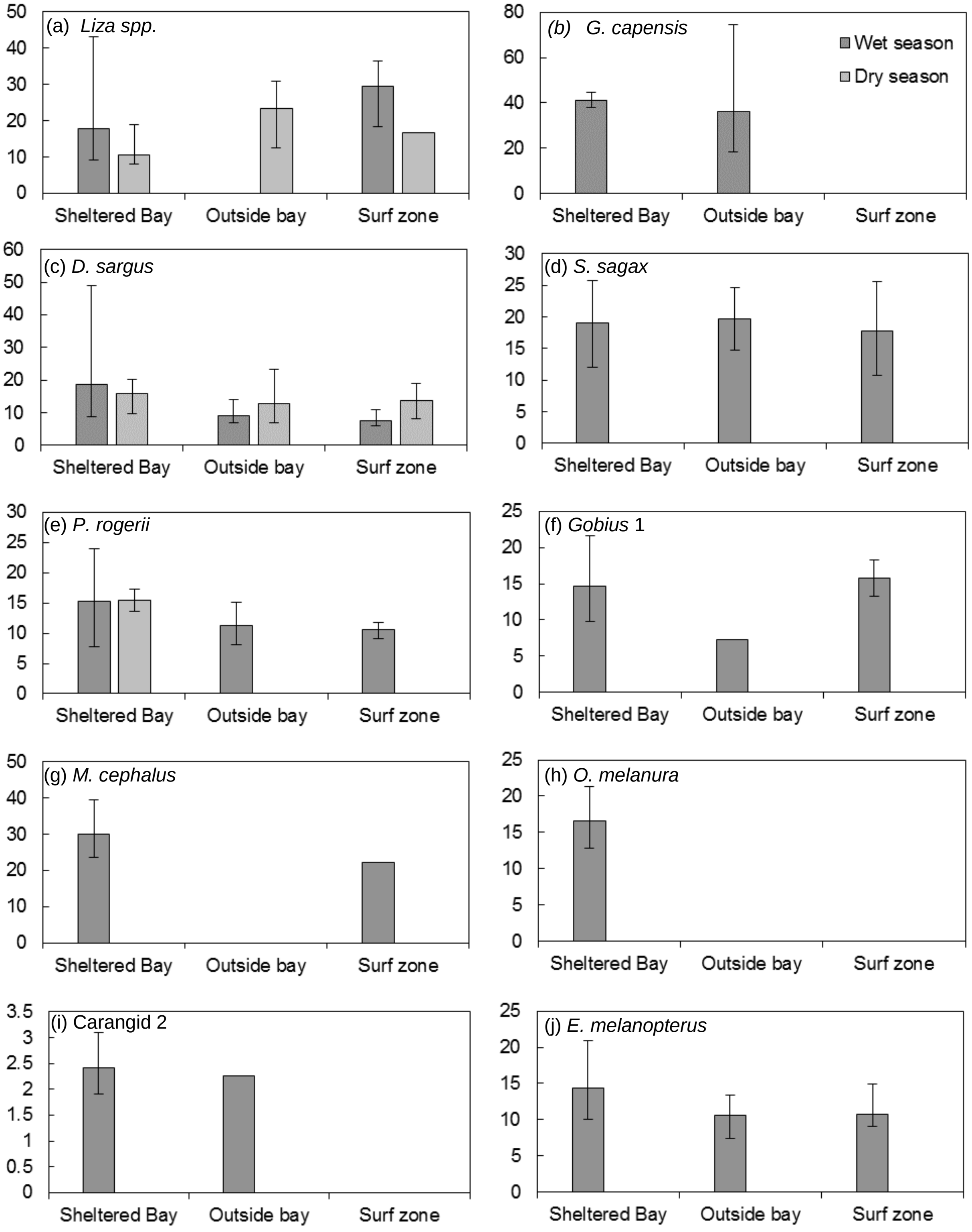

Figure 3.6: Mean body length SL (mm) of the 10 dominant (>1%) species across habitat and season. (a) *Liza species*; (b) *Gymnammodytes capensis*; (c) *Diplodus sargus*; (d) *Sardinops sagax*; (e) *Pomadasys rogerii*; (f) *Gobius* 1; (g) *Mugil cephalus*; (h) *Oblada melanura*; (i) Carangid 2; (j) *Eucinostomus melanopterus*

Discussion

The shallow water (±1.5m) habitats of the southern Angolan coast host a diverse suite of larval and early juvenile fishes. In total, 51 species from 18 families were captured from the SB, OB and SZ. The number of taxa observed in this study was comparable to warm temperate surf zone studies globally, including New Jersey, 47 taxa (Able et al. 2010); Taiwan, 47 taxa (Yang and Senta 1993) and the Gulf of Mexico, 69 taxa (Ruple 1984). Mugilidae, Engraulidae, Clupeidae, Carangidae, Sparidae and Gobiidae were families common to all these studies, and coupled with the similitude of species and genera (e.g. *Engraulis*, *Mugil*, *Liza*), there appears to be evidence for the global use of this habitat by a specialized group of species that have evolved to utilize this dynamic environment (Pattrick and Strydom, 2014).

The number of taxa observed was greater than several warm-temperate surf zone studies on South Africa's east coast (Whitfield 1989, Cowley et al. 2001, Strydom 2003, Watt-Pringle and Strydom 2003, Strydom and d'Hotman 2005). Typically, the number of taxa observed was considerably lower than that in the surf zone (Harris and Cyrus, 1996) and large coastal embayments (Harris and Cyrus 1997, Harris and Cyrus 1999) along the sub-tropical KwaZulu-Natal coast of RSA. Southern Africa's Atlantic seaboard is known for lower ichthyofaunal diversity than its east coast, attributed to the tropical-subtraction effect (Turpie et al. 2000). Contrastingly, the higher diversity of the current study than preceding warm-temperate, surf zone studies is attributed to a larger sampling area and effort, and higher overall habitat complexity. Furthermore, the position of the study area within the ABFZ likely explains the higher diversity, as frontal systems are known for high diversity through species accumulation (Scales et al. 2014). The high diversity and endemism of the Indian Ocean is well documented (Turpie et al. 2000, Joyeux et al. 2008, Floeter et al. 2008), so it is unsurprising that the subtropical surf zones and embayments are more diverse than the current study area. However, the disparity in diversity between the current study and those from sub-tropical South

Africa is amplified by the capture of many exclusively marine species in these subtropical embayments using dissimilar offshore sampling techniques (Harris and Cyrus 1997, 1999). While there is high similarity between the current study and studies of South African warm-temperate surf zones, sound comparisons are troublesome due to differing physical habitat, oceanographical conditions and sampling techniques.

As most studies of large coastal embayments employ boat based sampling techniques (Herman 1963, Jenkins 1986, Beckley 1987, Harris and Cyrus 1997, 1999), the number of studies with comparable shore-based sampling methodology across a similar habitat spectrum was low. This study differs fundamentally from most ichthyoplankton surf zone studies, as it includes shore based surf zone samples from an exposed surf zone (SZ), a moderately exposed sandy beach (OB) and a completely sheltered sandy shoreline (SB). Fortunately, work by Pattrick and Strydom (2014) employed identical sampling techniques along a similar array of habitats, namely the sheltered and exposed shores of Algoa Bay, a large coastal embayment in warm-temperate South Africa. The number of taxa they observed (57 species; 23 families) is similar to that of this study (51 species; 18 families), with several families common to both studies, namely Blennidae, Carangidae, Clupeidae, Engraulidae, Gobiidae, Haemulidae, Kyphosidae, Mugilidae, Sciaenidae, Soleidae, Sparidae and Tripterygiidae. Several species were also common to both studies, including *Parablennius pilicornis, Mugil cephalus, Engraulis encrasicolus, Heteromycteris capensis* and *Sarpa salpa.* Three vicariant sister species were also observed in both studies, including members of the *Spondyliosoma emarginatum, Diplodus cervinus* and *Diplodus sargus* species complexes. Not only does this provide evidence for the historical connection of these two warm-temperate regions, it further highlights the utilization of shallow water habitats (surf zones and coastal bays) as nursery areas for a specialized group of fishes.

Overall, the shallow water study area was dominated (>1% total catch) by 10 species. Several coastal, estuarine associated species were dominant, namely *Liza species Diplodus sargus, Pomadasys rogerii, Mugil cephalus* and *Eucinostomus melanopterus*. Exclusively marine species were also dominant, namely *Gymnammodytes capensis*, *Sardinops sagax* and *Oblada melanura*, as were *Gobius* spp. 1 and *Carangidae* 2. Estuarine associated taxa (MEO and MED) were an important part of the shallow water ichthyoplankton assemblage in this study, representing 50% of the taxa observed, and 56% of the total catch by number. The catch was dominated by MEO taxa (44%), similar to surf zone studies from warm-temperate South Africa, most of which are located near to estuaries e.g. Watt-Pringle and Strydom (2003), 44%; Strydom (2003), 52% and Whitfield (1998), 47%. While estuarine associated taxa dominated in this study, the relative proportion of MED taxa was lower (6% of taxa; 3% of catch) than other warm-temperate studies (7–24% of taxa; 80–98% of catch; Strydom 2003, Whitfield 1989). Exclusively marine species are typically encountered in low numbers in South African surf zones (Strydom and d'Hotman 2005), but they represent a larger component of the southern Angolan community (13% of taxa; 13% of total catch). It therefore appears that the absence of functional estuaries has affected the structure and composition of the shallow water ichthyoplankton community. The absence of functional estuaries in southern Angola likely resulted in the extirpation of more sensitive MED taxa, and as a result the community has evolved a larger marine centric (EMS and MES) component.

The predominance of typically estuarine associated species in a region devoid of estuaries suggests a degree of adaptability among this group. It appears that some MEOs have adapted to utilize alternative, non-estuarine habitats, and the presence of a MED species (*Mugil cephalus*) in a region devoid of estuaries challenges its classification. Based on this observation, in Chapter 2 it was suggested that strict estuarine dependence is likely regionally specific, and more a factor of alternative habitat availability than intrinsic reliance on estuarine function. The suitability of habitats such as coastal embayments to serve as alternative habitats to estuaries therefore depends on their ability to serve similar ecosystem functions, such as the provision of food, refuge from current and predation and favourable physico-chemical factors such as temperature and turbidity.

This study includes samples from three physically and environmentally contrasting shallow water habitats across an exposure gradient, from a completely sheltered bay (SB) to a completely exposed surf zone (SZ). Typically estuarine associated taxa dominated both the SB (60%) and the SZ (50%), and these two habitats showed approximately equal proportions of EMS (SB = 27%; SZ = 29%). Conversely, the OB sites showed a considerably higher proportion of EMS (41%) and MES (18%) taxa than other sites. The relative abundance of MEO species is similar between the SB (83%) and SZ (84%), but very low at OB (10%) sites, which were dominated by EMS (68%). While the MED were observed in all habitats, the relative contribution of this guild to catches was considerably higher in the SB (7%) and negligible at the OB (<1%) and SZ (<1%) sites. The proximity of OB sampling sites to deep water likely resulted in the observation of several solely marine taxa near the shore (i.e. *Sardinella aurita, Decapterus punctatus, Trachurus* spp. *1* and *G. capensis*), while it appears that the SB and SZ sites are utilized by a similar suite of estuarine associated species. However, the higher relative abundance of MEO and particularly MED species in the SB highlights the importance of this sheltered habitat for these estuarine associated guilds.

Overall, larval and early juvenile fish density was highest in the most sheltered habitat (SB), and lowest in the most exposed habitat (SZ). There has been much debate over the effect of exposure to wave energy and high turbulence on surf zone ichthyoplankton assemblages. Some workers suggest that the turbulence from breaking waves provides refuge from predators (Lasiak 1986), and that high turbidity affords juvenile fishes protection from piscivores (Blaber 1980, Cyrus and Blaber 1987). Conversely, there is evidence to suggest that turbidity hampers the feeding of juveniles due to reduced visibility (Moore and Moore 1976), and that the increased energy demand of maintaining position in high current velocity is a selective disadvantage (Gibson 1994). It is difficult for researchers to uncouple the effect of exposure from other associated abiotic factors such as salinity, turbidity and macrophyte abundance (Clark 1997), particularly when studies do not incorporate an adequate spectrum of exposure. While some species are known to seek refuge from turbulence in microhabitats, even in exposed areas (Watt-Pringle and Strydom 2003), there appears to be a general consensus that abundance of larval and juvenile fishes in sandy beach surf zones is highest in areas with lowest exposure (Hillman et al. 1977, Romer 1990, Clark et al. 1994, Clark 1997, Pattrick and Strydom 2014). As such, it is safe to suggest that larval and early juvenile fish abundance appears to correlate negatively with exposure, as the shelter of the embayment yielded the highest CPUE, and the exposed surf zone the lowest overall CPUE.

Larval and early juvenile density was positively correlated with temperature, and negatively correlated with turbidity. This is highlighted by the highest CPUE, which was observed during the warmest season and in the SB (Figure 3.4). In comparison, the lowest CPUE was observed during the coldest season in the exposed SZ (Figure 3.4). The variable physical nature of the surf zone environment promotes an inconstant ichthyofaunal assemblage, with temperature, turbidity, habitat complexity and exposure known as major drivers of early stage fish abundance (Ruple 1984, Harris and Cyrus 1996, Strydom 2003, Watt-Pringle and Strydom 2003, Pattrick and Strydom 2014). Apart from the advantage provided by shelter, the large expanse of very shallow habitat along the shores of the SB are also significantly warmer than other sampling areas, reaching 30°C as a result of solar radiation. This warm, sheltered habitat supports high primary productivity, evidenced by a profusion of Chlorophyta, specifically *Ulva* spp. Members of the genus *Ulva* are known to occur in nutrient rich waters (Fletcher 1996), and the plethora of this chlorophyte inside the embayment further illustrates the high nutrient availability in this habitat. Not only does this indicate high productivity, but *Ulva lactuca* is known to provide effective refuge for juvenile blue crabs (*Callinectes sapidus*), reducing predation to 9% of adjacent non-vegetated habitats (Wilson et al. 1990). Similarly, accumulations of detached macrophytes in an Australian surf zone have been shown to not only increase habitat complexity and provide refuge for ichthyoplankton, but also host associated epifaunal and detrital food items (Lenanton et al. 1982, Pollard 1984). The density of suspended macrophytes is a known driver of abundance and community structure of fishes in surf zones (Robertson and Lenanton 1984, Clark et al. 1996, Crawley et al. 2006). Clark et al. (1996) attributed the high abundance of invertebrate and detritus feeding fishes to the presence of macrophytes associated with low wave exposure sites in Saldahna Bay, South Africa, and littoral macrophytes are known as favoured habitats for many estuarine associated taxa (Whitfield 2016). Similarly, the abundance of juvenile fish was positively correlated with macrophyte levels at King’s Beach, RSA (Rishworth et al. 2014). As such, it is safe to suggest that the SB habitat provides favourable conditions for early stage fish development, through provision of shelter, refuge, food and favourable temperatures similar to estuaries.

Liza spp. and *P. rogerii*, were significantly more abundant in the SB than other habitats, with CPUE for both species decreasing with habitat progression towards the SZ. Unlike these two species, *D. sargus* was significantly more abundant in the OB exposed sandy beach outside the embayment. In warm-temperate South Africa, larval, juvenile and adult members of the genus *Liza* are an important component of estuarine communities (Clarke et al. 1994). While not strictly dependent on estuaries, *Liza richardsonii* commonly utilizes warm-temperate estuaries as a nursery and feeding areas (Whitfield 1998, Lamberth et al. 2008). Similarly, the closely related *Pomadasys kakaan* is categorized as MEO and the closely related *Pomadasys commersonnii* classified as MED. Members of the *D. sargus* sub species complex, however, are typically coastal specialists, preferring rocky coastal habitats as nursery areas, although they do utilize the lower reaches of estuaries opportunistically as juveniles. It appears that typically estuarine associated *P. rogerii* and *Liza* spp. actively select the estuarine like environmental conditions of the SB, while the coastal *D. sargus* favours the moderately exposed OB sites. Furthermore, it appears that exposure and associated physical factors, in conjunction with diet and food source availability, affect how individual species utilize these habitats throughout their development.

The mean body length of *Liza* spp. increased with exposure, with the largest individuals present in the surf zone, and the smallest inside the embayment. Conversely, there was no considerable difference in the mean or range of body lengths of *L. richardsonii* observed between exposed (15.8 mm) and sheltered sites (11.5 mm) in Algoa Bay (Pattrick and Strydom 2014). However, the smallest *Liza* spp. larva observed in the SB (8 mm BL; Table 3.2) was considerably smaller than that observed in South African warm-temperate surf zones (e.g. Watt-Pringle and Strydom 2003: min = 20 mm; Strydom 2003: min = 11.9 mm) and large coastal embayments (e.g. Pattrick and Strydom: 2014: min = 11.5 mm). As such, it appears that the SB affords protection during their development to smaller postflexion larvae (>8 mm) and early juveniles (<20 mm), which likely feed principally on copepods and macruran larvae (Whitfield 1998) that were regularly observed in zooplankton samples in this habitat (Matthew Farthing, pers. obs.). As *Liza* spp. complete metamorphosis, they likely migrate towards more exposed coastal waters, to join the adult population, feeding principally on phytoplankton and detritus (Romer 1986). Alternatively, the presence of smaller larvae in the SB than other habitats may simply be the result of closer proximity to adult spawning grounds.

The opposite trend was observed for *D. sargus*, with significantly larger individuals present in the SB, with a decreasing trend in mean body length with increasing exposure. Similarly, the mean body length of the closely related *D. capensis* was significantly larger in the sheltered sites of Algoa Bay in warm-temperate South Africa (Pattrick and Strydom 2014).

The postflexion larvae of *D. sargus* are known to utilize the shallow nearshore (<15m) and surf zones as nursery areas (Watt-Pringle and Strydom 2003, Strydom and d'Hotman 2005), entering estuary mouths opportunistically as juveniles (Whitfield 1999). As postflexion larvae, *D. sargus* feed principally on copepod nauplii and copepod eggs associated with sandy substrate in the shallow nearshore (Sánchez-Velasco and Norbis 1997) and Copepoda associated with rocky shore littoral zones (Strydom 2008), whereas juvenile *D. sargus* feed principally on chlorophytes (Coetzee 1986, Lasiak 1986, Figueiredo et al. 2005, Richardson et al. 2011). The onset of omnivory associated with metamorphosis (Coetzee 1986, Sánchez-Velasco and Norbis 1997, Richardson et al. 2011) results in a shift in the dominant food items from zooplankton to chlorophytes, which are abundant in warm, sheltered waters such as the SB. Therefore, the increasing trend in mean body length as habitats become more sheltered may be attributed to the steady incorporation of chlorophyta in *D. sargus* diet throughout development from larvae to juvenile (Coetzee 1986, Sánchez-Velasco and Norbis 1997, Richardson et al. 2011).

Significantly larger *P. rogerii* were present in the SB, with a decreasing trend in mean body length with increasing exposure. This ontogenetic progression in habitat utilization is similar to that observed in the related, MED *Pomadasys commersonnii,* the larvae of which typically enter surf zones before recruitment into more sheltered habitats such as estuaries and lagoons (Strydom and d'Hotman 2005), which they utilize intermittently as adults (Wallace 1975, van der Elst 1993, Whitfield 1998). Similarly, many members of the genus *Pomadasys* are known to spawn at sea, with postflexion larvae recruiting into estuaries (e.g. *Pomadasys kakaan* and *Pomadasys commersonnii*) (Wallace 1975, Joubert 1981, van der Elst 1993, Connell 2012). It is likely that *P. rogerii* spawns at sea, with progeny recruiting into low energy surf zones as postflexion larvae, using this habitat as a transient route to more sheltered habitats such as the SB. The presence of larger *P. rogerii* individuals inside the SB concurs with the general trend in this genus, whereby juveniles actively select warmer, sheltered habitats with high prey item availability (Wallace 1975, van der Elst 1993, Connell 2012).

In this study, temperature best explained the presence/absence of species, with samples becoming more speciose during the warmer, wet season. Seasonal changes in oceanographical conditions, coupled with innate biological drivers such as spawning seasonality and thermal tolerance have been found to shape fish communities (Jenkins 1986, Harris and Cyrus 1997, Harris and Cyrus 1999, Bell et al. 2001, Strydom 2003, Pattrick and Strydom 2008, Kruger and Strydom 2010). Greater species diversity has been observed in surf zones globally during warmer months (McFarland 1961, Modde and Ross 1980, Strydom 2003, Félix et al. 2007, Pattrick and Strydom 2014), attributed to the influx of spring/summer spawning coastal species that concentrate spawning effort in warmer months. Therefore, there is evidence to suggest that the increased diversity and abundance of the warm, wet season is attributed to the influx of summer/spring spawning species.

Catches during the wet season were characterized by *D. sargus*, *S. sagax*, *P. rogerii* and *G. capensis*, while catches during the dry season were characterized by *D. sargus*, *Liza* spp. and *S. salpa.* Both *D. sargus* and *Liza* spp. were observed in both seasons and all habitats, and appear to be year-round residents in the sampling area, while *S. salpa* was only observed during the dry season. Apart from the two year-round residents, the wet season was characterized by two coastal species with tropical affinity (*P. rogerii* and *G. capensis*), and the highly migratory pelagic *S. sagax*. The observation of *S. salpa* in the dry season exclusively is unsurprising, as temperate sparids are known for spawning in the cooler months in the warmer parts of their distribution (Sheaves 2006, Potts et al.2014). It appears that the increase in temperature facilitates the spawning of taxa with greater limiting isotherms (e.g. *P. rogerii* and *G. capensis*), and the reduced wave energy associated with the wet season eases the entry of weaker swimming pelagic taxa (e.g. *S. sagax*) into the SZ.

In the SZ, the seasonal difference in CPUE is stark, with little catch observed during the dry season. While this is partly attributed to the spring/summer spawning seasonality of the predominately temperate coastal fish assemblage, the seasonal changes in wave energy in the SZ may also contribute. The more protected SB and OB environments showed no significant difference in overall CPUE, which highlights the year round stability of surf energy in these habitats. The increased frequency of high energy surf events (MW Farthing pers. obs.) during the dry season may preclude sensitive ichthyoplankton from the wading depths of the primary surf zone; however, there is potential for early stage fishes to make use of micro refuges during these high energy events, rather than vacating the surf zone entirely.

In summary, the results from this study highlight the effect of physical habitat, exposure and seasonality on larval and early juvenile fish community structure. The prevalence of typically estuary associated taxa in an area devoid of estuaries suggests that these taxa have adapted to utilize alternative nursery areas. This study challenges the popular belief that *M. cephalus* is estuarine dependant, and suggests that the presence of this species in southern Angola indicates a higher level of adaptability than previously assumed. The sheltered environment inside the embayment appears to serve as an alternative habitat to estuaries and likely facilitates the success of *M. cephalus* and several other marine estuarine associated species that were abundant in this habitat. The high abundance of several important fishery species inside the embayment is attributed to the accumulation of chlorophytes in this area. It is suggested that the accumulation of chlorophytes serves several important ecosystem functions, including the provision of refuges and associated epifaunal prey items. The proportion of EMS and MES taxa was higher than comparable preceding warm-temperate studies. The absence of estuaries along the southern Angolan coastline likely extirpated taxa with a stricter dependence on the estuarine environment, allowing marine and marine straggler guilds to fill niches in the surf zone and nearshore. The study area showed higher diversity than comparable preceding studies from warm-temperate South Africa, attributed to the species accumulator affect within the Angola Benguela Frontal Zone, and the proximity of study areas to deep waters that host marine taxa. There was a strong relationship between composition structure and exposure, with more sheltered habitats supporting higher abundance and diversity. It is however suggested that the relationship between species abundance and exposure is complicated by other factors, such as ontogenetic shift in diet and physico-chemical variables.

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Chapter 4

General discussion

This study is the first assessment of the early stages of fishes conducted in Angola. To date, investigations in the region have been limited to pelagic or nearshore ichthyoplankton assemblages associated with large scale research cruises (e.g. Ekau et al. 2001, John et al. 2001, Verheye and Ekau 2005a, b), with no focus on the important fishery species inhabiting shallow water habitats such as surf zones and coastal embayments. Angola's unstable political climate and history of civil war thwarted progress in scientific investigations in the region for 60 years, and as a result much of the regions ichthyofauna is poorly understood. Since the advent of peace and stability (2002), Angola's population and reliance on the ocean for protein have grown exponentially, with fish being the principal animal protein consumed (18.6kg per capita, per annum: IFAD 2014). The dependence of individuals and industry on the sea is particularly high on the southern Angolan coastline, adjacent to the non-arable lands of the Namib Desert. Currently, Angola's principle mandate is one of basic infrastructural and civil rights restoration, with 68% of the population below the poverty line (IFAD 2014). It is safe to suggest that scientific research, conservation and fisheries management are not state priorities, and the fisheries department has little and inadequate capacity for monitoring, enforcement or development of marine living resource legislation (Duarte et al. 2005). The current level of ichthyological understanding is insufficient for effective management and conservation, and never before has there been such a need to establish critical biological, ecological and ecophysiological baseline information. This study has endeavoured to address the lack of understanding of the early life history of fishes from this biodiversity and climate change hotspot, and makes a major contribution to previous, ongoing and future ecological ichthyofaunal investigations from the region (e.g. Richardson et al. 2011, Potts et al. 2014, Winkler et al. 2014, Parkinson in prep.).

Overall, the shallow water of the southern Angolan coast hosts a diverse, typically warm-temperate early stage fish assemblage. A total of 51 species were identified, with common species highlighting the biogeographic connections between the study area and warm-temperate South Africa and the Mediterranean. Most commonality across warm-temperate regions was within the family Sparidae (e.g. *Diplodus sargus, Diplodus cervinus, Sarpa salpa, Spondyliosoma emarginatum* and *Oblada melanura*), which contributed 11 species to the study area assemblage. The scarcity of meristic, morphometric and developmental information is noted as one of the principal impediments in this study, with nine taxa remaining unidentified, and a further 12 species remaining identified to family level only. The Sparidae were particularly troublesome, with six distinctly different taxa suspected to be from the *Pagrus, Sparus* and *Dentex* genera remaining unidentified due to insufficient or inadequate adult descriptions, despite specimens having developed passed flexion where more characters are available for use.

This study addressed the call made by Richardson (2010) and Winkler (2013) for an assessment of the coastal ichthyoplankton assemblage to validate the reproductive periodicity of *Diplodus sargus* and *Diplodus cervinus*. The observation of larvae of both aforementioned species corroborates observations of shallow nearshore spawning aggregations of *D. sargus* and *D. cervinus*, and the timing supports the reported spawning periodicity for these species in southern Angola. The age and timing of *D. sargus* larvae observed supports the hypothesis that the cold water anomaly (Richardson 2010, Winkler 2013), which has subsequently been described an as annual upwelling event (M. Roualt, pers. comm.) in December/January, provides an important alternative spawning opportunity for these species. Furthermore, this study presents evidence that supports the recent paradigm shift that spawning of Sparidae is linked to temperature, and not photoperiod (Sheaves 2006, Potts et al.2014).

This study provides the first larval record of *Argyrosomus coronus*, an important recreational, subsistence and commercial fishery species in southern Angola. This observation corroborates observations of ripe adults in the study area (Potts et al. 2010), and the timing of observation contributes to inferences of spawning in ongoing multi-method studies of seasonal movement and behaviour using acoustic telemetry (Parkinson et al. in prep.). While adults are common both inshore in the dry season and further offshore in the wet season, there are limited observations of smaller (<300 mm TL) juveniles. In South Africa, the closely related *Argyrosmous japonicus* makes regular use of estuaries as a nursery area, although they are not considered strictly dependent on this environment. Similarly, *A. coronus* juveniles (300–600 mm TL) and sub adults (600–870 mm TL) have been regularly observed near the mouth of the Cunene River (Potts et al. 2010), which represents the only estuarine environment in southern Angola. Furthermore, Potts et al. (2010) suggest that juveniles (<300 mm TL) are prevalent offshore (50–100 m), recruiting into the shallow nearshore and littoral zones from 300 mm TL. The observation of postflexion larvae inside Tombua Bay gives an indication of habitat utilization during this early developmental phase. It is difficult to deduce any nursery importance from a single observation, but based on the selection of sheltered habitats such as estuaries by closely related species such as *Argyrosomus japonicus* in South Africa (Cowley et al. 2010) and Australia (Gray and McDonall 1993), it is theorised that sheltered coastal embayments may serve an important nursery role for this species. Baia dos Tigres is southern Angola’s largest coastal embayment, located approximately 120 km south of the study area, in the core of the region’s *A. coronus* distribution (Potts et al.2010). It is likely that this massive coastal embayment represents an important habitat for the early development of *A. coronus* and several other species in the absence of estuaries.

The use of estuaries by early developmental phases of warm-temperate coastal fishes is well documented in South Africa (Strydom 2002). The close biogeographic relationship between southern Africa's warm temperate regions, and the recent (approximately 2 mya) oceanographic changes and subsequent allopatric event (Henriques et al. 2014), which is thought to have isolated the coastal marine fauna has provided an ideal natural laboratory to investigate the response of warm-temperate coastal fishes to the absence of functional estuaries. This study compared the relative abundance of fishes belonging to the different estuarine utilization categories to investigate the impact of the absence of estuaries on community composition. In Chapter 2, it was found that the surf zone assemblage included fewer marine estuarine opportunist taxa than comparable surf zone studies in South Africa. Furthermore, only a single estuarine dependent species was observed, which suggests that the absence of functional estuaries may have resulted in the extirpation of strictly estuarine dependent species (e.g. *Rhabdosargus globiceps*) that dominate warm-temperate South African surf zones. Nevertheless, it appears that some taxa, which only use estuaries intermittently or opportunistically, were able to adapt (e.g. *Diplodus sargus, Liza* spp.*, Sarpa salpa*), and the high abundance of estuary associated taxa inside Tombua Bay highlights the importance of this sheltered, food rich environment for this group. Furthermore, the observation of the MED *Mugil cephalus* in the study region challenges its traditional classification as strictly dependent on estuaries (Wallace 1984).

In this study, it is suggested that dependence on the estuarine environment may be regionally specific for some taxa. While it is acknowledged that some marine taxa do depend on specific estuarine functions and ecosystem services, the presence of the MED *Mugil cephalus* in southern Angola suggests a degree of adaptability. Potter et al. (1990) suggested that warm-temperate, MED taxa had adapted to utilize coastal embayments as alternative nursery areas in arid South Western Australia. Based on this, it was suggested that some taxa may find the essential ecosystem services normally provided by estuaries in alternative habitats such as coastal embayments. In Chapter 3, it is suggested that the warm, productive and sheltered habitat inside Tombua Bay provides *Mugil cephalus* with the necessary ecosystem functions for which it typically seeks out in estuaries in South Africa and South Western Australia. While this does indicate a degree of adaptability, the ability of MED taxa to survive the loss of estuarine habitats depends on species specific ecosystem requirements and the availability of alternative habitats that serve these functions.

The role of the estuarine environment in the life cycles of important warm-temperate fishery species is well understood in South Africa (e.g. Blaber 1973, Potter et al. 1990, Whitfield 1994, James et al. 2007, Cowley et al. 2010). Several marine species utilize estuaries as larvae (e.g. *Rhabdosargus holubi*), early juveniles (e.g. *Argyrosomus japonicus*, *Pomatomus saltatrix*) and intermittently as adults (e.g. *Pomadasys commersonnii*). The use of estuaries as feeding areas by several large, prized sport angling (e.g. *Lichia amia*) and food fishes (e.g. *Rhabdosargus holubi*) has resulted in high levels of fishing pressure (Cowley et al. 2013). Furthermore, estuaries are particularly susceptible to other anthropogenic disturbances such as pollution by eutrophication, artificial lighting associated with urbanization (Becker et al. 2013), water abstraction and disturbance by recreational activities such as water-skiing (Lamberth et al. 2008). This suggests that these environments may represent survival bottlenecks for some species or life stages. With forecasted changes in precipitation due to anthropogenically caused climate change, it is likely that estuarine function is further under threat, as rainfall plays a major role in estuarine mouth state (open/closed) and nutrient availability (James et al. 2007). As such, it is safe to suggest that South Africa’s estuaries are under threat (Wallace et al. 1984), and therefore so are the important species that rely on this habitat. The understanding that some more strictly estuarine dependent taxa may experience distributional shifts, reductions in range and extirpation warrants efforts to conserve these important habitats throughout southern Africa.

While the conservation of estuaries throughout the world on the basis of their importance to some fish species is critical, there is evidence that the importance of this habitat has previously been overemphasized (Able 2005) for some fishes in RSA (Strydom 2008). The absence of rigorous assessments of alternative, non-estuarine nurseries on RSA's coast may be to blame for this over-emphasis. Strydom (2008) suggested that sub-tidal bays associated with rocky shores provide examples of alternative, non-estuarine nursery areas for early stage fishes, and highlights the difficulty of sampling rocky shores as a reason for the few assessments of these habitats. While it is likely that estuaries are model habitats for early stage fish development, the results of this study challenge the premise that estuarine use is obligatory for many coastal fishes (e.g. *Mugil cephalus*). While I acknowledge that some, more sensitive taxa may require estuaries for success, I suggest that the facultative use of these habitats by coastal ichthyofauna in RSA has been assumed to be obligate and thereby overemphasized in the absence of studies of alternative, non-estuarine habitats. Conversely, it cannot be ignored that the importance of a nursery habitat to a particular population must factor in area and extent (Beck et al. 2001, Dahlgren et al. 2003). While an individual species may not be an obligate user of estuaries, if estuaries stand to contribute above average recruitment to adult populations, then their importance to that species must be acknowledged, regardless of the nature of their apparent independence or dependence upon the estuarine environment.

While the distance of southern Angola's only functional estuary from the study area precludes its effect on the early fish community observed, there is still potential for the Cunene Estuary to play a large role in the maintenance of estuarine dependent fish populations in the region. Many species (e.g. *Argyrosomous japonicus*) are considered MED in South Africa, and it is possible that the Cunene Estuary may be the only major nursery habitat for the closely related *Arygyrosomous coronus* in southern Angola. Only three individual *A. coronus* larvae were observed from a single seine haul in this study in Tombua Bay. Similarly, *Lichia amia* also show a strong estuarine association in South Africa (Whitfield 1998), but larvae and juveniles were absent from catches in this study. Juvenile *L. amia* have been observed at the Cunene Estuary mouth (MW Farthing, pers. obs.), and it is likely that this habitat plays a larger role than previously assumed in maintaining these populations.

It is possible that the Cunene Estuary represents a bottleneck for the survival and success of some estuarine associated species in southern Angola, some of which are important artisanal, commercial and recreational angling species in the region (e.g. *A. coronus, L. amia*). This is particularly concerning in light of the proposed hydroelectric power generation scheme (Baynes Hydropower Project), which requires the construction of Orakawe Dam on the Cunene River. Fish depend on the characteristics of their aquatic environment, which provide them the necessary ecosystem services required for success and survival. The hydroelectric damming of natural watercourses has been termed cataclysmic for riverine biota (Gupp 1994), and is highlighted as cause for decline in estuarine fisheries (Baisre and Arboleya 2006) and aquatic biota impoverishment in the temperate new world (Pringle et al. 2000). Until we have a succinct understanding of which ecosystem services provided by estuaries are sought out by these estuarine associated species, it can only be assumed that altered or reduced flow regimes will affect the ecological dynamics of this sensitive habitat. Furthermore, the insidious threat of climate change and its associated effect on rainfall, estuarine function and fish distribution is also cause for concern. It is therefore critical to assess the ecological importance of the Cunene Estuary to southern Angolan fishes, and to limit the levels of localized exploitation to ensure its ecological integrity.

Based on the results of this study, the following research priorities have been identified for the southern Angolan study region:

1. A fine scale, micro-habitat utilization assessment of the surf zone is required to assess the importance of different habitats identified in the surf zone to different taxa. While comparable with other studies, the sampling methodology employed in this study was unable to definitively separate ichthyoplankton communities into habitat types.
2. A comprehensive ichthyoplankton assessment of the sheltered coastal embayment, Baia dos Tigres, to determine the utilization and regional importance of this habitat as a nursery area. Based on the high abundance of marine estuarine associated taxa in Tombua Bay, it is likely that this group will utilize other large coastal embayments such as Baia dos Tigres, and the magnitude of this environment suggests that it will facilitate proportionally greater recruitment to adult populations.
3. A comprehensive larval and juvenile assessment of the surf zone adjacent to the Cunene River mouth, to assess the importance of the only estuarine habitat in southern Angola to taxa from the region. It is likely that some, more estuarine dependent taxa not observed in the study area utilize the Cunene Estuary as a nursery area. The almost exclusive observation of juvenile *Lichia amia* and *Argyrosomus coronus* in proximity to the Cunene River highlights the potential importance of this region to important recreational and subsistence fishery species.
4. A study of the natal origin and ontogenetic migration ecology of important fishery species (e.g. *Lichia amia, Argyrosomus coronous, Pomatomus saltatrix*) along the southern Angolan coastline. It is critical to determine the importance of regional nursery habitats to the southern Angolan populations as whole. It is hypothesized that nursery role of the Cunene River and Baia dos Tigres is greater than assumed and determining

centres of spawning and nursery importance along the Angolan coast is critical for effective conservation.

5. An ecophysiological assessment of the thermal tolerance of important southern Angolan fishery species throughout development. Rapid ocean warming, coupled with the seasonal shift of the ABFZ suggests that future changes in sea temperature are imminent, and the reproductive scope and ontogenetic migration ecology of important taxa is likely to change as a result.

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