LARVAL FISH DYNAMICS WITHIN THE COASTAL NEARSHORE OF THE EASTERN CAPE, SOUTH AFRICA.

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ABSTRACT

The coastal nearshore is important for the early development of fishes as it is used for spawning and/or as a nursery. One of the central concerns in coastal ecology is understanding the role of the nearshore for larvae, ultimately providing key knowledge on population dynamics and hence helping in making decisions pertaining to conservation and resource management. The aim of this study was to investigate the alongshore and cross-shore distribution of larval fishes and the links to the physio-chemical conditions (including prevailing winds) and hydrodynamics in the region of Algoa Bay, situated on the south east coast in the warm temperate region of South Africa. Fish larvae were sampled at nine sites for the first component of the study (January 2016 –March 2017) and at four sites for the second component (November 2019), near the surface and bottom (15-50 m) of the water column as well as at two different distances from shore (~400 m/~3 km) using a set of bongo plankton nets towed behind a boat. Environmental data were simultaneously collected using and acoustic Doppler current profiler (ADCP) and conductivity, temperature, depth (CTD) profiler. Larval fish abundance generally decreased with increasing distance from the shore, however, this varied in space and time, with some larval species recorded in high abundances offshore. Close inshore the larvae of coastal fish species producing benthic eggs (CBE) including the Blenniidae and Gobiesocidae mostly dominated, while offshore the larvae of coastal fish species producing pelagic eggs (CPE) i.e. Sparidae and Cynoglossidae, as well as pelagic fish species producing pelagic eggs (PPE) i.e. Clupeidae and Engraulidae mostly dominated. Vertical distribution of larvae differed according to taxon, with the Callionymidae (CPE), Cynoglossidae and Gobiesocidae occurring at high densities at the bottom of the water column, while the Blenniidae dominated near the surface.

Fluorescence, temperature and salinity varied with depth (surface/bottom), being particularly high at the surface; currents moved faster at the surface than the bottom of the water column.

Increased abundances of larval fishes were evident after upwelling events (associated with easterly winds) in the Bay, while during downwelling (associated with westerly winds), low densities were generally recorded, except for the sites situated near headlands/capes where there were higher densities of fish larvae during downwelling events. Overall, the results of this study suggest that spawning mode of the adults, oceanography and environmental conditions coupled with what is known of the behaviour of fish larvae, were important in shaping the larval fish community of the Algoa Bay region. These results highlight the importance of incorporating multiple biological (developmental stage, reproductive mode, species) and physical (currents, fluorescence, wind-driven up/down-welling) factors when addressing the mechanims of transport of larval fish in the coastal nearshore.

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CHAPTER I

GENERAL INTRODUCTION

1.1 Introduction

The structure of marine fish populations largely depends on the successful transport and survival of larvae and their juvenile settlement within suitable nursery habitats (Wittle *et al*., 1999; Brothers *et al*., 1983; Scheltema, 1986; Sponaugle and Cowen, 1996). Studies on the early life histories of fish and related early demographics are therefore important to understand the ecological drivers of population dynamics. As such, this knowledge helps in the management of commercial species and the conservation of exploited/threatened species (Largier, 2003; Shanks *et al*., 2003; Hastings and Botsford 1999, Palumbi 2001; Selkoe *et al*., 2016).

Studies in larval ecology are based on specific and important definitions of factors and processes that help with the understanding of proper concepts regarding population connectivity (Largier, 2003; Pineda, 2007; Selkoe *et al*., 2016). The term fish larvae, or ichthyoplankton, refers to the early developmental phase of fishes that occurs, for most species, immediately after hatching from the egg and ends with the juvenile stage of development (Leis 2006; Leis *et al*., 2009). Depending on the species, in the marine environment, larval fish can spend from a few days to several months in the pelagic environment, until they reach settlement stage (Leis, 1991b). After completion of the larval stage, fish larvae undergo a further morphological, behavioural and physical transition associated with their search for suitable juvenile habitat to settle upon (Valesini *et al*., 1997; Harris *et al.,* 2001). The movement of a larva from its spawning area to juvenile settlement habitats is referred to as larval dispersal (Pineda *et al*., 2007). This dispersal phase is largely influenced by hydrodynamics and other environmental physico-chemical processes (Selkoe *et al*., 2010), as well as the larva's behavioural capabilities (Blaxter, 1969; Stobutzki, 1997; Leis, 2006). It is at the youngest developmental stage (yolk-sac and preflexion stage) that larvae of coastal nearshore species are most susceptible to advection offshore by oceanographic currents (Hunter, 1972). The flexion stage follows the preflexion stage, when a larva starts and completes notochord flexion, setting up the base for the development of the caudal fin which helps to enhance their ability to move horizontally (Kendall and Matarese, 1987). Once larvae have reached the flexion developmental stage, they are able to not only adjust their vertical position in the water column and utilise suitable onshore currents to remain closer to shore (Cowen *et al.*, 2000; Cowen, 2002; Leis, 2006; Pattrick and Strydom, 2009), but also have active horizontal swimming abilities (Fisher *et al.*, 2000; Clark *et al.*, 2002). In so doing, larvae are able to greatly influence their dispersal.

The abundance of predators, availability of prey and physical oceanographic features are major factors influencing the dispersal of larval fish in the coastal nearshore (Hjort, 1914; Hunter, 1976; 1981; McGurk, 1989). The coastal nearshore, in relation to larval fishes, refers to waters shallower than 50 m in depth (Leis, 1991a; Pattrick *et al.*, 2016), and is known to serve as an important habitat for the early developmental stages of many fishes as it is commonly utilised as a spawning and/or nursery ground (Leis, 1982; Beckely, 1986; Whitfield, 1989; Potter *et al.*, 1990; Sponaugle and Cowen, 1996; Whitfield, 1999; Strydom, 2003; Pattrick and Strydom, 2008). Oceanographic features and the variability of environmental physico-chemical parameters in the coastal nearshore make this environment extremely dynamic, especially for larvae (Leis, 1991b; Pineda *et al.*, 2007; Rabbaniha *et al.*, 2015). For example, a decrease in temperature followed by an increase in chlorophyll-*a* levels are associated with coastal upwelling events, which foster conducive conditions for successful spawning of adult fishes and the subsequent growth and development of larvae (Rabbaniha *et al.*, 2015). The presence of estuaries/rivers creates changes in salinity and turbidity in the coastal nearshore, also highly influencing the distribution of larvae (Leis and Goldman, 1983; Beckley, 1986; Tilney and Buxton, 1994). Oceanographic features in the coastal nearshore such as eddies and fronts promote retention and transport of larvae (Hernández-Miranda *et al.*, 2003; Wilson *et al.*, 2008;

Inda-diaz *et al.*, 2010; Chang *et al.*, 2017; Diaz-Astudillo *et al.*, 2017; Chang *et al.*, 2018). Larvae can also be retained in the coastal nearshore due to slower current flow that occurs at the coastal boundary layer (Churchill 1985; Morgan and Fisher, 2010; Nickols *et al.*, 2012; Stansby *et al.*, 2016), which is the reduced flow and transport that often happens at depths of <30 m along the coast (Csanady, 1972). Coastal currents moving adjacent to the shore decrease in velocity when they reach the coastline (Churchill 1985, Lentz *et al.*, 1999; Wolanski 1992; Hamilton *et al.* 2006). Larvae can potentially spend their pelagic larval stage within the coastal boundary layer, thus limiting their offshore dispersal and increasing their alongshore retention and survival (Churchill 1985; Morgan and Fisher, 2010; Nickols *et al.*, 2012; Stansby *et al.*, 2016).

Topographical features also play an important role in structuring larval fish assemblages in the coastal nearshore (Yasso, 1965; Hsu *et al.,* 1987). Larvae tend to accumulate in bays and at headlands/capes (Strub *et al.*, 1991; Rojas and Landaeta, 2014; Morgan *et al.*, 2009; Morgan *et al.*, 2012; Morgan *et al.*, 2014; Morgan *et al.*, 2018). Bays also provide shelter for adult fishes to spawn and a suitable sheltered environment for both benthic and pelagic larval species to inhabit, ensuring maximum growth of larvae (Haegele and Schweigert, 1985; Hutchings *et al.*, 2002; Morgan *et al.*, 2009; Morgan *et al.*, 2012; Morgan *et al.*, 2014; Morgan *et al.*, 2018). In bays, water circulation tends to promote retention and also facilitate transport to nursery areas such as nearby estuaries (Gazeau *et al.*, 2005). Headlands or capes, acting as barriers to continuous flow, are also able to influence alongshore larval retention and facilitate their survival (Yasso, 1965; Hsu *et al.,* 1987). The shallow nature of the nearshore favours a flow that is more dynamic relative to the offshore, which is more stable and deeper (Lindner *et al.,* 2008).

1.2 Study Rationale

In the coastal nearshore of South Africa, studies have been conducted on the warm temperate south east coast to understand the extent of larval dispersal within the Tsitsikamma Marine Protected Area (MPA) (Tilney and Buxton, 1994; Tilney *et al.,* 1996). In the subtropical east coast region of South Africa (Harris *et al.*, 1999; Harris *et al.,* 2001), studies have focused mainly on the larval fish distribution and composition. The majority of research on coastal nearshore larval assemblages has been done in the Algoa Bay region (Beckley 1986; Strydom, 2007; Pattrick and Strydom, 2008; Pattrick *et al.*, 2013; Pattrick and Strydom, 2014a; b; Pattrick *et al*., 2016). These studies have, however, not assessed the relationship of fish larvae and *in situ* water current measurements to determine the functional relationships between fish larvae and their coupled hydrodynamic environment.

1.3 Aims and Objectives

The aim of this thesis was to investigate the composition of the larval fish assemblages in relation to environmental variables, including water currents and coastal winds, within the coastal nearshore of the Algoa Bay region. The specific objectives of this study were to describe the alongshore and cross-shore distribution, composition and abundance patterns of larval fishes in the coastal nearshore of the Algoa Bay region (Chapter 2). In addition to sampling for larval fishes, coastal nearshore current flow patterns as well as the physio-chemical environmental factors were analysed to determine the role they play in the larval fish patterns. The second objective of this study was to investigate the influence of local winds on the distribution and abundance of larval fishes in the Algoa Bay region (Chapter 3).

1.4 Thesis Structure

This thesis is divided into four chapters and includes a general introduction providing an overview of the importance and definitions of the processes that determine larval fish connectivity and the roles of nearshore alongshore and cross-shore circulation for the transport of larval fish (Chapter I). Chapter II focuses on the influence of currents and environmental physico-chemical factors on the composition, distribution and abundance of larval fish in the coastal nearshore of the Algoa Bay region. Chapter III assesses the effects of winds on the larval community in the region. A final chapter (Chapter IV) is a general discussion/synthesis, identifying the main components that drive larval fish assemblages in the coastal nearshore of the Algoa Bay region.

CHAPTER II

DISTRIBUTION, COMPOSITION AND ABUNDANCE OF FISH LARVAE IN THE COASTAL NEARSHORE OF THE ALGOA BAY REGION, EASTERN CAPE, SOUTH AFRICA

2.1 Introduction

Coastal fishes known to occur in the nearshore (Hernandez-Miranda *et al.*, 2002; Borges *et al.*, 2007; Cowen, 2009), mostly reproduce by brooding and/or broadcast spawning. Broadcast spawning occurs when fertilised eggs are released into the water column, where they hatch into pelagic larvae that disperses for a certain period and distance (Leis 2006; Leis *et al.*, 2009), whereas brooding is when fertilised eggs are maintained internally and are released into the water column at the larval stage (Dunn, 1975). The temporal and spatial extent of dispersal depends on the pelagic larval duration (hereafter PLD), which is the amount of time a larva spends in the pelagic environment before it is competent to settle into a coastal nearshore juvenile nursery habitat (Wittle, 2003). The PLD of a larva can range from a few days to several months (Brothers *et al.*, 1983; Scheltema, 1986; Sponaugle and Cowen, 1996). The timing, location and mode of spawning, together with the environment are also linked to the spatio-temporal variability of larval fish dispersal (Gray & Miskiewicz, 2000). Depending on the species, two types of eggs, benthic or pelagic, where benthic eggs are laid onto the substratum (seabed) or deposited in nests while pelagic eggs are released directly into the water column (Lambert and Ware, 1984) are generally spawned by marine fishes. Spawning modes (brooders vs broadcast) and location of egg development (benthic vs pelagic) can greatly influence the dispersal distances of many larval fishes (Beckley, 1986; Leis, 1991a; Cowen, 2009). Larvae that hatch from benthic eggs are known to be abundant closer inshore and near to the reefs where they are spawned (Johannes, 1978; Norcross & Shaw,1984; Dudley *et al.*, 2000; Armsworth *et al.*, 2001). Almost all offshore marine species produce pelagic eggs, which are buoyant and therefore more subject to wider dispersal (Leis &Miller, 1976; Young *et al.*, 1986; Gray & Miskiewicz, 2000; Auth & Brodeur *et al.,* 2007; Kent *et al.*, 2013).

The abundance and distribution of larvae, particularly in the coastal nearshore as compared to further offshore, are distinct (Leis and Miller, 1976; Borges *et al.,* 2007; Tinley *et al.*, 1996), supporting both a high diversity and density of fish larvae (Kingsford & Choat, 1989; Harris *et al.,* 1999; Hernandez- Miranda *et al.,* 2003). The coastal nearshore is also rich in phytoplankton and zooplankton biomass and diversity (Rekkik *et al*., 2013), providing a suitable food source for larval fishes (Franco-Gordo, 2004). Bays are an ideal habitat for adult fish to spawn in as they provide them with shelter (Frank and Leggett, 1983), while headlands surrounding bays reduce the strength of winds and wave action, also favouring within-bay water circulation and hence accumulation of larvae within the nearshore (Yasso, 1965; Velez *et al*., 2005; Delpey *et al*., 2014). In contrast, offshore waters are less productive than coastal nearshore habitats, containing less food sources for larval fishes (Johannes, 1978).

Worldwide, there has been significant research effort targeted at understanding the utilisation of the coastal nearshore by larval fishes (Hernandez-Miranda *et al*., 2002; Borges *et al*., 2007; Cowen, 2009). Larval fish assemblages within the coastal nearshore are dynamic in terms of distribution, with the oceanography of this environment driving most of the distribution of larval fishes (Thorson, 1964; Hamilton and May, 1977; Paris & Cowen, 2004). The coastal nearshore is shaped by local scale hydrodynamic processes influenced by wind, waves, tides and storms (Dingler and Inman, 1977; Plant and Griggs, 1992) which affect the dispersal and transport of larval fishes therein (Largier, 2003; Pineda, 2007; Selkoe, 2016). In addition, fish larvae are most likely to be retained within the coastal nearshore because of the presence of the coastal boundary layer that prevents offshore transport of ichthyoplankton (Cowen and Sponaugle, 2009). Oceanographic coastal features that can also retain larvae in the nearshore include eddies and fronts, while strong upwelling events can cause offshore advection of larvae (Lobel and Robinson, 1986; Govoni *et al*., 2009).

Swimming ability also influences larval distribution, with its strength varying exponentially through ontogeny (Stobutzki and Bellwood, 1997; Stobutzki, 1997; Leis and Carson-Ewart, 1997; Dudley *et al*., 2000). At the preflexion stage, larval fishes can move vertically in the water column via the use of their gas bladder, but are unable to actively swim great distances horizontally (Clark *et al*., 2005). After notochord flexion, with the development of the caudal fin, horizontal swimming increases significantly (Clark *et al*., 2005). At the last stage of larval development referred to as postflexion, larval fishes possess active swimming abilities, being capable to move against fast-flowing local currents (some species at speeds of up to 60 cm/s^{1}), avoiding passive drift (Stobutzki and Bellwood, 1994; Fisher *et al*., 2000; Clark *et al.,* 2005; Fisher, 2005; Pattrick and Strydom, 2009). In addition to this active horizontal swimming, larvae use other behaviours to retain themselves within the coastal nearshore. By strategically positioning themselves vertically in the water column, larvae can entrain themselves in currents for onshore retention in order to avoid offshore transport (Kent *et al*., 2013; Paris and Cowen, 2004). As such, both the horizontal and vertical patterns of current speed and direction play important roles in influencing the spatial and temporal transport of larval fish in the coastal nearshore (Leis and Goldman, 1983; Leis, 2006).

In South Africa, research on larval fish ecology has mostly been conducted within the estuarine environment (Melville-Smith, 1981; Melville-Smith & Baird, 1980, 1981; Beckley, 1984; Whitfield, 1985; Beckley, 1985; Harrison & Whitfield, 1990; Strydom & Hotman, 2005; Harris *et al*., 1999; Strydom *et al*., 2003). There has been some research assessing the role of surf zones for larval fishes (Whitfield, 1989; Harris and Cyrus, 1996; Cowley *et al*., 2001; Watt-Pringle Strydom, 2003; Strydom, 2003). Offshore studies (at depths >50 m) have mainly dominated the literature (O'Toole and King, 1974; Olivar and Beckley, 1994; Olivar and Beckley, 1994; Roel *et al*., 1994; Beckley and Connell, 1996; Olivar *et al*., 1999; Beckley and Leis, 2000) and in the coastal nearshore, only isolated, localised studies have been undertaken

(Beckley, 1989; Tilney & Buxton, 1994; Harris *et al.*, 1999; Pattrick & Strydom, 2008; Pattrick *et al.*, 2013, Pattrick *et al.*, 2016).

The distribution, composition and abundance of larval fishes has been previously described within the coastal nearshore of Algoa Bay, one of the largest sheltered bays on the southeast coast of South Africa (Beckley, 1989; Pattrick & Strydom, 2008; Pattrick *et al.,* 2013; Pattrick *et al.*, 2016). The role played by local ocean hydrodynamics and environmental conditions on the dynamics of fish larvae is however poorly understood, especially directly outside the bay, along the headlands, where research is completely lacking. The primary aim of this study was therefore to test the hypothesis that larval fish assemblages within the Algoa Bay region differ both along and across-shore and to relate this to the local coastal nearshore environmental conditions. I hypothesised that the abundance of fish larvae decreases with an increase in distance from the shore, with more larvae occurring near the surface than the bottom of the water column. Additionally, I hypothesise that larvae hatching from benthic eggs are expected to be more abundant closer inshore than offshore, while larvae hatching from pelagic eggs would be most abundant offshore. Studies have shown species than inhabit the offshore to spawn pelagic eggs while onshore species spawn benthic eggs (Wootton, 1990; Leis, 1991). Finally, I also hypothesise that fish larvae would accumulate more at the sites within the bay than those sites outside of the bay along the open coastline. This is due to the shape of the Bay, which is sheltered, providing suitable habitat for fish to spawn in (Hutchings *et al.*, 2002). The physical features such as currents also aid survival of eggs and larvae by recirculating water within the Bay area facilitating their retention (Yasso, 1965; Velez *et al.*, 2005; Delpey *et al.*, 2014).

2.2 Methods and Materials

2.2.1 Study Area

The sampling area for this study falls within the South African Environmental Observation Network (SAEON) Algoa Bay Sentinel Site, on the southeast coast of South Africa, which extends from Cape St Francis Bay in the west to Port Alfred in the east and includes Algoa Bay entirely (Figure 2.1). Sampling stretched from Kini Bay in the west (34°1'17.44"S, 25°21'24.70"E) to Kenton-on-Sea (33°46'12"S, 26°40'47"E) in the east (Figure 2.1).

Algoa Bay is the largest embayment on the east coast of South Africa, west of the Agulhas Bank with its mouth ~80 km wide (Harris 1999; Schumann *et al*., 2005), reaching a maximum depth of 70 m (Coetzee and Baird, 1981). The sea surface temperatures in the area range from 10 - 24°C all year round (Smit *et al.,* 2013). The area is highly influenced by the warm Agulhas Current (Goschen and Schumann, 1988), which flows south west along the continental shelf ~50 km offshore of Algoa Bay (Goschen and Schumann, 2011), increasing sea surface temperatures in the area (Schumann, 1987, 1998). Upwelling of cold water is known to occur at the headlands of Algoa Bay, namely Cape Padrone in the east of the Bay and Cape Recife in the west, reducing ocean temperatures in the Bay to as low as 10°C (Goschen and Schumann, 2011; Goschen *et al*., 2012). Upwelling in the eastern sector of the Bay is largely influenced by the Agulhas Current and easterly winds (Goschen, 1991), while upwelling in the western sector is mainly associated with the easterly winds (Goschen and Schumann, 2011). Easterly winds can occur mostly in summer (Schumann *et al*., 1988), while westerly winds occur all year round in the Bay region (Schumann and Martin, 1991), but are more prevalent in winter (Roberts, 2010). The mean sea surface temperatures in the eastern sector of Algoa Bay are generally warmer in summer and colder in winter than the western side of the Bay (Goschen, 1991). Hydrodynamics in Algoa Bay are driven by the coastal bathymetry, shoreline contours, oceanographic processes, local weather and adjacent continental shelf (Goschen & Schumann, 2011).

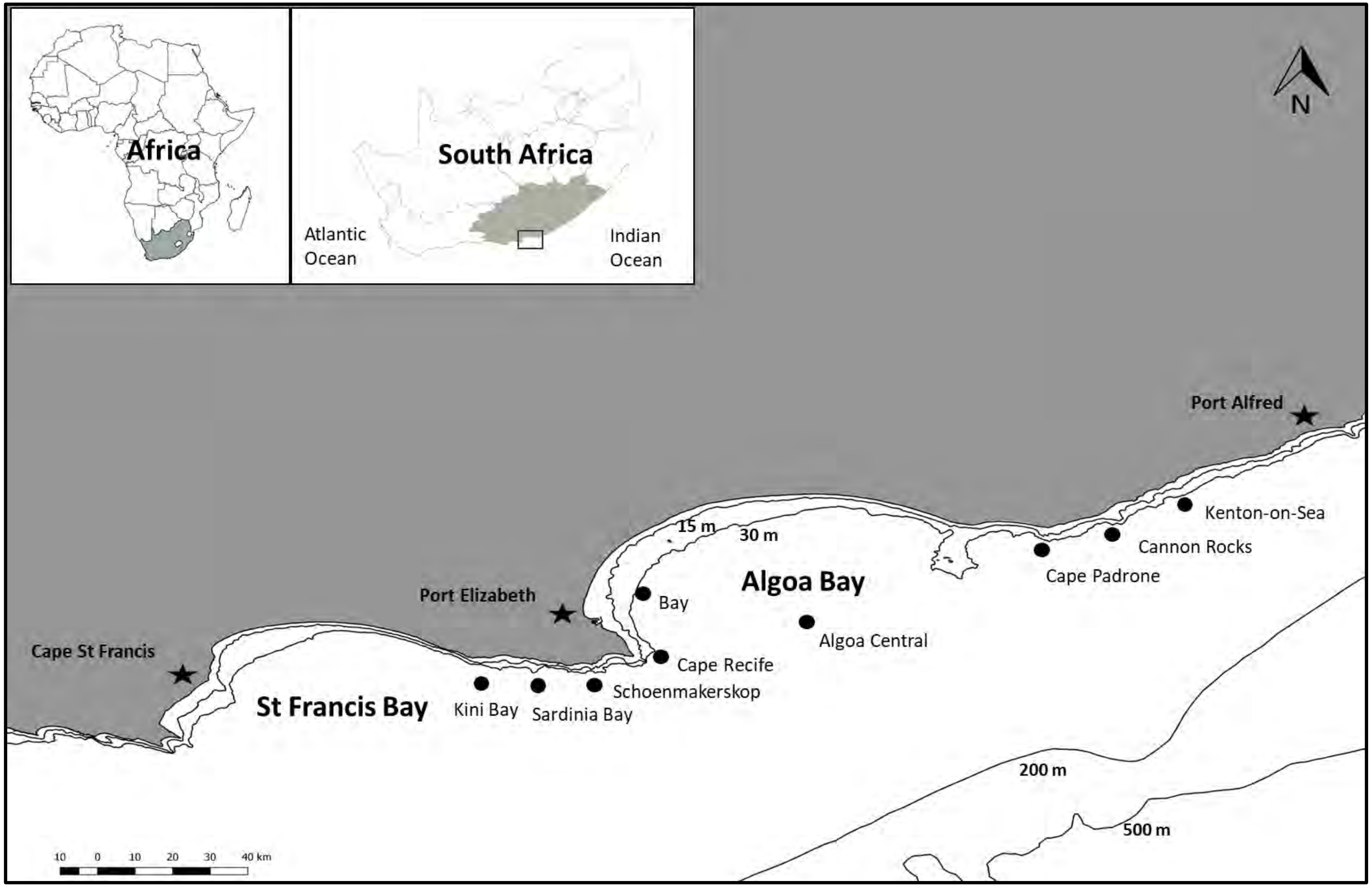


Figure 2.1: Map of Africa, South Africa and the sampling region on the south east coast of South Africa to show the approximate position of the nine sampling sites (black circles) in the Algoa Bay region. The three main metropolitan centres are also highlighted (black stars).

2.2.2 Field Sampling

Larval fishes were collected during several sampling events (Table 2.1) over two main sampling periods comprising Trip 1 (summer; January 2016 – early winter; May 2016) and Trip 2 (spring; October 2016 – late summer; March 2017). The lowest sea surface temperatures are recorded in April/May (Winter) in the Algoa Bay region while the highest sea surface temperatures are recorded in January/February (Summer) and October/November (Spring) (Schuman *et al.,* 1995). Sampling was carried out at nine sites situated in the coastal nearshore between Kini Bay, in the west, to Kenton-on-Sea, in the east (Figure 2.1). Larval fish samples were collected by means of boat-based plankton net tows using a set of bongo nets (mesh size 500 µm). Each net was 3.5 m in length with a 0.57 m mouth diameter. A General Oceanics flowmeter was attached to each net frame to determine the volume of water filtered during a tow. At each site, two stations (for the purposes of this study termed "Distance" with relative onshore and offshore positions selected) were sampled by towing the bongo nets twice (2 replicates per station), parallel to the shore at both the surface and near the bottom of the water column at a speed of ~2 knots for 3 minutes. When the net is hauled up onto the boat, the mouth of the net is closed off and does not sample the entire water column and therefore, only the bottom was sampled, not the entire water column. The onshore stations were located ~400 m from the shore and in water depths <30 m while the offshore stations were ~3 km from shore and in water depths >30 m, baring Algoa Central, located at the mouth of Bay (Table 2.1). After each tow, samples were rinsed over a sieve with mesh size of 500 µm, collected in jars and preserved in ethanol.

Table 2.1: Sampling dates for the nine sites during Trip 1 (summer – early winter) and Trip 2 (spring – late summer). See Figure 2.1 for location of the sampling sites.

Sites	**Trip 1 (summer-early winter)**	**Trip 2 (spring– late summer)**	**Average depth onshore**	**Average depth offshore**
Kini Bay	10/05/2016	06/11/2016	20	35
Sardinia Bay	11/05/2016	25/10/2016	16	33
Schoenmakerskop	23/02/2016	24/10/2016	15	37
Cape Recife	27/02/2016	22/10/2016	16	34
Bay	04/02/2016	22/10/2016	12	16
Algoa Central	22/01/2016	09/11/2016	45	50
Cape Padrone	12/04/2016	17/03/2017	18	32
Cannon Rocks	19/04/2016	17/02/2017	28	30
Kenton-on-Sea	13/04/2016	08/02/2017	15	27

Environmental parameters (11) were also recorded during the collection of the larval fish samples. Physical oceanographic data were collected at each station (onshore and offshore), using a 600 kHz acoustic Doppler current profiler (ADCP, RD Instruments®), mounted via a pole on the vessel which was lowered alongside of a fixed boat to measure zonal (Avg E cm/s), meridional (Avg N cm/s) and vertical (Avg V cm/s) current speed and direction in 1 m depth intervals for a minimum sampling period of 30 minutes. During the time of sampling, the boat was at anchor. Rayleigh test statistics were used to test for uniformity for the distribution of the oceanographic currents within each site and distance. Circular-linear correlations were then used to calculate correlations between currents speed and direction among sites and between distances. A Seabird SBE 9/11 plus CTD (conductivity, temperature, depth) profiler was also lowered to the bottom of the water column to measure water temperature (°C), fluorescence (mg/m^3), turbidity (NTU), salinity, dissolved oxygen (ml/L) and pH at each station. The raw CTD data were processed using SBE Data Processing, V7.26.7 software. The temperature data for the integrated environmental parameters were obtained from SAEON, using underwater temperature recorders (UTR's) located at Cape Recife and Cape Padrone at depths of ~15 m. The temperature data from the UTR's was used together with wind data in order to characterise the conditions at the west and east entrances of the Bay at least three days prior to sampling. Hourly measurements of wind speed and direction were obtained from the Port Elizabeth Airport meteorological station (to represent the Bay, Cape Recife, Schoenmakerskop, Sardinia Bay and Kini Bay sites in the west) and the Bird Island meteorological station (to represent the Algoa Central, Cape Padrone, Cannon Rocks and Kenton-on-Sea sites in the east). The meteorological stations are located at a height of 60 m (Port Elizabeth Airport) and 3 m (Bird Island) above sea level. The following equation was used to correct/adjust the wind data due to the varying heights of the weather stations:

$$V_{3m=} V_{h}\,(3/h)^{0.11}$$

Where V_{3m} is the wind speed at 3 m altitude at the Bird Island weather station, V_h is wind velocity measured at each station and h is the height at each meteorological (Hsu *et al.*, 1994).

From the wind data, an upwelling index, as zonal Ekman transport, was calculated with positive and negative values to indicate onshore and offshore displacement of surface waters, respectively (Bakun, 1973). Hourly tidal amplitude (m) data were retrieved using the WXTide32 software version 4.7.

2.2.3 Laboratory Analysis

Larval fishes were individually removed from each plankton sample, counted, measured and identified under a stereo microscope (Zeiss stemi 508) to the lowest possible taxon using the following literature: Leis and Rennis, 1978; Leis and Rennis, 1983; Leis and Trnski, 1989; Olivar and Fortuño, 1991; Griffiths and Heemstra, 1995; Neira *et al.*, 1998; Leis and Carson-Ewart, 2000; Azeiteiro *et al.*, 2006. Notochord length in preflexion and flexion larvae and standard length in postflexion larvae were measured to the nearest 0.1 mm and were referred to as body length (BL).

2.2.4 Statistical Analysis

2.2.4.1 Environmental Data

Cross-correlations among the environmental parameters recorded during the study were assessed using Draftsman plots. No significant correlations were found hence all environmental parameters were included in subsequent multivariate analyses. Patterns in environmental variables for the different trips and depths were observed using the Principal Component Analysis (PCA). A PCA was performed for each trip (i.e. Trip 1 and Trip 2; see details below on this approach due to the outcome of the pre-analysis of the biological data) on a normalised Euclidean distance similarity matrix to examine trends/patterns considering all the measured environmental parameters: temperature, fluorescence, pH, turbidity, salinity, dissolved oxygen and zonal flow, meridional flow, vertical flow, wind speed and wind direction. Since the temporal variability was not the primary scope of the study and due to heterogeneous distribution of data for trips, separate analyses were run for each trip. PCAs help simplify dimensions of data while retaining important information, it does this by projecting data onto lower dimensions called principal components (PC's) (Clarke & Gorley, 2015). Euclidean distance similarity matrix to examine trends/patterns considering all the measured environmental parameters: temperature, fluorescence, pH, turbidity, salinity, dissolved oxygen and zonal flow, meridional flow, vertical flow, wind speed and wind direction. All analyses of environmental data were performed using PRIMER V6.1.15 with PERMANOVA + V1.0.5 add-on.

2.2.4.2 Biological Data

The volume of water strained through each bongo net was calculated using the following formula:

> Volume of water filtered = Total flow meter revolutions (Flow meter end – flow meter start) * 3.0365 (meters per 1 revolution, calibrated in a swimming pool) * 0.26 (area of 57 cm bongo net)

The average for each replicate (pooling the two adjacent nets) was then calculated. The density of larvae (no. of larvae/100 m^3) was calculated using the following formula:

> Total density = total count / volume of water filtered x 100

Multivariate analyses were performed with the PRIMER V6.1.15 with PERMANOVA + V1.0.5 add-on (Clarke and Warwick, 1994). Possible along, cross-shore and depth effects on the larval abundance data were analysed. The homogeneity of variance of untransformed and, whenever necessary, transformed datasets was tested using the dispersion analysis (PERMDISP). The distance-based test for homogeneity of multivariate dispersions (PERMDISP), accompanies a PERMANOVA, and is used to determine the deviation of individual observations to their own group centroid (Anderson, 2017). The PERMDISP, used to test the hypothesis of no difference in dispersions among groups (Anderson, 2006), was used to test for homogeneity of data among sites and between trips (Trip 1 and Trip 2), distances (Onshore/Offshore) and depths (Surface/Bottom). The results of the PERMDISP on the square root transformed data showed the following factors: Site ($F= 0.85$, $p= 0.83$), Distance ($F= 1.03$, $p= 0.42$) and Depth ($F= 4,76$, $p= 0.08$) to be homogenous. The factor Trip ($F= 4.02$, $p< 0.05$)

was found to be heterogeneous, hence the analysis on the biological data was done separately for the two trips. PERMANOVA is robust against non-normality of data (Anderson, 2006) and so three-way permutational multivariate analyses of variance (PERMANOVA) were performed on the abundance data to test for significant differences among Site (9 levels, random), Distance (2 levels, fixed) and Depth (2 levels, fixed), separately for Trip 1 and 2. The analyses were based on the Bray-Curtis similarity matrix using 9999 permutations. Pairwise tests were run to assess significant factors and interactions identified during PERMANOVA tests. SIMPER analyses were used to detect the key contributing taxa to differences among Sites, and between Trips, Depth and Distances. Distance-based linear models (DistLM) were performed to determine the most influential environmental factors driving the overall larval fish abundances. The DistLM were based on 9999 permutations using the step-wise selection procedure based on Akaike's Information Criterion (AIC) and graphically visualised using redundancy analysis (db-RDA) ordination.

For the present study, larvae were grouped into four categories based on the adult distribution and the eggs that are produced: 1) Coastal species with Benthic Eggs (CBE), these are species that spawn in the nearshore but produce benthic eggs which get spawned onto the ocean floor (e.g. reefs) or vegetation (Barros *et al.*, 2001). 2) Coastal species with Pelagic Eggs (CPE) also spawn in the nearshore but produce pelagic eggs which are found in the water column. 3) Pelagic species with Pelagic Eggs (PPE) produce pelagic eggs and they spawn both in the nearshore and offshore environment. 4) Live-Bearers (LB) being either ovoviviparous or viviparous (Beckley, 1989; Sommer *et al.*, 2012).

2.3 Results

2.3.1 Species Composition

In total, 358 larval fishes were collected and were represented by 20 families and 36 species. Larvae from the CBE dominated overall catches comprising 49%, with the larvae of CPE contributing 31% towards the overall catch while the larvae of PPE and LB contributing 12% and 8% respectively. Blenniidae family dominated the total overall catch in coastal nearshore of the Algoa Bay region while in terms of species, *Parablennius pilicornis* (Blenniidae) contributed the most towards the total larval fish catch on the coastal nearshore. The flexion stage of larval development dominated the overall catch, comprising 63%. The preflexion stage of development contributed 29% with only 8% of the total catch consisting of postflexion stage larvae (Table 2.2).

Table 2.2: Species composition by total number of larvae (N) and as percentage of the total catch (%), developmental stage (Pr= preflexion, F= flexion, Po= postflexion), range in body length and spawning mode (CBE= Coastal species with benthic eggs, CPE= Coastal species with pelagic eggs, PPE= Pelagic species with pelagic eggs and LB= Live-bearers) in the coastal nearshore of the Algoa Bay region.

Family	**Species**	**N**	**%**	**Developmental stage**	**Body length (range) in mm**	**Spawning mode**
Blenniidae	Blenniidae sp. 1	7	2.0	F, Pr	0.6-6.6	CBE
	Blenniidae sp. 2	1	0.3	F	5.4	CBE
	Blenniidae sp. 3	3	0.8	F, Pr	2.9-4.9	CBE
	Omobranchus woodi	4	1.1	F, Pr	3.5-4.3	CBE
	Parablennius cornutus	11	3.1	F	8.2-8.9	CBE
	Parablennius pilicornis	114	31.8	Pr, F, Po	0.9-13.3	CBE
Callionymidae	Callionymidae sp. 1	11	3.1	Pr, F, Po	0.8-6.7	CPE
Clinidae	Clinidae sp. 1	21	5.9	F, Pr, Po	0.5-9.5	LB
Clupeidae	*Etrumeus whiteheadi*	22	6.1	F	12.1-24	PPE
	Sardinops sagax	3	0.8	F	6.7-10	PPE
Cynoglossidae	Cynoglossidae sp. 1	37	10.3	F, Pr, Po	1.0-11.7	CPE
Engraulidae	*Engraulis encrasicolus*	17	4.7	Pr, F, Po	1.2-14.6	PPE
Gobiidae	*Caffrogobius gilchristi*	4	1.1	F, Pr	0.9-1.3	CBE
	Glossogobius callidus	1	0.3	Pr	0.9	CBE
Gobiesocidae	*Chorisochismus dentex*	2	0.6	Pr	0.8-4.7	CBE
	Diplecogaster megalops	22	6.1	Pr, F, Po	0.7-6.4	CBE
Haemulidae	*Pomadasys* sp. 1	2	0.6	F	1.4	CPE
Hemiramphidae	*Hyporhamphus capensis*	1	0.3	Po	32.2	CBE
Mugilidae	Mugilidae sp. 1	10	2.8	Po	8.8	CPE
Scomberesocidae	Scomberesocidae sp. 1	2	0.6	F	0.6	CPE
Scorpaenidae	Scorpanidae sp. 1	3	0.8	F	0.9	CPE
Serranidae	*Acanthistius* sp. 1	1	0.3	Po	20.0	CPE
Soleidae	*Heteromycteris capensis*	8	2.2	F	3.8-8.0	CPE
	Solea turbynei	6	1.7	Pr, F	3.1-14.0	CPE

	Soleidae sp. 1	8	2.2	Pr, F	2.6-8.8	CPE
Sparidae	*Diplodus capensis*	9	2.5	F	0.7-7.9	CPE
	Pachymetopon blochii	7	2.0	F, Pr	0.9-10.6	CPE
	Pagellus natalensis	1	0.3	F	1.3	CPE
	Rhabdosargus holubi	1	0.3	Po	1.0	CPE
	Sparidae sp. 1	4	1.1	Pr	0.9-6.4	CPE
	Spondyliosoma emarginatum	5	1.4	F	4.6-11.5	CBE
Syngnathidae	*Syngnathus* sp. 1	6	1.7	Po	10.1-79.4	LB
Tetraodontidae	Tetraodontidae sp. 1	1	0.3	Pr	2.0	CPE
Triglidae	Triglidae sp. 1	2	0.6	Po	0.6-12.2	CPE
Unidentified sp.	Unidentified sp. 1	1	0.3	F	5.3	
Total no. of individuals		358	100			

Overall, the density of fish larvae was higher in the onshore than offshore, with more larvae occurring at the surface of the water column than at the bottom (Figure 2.10). The density of larvae from CBE decreased with increasing distance from the shore and occurred mostly at the surface of the water column. Generally, a higher density of both CPE and PPE occurred in the offshore, with more larvae particularly at the bottom of the water column. The highest density of larvae of LB occurred in the onshore at the bottom of the water column (Figure 2.2).

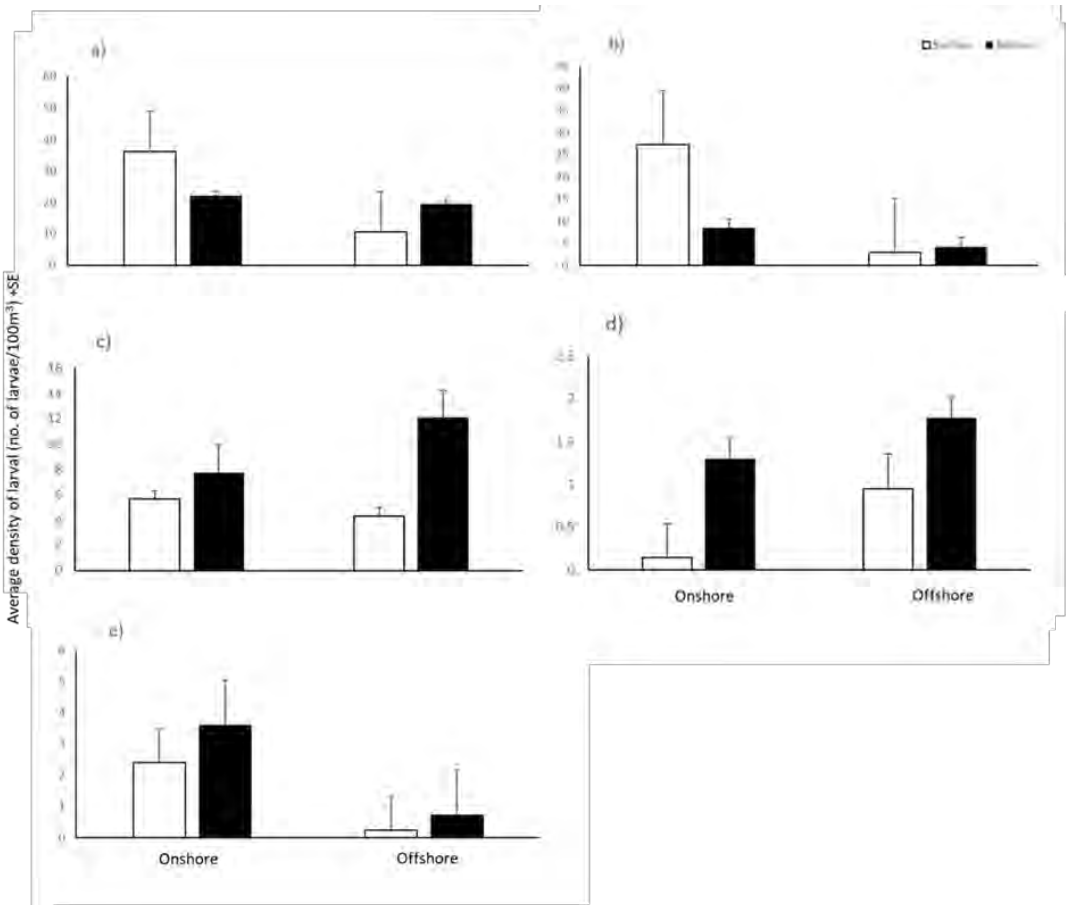


Figure 2.2: Larval fish density (error bars indicate standard errors) for a) the total density, b) Coastal species with Benthic Eggs= CBE, c) Coastal species with Pelagic Eggs= CPE, d) Pelagic species with Pelagic Eggs= PPE and e) Live Bearers= LB at the two Depths (surface/bottom) and Distances (onshore/offshore) sampled in the coastal nearshore of the Algoa Bay region.

During Trip 1, 107 larval fishes (10 families and 15 species) were collected, with 251 fish larvae (17 families and 30 species) collected during Trip 2. The Blenniidae and Cynoglossidae dominated the catches during both Trip 1 and Trip 2 (Figure 2.3).

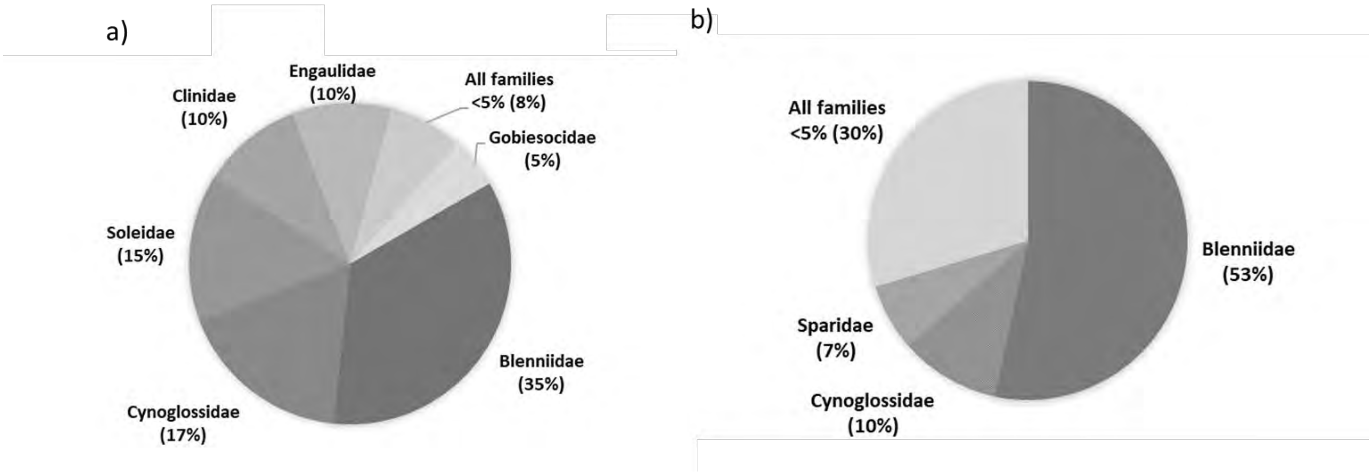


Figure 2.3 Percentage contribution of larvae of the dominant fish families (>5%) captured during a) Trip 1 and b) Trip 2 in the coastal nearshore of the Algoa region.

During Trip 1, the larvae of Coastal species with Pelagic Eggs (CPE) dominated the catches while during Trip 2, Coastal species with Benthic Eggs (CBE) were dominant in the coastal nearshore of the Algoa Bay region (Figure 2.4).

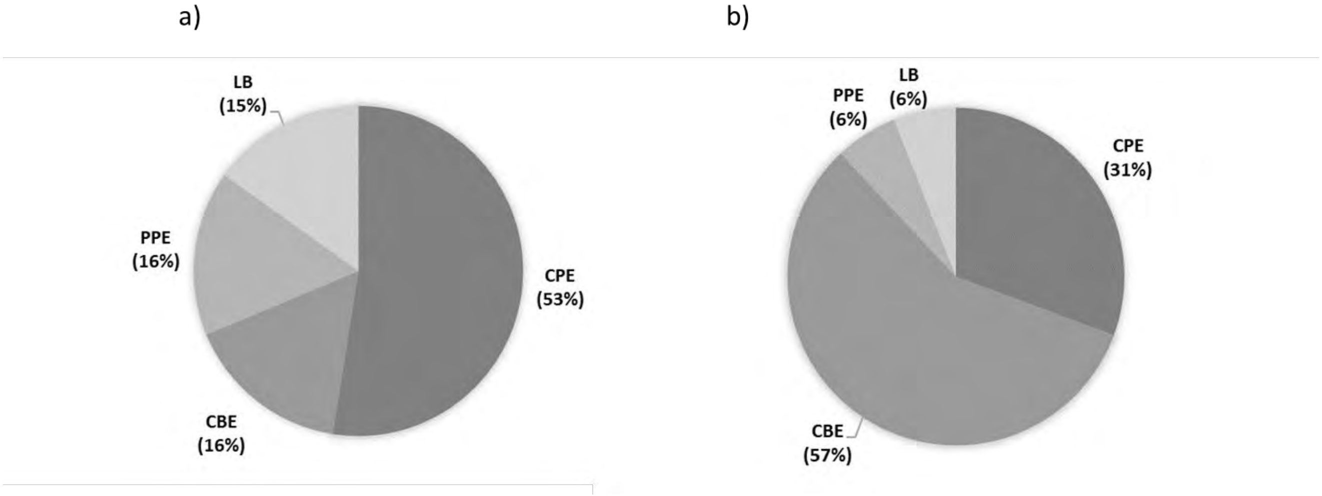


Figure 2.4 Percentage contribution of larvae of CBE, CPE, PPE and LB sampled during a) Trip 1 and b) Trip 2 in the coastal nearshore of the Algoa Bay region.

At the surface of the water column, during Trip 1, the Blenniidae contributed the most towards the overall catch (Figure 2.4a) while Soleidae made important contributions at the bottom of the water column (Figure 2.4b). Cynoglossidae dominated both the onshore (Figure 2.4c) and offshore in the Algoa Bay region during Trip 1 (Figure 2.4d).

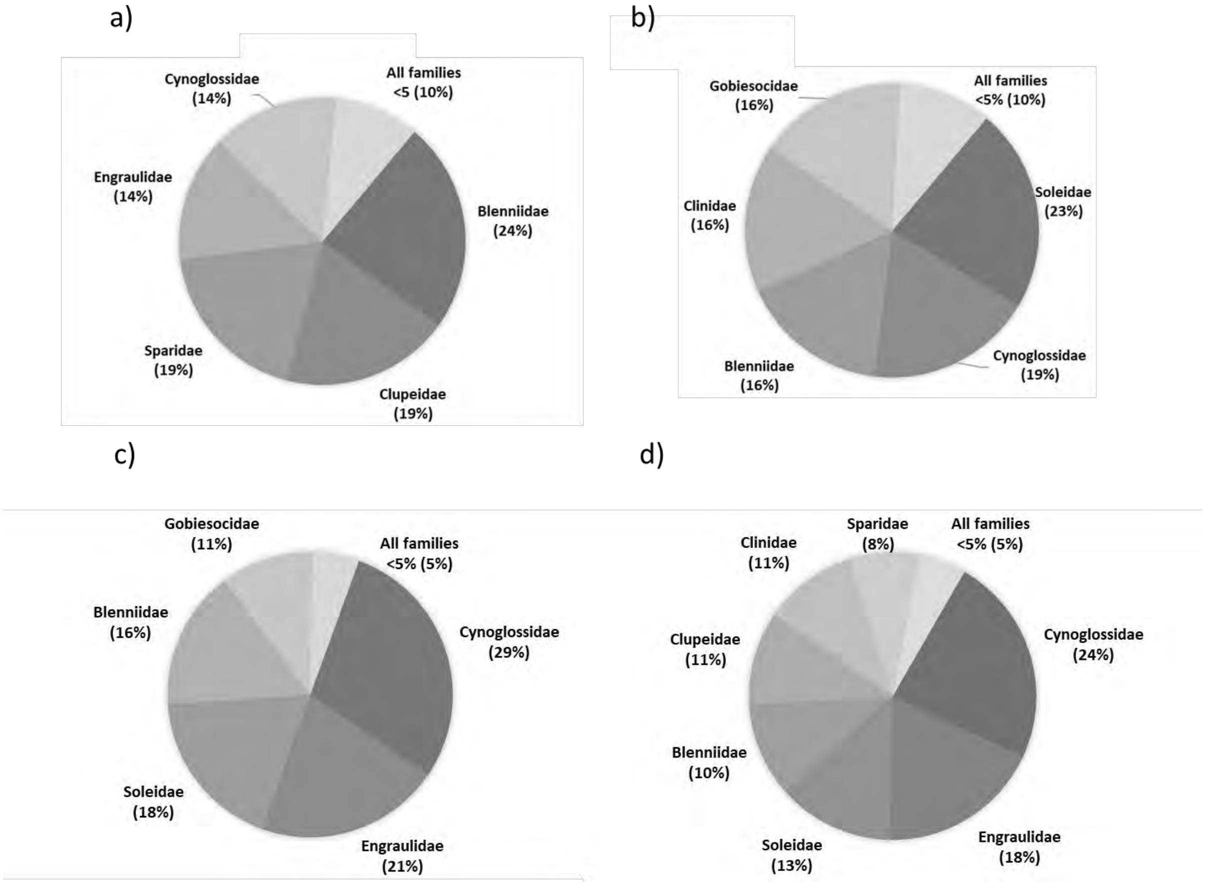


Figure 2.5 Percentage contribution of the dominant families during Trip 1 at the a) Surface b) Bottom c) Onshore d) Offshore sampled in the coastal nearshore of the Algoa Bay region.

For Trip 2, Blenniidae made important contributions at the surface of the water column (Figure 2.5a) while Cynoglossidae contributed the most towards the bottom (Figure 2.5b). In the onshore, Blenniidae contributed the most towards the total catch (Figure 2.5c), while Cynoglossidae dominated the offshore on the coastal nearshore waters in the Algoa Bay region (Figure 2.5d).

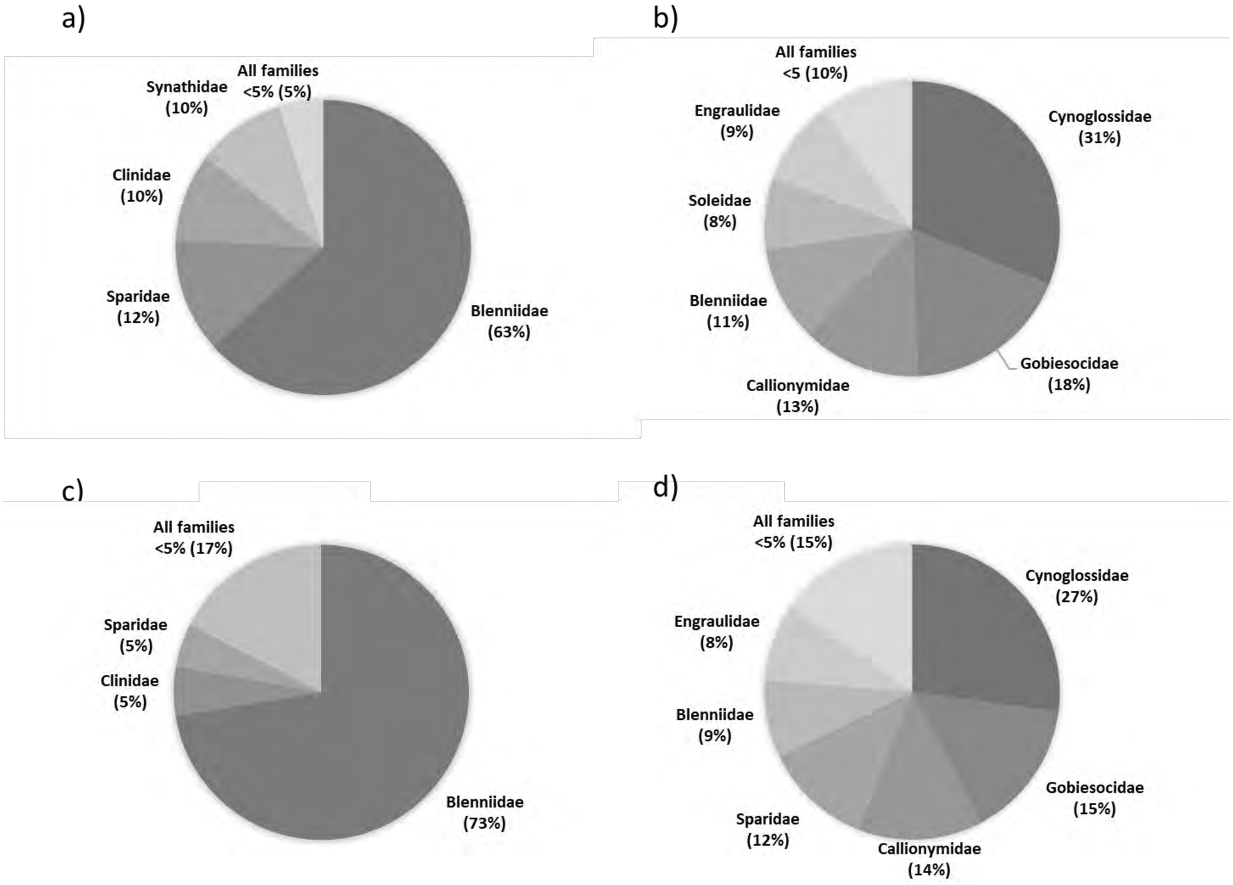


Figure 2.5 Percentage contribution of the dominant families during Trip 2 at the a) Surface b) Bottom c) Onshore d) Offshore sampled in the coastal nearshore of the Algoa Bay region.

2.3.2 Alongshore, Cross-shore and Depth Variability in Larval Fish Community

The results of the PERMANOVA conducted on the abundance of larvae for Trip 1 indicated that there was high variability in larval fish composition according to Site, Distance and Depth. The interaction between Site and Depth and the interaction among Site, Distance from the shore and Depth during Trip 1 (Table 2.3) were also found to be significant.

Table 2.3: Results of PERMANOVA on square root transformed larval abundance data recorded in the coastal nearshore of the Algoa Bay region during Trip 1 (added as root values in the table). Df= Degrees of freedom, SS= Sum of Squares, MS= Mean Squares, Pseudo-F= F-ratio, P= Probability value. Significant results in bold.

Source	Df	SS	MS	Pseudo-F	P
Site (Si)	8	12071.0	1508.9	1.6	**0.005**
Distance (Di)	1	2361.3	2361.3	2.8	**0.01**
Depth (De)	1	2788.5	2788.5	2.1	**0.04**
Si x Di	8	6824.9	853.1	0.9	0.6
Si x De	8	10395.0	1299.4	1.4	**0.01**
Di x De	1	2466.7	2466.7	1.8	0.1
SI x Di x De	8	10685.0	1335.6	1.5	**0.02**
Res	35	31938.0	912.5		
Total	70	79294.0			

During Trip 1, the highest mean densities of larval fish were recorded at the surface of the water column at Sardinia Bay, Schoenmakerskop and Cape Recife, while at Kini Bay and Algoa Central most larvae were found at the bottom (Figure 6a; Table 2.4). At Cape Recife, larvae were most abundant onshore at the surface, while at Algoa Central and Cannon Rocks more larvae were recorded onshore at the bottom (Figure 2.6a, b; Table 2.4). Larvae were abundant offshore at the bottom of the water column at Kini Bay, while at Sardinia Bay more larvae were recorded offshore at the surface (Figure 2.6a, b; Table 2.4).

Table 2.4: Pairwise test results showing significant interaction among Site, Depth (surface/bottom) and Distance (onshore/offshore) during Trip 1.

Interaction	Site	Distance	Depth
Si x De	Kini Bay		Bottom>Surface
	Sardinia Bay		Surface>Bottom
	Schoenmakerskop		Surface>Bottom
	Cape Recife		Surface>Bottom
	Algoa Central		Bottom>Surface
Si x De X Di			
	Kini Bay	Offshore>Onshore	Bottom>Surface
	Sardinia Bay	Offshore>Onshore	Surface>Bottom
	Cape Recife	Onshore>Offshore	Surface>Bottom
	Algoa Central	Onshore>Offshore	Bottom>Surface
	Cannon Rocks	Onshore>Offshore	Bottom>Surface

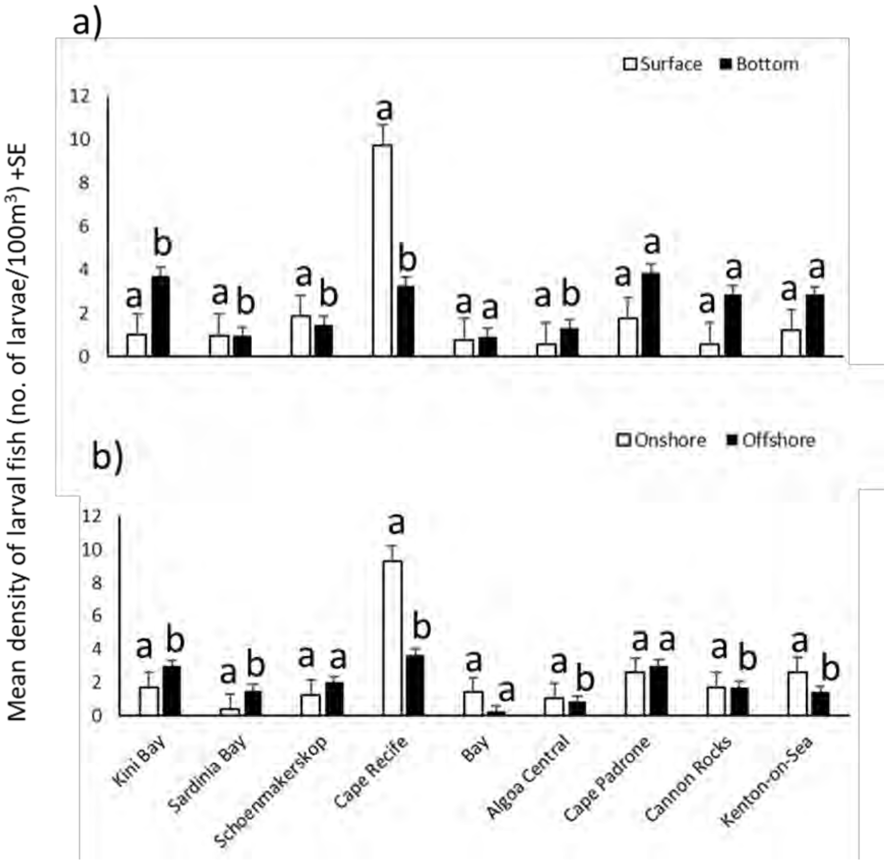


Figure 2.6: Mean density of larvae (no./100 m^3) during Trip 1 for a) Depth (surface/bottom) and b) Distance (onshore/offshore) in the coastal nearshore of the Algoa Bay region. Error bars indicate standard error and the letters above the bars indicate within site homogenous group identified by ‘Site X Depth’ pairwise results.

The SIMPER results indicated that *P. pilicornis* drove the separation between the onshore and offshore (mostly in the onshore), while *Sardinops sagax* were exclusively offshore and *D. megalops* were found exclusively onshore at Cape Recife (Table 2.5). At Cape Recife, the species that contributed the most towards the observed patterns between Depth (surface/bottom) was *P. pilicornis,* while *S. sagax* and *D. megalops* were found exclusively at the bottom of the water column (Table 2.6). *Parablennius pilicornis*, Cynoglossidae sp. 1, *D. megalops* and *Engraulis encrasicolus* contributed the most towards the observed patterns in Depth (surface/bottom) during Trip 1 in the coastal nearshore of the Algoa Bay region (Table 2.7). For the differences between Distance (onshore/offshore), the following species contributed the most towards the observed patterns: *P. pilicornis*, Cynoglossidae sp. 1, *D. megalops* and *Diplodus capensis* (Table 2.8).

Table 2.5: SIMPER results for the percentage contribution of species to dissimilarity of Distance (onshore/offshore) in the coastal nearshore of Cape Recife in the Algoa Bay region during Trip 1. Av.Abund.= Average abundance of species, Av.Diss.= Average dissimilarity of species, Contrib.%= contribution percentage of each species and Cum.%= cumulative contribution of each species. The cut off for including species in the table was 8% contribution.

Species	**Av.Abund. offshore**	**Av.Abund. onshore**	**Av.Diss.**	**Contrib.%**	**Cum.%**
Parablennius pilicornis	0.1	1.6	28.9	29.8	29.8
Sardinops sagax	0	0.1	9.4	9.7	39.6
Diplecogaster megalops	0	0.3	8.5	8.8	48.4

Table 2.6: SIMPER results for the percentage contribution of species to dissimilarity of depth (surface/bottom) in the coastal nearshore of Cape Recife during Trip 1 in the Algoa Bay region. Av.Abund.= Average abundance of species, Av.Diss.= Average dissimilarity of species, Contrib.%= contribution percentage of each species and Cum.%= cumulative contribution of each species. The cut off for including species in the table was 8% contribution.

Species	**Av.Abund. Bottom**	**Av.Abund. surface**	**Av.Diss.**	**Contrib.%**	**Cum.%**
Parablennius pilicornis	0.2	1.5	28.0	29.0	29.0
Sardinops sagax	0.1	0	8.4	8.7	37.7
Diplecogaster megalops	0.3	0	8.3	8.5	46.2

During Trip 2, there were significant effects for Site and the interaction between Site and Depth in the coastal nearshore of the Algoa Bay region (Tables 2.7 and 2.8). There is a significant correlation between the SS for both trips, suggesting that the factors in isolation or combination, are behaving similarly, whilst there were also similar residuals (Tables 2.7 and 2.8). For Trip 1, the significant interaction between site and distance as well as the interaction among site, distance and depth were taken into consideration. During Trip 2 only the interaction between site and depth was significantly (Tables 2.7 and 2.8). The highest densities of larval fish were recorded at Kini Bay, Schoenmakerskop, Cape Recife and Kenton-on-Sea, with more larvae at the surface than bottom; within Bay, Cape Padrone and Cannon Rocks, more larvae were at the bottom than surface (Figure 2.7). The species that contributed the most towards the observed differences between depths during Trip 2 were Blenniidae sp. 1, Clinidae sp. 1, *D. megalops*, Cynoglossidae sp. 1 and *E. encrasicolus* (Table 2.9).

Table 2.7: PERMANOVA results conducted on a square root transformed larval abundance data recorded in the coastal nearshore of the Algoa Bay region for Trip 2 (added as root values in the table). Df= Degrees freedom, SS= Sum of Squares, MS= Mean Squares, Pseudo-F= F-ratio. Significant results in bold.

Source	**Df**	**SS**	**MS**	**Pseudo-F**	**P**
Site (Si)	8	9093.5	1136.7	1.9	**0.003**
Distance (Di)	1	1201.8	1201.8	1.5	0.2
Depth (De)	1	1967.2	1967.2	2.1	0.1
Si x Di	8	6395.1	799.4	1.3	0.1
Si x De	8	7577.3	947.3	1.6	**0.001**
Di x De	1	636.3	636.3	1.1	0.4
Si x Di x De	8	4557.5	569.7	0.9	0.6
Res	36	21635.0	600.9		
Total	71	53063.0			

Table 2.8: Pairwise test results resulting from the significant interaction among site and depth (surface/bottom) during Trip 2.

Interaction	Site	Depth
SiXDe	Kini Bay	Surface>Bottom
	Schoenmakerskop	Surface>Bottom
	Cape Recife	Surface>Bottom
	Bay	Bottom>Surface
	Cape Padrone	Bottom>Surface
	Cannon Rocks	Bottom>Surface
	Kenton-on-Sea	Surface>Bottom

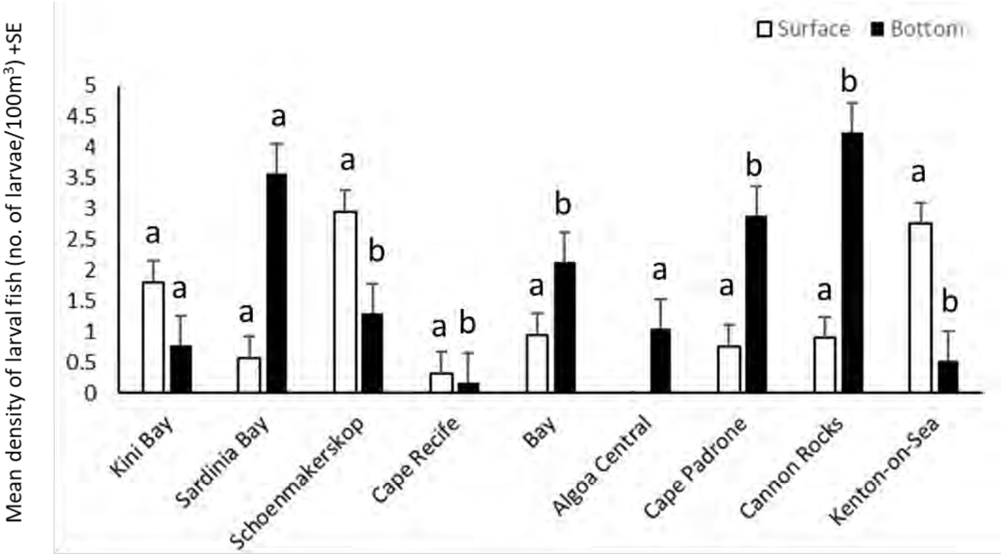


Figure 2.7: Total density of larvae (no./100 m^3) during Trip 2 for depth (surface/bottom) in the coastal nearshore of the Algoa Bay region. Error bars indicate standard error and the letters above the bars indicate within site homogenous group identified by 'Site X Depth' pairwise results.

Table 2.9: SIMPER results for the percentage contribution of species to dissimilarity of depth (surface/bottom) in the coastal nearshore during Trip 2 in the Algoa Bay region. Av.Abund.= Average abundance of species, Av.Diss.= Average dissimilarity of species, Contrib.%= contribution percentage of each species and Cum.%= cumulative contribution of each species. The cut off for including species in the table was 8%.

Species	Av.Abund. bottom	Av.Abund. surface	Av.Diss.	Contrib.%	Cum.%
Blenniidae sp. 1	0.03	0.1	10.2	10.6	10.6
Clinidae sp. 1	0.1	0.05	9.9	10.3	20.9
Diplecogaster megalops	0.1	0.03	9.8	10.1	31.0
Cynoglossidae sp. 1	0.1	0.03	9.2	9.6	40.6

2.3.3 Environmental Variability in the Coastal Nearshore

The PCA performed on the environmental variables revealed high variability for both Trip 1 and 2 and no clear, cross-shore (onshore vs offshore) or alongshore (amongst the sites) differences (Figure 2.8). A clear spatial variation was evident between depths (surface and bottom) in the coastal nearshore, but only for Trip 1. The PCAs (Figure 2.2) revealed that the eleven environmental variables explained ~40% of the dataset variability in the first two axes, for both Trip 1 and Trip 2. For Trip 1, the data according to depth were mainly separated vertically, hence mostly driven by PC 2 (15.9%) where the data at the surface were positively correlated with meridional and vertical currents. During Trip 2, data according to depth were mainly characterised by a negative correlation with wind speed and wind direction and positive correlation with meridional flow (PC 1, 22.3%), while PC 2 explained 19.6% and was mainly explained by a negative correlation with both fluorescence and turbidity and a positive correlation with pH (Table 2.10).

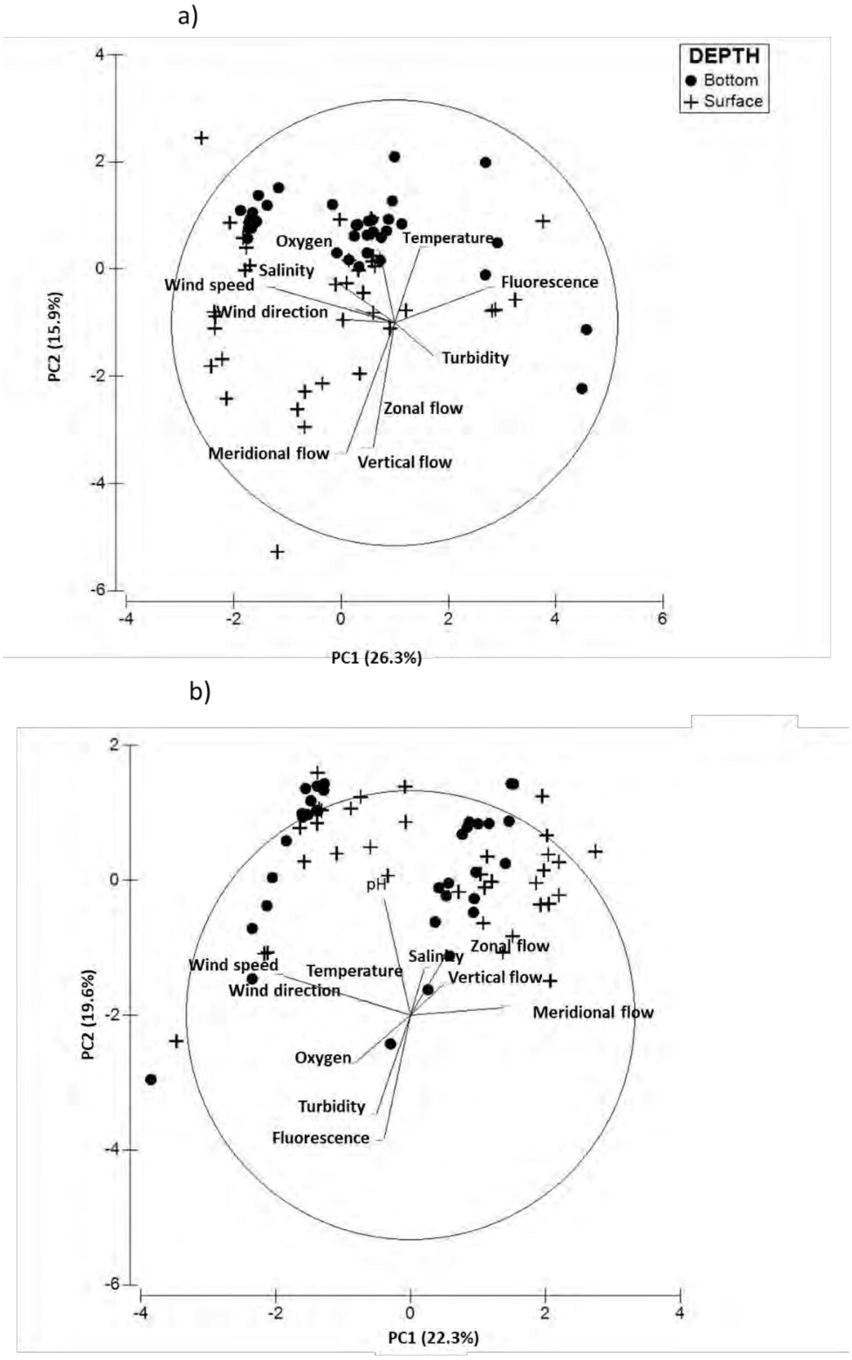


Figure 2.8: PCA two-dimensional biplots of the first and second components of the environmental variables for a) Trip 1 and b) Trip 2.

Table 2.10: A summary of eigenvectors of the first two Principal Components (PC1 and PC2) for each environmental variable in the coastal nearshore of the Algoa Bay region during Trip 1 (summer – early spring) and Trip 2 (late summer – late spring).

Variable	**Trip 1**		**Trip 2**	
	PC1 (26.3%)	PC2 (15.9%)	PC1 (22.3%)	PC2 (19.6%)
Zonal flow	-0.18	0.06	0.15	0.26
Meridional flow	-0.22	-0.58	0.41	0.03
Vertical flow	-0.09	-0.56	0.15	0.14
Temperature	0.11	0.33	-0.18	0.05
Fluorescence	0.4	0.15	-0.12	-0.55
Turbidity	0.17	-0.14	-0.15	-0.44
pH	-0.25	0.02	-0.12	0.51
Salinity	-0.28	0.2	0.06	0.21
Oxygen	-0.07	0.32	-0.24	-0.21
Wind speed	-0.53	0.15	-0.57	0.17
Wind direction	-0.53	0.15	-0.57	0.17

2.3.4 Alongshore and Cross-shore Spatial Trends in Current Direction

The results of the Rayleigh test for potential differences in flow of currents along and across-shore for Trip 1 indicated that current speed and direction in both the onshore and offshore for all sites (baring Bay and Schoenmakerskop offshore) were not uniformly distributed (Table 2.11). The circular linear correlation tests to assess the differences in current flow provided significant results for all the sites, except for Kini Bay onshore, indicating that current speed and direction were strongly correlated (Table 2.12).

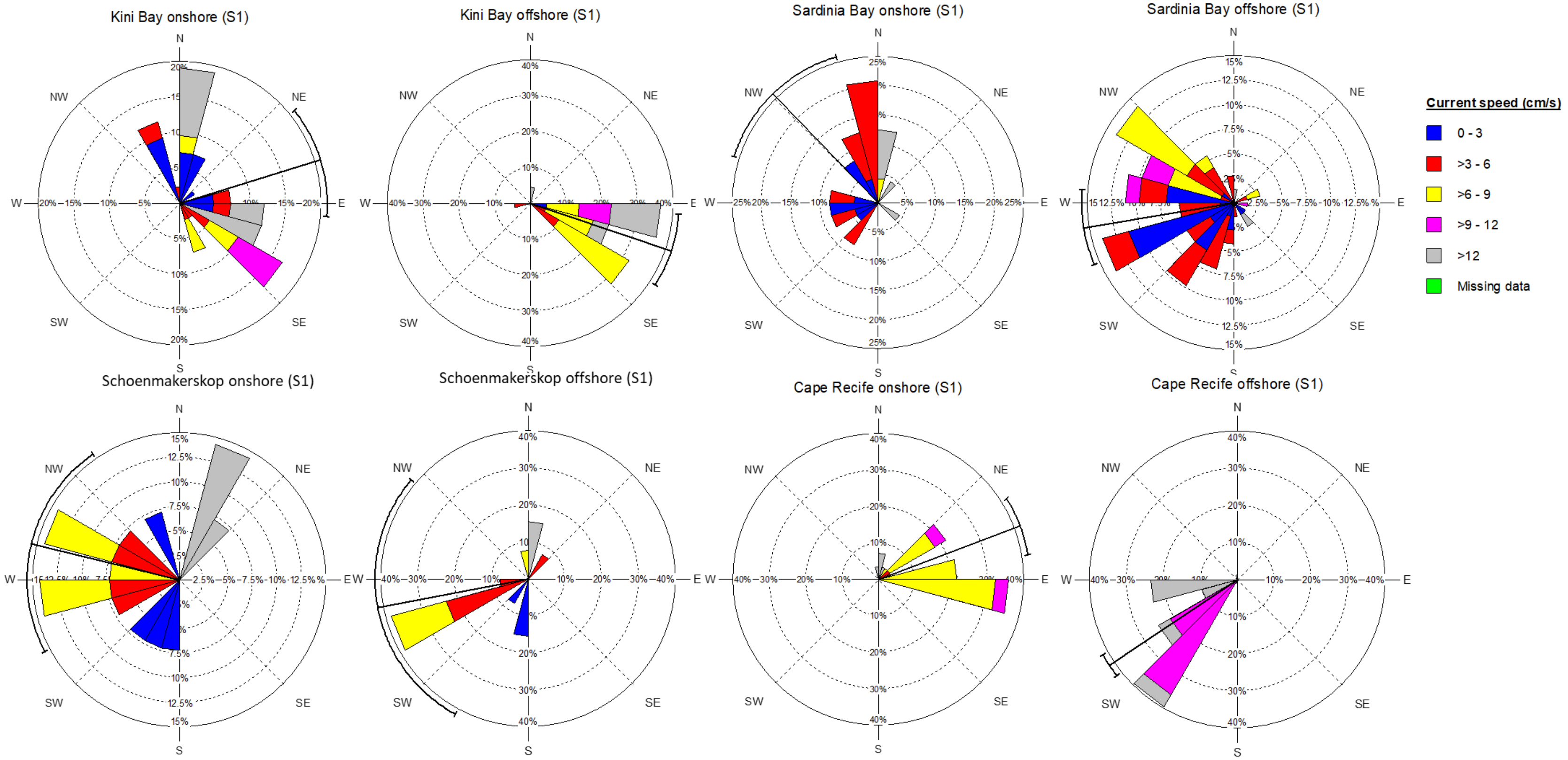
At Sardinia Bay, Cape Recife, Bay, Cape Padrone, Cannon Rocks and Kenton-on-Sea the currents were slower in the onshore than in the offshore. In the western sector, outside of Algoa Bay, at Schoenmakerskop the current velocities were faster onshore than offshore. At Kini Bay and Algoa Central the ocean currents in the onshore and offshore were greater than 12 m/s during Trip 1 (Figure 2.9 and 2.10).

Table 2.11: Results of the Rayleigh test for Trip 1 for differences on currents between distance (onshore/offshore) for Kini Bay, Sardinia Bay, Schoenmakerskop, Cape Recife, Bay, Algoa Central, Cape Padrone, Cannon Rocks and Kenton-on-Sea in the Algoa Bay region. P-values in bold are significant.

	Kini Bay Onshore	**Kini Bay Offshore**	**Sardinia Bay Onshore**	**Sardinia Bay Offshore**
Rayleigh Test (Z)	11.128	15.155	6.776	24.915
Rayleigh Test (p)	**7.00E-06**	**1.00E-07**	**8.00E-04**	**1.00E-11**
	Schoenmakerskop Onshore	Schoenmakerskop Offshore	Cape Recife Onshore	Cape Recife Offshore
Rayleigh Test (Z)	3.523	2.592	20.925	70.384
Rayleigh Test (p)	**0.03**	0.07	**1.86E-09**	**< 1E-12**
	Algoa Bay Onshore	Algoa Bay Offshore	Algoa Central Onshore	Algoa Central Offshore
Rayleigh Test (Z)	0.427	2.662	18.47	5.779
Rayleigh Test (p)	0.66	0.07	**9.00E-09**	**0.003**
	Cape Padrone Onshore	Cape Padrone Offshore	Cape Rocks Onshore	Cannon Rocks Offshore
Rayleigh Test (Z)	11.185	9.667	8.087	47.663
Rayleigh Test (p)	**3.00E-06**	**6.00E-05**	**2.00E-04**	**< 1E-12**
	Kenton-on-Sea Onshore	Kenton-on-Sea Offshore		
Rayleigh Test (Z)	4.954	8.265		
Rayleigh Test (p)	**0.006**	**3.00E-04**		

Table 2.12: Results of the circular linear correlation between current speed and direction at the onshore/offshore during Trip 1 for KOS= Kenton-on-Sea, CR= Cannon Rocks, CP= Cape Padrone, B= Bay, CRF= Cape Recife, SK= Schoenmakerskop, SB= Sardinia Bay and KB= Kini Bay in the Aloga Bay region. P-values in bold are significant.

Variables (& observations)	**R**	**P**
KOS-Onshore direction & speed	0.347	**0.03**
KOS-Offshore direction & speed	0.729	**< 1E-12**
CR-Onshore direction & speed	0.293	**0.0151**
CR-Offshore direction & speed	0.586	**1.56E-10**
CP-Onshore direction & speed	0.699	**2.31E-05**
CP-Offshore direction & speed	0.257	**0.036**
AC-Onshore direction & speed	0.479	**9.51E-09**
AC-Offshore direction & speed	0.76	**< 1E-12**
B-Onshore direction & speed	0.907	**9.28E-04**
B-Offshore direction & speed	0.712	**0.035**
CRF-Onshore direction & speed	0.965	**< 1E-12**
CRF-Offshore direction & speed	0.697	**< 1E-12**
SK-Onshore direction & speed	0.822	**1.19E-04**
SK-Offshore direction & speed	0.625	**0.016**
SB-Onshore direction & speed	0.873	**7.40E-10**
SB-Offshore direction & speed	0.416	**5.86E-06**
KB-Onshore direction & speed	0.059	0.875
KB-Offshore direction & speed	0.52	**0.005**



Kini Bay onshore (S1)

Kini Bay offshore (S1)

Sardinia Bay onshore (S1)

Sardinia Bay offshore (S1)

Schoenmakerskop onshore (S1)

Schoenmakerskop offshore (S1)

Cape Recife onshore (S1)

Cape Recife offshore (S1)

Figure 2.9: Current roses showing cross-shore variability in oceanographic currents at sites (Kini Bay, Sardinia Bay and Schoenmakerskop and Cape Recife) situated in the western extent of the Algoa Bay study region for Trip 1 (summer – early winter). The colour of the bands indicates the range of current speed (cm/s). The length of the vector spokes shows how consistent the mean direction is. The black long curved line indicates the average current direction; the arch on the outside of the circles shows the variability around the mean in current direction.

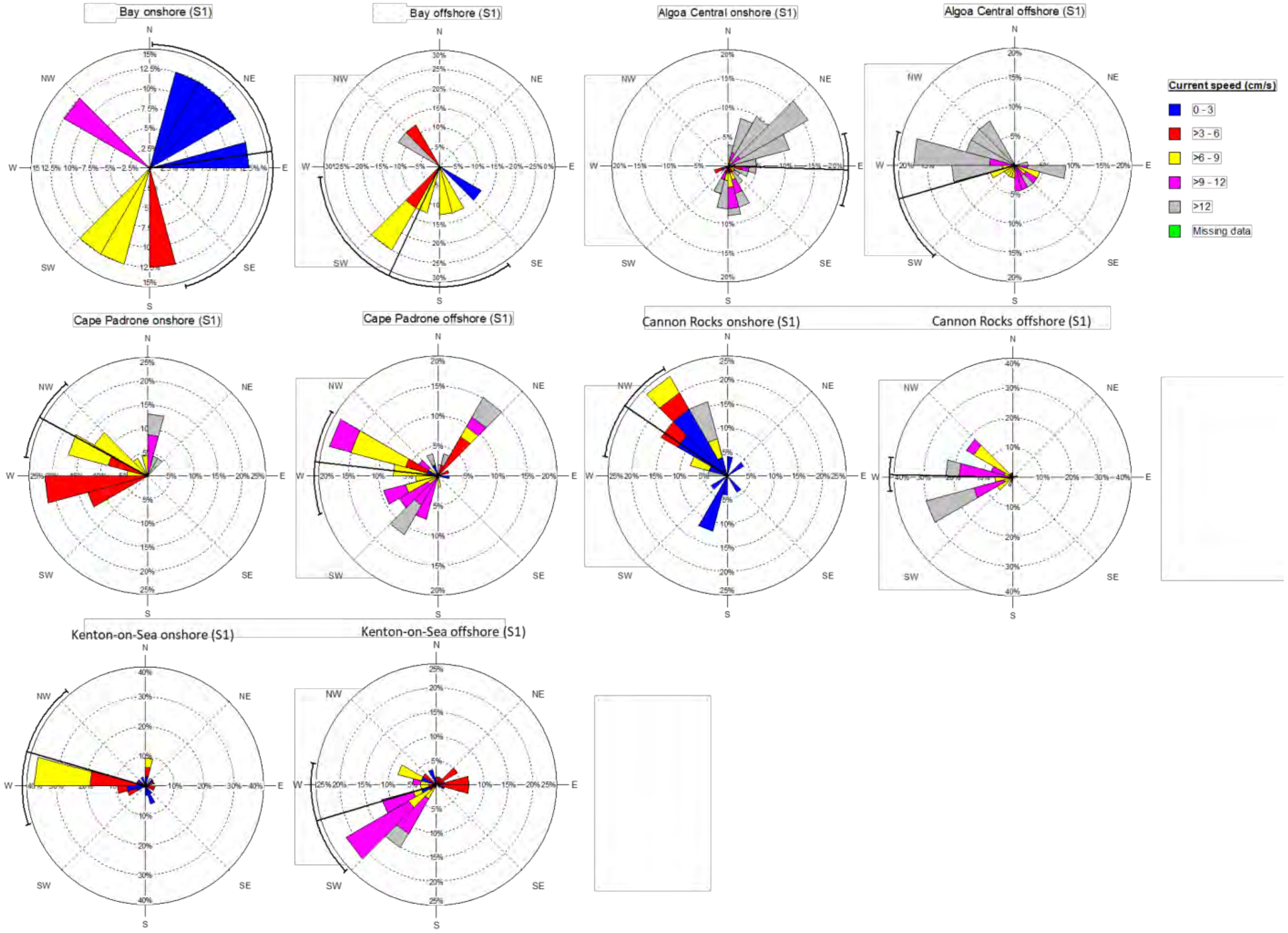


Figure 2.10: Figure 2.4: Current roses showing cross-shore variability in oceanographic currents at sites (Bay and Algoa Central, Cape Padrone, Cannon Rocks and Kenton-on-Sea) situated in the central and western sector of the Algoa Bay study region for Trip 1 (summer – early winter). The colour of the bands indicates the range of current speed (cm/s). The length of the vector spokes shows how consistent the mean direction is. The black long curved line indicates the average current direction; the arch on the outside of the circles shows the variability in current direction.

The results of the Rayleigh tests for potential differences in flow of currents along and cross-shore for each site and station for Trip 2 indicated that current speed and direction at both the onshore/offshore for all sites were not uniformly distributed (Table 2.13). The circular linear correlation tests to assess the differences in the flow of currents provided significant results for all the sites indicating that current speed and direction were strongly correlated except for Algoa Central and Sardinia Bay onshore and Kini Bay offshore (Table 2.14).

At Sardinia Bay, Schoenmakerskop and Algoa Central the ocean currents were slower on the onshore during Trip 2, than in the offshore. The opposite pattern of current speeds (onshore >offshore) was recorded at Kini Bay and Bay. The ocean currents within the eastern sector of the study area, at Cape Padrone, Cannon Rocks and Kenton-on-Sea were greater than 12 m/s at both distances (onshore/offshore) while for Cape Recife, currents were greater than 6-9 m/s at both distances (Figure 2.11 and 2.12).

Table 2.13 Results of the Rayleigh test for Trip 1 for differences on currents between distance at the onshore/offshore for Kini Bay, Sardinia Bay, Schoenmakerskop, Cape Recife, Bay, Algoa Central, Cape Padrone, Cannon Rocks and Kenton-on-Sea in the Algoa Bay region. P-values in bold are significant.

	Kini Bay Onshore	Kini Bay Offshore	Sardinia Bay Onshore	Sardinia Bay Offshore
Rayleigh Test (Z)	24.073	1.585	18.126	35.598
Rayleigh Test (p)	**9.05E-11**	0.208	**2.29E-08**	**< 1E-12**
	Schoenmakerskop Onshore	Schoenmakerskop Offshore	Cape Recife Onshore	Cape Recife Offshore
Rayleigh Test (Z)	12.289	16.479	24.505	1.101
Rayleigh Test (p)	**1.12E-06**	**6.03E-08**	**7.55E-11**	0.333
	Bay Onshore	Bay Offshore	Algoa Central Onshore	Algoa Central Offshore
Rayleigh Test (Z)	15.132	15.435	10.449	12.259
Rayleigh Test (p)	**1.37E-07**	**7.61E-08**	**4.24E-06**	**8.37E-07**
	Cape Padrone Onshore	Cape Padrone Offshore	Cape Rocks Onshore	Cannon Rocks Offshore
Rayleigh Test (Z)	13.117	41.866	1.683	63.632
Rayleigh Test (p)	**3.93E-07**	**< 1E-12**	0.187	**< 1E-12**
	Kenton-on-Sea Onshore	Kenton-on-Sea Offshore		
Rayleigh Test (Z)	21.709	31.335		
Rayleigh Test (p)	**1.99E-09**	**< 1E-12**		

Table 2.14: Table 2.6: Results of the circular linear correlation between current speed and direction (onshore/offshore) during Trip 2 for KOS= Kenton-on-Sea, CR= Cannon Rocks, CP= Cape Padrone, B= Bay, CRF= Cape Recife, SK= Schoenmakerskop, SB= Sardinia Bay and KB= Kini Bay in the Aloga Bay region. P-values in bold are significant.

Variables (& observations)	**R**	**P-value**
KOS-Onshore direction & speed	0.725	**1.54E-05**
KOS-Offshore direction & speed	0.709	**2.68E-11**
CR-Onshore direction & speed	0.864	**3.48E-11**
CR-Offshore direction & speed	0.498	**3.20E-08**
CP-Onshore direction & speed	0.857	**1.19E-07**
CP-Offshore direction & speed	0.305	**0.014**
AC-Onshore direction & speed	0.342	0.17
AC-Offshore direction & speed	0.666	**7.20E-05**
B-Onshore direction & speed	0.589	**0.001**
B-Offshore direction & speed	0.714	**4.21E-06**
CRF-Onshore direction & speed	0.826	**2.62E-12**
CRF-Offshore direction & speed	0.436	**2.11E-06**
SK-Onshore direction & speed	0.388	**0.023**
SK-Offshore direction & speed	0.41	**0.04**
SB-Onshore direction & speed	0.255	0.29
SB-Offshore direction & speed	0.397	**3.79E-05**
KB-Onshore direction & speed	0.581	**6.44E-06**
KB-Offshore direction & speed	0.176	0.76

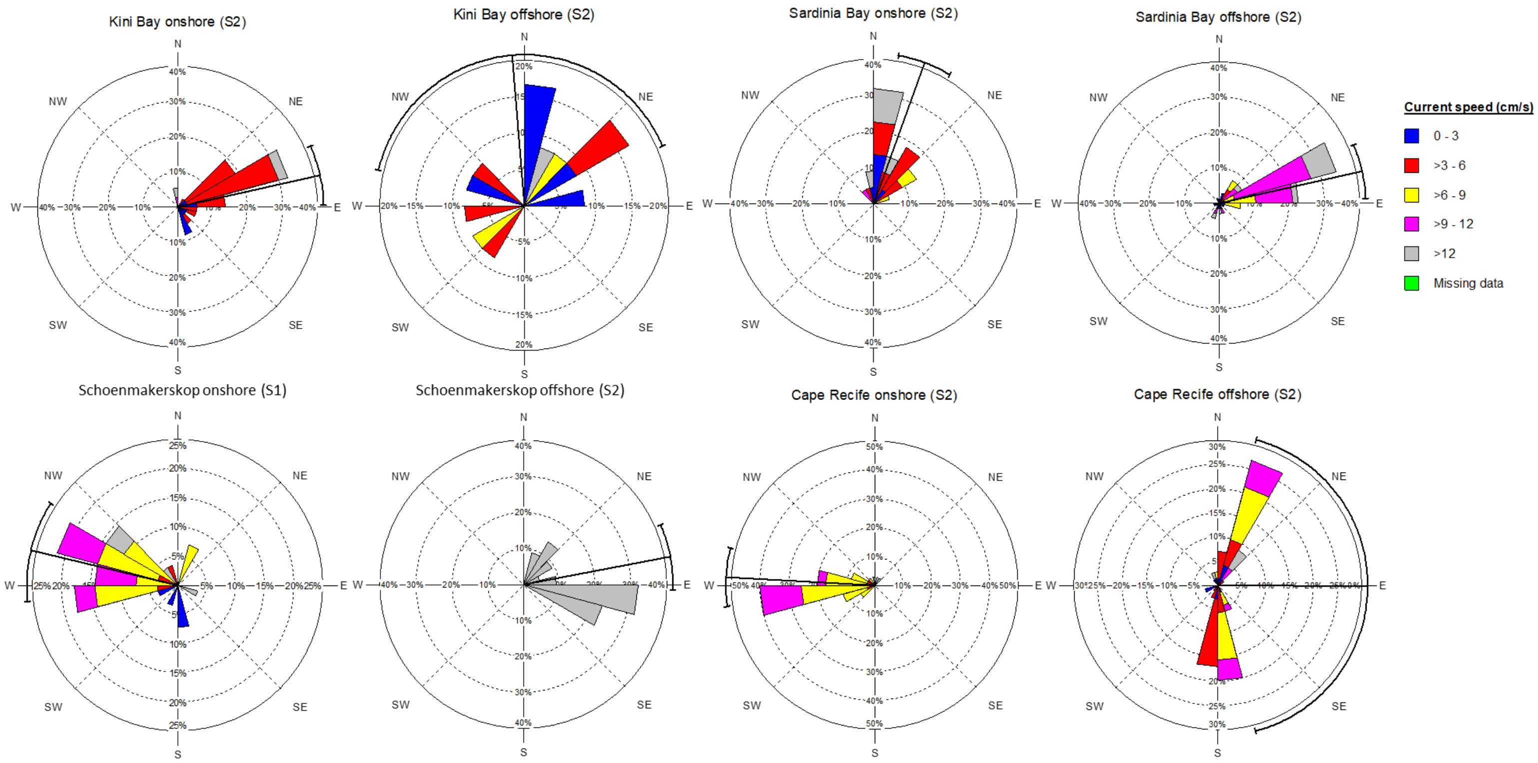


Figure 2.11: Current roses showing cross-shore variability in oceanographic currents at sites (Kini Bay, Sardinia Bay, Schoenmakerskop, Cape Recife) situated in the central and western sector of the Algoa Bay study region for Trip 2 (late summer – late spring). The colour of the bands indicates the range of current speed (cm/s). The length of the vector spokes shows how consistent the mean direction is. The black long curved line indicates the average current direction; the arch on the outside of the circles shows the variability in current direction.

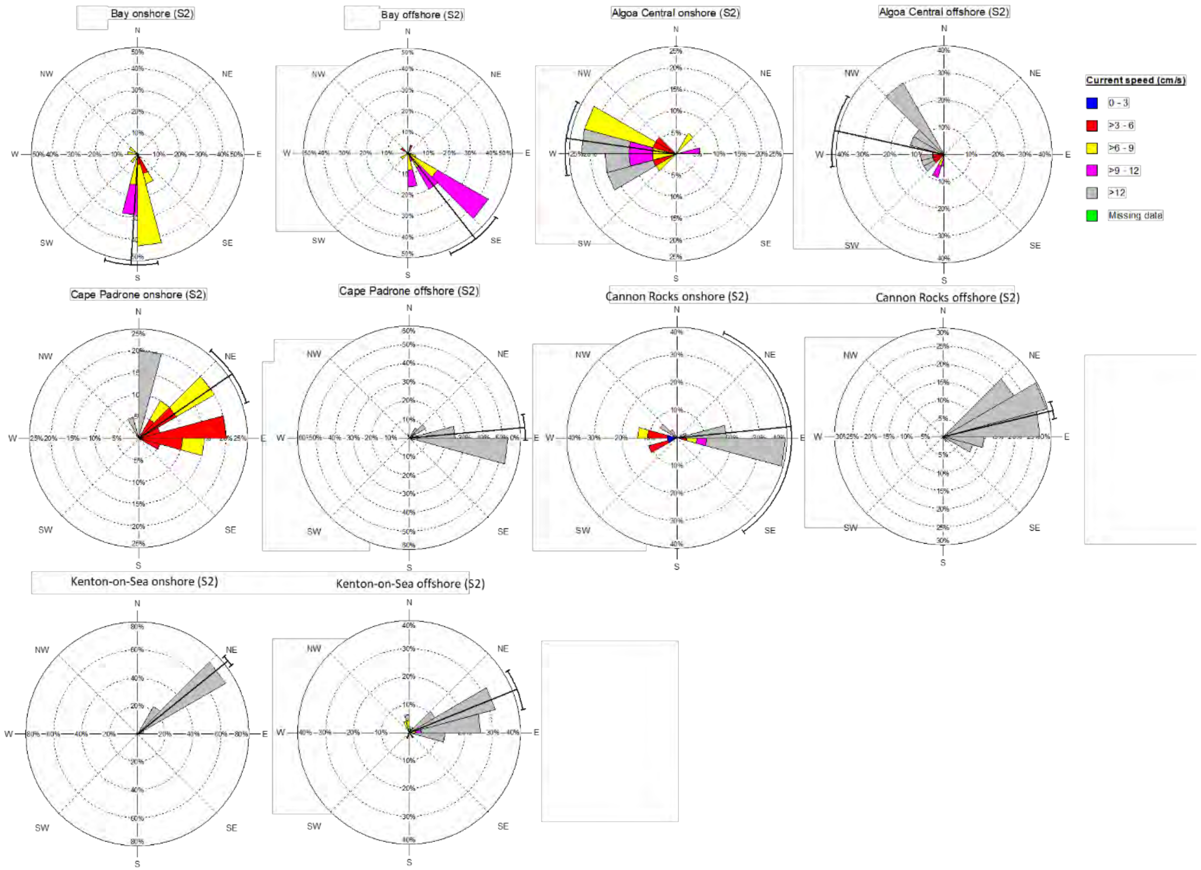


Figure 2.12: Current roses showing cross-shore variability in oceanographic currents at sites (Bay, Algoa Central, Cape Padrone, Cannon Rocks and Kenton-on-Sea) situated in the eastern sector of the Algoa Bay study region for Trip 2 (late summer – late spring). The colour of the bands indicates the range of current speed (cm/s). The length of the vector spokes shows how consistent the mean direction is. The black long curved line indicates the average current direction; the arch on the outside of the circles shows the variability in current direction.

2.3.5 Patterns in Wind Speed and Direction

To characterise the wind details at the west and east entrances to the Bay, on the eastern headland (Cape Padrone) of Algoa Bay during Trip 1 (April 2016) and Trip 2 (March 2016) a north easterly and south westerly wind blew two days preceding sampling respectively (Figure 2.13). On the western headland of the Bay (Cape Recife) there were strong south westerly winds three days before sampling during Trip 1 (February 2016) and a two days preceding sampling for Trip 2 (October 2016) (Figure 2.14).

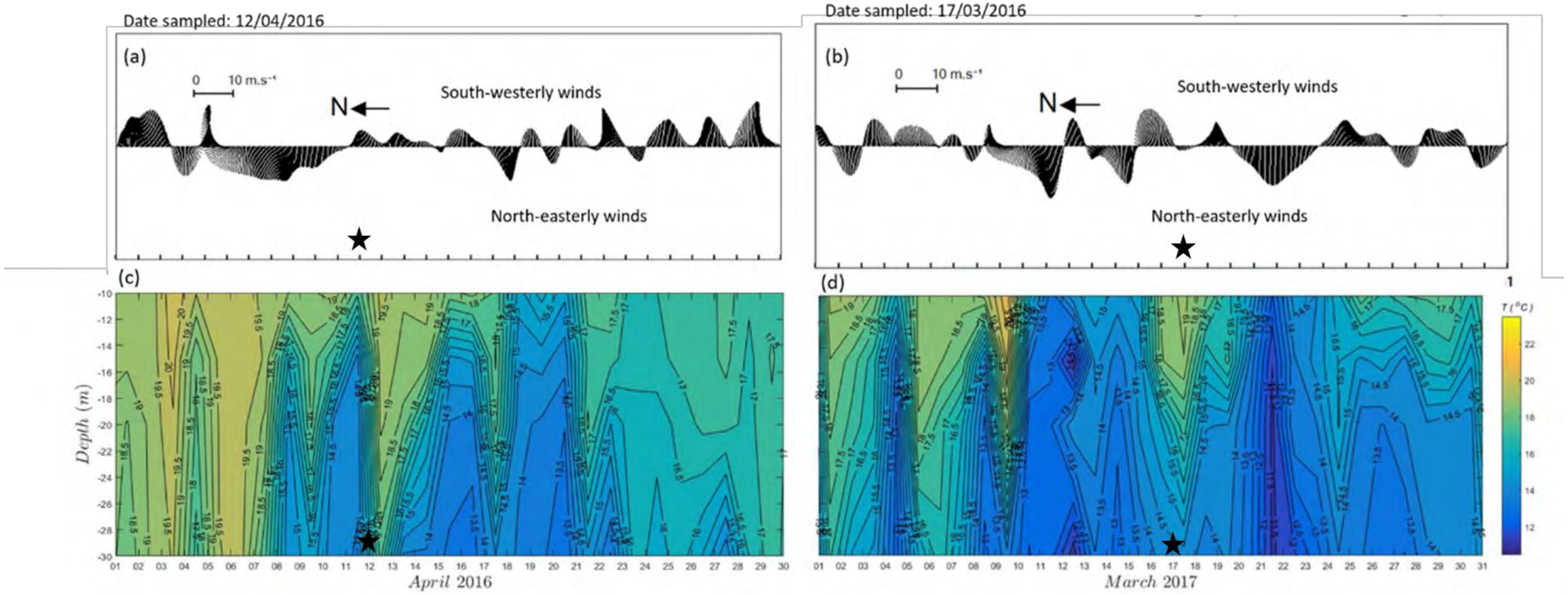


Figure 2.13: Wind stick vector plots for Bird Island weather station (a) April 2016 (b) March 2017 with corresponding sea temperatures measured by the underwater temperature recorder (UTR) chain mooring in (c) April 2016 (d) March 2017 at Cape Padrone. The star signs indicate the days when sampling was conducted.

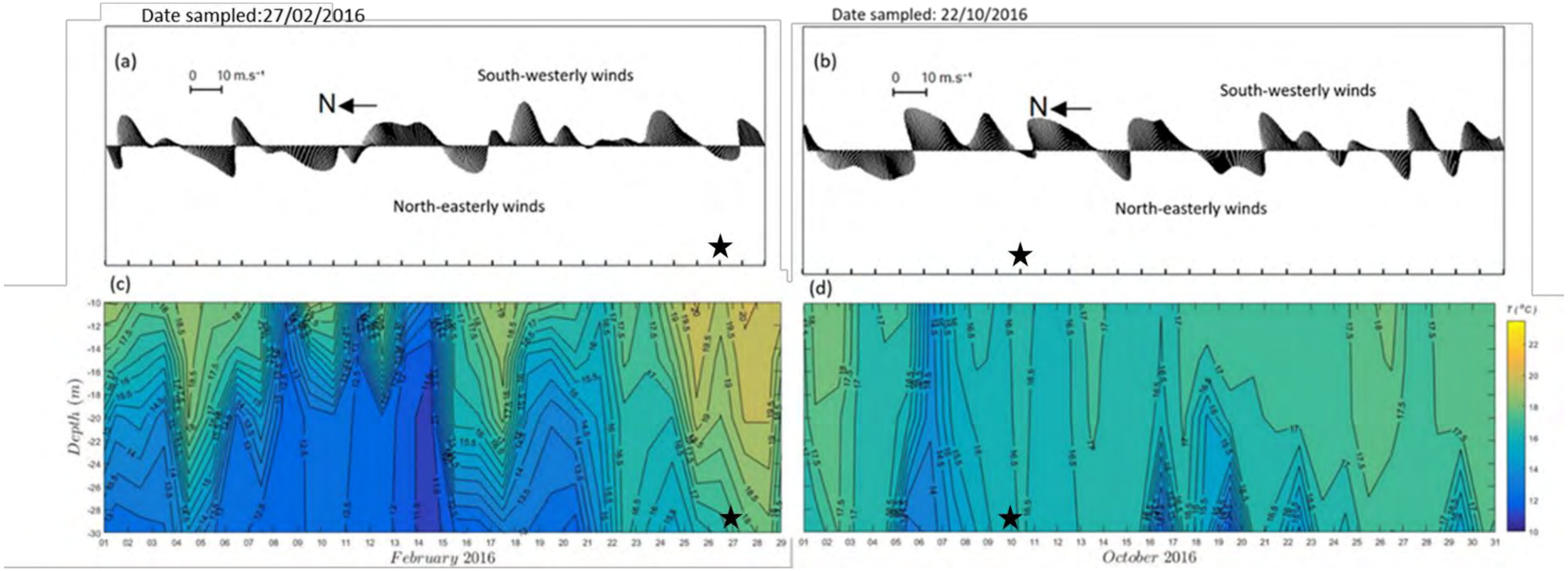


Figure 2.14: Wind stick vectors for Port Elizabeth Airport (a) February 2016 (b) October 2016 with corresponding temperature measured with the underwater temperature recorder (UTR) chain mooring (c) February 2016 (d) October 2016 near Cape Recife. The star signs indicate the days in which sampling was conducted.

2.3.6 Wind-Derived Upwelling

At the sites situated in the east of Algoa Bay (Cape Padrone), and the adjacent sites of Kenton-on-Sea and Cannon Rocks, upwelling occurred a few days preceding sampling and on the day of sampling, during both Trip 1 and Trip 2 (barring Cape Padrone during Trip 2), while upwelling was evident only during Trip 2 at Algoa Central (Figure 2. 8) and Cape Recife (western headland) respectively (Figure 2. 9). Cape Padrone was sampled on the 12 April 2016 (early winter; Trip 1) and again on the 17 March 2017 (early winter; Trip 2). In April 2016, at Cape Padrone, six days preceding sampling there were consistent north easterly winds that blew and there was a strong thermocline/stratification in the water column particularly on the day of sampling. In addition, from the 10 - 16 March 2017 at Cape Padrone, a strong upwelling event occurred resulting in temperatures dropping from 18°C to 12°C in the vicinity of the sampling area (Figure 2.6). At Kenton-on-Sea and Cannon Rocks, upwelling was persistent, occurring three days before sampling and on the day of sampling. At Kini Bay, Sardinia Bay, Schonemakerskop, Bay and during both trips, as well as Cape Recife (Trip 1) there were downwelling events that occurred three days prior to sampling and on the day of sampling (Figure 2.15 and 2.16).

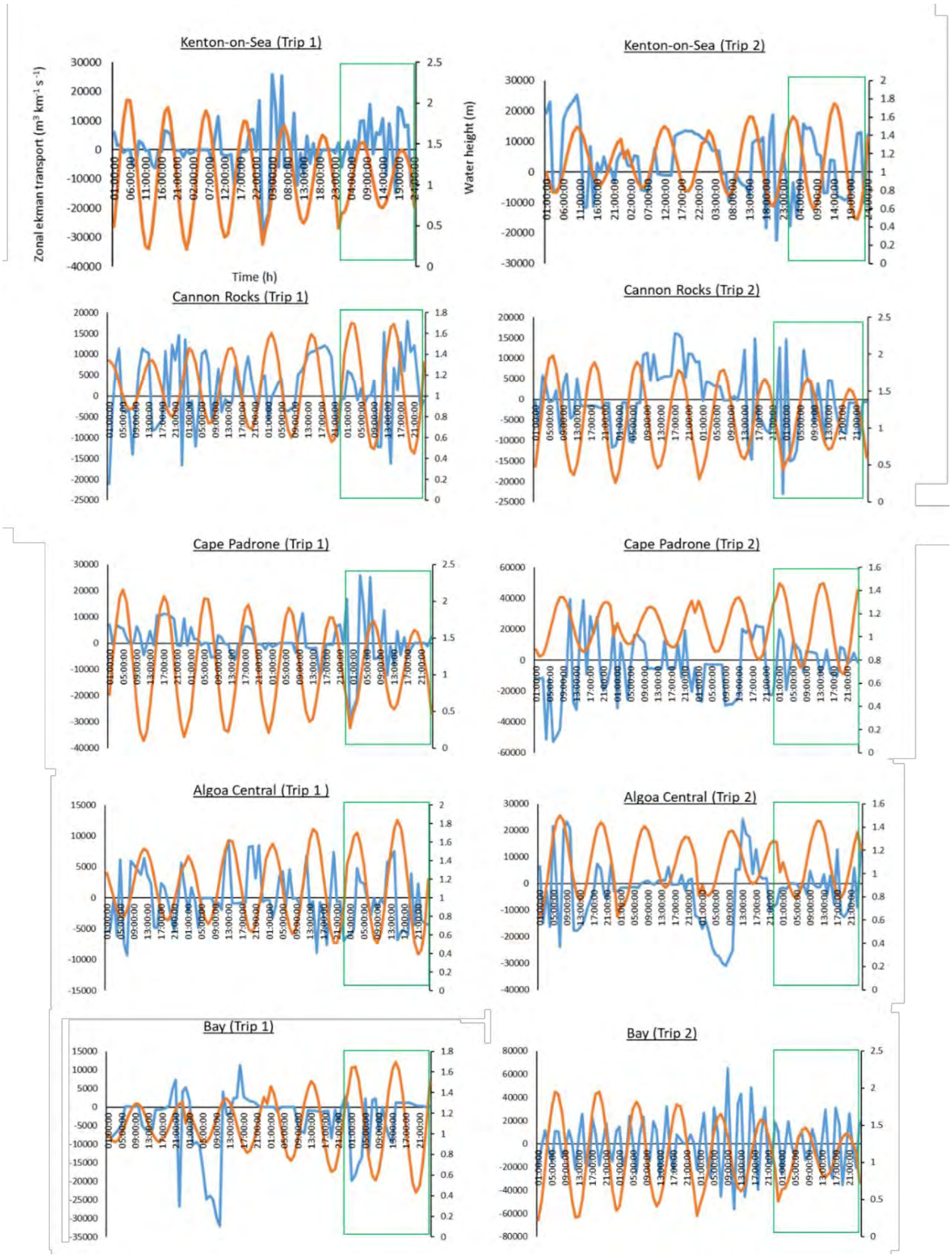


Figure 2.15: Time series of zonal Ekman transport (blue lines) and water height (orange lines) for Kenton-on-Sea, Cannon Rocks, Cape Padrone, Algoa Central and Bay during Trip 1 and Trip 2 in the Algoa Bay region. For lines (blue/orange) positive values signify upwelling, negative values indicate downwelling. Green rectangles indicate the days when the nearshore was sampled.

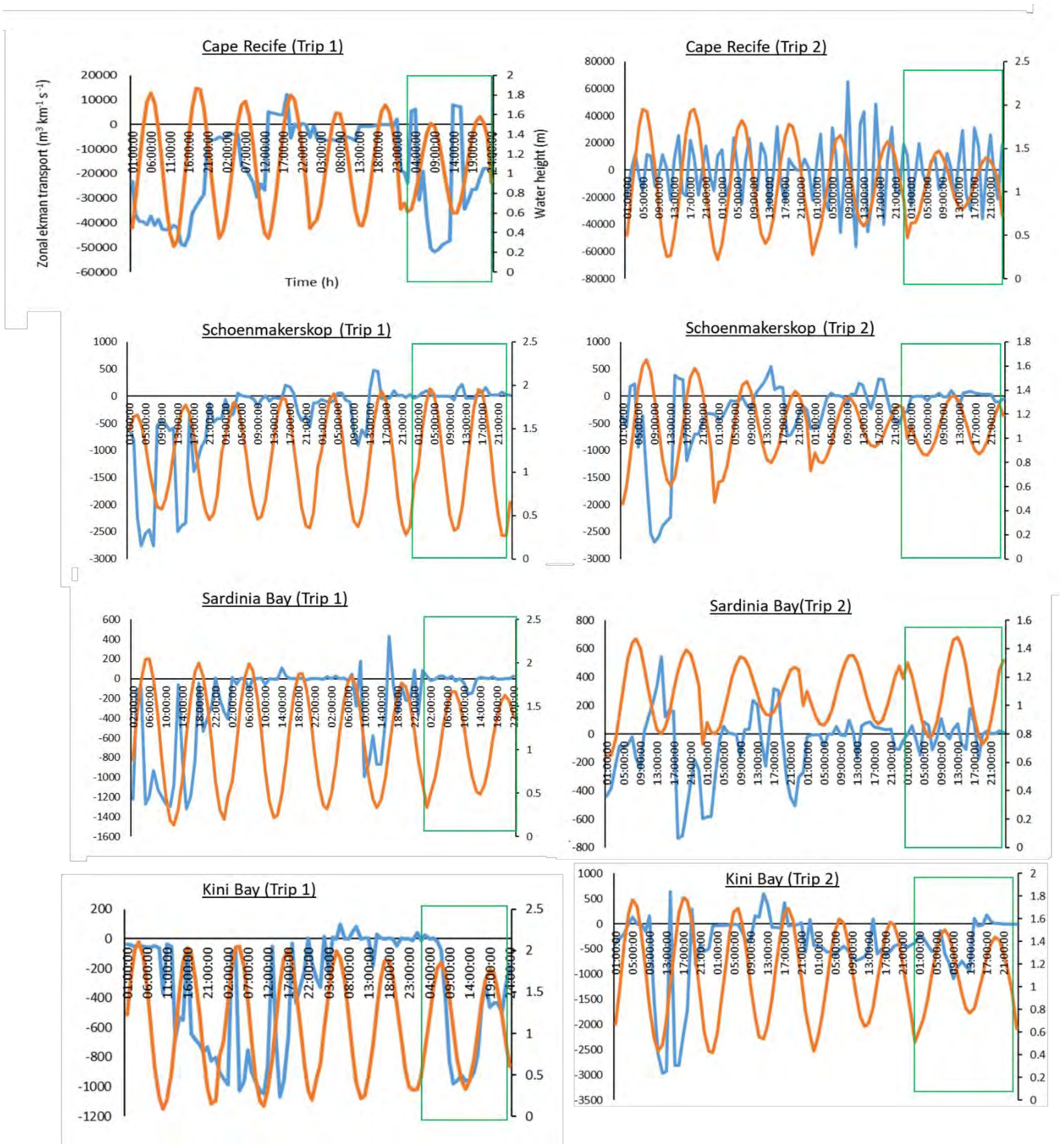


Figure 2.16: Time series of zonal Ekman transport (blue lines) and water height (orange lines) for Cape Recife, Schoenmakerskop, Sardinia Bay and Kini Bay during Trip 1 and Trip 2 in the Algoa Bay region. For lines (blue/orange) positive values signify upwelling, negative values indicate downwelling. Green rectangles show the days when the nearshore was sampled.

2.3.7 Relationship between Environmental Parameters and Larval Fish Community

The results of the Distance based redundancy analysis (dbRDA) indicated that for Trip 1, at Cape Recife ~60% of the total variability in the larval fish community was explained by the environmental variables, while for Algoa Central, Cape Padrone and Kenton-on-Sea the environmental variables explained ~50% of the larval distribution. For the other sites <50% of the variability in the larval fish assemblages could be explained by the environmental parameters (Figure 2.17; Table 2.15).

The relationship between the larval fish community and the environmental variables was investigated by distance-based linear models (DISTLM). The DISTLM model was built using step-wise selection procedure, AIC, and applying 9999 permutations at a significance level of $p<0.05$. The results of the marginal (Table 2.15) and sequential tests (Table 2.16) indicated that, for Algoa Central and Sardinia Bay during Trip 1, larval fish community structure was significantly influenced by the individual effect of oxygen and fluorescence, contributing 35% and 31% respectively to the model. In the results of the sequential and marginal tests, significant effects solely for turbidity and pH (Bay) were confirmed, cumulatively contributing 79% to the model, while significant effects for vertical and meridional flow (Cape Recife), cumulatively contributing 87% to the model (Tables 2.15, 2.16).

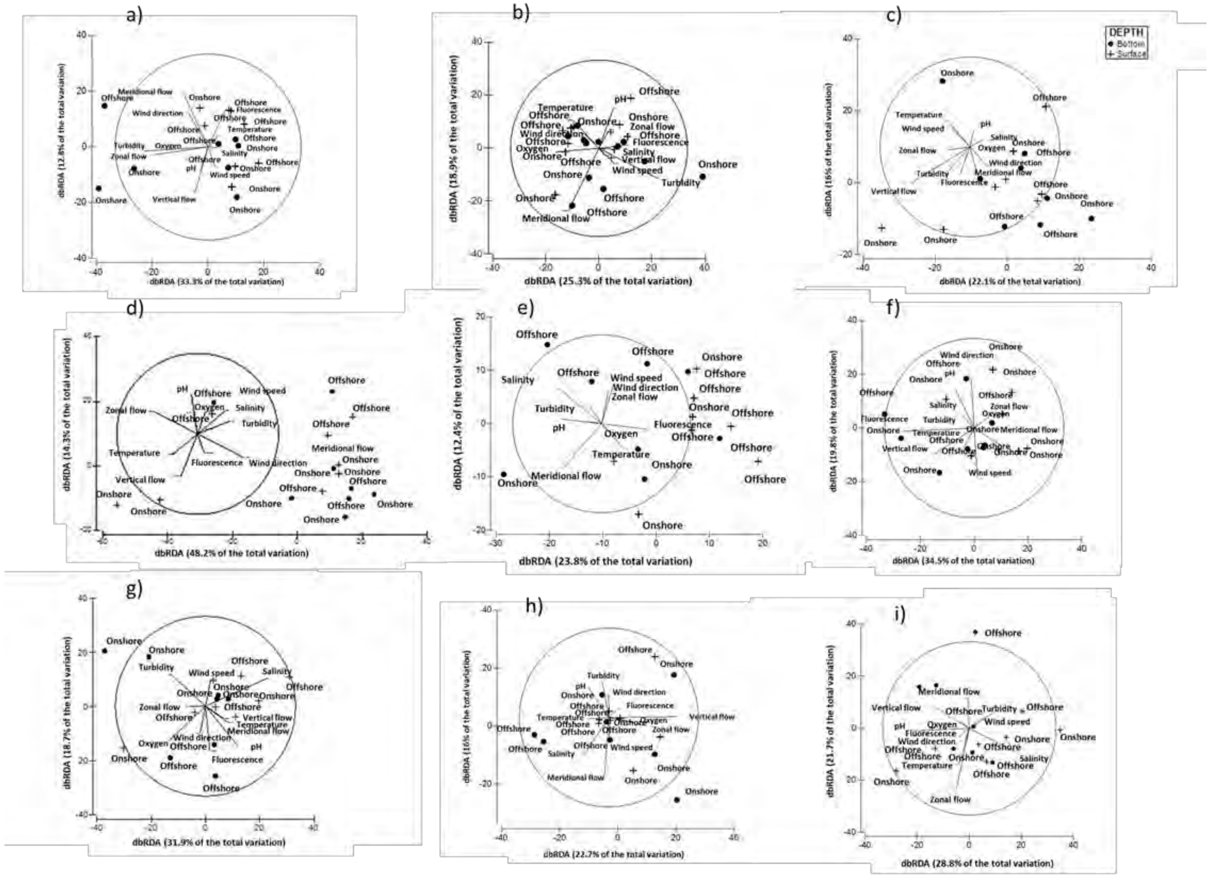


Figure 2.17: Results of the distance based redundancy analysis (dbRDA) for Trip 1 to show the relationships between larval fish community and environmental parameters for: a) Kini Bay, b) Sardinia Bay, c) Schoenmakerskop, d) Cape Recife, e) Bay, f) Algoa Central, g) Cape Padrone, h) Cannon Rocks, j) Kenton-on-Sea.

Table 2.15: The results of the DistLM marginal tests followed by results from the step-wise selection procedure using the Akaike Information Criterion (AIC) from the coastal nearshore for Trip 1 in the region of Kini Bay, Sardinia Bay, Schoenmakerskop, Cape Recife, Bay, Algoa Central, Cape Padrone, Cannon Rocks and Kenton-on-Sea (Prop = proportion of variance explained by each variable). P-values in bold are significant.

	Kini Bay			**Sardinia Bay**			**Schoenmakerskop**			**Cape Recife**			**Bay**		
MARGINAL TESTS															
Variable	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.
1.Zonal flow	1.11	0.33	0.16	0.57	0.73	0.09	1.36	0.27	0.18	0.48	0.78	0.07	1.03	0.42	0.15
2.Meridional flow	0.76	0.57	0.11	0.43	0.59	0.07	0.5	0.81	0.07	4.82	**0.02**	0.44	2.09	0.16	0.26
3.Vertical flow	1.03	0.41	0.15	0.6	0.52	0.09	2.03	0.19	0.25	4.56	**0.007**	0.43	2.62	0.1	0.3
4.Temperature	0.44	0.85	0.07	1.22	0.32	0.17	0.1	0.96	0.02	0.66	0.63	0.09	1.17	0.3	0.16
5.Fluorescence	0.91	0.48	0.13	2.67	**0.03**	0.31	0.07	0.99	0.01	1.39	0.24	0.19	0.69	0.58	0.1
6.Turbidity	1.02	0.45	0.14	0.05	0.99	0.08	2.34	0.1	0.28	1.09	0.35	0.15	4.03	**0.001**	0.4
7.pH	0.34	0.91	0.05	1.11	0.35	0.16	0.47	0.77	0.07	0.93	0.61	0.13	3.91	**0.002**	0.39
8.Salinity	0.77	0.53	0.11	1.59	0.22	0.21	0.22	0.86	0.04	0.99	0.4	0.14	1.14	0.34	0.16
9.Oxygen	0.79	0.5	0.12	2.23	0.2	0.27	1.02	0.47	0.14	1.17	0.29	0.16	0.74	0.62	0.11
10.Wind speed	0.83	0.62	0.12	0.148	1	0.02	2.28	0.26	0.27	0.002	1	0.003	0.005	1	0.009
11.Wind direction	0.83	0.63	0.12	0.148	1	0.02	2.28	0.24	0.27	0.002	1	0.003	0.005	1	0.009
	Algoa Central			**Cape Padrone**			**Cannon Rocks**			**Kenton-on-Sea**					
MARGINAL TESTS															
Variable	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.			
1.Zonal flow	1.25	0.33	0.17	0.11	0.99	0.02	0.58	0.74	0.09	0.46	0.8	0.07			
2.Meridional flow	0.23	0.97	0.04	0.65	0.69	0.02	0.38	0.88	0.06	0.61	0.66	0.09			
3.Vertical flow	0.83	0.52	0.12	0.35	0.87	0.06	0.16	0.98	0.03	1.92	0.09	0.24			
4.Temperature	1.75	0.14	0.23	0.29	0.95	0.06	1.15	0.34	0.16	0.55	0.72	0.08			
5.Fluorescence	0.84	0.52	0.12	0.35	0.89	0.06	0.55	0.78	0.08	0.7	0.58	0.12			
6.Turbidity	0.61	0.64	0.09	0.57	0.76	0.09	1.23	0.3	0.17	0.68	0.67	0.1			
7. pH	1.64	0.17	0.21	0.63	0.72	0.09	1.02	0.41	0.14	0.84	0.54	0.12			
8.Salinity	1.27	0.29	0.17	1.02	0.45	0.14	0.66	0.66	0.09	0.61	0.74	0.09			
9.Oxygen	3.267	**0.01**	0.35	0.57	0.71	0.09	1.2	33	0.17	0.89	0.52	0.13			
10.Wind speed	0.007	1	0.001	0.009	1	0.001	0.01	1	0.02	0.46	1	0.07			
11.Wind direction	7	1	0.001	0.009	1	0.001	0.01	1	0.02	0.46	1	0.07			

Table 2.16: Results of the DistLM sequential tests followed by results from the step-wise selection procedure using the Akaike information Criterion (AIC) from the coastal nearshore during Trip 1 in the region of Kini Bay, Sardinia Bay, Schoenmakerskop, Cape Recife, Bay, Algoa Central, Cape Padrone, Cannon Rocks and Kenton-on-Sea (Prop=proportion of variance explained by each variable, Cumul.= cumulative contribution to the overall variance of larval fish assemblages, R^2 = adjusted R-Squared, RSS= Residual sum of squared deviations, No. Vars= number of variance). For "selections" refer to the previous table of the marginal tests. P-values in bold are significant.

Kenton-on-Sea						**Cannon Rocks**					
SEQUENTIAL TESTS						*SEQUENTIAL TESTS*					
Variable	AIC	Pseudo-F	P	Prop.	Cumul.	Variable	AIC	Pseudo-F	P	Prop.	Cumul.
3.Vertical flow	54.98	1.92	0.09	0.25	0.25	6.Turbidity	49.61	0.55	0.78	0.17	0.17
8.Oxygen	53.63	0.89	0.52	0.13	0.38	9.Oxygen	44.65	1.20	0.33	0.17	0.34
BEST SOLUTION						*BEST SOLUTION*					
AIC	R^2	RSS	No.Vars	Selections		AIC	R^2	RSS	No.Vars	Selections	
53.63	0.46	911.81	2	3;8		44.65	0.52	473.84	2.00	6;9	
Cape Padrone						**Algoa Central**					
SEQUENTIAL TESTS						*SEQUENTIAL TESTS*					
Variable	AIC	Pseudo-F	P	Prop.	Cumul.	Variable	AIC	Pseudo-F	P	Prop.	Cumul.
6.Turbidity	54.84	1.12	0.43	0.07	0.07	9.Oxygen	44.86	3.27	**0.01**	0.35	0.35
8.Salinity	46.23	1.34	0.26	0.18	0.25	4.Temperature	32.52	1.75	0.14	0.23	0.58
BEST SOLUTION						*BEST SOLUTION*					
AIC	R^2	RSS	No.Vars	Selections		AIC	R^2	RSS	No.Vars	Selections	
46.2	0.5	590.84	2	6;8		32.52	0.53	740.54	2	4;9	
Bay						**Cape Recife**					
SEQUENTIAL TESTS						*SEQUENTIAL TESTS*					
Variable	AIC	Pseudo-F	P	Prop.	Cumul.	Variable	AIC	Pseudo-F	P	Prop.	Cumul.
6.Turbidity	49.61	4.03	**0.001**	0.40	0.40	2.Meridional flow	37.13	4.83	**0.02**	0.44	0.44
7.pH	44.65	3.91	**0.002**	0.39	0.79	3.Vertical flow	36.23	4.56	**0.008**	0.43	0.87
BEST SOLUTION						*BEST SOLUTION*					
AIC	R^2	RSS	No.Vars	Selections		AIC	R^2	RSS	No.Vars	Selections	
44.65	0.45	657	2	6;7		36.23	0.59	602.59	2	2;3	

Schoenmakerskop

SEQUENTIAL TESTS

Variable	AIC	Pseudo-F	P	Prop.	Cumul.
6.Turbidity	55.87	2.21	0.26	0.17	0.17
10.Wind speed	32.30	2.16	0.34	0.16	0.33
11.Wind direction	32.30	2.16	0.35	0.16	0.48

BEST SOLUTION

AIC	R^2	RSS	No.Vars	Selections
32.30	0.24	5236.60	3	6;10;11

Sardinia Bay

SEQUENTIAL TESTS

Variable	AIC	Pseudo-F	P	Prop.	Cumul.
8.Salinity	54.98	1.59	0.57	0.14	0.14
5.Fluorescence	53.63	2.67	**0.02**	0.31	0.45
9.Oxygen	52.15	1.62	0.32	0.14	0.60

BEST SOLUTION

AIC	R^2	RSS	No.Vars	Selections
52.154	0.86	911.81	3	5;8;9

Kini Bay

SEQUENTIAL TESTS

Variable	AIC	Pseudo-F	P	Prop.	Cumul.
1.Zonal flow	54.94	1.29	0.27	0.18	0.18
6.Turbidity	52.70	1.16	0.33	0.13	0.32

BEST SOLUTION

AIC	R^2	RSS	No.Vars	Selections
52.70	0.99	56.36	2	1;6

During Trip 2, the first and the second dbRDA axes explained 100% of the total variability of distribution of the larval fish community at Cape Recife. At Kini Bay, Algoa Central and Kenton-on-Sea the environmental variables explained 80% of the variation in the larval fish community while at Sardinia Bay, Bay, Cannon Rocks the environmental variables explained ~70%, and at Schoenmakerskop and Cape Padrone just over 60% (Figure 2.18; Table 2.17).

For Schoenmakerskop during Trip 2, the marginal (Table 2.17) and sequential tests (Table 2.18) indicated that, larval fish community were significantly explained by turbidity (33% of variability). The sequential tests for Cannon Rocks and Bay confirmed the significant effects of pH and vertical flow, which contributed 27% and 29% respectively to the model. Significant effects solely for meridional flow and salinity were confirmed for Cape Recife, cumulatively contributing 67% to the model.

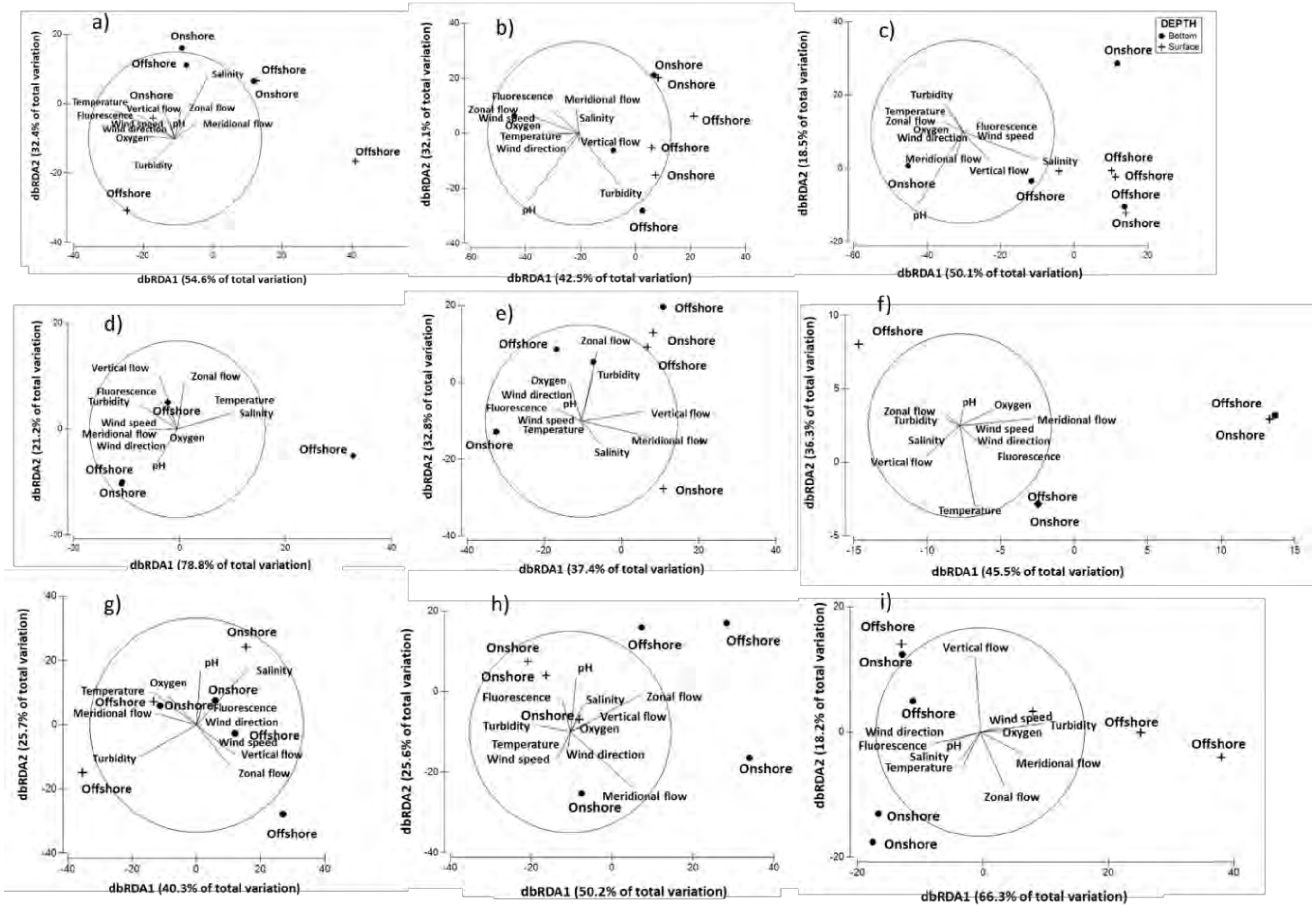


Figure 2.18: Distance based redundancy analysis (dbRDA) for Trip 2 of the DistLM show the relationships between larval fish community and environmental parameters for: a) Kini Bay, b) Sardinia Bay, c) Schoenmakerskop, d) Cape Recife, e) Bay, f) Algoa Central, g) Cape Padrone, h) Cannon Rocks, j) Kenton-on-Sea.

Table 2.17: DistLM marginal tests followed by results from the step-wise selection procedure using the corrected Akaike Information Criterion (AIC) and sequential tests from the coastal nearshore for Trip 2 in the region of Kini Bay, Sardinia Bay, Schoenmakerskop, Cape Recife, Bay, Algoa Central, Cape Padrone, Cannon Rocks and Kenton-on-Sea (Prop = proportion of variance explained by each variable). P-values in bold are significant.

	Kini Bay			**Sardinia Bay**			**Schoenmakerskop**			**Cape Recife**			**Bay**		
MARGINAL TESTS															
Variable	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.
1.Zonal flow	0.29	0.89	0.04	2.05	0.10	0.25	0.54	0.74	0.1	0.24	0.88	0.04	0.9	0.55	0.13
2.Meridional flow	0.59	0.68	0.09	1.51	0.22	0.2	0.45	0.86	0.08	0.61	0.59	0.09	2.52	**0.01**	0.29
3.Vertical flow	0.56	0.62	0.08	0.79	0.57	0.12	0.68	0.64	0.12	0.13	0.93	0.02	1.58	0.15	0.21
4.Temperature	0.65	0.53	0.10	0.48	0.79	0.07	0.61	0.75	0.11	0.7	0.55	0.1	1.46	0.24	0.19
5.Fluorescence	0.80	0.49	0.12	0.70	0.64	0.10	0.55	0.81	0.1	0.78	0.48	0.11	1.09	0.31	0.15
6.Turbidity	0.59	0.67	0.09	0.34	0.88	0.05	2.45	**0.01**	0.33	0.33	0.63	0.05	0.28	0.92	0.04
7.pH	0.29	0.77	0.05	1.33	0.28	0.18	0.61	0.79	0.11	0.56	0.64	0.08	0.71	0.67	0.1
8.Salinity	0.55	0.67	0.08	0.99	0.43	0.14	2.37	0.08	0.32	0.61	0.61	0.09	1.31	0.26	0.18
9.Oxygen	0.23	0.89	0.04	0.47	0.87	0.07	0.54	0.84	0.10	0.59	0.63	0.1	1.11	0.27	0.16
10.Wind speed	0.27	0.86	0.04	0.54	0.76	0.0008	0.004	1	0.0008	0.006	1	0.0001	0.002	1	0.004
11.Wind direction	0.27	0.87	0.04	0.54	0.72	0.0008	0.004	1	0.0008	0.006	1	0.0001	0.002	1	0.004

	Algoa Central			**Cape Padrone**			**Cannon Rocks**			**Kenton-on-Sea**		
MARGINAL TESTS												
Variable	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.	Pseudo-F	P	Prop.
1.Zonal flow	1.11	0.45	0.16	1.90	0.12	0.24	1.12	0.39	0.16	0.84	0.49	0.12
2.Meridional flow	0.79	0.53	0.12	0.85	0.53	0.12	1.52	0.23	0.20	0.29	0.84	0.05
3.Vertical flow	0.57	0.48	0.09	0.78	0.52	0.11	0.51	0.74	0.08	1.05	0.36	0.15
4.Temperature	3.86	0.13	0.39	0.89	0.56	0.13	1.27	0.29	0.17	3.29	**0.05**	0.35
5.Fluorescence	0.47	0.50	0.07	1.11	0.33	0.16	0.64	0.69	0.1	1.26	0.28	0.17
6.Turbidity	0.40	0.58	0.06	2.15	**0.05**	0.26	0.78	0.59	0.11	2.04	0.17	0.25
7.pH	0.31	0.75	0.05	1.34	0.25	0.18	2.43	**0.03**	0.29	0.82	0.48	0.12
8.Salinity	3.10	0.11	0.34	2.97	**0.04**	0.33	0.97	0.50	0.14	2.76	0.15	0.31
9.Oxygen	0.63	0.49	0.09	1.36	0.23	0.18	1.26	0.28	0.10	2.01	0.11	0.25

10.Wind speed	0.09	1	0.01	0.05	1	0.09	0.006	1	0.09	0.47	0.66	0.07
11.Wind direction	0.09	1	0.01	0.05	1	0.09	6	1	0.09	0.47	0.62	0.07

Table 2.18 Results of the DistLM sequential tests followed by results from the step-wise selection procedure using the Akaike information Criterion (AIC) from the coastal nearshore during Trip 2 in the region of Kini Bay, Sardinia Bay, Schoenmakerskop, Cape Recife, Bay, Algoa Central, Cape Padrone, Cannon Rocks and Kenton-on-Sea. (Prop=proportion of variance explained by each variable, Cumul.= cumulative contribution to the overall variance of larval fish assemblages, R^2 = adjusted R-Squared, RSS= Residual sum of squared deviations, No. Vars= number of variance). For “selections” refer to the previous table of the marginal tests. P-values in bold are significant.

Kini Bay						**Sardinia Bay**					
SEQUENTIAL TESTS						*SEQUENTIAL TESTS*					
Variable	AIC	Pseudo-F	P	Prop.	Cumul.	Variable	AIC	Pseudo-F	P	Prop.	Cumul.
4.Temperature	55.85	1.18	0.09	0.23	0.23	7.pH	44.24	2.14	0.12	0.19	0.19
5.Fluorescence	55.29	1.03	0.05	0.25	0.48	8.Salinity	39.02	2.44	0.15	0.17	0.37
BEST SOLUTION						*BEST SOLUTION*					
AIC	R^2	RSS	No.Vars	Selections		AIC	R^2	RSS	No.Vars	Selections	
55.29	0.44	3790.6	2	4;5		39.02	0.96	182.58	6	7;8	
Schoenmakerskop						**Cape Recife**					
SEQUENTIAL TESTS						*SEQUENTIAL TESTS*					
Variable	AIC	Pseudo-F	P	Prop.	Cumul.	Variable	AIC	Pseudo-F	P	Prop.	Cumul.
6.Turbidity	47.28	2.45	**0.01**	0.33	0.33	2.Meridional flow	52.53	4.09	**0.006**	0.27	0.27
8.Salinity	44.86	3.25	0.22	0.17	0.51	8.Salinity	47.41	3.89	**0.032**	0.4	0.67
BEST SOLUTION						*BEST SOLUTION*					
AIC	R^2	RSS	No.Vars	Selections		AIC	R^2	RSS	No.Vars	Selections	
44.86	0.76	1354.2	2	6;8		47.41	0.96	521.19	2	2;8	
Bay						**Algoa Central**					
SEQUENTIAL TESTS						*SEQUENTIAL TESTS*					
Variable	AIC	Pseudo-F	P	Prop.	Cumul.	Variable	AIC	Pseudo-F	P	Prop.	Cumul.
2.Meridional flow	54.64	1.72	0.14	0.23	0.23	4.Temperature	52.76	2.86	0.29	0.35	0.35

3.Vertical flow	53.86	2.52	**0.01**	0.29	0.52	5.Fluorescence	51.97	2.79	0.12	0.31	0.61
BEST SOLUTION						*BEST SOLUTION*					
AIC	R^2	RSS	No.Vars	Selections		AIC	R^2	RSS	No.Vars	Selections	
53.86	0.58	2394.5	2	2;3		51.97	0.97	203.83	2	4;5	
Cape Padrone						**Cannon Rocks**					
SEQUENTIAL TESTS						*SEQUENTIAL TESTS*					
Variable	AIC	Pseudo-F	P	Prop.	Cumul.	Variable	AIC	Pseudo-F	P	Prop.	Cumul.
7.pH	57.46	1.63	0.21	0.21	0.21	5.Fluorescence	54.87	2.41	0.08	0.24	0.24
8.Salinity	42.33	1.56	0.19	0.21	0.42	7.pH	53.85	2.08	**0.01**	0.27	0.51
BEST SOLUTION						*BEST SOLUTION*					
AIC	R^2	RSS	No.Vars	Selections		AIC	R^2	RSS	No.Vars	Selections	
42.33	0.52	8189.5	2	7;8		53.85	0.5	3166	2	5;7	
Kenton-on-Sea											
SEQUENTIAL TESTS											
Variable	AIC	Pseudo-F	P	Prop.	Cumul.						
4.Temperature	51.91	2.49	0.05	0.29	0.29						
8.Salinity	51.09	2.89	0.05	0.26	0.55						
9.Oxygen	42.31	1.38	0.33	0.11	0.66						
BEST SOLUTION											
AIC	R^2	RSS	No.Vars	Selections							
42.31	0.99	73.57	3	4;8;9							

2.4 Discussion

The composition and abundance of the larval fish community in the coastal nearshore of the Algoa Bay region varied considerably both along and cross-shore, with depth. In addition, whilst distance and depth were important for Trip 1, not so for Trip 2. In the present study a total of 36 species were recorded belonging to 20 families. The most numerically abundant species were from family Blenniidae (CBE), Cynoglossidae (CPE), Gobiesocidae (CBE), Soleidae (CPE), Clinidae (LB) and Sparidae (CPE). Six species of family Blenniidae and Sparidae were recorded in this study and for family Soleidae, three species, Gobiesocidae ,two species, and only one species each for Cynoglossidae and Clinidae. In previous studies within the coastal nearshore (depth <15 m) of Algoa Bay itself, Cynoglossidae and Sparidae larvae have also been found among the most abundant families, in addition to Clupeidae (PPE), Engraulidae (PPE) and Gobiidae (CBE) (Beckley, 1986; Pattrick and Strydom, 2008). The fish families found in the present study are also common in the coastal nearshore further south, in the same warm temperate region (Tilney and Buxton, 1994) of South Africa.

At Cape Recife, the blenniid, *Parablennius pilicornis* (CBE) was mostly abundant in the onshore, with more larvae at the surface of the water column than at the bottom. In the warm-temperate Tsitsikamma region of Southern Africa, situated 150 km to the west of Algoa Bay, the occurrence of blenniid larvae (*Chalaroderma oceliata, Parablennius cornutus* and *P. pilicornis)* onshore has been associated with the proximity of reef habitats, hence vicinity to adult habitats (Tinley and Buxton, 1994). The same association of Blenniidae larvae with reefs has been noticeable in the tropical waters of Hawaii, on the windward side of the Oahu Island (Watson, 1987). Blenniidae larvae hatch from benthic eggs which are adhesive and often stick onto vegetation (Thresher, 1984; Brogan, 1994; Leis *et al.,* 2013). In other parts of the world including Portugal (Borges *et al.,* 2006), Hawaii (Leis and Miller, 1976), California (Barnett *et* *al*., 1984) and New Zealand (Kingsford and Choat, 1989) the onshore distribution of larvae of blenniids has been attributed to the spawning modes, spatio-temporal occurence of the adults, which influences the egg release and dispersal (Leis and Miller, 1976; Barnett *et al*., 1984; Borges *et al.,* 2007). The eggs are therefore not subject to any pelagic dispersal, with the larvae subsequently only entering into the coastal nearshore much later in their development. In addition, by not having a yolk-sac stage, larvae from benthic eggs hatch in a more developed condition than those from pelagic eggs, with larvae having a yolk-sac (Thresher, 1984; Brogan 1994; Leis and Miller, 1976; Barnett *et al*., 1984; Borges *et al.,* 2007). Generally, blenniid larvae at the preflexion stage of development have enhanced developed sensory abilities and can also actively swim in water and maintain vertical position (Stobutski and Bellwood, 1994; Leis and Carson-Ewart, 1997; Fisher *et al*., 2000), which favours their growth and reduces their mortality rate in the dynamic coastal nearshore environment (Brogan, 1994; Leis *et al.,* 2013).

In the Algoa Bay study region, the highest densities of larval fishes were recorded at Cape Recife, particularily in the onshore, especially during Trip 1. The variance in larval fish communities at Cape Recife during Trip 1 was explained mostly by currents (meridional flow and vertical flow). In terms of topography, Cape Recife is a headland, situated on the western edge of Algoa Bay (Goschen *et al*., 2012), with larval fish samples collected from a maximum depth of 17 m in the onshore and 35 m in the offshore. At Cape Recife the currents were faster offshore than onshore. Since hydrodynamics are important processes in shaping larval fish assemblages in the coastal nearshore (Leis, 2006; Pattrick *et al*., 2013), the varying densities of larval fish recorded at Cape Recife may be due to the favourable, slower onshore currents recorded and shallower depths. Perhaps shallower sites provide a suitable and safe habitat for egg laying to occur in and therefore increasing chances for larvae to hatch in coastal nearshore of the Algoa Bay region.

During both trips, larvae of the family Blenniidae were found to be dominant onshore at the surface while Soleidae and Cynoglossidae dominated the offshore with the highest abundance recorded at the bottom of the water column. The onshore distribution of blenniids and offshore distribution of soleids and Cynoglossidae supports the hypothesis of the abundance of coastal species with benthic eggs onshore and abundance of coastal species with pelagic eggs offshore. Similar studies have also observed the offshore distribution of coastal species with pelagic eggs from family Soleidae and Cynoglossidae but only in particular species of these families, making the distribution of these larvae quite variable (Heemstra and Heemstra, 2004; Trassierra, 2018). For family both soleids and cynoglossids, the larvae recorded were mostly at preflexion stage of development. The larvae of these families could have been pasively transported offshore by currents, as the larvae at preflexion stage are still underdeveloped and unable to swim properly. Larval fish species produced from pelagic eggs are also generally less developed than benthic eggs when they hatch (Leis, 1991), therefore, making their distribution to be affected by local oceanographic features such as currents.

The Algoa Bay area is known to be an important habitat for the larvae of sardine, *Sardinops sagax* (PPE), and anchovy, *Engraulis encrasicolus* (PPE) (Beckely, 1989; Pattrick and Strydom, 2008). In addition, *S. sagax* larvae are also known to occur in high numbers within the coastal nearshore west of Algoa Bay, in the Tsitsikamma Nature Reserve marine protected area (Tilney and Buxton, 1994). In the present study however, the densities of *S. sagax* and *E. encrasicolus* were considerably lower than previously recorded in the Algoa Bay region (Beckley, 1986; Pattrick and Strydom, 2008). Since the 1980s, there have been fluctuations in the adult population size of *S. sagax* and *E. encrasicolus* in South Africa, with low abundance recorded in recent years in 2011-2018 for *S. sagax* while biomass for *E. encrasicolus* is still very high (Van de Sleen *et al*., 2018)., The decrease in abundance of *S. sagax* has been attributed to mainly overfishing and global warming (Boyd and Badenhorst, 1981; Crawford, 1981; Van der Lingen *et al.*, 2006; Costalago *et al.*, 2018). The low abundance of *S. sagax* larvae observed in this study may also be due to the fact that this species only occassionally spawns within the Algoa Bay region, with the primary spawning area for sardine occuring in colder waters of the west coast of South Africa (Costalago *et al.,* 2018) and in the offshore areas of the Agulhas Bank (Hampton 1992; Roel *et al.,* 1994). In the Tsitsikamma National Park, larvae of *E. encrasicolus* were recorded along the continental shelf at depths <90 m (Tilney *et al.*, 1996), but the presence of larvae has been recorded at depths <15 m in Algoa Bay (Pattrick and Strydom, 2008) and occasionally within the Swartkops Estuary mouth, in Algoa Bay (Beckley, 1986). The larvae of *E. encrasicolus* are spawned much closer to shore in the Algoa Bay region, as these larvae were found particularily, at depths of 30 m in the present study.

During both trips, larval density was higher at the surface than bottom of the water column at Schoenmakerskop and Cape Recife, with species of the Blenniidae contributing the most towards the observed distribution. The Blenniidae larvae were mostly at the very early stage of development (preflexion). In contrast, at Algoa Central, Cape Padrone and Cannon Rocks, larvae were more abundant at the bottom of the water column. Callionymidae and Gobiesocidae made important contributions towards the larval fish compostion at Algoa Central, while Gobiesocidae and Cynoglossidae dominated the catches at Cannon Rocks and Cape Padrone. Later stages of development contributed the most towards the catches of Callionymidae and Cynoglossidae. Late stages of larvae are normally well developed and able to swim vertically (up and down) in the water column, tracking areas where their prey are highly abundant (Batty, 1987). Generally, currents are known to be faster at the surface of the water column than at the bottom (Boyd *et al.*, 1992; Goschen & Schumann, 1994; Schumann *et al.*, 2005; Goschen *et al.*, 2012). As such, the young blenniid larvae contributing to the higher abundance of larvae observed at the surface at Schoenmakerskop and Cape Recife, could be forced to the surface due to their poor swimming abilities, unable to depth regulate due to thefast flowing surface currrents and thus drift passively with (Hunter, 1972; Borges *et al*., 2007). The older larvae observed at the bottom of the water column at Algoa Central, Cape Padrone and Cannon Rocks could utilise the slower moving currents at the bottom of the water column in order to remain closer to shore. Distribution of species from the Gobiesocidae family at the bottom depths is common in the coastal nearshore, mainly caused by their specialised suction disk that helps attach themselves on rocky substrates or vegetation in order to avoid being dispersed offshore (Allen, 1984). Studies on the vertical distribution of larvae in the coastal nearshore have reported the occurence of Callionymidae (Gray, 1998), Gobiesocidae (Kingford, 2001) and Cynoglossidae (Campos and Santillan, 2005, 2006) in deep waters during the day to be common due to predator avoidance (Ahlstrom, 1959; Loeb, 1979; Boehlert *et al*., 1985; Brodeur and Rugen, 1994; Gray and Miskiewicz, 2000; Kingford, 2001; Campos and Santillan, 2005). The factors that contributed to the family-specific distributions of larvae in the present study could therefore include ontogeny (i.e preflexion larvae occuring at the surface and postflexion larvae found mostly at the bottom of the water column), currents (i.e faster currents at the surface and slow moving currents at the bottom) as well as availability of predators and prey.

Cape Recife, Cape Padrone and Cannon Rocks (eastern edge of Algoa Bay) experience upwelling events associated with easterly winds, especially in summer (Goschen *et al*., 2012). This was the case, especially during Trip 2 at Cape Recife and both trips at Cape Padrone and Cannon Rocks. During an upwelling event, cold deep water rich in nutrients is brought to the surface triggering spawning of some adult coastal fishes (Parrish *et al.,* 1981; Neilson and Perry, 1990; Tinley and Buxton, 1994; Hutchings *et al.,* 2002). The associated increase in biological productivity within an upwelling area can hence ehance the survival of larval fishes through increased food supply (Morgan, 2014; Morgan *et al*., 2018). At Kenton-on-Sea, Cannon Rocks and Cape Padrone, Cynoglossidae (Cynoglossidae sp. 1) and Soleidae (*Heteromycteris capensis* and Soleidae sp. 1) were among the dominant species. Pattrick and Strydom (2014), found upwelling to be favourable for certain species in Algoa Bay, including Soleidae (*Austroglossus pectoralis* and *Heteromycteris capensis*) and Cynoglossidae (*Cynoglossus capensis*). Good feeding conditions and availability of approriate food are likely to aid growth and survival of larvae in upwelling systems (Cushing, 1971).

At Bay (Trip 1), Cape Recife (Trip 1) Schoenmakerskop (Trip 1 and 2), Sardinia Bay (Trip 1 and 2) and Kini Bay (Trip 1 and 2), all located on the western edge of the sampling region, there were strong downwelling events a few days before sampling and on the day of sampling. The effect of downwelling on the distribution of larvae can differ depending on the swimming capabilities of larvae (Shanks and Brink, 2005). During downwelling, the surface occupying larvae are transported shorewards, however during strong downwelling from winds or storms larvae are transported into deeper water offshore (Ma and Grassle, 2005). The lowest densities of larval fishes were recorded at Bay, Schoenmakerskop, Sardinia Bay and Kini Bay, suggesting downwelling in these areas could be associated with offshore transport of larval fish, while at Cape Recife, downwelling was associated with high densities of fish larvae. Larvae at the flexion developmental stage dominated the catches at Cape Recife while at Bay, Schoenmakerksop, Sardinia Bay and Kini larvae at a later stage of development (postflexion larvae) dominated. The highest densites of larval fish were recorded at Cape Recife possibly because this site is close to the lee of the headland, where larvae are mostly concentrated during downwelling events (Morgan *et al*., 2009).

At Kenton-on-Sea during Trip 2, sea temperature was higher in the onshore at the surface than at the bottom of the water column (Appendix A). Like elsewhere, Goschen and Schumann (2011), have highlighted that the surface waters are heated to a greater extent by solar radiation in the eastern Agulhas bank (offshore Algoa Bay) especially in summer corresponding to when sampling was conducted for Kenton-on-Sea (Trip 2).Oxygen was higher offshore at the surface of the water column at Algoa Central during Trip 1. At Cannon Rocks pH was the same at both distances (onshore/offshore) and was particularily higher at the bottom than the surface during Trip 2. The concentration of pH and oxygen corresponded with the larval densities at both of these sites. Larval fish tended to avoid depths with low dissolved oxygen and pH levels, as this is capable of reducing their growth and survival (Breitburg, 1994; Saleh *et al.*, 2013). Fluorescence was higher offshore at the surface during Trip 1. The larval fish also shown the same distribution with fluorescence at Algoa Central, with larval densities particularily higher offshore at the surface of the water column. Fluorescence serves an indication for chlrophyll-*a* which is an proxy for phytoplankton biomass and hence food for larvae (Rabbaniha *et al.*, 2015). Turbidity was higher in the onshore than offshore at Bay (Trip 1) while the reversed patterns was observed at Schoenmakerskop (Trip 2) (Appendix A) and seemed to influence the larval distribution at those sites during the relative trips. Generally, increased turbidity can result in low predation, hence more chance of larvae avoiding predators, therefore reducing mortality rates of larval fish (Fiksen *et al.*, 2002; Fuiman and Werner, 2009). At sites situated near capes, where downwelling was prominent, nutrient influx at the surface waters fuels phytoplankton productivity which might explain the high turbidity recorded at the surface at Bay (Trip 1) and Schoenmakerskop (Trip 2) (Wieters *et al.,* 2003), as higher concentration of phytoplankton can alter turbidity in the nearshore (Wang *et al.*, 2019). Turbidity was generally higher at bottom depths during the present study. Although extreme caution was taken to avoid touching of the bottom substrate during sampling, the general increase of turbidity with depth may have occurred when occasionally the CTD might have hit the seabed causing the sediment to stir. In addition, salinity explained the variation in larval fish distribution at Cape Recife (Trip 2), with salinity slightly higher in the offshore at the surface of the water column

(Appendix A). At Cape Recife during Trip 2, more larvae were recorded at the surface of the water column than at the bottom, suggesting that larvae prefered less saline waters at this site. The observed patterns of lowest salinity onshore at Cape Recife (Trip 2) and highest turbidity at Bay (Trip 1) and Schoenmakerskop (Trip 2) may also be due to the influence of fresh water from five rivers flowing into the Bay area where sampling was conducted, i.e., Swarkops, PE Harbour (Baakens), Papenkuils, Coega and Sundays (Whitfield, 1998; Able, 2005; Goschen *et al.,* 2012).

The distribution and composition of larval fishes in the coastal nearshore in the present study could be attributed to the habitat type, as the spawning of the adults and whether the eggs are pelagic or demersal had a large part to play in larval distribution. Larvae spawned from reef-associated adults (Blenniidae) with benthic eggs dominated in the onshore and the larvae of pelagic adults (Soleidae and Cynoglossidae) were dominant offshore. In addition, larval fish assemblages displayed a strong cross-shore and alongshore distribution in the coastal nearshore of the Algoa Bay region that was significantly linked to different environmental conditions, depending on the sites, but with larval fish community at Cape Recife influenced mainly by meridional and vertical flows. Currents played an important role in the spatial distribution of larval fishes, with the lowest densities of larvae recorded in fast moving currents offshore and highest densities recorded in slow moving currents onshore Wind direction, as a driving factor of coastal upwelling/downwelling (occurring at least three days preceding sampling), could have influence alongshore distribution of larval fish in the Algoa Bay region. High abundances were recorded at sites sampled after upwelling events (easterly wind-driven), while the least densities were recorded in downwelling areas, particularly at sites not situated around capes/headlands. The western headland of Cape Recife was however an exception because highest densities of larvae were recorded a day before downwelling (westerly wind-driven). To conclude, oceanographic conditions therefore played an important role in the larval fish distribution as a direct mechanism of transport and indirectly influencing the nutrients and hence possible predator avoidance and therefore survival of larval fish in the Algoa Bay region. This study contributes to the understanding the distribution and abundance of larval fish on the coastal nearshore of the Algoa Bay region and also role played by environmental conditions including hydrodynamics on the structuring of larval fish assemblages.

CHAPTER III

INTERACTIONS OF WIND AND LARVAL FISH ASSEMBLAGES IN THE COASTAL NEARSHORE OF ALGOA BAY

3.1 Introduction

Winds are one of the main drivers of hydrodynamics in the coastal nearshore, influencing mostly the surface of the water column causing currents to move faster at the surface than at the bottom (Tapia *et al*., 2004; Robert, 2010; Solokov and Chubarenko, 2012; Kampf, 2017). This localized effect on coastal nearshore hydrodynamics hence makes wind-driven circulation particularly relevant for the transport of early stages of fish (Graham and Largier, 2007). Wind-driven circulation occurring at different spatial and temporal scales in the coastal nearshore plays a pivotal role in retention, dispersal, recruitment and settlement of fish larvae (Castro *et al*., 2000; Sponaugle *et al*., 2005; Chang *et al*., 2017). In addition, some adult fishes adjust their spawning activity coincide with favorable wind-driven ocean features, such as coastal upwelling, so as to provide an immediate food source for larvae to increase their survival in the dynamic coastal nearshore (James *et al*., 2002; Tapia *et al*., 2004; Norcross *et al*., 2011; Comerford and Brophy, 2013).

Furthermore, the topography of the coastal nearshore, coupled with the influence of winds, strongly affects the oceanography of localised areas (Mace *et al*., 2005; Graham and Largier, 2007; Morgan *et al*., 2009; Morgan *et al*., 2012; Morgan, 2014). Around headlands, winds are more intense on the windward side, generating currents capable of transporting ichthyoplankton offshore, which results in limited recruitment back to the nearshore (Graham and Largier, 2007; Morgan *et al*., 2009; Morgan *et al*., 2012; Morgan, 2014). On the leeward side of a headland however, the retention of larvae inshore is observed due to the occurrence of mesoscale eddies and fronts (Roughan *et al*., 2006).

Several studies have investigated the influence of wind on larval fish distribution (Tapia *et al*., 2004; Comerford and Brophy., 2013). Expectedly, the extent to which winds influence larval transport in the coastal nearshore differs across the world (Croz *et al*., 1999; Dalley *et al.*, 2002). The strength and direction of the wind are among the main factors driving larval fish distribution in the coastal nearshore of both temperate (Comerford and Brophy, 2013) and tropical regions (Croz *et al*., 1999), where strong winds events are associated with the offshore dispersal of early stages of fish larvae that are still underdeveloped in terms of swimming abilities.

Wind-driven oceanographic studies that assess larval dispersal have been done extensively across the world in Northern California (Largier, 2003; Morgan *et al*., 2009; Morgan *et al*., 2012; Morgan *et al*., 2014; Morgan *et al*., 2018), central California (Wilson *et al*., 2008; Indiaz-diaz, 2014), central Chile (Hernández-Miranda *et al*., 2003) the northern Pacific Ocean (Chang *et al*., 2017; Chang *et al*., 2018), south-east Pacific Ocean (Vasquez *et al*., 2013) and north-east Atlantic Ocean (Moyano *et al.,* 2014; Shulzitski *et al.,* 2016). Studies along the north Atlantic Ocean, north and south-east Pacific Ocean, for example, have focused on the effects of oceanographic conditions on larval transport, with an emphasis on single species, especially on those that are important from a commercial fishery perspective such as *Trachurus murphyi* (Vasquez *et al*., 2013), *Anguilla japonica* (Chang *et al*., 2017; Chang *et al*., 2018), *Sardinops sagax* and *Engraulis mordax* (Inda-diaz *et al*., 2010), with only isolated studies having assessed the relationship between wind driven oceanographic features and larval fish communities (Hernández-Miranda *et al*., 2003; Wilson *et al*., 2008; Diaz-Astudillo *et al*., 2017).

Much research has focused on understanding the interaction of larvae with wind induced coastal upwelling (Morgan *et al*., 2012; Morgan, 2014; Tiedeman *et al*., 2016; Morgan *et al*., 2018). Coastal upwelling is caused when the Ekman layer is forced offshore and must be compensated by upward movement of deep nutrient-rich water to the surface, where sunlight then fuels blooms of phytoplankton (Morgan *et al*., 2009; Morgan, 2014; Kampf and Chapman, 2016; Kampf, 2017). Areas of coastal upwelling are known to be favourable habitats for many larval fishes due to the high abundance in zooplankton which spawn and produce (especially) nauplii, the main food source for first-feeding larval fish (Shulzitski *et al.,* 2016; Chang *et al*., 2017; Chang *et al*., 2018).

As highlighted in the previous chapter, research on ichthyoplankton composition and distribution has been carried out in Algoa Bay (Beckley, 1986; Pattrick and Strydom, 2007; 2008; 2014; Pattrick *et al*., 2013; 2016; Costalago *et al*., 2018), but the influence by winds on larval fish assemblages remains unknown for this region. Algoa Bay is defined by the eastern (Cape Padrone) and western (Cape Recife) headlands/capes, with ocean circulation and wind forcing varying according to these topographical features (i.e. the windward vs leeward areas; Goschen and Schuman, 2011). As a result of easterly winds, upwelling occurs both at the western (Schuman *et al*., 1988) and eastern (Goschen *et al*., 2012) headlands. Easterly- winds are most common in summer, while westerlies- occurring throughout the year (Schuman and Martin,1991). When coastal upwelling takes place at the western headland, the cold upwelled water is brought into the Bay via westerly winds, thus reducing the sea surface temperatures in the vicinity (Goschen and Schuman, 1995). This study was specifically designed to identify possible links between local wind events, with coupled environmental factors, and the distribution of ichthyoplankton at the headlands of Algoa Bay, situated in the warm-temperate coastal nearshore of the Eastern Cape, South Africa.

3.2 Methods and Materials

3.2.1 Study Area

The sampling for this study was conducted in the coastal nearshore of Algoa Bay (Figure 3.1), in November 2019. Due to the sheer extent of the Bay and the travelling time via boat to sample the distant headlands in one day, the study was restricted to four sampling sites. Two sites were located on either sides (windward vs leeward) of the western headland (Cape Recife) and two sites on either sides of the eastern headland (Cape Padrone). For the purposes of this study, the sampling sites were named from west to east: West outside (33°47'53"S, 26°19'07"E), West inside (33°47'49"S, 26°36'32"E), East inside (34°00'41"S, 25°45'46"E) and East outside (34°04'51"S, 25°42'30"E).

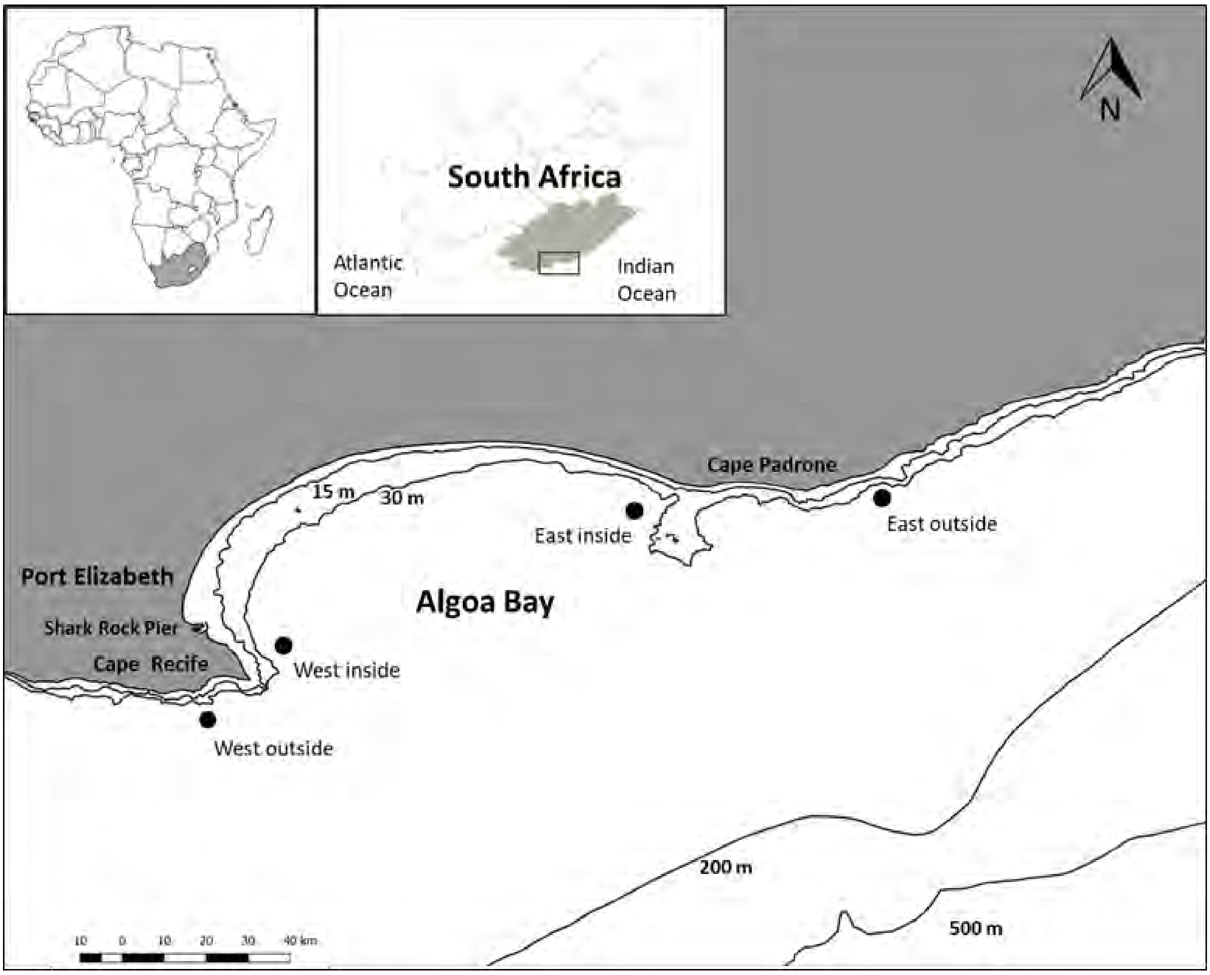


Figure 3.1: Position of the four sampling sites (black circles) in the Algoa Bay region, situated on the south east coast of South Africa. The sites for the study (black circles) were selected on the two prominent headlands of Algoa Bay, on the western sector (Cape Recife) and eastern sector (Cape Padrone). The location Shark Rock Pier corresponds to the position from where wind data were recorded.

3.2.2 Field Sampling

The effects of easterly and westerly wind events were investigated. Sampling was conducted on the 13th (Trip 1) 14th (Trip 2) and 20th (Trip 3) of November 2019. There is a gap between Trip 2 and Trip 3 because in order for sampling to be conducted it has to be done within a good weather window, when wave heights are <1.5 m and wind speeds <14 knots. The sampling occurred during early summer, when easterly winds are dominant (Schumann *et al.*, 1988) and larval fish are known to be abundant in Algoa Bay (Beckley, 1986). Three factors were included in the experimental design: Site (inside/outside), Distance (onshore/offshore) and Depth (surface/bottom). The focus here was to assess the along and cross-shore distribution and composition of larval fish in the coastal nearshore of the Algoa Bay region. The onshore stations were located ~200 m from the shore, while the offshore stations were ~3 km from the shore. A reference to Chapter 2 should be made for further details on this methodology.

The volume of water strained through each bongo net was calculated using the following formula:

> Volume of water filtered = Total flow meter revolutions (flow meter end – flow meter start) * 3.0365 (meters per 1 revolution, calibrated in a swimming pool) * 0.26 (area of 57 cm bongo net).

The average larval density for each replicate (two adjacent nets were pooled) was then calculated. The density of larvae (no. of larvae/100 m^3) was calculated using the following formula:

> Larval fish density = total count / volume of water filtered x 100.

Salinity, water temperature (°C), oxygen (ml/L), pH, fluorescence (mg/m^3) and turbidity (NTU) were collected at each of the sampling stations using a Seabird SBE 9/11 plus CTD which was lowered alongside the boat to measure these environmental parameters at 1 m depth intervals within 1 m of the seabed. During Trip 3 (20th November 2019), the CTD was accidentally lowered into the water column without being switched on and therefore no CTD data were recorded for this sampling day for the entire sampling duration.

3.2.3 Environmental Data

Hourly measurements of wind speed and direction were obtained from an automatic weather station installed by the South African Weather Services (SAWS) at Shark Rock Pier (Figure 1), located 3 m above sea level in the western sector of Algoa Bay, on the days of sampling (13th, 14th and 20th November 2019) as well as two days before each Trip. No data could unfortunately be retrieved for the eastern sector of the Bay (Bird Island meteorological station), due to SAWS operational issues and only data from the western sector of the Bay were therefore used (Shark Rock Pier; Figure 3.1). The following equation was used to correct/adjust for the height of the weather station:

$$V_{3m} = V_h \, (3/h)^{0.11}$$

Where V_{3m} is the wind speed at 3 m altitude at Shark Rock Pier, V_h is wind velocity measured at height h and h is the height at the meteorological station (Hsu *et al.*, 1994).

From the wind data, an upwelling index as zonal Ekman transport was calculated, with positive and negative values to indicate onshore and offshore displacement of surface waters, respectively (Bakun, 1973), at Shark Rock Pier situated on the west of Algoa Bay (Figure 3.1). Hourly data for tidal amplitude (m) was retrieved using the WXTide32 software version 4.7.

3.2.4 Laboratory Analysis

Biological samples were processed and analysed using the same protocol as described in Chapter 2, therefore reference to Chapter 2 should be made for further details.

3.2.5 Statistical Analysis

3.2.5.1 Rayleigh test statistics were used to test for uniformity for the distribution of the winds within each site and distance. Circular-linear correlations for wind data were then used to calculate correlations between wind speed and direction among sites and between distances.

3.2.5.2 Environmental and Biological Data

Draftsman plots were used to assess cross-correlation among the environmental parameters water temperature (°C), fluorescence (mg/m^3), turbidity (NTU), salinity, dissolved oxygen (ml/L), pH, wind speed and wind direction at each station. No significant correlations were found. A Principal Component Analysis (PCA) was used to outline and visualize the relationships among the environmental parameters. PCA reduces dimensions of data set while retaining important information (Clarke & Gorley, 2015). Patterns in environmental variables were examined using a Principal Component Analysis on a Euclidean distance matrix generated from normalised data. PCA were done separately by trip (see below details on this approach due to the outcome of the pre-analysis of the biological data). The strength of the zonal Ekman transport was assigned based on that of Kassi *et al*., (2018) where a range of 800 – 1400 m^3 km^{-1} s^{-1} is considered to actively influence larval fish distribution.

The biological data were square root transformed to address heteroscedasticity. Even after this transformation the biological data did not conform to the homogeneity of variances. A four-way Welch's multivariate ANOVA was hence preferred over PERMANOVA (Alyeseyenko 2016). The Welch's multivariate ANOVA was used because data according to depth were also heterogeneous, they were included in the analysis due to specific relevance to the hypothesis of the study and the permutational analysis being more robust than individual non-parametric tests, such as Kruskal-Wallis (Liu, 2015). Since the temporal variability was not the primary scope of the study and due to heterogeneous distribution of data for trips, separate analyses were run for each trip. Games-Howell post hoc tests (pairwise tests) were run to assess significant main effects and interactions. A non-parametric multidimensional scaling (NMDS) (Kruskal and Wish, 1978), was used to detect the variability in the biological data. ANOSIM was performed on the larval fish community to test for differences among trip (3 levels), site (4 levels), distance (as defined in the previous chapter; 2 levels) and depth (2 levels). SIMPER analysis was used to identify species responsible for characterising the significant differences detected by the ANOSIM.

A Biota-Environment (BIOENV) analysis was hence performed to examine the relationship between the biological community structure and the environmental variables. The strength of the relationship was assessed through Spearman correlation using 9999 permutations. Distance-based redundancy analysis (db-RDA) ordination plots were used to graphically illustrate the relationship between environmental variables and larval fish assemblages.

Larval fish community analyses were performed using the software package PRIMER V6.1.15 with PERMANOVA + V1.0.5 add-on (Clarke and Warwick, 1994). Welch's multivariate ANOVA was performed in R environment for computing statistics (R version 1.2.1335) (R Development Core Team, 2019) using the *car* package (Welch's ANOVA; Fox and Weisberg, 2009).

3.3 Results

3.3.1 Larval Fish Composition

A total of 522 larval fish were collected during the sampling period representing 15 fish families and 29 species. The family that contributed the most towards the total larval fish catch in the Algoa Bay region included Gobiesocidae and in terms of species *Chorisochismus dentex* dominated the larval fish catches for all the trips (Table 3.1). Preflexion and flexion larvae across all sites contributed the most during Trip 1 while post flexion larvae were dominant during Trip 3 in the coastal nearshore (Figure 3.2).

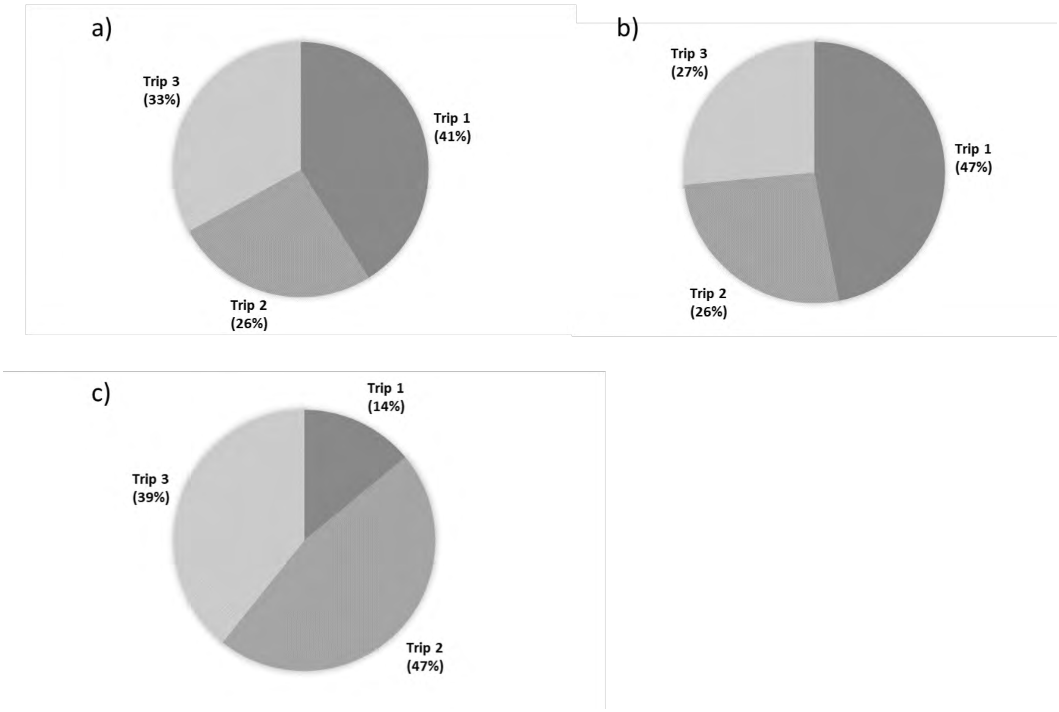


Figure 3.2: Percentage contribution of larval fish at a) preflexion and b) flexion and c) postflexion stages of development during Trip 1, Trip 2 and Trip 3 in the coastal nearshores of the Algoa Bay region.

Table 3.1: Species composition by total counts (N); as percentage of the total catch (%); developmental stage (DS) (Pr= preflexion, F= flexion, Po= postflexion) and body length (BL) range of fish larvae in Algoa Bay during Trip 1, Trip 2 and Trip 3.

		Trip 1				**Trip 2**				**Trip 3**			
Family	Species	N	%	DS	BL (range) in mm	N	%	DS	BL (range) in mm	N	%	DS	BL (range) in mm
Blenniidae	*Parablennius pilicornis*	4	2.2	Pr,F,Po	2.7-8.7	48	36.6	Pr,F,Po	3.3-11.7	34	16.5	Pr,F,Po	3.1-12.2
Callionymidae	Callionymidae sp. 1	2	1.1	Pr,F	2-4.2.0								
Cheilodactylidae	*Cheilodactylus* sp. 1									1	0.5		7.9
Clinidae	Clinidae sp. 1	23	12.4	F,Po	5.2-13.7	12	9.2	F,Po	5.2-6.9	12	5.8	F,Po	3.8-11.2
Clupeidae	*Etrumeus whiteheadi*	3	1.6	Po	17.7-18.7	2	1.5	Po	14.9-15.9				
	Sardinops sagax	1	0.5	Po	13.3								
Cynoglossidae						5	3.8	Pr,F,Po	5.3	10	4.9	F,Po	5-9.9
Engraulidae	*Engraulis encrasicolus*	6	3.2	F,Po	11.0-21.3	2	1.5	Po	13.7-14.0	16	7.8	F,Po	7.1-12.2
Gobiesocidae	*Chorisochismus dentex*	99	53.5	Pr,F,Po	3.1-9.0	36	27.5	Pr,F,Po	3.2-6.9	70	34.0	Pr,F,Po	3.4-7.2
	Eckloniaichtys scylliorhiniceps	3	1.6	Pr	4.4-4.9					2	1.0	Pr,Po	4.5-7.1
Gobiidae	*Caffrogobius gilchristi*	1	0.5	F	5.5					1	0.5	F	5.1
	Caffrogobius nudiceps	2	1.1	Pr	2.2-3.0								
	Caffrogobius sp. 1	1	0.5	Pr	4.5					1	0.5	Pr	3.9
	Caffrogobius sp. 2	2	1.1	F	4.4-4.7								
	Glossogobius callidus	10	5.4	Pr,F	4.5-6.8	4	3.1	Pr	2.5-3.9	4	1.9	Pr,F	3.8-4.5

	Gobiidae sp. 1	12	6.5	Pr,F	3.8-6.5	2	1.5	F	5.6-6.4	2	1.0	Po	6.2-7.4
	Gobiidae sp. 2	3	1.6	Pr,F	3.8-6.5					1	0.5	Po	5.4
	Psammogobius knysnaensis	2	1.1	F	4.2-5.0								
Mugilidae	Mugilidae sp. 1									1	0.5	Po	17.0
Sciaenidae	Sciaenidae sp. 1									1	0.5	F	3.9
	Sciaenidae sp. 2	1	0.5	Pr	2.7					1	0.5	Po	6.6
Scomberesocidae	Scomberesocidae sp. 1									1	0.5	Po	5.5
Scorpaenidae	Scorpaenidae sp. 1									1	0.5	Po	12.4
Soleidae	*Heteromycteris capensis*	2	1.1	Pr,Po	2.7-8.6	4	3.1	Pr,F	3.7-5.6	26	12.6	Pr,F,Po	3.2-11.9
	Solea turbynei					10	7.6	F,Po	4.2-5.3				
Sparidae	Sparidae sp. 1	2	1.1	Po	8.2					8	3.9	F,Po	4-6.6
	Spondyliosoma emarginatum	5	2.7	Pr	3.7-5.5	6	4.6	Pr,F	2.6-5.8	13	6.3	Pr,F,Po	3.7-8.5
	Total number of individuals	185	100			131	100			206	100		

One hundred and eighty-five larval fish specimens (10 families, 21 species) were recorded during Trip 1, with Gobiesocidae dominating the coastal nearshore (Figure 3.3a). In terms of species, *Chorisochismus dentex* dominated the catches (Figure 3.3b).

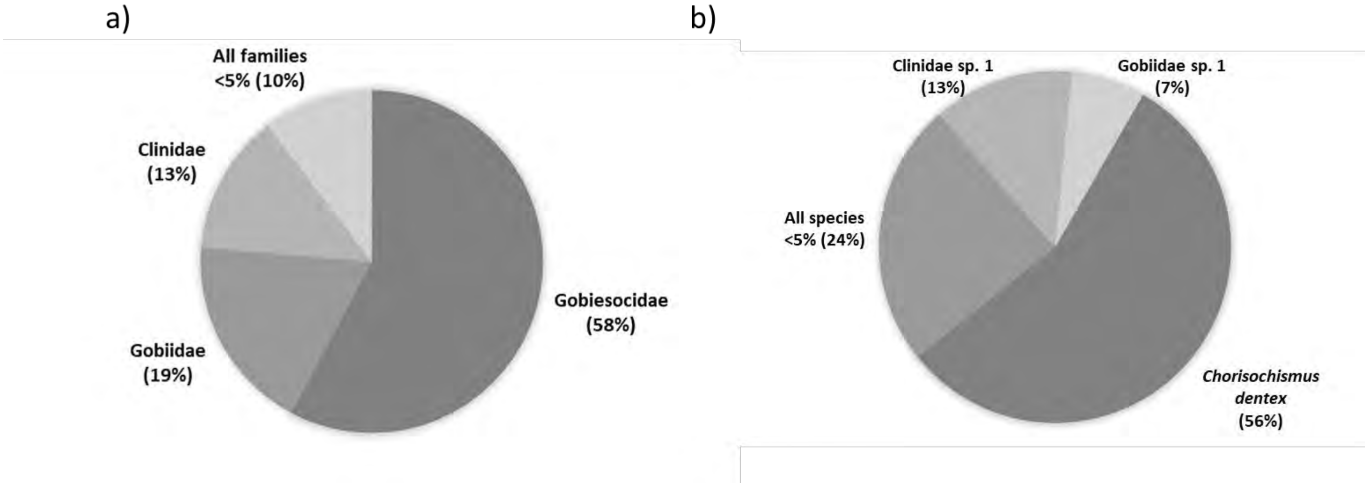


Figure 3.3: Percentage contribution of larvae of dominant (>5%) fish a) families and b) species sampled during Trip 1 in the coastal nearshores of the Algoa Bay region.

The fish family that dominated the surface of the water column included Clinidae (Figure 3.4a) while Gobiesocidae dominated at the bottom of the water column during Trip 1 (Figure 3.4b). During Trip 1, the onshore and offshore were both dominated by Gobiesocidae (Figure 3.4c, d).

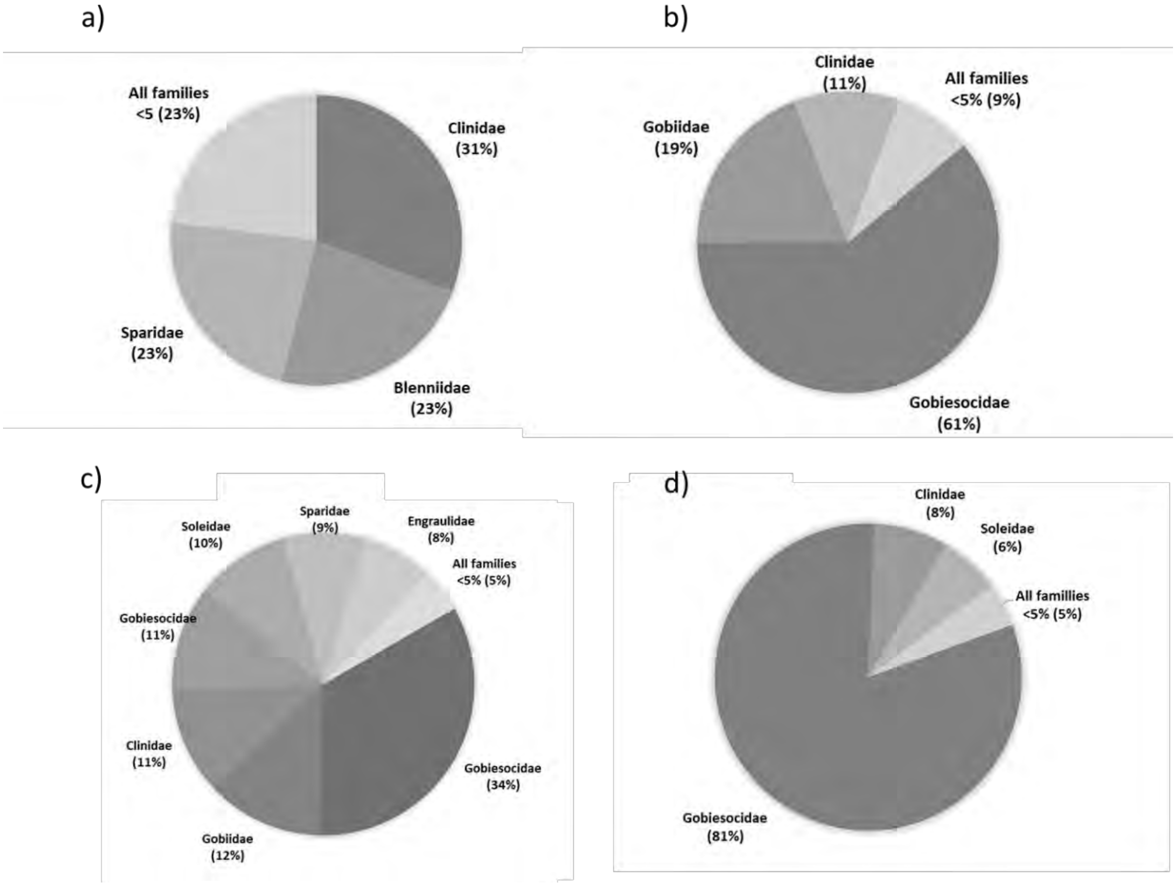


Figure 3.4: Percentage contribution of the dominant families during Trip 1 at the a) Surface b) Bottom c) Onshore d) Offshore sampled in the coastal nearshore of the Algoa Bay region.

During Trip 2, 131 larval fish specimens (9 families, 11 species) were recorded with Gobiesocidae the most representative family with *C. dentex* the most dominant species (Figure 3.5).

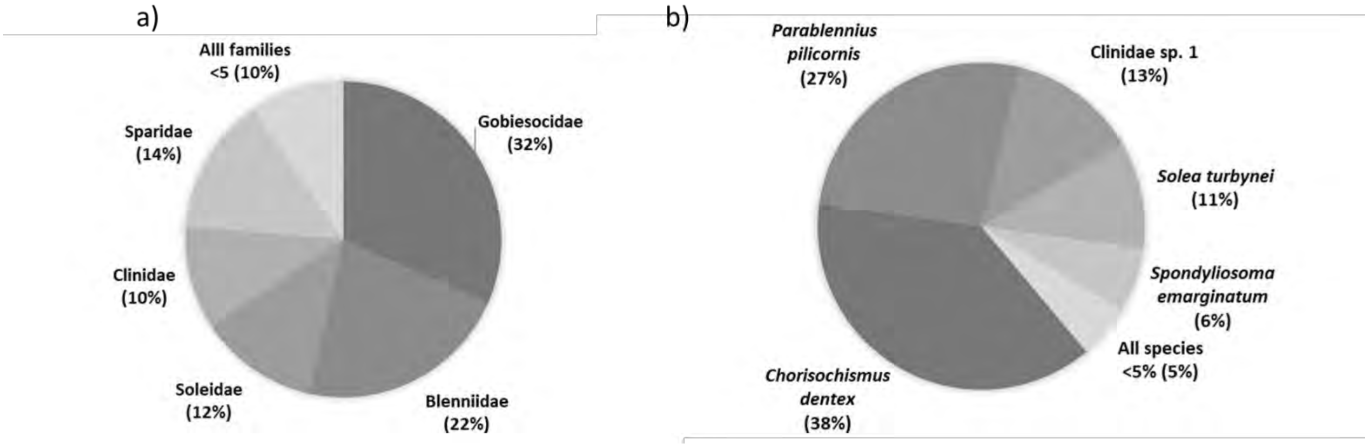


Figure 3.5 Percentage contribution of dominant fish a) families and b) species (>5%) sampled during Trip 2 in the coastal nearshores of the Algoa Bay region.

The families that made important contributions at the surface of the water column during Trip 2 included Blenniidae while at the bottom of the water column Gobiesocidae. In both the onshore and offshore, Gobiesocidae and Blenniidae dominated the catches (Figure 3.6).

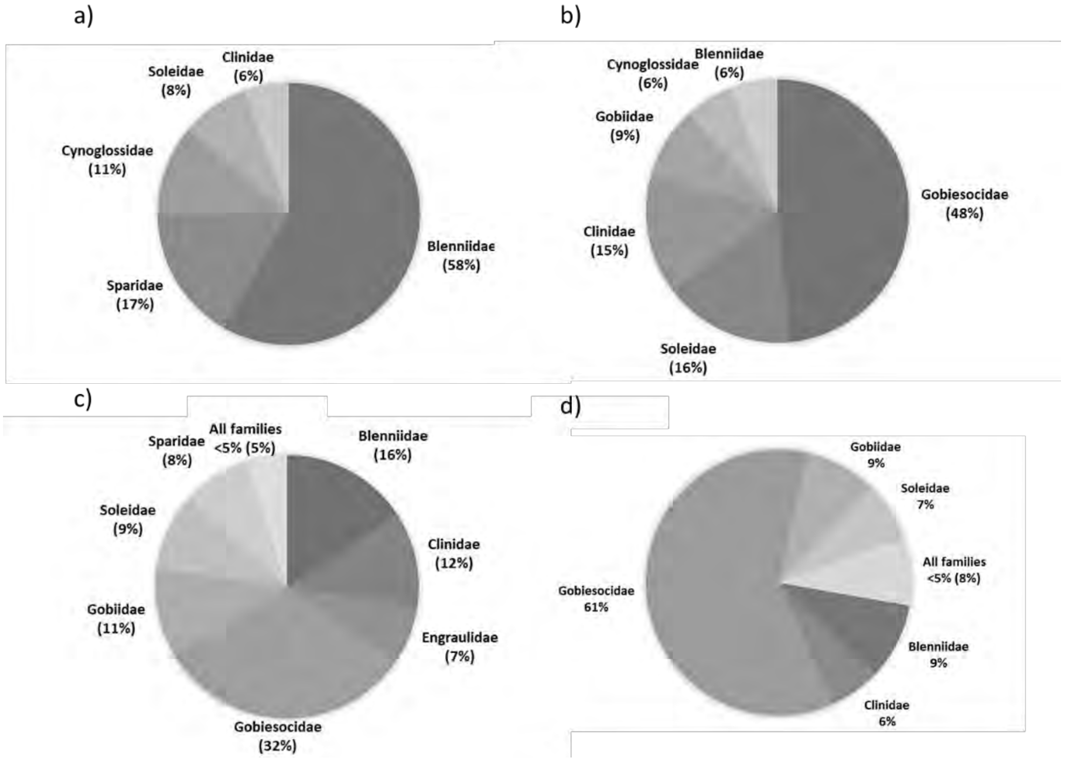


Figure 3.6 Percentage contribution of the dominant families during Trip 2 at the a) Surface b) Bottom c) Onshore d) Offshore sampled in the coastal nearshore of the Algoa Bay region.

During Trip 3, 206 larval fish were recorded (12 families, 22 species), with the catch similarly dominated by Gobiesocidae. As before, *C. dentex* dominated the overall catches (Figure 3.7).

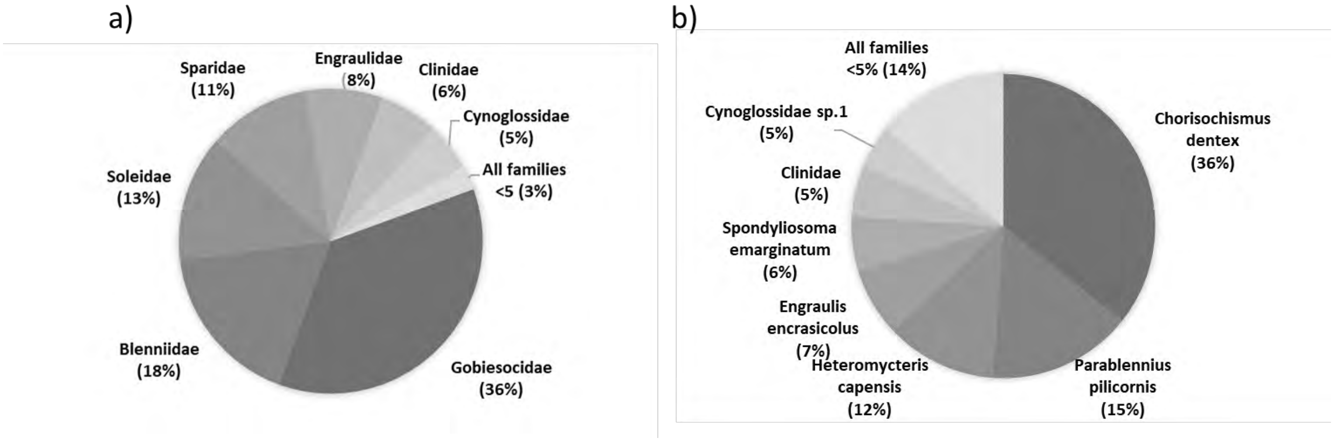


Figure 3.7: Percentage contribution of dominant fish a) families and b) species (>5%) sampled during Trip 3 in the coastal nearshores of the Algoa Bay region.

At the surface of the water column during Trip 3, Blenniidae dominated (Figure 3.8a), while at the bottom of the water column the family that contributed the most was Gobiesocidae (Figure 3.8b). In the onshore, Gobiesocidae dominated the total larval fish catch while the offshore was dominated by Soleidae (Figure 3.8c, d).

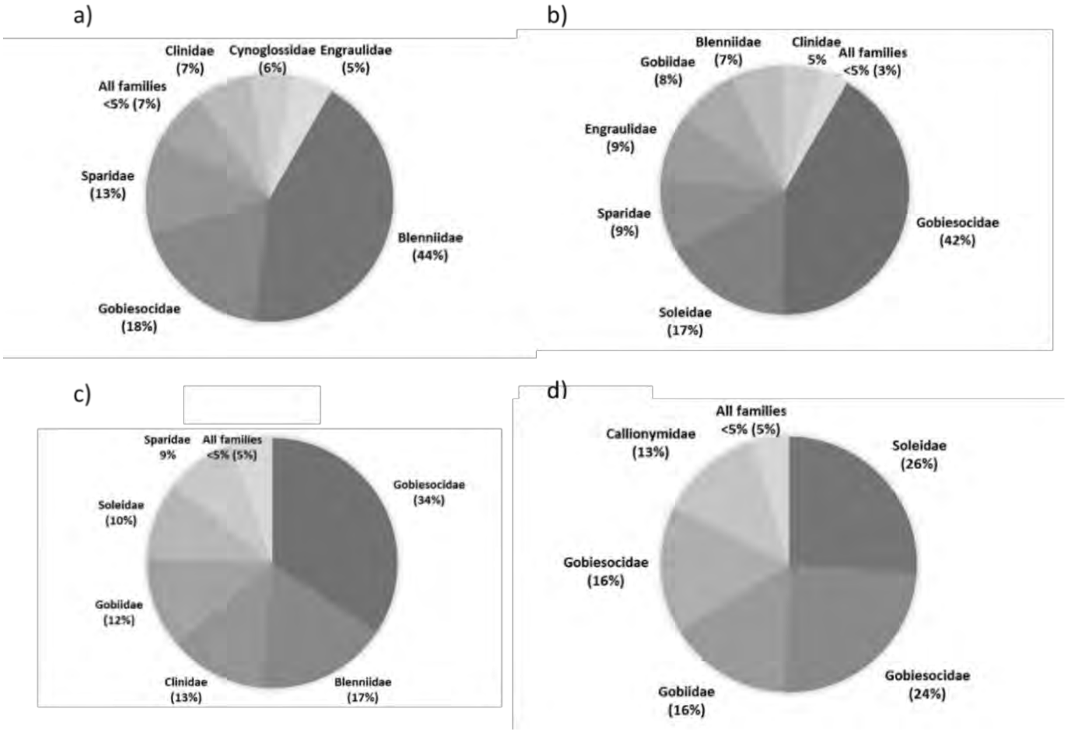


Figure 3.8: Percentage contribution of the dominant families during Trip 3 at the a) Surface b) Bottom c) Onshore d) Offshore sampled in the coastal nearshore of the Algoa Bay region.

3.3.2 Alongshore, Cross-shore and Depth Variability in Larval Fish Assemblages

The results of the four-way Welch's ANOVA indicated significant differences in the larval fish assemblages for depth and for interaction between distance and trip (Table 3.2).

Table 3.2: Results of the four-way Welch's ANOVA for the total abundance of all taxa at East outside, East inside, West inside and West outside (added as root values in the table). Df= Degrees of freedom, SS= Sum of squares, MS= Mean squares, F= Pseudo F-ratios. P-values in bold are significant.

	Df	**SS**	**MS**	**F**	**P-value**
Site (Si)	3	0.07	0.02	0.68	0.57
Depth (De)	1	0.60	0.60	21.86	**0.00002**
Distance (Di)	2	0.08	0.04	1.54	0.22
Trip (Tr)	2	0.12	0.06	2.11	0.13
Si X De	3	0.04	0.01	0.53	0.66
Si X De	3	0.04	0.01	0.52	0.67
De X Di	1	0.001	0.001	0.03	0.85
Si X Tr	6	0.13	0.02	0.78	0.59
De X Tr	2	0.02	0.01	0.44	0.65
Di X Tr	2	0.21	0.10	3.77	**0.03**
Si X De X Di	3	0.11	0.03	1.29	0.29
Si X De X Tr	6	0.15	0.02	0.91	0.49
Si X Di X Tr	6	0.31	0.05	1.85	0.11
De X Di X Tr	2	0.17	0.08	3.03	0.06
Si X De X Di X Tr	6	0.23	0.04	1.39	0.24
Residuals	47	1.29	0.03		

The results of the pairwise test indicated that fish larval density was significantly higher at the bottom of the water column than at the surface during each trip in the coastal nearshore of the Algoa Bay region (Figure 3.9)

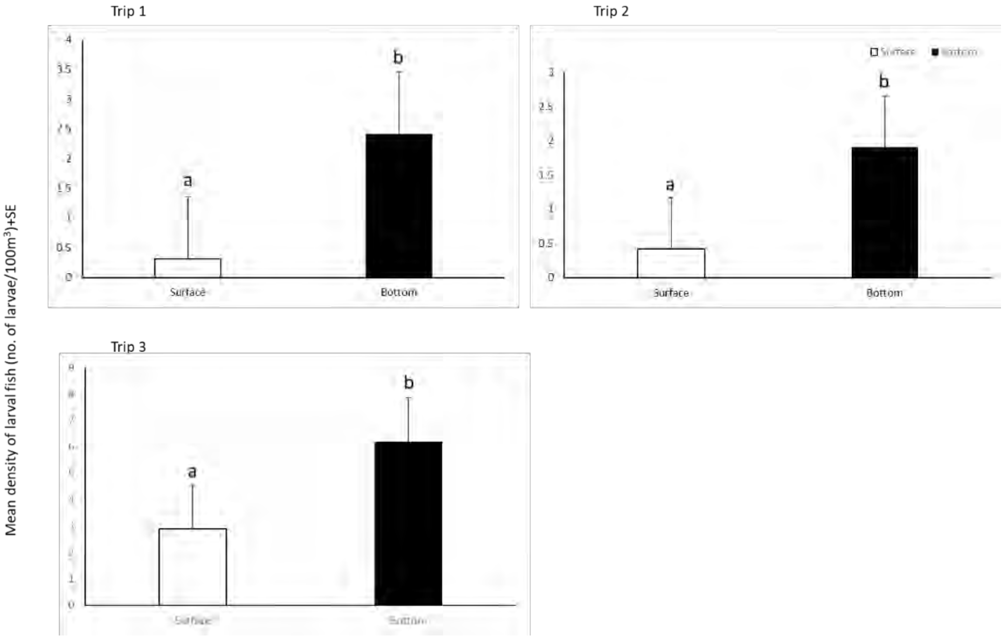


Figure 3.9: Mean total larval fish densities by depth (surface/bottom) during Trip 1, 2 and 3 in the Algoa Bay region. Error bars indicate standard error and the letters above the bars indicate within site homogenous group identified by 'Trip X Depth' pairwise results.

During Trip 2, significantly higher densities of larvae were recorded in the onshore (Figure 3.10).

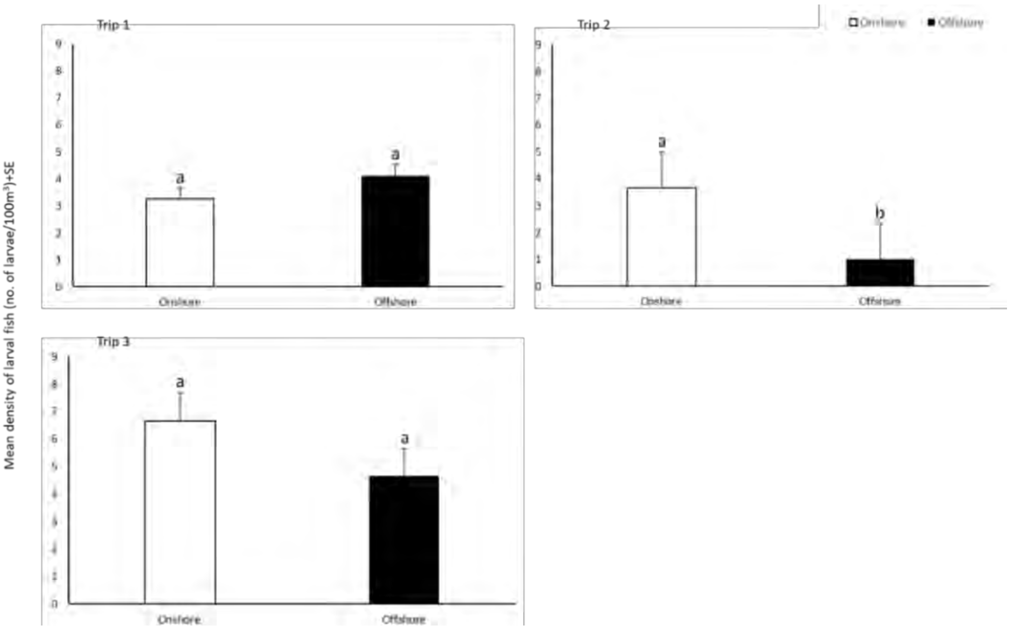


Figure 3.10: Mean total larval fish densities by distance (onshore/offshore) during Trip 1, 2 and 3 in the Algoa Bay region. Error bars indicate standard error and the letters above the bars indicate within site homogenous group identified by 'Trip X Distance' pairwise results.

The findings highlighted by the results of the Welch's ANOVA were confirmed by the NMDS plots (Figures 3.11 and 3.12). The results of the ANOSIM analysis also confirmed a significant effect of depth (Table 3.2).

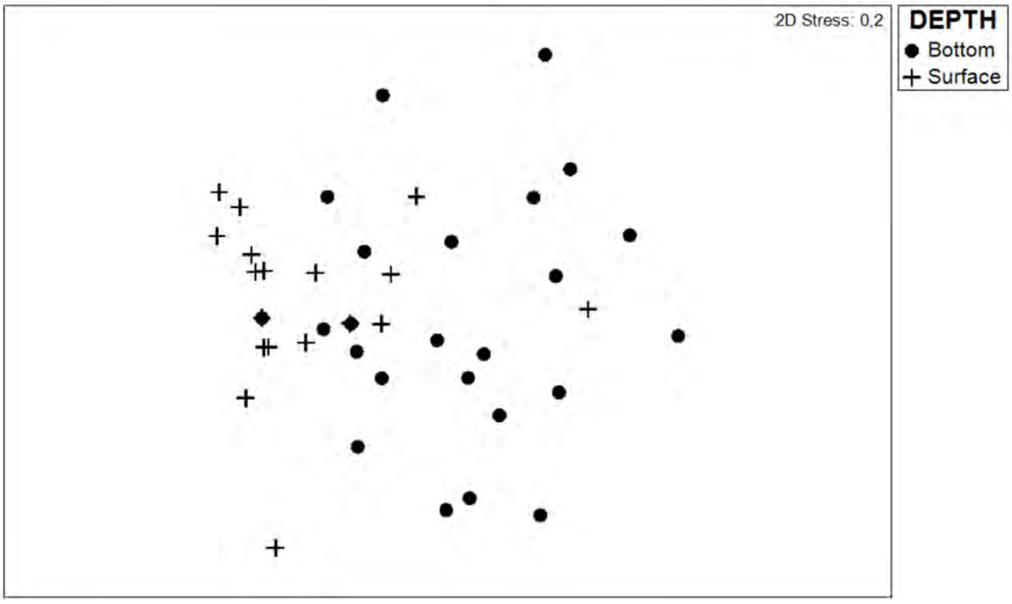


Figure 3.11: Non-parametric multidimensional scaling (NMDS) plot of Bray-Curtis distances in 2D of all larval fish samples at the two different depths in the coastal nearshore of the Algoa Bay region.

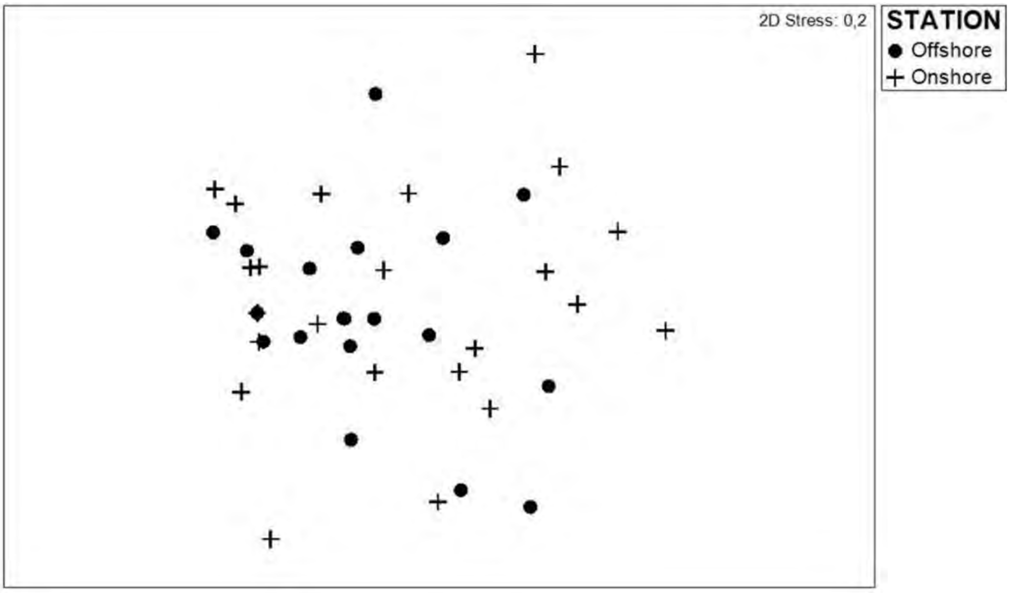


Figure 3.12: Non-parametric multidimensional scaling (NMDS) plot of Bray-Curtis distances in 2D of all larval fish samples at the two different distances in the coastal nearshore of the Algoa Bay region.

Table 3.3: Results of the three-Way ANOSIM for larval fish density between depth (surface/bottom), distance (onshore/offshore) and among trips (1, 2 and 3) in the coastal nearshore of the Algoa Bay region. The analysis produces an R statistic ranging from 0 to 1. An R-value of 1 means there are dissimilarities between groups while R-value of 0 means an even distribution. P-values in bold are significant.

Groups	R-value	P-value
Depth	0.28	**0.01**
Distance	0.05	4.40
Trip	0.05	1.20

The results of the SIMPER for the factor depth showed that *C. dentex*, *P. pilicornis* and *H. capensis* were more abundant at the bottom than the surface of the water column (Table 3.4). In addition, the results of the SIMPER on the factor distance (although not significant) showed that *Chorisochismus dentex* were more abundant in the offshore, with Clinidae sp. 1 and *Parablennius pilicornis* in the onshore (Table 3.5).

Table 3.4: SIMPER results for the percentage contribution of species to dissimilarity of depth (surface/bottom) in the coastal nearshore in the Algoa Bay region during all trips combined. Av.Abund.= Average abundance of species, Av.Diss.= Average dissimilarity of species, Contrib.%= contribution percentage of each species and Cum.%= cumulative contribution of each species. The cut off for including species in the table was 5% contribution.

Species	Av.Abund. bottom	Av.Abund. surface	Av.Diss.	Contrib.%	Cum.%
Chorisochismus dentex	0.49	0.01	42.39	45.02	45.02
Parablennius pilicornis	0.08	0.01	12.54	13.32	58.34
Clinidae sp. 1	0.05	0.01	4.88	5.19	63.53

Table 3.5: SIMPER results for the percentage contribution of species to dissimilarity of distance (onshore/offshore) in the coastal nearshore in the Algoa Bay region during all trips combined. Av.Abund.= Average abundance of species, Av.Diss.= Average dissimilarity of species, Contrib.%= contribution percentage of each species and Cum.%= cumulative contribution of each species. The cut off for including species in the table was 5% contribution.

Species	Av.Abund. offshore	Av.Abund. Onshore	Av.Diss.	Contrib.%	Cum.%
Chorisochismus dentex	0.38	0.12	33.18	36.85	36.85
Clinidae sp. 1	0.04	0.06	15.31	17.00	53.86
Parablennius pilicornis	0.02	0.04	7.94	8.82	62.68

3.3.3 Environmental Variability

Principal component analysis (PCA) performed on environmental variables during Trip 1 and Trip 2 revealed strong depth (surface/bottom) variability (Figure 3.13). The eight environmental variables namely temperature, fluorescence, turbidity, pH, oxygen, salinity, wind speed and wind direction collectively explained ~80% of the variability in the environment during Trip 1 and ~75% during Trip 2. For Trip 1, two distinct grouping by depth were observed. PC 1, explained almost 50% of the total variation and was correlated with oxygen, pH and temperature, while PC 2 explained a third of the variation and was driven by pH, salinity, and turbidity (Table 3.1). During Trip 2, the distribution of larvae was also grouped by depth with PC 1 (47.7%), which was correlated with salinity, temperature and pH (Table 3.1). A clear outlier was identified at one of the depths particularily, at the bottom, at the site situated at the west outside of the Algoa Bay region during Trip 1 (Table 3.6).

a)

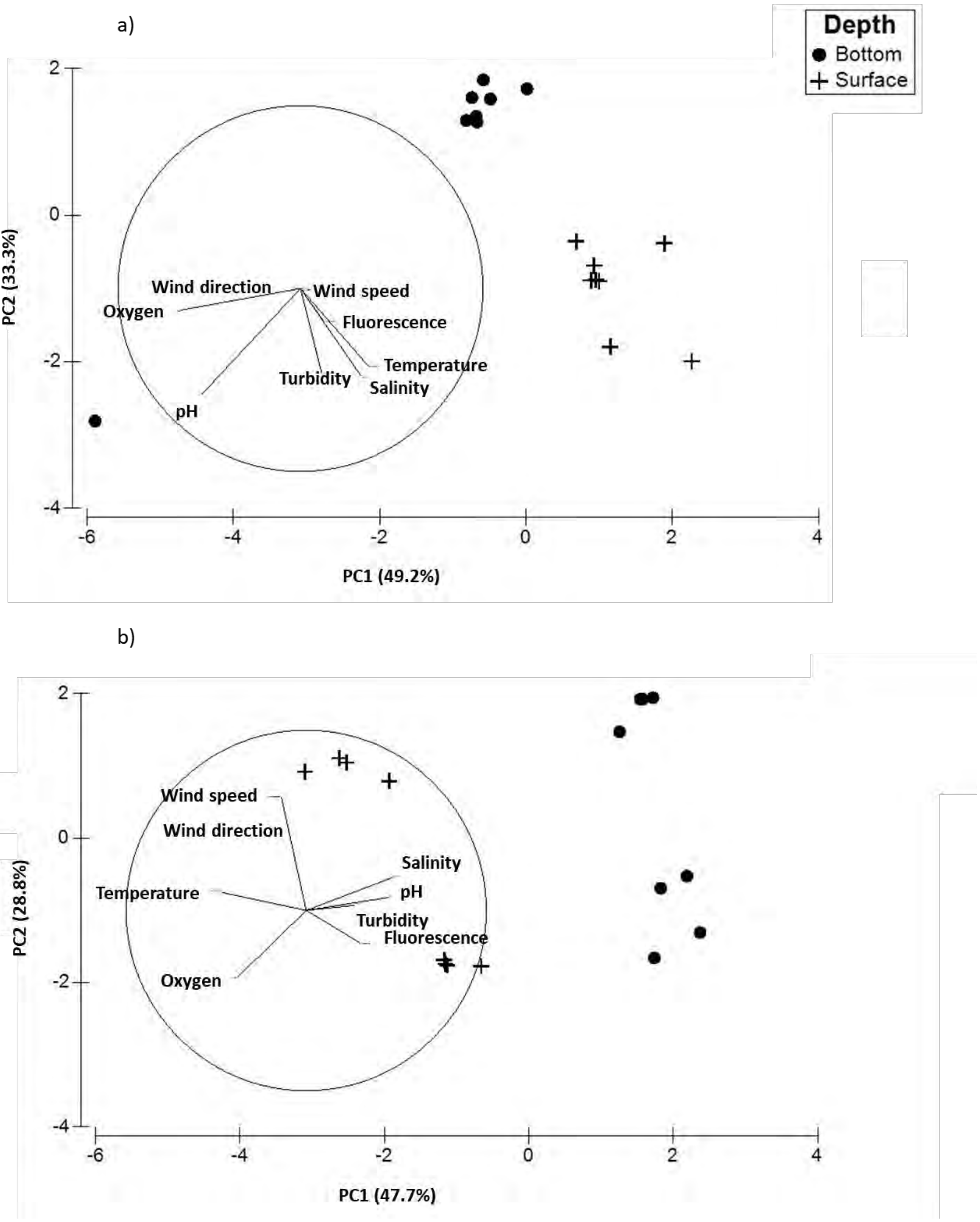


Figure 3.13: Principal component analysis conducted on the environmental variables during a) Trip 1 and b) Trip 2 in the coastal nearshore of the Algoa Bay region.

Table 3.6: Eigenvectors determined from PCA for each environmental variable in the coastal nearshore of the Algoa Bay region during Trip 1 and Trip 2.

Variable	**Trip 1**		**Trip 2**	
	PC1(49.2%)	PC2 (33.3%)	PC1 (47.7%)	PC2 (28.8%)
Temperature	-0.37	0.42	-0.47	-0.09
Fluorescence	0.12	0.18	0.29	-0.18
Turbidity	0.12	0.46	0.27	-0.03
pH	-0.54	0.58	0.46	0.07
Salinity	0.33	0.48	0.48	-0.18
Oxygen	-0.65	0.12	-0.40	0.37
Wind speed	0.01	0.20	0.14	0.62
Wind direction	0.01	-0.20	0.14	0.62

3.3.4 Wind Variability

The results of the Rayleigh test for potential differences in flow of currents alongshore and cross-shore for Trip 1 indicated that current speed and direction in both the onshore/offshore for all sites (baring Bay and Schoenmakerskop offshore) were not uniformly distributed (Table 2.3). The circular linear correlation tests to assess the differences in currents flow provided significant results for all the sites (except for Kini Bay onshore) indicating that current speed and direction were strongly correlated (Table 2.4).

The results of the Rayleigh test to assess the differences in the distribution of winds two days prior to sampling and on the day of sampling and on the day of sampling for all the three trips indicated that wind speed and direction were not uniformly distributed (Table 3.7 and 3.9). The circular linear correlation tests to assess the distribution of winds provided significant results for two days prior to sampling and on the day of sampling for all the three trips, indicating that wind speed and direction were strongly correlated (Table 3.8 and 3.10).

The winds were stronger two days preceding sampling for Trip 1 and Trip 3, and winds were weaker a day before sampling for Trip 2 (Figure 3.14 and 3.15).

Table 3.7 Results of the Rayleigh test between wind speed and direction for two days prior to Trip 1 (11th November), b) one day prior to (12th November) and c) on the day of sampling for Trip 1 (13th November) and d) Trip 2 (14th November) in the Algoa Bay region. P-values in bold are significant.

One Sample Tests	**10-Nov**	**11-Nov**	**12-Nov**	**13-Nov**	**14-Nov**
Rayleigh Test (Z)	4.828	22.645	23.559	22.575	16.689
Rayleigh Test (p)	0.007	8.02E-10	4.03E-10	8.45E-10	4.21E-08

Table 3.8: Results of the circular linear correlation between wind speed and direction for two days prior to Trip 1 (11th November), b) one day prior to (12th November) and c) on the day of sampling for Trip 1 (13th November) and d) Trip 2 (14th November) in the Algoa Bay region. P-values in bold are significant.

Variables (& observations)	**r**	**p**
10 November wind direction & 10 November wind speed	0.57	8.51E-04
11 November wind direction & 11 November wind speed	0.715	7.13E-06
12 November wind direction & 12 November wind speed	0.484	0.007
13 November wind direction & 13 November wind speed	0.571	8.21E-04
14 November wind direction & 14 November wind speed	0.542	0.002

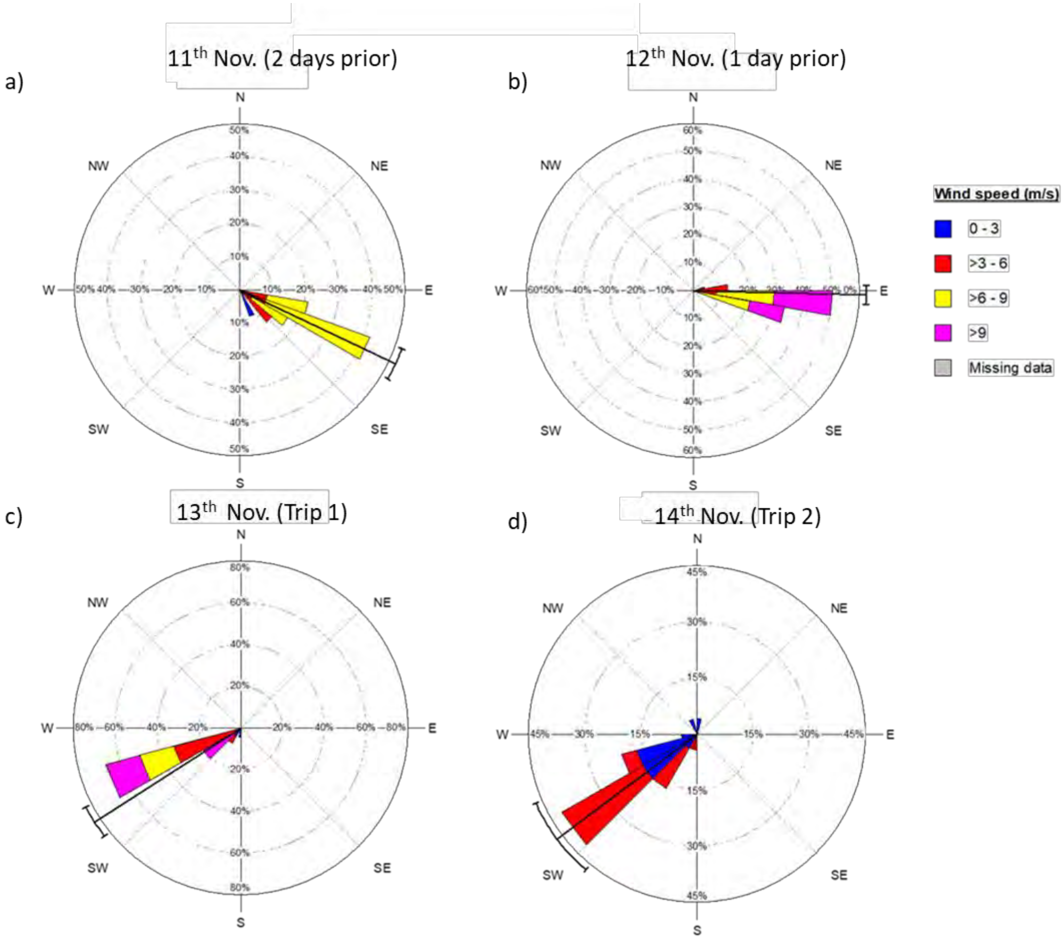


Figure 3.14: Wind roses showing variability in wind speed and direction for a) two days prior to Trip 1 (11th November), b) one day prior to (12th November) and c) on the day of sampling for Trip 1 (13th November) and d) Trip 2 (14th November). The colour of the bands indicates the range of wind speed (cm/s). The length of the vector spokes shows how consistent the mean direction is. The black long curved line indicates the average wind direction; the arch on the outside of the circles shows the variability in wind direction.

Table 3.9: Results of the Rayleigh Test between wind speed and direction for two days prior to sampling for Trip 3 (18th November), one day prior to (19th November) and on the day of sampling (Trip 3; 20th November 2019).

One Sample Tests	**17-Nov**	**18-Nov**	**19-Nov**	**20-Nov**
Rayleigh Test (Z)	22.14	3.75	19.781	23.181
Rayleigh Test (p)	1.17E-09	0.022	6.17E-09	5.37E-10

Table 3.10: Results of the circular linear correlation between wind speed and direction for for two days prior to sampling for Trip 3 (18th November), one day prior (19th November) and on the day of sampling (Trip 3; 20th November 2019)

Variables (& observations)	**R**	**P-value**
17 November wind direction & wind speed	0.465	0.01
18 November wind direction & wind speed	0.703	1.15E-05
19 November wind direction & wind speed	0.647	8.56E-05
20 November wind direction & wind speed	0.451	0.013

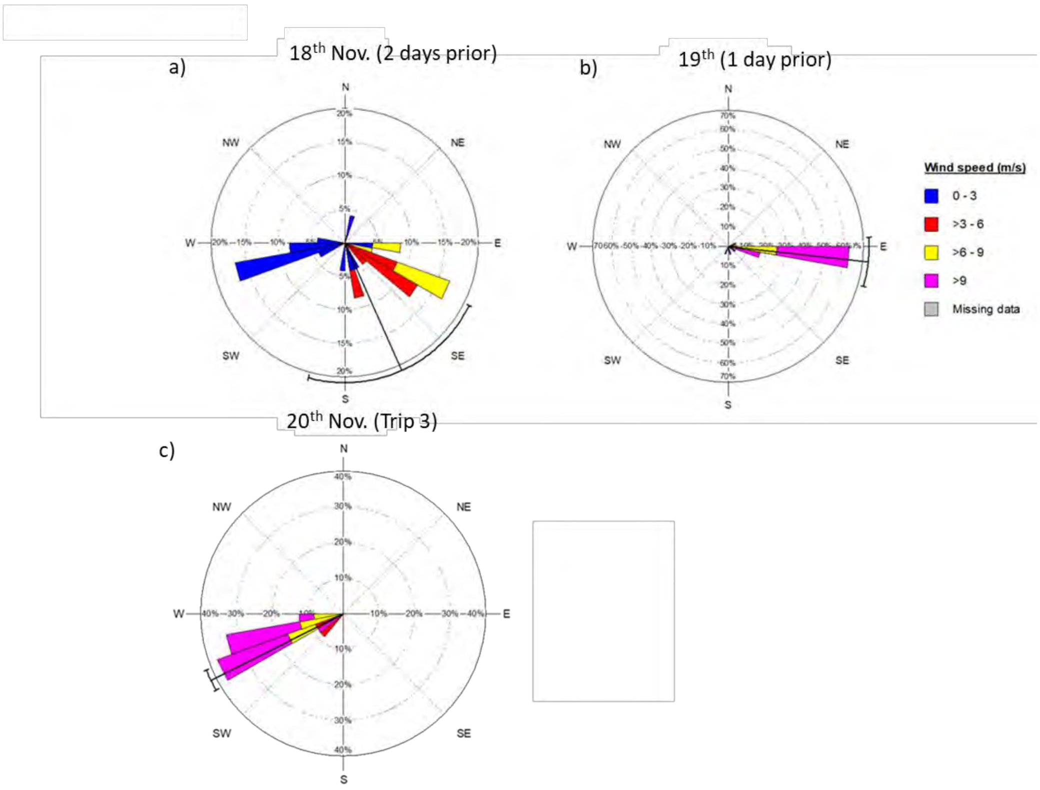


Figure 3.15: Wind roses showing variability in wind speed and direction for a) two days prior to sampling for Trip 3 (18th November), b) one day prior to (19th November) and c) on the day of sampling (Trip 3; 20th November 2019). The colour of the bands indicates the range of wind speed (cm/s). The length of the vector spokes shows how consistent the mean direction is. The black long curved line indicates the average wind direction; the arch on the outside of the circles shows the variability in wind direction.

3.3.5 Wind-derived upwelling

Wind forcing was relatively weak during the present study, with maximum wind speeds not exceeding 14 m/s and Ekman transport between 600 - 800 $m^3 km^{-1} s^{-1}$ while water height was between 1.6 – 1.8 m (Figure 3.16. The zonal Ekman transport of during Trip 1 and Trip 3 was >800 $m^3 km^{-1} s^{-1}$, suggesting that upwelling recorded during these trips could have affected the larval fish community, however downwelling was more prevalent than upwelling (Table 3.11).

Table 3.11: Zonal Ekman transport (minimum/maximum) and its strength (weak/strong) in the coastal nearshore two days prior sampling for Trip 1, Trip 2 and Trip 3 in the western sector of the Algoa Bay region.

Trips	**Minimum Ekman transport ($m^3 km^{-1} s^{-1}$)**	**Maximum Ekman transport ($m^3 km^{-1} s^{-1}$)**	**Strength relative to larval fish control (weak/strong)(Kassi *et al.*, 2018)**
Trip 1	-1752.19	862.10	Strong
Trip 2	-1752.19	610.95	Weak
Trip 3	-1914.44	893.99	Strong

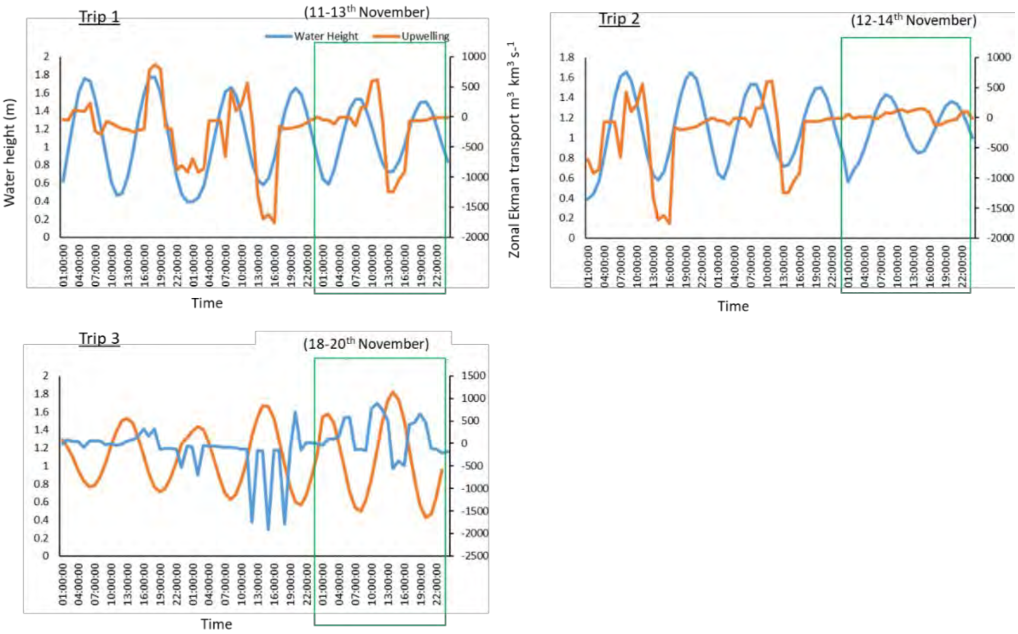


Figure 3.16: Time series of zonal Ekman transport (blue lines) and water height (orange lines) for Trip 1, Trip 2 and Trip 3. For lines (blue/orange), positive values signify upwelling, negative values signify downwelling. Green rectangles indicate the days in which the coastal nearshore was sampled.

3.5.6 Relationship between Environmental Parameters and Larval Fish

In the Algoa Bay region, the fitted model visualised by the dbRDA explained ~44.9% of the total larval fish community during Trip 1 and Trip 2 combined (Figure 3.17). The results of the BIOENV analysis indicated that the environmental variables that were best correlated with observed patterns of the larval fish community during the two trips included temperature, fluorescence and salinity. A clear outlier was identified at at the bottom at the site situated at the west outside of Algoa Bay (Figure 3.17).

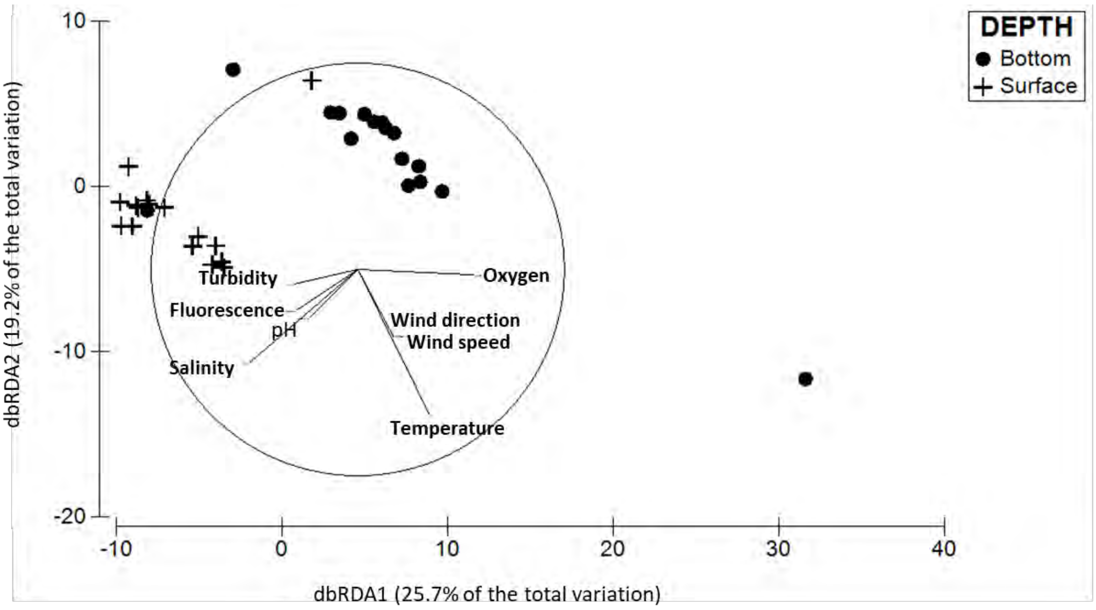


Figure 3.17: Distance based redundancy analysis (dbRDA) shows the relationship between the larval fish community and environmental parameters in the coastal nearshore of the Algoa Bay region during Trip 1 and Trip 2 combined.

Table 3.12: Results of the BIOENV correlation analysis in the coastal nearshores of the Algoa Bay region showing the best combination of environmental variables associated with the highest corrrelation between larval fish community and environmental variables and environmental data matrices in the Algoa Bay region. Spearman's rank correlation for the best correlation model is shown in bold. Correlation values correspond to Spearman's rank correlation coefficient (p).

No. of Variances	**Correlation**	**Selections**
3	0.328	Temperature; Fluorescence; Salinity
2	0.302	pH; Wind speed
3	0.302	pH; Salinity; Wind direction
1	0.299	Turbidity
3	0.291	Turbidity; Salinity; Oxygen
4	0.279	Turbidity; Salinity; Oxygen; Wind speed
4	0.279	Turbidity; Salinity; Oxygen
2	0.267	pH; Oxygen
3	0.267	Salinity; Oxygen; Wind speed
3	0.267	Salinity; Oxygen ;Wind direction

Discussion

In the Algoa Bay region, after both easterly and westerly wind events, the dynamics of larval fishes differed between depths and, less so, with distance from the shore. A higher density of fish larvae were generally observed at the bottom of the water column. Despite this clear cut trend, there were some additional noticeable influences, with more larvae being collected at the bottom at the two sites inside (leeward) of the Bay than outside (windward). Generally, nearshore larval fish distribution is known to be restricted to the bottom of the water column during the day (the time when all sampling was carried out in the present study), due to predator avoidance, as sunlight penetration at the surface of the water column makes larvae more visible to predators (Fortier and Harris, 1989; Olla and Davis, 1990; Leis, 1991a; Bolhert *et al.*, 1992). The presence of fish larvae at the bottom of the water column may also be attributed to bottom currents being slower than surface currents therefore making the coastal floor more suitable for larval accumulation (Leis, 1991b; Bolhert *et al.*, 1992; Cowen and Castro, 1994). Some larvae remain at the surface during the day, especially during the very early stages of larval development (preflexion), drifting passively in the pelagic environment until they start developing fins and are able to swim against surface currents (Morgan *et al.*, 2009).

Coastal species, including the gobiesocid, *Chorisochismus dentex*, a blenniid, *Parablennius pilicornis*, and a soleid *Heteromycteris capensis* were more abundant at the bottom of the water column during this study. In addition, *C. dentex* was the most dominant species during all three trips. This species was followed, in terms of abundance, by Clinidae sp. 1 during Trip 1, and *P. pilicornis*, for both Trip 2 and 3. The larvae of Gobiesocidae species spend most of their pelagic phase at the bottom of the water column until they are ready to settle in nursery habitats (Brothers *et al.*, 1983; Scheltema, 1986; Sponaugle and Cowen, 1996). Even at the early larval stage, these species have specialised ventral sucking disks that enable them to stick onto rocky substrates resisting being dispersed by fast moving currents (Allen, 1984). Clinidae and Blenniidae larvae recorded in the present study were mostly at the postflexion stage of development, suggesting that at this late stage development of larvae from these families were able to swim and move vertically (up and down) in the water column and select favourable bottom currents for retention (Stobutzki and Bellwood, 1994; Fisher *et al.*, 2000; Clark *et al.,* 2005; Fisher, 2005; Pattrick and Strydom, 2009).

Other fish families, which were most abundant during all trips combined, included Gobiidae and Soleidae. All dominant fish families recorded in the present study also generally prevail in the eastern and western sectors of the coastal neashore of Algoa Bay (Beckely, 1986; Pattrick and Strydom, 2008) and in the Tsitsikamma Nature Reserve, located 150 km west of Algoa Bay (Tinley and Buxton, 1994). Similar trends in the most dominant families in the present study are also observed in the warm temperate Mediterranean (Beldade *et al.*, 2006) and New Zealand (Kingsford and Choat, 1989), as well as the tropical waters of Hawaii (Leis and Miller, 1976) and Australia (Gray, 1993) with however family ranks differing among regions.

All developmental stages of the Soleidae, *Heteromycteris capensis*, were found in the inside of the Bay (leeward) of both headlands. Pattrick and Strydom (2008) recorded highest densities of *H. capensis* in spring in the Algoa Bay region, with this species represented by all developmental stages, suggesting that Algoa Bay could serve as a nursery area for the larvae of this species, particularly during spring. My results confirm these authors' hypothesis suggesting that grow out (which is the complete development of larval stage) of this particular species is occurring in specific areas of Algoa Bay. For the Clinidae fish family, only flexion and postflexion larvae were recorded and mostly outside of the Bay (windward) at both the headlands (Cape Recife and Cape Padrone). Clinids spawn both in estuaries and in the coastal nearshore and are known to be brooders, keeping their larvae internally until the flexion stage

(Day *et al*., 1981). The numbers of Clinidae larvae recorded in the present study were higher than those recorded in Algoa Bay by Beckely (1989) and Pattrick and Strydom, (2008), suggesting that these species could have a preference for headlands in the Algoa Bay region, outside of the Bay itself. The larval densities of sparids were substantially lower than previously recorded in this region, possibly because the spawning season of Sparidae appears to be towards mid-summer and winter, with larvae most abundant during winter in Algoa Bay (Pattrick and Strydom, 2008). Coastal species which produce benthic eggs such as species of the Gobiidae family are diverse in South African waters (Heemstra and Heemstra, 2004). *Caffrogobius gilchristi* had lower densities in this study than previously recorded in the same region (Pattrick and Strydom, 2008). These species are known to be flushed into the coastal nearshore from nearby estuaries during the ebb tide (Heemstra and Heemstra, 2004; Beckley, 1985; Strydom and Wooldridge, 2005; Pattrick and Strydom, 2014a). This may therefore suggest that preflexion larvae of this species are observed closer to the entrance of estuaries, with older larvae having a much broader distribution.

The winds were strongest the day before sampling for both Trip 1 and Trip 3, with winds blowing at an average speed of 7.8 m/s and 8.4 m/s in an east direction. During Trip 2, the average wind speed was only 4.7 m/s in a south west direction. The highest densities of larval fish were recorded during Trip 3 (206 larvae), followed by Trip 1 (185 larvae) then Trip 2 (131 larvae). The zonal Ekman transport was strongest during Trip 1 and Trip 3 during the present study, suggesting that physical conditions (upwelling events) prior the two trips were optimal for larval fish dispersal (Kassi *et al*., 2018). This is evident as the highest densities of fish larvae were recorded when upwelling was persistent for at least two days before sampling and on the day of sampling. Larvae at a postflexion stage of development dominated the catches in the present study especially during Trip 2, suggesting that larvae were able to control their position in the water column due to the improved swimming capabilities of late stage larvae which could counteract the current strength at the surface (Cowen & Castro, 1994; Paris & Cowen, 2004), or, like it seems, avoided the surface currents and swam to the bottom.

The most important environmental variables affecting larval fish assemblages were temperature, fluorescence and salinity in the coastal nearshore of the Algoa Bay region. Fluorescence and salinity were generally higher in the onshore during Trip 1 than Trip 2, particularily at the surface of the water column while temperature was higher offshore at the surface than onshore (Appendix B and C). During upwelling, cold, nutrient rich and more saline waters are brought to the surface, where they get direct heat from the sun (Shannon *et al.*, 1984; Thomposon and Bonham, 2011; Beckley *et al.*, 2019), enhanced chlorophyll-*a* which is a proxy for productivity, is fuelled by higher availability of nutrients in the upper layers of the water colum (Cushing, 1971; Wieters *et al.,* 2003). In addition, these conditions are generally followed by a succession of zooplankton and copepod nauplii, a favourable food source for many larval fishes (Brodeur and Rugen, 1994; Kendall and Matarese, 1987), although this was not tested in the current study. Larval fish were generally caught at close to the seabedduring this study, with late stages dominating the catches, suggesting the early stages of larvae could have been transported offshore in the Ekman layer by upwelling. A high probability of survival and growth of larval fish is however, observed in environments where there is availability of appropriate food, especially during and after upwelling and relaxation events (Cushing, 1971). Perhaps, the late stages of larvae were found at the bottom of the water column because they are not as closely affected by the most influential environmental parameters (temperature, turbidity, salinity, pH, fluorescence, wind speed and direction) measured during this study as the early stages may be more physiologically vulnerable to these parameters (Preston, 1985; Zacharia and Kakati, 2004; Anger, 2003; Crisp, 2017). Given the time of sampling, daylight risk of being predated could have caused late stages of larvae to preferentially remainat the bottom during upwelling (Fortier and Harris, 1989; Olla and Davis, 1990; Leis, 1991a; Bolhert *et al*., 1992). Jury (2019) recorded higher fluorescence around the capes at St Francis Bay, which is situated just 80 km south of Algoa Bay and associated this with shelf edge upwelling, further suggesting that environmental variables such as temperature, fluorescence and salinity are important in areas prone to easterly-driven upwelling, as indicative of upwelling events (Pizarro, 2014; Ismail *et al*., 2015).

During both Trip 2 and 3, higher densities of fish larvae were recorded in the onshore than the offshore. A decrease in the density of fish larvae with increasing distance from the shore is common in the coastal nearshore around the globe (Borges *et al*., 2007; Pattrick and Strydom, 2008; Salinas-de-Leon *et al*., 2012), although this tendency was not pervasive during this study. Generally, larvae of many nearshore species remain in the onshore, where across-shore and along-shore currents tend to be reduced (Largier, 1993; Roughan *et al*., 2006).

More fish larvae were recorded offshore, particularily at the bottom of the water column during Trip 1 (Appendix E). Preflexion larvae dominated the catches during Trip 1, while for the other two trips postflexion larvae dominated. During downwelling, which was more prevalent than upwelling in this study, currents flow shoreward at the surface layers of the water column and seaward at the bottom (Shanks and Brinks, 2005; Ben-Tzivi, 2007). Thus, preflexion larvae in this study may have been unable to swim against vertical currents resulting in them sinking with surface waters moving towards the bottom during downwelling slightly prevailing offshore (during Trip 1). The older larvae inhabiting the deep strata of the water column may be able to return onshore after downwelling because they have better swimming abilities than early stages (Stobutzki and Bellwood, 1994; Shanks and Brinks, 2005; Stanley *et al*., 2012) (especially during Trips 2 and 3). Even though fish larvae are advected offshore at the surface during upwelling, larvae of some species remain in the onshore throughout their lives, just below the Ekman layer (Largier *et al.,* 1993; Roughan *et al.,* 2006). When upwelling relaxes or reverses, larvae become concentrated on the lee side of the headlands hence larvae were generally caught within the Bay in the present study where alongshore and crosshore flow is reduced (Farrell *et al*., 1991; Roughgarden *et al*., 1992; Morgan *et al*., 2009; Morgan *et al*., 2012) which accounts for larvae generally being caught within the Bay in the present study.

This study presents for the first time, the influence of prevailing winds on the larval fish community in the Algoa Bay region. Larval fish assemblages varied according to depth (bottom prevalence) and distance from the shore (although not pervasive as contrasting/different patterns were observed in each trip), with larvae inhabiting the bottom layers of the water column in the coastal nearshore of the capes/headlands. The distribution of larvae around the headlands in Algoa Bay was largely infuenced by direction of prevailing winds, with easterly component winds responsible for upwelling, while downwelling was driven mainly by westerly winds. Oceanographic features such as upwelling were most likely responsible for the variability of environmental conditions (particularily temperature, fluorescence and salinity) in the Algoa Bay region which in turn further contributed to the depth effect of fish larvae.

CHAPTER IV

SYNTHESIS

The results of this study highlight important environmental links to larval fish composition and distribution in the coastal nearshore of the Algoa Bay region, hence filling up some of the gaps of knowledge for this important, dynamic and diverse coastal region. This study has also helped in identifying possible spatial hotspots for larval fish assemblages, driven by physical factors such as currents and upwelling events. Wind speed and direction were the main oceanographic features driving larval assemblages, especially through upwelling/downwelling, which differed in space and time. Larvae exhibited different vertical and horizontal distributions depending on ontogenetic stages of development in relation to local oceanography. The spawning mode of adults and the types of eggs produced were also relevant for the vertical (depth) and horizontal (cross-shore) distribution patterns of larvae in the coastal nearshore of the region. The planktonic larval stage is vulnerable to the oceanic forcing because larvae can spend several days/months in the pelagic environment before reaching the settlement stage (Brothers *et al.*, 1983; Scheltema, 1986; Sponaugle and Cowen, 1996). This lengthy permanence in the physical environment makes larval growth and development highly dependent on the water masses they are found in, making the bio-physical understanding of stage dynamics essential for connectivity studies (Largier, 2003; Shanks *et al.*, 2003; Hastings and Botsford 1999, Palumbi 2001; Selkoe *et al.*, 2016).

Larval density was generally higher in the onshore than offshore, with this pattern varying in time and space for some species. The larvae of pelagic species producing pelagic eggs (PPE), such as Engraulidae and Clupeidae, as well as coastal species with pelagic eggs (CPE) including Cynoglossidae and Sparidae, occurred in higher densities in the offshore, while the onshore was dominated by the larvae of coastal species with benthic eggs (CBE) and these included Blenniidae and Gobiesocidae. Several factors such as hydrodynamics, egg type, ontogenetic stages and size of larvae seem to affected the distribution of larval fish vertically and horizontally during the present study. Abundance was not only limited to the reproductive strategies of the adult fish populations, but also often associated with oceanographic features (i.e currents, upwelling/downwelling). These oceanographic features not only relate to the transport of larvae in the coastal nearshore, but could also affect their feeding conditions and subsequent survival success (Ahlstrom and Moser, 1976).

The easterly and westerly wind components in the Algoa Bay region were highly associated with upwelling and downwelling/relaxation events. The direction and speed of winds appear to be the main driving factor of the local oceanography during this study, especially slow moving currents and upwelling/downwelling events, which were in turn responsible for the cross-shore variability of larval fish assemblages. Prevailing winds are known to influence mostly the upper layers of the water column (Roberts, 1990), and was the case in this study too, increased average speed of surface currents in the Bay were highly associated with strong winds, while light winds accompanied slower current speeds to which the advanced developmental stages of larvae mostly associated, particularly with the bottom of the water column with larvae persisting onshore. It is however known that for winds to be effective in driving oceanographic features and thereafter larval fish transport and overall larval abundance, they need to blow at considerable speeds or for several days (Kassi *et al*., 2018).

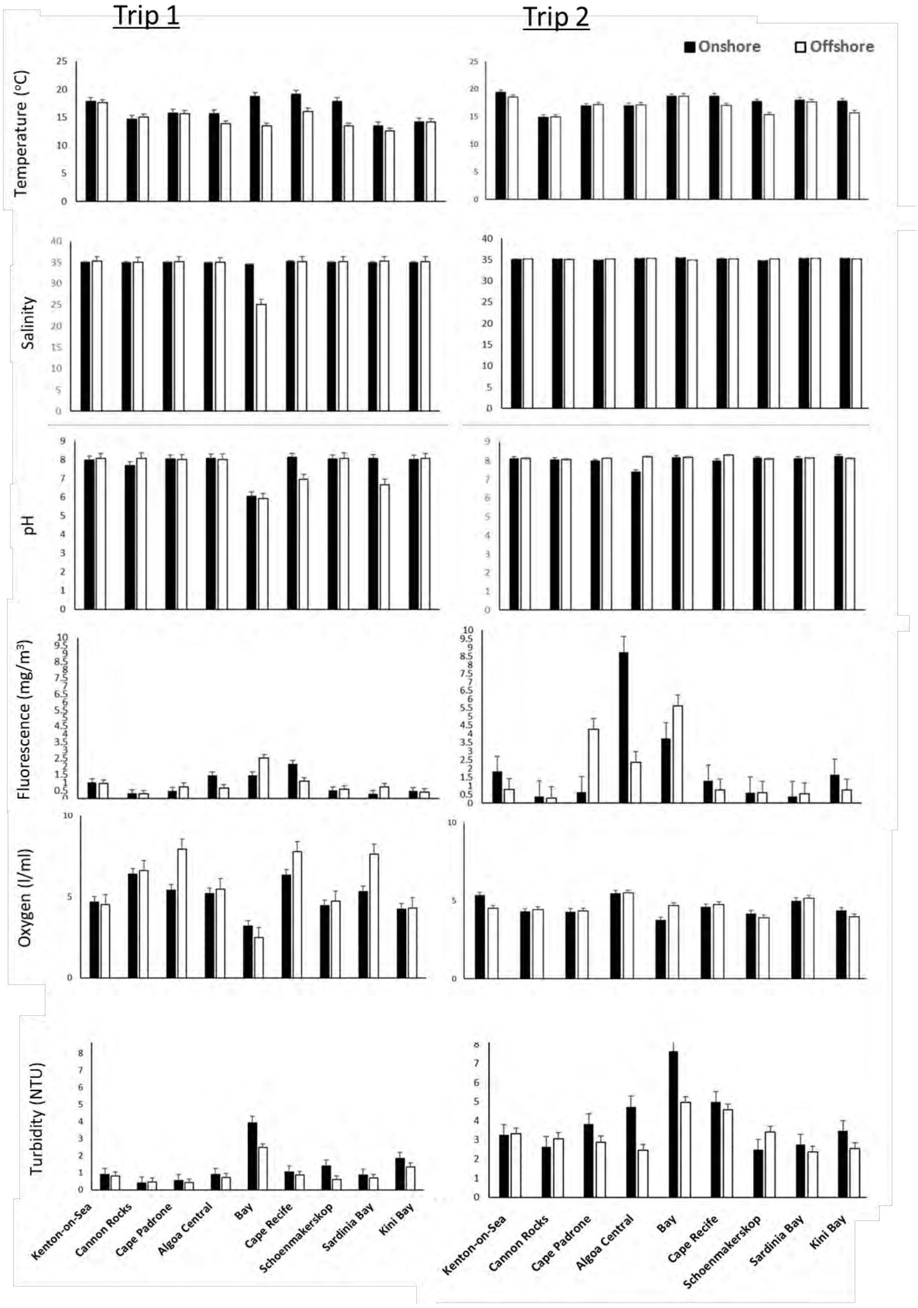
The most important environmental parameters driving the variability of larval fish assemblages in the coastal nearshore of the Algoa Bay region were temperature, fluorescence and salinity. These variables were mostly driven by oceanographic features such as upwelling. During upwelling temperature decreased drastically while salinity, oxygen and fluorescence increased, indicating arrival of newly upwelled nutrient rich water followed by production of phytoplankton and zooplankton and hence food for larvae (Morgan *et al*., 2009; Morgan, 2014; Kampf and Chapman, 2016; Kampf, 2017).

During periods of upwelling, postflexion larvae were mostly associated with the bottom of the water column where currents are known to flow towards the shore (Roberts, 2010). After upwelling events, more larvae occurred in the onshore. This suggests some degree of onshore retention, with these larvae capable of utilising the currents to move/persist onshore. In addition, the early developmental stages were recorded mostly offshore during upwelling in this study, the reason being that larvae at the preflexion stage of development are often susceptible to offshore transport due to the offshore current flow that occurs in the Ekman layer at the surface (Shanks and Brinks, 2005; Ben-Tzivi, 2007). In contrast, the opposite pattern occurred during downwelling, with surface currents flowing towards the coast and currents flowing offshore at the bottom of the water column (Shanks and Brinks, 2005; Ben-Tzivi, 2007). The influence of upwelling/downwelling on the distribution of larvae is thus very much mediated by ontogeny, with early stage larvae unable to swim against upwelling or downwelling currents, hence sinking to the bottom during downwelling and remaining at the surface during upwelling (Shanks and Brinks, 2005). Around the capes/headlands in the Algoa Bay region especially during summer, offshore transport due to upwelling is likely (Goschen and Schumann, 2010), but these areas also acts as a retentive zone during relaxation events. Larvae which are at the late stage of development appear to use the bottom currents in order to remain onshore after upwelling events. The reason for the abundance of postflexion larvae onshore could also be because there are high abundances of prey in the coastal nearshore thus favoring their growth and survival (Peterson *et al*., 1979; Grantham, 1997; Peterson, 1998; Papastephanou *et al*., 2006). Upwelling events were favourable for certain species in the Bay (i.e. species of Cynoglossidae and Soleidae). These species appear to be timing their spawning to occur during peak phytoplankton production, thus ensuring availability of enough food sources for larval fish in the coastal nearshore of the Algoa Bay region (Pattrick and Strydom, 2014 b).

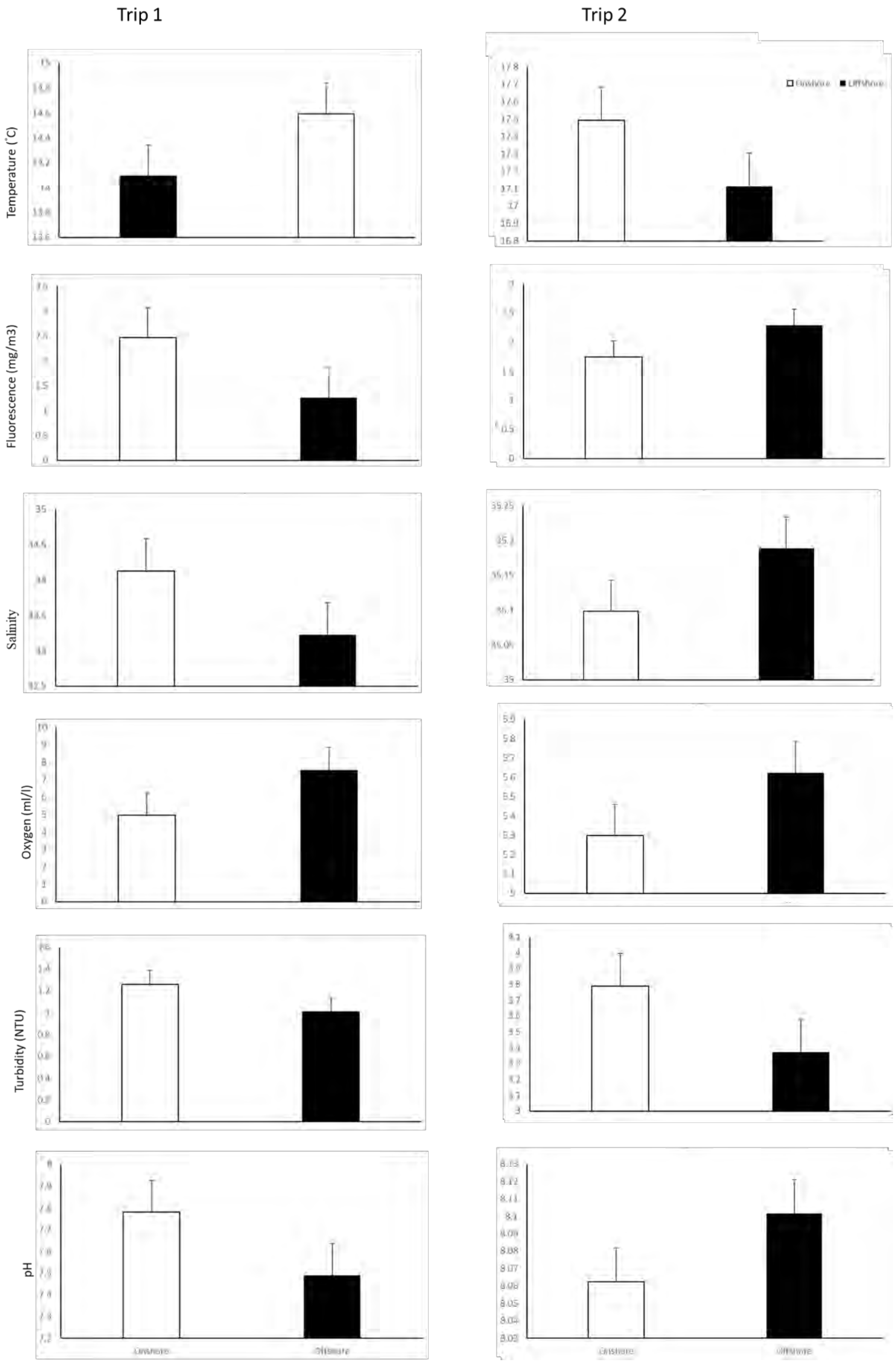
Most larvae occurred on the western edge of the Bay near Cape Recife in particular. Generally, average current speeds were faster at Cape Padrone (eastern sector) than in the western sector of the Bay (Cape Recife). The eastern headland/cape of the Bay is exposed and frequently receives warm plumes from the fast flowing Agulhas Current with net transport effects into the west which could transport incompetent larvae offshore, towards the direction in which currents flow (Schumann *et al*., 2005; Roberts, 2010; Porri *et al*., 2014; Weidberg *et al*., 2015). The western sector can nevertheless also experience reduced current speed due to greater bottom friction and reduced wind shear favoring entrainment and possibly survival of many larval fish species (Roberts, 1990). There was a high abundance of unidentified taxon from the Clinidae fish family around the two prominent capes in the Bay, suggesting that this species was able to withstand harsh hydrodynamic conditions near the capes. Factors that attributed to the observed distribution patterns at the capes include shape of the coastline, local oceanography and hydrodynamics which all play an important role in shaping larval fish communities near the headlands.

This study has shed light about the role played by hydrodynamics and environmental variables in the composition, distribution and abundance of larval fishes in the coastal nearshore of the Algoa Bay region. Mechanisms that promote larval fish retention in the coastal nearshore were quantified in this study. My work has also identified that larval fish distribution is characterised by temporal heterogeneity related to hydrodynamic and environmental factors with the importance of also assessing the behavioral capabilities of larval fish. The combination of the variability of environmental conditions such as salinity and turbidity with increasing distance from the shore caused mainly by freshwater inflow into the coastal nearshore from nearby estuaries/rivers and upwelling/downwelling events within the Bay create a dynamic environment for larval fish in the Algoa Bay region. I would suggest that for future research on larval dispersal, ADCP data be included to quantify currents as no previous published research in Algoa Bay has done this. Larval fish play a significant role in how adult fish populations are structured (Largier, 2003; Shanks *et al*., 2003; Hastings and Botsford 1999, Palumbi 2001; Selkoe *et al*., 2016) and therefore, bio-physical interactions and spatial hotspots of larval fish need to be considered/included in management plans of fisheries and marine reserves. It is therefore important to understand the degree to which environmental variables including current speed and direction influence fish larvae as this information can determine larval dispersal and their fate in the coastal nearshore.

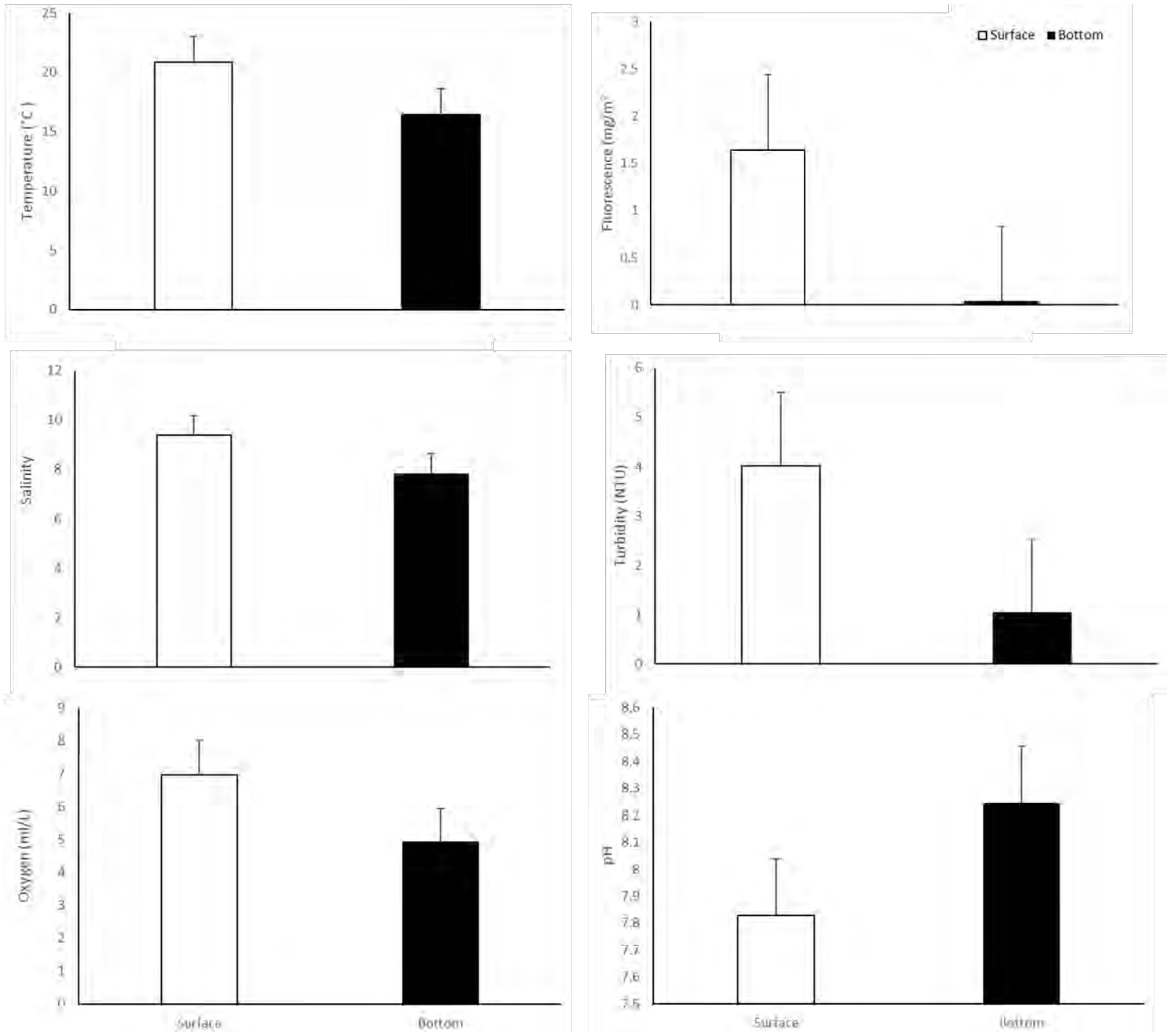
Appendices



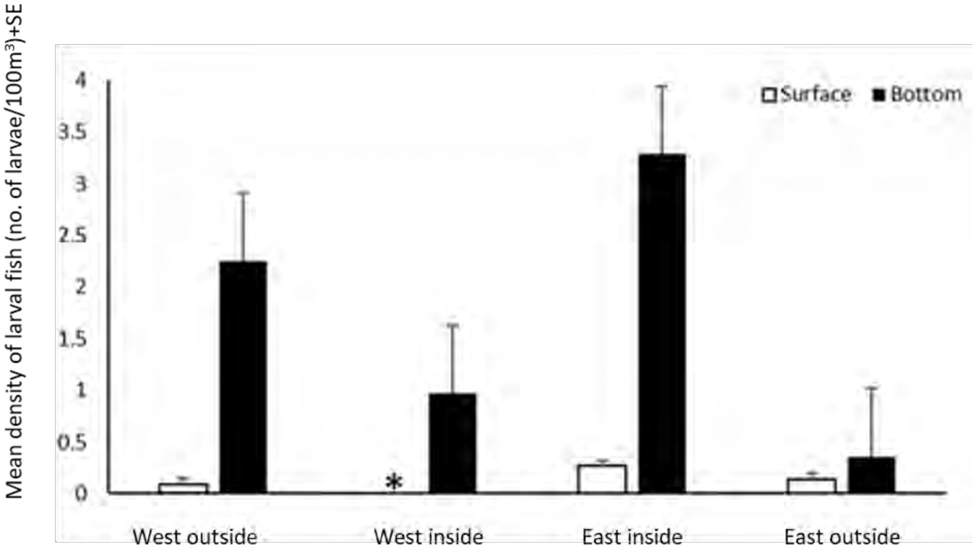
Appendix A: The onshore and offshore variability of the six environmental variables showing averages (+SE) measured at all the nine sites during both Trip 1 and Trip 2.



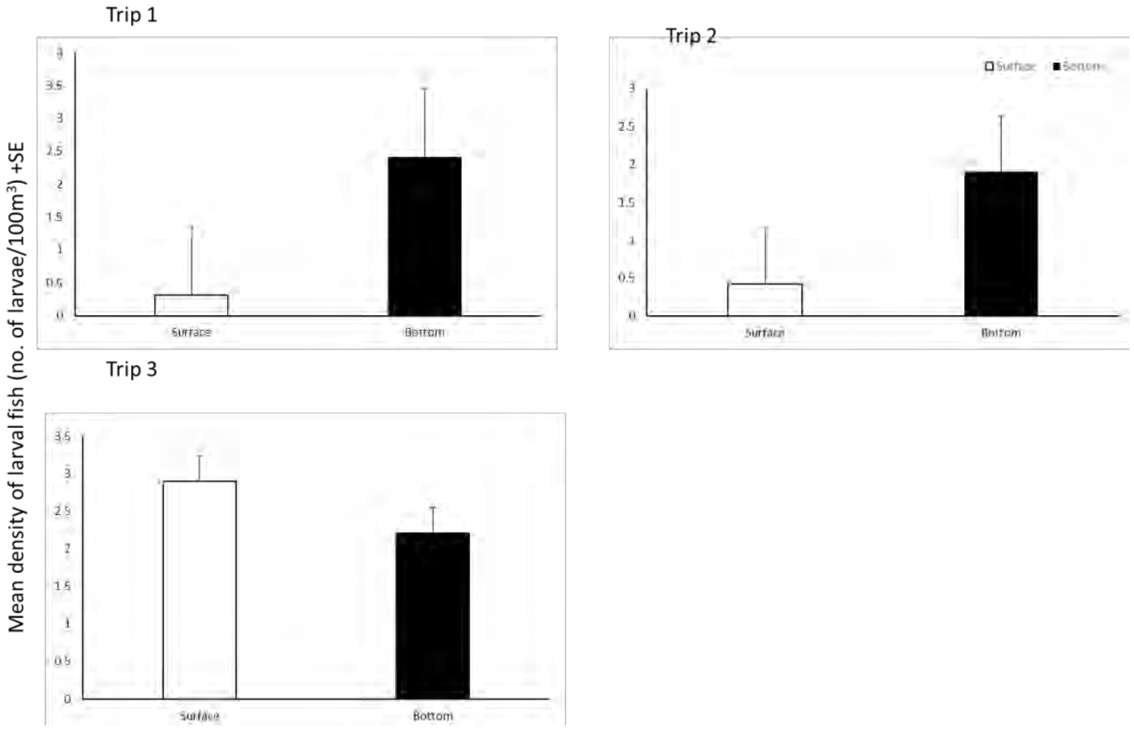
Appendix B: The onshore and offshore distribution of the six environmental variables showing averages (+SE) measured at all six sites during Trip 1 and Trip 2.



Appendix C: The surface and bottom distribution of the six environmental variables showing averages (+SE) measured at all the six sites during both Trip 1 and Trip 2 combined.



Appendix D: Mean densities for all taxa during Trip 1 for depth (surface/bottom) for East outside, East inside, West inside and West outside in the Algoa Bay region.



Appendix E**:** Mean total larval fish densities by distance (surface/bottom) during Trip 1, 2 and 3 in the Algoa Bay region. Error bars indicate standard error.

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