ENVIRONMENTAL DRIVERS OF THE COMPOSITION AND DISTRIBUTION OF LARVAL FISH ASSEMBLAGES OFF THE SOUTH COAST OF SOUTH AFRICA

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General Abstract

The species composition, distribution and patterns of vertical migration of larval fish assemblages were investigated in March and in September 2013 within two adjacent log spiral bays, Algoa Bay and St Francis Bay, on the south coast of South Africa. Fish larvae were collected by means of a boat towed bongo net (57 cm diameter; mesh aperture 500 µm). An onshore (2 km) and an offshore (3 km) station were each sampled twice during the daytime (06:00 – 18:00) with two horizontal tows: near the surface (0.5 m) and close to the bottom (12 m). Tows were repeated at night (18:00 – 23:00) for onshore sites. Larval catches included 16 fish families and 40 species. A multivariate analysis indicated that the species composition was significantly different between Algoa Bay and St Francis Bay, with Engraulidae, Blenniidae, Sparidae, Soleidae and Cynoglossidae making important contributions to the larval fish catch in Algoa Bay, while Blenniidae, Engraulidae, Tripterygiidae, Sparidae and Gobiesocidae contributed significantly in St Francis Bay. Differences in assemblage composition were noted between the Spring (September–October) and Autumn (March-April) months. The species composition of larval fish assemblages was related to wind speed, wave height, cloud cover, sea water temperature, depth, average current speed and direction. Wind speed, wave height, temperature and depth significantly contributed to the variation in larval fish densities. Abundances of larval fishes were greater offshore than onshore, larvae from pelagic eggs dominated catches offshore, while larvae from demersal eggs dominated onshore catches. Habitat structure strongly influenced the composition of larval fishes between the bays and abundances were significantly greater at night than during the day. Most larval fishes displayed a reverse diel vertical migration pattern and were most influenced by predators, wind speed and cloud cover. This study shows that larval fish assemblages are highly complex and patchy. Spawning mode, individual species behaviour, diel vertical migration, current structure, depth, temperature, wind speed, cloud cover and type of habitat substratum all influence larval fish composition and distribution in the nearshore waters of South Africa.

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In dedication to my father

Eduardo Trassierra Ferrarons

The one person I wish could read this

You are forever in my heart dad.

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Declaration

I hereby declare that the following thesis has not been submitted to a university other than Rhodes University, Grahamstown, South Africa. The work presented here is that of my own.

Jaqueline Anne Trassierra

Chapter 1

General Introduction

The biology of adult fishes cannot be fully understood without the knowledge of the early life history of their larvae. Larval fishes are morphologically different from conspecific adults and often difficult to identify morphologically, sometimes being classed into the wrong taxon (Matsumoto, 1958; Leis, 1991a; Leis *et al.*, 2002; Weigt *et al.*, 2012). Larval fishes occupy different habitats to their adults (King, 2004; Lecchini *et al.*, 2005; Bakun, 2006), feed differently (Houde & Schekter, 1980; Hunter, 1981; Govoni *et al.*, 1986) and display different patterns of behaviour (Huntingford, 1986). The investigation of larval fish dynamics can improve our understanding of adult fish populations, allowing us to assess and manage future adult fish stocks (Runnström, 1941; Williams & Hart, 1974; Shepherd & Cushing, 1980; Hewitt, 1981).

Distributions of larval fishes are, however, patchy (Richardson & Pearcy, 1977; Jenkins, 1986; Vélez *et al.*, 2005; Pattrick *et al.*, 2013). Spawning modes (Leis & Miller, 1976; Sanvicente-Añorve *et al.*, 1998; Kent *et al.*, 2013), habitat (Jenkins *et al.*, 1997; Pattrick & Strydom, 2017), diel vertical migration (Leis, 1991b; Pearre, 2003) and environmental features such as currents, temperature, salinity, wind and turbidity can all drive the distribution of larval fishes (Leis, 1991a). Survival through the larval phase into adulthood is however vital for future adult fish populations and understanding their distribution can provide more insight into their survival.

The larval stage of most marine fishes is pelagic and may last from several days to months (Leis, 2010). It is during this early life history stage of marine fishes that they are most vulnerable to mortality (Hjort, 1914). Starvation, predation and extensive offshore transport by currents are three of the most critical factors leading to larval fish mortality (Hjort, 1914; Hunter, 1976, 1981; McGurk, 1989). During their pelagic stage, larval fishes require a suitable habitat for survival while they develop into juveniles. Many coastal regions, such as embayments (Watson, 1974; Richardson & Pearcy, 1977; Yamashita & Aoyama, 1984; Olney & Boehlert, 1988; Graham & Largier, 1997; Jenkins *et al.*, 1997; Powell, 2002; Vélez *et al.*, 2005; Allain *et al.*, 2007), lagoons (Leis, 1986, 1991b; Thorrold, 1990; Abecasis & Erzini, 2008; Aceves-Medina *et al.*, 2008), coral atolls (Boehlert *et al.*, 1992; Leis, 1993; Cowen &

Castro, 1994) and shelf waters (Young *et al.*, 1986; Sabatés & Masó, 1990; Munk *et al.*, 1999) have high productivity of phytoplankton and zooplankton, providing a stable source of food for larval fishes. These environments are characterised by oceanographic features such as eddies (Lobel & Robinson, 1986; Nakata *et al.*, 2000; Okazaki *et al.*, 2002), fronts (Pingree *et al.*, 1974; Shanks, 1983; Kingsford *et al.*, 1991; Munk *et al.*, 1999) and onshore currents (Cowen & Castro, 1994; Porch, 1998) which prevent larvae from being transported extensive distances from their natal habitats.

Larval fishes, however can be dispersed by ocean currents up to great distances from the shore (Richardson & Pearcy, 1977; Muhling *et al.*, 2007; Shanks, 2009). In order to avoid offshore advection, pelagic larval fishes will often make use of oceanographic features such as eddies, as a means of retention and food supply (Lobel & Robinson, 1986; Nakata *et al.*, 2000; Logerwell *et al.*, 2001; Nishimoto & Washburn, 2002; Bakun, 2006). By using olfactory cues (Kingsford *et al.*, 2002; Gerlach *et al.*, 2007), larvae of coral reef fishes are able to find and swim back to their natal reefs (Taylor & Hellberg, 2003; Paris & Cowen, 2004). Larval fishes will also make use of favourable ocean currents flowing shore wards to avoid offshore advection (Cowen & Castro, 1994; Paris & Cowen, 2004; Kent *et al.*, 2013).

Distribution of larval fish, however, is initially determined by spawning mode. Three modes of spawning are commonly used by adults: pelagic spawning, benthic spawning and brooding (Leis, 1991a). Offshore marine species and most coral reef species spawn pelagic eggs (Wootton, 1990; Leis, 1991a), while inshore coastal marine species can spawn pelagic eggs or lay demersal eggs (Leis, 1991a). Generally, coastal adults spawning pelagic eggs will spawn in or near areas of known hydrodynamic retention or weak offshore currents to maximise retention near the natal sites and reduce mortality of eggs (Johannes, 1978; Norcross & Shaw, 1984). Pelagic eggs are mostly transparent compared to demersal eggs, which are usually heavily pigmented (Breder, 1962). The pelagic eggs are buoyant and float at or close to the surface making them vulnerable to surface currents (Sundby, 1991). Larvae from pelagic eggs hatch within 48 hours and are less developed than demersal eggs, which can take up to a week or even more before hatching (Breder, 1962; Leis, 1991a, 1994). Newly hatched larvae from pelagic eggs still have their yolk sac intact which provides the larvae nutrients for a longer period of time while their digestive tract develops (Breder, 1962; Hunter, 1981). Most yolk sac larvae swim with short energetic bouts followed by long rest periods (Hunter, 1972, 1981; Weihs, 1980; Bailey & Yen, 1983). Because they are still underdeveloped and lack differentiated fins, yolk sac larvae are still very much susceptible to offshore transport (Hunter, 1972). Yolk sac larvae do not respond to predators (Bailey & Houde, 1989) and so the transparency of the egg sac and the larvae help to avoid predators during this passive stage of their life (Breder, 1962). Larvae from demersal eggs on the other hand, hatch after the yolk sac has been absorbed skipping the yolk sac stage and hatch as preflexion larvae. Larvae in the preflexion stage have a functioning digestive system and their permanent fins and fin rays are present (Breder, 1962). Preflexion larvae are able to swim short distances (< 5 cms^{-1}) for short periods of time (Hunter, 1972; Weihs, 1980; Batty, 1987; Fisher *et al.*, 2000), thus enabling them to actively search for food (Breder, 1962). Although, preflexion larvae may not be able to swim great distances horizontally, vertical swimming would be possible for these weak swimmers, enabling them to adjust their vertical distributions (Fisher *et al.*, 2000). The flexion stage in larval fishes follows the development of flexion in the notochord. During the flexion stage, body shape, fin rays, swimming ability and feeding techniques rapidly develop and change (Kendall *et al.*, 1984). It is at this stage of development that larval fish start to swim greater distances for longer periods of time (Clark *et al.*, 2005). Flexion stage larvae are able to swim at speeds between 5 and 10 cms^{-1} and reach distances up to 2 km (Clark *et al.*, 2005), this gives larvae the potential to swim small scale distances (Fisher *et al.*, 2000). Postflexion larvae have furthermore developed gill rakers and photophores and are active swimmers (>10 cms^{-1}), which can successfully swim against strong currents (Fisher *et al.*, 2000; Fisher & Bellwood, 2002; Clark *et al.*, 2005; Pattrick & Strydom, 2009).

Fast, successful development through the larval phase is crucial for survival. Larval fish feed mainly on copepods and their nauplii (Houde & Taniguchi, 1979) and are preyed upon by larger zooplanktivorous copepods, chaetognaths, medusa, amphipods and mysids (Bailey & Houde, 1989; Cowan *et al.*, 1996). To avoid starvation and predation, larval fishes adopt a variety of mechanisms including prey selection size (Hunter, 1981), burst swimming modes, (Osse *et al.*, 1997), swim bladder inflation (Blaxter, 1986) and being inactive (Bailey & Yen, 1983). An additional, important mechanism promoting larval fish survival is vertical migration. Larval fishes will move vertically up and down in the water column tracking high abundances of food (Fortier & Leggett, 1983; Batty, 1987). They will also actively switch their vertical position from either the surface of the water column to the bottom, or vice versa, to avoid predators (Hobson, 1973; Ohman *et al.*, 1983; Ohman, 1990; Brodeur & Rugen, 1994). Vertical migration is also used to avoid offshore transport via currents; by moving into depths with favourable onshore currents, larvae are able to retain themselves close to shore (Cowen & Castro, 1994; Paris & Cowen, 2004; Kent *et al.*, 2013).

Study Rationale

Coastal nearshore marine habitats are particularly important areas for coastal adults to spawn and larval fish to develop into juveniles (Leis & Miller, 1976; Richardson & Pearcy, 1977; Beckley, 1986; Jenkins, 1986; Hernández-Miranda *et al.*, 2003; Pattrick & Strydom, 2008; Kent *et al.*, 2013). In South Africa, research on larval fishes has mainly focused on estuarine (Melville-Smith & Baird, 1980; Melville-Smith, 1981; Beckley, 1984; Harrison & Whitfield, 1990; Martin *et al.*, 1992; Whitfield, 1994, 1999, Harris & Cyrus, 1995, 1997, 1999; Harris *et al.*, 1995; Strydom *et al.*, 2003; Pattrick *et al.*, 2007; Montoya-Maya *et al.*, 2009; Wasserman *et al.*, 2010; Pattrick & Strydom, 2014; Strydom, 2015; *inter alia*), surf zone (Whitfield, 1989; Harris & Cyrus, 1996; Cowley *et al.*, 2001; Strydom, 2003; Watt-Pringle & Strydom, 2003; Strydom & d'Hotman, 2005) and commercially important pelagic species (Thomas, 1986; Olivar *et al.*, 1988; Olivar & Shelton, 1993; Beckley & Hewitson, 1994; Beckley & Leis, 2000; Huggett *et al.*, 2003; van der Lingen & Huggett, 2003; Grote *et al.*, 2012).

The composition of larval fish assemblages, species abundances and distributions in the nearshore (< 30 m deep; Pineda *et al.*, 2007) have been investigated in the sub-tropical waters off the St Lucia Estuary in the KwaZulu-Natal province (Harris *et al.*, 1999). Larval fish and fish egg surveys were conducted in 1991 and 1992 within the warm temperate Tsitsikamma National Park marine reserve, located in the Eastern Cape province (Tilney & Buxton, 1994). Tilney et al., (1996) then published data from this study, focusing on the Blenniidae, Gobiesocidae, Sparidae and Engraulidae fish families (Tilney *et al.*, 1996). A study looking at jetski based towing to investigate nearshore composition of larval fish assemblages occurred off the warm temperate south coast in Port Alfred, Eastern Cape (Strydom, 2007). And finally Algoa Bay, along the warm temperate south coast, has received the most attention in terms of nearshore composition and distribution of larval fishes (Beckley, 1986; Pattrick & Strydom, 2008, 2014, 2017; Pattrick *et al.*, 2013).

The South African coastline is mostly linear, with very few bays or inlets. Hutchings *et al.* (2002) has suggested that due to this, enormous constraints are placed on the reproductive strategies of many fish species occurring within the region. Several economically and ecologically important species spawn on the edge of current systems where eggs and larvae are transported into productive inshore nursery grounds (Hutchings *et al.*, 2002). Due to the paucity in larval fish research in the nearshore of South Africa, there is a need to continue research within the nearshore, to fill the gaps in our understanding of the dynamics of larval fishes. Algoa Bay and St Francis Bay are two large embayments on the south coast of South Africa and are likely to be important areas for the development of larval fishes.

Study Aims and Objectives

The aim of this study was to investigate the assemblages of larval fishes in the nearshore waters of Algoa Bay and St Francis Bay, two adjacent shallow coastal bays on the south coast of South Africa. The specific objectives of this study were: 1) to assess how the species composition and abundance of the larval fish assemblages are influenced by depth and distance offshore within the two bays and determine what role physical environmental factors may play in shaping the distributions of these larval fishes (Chapter 2); 2) to assess diel vertical migration patterns of larval fishes by comparing day and night samples and investigate environmental conditions that may influence these patterns (Chapter 3); 3) to evaluate the use of open bongo nets in the sampling procedure by asking whether contamination during recovery of the net from depth significantly affects estimates of larval abundances derived from horizontal tows near the bottom (Chapter 4). Chapter 4 is therefore a methodological section analysing the stratum-specific method used in this study for the sampling of larval fishes.

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Chapter 2

Ichthyoplankton composition and distribution in two adjacent bays off the south coast of South Africa

1 Introduction

Mortality of fishes is greatest during the early larval stages (Cushing, 1974; Hjort, 1914; Houde, 1987). In order to ensure maximum survival and successful development, larval fishes need to find a favourable environment that will not lead to starvation or extensive passive transport due to currents (Cushing, 1974; Hjort, 1914; Houde, 1987). Due to their shape, physical features and circulation patterns, coastal embayments, or bays, provide suitable habitats for planktonic species. Many bays are in the shape of half a heart and are known as half-heart bays, or more formally as log-spiral bays (Yasso, 1965). The major topographic feature that defines a bay is the headland, which acts as a barrier for incoming waves (Yasso, 1965). By either refraction or diffraction waves are dissipated and redistributed into the bay (Yasso, 1965; Hsu *et al.*, 1987). Coastal bays can also provide a sheltered region for species of adult fish that spawn pelagic eggs and ensure maximum survival of eggs and larvae (Haegele & Schweigert, 1985; Hutchings *et al.*, 2002). The currents in bays often recirculate water within them (Signorini, 1980; Heath, 1985; Goschen & Schumann, 1988; Geyer *et al.*, 1992; Graham & Largier, 1997; Vélez *et al.*, 2005) and can act as a retention zone. This helps to retain fish eggs and larvae and reduces loss from offshore transport (Haegele & Schweigert, 1985; Hutchings *et al.*, 2002; Largier, 2004; Álvarez *et al.*, 2015). Being good retention zones, bays also support high accumulation of phytoplankton (Kang *et al.*, 2003) and zooplankton (Archambault *et al.*, 1998; Roughan *et al.*, 2005; Morgan & Fisher, 2010) and so are a stable source of food for larval fishes. Due to their reduced wave action (Yasso, 1965) bays provide a sheltered environment for larval fishes. All these factors combined make bays a highly suitable habitat for the development of larval fishes.

Larval fish assemblages in bays are often patchy, with physical mechanisms such as currents, temperature and depth determining their distribution (Richardson & Pearcy, 1977; Jenkins, 1986; Vélez *et al.*, 2005; Pattrick *et al.*, 2013). Habitat type within bays is known to affect larval distribution of some species, with some presettlement larvae preferring less structurally complex, reef-associated sand habitats before they settle as juveniles (Pattrick & Strydom, 2017). Furthermore, biological factors too can alter larval fish assemblages. Different spawning strategies can also greatly alter larval fish assemblages within bays. In the tropics, specifically Hawaii, larvae of reef species that have non-pelagic eggs have been found closest to the coast, while larvae of reef species with pelagic eggs were located further offshore (Leis & Miller, 1976). Furthermore, the larvae of adults which occur in bays dominate larval catches, suggesting that adults are making use of the protective features of bays to spawn (Leis & Miller, 1976). In temperate south eastern Australia (Victoria Bay), larvae of species with non-pelagic eggs were found in highest abundances 1 km offshore from the coast, while larvae of species with pelagic eggs had no horizontal spatial differences (Kent *et al.*, 2013). In the southern Gulf of Mexico, larvae of estuarine associated species were found in the shallow nearshore waters, while larvae from adults found above the coastal shelf and the mesopelagic zone were found in the same areas respectively (Sanvicente-Añorve *et al.*, 1998). Studies in Peru (Vélez *et al.*, 2005), Oregon (Richardson & Pearcy, 1977), Australia (Jenkins, 1986; Kent *et al.*, 2013), Japan (Yamashita & Aoyama, 1984), Hawaii (Leis & Miller, 1976) and South Africa (Beckley, 1986; Pattrick & Strydom, 2008) have found clear onshore and offshore differences in larval fish assemblages in bays, where larvae of adults which occur in the bay dominate catches. Furthermore, the above studies found bays to be good spawning and nursery areas, with most spawning taking place from late winter to spring and summer (Leis & Miller, 1976; Richardson & Pearcy, 1977; Beckley, 1986; Jenkins, 1986; Vélez *et al.*, 2005; Pattrick & Strydom, 2008; Kent *et al.*, 2013).

Larval fish research in South Africa has focused on the estuarine (Melville-Smith & Baird, 1980; Melville-Smith, 1981; Beckley, 1984; Harrison & Whitfield, 1990; Martin *et al.*, 1992; Whitfield, 1994, 1999, Harris & Cyrus, 1995, 1997; Harris *et al.*, 1995; Strydom *et al.*, 2003; Pattrick *et al.*, 2007; Montoya-Maya *et al.*, 2009; Wasserman *et al.*, 2010; Pattrick & Strydom, 2014; Strydom, 2015; *inter alia*) and surf zone (Whitfield, 1989; Harris & Cyrus, 1996; Cowley *et al.*, 2001; Strydom, 2003; Watt-Pringle & Strydom, 2003; Strydom & d'Hotman, 2005; *Inter alia*) environments, as well as the tidal exchange of ichthyoplankton between ocean and estuary (Beckley, 1985; Whitfield, 1989; Harris & Cyrus, 1995, 1999; Cowley *et al.*, 2001; Kemp & Froneman, 2004; Strydom & Wooldridge, 2005 *inter alia*). Research in the marine offshore environment of South Africa has mostly focused on commercially important pelagic species:

anchovy, *Engraulis encrasicolus* (Family: Engraulidae), sardine, *Sardinops sagax* (Family: Clupeidae), round herring, *Etrumeus whiteheadi* (Family: Dussumieriidae; Thomas, 1986; Olivar & Shelton, 1993; Beckley & Hewitson, 1994; Huggett *et al.*, 2003; van der Lingen & Huggett, 2003), lanternfish, *Lampanyctodes hectoris* (Family: Myctophidae; Ahlstrom *et al.*, 1976; Olivar *et al.*, 1999), hake, *Merluccius capensis* and *M. paradoxus* (Family: Merlucciidae; Olivar *et al.*, 1988; Grote *et al.*, 2012) and species from the family Scombridae (Beckley & Leis, 2000). All the studies mentioned above have either been carried out in the Benguela and Agulhas Currents or offshore of the South African coast including Namibia.

Investigations into the nearshore larval fish assemblages off the South African coastline have been isolated. Sparse studies have been carried out off the subtropical east coast, in the nearshore waters off the St Lucia Estuary, (Harris *et al.*, 1999), south coast, Tsitsikamma National Park MPA, (Tilney & Buxton, 1994; Tilney *et al.*, 1996) and Port Alfred (Strydom, 2007). The coast of southern Africa has only a few bays or semi-enclosed areas, with four prominent bays along the south coast belonging to a type known as half-heart or log-spiral bays because of their shape (Yasso, 1965). Algoa Bay, the most easterly of these bays has received the most attention in terms of nearshore distribution of larval fishes (Beckley, 1986; Pattrick & Strydom, 2008, 2014, 2017; Pattrick *et al.*, 2013). The other bays to the west, in particular St Francis Bay, have supported no investigations of larval fishes.

The aim of this study was to investigate the assemblages of larval fishes, in two adjacent shallow coastal bays, on the south coast of South Africa. The specific objectives of the present study were to 1) assess the species composition, abundance and developmental stages of larval fishes in the nearshore environment of Algoa Bay and St Francis Bay, 2) to assess larval fish assemblages with increasing distance from shore within the two bays, and 3) to determine what physical environmental factors played a role in the distribution of larval fishes. Because Algoa Bay and St Francis Bay are in such close proximity and of a similar shape one would expect the two bays to comprise similar larval fish species.

2 Material and Methods

2.1 Sample Sites

Algoa Bay (33.928100°S 25.618710°E) and St Francis Bay (34.167830°S 24.851370°W) are two adjacent, coastal bays on the warm temperate south coast of South Africa (Figure 2.1). The bays are two of the largest of four log-spiral bays on the south coast of South Africa (Bremner, 1983). Both Algoa Bay and St Francis Bay are roughly 80 km across, with Algoa Bay approximately 40 km in width perpendicular to the shore and St Francis Bay 30 km perpendicular to the shore. Both bays are shallow, with depths not exceeding 80 m and are sheltered and experience moderate wave action (Lasiak, 1984; Bruton *et al.*, 1991; Schumann *et al.*, 2005). The wave force in both bays is under 8 $N.m^{-2}$ compared to 14 $N.m^{-2}$ on the open coast (Nicastro *et al.*, 2008). The Agulhas Current is the major western boundary current flowing south-westwards approximately 70 km from the coastline of the bays (Gründlingh, 1983; Lutjeharms, 2006). Just south of St Francis Bay, the continental shelf widens and the core flow of the Agulhas Current moves offshore (Schumann *et al.*, 2005). Although the Agulhas Current has no constant influence on the bays, occasional large meanders in the Agulhas Current circulate warmer water into the bays (Schumann, 1987; Goschen & Schumann, 1988) and large physical features like the Natal Pulse can at times export subsidies from the bays (Jackson *et al.*, 2012; Porri *et al.*, 2014). Predominantly south westerly winds blow in Algoa Bay and St Francis Bay throughout the year (Schumann *et al.*, 2005). During summer however, easterly winds predominate (Hunter, 1987), with upwelling occurring off the headlands of the bays (Schumann *et al.*, 2005).

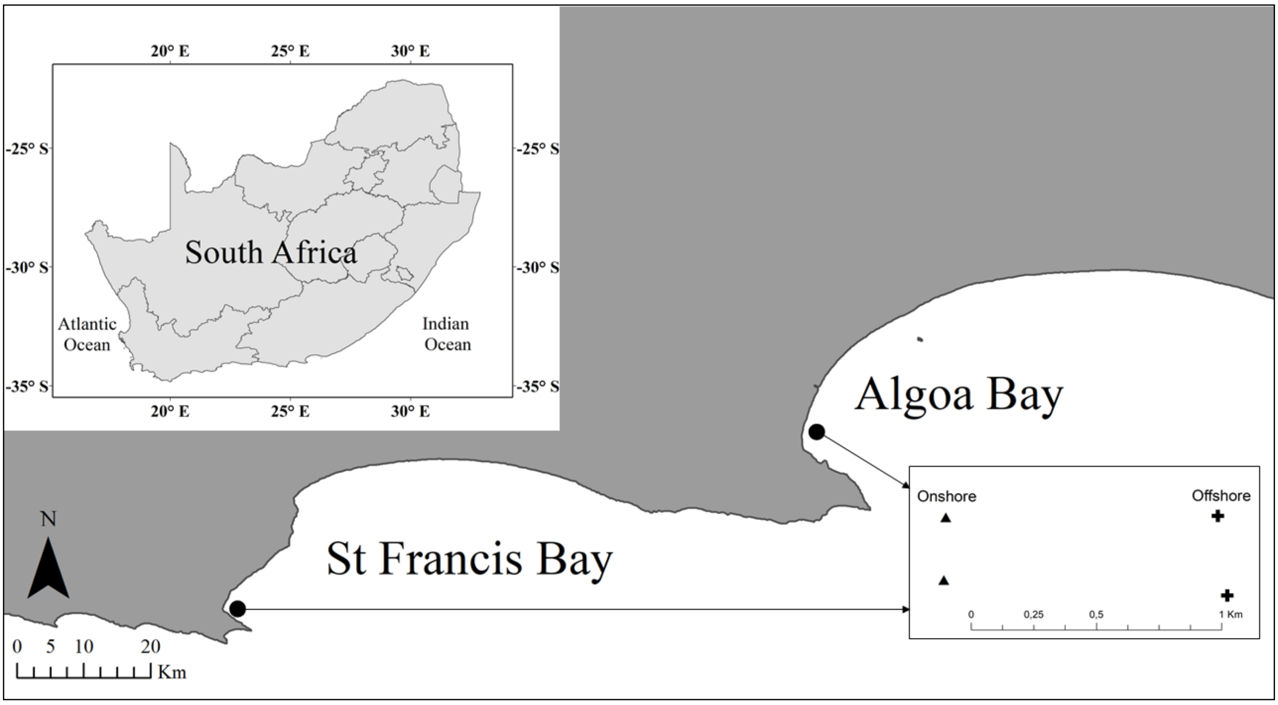

Figure 2.1 The geographical position of Algoa Bay and St Francis Bay on the south coast of South Africa showing the location of the two sampling sites indicated by black circles and the two onshore stations (black triangles) and two offshore stations (black crosses) in the insert

Algoa Bay and St Francis Bay were selected to investigate the composition, distribution and abundance of larval fishes (Figure 2.1). Sampling was conducted during known peak larval fish abundances in the region (Beckley, 1986; Pattrick & Strydom, 2008), in March/April (autumn) and September/October (spring) 2013. Although seasonality was not taken into account for this study as sampling only took place once during these distinct times, seasons do play a clear role in determining larval fish abundances in the area (Beckley, 1986; Pattrick & Strydom, 2008) and reference to seasonality has been made in the discussion of this chapter. Within each bay, four stations; two onshore and two offshore, were selected (Figure 2.1). The two onshore stations were located 1 km from the coast and ~200 m apart and the two offshore stations were 2.4 km from the coast and also ~200 m apart. For the purpose of this study, the offshore stations are named offshore even though they are close enough to the coast to still be considered nearshore. Sampling at the onshore stations was repeated during night. The night samples were however not included in the analysis for this chapter of the thesis. Due to time constraints offshore stations could not be sampled at night.

The first sampling period was over March and April 2013, with Algoa Bay sampled in March and St Francis Bay, six weeks later, in April. Samples and data from these sampling times will be referred to as March samples/data. The second sampling period was in September and

October 2013, with Algoa Bay in September and St Francis Bay, one and a half weeks later, in October. Samples/data from this period will be referred to as September samples/data.

At each station, current speed and direction were measured using a boat-based acoustic Doppler current profiler (ADCP, Teledyne RDI Workhorse monitor 300KHz). Currents were measured in 0.5 m vertical bins and averaged over 30-60 minutes. Data corresponding to depths less than 2.25 m from the surface were discarded due to backscatter. Temperature and depth were recorded using either a YSI 6920 multi-parameter water quality logger or a Seabird SBE19plusV2 CTD depending on availability. On two occasions, during the September (spring) sampling at St Francis Bay, a SUUNTO D4 dive computer was used to obtain temperature and depth values due to the malfunctioning of the CTD. For this reason, only temperature could be used in the analysis. All instruments were calibrated against one another to ensure that the data collected were standardised and there were no discrepancies in the data set. v cover was estimated as a fraction of total cloud cover out of a possible 8 oktas as described in the International Cloud Atlas (World meteorological organization, 1975; World meteorological Organization, 2011). Wind speed and wave height were boat based estimates and later compared to the Weather Research and Forecasting (WRF) model station located at Port Elizabeth and Cape St Francis (Windguru www.windguru.cz).

2.2 Larval Fish Collection and Identification

At each station, larval fish were collected by means of a set of bongo nets, each net with a 57 cm diameter and mesh aperture of 500 µm, deployed from a davit and winch system on the 13 m Category B research vessel uKwabelana. A one way clutch General Oceanics flowmeter was suspended from the frame of the net to quantify the volume of water sampled. The bongo nets were pulled parallel to the shore while the boat maintained a speed of ~2 knots for three minutes. Horizontal tows were repeated twice at one meter above the seafloor (referred to as bottom tows) and twice at one meter below the sea surface (referred to as surface tows). The depth of the bongo nets was determined by the altimeter on board the boat and the rope connected to the bongo nets was let out 1 m short the depth of the sea floor. A vertical tow was done for each bottom tow to correct for larval fish that could have been caught while hauling the nets to the surface (Figure 2.2). Nets were rinsed into a 250 µm sieve, samples were transferred into 500 ml sample jars and fixed in 10% formaldehyde in seawater. During the September sampling, samples were preserved in absolute ethanol for possible DNA analysis. Samples from each of the bongos were pooled and analysed as one sample. In the laboratory, larval fish were separated from the rest of the sample, counted and identified to the lowest possible taxon (Olivar, 1986; Beckley, 1989; Cambray & Bok, 1989; Neira *et al.*, 1998; Leis & Carson-Ewart, 1999; Leis *et al.*, 2002; Wood, 2003; Richards, 2005; Strydom & Neira, 2006). The standard length of each larva was measured to the nearest 0.1 mm, using the methods from Neira *et al.* (1998) under a stereomicroscope fitted with an eyepiece micrometer with 0.1 mm precision. Larvae were further categorised into preflexion, flexion and postflexion stages.

2.3 **Bathymetric Data**

Bathymetric details of Algoa Bay and St Francis Bay were provided by the South African Navy Hydrographic Office. Depth contours and seabed features were plotted in ArcGIS 10.3.

2.4 **Statistical Analysis**

2.4.1 Environmental Data

Patterns of environmental data (wind speed (knots), wave height (m), cloud cover (oktas), temperature (°C), depth (m), average current speed ($cm.s^{-1}$) and average current direction were examined using the Primer 6 PERMANOVA+ software package (version 6.1.15). Draftsman plots were produced to assess skewness of the data. Current speed and direction, depth and temperature were subsequently log (x+1) transformed to correct for skewness. Patterns in environmental variables were observed between sites (Algoa Bay/St Francis Bay), position (onshore/offshore) and depth (surface/bottom) by performing a Principle Component Analysis (PCA; Clarke & Warwick, 2001) on the normalised Euclidean distance similarity matrices of the environmental variables (Clarke & Gorley, 2006). PCA reduces the dimensions of the data set without loss of important information. It does this by transforming a number of correlated variables into a smaller number of uncorrelated variables called principal components. The first principal component (Principal Component 1) is the linear combination of x-variables that has the maximum variance accounting for as much variation in the data as possible. The second principal component (Principal component 2) accounts for as much of the remaining variation as possible. The PCA explains the maximum variance with the fewest possible number of principal components (Clarke & Gorley, 2015).

2.4.2 Biological Data

Because the bongo nets could not be closed, it was necessary to correct values from the horizontal bottom tows for contamination by larval fish caught while bringing the net up from the bottom to the surface. Although the results of Chapter 4 indicate that such contamination did not have a significant effect on the results, the present data were corrected before analysis to provide the most accurate results. To correct for contamination, the number of larvae potentially caught in the vertical tows was subtracted from the number of larvae caught in the bottom tows to produce a true value for the horizontal bottom tow ($\underline{X}$). To do this the following calculations and methods (Figure 2.2) were used:

$$\underline{X} = X - (Y - Z)$$

Where X = number of larvae in the bottom tow, including larvae caught while bringing the net to the surface, Y = number of larvae in the vertical tow and Z = proportion of larvae within the vertical tow that would also be included in the bottom tow (Figure 2.2).

Z was calculated as follows:

$$Z = \frac{Y * B}{A}$$

Where A is the volume sampled for the vertical tow and B is the volume sampled for the bottom horizontal tow (Figure 2.2).

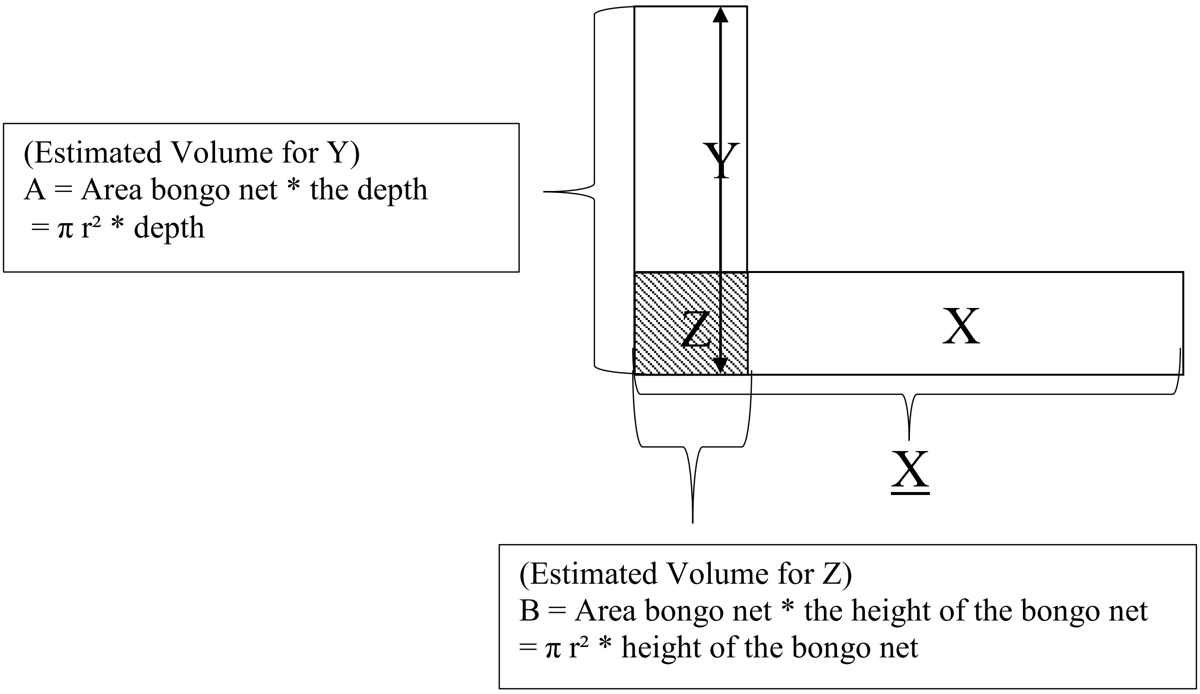

Figure 2.2 To correct for contamination larvae caught while returning the net to the surface, (Y) must be removed from the larvae caught in the horizontal tows (X). However, the area shaded is an overlap of the two tows, so these larvae (Z) need to be excluded from the vertical component (Y) before correction to give a true value for the horizontal tow ($\underline{X}$). To do this, the volumes of Y (A) and of Z (B) were calculated and used as a proportion to estimate the number of larvae caught within those areas

Once true values ($\underline{X}$ calculated above) for all bottom tows were calculated, mean density (MD) of larvae was calculated using the following formula to give a density per 100m^3.

$$\mathrm{MD} = \frac{\text{No. of larvae}}{\text{flow meter revolutions } \div \text{ calibration value in m}^3} \times 100$$

Larval fish community analyses were run on Primer 6 version 6.1.15 and PERMANOVA+ (PRIMER v6 & PERMANOVA +v1, PRIMER-E Ltd.). Densities of larvae were square-root transformed and Bray-Curtis similarities between samples were used to construct a similarity matrix (Bray & Curtis, 1957). The distance-based test for homogeneity of multivariate dispersions, PERMDISP (Anderson, 2006) was used to test for homogeneity of site (Algoa Bay and St Francis Bay), season (March and September), position (onshore and offshore) and depth (surface and bottom). Season was heterogeneous, and so analyses for March and September data were run independently of each other. A distance-based test for homogeneity was repeated for March and September individually.

A three-way PERMANOVA (PERMANOVA + for Primer-6; Anderson, 2005) was employed to assess the effects of the factors: site (Random, 2 levels: Algoa Bay, St Francis Bay), position (Fixed, 2 levels: onshore, offshore), depth (Fixed, 2 levels: surface, bottom) and of all factor combinations on the larval fish community separately for March and September. Permutated pairwise tests were run on significant combination of factors to assess the interactive effects within the factors combined.

Species contributing most to the average dissimilarities between the groups: site, position and depth were obtained using the SIMPER (similarity percentages) routine. (Warwick *et al.*, 1990).

The relationship between the environmental variables and larval fish densities were examined using a distance based linear model (DistLM) and observed using a distance-based redundancy analysis ordination (dbRDA; Legendre & Anderson, 1999). Marginal tests (999 permutations) were performed to determine the most influential environmental factors on larval fish densities.

3 Results

3.1 Environmental Analyses

Mean sea water temperatures in Algoa Bay were 21.6 °C (with a range of ± 1.23 °C) in March and 17.9 °C (± 0.42 °C) in September. Mean sea water temperatures in St Francis Bay were 17.8 °C (± 1.37 °C) in March and 18.3 °C (± 1.35 °C) in September. During March mean bottom depth sampled in Algoa Bay, was 9.5 m onshore and 12.5 m offshore. St Francis Bay was 6.2 m onshore and 9.9 m offshore. During September, mean bottom depth sampled in Algoa Bay was 9.6 m onshore and 11.6 m offshore. St Francis Bay was 5.5 m onshore and 11.5 m offshore. Algoa Bay in March experienced an average wind speed of 2.1 knots, with an average wave height of 0.9 m, while in September, the average wind speed was 1.6 knots with average wave height increasing to 1.5 m. St Francis Bay in March experienced an average wind speed of 1.3 knots and average wave height of 1.6 m, in September average wind speed was 0.8 knots and wave height was 0.8 m. During March, average surface current for Algoa Bay was 4.64 cms^{-1} and average bottom current was 6.94 cms^{-1}. In St Francis Bay, average surface current was 5.32 cms^{-1} and average bottom current was 7.66 cms^{-1}. During September, Algoa Bay's average surface current was 4.31 cms^{-1} and average bottom current was 11.18 cms^{-1}. St Francis Bay's average surface current was 3.68 cms^{-1} and average bottom current was 7.17 cms^{-1}. There were clear current directions in September with surface currents flowing predominantly south and bottom currents flowing predominantly west (Table 2.1 and Table 2.2).

Table 2.1 Mean (n=2) environmental variables for Algoa Bay and St Francis Bay during March 2013. Wind speed (knots), wave height (m), clouds (oktas), temperature (°C), depth (m), average current speed (cms^{-1}), average current direction and average volume of water filtered through the bongos (m³)

Environmental Variable	Algoa Bay				St Francis Bay			
	Onshore		Offshore		Onshore		Offshore	
	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
Wind speed	2,0	2,5	2,0	2,0	1,0	1,0	1,5	1,5
Wave height	1,0	1,5	0,5	0,5	1,7	1,7	1,5	1,5
Clouds	2,0	2,0	1,5	1,5	2,0	2,0	4,0	4,0
Temperature	22,2	21,6	21,9	21,1	18,0	17,8	18,2	17,2
Depth	1,5	9,5	1,8	12,5	1,5	6,2	1,6	9,9
Current speed	4,7	6,8	4,6	7,1	3,6	6,1	7,1	9,2
Current direction	26,0	170,5	294,1	129,5	108,3	302,7	197,3	255,4
Volume water filtered	384,4	410,2	464,1	185,1	508,0	460,3	335,5	546,8

Table 2.2 Mean (n=2) environmental variables for Algoa Bay and St Francis Bay during September 2013. Wind speed (knots), wave height (m), clouds (oktas), temperature (°C), depth (m), average current speed (cms^{-1}), average current direction and average volume of water filtered through the bongos (m³)

Environmental Variable	Algoa Bay				St Francis Bay			
	Onshore		Offshore		Onshore		Offshore	
	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
Wind speed	1,5	1,5	1,8	1,8	0,5	0,5	1,0	1,0
Wave height	1,5	1,5	1,5	1,5	0,8	0,8	0,8	0,8
Clouds	1,0	1,0	0,0	0,0	3,5	3,5	2,0	2,0
Temperature	17,8	17,8	18,1	17,8	18,3	18,0	19,0	17,9
Depth	1,6	9,6	1,5	11,5	1,6	5,5	1,5	11,5
Current speed	3,8	12,7	4,8	9,7	2,9	5,4	11,4	2,0
Current direction	192,9	298,7	150,5	252,9	185,4	283,2	207,2	161,4
Volume water filtered	722,8	324,7	312,3	319,9	648,5	502,8	403,9	386,5

The PCA performed on the environmental variables revealed that St Francis Bay and Algoa Bay in March were noticeably different (Figure 2.3). To ease discussion, the outcome plot of the PCA is split into four quadrants (Figure 2.3) Environmental variables from St Francis Bay were distributed within quadrants 2 and 3, barring one point (St Francis Bay, offshore, September). Data from Algoa Bay was more dispersed. The linear coefficients linking the environmental variables to the principle components showed cloud cover and wind speed to be driving the separation between Algoa Bay and St Francis Bay. In March, Algoa Bay and St Francis Bay were separated along the principal component 1, Algoa Bay distributed between quadrants 1 and 4 and St Francis Bay distributed between quadrants 2 and 3. The linear coefficients linking the environmental variables to the principal component 1 showed temperature and current direction driving the separation between Algoa Bay and St Francis Bay in March. In September, Algoa Bay and St Francis Bay were separated along the principal component 2, Algoa Bay distributed between quadrants 1 and 2 and St Francis Bay distributed between quadrants 3 and 4. The linear coefficients linking the environmental variables to the principal component 2 show wind speed, cloud cover, current speed and depth to be driving the separation between Algoa Bay and St Francis Bay in September (Figure 2.3).

PCA indicated that 27.6% of the variability could be explained by the first component (PC 1) and 23.9% by the second component (PC 2) with the first two principal components alone explaining more than 50% of the total variability. PC 1 shows a strong negative relationship with wind speed and temperature, with a strong positive correlation with wave height, cloud cover and depth (Table 2.3).

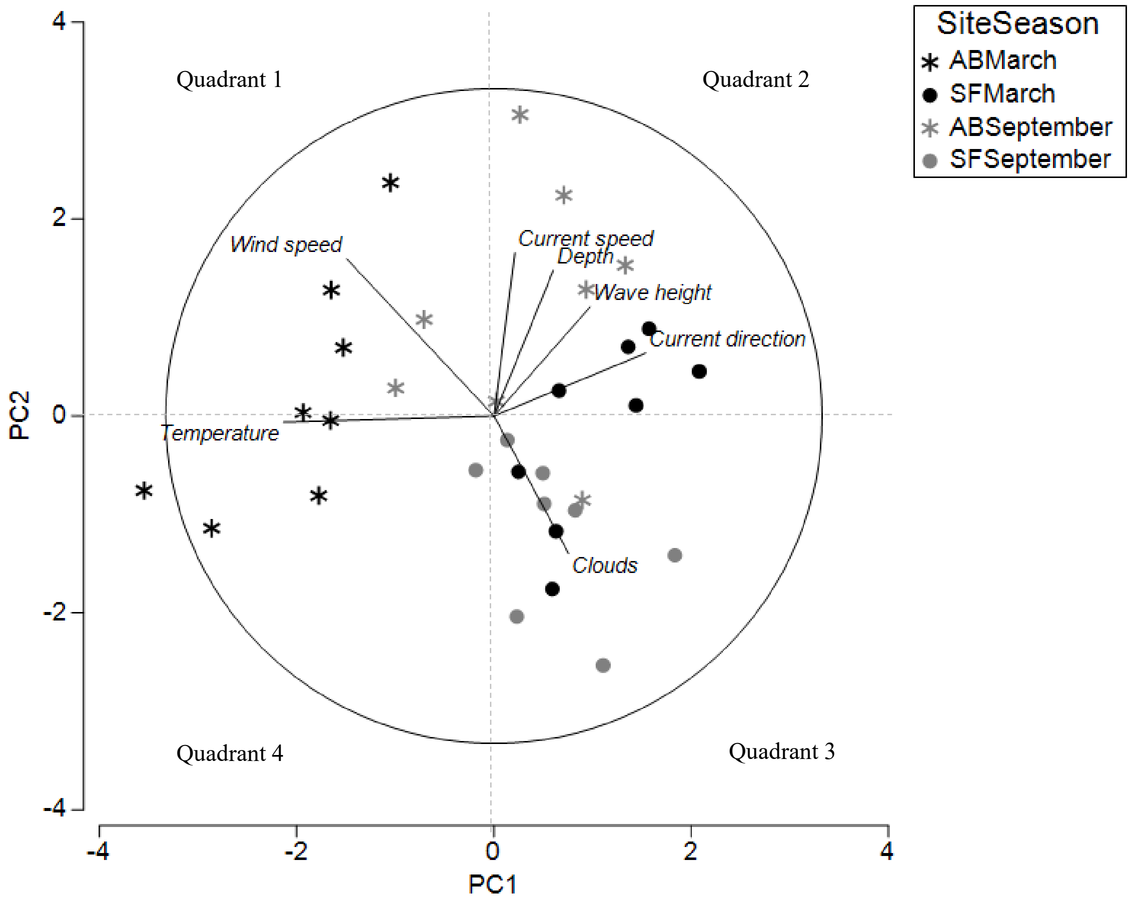

Figure 2.3 Two-dimensional scatter plot of the first and second principal components of environmental variables (wind speed (knots), wave height (m), clouds (oktas), temperature (°C), depth (m), average current speed (cms^{-1}) and average current direction) surface and bottom for March and September in Algoa Bay (AB) and St Francis Bay (SF). Vectors of the linear correlations between individual variables are superimposed on the graph

Table 2.3 Eigenvectors determined from PCA for environmental variables (wind speed, wave height, cloud (oktas), temperature, depth, average current speed and average current direction)

Variable	PC1	PC2	PC3	PC4	PC5
%Variation	27.60	23.90	16.90	11.90	9.10
Wind speed	-0.45	0.48	-0.07	0.05	0.30
Wave height	0.29	0.33	-0.66	0.15	0.32
Clouds	0.23	-0.42	0.28	0.64	0.48
Temperature	-0.64	-0.02	0.28	0.07	0.03
Depth	0.18	0.45	0.49	-0.20	0.54
Current speed	0.06	0.50	0.16	0.68	-0.48
Current direction	0.46	0.19	0.39	-0.27	-0.25

3.2 Larval Fish Assemblages

3.2.1 Species Composition

A total of 790 larval fishes were collected, comprising 17 fish families and 34 species. Of the total, 30 larval fishes were caught in the vertical tows and the corrected proportions were subtracted from the values for their respective species in the bottom catches. In Algoa Bay, the larval fish catch was dominated by Engraulidae (67%), with important contributions from Blenniidae (15%), Sparidae (8%) Soleidae (6%) and Cynoglossidae (2%). While in St Francis Bay the larval fish catch was dominated by Blenniidae (26%), with important contributions from Engraulidae (22%), Tripterygiidae (20%), Sparidae (11%) and Gobiesocidae (7%). All other fish families made up < 2% of the catches in both bays. March samples made up only 8% of the total catch while September made up 92%. Preflexion larvae made up more than 90% of the total catch during both March and September.

The distance-based test for homogeneity of multivariate dispersions (PERMDISP) showed site ($F_{1,30} = 0.17$, $p > 0.7$), position ($F_{1,30} = 1.17$, $p > 0.4$) and depth ($F_{1,30} = 4.88$, $p > 0.1$) to be homogenous. Season however, was significantly heterogeneous ($F_{1,30} = 48.77$, $p < 0.001$) and therefore analysed separately.

3.2.2 March Analysis

Results of the PERMDISP analysis for March, site ($F_{1,14} = 4.10$, $p > 0.1$), position ($F_{1,14} = 0.36$, $p > 0.6$) and depth ($F_{1,14} = 0.11$, $p > 0.8$) indicated homogeneity of data according to the factors considered.

During March (autumn), a total of 62 larval fish were captured between the two bays (excluding the vertical tows). In Algoa Bay, 50 larval fish were captured while in St Francis Bay only 12 larval fish were captured (Table 2.4). Nine species were captured in Algoa Bay with *Engraulis encrasicolus* (Family: Engraulidae) contributing 93% towards the total catch. In St Francis Bay only five species were captured, with a blennid species, Blenniidae 4 and a Tripterygiidae species dominating the larval fish catch, contributing 77% and 23% respectively.

Table 2.4 Species, total catch, mean density per 100m^3 (n=2) and standard deviation (in brackets), for Algoa Bay and St Francis Bay, onshore and offshore, surface and bottom in March 2013

Family	Species	Total Catch	Algoa Bay				St Francis Bay			
			Onshore		Offshore		Onshore		Offshore	
			Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
Blenniidae	Blenniidae 1	2	0.2 (0.3)	-	-	-	-	-	-	-
	Blenniidae 2	1	-	-	0.9 (0.1)	-	-	-	-	-
	Blenniidae 3	2	-	-	0.9 (0.1)	-	0.9 (0.1)	-	-	-
	Blenniidae 4	5	-	-	-	-	0.2 (0.4)	0.2 (0.6)	0.1 (0.2)	-
	Parablennius 1	2	-	0.1 (0.3)	0.9 (0.1)	-	-	-	-	-
Engraulidae	*Engraulis encrasicolus*	36	1.4 (0.6)	0.8 (0.9)	1.3 (1.5)	1.3 (1.2)	-	-	-	-
Gobiesocidae	Gobiesocidae 1	1	-	-	-	0.3 (0.4)	-	-	-	-
Gobiidae	*Caffrogobius nudiceps*	2	-	0.2 (0.2)	-	0.3 (0.4)	-	-	-	-
	Psammogobius knysnaensis	1	-	-	0.1 (0.2)	-	-	-	-	-
Leiognathidae	Leiognathidae 1	1	-	-	-	-	-	0.1 (0.2)	-	-
Soleidae	*Solea turbynei*	4	0.1 (0.2)	0.2 (0.2)	-	0.6 (0.8)	-	-	-	-
Syngnathidae	*Syngnathus temminckii*	1	-	-	-	-	-	0.1 (0.2)	-	-
Tripterygiidae	Tripterygiidae 1	4	-	-	-	-	0.3 (0.8)	-	0.1 (0.2)	-

A three-way PERMANOVA indicated that species composition differed significantly between sites, with no other factors or interactions showing a significant effect (Table 2.5). A permutational pairwise test was not run as site was the only significant factor.

Table 2.5 Results of the three-way PERMANOVA conducted on square-root-transformed abundance data for March 2013. Site (Random, 2 levels: Algoa Bay, St Francis Bay), position (Fixed, 2 levels: onshore, offshore), depth (Fixed, 2 levels: surface, bottom). **p<0.01

Source	df	SS	MS	F
Site	1	2245.10	2245.10	13.16**
Position	1	66.13	66.12	0.41
Depth	1	204.22	204.22	1.48
Site x Position	1	160.10	160.10	0.94
Site x Depth	1	138.21	138.21	0.81
Position x Depth	1	70.53	70.53	0.48
Site x Position x Depth	1	146.56	146.56	0.86
Res	8	1365.20	170.65	
Total	15	4396.10		

The DistLM marginal tests indicated that wind speed, wave height and temperature were the environmental factors that contributed significantly to the variation in larval fish density (Table 2.6).

Table 2.6 DistLM marginal test results for March 2013 . Prop = proportion of variance explained by each variable. **p<0.01

Variable	SS	F	Prop
Wind speed	1216.70	5.36	0.28**
Wave height	1518.10	7.39	0.35**
Clouds	617.94	2.29	0.14
Temperature	2000.30	11.69	0.46**
Depth	282.33	0.96	0.06
Current speed	105.12	0.34	0.02
Current direction	308.70	1.06	0.07

The fitted model visualised by the dbRDA plot explained a total of 63.5% of the variance (Figure 2.4). Temperature, wave height and current direction were the environmental variables mostly responsible for the separation between Algoa Bay and St Francis Bay.

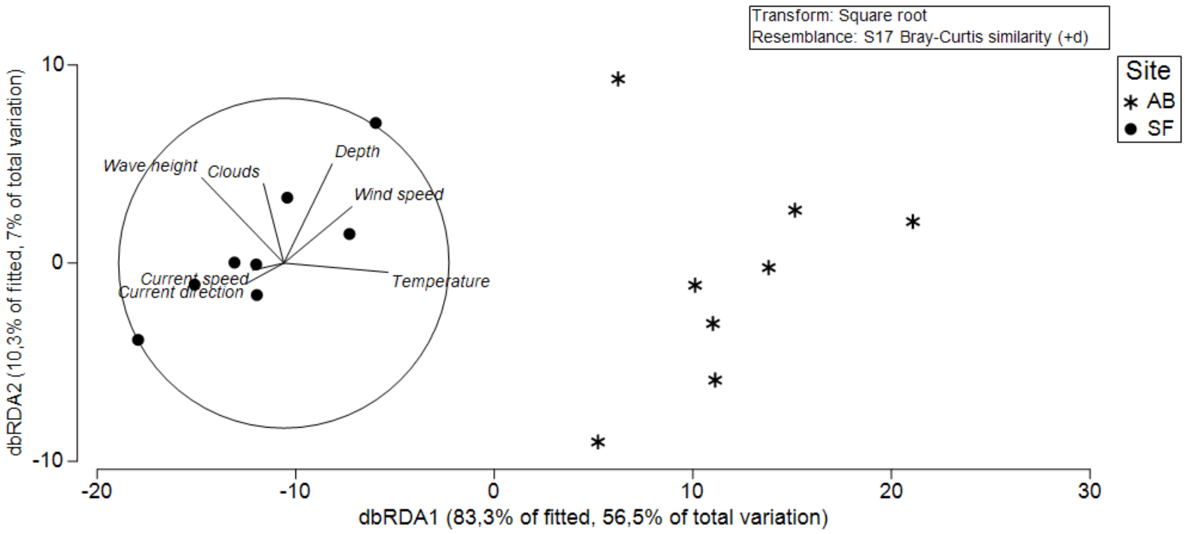

Figure 2.4 Distance based redundancy analysis for March 2013 samples plotted against environmental variables. (AB = Algoa Bay, SF = St Francis Bay)

3.2.3 September Analysis

Results of the PERMDISP analysis for September, site ($F_{1,14} = 4.16$, $p > 0.06$), position ($F_{1,14} = 0.22$, $p > 0.6$) and depth ($F_{1,14} = 1.00$, $p < 0.3$) indicated homogeneity of data according to the factors considered.

During September (spring) a total of 675 larval fish were captured between the two bays (excluding vertical tows). In Algoa Bay 442 larval fish were captured, while in St Francis Bay 233 larval fish were captured. In Algoa Bay, 20 species were recorded and 21 species in St Francis Bay (Table 2.7).

Table 2.7 Species, total catch, mean density per $100m^3$ and standard deviation (in brackets), for Algoa Bay and St Francis Bay, onshore and offshore, surface and bottom in September 2013

Family	Species	Total Catch	Algoa Bay				St Francis Bay			
			Onshore		Offshore		Onshore		Offshore	
			Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
Blenniidae	Blenniidae 1	7	-	-	0.9 (0.6)	0.3 (0.1)	-	-	-	-
	Blenniidae 3	3	-	0.2 (0.3)	-	-	-	-	0.2 (0.3)	-
	Blenniidae 4	19	1.0 (1.1)	0.4 (0.9)	1.3 (1.8)	-	-	-	-	-
	Blenniidae 5	7	-	-	0.6 (0.9)	0.3 (0.5)	-	-	-	-
	Blenniidae 6	18	-	-	-	-	1.0 (1.4)	0.1 (0.2)	0.4 (0.6)	-
Carangidae	Carangidae 1	17	-	-	0.2 (0.4)	0.2 (0.2)	-	0.9 (0.2)	-	0.9 (1.3)
Clupeidae	*Sardinops sagax*	2	-	-	-	-	-	0.3 (0.6)	-	-
Cynoglossidae	*Cynoglossus capensis*	88	-	3.8 (4.0)	-	1.4 (1.08)	-	-	0.1 (0.2)	0.1 (0.2)
	Cynoglossus zanzibarensis	7	-	-	-	1.9 (0.2)	-	-	-	-
Dussumieriida	*Etrumeus whiteheadi*	2	-	0.4 (0.6)	-	-	-	-	-	-
Engraulidae	*Engraulis encrasicolus*	316	2.8 (1.8)	13.6 (2.1)	0.5 (0.5)	13.7 (1.0)	0.6 (0.4)	3.0 (0.6)	2.8 (0.7)	7.0 (2.4)
Gobiesocidae	Gobiesocidae 1	2	-	-	-	-	0.8 (0.2)	0.1 (0.2)	0.1 (0.2)	-
	Gobiesocidae 3	3	-	-	-	-	-	0.3 (0.6)	-	0.1 (0.2)
Gobiidae	*Caffrogobius nudiceps*	4	-	-	-	-	-	0.2 (0.2)	-	0.2 (0.3)
	Psammogobius knysnaensis	2	-	-	-	-	0.2 (0.2)	-	-	-
Sciaenidae	*Argyrosomus inodorus*	1	-	-	-	0.2 (0.2)	-	-	-	-
Scorpaenidae	*Scorpaenidae 1*	8	-	-	-	-	0.8 (0.2)	0.4 (0.1)	-	0.4 (0.1)
Soleidae	*Heteromycteris capensis*	23	-	0.1 (0.2)	-	1.9 (1.0)	0.2 (0.2)	-	0.5 (0.9)	0.5 (0.6)
	Solea turbynei	20	0.3 (0.5)	0.9 (1.3)	-	1.4 (2.5)	-	0.1 (0.2)	-	-
Sparidae	*Chrysoblephus laticeps*	10	-	-	-	0.9 (1.1)	-	0.3 (0.6)	0.2 (0.3)	0.1 (0.2)
	Diplodus capensis	56	1.1 (0.4)	0.3 (0.4)	3.9 (1.3)	0.6 (0.5)	-	0.8 (0.1)	0.6 (0.7)	-
	Lithognathus 1	3	-	-	0.6 (0.9)	-	-	-	-	-
	Pagellus natalensis	1	-	-	-	-	-	0.8 (0.1)	-	-
	Rhabdosargus globiceps	5	0.6 (0.8)	-	0.1 (0.2)	-	0.8 (0.2)	0.8 (0.1)	-	0.1 (0.2)
	Sparidae 1	2	0.1 (0.2)	-	-	0.2 (0.2)	-	-	-	-
	Sparidae 2	2	-	0.1 (0.2)	-	0.2 (0.2)	-	-	-	-
	Sparidae 3	1	0.1 (0.2)	-	-	-	-	-	-	-
	Spondyliosoma emarginatum	24	0.03	-	0.7 (0.4)	0.3 (0.4)	0.4 (0.2)	0.2 (0.3)	0.7 (0.9)	0.3 (0.5)
Syngnathidae	*Syngnathus temminckii*	1	-	-	-	-	-	-	-	0.1 (0.2)
Tetraodontidae	Tetraodontidae 1	9	-	-	-	-	0.4 (0.4)	0.4 (0.1)	-	0.1 (0.2)
Tripterygiidae	Tripterygiidae 1	11	-	-	-	-	0.2 (0.3)	0.4 (0.2)	0.6 (0.4)	-

During September, the results of the three-way PERMANOVA revealed that larval fish communities differed significantly in relation to site and its interaction with position and depth. (Table 2.8).

Table 2.8 Results of the three-way PERMANOVA conducted on square-root-transformed abundance data for September 2013. Site (Random, 2 levels: Algoa Bay, St Francis Bay), position (Fixed, 2 levels: onshore, offshore), depth (Fixed, 2 levels: surface, bottom). *p<0.05, **p<0.01

Source	df	SS	MS	F
Site	1	3761.30	3761.30	8.34**
Position	1	1068.50	1068.50	0.87
Depth	1	3652.90	3652.90	1.86
Site x Position	1	1228.50	1228.50	2.73*
Site x Depth	1	1967.50	1967.50	4.36**
Position x Depth	1	202.23	202.23	0.39
Site x Position x Depth	1	514.36	514.36	1.14
Res	8	3606.60	450.83	
Total	15	16002.00		

Pairwise tests for the significant interaction between site (Algoa Bay and St Francis Bay) and position (onshore and offshore) indicated there were significant differences between onshore and offshore in Algoa Bay only. Pairwise tests of the interaction between site (Algoa Bay and St Francis Bay) and depth (surface and bottom) indicated there were significant differences between surface and bottom within and between Algoa Bay and St Francis Bay.

The DistLM marginal tests indicated wind speed, wave height, temperature and depth were the environmental factors that significantly contributed to the variation in larval fish density (Table 2.9).

Table 2.9 DistLM marginal test results for September 2013 . Prop = proportion of variance explained by each variable. *p<0.05, **p<0.01

Variable	SS	F	Prop.
Wind speed	2531.90	2.63*	0.16
Wave height	3761.30	4.30**	0.24
Clouds	4097.90	4.82**	0.26
Temperature	1616.70	1.57	0.10
Depth	3998.70	4.66**	0.25
Current speed	1461.40	1.41	0.09
Current direction	1485.60	1.43	0.09

The fitted model visualised by the db-RDA plot indicated that a total of 54.4% of the variance in the larval fish community was explained by the first two axes (Figure 2.5). Cloud cover, wave height and wind speed drove the separation between Algoa Bay and St Francis Bay. Current direction drove the separation between the surface and bottom larval fish assemblages (Figure 2.5).

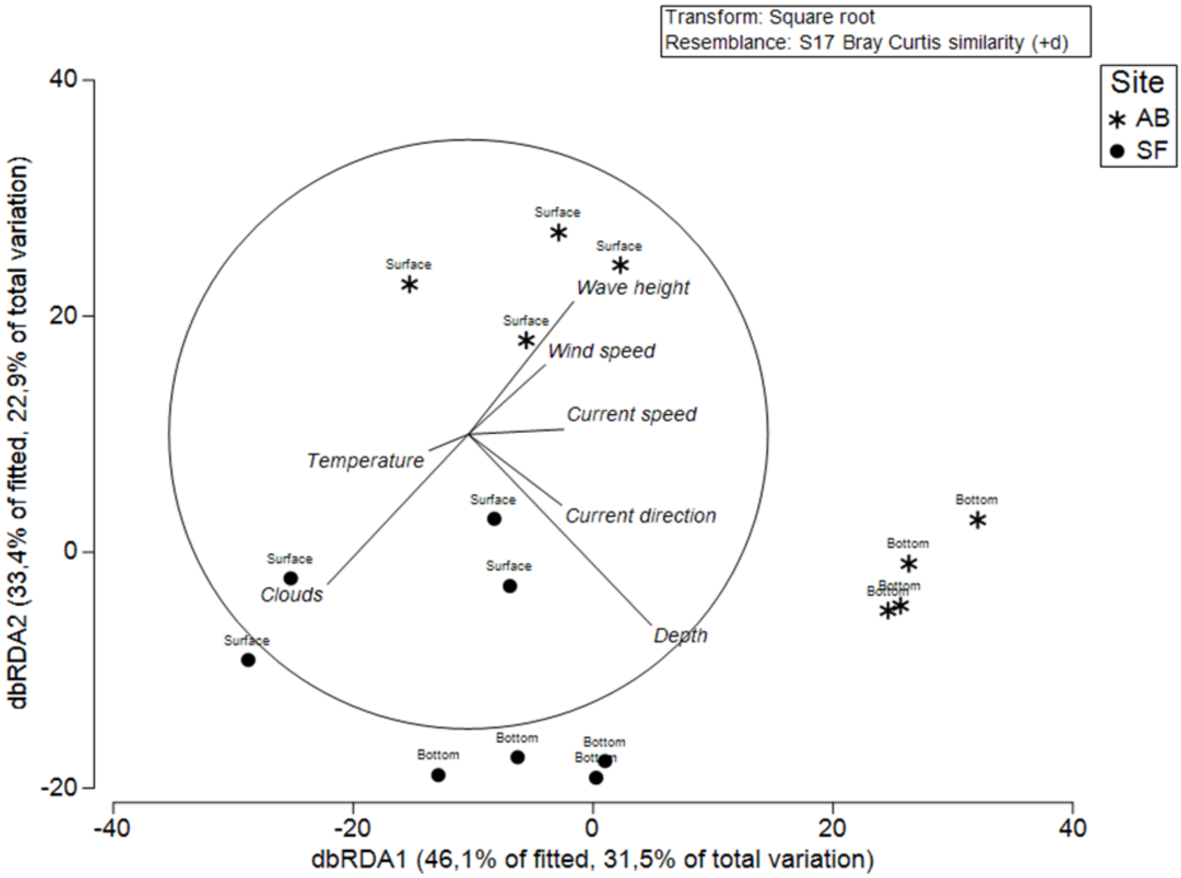

Figure 2.5 Distance based redundancy analysis for September 2013 samples. Site and depth plotted against environmental variables with site labelled on each plot (AB = Algoa Bay, SF = St Francis Bay)

Results from the SIMPER analysis showed that *Engraulis encrasicolus, Diplodus capensis* (Family: Sparidae), Blenniidae 4, *Cynoglossus capensis* (Family: Cynoglossidae) and *Spondyliosoma emarginatum* (Family: Sparidae) dominated Algoa Bay (Table 2.10). St Francis Bay was dominated by *E. encrasicolus*, Tripterygiidae 1, *S. emarginatum*, Tetraodontidae 1 and *Heteromycteris capensis* (Family Soleidae; Table 2.11).

Onshore stations were dominated by *E. encrasicolus*, *S. emarginatum*, *D. capensis*, Tetraodontidae 1 and Blenniidae 4 (Table 2.12). Offshore stations were dominated by *E.*

encrasicolus, D. capensis, S. emarginatum, H. capensis and C. capensis (Table 2.13). Surface samples were dominated by *E. encrasicolus*, *D. capensis*, *S. emarginatum*, Tripterygiidae 1 and *H. capensis* (Table 2.14). Bottom samples were dominated by *E. encrasicolus*, *C. capensis*, *H. capensis*, Carangidae 1 and Scorpaenidae 1 (Table 2.15). *Engraulis encrasicolus* contributed the most to all groups.

Table 2.10 SIMPER results of contributing species in Algoa Bay during September 2013

Species	Av.Abund	Contrib%	Cum.%
Engraulis encrasicolus	0.74	44.33	44.33
Diplodus capensis	0.33	21.97	66.30
Blenniidae 4	0.19	8.68	74.98
Cynoglossus capensis	0.38	7.46	82.44
Spondyliosoma emarginatum	0.13	6.60	89.04

Table 2.11 SIMPER results of contributing species in St Francis Bay during September 2013

Species	Av.Abund	Contrib%	Cum.%
Engraulis encrasicolus	0.53	47.12	47.12
Tripterygiidae 1	0.14	9.78	56.91
Spondyliosoma emarginatum	0.15	7.70	64.60
Tetraodontidae 1	0.11	7.53	72.13
Heteromycteris capensis	0.12	6.12	78.26

Table 2.12 SIMPER results of contributing species to onshore stations during September 2013

Species	Av.Abund	Contrib%	Cum.%
Engraulis encrasicolus	0.60	55.28	55.28
Spondyliosoma emarginatum	0.10	8.64	63.92
Diplodus capensis	0.13	6.46	70.38
Tetraodontidae 1	0.09	6.32	76.70
Blenniidae 4	0.12	5.35	82.05

Table 2.13 SIMPER results of contributing species to offshore stations during September 2013

Species	Av.Abund	Contrib%	Cum.%
Engraulis encrasicolus	0.68	50.05	50.05
Diplodus capensis	0.28	15.11	65.15
Spondyliosoma emarginatum	0.18	10.30	75.45
Heteromycteris capensis	0.20	9.55	85.00
Cynoglossus capensis	0.27	3.84	88.85

Table 2.14 SIMPER results of contributing species to surface samples during September 2013

Species	Av.Abund	Contrib%	Cum.%
Engraulis encrasicolus	0.35	41.98	41.98
Diplodus capensis	0.30	23.27	65.25
Spondyliosoma emarginatum	0.18	16.64	81.89
Tripterygiidae 1	0.09	4.93	86.82
Heteromycteris capensis	0.08	3.61	90.44

Table 2.15 SIMPER results of contributing species to bottom samples during September 2013

Species	Av.Abund	Contrib%	Cum.%
Engraulis encrasicolus	0.93	62.60	62.60
Cynoglossus capensis	0.40	8.88	71.48
Heteromycteris capensis	0.17	4.24	75.72
Carangidae 1	0.15	4.17	79.89
Scorpaenidae 1	0.10	4.05	83.94

During September, species richness and abundance differed between bays. Within Algoa Bay, three species of Blenniidae, *Cynoglossus capensis*, *Lithognathus* 1 and two species of Sparidae were found that were not found in St Francis Bay. On the other hand, Blenniidae 6, two species of Gobiesocidae, Tripterygiidae 1, *Caffrogobius nudiceps* (Family: Gobiidae), *Psammogobius knysnaensis* (Family: Gobiidae), Scorpaenidae 1 and Tetraodontidae 1 were all found in St Francis Bay, with none being caught in Algoa Bay (Figure 2.6).

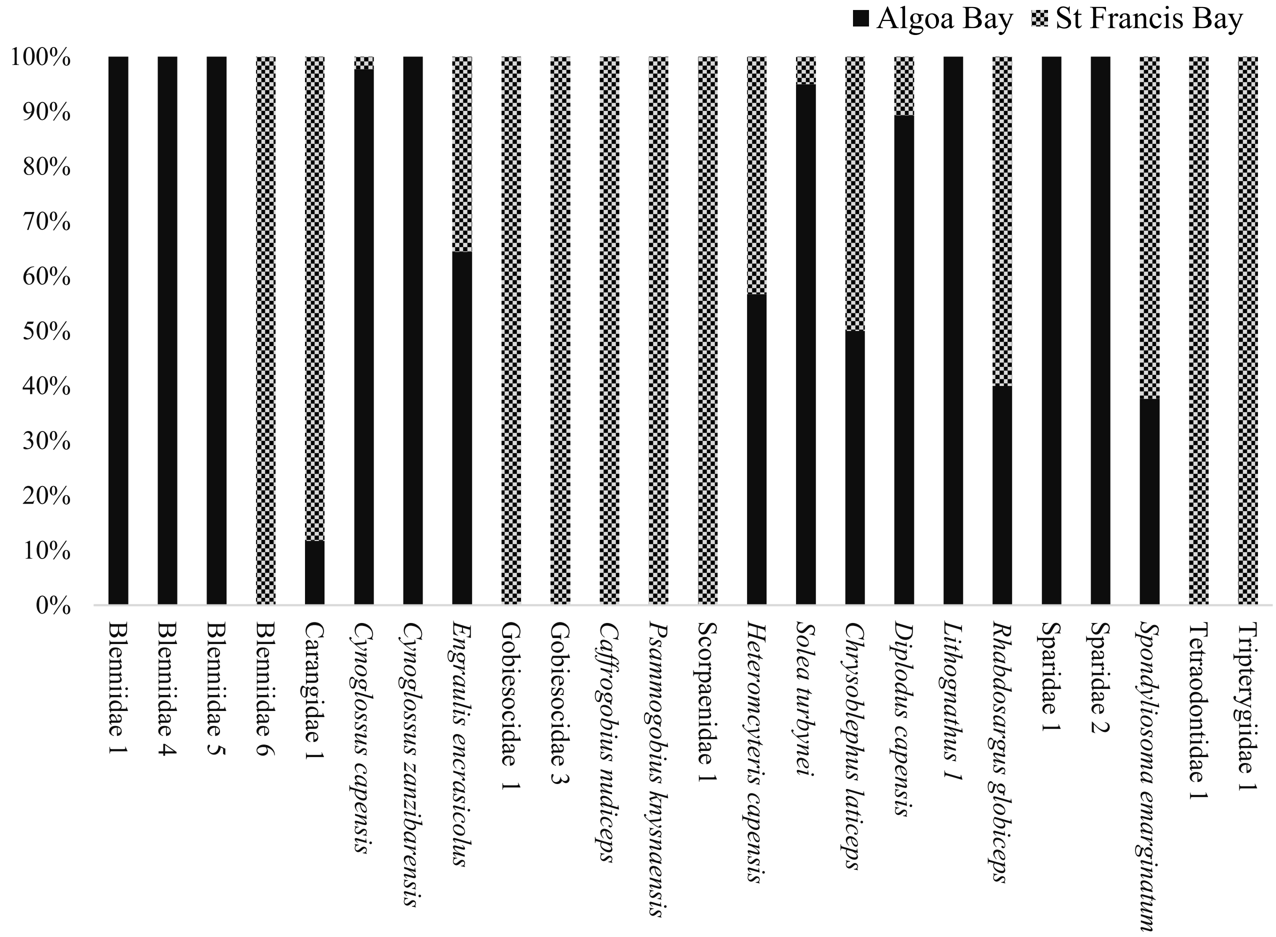

Figure 2.6 Proportion of species density with original abundances of n > 3 caught in each bay during September 2013. Algoa Bay solid and St Francis Bay hatched.

3.3 **Bathymetric Map**

The bathymetric data provided by the South African Navy Hydrographic Office showed the seabed of Algoa Bay to consist mostly of sand and mud, or a combination of the two. St Francis Bay, although still largely sandy, contained more rock features on the seabed than Algoa Bay. These rock features, which are very likely rocky reefs, were in close proximity of the St Francis Bay sampling site. Algoa Bay sampling site on the other hand was all sand and mud (Figure 2.7).

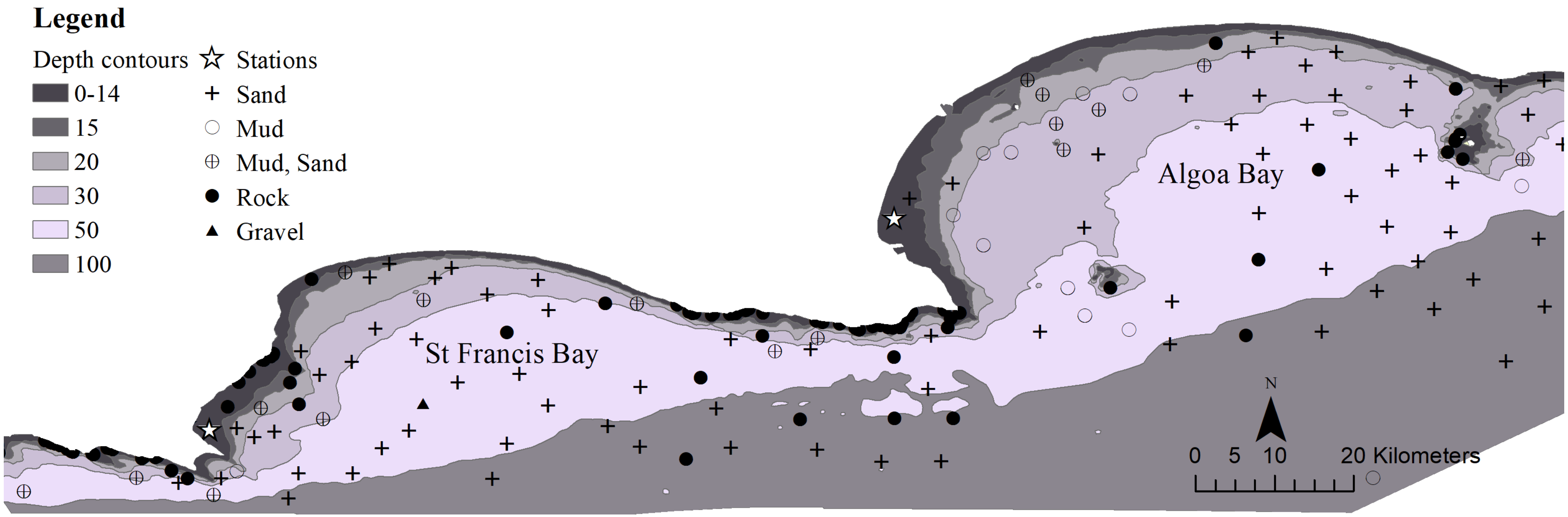

Figure 2.7 Bathymetric map of Algoa Bay and St Francis Bay showing depth contours and seabed features including substratum type. White asterisks (stations) indicate the sampling sites for Algoa Bay and St Francis Bay. Data provided by the South African Navy Hydrographic Office and map created using ArcGIS 10.3

4 Discussion

The composition and abundance of larval fish communities differed substantially in Algoa Bay and St Francis Bay between March (autumn) and September (spring). The majority of coastal fishes spawn in late winter through to spring (Booth & Beretta, 1994; Gray & Miskiewicz, 2000; Pattrick & Strydom, 2008; Garrido *et al.*, 2009), supporting the results of the present study with higher abundances of larval fishes occurring in September. Clear differences in larval fish composition between Algoa Bay and St Francis Bay, onshore and offshore stations as well as between surface and bottom depth strata were observed during September. During March, larval fish catches in Algoa Bay were dominated by the anchovy, *Engraulis encrasicolus*. The larvae of this species dominates the coastal waters of most warm-temperate regions and can usually be found throughout the year, with density peaks occurring in spring through to summer (hence the high numbers in the March catches). Within the shallow nearshore of Algoa Bay, Beckley (1986) and Pattrick & Strydom (2008), found *Caffrogobius* spp to dominate larval fish catches in autumn. In the present study, however, only two individuals of *Caffrogobius nudiceps* were captured in March 2013. In St Francis Bay, no *E. encrasicolus* or *C. nudiceps* larvae were captured. Instead the most abundant species included larvae from Blenniidae and Tripterygiidae fish families, though both were low in numbers (n < 5). It is difficult to deduce any possible conclusion in March due to such low numbers of larval fishes being caught.

In September, greater densities of larval fishes were caught at the bottom during the day, at both the onshore and offshore stations. Similarly, higher densities of larval fishes at the bottom have been observed in the nearshore region of the subtropical east coast of South Africa (Harris & Cyrus, 1999). Generally, higher abundances of larval fish can be found at deeper depths and/or close to the bottom of the sea floor during the day (Brewer & Kleppel, 1986; Ruso & Bayle-Sempere, 2006; Auth *et al.*, 2007; Stenevik *et al.*, 2007). Many authors suggest this is either a way to avoid predators or to optimise feeding conditions (Hobson, 1973; Munk *et al.*, 1989; Miner & Stein, 1993; see Chapter 3 of this thesis for more detail). Furthermore, differences between the surface and the bottom in the species composition of larval fish communities were explained by current speed. The surface currents, apart from the offshore station in St Francis Bay, were slower than bottom currents. This is unusual as surface currents are generally faster than bottom currents (Boyd *et al.*, 1992; Goschen & Schumann, 1994; Schumann *et al.*, 2005; Goschen *et al.*, 2012). Sampling during this study was confined to periods of low wind speeds (<15 knots) to increase efficiency of sampling. Surface winds drive surface currents (Roberts, 1990), however, surface winds can have little influence on bottom currents (Schumann *et al.*, 2005). Presumably, because there was low wind speed during the time of the study, surface currents would be slower. Roberts (1990) found that the surface and bottom currents also flow in different directions, this study supports that as surface currents flowed predominantly in a southerly direction, which was parallel with the coast, while the bottom currents flowed more westerly, onshore to the coast.

The species (*E. encrasicolus, C. capensis, H. capensis,* Carangidae 1 and Scorpaenidae 1) contributing most to bottom samples all hatch from pelagic eggs. Larval fish from pelagic eggs hatch at smaller sizes and are less developed than larvae from benthic eggs (Leis, 1991) and so their distribution can be more strongly affected by currents. However, even as preflexion larvae, they are still able to swim for short periods of time, and even though horizontal swimming may not be probable, they can swim vertically (Fisher *et al.*, 2000). So perhaps fish larvae position themselves vertically where offshore transport would be the least, i.e. at the bottom with currents transporting larvae closer inshore. In the tropical waters off Barbados, densities of larval fish are greater in deeper onshore currents than slower currents flowing parallel to the shore (Cowen & Castro, 1994; Paris & Cowen, 2004). Off the warm temperate southeast coast of Australia, it was suggested that *Engraulis australis* (Family: Engraulidae) larvae use the currents to stay close to the shore (Kent et al., 2013). These studies, including the present study, conform to Armsworth's (2001) model that larval fish take advantage of favourable currents to maximise the efficiency of their dispersal (Armsworth, 2001).

During September, offshore larval fish densities were higher than onshore for both Algoa Bay and St Francis Bay. This was similarly observed in the western sector of the nearshore in Algoa Bay (Pattrick & Strydom, 2008), where densities of larval fishes were greater at the 15 m depth contour than the 5 m depth contour. Likewise, off the subtropical east coast of South Africa (2.5 km offshore, 28 m deep; Harris *et al.*, 1999) and in the warm-temperature region of the Tsitsikamma National Park MPA (3.8 km offshore, 80 m deep; Tilney & Buxton, 1994) larval fish densities increased with depth. A similar trend was also observed off the north-eastern temperate New Zealand coast, where abundances of larvae where greater at 3.2 km and 6 km offshore than 0.5 km offshore (Tricklebank *et al.*, 2006). In a summative assessment of the larval fishes off the Island of Oahu in tropical Hawaii, it was found that larvae of reef species with pelagic eggs are most abundant offshore (10-12 km, 1800 m deep; Leis & Miller, 1976). Species contributing to offshore assemblages for the present study included sand, reef and pelagic species: *Engraulis encrasicolus*, *Diplodus capensis*, *Spondyliosoma emarginatum*, *Heteromycteris capensis* and *Cynoglossus capensis* (Heemstra & Heemstra, 2004). Apart from *E. encrasicolus*, a pelagic species, and *S. emarginatum* which lays benthic eggs (Heemstra & Heemstra, 2004), all of the above mentioned species are coastal with pelagic eggs (Brownwell, 1979; Beckley, 1986). The larval fishes contributing most to the onshore stations included reef associated species: Tetraodontidae 1 and Blenniidae 4. Although *E. encrasicolus, S. emarginatum* and *D. capensis* also contributed to the onshore assemblages, their densities were greater offshore than onshore. Tetraodontidae and Blenniidae are both benthic taxa, which produce benthic eggs. Similar trends have been observed off the coast of central Chile (Hernández-Miranda *et al.*, 2003) and off the Island of Oahu in Hawaii (Leis & Miller, 1976), where the larvae of species laying benthic eggs are more abundant closer to the shore. Likewise, in Algoa Bay, Pattrick & Strydom (2008) observed that coastal species that produce benthic eggs decrease in density with an increase in distance from the shore. The distribution of *S. emarginatum*, however, did not follow this general trend; despite being a species that lays benthic eggs it was found further offshore. Pattrick & Strydom (2008) found a similar trend in Algoa Bay where *S. emarginatum* had greater densities at the 15 m depth contour than the 5 m depth contour. *Spondyliosoma emarginatum* is only one of two sparid species that lay demersal eggs (Leis *et al.*, 2002). The eggs are laid in a depression they create out of the sand (Heemstra & Heemstra, 2004) and perhaps the deeper sites provide a better habitat for egg-laying and are a more suitable and safer environment for the hatched larvae. However, little is known about the early life history of *S. emarginatum* and so to fully understand their distribution, more work is needed on their early life histories (Beckley, 1989; Leis *et al.*, 2002).

During September, larval fish assemblages in Algoa Bay were dominated by Engraulidae, Sparidae, Blenniidae and Cynoglossidae. In previous studies in the Bay (Beckley, 1986; Pattrick & Strydom, 2008), Gobiidae and Clupeidae contributed the most to the overall larval fish catches. In the present study, neither Gobiidae nor Clupeidae were found in Algoa Bay. Off the temperate west coast of Portugal (Garrido *et al.*, 2009) and off the tropical south eastern coast of Mexico (Vásquez-Yeomans *et al.*, 1998), Gobiidae larvae were predominantly found at night with few being caught during the day. This is supported in the present study in Chapter 3, where densities of Gobiidae larvae were higher at night than during the day. Beckley (1986) found very few Sparidae in Algoa Bay compared to the present study, where Sparidae contributed to the dominant taxa. Pattrick & Strydom (2008) similarly found higher abundances of Sparidae larvae compared to Beckley (1986). The presence of sparid larvae in the present study supports the results of Pattrick & Strydom (2008), suggesting that spawning is occurring closer to shore.

No previous study has focussed on assessing the nearshore composition of larval fish in St Francis Bay. Studies within the bay have focused on estuaries and their adjacent surf zones (Strydom, 2003; Strydom *et al.*, 2003; James & Harrison, 2010). A comparison of the larval fish assemblages between St Francis Bay and Algoa Bay highlighted very different species compositions. St Francis Bay was dominated by *E. encrasicolus*, Tripterygiidae 1, *S. emarginatum*, Tetraodontidae 1 and *H. capensis*. Furthermore, Gobiesocidae 1, Tripterygiidae 1, Scorpaenidae 1, Tetraodontidae 1 and Blenniidae 6 were found exclusively in St Francis Bay. Carangidae 1 and *S. emarginatum*, although not exclusive, had greater densities in St Francis Bay than in Algoa Bay. Although Gobiesocidae, Tripterygiidae, Scorpaenidae, Tetraodontidae, Carangidae and *S. emarginatum* have previously been found in Algoa Bay their abundances and percentages to the total larval fish catch were low (Beckley, 1986; Pattrick & Strydom, 2008).

Notable differences exist in the bathymetric features of the two bays. The underwater terrain in Algoa Bay is characterised by mostly sand and mud, with a few rocky features. The Algoa Bay sampling site was exclusively sand and the larval fish assemblages comprised predominately of pelagic and sand associated species: *E. encrasicolus*, *Cynoglossus capensis*, *Cynoglossus zanzibarensis*, *Solea turbynei* (Family: Soleidae), *H. capensis* and *Lithognathus* spp (Family: Sparidae). Beckley (1986) and Pattrick & Strydom (2008) found the above mentioned species, apart from *Lithognathus*, to dominate the catches in Algoa Bay. Juvenile *Lithognathus mormyrus* have been found to dominate juvenile fish assemblages in surf zones within Algoa Bay (Lasiak, 1986) suggesting Algoa Bay could be a spawning and nursery area for *Lithognathus* spp (Lasiak, 1986). St Francis Bay on the other hand, presents a mixture of rocky features, sand and gravel, indicating the presence of rocky reefs, particularly around the present study's sampling site. The species found exclusively in St Francis Bay: Gobiesocidae 1, Tripterygiidae 1, Scorpaenidae 1, Tetraodontidae 1, *S. emarginatum*, Carangidae 1 and Blenniidae 6, are all reef associated species (Heemstra & Heemstra, 2004). Off the west coast of Portugal, species dominating the larval assemblage from a rocky reef habitat were predominantly species from adults which lay demersal eggs including species in the families Blenniidae, Gobiidae and Tripterygiidae (Borges *et al.*, 2007). The rocky reef larval composition for the above mentioned study is very similar to that found in St Francis Bay and this could confirm the rocky reef prevailing nature of St Francis Bay and hence the prevalence of reef associated species.

5 Conclusion

The results from this study shed a bit more light on the composition and distribution of larval fish assemblages in Algoa Bay and St Francis Bay, South Africa. St Francis Bay is an area that has had no previous work on larval fish dynamics and so this study provides baseline information on species composition and distribution. The difference in larval fish assemblages between Algoa Bay and St Francis Bay strongly suggests that the different habitats are influencing the larval fish compositions. Currents could play an important role in the spatial distributions of the larval fishes, with larvae potentially vertically positioning themselves within favourable current regimes. The results of this study show how complex larval distribution can be in coastal bays, with not only spawning modes and behaviour, but also environmental factors driving larval fish distributions. To better our understanding of these larval fish assemblages, further studies, particularly in St Francis Bay need to be completed, keeping in mind the spatial and temporal complexities of the larval fish assemblages.

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Chapter 3

Diel vertical migration of ichthyoplankton in two adjacent bays off the south coast of South Africa

1 Introduction

Diel vertical migration (hereafter, DVM) is a phenomenon common among most zooplankton and ichthyoplankton (Leis, 1986; Lampert, 1989; Pearre, 2003). It is described as the vertical migration of aquatic animals over a 24-hour period from one depth stratum in the water column to another. Plankton generally follow two types of diel vertical migration: type I and type II (Neilson & Perry, 1990). Type I DVM is the upward movement from the bottom of the water column (where they occur during the day) to the surface at dusk/night. Type II DVM is the downward movement from the surface layers of the water column (where they occur during the day) to the bottom at night. Type II DVM is not limited to animals, with flagellates and dinoflagellates also showing this type of movement (Eppley *et al.*, 1968; Cullen, 1985; Passow, 1991). Zooplankton, including euphausiids (Fragopoulu & Lykakis, 1990), copepods (Williams & Conway, 1984) amphipods (Heywood, 1996) and chaetognaths (Irigoien *et al.*, 2004) generally, though not always, follow a type I DVM.

Diel vertical migration has long been associated as a mechanism for predator avoidance and prey selection (Pearre, 1979; Garrido *et al.*, 2009). These two processes can greatly alter the behaviour of planktonic animals. Zooplankton and ichthyoplankton follow large assemblages of food and or prey (Huntley & Brooks, 1982; Fortier & Leggett, 1983). However, in the case of the presence of predators, quite often zooplankton and ichthyoplankton will switch to a type II migration pattern, actively trying to avoid visual predators using Type I migration (Hobson, 1973; Ohman *et al.*, 1983; Ohman, 1990; Brodeur & Rugen, 1994).

In addition to biological mediation of DVM, abiotic components can also switch diel migration on and off. Light, for example, is a major and most obvious cue for the onset of DVM. Fish larvae are visual feeders (Munk *et al.*, 1989) and move up and down the water column where there is optimal light for feeding while seeking light levels that are still low enough to avoid detection by predators (Clark & Levy, 1988). In relation to this, turbidity, which decreases the light intensity in the water, also affects the DVM, with larval fish occupying the surface during the day only when the top layers of the water column are turbid (Palomera, 1991). Temperature can also alter the depth at which animals are found as fish larvae tend to aggregate around the thermocline during the day (Heath *et al.*, 1988).

The diel vertical migration of larval fishes, thus does not often follow the simple upwards movement (type I DVM) seen in many species of zooplankton. In the northern Gulf of Alaska, the larval fishes dominating catches show a Type II migration (Brodeur & Rugen, 1994). While in Santa Monica Bay, California (Brewer & Kleppel, 1986) and the Great Barrier Reef, Australia (Leis, 1991), larval fishes accumulate at bottom depths during the day, whereas at night they are dispersed throughout the water column. Differential diel vertical migration patterns can also be determined according to ontogeny (Brewer & Kleppel, 1986; Conway *et al.*, 1997). DVM is thus a complex mechanism and varies according to developmental stage, behaviour and environmental stimuli. It is therefore clear that DVM in larval fishes should be considered at the family/species level.

In South Africa, surf zone larval accumulation areas (Whitfield, 1989; Harris & Cyrus, 1996; Cowley *et al.*, 2001; Hutchings *et al.*, 2002; Watt-Pringle & Strydom, 2003) and estuarine nursery habitats (Beckley, 1984; Whitfield, 1999; Strydom, 2015) have been well identified and studied. Investigations into the coastal nearshore larval fish assemblages off the South African coastline have, however, been isolated (Beckley, 1986; Tilney & Buxton, 1994; Tilney *et al.*, 1996; Harris *et al.*, 1999; Pattrick & Strydom, 2008) and focus on the larval fish composition and more notably, the diel vertical migration patterns of larval fishes is still scarce. The understanding of diel migration patterns can greatly improve our understanding of larval fish lifecycles, settlement success and survival.

The aim of this study was to investigate the DVM of larval fishes, in two adjacent shallow coastal bays. Algoa Bay and St Francis Bay are two large, relatively sheltered bays situated in the province of the Eastern Cape. The specific objectives of the present study were to: a) increase our understanding of the diel vertical migration patterns of the larval fish assemblages in Algoa Bay and St Francis Bay, b) determine which species exhibit diel vertical migration patterns, and if so the specific patterns they display, and c) assess the environmental conditions that may influence these diel migration patterns.

2 Material and Methods

2.1 Study Site

Study sites for this part of the study have been explained in full in Chapter 2, therefore, to avoid repetition, please refer to Chapter 2 for a more detailed descriptive account and geographical map. Algoa Bay (33.928100°S 25.618710°E) and St Francis Bay (34.167830°S 24.851370°W; Figure 2.1) were selected to investigate the composition, distribution and abundance of larval fishes within the coastal nearshore. Sampling was conducted during known peak larval abundance in the region (Beckley, 1986; Pattrick & Strydom, 2008), in March/April (autumn) and September/October (spring) 2013. Although seasonality was not taken into account for this study as sampling only took place once during these distinct times, seasons do play a clear role in determining larval fish abundances in the area (Pattrick & Strydom, 2008) and reference to seasonality has therefore been made to some extent. Within each bay, two nearshore stations, ~ 200 m apart and ~1 km from the coast were selected. At each station, sampling was conducted during the daytime (06:00-18:00) and repeated again after dark (18:00-23.00).

2.2 Environmental Variables

Environmental variables measured for this study were identical to Chapter 2, therefore please refer to Chapter 2 for a detailed description of the methodology used for the collection of the environmental data.

2.3 Larval fish Collection and Identification

At each station, larval fishes were collected by means of a set of bongo nets with a 57 cm diameter and mesh aperture of 500 µm, deployed from a davit and winch system on a 13 m Category B research vessel, uKwabelana. A one way clutch General Oceanics flowmeter was suspended from the frame of the net to quantify the volume of water sampled. The bongo nets were pulled parallel to the shore while the boat maintained a speed of 2 knots for three minutes. Horizontal tows were repeated twice at one meter above the seafloor (referred to as bottom tows) and twice at one meter below the sea surface (referred to as surface tows). The depth of the bongo nets was determined by the altimeter on board the boat and the rope connected to the bongo nets was let out 1 m short the depth of the sea floor. A vertical tow was done for each bottom tow to correct for larval fish that could have been caught while hauling the nets to the surface (Figure 2.2). Nets were rinsed into a 250 µm sieve, samples were transferred into 500 ml sample jars and fixed in 10% formaldehyde in seawater. During the September sampling, samples were preserved in absolute ethanol for possible DNA analysis. Samples from each of the bongos were pooled and analysed as one sample. In the laboratory, larval fish were separated from the rest of the sample, counted and identified to the lowest possible taxon (Olivar, 1986; Beckley, 1989; Cambray & Bok, 1989; Neira *et al.*, 1998; Leis & Carson-Ewart, 1999; Leis *et al.*, 2002; Wood, 2003; Richards, 2005; Strydom & Neira, 2006). The standard length of each larva was measured to the nearest 0.1 mm, using the methods from Neira *et al.* (1998) under a stereomicroscope fitted with an eyepiece micrometer with 0.1 mm precision. Larvae were further categorised into preflexion, flexion and postflexion stages. The remaining zooplankton in each sample were placed into a measuring cylinder and allowed to settle for 10 minutes and a settled volume estimate of zooplankton was recorded in millilitres to the nearest ml. It should be noted that the day samples for this part of the study are the same samples as the onshore samples in Chapter 2.

2.4 Statistical Analysis

2.4.1 Environmental Data

Patterns of environmental data were examined using the Primer 6 PERMANOVA+ software package (version 6.1.15). Draftsman plots were produced to check for skewedness in the distribution of data. Current speed and direction, depth, temperature and zooplankton were log (x+1) transformed to correct for skewedness. Patterns in environmental variables were observed by performing a Principle Component Analysis (PCA; Clarke & Warwick, 2001) on the normalised Euclidean distance similarity matrices of the environmental variables (Clarke & Gorley, 2006). PCA reduces the dimensions of the data set without loss of important information. It does this by transforming a number of correlated variables into a smaller number of uncorrelated variables called principal components. The first principal component (Principal Component 1) is the linear combination of x-variables that has the maximum variance accounting for as much variation in the data as possible. The second principal component (Principal component 2) accounts for as much of the remaining variation as possible. The PCA explains the maximum variance with the fewest possible number of principal components (Clarke & Gorley, 2015).

2.4.2 Biological Data

All bottom tows were corrected for possible contamination of larval fishes unintentionally caught in the vertical column of water while hauling the net to the surface. Please refer to Chapter 2 for a descriptive account on how this was calculated.

Mean densities (MD) of all larvae and settled zooplankton volumes (referred to as zooplankton) were calculated using the following formula to determine the density per 100m^3.

$$\mathrm{MD} = \frac{\text{No. of larvae or ml of zooplankton}}{(\text{flow meter revolutions} \div \text{calibration value in m}^3)} \times 100$$

Larval fish community analyses were run on Primer 6 PERMANOVA+ software package (version 6.1.15). Densities of larvae were all square-root transformed and Bray-Curtis similarities between samples were used to construct a similarity matrix (Bray & Curtis, 1957). The distance-based test for homogeneity of multivariate dispersions, PERMDISP (Anderson, 2006) was used to test for homogeneity of site (Algoa Bay and St Francis Bay), season (March and September), time (day and night) and depth (surface and bottom). Season was heterogeneous, and so analyses for the March and September data were run independently of each other. A distance-based test for homogeneity was repeated for March and September individually.

A three-way PERMANOVA (PERMANOVA + for Primer-6; Anderson, 2005) was employed to assess the effects of the factors: site (Random, 2 levels: Algoa Bay, St Francis Bay), time (Fixed, 2 levels: day, night), depth (Fixed, 2 levels: surface, bottom) and of all factor combinations on the larval fish community separately for March and September. Permutated pairwise tests were run on significant combination of factors.

Species contributing most to the average dissimilarities between the groups: site, time and depth were obtained using the SIMPER (similarity percentages) routine (Warwick *et al.*, 1990).

The relationships between environmental variables and the larval fish community were examined using a distance-based linear model (DistLM) and observed using distance-based redundancy analysis ordination (db-RDA; Legendre & Anderson, 1999). Marginal tests (999 permutations) were performed to determine the environmental factors with the greatest influence on the larval fish communities.

Weighted mean depth (WMD) for larval fish and zooplankton occurrence was calculated for the surface and bottom as follows:

$$\mathrm{WMD} = \sum (d_i * n_i)/\sum n_i$$

(Worthington, 1931; Pearre, 2003), where d_i = the depth stratum sampled and n_i = the density of larval fish caught at d_i.

Only six taxa for March and 19 taxa for September were present in enough sample sets ($n > 2$) to allow for analysis on WMD.

Diel vertical migration (DVM) was calculated by subtracting the night WMD from the day WMD. Positive values indicate a positive DVM (moving upwards in the water column during the night), while negative values indicate a reverse diel vertical migration (RDVM; moving downwards in the water column during the night; Pearre, 2003). Species present at only one of the two depths were excluded from this estimate.

A general linear factorial model was run on species showing either DVM or RDVM, to test for significant differences in density of individual taxa between times (Fixed, 2 levels: day and night) and/or depths (Fixed, 2 levels: surface and bottom; STATISTICA Version 13).

Larval fish exhibiting DVM were correlated to zooplankton using a simple linear (Pearson r) correlation. P-values were Bonferroni adjusted (Feise, 2002).

3 Results

3.1 Environmental Variability

Mean sea water temperatures in Algoa Bay in March were 21.6 °C (SD ± 0.46 °C) and 17.9 °C (SD ± 0.13 °C) in September. Mean sea water temperatures in St Francis Bay in March were 17.8 °C (SD ± 0.40 °C) and 18.3 °C (± 0.30 °C) in September. Mean bottom depth sampled in Algoa Bay for both March and September was 10.9 m, with the maximum depth reaching 12.6 m. Mean bottom depth sampled in St Francis Bay was 8.2 m with the maximum depth reaching 10.6 m. Algoa Bay in March experienced an average wind speed of 2.1 knots and 0.8 m wave height. In September, average wind speed was 1.6 knots with 1.6 m waves. St Francis Bay in March experienced an average wind speed of 1 knot and average wave height of 1.6 m, in September average wind speed was 1 knot and 0.8 m wave height (Table 3.1 and Table 3.2).

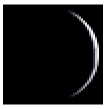
Table 3.1 Mean (n=2) environmental variables for Algoa Bay and St Francis Bay during March 2013. Wind speed (knots), wave height (m), clouds (oktas), temperature (°C), depth (m), average current speed (cms^{-1}), average current direction, zooplankton density (per $100m^3$) and average volume of water filtered through the bongos (m^3)

Environmental Variable	Algoa Bay				St Francis Bay			
	Day		Night		Day		Night	
	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
Wind speed	2,0	2,5	2,0	2,0	1,0	1,0	1,0	1,0
Wave height	1,0	1,5	0,5	0,5	1,7	1,7	1,5	1,5
Clouds	2,0	2,0	1,0	1,0	2,0	2,0	2,0	2,0
Temperature	22,2	21,6	21,6	21,1	18,0	17,8	18,2	17,2
Depth	1,5	9,5	1,6	12,5	1,5	6,2	1,0	10,4
Current speed	4,7	6,8	7,1	10,0	3,6	6,1	2,5	8,0
Current direction	26,0	170,5	336,9	265,0	108,3	302,7	278,6	267,3
Zooplankton	16,9	2,5	24,5	184,4	12,7	15,3	0,2	0,2
Volume water filtered	464,1	185,1	384,4	410,2	335,5	546,8	508,0	460,3

Table 3.2 Mean (n=2) environmental variables for Algoa Bay and St Francis Bay during March 2013. Wind speed (knots), wave height (m), clouds (oktas), temperature (°C), depth (m), average current speed (cms^{-1}), average current direction, zooplankton density (per $100m^3$) and average volume of water filtered through the bongos (m^3)

Environmental Variable	Algoa Bay				St Francis Bay			
	Day		Night		Day		Night	
	Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
Wind speed	1,5	1,5	1,8	1,8	0,5	0,5	1,5	1,5
Wave height	1,5	1,5	1,8	1,8	0,8	0,8	0,8	0,8
Clouds	1,0	1,0	0,0	0,0	3,5	3,5	3,0	3,0
Temperature	17,8	17,8	18,1	17,9	18,3	18,0	18,7	18,1
Depth	1,6	9,6	1,4	12,2	1,6	5,5	1,5	10,6
Current speed	3,8	12,7	5,8	5,0	2,9	5,4	3,9	14,0
Current direction	192,9	298,7	40,1	201,3	185,4	283,2	211,8	306,2
Zooplankton	7,1	3,2	21,1	14,8	16,7	27,6	1,2	1,4
Volume water filtered	312,3	319,9	722,8	324,7	403,9	386,5	648,5	502,8

Table 3.3 Sampling dates and times with the respective moon phase, sunrise and sunset.

Site	Algoa Bay	St Francis Bay	Algoa Bay	St Francis Bay
Date	3rd March	15th April	23rd September	3rd October
Moon Phase				
Sunrise	06:09	06:40	06:05	05:51
Sunset	18:47	17:54	18:14	18:21
Sample times	10:30-11:20	13:00-14:00	15:00-17:00	16:00-17:00
	19:00-20:30	20:00-21:00	21:00-23:00	20:30-22:00

Clear spatial variation between St Francis Bay and Algoa Bay was evident in the PCA (Figure 3.1). Samples from St Francis Bay were distributed within the negative quadrant of the Principal Component 1, while those from Algoa Bay were distributed within the positive quadrant, apart from one datum point. The majority of bottom samples were distributed within the negative quadrant of the Principal Component 2, barring three data points, while surface samples were more randomly distributed (Figure 3.1). The linear coefficients linking the environmental variables to the principle components showed cloud cover, temperature and wind speed separating Algoa Bay and St Francis Bay along the Principal Component 1 (Figure 3.1).

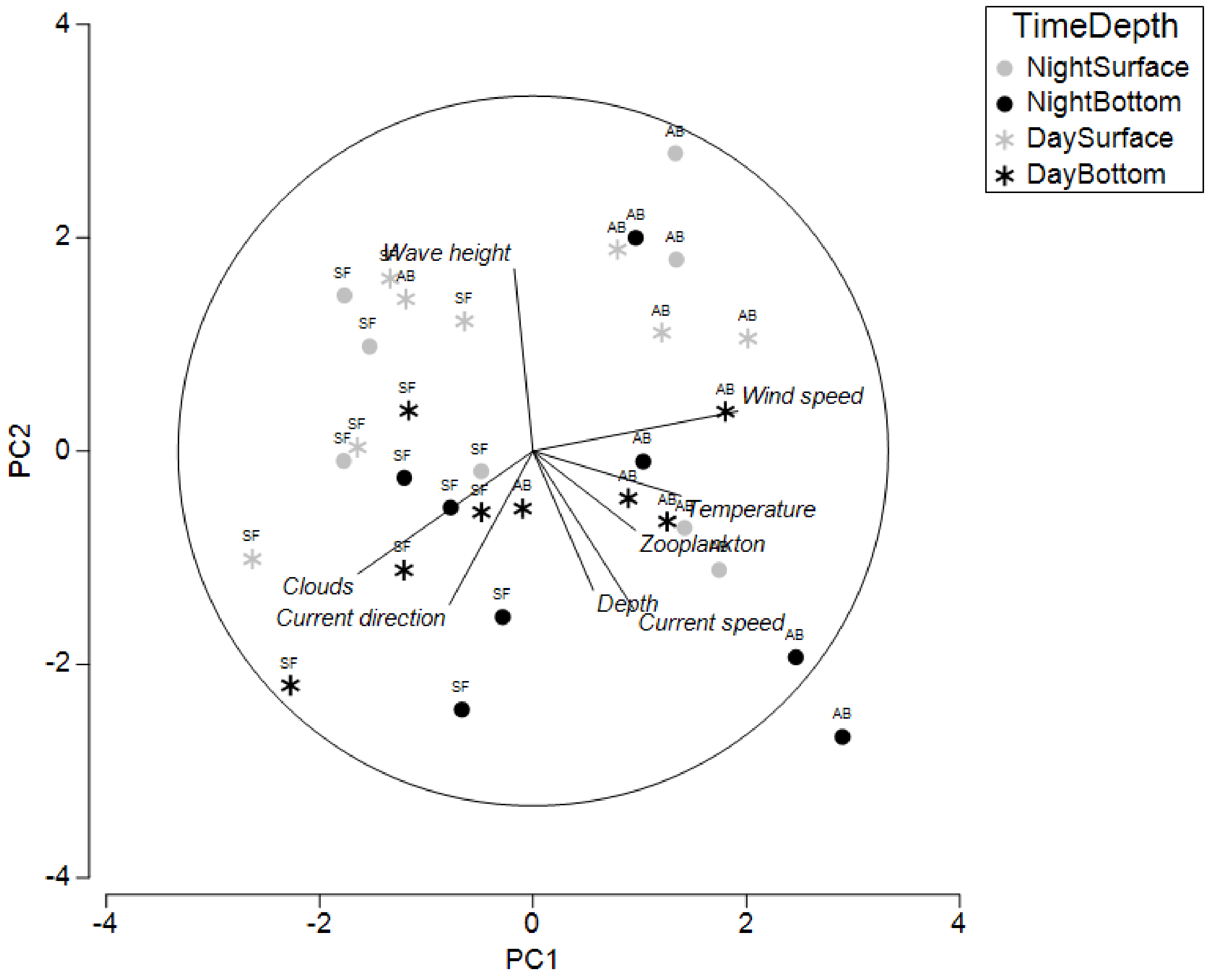


Figure 3.1 Two-dimensional scatter plot of the first and second principal components of environmental variables (wind speed (knots), wave height (m), cloud (oktas), temperature (°C), depth (m), average current speed (cms^{-1}), average current direction) and zooplankton during day and night, surface and bottom for March and September 2013 in Algoa Bay (AB) and St Francis Bay (SF). Vectors of the linear correlations between individual variables are superimposed on the graph

PCA indicated that 27.4% of the variability among all the environmental parameters could be explained by the first component (PC 1) and 23.6% by the second component (PC 2) with the first two principal components alone explaining more than 50% of the total environmental variability. PC 1 showed high correlation with clouds and current direction, with a strong yet negative relationship with wind speed, temperature, current speed and zooplankton volume (Table 3.4).

Table 3.4 Eigenvectors determined from PCA for environmental variables (wind speed, wave height, clouds, temperature, depth, average current speed, average current direction) and zooplankton

Variable	PC1	PC2	PC3	PC4	PC5
% Variation	27.40	23.60	20.30	10.90	8.80
Wind speed	-0.58	0.11	-0.01	0.29	-0.44
Wave height	0.05	0.51	-0.48	0.02	0.03
Clouds	0.49	-0.35	0.31	0.43	-0.01
Temperature	-0.42	-0.13	0.43	0.13	-0.27
Depth	-0.17	-0.39	-0.51	-0.05	-0.13
Current speed	-0.28	-0.45	-0.32	0.41	0.52
Current direction	0.24	-0.43	-0.28	-0.31	-0.58
Zooplankton	-0.29	-0.22	0.23	-0.67	0.34

Zooplankton showed variable results among the two sampling periods as well as the sites. Although there was no community analysis, some overall observations could be made (Table 3.5). Zooplankton biomass was greater at night than during the day, apart from one instance in St Francis Bay in September, where zooplankton biomass was greater during the day at the bottom. At night, zooplankton was relatively similar for the surface and bottom, apart from in Algoa Bay during March, where a very large volume was found at the bottom, consisting mainly of mysids (± 90%). Algoa Bay (March) and St Francis Bay (September) showed a greater volume of zooplankton at the surface during the day. It was noted that a large amount of chaetognaths in St Francis Bay were collected at the surface during the night in September.

Table 3.5 Mean (n=2) estimated settled volume (ml) of zooplankton in ml for Algoa Bay and St Francis Bay, during day and night at the surface (S) and at the bottom (B)

March								Sept							
Algoa Bay				St Francis Bay				Algoa Bay				St Francis Bay			
Day		Night		Day		Night		Day		Night		Day		Night	
S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B
64	9	113	500	1	1	11	10	88	144	129	127	84	23	126	104

3.2 Larval Fish Assemblages

3.2.1 Overall Larval Fish Composition and Developmental Stages

A total of 1102 larval fishes were collected, comprising 16 fish families and 36 species. Only 112 larvae were caught in the vertical tows and the corrected proportions (see Chapter 2, Figure 2.2) were subtracted from the values for their respective species in the bottom catches. The following results are based on the density values (per 100m³) of the larval fishes. Day catches made up 32% of the total larval fish catch, while night catches made up 68%. During the day, 27% of the larval fish catch occurred at the surface while 73% were at the bottom. At night, surface catches comprised 52% of the total larval fish catch and bottom catches were 48%. Preflexion larvae contributed the most to the overall catch, contributing 79% towards the total catch, with flexion stage larvae contributing 14% and postflexion larvae only contributing 7%. Only one juvenile, a Mugilidae, was caught. During night sampling, the proportional catches of flexion and postflexion larvae increased (Figure 3.2).

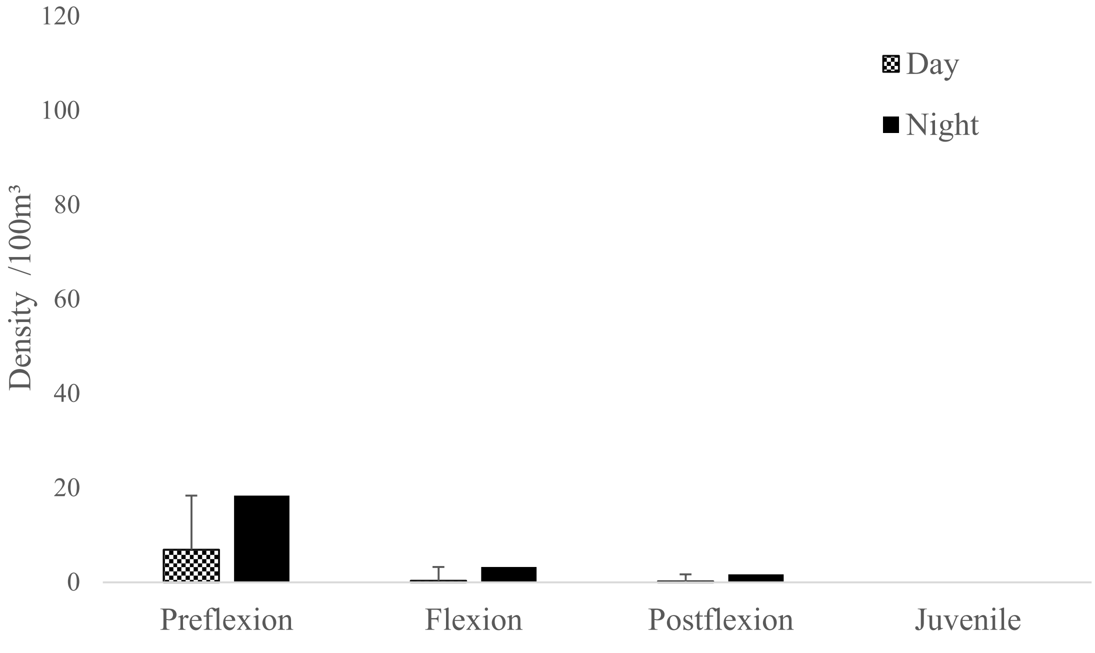


Figure 3.2 Percentages of densities of larval fish stages caught during the day and night. Larval fish densities pooled for Algoa Bay, St Francis Bay March and September.

Algoa Bay was dominated by two fish families. Engraulidae made a total contribution of 62% to the total larval fish catch and Gobiidae, 14%. St Francis Bay larval fish catches were dominated by Engraulidae (46%) with Gobiesocidae (15%) and Blenniidae (15%), making equal contributions. The rest of the fish families made up <1% of the total larval fish catches in both bays. March samples made up only 9% of the total catch while September made up 91%.

The distance-based test for homogeneity of multivariate dispersions (PERMDISP) showed site ($F_{1,30} = 1.31$, $p > 0.3$), time ($F_{1,30} = 0.09$, $p > 0.8$) and depth ($F_{1,30} = 0.30$, $p > 0.6$) to be homogenous. Season however was significantly heterogeneous ($F_{1,30} = 42.16$, $p < 0.001$) and therefore analysed separately.

3.2.2 March Larval Fish Composition and Developmental Stages

During March (autumn), a total of 90 larval fish were captured between the two bays (excluding the vertical tows). Day time catches of larval fish contributed 37% to the total catch in March while 63% were caught at night. During the day, 61% of the larval fish were found at the surface, while 39% were at the bottom. During the night, 35% of the larval fish were found at the surface, while 65% were found at the bottom. *Engraulis encrasicolus* (Family: Engraulidae), the only species within the family, contributed 81% towards the overall larval fish catches in Algoa Bay while in St Francis Bay, Blenniidae 4 and Tripterygiidae 1 contributed 45% and 28% respectively.

PERMDISP for March indicated site ($F_{1,14}= 1.62, p > 0.2$), time ($F_{1,14} = 0.19, p > 0.6$) and depth ($F_{1,14}= 045, p > 0.5$) to be homogenous.

During March, preflexion larvae dominated the day catches, with only a small percentage of flexion and postflexion individuals found at the bottom. At night, again preflexion larvae dominated, but with an increased representation of all larval stages, especially at the bottom (Figure 3.3).

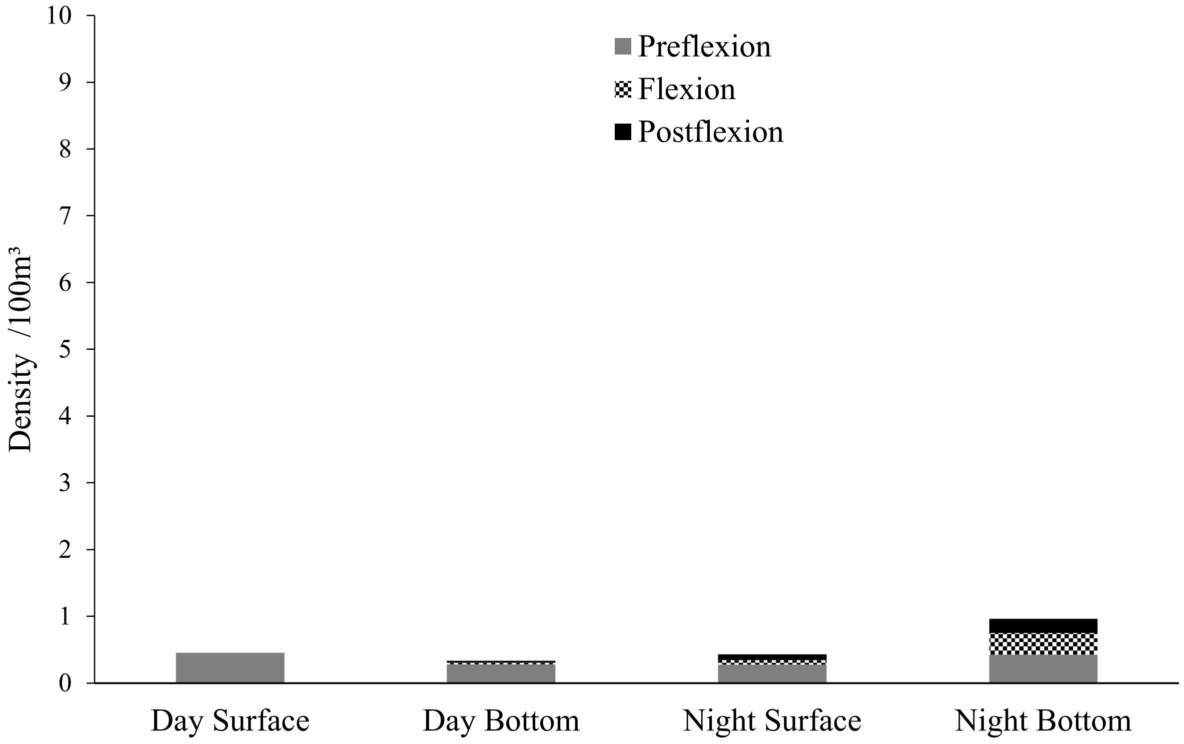


Figure 3.3 Density of flexion stages during March at the surface and the bottom during day and night, for Algoa Bay and St Francis Bay combined

Table 3.6 Total count, mean density per 100m^3 and standard deviation (in brackets) of species, for Algoa Bay and St Francis Bay, during day and night, surface and bottom in March 2013

Family	Species	Total Count	Algoa Bay				St Francis Bay			
			Day		Night		Day		Night	
			Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
Blenniidae	Blenniidae 1	2	0.2 (0.3)	-	-	-	-	-	-	-
	Blenniidae 3	1	-	-	-	-	0.1 (0.1)	-	-	-
	Blenniidae 4	4	-	-	-	-	0.2 (0.0)	0.2 (0.1)	-	-
	Parablennius 1	1	-	0.1 (0.2)	-	-	-	-	-	-
Dussumieriidae	*Etrumeus whiteheadi*	5	-	-	-	-	-	-	-	0.6 (0.5)
Engraulidae	*Engraulis encrasicolus*	45	1.4 (0.6)	0.8 (0.9)	1.2 (1.6)	2.4 (0.2)	-	-	0.1 (0.2)	0.3 (0.4)
Gobiesocidae	Gobiesocidae 1	7	-	-	-	-	-	-	0.1 (0.1)	0.6 (0.4)
Gobiidae	*Caffrogobius gilchristi*	1	-	-	-	-	-	-	-	0.1 (0.2)
	Caffrogobius nudiceps	12	-	0.1 (0.2)	0.2 (0.3)	0.5 (0.1)	-	-	0.1 (0.1)	0.5 (0.3)
	Redigobius dewaali	1	-	-	0.1 (0.2)	-	-	-	-	-
Leiognathidae	Leiognathidae 1	1	-	-	-	-	-	0.1 (0.2)	-	-
Mugilidae	Mugilidae 1	1	-	-	0.1 (0.2)	-	-	-	-	-
Soleidae	*Solea turbynei*	3	0.1 (0.2)	0.1 (0.2)	0.1 (0.2)	-	-	-	-	-
Syngnathidae	*Syngnathus temminckii*	1	-	-	-	-	-	0.1 (0.2)	-	-
Tripterygiidae	Tripterygiidae 1	5	-	-	-	-	0.3 (0.1)	-	0.1 (0.1)	0.1 (0.2)

A three-way PERMANOVA revealed that species composition differed significantly between sites, with no other factors or interactions showing a significant effect (Table 3.7). No permutational pairwise test was run as specific differences among sites, the only significant factor, were not of relevance to the specific question of the study.

Table 3.7 Results of the three-way PERMANOVA conducted on square-root-transformed density data for March 2013. **p<0.01

Source	df	SS	MS	F
Site	1	1796.60	1796.60	8.39**
Time	1	874.90	874.90	2.45
Depth	1	343.89	343.89	2.92
Site x Time	1	357.11	357.11	1.67
Site x Depth	1	117.61	117.61	0.55
Time x Depth	1	360.14	360.14	1.68
Site x Time x Depth	1	214.44	214.44	1.00
Residual	8	1712.70	214.09	
Total	15	5777.50		

The DistLM marginal tests indicated that wind speed, wave height and sea temperature were the environmental factors to significantly explain the variation in larval fish density (Table 3.8).

Table 3.8 DistLM marginal test results for March 2013. Prop = proportion of variance explained by each variable. **p<0.01

Variable	SS	F	Prop
Wind speed	1398.40	4.47	0.24**
Wave height	1171.90	3.56	0.20**
Clouds	560.93	1.51	0.10
Temperature	1769.00	6.18	0.31**
Depth	524.87	1.40	0.09
Current speed	488.08	1.29	0.08
Current direction	332.24	0.85	0.06
Zooplankton	606.97	1.64	0.11

The fitted model visualised by the db-RDA plot explained a total of 67% of the variance in the larval fish community (Figure 3.4). Wave height and wind speed were the environmental variables driving the separation between Algoa Bay and St Francis Bay. Within St Francis Bay, depth drove the separation between day and night as well as surface and bottom during the night (Figure 3.4).

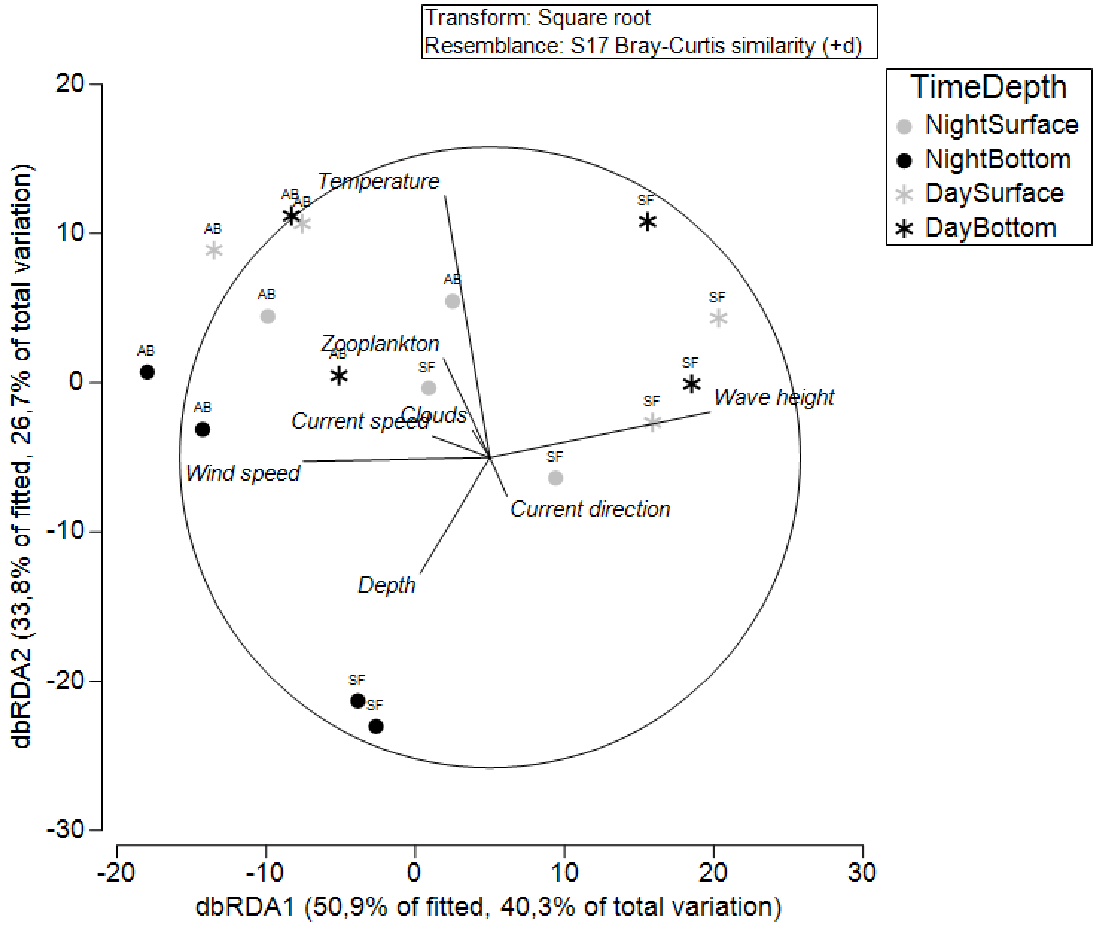


Figure 3.4 Distance based redundancy analysis for March 2013 larval fish assemblages. Time (day and night) and depth (surface and bottom) plotted against environmental variables with site labelled on each plot (AB = Algoa Bay, SF = St Francis Bay)

Results from the SIMPER analysis showed that the species contributing most towards the patterns of larval fish assemblages in both bays were *Engraulis encrasicolus*, *Caffrogobius nudiceps* (Family: Gobiidae), Gobiesocidae 1, Blenniidae 4 and Tripterygiidae 1. *Engraulis encrasicolus* dominated all four groups: night, day, surface and bottom, with highest densities at night (contributing ~50% of the dissimilarity between day and night) and at the surface (contributing >50% of the dissimilarity between surface and bottom; Table 3.9, Table 3.10, Table 3.11 and Table 3.12). *Caffrogobius nudiceps* contributed the second highest to the density of larval fish in the night and bottom samples (Table 3.9 and Table 3.12). Gobiesocidae 1, Blenniidae 4 and Tripterygiidae 1 were only found in St Francis Bay. Gobiesocidae 1 was only found at night with greater densities at the bottom. Blenniidae 4 was only found during the day, with no difference between surface and bottom. Tripterygiidae 1 had similar densities during day and night, but was found only at the surface during the day with similar densities between surface and bottom during the night (Table 3.6).

Table 3.9 SIMPER results of contributing species to night samples in Algoa Bay and St Francis Bay during March 2013

Species	Av.Abund	Contrib%	Cum.%
Engraulis encrasicolus	0.23	48.58	48.58
Caffrogobius nudiceps	0.16	40.57	89.15
Gobiesocidae 1	0.08	6.71	95.86

Table 3.10 SIMPER results of contributing species to day samples in Algoa Bay and St Francis Bay during March 2013

Species	Av.Abund	Contrib%	Cum.%
Engraulis encrasicolus	0.16	46.75	46.75
Blenniidae 4	0.07	42.38	89.13
Tripterygiidae 1	0.04	6.84	95.97

Table 3.11 SIMPER results of contributing species to surface in Algoa Bay and St Francis Bay during March 2013

Species	Av.Abund	Contrib%	Cum.%
Engraulis encrasicolus	0.17	61.84	61.84
Tripterygiidae 1	0.06	21.73	83.57
Blenniidae 4	0.04	6.79	9.36

Table 3.12 SIMPER results of contributing species to bottom in Algoa Bay and St Francis Bay during March 2013

Species	Av.Abund	Contrib%	Cum.%
Engraulis encrasicolus	0.22	53.57	53.57
Caffrogobius nudiceps	0.13	33.28	86.85
Blenniidae 4	0.04	7.67	94.53

3.2.3 September Larval Fish Composition and Developmental Stages

During September (spring) a total of 800 larval fishes were captured between the two bays (excluding the vertical tows). Day time catches of larval fish contributed 36% to the total catch in September while 64% were caught at night. During the day, 33% of the larval fish were found at the surface, while 67% were at the bottom. During the night, 52% of the larval fish were found at the surface, while 48% were found at the bottom. In Algoa Bay, three species, *Engraulis encrasicolus*, *Solea turbynei* (Family: Soleidae) and *Caffrogobius nudiceps* contributed 58%, 11% and 10% to the total larval fish catch respectively. In St Francis Bay, 5 species; *Engraulis encrasicolus*, (32%) Tripterygiidae 1 (13%), Tetraodontidae 1 (9%), *Spondyliosoma emarginatum* (Family: Sparidae; 9%) and Carangidae 1 (8%), contributed a total of ~70%.

During the September sampling, preflexion larvae dominated day and night and surface and bottom. Flexion stages had greater densities at night than during the day (Figure 3.5).

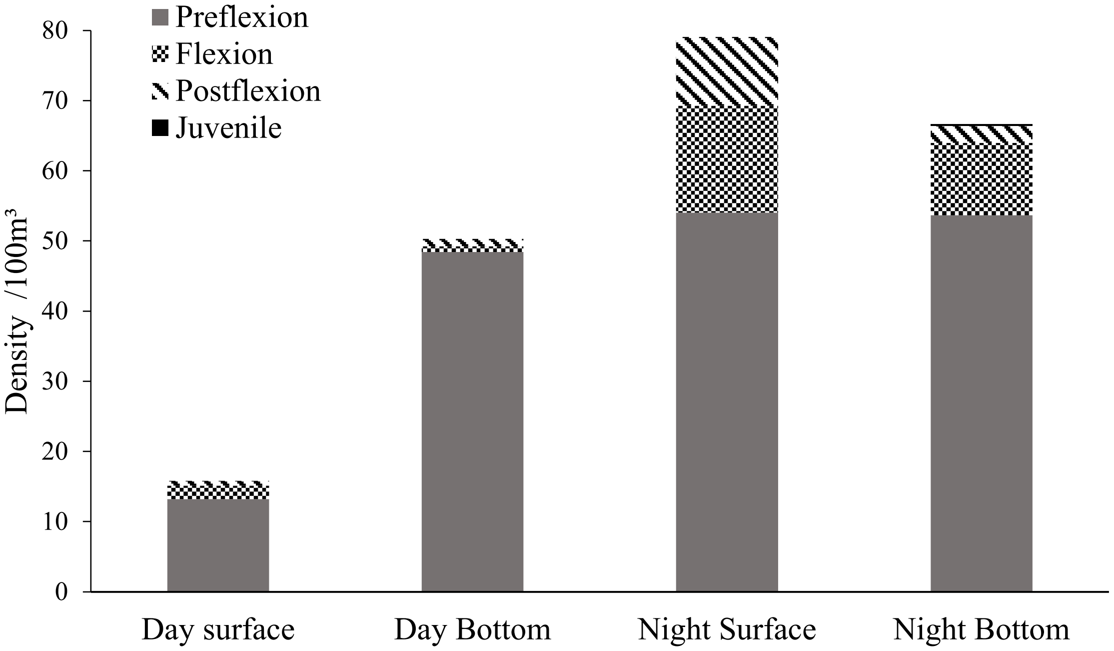


Figure 3.5 Density of flexion stages during September at the surface and at the bottom during day and night, for Algoa Bay and St Francis Bay combined

Table 3.13 Species total count, mean density per 100m^3 and standard deviation (in brackets), for Algoa Bay and St Francis Bay, during day and night, surface and bottom in September 2013

Family	Species	Total Count	Algoa Bay				St Francis Bay			
			Day		Night		Day		Night	
			Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
Blenniidae	Blenniidae 2	1	-	-	-	-	-	-	-	0.1 (0.2)
	Blenniidae 3	1	-	0.2 (0.3)	-	-	-	-	-	-
	Blenniidae 4	13	1.0 (1.1)	0.4 (0.1)	-	-	-	-	-	-
	Blenniidae 5	3	-	-	-	-	-	-	0.3 (0.4)	-
	Blenniidae 6	30	-	-	-	-	1.0 (1.4)	0.1 (0.2)	0.7 (0.9)	1.0 (0.3)
Carangidae	Carangidae 1	16	-	-	-	-	-	0.9 (0.2)	0.4 (0.1)	0.4 (0.1)
Clupeidae	*Sardinops sagax*	4	-	-	0.4 (0.5)	-	-	0.2 (0.1)	-	-
Cynoglossidae	*Cynoglossus capensis*	23	-	3.8 (4.0)	0.2 (0.3)	0.2 (0.3)	-	-	-	-
Dussumieriidae	*Etrumeus whiteheadi*	5	-	0.4 (0.6)	0.5 (0.8)	-	-	-	-	-
Engraulidae	*Engraulis encrasicolus*	448	2.1 (1.8)	13.6 (2.1)	17.1 (8.4)	12.7 (16.0)	0.6 (0.4)	3.0 (0.6)	2.0 (1.0)	12.3 (3.0)
Gobiesocidae	Gobiesocidae 1	7	-	-	-	-	0.1 (0.1)	-	0.3 (0.2)	0.4 (0.1)
	Gobiesocidae 2	1	-	-	-	-	-	-	0.1 (0.1)	-
	Gobiesocidae 3	2	-	-	-	-	-	0.2 (0.1)	-	-
Gobiidae	*Caffrogobius gilchristi*	5	-	-	0.6 (0.4)	0.1 (0.2)	-	-	-	-
	Caffrogobius nudiceps	116	-	-	14.5 (2.5)	2.6 (1.5)	-	0.2 (0.2)	0.3 (0.5)	0.3 (0.4)
	Psammogobius knysnaensis	2	-	-	-	-	0.2 (0.2)	-	-	-
Mugilidae	Mugilidae 2	1	-	-	-	-	-	-	-	0.1 (0.2)
Scorpaenidae	Scorpaenidae 1	7	-	-	-	-	0.1 (0.1)	0.4 (0.1)	-	0.2 (0.0)
Soleidae	Heteromycteris capensis	17	-	0.1 (0.2)	0.3 (0.0)	-	0.2 (0.2)		0.6 (0.0)	0.6 (0.5)
	Solea turbynei	22	0.3 (0.5)	0.9 (1.3)	0.6 (0.4)	0.9 (0.7)	-	0.1 (0.2)	-	0.1 (0.2)

Table 3.13 continued

Family	Species	Total Count	Algoa Bay				St Francis Bay			
			Day		Night		Day		Night	
			Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
Sparidae	*Chrysoblephus laticeps*	3	-	-	-	-	-	0.2 (0.1)	0.1 (0.1)	-
	Diplodus capensis	26	1.1 (0.4)	0.3 (0.4)	-	0.3 (0.1)	-	0.1 (0.1)	0.1 (0.1)	0.2 (0.0)
	Pagellus Natalensis	1	-	-	-	-	-	0.1 (0.1)	-	-
	Rhabdosargus globiceps	4	0.1 (0.1)	-	-	-	0.1 (0.1)	0.1 (0.1)	-	0.1 (0.2)
	Sparidae 1	1	0.1 (0.2)	-	-	-	-	-	-	-
	Sparidae 2	1	-	0.1 (0.2)	-	-	-	-	-	-
	Sparidae 3	1	0.1 (0.2)	-	-	-	-	-	-	-
	Spondyliosoma emarginatum	13	0.2 (0.1)	-	-	-	0.3 (0.2)	0.2 (0.3)	0.4 (0.1)	0.1 (0.2)
Tetraodontidae	Tetraodontidae 1	11	-	-	-	-	0.3 (0.0)	0.4 (0.1)	0.1 (0.1)	0.2 (0.3)
Tripterygiidae	Tripterygiidae 1	15	-	-	-	-	0.2 (0.0)	0.4 (0.2)	0.3 (0.1)	0.8 (0.8)

The PERMDISP for September (spring) showed site ($F_{1,14} = 2.46$, $p > 0.1$), time ($F_{1,14} = 1.26$, $p > 0.2$) and depth ($F_{1,14} = 0.7$, $p > 0.4$) to be homogenous.

During September, the results of the three-way PERMANOVA on the larval fish community yielded significant differences between site, the interaction between site and time, and the interaction between site, time and depth (Table 3.14).

Table 3.14 Results of the three-way PERMANOVA conducted on square-root-transformed density data for September 2013 samples on all larval fish species in Algoa Bay and St Francis Bay. **p<0.01

Source	df	SS	MS	F
Site	1	5098.00	5098.00	14.64**
Time	1	2048.40	2048.40	1.67
Depth	1	1015.20	1015.20	2.97
Site x Time	1	1229.10	1229.10	3.53**
Site x Depth	1	341.50	341.45	0.98
Time x Depth	1	905.50	905.50	0.56
Site x Time x Depth	1	1613.00	1613.00	4.63**
Res	8	2785.70	348.21	
Total	15	15036.00		

Pairwise tests of the interaction between site (Algoa Bay and St Francis Bay) and time (day and night) indicated there were significant differences between day and night in Algoa Bay and in St Francis Bay. Pairwise tests on site*time*depth showed no significant results on all levels.

The results of the DistLM marginal tests indicated that wind speed, wave height, cloud cover and sea temperature were the environmental factors that significantly contributed to the variation in larval fish density (Table 3.15).

The fitted model visualised by the db-RDA plot indicated that a total of 55.6% of the variance in the larval fish community was explained by the first two axes (Figure 3.6). Cloud cover and wave height drove the separation between Algoa Bay and St Francis Bay. Separation between surface and bottom larval densities during the day for both Algoa Bay and St Francis Bay was driven by current speed, depth and zooplankton. Night time samples showed no clear separation (Figure 3.6).

Table 3.15 DistLM marginal test results for September 2013. Prop = proportion of variance explained by each variable. *p<0.05, **p<0.01

Variable	SS	F	Prop.
Wind speed	2112.80	2.29*	0.14
Wave height	4588.70	6.15**	0.31
Clouds	5432.00	7.92**	0.36
Temperature	2591.00	2.92**	0.17
Depth	1048.50	1.05	0.07
Current speed	2063.40	2.23	0.14
Current direction	1286.60	1.31	0.09
Zooplankton	992.25	0.99	0.07

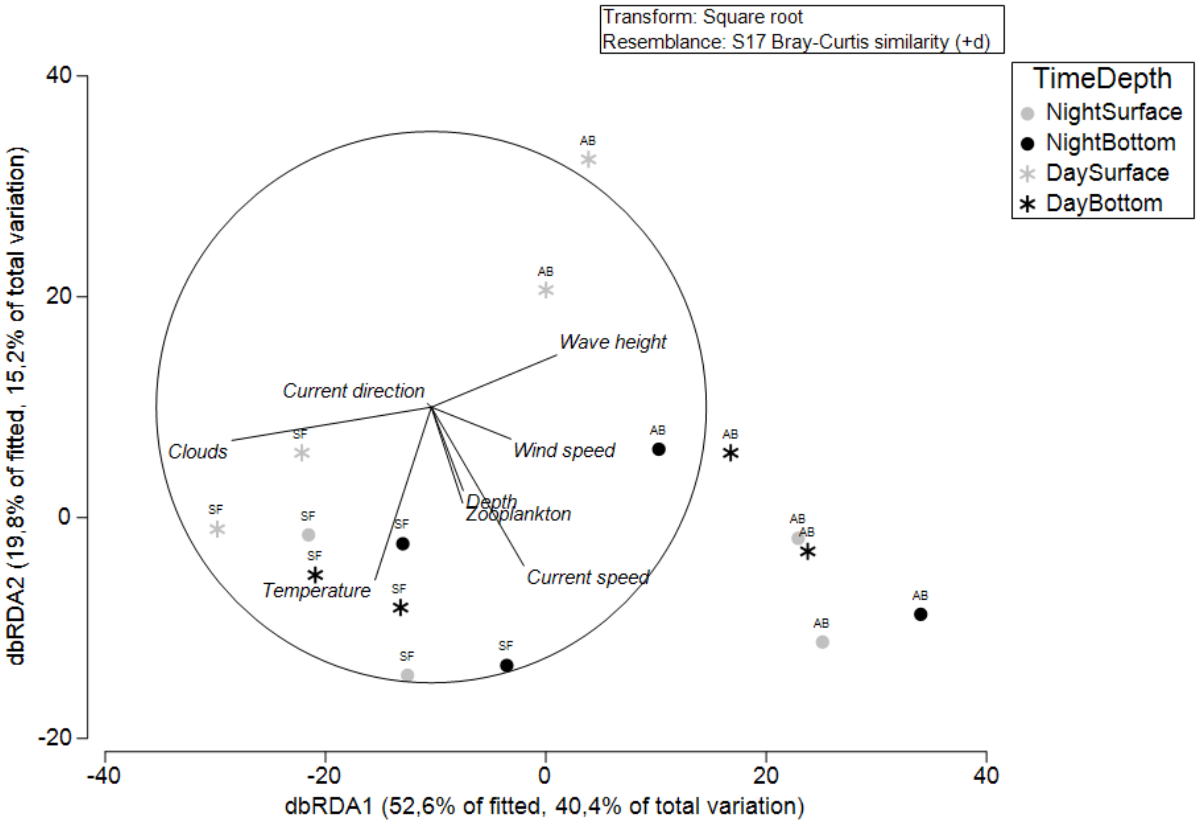


Figure 3.6 Distance based redundancy analysis for September 2013 larval fish assemblages. Time and depth plotted against environmental variables with site labelled on each plot (AB = Algoa Bay, SF = St Francis Bay)

Results from the SIMPER analysis showed night samples were dominated by *Engraulis encrasicolus, Caffrogobius nudiceps* and *Heteromycteris capensis* (Family: Soleidae; Table 3.16), while the day samples were dominated by *E. encrasicolus*, *Spondyliosoma emarginatum* and *Diplodus capensis* (Family: Sparidae; Table 3.17). Surface samples were dominated by *E.*

encrasicolus, S. emarginatum and *H. capensis* (Table 3.18). Bottom samples were dominated by *E. encrasicolus, D. capensis* and *Solea turbynei* (Family: Soleidae; Table 3.19). *Engraulis encrasicolus* contributed to > 50% in all four groups.

Table 3.16 SIMPER results of contributing species to night samples in Algoa Bay and St Francis Bay during September 2013

Species	Av.Abund	Contrib%	Cum.%
Engraulis encrasicolus	0.95	50.34	50.34
Caffrogobius nudiceps	0.48	16.20	66.55
Heteromycteris capensis	0.17	7.75	74.30

Table 3.17 SIMPER results of contributing species to day samples in Algoa Bay and St Francis Bay during September 2013

Species	Av.Abund	Contrib%	Cum.%
Engraulis encrasicolus	0.60	55.28	55.28
Spondyliosoma emarginatum	0.10	8.64	63.92
Diplodus capensis	0.13	6.46	70.38

Table 3.18 SIMPER results of contributing species to surface samples in Algoa Bay and St Francis Bay during September 2013

Species	Av.Abund	Av.Sim	Cum.%
Engraulis encrasicolus	0.60	50.02	50.02
Spondyliosoma emarginatum	0.12	13.46	63.48
Heteromycteris capensis	0.13	8.90	72.38

Table 3.19 SIMPER results of contributing species to bottom samples in Algoa Bay and St Francis Bay during September 2013

Species	Av.Abund	Av.Sim	Cum.%
Engraulis encrasicolus	0.94	60.92	60.92
Diplodus capensis	0.13	7.19	68.10
Solea turbynei	0.17	6.27	74.37

3.2.4 Diel Vertical Migration

In March, *Caffrogobius nudiceps* and *Solea turbynei* showed positive DVM, while *Engraulis encrasicolus* showed reverse DVM. In St Francis Bay, Blenniidae 4 and Tripterygiidae 1 showed RDVM. Zooplankton showed RDVM for both sites (Table 3.20). All other species were excluded due to not being sufficiently abundant (n ≤ 2).

Table 3.20 Weighted mean depths of species and zooplankton in March 2013 for Algoa Bay and St Frances Bay with diel vertical migration (DVM) calculated. Positive values indicate positive DVM, while negative values indicate a reverse DVM (RDVM). Species with abundances < 2 were excluded

	Algoa Bay			St Francis Bay		
Species	Day	Night	DVM	Day	Night	DVM
Caffrogobius nudiceps	9.48	9.40	0.08	-	-	-
Engraulis encrasicolus	4.52	8.96	-4.43	-	-	-
Blenniidae 4	-	-	-	4.05	11.47	-7.42
Solea turbynei	5.44	2.27	3.17	-	-	-
Tripterygiidae 1	-	-	-	1.59	5.85	-4.26
Zooplankton	2.52	11.23	-8.72	3.71	7.57	-3.86

In March, the general linear factorial model, showed a significant effect of time (day and night) and depth (surface and bottom)for *Caffrogobius nudiceps* and a significant interaction between site (Algoa Bay and St Francis) and time (day and night) for Blenniidae 4 (Table 3.21).

Table 3.21 General linear factorial model of species in March showing significant differences between site, time and depth including the interactions between the three. All other species were found to have no significance and not shown. *p<0.05; **p<0.01

Species	df	MS	F	Effect
Caffrogobius nudiceps	1	0.004	4809.902*	Time
Caffrogobius nudiceps	1	0.002	41262.266**	Depth
Blenniidae 4	1	0.000	466.326*	Site*Time

In September, *Engraulis encrasicolus*, *Etrumeus whiteheadi* (Family: Dussumieriidae), *Heteromycteris capensis* and *Cynoglossus capensis* (Family: Cynoglossidae) all showed DVM in Algoa Bay, while *Diplodus capensis*, *Spondyliosoma emarginatum* and *Solea turbynei* showed RDVM. St Francis Bay had a greater number of species showing DVM and RDVM than for Algoa Bay. *Caffrogobius nudiceps* and *Chrysoblephus laticeps* (Family: Sparidae) were the only two species to show positive DVM, the rest all showed RDVM. Zooplankton showed RDVM for both sites (Table 3.22). All other species were excluded due to not being sufficiently abundant (n ≤ 2).

Table 3.22 Weighted mean depths of species and zooplankton in September 2013 for Algoa Bay and St Frances Bay with diel vertical migration (DVM) calculated. Positive values indicate positive DVM, while negative values indicate reverse DVM (RDVM). Species with abundances < 2 were excluded

	Algoa Bay			St Francis Bay		
Species	Day	Night	DVM	Day	Night	DVM
Caffrogobius nudiceps	-	-	-	5.50	5.45	0.05
Diplodus capensis	3.11	12.07	-8.96	5.50	7.84	-2.34
Spondyliosoma emarginatum	-	-	-	3.37	3.83	-0.46
Rhabdosargus globiceps	-	-	-	3.68	10.58	-6.90
Chrysoblephus laticeps	-	-	-	5.52	1.54	3.98
Engraulis encrasicolus	8.52	5.88	2.64	4.84	9.32	-4.48
Etrumeus whiteheadi	9.48	1.57	7.91	-	-	-
Blenniidae 6	-	-	-	2.10	6.85	-4.75
Solea turbynei	7.45	7.71	-0.27	-	-	-
Heteromycteris capensis	9.64	1.43	8.22	1.51	5.81	-4.31
Tetraodontidae 1	-	-	-	3.84	7.73	-3.89
Gobiesocidae 1	-	-	-	2.23	6.49	-4.26
Tripterygiidae 1	-	-	-	4.37	8.17	-3.81
Cynoglossus capensis	9.51	6.70	2.81	-	-	-
Scorpaenidae 1	-	-	-	4.92	10.56	-5.64
Carangidae 1	-	-	-	5.52	5.92	-0.41
Zooplankton	5.73	7.18	-1.46	2.85	5.24	-2.40

In September, the results of the general linear factorial model showed *Caffrogobius nudiceps*, *Diplodus capensis*, *Chrysoblephus laticeps*, Tetraodontidae 1 and Carangidae 1 had a significant interaction among site, time and depth (Table 3.23). *Rhabdosargus globiceps* (Family: Sparidae) showed a significant difference between day and night, whereas *Heteromycteris capensis* showed a significant difference between surface and bottom (Table 3.23).

Table 3.23 General linear factorial model of species in September showing significant differences between site, time and depth including the interactions between the three. All other species were found to have no significance and not shown *p<0.05; **p<0.01

Species	df	MS	F	Effect
Caffrogobius nudiceps	1	0.339	30.123**	Site*Time*Depth
Diplodus capensis	1	0.003	8.050*	Site*Time*Depth
Rhabdosargus globiceps	1	0.000	591.676*	Time
Chrysoblephus laticeps	1	0.000	7.711*	Site*Time*Depth
Heteromycteris capensis	1	0.000	262.003*	Depth
Tetraodontidae 1	1	0.000	446.799*	Site*Time
Carangidae 1	1	0.002	26.815**	Site*Time*Depth

Zooplankton and larval fish showed no correlation between each other after Bonferroni adjustments except in March, where *Caffrogobius capensis* showed a positive correlation with zooplankton in Algoa Bay and Blenniidae 4 showed a positive correlation with zooplankton in St Francis Bay. Before Bonferroni adjustment, however, *C. capensis* showed positive correlation with zooplankton in Algoa Bay in September, as well as *Heteromycteris capensis* and Gobiesocidae 1 in St Francis in September (Table 3.24).

Table 3.24 Results of simple linear (Pearson r) correlation between zooplankton and larval fish exhibiting DVM with original p values and Bonferroni corrected p values for Algoa Bay (AB) and St Francis Bay (SF) during March and September. *Significant p value after Bonferroni adjustment

Site and Season	Species	r	r^2	Original p	Bonferroni adjusted p
AB March	*Caffrogobius nudiceps*	0.807	0.652	0.015*	0.017
SF March	Blenniidae 4	0.934	0.872	0.001*	0.008
AB September	*Caffrogobius nudiceps*	0.832	0.692	0.010	0.005
SF September	*Heteromycteris capensis*	-0.863	0.745	0.006	0.004
	Gobiesocidae 1	-0.764	0.584	0.027	0.004

In summary, larval fish communities differed between seasons and sites. Communities were dominated by *Engraulis encrasicolus* except for St Francis Bay in March. In March no significant DVM was present. In September majority of larvae had RDVM similar to zooplankton, although correlation analyses do not support this. Environmental variables driving the assemblages and most likely DVM are wave height, wind speed and cloud cover.

4 Discussion

Time of year and day, location and depth were important factors contributing to the distribution and composition of the larval fish community in the shallow nearshore, warm-temperate waters of the south coast of South Africa. A clear difference in larval fish assemblages between Algoa Bay and St Francis Bay was observed, while taxon specific, diel vertical migration patterns were also identified. As recorded in several previous studies, larval fish abundance was significantly greater at night than during the day (Harris & Cyrus, 1996; Auth *et al.*, 2007; Primo *et al.*, 2012). During the daytime catches, the majority of fish larvae caught were in the preflexion stage of development. Older larvae in the flexion and postflexion stages have an increased swimming ability (Dudley *et al.*, 2000; Clark *et al.*, 2005; Pattrick & Strydom, 2009) and are able to visually avoid the net (Richardson & Pearcy, 1977; Trnski, 2001; Pearre, 2003). This study confirmed this pattern, with the increase in catches of flexion and postflexion larvae at night, suggesting that the later stage larvae were potentially avoiding the net during the day. Because preflexion larvae dominated all catches, day and night, net avoidance by older larvae would however not alter the fact there were higher abundances of larvae at night than during the day.

4.1 Diel Vertical Migration

Of all 36 taxa that were identified, only eight showed DVM. It should be taken into consideration, however, that some larval fishes e.g. *Etrumeus whiteheadi* did present patterns of DVM, but did not show a significant result because their densities were similar for bottom day and surface night.

Larval fish densities differed considerably between March and September 2013 sampling events, with greater densities in September. Seasonal differences of larval fish abundances in temperate regions have been observed around the world (Booth & Beretta, 1994; Gray & Miskiewicz, 2000; Garrido *et al.*, 2009), with most taxa spawning in late winter to spring. This is true for South Africa (Beckley, 1986; Harris *et al.*, 1999; Pattrick & Strydom, 2008), where abundances of fish larvae are greater during spring than autumn. During the autumn months, *Caffrogobius* species, *Engraulis encrasicolus*, Tripterygiidae species and Blenniidae species show small spawning peaks in Algoa Bay (Beckley, 1986; Pattrick & Strydom, 2008), the present study supports this as these taxa dominated catches during March. Even so, these low numbers caught in March made it impossible to determine any possible DVM for species with the exception of *Engraulis encrasicolus*.

Temperature was shown to influence the larval fish composition in March 2013. During this time, St Francis Bay experienced the lower water temperatures (17.2 °C), specifically at the bottom of the water column, during the night. Temperature can alter DVM if a thermocline is present (Palomera, 1991; Olivar *et al.*, 2014), however no thermocline was present at such shallow depths where sampling was done.

Cloud cover also contributed to the significant spatial difference in larval fish assemblages, especially during the September, spring sampling. When there is an increase in cloud cover, the light intensity penetrating into the column water decreases. Light intensity is a visual cue for the onset of DVM and is particularly relevant for prey-predator interactions (Munk *et al.*, 1989; Miner & Stein, 1993). Larval fishes are visual feeders and during low light levels, larvae move to the upper water column to obtain maximum light intensity for feeding (Munk *et al.*, 1989; Miner & Stein, 1993; Job & Bellwood, 2000). Furthermore, larval fish need to avoid being seen by predators themselves (Nesbitt *et al.*, 1996). Clark & Levy (1988) proposed an "antipredation window", where the light intensity is great enough to feed, but also low enough to avoid predators. They hypothesised that this window occurs at dawn and dusk. However, on cloudy days in the North Sea, clupeids have been found at the surface during the day (Bridger, 1956). Perhaps when it is cloudy and overcast, a third "antipredation window" is provided and the larvae use it to their advantage. It should be noted, however, that in the present study, St Francis Bay did have relatively more cloud cover; it was not completely overcast, but rather patchy where sunlight could still shine through.

Prey availability can alter larval fish DVM as larvae follow the distribution patterns of their prey (Fortier & Leggett, 1983; Batty, 1987). In St Francis Bay (September) the majority of larvae showed RDVM, as did the zooplankton assemblages. No correlations were however present and considering the mesh size of the nets (500µm) would allow smaller prey items to pass through the net it would be speculative to assume that larvae follow their prey.

In St Francis Bay (September), *Engraulis encrasicolus*, *Diplodus capensis*, Tetraodontidae 1 and Tripterygiidae 1 all had higher abundances at the bottom of the water. This coincided with a larger abundance of chaetognaths at the surface than at the bottom. Chaetognaths are planktonic predators (Fortier & Harris, 1989), including predators of larval fishes (Williams & Hart, 1974). The larvae of *E. encrasicolus*, *D. capensis*, Tetraodontidae 1 and Tripterygiidae 1 could have therefore, avoided the predator abundant surface waters, taking refuge at the bottom. *Engraulis encrasicolus* larvae feed at the bottom during the day (Olivar *et al.*, 2001) and migrate to the surface at night by inflating their gas bladder and hence reducing energy expenditure (Uotani, 1973; Hunter & Sanchez, 1976; Olivar *et al.*, 2001). The presence of night feeder predators (Øresland, 1987), however, can greatly alter the typical DVM of *E. encrasicolus* (reviewed in Neilson & Perry, 1990). Moving fish larvae are more likely to be preyed upon (Bailey & Yen, 1983; Brewer *et al.*, 1984), hence, becoming passive and sinking to the bottom will aid in predator avoidance.

4.1.1 Blenniidae

Blenniidae larvae are phototaxic and are usually found at the surface during the day (Watson, 1974; Fishelson, 1976; Labelle & Nursall, 1985; Olivar, 1990; Tilney *et al.*, 1996; Borges *et al.*, 2007), where they feed mostly on copepods (Qasim, 1955; June & Carlson, 1971; Watson, 1974). This behaviour is thought to avoid predators as day time abundances of zooplankton and larval fishes and subsequently larval fish predators are low at the surface (Hempel & Weikert, 1972). Thereby Blenniidae that inhabit the surface during the day are actively avoiding predators without risking starvation due to low competition for the low food availability. The blennid larvae in the present study exhibited these trends, most being at the surface during the day and dispersed at night. This would also indicate that at night, swimming activity is reduced, as Blenniidae larvae are inactive at night (Qasim, 1955), and they are then able to passively sink back down to the bottom.

4.1.2 Carangidae

Only one species of Carangidae was identified from St Francis Bay during September. This species was found at the bottom during the day and had an equal distribution between the surface and the bottom at night. Carangidae larvae are either found in low numbers at the surface (Garrido *et al.*, 2009) or at the bottom (Ruso & Bayle-Sempere, 2006) of the water column. Carangidae adults spawn pelagic eggs in the neritic zone, over the shelf and as far as the oceanic zone (von Westernhagen, 1974; Garratt, 1988; Flores-Coto & Sanchez-Ramirez, 1989; Jordan *et al.*, 1995), and the larvae are commonly found in abundance in the mid-water strata (Gray & Miskiewicz, 2000). Being pelagic larvae (Sale, 1991), Carangidae would therefore be more abundant in midwater and possibly further offshore due to offshore transport of currents. This could explain why Carangidae larvae are found in low numbers either at the surface or at the bottom.

4.1.3 Engraulidae

Engraulis encrasicolus, the only representative of the family Engraulidae contributed most towards all larval fish catches. Engraulid larvae are known to dominate larval fish communities around the world, ranging from the coastal waters of Japan (Tsukamoto *et al.*, 2001), to the west coast of the USA (Richardson & Pearcy, 1977), Spain (Ruso & Bayle-Sempere, 2006), Chile (Hernández-Miranda *et al.*, 2003), Australia (Leis, 1993; Muhling & Beckley, 2007) and South Africa (Beckley, 1986; Tilney & Buxton, 1994; Harris & Cyrus, 1997). Engraulid larvae exhibit strong and consistent DVM, moving from the bottom of the water column during the day to the surface at night. This diel behaviour has been observed in the field (Olivar *et al.*, 2001; Sabatés *et al.*, 2008) as well as in laboratory-based studies (Hunter & Sanchez, 1976). Engraulid larvae inflate their gas bladder at night by engulfing air at the surface, this enables them to conserve energy and maintain themselves at the surface (Uotani, 1973; Hunter & Sanchez, 1976). This common feature most likely explains the pervasive positive DVM trend in engraulid larvae from around the world. In the present study, however, *E. encrasicolus* did not exhibit DVM during March. Seemingly, this pattern resulted from the very low abundances of larvae at St Francis, and with Algoa Bay presenting similar distributions between surface and bottom, with a slight increase in abundance at night. During September, *E. encrasicolus* abundances were more structured during the day, occupying the bottom, while at night, their distribution was spread between surface and bottom. A similar trend to this study has been previously recorded in the larvae of *Clupea haiengus* (Family: Clupeidae), collected from the north coast of Scotland (Heath *et al.*, 1988). Likewise, in the Northern Benguela, *E. encrasicolus* larvae have been found to be dispersed during the night, through the common mechanisms of inflated gas bladders (Stenevik *et al.*, 2007). *Engraulis encrasicolus* are generally found where there are higher abundances of prey (Sabatés *et al.*, 2008). This possible explanation for such triggers of DVM seem to match the September results in Algoa Bay, when there was no significant difference between zooplankton volumes between the surface and the bottom at night, hence equal night distribution of *E. encrasicolus*.

4.1.4 Gobiidae

Most of the Gobiidae larvae caught in this study occurred at the bottom during the day, but moved throughout the water column at night, having almost equal abundances between surface and bottom. The distribution of Gobiidae larvae off the southeast coast of Spain (Ruso & Bayle-Sempere, 2006) and west coast of Portugal (Garrido *et al.*, 2009) showed similar patterns to this study, with greater abundances at deeper depths during the day and disperse throughout the water column at night. In Algoa Bay, during September, *C. nudiceps* was only found at night and in high abundances at the surface. Although this would yield a non-significant result, because no specimens were found during the day, one could assume that DVM occurred due to the general presence of larvae at the bottom during the day.

4.1.5 Soleidae

In March, larvae of *Solea turbynei* showed a non-significant trend for positive DVM, while in September, when abundances were higher, this species was evenly distributed throughout the water column, during both the day and night. In the Bay of Biscay (NE Atlantic), the common sole, *Solea solea,* larvae do show DVM, depending on the specific ontogenetic larval stage. Preflexion larvae are evenly distributed in the water column with no diel differences, while later stage larvae perform positive DVM (Koutsikopoulos *et al.*, 1991; Lagardère *et al.*, 1999). Similarly, in the present study, the larvae collected in September that were evenly distributed through the water column, all belonged to the preflexion stage of development. Larvae collected in March included some flexion larvae, which possibly yielded to the occurrence of positive DVM. The patterns detected in March however should be interpreted with caution, due to the overall low abundances of *S. turbynei* larvae found ($n < 5$). *Heteromycteris capensis* had variable DVM. In Algoa Bay, a typical positive DVM was observed, although again, this should be considered cautiously as only four individuals were collected. In St Francis Bay on the other hand, where the abundance of *H. capensis* larvae was higher, larvae were evenly distributed at night, with almost equal abundances at the surface and at the bottom. Larvae collected in St Francis Bay, however, mostly belonged to the flexion stage of development, contradicting the findings of *S. turbynei* and *S. solea* (Koutsikopoulos *et al.*, 1991; Lagardère *et al.*, 1999). In the NW Mediterranean Sea, decreased abundances of Soleidae larvae have, however, been found at the bottom during the day, with an increase in abundance at night and a variable distribution throughout the water column (Olivar & Sabatés, 1997), similar to the assemblages of *H. capensis* in St Francis Bay in the present study.

4.1.6 Sparidae

Within the Sparidae fish family, three species showed significant DVM: *Chrysoblephus laticeps*, *Diplodus capensis* and *Rhabdosargus globiceps*. The latter two exhibited a reverse DVM, while *Chrysoblephus laticeps* showed positive DVM. These results should, however, be considered with caution as only three individuals were identified. Similarly, for *R. globiceps*, although a reverse DVM pattern was observed, only three individuals were identified. *Spondyliosoma emarginatum* showed no significant DVM and had equal abundances at the surface and bottom during both day and night. Off the northwest Iberian Peninsula, *Spondyliosoma cantharus* has a similar pattern to the one for this study, with equal distributions among all depth strata day and night (Rodriguez *et al.*, 2015). *Diplodus capensis* dominated sparid abundances. In contrast to the present study, in which *Diplodus capensis* showed RDVM, off the southeast coast of Spain, *Diplodus* species appear to have no significant DVM pattern (Olivar & Sabatés, 1997; Ruso & Bayle-Sempere, 2006), except off the west coast of Portugal (Garrido *et al.*, 2009), where *Diplodus* species exhibited positive DVM. The family Sparidae does show complex distribution patterns in the region of this study, where low numbers of sparid larvae are often found in nearshore waters (Tilney & Buxton, 1994). The limited numbers of all sparid species except *D. capensis,* could obscure possible DVM patterns.

4.1.7 Tetraodontidae

A Tetraodontidae species, only observed in St Francis Bay during September, showed reverse DVM. Greater abundances were found during the day, with even spread between surface and bottom depths. At night, however, although still being found at the surface, greater abundances were found at the bottom. In the Straits of Florida, larvae of Tetraodontidae have similarly been found in highest abundances during the day, particularly at the surface of the water column (Huebert *et al.*, 2011). Similar to the pattern observed in the present study, night time densities of Tetraodontidae larvae decreased with an increase in dispersal in the water column (Huebert *et al.*, 2011).

5 Conclusion

It is clear that the distribution, species composition and diel vertical migrations of larval fish communities are complex in both time and space and that patterns of diel vertical migration vary among and within larval fish families. External influences can also drive diel migration patterns. Currents (Bartsch & Backhaus, 1988), winds (Gray & Miskiewicz, 2000) and sensory cues (Kingsford *et al.*, 2002) can further alter larval fish distributions. It is clear nevertheless that there were variable DVM patterns among all the larval fishes, although the majority exhibited RDVM. Some of the fish larvae, particularly the engraulids, seem to actively avoid predators. Overall, the diverse and variable patterns of DVM highlighted by this study are of particular relevance as globally, the present study is one of few completed in very shallow nearshore waters (< 15 m). DVM patterns could differ drastically from patterns observed in offshore waters, considered by most studies. Further studies in DVM of larval fishes in inshore waters could greatly improve our understanding of the larval fish community composition and distribution and highlight the specific role and links of shallow depths and bathymetry, potential association to unique fish assemblages and availability and proximity to nursery habitats.

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Chapter 4

A stratum-specific method for sampling larval fishes

1 Introduction

Quantitative zooplankton sampling began in the late 1800s, with the first pioneer plankton collection, using a single conical net that was deployed vertically (Hensen, 1887; referenced in Bone & Noble, 2016). Hensen (1887) believed plankton were evenly distributed throughout the ocean and small scale vertical tows would be able to provide realistic estimates of the oceans plankton diversity and size (Wiebe & Benfield, 2003). Hensen's theory was, however, heavily criticised (Haeckel, 1890; referenced in Bone & Noble, 2016), but only in the early 1900s did people start to question Hensen's uniformity belief, with studies such as Johnstone (1908), Herdman (1918), Johnstone *et al.* (1924), Gardiner (1931) and Winsor & Walford (1936) producing results that indicate plankton are not uniformly distributed. Kofoid (1912) designed a net that could be opened and closed at depths for horizontal towing (Figure 4.1 (A)), thus allowing samples to be collected at discrete depths to assess vertical movements of plankton (Kofoid, 1912). However, Kofoid's (1912) net, besides the high costs and complicated manufacture, was heavy and required the use of strong cables (Bigelow, 1913). Nansen (1915), finally published his methods for a simple and easy to use net with a mechanism to close vertically and horizontally towed nets for discrete plankton sampling (Nansen, 1915). The mechanism consisted of a messenger that released a hook in the frame of the net so that the net collapsed and hung vertically when lowered or hauled up (Figure 4.1 (B); Nansen, 1915). Nets based on Hensen's original design and Nansen's open/closing mechanisms were continuously re-developed to improve the accuracy of plankton sampling. Later on researchers soon came to realise that swimming organisms were able to avoid the nets (Clutter & Anraku, 1968) and a net with an unobstructed opening was therefore needed. McGowan & Brown (1966) built the first open/close bongo net, a set of two circular nets joined by a central point that was attached to a cable, thereby leaving the mouth of the nets unobstructed (Figure 4.1 (C); McGowan & Brown, 1966). Posgay and Marak, (1980) designed a net based on the McGowan & Brown (1966) bongo net to use for oblique towing (Posgay & Marak, 1980).

Because the net would be open throughout the sampling, no open close mechanism was needed and so the open Marine Resources Monitoring, Assessment and Prediction (MARMAP) bongo net was developed (Figure 4.1 (D); Posgay & Marak, 1980). Bongo nets were more efficient at sampling larval fishes than most other plankton samplers (Posgay & Marak, 1980). The open MARMAP bongo net design is still used widely today and is very popular in larval fish studies using oblique tows (Ingram *et al.*, 2015; Rabbaniha *et al.*, 2015; Sabatés *et al.*, 2015; Kitchens *et al.*, 2017; Siddon *et al.*, 2018). Due to its popularity, the open bongo net is widely available and studies, such as this one, often use the open bongo net for discrete depth sampling. The issue with the recovery of an open bongo net to the surface from depth, is that there is a possibility of inadvertently collecting larval fishes as the net is retrieved, thus contaminating the sample. To overcome this, nets are pulled to the surface as quickly as possible (Richardson & Pearcy, 1977; Leis, 1991). If an open/close bongo net is available and used for discrete depth sampling there is a similar problem in that sometimes the messenger and/or the mechanism to close the net fails and nets are then hauled to the surface open (Merriman, 1941; Leis, 1991).

As this thesis involved the use of an open bongo net to sample larval fishes near the bottom of the water column, the aim of this study was to determine whether contamination during recovery of the net from depth, significantly affects estimates of larval abundances derived from horizontal tows near the bottom.

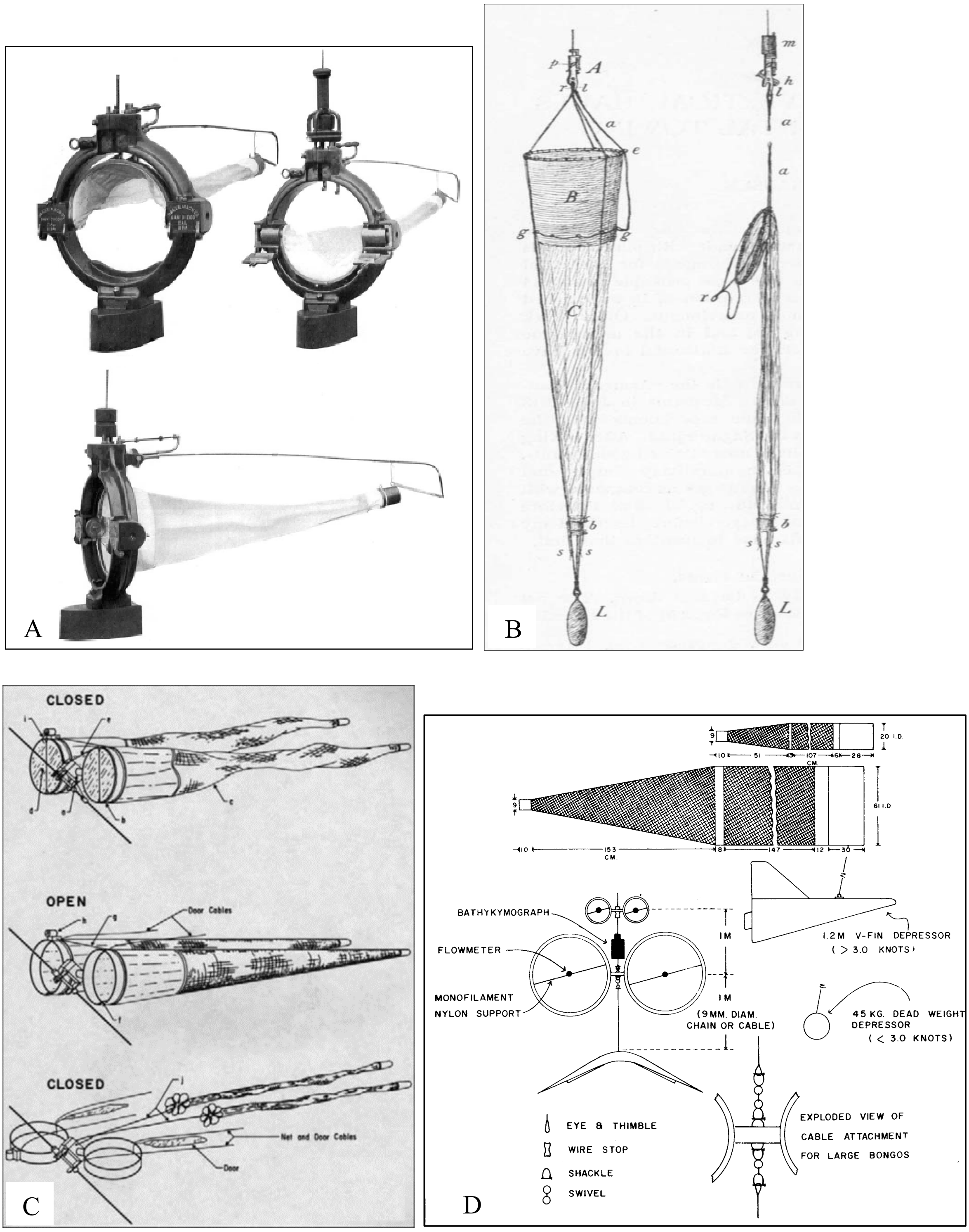

Figure 4.1 (A) Kofoid's self-closing net with an unobstructed mouth opening. Top left is the closed mouth on lowering the net, top right is the messenger releasing the net mouth, bottom is the open mouth ready for horizontal towing (figure from Kofoid, (1912)). (B) Nansen's closing net for vertical and horizontal tows. To the left is the net open. To the right is the net closed (figure from Nansen (1915)). (C) McGowan & Brown's open/close bongo net (figure from McGowan & Brown, (1966)). (D) The Posgay & Marak open MARMAP bongo net design (figure from Posgay & Marak, (1980))

2 Methods

Algoa Bay and St Francis Bay (See Chapter 2, section 2.1), located on the south coast of South Africa, were sampled both onshore and offshore (Chapter 2), and day and night (Chapter 3) in March and September 2013. For details on the sampling procedure, please refer to those specific chapters. Because an open/close mechanism was not available for the bongo net used throughout the study, all sampling was coupled with deployment of vertical hauls. Using the larval fish abundances from the original bottom tows and the abundances from the vertical tows, a true value of the abundance of larval fishes caught at the bottom could be calculated (Chapter 2, section 2.5.2). From those calculations two values were obtained, an original bottom tow abundance and a corrected bottom tow abundance.

Corrected abundances of larvae were calculated as follows:

$$\underline{X} = X - (Y - Z)$$

Where X = number larvae in the horizontal tow, including larvae caught while bringing the net to the surface, Y = number larvae in the vertical (recovery) tow and Z = proportion of larvae within the vertical tow that would also be included in the horizontal tow. Please see Chapter 2, 2.5.2 for an illustrative diagram.

Z was calculated as follows:

$$Z = \frac{Y * B}{A}$$

Where A is the volume sampled for the vertical tow and B is the area sampled for the horizontal.

A percentage of correction was calculated for each species of larval fish and for the total using the following formula:

$$\% \text{ of Correction} = \frac{(X - \underline{X})}{X} * 100$$

3 Results

Out of a total of 1540 larval fishes collected during the entire study period, 127 specimens were caught in the vertical tows. A total of 12 bottom and 12 vertical tows (from Chapters 2 and 3) were completed and used in the analysis. The total catch of larval fishes comprised 18 families and 36 species, of which, 10 families and 16 species were caught in the vertical tows (Table 4.1). Algoa Bay had a total of 1037 larval fish, with 110 larvae caught in the vertical tows. St Francis Bay had a total of 503 larval fish with only 17 larvae in the vertical tows. The bottom tows consisted of 882 larvae, 514 were caught during the day, including the daytime offshore samples and 368 larval fish were caught at night. During the day, 31 larvae were caught in the vertical tows, while at night 96 larvae were caught in the vertical tows. (Table 4.1). Onshore and offshore bottom tows contained 219 and 295 larval fishes respectively whereas onshore and offshore vertical tows had 16 and 15 larval fishes respectively.

Engraulis encrasicolus (Family: Engraulidae) was the most abundant species with a total of 851 individuals being caught throughout the study, 89 of which were captured in the vertical tows.

The percentage of correction calculated for the total larval catch was 13%. *Caffrogobius nudiceps* (Family: Gobiidae) had the maximum percentage of correction calculated at 25% (Table 4.1). The average percentage of correction was 4%.

Table 4.1 Total abundances of larval fish caught in the bottom tows, the vertical tows, the calculated corrected bottom abundances (see calculation above) and the percentage of the correction. N/A indicates an invalid number as those larvae were only found in the vertical tows

Family	Species	Original Bottom	Vertical	Corrected Bottom	Percentage of correction
Blenniidae	Blenniidae 1	2	0	2	0%
	Blenniidae 2	1	0	1	0%
	Blenniidae 3	1	0	1	0%
	Blenniidae 4	6	1	5	16%
	Blenniidae 5	2	0	2	0%
	Blenniidae 6	9	0	9	0%
	Parablennius 1	1	1	1	0%
Callionymidae	Callionymidae 1	0	1	0	N/A
Carangidae	Carangidae 1	20	3	19	5%
Clupeidae	*Sardinops sagax*	2	0	2	0%
Cynoglossidae	*Cynoglossus capensis*	92	4	88	4%
	Cynoglossus zanzibarensis	7	0	7	0%
Dussumieriidae	*Etrumeus whiteheadi*	7	0	7	0%
Engraulidae	*Engraulis encrasicolus*	545	89	460	16%
Gobiesocidae	Gobiesocidae 1	11	1	10	8%
	Gobiesocidae 3	3	0	3	0%
Gobiidae	*Caffrogobius gilchristi*	2	0	2	0%
	Caffrogobius nudiceps	49	14	37	25%
	Psammogobius knysnaensis	0	1	0	N/A
Leiognathidae	Leiognathidae 1	1	0	1	0%
Mugilidae	Mugilidae 2	1	0	1	0%
Sciaenidae	*Argyrosomus inodorus*	1	0	1	0%
Scorpaenidae	Scorpaenidae 1	10	1	9	10%
Soleidae	*Heteromycteris capensis*	24	3	22	8%
	Solea turbynei	28	2	27	3%
Sparidae	*Chrysoblephus laticeps*	8	2	8	0%
	Diplodus capensis	12	1	11	8%
	Pagellus Natalensis	1	0	1	0%
	Rhabdosargus globiceps	3	0	3	0%
	Sparidae 1	1	0	1	0%
	Sparidae 2	2	0	2	0%
	Sparidae 3	0	1	0	N/A
	Spondyliosoma emarginatum	10	2	8	19%
Syngnathidae	*Syngnathus temminckii*	2	0	2	0%
Tetraodontidae	Tetraodontidae 1	7	0	7	0%
Tripterygiidae	Tripterygiidae 1	11	0	11	0%
Total		882	127	772	13%

4 Discussion

The percentage corrections found between the abundance of larval fishes caught in the original bottom tow and the corrected abundance of larvae for either day/night samples or onshore/offshore samples were all low. It is noteworthy that larvae with a total percentage of corrections larger than 10%, i.e. *Caffrogobius nudiceps*, *Engraulis encrasicolus*, *Spondyliosoma emarginatum* (Family: Sparidae) and Blenniidae 4, all had low (< 15%) percentage of corrections when considering only the day time samples.

Caffrogobius nudiceps had the highest total percentage of correction and throughout the study, the majority of *C. nudiceps* were caught at night. During the day *C. nudiceps* was found closer to the sea floor, however, at night it was dispersed throughout the water column (refer to Chapters 2 and 3). Occurring at the bottom and able to avoid nets during the day (Richardson & Pearcy, 1977; Trnski, 2001; Pearre, 2003) in addition to being dispersed within the water column at night (Ruso & Bayle-Sempere, 2006; Garrido *et al.*, 2009; Chapter 3 from this thesis), could explain why higher abundances of *C. nudiceps* were captured in the vertical tows relative to the bottom tows, resulting in a high percentage of correction. *Engraulis encrasicolus* inflate their gas bladders at night in order to conserve energy (Uotani, 1973; Hunter & Sanchez, 1976). Once the gas bladder is inflated *E. encrasicolus* start to slowly sink to the bottom during the night (Stenevik *et al.*, 2007) thereby becoming somewhat passive particles and are therefore easily captured in the vertical hauls. In the case of *Spondyliosoma emarginatum* and Blenniidae 4, abundances in the bottom tows were relatively low and so the 1 or 2 larvae caught in the vertical tows would give them a high percentage of correction. Interestingly, both *S. emarginatum* and Blenniidae 4 were more abundant in surface tows (See Chapters 2 and 3) and similar trends of *S. emarginatum* (Garrido *et al.*, 2009) and Blenniidae (Tilney *et al.*, 1996) being more abundant at the surface of the water column have been found in other studies. Even with the high percentages of correction the vertical abundances did not significantly change the original bottom abundances. Two species captured exclusively in the vertical tows were found just once during the study period. Callionymidae and *Psammogobius knysnaensis* larvae are rare within the study area (Beckley, 1983; Pattrick & Strydom, 2008, 2014, 2017). *Psammogobius knysnaensis* is an estuary dependant species and spawn in estuaries (Beckley, 1985; Whitfield, 1998) and the larvae are more commonly found in estuaries (Melville-Smith & Baird, 1980; Strydom *et al.*, 2003). Callionymidae are offshore species (Fröiland & Greve, 1976; Olney & Sedberry, 1983; Sánchez-Velasco, 1998) and would rarely be found in nearshore waters. Furthermore, Callionymidae are more abundant in winter while *Psammogobius knysnaensis* (Whitfield, 1998) are more abundant in summer (Beckley, 1983; Pattrick & Strydom, 2008, 2014, 2017). This could indicate why both species were not caught in any horizontal tows.

The results from this study suggest that the larval fishes caught in the vertical nets, potentially contaminating the bottom tow abundances, did not alter estimates of larval fish abundances at the bottom of the water column. Whether original or corrected abundances are used, it does not change the overall results of this type of study. Correction for contamination by vertical tows is therefore not necessary when sampling a discrete bottom layer of the water column. When using an open/close bongo net and the mechanism fails, such as in the case in Chesapeake Bay (Merriman, 1941) and in the Great Barrier Reef Lagoon (Leis, 1991) bringing the net open to the surface will not affect the bottom samples. The results of this study indicate that vertical tows to determine vertical profiles of larval fish such as in the case in Georges Bank, where a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) was used to sample discrete depths of larval fishes (Lough *et al.*, 1996) would not be necessary. The vertical tows would not provide accurate species richness or diversity.

This study further indicates that it is acceptable to avoid vertical correctional tows in future studies. This is not only time and effort saving but also saves one the trouble of finding/making an open/close bongo net should one not be available. The maximum depth sampled during the current study, however, was ±12 m and vertical tows were hauled at a winch speed of approximately 1 ms^{-1}. It would be beneficial to replicate this study at different depths and different speeds to determine if depth and speed have an effect. It should also be noted that individual larval fish behaviour may also change the results. This methodological study provides robust guidelines for the nearshore use of an open bongo net to collect discrete depth samples without the need to correct for contamination.

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Chapter 5

Synthesis and Conclusions

The present study assessed the nearshore larval fish species composition, distribution and possible vertical migration patterns within two adjacent log spiral bays, Algoa Bay and St Francis Bay, on the south coast of South Africa, in March and in September 2013. The composition of larval fish assemblages was related to wind speed, wave height, cloud cover, sea water temperature, depth, average current speed and direction.

Although there was only one sampling occasion in each month, differences between them probably partially reflect the effects of seasonality. Notable seasonal differences in larval fish densities occurred between March and September, with significantly greater densities in September. Globally, the majority of fish spawn in late winter through to spring (Booth & Beretta, 1994; Gray & Miskiewicz, 2000; Pattrick & Strydom, 2008; Garrido *et al.*, 2009). September is the South African spring and so it is of no surprise that the densities were far greater during this time period.

Besides the seasonal differences, the results from this study confirm that larval fish assemblages are highly complex and patchy, and are influenced by spawning, individual species behaviour, currents, depth, temperature, wind speed and cloud cover. In addition, habitat structure seems to play a major role in the composition of these larval fish assemblages. The nearshore habitat structures within each bay differed considerably. Although the bays chosen for this study were comparable in size, shape and orientation, the seabed surrounding the sampling sites of Algoa Bay were composed of sand and mud, while St Francis Bay sampling sites comprised more rocky reef habitat and the larval fish assemblages within each bay reflected these differences. Densities of larval fish in Algoa Bay were dominated by the fish families Engraulidae, Blenniidae, Sparidae, Soleidae and Cynoglossidae. These are either pelagic and/or sandy and bottom associated families. Densities of larval fishes in St Francis Bay were dominated by Blenniidae, Engraulidae, Tripterygiidae, Sparidae and Gobiesocidae. Furthermore, Syngnathidae, Tetraodontidae and Scorpaenidae were exclusively captured in St Francis Bay and Carangidae were far more abundant in St Francis Bay than Algoa Bay. All of the St Francis Bay families are associated with reefs. *Engraulis encrasicolus*, the only representative species from the Engraulidae family is a pelagic species, but still dominates larval fish catches surrounding reefs (Pattrick & Strydom, 2017).

Within both bays, there were clear horizontal spatial differences in larval fish assemblages. Larvae from adults that lay demersal eggs were found closer inshore (~ 1 km from the coast), while larvae from adults that lay pelagic eggs were found farther offshore (~ 2 km from the coast). This is a common pattern seen worldwide among most larval fishes occurring in tropical to warm temperate areas (Leis & Miller, 1976; Richardson & Pearcy, 1977; Yamashita & Aoyama, 1984; Sanvicente-Añorve *et al.*, 1998; Vélez *et al.*, 2005; Kent *et al.*, 2013). Fish larvae from benthic eggs hatch at a more advanced developmental stage than larvae from pelagic eggs (Breder, 1962; Leis, 1991, 1994). Larvae from benthic eggs hatch with their permanent fins and fin rays present, and therefore attain swimming abilities more quickly than pelagic larvae and are able to retain themselves closer inshore (Breder, 1962; Fisher & Bellwood, 2002). Larvae from pelagic eggs are more susceptible to passive offshore transport due to currents (Hunter, 1972). So even from a hatchling, larval fish distribution has already been pre-determined to some degree.

As pressure is high on fish during their early life stages as larvae (Hjort, 1914), larval fishes must adopt different means to distribute themselves in the water column to avoid starvation, predation and extensive offshore transport (Hjort, 1914; Hunter, 1976, 1981). Diel vertical migration (DVM) is one strategy that larval fishes use to avoid mortality, but given its complexity, DVM should be evaluated at the individual species level (Hempel & Weikert, 1972; Williams, 1991). Nevertheless, this study showed that individual behaviour, and external biotic and abiotic factors can drive different modes of DVM and thus, different larval distributions. One such driver is the presence of zooplankton. Larval fishes are visual feeders and so follow their prey to the surface at dusk where light intensity is optimal for feeding (Fortier & Leggett, 1983; Batty, 1987). Zooplankton usually show a type I DVM pattern (moving from the bottom to the surface of the water column at night; Williams & Conway, 1984; Fragopoulu & Lykakis, 1990; Heywood, 1996; Irigoien *et al.*, 2004), however, in the present study they showed more of a type II DVM pattern, with higher densities of zooplankton occurring at the bottom during the night. The majority of the larval fishes in the present study displayed the similar type II DVM to the zooplankton, indicating that they followed their prey. This pattern should however be considered with caution as the 500µm nets would allow smaller prey items to pass through, and so the settled zooplankton would not necessarily contain prey for the preflexion larvae. The switch to the type II DVM by zooplankton and to some extent larval fishes, was affected by high densities of chaetognaths present in the surface layers at night in St Francis Bay, at least in September. Chaetognaths are largely zooplankton feeders (Øresland, 1987; Fortier & Harris, 1989) but have been known to feed on larval fishes (Fraser, 1969; Williams & Hart, 1974). Quite often zooplankton and larval fishes will switch over to a type II DVM to avoid predators using type I DVM (Hobson, 1973; Ohman *et al.*, 1983; Ohman, 1990; Brodeur & Rugen, 1994).

Engraulis encrasicolus (Engraulidae) and Blenniidae larval fishes exhibit behavioural mechanisms to avoid predators. *Engraulis encrasicolus* larvae move to the surface of the water column at dusk to engulf air to conserve energy while maintaining their vertical position in the water during the night (Uotani, 1973; Hunter & Sanchez, 1976). However, even with an inflated gas bladder, *E. encrasicolus* still manages to passively sink to the bottom (Stenevik *et al.*, 2007). This form of passive sinking is in a way a predator avoidance mechanism. Predators are more inclined to attack moving prey (Bailey & Yen, 1983; Brewer *et al.*, 1984), thus by using an inflated gas bladder, *E. encrasicolus* can safely passively sink away from the predators occupying the surface waters at night time.

Blenniidae larvae are phototaxic, they feed during the day (Qasim, 1955; June & Carlson, 1971; Watson, 1974) and use more of a type II DVM pattern. The Blenniidae larvae in the present study conformed to this behaviour being more abundant at the surface during the day than at night. Feeding at the surface during the day decreases the chance of encountering predators that mostly feed at night (Øresland, 1987).

Larval fish not showing these individual adaptations to avoid predators find themselves in a predicament, either they do not feed and avoid predators in the dark or they feed and risk predation. Larval fish must find optimal light levels that will enable them to see prey but at the same time not be seen by predators (Clark & Levy, 1988). During the present study, a "third antipredation window" (sensu Clark & Levy, 1988) presented itself in the form of cloud cover as mostly observed for the surface preference by *Engraulis encrasicolus*. Clouds decrease the light intensity absorbed into the water column giving it a somewhat similar optimum light as dawn and dusk would. Clupeid larvae in the North Sea have also been found at the surface on overcast days (Bridger, 1956). This could reflect the fact that some larval fishes are using the decreased light intensity due to cloud cover to move closer to the surface to feed.

In addition to using DVM to avoid predators, larvae can move up or down to take advantage of currents and overcome extensive offshore transport. (Cowen & Castro, 1994; Paris &

Cowen, 2004; Kent *et al.*, 2013). The present study supported this as the larval fish species contributing the most to the bottom samples were all from pelagic eggs. Larvae from pelagic eggs are more susceptible to passive transport by currents due to their poor development at hatching (Breder, 1962; Leis, 1991, 1994). During the September sampling period, the bottom currents were all flowing onshore, in a westerly direction, while surface currents were flowing alongshore in a southerly direction. The pelagic larvae dominating the bottom assemblages could have been taking advantage of the bottom currents to retain themselves in the nearshore waters.

The results from this study shed some light on the composition and distribution of larval fish assemblages in Algoa Bay and St Francis Bay. St Francis Bay is an area that has had no previous work on larval fishes in the coastal nearshore. The South African Environmental Observation Network (SAEON) incorporated St Francis Bay into its long term monitoring programme in 2016 (Bornman, 2016; Hermes *et al.*, 2016), however focus of this programme is primarily on phytoplankton. This study, thus provides baseline information on larval fish species composition and distribution within St Francis Bay. The results highlight the presence of Sparidae and Carangidae larvae in both Algoa Bay and St Francis Bay, two important commercial and recreational linefish (fish caught by rod and reel rather than by nets) families in South Africa (Heemstra & Heemstra, 2004). Many of the species in these two families are either on the orange or red South African Sustainable Seafood Initiative (SASSI) list. The SASSI list is a guide for consumers of fish in South Africa. Species on the green list are your best choice to eat/buy, species on the orange list should be considered twice before eating or buying and species on the red list are highly recommended to avoid. Species on the orange or red list are of concern as it means the species are either depleted due to over fishing (orange list) or they are unsustainable due to the population collapsing (red list). Because the two bays are very attractive sites for linefisherman, the species within Sparidae and Carangidae need protection. In 2016 the Minister of Environmental Affairs, South Africa proposed 22 new MPAs along the entire stretch of the South African coastline. Although one of the MPAs is planned for Algoa Bay, St Francis Bay has no MPAs planned for the future.

In conclusion, the outcome of this study indicates the highly complex dynamics of assemblages of larval fishes in the shallow nearshore of South Africa. Habitat has a major influence on the species composition. Over the sandy bottom habitat of Algoa Bay, larval fish assemblages were dominated by pelagic and sand associated larvae. The rocky reef habitat in St Francis Bay was dominated by reef associated species. In addition to this, external abiotic and biotic factors greatly influenced the distribution of larval fishes. The main issues leading to larval fish mortality are starvation, predation and extensive offshore transport. Finding the optimum light intensity where they can feed and where food is present while still avoiding predators and at the same time avoiding strong offshore currents becomes a complicated issue. It hence appears that one needs to take into consideration a broad range of possible drivers when investigating the mechanisms that can influence larval fish assemblages in coastal nearshore areas.

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