

# **Patterns and influencing factors of the larval fish assemblage of the KwaZulu-Natal Bight, South Africa**

by

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## ABSTRACT

Processes that control population dynamics occur early in the life history of most fish species. Studies of fish larvae can indicate relative size classes and abundance of spawning fish stocks and therefore help with management decisions pertaining to fisheries and conservation. However, little is known of marine larval fishes of the east coast of South Africa, with the only previous study dating back to 1990/1991. The African Coelacanth Ecosystem Programme (ACEP) KZN Bight Functioning Project, which examined nutrient sources and trophic ecology of the Bight, presented an opportunity to study larval fishes in this area. This study reports on results from two synoptic surveys conducted off central KwaZulu-Natal in January (Wet season) and July (Dry season) of 2010. Although designated as Wet and Dry seasons here (for consistency with other studies in the KZN Bight Functioning Project) they could also be regarded as Summer and Winter seasons respectively. Oblique hauls from 80 m depth by Bongo nets (2 x 500  $\mu\text{m}$  mesh) were undertaken at stations on the Shelf, Mid-slope and Deep-slope (in <100m, 100-600m and ~1 000m water depths respectively) along 15 coast-perpendicular transects.

The MSc project commenced in 2013, with bursary support from the National Research Foundation's Scarce Skills funding programme. Taxonomic skills in the identification of fish larvae in South Africa, especially subtropical species, are poorly developed. Several international larval keys and expert input from Dr Allan Connell, however, allowed the majority of larvae to be systematically identified to family level. In addition to the depth stratification, transects were grouped into three geographic areas based on putative nutrient influences: Durban, Thukela and Richards Bay. In the 107 samples collected, 2 537 fish larvae, representing 116 taxa from 68 families, were identified. The Durban shelf had the highest larval density (392.74 larvae/100m<sup>-3</sup>) during the Dry season, and the lowest (2.08 larvae/100m<sup>-3</sup>) during the Wet season. The most abundant families found during this study were Leiognathidae, Callionymidae and Tripterygiidae, which have demersal adult phases. The most ubiquitous (widely occurring) taxa were Myctophidae, Engraulidae and Bregmacerotidae.

Multivariate analyses, which included consideration of environmental factors, were undertaken to elucidate patterns in larval distribution, some of which displayed strong seasonality, likely due to varying spawning seasons of fishes. Larval distribution was also influenced by large-scale differences in water masses, with assemblages collected in the

Agulhas Current waters differing significantly from those from shelf waters. Samples collected over the Deep-slope were influenced by the encroaching Agulhas Current which is characterised by increased Sea Surface Temperature and surface salinity, low nutrients and the presence of deep water larval taxa. Assemblages sampled off Durban and the Thukela, where the shelf is wider, were characterised by in-shore species. This contrasted with the assemblages off Richards Bay where the shelf is narrower, and where the influence of the Agulhas Current was greater. This influence was more apparent in the Wet season, during which Durban and Thukela shelf samples differed significantly from all others. During the Dry season, larval fish patterns were more homogenous, with the only significant differences being between samples from the shelf and the deep slope off Durban and Thukela. Overall, season, depth and the dynamic oceanographic environment accounted for most of the observed patterns. Larval fish assemblages studied here therefore showed significant structure and spatial variability which were attributed to the area's main oceanographic features.

## **DECLARATION**

The work described in this dissertation was carried out at the Oceanographic Research Institute, the Council for Scientific and Industrial Research and the School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, under the supervision of Dr Sean Fennessy and co-supervised by Mr Steven Weerts. This work took place between June 2013 and January 2016.

I declare that the work submitted within this thesis is my own work. This work is submitted for the fulfilment of a Master in Science in Zoology at the University of KwaZulu-Natal.

This full work, or partial sections, has not been submitted for any other degree or examination at this university or any other tertiary institution.

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NRF Declaration:

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# CHAPTER 1: INTRODUCTION

## 1.1 Fishes of South Africa

South Africa is a region of high marine fish diversity. Few other regions share the same ichthyofaunal richness, with 1 970 recorded species from 280 families (Fishbase, 2015). Estimates for the wider southern African region are that there are more than 2 000 coastal species alone (Heemstra and Heemstra, 2004). Smith and Heemstra (1995) noted that the tropical Indo-Pacific region is the largest contributor of species (> 50%) to the southern African fish community. The second largest contribution (29%) is from deep-sea species found in the wider southern hemisphere (Smith and Heemstra, 1995). The remainder is made up of taxa from the Atlantic and temperate Southern oceans, and cosmopolitan species. There are reportedly 48 species endemic to South African marine waters (Fishbase, 2015). A review by van der Elst et al. (2005) lists five main families of endemic fishes off eastern South Africa, with notable contributions from the Clinidae, Gobiidae and Sparidae.

There is a convergence of three oceans off the southern tip of continental Africa, namely the Indian, Pacific and Southern Oceans. The resulting unique environment has contributed to the high level of endemism in marine fishes. For example, on the east coast of South Africa, the prominent Agulhas Current that flows southwards along the coast results in distinct environmental conditions through the influence of warm tropical waters and the introduction of tropical fauna and flora from the Western Indian Ocean (Beckley, 1998). However, the east coast of South Africa is the only coastal region in the Western Indian Ocean that has a temperate climate driven by the influence of cooler Southern and Atlantic Oceans (Beckley, 1998). The diversity of species and variety of habitats has engendered a wide array of fishery types in the region (van der Elst, 1989; Everett, 2014). Each fishery type has unique characteristics depending on regional fish diversity, climate and oceanographic conditions. The southeast Atlantic on the west coast of South Africa supports the country's large commercial fisheries which produce catches of 4.1 kg of fishes per 10 km<sup>2</sup> of marine surface area (van der Elst et al., 2005). These fisheries particularly target the high abundances of small pelagic fishes found there, as well as demersal fishes. In comparison, fisheries of the Western Indian Ocean region, which includes part of the east coast of South Africa, produce just 1.35 kg per 10 km<sup>2</sup> (FAO, 2003). This disparity reflects the relatively low productivity of the South African east coast, and stems from the absence of a large nutrient upwelling system, such as that present on the west coast (Andrews and Hutchings, 1980; Brundrit,

1981). One consequence of the absence of large-scale fisheries on the east coast is the lack of information on larval fishes, other than that described below. The current study aims to remedy this situation, by describing the larval ichthyofauna of the KwaZulu-Natal Bight on the east coast – an area that has not been well described in terms of this particular life history stage of its fishes.

## **1.2 Larval fishes and research in South Africa**

### **1.2.1 Fish larvae**

The term “fish larvae” refers to a short period within the planktonic phase (ichthyoplankton) of most fish species. The larval phase falls between hatching from the egg, and the development of complete fin ray counts and the beginning of squamation prior to the juvenile fish stage (Kendall et al., 1984). Larvae of most fishes occur in the photic zone of the water column, upward of 200 m depths (also known as the epipelagic zone). The nature of a larval fish assemblage depends on a number of spatial and temporal factors. Spatially, larval fish may display habitat preference/association, as a reflection of that of the adult phase (Dudley et al., 2000; Armsworth et al., 2001). Additionally, there are a variety of spawning techniques, which can also influence larval distribution. Broadcast spawners release eggs directly into the water column, therefore dispersal begins prior to the larval phase, which potentially allows for a greater dispersal of progeny. Examples are the family Acanthuridae (unicorn fish), which have a specialized Acronurus larval phase that is well adapted for a relatively long pelagic existence before settlement onto reefs (Leis and Rennis, 1983). The pelagic phase of Labridae (wrasses) and Chaetodontidae (butterflyfish) larvae also have long durations which results in wide dispersal (Victor, 1986; Leis, 1989). In contrast, demersal spawners such as Tripterygiidae (triplefin blennies), Pomacentridae (damselfish and clownfish) and Gobiidae (gobies) attach eggs to the seabed (Leis and Rennis, 1983; Eyberg, 1984). While demersal eggs restrict dispersal during the egg phase, once hatched, their larvae are still potentially exposed to dispersal mechanisms, such as currents.

Habitat association may also result from active movement by the larvae towards areas with optimal physico-chemical conditions for survival. For example, there is evidence that larval recruitment into estuaries is due to active movement by the larvae, which respond to changes in turbidity and salinity (Whitfield, 1989a and b; Strydom, 2002; James et al., 2008). It was originally thought that fish larvae could not migrate very effectively for long distances. However, most larvae are effective swimmers, capable of travelling speeds greater than that

observed in local current regimes (Leis and Stobutzki, 1999; Dudley et al., 2000; Fisher and Bellwood, 2002 and 2003; Fisher, 2005; Leis et al., 2006). Larval fishes are able to adjust their vertical position in the water column and thus can take advantage of current flow to areas with more favourable physico-chemical conditions of temperature, salinity and nutrients (Leis and Stobutzki, 1999; Leis, 2006; Leis et al., 2006). Fish larvae therefore, may actively control their location to a much greater degree than previously thought (Armstrong et al., 2001; Leis, 2006).

The physico-chemical conditions of a marine water body depend on a variety of oceanographic features, bathymetry, currents and upwelling zones. Proximity to terrestrial influences (rivers) will further affect the physico-chemical qualities of a water body, as well as the bottom sediment composition. These in turn play an important role in determining the distribution of larval fishes in the marine environment, with currents in particular being influential (Leis and Goldman, 1983). Currents also act as transport towards, and retention mechanisms within, nursery areas (van der Lingen et al., 2010). For larvae that survive the critical transition stage from yolk sac to particulate feeding, survival largely depends on obtaining adequate food and escaping predation (Ahlstrom and Moser, 1976), which appropriate nursery areas must provide. Seasonal and annual variation in the above factors provides further complexity to the larval fish assemblage.

Processes that control population dynamics begin early in the life history of most fishes (Ahlstrom and Moser, 1976). Study of larval fish assemblages provides information of the potential variation in recruitment to adult populations (Bailey, 1981; Iles and Sinclair, 1982; Nakata et al., 2000). For example, early larval fish studies can be used to predict year-class strength of targeted fisheries species through quantitative surveys (Bowles et al., 1978). At the start of the 1900s, international research interest in larval fishes expanded when it emerged that, if sampled quantitatively, larval fish abundances could indicate the relative size or abundance of spawning fish stocks (Bowles et al., 1978). Thus, the proportion of the larval population surviving to the post-planktonic stage has a direct relationship to the size of that year-class when it reaches commercial size (Ahlstrom, 1954).

### **1.2.2 Taxonomic and descriptive studies**

Research on larval fishes in South Africa first commenced in the Western Cape in the early twentieth century by ichthyologist JDF Gilchrist from Scotland. Gilchrist came to South Africa as Government Marine Biologist at the Cape of Good Hope in 1895. He subsequently

produced episodic annotated illustrations on the eggs and larvae of some 91 species from the genera *Paralichthodes* (flounders), *Selachophidium* (cusk-eels), *Neocyttus* and *Psuedocyttus* (oreos), *Lyconodes* (hake), *Neoscombrops* (ocean-basses) and tinseltfish, *Xenolepidichthys* (Gilchrist, 1903, 1904, 1916 and 1921; Gilchrist and Hunter, 1919). In the mid-1900s, the larval taxonomy and ontogeny of commercially important fish species on the west coast of South Africa such as *Merluccius capensis* (South African hake), *Thyrsites atun* (snoek) and *Helicolenus dactylopterus* (jacopever) gained emphasis (Matthews and Van Dyk de Jager, 1951; De Jager, 1955; Haigh, 1972).

This descriptive work on important fisheries species on the west coast continued into the late 1900s with the focus on *Sardinops sagax* (pilchard), *Austroglossus microlepis* (west coast sole) and the anchovy, *Engraulis capensis* (O'Toole, 1977; Louw and O'Toole, 1977; King et al., 1978). Bronwell (1979), who examined the rearing of 40 marine fish species around the Cape Peninsula, followed this. Descriptions of the egg and larval development of the South African mullet *Liza richardsonii* (Cambray and Bok, 1989), the dusky kob *Argyrosomus japonicus* (Beckley, 1990) and the steentjie seabream *Spondyllosoma emarginatum* (Beckley, 1989) followed. Olivar and Fortuño (1991) described spawning areas and seasons of several fishes from the Benguela Current region of the southeast Atlantic and included their larvae in a comprehensive guide. These included, amongst others, species from the orders Clupeiformes, Gadiformes, Gobiesociformes, Myctophiformes, Ophidiiformes, Perciformes, Pleuronectiformes, and Zeiformes (Olivar and Fortuño, 1991).

Several research cruises, conducted by the Sea Fisheries Branch from 1951 to 1969, focused on the spawning of *E. capensis* and *S. sagax* from the east coast of South Africa (Anders, 1975). A South African east coast study on larval fish by Eyberg (1984) then observed the spawning period and size at hatching of the in-shore blennioid, *Parablennius cornutus*. Subsequently, the last decade of the 20th century produced most of the descriptive studies of east coast fish larvae under the influence of the Agulhas Current. Myctophidae (lantern-fish) larvae from the genera *Benthoosema*, *Diogenichthys*, *Myctophum*, among others, were described (Olivar and Beckley, 1995; Olivar et al., 1999). Carpenter seabream *Argyrozona argyrozona* (Davis and Buxton, 1996), galjoen *Dichistius capensis* (Leis and van der Lingen, 1997), santer seabream *Cheimerius nufar* (Connell et al., 1999) and red tjor-tjor *Pagellus natalensis* (Leis et al., 2002) were described more recently. The mud sole *Austroglossus pectoralis* and the tonguesole *Cynoglossus zanzibarensis* (Wood, 2000 and 2003) and the white-margined sole *Dagetichthys marginatus* (Thompson et al., 2007) followed.

Lastly, Connell (2007) has documented and described numerous marine fish eggs and larvae off the east coast of South Africa. He described eggs and early larvae of some 226 fish species. Their annual spawning period, and egg abundance trends, are also provided and can be found at the following link: <http://fisheggs-and-larvae.saiab.ac.za/>. In recent years, Connell's work was further verified through DNA barcoding.

### **1.2.3 In-shore life history, population and community studies**

Surveys of South African larval fish assemblages commenced in the late 1900s. Most in-shore studies to date have taken place in warm-temperate waters of the Eastern Cape. Beckley (1986) conducted the first study in Algoa Bay, describing taxa in terms of their distributions, breeding biology and early life histories. Surf zone studies described assemblages of juvenile fishes and found this habitat to function as a nursery for some species of coastal fishes (Lasiak, 1981 and 1986; Bennett, 1989). In the 1990s, a study was undertaken to investigate the role played by the Tsitsikamma National Park marine reserve as a source of eggs and larvae to adjacent fished areas. In doing so, this study assessed the composition of larvae occurring in the area (Tilney and Buxton, 1994; Tilney et al., 1996).

More recently, Cowley et al. (2001) observed larval fish assemblages adjacent to the mouths of intermittently open estuaries in the Eastern Cape, and immigration of larvae to estuaries during marine over-wash events. It is apparent that the presence of estuarine water in the surf zone triggers an accumulation response by larvae of estuarine-associated fishes (Strydom, 2003). Investigations of habitat use by estuarine larval fishes suggested that they actively select areas of weaker current flow in topographical depressions associated with dissipative beach surf zones (Watt-Pringle and Strydom, 2003). A study of larval fishes in a surf zone not associated with an estuary provided evidence that aggregations of estuarine-associated larvae occurred in this habitat, irrespective of proximity to estuary mouths (Strydom and d'Hotman, 2005). Also in this habitat, Strydom (2007) observed a size gradient in larval fishes between the surf waters and adjacent shallow near-shore waters with larger individuals occurring in the surf.

Turning specifically to the east coast province of KwaZulu-Natal (KZN), Whitfield (1989a) examined larvae in the surf zone adjacent to estuaries and found seasonal shifts in larval abundance similar to that found in estuaries (Whitfield, 1989b), with an increase between spring and early autumn. In the late 1990s, Harris (1996) described the larval fish assemblages of three estuarine habitats along the KZN coastline, namely Durban harbour,

Richards Bay harbour and the St. Lucia estuary (Harris, 1996; Harris and Cyrus, 1998). The St. Lucia work revealed that Gobiidae larvae were by far the most dominant occurring larvae in that area. In Richards Bay harbour gobiid larvae were also most dominant, together with larvae of the family Engraulidae (Harris, 1996). Durban harbour revealed a dominance of Clupeidae larvae (30 % of total catch; Harris and Cyrus, 1998). Beckley and Naidoo (2003) subsequently used light-traps to investigate larvae in the vicinity of the entrance channel of Durban harbour and also found catches to be dominated by clupeid larvae (72.3 % of total catch).

Congruently to her studies of estuarine habitat, Harris et al. (1999) studied the surf zone and near-shore habitats in proximity to the St. Lucia estuary in the subtropical northern region of the province. The larval fish assemblage off the estuary mouth was compared to that found in the adjacent surf zone (Harris and Cyrus, 1996) and in the St. Lucia estuary (Harris and Cyrus, 1995). Larvae of the family Sparidae (seabreams) were most abundant in the surf zone (Harris et al., 1999). The study also assessed assemblages along an ocean-estuarine gradient and related these to the physical characteristics of each environment (Harris et al., 2001). Diversity increased with distance from shore and with distance for estuary mouth. Species assemblages differed amongst estuarine, surf zone and near-shore waters and this correlated best with turbidity. Occurrence of partially estuarine-dependent species in all three environments suggested that ocean-estuarine coupling was an important process for the recruitment success of these species; however, the near-shore zone was a preferred habitat for marine species which do not associate with estuaries, such as Tripterygiidae (triplefin blennies), *Bregmaceros atlanticus* (antenna codlet), *Engyprosopon grandisquama* (largescale flounder) and *Benthoosema pterotum* (skinnycheeked lantern-fish) (Harris et al., 2001).

#### **1.2.4 Off-shore life history, population and community studies**

Off-shore larval fish assemblage research in South Africa gained momentum in the late 1900s (Castle, 1968 and 1969; Haigh, 1972; Louw and O'Toole, 1977; King et al., 1978). The first major off-shore survey was conducted by the Sea Fisheries Branch on the west coast in 1972 (O'Toole, 1974), and investigated the spawning and geographical limits of commercially important pelagic *S. sagax*, *E. capensis* and *Trachurus trachurus* (Atlantic horse mackerel), as a contribution to stock assessment. O'Toole (1974) also described the distribution, abundance and ecology of the larval stages of *A. microlepis*, *Dicloglossa cuneata* (wedge sole), *Sufflogobius bibarbatus* (bearded goby), *M. capensis* and other species important to

fisheries. During the early 1980's the spawning and transport of *E. capensis* eggs and larvae via shelf-edge frontal jet currents near Cape Point received much research attention (Badenhorst and Boyd, 1980; Shelton and Hutchings, 1981 and 1982; Shelton, 1984).

The first off-shore larval fish assemblage study on the subtropical east coast of South Africa was that of Anders (1975). In these surveys the eggs and larvae of Clupeids (*Sardinops sagax*) were found to coincide with the annual migration of adults of this sardine on the east coast, well-known as the “sardine run”. In mid-1986, a study on marine fish eggs commenced some 60 km south of Durban on the east coast, about 5 km off-shore of Park Rynie, to investigate the spawning patterns of fishes (Connell, 2010). This study is ongoing and has documented the spawning intensity and periodicity of over 200 species of marine fishes. This study supported the findings of Anders (1975), providing evidence of annual spawning of the sardine *S. sagax* off KZN. Also based on these observations, Beckley and Connell (1996) have reported on spawning patterns of shad (*Pomatomus saltatrix*) which was found to spawn on the shelf in 30 – 50 m water depth, some 25 – 30 km inside the inner edge of the Agulhas Current (Beckley and Connell, 1996).

Subsequent off-shore surveys in 1990/1991 on the east coast focussed on the Agulhas Current and adjacent shelf waters, and involved sampling four transects off southern and central KZN (Beckley and van Ballegooyen, 1992). Owing to their high relative abundance in samples, greatest attention centred on the overall spatial and temporal distributions of Myctophidae, Scombridae (tuna, mackerel and bonitos) and clupeoid larvae (Beckley and Hewitson, 1994; Olivar and Beckley, 1994 and 1995; Olivar et al., 1999; Beckley and Leis, 2000). Based on these surveys, Beckley (1993) observed that ichthyoplankton of linefish species (including many Sparidae) were not prominent in the Agulhas Current, contrary to previous thinking (Heydorn et al., 1977; van der Elst, 1988). Greatest densities of Myctophidae larvae occurred close in-shore (50 – 100 m water depth), and this was ascribed to shoreward intrusions of the Agulhas Current surface water (Beckley and van Ballegooyen, 1992; Olivar and Beckley, 1994). Scombridae larvae showed distinct spatial and temporal variation in distribution and abundance linked to seasonal oceanographic conditions (Beckley and Leis, 2000). Since these cruises in 1990/1991, no off-shore larval assemblage studies have been conducted off KZN.

### **1.3 Objectives and aims**

The present study was conducted as part of the “Ecosystem functioning in the KwaZulu-Natal Bight” project that was undertaken during the second phase of the African Coelacanth

Ecosystem Programme (ACEP II). The aim of this project was to examine the physical, geological and biological processes that influence the marine ecosystem off the central KZN coast with emphasis on the roles of different nutrient sources. As indicated above, previous off-shore surveys in the region are limited, dating back to 1990/91 and were confined to four transects in the southern half of the province. The incorporation of measurements of physico-chemical characteristics of the water column as potential explanatory factors in the current study was intended to improve understanding of potential environmental factors influencing the larval fish assemblage, thereby improving knowledge of the ichthyofauna of a unique region of the South African marine environment.

The aims of the present study were therefore to:

1. Characterize the assemblage of larval fishes present off central KwaZulu-Natal.
2. Determine the potential role of physico-chemical characteristics of the water column in the abundance and distribution of larval fishes off central KwaZulu-Natal.
3. Compare observed patterns in ichthyofaunal larval assemblages to available information on the ichthyofauna of KwaZulu-Natal and elsewhere.

#### **1.4 Thesis outline**

This thesis comprises five chapters. Chapter 1 (this chapter) serves as an introduction, describing previous work and providing motivation for the work performed in this thesis. Chapter 2 presents the study area in the context of early life histories of KZN marine fishes, and the potential for retention and survival of fish larvae off central KZN. Chapter 3 reviews sampling methods for fish larvae and the sampling design, procedures and analyses used in this study. Chapter 4 presents the observational and statistical results. Chapter 5 discusses the significance of the results, observed trends in relation to existing knowledge, summarizes the main conclusions of this thesis, and presents an outlook for future work.

## CHAPTER 2: DESCRIPTION OF STUDY AREA

### 2.1 Locality and climate

The “Ecosystem functioning in the KwaZulu-Natal Bight” project study area encompassed a region of the east coast of South Africa known as the KwaZulu-Natal (KZN) Bight (Figure 1). The KZN Bight is formed by an indentation in the coastline and roughly extends from 30° S in the south to 28° 30' S in the north. The otherwise linear coastline runs at about 30° east of north (Figure 1).

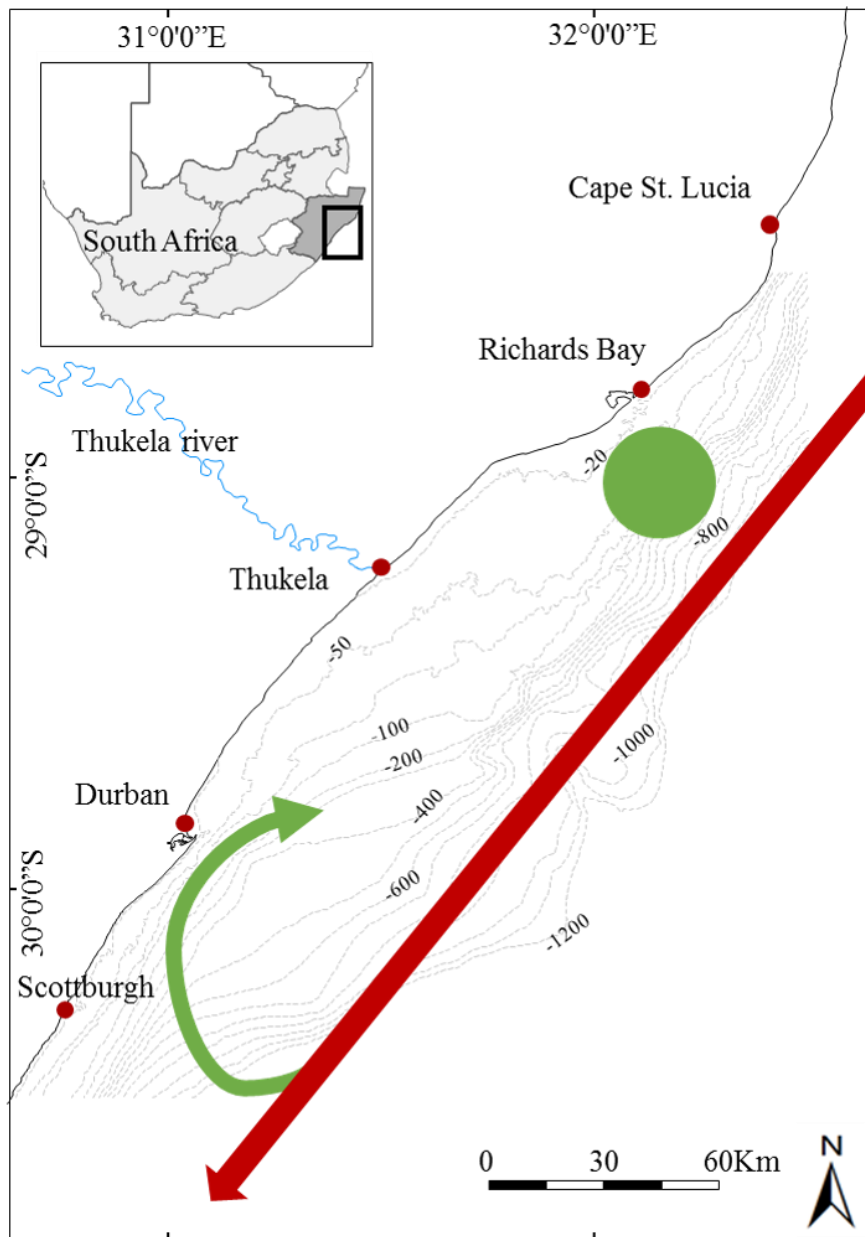


Figure 1. KwaZulu-Natal Bight showing bathymetry and major oceanographic features. Red arrow = Agulhas Current; green arrow = Durban eddy, green dot = Richards Bay upwelling.

This coastal belt is humid and subtropical with two dominant winds which blow parallel to the coast, a north-easterly and a south-westerly (Hunter, 1988). The north-east and south-west winds are equally prevalent in summer while during winter the south-west winds are slightly more frequent and stronger. The winter south-westerly winds are associated with cold fronts which are preceded by coastal lows (Hunter, 1988). The region experiences high rainfall in summer and low rainfall in winter (Figure 2).

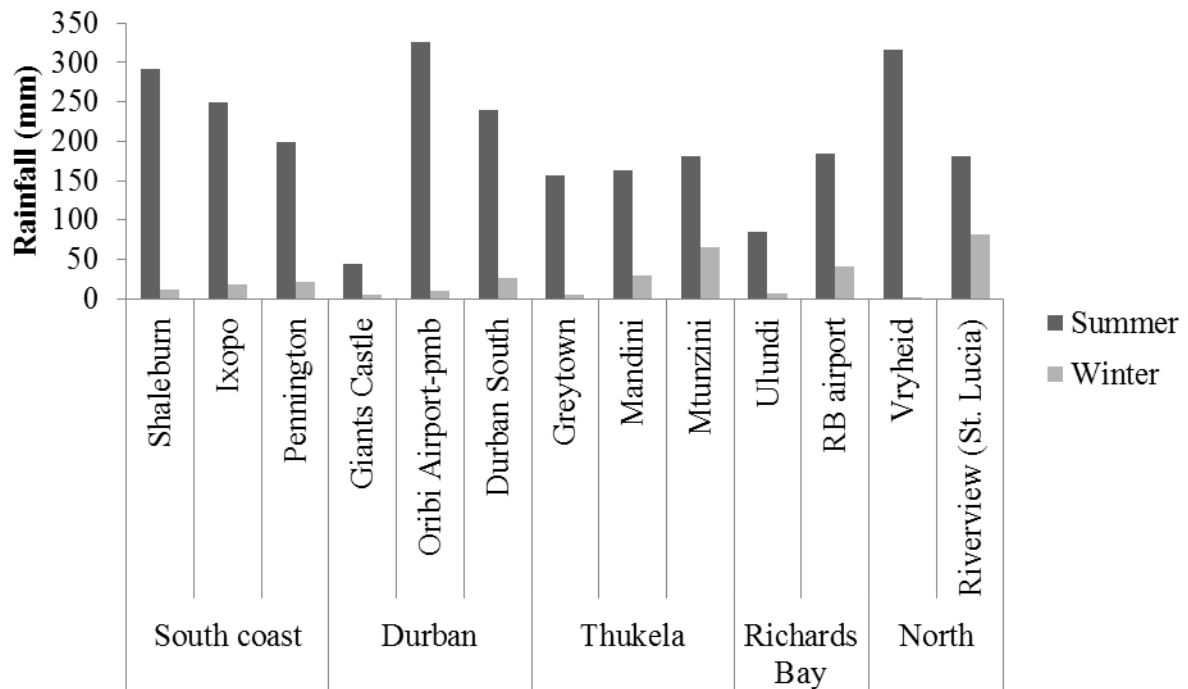


Figure 2. Rainfall experienced at various inland and coastal localities in KwaZulu-Natal during sampling in the KZN Bight in December/January (summer) and June/July (winter) 2010. Inland localities included are in catchments draining into different regions of KZN's coastal waters.

## 2.2 Oceanography

The dominant feature along the KZN coastline is the Agulhas Current (Shannon, 1989). With surface core velocities which exceed  $2.5 \text{ m s}^{-1}$ , an average depth of 200-300 m, a width of 70-90 km and an average mass transport of 70 Sv (Grundlingh, 1980; Bryden et al., 2005), the Agulhas Current is the largest of the five major western boundary currents in the world (Lutjeharms, 2006). The narrow continental shelf heavily influences the oceanography of the KZN Bight. The shelf extends approximately 40 km off-shore at the widest central point of the KZN Bight and the outer edge of the shelf is at an average depth of around 100 m

(Roberts et al., 2010). The widening of the relatively shallow shelf restricts the Agulhas Current off-shore (Roberts et al., 2010), with the midpoint of the Agulhas Current being between 40 and 60 km off-shore of the KZN Bight, although this distance can vary up to 30 km a day. The core temperature of the Agulhas Current ranges between 23 and 28 °C (Pearce, 1978; Schumann, 1988). Agulhas Current waters are warm relative to shelf waters and occasionally the Agulhas Current veers on to the shelf, resulting in warmer in-shore waters.

Large singular meanders, called the Natal Pulses, occur in the trajectory of the Agulhas Current approximately five times a year (Lutjeharms and Roberts, 1988). These pulses originate in the KZN Bight and grow in amplitude as they move south at a rate of about 20 km a day. South of the KZN Bight, the shelf width decreases and there is a change in orientation of the coast relative to the southward-flowing Agulhas Current. These traits, together with cyclonic circulation embedded in these pulses (Lutjeharms and Roberts, 1988; Lutjeharms et al., 2003), result in the generation of a semi-permanent gyre or cyclonic eddy off Durban (green arrow, Figure 1; Gill and Schumann, 1979; Schumann, 1981).

Off Richards Bay a persistent upwelling cell is generated by the change in the topographical nature of the northern KZN Bight (green dot, Figure 1; Lutjeharms et al., 1989a). This upwelling off Richards Bay and the semi-permanent eddy off Durban contribute to a complex flow of shelf currents in the region (Flemming and Hay, 1988). Together with a similar eddy south of Port St. Johns on the Transkei coast, these features have been proposed to form migratory stepping stones for fishes migrating up the coast along the predominantly north-flowing currents on the in-shore edge of the prevailing south-flowing Agulhas Current (Roberts et al., 2010). Like other western boundary currents, the Agulhas Current generates a northward undercurrent on the continental slope at depths of between 800 m and 3 000 m, which may aid with northward migrations of deep-water fauna (Beal and Bryden, 1997).

Another oceanographic feature to consider are mesoscale eddies which form in the Mozambique Channel, some of which travel westwards towards the east coast of South Africa. It is suspected that they are guided by the Mozambique ridge which runs south-westwards along the eastern side of Africa at a 35° angle. These eddies are thought to entrain and transport biological material from Madagascar to the south-east coast of Africa, including the KZN Bight (Quartly and Srokosz, 2004).

### **2.3 Substrate**

Shelf sediments of the KZN Bight are mainly sandy and are interspersed with areas of reef (Green and MacKay, in press). These reefs often take the form of submerged shorelines in linear ridges (Martin and Flemming, 1988). They are widely dispersed in the central KZN Bight owing to the width of the shelf, but are more concentrated off Durban and Richards Bay where the shelf is narrower. Additionally there is a large concentration of reef area just south of Richards Bay (Green and MacKay, in press).

The Thukela River is the third largest river in southern Africa and flows into the sea midway along the KZN Bight coastline. It has a high sediment output of  $6.79 \times 10^3 \text{ m}^3/\text{year}$  (Birch, 1996) which is fed onto the Thukela Shelf. High sediment input from the Thukela River results in a fine silt depocentre off the river mouth (Flemming and Hay, 1988). The outer shelf (60 to 100 m depths) is characterized by gravel and large bedforms that are produced by the southerly-flowing Agulhas Current (Bosman et al., 2007). Two large patches of gravel are present, one on the shelf edge south of Durban and one on the shelf between Thukela and Durban. A number of canyons break up the shelf edge (Green and MacKay, in press).

### **2.4 Nutrients and primary productivity**

In comparison to the Benguela system on the west coast of South Africa, waters of the KZN Bight have low nutrient concentrations and are oligotrophic (Lutjeharms, 2006). Nitrate concentrations of the KZN Bight range between 1 and 2  $\mu\text{mol/L}$  in the south and central areas, but can reach 9  $\mu\text{mol/L}$  in the north during Richards Bay upwelling events (Meyer et al., 2002). In comparison, nitrate concentrations in the Southern Benguela are usually around 20  $\mu\text{mol/L}$  (Giraudeau and Bailey, 1995).

Nutrient concentrations in the Agulhas Current itself increase with increased depth. In the KZN Bight, surface waters decrease in nutrient concentration with increased distance from shore, towards the Agulhas Current (Pearce, 1977a). Therefore, the Agulhas Current itself provides little nutrients. However, it plays a major role in nutrient loading on the shelf off the KZN Bight as it drives processes that supply nutrients to the KZN Bight, increasing the productivity of the KZN Bight waters (Lutjeharms et al., 2000; Meyer et al., 2002). The continuous Eckman veering of the Agulhas Current waters at the shelf edge causes upwelling of cooler, nutrient-rich water onto the shelf and results in cooler in-shore waters with elevated concentrations of inorganic nutrients (N, P and Si) relative to the core surface water of the Agulhas Current.

The eddy located off Durban (Pearce, 1977b), and upwelling off Richards Bay (Lutjeharms et al., 1999), are further sources of cooler nutrient-rich water. The upwelling off Richards Bay contributes to a near-continuous supply of nutrients onto the adjacent Thukela Bank (Carter and d'Aubrey, 1988; Roberts and Nieuwenhuys, in press) resulting in a distinct region of enriched biological production (Carter and Schleyer, 1988). Rivers along the coast, particularly the Thukela, are further sources of nutrients (Pearce et al., 1978; Carter and D'Aubrey, 1988; Lutjeharms et al., 1989b; Ayers and Scharler, 2011; de Lecea et al., 2013). Influenced by these features, the waters of the KZN Bight therefore have higher primary productivity than elsewhere on the KZN coast, and this is reflected in elevated chlorophyll-*a* concentrations.

## **2.5 Secondary productivity**

Increased phytoplankton (primary production), driven by nutrient input, is important for maintenance of local zooplankton communities. Over the past twenty years South African zooplankton research has focused on the Benguela upwelling ecosystem and on the Agulhas Bank off the Cape south coast where commercially important pelagic fish species are most abundant. Zooplankton research on the east coast comprises only a few early surveys (Carter, 1977; Schleyer, 1985; Carter and Schleyer, 1988) and more recent studies which mostly focussed on gelatinous zooplankton (Thibault-Botha et al., 2004; Buecher et al., 2005; Thibault-Botha and Gibbons, 2005).

Transects across the Agulhas Current have shown a higher zooplankton biomass in-shore (Carter, 1977), and the bulk of the zooplankton biomass (70%) occurs in the upper 100 m (Carter and Schleyer, 1988). The dominant copepod species in the core of the Agulhas Current was *Paracalanus parvus*, but on the shelf, *Centropages chierchiae* and *Calanoides carinatus* were dominant (Carter, 1977). Carter (1977) recorded a dry (austral winter) season biomass bloom dominated by the large calanoid, *C. carinatus*. Most recently, Pretorius et al. (in press), as part of the ACEP II: "Ecosystem functioning in the KZN Bight" project, conducted a synoptic analysis of zooplankton biomass (which comprised mainly copepods) across the wet and dry season in the KZN Bight. Zooplankton biomass was significantly higher in the Dry season, and was patchy in distribution, with highest concentrations located off-shore at Richards Bay and farther north off St. Lucia. During the Wet season, zooplankton biomass was more evenly distributed, with highest concentrations off Durban. This contrasts with Carter (1977) who found a shelf biomass minimum in the Durban area in

the late Wet season (March). Pretorius et al. (in press) also noted that the persistent nutrient enrichment from the upwelling off Durban and Richards Bay appears to have a greater influence on zooplankton biomass and distribution in the KZN Bight than the strongly seasonal nutrient input from the Thukela River.

Despite this elevated secondary productivity apparently being associated with the upwelling systems, trophic flows of the KZN Bight are driven by detritus (Ayers and Scharler, 2011). Riverine input is a large source of detritus along the KZN coastline, especially by the Thukela River (de Lecea et al., 2013). In comparison to the west coast of South Africa (an upwelled/phytoplankton-driven system), fish abundances of the KZN Bight are relatively low. The Southern Benguela on the west coast is nutrient-rich with high plankton biomass and fishery landings (Shannon et al., 2003). In this area, pelagic fish predators on zooplankton are mainly represented by sardine (*S. sagax*), red-eye round herring (*Etrumeus whiteheadi*), Cape-anchovy (*E. capensis*) and Cape horse mackerel (*Trachurus capensis*) (Crawford et al., 1987; Japp et al., 1994). These species are not nearly as common off KZN, which does not support an abundance of pelagic fishes, except during the sardine run in June-August (van der Lingen et al., 2010). Van der Elst (1989) compared the coastal fisheries of South Africa and reported that the KZN shelf does not support any year-round pelagic fisheries and yields only 1 500 to 2 000 tonnes of linefish per year (mostly demersal species) and about 500 tonnes of shoaling sardine-like pelagic fishes per year. The low productivity of the east coast is also reflected in the beach-seine and gill-net fisheries of South Africa. Catch per unit effort in these fisheries declines from 115-294 kg per net-day off the west coast to 5-48 kg per net-day off the east coast (Lamberth et al., 1997). Broadly, a trend is observed from highly productive, largely industrial fisheries on the west coast to low production, small-scale fisheries on the east coast (Lamberth et al., 1997). The small scale of the KZN fisheries notwithstanding, the larval fishes of the KZN Bight could be expected to reflect the catch composition of fisheries in the area to some extent at least.

## **CHAPTER 3: MATERIALS AND METHODS**

### **3.1 Larval fish sampling**

#### **3.1.1 Factors affecting larval fish sampling**

When sampling larval fish, gear selection must include consideration of the advantages and disadvantages of each gear type (Bowles et al., 1978; Marcy and Dahlberg, 1980; Kelso and Rutherford, 1996). Gear choice must take into consideration characteristics of the sampled organisms (biotic factors) and the habitat being sampled (abiotic factors). The most common abiotic factors affecting larval fish sampling are the hydraulic characteristics of both the gear and the flow conditions near the gear. For example, turbulence within and around the gear may reduce its filtering efficiency (Bowles et al., 1978). Variation in mesh size regulates clogging during filtration. Small mesh size is prone to clogging in waters with high biomass. However, too large a mesh size might facilitate extrusion of targeted fish larvae which can pass through the gear.

Biotic factors affecting larval fish sampling include active avoidance of gear by larger, more developed larval fish. Well-developed, larger larval fish are able to move through the water column by swimming. Towed gear may cause turbulence in the water column, alerting larger larval fish and leading to avoidance of the gear (Tranter and Smith, 1968). Larvae may also be excluded by extrusion depending on the compressibility of the organism and mesh flexibility (Vannucci, 1968). The organism may orientate itself in such a way as to facilitate escape.

Variations in horizontal distribution and diurnal vertical migration of larvae through the water column are also potentially influential biotic characteristics. In comparison with current speeds the swimming ability of larval fish is often of minor importance. However, larvae can migrate vertically in the water column and so influence their horizontal transport, using currents that change with depth in speed and direction (Fortier and Leggett, 1983; Sclafani et al., 1993). Three categories of vertical migrations occur. Type I migrations occur as upward movement at the beginning of night and downward movement at the beginning of day. Type II occur in the opposite directions, downwards at dusk and upwards at dawn (Neilson and Perry, 1990). Type III migrations occur as aggregations during the day and dispersals at night (Leis, 1991; Olivar and Sabatés, 1997; Gray, 1998).

The vertical distribution of larval fish in a water column varies amongst taxa as well as age classes. Size and consequently swimming ability change throughout larval fish development and the larvae of many species exhibit changes in vertical migratory patterns as they develop (Neilson and Perry, 1990). Younger larvae and particularly those in poor condition may be more strongly influenced by buoyancy or lack thereof (Sclafani et al., 1993). However, even in their earliest stages, larvae are able to migrate if conditions become unfavourable (Grønkjær and Wieland, 1997). Factors that may influence these migratory patterns include light, prey and predator distribution, as well temperature and salinity effects. However, individuals of given species and guilds often exhibit similar distribution patterns, regardless of the prevailing environmental conditions, and form distinct assemblages at different depths (Southward and Barrett, 1983; Röpke, 1989; Olivar and Sabatés, 1997; Gray and Kingsford, 2003).

Modification of gear design and sampling method must be made to reduce the effects of turbulence, avoidance, clogging and extrusion. The efficiency of each gear type is based on the ability of the gear to collect an accurate representation of the aquatic community being studied (Bowles et al., 1978). Given the natural variations in vertical distribution of larval fishes, it is important to sample adequate depths to ensure a full representation of the sampled community. When comparing larval fish communities, sampling should ideally be restricted to a consistent time of day, or else include consideration of these migrations during analysis.

### **3.1.2 Larval fish sampling gear**

#### ***Evolution of sampling gear***

Larval fish sampling gear has changed over time in attempts to alleviate the problems posed by turbulence, clogging and extrusion; larval fish surveys commenced in Europe in 1828 utilizing plankton nets (Fraser, 1968). The early plankton nets consisted of metal rings with conical nets of silk bolting cloth, originally designed for milling flour (Heron, 1968). Modern day plankton nets consist of non-perishable synthetic fibre such as nylon or metal screening to maintain a constant mesh size to assure retention of plankton of a desired size class (Bowles et al., 1978). A diversity of sampling gears and methods has developed in response to the diversity of fish reproductive modes and species-specific differences in spawning habitats, larval fish growth and behaviour and to suit specific sampling conditions (Kelso and Rutherford, 1996). There are several general categories of larval fish sampling gear, namely pump samplers and diver-operated gear, high-speed nets, plankton recorders, and low-speed,

mid-water and multi-level nets. Less frequently used are grab samplers, plankton purse seines, electrofishing and traps (Bowles et al., 1978; Marcy and Dahlberg, 1980).

### ***Pump samplers and diver-operated gear***

Pumps are best used to sample turbulent water and sites that are inaccessible to nets. Since 1887, studies of demersal eggs and larvae, and the spatial distribution of pelagic larval fishes, have utilized centrifugal pumps (Aron, 1958). Their use typically requires less labour once in a fixed position and it is therefore easier to replicate samples, as gear position in the environment is easily controlled (Harris et al., 1986; Kelso and Rutherford, 1996). Stauffer (1981) tested three pump designs for collecting lake trout eggs and early life stages and reported adequate collections with a system incorporating a diver-directed intake.

Dorr et al. (1981) used diver-operated underwater diaphragm pumps to sample alewife and lake trout eggs as well as age-0 sculpins. Diver-operated gear is best for highly specialized sampling. Vogeleson et al. (1971) used compressed air from a scuba cylinder in a portable, diver-operated suction device for collection of sunfish eggs and larvae. Novak and Sheets (1969) also used scuba divers to direct the pump intake for collecting smallmouth bass larvae. Diver operated gear however, requires training, limits the study area and it is difficult to quantify the volume of water sampled (Bowles et al., 1978). Leithiser et al. (1979) found that avoidance by larger larval fish was also significantly less in pump samples than in concurrent samples taken with plankton nets. Due to their large size however, pumps can be difficult to work with as a mobile sampler in the field (Bowles et al., 1978; Kelso and Rutherford, 1996). In addition, Aron (1958) reported that plankton nets are as efficient at sampling pelagic larval fishes as pump samplers.

### ***High-speed nets and plankton recorders***

Plankton nets are able to sample larger spans of water than pumps and are more suitable for whole community analysis, giving a true pelagic sample. Although a lesser volume of water is sampled compared to other gear types, efficiency is increased by sampling larger areas in a short period of time (Kelso and Rutherford, 1996), particularly when using high-speed plankton nets. High-speed plankton nets are typically large (>50 kg), susceptible to clogging and samples are frequently damaged. The high speed of towing may also increase extrusion of smaller organisms through the net by distortion of the mesh, which affects retention and selectivity. Furthermore, large vessels and winches are needed for deployment. Although high-speed samplers reduce net avoidance by mobile larval fish, avoidance can still occur

(Bjorke et al., 1974). Modifications have been made on numerous occasions to correct for these inefficiencies (Schnack, 1974; Coles et al., 1977). An alternative design is the jet net which was developed to reduce damage to collected organisms by slowing the velocity of water as it moved through the sampler into the collecting net (Clarke, 1964).

Another modification of high-speed plankton nets is the plankton recorder. Developed by Longhurst et al. (1966) from a Hardy plankton recorder (Hardy, 1936), they sample a narrow band of water over a long distance. The Longhurst-Hardy plankton recorder incorporated at the end of plankton nets is a unique collection box that continuously filters collected organisms through a gauze strip, which is overlaid by a second strip, both of which are wound up in the box. The plankton recorder has been used extensively and has been reported to be more effective than normal high-speed plankton nets (Colton et al., 1961) and pump samplers (Brander and Thompson, 1989). However, the recorder may not be effective at low concentrations of larvae ( $<0.1/\text{m}^3$ ; Colton et al., 1961), and problems occur with extended residence of organisms in the netting before capture in the recorder (Haury et al., 1976). These samples are frequently mutilated due to extrusion of samples through the nets, which is not ideal for examination of delicate organisms. Sampling is also limited by bottom topography.

### ***Low speed nets and multi-level systems***

Low-speed nets are trawled horizontally, obliquely or vertically at speeds of less than 2 m/s (~5 knots) and for periods ranging from 30 seconds to an hour. These plankton nets cause less damage to the sampled organisms and are therefore better when identifying organisms visually. Several low-speed, mid-water nets have been developed to sample early life stages of pelagic fishes. For example, the Isaacs-Kidd mid-water trawl (Isaacs and Kidd, 1953) has been used extensively to sample large larvae and small juveniles in pelagic waters (Pearcy, 1980). Low speed nets however, have labour requirements and the boat from which they are deployed must be able to maintain a constant speed (Bowles et al., 1978). Further, mid-water (and horizontal) tows do not give a true representation of community changes with depth. The need to sample eggs and larvae on or just above the ocean bed in order to investigate relationships with bottom hydrography led to the development of benthic plankton sleds (Frolander and Pratt, 1962; Dovel, 1964; Yocum and Tesar, 1980; Madenjian and Jude, 1985; Phillips and Mason, 1986). In addition, speed of tow must be kept constant as it could alter

the depth of the sampler and over-emphasize abundance of organisms from a specific depth (Bowles et al., 1978).

A steel-framed trawl developed by Tucker (1951) was used by Haldorson et al. (1993) to monitor larval fish abundances and was modified by Houser (1983) to include a diving plane for maintenance of position in the water column without the use of ballast. La Bolle et al. (1985) included an adjustable net that could effectively sample the entire water column in a range of depths.

Closing mechanisms fitted to low speed nets allow collection of samples from discrete depths, together with flow measurements. Early closing mechanisms used weighted messengers to close the net at selected depths before retrieval. Various opening and closing mechanisms have been developed using acoustics (Clarke, 1969; Baker et al., 1973). In 1976 a system was introduced whereby electronic signals triggered the opening and closing of nets sequentially, thus eliminating the inadvertent collection of plankton from other strata during deployment and recovery (Wiebe et al., 1976). The MOCHNESS trawl (multiple opening-closing net and environmental sensing system; Wiebe et al., 1976) incorporated sensors to monitor depth, temperature, specific conductance, flow, net angle, and net deployment. Sameoto et al. (1977) incorporated similar environmental sensing systems in the BIONESS (Bedford Institute of Oceanography Net Environmental Sampling System) net and modifications to this net resulted in the LOCHNESS (large opening closing high-speed net and environmental sampling system) sampler (Dunn et al., 1993). These sampling systems, however, are expensive and demand high maintenance (Kelso and Rutherford, 1996).

### ***Low-speed oblique Bongo nets***

Oblique (as well as vertical) tows give a representation of the larval fish community through the entire water column (Kelso and Rutherford, 1996). Low-speed, oblique Bongo nets (Figure 3) can be deployed off relatively small vessels, fished from a fixed position or towed, and are relatively inexpensive. The mesh is easily clogged and larger larvae may avoid capture (Bowles et al., 1978), however, mesh selection can limit clogging. The best mesh design is square with uniform aperture and is stiff enough to resist bending but flexible enough to allow self-cleaning (Heron, 1968). Increased mouth diameter of the net reduces net avoidance as an organism must travel further in order to avoid capture (Barkley, 1972). Generally, larger diameter nets are more efficient but a diameter of more than one meter is impractical due to difficulties in handling and towing (Aron, 1962). In order to increase

sample volume the length of tow can be increased rather than increasing net mouth (Wiebe, 1972). The duration of tow should be long enough to sample an adequate volume of water while not being so long as to cause clogging. Bongo nets in particular sample large volumes as they provide side-by-side simultaneous net samples (McGowen and Brown, 1966; Bowles et al., 1978). The volume of water that passes through the net must be calculated to provide quantitative analysis of plankton samples. Originally it was thought that the volume of water sampled was that presented at the mouth of the net, however, due to clogging of the mesh, filtered water volume is reduced as sampling progresses (Fraser, 1966; Tranter and Heron, 1967; Tranter and Smith, 1968). Therefore, an accurate flow meter must be used which records the flow rate of water through the net while sampling. This velocity together with gear dimensions allows for calculated volume sampled which accounts for clogging as well as for differences in field conditions at different sampling stations, such as turbulence (Bowles et al., 1978).

Low-speed Bongos have been successfully used in South Africa for several years. Zooplankton in South Africa are most often sampled using vertical Bongo nets (Sono, 2008) and zooplankton sampling during the current survey (ACEP II: ecosystem functioning of the KZN Bight) also made use of this gear type (Pretorius et al., in press). Bongo nets are a standard gear used in many larval fish surveys (Smith and Richardson, 1977; Johnson and Morse, 1994; Shima and Bailey, 1994; Pepin and Shears, 1997). Several larval fish studies in South Africa have successfully used Bongo nets (eg. Olivar and Shelton, 1993; Tilney and Buxton 1994; Wood, 1999; Patrick, 2008). In particular, Bongo nets were utilized during the 1990/1991 survey of fish larvae of the east coast of South Africa (Beckley and van Ballegooyen, 1992) and were therefore chosen for this study (Figure 3).

### **3.1.3 Larval fish sampling for the present study**

The FRS Algoa research vessel, then owned by the Department of Environmental Affairs and Tourism, provided the platform to undertake two 10-day synoptic surveys of the KwaZulu-Natal (KZN) Bight for the ACEP II: “Ecosystem functioning in the KZN Bight” project (Fennessy et al., in press). These surveys took place in January/February 2010 (during the Wet season) and July/August 2010 (during the Dry season). During the surveys, larval fishes were sampled along 15 coast-perpendicular transects across the KZN Bight from just south of Durban to Cape St. Lucia in the north (Figure 4). Locations of stations and transects were pre-determined based on the predicted time required to undertake a range of sampling

(including for larval fishes) during the 10 day surveys (Fennessy et al., in press). Transects consisted of a minimum of three larval fish stations, but four stations were sampled as the shelf widened in the central KZN Bight. Three bathymetric Zones were defined, separating the stations into Shelf (20-100 m), Mid-slope (100-700 m) and Deep-slope (about 1 000 m depth) (Figure 4). No Mid-slope stations were sampled in the Thukela Area. This was due to the natural morphology of the shelf. In this section of the central KZN Bight, the shallow Thukela Shelf widens and there is a very narrow area at depths between 100 and 700 m (see Figure 4).



Figure 3. Photograph of Bongo net taken during sampling by Prof. AJ Smit.

At each of the preselected stations, larval fishes were sampled using a low-speed Bongo net (Figure 3) hauled obliquely through the water column. The Bongo comprised two nets, each with a mouth diameter of 57 cm (area of  $0.26 \text{ m}^2$ ). For the purposes of this study, larval fishes were collected from only one of the Bongo nets, with 500  $\mu\text{m}$  mesh size, were included in the analysis. Samples from the other net were used for isotope analysis in a separate study. A Series U3 flow meter attached to the mouth of the net was used to allow for the calculation of volume of water sampled during each tow. On the approach to each station the net was lowered to a depth of 80 m, or 5 m from the seafloor (whichever was shallower). The

maximum depth of 80 m was selected to correspond with that of the previous off-shore study in KZN by Beckley and van Ballegooyen (1992). Once the net reached the chosen sampling depth the ship motored at 2 knots and the net was retrieved at 0.5 m/s. On retrieval the contents of the nets were washed into 350 ml plastic jars and preserved in 10 % buffered seawater formalin. Samples were collected during both the day and the night to fit in with the fieldwork required for other components of the wider research project. Time of sampling was recorded at each station to allow for analysis of possible diurnal effects on larval fish abundances. Any circumstances that could have influenced the efficiency of sampling (e.g. rough seas, wind) were recorded on field sheets.

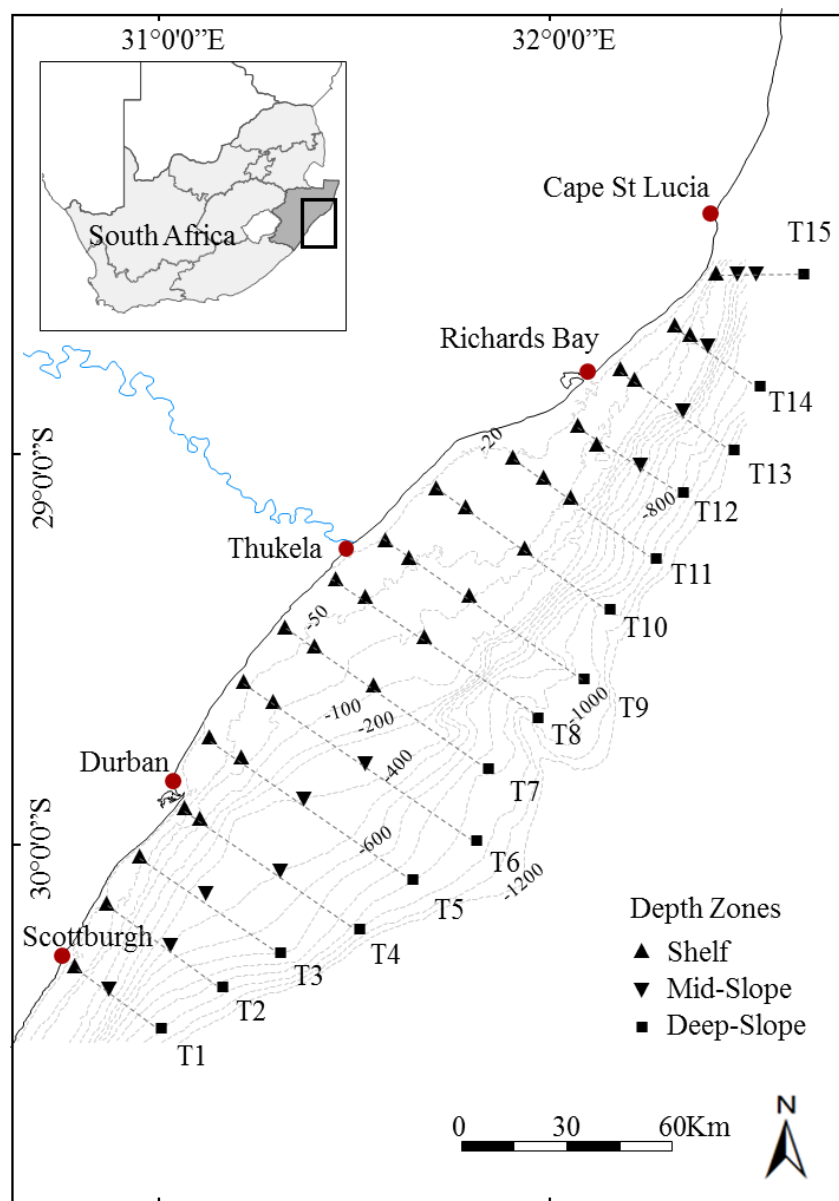


Figure 4. KwaZulu-Natal Bight (bathymetry indicated in m) and the localities of transects (T) and stations sampled during Wet and Dry seasons, 2010.

## **3.2 Environmental parameters**

### **3.2.1 Environmental variables affecting larval fish assemblage**

Larval fishes are influenced by a variety of environmental factors, operating at a range of temporal and spatial scales, particularly those that affect their feeding, survival and transport (Muhling, 2006). At larger spatial scales (e.g. between water masses), larval fishes distribution is influenced by hydrographic boundaries and water masses, in the manner of passive particles (Olivar and Beckley, 1994). Water-mass history is considered to be one of the most important factors in structuring large-scale larval fish assemblages (Cowen et al., 1993). Larval fishes make use of oceanographic features and water masses with recurrent and predictable properties to ensure dispersal or retention in waters suitable for feeding, growth and subsequent survival (e.g. Moser and Smith, 1993; Olivar and Shelton, 1993; Grothues and Cowen, 1999; Hare et al., 2001). Other oceanographic processes such as upwelling (Olivar and Shelton, 1993), advection and direction of flow (Franco-Gordo et al., 2001) and position and strength of currents (Hare et al., 2001; Hsieh et al., 2005) are also important in shaping larval fish assemblages. These features may be readily defined on a cruise-by-cruise basis by observing measures of Sea Surface Temperature (SST) and salinity (Muhling, 2006), and therefore should be used to ascertain large-scale structuring of water masses and their relevant larval fish assemblages.

At smaller spatial scales (e.g. within water masses), larval fish behaviour appears to modify assemblage patterns (Leis and Carson-Ewart, 1998; Kingsford et al., 2002). Larval fishes actively migrate towards waters with preferable conditions. These patterns may be influenced by hydrographic fronts (Moser and Smith, 1993; Sabatés et al., 2007) and local variations in temperature, salinity and Chlorophyll-*a* concentration (Grioche et al., 1999; Espinosa-Fuentes and Flore-Coto, 2004). For example, temperature is known to be one of a suite of important environmental variables influencing larval fish assemblages in coastal waters (Kingsford, 1988; Tzeng and Wang, 1993; Harris et al., 1999). Differences in swimming performances of temperate and tropical species have been related to water temperature (Wardle, 1975; Wieser and Kaufmann, 1998). From South African studies, too, SST is most often ascertained to be the driving parameter of larval fish assemblages (Beckley, 1985; Olivar and Beckley, 1994; Tilney and Buxton, 1994; Strydom, 2002; Muhling, 2006; Harris et al., 2001; Pattrick, 2008). Salinity was also considered in each of these studies, but not found to be a driving factor in larval fish assemblages. While temperatures and salinities vary with depth through the water

column, surface values are most frequently and adequately used to ascertain water mass structures (Muhling, 2006; Muhling et al., 2008).

Muhling (2006) emphasized the role of surface Chlorophyll-*a* in marine environments as an influencing factor in larval fish assemblages, by observing larvae in proximity to nutrient sources such as river mouths and upwelling cells. Similarly to the effect of Chlorophyll-*a*, as a proxy for nutrients/productivity, zooplankton dry weight is a proxy for productivity and a possible explanatory factor for larval fish assemblages. Zooplankton feed on phytoplankton blooms, and in turn form important prey for various developmental stages of a variety of fishes, and are particularly important for the larval fish phase. A number of dietary studies have shown the preference by larval fishes for copepodites, a development stage of copepods (Gaughan, 1991) which are the dominant constituent in most sea-surface zooplankton samples.

Zooplankton are known to accumulate at hydrographic fronts and upwelling areas because of phytoplankton blooms, and these areas are often targeted by adult fishes as food sources. This in turn might be correlated with an increase in fish spawning activity and hence larval occurrence near the fronts (Dr A. Connell pers. comm., 2014, alconnelli@gmail.com). In addition, zooplankton biomass may be indicative of previously nutrient-enriched waters. These four factors (Temperature (SST), Salinity (surface), Chlorophyll-*a* and Zooplankton dry weight) were considered as environmental factors in this study.

### **3.2.2 Environmental measurements**

At all stations, water column profiling of Temperature and Salinity was conducted using a Conductivity Temperature and Depth (CTD) probe. These environmental data were recorded on arrival at each station with an SBE 9plus CTD underwater unit which was lowered by a hydrographic winch to within 5 m of the sea floor. Seawater was collected at selected depths according to the fluorescence profile. Analyses of these water samples included measurement of Chlorophyll-*a*. Pigment samples were stored frozen in liquid nitrogen and analysed ashore by liquid chromatography in order to determine total Chlorophyll-*a* ( $\mu\text{g/L}$ ; Barlow and Lamont, 2012). These values were subsequently made available to the present study.

Zooplankton biomass was collected concurrently using vertically-deployed Bongo nets (200  $\mu\text{m}$  mesh). The samples were split at sea using a Folsom splitter; part of the split samples was used to determine zooplankton dry weight ( $\text{mg/m}^3$ ). Samples were filtered onto GF/F filter papers from which excess water was removed using a vacuum pump. The filters were

weighed before and after sample filtration and then dried in an oven at 60 °C for 24 hrs and reweighed (Lovegrove, 1962 and 1966) and these values were subsequently made available to the present study (Pretorius et al., in press).

### **3.3 Laboratory procedures for larval fishes**

With the use of a dissecting microscope (20x magnification) the larval fishes were separated from the samples which also comprised algae, cephalopods, chaetognaths, cnidarians, copepods, crustaceans, echinoderms, fish eggs, larvaceans, mollusca, ostracods and polychaetes. Qualitative notes were made on the presence and relative abundance of these other biota. The larval fishes were then preserved in 70% ethanol and stored in darkness to prevent loss of pigmentation.

Larval fishes were identified to the lowest possible taxonomic classification under a dissecting microscope (10-100x magnification) using available taxonomic resources, including Smith and Heemstra (1995), Leis and Carson-Ewart (2000), Richards (2006) and Connell (2007). Appendix Ia shows a diagram of a typical fish larvae (specifically a Clupeiod larva) taken from Leis and Carson-Ewart (2000) annotated with the basic characteristics of importance for identification, namely length vs. gut length, length vs. width, number of myomeres and gut shape. In addition to these characteristics, each family was identified using various traits specific to that family/taxon. Larval fish were counted and photographs were taken of each taxon encountered and a catalogue was developed for reference. Identifications were verified by Dr Allan Connell (Research Associate, South African Association for Aquatic Biodiversity, Grahamstown) and in the case of some taxa other experts in the field were consulted for further confirmation of identity.

### **3.4 Data analysis**

#### **3.4.1 Conceptual model**

Sample stations were categorised by Area-Zone based on criteria of latitude and depth. Three broad Areas were recognised: Richards Bay, Thukela and Durban. These can be separated on the basis of their proximities to different nutrient sources, an upwelling cell in the case of Richards Bay, the Thukela River in the case of the Thukela Area, and a cyclonic eddy in the case of Durban (de Lecea et al., 2013; Fennessy et al., in press). They also represent northern, central and southern regions of the KZN Bight respectively. Transects T1 to T6 were designated as occurring in the “Durban” Area, T7 to T10 in the “Thukela” Area and T11 to

T15 in the “Richards Bay” Area (Figure 4). With the further definition of sites by depth zone (Shelf, Mid-slope and Deep-slope), this separated the KZN Bight into eight Area-Zones in a spatially structured sampling grid (Figure 5) that was consistent with a conceptual model of larval fish distribution over the KZN Bight. This allowed stations to be treated as replicates in the investigation of the spatial patterns of larval fish abundances and allowed the development of a number of *a priori* hypotheses, informed by the typical oceanographic conditions found in the KZN Bight, and the likely drivers of larval fish assemblages.

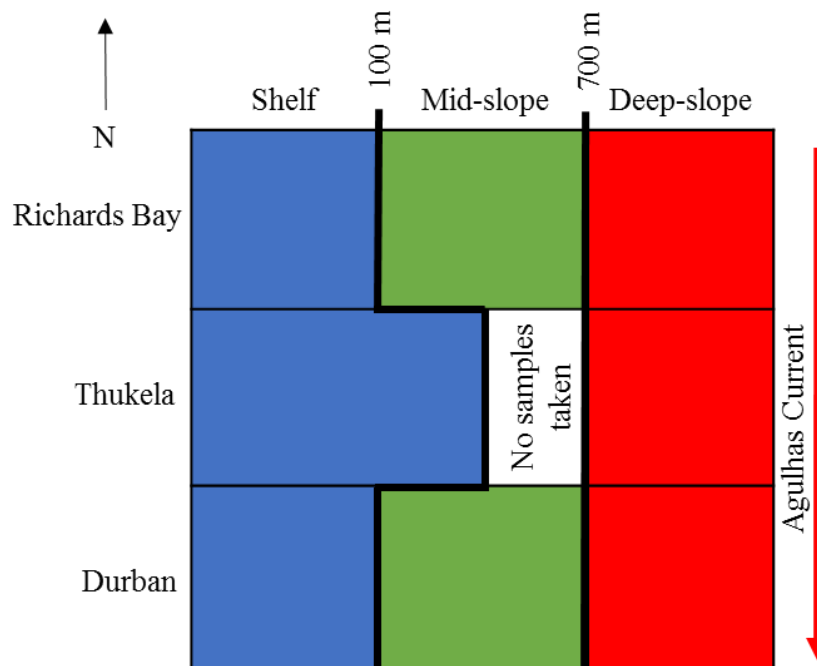


Figure 5. Conceptual spatial model categorising sampling stations for larval fishes in the KwaZulu-Natal Bight. “No samples taken” refers to the lack of samples from that Area-Zone owing to the much greater width of the adjacent shelf and the rapid increase in depth beyond the shelf break (see text).

*A priori* predictions were that: 1) the larval fish assemblage of the Deep-slope Zone would be homogenous due to the prevalence of Agulhas Current waters (red colouring). 2) The larval fish assemblage of the Mid-slope Zone (off Durban and Richards Bay) would be similar due to inputs of nutrient-enriched waters from the Durban eddy and the Richards Bay upwelling (green colouring). 3) The assemblage of the Shelf Zone would be homogenous owing to the well-mixed nature of shelf waters, combined with larval supply from distinct coastal/shelf communities 4) Richards Bay, Thukela and Durban Areas were hypothesized to support distinct larval fish communities due to differences in their nutrient sources (upwelling versus riverine).

Albeit that the Thukela shelf is known to be different to the other shelf habitats (Fennessy, in press), this could not be tested *a priori* owing to the unbalanced design of the sampling grid; so the most conservative and statistically appropriate approach was to test for broad Area and Zone influences.

### **3.4.2 Potential effect of day and night sampling**

As indicated previously, diurnal migration can play a role in the distribution of fish larvae in marine waters. It was therefore important to assess the possible confounding influence of time of sampling (day versus night) on larval fish catches before conducting wider spatial and temporal analyses. This was achieved by univariate as well as multivariate analyses. Univariate tests (ANOVA) were performed on two community metrics (number of taxa and larval density (larvae/100m<sup>3</sup>) using the SigmaPlot Statistical Package. Prior to analysis data were checked for normality and homogeneity (Levene's test). In cases where the assumptions of ANOVA were not met and could not be achieved by transformation, Kruskal–Wallis non-parametric tests were conducted.

Multivariate comparison was conducted through Analysis of Similarity (ANOSIM) using Primer 6.1.16. ANOSIM calculates a *p*-value similar to that of an Analysis Of Variance (ANOVA), where values of *p* < 0.05 indicate significant differences. *p*-Values are also associated with an R-statistic which is scaled between -1 and 1, which indicates the biological importance of a calculated statistical difference. Biological importance of differences increases as R approaches 1, with values greater than 0.4 considered biologically important (Clarke and Warwick, 2001).

### **3.4.3 Environmental conditions**

Contour plots of environmental variables (SST, surface Salinity, Chlorophyll-*a* (f-surface) and Zooplankton dry weight) were plotted in Ocean Data View 4 (Schlitzer, 2015) using variational data interpolation (DIVA). This allowed a visual interpretation of these data. Data were also analysed using formal statistical methods. Prior to statistical analyses, environmental variables were normalized, using the normalize function in PRIMER 6.1.16, so that variables with differing units of measurement were comparable with one another. Variables were checked for homogeneity using draftsman plots, no pair of environmental variables correlated where *R* > 0.7 and therefore each variable met the requirement of homogeneity of variance (Link et al., 2013). Statistical analysis was then conducted using Principal Components Analysis (PCA) in PRIMER 6.1.16 (Clarke and Gorley, 2001).

Tests for differences in environmental variables across the *a priori* identified factors of Season, Area and Zone were made using PERMANOVA+ 1.0.6 (Anderson et al., 2008). The similarity matrix used for the basis of the PERMANOVA tests was generated based on Euclidean distance. PERMANOVA is a non-parametric method that uses permutation methods to test for differences among groups by testing the simultaneous response of variables (in this case environmental) to one or more *a priori* factors from a specified experimental design (Anderson et al., 2008). The routine partitions the total sum of squares according to the *a priori* factors in the specified experimental design, including appropriate treatment of factors that are fixed or random, crossed or nested, and all interaction terms. In this study, to test the *a priori* hypotheses, Season, Area and Zone were treated as fixed factors that were crossed (every level of one factor is present in every level of the other factor, and vice versa). A distance-based pseudo-*F* statistic is computed (analogous to the *F* statistic for multi-factorial ANOVA models) and *p*-values are subsequently obtained by permutation.  $p < 0.05$  is considered a significant difference between environmental variables associated with the *a priori* factors.

### 3.4.4 Analysis of biological data

The volume of water filtered by the Bongo net was calculated using the following equation:

$$\text{Vol. Filtered (m}^3\text{)} = ((\text{Flow meter count}/10)/\text{calibration factor}^*) \times \text{net mouth area of } 0.25 \text{ m}^2$$

\*Calibration factor = 3.3751 determined for the specific flow meter used.

Density of larvae was subsequently calculated as number of larvae per 100 m<sup>3</sup> of water filtered (larvae/100m<sup>3</sup>). Larval density was then tested for normality and homogeneity of variances using Levene's test; attempts to normalize data were conducted via transformations where possible. One-way ANOVA (normally distributed data) and Kruskal–Wallis (non-normal data) tests were conducted to detect differences within a number of community metrics (number of taxa, density (larvae/100m<sup>3</sup>), Margalef's species richness, species evenness and Shannon–Wiener diversity) between Season, Zone and Area using the SigmaPlot statistical package. Post Hoc analyses using Dunn's Method on non-normal data and Tukey's tests on normally-distributed data were performed.

Following square root transformation, to reduce the influence of abundant taxa, and which is a transformation best used for count data (McDonald, 2014), patterns in the larval fish assemblage in terms of factors Season, Area and Zone were tested using PRIMER 6.1.16 (Clarke and Warwick, 2001). Firstly, a similarity matrix between all sample combinations using the Bray-Curtis distance measure (Clarke and Gorely, 2001) was generated. Cluster analyses (group average) and non-metric Multidimensional Scaling (MDS; Shepard, 1962; Kruskal, 1964; Kruskal and Wish, 1978) were then performed using the similarity data, as a means of visualizing similarities amongst samples in a two dimensional plane. MDS is an unconstrained ordination procedure that relates the data points based on a general criterion, such as minimizing residual variance (Meulman 1986 and 1992). Unconstrained ordinations are useful for visualizing broad patterns across entire data clouds that may not fit with a theoretical design. In addition, once the ordination has been plotted, *a priori* factors (such as the Season, Area and Zone factors used in this study) can be overlaid on the data cloud to visualize expected potential patterns of differences in the location or relative dispersion.

However, real patterns of differences in multivariate location among groups can sometimes be masked by patterns of overall dispersion in an unconstrained ordination (Anderson and Willis, 2003). Therefore, canonical analysis of principal co-ordinates (CAP) was also conducted using Primer 6.1.16, taking into account the *a priori* hypotheses depicted in the conceptual design (Figure 5). CAP is a flexible and particularly useful constrained ordination procedure for ecology (Anderson and Willis, 2003). It has the advantage of allowing any distance or dissimilarity measure to be used, but (like the traditional canonical methods) also takes into account correlation structure among *a priori* factors in the response data cloud (e.g. Neter et al., 1996; Legendre and Anderson, 1999). CAP uses the trace statistic (sum of canonical eigenvalues = sum of squared canonical correlations) and obtains a *p*-value by permutation (e.g. Anderson, 2001). Anderson and Willis (2003) suggest that both a CAP ordination and an unconstrained ordination such as MDS be used together.

Lastly, differences in larval density across Season, Areas and Zones were tested using PERMANOVA+ 1.0.6 (Anderson et al., 2008). Here Season, Area and Zone were regarded as fixed factors, which were crossed. Pairwise PERMANOVA procedures were conducted within groups found to be significantly different. Species that contributed most to the similarity within and between groups, based on Season, Area and Zone were identified using the SIMPER (Similarity Percentages Routine) routine. SIMPER decomposes the average Bray-Curtis dissimilarities between all pairs of samples, one from each group (or decomposes

all similarities among samples within a group), into percentage contributions from each taxa, listing the taxa in decreasing order of such contributions.

### **3.4.5 Relationship between fish larvae and environmental data**

Multivariate patterns were explored using the Distance-Based Linear Model (DistLM) in the PERMANOVA+ 1.0.6 menu. Modelling was performed on Bray–Curtis similarity matrices based on square-root transformed data and included the full suite of taxa identified. Environmental variables were tested for co-linearity before being included in the model. Firstly a marginal test was conducted which determines how much of the variance in the biological community (larval fish densities in this case) can be explained by each environmental variable individually (Anderson et al., 2008). This is expressed as a  $p$ -value, and when  $p < 0.05$  the variable is considered to be significant in explaining variation.

Following this, a sequential test was conducted in DistLM. This test partitions the variations in biological data distribution according to a multiple regression model (based on environmental variables), using a selection procedure chosen by the user (e.g. forward, step-wise, best fit). In this study the selection procedure used was the “step-wise” option which successively adds and removes environmental variables based on a chosen selection criterion. The selection criterion (a measure of model quality balancing goodness of fit with model complexity) used in this study was Akaike’s Information Criterion (AIC; Akaike, 1973). AIC excluded environmental variables in the model if they added no more to the explained sum of squares than would be expected by adding some random variable. The resulting sequential DistLM shows the portion of the variation in the data explained by important variables only. A distance-based Redundancy Analysis (dbRDA) was used as a visualization tool to model the DistLM model in a multi-dimensional space using vector overlays and Eigen-analysis of the fitted data cloud (Anderson et al., 2008).

## CHAPTER 4: RESULTS

### 4.1 General

#### 4.1.1 Sampling success

Larval fish sampling was successfully conducted at 108 of 116 planned stations across the two seasons (53 Wet and 55 Dry). Adverse weather conditions and net entanglement were responsible for larval samples not being collected at eight stations. Further to this, water samples were not collected at one station, and this station was also omitted from analyses. Full data sets including physico-chemical measurements, nutrient concentrations and larval fish abundances were therefore available from 107 sampling stations over the two seasons sampled. Stations clustered into three groups by depth (sounding) which corresponded to the Shelf, Mid-slope and Deep-slope categories of the conceptual design (Figures 5 and 6).

A plot of the volumes of water sampled against sampled depths of each tow showed an expected positive relationship. Variability in volume of water sampled increased with depth sampled. Many factors may cause this, including variable current speeds, especially at the deeper stations further off-shore, where there was a likely greater influence of the Agulhas Current. Other factors include angle of the net and speed lowered and hauled. At seven stations, flow meter readings were compromised by either non-recording or equipment (flow meter) malfunction. Clear outliers were also identified at some stations, which in some cases corresponded with field notes that indicated possible problematic readings. Flow data from those stations were omitted and substituted with the estimated flow derived from a regression formula:

$$\text{Volume filtered} = 0.7011(\text{depth (m)}) + 14.067$$

This is a standard conversion used for Bongo net sampling on the FRS Algoa (J.A. Huggett pers. comm., 2013, Department of Environmental Affairs, Cape Town).

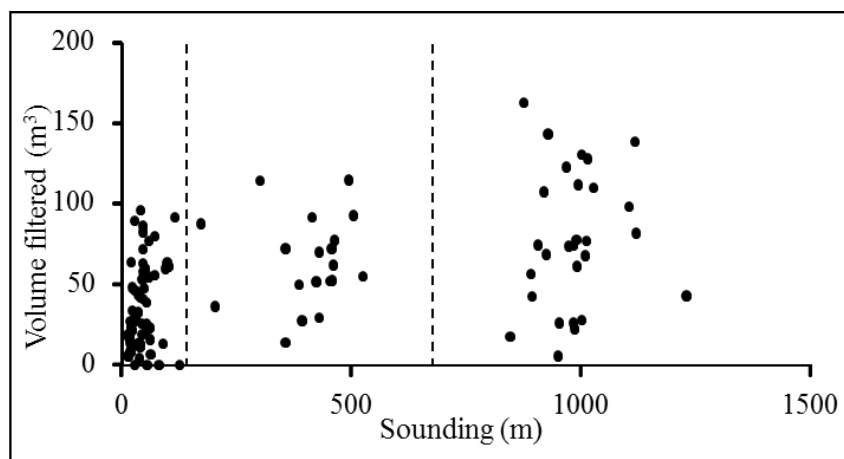


Figure 6. Volume of water filtered at the respective soundings during Wet and Dry season surveys of the KwaZulu-Natal Bight, 2010. The dashed lines delineate three broad depth clusters corresponding to Shelf, Mid-slope and Deep-slope Zones.

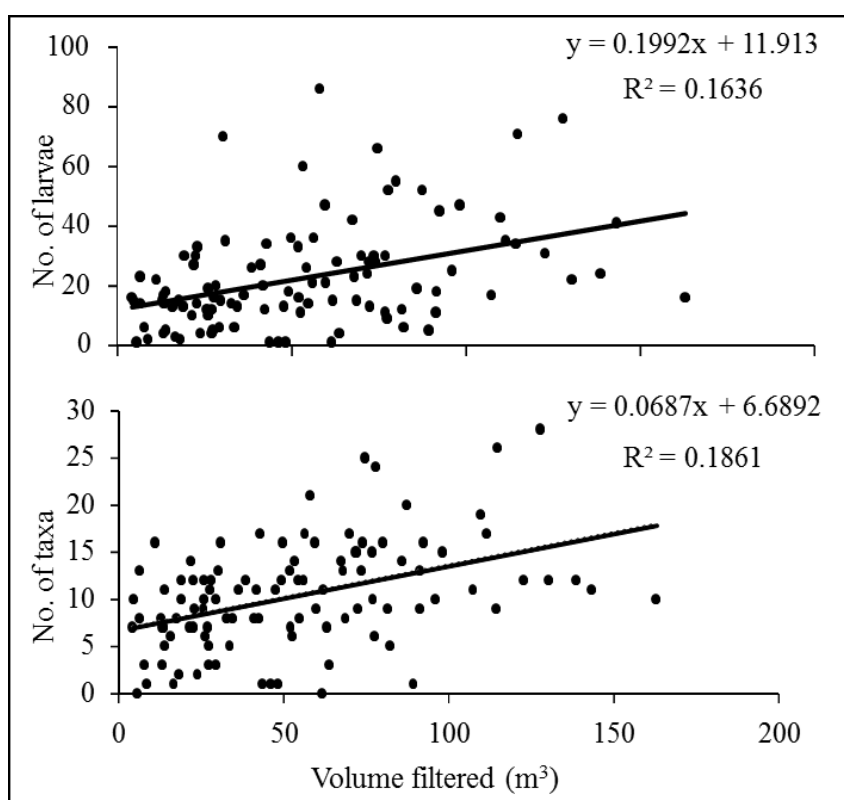


Figure 7. Number of fish larvae and taxa against calculated volumes of water filtered per tow during Wet and Dry season surveys of the KwaZulu-Natal Bight, 2010.

Over the two sampled seasons 2 537 larvae were collected (1 174 Wet and 1 363 Dry). Overall, an average of 23 ( $\pm 18$  SD) larvae was caught per sample ( $22 \pm 17$  SD in the Wet and

24  $\pm$  18 SD in the Dry), with the highest number (76) in a single sample being caught over the Deep-slope of transect T10 in the Thukela Area. Two samples had no larvae, both during the Wet season, one on the Shelf (T2) and the other over the Mid-slope (T14). Larval abundances were standardized to numbers of larvae per unit volume (100 m<sup>3</sup>) filtered. A weak positive relationship was found to exist between number of larvae and volume filtered, and between numbers of taxa caught and volume filtered (Figure 7).

#### 4.1.2 Potential effect of day and night sampling on larval fishes

During the two surveys, 59 and 50 samples were taken during the day and at night respectively. Univariate tests were used to detect the potential occurrence of diurnal migration by larval fishes. There were no significant differences in larval fish densities or numbers of taxa sampled during daylight versus night-time hours when data were pooled across season (Figure 8). Analysis of community differences using ANOSIM also found no significant difference between day and night larval fish composition. This indicated that larval fish communities sampled during the day were not different to those sampled at night and allowed further analyses to be conducted without consideration of potential confounding effects of sampling time.

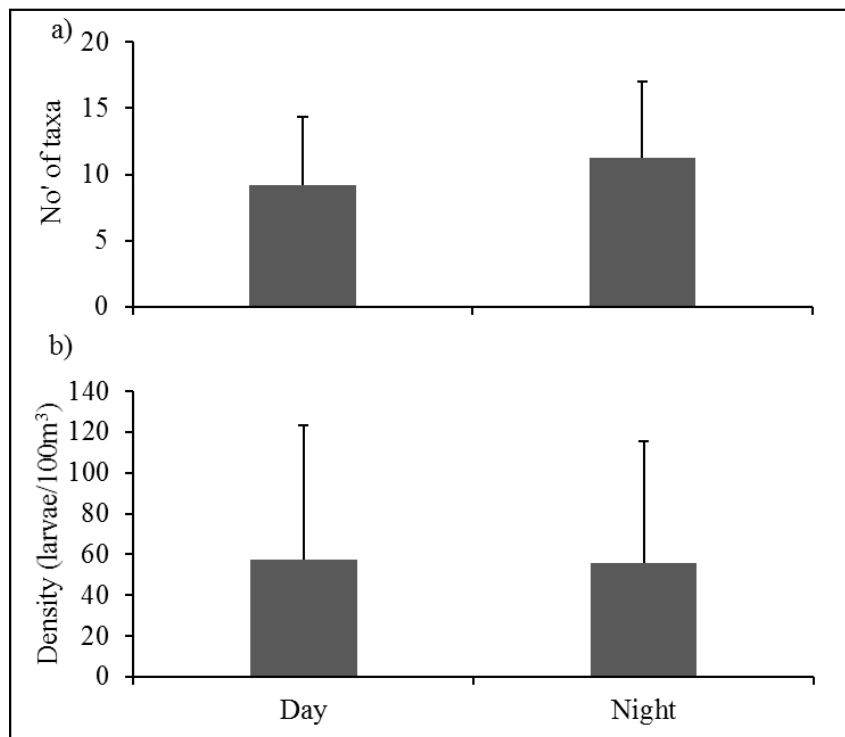


Figure 8. Mean numbers of taxa and densities ( $\pm 1$  SD) of larval fishes sampled during the day and night pooled across Wet and Dry season surveys of the KwaZulu-Natal Bight, 2010.

## 4.2 Environmental conditions

Marked seasonal variation was evident in all environmental parameters. Mean SST was considerably higher and with a greater range in the Wet than the Dry season (Table 1). In both seasons, SST increased with distance from shore (Figure 9a). The off-shore influence of the Agulhas Current, particularly apparent in the Wet season, was indicated by the areas with  $SST > 27^{\circ}\text{C}$  in the Wet season and  $22.5^{\circ}\text{C}$  in the Dry season. Warm Agulhas Current waters reached close in-shore in the north (Figure 9a). The effect of the KZN Bight's widened shelf in displacing the Agulhas Current off-shore in the Thukela and Durban areas was also apparent (Figure 9a).

Table 1. Mean and range of environmental parameters measured during Wet and Dry season surveys of the KwaZulu-Natal Bight, 2010. SST = Sea Surface Temperature.

Season		SST ( $^{\circ}\text{C}$ )	Surface salinity	Chlorophyll- <i>a</i> ( $\mu\text{g/L}$ )	Zooplankton Dry weight ( $\text{mg/m}^3$ )
Wet	Mean	26.10	35.32	0.28	11.72
	Min	20.36	34.77	0.08	0.54
	Max	28.77	35.56	1.28	42.60
Dry	Mean	21.53	35.43	0.87	18.63
	Min	19.98	35.37	0.31	3.21
	Max	23.23	35.49	2.78	72.13

Mean surface salinity was similar between each season (Table 1). However, pockets of lower salinity were detected during the Wet season, most notably near the mouth of the Thukela River (Figure 9b). The higher rainfall during the Wet season (Chapter 2, Figure 2) and the locality of Thukela River mouth likely account for this. Higher surface salinities off-shore in the Wet season were likely due to increased temperatures and evaporation in the Agulhas Current. Conversely, salinity in the Dry season was less patchy with a gradient of decreasing salinity with distance from shore (Figure 9b), likely related to the weakened influence of the Agulhas Current in this season.

Chlorophyll-*a* levels were generally very low in both seasons (Table 1). Mean and range (difference between minimum and maximum values) in Chlorophyll-*a* were highest in the Dry season, particularly over the Mid-slope off Durban and on the Shelf near the Thukela River mouth (Table 1, Figure 9c). During the Wet season very low levels of Chlorophyll-*a*

were recorded across the wider bight, with the exception of close in-shore near the Thukela River mouth (Figure 9c).

Zooplankton Dry weight showed a similar pattern to the Chlorophyll-*a* measurements (Table 1). Highest readings occurred close in shore along the entire coastline in both seasons with peaks in the far North and South edges of the Dry season (Figure 9d). In general, zooplankton Dry weight was lower and more homogenous with distance off-shore, especially so in the Wet season (Figure 9d).

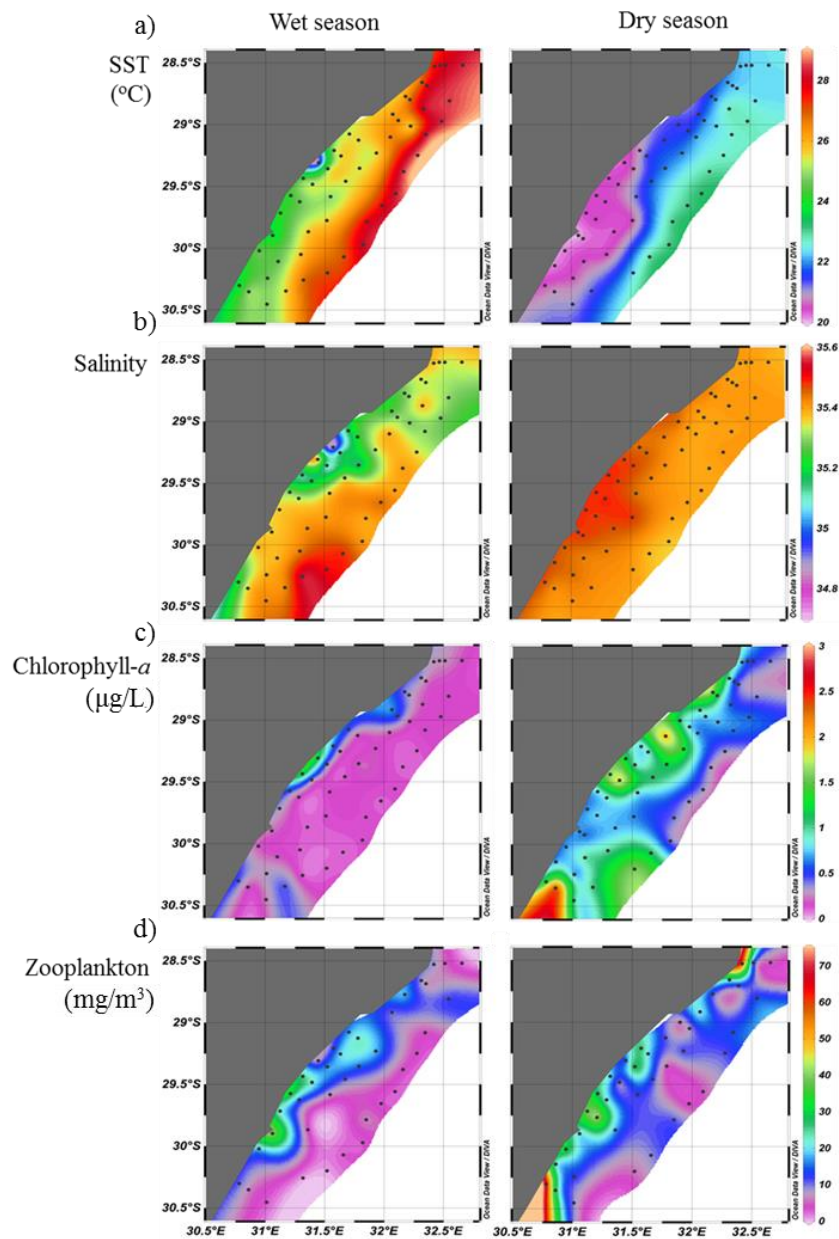


Figure 9. Surface environmental variables during Wet and Dry season surveys of the KwaZulu-Natal Bight, 2010.

Principle Components Analysis (Figure 10) showed clear seasonal differences in environmental water qualities and zooplankton biomass. Parameters most influential in these differences (as indicated by vector overlays) were SST, which was higher in the Wet season, and Chlorophyll-*a*, which was higher in the Dry season. Overall, SST was the primary source of significant seasonal difference in environmental variables during the study (PERMANOVA, Table 2). There was a significant interaction between season and locality (both Zone and Area), which was most marked in surface salinity. During the Wet season, salinity on the Shelf (particularly in the Thukela Area) was lower than in the Mid- and Deep-slope Zones. This was much less evident in the Dry season (Figures 9b and 10). Zooplankton Dry weight also exhibited some spatial variation and this was also reflected along Principal Components Axis 2 (Figure 10). High zooplankton Dry weight was recorded at several stations on the Shelf compared to waters further off-shore (Figure 9d).

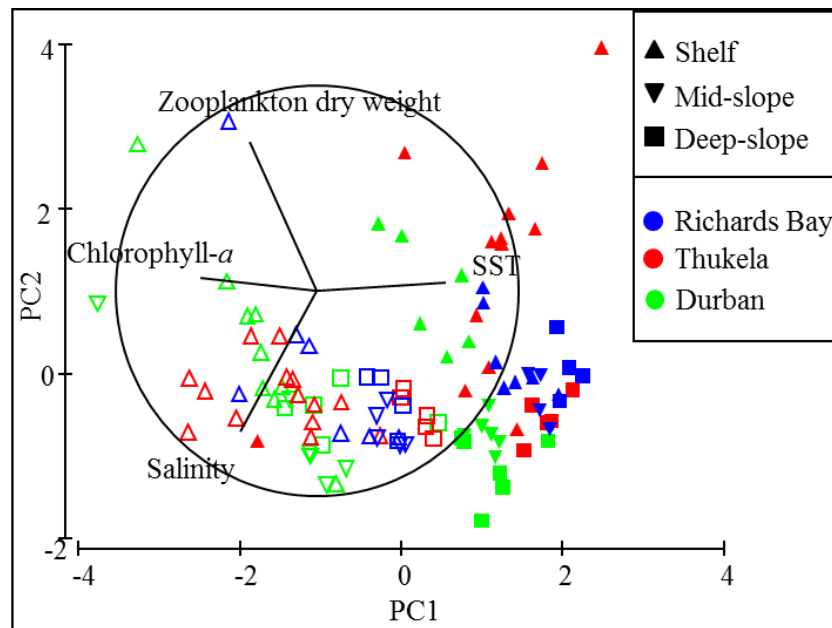


Figure 10. Principle component plot of environmental variables measured during Wet and Dry season surveys of the KwaZulu-Natal Bight, 2010. Vectors show the degree of influence and direction of the different environmental variables. Solid symbols = Wet season, open symbols = Dry season.

Table 2. PERMANOVA of environmental variables recorded on Wet and Dry season surveys of the KwaZulu-Natal Bight, 2010. \* = significant,  $p$ -perm <0.05.

Source	df	Pseudo-F	$p$ -perm
Season	1	61.28	0.0001*
Area	2	4.71	0.0001*
Zone	2	12.05	0.0001*
Season X Area	2	1.50	0.17
Season X Zone	2	3.12	0.0042*
Area X Zone	3	2.98	0.0014*
Season X Area X Zone	3	1.66	0.091

### 4.3 Larval fish assemblage

#### 4.3.1 Larval fish abundance

Mean larval density per site in the present study was 55 larvae/100m<sup>3</sup> (SD 59). The highest larval fish density of the KZN Bight in 2010 was recorded in the Shelf Zone of transect T5 (392.74 larvae/100m<sup>3</sup>) during the Dry season. The lowest larval fish density occurred during the Wet season in the Shelf Zone of transect T1 (2.08 larvae/100m<sup>3</sup>). Averaged within sampled Area-Zones, the highest mean density occurred over the Durban Shelf and the lowest over the Thukela Deep-slope, both during the Dry season (Table 3). Densities were consistently highest on the Shelf compared to other depth Zones in both seasons, except for in the Richards Bay Area in the Dry season where a slightly higher density occurred over the Mid-slope (Table 3). While mean densities on the Shelf were high, so too were their standard deviations, suggesting a patchily distributed community. There was a decrease in larval fish abundance from south to north in the Shelf Zone during both seasons, but no other obvious patterns amongst Area-Zones were evident (Table 3).

Table 3. Number of samples (N), mean number of larvae (larvae/100m<sup>3</sup>) and standard deviation (SD) of Area-Zones during Wet and Dry season surveys of the KwaZulu-Natal Bight, 2010. (- = no sample).

Season	Zone		Area		
			Durban	Thukela	Richards Bay
Wet	Shelf	N	7	13	7
		Mean	<b>110.12</b>	<b>86.6</b>	<b>53.48</b>
		SD	120.1	89.2	49.88
	Mid-slope	N	6	-	5
		Mean	<b>26.7</b>	-	<b>29.57</b>
		SD	12.6	-	18.8
	Deep-slope	N	6	5	4
		Mean	<b>55.3</b>	<b>65.3</b>	<b>31.4</b>
		SD	42.53	15.59	12.56
Dry	Shelf	N	9	14	7
		Mean	<b>134.76</b>	<b>56.9</b>	<b>41.37</b>
		SD	125.4	41.01	24.9
	Mid-slope	N	6	-	5
		Mean	<b>39.1</b>	-	<b>54.54</b>
		SD	28.1	-	29.29
	Deep-slope	N	5	5	4
		Mean	<b>51</b>	<b>21.7</b>	<b>45.1</b>
		SD	25.45	12.65	30.54

#### 4.3.2 Taxonomic composition

In total, 116 taxa were sampled over the KZN Bight in the Wet and Dry seasons of 2010. These taxa comprised 67 families and 7 unidentified taxa. Fifty-eight damaged specimens and 145 newly hatched (yolk sac) larvae were unidentifiable, and were omitted from the analyses. These contributed < 8% to the total number of larvae sampled. In both Wet and Dry seasons ninety-five taxa were sampled (Table 4).

The most dominant family during both seasons was Leiognathidae (22.4 larvae/100m<sup>3</sup>, 7.2% of the total). Percentage contributions were low for all families in both seasons i.e. many taxa contributed small amounts to overall composition. The highest percentage contribution during the Wet season was by Leiognathidae, Bregmacerotidae, Callionymidae and Tripterygiidae. Leiognathidae, Zeidae, Synodontidae, Priacanthidae and Tripterygiidae

contributed the most during the Dry season. Eighteen families were present during one season only, nine exclusively in the Wet season and nine exclusive to the Dry season (Table 4).

Some variation in composition of fish larvae amongst Zones was apparent. Notably, Myctophidae and Engraulidae were relatively abundant in Mid- and Deep-slope Zones, but much less so over the Shelf. Conversely, Callionymidae were relatively more abundant in Shelf waters (Figure 11). Leiognathidae and Tripterygiidae both occurred in relatively high abundance in the Mid-slope, but, while present over the Deep-slope, were not amongst the most common taxa found there. Myctophidae, Mullidae and Engraulidae were most common on the Deep-slope (Figure 11).

A similar pattern emerged across the three sampling Areas, with many families at similar low percentages of abundance. An abundance of Leiognathidae, Callionymidae and Priacanthidae larvae typified Durban. Tripterygiidae, Leiognathidae and Pinguipedidae were the most abundant larvae in the Thukela Area, and the Myctophidae, Bregmacerotidae and Tripterygiidae were the most abundant taxa off Richards Bay (Figure 12).

Table 4. Mean densities (also expressed as % contribution to the total density per season) of larval fish families and total % occurrence (presence in samples) of each family across all samples recorded in the KwaZulu-Natal Bight during the Wet and Dry seasons, 2010. Adult position in the water column is indicated, P = Pelagic and D = Demersal.

Family	Pelagic / Demersal	Wet season		Dry season		Totals	
		Density (larvae/100m <sup>3</sup> )	% Contribution	Density (larvae/100m <sup>3</sup> )	% Contribution	Total Density (larvae/100m <sup>3</sup> )	Total % Occurrence
Leiognathidae	D	12.55	4.85	27.34	10.64	22.41	16.98
Callionymidae	D	11.18	4.32	5	1.95	11.18	22.64
Tripterygiidae	D	11.35	4.39	10.69	4.16	10.94	36.79
Percophidae	D	-	-	9.41	3.66	9.41	1.89
Myctophidae	P	8.74	3.38	9.88	3.85	9.39	66.98
Cirrhitidae	D	9.85	3.81	4.73	1.84	9.06	12.26
Synodontidae	D	5.88	2.27	11.31	4.4	8.8	36.79
Chaetodontidae	D	-	-	8.45	3.29	8.45	1.89
Sciaenidae	D	4.64	1.79	9.05	3.52	7.9	21.70
Priacanthidae	D	6.04	2.33	11.14	4.34	7.74	8.49
Bregmacerotidae	D/P	12.33	4.77	4.02	1.57	7.56	50.94
Triglidae	D	9.67	3.74	4.34	1.69	7.26	29.25
Engraulidae	P	6.83	2.64	7.23	2.81	7.06	59.43
Zeidae	D	2.08	0.81	14.29	5.56	6.97	4.72
Scombridae	P	8.21	3.17	3.66	1.42	6.88	38.68
Clinidae	D	-	-	6.61	2.57	6.61	0.94
Mullidae	D	7.5	2.9	5.15	2.01	6.57	45.28
Cynoglossidae	D	8.63	3.34	2.91	1.13	6.43	12.26
Trichonotidae	D	-	-	5.8	2.26	5.8	0.94
Pinguipedidae	D	7.54	2.91	4.69	1.83	5.64	11.32

Labridae	D	7.06	2.73	1.87	0.73	5.14	25.47
Sparidae	D	2.86	1.1	6.62	2.58	5.05	11.32
Sillaginidae	D	6.97	2.69	2.92	1.14	4.82	16.04
Pseudochromidae	D	4.05	1.57	5.29	2.06	4.67	5.66
Carangidae	P	5.17	2	3.88	1.51	4.66	26.42
Ostraciidae	D	4.43	1.71	-	-	4.43	3.77
Apogonidae	D	5.15	1.99	2.76	1.07	4.35	2.83
Champsodontidae	D	4.81	1.86	3.84	1.5	4.25	17.92
Paralichthyidae	D	5.08	1.96	2.42	0.94	4.19	14.15
Gobiidae	D	4.52	1.75	1.83	0.71	3.9	12.26
Trichiuridae	P	-	-	3.86	1.5	3.86	0.94
Bothidae	D	4.33	1.67	2.45	0.95	3.68	33.02
Pomatomidae	P	7.22	2.79	1.73	0.67	3.56	2.83
Microdesmidae	D	3.52	1.36	-	-	3.52	2.83
Balistidae	D	3.25	1.26	4.41	1.72	3.36	10.38
Nemipteridae	D	3.24	1.25	-	-	3.24	0.94
Gonostomatidae	P	3.64	1.41	2.61	1.02	3.2	31.13
Acanthuridae	D	3.78	1.46	0.9	0.35	2.82	5.66
Lutjanidae	D	3.77	1.46	1.48	0.58	2.79	13.21
Chiasmodontidae	P	-	-	2.74	1.07	2.74	8.49
Pomacentridae	D	3.05	1.18	2.06	0.8	2.63	24.53
Bathylagidae	P	1.76	0.68	2.69	1.05	2.55	12.26
Syngnathidae	D	3.7	1.43	1.38	0.54	2.54	1.89
Malacanthidae	D	4.46	1.72	1.47	0.57	2.47	2.83
Istiophoridae	P	2.68	1.04	1.3	0.51	2.22	2.83
Serranidae	D	1.36	0.52	3.88	1.51	2.2	2.83
Nemichthyidae	D	2.68	1.04	1.31	0.51	2.13	4.72
Elopidae	P	2.33	0.9	1.63	0.63	2.05	4.72

Bramidae	P	0.78	0.3	2.14	0.83	2.03	12.26
Astronesthidae	P	1.08	0.42	2.2	0.86	1.98	4.72
Chaunacidae	D	0.84	0.32	3.86	1.5	1.85	2.83
Aploactinidae	D	1.84	0.71	-	-	1.84	0.94
Holocentridae	D	1.84	0.71	-	-	1.84	0.94
Terapontidae	D	1.24	0.48	3.86	1.5	1.76	4.72
Exocetidae	P	1.62	0.63	-	-	1.62	0.94
Phosichthyidae	P	1.41	0.55	1.77	0.69	1.59	5.66
Ophidiidae	D	1.53	0.59	1.52	0.59	1.53	4.72
Nomeidae	P	1.57	0.61	1.32	0.51	1.44	3.77
Opistognathidae	D	1.43	0.55	-	-	1.43	0.94
Muraenidae	D	1.45	0.56	1.25	0.49	1.4	3.77
Isonidae	P	-	-	1.39	0.54	1.39	0.94
Malacosteidae	P	-	-	1.3	0.51	1.3	2.83
Hoplichthyidae	D	1.57	0.61	0.87	0.34	1.22	1.89
Sphyraenidae	D	1.18	0.46	1.15	0.45	1.17	2.83
Emmylichthyidae	P	-	-	1.15	0.45	1.15	1.89
Haemulidae	D	0.78	0.3	-	-	0.78	0.94
Lethrinidae	D	0.7	0.27	-	-	0.7	0.94

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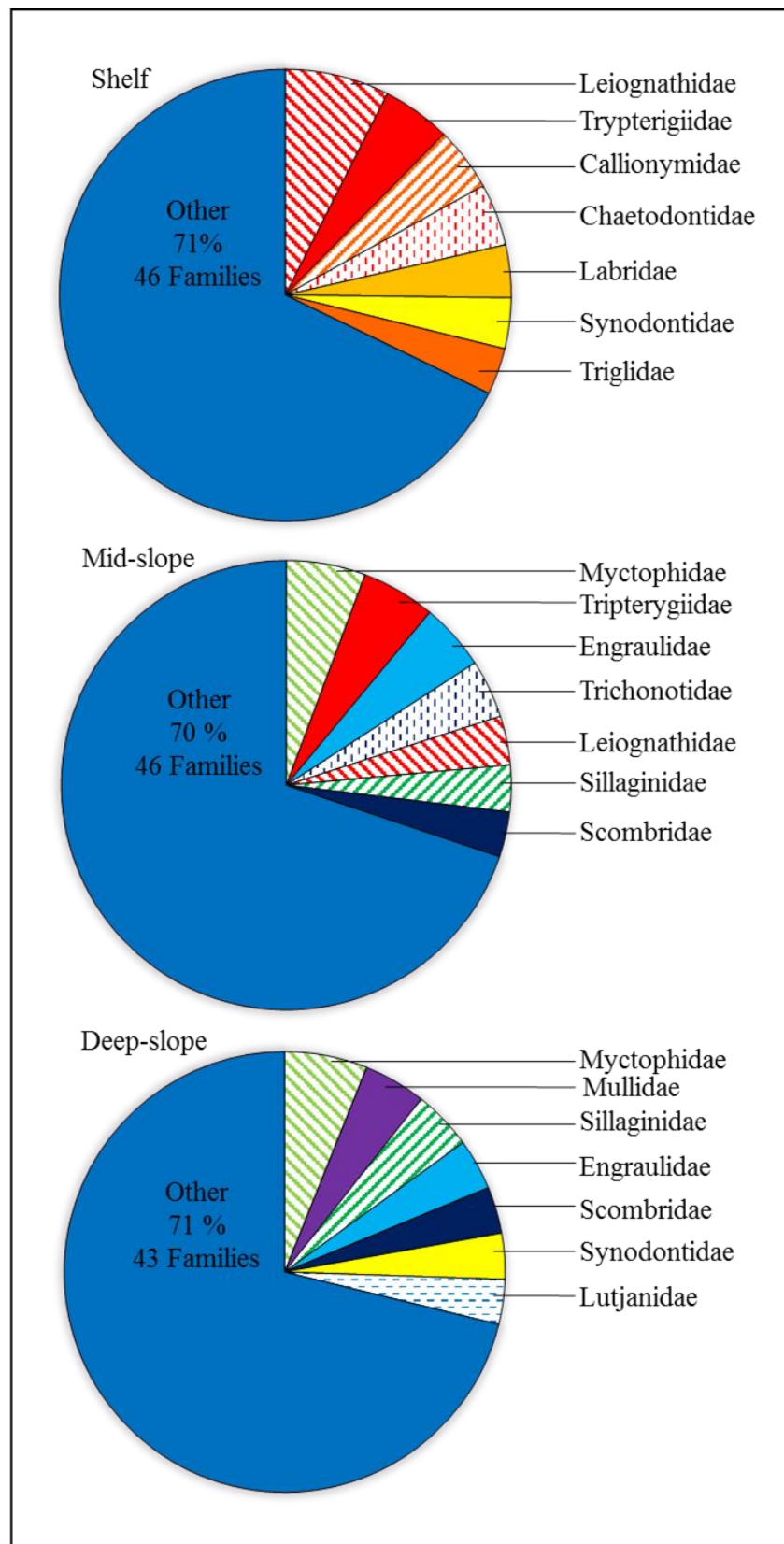


Figure 11. Contributions (by percentage of overall larval fish density) of commonly-occurring larval fish families on the Shelf, Mid-slope and Deep-slope of the KwaZulu-Natal Bight, 2010.

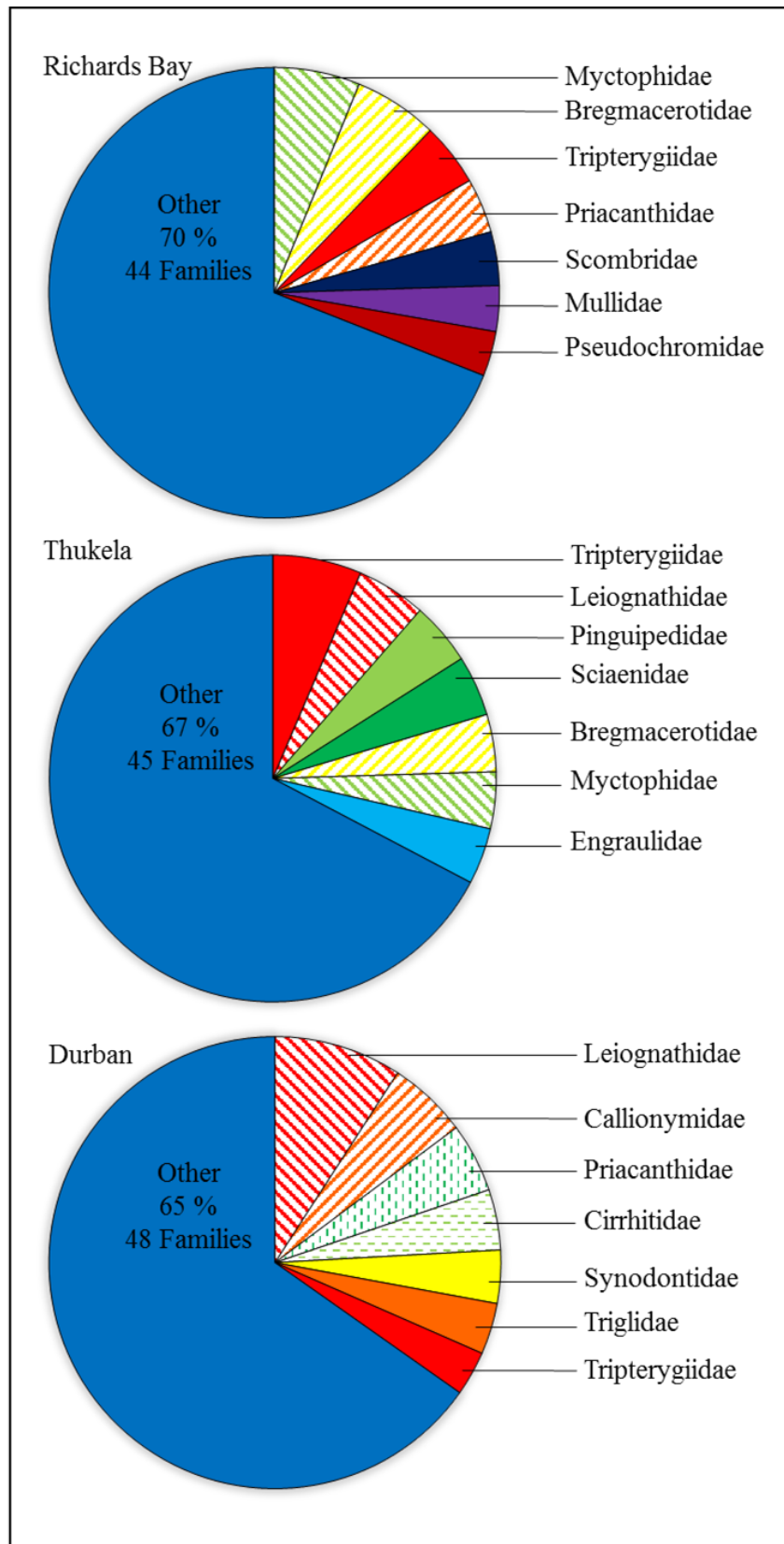


Figure 12. Contributions (by percentage of overall larval fish density) of commonly-occurring larval fish families off Durban, Thukela and Richards Bay along the KwaZulu-Natal Bight, 2010.

#### 4.3.3 Univariate analyses

There were no significant differences in any of the diversity indices nor in larval fish densities between Seasons or Areas (Table 5), but there was a gradual and significant increase in numbers of taxa, species richness and Shannon-Weiner diversity with increased distance off-shore ( $p < 0.05$ ; Figure 13; Table 5). Post hoc analyses determined that diversity and number of taxa on the Deep-slope were significantly higher than on the Shelf ( $Q = 3.708$ ,  $p < 0.05$  and  $Q = 3.411$ ,  $p < 0.05$  respectively). Species richness on the Shelf was significantly lower than on the Mid-slope ( $q = 34.998$ ,  $p = 0.002$ ) and Deep-slope ( $q = 37.81$ ,  $p < 0.001$ ).

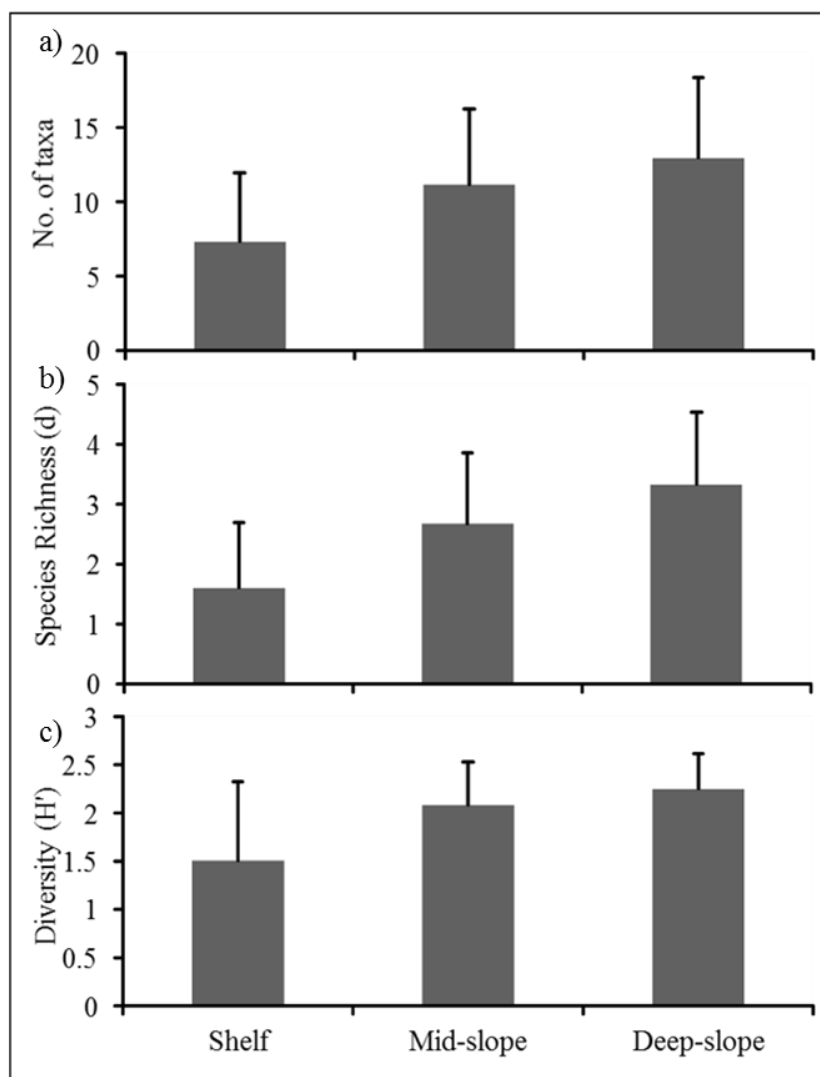


Figure 13. Mean number of taxa, species richness and diversity ( $\pm 1$ SD) of larval fishes sampled in each Zone (Shelf, Mid-slope and Deep-slope) of the KwaZulu-Natal Bight.

Table 5. Results of ANOVAs of univariate indices of the KwaZulu-Natal Bight larval fish community by Season, Area and Zone. \* indicates a significant difference between groups. F = ANOVA, H = Kruskal–Wallis test result.

Index	Season		Area		Zone	
	Statistic	<i>p</i>	Statistic	<i>p</i>	Statistic	<i>p</i>
No of taxa	<i>H</i> = 0.40	0.528	<i>F</i> = 0.89	0.570	<i>H</i> = 14.12	0.001*
Density (larvae/100m <sup>3</sup> )	<i>H</i> = 0.22	0.638	<i>H</i> = 15.26	0.360	<i>H</i> = 1.95	0.377
Species richness (d)	<i>F</i> = 0.03	0.875	<i>F</i> = 1.02	0.443	<i>F</i> = 18.56	0.001*
Evenness	<i>H</i> = 1.55	0.213	<i>H</i> = 9.77	0.779	<i>H</i> = 0.23	0.890
Diversity (H')	<i>H</i> = 0.61	0.435	<i>H</i> = 11.11	0.677	<i>H</i> = 17.34	0.001*

#### 4.4 Multivariate analyses

##### 4.4.1 Combined analysis

While non-metric multidimensional scaling (MDS) did not show strong clustering some gradients were apparent in the ordination plot (Figure 14). Deep-slope assemblages tended to separate from those taken over Shelf and Mid-slope. Similarly, Richards Bay assemblages also tended to separate spatially and show less spread than those from other Areas. At face value, this suggested that Zone (depth) and Area were more influential than Season in explaining larval fish community patterns. However, the high stress value obtained for the 2-dimensional ordination suggested that the ordination plot should be interpreted with caution and might not clearly reflect similarities (or dissimilarities) in the sampled larval fish communities.

When *a priori* groupings were analysed using canonical analysis of principal co-ordinates (CAP) (Figure 14), Deep-slope and Shelf separation was more pronounced and Richards Bay aggregated within the Dry season cluster only. However, there was a clear seasonal shift (Figure 14). Statistical analysis using PERMANOVA showed that seasonality played a substantial and significant role in the larval fish community of the KZN Bight (Table 6) although Area and Zone were also influential.

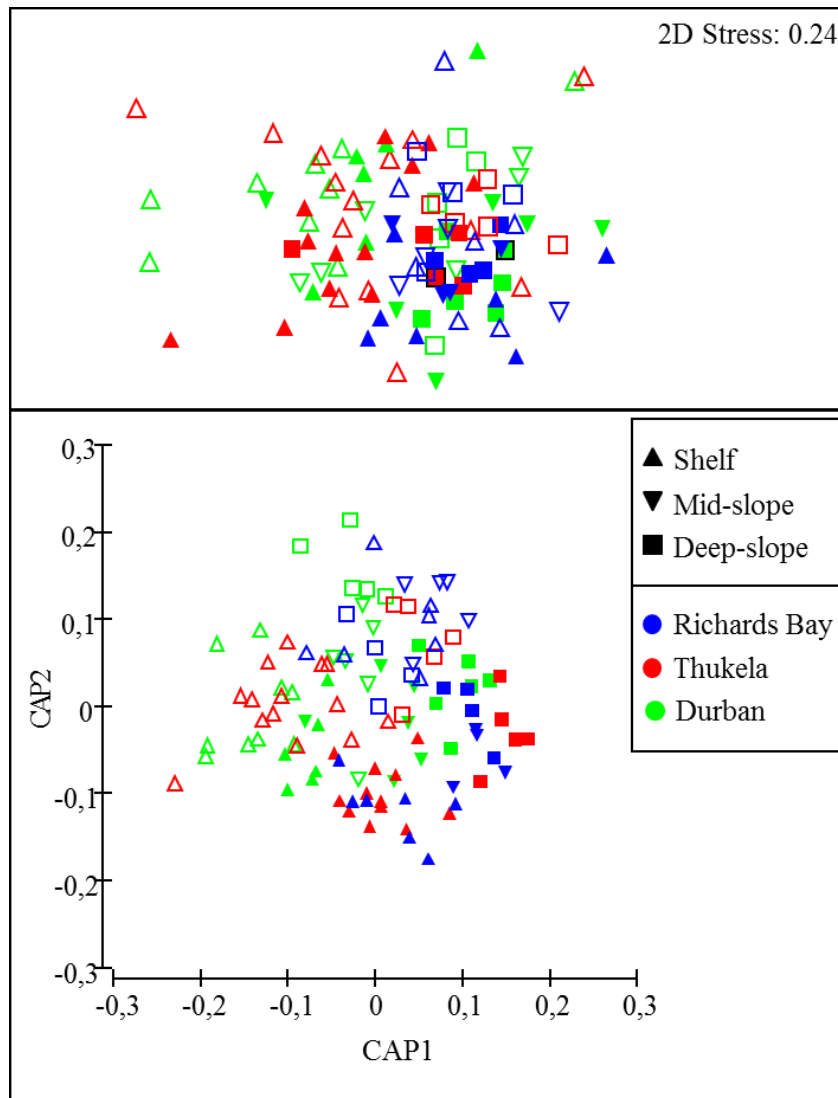


Figure 14. MDS ordination and CAP plot of larval fish sampled in the KwaZulu-Natal Bight, 2010. Solid symbols = Wet season, open symbols = Dry season.

The significant difference between Zones is apparent in both seasons (Figure 14). Pairwise PERMANOVA provided further clarity; ignoring Season and Area, the Shelf Zone was significantly different from both slope Zones (Table 7). However, separation between Areas was also noticeable in the Dry season between Richards Bay and Durban (CAP, Figure 14). Therefore, ignoring Season and Zone, Richards Bay was indeed significantly different to Durban (Table 7). In order to further investigate the role of Zone and Area, multivariate analyses were subsequently conducted on Wet and Dry season separately to remove the high influence of season.

Table 6. PERMANOVA of the larval fish community recorded in the Wet and Dry season across the KwaZulu-Natal Bight, 2010.

Source	df	Pseudo-F	<i>p</i> -perm
Season	1	3.40	0.0001*
Area	2	1.45	0.0237*
Zone	2	3.25	0.0001*
Season X Area	2	1.34	0.055
Season X Zone	2	1.34	0.057
Area X Zone	3	1.21	0.11
Season X Area X Zone	3	0.85	0.81

Table 7. Results of Pairwise PERMANOVA of the larval fish community between Areas and Zones recorded in the Wet and Dry season across the KwaZulu-Natal Bight, 2010.

Group comparisons	t	P(perm)
Shelf vs. Mid-slope	1.23	0.02*
Shelf vs. Deep-slope	2.32	0.0001*
Mid-slope vs. Deep-slope	1.20	0.09
Durban vs. Thukela	1.07	0.29
Durban vs. Richards Bay	1.35	0.01*
Thukela vs. Richards Bay	1.14	0.15

SIMPER analyses to determine which taxa accounted for similarities within *a priori* identified groups and dissimilarities between them, showed that mean similarities in the Wet and Dry season larval fish communities were both relatively low at around 15%, while mean dissimilarity between the seasons was high at around 87% (Table 8). This indicated that larval fish communities in these seasons were distinct although within-season communities varied greatly amongst the sampled stations. Four taxa contributed ~41% to the overall mean similarity in the Wet season, and five taxa contributed ~48% to the Dry season overall mean similarity (Table 8). These characteristic taxa differed between the seasons: Scombrid A contributed most to similarity during the Wet season, followed by Mullid B. Engraulid B and Tripterygiid A contributed most to similarities within the Dry season (Table 8). These four taxa also contributed most to the dissimilarity between the larval fish communities of each sampled season (i.e. accounted for the distinction between the seasons), followed by

Bregmacerotid A and Leiognathid A (Table 8). The Wet season was further represented by Bothid A and Gonostomatid A, and the Dry season by Myctophid F, Bregmacerotid B and Phosichthyid B (Table 8).

Table 8: Results of SIMPER analyses showing the dominant larval fish taxa that characterize and discriminate Wet and Dry season of the KwaZulu-Natal Bight, 2010. Dominant taxa are those contributing >6% and >3% respectively to overall mean similarity and dissimilarity.

Taxa	Mean abundance	Mean similarity	% Contribution	% Cumulative
<i>Wet season: mean similarity within group = 15.57%</i>				
<i>Scombrid A</i>	1.43	2.42	15.57	15.57
<i>Mullid B</i>	1	1.57	10.1	25.68
<i>Bothid A</i>	0.88	1.37	8.78	34.46
<i>Gonostomatid A</i>	0.66	0.99	6.38	40.84
<i>Dry season: mean similarity within group = 15.10%</i>				
<i>Engraulid B</i>	1.15	2.02	13.37	13.37
<i>Tripterygiid A</i>	1.25	1.66	11	24.36
<i>Myctophid F</i>	0.69	1.29	8.52	32.88
<i>Bregmacerotid B</i>	0.74	1.22	8.05	40.93
<i>Phosichthyid B</i>	0.74	1.09	7.24	48.17
<i>Mean dissimilarity between Wet and Dry seasons = 86.86%</i>				
	Wet season	Dry season	Mean dissimilarity	
<i>Tripterygiid A</i>	0.86	1.25	3.96	4.56
<i>Engraulid B</i>	0.61	1.15	3.53	8.62
<i>Scombrid A</i>	1.43	0.33	3.46	12.6
<i>Mullid B</i>	1	0.52	3.06	16.12
<i>Bregmacerotid A</i>	0.94	0.42	3	19.58
<i>Leiognathid A</i>	0.39	0.89	2.77	22.77

A Distance Based Linear Model (DistLM) was used to explore the amount of variation in the larval fish distribution patterns that could be explained by SST, Chlorophyll-*a*, Salinity and Zooplankton Dry weight. Marginal tests show that all of these significantly explained some, but not much, of the variation observed in the larval fish community independently of the other variables (Table 9). SST explained 5%, Zooplankton more than 3% and surface Chlorophyll-*a* and Salinity 2% each (Table 9).

The full model was visualized on the dbRDA plot (Figure 15). The two axes capture > 82% of the fitted variability, showing the plot to be a good joint representation of the biotic community and the influencing abiotic factors. The seasonal differences in biota correlated best with SST, while the spatial differences in biota (Area-Zones, especially in Wet season) were best correlated with Zooplankton Dry weight (which was highest on the Shelf) and Salinity (which was highest on the Deep-slope).

Total explained variation (7.3%) was low, indicating that a large amount of the larval community variation was not explained by the measured environmental variables. However, the sequential test determined the best solution of parameters by determining whether adding another parameter explained significantly more (increased AIC) than some random variable would. Once SST had been considered in the model, no other environmental variables explained significantly more variation of the larval fish community (Table 9). Therefore, in considering the full dataset from both Wet and Dry seasons, SST was identified as the most influential of the measured environmental variables in predicting larval fish communities. This does not imply that temperature was causative. Rather the seasonal differences in fish community were best correlated with seasonal differences in temperature.

Table 9. DistLM results (marginal and sequential tests) describing the relationship between larval fish community and environmental variables of the KwaZulu-Natal Bight, 2010. AIC = Akaike's Information Criterion: a measure of model quality balancing goodness of fit with model complexity.

Variable	<i>Marginal test</i>		
	Proportion of observed variation	Pseudo-F	<i>p</i>
SST	0.05	5.29	0.0001*
Zooplankton	0.03	2.83	0.0001*
Chlorophyll- <i>a</i>	0.02	2.14	0.001*
Salinity	0.02	1.80	0.0108*
	<i>Sequential test</i>		
	AIC	Pseudo-F	<i>p</i>
+SST	861.76	5.29	0.0001*

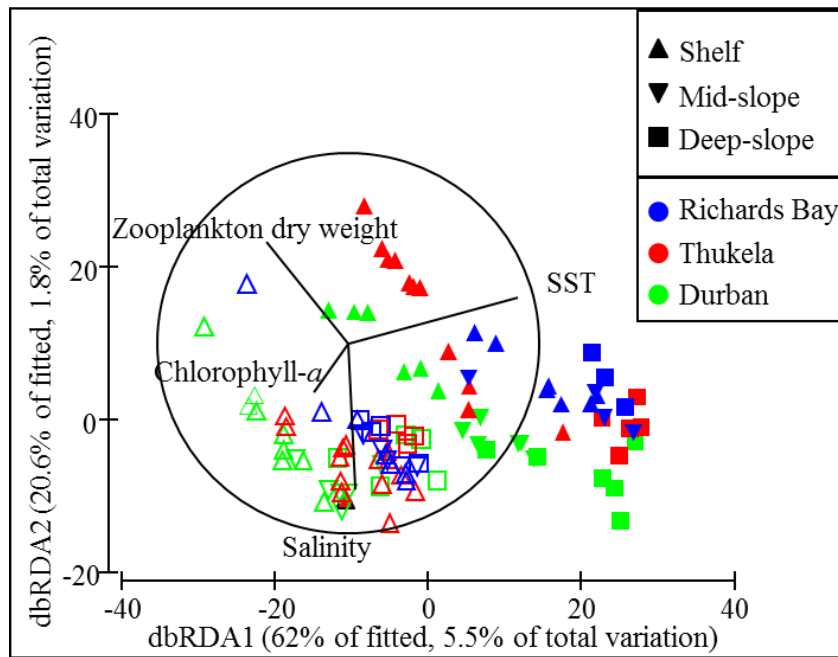


Figure 15. dbRDA plot of larval fish community of the KwaZulu-Natal Bight (2010) overlaid with the environmental parameters. Solid symbols = Wet season, open symbols = Dry season).

In order to investigate the role of Zone and Area and remove the high influence of season, multivariate analyses were subsequently conducted on separately Wet and Dry season data.

#### 4.4.2 Wet season multivariate analyses

CAP analysis of the combined Wet/Dry season data provided a clearer depiction of 2-dimensional spatial relationships between larval assemblages than MDS, and was adopted as the preferred approach in the separate Wet and Dry season analyses. During the Wet season, the larval fish community displayed separation on the basis of Area and Zone (Figure 16). PERMANOVA showed these differences in Area and Zone to be significant, but without a significant interactive effect (Table 10). Pairwise PERMANOVA between Zones in the Wet season showed the larval fish community of the Deep-slope to be significantly different from that over the Shelf (Table 10). Likewise, tests across the Areas confirmed significant differences between fish larvae off Richards Bay and Thukela as well as between Richards Bay and Durban (Table 10).

Table 10. PERMANOVA of the larval fish community across Areas and Zones recorded in the Wet season across the KwaZulu-Natal Bight, 2010.

Source	df	Pseudo-F	<i>p</i> -perm
Area	2	1.62	0.0039*
Zone	2	2.64	0.0001*
Area X Zone	3	1.06	0.3464
<hr/>			
Pairwise analyses		t	<i>p</i> -perm
Area:			
Richards Bay vs. Thukela		1.29	0.023*
Richards Bay vs. Durban		1.29	0.0237*
Zone:			
Shelf vs. Deep-slope		2.12	0.0001*
Durban:			
Mid-slope vs. Deep-slope		1.4	0.0018*
Shelf:			
Richards Bay vs. Thukela		1.36	0.012*
Richards Bay vs. Durban		1.21	0.05*

In addition, although Area and Zone did not show a significant interaction (Table 10), there were apparent differences between larval fish communities from the Durban and Richards Bay Mid-slope Zones (Figure 16). Pairwise PERMANOVA of each Mid-slope Area-Zone revealed the only significant difference to be between larvae over the Durban Mid-slope and Durban Deep slope. Also, pairwise tests on Area-Zone terms across Zones detected that the overall difference of Richards Bay from Thukela was driven by Shelf communities (Table 10). Similarly, Durban Shelf was significantly different from the Richards Bay Shelf. Using these results it can be inferred that while several Area-Zones supported significantly different larval fish assemblages in the Wet season of 2010, three broad regions of the KZN Bight supported characteristic assemblages, based on a lack of significant difference between Area-Zones. First was the region encompassing the Deep-slope Zone as well as the Richards Bay Mid-slope. Secondly, was that of the Thukela and Durban Shelf together with the Durban Mid-slope. The third distinct region was that of Richards Bay Shelf which is significantly different from all other regions.

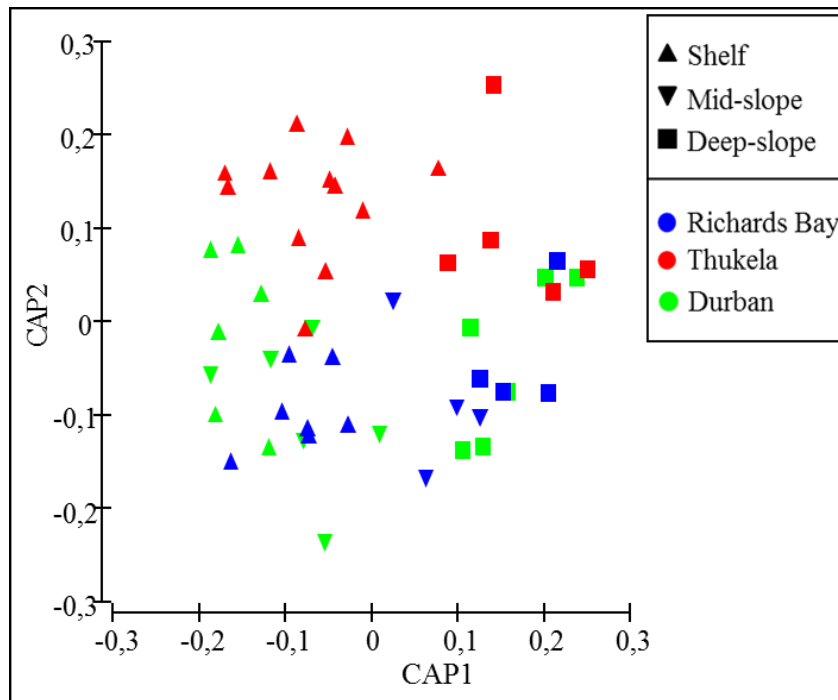


Figure 16. CAP plot of the larval fish community across Area-Zones of the KwaZulu-Natal Bight during the Wet season, 2010.

Overall, mean within-group similarities were low for all Areas-Zones (Table 11) while dissimilarities between-groups were high (Table 12). Mean similarities were highest in the Deep-slope Zones (Table 11), driven by four taxa (Mullid B, Bothid A, Scombrid A and Gonostomatid B) that contributed ~ 55% to within-group similarities in this Zone. The top taxa (Bregmacerotid A and Scombrid A) driving within-group similarities over the Shelf Zone (which the pair-wise tests above showed was significantly different to the Deep-slope), contributed ~25% to within group similarities. These taxa also contributed most to the dissimilarity between the two Zones (Table 12).

Durban Mid-slope, similarly to the Shelf Zone, differed significantly from the Deep-slope. The main three species contributing to within-group similarity of the Durban Mid-slope (Bregmacerotid B, Phosichthyid B and Myctophid B - Table 11) differed from the main species characterising the Deep-slope. However, the dissimilarity was driven rather by characteristically Deep-slope taxa (Gonostomatid A, Mullid B, Bothid A, Myctophid D and Scombrid A). Phosichthyid B contributed to within group similarities of both Mid-slope and Deep-slope off Durban, however, this taxon was significantly more characteristic of the Deep-slope (Tables 11 and 12).

Mean similarities within Area increased northwards from Durban to Richards Bay (Table 11). Pairwise analyses above confined the significant differences between Areas to the Shelf Zones. A large portion of the similarity in larval fish assemblages from the Richards Bay shelf was attributable to the presence of Bregmacerotid A, which contributed 53.82% to the overall similarity. The Richards Bay Shelf was also characterized by Scombrid A and Myctophid D (Table 11). Scombrid A also contributed substantially to similarities in larval fishes in the Thukela Shelf Area Zone, together with Tripterygiid A, Cirrhitid A and Mullid A (Table 11). These taxa (from both Area-Zones) contributed to the dissimilarity between these two Area-Zones (Table 12).

Likewise, the Durban Shelf taxa were different to those of the Richards Bay Shelf (Table 11). Engraulid B, Carangid A, Cynoglossid A and Leiognathid A contributed markedly to similarity on the Durban Shelf (Table 11). As a result, Bregmacerotid A and Scombrid A off Richards Bay and Engraulid B and Callionymid B off Durban contributed most to dissimilarity between the two Area-Zones.

Table 11. SIMPER results showing mean within-group similarity (indicated with an \*) and dominant larval fishes (percentage contribution to within-group similarity > 4%) per Area-Zone in the KwaZulu-Natal Bight in the Wet season, 2010. Dashed line = non-significant difference between Area-Zones.

Area	Zone					
	Shelf	%	Mid-slope	%	Deep-slope	%
Richards Bay	<i>Bregmacerotid A</i>	53.82	<i>Scombrid A</i>	31.38	<i>Mullid B</i>	23.15
	<i>Scombrid A</i>	8.65	<i>Bothid A</i>	20.64	<i>Pomacentrid A</i>	19.49
	<i>Myctophid D</i>	8.37	<i>Sillaginid A</i>	11.58	<i>Scombrid A</i>	17.45
			<i>Gonostomatid A</i>	10.76	<i>Engraulid A</i>	10.15
		15.36*		31.66*		38.26*
Thukela	<i>Tripterygiid A</i>	13.5	<i>No samples collected</i>		<i>Scombrid A</i>	15.29
	<i>Scombrid A</i>	13.11			<i>Bothid A</i>	13.26
	<i>Cirrhitid A</i>	11.61			<i>Mullid B</i>	12.39
	<i>Mullid A</i>	10.95				
		16.23*				32.85*
Durban	<i>Engraulid B</i>	14.69	<i>Bregmacerotid B</i>	25.39	<i>Bothid A</i>	18.43
	<i>Carangid A</i>	11.34	<i>Phosichthyid B</i>	22.13	<i>Gonostomatid A</i>	17.63
	<i>Cynoglossid A</i>	11.08	<i>Myctophid B</i>	18.91	<i>Phosichthyid B</i>	15.74
	<i>Leiognathid A</i>	10.96			<i>Mullid B</i>	14.2
		11.18*		7.78*		31.04*

Table 12. SIMPER results showing mean between-group dissimilarity and dominant larval fishes (contributing > 3% to dissimilarity between-groups) of significantly different Area-Zones of the KwaZulu-Natal Bight recorded in the Wet season, 2010.

Taxa	Mean abundance		Mean dissimilarity	% Contribution	% Cumulative
Mean dissimilarity between Shelf and Deep-slope = 84.56%					
	Shelf	Deep- slope			
Mullid B	0.76	1.84	4.18	4.94	4.94
Scombrid A	1.49	1.59	3.93	4.64	9.59
Bothid A	0.37	1.69	3.73	4.41	14.00
Bregmacerotid A	1.59	0.00	3.44	4.07	18.07
Mean dissimilarity between Durban Mid-slope and Deep-slope = 87.53%					
	Durban Mid- slope	Durban Deep- slope			
Gonostomatid A	0.52	1.86	5.19	5.93	5.93
Mullid B	0.17	1.66	5.16	5.9	11.82
Bothid A	0.3	1.65	4.34	4.96	16.78
Myctophid D	0.00	1.48	3.96	4.52	21.30
Scombrid A	0.21	1.28	3.77	4.30	25.60
Phosichthyid B	0.90	1.46	3.69	4.22	29.82
Mean dissimilarity between Durban and Richards Bay Shelf = 90.29%					
	Durban Shelf	Richards Bay Shelf			
Bregmacerotid A	0.76	3.08	7.38	8.17	8.17
Scombrid A	1.43	1.53	4.76	5.27	13.44
Engraulid B	1.19	0.26	4.62	5.12	18.56
Callionymid B	2.52	0.00	3.84	4.26	22.82
Mean dissimilarity between Thukela and Richards Bay Shelf = 88.52%					
	Thukela Shelf	Richards Bay Shelf			
Bregmacerotid A	1.14	3.08	8.13	9.19	9.19
Scombrid A	1.5	1.53	4.90	5.54	14.73
Tripterygiid A	1.79	0.00	4.68	5.29	20.02
Cirrhitid A	1.30	0.53	4.32	4.88	24.89
Mullid A	1.23	0.26	3.93	4.44	29.33

DistLM marginal tests on the Wet season data indicated that little variation in the larval fish community was explained by environmental variables (Table 13). Individually, SST and Zooplankton Dry weight explained 6% each, while Surface Salinity and Chlorophyll-*a* explained 4% and 3% respectively (Table 13).

The Wet season full model was visualized on the dbRDA plot (Figure 17). The two axes capture >73% of the fitted variability, showing that the plot is a good joint representation of the biotic community and the influencing abiotic factors. The Zonal differences in larvae correlated best with SST and Zooplankton, with SST highest on the Deep-slope and Zooplankton highest on the Shelf (Figure 17). The spatial differences in larvae between Areas were best correlated with Salinity, highest in Richards Bay, and particularly between Shelf Areas. Richards Bay Mid-slope and Deep-slope larvae were associated with higher SST, while Durban Mid-slope larvae were associated with lower SST and salinities similarly to Durban and Thukela Shelf (Figure 17). Total explained variation (10.4%) was low, indicating that a large amount of the biological community variation was not explained by the measured environmental variables. However, the sequential test determined that once SST had been considered in the Wet season model, no other environmental variables explained significantly more variation of the larval fish community (Table 14), i.e. this variable was the most influential.

Table 13. DistLM results (marginal and sequential tests) describing the relationship between larval fish community and environmental variables during the Wet season of KwaZulu-Natal Bight, 2010. AIC = Akaike's Information Criterion: a measure of model quality balancing goodness of fit with model complexity.

Variable	<i>Marginal test</i>		
	Proportion of variance explained	Pseudo-F	<i>P</i>
SST	0.06	3.09	0.0001*
Zooplankton	0.06	2.81	0.0001*
Salinity	0.04	1.96	0.0045*
Chlorophyll- <i>a</i>	0.03	1.69	0.0223*
	<i>Sequential test</i>		
	AIC	Pseudo-F	<i>P</i>
+SST	409.82	3.09	0.0001*

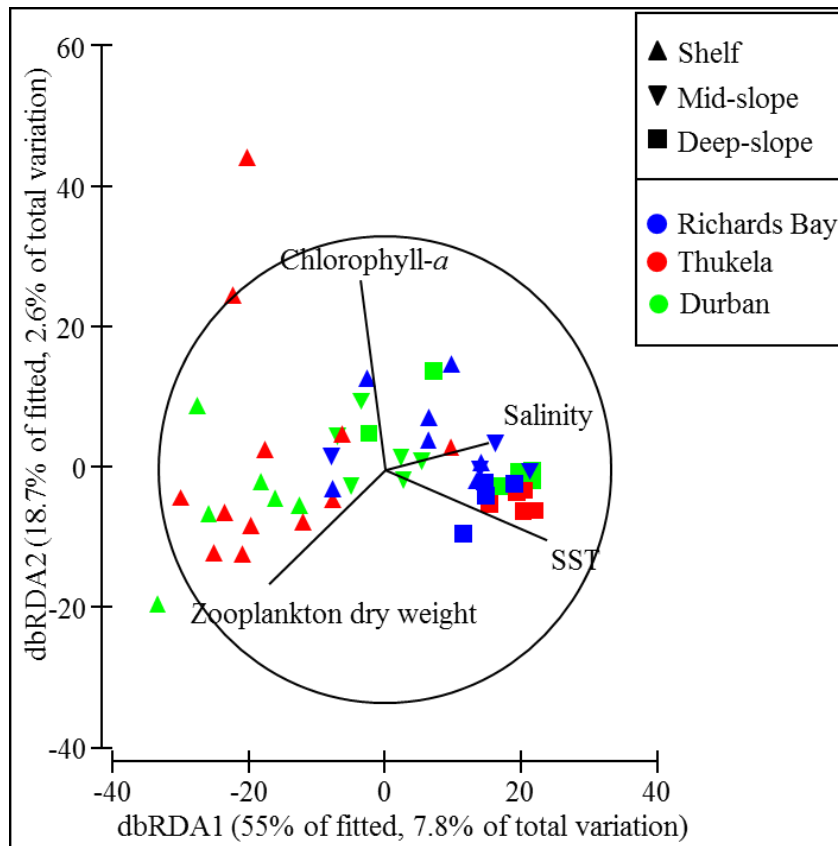


Figure 17. dbRDA plot of the larval fish community of the KwaZulu-Natal Bight (2010) overlaid with the environmental variables, during the Wet season, 2010.

#### 4.4.3 Dry season multivariate analyses

Separation between larvae in different Zones is apparent through CAP analysis (Figure 18) of the larval fish community in the Dry season. This is supported by the significant differences that were measured between Zones only (PERMANOVA; Table 14). Deeper statistical analyses using Pairwise PERMANOVA across Zones in the Dry season revealed this difference again held significantly between communities over the Shelf and Deep-slope only (Table 14). Neither Deep-slope nor Shelf communities were significantly different to Mid-slope. Similarly to the Wet season, inferences can therefore be made that KZN Bight larval fish assemblages in the Dry season of 2010 fell into distinct regions. The first was that over the Deep-slope, and the second was that on the Shelf. The Mid-slope Zone between the two regions had a larval fish community that shared attributes with the communities of both the Shelf and the Deep-slope.

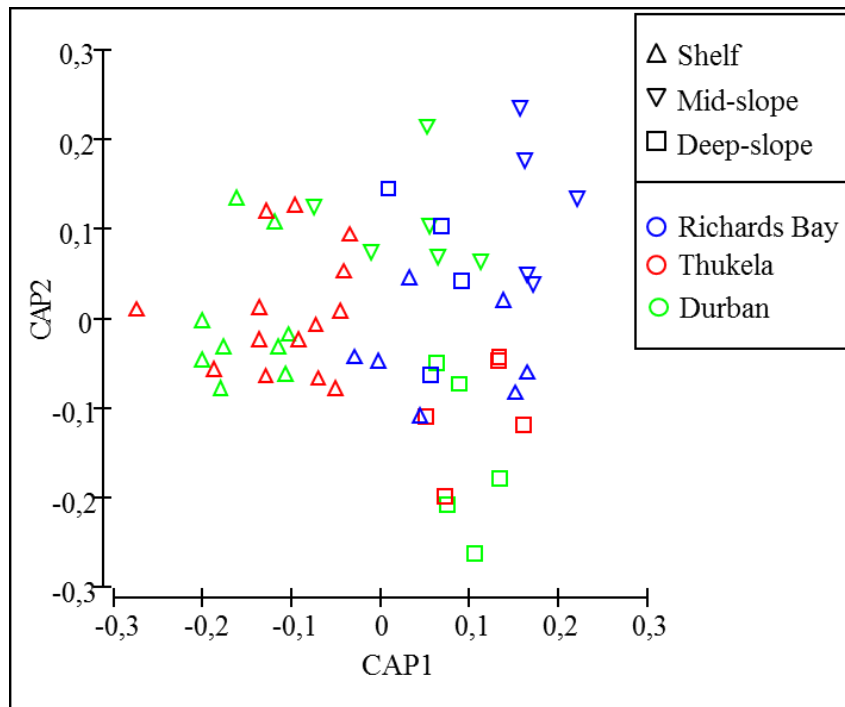


Figure 18. CAP plot of the larval fish community across Area-Zones of the KwaZulu-Natal Bight during the Dry season, 2010.

Table 14. PERMANOVA of larval fish community recorded in the Dry season across Areas and Zones of the KwaZulu-Natal Bight, 2010.

Source	df	Pseudo-F	<i>p</i> -perm
Area	2	1.19	0.1915
Zone	2	1.97	0.0006*
Area X Zone	3	1.00	0.4715
<hr/>			
Pairwise analyses		t	<i>p</i> -perm
Zone:			
Shelf vs. Deep-slope		1.66	0.0002*

Several different taxa of the family Myctophidae are notably present in all Area-Zones except Durban Shelf and Mid-slope and Thukela Shelf in the Dry season (Table 15). The family Bregmacerotidae also showed a noteworthy trend, being absent in all Deep-slope Zones. Leiognathid A, Sciaenid C and Trypterigiid A of the Shelf Zones and Phosichthyid B, Engraulid B, and family Myctophidae of the Deep-slope drove the significant dissimilarity between the two Zones (Table 16).

Table 15. SIMPER results showing mean within-group similarity (indicated with an \*) and dominant larval fishes (percentage contribution to within-group similarity > 4%) per Area-Zone in the KwaZulu-Natal Bight in the Dry season, 2010. Dashed line = non-significant difference between Area-Zones. Bold dashed lines show no significant difference with Mid-slope but a significant difference between Shelf and Deep-slope.

Area	Zone					
	Shelf	%	Mid-slope	%	Deep-slope	%
Richards Bay	<i>Bregmacerotid B</i>	21.75	<i>Bregmacerotid B</i>	21.66	<i>Mullid B</i>	21.31
	<i>Engraulid B</i>	17.87	<i>Myctophid E</i>	13.97	<i>Myctophid F</i>	17.72
	<i>Myctophid D</i>	16.48	<i>Bothid A</i>	8.53	<i>Champsodontid A</i>	16.09
			<i>Tripterygiid A</i>	8.44	<i>Tripterygiid A</i>	14.85
					<i>Engraulid B</i>	14.52
		19.58*		30.49*		21.4*
Thukela	<i>Leiognathid A</i>	22.22	<i>No samples collected</i>		<i>Phosichthyid B</i>	29.2
	<i>Engraulid B</i>	11.44			<i>Myctophid F</i>	20.53
	<i>Bregmacerotid A</i>	8.02			<i>Scombrid A</i>	13.39
	<i>Sciaenid C</i>	7.72				
		13.25*				30.05*
Durban	<i>Leiognathid A</i>	22.51	<i>Tripterygiid A</i>	23.2	<i>Phosichthyid B</i>	23.27
	<i>Tripterygiid A</i>	20.12	<i>Bregmacerotid B</i>	18.16	<i>Myctophid B</i>	11.04
	<i>Sciaenid C</i>	18.39	<i>Engraulid A</i>	12.48	<i>Bathylagid A</i>	8.79
					<i>Myctophid F</i>	8.61
		12.04*		12.96*		24.37*

Table 16. SIMPER results showing mean between-group dissimilarity and dominant larval fishes (contributing > 3% to dissimilarity between-groups) of significantly different Area-Zones of the KwaZulu-Natal Bight recorded in the Dry season, 2010.

Taxa	Mean abundance		Mean dissimilarity	% Contribution	% Cumulative
<i>Mean dissimilarity between Durban Shelf and Deep-slope = 90.38%</i>					
	Durban Shelf	Durban Deep-slope			
<i>Leiognathid A</i>	3.15	0	6.33	7	7
<i>Sciaenid C</i>	1.48	0	4.53	5.02	12.02
<i>Tripterygiid A</i>	2.1	0.82	4.53	5.01	17.03
<i>Phosichthyid B</i>	0.17	1.71	4.31	4.77	21.8
<i>Myctophid D</i>	0	1.49	4.18	4.63	26.43
<i>Synodontid B</i>	1.6	0.8	4.18	4.63	31.06
<i>Engraulid B</i>	1.07	1.38	3.94	4.36	35.42
<i>Mean dissimilarity between Thukela Shelf and Deep-slope = 86.11%</i>					
	Durban Mid-slope	Durban Deep-slope			
<i>Phosichthyid B</i>	0.14	1.58	5.65	6.56	6.56
<i>Leiognathid A</i>	1.39	0	5.01	5.82	12.37
<i>Engraulid B</i>	1.28	0.89	4.75	5.51	17.89
<i>Myctophid F</i>	0.33	1.23	4.14	4.81	22.7
<i>Tripterygiid A</i>	1.04	0.61	4.05	4.7	27.4
<i>Scombrid A</i>	0.13	1	3.67	4.27	31.66
<i>Myctophid A</i>	0.95	0.38	3.49	4.05	35.71

DistLM marginal tests showed that during the Dry season all the environmental variables except surface Chlorophyll-*a* explained some, although little, of the variation observed in the larval fish community independently of the other variables (Table 17). Surface salinity explained 9 %, SST 8% and Zooplankton 3% each (Table 17). The Dry season full model was visualized on the dbRDA plot (Figure 19). The two axes capture >81% of the fitted variability, showing that the plot is a good joint representation of the biotic community and the influencing abiotic factors. The Zonal differences in biota correlated best with Salinity. High salinities correlated with larval fishes of the Deep-slope and Richards Bay Shelf and Mid-slope (Figure 19). Thukela Shelf correlated with higher Chlorophyll-*a* and Durban Shelf with high Zooplankton Dry weight, however the assemblage of larval fishes was not

significantly different between Areas. Total explained variation (11.2%) was low, indicating that a large amount of the biological community variation was not explained by the measured environmental variables. However, the sequential test determined that once Salinity had been considered in the Dry season model, no other environmental variables explained significantly more variation of the larval fish community (Table 17) i.e. this variable was the most influential.

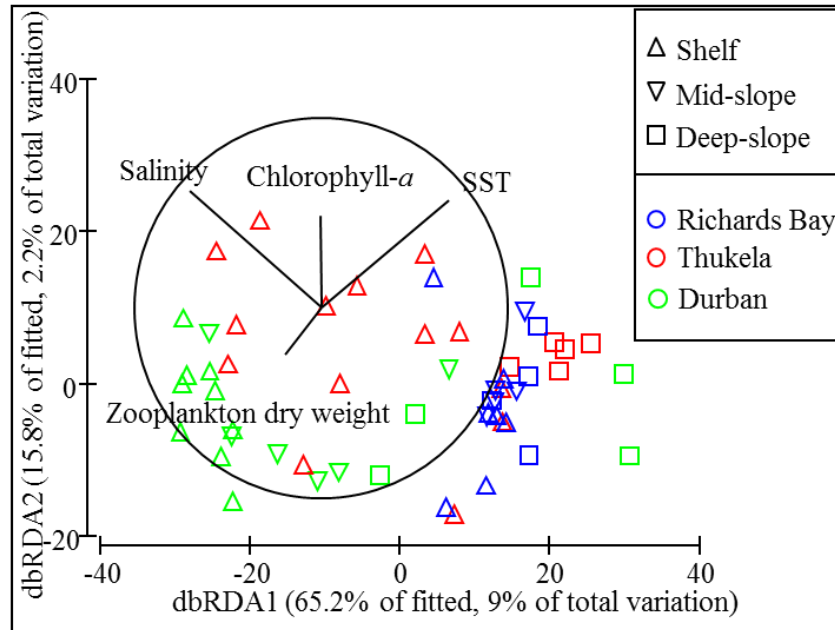


Figure 19. dbRDA plot of larval fish community overlaid with the environmental variables during the Dry season, 2010. The horizontal axis accounts for 9% of the total variation.

Table 17. DistLM results (marginal and sequential tests) for the relationship between larval fish community and environmental variables during the Dry season, 2010.

Variable	<i>Marginal test</i>		
	Proportion	Pseudo-F	<i>P</i>
SST	0.08	4.77	0.0001*
Chlorophyll- <i>a</i>	0.01	0.77	0.7759
Salinity	0.09	4.97	0.0001*
Zooplankton	0.03	1.59	0.0398*
	<i>Sequential test</i>		
	AIC	Pseudo-F	<i>P</i>
+SST	449.66	4.97	0.0001*

## CHAPTER 5: DISCUSSION

### 5.1 General

Studies of fish larvae provide understanding of fish biology and ecological processes such as spawning, recruitment and utilization of nursery areas by fishes. Little is known of the off-shore larval fish community of the KZN Bight. In contrast a number of studies of larval assemblages have been conducted in near-shore KZN waters ( $< 5$  m water depth) and estuaries (Whitfield, 1989a and b; Harris, 1996; Harris and Cyrus, 1995 and 1996; Harris et al., 1999 and 2001; Beckley and Naidoo, 2003). Sampling of fish eggs and larvae in shelf waters just south of the KZN Bight has also been valuable in building knowledge of these life history stages (Connell, 2007). Other than this, published research on off-shore larval fishes has been limited to surveys during regional sampling conducted between Algoa Bay and the Thukela River in 1990/1991 (Beckley and van Ballegooyen, 1992; Beckley and Hewitson, 1994; Beckley and Connell, 1996; Olivar et al., 1999; Hutchings et al., 2003). The ACEP II “Ecosystem functioning of the KZN Bight” project therefore afforded a unique opportunity to study the relatively poorly-known larvae from off-shore.

Larval fish sampling was one of numerous components of the afore-mentioned multidisciplinary project. The design of the sampling programme and fieldwork was constrained by the overall research questions posed in the ACEP KZN Bight project (Fennessy et al., in press) and by the capabilities and availability of the research vessel. For example, there was no systematic attempt to sample nocturnally and diurnally. However, on examination, the larval fish assemblage in the present study did not exhibit marked diel vertical migrations over the range of depths sampled (maximum of 80 m), with similar densities, numbers of taxa and species composition occurring irrespective of day or night time sampling. Stations in water depths shallower than 80 m included the full water column and so would have sampled the full range of vertical migration by the larvae present. The 80 m maximum in this study was chosen to correspond with that sampled by Beckley and van Ballegooyen (1992), to permit comparisons when appropriate. It is possible that the taxa sampled here occur naturally in upper waters as larvae, regardless of time of day. In support of this, a study of diurnal migration of larval fishes associated with two eddy systems off the south-west coast of Australia in the Leeuwin current found that the majority of the larvae occurred in the upper 150 m regardless of time of day (Muhling, 2006).

Also, assemblages in a warm-core down-welling eddy off Western Australia were patchy and varied significantly with distance from the eddy centre and with depth, which was attributed to the depth of the mixed layer (Muhling, 2006). The mixed-layer is a region of variable depth adjacent to the sea surface, and in which temperature and salinity (and hence density) are uniform, as a function of the mixing caused by wind and wave action. This warm-core eddy off Western Australia was associated with warm, oligotrophic waters similar to those of the KZN Bight, suggesting that in such waters, fish larvae do not display typical vertical migration corresponding with day and night, but rather might coincide with the depth of the mixed layer.

The application of a conceptual model to the current study allowed samples to be treated as replicates, and for statistically valid inferences to be made. The first delineation, that of distance from shore, separating each transect into Shelf, Mid-slope and Deep-slope zones, may be coupled with the predicted presence of the Agulhas Current in the Deep-slope vs. Shelf waters (Shannon, 1989; Beckley and van Ballegooyen, 1992). This first delineation was well conceived, as there was indeed a strong presence of the Agulhas Current over the Deep-slope during the present study, particularly in the Wet season (Figure 9). The second delineation was based on proximity to likely nutrient sources and/or potential sources of off-shore fish larvae, i.e. the Durban Eddy, the Richards Bay upwelling cell and the Thukela River (Meyer et al., 2002; de Lecea et al., 2013; Fennessy et al., in press). Environmental conditions at the time of study reflected the expected high Wet season and low Dry season rainfall patterns for the area (Figure 2), driving expected higher Wet season flow of nutrients from the Thukela river (Omarjee, 2012; Figure 9). However, the hypothesized increase in nutrients produced in the upper water layers by the eddy-induced upwelling off Durban was not evident at the time of sampling (Roberts and Nieuwenhuys, in press). The nutrient concentrations found in the KZN Bight during the time of this study were also not indicative of nutrient-producing oceanographic features such as the Durban eddy or Richards Bay upwelling, and were more representative of riverine influence (Omarjee, 2012). Further, Pretorius et al. (in press) reported that nutrient enrichment from the Durban eddy and Richards Bay upwelling in 2010 appeared to have a greater seasonal influence on zooplankton biomass and distribution on the KZN Bight than the strongly seasonal nutrient input from the Thukela River, even in the absence of these two oceanographic features during sampling. In contrast, de Lecea et al., (2015) demonstrated that zooplankton diets relied on riverine organic matter in-shore in the central Bight during the Wet season. Thus, recent

findings from the ACEP study suggest the nutrients provided by oceanographic features have more of a seasonal influence than the predicted spatial effect.

A further factor which could have been influential was that of proximity of sampling localities to various bottom substrates. The Durban and Richards Bay Shelf areas sampled are characterized by a higher proportion of reef substrate than the Thukela Shelf area, which more typically comprises soft sediments (Green and MacKay, in press). This could potentially have influenced larval assemblage patterns through habitat association, and was accounted for in the testing of interactive effects of the various factors.

Overall, while upwelling was not occurring at the time of sampling, the effects thereof still appeared to have been manifested, and other spatial tenets of the conceptual model (proximity to shore and Agulhas Current, depth, latitude and habitat) were still applicable i.e. the framework of the conceptual model is still considered valid.

Thus, despite some shortcomings in the sampling design and data collected (e.g. disparity in Day/Night sampling effort) these are not considered sufficiently influential to negate the findings or value of the work presented here. The KZN Bight is a unique environment, and the large spatial coverage of the synoptic sampling grid surveyed here over two seasons has produced the most intensive study of its fish larvae to date. As such, the data in the present study are considered fit for purpose and the results are considered to have substantial value towards improving understanding of this part of the life history of KZN fishes.

## **5.2 Broad patterns in KZN Bight fish larvae**

### **5.2.1 Densities**

Observed larval fish densities in this study (min = 2.08, max = 392.74 larvae/100 m<sup>3</sup>) are similar to those reported on the South African east coast (including part of KZN) by Beckley and van Ballegooyen (1992). A general decrease in larval density with distance from shore in the Durban and Thukela areas was observed in both this study and that of Beckley and van Ballegooyen (1992). The KZN Bight fish larval community is patchily distributed, particularly in the Durban Shelf area, as seen by the wide range and the high variance in larval density. Beckley and van Ballegooyen (1992) reported similar high variability. This variability also characterizes marine waters at similar subtropical latitudes off Eastern and South-Western Australia and Eastern Brazil (Smith and Suthers, 1999; Nonaka et al., 2000; Muhling et al., 2008). Similar variability in density was also reported in the Benguela current

on the west coast of South Africa (Olivar and Shelton, 1993). Variability in abundance therefore appears to be a common feature in larval fishes in marine systems.

Larval fish densities in the KZN Bight are lower than those recorded on the South and West coasts of South Africa (e.g. in comparison with Tilney and Buxton, 1994; Table 18). Other studies along the South African coast have detected this eastward trend of declining density even within the smaller spatial scales of their respective study areas (Whitfield, 1989b; Harris and Cyrus, 1996; Harris et al., 1999; Cowley et al., 2001; Strydom, 2003). This decrease in larval fish densities coincides with change from cool temperate waters in the west to warmer subtropical waters in the east. Cooler waters are more productive and support larger stocks of fishes which produce higher densities of larvae (Pepin, 1991; Morales-Nin, 2009). Coastal upwelling on the West coast of South Africa is caused by Ekman transport interacting with the Benguela Current resulting in very high levels of primary production (Behrenfeld and Falkowski, 1997; Carr and Kearns, 2003; Trujillo and Thurman, 2005). Chlorophyll-*a* concentrations in the Benguela upwelling region typically range between 5 – <15 µg/L depending on the season (Carr and Kearns, 2003). However, a maximum Chlorophyll-*a* concentration of 117 µg/L has recently been noted in the Benguela ecosystem (Barlow and Lamont, 2012). In the KZN Bight, a study near to the time of sampling of the present study recorded Chlorophyll-*a* levels between 0.10 – 1.44 µg/L (Lamont and Barlow, 2014), similar to what was recorded during the present study. The reason for the difference between the east and west regions is that the west coast experiences much higher nutrient concentrations than the KZN Bight which is oligotrophic (Verheye-Dua and Lucas, 1988; Bustamante et al., 1995; Carr and Kearns, 2003).

Similar trends of declining densities/biomasses from west coast to the east coast in South Africa have been observed in other organisms. For example, there is a noted reduced mussel biomass in KZN compared to the Cape (van Erkom Schurink and Griffiths, 1990). Maximum zooplankton biomass recorded for the northern Benguela by Kollmer (1963) was double that recorded in the KZN Bight (Pretorius et al., in press), as was mean copepod biomass in the southern Benguela during annual autumn and summer cruises over a 16-year time series (Huggett et al., 2009).

### **5.2.2 Number of taxa**

Densities of larval fishes were spread relatively evenly across taxa i.e. the KZN Bight assemblage was not strongly dominated by few highly abundant taxa but rather a large

number of taxa in similar low abundances. This was similarly the case in the study by Beckley and van Ballegooyen (1992) in their off-shore study between Algoa Bay and the Thukela River. In Australia, Smith and Suthers (1999) and Muhling et al. (2008) reported similar off-shore taxon counts to those obtained in the present KZN Bight study (Table 18) and attributed high larval diversity to the convergence of tropical and temperate waters.

While larval fish densities were relatively low (discussed above) in comparison to other South African areas, the number of larval taxa recorded in the KZN Bight in this study was higher than those recorded in off-shore studies on the west, south and south-east coasts (e.g. Olivar and Shelton, 1993; Tilney and Buxton, 1994).

In contrast to the west-east declining gradient in larval fish density, there is increasing diversity, with eastern waters supporting more larval fish species. In the current study, in similar fashion while density decreased, number of taxa increased with distance from shore (Table 3). Harris et al. (2001) noted a similar trend, albeit that their study was located considerably closer in-shore and also only sampled surface water.

Table 18. Comparative numbers of samples, taxa, families and mean densities of larval fishes from off-shore marine waters.

		Number of samples	Number of taxa	Number of families	Average no. larvae/100m <sup>3</sup>	Reference
South Africa						
	Benguela Current	unspecified (120 sites)	19	-	-	(Olivar and Shelton, 1993)
	Tsitsikamma National Park	16 (4 sites)	55	24	282	(Tilney and Buxton, 1994)
	South-east coast	57 (4 sites)	-	75	-	(Wood, 1999)
	Algoa - Thukela	106 (36 sites)	-	-	80.5	(Beckley, 1992)
28.3 – 30.0 ° S	KwaZulu-Natal Bight	108 (55 sites)	116	67	54.5	This study
International						
31.3 – 31.5 ° S	South western Australia	102 (5 sites)	148	93	6 - 743	(Muhling et al., 2008)
33.5 – 34.0 ° S	Eastern Australia	35 (5 sites)	137	111	-	(Smith and Suthers, 1999)
16.0 – 23.0 ° S	Eastern Brazil	192 (64 sites)	83	77	-	(Nonaka et al., 2000)

### 5.3 Commonly-occurring KZN Bight fish larvae

Most fish larvae obtained in this study were from families which are widespread across the Indo-West Pacific (Leis and Carson-Ewart, 2000; Mwaluma et al., 2014). The most abundant families found were Leiognathidae, Callionymidae and Tripterygiidae (Appendix Ib). However, differences between assemblages in this study were driven by frequency of occurrence (ubiquity) within each area-zone (reflected in the SIMPER analyses; Table 4). Myctophidae occurred most frequently and also in high abundance (Table 4). Other ubiquitous families included Bregmacerotidae and Engraulidae (Appendix Ic). More detailed consideration of the characteristics of the commonly-occurring taxa is provided below, in an attempt to contextualize their occurrence with known features of the biogeography of KZN fishes.

#### 5.3.1 Leiognathidae

Leiognathidae (pony fishes and slimies) was the most abundant family during this study. This is perhaps surprising as they were not recorded in the off-shore study by Beckley and van Ballegooyen (1992). They also do not feature in other off-shore larval studies around South Africa, nor are they recorded in studies at similar latitudes elsewhere. However, adult Leiognathidae are widespread in the Indo-Pacific region, where they are frequently abundant. They typically inhabit shallower shelf waters, although some taxa occur in water up to 160 m in depth (Woodland et al., 2001).

Adult leiognathids were also the most abundantly occurring fish in a study of near-shore waters off Durban in the southern KZN Bight, based on catches from a beach seine-net fishery (Beckley and Fennessy, 1996). Similarly, they were also among the most abundant fish in a study of the Thukela Bank trawl fishery in the central KZN Bight (Mkhize, 2006), although their numbers appear to fluctuate markedly here, as this family was far less common in the trawl fishery in the 1990s (Fennessy et al., 1994). The abundance of adult leiognathids in these areas explains their abundance in the larval fish assemblage.

Mkhize (2006) reported two leiognathid species, *Gazza minuta* and *Secutor ruconius* in the Thukela trawl bycatch and these were also recorded in the Durban beach seine fishery together with *Secutor insidiator* and *Leiognathus equula* (Beckley and Fennessy, 1996). Hence these species are likely to form the bulk of the leiognathid larvae sampled in this study. Adults Leiognathidae feed on benthic invertebrates and are considered to be bottom-living fishes (Smith and Heemstra, 1995) which might account for their presence as by-catch

in trawl-fisheries. Leiognathid larvae in the present study show similar trends to their adult counterparts, occurring in shallow in-shore waters in both seasons (Figure 20a).

Although abundant during both seasons, higher concentrations of leiognathid larvae were apparent on the shelf south of Durban in the Wet season and on the Thukela shelf in the Dry season (Figure 20a). Connell (2007) noted that off Park Rynie, to the south of the KZN Bight, the Leiognathidae are indeed a summer spawning family, which agrees with the high larval abundances observed south of Durban in the Wet season in this study (Figure 20a).

### **5.3.2 Callionymidae**

The second most commonly-occurring larvae in this study, the callionymids (dragonets), were found to be characteristic of the central bight in the Wet season (Figure 20b). Callionymidae adults typically live on sandy bottoms such as that which occurs across the central bight (Green and MacKay, in press) and feed on small benthic invertebrates, although some species are reef dwellers. Fennessy (in press) recorded *Callionymus marleyi* and *Callionymus regani* adults in mid-shelf water of the central KZN Bight, albeit in low numbers, during a trawl survey of soft sediments in 2010. Connell (2007) considered *C. marleyi* off KZN to spawn all year round with peaks over the summer months. In contrast, a study of spawning of Callionymidae in continental shelf waters off the eastern United States revealed peak spawning in late summer and early autumn over the Mid-slope of the South Atlantic Bight (Olney and Sedberry, 1983). Persad (2005) also recorded *C. marleyi* from the off-shore (300 – 500m depth) demersal trawl fishery for crustaceans in the KZN Bight. Weerts (2002) recorded the species with some consistency from shallow sandbanks in the Port of Richards Bay. It is therefore likely that the two callionymid taxa in the present study belong to the species *C. marleyi* and *C. regani*. Their abundance in the larvae is perhaps surprising given that they do not feature strongly in local trawl catches, but this could be a result of trawling mainly on muddy sediments, while callionymids prefer sandy substrata (Smith and Heemstra, 1995).

### **5.3.3 Tripterygiidae**

This family (triplefin blennies) was third highest in abundance in the present study and also featured strongly in the study of near-shore larvae by Harris et al. (2001) near Lake St. Lucia (to the north of the KZN Bight). Their occurrence in the present study is notable however, as Tripterygiidae are not characteristic of any other off-shore South African larval studies, despite their being cosmopolitan in tropical and temperate regions (Smith and Heemstra,

1995). Connell (2007) does not report the occurrence of any tripterygiid eggs or larvae from south of the Bight. In comparison with similar studies at similar latitudes, although also absent in the study by Smith and Suthers (1999) on the east coast of Australia, they were reported (in low numbers) off south-western Australia (Muhling et al., 2008) and the east coast of Brazil (Nonaka et al., 2000).

Tripterygiidae are more abundant in warmer waters (Smith and Heemstra, 1995) where they were originally thought to be year round spawners (Thresher, 1984). Other studies have shown a greater off-shore distribution in summer months (Muhling and Beckley, 2007) and Nonaka et al. (2000) reported their presence during autumn months only. However, in the present study, Tripterygiidae was amongst the dominant families in both the Wet and Dry seasons. The tripterygiids in the present study were largely concentrated in shelf waters (Figure 20c), particularly south of Durban in the Wet season and off Richards Bay in the Dry season (Figure 20c). Tripterygiidae adults live in shallow shelf waters on subtidal rocky or coral reef or in intertidal rock pools (Thresher, 1984; Wheeler, 1985; Smith and Heemstra, 1995; Springer, 1998; Allen and Robertson, 1994; Nelson, 1994; Beckley 1999). They are demersal spawners; the eggs covered with numerous sticky threads are anchored in the algae of the nesting sites where male triplefin blennies remain nearby to guard them until they hatch (Thresher, 1984). However, post-hatching, the larvae are planktonic and occur primarily in shallow, near-shore waters (Thresher, 1984), as in this study (Figure 20c). Again, the larvae appear to be greatly influenced by the spatial dynamics of the adult fishes. Their abundance is also perhaps surprising given the low proportion of reef habitat relative to soft substrata in the Bight.

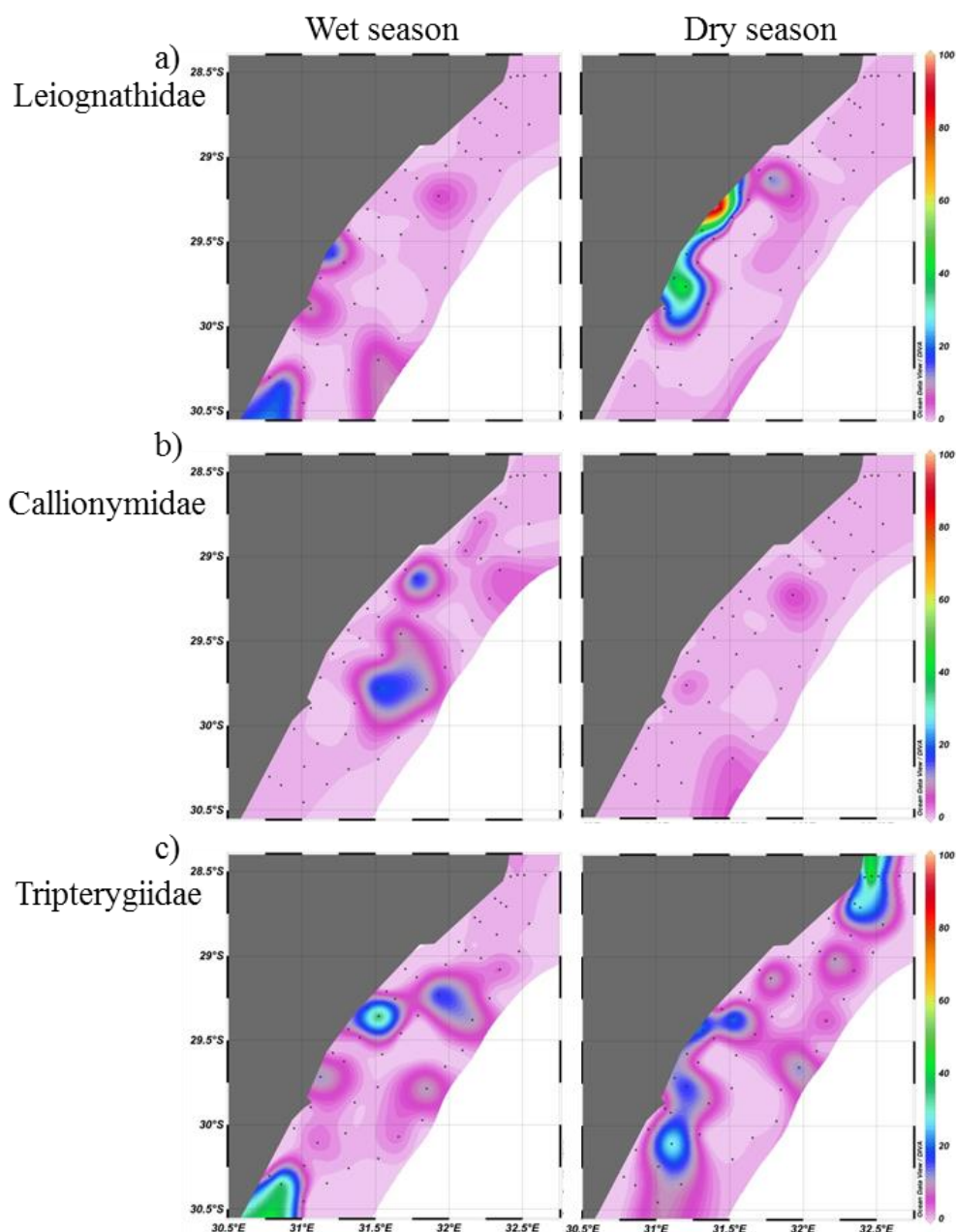


Figure 20. Percentage contributions to overall densities of the most abundant families at stations on the KwaZulu-Natal Bight in the Wet and Dry seasons, 2010.

### 5.3.4 Myctophidae

Not surprisingly myctophids (lanternfishes) were the most ubiquitous, speciose and in high abundance in this study (Figure 21a; Appendix II). Individuals of various species featured in high abundance in all studies compared in Table 18 above, excepting that of Tilney and Buxton (1994) of the Tsitsikamma National Park. The family is considered to make up approximately half of all fish larvae taken in oceanic plankton tows around the world (Ahlstrom et al., 1976).

Myctophids are particularly prolific in oceanic midwaters (Ahlstrom et al., 1976) and aggregate in extensive shoals in slope waters (Backus et al., 1968; Barham, 1971). This behaviour likely explains the regular appearance of *Diaphus knappi* in the off-shore (300 – 500m depth) demersal trawl fishery for crustaceans in the KZN Bight (Fennessy and Groeneveld, 1997; Persad, 2005). Olivar and Beckley (1994) described several species of the genus *Diaphus* which were encountered on the east coast of South Africa as well as some 32 other taxa. Lanternfish (Myctophidae) larvae can be separated into two groups based on eye shape. The group Myctophinae includes larvae with narrow, elliptical eyes (most taxa encountered in this study) while the Lampanyctinae is comprised of individuals with round or nearly round eyes (one taxon in this study) (Moser and Ahlstrom, 1970, 1972 and 1996).

Studies indicate that lanternfishes are important grazers on herbivorous zooplankton (Paxton, 1967; Holton, 1969; Legand and Rivaton, 1969; Collard, 1970; Baird et al., 1975). These fishes mainly live in mid-water, and some species undergo vertical migration; a behaviour which suggests that they play an important role in transferring energy from the upper to the deeper layers as they feed near the surface and defecate near the bottom (Angel, 2003; Conley and Hopkins, 2004).

### **5.3.5 Engraulidae**

Engraulids are small, pelagic, schooling fishes, mostly found in shallow coastal waters and estuaries in both tropical and temperate regions (Beckley, 1993; Smith and Heemstra, 1995; Muhling et al., 2008). They are commercially important for food and fishmeal, and are also used as bait (Smith and Heemstra, 1995). However, there are no directed fisheries for engraulids in KZN (Everett, 2014) so little is known of the occurrence of non-larval life history stages for this group in this region. Second in ubiquity (i.e. frequency of occurrence) amongst families of this study (Table 4), the engraulids were equally abundant in the Wet and the Dry season but were particularly characteristic of the Dry season due to greater ubiquity during that survey. In the Wet season a hotspot of high abundance was detected on the shelf south of Durban in the Wet season (Figure 21b). Connell (2007) has reported the eggs and larvae of five engraulid taxa consistently in this area, namely *Engraulis encrasicolus*, *Encrasicholina punctifer*, *Stolephorus holodon*, *Thryssa vitrirostris* and one unidentified taxon. Based on relative abundance of their eggs, these taxa were all reported to be Wet season spawners, although some were recorded in other months. Summer spawning of engraulids was also observed off eastern Australia and Brazil (Smith and Suthers, 1999; Nonaka et al., 2000).

Two morphotypes of engraulid were observed during the current study (Appendix II). Beckley and van Ballegooyen (1992) reported engraulid larvae to be abundant in that survey of 1990/1. Of the four afore-mentioned taxa observed by Connell (2007), *E. punctifer* and particularly *T. vitrirostris* adults have been found to be in high abundance during trawls on the Thukela Bank (Fennessy, 1994; Mkhize, 2006). In addition, two *Thryssa* species were found to contribute 14% by number to catches in the beach seine fishery off Durban (Beckley and Fennessy, 1996).

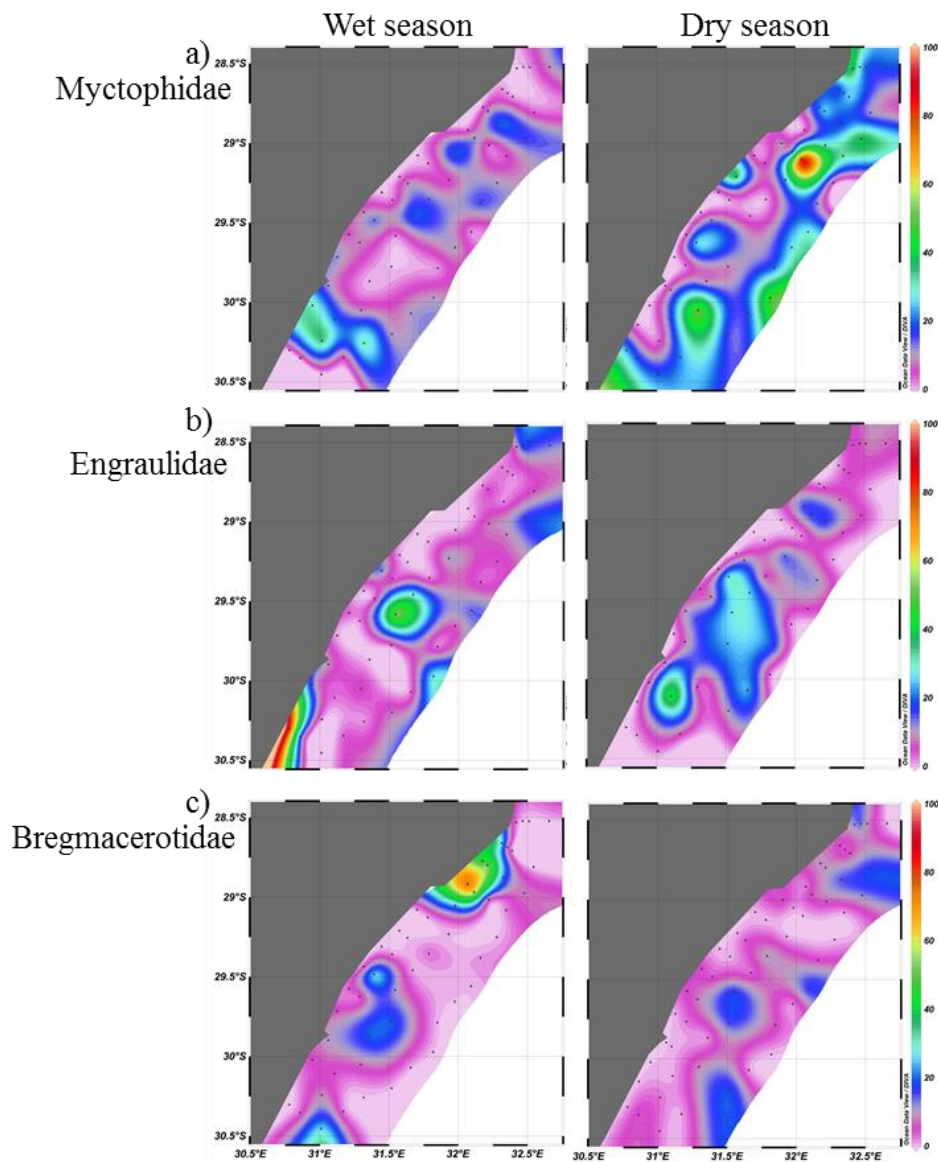


Figure 21. Percentage contributions to overall densities of the most ubiquitous families at stations on the KwaZulu-Natal Bight in the Wet and Dry seasons, 2010.

### 5.3.6 Bregmacerotidae

Third most ubiquitous of larvae in this study, Bregmacerotidae is a family of small, pelagic fishes (Smith and Heemstra, 1995). It is a monotypic family with just one genus, *Bregmaceros*, and three species known on the east coast of South Africa, *B. maclellandii*, *B. atlanticus* and *B. nectabanus* (Smith and Heemstra, 1995). A high concentration was particularly noticeable over the shelf near Richards Bay in the Wet season (Figure 21c) driving the unique larval fish assemblage observed there. In a nearby larval fish study of near-shore waters off St. Lucia (to the north of the KZN Bight) by Harris et al. (2001), *B. atlanticus* were the second most ubiquitous larvae. Beckley (1992) also reported *B. atlanticus* from the previous off-shore surveys of 1990/1.

While concentrations were associated with shallower sites during the Wet season, in the Dry season Bregmacerotidae characterized the Deep-slope (Figure 21c). Elsewhere, the plankton-eating Bregmacerotidae are widespread from shallow shelf waters to deeper oceanic waters (Muhling et al., 2008; Bray, 2012).

### 5.3.7 Larvae of species with fisheries' importance

#### *Migratory fishes*

Beckley (1993) reported several linefish larvae present along the east coast of South Africa particularly the families Pomatomidae, Sciaenidae, Carangidae, Sparidae, Haemulidae and Scombridae. Larvae of all these families were present during the current study. The monospecific Pomatomidae were represented by *Pomatomus saltatrix* (shad), and is the most commonly caught fish by KZN's shore anglers (Beckley, 1993; Dunlop and Mann, 2012); their larvae are known to be associated with shelf waters (Beckley, 1993; Kendall and Walford, 1979). This species, and others such as some sciaenids and sparids, are known for their annual spawning migration northwards to KZN waters in winter (van der Elst, 1988; Hutchings et al., 2003). It was originally believed that shad spawned in the Agulhas Current as a means of southward transport of their larvae (Thresher, 1984). However, Beckley and Connell (1996), found shad to be summer spawners on the shelf, south of Durban. They were indeed more abundant in the Wet season during the present study and, excluding a single Deep-slope specimen in the Agulhas Current, were shelf-associated (Table 4), corroborating the finding of Beckley and Connell (1996).

Sciaenids are another family which has species known to undergo spawning migration to KZN Bight waters in winter (van der Elst, 1988; Hutchings et al., 2003). In support of this, in

the present study the majority of these larvae were caught in the Dry (winter) season in all three areas. Sciaenid larvae have also been reported to occur in the Dry season off the west coast of Brazil Nonaka et al. (2000). Known for predominance in KZN trawl fisheries (Fennessy, 1994) sciaenids were expected to be prominent in this study, similarly to what was found by Beckley (1993). However, they were largely restricted to the shelf zones with just 11 of the 65 individuals captured over the Mid- and Deep-slope. *Atractoscion aequidens* (geelbek) larvae commonly occur along our coastline (Tilney and Buxton, 1994; Wood, 1999; Beckley, 1993) and may be the more numerous of the three sciaenid taxa noted in the present study. Two other possible taxa are *Argyrosomus* and *Umbrina*, although Fennessy, (1994) reported other sciaenids (*Otolithes* and *Johnius*) to be abundant in the northern part of the KZN Bight.

A similar spawning migration, the well-known sardine run (Family Clupeidae) up to the east coast takes place in the Dry season (Beckley and Hewitson, 1994; Connell, 2010). The migration to KZN is a fundamental component of the life history of this sardine population (Beckley, 1998). In the study of the Durban seine net fishery, Clupeidae (*Sardinops sagax*) were third highest in abundance (Beckley and Fennessy, 1996). Larvae of the family Clupeidae were also present during the 1990/1 larval survey, however in the present study no clupeid larvae were sampled. This is surprising given their prominence in other studies. The dynamic nature of larval assemblages which are at the mercy of oceanographic phenomena can result in non-sampling of expected taxa. Thus, it is possible that *Sardinops* larvae were present during the Dry season survey, but were not encountered by the net. It is also possible that the survey was conducted too early in the run and spawning had not yet occurred. It has also been observed that, increasingly, the sardine run has reduced its northward extent (Fréon et al., 2010), which may have accounted for the absence of these larvae in the present study.

### ***Resident fishes***

A review by van der Elst et al. (2005) lists five main groups of endemic fishes off eastern South Africa. These include the family Sparidae (van der Elst et al., 2005), four taxa of which were encountered during the present study. Beckley (1993) described the high abundance of sparid larvae, chiefly represented by *Pagellus natalensis* (Natal Pandora) on the shelf. In the present study, the larva Sparid D was particularly prominent and proved to be *P. natalensis* (confirmed by Dr A. Connell pers. comm., 2014). Fennessy (in press) reported *P. natalensis* to be the most commonly trawled demersal fish in the Bight. Another characteristic sparid of the east coast of South Africa is *Diplodus capensis* (blacktail; denoted in this study as Sparid

A). During this study just seven blacktail larvae were recorded, largely in the Wet season and surprisingly only over the slope zones. However, the peak of spawning activity of this sparid (July to September; Joubert, 1981) occurs outside the sampling period, which may explain their low occurrence. Harris et al. (1999) found Sparidae larvae to be most abundant in the surf zone (which was not sampled in the present study) and therefore this family may be more prominent in the larvae of KZN Bight waters than is portrayed here.

Two carangid taxa were identified in the present study (Appendix II), one of which was numerically dominant, comprising 43 specimens which were largely sampled over the shelf. These larvae are likely to be either *Trachurus sp.* or *Decapterus sp.*, which are common, small, shoaling fishes in south-east African shelf waters (Smith and Heemstra, 1995), and were also reported as dominant larvae by Beckley (1993). The other carangid taxon in the present study comprised just three individuals which were all sampled over the Deep-slope, two off Durban and one off Richards Bay.

*Pomadourys olivaceus* of the family Haemulidae are extremely common in the study area (Fennessy, in press). Characteristic of soft sediment habitats, larvae in the present study are likely to be this species, similar to the Beckley (1993) study which associated them with shelf waters in 1990/1.

Scombridae (tuna and mackerel) larvae were characteristic of samples in the Wet season in the present study, similar to that found by Beckley (1993). In the present study two taxa were observed; both Scombrid A and B were large-mouthed larvae and belonged to taxa of the larger oceanic Scombridae (Leis and Carson-Ewart, 2000). Scombrid B was found exclusively over the Deep-slope, similar to what was observed by Beckley (1993). However, Scombrid A, the more abundant of the two taxa, occurred across all depth zones and areas.

#### ***Other noteworthy taxa***

While some of the findings in this study resonate with the limited other larval fish studies of South Africa and similar latitudes, as well as what is known of fish assemblages from fisheries studies in the study area, there were some notable occurrences. Larvae of the coral-associated Chaetodontidae, Labridae and Acanthuridae were surprisingly found across all depth-zones during the present study. Also, described by Beckley (1993) as deep-slope larvae, they likely originated from waters to the north of the Bight, and were dispersed in KZN Bight shelf waters, further portraying the great influence of the Agulhas Current on larval fish composition of the KZN Bight. Furthermore, as previously described, members of

these families have a specialized long lived larval phase that is well adapted for a relatively long pelagic existence before settlement onto reefs (Leis and Rennis, 1983; Victor, 1986; Leis, 1989). Therefore, fishes with long larval durations could in fact be expected to disperse over great areas and hence occur over a wider area, including places far away from their adult spawning grounds/habitats/depths.

Around 70% of the families encountered as larvae in this study are demersal as adult fishes (Table 4). Among these demersal taxa, four families in particular, Clinidae, Mullidae, Gobiidae and Bothidae were noteworthy in this study. Not recorded by Beckley (1993) or Connell (2007), the families Clinidae and Gobiidae also contain many fishes endemic to eastern South Africa (van der Elst et al., 2005). Clinids (klipfishes) are viviparous shallow water taxa (Smith and Heemstra, 1995) and therefore it is surprising that these larvae were encountered in this study. However, these larvae were only found in one sample on the Durban Shelf. Gobiidae (gobies) in this study were mostly encountered in the Wet season in the Thukela area. Two taxa were observed (Appendix II), Gobiid A being found exclusively in the Shelf zone. Adults of the other two families, Bothidae and Mullidae, are bottom dwellers inhabiting continental shelves of tropical and subtropical areas (Smith and Heemstra, 1995). It is therefore interesting that the bothids (left-eye flounders) were abundant and characteristic of the Deep-slope in the present study. Connell (2007) reports an unidentified Bothid most abundant in off-shore samples off Park Rynie south of Durban. Several bothid species have been recorded in trawl catches on the east coast of South Africa; *Laeops pectoralis*, *L. nigromaculatus* and *Chascanopsetta lugubris* (Persad, 2005; Fennessy et al., in press). The trawling grounds that these species have been reported from fall within the Mid-slope depth range of the current study. Mullidae (goatfishes) are common shelf fishes (Fennessy, in press), but were characteristic of the Deep-slope in the present study, although their larvae were also present in the other depth zones. Connell (2007) reported two morphotypes. One, *Upeneus guttatus*, displays preference for shallower waters similar to that of Mullid A in the current study. The other morphotype, a combination of *Parupeneus fraserorum* and *P. rubescens*, reported by Connell (2007) to have a slight preference for off-shore waters, is similar to Mullid B and C in the present study.

From the above taxon analysis it is evident that there is some exchange between shallow coastal waters and deep oceanic waters (in both directions), which indicates that it is a partially open system. This is evidenced by the ubiquitous families such as Myctophidae. Myctophidae larvae close in-shore can be ascribed to shoreward intrusions of the Agulhas

Current surface water (Beckley and van Ballegooyen, 1992; Olivar and Beckley, 1994). However, these are exceptions rather than the rule, as there is also some degree of retention (either oceanographically or biologically mediated) to ensure that these fishes persist. For example, larvae of the migratory Pomatomidae and Sciaenidae are retained in shallow waters which are utilized as nursery grounds (Beckley, 1993; Hutchings et al., 2003). Demersal resident taxa such as Leiognathidae, Tripterygiidae and Callionymidae were also relatively more abundant in Shelf waters while Myctophidae (although ubiquitous in all zones), Engraulidae and Scombridae featured in deeper Agulhas Current waters.

#### **5.4 Distribution of fish larvae in Wet and Dry seasons**

Figure 22 shows the graphically summarized results of Permanova in the present study, supporting the distinct larval fish assemblages in the three regions during the Wet season, compared to the less well defined assemblages in different regions during the Dry season. In the Wet season SST was best related to larval fish distribution which suggests that assemblage was mediated by the Agulhas Current. This postulation is supported by the homogeneity across all Deep-slope Zones coinciding with the Agulhas Current influenced Deep-slope waters. Intrusion of Agulhas Current waters onto the Richards Bay Mid-slope was suggested by the similarity in SST and explains the correspondence of larval fish assemblages there with those over the wider Deep-slope zones. Richards Bay is situated just below a very narrow section of shelf where the Agulhas current comes closest (~5 km) to the shore along the KZN coast (Bang et al., 1978). By a similar logic the widening of the shelf (forming the Bight) is such that the Agulhas Current is forced off-shore even in the Durban area where the shelf width tapers, and as a result, larvae of the Durban Mid-slope conformed to a “shelf” assemblage (Figure 22). A comparatively unique larval fish assemblage occurred in Richards Bay Shelf waters in the Wet season that was different from that occurring in Shelf waters off Thukela and Durban. This assemblage was characterised by a relatively higher abundance of Bregmacerotid A larvae.

The Dry season displayed less spatial structuring of larval assemblages (Figure 22). Fish larvae were homogenous across the three delineated areas (Durban, Thukela and Richards Bay). The effect of the Agulhas Current on temperature, while less prominent, was still evident off-shore (Figure 9a). While fish larvae were found to correlate with salinity more than temperature (Figure 19), differences were marginal. Salinity was slightly higher over the shelf while temperatures were warmer off-shore. Again, larvae of “shelf” waters differed from “Agulhas” (Deep-slope) waters. At the time of sampling the Mid-slope appeared to be

an intermediate zone with a gradual change in taxa from shelf to Agulhas waters, as might be anticipated. This transition is mirrored by a change from shallow water to deep-water taxa. Shallow water leiognathids, sciaenids and tripterygiids were characteristic of the shelf waters while deep water phosichthyids, several myctophids, scombrids and bathylagids featured in off-shelf samples.

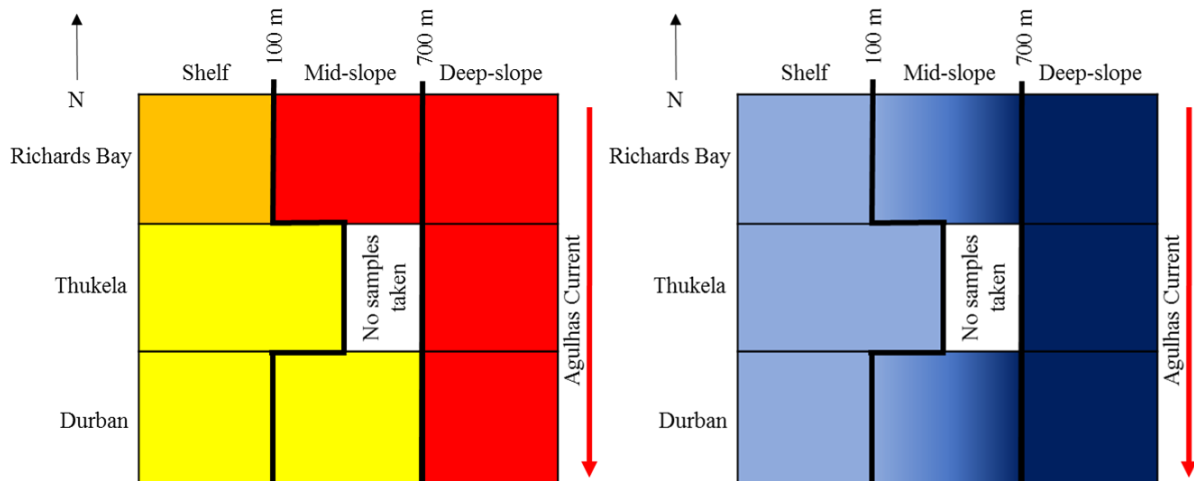


Figure 22. Larval fish patterns within the conceptual framework of the KwaZulu-Natal Bight, 2010. Different colours denote different assemblages. Left = Wet season, right = Dry season.

Water mass history is considered to be one of the most important factors in structuring large-scale larval fish assemblages (Cowen et al., 1993). With the uncharacteristic absence of upwelling and eddy systems during the present study it is perhaps not surprising that Zooplankton dry weight (a proxy for productivity) and Chlorophyll-*a* concentration did not appear influential in the structuring of larval fish assemblages.

It has long been known that the oceanography of the east coast of South Africa has a great influence on the marine biological communities (McNae, 1962; Heydorn et al., 1977). Larval fish assemblages studied here showed significant structure and spatial variability which were attributed to the main oceanographic features, and the Agulhas Current played a particularly significant role in this. Heydorn et al. (1977) detected three influential processes through which the oceanography might affect the biological communities, the first being that of temperature-induced responses, whether through seasonal differences or the difference between warmer Agulhas Current and cooler inner shelf waters. There is consistency with this observed in the present study, with SST being the most reliable abiotic predictor of the larval fish communities. Regarding season, this is expected although not necessarily related

to temperature directly, but more likely via the biology of the species, especially their spawning periodicity. Spatially-mediated effects on larval assemblages may be an artefact of the location of spawning areas to some extent, but also may reflect the influence of different water masses, e.g. Agulhas vs coastal/shelf water.

The second influencing process detected by Heydorn et al. (1977) is that through utilization of current transport mechanisms. Connectivity with marine waters further afield and neighbouring coastal systems is suggested in the present study through the presence of larvae of several families that include migratory species (e.g. Pomatomidae and Sciaenidae). However, it is difficult to ascertain connectivity with other locations without better taxonomic resolution. The third influencing process by oceanographic features is through larval retention mechanisms and marine/estuarine interaction (Heydorn et al., 1977). Some estuarine associations are also evidenced by larval studies within estuaries (Harris et al., 2001). While there is some evidence of retention within water masses in the current study, further studies are required to ascertain definitive mechanisms which permit local fish communities to persist.

The environmental factors examined explained a large part of the fitted variation but only a limited amount of the total explained variation in the testing of the conceptual model. This is a likely consequence of the dynamic oceanographic environment (Roberts and Nieuwenhuys, in press). Historical studies have shown that the Agulhas Current is present 80% of the time off Durban, and that its in-shore boundary is found, on average, some 40 km off-shore (minimum 10 km; maximum 100 km) but this is highly variable on a daily time-scale (Schumann, 1981). Gründlingh (1980) showed that in-shore currents in the northern Bight reverse regularly, especially with the emergence and passing of eddies. Schumann (1981) found that the alongshore wind component plays a major role in the circulation dynamics — but acknowledged that topography and the flow from the Agulhas Current also serve to produce markedly different regimes. Roberts and Nieuwenhuys (in press) note that, at times, the entire KZN shelf can be flooded with Agulhas water. Thus, the spatial and seasonal influences on larval patterns may be disrupted on shorter time scales than examined here.

## **5.5 Future studies**

Perhaps the most obvious requirement of future studies would be improvement of our taxonomic knowledge of local species. This is a basic requirement of understanding fish biology, and is especially important in the case of species of economic or conservation

significance. Recent advances in genetic techniques would facilitate greater taxonomic resolution for future studies. Repeated sampling at each site at varying times of day would allow for verification of the apparent non-significant role of diurnal migration observed on the KZN Bight in this study. Discrete sampling at multiple depths would also shed some light on vertical movement of fish larvae in the water column; surveys at different times of the year, and over several years, would better account for the role of spawning seasonality on larval abundance and seasonality, as well as interannual variability.

On a larger spatial scale, it has been hypothesized that there is biological connectivity with communities of southern Madagascar driven by regular eddies, which move across the Mozambique Channel. This connectivity is currently being examined as part of the multi-disciplinary programme, the ACEP “Suitcase Project” (Fennessy, 2014). Preliminary results presented at the recent South African Marine Science Symposium show coastal fish eggs and larvae to be abundant on the Madagascan shelf as well as in mid-channel eddies (Ockhuis et al., 2014). Similarly, offshore larval connectivity with Mozambique is uncertain due to a lack of such studies there.

Consideration must be given to other potential environmental drivers such as the depth of the mixed layer as discussed. Another aspect for consideration is active selection of settlement habitats by fish larvae and their proximity to bottom substrate. For example, a study by Myberg and Fuiman (2002) indicated that tripterygiid larvae aggregate towards reefs by using auditory cues. Other unmeasured variables are predator presence, spawning time, history of water masses (e.g. previous upwelling events). All of these factors could be taken into consideration during planning of future research.

## **5.6 Conclusion**

In summary, previous larval studies in the KZN Bight system are limited. The ACEP II “Ecosystem functioning of the KZN Bight” project afforded a unique opportunity to study the relatively poorly-known larvae from off-shore. There were three aims in this study: 1) To characterize the assemblage of larval fishes present off central KZN, 2) to determine the potential role of physico-chemical characteristics of the water column in the abundance and distribution of larval fishes off central KZN and 3) to compare observed patterns in larval fish assemblages to available information on the larval and adult fish of KZN and elsewhere. The original aims of the thesis were all achieved to varying degrees.

To summarise the results associated with these aims:

1. Larval fishes were largely those of families which are widespread in the Indo-West-Pacific region, and were dominated by demersal taxa.
2. Larval distribution displayed strong seasonality, due to the influence of local oceanography, but probably also mediated by varying spawning seasons of the adults. Samples collected over the Deep-slope were influenced by the encroaching Agulhas Current which is characterised by increased SST and surface salinity. This difference in Agulhas and shelf water masses was reflected in the larval assemblages, with deep water taxa synonymous with Agulhas waters and shallow water taxa collected where the shelf is wider. This influence was more apparent in the Wet season. During the Dry season, larval fish patterns were more homogenous and structured along a gradient with distance off-shore and proximity to the Agulhas Current.
3. Comparisons with previous larval fish surveys of the KZN Bight and elsewhere have been made, although limited comparable studies are available. Notable was the occurrence in abundance of several families which are not characteristic of fisheries in the region, evidence that the biodiversity of fishes in the KZN Bight has been under-sampled, particularly over soft sediments. Recent oceanographic studies have re-emphasized the dynamic and turbulent nature of KZN Bight waters. This study has allowed greater understanding of the roles of these forces on fish larvae, but much remains to be learnt.

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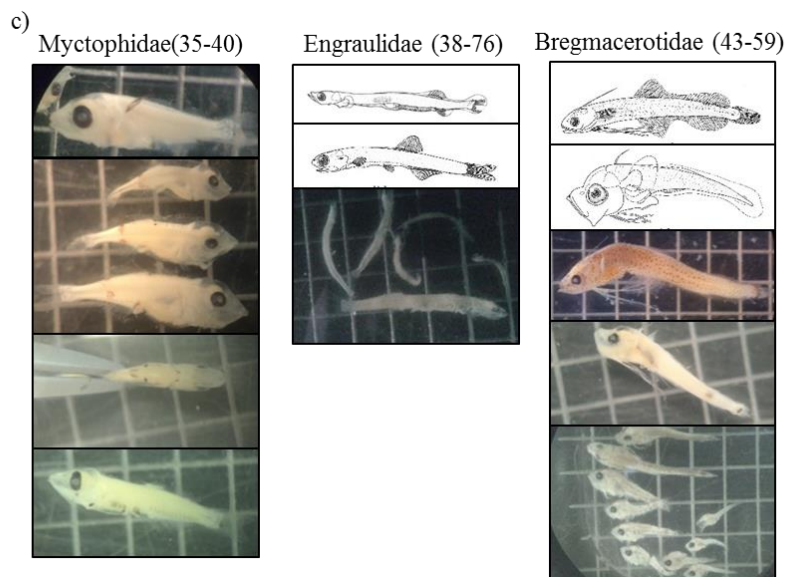
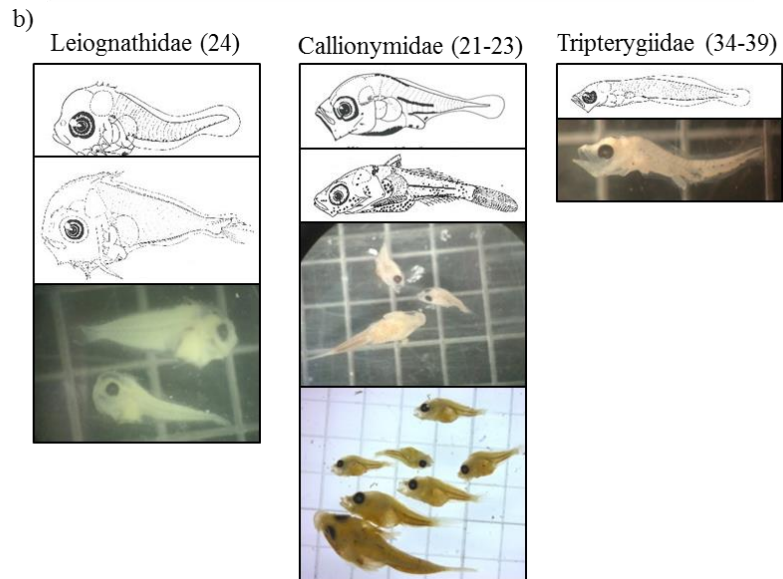
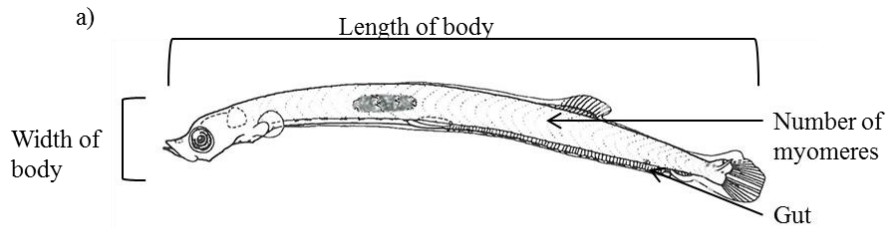
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## APPENDICES

Appendix I. a) Diagram of a typical clupeoid fish larva showing the initial characteristics to be ascertained during identification together with photographs and diagrams of b) the most abundant and c) the most ubiquitous larvae encountered during the current study. Diagrams taken from Leis and Carson-Ewart (2000). Number of myomeres for each family is presented in parentheses.



Appendix II. Mean densities of larval fish families with multiple taxa recorded in the KwaZulu-Natal Bight during the Wet and Dry seasons, 2010.

Family	Taxa	Wet season		Dry season	
		Mean density (larvae/100m <sup>3</sup> )	% Occurrence	Mean density (larvae/100m <sup>3</sup> )	% Occurrence
Apogonidae	Apogonid A	5.15	3.92	-	-
	Apogonid B	-	-	2.76	1.82
Balistidae	Balistid A	3.25	17.65	-	-
	Balistid B	3.24	1.96	4.41	1.82
Bregmacerotidae	Bregmacerotid A	15.70	27.45	2.68	27.27
	Bregmacerotid B	5.32	23.53	3.84	40
Carangidae	Carangid A	5.32	29.41	3.88	20
	Carangid B	4.00	3.92	-	-
Cynoglossidae	Cynoglossid A	9.35	7.84	3.60	5.45
	Cynoglossid B	1.84	1.96	-	-
	Cynoglossid C	9.93	5.88	1.88	3.64
Engraulidae	Engraulid A	7.07	29.41	6.28	21.82
	Engraulid B	5.60	27.45	7.11	47.27
Gobiidae	Gobiid A	9.63	3.92	1.48	1.82
	Gobiid B	3.25	15.69	2.00	3.64

CONT.		Wet season		Dry season	
Family	Taxa	Mean density (larvae/100m <sup>3</sup> )	% Occurrence	Mean density (larvae/100m <sup>3</sup> )	% Occurrence
Labridae					
	Labrid B	6.67	13.73	1.92	9.09
	Labrid C	11.65	3.92	-	-
	Labrid D	9.40	7.84	1.90	5.45
Lutjanidae					
	Lutjanid A	3.77	15.69	1.89	3.64
	Lutjanid B	-	-	1.28	7.27
Microdesmidae					
	Microdesmid A	1.70	3.92	-	-
	Microdesmid B	7.17	1.96	-	-
Mullidae					
	Mullid A	8.97	19.61	2.85	10.91
	Mullid B	5.55	45.10	4.35	27.27
	Mullid C	-	-	15.52	1.82
Myctophidae					
	Myctophid A	3.26	11.76	5.95	30.91
	Myctophid B	2.77	19.61	5.13	23.64
	Myctophid C	0.78	1.96	1.34	1.82
	Myctophid D	8.65	25.49	5.36	32.73
	Myctophid E	5.20	3.92	2.65	20
	Myctophid F	9.33	15.69	4.44	36.36
	Myctophid G	2.06	9.80	2.81	7.27
	Myctophid H	1.78	1.96	3.39	1.82
	Myctophid I	-	-	2.97	1.82
	Myctophid J	2.17	3.92	1.25	5.45

CONT.		Wet season		Dry season	
Family	Taxa	Mean density (larvae/100m <sup>3</sup> )	% Occurrence	Mean density (larvae/100m <sup>3</sup> )	% Occurrence
Nomeidae	Nomeid A	1.84	1.96	1.32	3.64
	Nomeid B	1.29	1.96	-	-
Paralichthyidae	Paralichthyid A	4.66	11.76	3.14	5.45
	Paralichthyid B	5.71	7.84	1.34	3.64
Phosichthyidae	Phosichthyid A	1.41	5.88	1.77	5.45
	Phosichthyid B	3.34	35.29	4.18	38.18
Pomacentridae	Pomacentrid A	2.71	25.49	2.26	16.36
	Pomacentrid B	9.01	1.96	-	-
	Pomacentrid C	1.63	1.96	1.15	3.64
Pseudochromidae	Psuedochromid A	4.05	5.88	-	-
	Psuedochromid B	-	-	5.29	5.45
Sciaenidae	Sciaenid A	4.61	3.92	6.98	9.09
	Sciaenid B	-	-	2.10	5.45
	Sciaenid C	3.72	9.80	10.24	20
Scombridae	Scombrid A	7.84	56.86	2.91	20
	Scombrid B	2.63	7.84	3.97	5.45
Sparidae	Sparid A ( <i>Diplodus capensis</i> )	2.66	7.84	2.85	1.82

CONT.		Wet season		Dry season	
Family	Taxa	Mean density (larvae/100m <sup>3</sup> )	% Occurrence	Mean density (larvae/100m <sup>3</sup> )	% Occurrence
	Sparid B	-	-	15.35	1.82
	Sparid C	3.66	1.96	-	-
	Sparid D ( <i>Pagellus natalensis</i> )	-	-	5.63	9.09
Synodontidae					
	Synodontid A	5.85	31.37	2.87	27.27
	Synodontid B	3.57	1.96	23.17	10.91
	Synodontid C	4.32	3.92	18.45	5.45
Triglidae					
	Triglid A	13.37	15.69	4.90	18.18
	Triglid B	-	-	2.40	1.82
	Triglid C	5.21	21.57	1.87	9.09