MESOSCALE ALONGSHORE AND CROSS-SHORE TRANSPORT AND SETTLEMENT OF INVERTEBRATE LARVAE ON THE SOUTH EAST COAST OF SOUTH AFRICA

THESIS SUBMITTED IN FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTERS IN SCIENCE

OF RHODES UNIVERSITY

BY

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DECEMBER 2018

ABSTRACT

Pelagic larval stages of most marine benthic species are important in maintaining coastal populations of adults. Several physio-chemical factors such as currents, winds, larval behaviour and time have an influence on the dispersal and transport of larvae to the adult habitat but their role is however still poorly understood. The aim of this study was to investigate the alongshore and cross-shore transport and temporal delivery of invertebrate larvae at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) along the south east coast of Eastern Cape, South Africa. Larval distribution of several taxa was determined during two sampling periods, by collecting water samples at nearshore line transects (3 distances: 900m, 1500m and 2400m – perpendicular to the shore) and at three depths (surface, thermocline/middle, bottom), which ranged from 15m (inshore) to 50m (offshore). Physical properties (current speed and direction, dissolved oxygen, fluorescence, turbidity, temperature, salinity, pH, pressure, density and conductivity) were measured and coupled in order to further understand larval distribution. The larvae were analysed as both total abundance and separately as the abundances of a variety of taxa which were: *Perna perna*, *Mytilus galloprovincialis*, oysters, early and late nauplii and cyprids. Larval settlement and recruitment on the rocky shores were measured by monthly deployment and collection of 20 (10 each for barnacles and mussels) artificial collectors at each site, which were preserved in ethanol or frozen for further processing. Multiple Permutational Multivariate Analysis of Variance (PERMANOVA) analyses were used to test the effects of site, depth and distance from the shore for the nearshore larvae (taxa analysed separately). In addition, a distance based linear model (distLM) was performed to analyse the relationship between the total larval abundance and the above mentioned physical variables. Multiple two-way analyses of variance (ANOVA) were performed to test the effects of months and sites on the settlement and recruitment of the larvae (*P. perna*, *M. galloprovincialis*, other bivalves, cyprids and juvenile barnacles) arriving on the shore.

For the nearshore larval distribution, results from the PERMANOVAs revealed that most taxa showed a significant site and depth interactions with the exception of ‘early nauplii’ taxon. Also nearly all taxa were found within the thermocline, besides ‘oyster’ and ‘cyprids’ which were located at thermocline or bottom. Larvae were also located at variable distances from the shore, with most occurring at the offshore stations. Furthermore, there was a geographical separation of larval abundance according to sites, with most larvae located at Cannon Rocks and Kenton on Sea and least at Schoenmakerskop and Cape St Francis. For the settlement and

recruitment, most taxa showed a seasonal trend, with the highest abundance of settlers and recruits expectedly appearing during the summer months of the sampling period. Additionally there was a site effect for most taxa (*P. perna*, *M. galloprovincialis*, other bivalves and juvenile barnacles), where settlers and recruits were mostly found at Cannon Rocks. Significant differences in abundance of settlers and recruits amongst the four sites indicate spatial and temporal variability for the targeted 180km stretch of coast.

Overall for this study, taxon and ontogenetic stage of larvae were important in the distribution and abundance of larvae. Throughout the time frame of nearshore and intertidal sampling, Cannon Rocks consistently resulted as a 'hot spot' for larval abundance, settlement and recruitment, while a broad west to east separation was also observed. These results hence highlight that within this stretch of c.180km coast, time, taxon, ontogeny and post-settlement factors influence early dynamics of benthic populations.

ACKNOWLEDGEMENTS

All glory and honour given to the Almighty and Everlasting God. If it was not for Him, I would have never been where I am today, and for that He deserves all the praise!

A special word of appreciation goes to my parents (Andile Dyantyi and Pamela Dyantyi) and family, your love and support while developing my career in the South African Institute for Aquatic Biodiversity (SAIAB) is simply immeasurable. I could have not done this without you. I would like to acknowledge and thank my supervisor, Dr Francesca Porri, for being such a vibrant, enthusiastic and wonderful person. I have never seen such passion for marine biology and I am truly inspired and honoured to have been a product of your hands. You consistently believed in me and you continued to push me till the end. I also want to thank my co-supervisor, Prof Christopher McQuaid, who is such an inspiration in the world of science. Your words of encouragement, advice, jokes and assistance will forever be remembered.

To my partner in crime, Afika Njwaxu, your love, support, advice and encouragement is deeply appreciated. You have been with me through the good times and the bad times. You have seen me grow and you have added fire to my spirit of science and the completion of my MSc would have never been possible without you.

This project would not have been possible without funding and in that regard I thank the National Research Foundation (NRF), African Coelacanth Ecosystem Programme (ACEP) and SAIAB for funding and supporting me for my MSc. Finally I would like to also extend my gratitude to the following people who assisted me with data collection during field work of this research project: Sandisiwe Mafanya, Zinzi Somana, Siseko Benya, Martinus Scheepers, Abongile Tsotsi, Ryan Palmer, Koos Smith, Paula Marchand, Jaqui Trassierra, Olwethu Duna and Christian Schultz, Matthew, Nick Riddin, Emily Moxham, Carlota Fernández Muńiz, Sethu Mnqotho and Ncumisa Matam. The endless hours of mining for PVC plates, getting soaked by the waves at the rocky shores, sorting samples in the lab and being sea sick on the boat will be forever remembered, appreciated and laughed at, as they will be used as a learning lesson for future generations.

Contents

CHAPTER 1

GENERAL INTRODUCTION

1.1 Degree of coupling and uncoupling of larval dispersal, settlement and recruitment

Most marine invertebrate species have a pelagic larval phase, which is an important determinant of adult benthic populations (Thorson, 1950; Underwood and Fairweather, 1989, Siegel *et al*., 2008; Gallego *et al*, 2017). Larval connectivity entails the exchange of propagules between two geographically separated populations (Pineda *et al*., 2007). This definition also encompasses larval dispersal and transport, where larvae are transported from the natal source of reproduction to the settlement site where they will recruit into the adult population (Cowen and Sponaugle, 2009). Up until the past 40 years, marine populations have been regarded as demographically open systems, in which replenishment of local benthic populations was dependant on propagules that potentially came from distant sources (Roughgarden *et al*., 1985; Scheltema, 1986; Hughes, 1990; Caley *et al*., 1996; Eble *et al*., 2010). In most cases, openness of populations was estimated by the physical dominant mechanisms that mostly influence the transport of larvae (Caley *et al*., 1996) In addition, the duration of the larval phase of invertebrates was inferred to be correlated with dispersal distance, the longer the time spent in the pelagic, the greater the distance of transport (Shanks *et al*., 2003; Shanks, 2009), although this was not a general rule, as pelagic larval duration can be negatively correlated with larval dispersal (Weersing and Toonen, 2009). It must, be noted that while larval duration and ocean hydrodynamics are important factors influencing the transport of larvae in the water column, they are not the only determinants of dispersal (Cowen *et al*., 2007).

Increasingly, marine systems are viewed as 'closed' systems and there are several factors responsible for this reclassification. Although larvae can be passively transported, they possess active swimming capabilities (Chia *et al*., 1984) and can alter their vertical position in the water column (Hunt and Scheibling, 1996, Dobretsov and Miron, 2001; Knights *et al*., 2006 Weidberg *et al*., 2015). Larvae can also delay metamorphosis if suitable substrata are not encountered during pre-competency/competency (Pechenik *et al*., 1998). Further delay in metamorphosis leads to a higher risk in becoming sink larvae lost to sea (Porri *et al*., 2014). There is more danger of being influenced by several small to large scale features in the sea. Potentially larvae can become source for distant populations. Oceanographic features are usually classified by scale, whereby small-scale can range from 100s of meters to a 10s kilometres; mesoscale can be 100s of kilometres and whilst large can be more around 100s to 1000s of kilometres. Though large scale oceanographic features, such as the Benguela Current can influence connectivity, there are mesoscale and small scale features that have a role in the

dispersal and transport of larvae including (but not limited to): meanders, eddies, coastal boundaries, wind, fronts (and associated internal waves), surf zone circulation (Clancy and Epifanio, 1989; Pineda, 1991; Largier 2003; Queiroga *et al*., 2007; Navarrete *et al*., 2015; Weidberg *et al*., 2018). In addition to such biophysical factors, studies have found that there is often retention of larvae in nearshore waters, which supports the idea of marine populations as being 'closed' (Graham and Largier, 1997; Morgan and Fisher, 2010; Porri *et al*., 2014; Weidberg *et al*., 2015). Understanding how biological and hydrographic processes such as the ones mentioned above influence larval dispersal will therefore lead to a better understanding of possible coupling and uncoupling of larvae, settlers and recruits (Cowen *et al*., 2007).

1.2 Larval dispersal and Marine Protected Areas

Marine Protected Areas or MPAs are clearly defined spaces used as a management tool to protect endangered species, ecosystem services, biodiversity, and marine/coastal habitats and ultimately conserve the functioning of ocean and coastal ecosystems (Jentoft *et al*., 2007, Ban *et al*., 2017). MPAs enhance marine resources by protecting source populations, which act as a source of larvae, by providing spill over to nearby areas (O'Leary *et al*., 2018). MPAs also serve to counteract the degradation of aquatic habitats and the over-exploitation of resources through anthropogenic activities such as mining and fishing respectively (Agardy, 2000). Where does the role of larval dispersal fit into MPAs? When designing and selecting an area that is designated as a MPA, there needs to be consideration of the larval transport over the relevant spatial scales as individual populations can act as either sinks (where larvae are lost to offshore waters) or sources of larvae and this can be highly variable from region to region (Jones, 2002). With most intertidal marine species having a dispersive stage (pelagic larval phase) in their life cycle, this makes management of resources difficult as larval dispersal, transport, settlement and recruitment is erratic, subject to several oceanic events, currents, fronts, upwelling and the like (Nickols *et al*., 2015). The concept is that MPAs can act as sources of propagules for other coastal areas to replenish stocks of marine organisms. If MPAs are to function well and conserve species, there is a need to know more about the scales (spatial and temporal) at which transport of larvae in the water column and settlement on the shore relate (Pineda *et al*., 2010).

Larval transport and delivery to the benthic zone is influenced by several mechanisms which still remain poorly understood in South Africa Since the majority of benthic organisms have a

pelagic larval stage, there is an inevitably strong interaction between physical oceanography and life history traits, which in turn most likely influences the spatial structure of adult populations. Settlement and post-settlement processes can further shape the final configurations of adult populations. It is therefore imperative to couple physical and biological processes in studies of larval dispersal, settlement and recruitment, so as to account for the effects of the offshore bio-physical as well as onshore settlement processes on the dynamics and structure of benthic populations The aim of this study was make a contribution to understand the degree of coupling between larvae in the water column and recruitment of benthic populations at the mesoscale level (200km) on the south east coast of South Africa. To assess larval recruitment coupling in the region, the abundance and distribution of the larvae of several intertidal taxa were measured in the nearshore waters. To further characterise and understand larval distribution patterns, physical drivers within the nearshore waters were also determined (Chapter 2). Additionally, to link larval abundance in the water to the adult populations in the benthic habitat, the temporal variability of larval delivery (settlement) was also estimated (Chapter 3). A final chapter (Chapter 4) involved a general discussion and comparison of onshore versus offshore larval densities to further establish the coupling of benthic populations.

CHAPTER 2

ALONGSHORE AND CROSS-SHORE TRANSPORT OF BENTHIC INVERTEBRATE LARVAE

2.1 Introduction

For marine organisms such as mussels and barnacles, the dispersal and transport of the pelagic larval phase have an influence on benthic populations (Pineda *et al* 2007). Dispersal includes all larval related processes from the source to the settlement sites, whilst larval transport involves the movement of larvae from one location to another while dispersed in the water column (Cowen and Sponaugle, 2009). Large scale physical mechanisms, such as the presence of boundary currents, upwelling and eddies can influence biological processes (such as behavioural response of larvae e.g. diel migration) and modulate small scale water dynamics in ways that enhance or suppress larval transport (Pineda *et al*., 2007). For example, Porri *et al*. (2014) described how the occurrence of solitary meanders, which have a leading and lagging end, can advect larvae offshore, contributing to larval transport and offshore sinks.

Upwelling is a process by which cold nutrient rich water from the bottom rises up to the surface layer in response to surface water that had been transported offshore by strong winds (Morgan *et al*., 2009). Upwelling is a physical process that has been extensively investigated worldwide for its effects on larval transport. Upwelling may potentially transport larvae offshore, increasing cross-shore transport (Menge *et al*., 2003). Additionally larvae of sea clams, *Spisula solidissima* and *Ensis directus*, have been found to be restricted below the thermocline during both upwelling and downwelling occurrences in North Carolina, USA, which affected cross-shore distribution as larvae were transported landward during upwelling and seaward during the downwelling (Shanks and Brink, 2005). In Chile, upwelling influences the offshore transport of larvae, however, cyclonic eddies in their leeward side can entrain the waters shoreward, reducing cross-shore transport (Hoffmann *et al*., 2012). Similarly, in Delaware Bay, USA, during the downwelling at fronts, larvae can concentrate below the pycnocline layer, aiding in nearshore retention (Clancy and Epifanio 1989). Though upwelling is a major physical driver of larval transport (both onshore and/or offshore) and delivery, however in some regions this is not the case as there are other dominant physical drivers such as surf zone hydrodynamics (see Shanks and Morgan, 2018). It must hence be noted that there are differences around regions of the world.

Regional to local spatial scale hydrodynamics, including nearshore oceanographic mechanisms, are also important determinants of larval transport (Pineda *et al.*, 2007). A shallow thermocline can create vertically sheared (change in speed and/or direction of water flow) environments that may restrict larval transport for species with diel vertical migration (Pineda *et al*., 2007). Recirculation of water in nearshore eddies can also act as a trap for propagules and therefore enhance local recruitment at particular locations (Largier 2003).

Coastal fronts are boundary layers that can have sharp temperature gradients on either horizontal side, which occur as a result of two converging water masses with different physio-chemical characteristics (Pineda, 1999). Converging water masses can carry larvae from both sides to this area, where buoyant and swimming larvae accumulate in the surface layer (Clancy and Epifanio, 1989), hence limiting their cross-shore dispersal (Woodsen *et al*., 2012). The coastal boundary layer is an interface between nearshore and offshore waters, which can have an alongshore flow caused by surface wind and alongshore pressure gradients (Nickols *et al*., 2012). The structure and size of coastal boundary layers depend on the shallowness of the water, bottom topography, wind forcing and stratification, making them distinct from other oceanic features (Churchill, 1985; Nickols *et al*., 2012). Flow speeds of water near the shore are generally slow and alongshore flows are also further slowed down by the shallow depth and bottom topography of the coastline, in addition, cross-shore flow can be limited by the proximity of the coastal boundary layer (Largier, 2003). This too can affect the transport of larvae. Once larvae have been transported offshore, they tend to be vulnerable to strong cross-shore and alongshore currents, which inevitably will transport larvae alongshore at great distances (Largier 2003).

Moving closer to shore, among other physical drivers of larval transport, wind forcing has a direct effect on water currents, through turbulence and wind-driven upwelling (Bertness *et al*., 1992; Morgan, 2014) and hence influences the nearshore distribution and transport of larvae (Morgan *et al*., 2009; Pfaff *et al*., 2011). Internal tidal bores cause upwelling by bringing up cold subsurface waters in a shoreward direction which in turn transport larvae towards nearshore populations (Pineda, 1991). Local cross-shore hydrodynamics operating at scales of hundreds of meters from the shore can also cause differential delivery of larvae to benthic sites (Porri *et al*., 2006; Rilov *et al*., 2008). Depending upon the characteristics of the nearshore environment of a region, surf zones can act as retention areas, where larvae are transported onshore by wind driven waves (Navarrete *et al*., 2015; Morgan *et al*., 2016). Within surf zones, surface waves transport larvae to adult sites by breaking near the shore (Pineda *et al*., 2007). Surf-zone turbulence can influence settlement by invoking transitioning (metamorphosis) of larvae to settle in suitable habitats and also give an indication that suitable substrata for settlement are nearby as hydrodynamics are different in nearshore waters as compared to offshore waters (Gaylord *et al*., 2013) Ultimately, larvae can perform swimming behaviour in the form of diel vertical migration through the water column which can alter offshore and

onshore dispersal as influenced by all the physical processes as discussed above (Hunt and Scheibling, 1996; Dobretsov and Miron, 2001; Knights *et al*., 2006; Adams *et al*., 2014; Weidberg *et al*., 2015). For example, early larvae (zoeae) of the crab *Hemigrapsus sanguineus* in Delaware Bay, USA, migrate to surface layers during ebb tides so as to be transported to the adjacent coastal areas for further ontogenic development (Cohen *et al*., 2015). The barnacle larvae, *Chthamalus* spp, and the larvae of the crab *Carcinus maenas*, actively migrate through the water column and accumulate in fronts (Franks, 1992; Weidberg *et al*., 2018) which act as retention zones, reducing offshore transport by upwelling (Queiroga *et al*., 2007).

The physical marine environment of the south-east coast of South Africa is mainly influenced by the western boundary Agulhas current which flows in a south west direction towards the pole, at a speed of around 2.5ms $^{-1}$ (Goshen and Schumann, 1994). The Agulhas Current closely follows the continental slope from Kwa-Zulu-Natal to the Eastern Cape and shows little divergence from its position for a large part of its length (Lutjeharms and Roberts, 1988). At about 34°S, south west of Port Elizabeth, where the continental shelf widens to form the Agulhas Bank (which is about 800km long and 270km wide), several large scale features such as meanders, Natal Pulses and eddies disrupt the flow of the current (Lutjeharms and Roberts, 1988, Jackson *et al*., 2012). These above features form on the landward edge of the Agulhas current where there are high velocity gradients (Lutjeharms, 1981; Jackson *et al*., 2012).

Algoa Bay is a temperate eastward facing bay with a maximum depth of approximately 73m and a width of about 80km, on the south east of South Africa (Harris, 1978; Pattrick and Strydom, 2008). Wind is the driving force of the surface layers in the nearshore regions of the bay, with south westerly winds dominating throughout the year, however north easterly winds do occur during the summer period (Roberts, 2010). There is a small amount of freshwater input in the region from the rivers within the bay, such as the Sundays River and Swartkops River; this is likely to increase during floods (Schumann *et al*., 2005), but is largely negligible. In and around the Algoa Bay, the region is susceptible to wind driven upwelling, which brings up cold nutrient rich water that enters the bay from Port Alfred and Cape Recife (east and west of Algoa Bay respectively, Lutjerharms *et al*., 2000; Roberts, 2010). The water is well mixed in the bay with no distinct thermocline due to upwelling (Goschen and Schumann, 1988). Several studies have been done in the region linking larval dispersal with physical processes in the nearshore environment. Studied taxa include the larvae of invertebrates such as mussels (McQuaid and Phillips, 2006; Porri *et al*., 2006; von der Meden *et al*., 2008), barnacles

(Weidberg *et al*., 2018), crabs (Du Preez and McLachlan, 1984, Pereyra Lago, 1993) ascidians (Pineda *et al*., 2012) and squid (Sauer *et al*., 1992) as well as the larvae of fish (Beckley, 1986; Pattrick and Strydom, 2008).

Extensive research on the effects of mesoscale oceanographic mechanisms on the distribution of larvae was recently carried out along the south coast of South Africa, where the highest abundances of mussel larvae were found within the nearshore waters (less than 4km from the coast; Porri *et al*., 2014; Weidberg *et al*., 2015). The present study follows a broad regional approach, with an investigation that focuses on the abundance and distribution of invertebrate larvae in the nearshore waters less than 3km offshore along a stretch of open coast, covering an alongshore and a cross-shore components. High spatial variability in larval abundances was expected among the four sites selected for this study, as larval distribution can vary among adjacent sites only a few km, or even metres apart (Porri *et al*., 2006; 2008). Physical variables were measured simultaneously to the collection of the biological data, to effectively understand the nearshore mechanisms that are involved in larval transport as these variables can affect the behaviour of larvae and the physiology (see Dekshenieks *et al*., 1996; Tapia *et al*., 2010).

2.2 Methods and Materials

2.2.1 Study site

Four study sites (all on the open coast) were selected along the south east coast of South Africa (Figure 2.1) namely: Kenton on Sea (33°41’58.06”S 26°40’45.19”E), Cannon Rocks (33°45’37.33”S 26°32’32.64”E), Schoenmakerskop (34°2’54.49”S 25°32’6.43”E) and Cape St Francis (34°12’50.51”S 24°49’8.36”E) covering a distance of 180km of coastline.

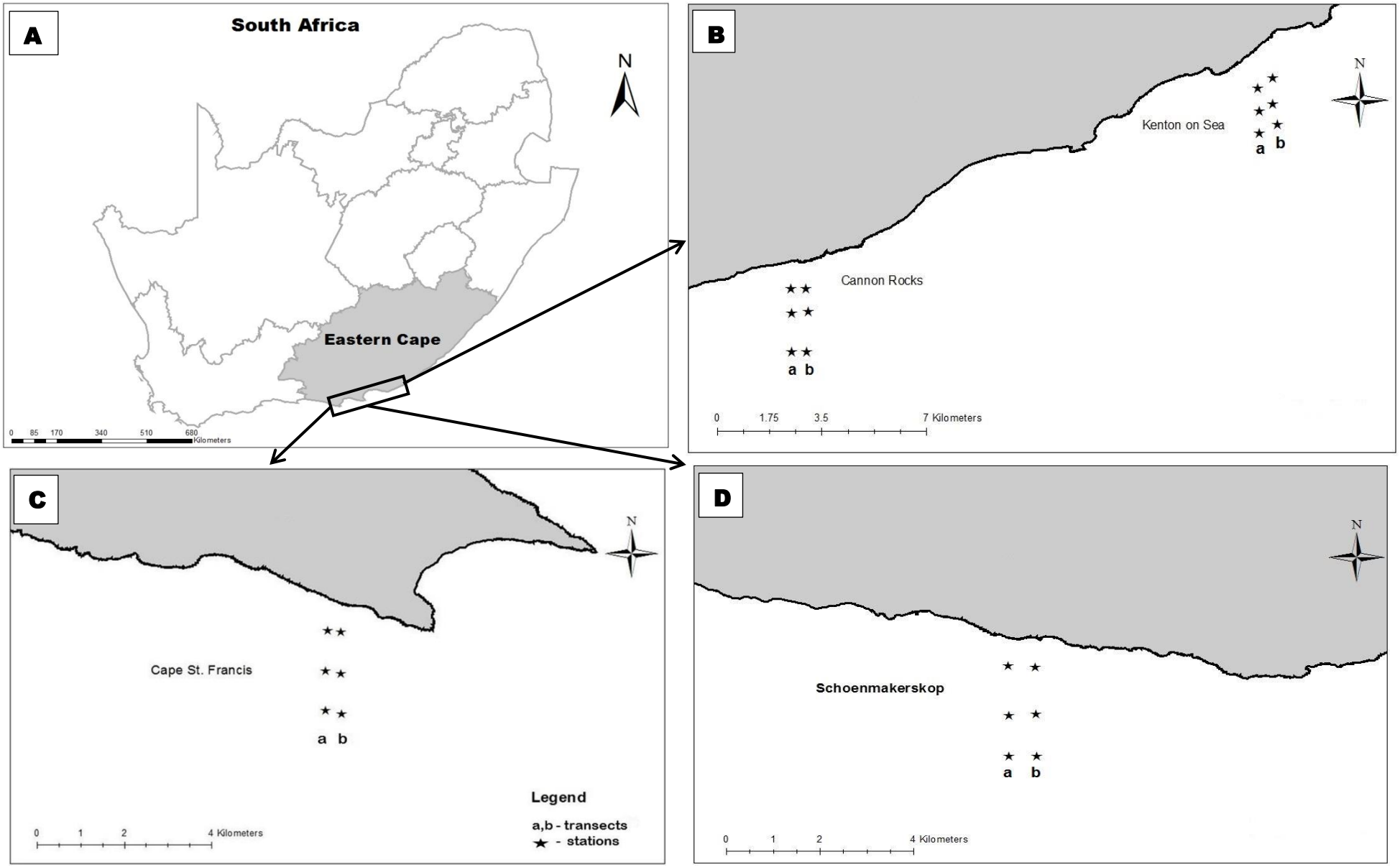

Figure 2.1: Maps of study area and sites; Map of South Africa and region, Eastern Cape (A), Kenton on Sea and Cannon Rocks (B), Cape St Francis (C) and Schoenmakerskop (D). Stars on the study sites indicate the sampling stations (onshore – offshore) for each transect (a, b).

2.2.2 Larval collection/experimental design

The study took place over two periods (conveniently referred to as Season one and Season two) during the reproductive seasons for benthic invertebrates in the region (Griffiths, 1977; Emmerson, 1994; van Erkom Schurink and Griffiths, 1991, Zardi *et al*., 2007). All sampling was carried out aboard the RV uKwabelana, a 13m research vessel. Sampling took place between 24th of February 2016 and the 17th of February 2017 (refer to Table 2.1 for exact dates of sampling). Although the design of this study aimed to sample all sites within the shortest time possible, the gaps between the sampling dates for each period were due to weather dependency and the fact that the study was part of a bigger project, focusing on ten sites along the south east coast of South Africa. At each site, the distribution of larvae in the water was determined by collecting nearshore water samples along two ('a' and 'b') parallel line transects, running in a seaward direction, perpendicular to the shore (i.e. n = 2). Each transect comprised three stations: onshore, midshore and offshore, with distances from the shore of 900m, 1500m and 2400m respectively. The samples were collected using a submersible 2.2 KC Denmark 23.580 plankton pump with a net of 60µm mesh. The pump was run for a fixed period of 7min which allowed the filtration of an average of 1400L, estimated from a flowmeter attached to the pump. The pump was deployed at three depths: surface (1m below the surface), mid/thermocline and bottom. The latter was sampled 5m above the seabed in order to reduce the amount of collected sand (Porri *et al*., 2014). The bottom depth at stations varied in depth across the four sites, ranging from 15m (inshore) to 50m (offshore). At the end of each run, the cod end (catch basket) of the pump was rinsed with filtered seawater into a 75µm sieve and the contents of the sieve were transferred into a labelled 250ml plastic jar and preserved in 100% ethanol. All jars were transported back to the laboratory for further analysis.

Table 2.1: Sampling dates of Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis for expected reproductive seasons, conveniently named "Season 1"and "Season 2".

Sampling Seasons	
Season 1	**Season 2**
Schoenmakerskop – 24/02/16	Schoenmakerskop – 24/10/16
Cape St Francis – 15/03/16	Cape St Francis – 21/11/16
Kenton on Sea – 14/04/16	Kenton on Sea – 09/02/17
Cannon Rocks – 20/04/16	Cannon Rocks – 17/02/17

2.2.3 Physical data collection

A moored Acoustic Doppler Current Profiler (ADCP) was used to collect *in situ* information on current speed (cm/s) and direction (degrees) at each station. A Seabird SBE 911 plus CTD (Conductivity, Temperature and Depth) with attached sensors (SBE 43 dissolved oxygen sensor, SBE 18 pH sensor and a WET Labs ECO-FLNTURT, chlorophyll and turbidity sensor) was lowered into the water at each station to measure the following physical variables: temperature (°C), salinity (g/kg), pH, dissolved oxygen (ml/l), pressure (db), turbidity (NTU), density (kg/m^3), fluorescence (mg/m^3) and conductivity (mS/cm).

2.2.4 Larval identification

All collected samples were processed using a Leica MZ75 stereoscopic dissecting microscope with an eye-piece micrometre. The larvae found in the samples were grouped into three main taxa: bivalves, decapods and barnacles.

Bivalves

Larvae of the two mussel species, *Perna perna* (indigenous) and *Mytilus galloprovincialis* (invasive), were identified following Bownes *et al.* (2008). The larvae of oysters and salt water clam, *Hiatella* spp., were identified after Waller (1981) and Booth (1983) respectively. 'D stage' larvae are the smallest pediveliger larval stage of all bivalves and were identified following Siddall (1980), though the author was describing the genus *Perna*. Three unidentified morphologically distinct bivalves were found: Bivalve spp. A, B and C. All other bivalves that could not be identified taxonomically were grouped together as 'other bivalves'.

Decapods

Decapod larvae were grouped into anomuran, brachyuran, pinnotherid, porcelanid zoeae and brachyuran megalopae using several references (Harvey *et al*, 2002; dos Santos and González-Gordillo, 2004; Chan *et al*., 2014).

Barnacles

Several naupliar stages of barnacle larvae were identified and thus, larvae were categorised into the following groups: early *Chthamalus dentatus* nauplii, late *Chthamalus dentatus* nauplii, *Octomeris angulosa* late nauplii, early balanid nauplii, late balanid nauplii (Sandison and Day, 1954; Achituv, 1986; Ross *et al*., 2003). There were two species of cyprids (Cyprid spp. A and B) that were unidentified.

2.2.5 Statistical analysis

Seven taxa were selected for analysis based on the occurrence of at least 10 individuals per station from each of the samples. Namely: total larval abundance (i.e. total collective larval abundance from all taxa), *Perna perna*, *Mytilus galloprovincialis*, oysters, barnacle early nauplii, barnacle late nauplii and cyprids. The data sets were incomplete as in each season there were samples that could not be collected due to either bad weather conditions at sea or malfunction of the plankton pump. During the first season (February – April 2016), the samples for the most offshore station (2400m) of transect 'a' for Cape St Francis could not be collected, due to bad weather conditions that developed during sampling. For this reason, analysis of "season one" was split into two. The first analysis included the factors: site (3 levels; excluding Cape St Francis), depth (3 levels) and distance (3 levels). A second analysis included the factors: site (4 levels), depth (3 levels) and distance (2 levels), with the offshore stations (2400m) removed. For "season two", the offshore 'bottom' sample of transect 'b' at Cannon Rocks was not collected due to pump malfunction. Because only one sample was missing however, this was corrected by performing an *a priori* hierarchical cluster analysis for the combined offshore stations of Cannon Rocks of transect 'a and b', which revealed clustering of samples that were similar in larval abundance and composition. Based on those results, which showed that samples from the thermocline (for both transect a and b) and bottom (for transect a) had a similarity of over 80%, the abundance of larvae for the missing sample at Cannon Rocks was interpolated by averaging the abundance of this thermocline/bottom cluster.

Multivariate and several univariate PERMANOVAs (Permutational Multivariate Analysis of Variance) were performed to test for significant effects among the three factors site (random), distance (fixed) and depth (fixed) (Anderson, 2003). Multivariate PERMANOVAs were based on 999 permutations using the Bray-Curtis resemblance matrix after square root transformation. Transformation was required to normalise the data and also to reduce the influence of very abundant species on the outcome. Univariate PERMANOVAs were also based on the same number of permutations using the Euclidean resemblance matrix after square root transformation. Pairwise tests were run for the significant factors and interactions between factors that were identified during the PERMANOVA tests. Since multiple tests for several taxa were performed, the Benjamini-Hochberg method for false discovery rates was used to reduce the possibility of type I errors (Benjamini *et al*., 2001; Table 2.2). Individual p-values from the PERMANOVAs of the seven taxa were arranged in order, from the smallest to the largest. The smallest p-value was ranked $i = 1$, which was followed by the next p-value, ranked as $i = 2$, etc. Each p-value was then compared to its own calculated Benjamini-Hochberg critical value $[(i/m)Q]$, where i was the rank, m the total number of tests, and Q the false rate discovery of 0.05. Starting off from the largest p-value (i.e. rank 147 = 0.969, Table 2.2) and working up the table, p-values were compared against their own calculated critical values. The largest p-value which was smaller or equal to its own critical value ($p \leq (i/m)Q$) was the cut off point for significance (in this case, the 47th ranked p-value, 0.016, Table 2.2). Therefore, all p-values smaller or equal to the 47th ranked p-value (0.016) were considered to be significant. All p-values below the 47th ranked p-value were considered as non-significant (Benjamini *et al*., 2001).

A multivariate analysis was performed on the 'total larval abundance' to investigate the possible oceanographic factors that influenced the spatial patterns in the numbers of larvae in the water. A Distance based linear model (DistLM) was performed to analyse the relationship between the total larval abundance and the following environmental variables: current speed (cm/s) and direction (degrees), temperature (°C), salinity (g/kg), pH, dissolved oxygen (ml/l), pressure (db), turbidity (NTU), density (kg/m^3), fluorescence (mg/m^3) and conductivity (mS/cm). After examining the Draftsman plot, multi-collinearity ($\geq$ 0.65%) was detected for: salinity, pH, density, pressure and conductivity, and therefore these factors were removed from the analysis. All variables were normalised, due to the variety of measuring units used, prior to DistLM analysis. For the model that was used for the DistLM, 999 permutations were selected, using the 'Best' procedure based on the Akaike Information Criterion (AIC). The analysis was

based on the Bray-Curtis resemblance matrix after square root transformation of ‘total larval abundance’. Visualisation for the DistLM was done using a distance-based redundancy analysis (dbRDA) plot, which provides a graphical indication of the relationship of species abundance and the environmental variable predictors. All statistical analysis was performed using PRIMER V6.1.15 with PERMANOVA+ V1.0.5. (Anderson *et al*., 2008)

2.3 Results

The outcomes of statistical tests on the abundance and distribution of invertebrate larvae were inconsistent through the analyses performed (with added variability because of the splitting of analyses in "season one"), with some taxa showing no significant effects of site, depth, distance or the interaction of all three factors. Generally though, there was some variability in the abundance and distribution of larvae at different sites, depths and distances. In several cases, there were significant interactions, but I have also discussed the main effects in order to clarify general patterns. Below are summaries of the outcomes of all analyses (Table 2.3 & 2.4) performed for each "season" indicating the overall significant and non-significant results from the PERMANOVAs.

Table 2.2: Results of the Benjamini-Hochberg method on all taxa: TL – Total larval abundance, P – *Perna perna*, M – *Mytilus galloprovincialis*, O – Oysters, EN – Early nauplii, LN – Late nauplii, C – Cyprids. Effects (Si – site, De – depth, Di – distance). (*i/m*)*Q* – Benjamini – Hochberg critical value where i – rank; m – total number of tests and Q – false discovery rate of 0.05. Bold 47th rank – Cut off point of significance.

Season	Analysis	Taxon	Effect	P value	Rank	(i/m)Q
2	Full	TL	Site	0.001	1	0.000340
2	Full	TL	SixDe	0.001	2	0.000680
2	Full	TL	SixDi	0.001	3	0.001020
2	Full	TL	SixDexDi	0.001	4	0.001361
2	Full	P	Site	0.001	5	0.001701
2	Full	P	SixDi	0.001	6	0.002041
2	Full	P	SixDexDi	0.001	7	0.002381
2	Full	M	Site	0.001	8	0.002721
2	Full	M	SixDe	0.001	9	0.003061
2	Full	M	SixDi	0.001	10	0.003401
2	Full	O	Site	0.001	11	0.003741
2	Full	O	SixDe	0.001	12	0.004082
2	Full	O	SixDi	0.001	13	0.004422
2	Full	O	SixDexDi	0.001	14	0.004762
2	Full	LN	Site	0.001	15	0.005102
2	Full	LN	SixDe	0.001	16	0.005442
2	Full	LN	SixDi	0.001	17	0.005782
2	Full	LN	SixDexDi	0.001	18	0.006122
2	Full	C	SixDe	0.001	19	0.006463

2	Full	C	SixDi	0.001	20	0.006803
1	No St Francis	TL	Site	0.001	21	0.007143
1	No St Francis	P	Site	0.001	22	0.007483
1	No St Francis	P	SixDe	0.001	23	0.007823
1	No St Francis	C	Site	0.001	24	0.008163
1	No offshore	TL	Site	0.001	25	0.008503
1	No offshore	P	Site	0.001	26	0.008844
1	No offshore	P	SixDe	0.001	27	0.009184
1	No offshore	M	Site	0.001	28	0.009524
1	No offshore	O	Site	0.001	29	0.009864
1	No offshore	O	SixDe	0.001	30	0.010204
1	No offshore	O	SixDi	0.001	31	0.010544
1	No offshore	C	Site	0.001	32	0.010884
2	Full	P	SixDe	0.002	33	0.011224
2	Full	M	SixDexDi	0.002	34	0.011565
1	No offshore	LN	Site	0.002	35	0.011905
2	Full	EN	SixDi	0.003	36	0.012245
2	Full	TL	Depth	0.004	37	0.012585
1	No St Francis	LN	SixDexDi	0.004	38	0.012925
1	No St Francis	TL	SixDe	0.005	39	0.013265
2	Full	C	SixDexDi	0.006	40	0.013605
1	No St Francis	LN	Site	0.007	41	0.013946
1	No offshore	TL	Depth	0.007	42	0.014286
1	No St Francis	TL	Depth	0.009	43	0.014626
1	No offshore	P	SixDexDi	0.012	44	0.014966
2	Full	C	Site	0.013	45	0.015306
1	No St Francis	TL	SixDi	0.016	46	0.015646
1	**No offshore**	**LN**	**SixDexDi**	**0.016**	**47**	**0.015986**
1	No St Francis	M	SixDi	0.017	48	0.016327
1	No offshore	TL	SixDe	0.019	49	0.016667
1	No offshore	TL	SixDi	0.019	50	0.017007
1	No offshore	C	DexDi	0.019	51	0.017347
1	No offshore	C	Depth	0.021	52	0.017687
1	No St Francis	O	SixDe	0.023	53	0.018027
1	No St Francis	O	Site	0.025	54	0.018367
2	Full	M	Depth	0.026	55	0.018707
2	Full	EN	Depth	0.032	56	0.019048
1	No St Francis	TL	SixDexDi	0.032	57	0.019388
1	No St Francis	P	SixDexDi	0.035	58	0.019728
1	No offshore	C	SixDi	0.037	59	0.020068
1	No St Francis	LN	Depth	0.04	60	0.020408
2	Full	EN	Site	0.042	61	0.020748
1	No St Francis	C	SixDexDi	0.042	62	0.021088
1	No offshore	O	SixDexDi	0.046	63	0.021429
1	No offshore	LN	SixDe	0.048	64	0.021769

1	No offshore	EN	Distance	0.055	65	0.022109
2	Full	O	Depth	0.056	66	0.022449
1	No offshore	TL	DexDi	0.057	67	0.022789
1	No St Francis	C	Depth	0.059	68	0.023129
1	No St Francis	O	SixDi	0.06	69	0.023469
1	No offshore	EN	Depth	0.063	70	0.023810
1	No St Francis	EN	Depth	0.069	71	0.024150
1	No St Francis	M	Site	0.082	72	0.024490
1	No St Francis	LN	Distance	0.086	73	0.024830
1	No St Francis	TL	DexDi	0.086	74	0.025170
1	No St Francis	M	SixDexDi	0.087	75	0.025510
1	No St Francis	O	DexDi	0.1	76	0.025850
1	No offshore	LN	Depth	0.121	77	0.026190
1	No St Francis	EN	Distance	0.125	78	0.026531
2	Full	TL	Distance	0.127	79	0.026871
1	No offshore	C	Distance	0.13	80	0.027211
1	No offshore	P	SixDi	0.133	81	0.027551
1	No St Francis	O	Distance	0.134	82	0.027891
2	Full	TL	DexDi	0.138	83	0.028231
1	No offshore	M	SixDi	0.173	84	0.028571
2	Full	C	Depth	0.186	85	0.028912
1	No offshore	M	SixDe	0.192	86	0.029252
1	No St Francis	O	Depth	0.202	87	0.029592
1	No offshore	TL	SixDexDi	0.207	88	0.029932
1	No St Francis	M	Depth	0.211	89	0.030272
1	No offshore	O	DexDi	0.218	90	0.030612
1	No St Francis	TL	Distance	0.221	91	0.030952
1	No offshore	EN	DexDi	0.229	92	0.031293
2	Full	P	Depth	0.234	93	0.031633
1	No offshore	C	SixDexDi	0.241	94	0.031973
1	No offshore	M	Depth	0.244	95	0.032313
2	Full	C	Distance	0.248	96	0.032653
1	No offshore	LN	SixDi	0.249	97	0.032993
1	No offshore	LN	Distance	0.257	98	0.033333
2	Full	O	DexDi	0.271	99	0.033673
1	No St Francis	P	SixDi	0.275	100	0.034014
2	Full	LN	Depth	0.291	101	0.034354
1	No offshore	M	SixDexDi	0.294	102	0.034694
1	No offshore	O	Depth	0.295	103	0.035034
1	No offshore	M	Distance	0.296	104	0.035374
1	No St Francis	C	SixDe	0.298	105	0.035714
1	No St Francis	O	SixDexDi	0.318	106	0.036054
1	No offshore	P	DexDi	0.323	107	0.036395
1	No St Francis	C	SixDi	0.326	108	0.036735
1	No St Francis	C	Distance	0.327	109	0.037075

1	No St Francis	M	Distance	0.331	110	0.037415
1	No offshore	TL	Distance	0.347	111	0.037755
1	No offshore	O	Distance	0.367	112	0.038095
2	Full	C	DexDi	0.382	113	0.038435
2	Full	O	Distance	0.44	114	0.038776
1	No offshore	C	SixDe	0.444	115	0.039116
1	No St Francis	LN	SixDe	0.448	116	0.039456
1	No St Francis	P	Depth	0.451	117	0.039796
1	No St Francis	P	DexDi	0.456	118	0.040136
1	No St Francis	LN	SixDi	0.459	119	0.040476
1	No St Francis	M	SixDe	0.469	120	0.040816
1	No offshore	P	Depth	0.47	121	0.041156
1	No offshore	P	Distance	0.485	122	0.041497
2	Full	EN	Distance	0.501	123	0.041837
1	No St Francis	C	DexDi	0.52	124	0.042177
2	Full	LN	DexDi	0.525	125	0.042517
1	No St Francis	P	Distance	0.534	126	0.042857
1	No offshore	EN	SixDe	0.573	127	0.043197
2	Full	M	DexDi	0.578	128	0.043537
2	Full	P	DexDi	0.594	129	0.043878
1	No St Francis	M	DexDi	0.602	130	0.044218
1	No St Francis	EN	SixDe	0.645	131	0.044558
1	No St Francis	EN	SixDexDi	0.697	132	0.044898
1	No St Francis	EN	DexDi	0.72	133	0.045238
1	No offshore	EN	Site	0.746	134	0.045578
1	No offshore	M	DexDi	0.772	135	0.045918
2	Full	EN	SixDexDi	0.773	136	0.046259
2	Full	LN	Distance	0.774	137	0.046599
1	No St Francis	EN	Site	0.796	138	0.046939
1	No St Francis	EN	SixDi	0.805	139	0.047279
2	Full	EN	SixDe	0.84	140	0.047619
1	No offshore	LN	DexDi	0.844	141	0.047959
2	Full	M	Distance	0.854	142	0.048299
2	Full	P	Distance	0.886	143	0.048639
1	No offshore	EN	SixDi	0.918	144	0.048980
1	No offshore	EN	SixDexDi	0.933	145	0.049320
2	Full	EN	DexDi	0.946	146	0.049660
1	No St Francis	LN	DexDi	0.969	147	0.050000

Table 2.3: A summary of the results of Permutational Multivariate Analyses of Variance (PERMANOVA) on all selected taxa, examining the effects of site, depth and distance on the square root transformed abundances of seven taxa of larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis). n – Not significant, **Y** - Significant.

	Season 1 (No St Francis)						
Factors	Total larvae	*Perna perna*	*Mytilus galloprovincialis*	Oysters	Early nauplii	Late nauplii	Cyprids
Site	**Y**	**Y**	n	n	n	**Y**	**Y**
Distance	n	n	n	n	n	n	n
Depth	**Y**	n	n	n	n	n	n
Site x Distance	**Y**	n	n	n	n	n	n
Site x Depth	**Y**	**Y**	n	n	n	n	n
Distance x Depth	n	n	n	n	n	n	n
Site x Distance x Depth	n	n	n	n	n	**Y**	n
	Season 1 (No offshore)						
	Total larvae	*Perna perna*	*Mytilus galloprovincialis*	Oysters	Early nauplii	Late nauplii	Cyprids
Site	**Y**	**Y**	**Y**	**Y**	n	**Y**	**Y**
Distance	n	n	n	n	n	n	n
Depth	**Y**	n	n	n	n	n	n
Site x Distance	n	n	n	**Y**	n	n	n
Site x Depth	n	**Y**	n	**Y**	n	n	n
Distance x Depth	n	n	n	n	n	n	n
Site x Distance x Depth	n	**Y**	n	n	n	**Y**	n

Table 2.4: A summary of the results of Permutational Multivariate Analysis of Variance (PERMANOVA) on all selected taxa examining the effects of site, depth and distance on the abundance of (square root transformed) seven taxa of larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis). n – Not significant, **Y** - Significant.

	Season 2						
Factors	Total larvae	*Perna perna*	*Mytilus galloprovincialis*	Oysters	Early nauplii	Late nauplii	Cyprids
Site	**Y**	**Y**	**Y**	**Y**	n	**Y**	**Y**
Distance	n	n	n	n	n	n	n
Depth	**Y**	n	n	n	n	n	n
Site x Distance	**Y**	**Y**	**Y**	**Y**	**Y**	**Y**	**Y**
Site x Depth	**Y**	**Y**	**Y**	**Y**	n	**Y**	**Y**
Distance x Depth	n	n	n	n	n	n	n
Site x Distance x Depth	**Y**	**Y**	**Y**	**Y**	n	**Y**	**Y**

2.3.1 Season 1

Total larval abundance (No Cape St Francis)

There was a significant effect of the interaction between site and depth, with consistently more total larvae present at the thermocline than at the other depths, the highest abundance being at Kenton on Sea (Table 2.5; Figure 2.2). More larvae were present at the offshore station (2400m) in Kenton on Sea, when compared to the rest of the distances and sites, (Table 2.5; Figure 2.3). The dbRDA1 showed that temperature and speed explained 10.7% of the total variation of the distribution of larvae, with temperatures and speed positively affecting the 'surface' and negatively affecting the 'bottom' depth (Figure 2.5). Vector direction and fluorescence explained only 6.5% total variation on dbRDA2, which mainly negatively influenced the distribution of larvae for the 'thermocline' depth (Figure 2.5).

Table 2.5: Results of the PERMANOVA examining the effects of site, depth and distance on the abundance (square root transformed) of total larvae collected at three sites (Kenton on Sea, Cannon Rocks and Schoenmakerskop) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	2	15845	7922.5	7.60	*
De - Depth	2	26166	13083	6.58	*
Di - Distance	2	4894.2	2447.1	1.35	n.s.
Si*De	4	7949.5	1987.4	1.91	*
Si*Di	4	7272.6	1818.1	1.74	*
De*Di	4	9767.4	2441.9	1.58	n.s.
Si*De*Di	8	12395	1549.3	1.49	n.s.
Residual	27	28162	1043		
Total	53	1.12E+05			

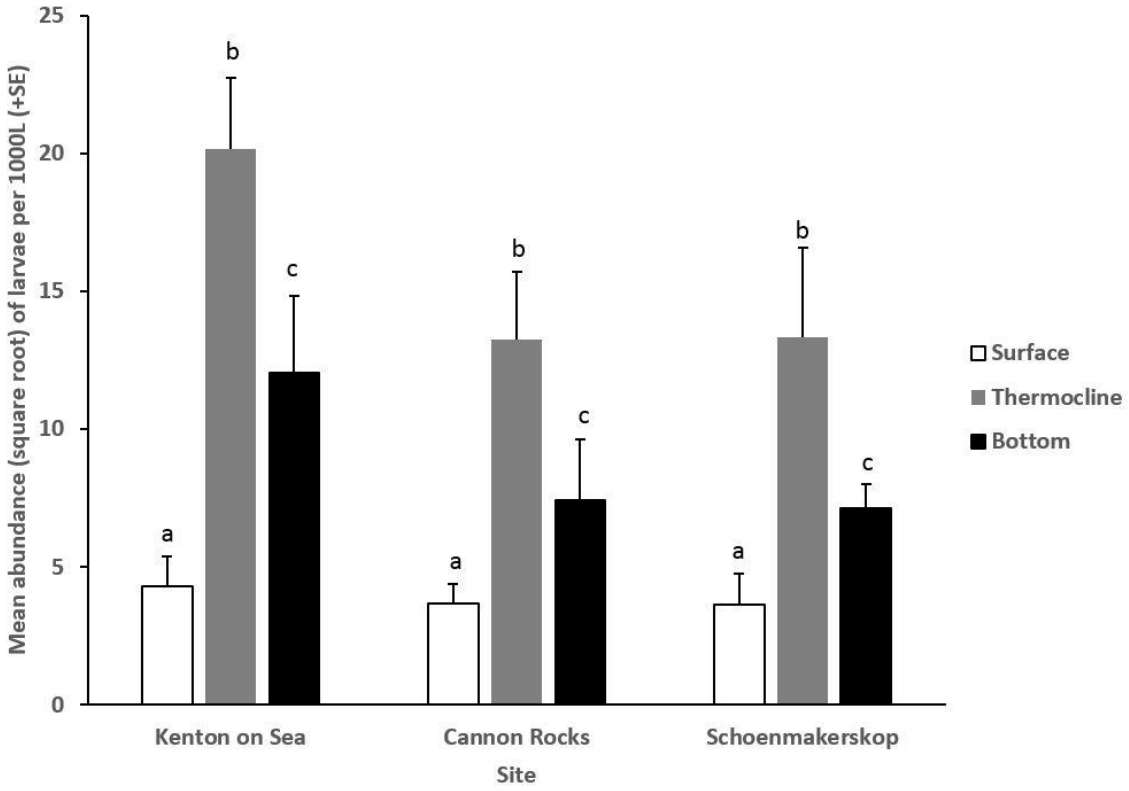

Figure 2.2: Mean abundance of (square root transformed) total larvae per 1000L collected at three depths at three sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by the 'site*depth' pair wise test.

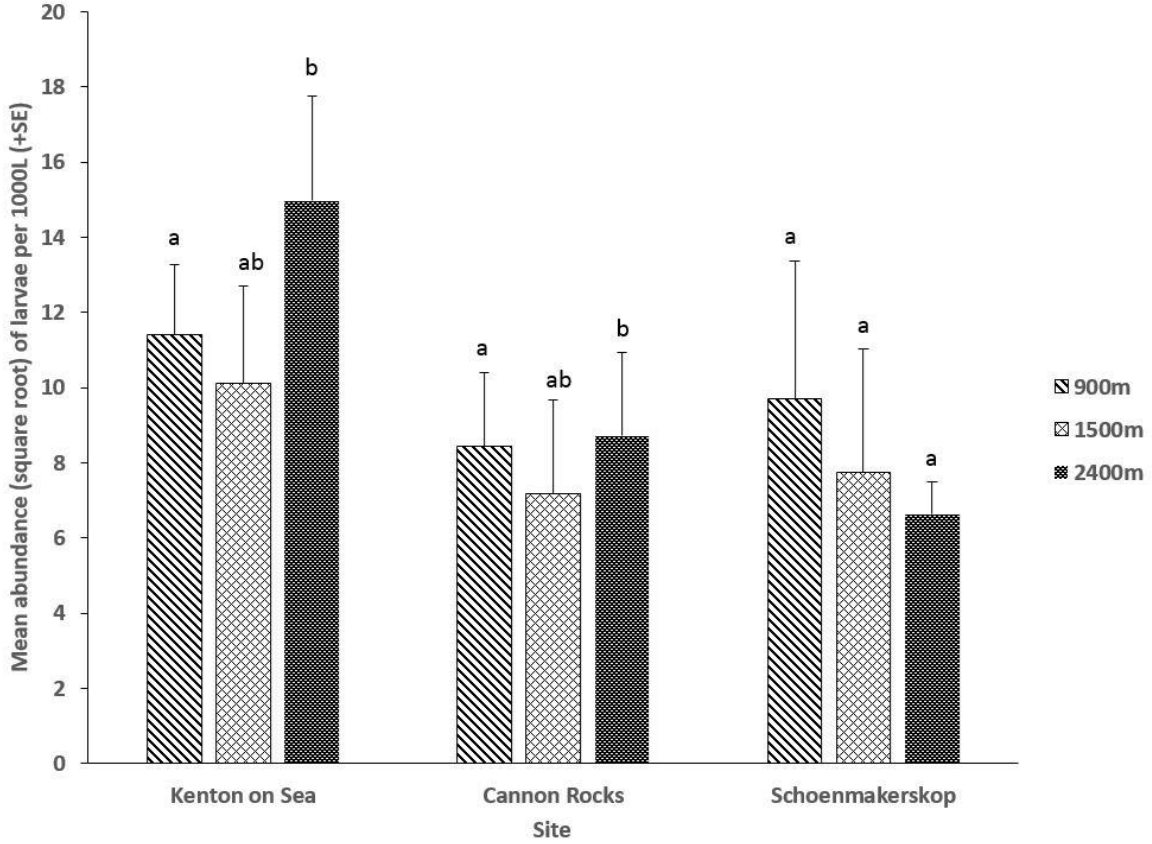

Figure 2.3: Mean abundance of (square root transformed) total larvae per 1000L collected at three nearshore distances, at three sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by the 'site*distance' pair wise test.

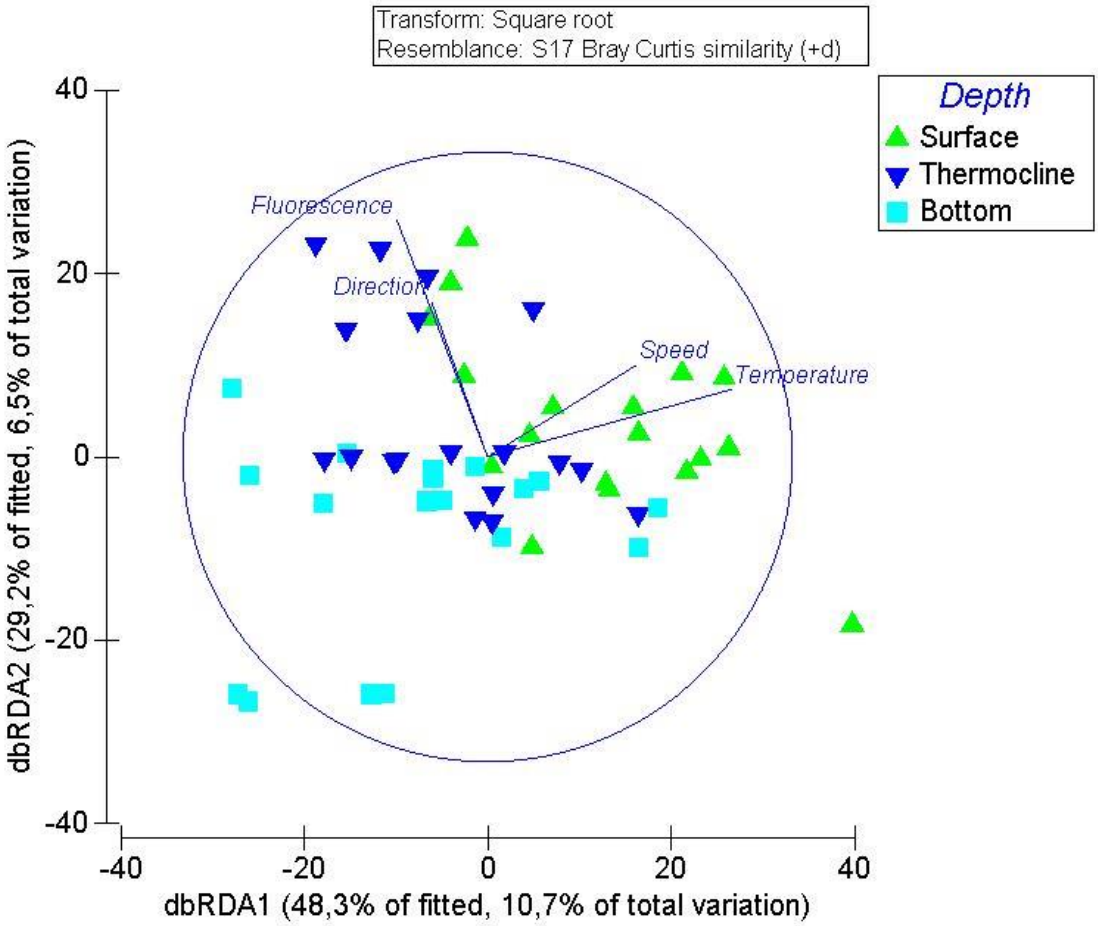

Figure 2.4: Distance based redundancy analysis (dbRDA) plot of the DistLM to show the relationship between 'Full taxa' larvae (no Cape St Francis, derived from a Bray-Curtis similarity matrix of data that had been square root transformed) and the physical parameters. Length and direction of vectors show the strength and direction of the relationship with regards to the larvae and the percentages indicate total variation explained by each axis.

Total larval abundance (No offshore stations)

There were significantly more larvae at Kenton on Sea than the other sites, which clarifies the significant effect of site (Figure 2.5; Table 2.6). The thermocline depth had the highest number of larvae which confirms the significant effect of depth for this taxon, followed by bottom and surface (Figure 2.6; Table 2.6). Though this analysis (which excluded the offshore stations) did not show a significant interaction between site, depth and distance, the results are consistent with the one from the analysis on the total larval abundance without Cape St Francis, in that larval abundance were greatest at thermocline at Kenton on Sea. Vectors turbidity and fluorescence, in the dbRDA1 plot were the main parameters that explained the separation in the distribution of larvae, especially for the 'surface' and 'thermocline' depths from the 'bottom' (negative relationship). The vectors however only explained 11.7% of the variation of larval distribution (Figure 2.7).

Table 2.6: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of total larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	19978	6659.4	5.90	*
De - Depth	2	15791	7895.3	4.38	*
Di - Distance	1	2481.8	2481.8	1.13	n.s
Si*De	6	10808	1801.4	1.60	n.s
Si*Di	3	6585.1	2195	1.95	n.s
De*Di	2	5746.6	2873.3	2.11	n.s
Si*De*Di	6	8187.5	1364.6	1.21	n.s
Residual	24	27087	1128.6		
Total	47	96665			

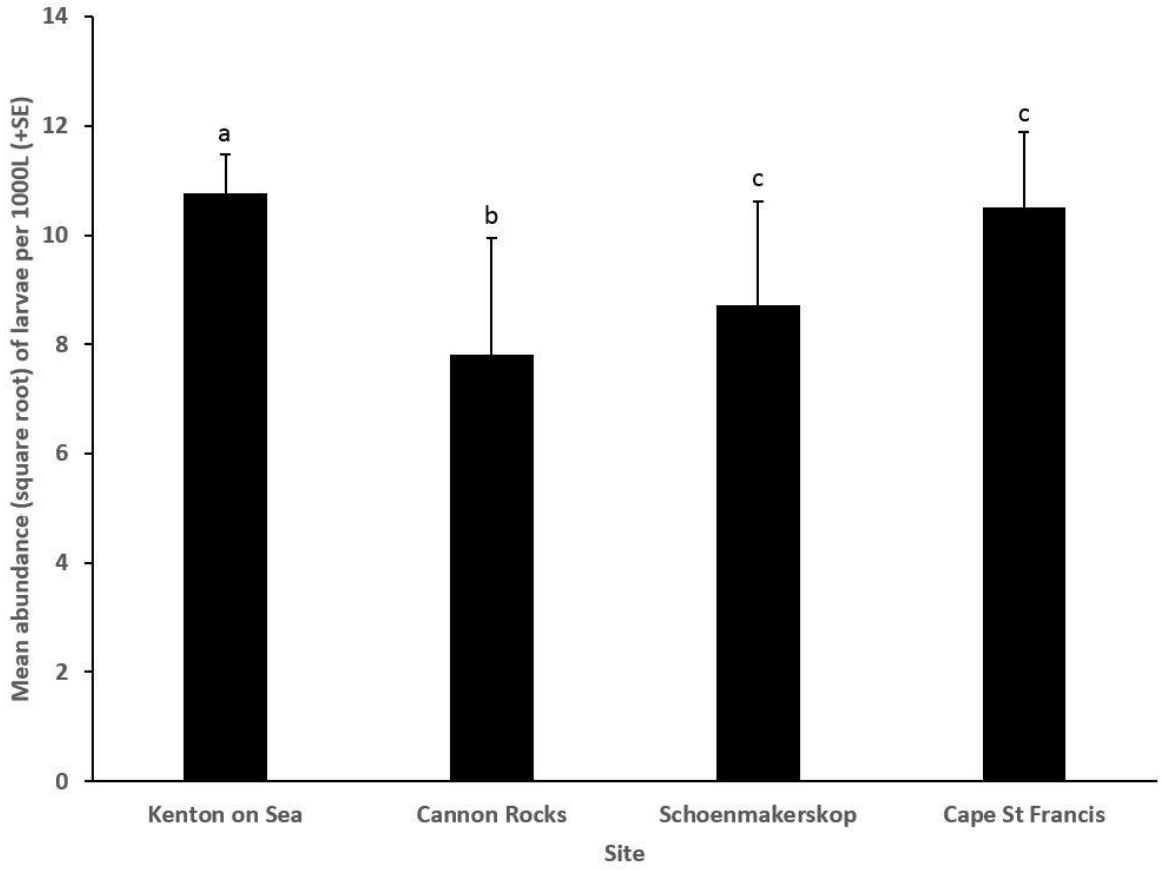

Figure 2.5: Mean abundance of (square root transformed) total larvae per 1000L collected at four sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by the 'site' pair wise test.

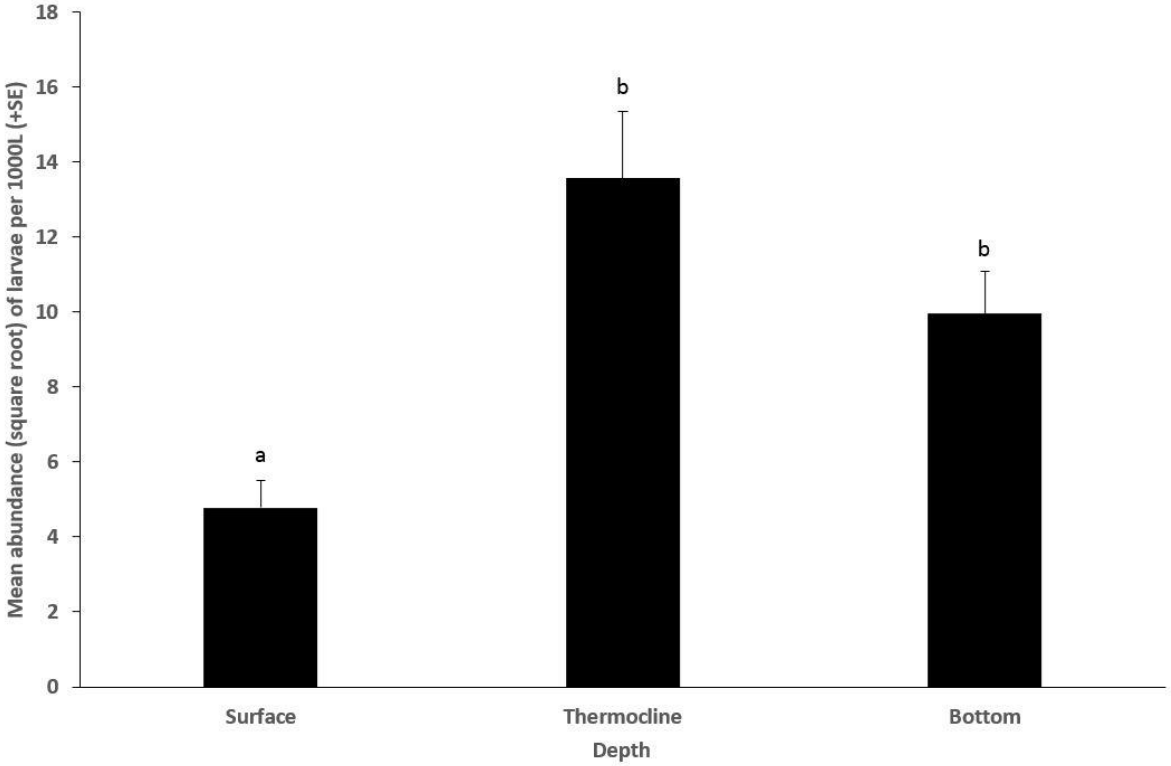

Figure 2.6: Mean abundance of (square root transformed) total larvae per 1000L collected in three depths. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by the 'depth' pair wise test.

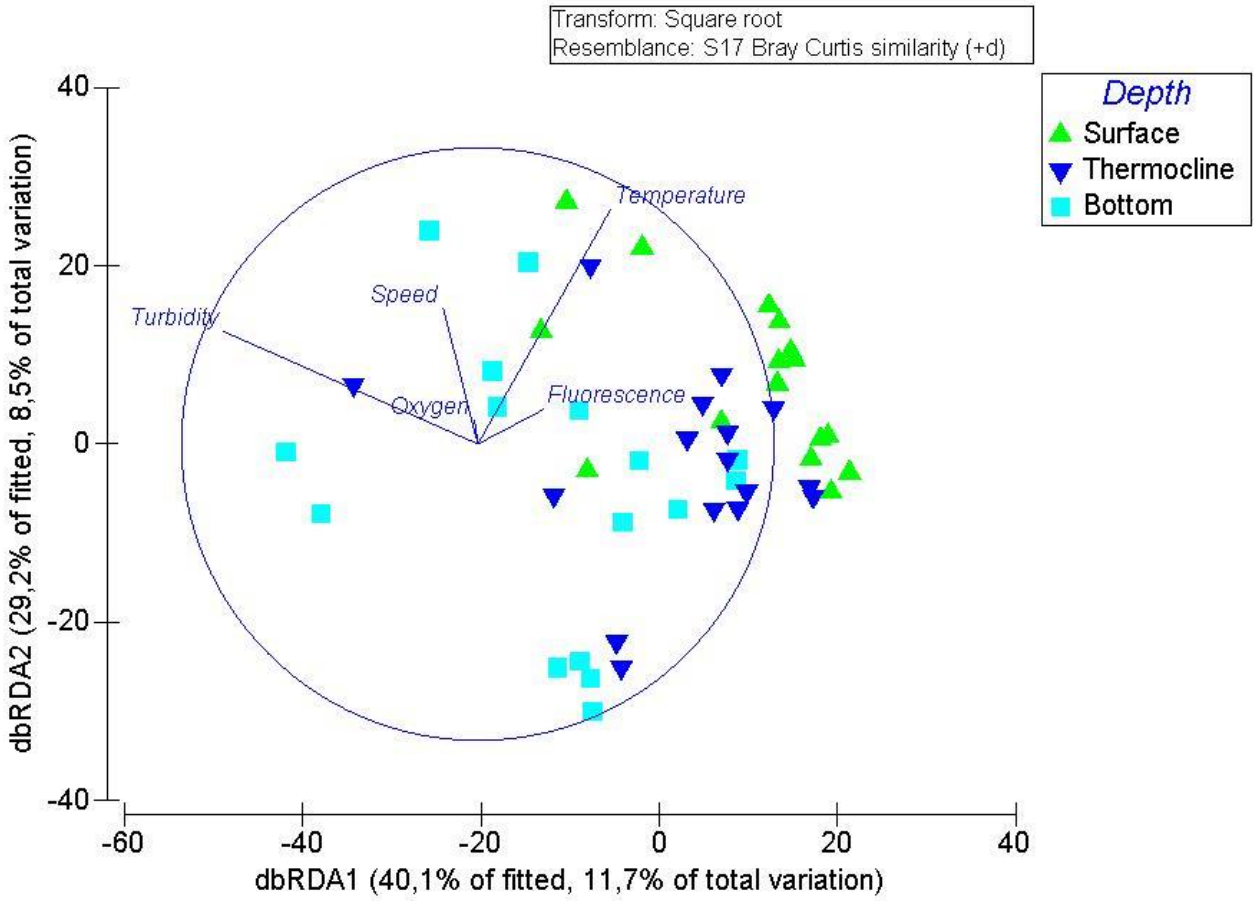

Figure 2.7: Distance based redundancy analysis (dbRDA) plot of the DistLM to show the relationship between the distribution of 'total larval abundance' larvae (no offshore station, derived from a Bray-Curtis similarity matrix of data that had been square root transformed) and the physical parameters. Length and direction of vectors show the strength and direction of the relationship with regards to the larvae and the percentages indicate total variation explained by each axis.

***Perna perna* larvae (No Cape St Francis)**

Kenton on Sea presented the highest abundance of *Perna perna* larvae, a trend confirmed by the significant effect of site (Figure 2.8; Table 2.7). The outcome of the PERMANOVA also revealed that the abundance of *Perna perna* larvae varied according to depth, but only at one site, Kenton on Sea, as supported by the significant effect of the interaction between site and depth (Table 2.7; Figure 2.8).

Table 2.7: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of *Perna perna* larvae collected at three sites (Kenton on Sea, Cannon Rocks, and Schoenmakerskop) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	2	79.88	39.94	40.79	*
De - Depth	2	2.27	1.14	0.79	n.s
Di - Distance	2	41.81	20.91	1.14	n.s
Si*De	4	5.72	1.43	1.46	*
Si*Di	4	73.71	18.43	18.82	n.s
De*Di	4	9.46	2.36	1.04	n.s
Si*De*Di	8	18.27	2.28	2.33	n.s
Residual	27	26.44	0.98		
Total	53	257.56			

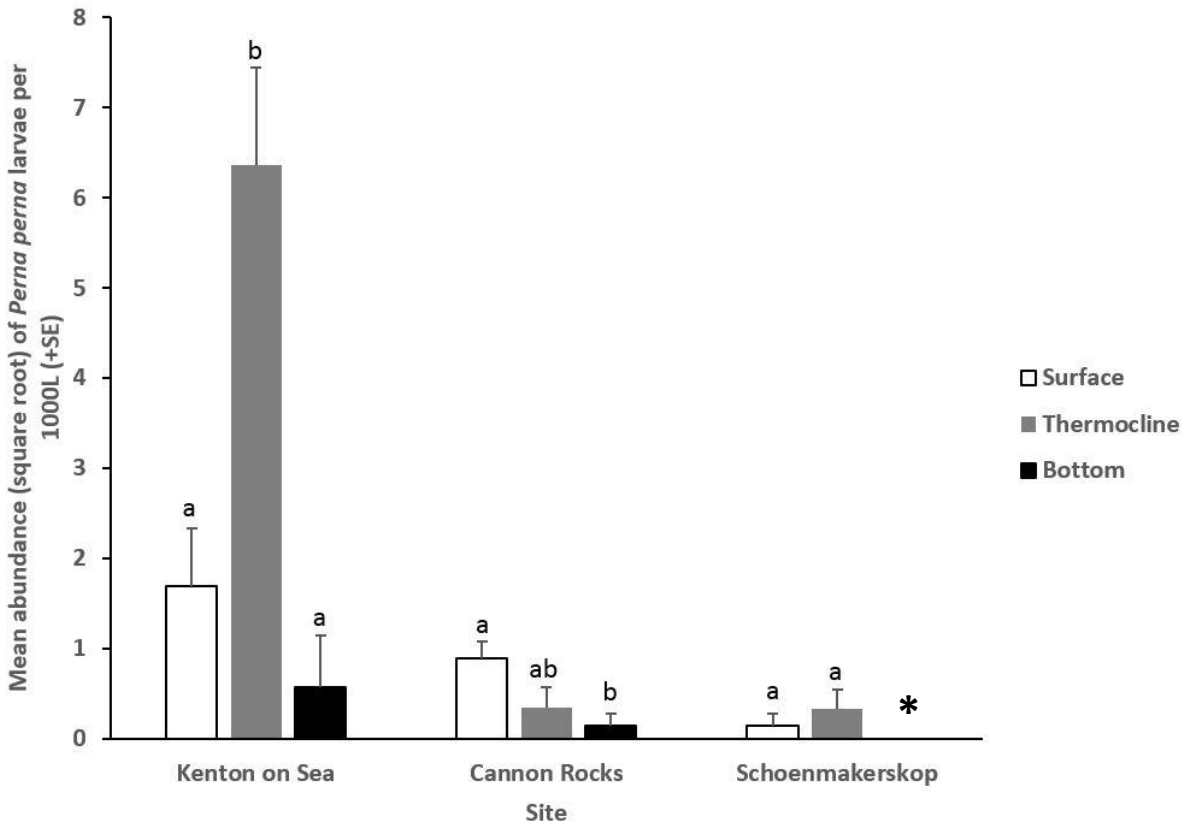

Figure 2.8: Mean abundance of (square root transformed) *Perna perna* larvae per 1000L collected at three depths at three sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by the 'site*depth' pair wise test. '*' indicates no larvae were captured.

***Perna perna* larvae (No offshore station)**

Results of the univariate PERMANOVA test showed a significant effect for the interaction of site and depth, which supports the varying pattern of the abundance of *Perna perna* larvae within the depths (surface, thermocline and bottom) over the four sites (Table 2.8; Figure 2.9). As with the previous analysis, when excluding the site Cape St Francis, the numbers of *Perna perna* larvae were highest at the thermocline in Kenton on Sea (Figure 2.9; Table 2.8). Generally, the abundance of *P. perna* varied among sites and depths and distances with no clear patterns, leading to a significant interaction of site, depth and distance (Table 2.8).

Table 2.8: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of *Perna perna* larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	70.28	23.43	26.21	*
De - Depth	2	21.17	10.58	1.06	n.s
Di - Distance	1	1.50	1.50	0.82	n.s
Si*De	6	59.64	9.94	11.12	*
Si*Di	3	5.48	1.83	2.04	n.s
De*Di	2	8.61	4.31	1.44	n.s
Si*De*Di	6	17.97	2.99	3.35	*
Residual	24	21.45	0.89		
Total	47	206.09			

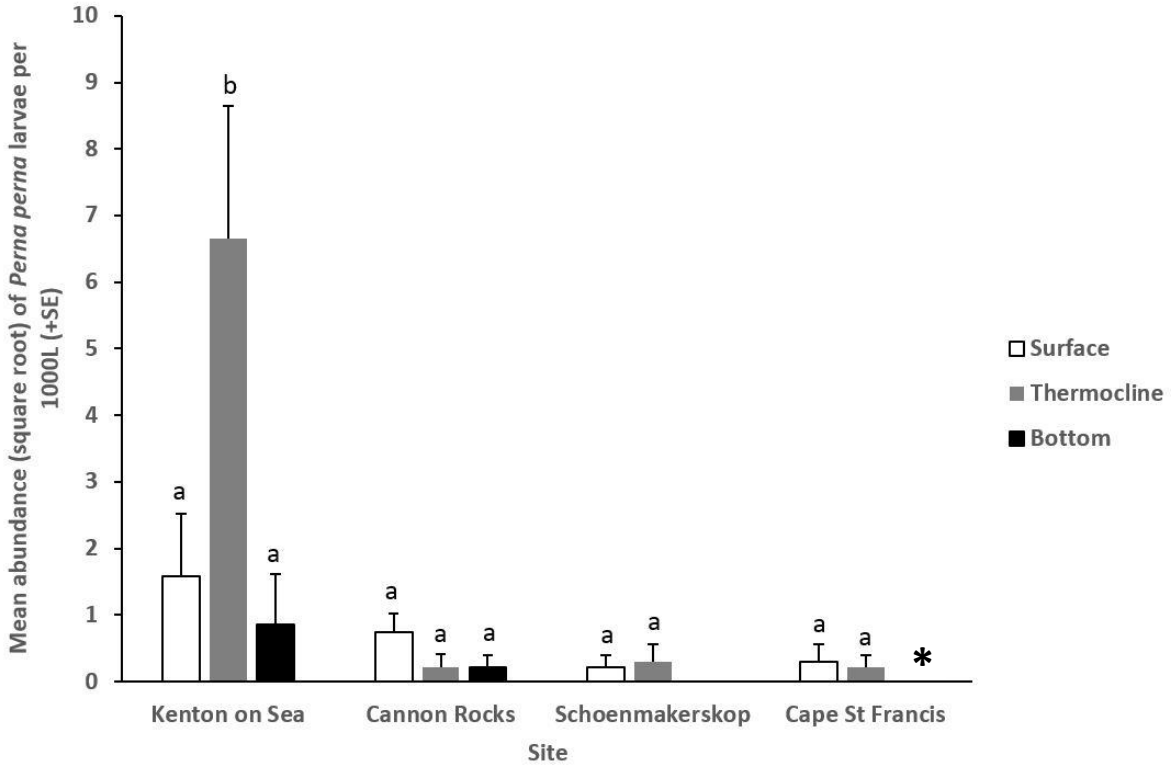

Figure 2.9: Mean abundance of (square root transformed) *Perna perna* larvae per 1000L collected at three depths at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*depth' pair wise test. '*' indicates that no larvae were captured.

Mytilus galloprovincialis larvae (No Cape St Francis)

Results from the univariate PERMANOVA showed no significant effects for any of the main factors or interactions for *Mytilus galloprovincialis* larvae (Table 2.9). The interaction between site and distance for this taxon was relatively close to significance (p = 0.017) with abundances of larvae at 900m offshore at Kenton on Sea larger than abundances at the other sites and distances. The p-value acceptance level was made more stringent due to the Benjamini-Hochberg correction (Table 2.1). The variability of larval abundance was however large (Figure 2.10). There were no larvae found at Cannon Rocks for this analysis.

Table 2.9 : Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of *Mytilus galloprovincialis* larvae collected at three sites (Kenton on Sea, Cannon Rocks, and Schoenmakerskop) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant

Source	Df	SS	MS	Pseudo - F	p
Si - Site	2	0.53	0.27	2.71	n.s
De - Depth	2	0.96	0.48	1.47	n.s
Di - Distance	2	0.45	0.23	2.57	n.s
Si*De	4	1.31	0.33	3.35	n.s
Si*Di	4	0.35	8.81E-02	0.90	n.s
De*Di	4	0.55	0.14	0.73	n.s
Si*De*Di	8	1.51	0.19	1.94	n.s
Residual	27	2.64	9.76E-02		
Total	53	8.30			

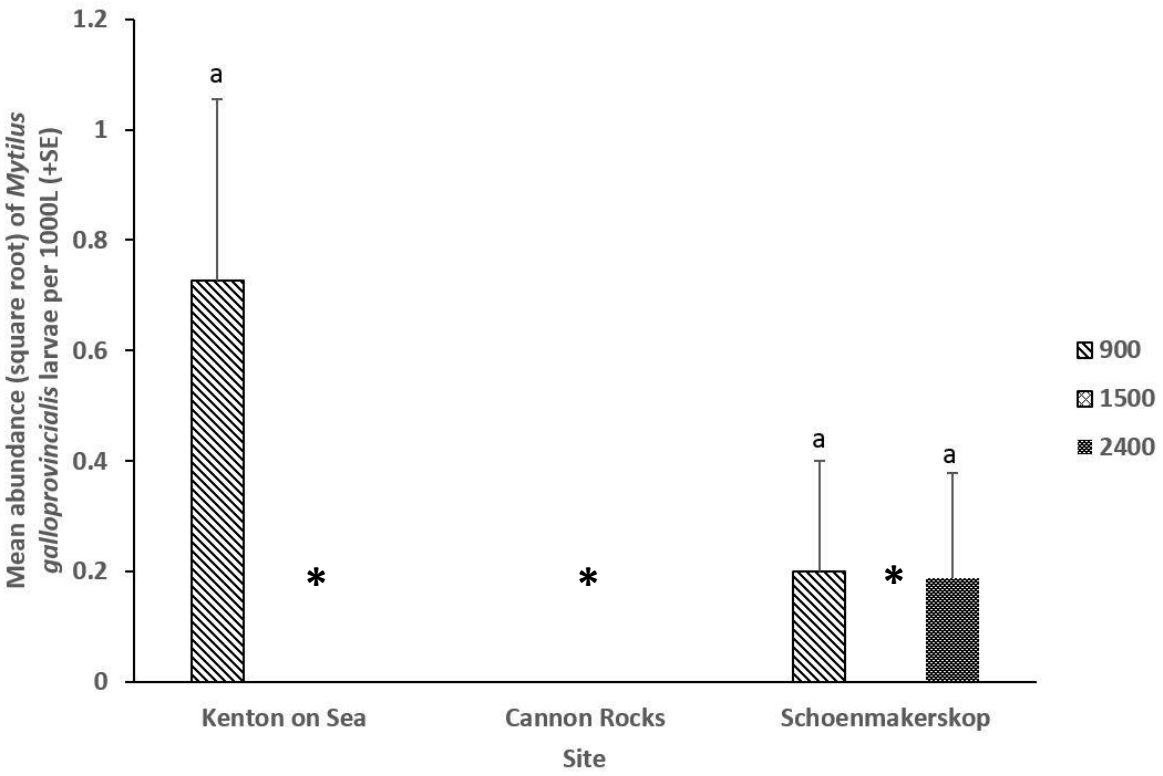

Figure 2.10: Mean abundance of (square root transformed) *Mytilus galloprovincialis* larvae per 1000L collected at three nearshore distances, at three sites. Error bars indicate standard errors and letters above the bar plots within-site indicate homogenous groups identified by 'site*distance' pair wise test. '*' indicates that no larvae were captured.

Mytilus galloprovincialis larvae (No offshore distance)

When (Cape St Francis) was included in the analysis, it was the only factor to have a significant effect from the univariate PERMANOVA (Table 2.10). There was a higher abundance of *M. galloprovincialis* larvae located in Cape St Francis than other sites, which confirmed the significant effect of site for this taxon (Figure 2.11; Table 2.10). As mentioned in the previous analysis, no larvae were found in Cannon Rocks for the first season.

Table 2.10: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of *Mytilus galloprovincialis* larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	5.08	1.69	9.47	*
De - Depth	2	0.97	0.49	1.78	n.s
Di - Distance	1	0.72	0.72	2.18	n.s
Si*De	6	1.64	0.27	1.53	n.s
Si*Di	3	1.00	0.33	1.86	n.s
De*Di	2	0.13	6.37E-02	0.28	n.s
Si*De*Di	6	1.38	0.23	1.28	n.s
Residual	24	4.29	0.18		
Total	47	15.20			

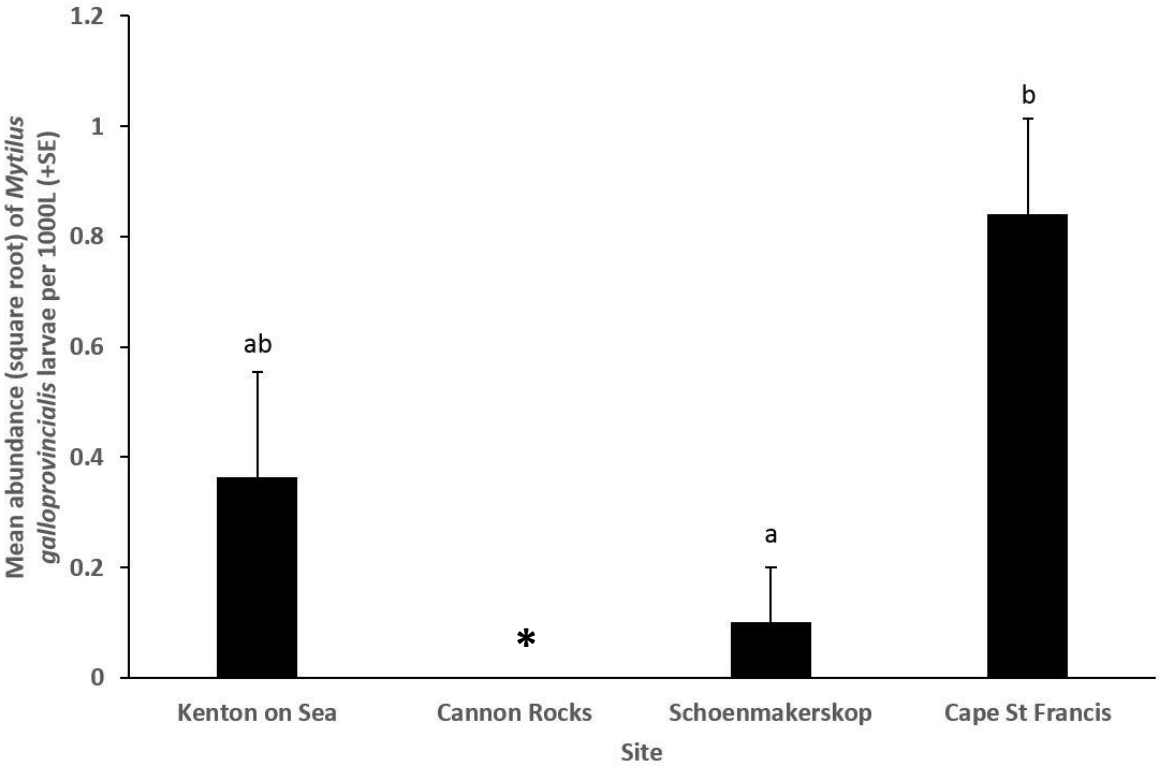

Figure 2.11: Mean abundance of (square root transformed) *Mytilus galloprovincialis* per 1000L collected at four sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by 'site' pair wise test. '*' indicates that no larvae were captured.

Oyster larvae (No Cape St Francis)

The results from the univariate PERMANOVA for all the factors of site, depth and distance on oyster larvae were not significant (Table 2.11). Even though there were no significant effects, the interaction of site and depth were relatively close to being considered significant (p = 0.023), with larvae at the thermocline and bottom in Schoenmakerskop higher (although not significantly) than the rest of the sites (Figure 2.12).

Table 2.11: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of oyster larvae collected at three sites (Kenton on Sea, Cannon Rocks, and Schoenmakerskop) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	2	7.21	3.60	4.35	n.s
De - Depth	2	16.01	8.00	3.52	n.s
Di - Distance	2	17.62	8.81	2.95	n.s
Si*De	4	9.105	2.28	2.75	n.s
Si*Di	4	11.94	2.99	3.60	n.s
De*Di	4	11.09	2.77	2.74	n.s
Si*De*Di	8	8.12	1.01	1.22	n.s
Residual	27	22.37	0.83		
Total	53	103.44			

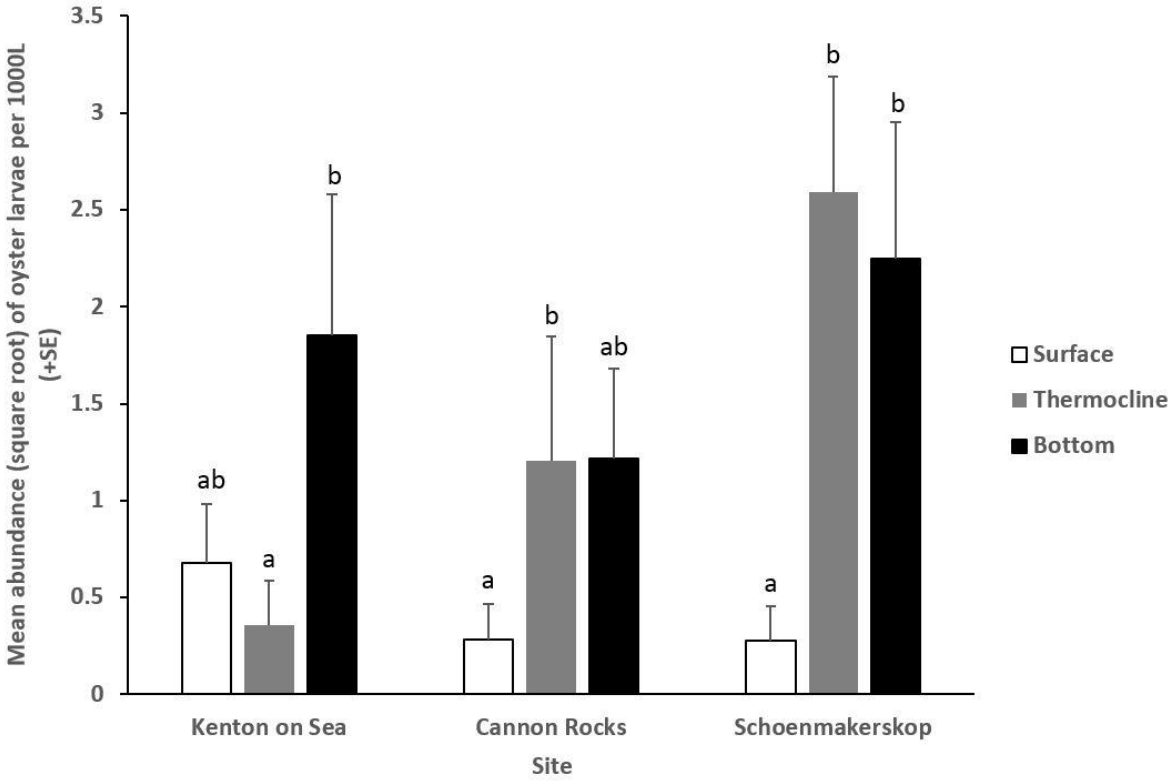

Figure 2.12: Mean abundance of (square root transformed) oyster larvae per 1000L collected at three depths at three sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*depth' pair wise test.

Oyster larvae (No offshore station)

The abundance of oyster larvae when including the fourth site varied from site to site at the different depths (Figure 2.13), as indicated by the significant interaction of site and depth (Table 2.12). There was also significant effect of the interaction of site and distance, which is shown by the increased abundance of larvae at the midshore station (1500m) in Cape St Francis (Figure 2.14). Considering both significant interactions (site*depth; site*distance), Cape St Francis was the site which had the highest abundance of oyster larvae, especially at 1500m offshore and at the bottom and thermocline(Figures 2.13 & 2.14; Table 2.12).

Table 2.12: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of oyster larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	138.89	46.30	25.09	*
De - Depth	2	50.13	25.06	1.66	n.s
Di - Distance	1	31.38	31.38	1.53	n.s
Si*De	6	90.60	15.1	8.18	*
Si*Di	3	61.42	20.47	11.10	*
De*Di	2	16.52	8.26	1.82	n.s
Si*De*Di	6	27.27	4.55	2.46	n.s
Residual	24	44.28	1.85		
Total	47	460.48			

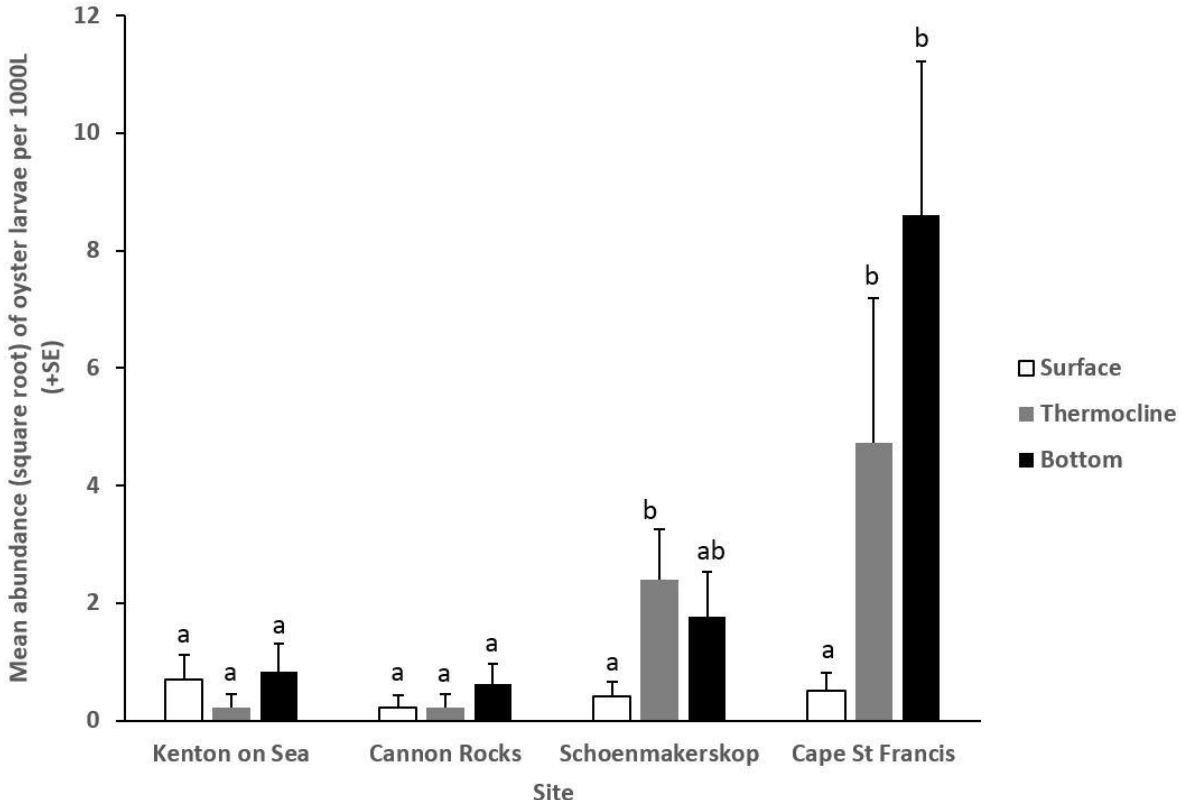

Figure 2.13: Mean abundance of (square root transformed) oyster larvae per 1000L collected at three depths at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by the 'site*depth' pair wise test.

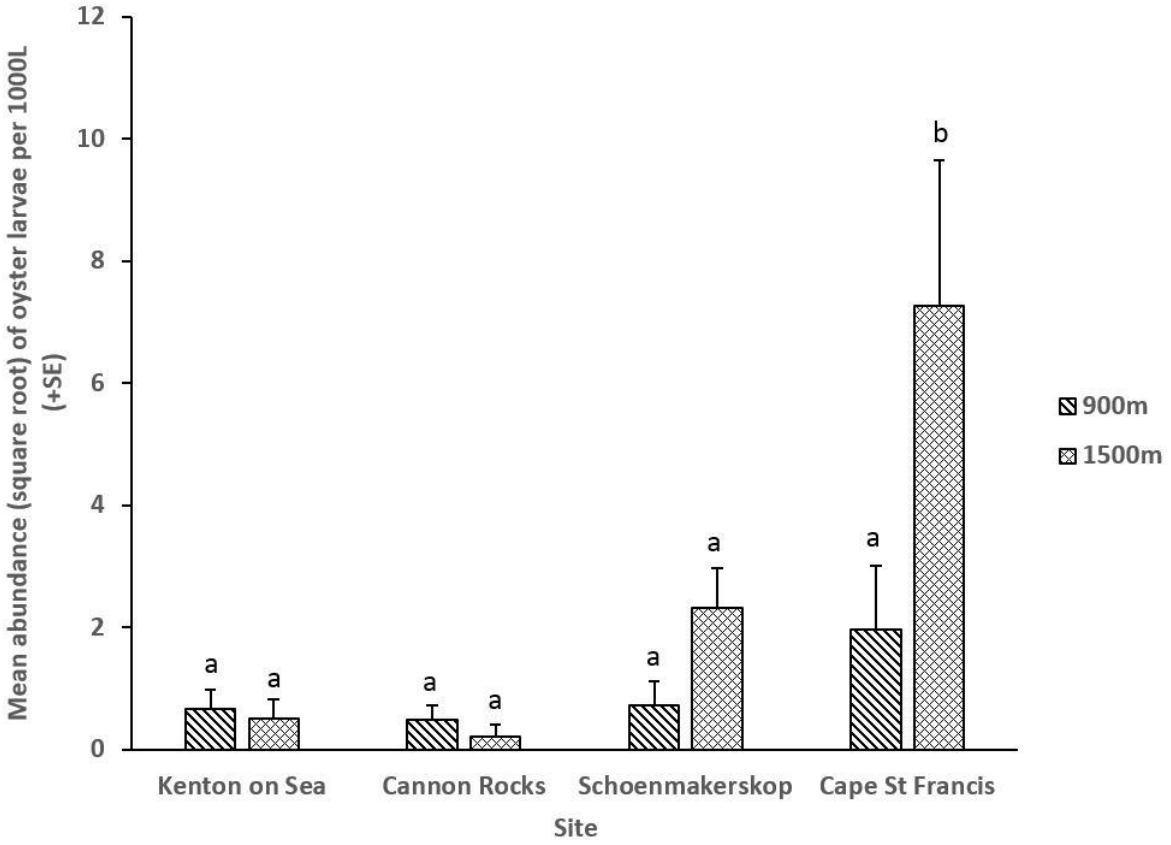

Figure 2.14: Mean abundance of (square root transformed) oyster larvae per 1000L collected at two nearshore distances, at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by the 'site*distance' pair wise test.

Early Nauplii (No Cape St Francis)

The results of the univariate PERMANOVA for early barnacle nauplii, as for *Mytilus galloprovincialis* (No Cape St Francis), were not significant for any of the factors or interactions (Table 2.13). The effect of depth was however relatively close to significant ($p<0.07$.), with more early nauplii larvae present within the thermocline as compared to the other two depths (Figure 2.15).

Table 2.13: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of early nauplii larvae collected at three sites (Kenton on Sea, Cannon Rocks, and Schoenmakerskop Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	2	6.56	3.28	0.21	n.s
De - Depth	2	51.12	25.56	3.63	n.s
Di - Distance	2	143.72	71.86	6.34	n.s
Si*De	4	28.18	7.04	0.45	n.s
Si*Di	4	45.35	11.34	0.73	n.s
De*Di	4	26.27	6.57	0.58	n.s
Si*De*Di	8	90.37	11.30	0.73	n.s
Residual	27	420.67	15.58		
Total	53	812.23			

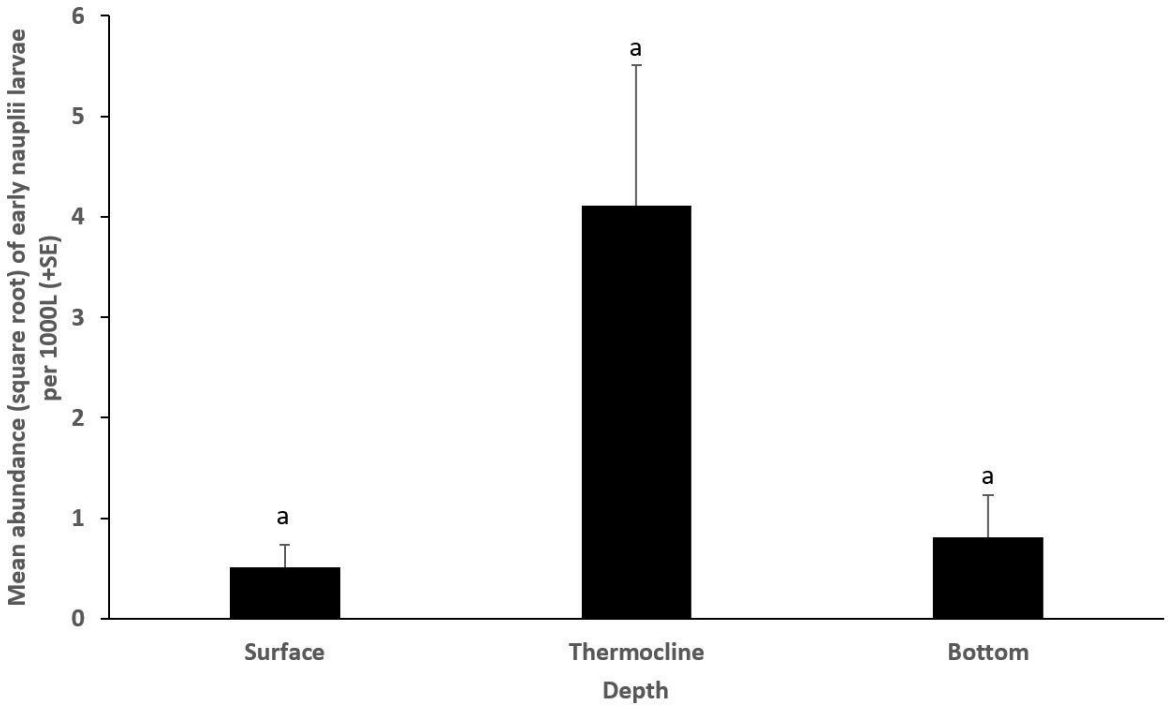

Figure 2.15: Mean abundance of (square root transformed) early nauplii larvae per 1000L collected in three depths. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by ‘depth’ pair wise test.

Early nauplii (No offshore station)

As for the previous analysis, the outcome of the univariate PERMANOVA by excluding the most offshore stations showed no significant results for any factors (site, depth and distance and interactions) for this taxon (Table 2.14). Nevertheless, there was a non-significant trend of distance, with more larvae present within the onshore (900m) than the midshore (1500m) (Figure 2.16).

Table 2.14: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of early nauplii larvae collected at three sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	26.43	8.81	0.44	n.s
De - Depth	2	151.72	75.86	4.46	n.s
Di - Distance	1	42.73	42.73	12.54	n.s
Si*De	6	102.01	17.00	0.85	n.s
Si*Di	3	10.22	3.41	0.17	n.s
De*Di	2	24.38	12.19	1.81	n.s
Si*De*Di	6	40.34	6.72	0.34	n.s
Residual	24	481.86	20.08		
Total	47	879.68			

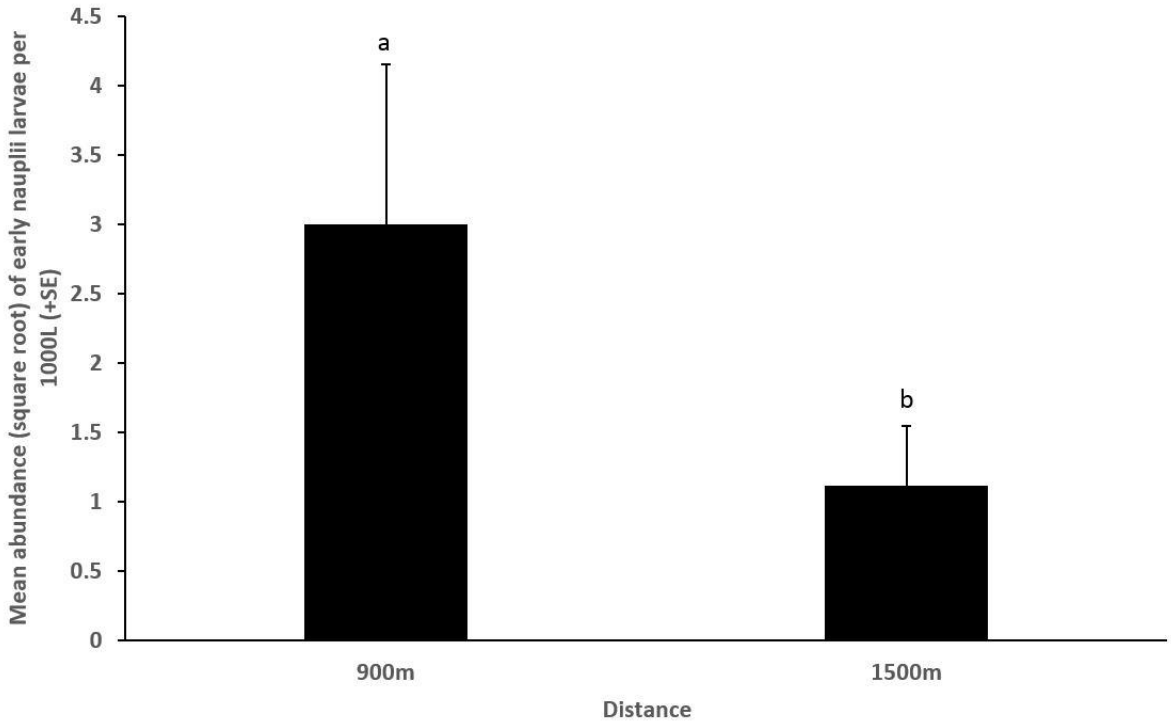

Figure 2.16: Mean abundance of (square root transformed) early nauplii larvae per 1000L collected at two nearshore distances. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by ‘distance’ pair wise test.

Late nauplii (No Cape St Francis)

Cannon Rocks had larger numbers of late nauplii larvae than the other sites, giving a significant effect of site (Figure 2.17; Table 2.15). Abundance of late nauplii also significantly varied over the sites at various depths and distance which was indicated by the significant interaction of all three factors mentioned above (Table 2.15).

Table 2.15: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of early nauplii larvae collected at three sites (Kenton on Sea, Cannon Rocks, and Schoenmakerskop) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	2	10.15	5.08	7.96	*
De - Depth	2	6.64	3.32	5.70	n.s
Di - Distance	2	28.87	14.44	23.94	n.s
Si*De	4	2.33	0.58	0.91	n.s
Si*Di	4	2.41	0.60	0.95	n.s
De*Di	4	1.23	0.31	0.11	n.s
Si*De*Di	8	21.69	2.71	4.25	*
Residual	27	17.22	0.64		
Total	53	90.56			

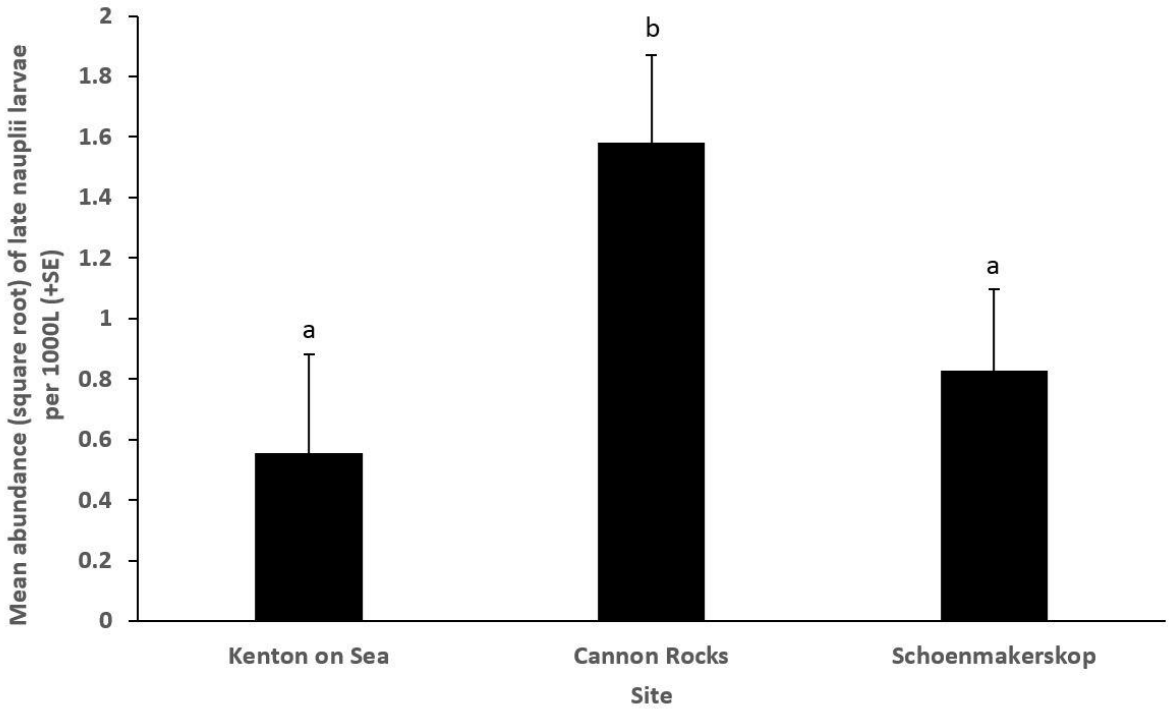

Figure 2.17: Mean abundance of (square root transformed) late nauplii larvae per 1000L collected at three sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by ‘site’ pair wise test.

Late nauplii (No offshore station)

Consistent with the previous analysis for the late nauplii (no Cape St Francis), there was a significantly higher abundance of late nauplii larvae at Cannon Rocks as compared to the other sites, whether the site, Cape St Francis, was included in the analysis or not (Figures 2.17 & 2.18; Tables 2.15 & 2.16). Overall, there was a variation in the number of larvae across all sites, at the various distances and depths, which yielded a significant effect of the interaction for all factors (Table 2.16).

Table 2.16: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of late nauplii larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	18.83	6.28	8.94	*
De - Depth	2	12.78	6.39	3.51	n.s
Di - Distance	1	2.65	2.65	2.61	n.s
Si*De	6	10.93	1.82	2.60	n.s
Si*Di	3	3.05	1.01	1.45	n.s
De*Di	2	0.76	0.38	0.17	n.s
Si*De*Di	6	13.31	2.22	3.16	*
Residual	24	16.85	0.70		
Total	47	79.15			

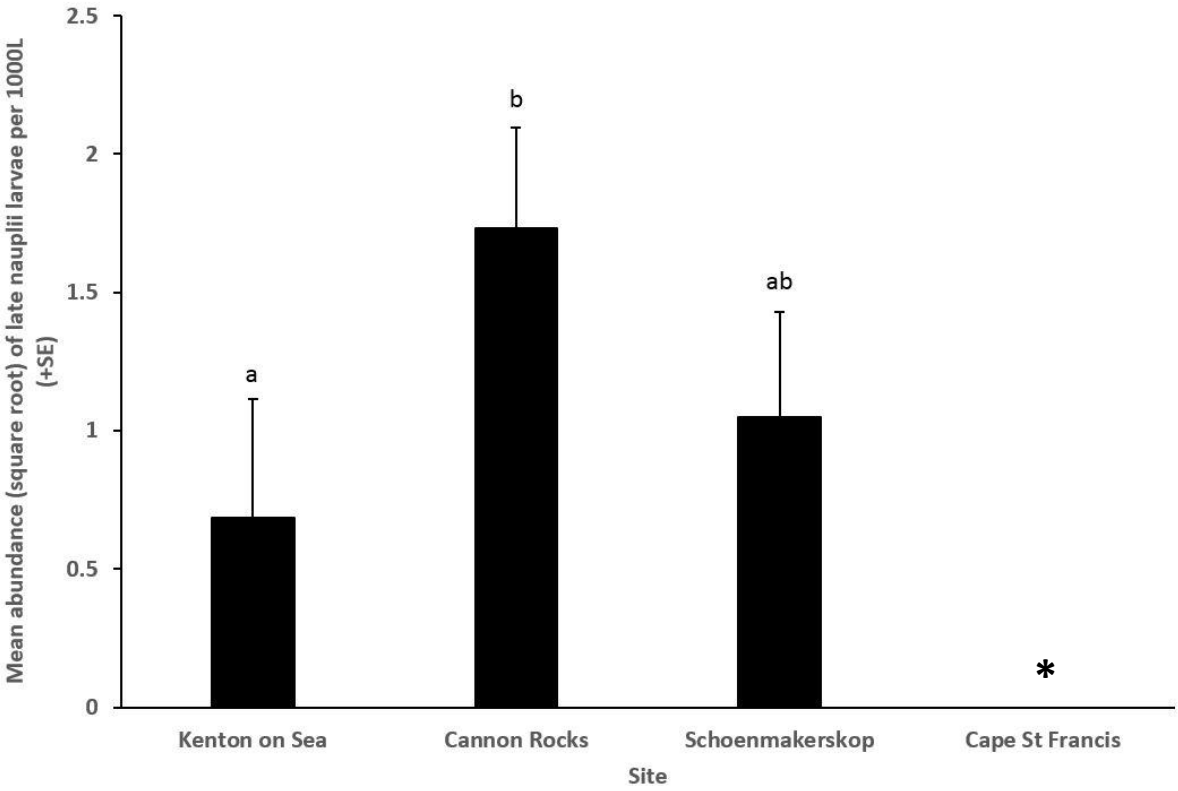

Figure 2.18: Mean abundance of (square root transformed) late nauplii larvae per 1000L collected at three sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by 'site' pair wise test. '*' indicates that no larvae were captured.

Cyprid larvae (No Cape St Francis)

Only the factor site had a significant effect (Table 2.17). Schoenmakerskop was the site that presented the highest number of cyprid larvae (Figure 2.19; Table 2.17).

Table 2.17: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of cyprid larvae collected at three sites (Kenton on Sea, Cannon Rocks, and Schoenmakerskop) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	2	97.11	48.55	19.48	*
De - Depth	2	10.28	5.14	1.73	n.s
Di - Distance	2	44.04	22.02	6.84	n.s
Si*De	4	11.87	2.97	1.19	n.s
Si*Di	4	12.88	3.22	1.29	n.s
De*Di	4	21.44	5.36	0.89	n.s
Si*De*Di	8	47.94	5.99	2.41	n.s
Residual	27	67.29	2.49		
Total	53	312.83			

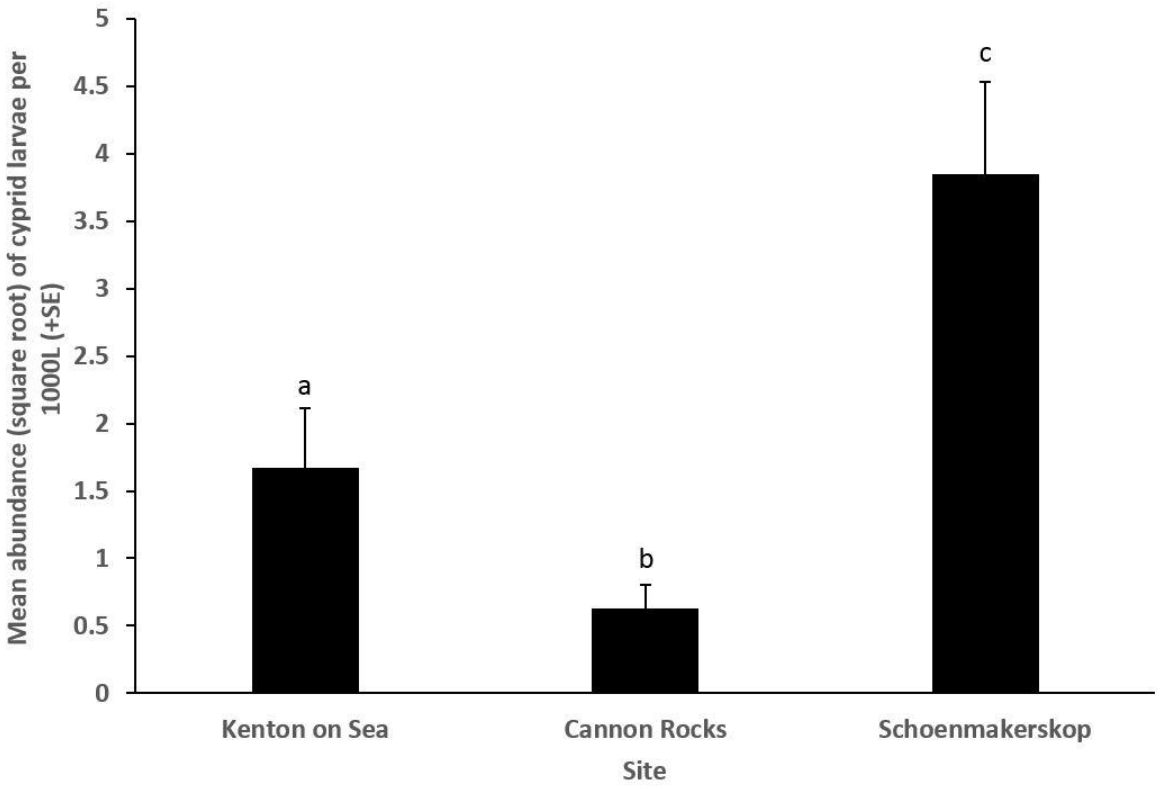

Figure 2.19: Mean abundance of (square root transformed) cyprid larvae per 1000L collected at three sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by 'site' pair wise test.

Cyprid larvae (No offshore station)

As with the previous analysis of cyprid larvae (no offshore station), only the site effect was significant, with a high abundance of larvae in Cape St Francis (Figure 2.20; Table 2.18). Noteworthy was also a geographical separation of sites, with cyprid larvae being more abundant in Cape St Francis and Schoenmakerskop (west of Algoa Bay) than Cannon Rocks and Kenton on Sea (east of Algoa Bay).

Table 2.18: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of late nauplii larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	153.48	51.16	25.66	*
De - Depth	2	42.58	21.29	10.98	n.s
Di - Distance	1	28.22	28.22	4.38	n.s
Si*De	6	11.63	1.94	0.97	n.s
Si*Di	3	19.33	6.44	3.23	n.s
De*Di	2	47.25	23.63	8.14	n.s
Si*De*Di	6	17.42	2.90	1.46	n.s
Residual	24	47.85	1.99		
Total	47	367.77			

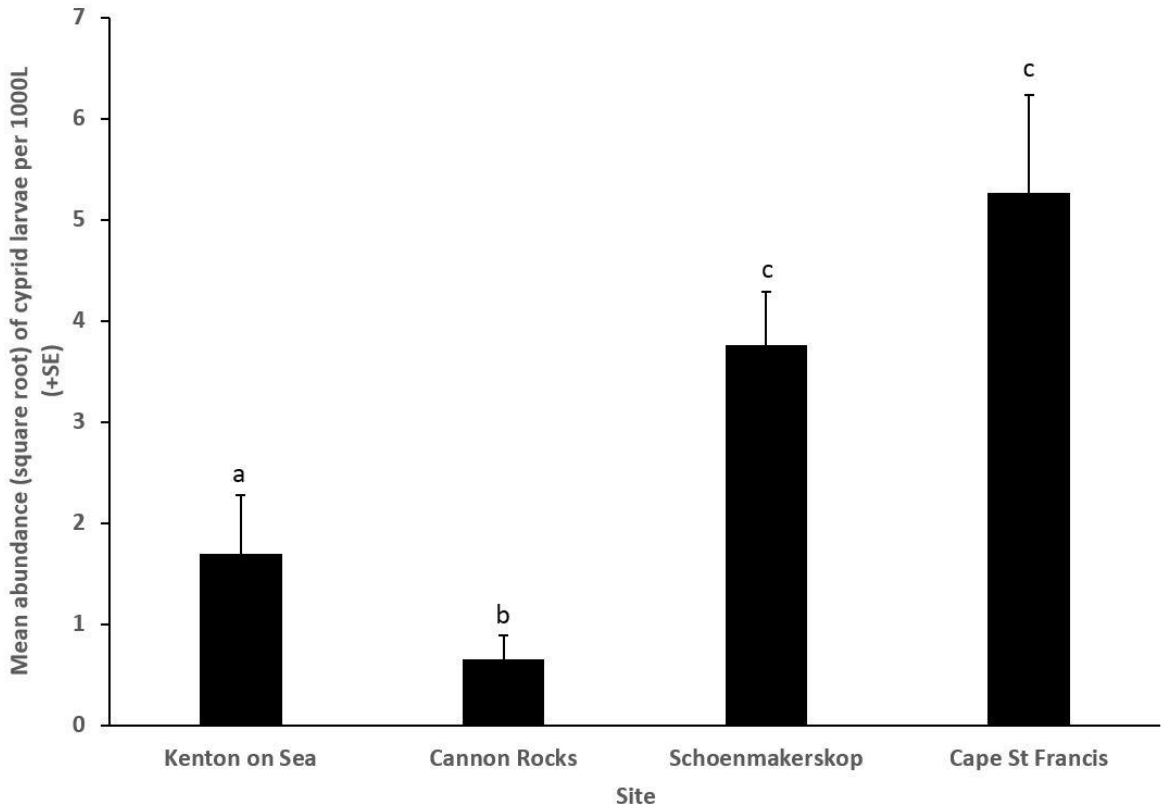

Figure 2.20: Mean abundance of (square root transformed) cyprid larvae per 1000L collected at four sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by 'site' pair wise test.

2.3.2 Season 2

Total larval abundance

Results from the Permutational Multivariate Analysis of Variance (PERMANOVA) revealed a significant effect of depth at certain sites (significant site*depth interaction), with a high larval abundance at the thermocline and low numbers at the surface across all four sites, particularly Kenton on Sea and Cannon Rocks (Table 2.19; Figure 2.21). Cannon Rocks had the highest abundances of larvae during "season two" (significant site effect, Table 2.19; Figure 2.21). There was a clear separation of sites, where Kenton on Sea and Cannon Rocks (both east of Algoa Bay) had higher abundances of larvae than Schoenmakerskop and Cape St Francis (both west of Algoa Bay). There was also a significant effect of site and distance, with the 2400m distance having the highest abundances of larvae at Cannon Rocks (Table 2.19; Figure 2.22). Overall however, the number of total larvae varied with depth and distance over the four sites, which was confirmed by the significant effect of site, depth and distance (Table 2.19; Figures 2.21 & 2.22). The dbRDA plot showed that 20.3% of total variation was explained by temperature and speed for larvae at the surface and turbidity, temperature and fluorescence for both the larval assemblages at the thermocline and bottom (Figure 2.23).

Table 2.19: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of total larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	P
Si - Site	3	14668	4889.3	6.17	*
De - Depth	2	33824	16912	5.59	*
Di - Distance	2	8077.5	4038.8	1.67	n.s
Si*De	6	18156	3026.1	3.82	*
Si*Di	6	14557	2426.2	3.06	*
De*Di	4	9680.8	2420.2	1.47	n.s
Si*De*Di	12	19790	1649.2	2.08	*
Residual	36	28531	792.54		
Total	71	1.4729E5			

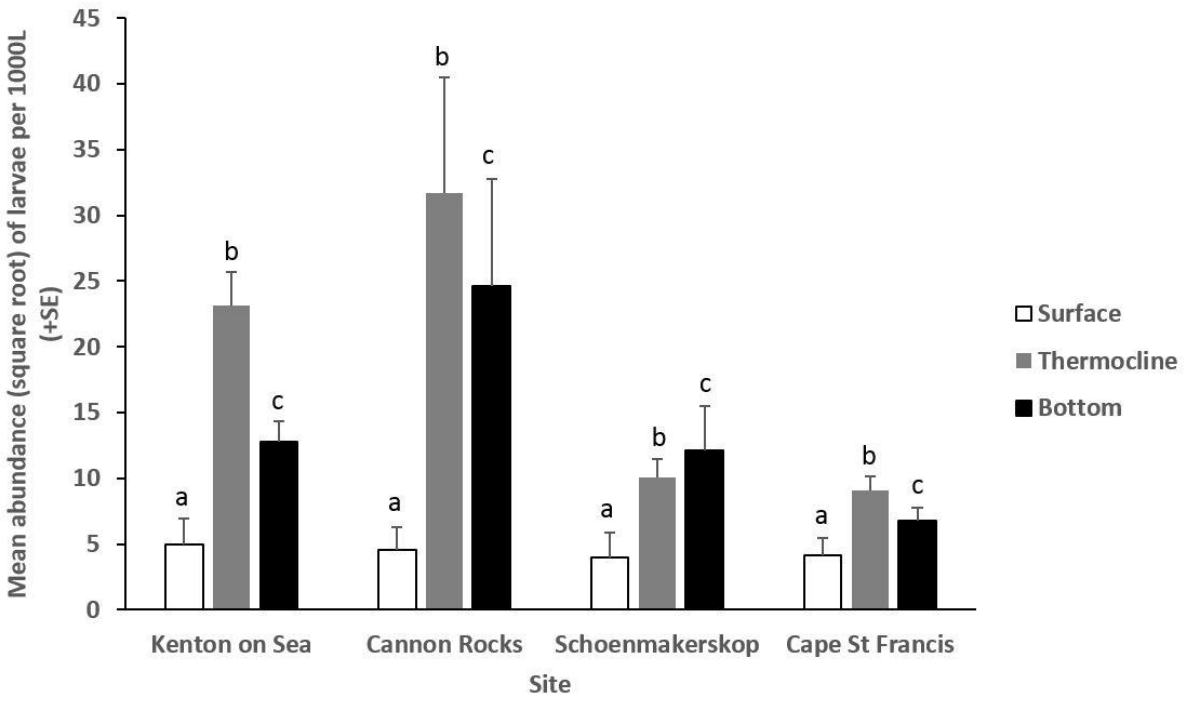

Figure 2.21: Mean abundance of (square root transformed) total larvae per 1000L collected at three depths at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*depth' pair wise test.

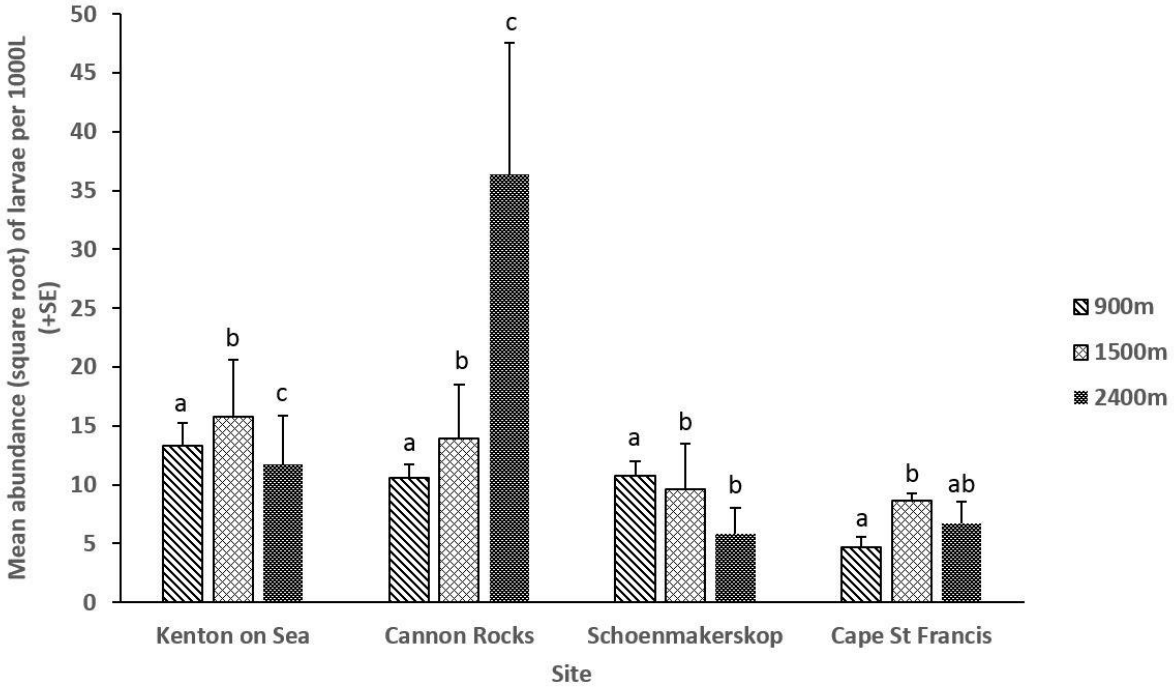

Figure 2.22: Mean abundance of (square root transformed) total larvae per 1000L collected at three nearshore distances, at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*distance' pair wise test.

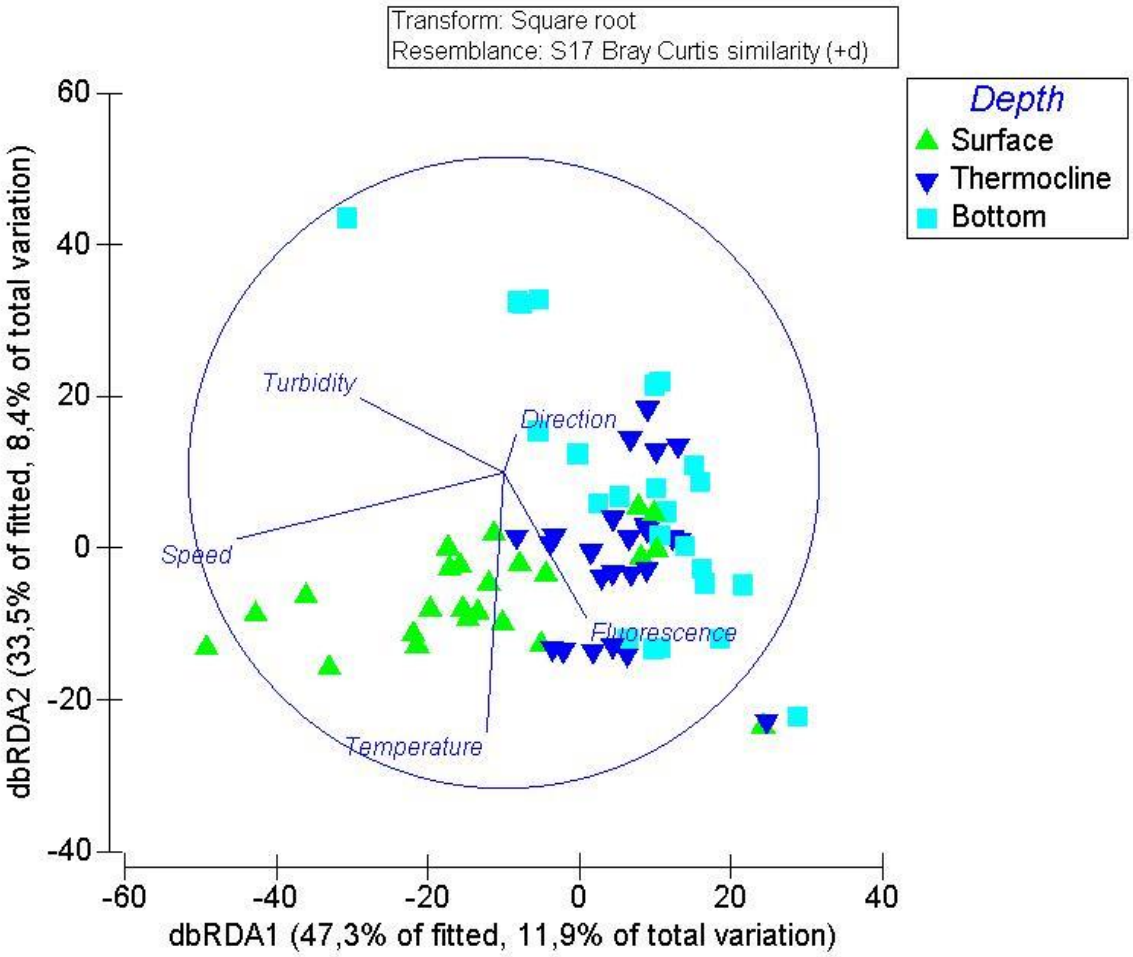

Figure 2.23: Distance based redundancy analysis (dbRDA) plot of the DistLM to show the relationship between 'Full taxa' larvae (derived from a Bray-Curtis similarity matrix of data that had been square root transformed) and the physical parameters. Length and direction of vectors show the strength and direction of the relationship with regards to the larvae and the percentages indicate total variation explained by each axis.

***Perna perna* larvae**

Generally, Cannon Rocks had the highest number of larvae, as confirmed by the significant effect of site (Table 2.20; Figures 2.24 & 2.25). Within this taxon, there was also a separation of sites with Kenton on Sea and Cannon Rocks, both east of Algoa Bay, presenting the highest numbers of larvae, while Schoenmakerskop and Cape St Francis, both west of Algoa Bay, had the lowest numbers. The highest abundances of *Perna perna* larvae were located in the thermocline depth for all sites but Cape St Francis (significant site and depth interaction, Table 2.20; Figure 2.24). Abundance of *Perna perna* larvae also varied according to distance among the sites, as was confirmed by the significant effect of the interaction site*distance (Table 2.20; Figure 2.25). Overall, there were variable numbers of larvae at different depths and distances among the four sites, which was affirmed by the significant effect of the interaction between all three factors (Table 2.20)

Table 2.20: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of *Perna perna* larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	104.36	34.79	19.62	*
De - Depth	2	34.50	17.25	2.00	n.s
Di - Distance	2	8.84	4.42	0.15	n.s
Si*De	6	51.73	8.62	4.86	*
Si*Di	6	172.78	28.80	16.24	*
De*Di	4	20.21	5.05	0.70	n.s
Si*De*Di	12	86.16	7.18	4.05	*
Residual	36	63.82	1.77		
Total	71	542.4			

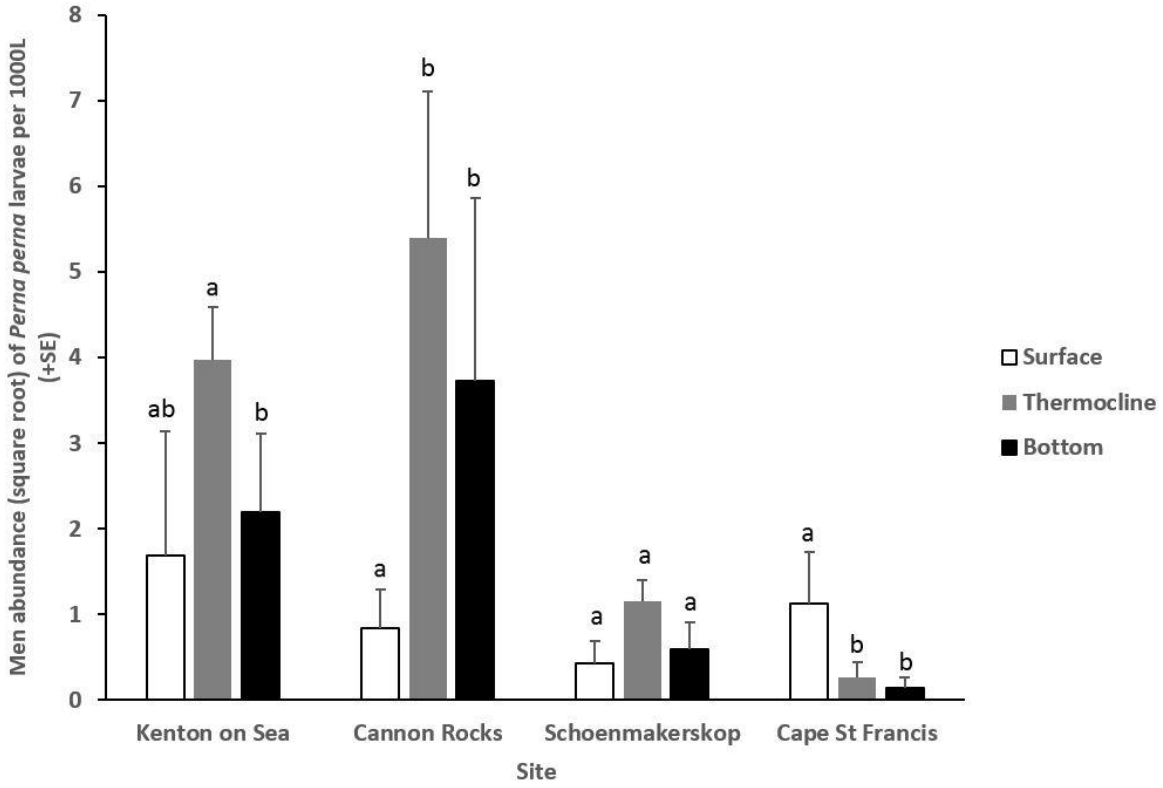

Figure 2.24: Mean abundance of (square root transformed) *Perna perna* larvae per 1000L collected at three depths, at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by site*depth pair wise test.

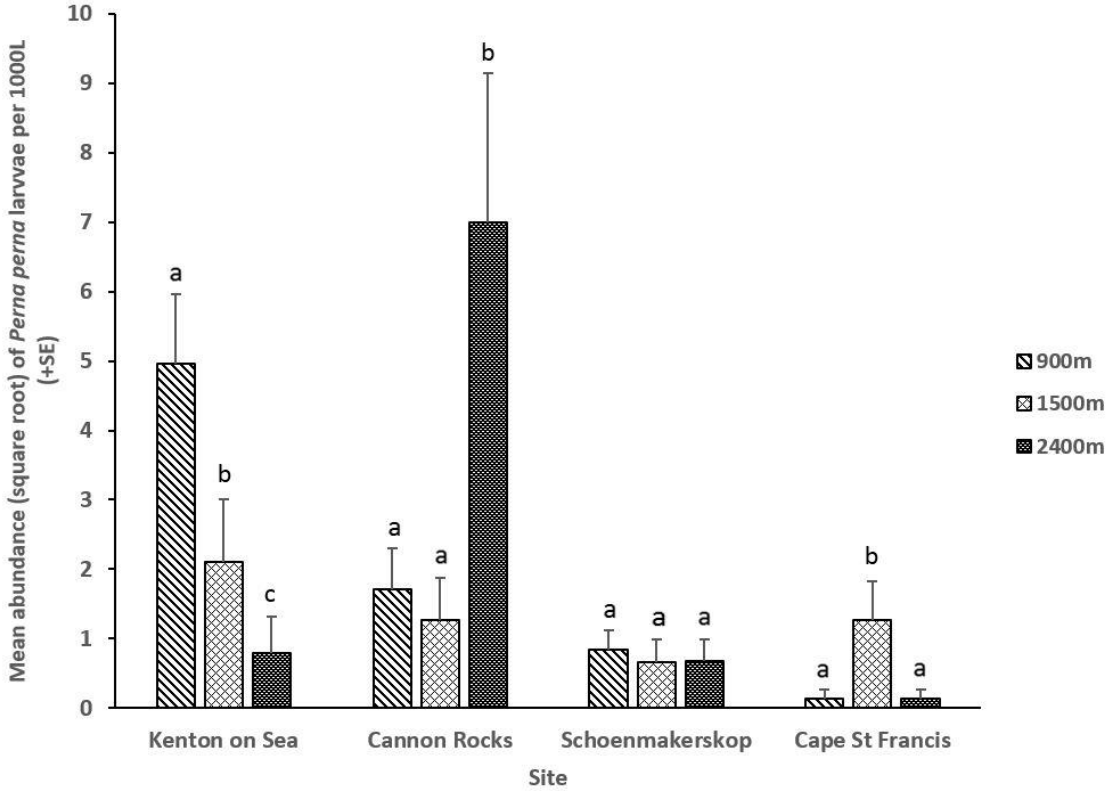

Figure 2.25: Mean abundance of (square root transformed) *Perna perna* larvae per 1000L collected at three nearshore distances, at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by site*distance pair wise test.

Mytilus galloprovincialis larvae

The abundances of *Mytilus galloprovincialis* larvae were high in the thermocline and quite low at the surface at all sites, but the difference between the two was significant only at Kenton on Sea, giving a significant effect of the site and depth interaction (Figure 2.26; Table 2.21). There was a significant effect of site and distance, with no consistent trend, highlighting the variability in the abundances of larvae among the three nearshore distances (Figure 2.27; Table 2.21). Kenton on Sea had the highest abundances of *M. galloprovincialis* larvae for both depth and distance factors (Figure 2.26 & 2.27). There was also a geographical separation of sites, with the highest abundances of larvae being found east of Algoa Bay (i.e. in Kenton on Sea and Cannon Rocks) and the lowest abundances to the west of Algoa Bay (i.e. in Schoenmakerskop and Cape St Francis, Figure 2.26 & 2.27). Overall for this taxon, there was variability of abundance of larvae for distances and depths among each site, which was explained by the significant interaction of all three factors (Figure 2.26 & 2.27; Table 2.21).

Table 2.21: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of *Mytilus galloprovincialis* larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	85.11	28.37	20,71	*
De - Depth	2	134.28	67.12	7,09	n.s
Di - Distance	2	2.31	1.16	0,13	n.s
Si*De	6	56.82	9.47	6,91	*
Si*Di	6	52.66	8.78	6,41	*
De*Di	4	15.52	3.88	0,77	n.s
Si*De*Di	12	60.76	5.06	3,70	*
Residual	36	49.31	1.37		
Total	71	456.76			

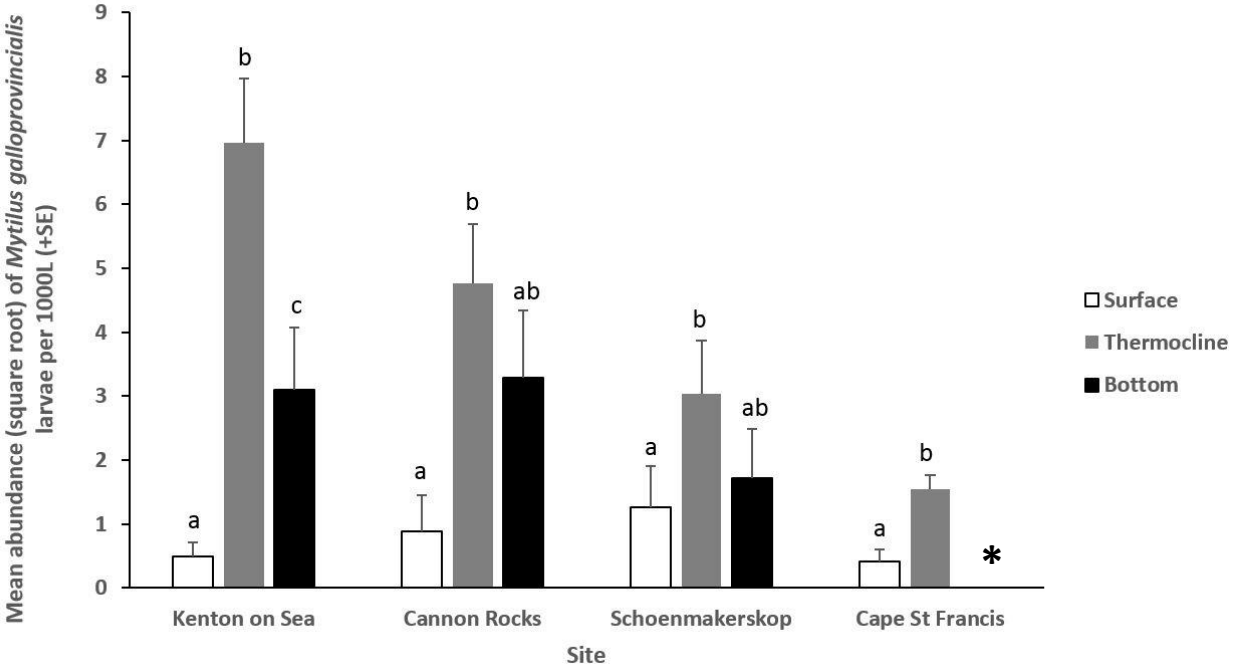

Figure 2.26: Mean abundance of (square root transformed) *Mytilus galloprovincialis* larvae per 1000L collected at three depths at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*depth' pair wise test. '*' indicates that no larvae were captured.

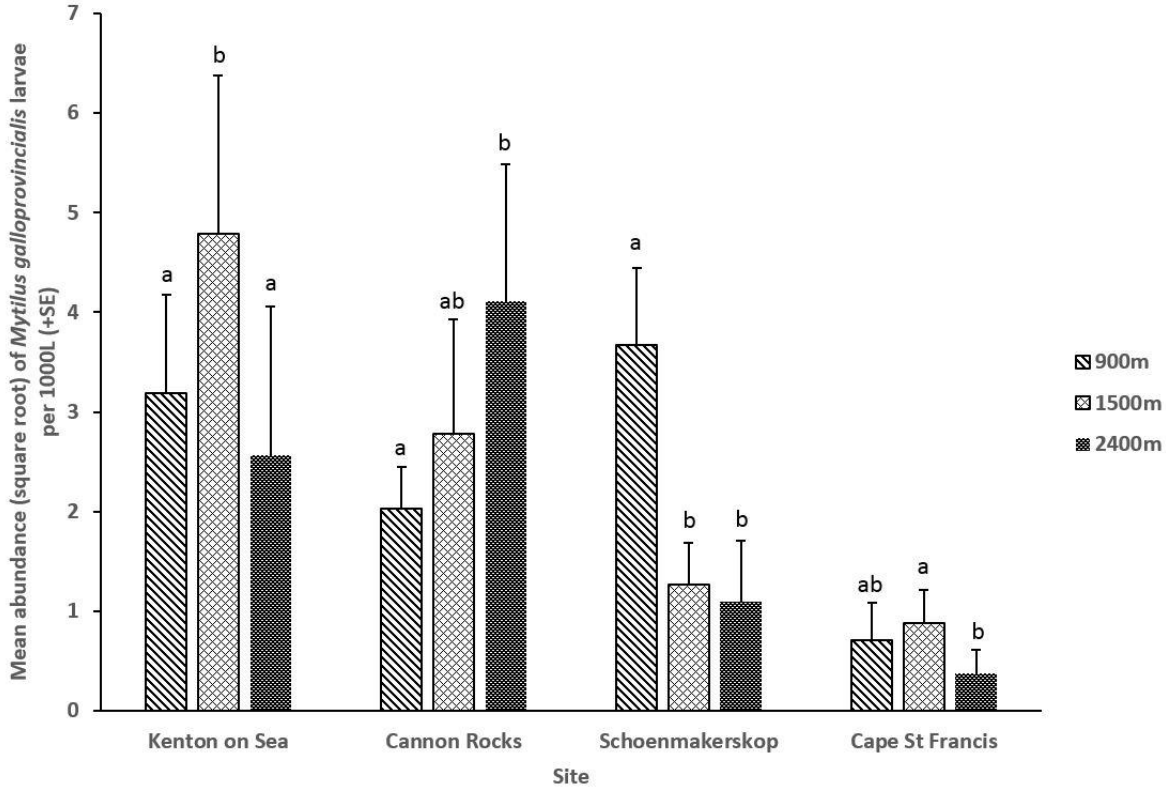

Figure 2.27: Mean abundance of (square root transformed) *Mytilus galloprovincialis* larvae per 1000L collected at three nearshore distances, at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*distance' pair wise test.

Oyster larvae

The outcome of the univariate PERMANOVA on the abundance of oyster larvae revealed that the number of larvae varied at different depths and distances over the four sites, which resulted in a significant three-way interaction (Figures 2.28 & 2.29 Table 2.22). There was also a significant effect between site and depth, where numbers of larvae were highest at the bottom depth in Cannon Rocks (Table 2.22; Figure 2.28). Noteworthy, there was a geographical separation of increased and uniform abundances of oyster larvae at the thermocline and bottom for the sites east of Algoa Bay (Kenton on Sea/Cannon Rocks), while west of Algoa Bay, abundance followed a (significant) gradient, with larvae increasing from the surface to the bottom (Schoenmakerskop/Cape St Francis; Figure 2.28). Due to slightly variable peaks in abundance of oyster larvae at different distances (2400m had the highest), there was a significant interaction of site and distance, which was likely caused by the high numbers at 2400m in Cannon Rocks (Figure 2.29; Table 2.22). Finally, Cannon Rocks had significantly more oyster larvae than any other site, and this was supported by the significant effect of site (Figures 2.28 & 2.29; Table 2.22).

Table 2.22: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of oyster larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	789.06	263.02	109.57	*
De - Depth	2	539.46	269.73	4.09	n.s
Di - Distance	2	366.8	183.4	1.10	n.s
Si*De	6	396	66.00	27.50	*
Si*Di	6	1003.1	167.18	69.65	*
De*Di	4	257.08	64.27	1.42	n.s
Si*De*Di	12	542.54	45.21	18.84	*
Residual	36	86.41	2.40		
Total	71	3980.4			

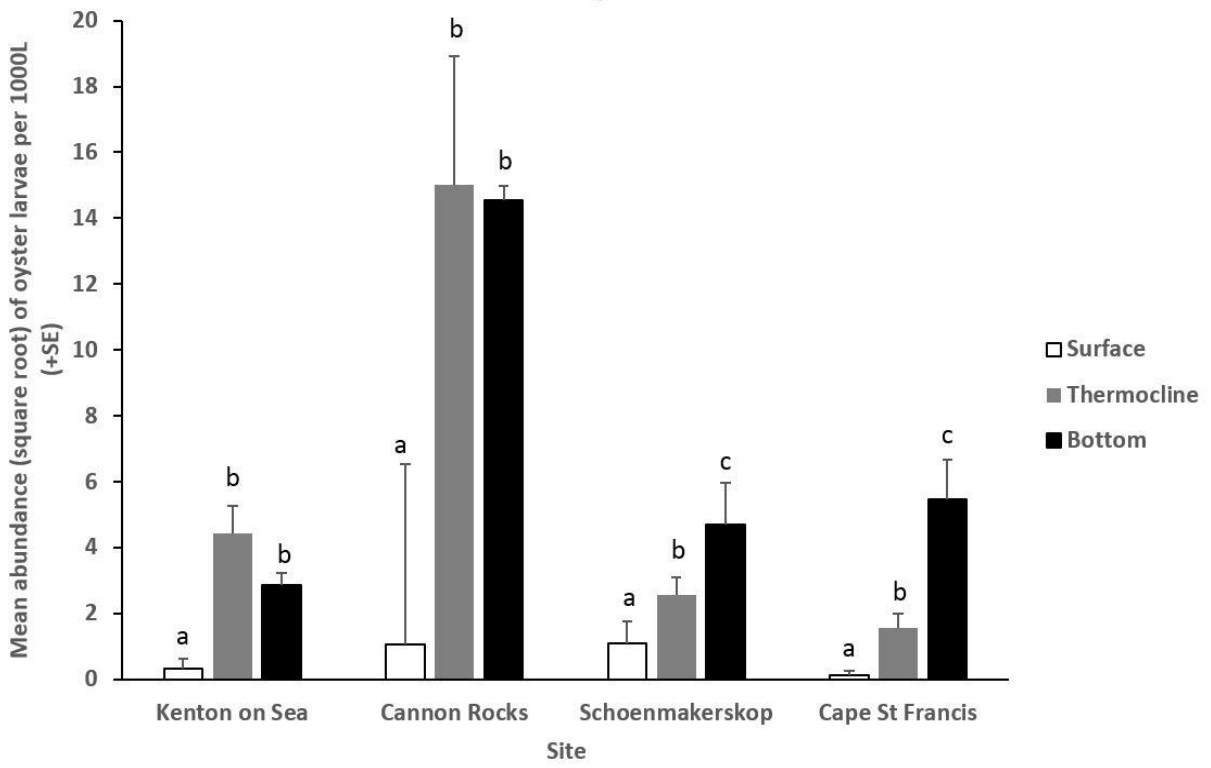

Figure 2.28: Mean abundance of (square root transformed) oyster larvae per 1000L collected at three depths at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*depth' pair wise test.

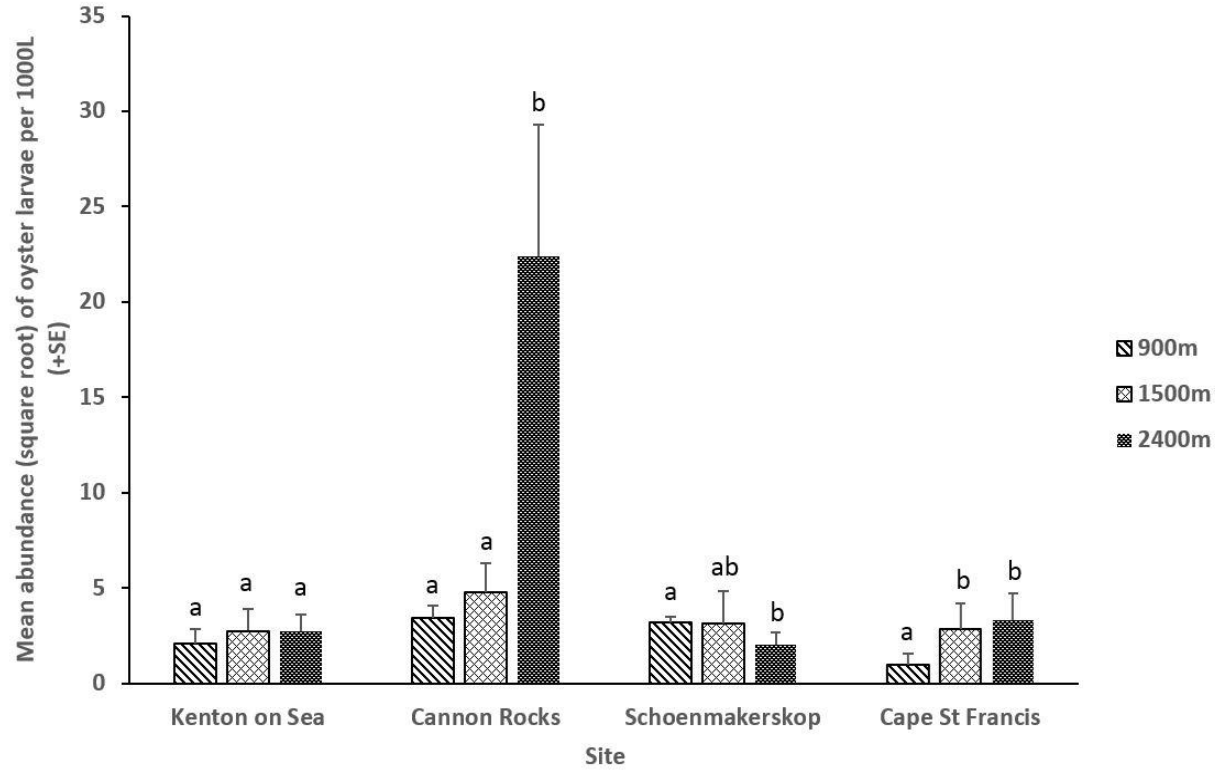

Figure 2.29: Mean abundance of (square root transformed) oyster larvae per 1000L collected at three nearshore distances, at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*distance' pair wise tests.

Early nauplii larvae

The numbers of early nauplii larvae varied among sites and distances, which was affirmed by the significant effect between site and distance (Figure 2.30; Table 2.23). This is the only taxon which did not show a significant effect of site, the combination of site and depth or the interaction for all three factors (Table 2.23).

Table 2.23: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of early nauplii larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	16.67	5.56	2.90	n.s
De - Depth	2	12.22	6.11	6.82	n.s
Di - Distance	2	18.40	9.20	0.84	n.s
Si*De	6	5.37	0.90	0.47	n.s
Si*Di	6	65.99	11.00	5.74	*
De*Di	4	1.00	0.25	0.19	n.s
Si*De*Di	12	16.05	1.34	0.70	n.s
Residual	36	68.95	1.92		
Total	71	204.65			

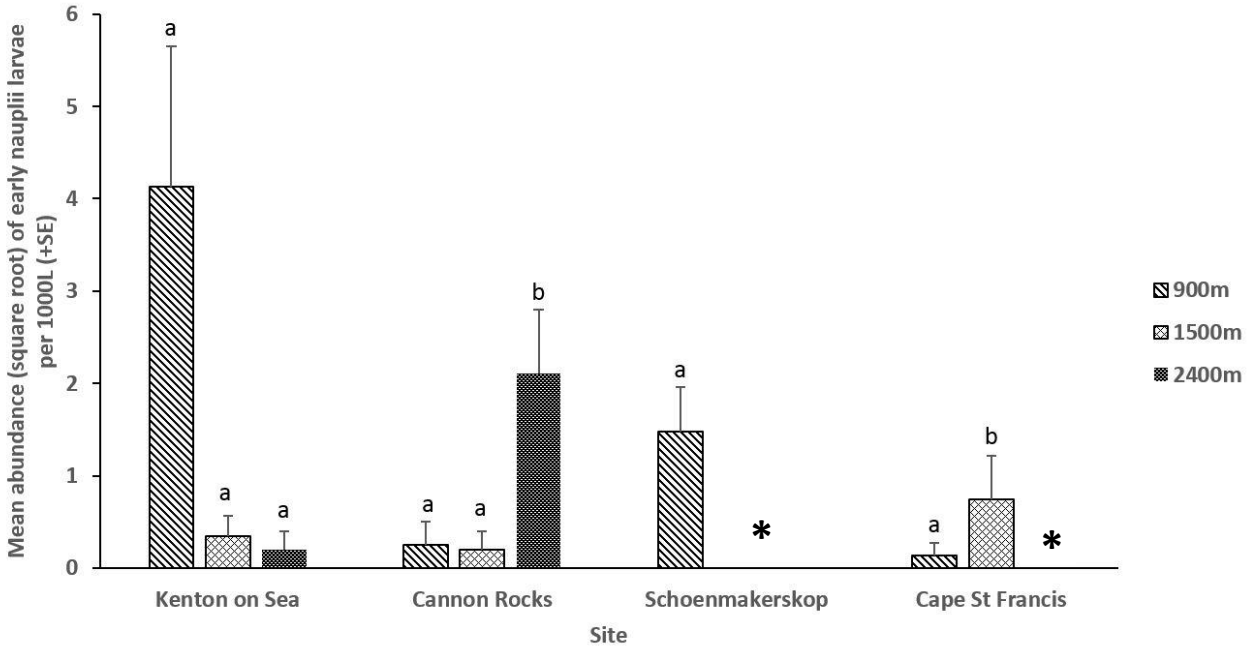

Figure 2.30: Mean abundance of (square root transformed) early nauplii larvae per 1000L collected at three nearshore distances, at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*distance' pair wise test. '*' indicates that no larvae were captured.

Late nauplii larvae

The outcome of the univariate PERMANOVA (Table 2.24) on the abundance of late nauplii larvae showed a significant effect of the interaction between site and depth, which was confirmed by the overall varying pattern of the late nauplii larvae during the sampling period at the four sites, although there was a consistent trend of higher abundances at the thermocline and bottom than at the surface (Figure 2.31). The number of late nauplii larvae also differed inconsistently among the three distances and the four sites, as confirmed by the significant effect of the interaction of site and distance (Figure 2.32; Table 2.24). Cannon Rocks generally had the highest abundances of late nauplii larvae, which was authenticated by the significant effect of site (Figure 2.33; Table 2.24). Although depth and distance had no significant effects (Table 2.24), there were variable peaks in abundance, visually, for thermocline and 2400m (Figures 2.31 & 2.32). The assorted pattern of abundance among site, depth and distance for the late nauplii (Figures 2.31 & 2.32) caused a significant effect three-way interaction (Table 2.24).

Table 2.24: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of late nauplii larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	10.47	3.49	7.09	*
De - Depth	2	11.23	5.62	1.64	n.s
Di - Distance	2	4.39	2.19	0.29	n.s
Si*De	6	20.57	3.43	6.96	*
Si*Di	6	44.75	7.46	15.15	*
De*Di	4	7.389	1.85	0.85	n.s
Si*De*Di	12	26.11	2.18	4.42	*
Residual	36	17.72	0.49		
Total	71	142.63			

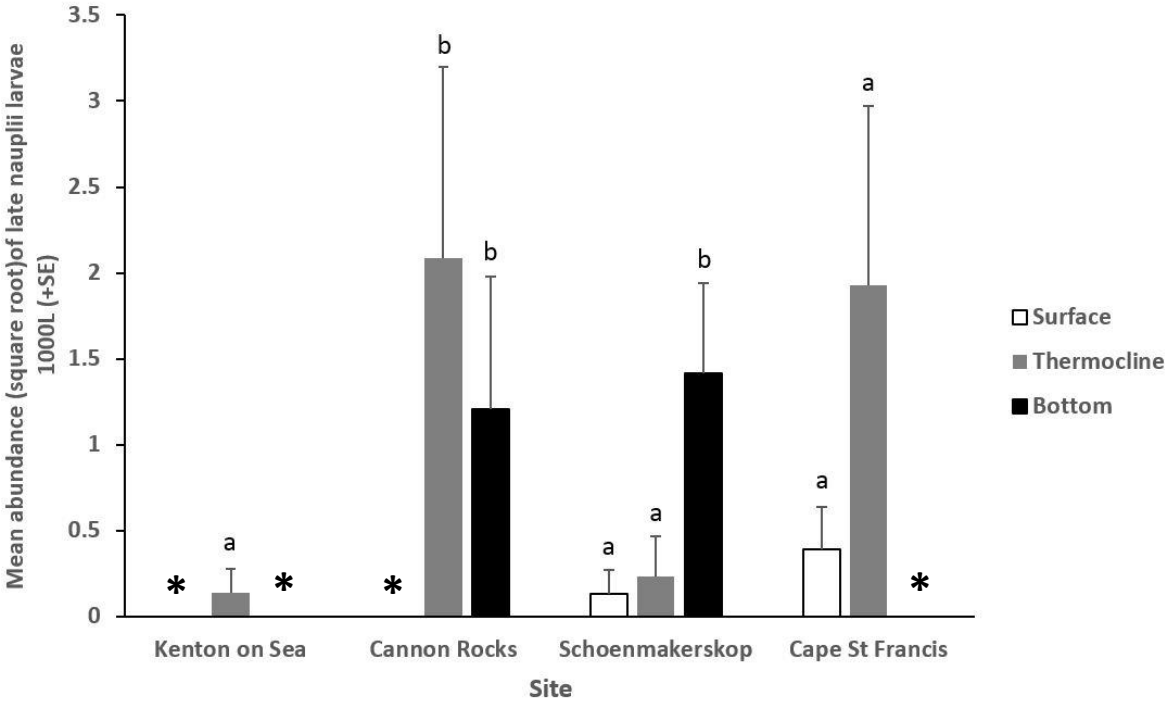

Figure 2.31: Mean abundance of (square root transformed) late nauplii larvae per 1000L collected at three depths at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*depth' pair wise test. '*' indicates that no larvae were captured.

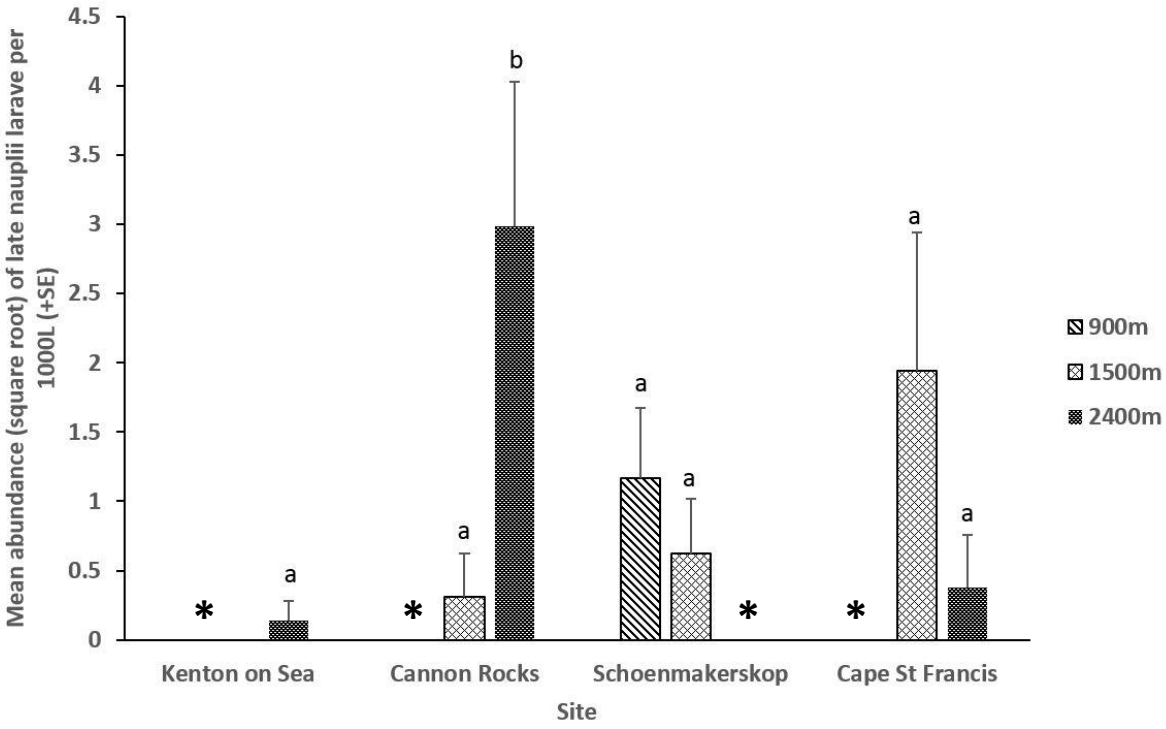

Figure 2.32: Mean abundance of (square root transformed) late nauplii larvae per 1000L collected at three nearshore distances, at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*distance' pair wise test. '*' indicates that no larvae were captured.

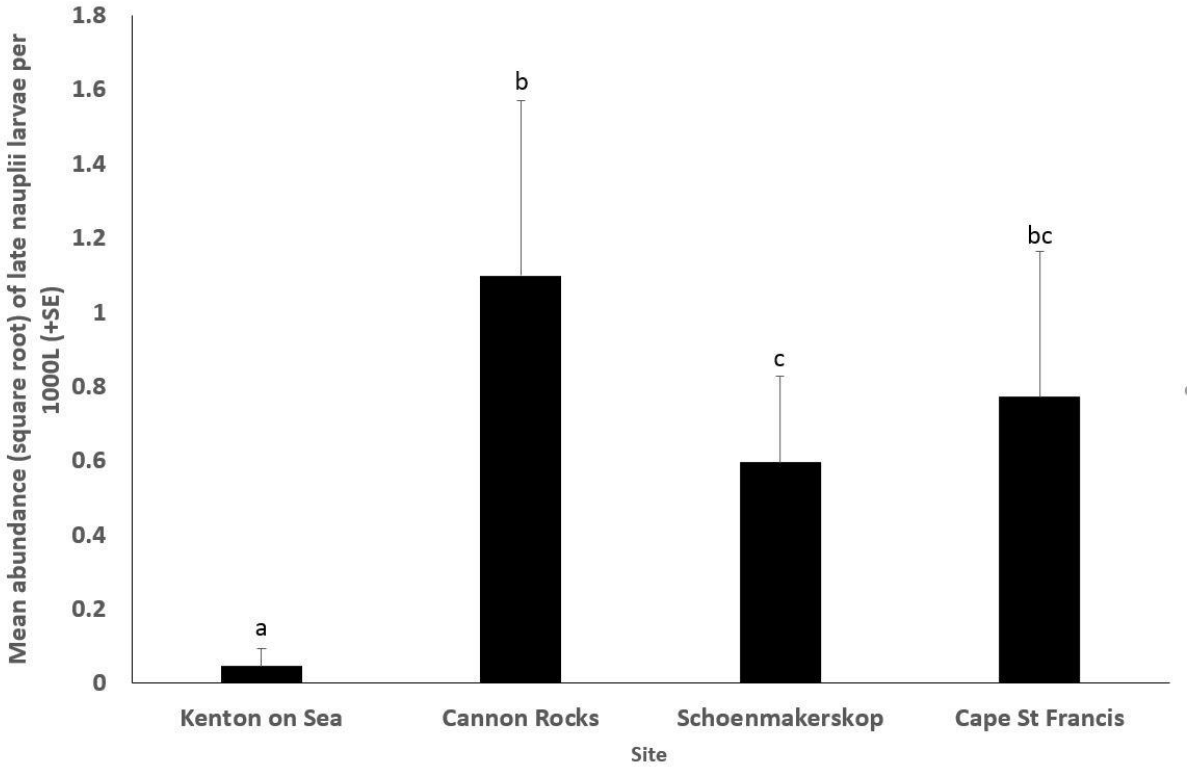

Figure 2.33: Mean abundance of (square root transformed) late nauplii larvae per 1000L collected at four sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by 'site' pair wise test.

Cyprid larvae

Consistent with the patterns for most of the analysis in the second season discussed above, there was a significant effect of site and depth, with cyprid larvae being more abundant in the bottom depth at Cannon Rocks and Cape St Francis (and even in Kenton on Sea, although highly variable) as compared to other sites and depths (Figure 2.34; Table 2.25). Results from the PERMANOVA also revealed a significant effect of site and distance, which was confirmed by the high abundance of cyprid larvae at the onshore distance (900m) for all sites except Cape St Francis (Figure 2.35; Table 2.25). Overall, however, the abundance of cyprid larvae varied over the different depths and distances, with cyprids being more abundant at particular depths and distances at the different sites (significant site, depth and distance interaction; Table 2.25).

Table 2.25: Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) examining the effects of site, depth and distance on the abundance (square root transformed) of cyprid larvae collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis) Df - Degrees of freedom; SS - Sum of Squares; MS – Mean Squares; Pseudo-F - F-ratio and p – probability– values; n.s. – non-significant; * = ≤ 0.016.

Source	Df	SS	MS	Pseudo - F	p
Si - Site	3	7.73	2.58	4.22	*
De - Depth	2	14.20	7.10	2.33	n.s
Di - Distance	2	13.70	6.85	1.85	n.s
Si*De	6	18.30	3.05	4.99	*
Si*Di	6	22.25	3.71	6.07	*
De*Di	4	8.08	2.02	1.06	n.s
Si*De*Di	12	22.86	1.91	3.12	*
Residual	36	22.01	0.61		
Total	71	129.12			

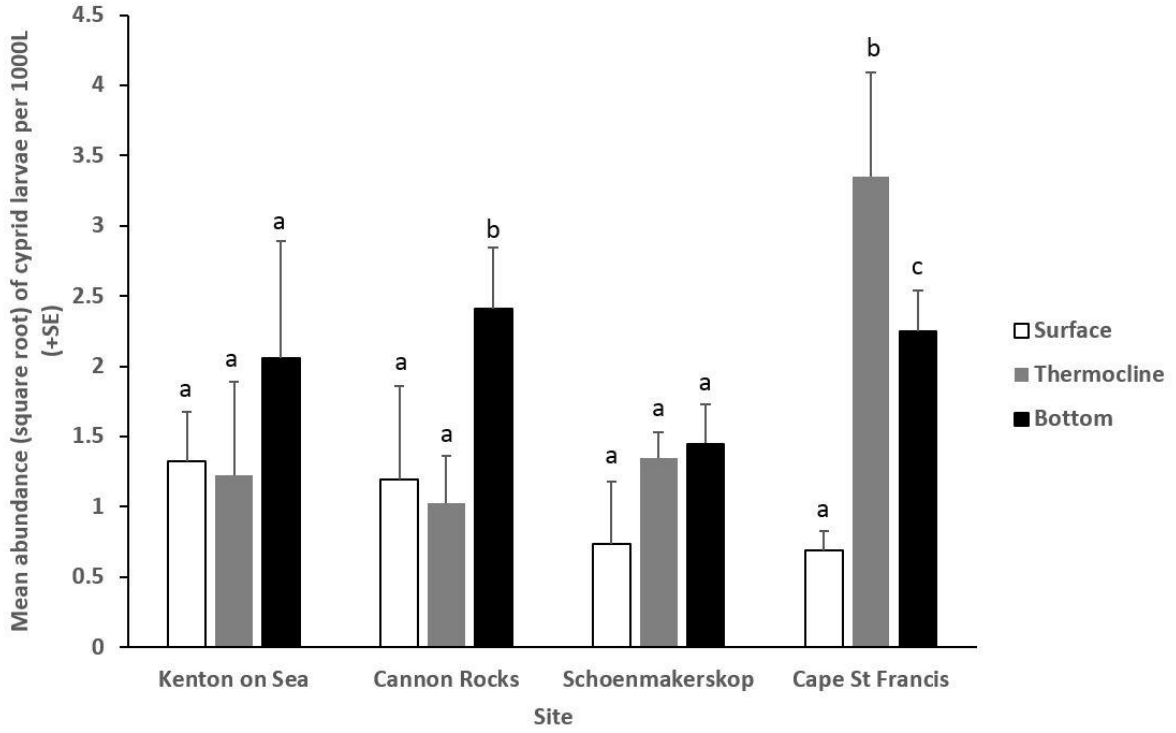

Figure 2.34: Mean abundance of (square root transformed) cyprid larvae per 1000L collected at three depths at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*depth' pair wise test.

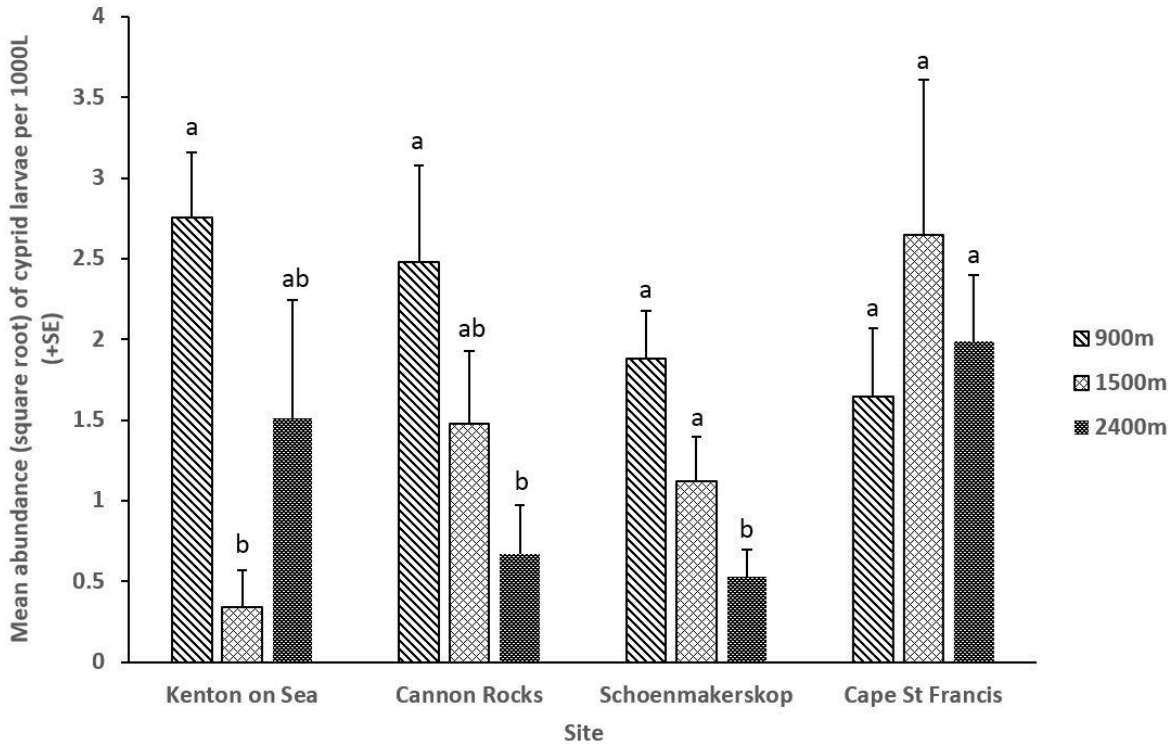

Figure 2.35: Mean abundance of (square root transformed) cyprid larvae per 1000L collected at three nearshore distances, at four sites. Error bars indicate standard errors and letters above the bar plots indicate within-site homogenous groups identified by 'site*distance' pair wise test.

Overall summary of results

Generally, the results from the PERMANOVA analyses showed that most taxa from both seasons exhibited significant site and depth interactions, except for the 'early nauplii' taxon. Nearly all taxa were found within the thermocline, with the exception of 'oysters' and 'cyprids' which were found at thermocline to bottom. The distribution of larvae according to distance had a variable pattern too in relation to site, although generally most larvae were detected at the offshore station (2400m), and the least in midshore (1500m) station. The pattern though seemed to vary according to taxon. There was a clear significant effect of site for nearly all analyses, with the most larvae being located at Cannon Rocks and Kenton on Sea followed by Schoenmakerskop then Cape St Francis. There was also a broader geographical separation of sites, especially with the total larval abundance, where the number of larvae were high to the east of Algoa Bay (Kenton and Cannon Rocks) and low on the west side of Algoa Bay (Schoenmakerskop and Cape St Francis). Though there was no significant differences, this was also the case for '*Mytilus galloprovincialis*', nevertheless only during "season one". "Season two" was the complete opposite (i.e. high abundance of larvae to the east of Algoa Bay).

2.4 Discussion

There was site variability for the whole sampling period, however Cannon Rocks was overall the site that presented the highest numbers of invertebrate larvae. Given the very nearshore scales of the study, there is a strong possibility of coupling of mechanisms that may have been at play during the sampling period in Cannon Rocks, such as local hydrodynamics which could have caused localised and differential abundance of larvae (Porri *et al*., 2006). Large scale mechanisms, such as the Agulhas current, can also alter larval transport and therefore can buffer if not suppress consistent local effects (Porri *et al*., 2014). Similar patterns have been observed both locally and internationally, with nearshore mechanisms helping to explain the distribution of larvae in a specific region (Pineda, 2000; Shanks *et al*., 2003; McQuaid and Lawrie, 2005; Pineda *et al*., 2007; Morgan *et al*., 2009; Duna, 2015; Shanks and Shearman, 2009; Weidberg *et al*., 2015; Morgan *et al*., 2018)

Generally, the results of this study highlight that larval abundance of most examined taxa varied according to site and depth during both sampling periods. Most of the larvae were located within the thermocline. Larval concentrations can increase at the thermocline, however some studies found the vertical distribution of larvae independent of thermal stratification and rather more associated with onshore transportation (Pineda and López, 2002; Gray and Kingsford, 2003). Association with specific depths is not uncommon, as zooplankton vertically migrate to lower depths within the water column to avoid predation from the surface during the day (Zaret and Suffern 1976; Lampert 1989; Loose and Dawidowicz, 1994; dos Santos *et al*., 2008). Vertical migration though is dependent on species and its ontogenetic phases. Cyprids were mostly associated with the bottom, while nauplii (early and late) were found in both thermocline and bottom depths. Nauplii have been observed to be located between mid and near-bottom depths (Shanks and Shearman, 2009, Morgan and Fisher, 2010), but can also occur closer to the surface due to a phototactic response that is intensified by starvation (Tapia *et al*., 2010).

Cyprids are lecithotropic (which makes them depend on the food reserves accumulated during the naupliar stages) and become specialised (for searching suitable substratum) just prior to benthic settlement (Walker 1987). Cooler temperatures at the bottom depths may explain the cyprid occurrence near the bottom (Tapia *et al*., 2010) as the metabolic rates and use of energy reserves slow down, enabling them to survive longer in the water prior to settlement (Enright, 1977). Overall, bottom temperatures varied during this study, ranging between 19.6°C – 8.7°C, however, the highest abundance of cyprids occurred between 17.0°C – 13.7°C in Cape St

Francis during the first sampling season, which may be the optimum temperature for survival of cyprids for this region, however this was not tested.

There was also an association of distance from shore and barnacle larvae, with cyprids generally located inshore, whilst early and late nauplii had an ubiquitous distribution, both occurring inshore and offshore. Similar patterns have been observed in other studies elsewhere where early nauplii have a wider cross-shore distribution than cyprids, while cyprids are more concentrated within the inshore (Tapia and Pineda, 2007; Hagerty *et al*., 2018). Thermal stratification can also be one of the key determinants which influences cross-shore transport and distribution as temperature evokes behaviour in barnacle larvae especially cyprids (Tapia and Pineda, 2007; Tapia *et al*., 2010; Hagerty *et al*., 2018; Pineda *et al*., 2018). Such ontogenetic shifts in relation to cross-shore distribution of larvae have been previously observed for the same taxon, in the same area as the current research (Mian, 2015). High numbers of nauplii (early and late) were found to the east of Algoa Bay, whilst cyprids were more abundant to the west of Algoa Bay. This regional pattern suggests that the larvae could have been transported alongshore by the westward flowing Agulhas current.

Oyster larvae were also found at the bottom depth and this can possibly be attributed to the density and overall mass of the shells of oysters. As oyster larvae grow, they develop thin shells, which increase the mass and make them to sink to the bottom depth of the water column (Dekshenieks *et al*., 1996). Furthermore, a decrease in salinity decreases larval activity, which lessens the capacity for active swimming and therefore favours passive sinking to the lower water depths (Dekshenieks *et al*., 1996). This was, however, not the case in this study, as salinity rarely differed among the depths, with surface having an average of 35.41g/kg, thermocline 35.35g/kg and bottom 35.27g/kg, making a general average of 35.34g/kg for the water column. A more likely explanation for the high abundance at the bottom depth could be the effect of larval swimming behaviour (North *et al*., 2008)

There was a separation of sites in the number of larvae according to species, with *P. perna* larvae, for both seasons, being more abundant to the east side of Algoa Bay (Kenton on Sea and Cannon Rocks). In contrast, *M. galloprovincialis* larvae had higher abundances to the west side of Algoa Bay (Schoenmakerskop and Cape St Francis) for the first sampling period with the opposite occurring during the second sampling season (i.e. high abundance on the east side of Algoa Bay). This geographic split could be explained by the fact that the epicentre of abundance for *M. galloprovincialis* is around Plettenberg Bay (located in the western region of

the south coast of South Africa), hence possibly corroborating the increased abundance of larvae of this species on the west side of Algoa Bay (von der Meden *et al*., 2008), although not entirely. The distribution of *M. galloprovincialis* is nevertheless site specific and populations are well established in some places, but not in others (Bownes and McQuaid, 2006), potentially explaining the occurrence of higher abundances of *M. galloprovincialis* larvae on the east side of the sampling region during the second season. Also, the lack of matching between the distribution of larvae and adjacent benthic populations has been highlighted before (Porri *et al*., 2006; Pineda *et al.* 2010).

One interesting outcome from all the analyses that were carried out was that there was no significant interaction between the factors depth and distance. A plausible explanation for this development was that the effect of depth prevailed over distance. Bivalve and barnacle larvae have been regarded as passive particles, however they do possess swimming capabilities (Metaxas, 2001). Vertical velocities of water are much slower (~ $2mm.s^{-1}$) than the horizontal currents and therefore larvae may have a better chance of influencing cross-shore and alongshore transport and distribution by altering their vertical position within the water column (Chia *et al*., 1984; Metaxas, 2001). Depending on the ontogenetic stages, larvae generally migrate above or below the Ekman layer during upwelling which causes the larvae to be transported offshore or retained nearshore (Tapia and Pineda, 2007; Morgan *et al*., 2009; Shanks and Shearman, 2009; Morgan and Fisher, 2010). The transportation and distribution of larvae in relation to depth and distance is driven differently depending upon the taxon, ontogenetic stage, behavioural responses and possibly the time of sampling, as specific taxa were found at different depths and distances when compared to the overall total abundance of larvae.

CHAPTER 3

SETTLEMENT AND RECRUITMENT OF BENTHIC INTERTIDAL INVERTEBRATES ON THE SOUTH EAST COAST OF SOUTH AFRICA

3.1 Introduction

For most benthic marine broadcast spawners, including mussels and barnacles, the pelagic larval phase can last from hours, to weeks to months (reviewed in Shanks *et* al, 2003; Fisher *et al*., 2014), but the planktotrophic larvae of mussels spend roughly 5 – 6 weeks in the water column (Kautsky, 1982), while for barnacles, the dispersive phase lasts 4 – 6 weeks (Brown and Roughgarden, 1985; Wares *et al*., 2009). The larval duration of invertebrates in the water column can have an effect on settlement. A short pelagic larval duration may lead to a short dispersal distance which increases the probability of larvae settling close to parental populations (Sponaugle *et al*., 2002). Although there is a broad correlation between pelagic larval duration and dispersal distance (e.g. Kinlan and Gaines 2003), some larvae can exhibit vertical migration behaviour within the water column and therefore can either increase or decrease dispersal distance (Shanks *et al*., 2003). The survival and final transport of the larvae to settlement sites are important determinants of the adult population (Epifanio and Garvine, 2001).

When considering larval connectivity of marine invertebrate populations, it is important to distinguish the processes of settlement and recruitment. Settlement involves competent larvae from the water column actively/passively encountering a suitable substratum, whereupon they may permanently attach to it. This contact can trigger metamorphosis which is followed by further ontogenetic events (Keough and Downes, 1982; Rodriguez *et al*., 1993). Recruitment follows after settlement, when the metamorphosed settlers have survived a period of post-settlement mortality and join the juvenile population on adult sites (Keough and Downes, 1982; McQuaid and Phillips, 2006, Pineda *et al*., 2007). The duration of this period is ill-defined, but it normally reflects a period of particularly high mortality after which rates of mortality decline.

Mussel settlers can attach and detach several times before permanently attaching to a substratum to recruit into the adult population. This theory was suggested by Bayne (1964) as primary and secondary settlement, where larvae attach to filamentous substrata for growth, detach for a secondary pelagic phase, which follows a series of attachments prior to the final settlement within adult mussel beds. Other authors such as Seed (1969) and Widdows (1991) have supported Bayne's (1964) theory with their own work. This theory has however been refuted by several authors, showing that the primary-secondary settlement does not apply universally. There is no empirical evidence of a "mandatory" secondary pelagic phase (Kautsky, 1982) as mussel larvae can settle and recruit directly among the adult beds (Beckley, 1979; McGrath *et al*., 1988 and Lasiak and Barnard, 1995).

The competent larvae of barnacles (cyprids) are lecithotropic and therefore do not feed and are dependent on the energy reserves accumulated during the preceding naupliar stages (Pechenik *et al*., 1998). Cyprids actively search for suitable surfaces to attach to permanently by use of stimuli such as chemical cues given off by the substratum (Pawlik, 1992) or conspecifics (Knight-Jones, 1953), and localised flow environments that will support post settlement growth and survival (Larsson and Jonsson, 2006). Cyprids can delay metamorphosis if suitable conditions or substrata are not encountered (Pechenik *et al*., 1998; Maki *et al*., 1988) however not for long periods, as this delay affects the overall post settlement survival of the juvenile barnacles (Pechenik *et* al., 1993; Larsson and Jonsson, 2006).

As larvae develop and transition from a pelagic way of life in the ocean to a benthic lifestyle in the intertidal, there are several biological, oceanographic and physical factors that influence the final stages of dispersal to settlement sites (Cowen and Sponaugle, 2009). Invertebrate larvae show swimming capabilities by actively or passively controlling benthic delivery through vertical migration in the water column (Genin *et al*., 2005), this increases larval retention in the water, ultimately affecting dispersal just prior settlement to the benthos (Fuchs *et al*., 2004).

The flow of water can affect the settlement of larvae by exerting hydrodynamic forces, which can induce larvae to actively select the substrata best suited for settlement and recruitment into the adult populations (Abelson and Denny, 1997; Larsson and Jonsson, 2006). Larvae require space to settle and the availability of suitable substrata has an influence on the settlement/recruitment of larvae to adult communities. Lack of substratum can also often result in increased settlement per available area, a process described as ‘settlement-intensification” (Pineda and Caswell, 1997; von der Meden *et al*, 2012a). This is however not always the case. *Chamaesipho tasmanica*, an Australian intertidal barnacle, was found to settle and recruit among the adult population due to differential larval supply and adult conspecifics (Jeffery, 2000). The benthic environment also offers chemical cues, and cues by biofilm, settler and adult conspecifics for larvae arriving ashore (Pawlik, 1992; von der Meden *et al*., 2010; Hadfield, 2011).

Research on mussel and barnacle settlement and recruitment in South Africa is relatively extensive (especially for mussels) and has mostly tackled the temporal and spatial variability of such processes (Lasiak and Barnard, 1995; Lawrie and McQuaid, 2001; Porri, 2006; McQuaid and Phillips, 2006; Pfaff *et al*., 2011, 2015; von der Meden, 2012b; Bell *et al*., 2015).

Several studies on settlement and/or recruitment on the south and south east coasts of South Africa have focused on the coastal topography, comparing rates of mussel settlement and recruitment in bays and on the open coast (McQuaid and Phillips, 2006; von der Meden, 2012b). The present study follows the alongshore approach (Porri *et al.*, 2006; Porri *et al*., 2014) taken and explained in the previous chapter on larval transport, where alongshore spatial and temporal scales of larval delivery of intertidal mussels and barnacles were investigated on the south east coast of South Africa. For this study, focus was given to comparing larval settlement and recruitment on a stretch of open coast of approximately 180km. Given that settlement and recruitment of intertidal organisms can vary from scales of 100s of meters (Porri et al., 2006) to 1000s km (Harris *et al*., 1998), high spatial variability in the delivery of mussel and barnacle larvae was expected among sites that are on average 60km apart, but within the same bioregion (Awad, *et al*. 2002). It was also expected that there would be temporal variability of settlement and recruitment of mussels and barnacles, with higher numbers settling and recruiting during the spring/summer season given previous studies within the region (Lasiak and Barnard, 1995; Zardi *et* al., 2007). Finally, increased settlement and recruitment were expected at the sites of highest adult cover due to local retention of larvae in the nearshore environment and delivery to "parental" sites (von der Meden *et al*., 2008).

3.2 Methods and Materials

3.2.1 Study sites

This study was conducted on the south east coast of South Africa (Figure 3.1), from February 2016 to February 2017. Four sites were selected on stretches of open coast namely: Kenton on Sea (33°41’23.68”S 26°40’28.73”E); Cannon Rocks (33°45’0.48”S 26°32’37.61”E); Schoenmakerskop (34°02’30.3”S 25°32’3.18”E); and Cape St Francis (34°12’36.42”S 24°49’32.76”E), overall covering about 180km of coast.

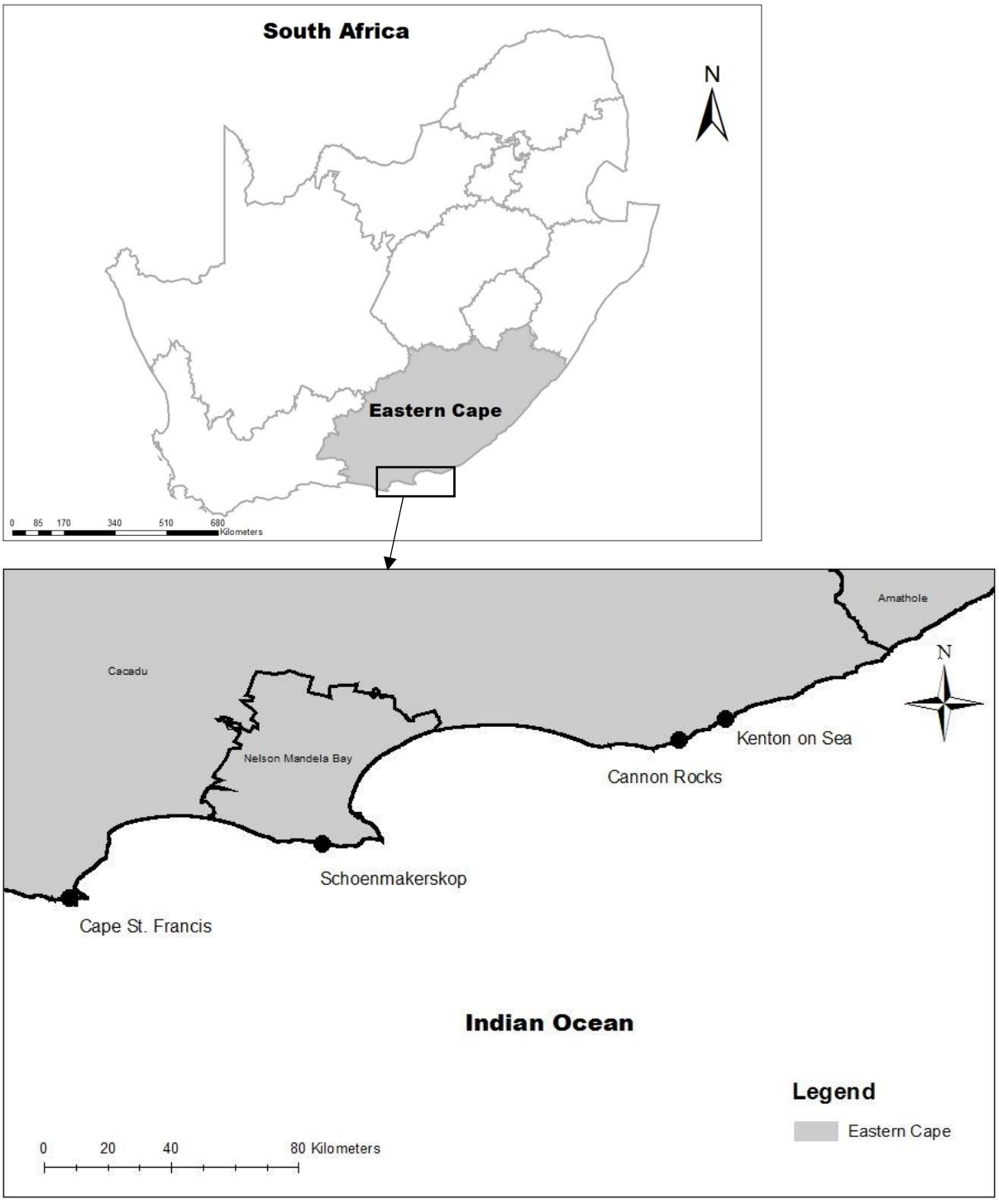

Figure 3.1: Map of the study area in South Africa, showing all sites: Kenton on sea; Cannon Rocks; Schoenmakerskop and Cape St Francis.

3.2.2 Experimental Design

The delivery of larvae (settlement) at each of the study sites in Chapter 2 was monitored by deploying artificial collectors. Artificial collectors for mussel and barnacle competent larvae (scouring pads and PVC – Polyvinyl chloride plates respectively) were deployed, which have been used widely in the past as settlement substrata (Shanks, 1986; Hunt and Scheibling 1996; Leslie *et al.*, 2005; Emlet and Sadro, 2006). Mussels (*Perna perna* and *Mytilus galloprovincialis*) and barnacles (*Chthamalus dentatus*, *Octomeris angulosa*, *Tetraclita serrata*) were the target species for the study. Ten plastic scouring pads, each separated by about 2m, were tied down with 4.7 x 200mm cable ties to 6 x 80mm eyebolts which had been drilled into the rocks, to collect mussel settlers at the low intertidal zone where mussel beds occur (Porri *et al*., 2006; Bownes *et al*., 2008; von der Meden *et al*., 2010; 2012) and settlement is highest (Porri *et al*., 2007). Ten Polyvinyl chloride (PVC) plates (78 x 59mm) each with anti-slip tape (with 60grit coarseness) sandpaper glued to them were tied down into holes drilled in the rocks using 6 x 40mm bolts and washers to collect barnacle cyprids. The plates and anti-slip tape were grey and black respectively, in order to mimic the natural rocks surfaces and placed in the mid intertidal zone. The pads and PVC plates were collected and replaced monthly on every full moon spring tide from 23 February 2016 till 13 February 2017. Collected pads were put in individual plastic jars and preserved with 100% ethanol on site, whilst each PVC plate was placed in a small plastic bag, then all 10 were placed in a bigger zip seal bag and then put in a freezer at -17.5°C upon return to the laboratory, for preservation till further processing. In addition, adult mussel and barnacle cover were determined at each site, during a once-off assessment of percentage cover. Mussel cover was determined in 30 50 x 50cm quadrats haphazardly deployed in the mid- and low intertidal, where most *Perna perna* occur (Bownes and McQuaid, 2006) and where the artificial collectors for settlers and recruits were also deployed. The point intercept method (Jonasson, 1988; Paddack *et al*., 2006) was used to assess percentage adult cover within each quadrat plot, where each intercept point (one percentage each, i.e. 100 points per quadrat) was represented by any adult mussel directly underneath the intercept. For the barnacles, the same method was applied using 30 replicates of haphazardly deployed 20 x 20cm quadrats in the mid- to higher intertidal zone where barnacle beds are found. The adult cover was sampled about 200m along the stretch of shore where the experiment was set up (von der Meden *et al.*, 2008; Cole and McQuaid, 2011).

3.2.3 Processing of mussel collectors

Out of 10 plastic jars containing scouring pads, a minimum of 3 jars were analysed. In the laboratory, just prior to processing, 5ml of sodium hypochlorite (bleach) was added to each jar, shaken well and left to soak for 5minutes to dissolve the byssal threads of mussel settlers, making it easier to detach them from the scouring pad (Davies, 1974). The contents of each jar were then poured through a 75µm sieve to collect all material. Each pad was then cut, unravelled and rinsed down with tap water using a hose over a 5L bucket, to remove any remaining debris which may have contained mussel settlers. The contents of the bucket were poured over the same 75µm sieve and the entire set of trapped material was then transferred into a plastic jar, where 15 – 20ml of 100% ethanol was added to preserve the sample until further examination.

3.2.4 Larval Identification

The samples from the processed mussel collectors were analysed under a Leica MZ75 stereoscopic dissecting microscope set with an eye-piece micrometer. Two mussel species, *Perna perna* (indigenous) and *Mytilus galloprovincialis* (invasive), were identified following Bownes *et al.,* (2008). The two species were present in assorted sizes, ranging from 300µm to about 2mm, therefore grouping by size was necessary. All specimens between 300µm to 360µm were classified as "settlers" and individuals >360µm were classified as "recruits" (Porri *et al.,* 2006). Other bivalve species that could not be taxonomically identified were classified as "other bivalves". For the barnacle settlement, PVC plates were removed from the freezer and examined under the same dissecting microscope used for mussels. On all plates, the barnacle larvae that were found were separated into two groups according to their morphology: cyprids and juvenile barnacles (Sandison and Day, 1954). Since settlers/recruits could not be identified to species, the broad categories 'cyprids' and 'juveniles' were used for two separate analyses (see details below). Sampling for the barnacles was conducted where there were *Chthamalus dentatus* beds (Hodgson, 1987) which could have led to the uniform barnacle species that were found, however this needs further exploration. After identification, both mussel and barnacle specimens were collected, counted and preserved in separate eppendorfs with 100% ethanol according to the site and month of collection.

3.2.5 Statistical Analysis

Three one-way ANOVAs were performed using Statistica (v13.2) software to test significant effects of sites for the adult mussels (*Perna perna* and *Mytilus galloprovincialis*) and barnacles (Figures 3.2 and 3.3 for the mussels and Figure 3.4 for the barnacles)

Several two-way Analyses of Variance (ANOVA) were performed to test for significant effects of the factors month and site, which were both considered random, for seven taxa (*Perna perna* settlers, *Perna perna* recruits, *Mytilus galloprovincialis* settlers, *Mytilus galloprovincialis* recruits, other bivalves, cyprids and juvenile barnacles). The data failed the tests of normality and homogeneity and were then transformed ($\log_{10}[X+1]$). After transformation the data then exhibited normality and homogeneity. As multiple tests for several taxa were performed, the Benjamini-Hochberg false discovery rate method (Benjamini *et al*., 2001; Table 3.1) was used to reduce the possibility of type I errors. Each individual p-value from the two-way ANOVAs of the seven taxa was arranged in order, from the smallest to the largest. The smallest p-value was ranked $i = 1$, which was followed by the next p-value, ranked as $i = 2$, etc. Each p-value was then compared to its own calculated Benjamini-Hochberg critical value, $[(i/m)Q]$, where i was the rank, m the total number of tests, and Q the false rate discovery of 0.05. Starting off from the largest p-value (i.e. 0.404047, Table 3.1) and working the way up the table by comparing p-values against their own calculated critical value, the cut-off point for significant acceptance was determined. The largest p-value, which was smaller than/equal to its own critical value ($p \leq (i/m)Q$), was the cut off point for significane (in this case, the 19th ranked p-value of 0.039857 in Table 3.1). Therefore, all p-values smaller or equal to the 19th ranked p-value (0.039857) were considered to be significant. All p-values ranked below the 19th p-value were then considered to be non-significant (Benjamini *et al*., 2001). Bar plots were plotted to visualise the data. Significant results of the ANOVAs were further invesitgated by the Student Newman-Keuls post-hoc test to compare the rank means of each group against the likelihood that they are the same.

3.3 Results

The outcomes of the statistical tests run on the abundances of invertebrate settlers and recruits, corrected using the Benjamini – Hochberg critical value (Table 3.1), were consistent through the analyses performed on seven taxa, highlighting significant effects of month, site and the interaction between month and site. This indicates that settlement and recruitment generally differed among sites and peaked during different months at different sites. In most cases, there were significant interactions but I have also discussed the main effects in order to clarify general patterns.

Table 3.1: Results of the Benjamini-Hochberg correction on all taxa. (*i/m*)*Q* – Benjamini – Hochberg critical value where i – rank; m – total number of tests and Q – false discovery rate of 0.05. PR – *P. perna* recruits; PS – *P. perna* settlers; MR – *M. galloprovincialis* recruits; MS – *M. galloprovincialis* settlers; OB – Other bivalves; C – Cyprids; J – barnacle juveniles.

Taxon	**Effect**	**p-value**	**Rank**	**(*i/m*)*Q***
PR	Site	0.000000	1	0.00238
PR	Month*site	0.000000	2	0.00476
C	Month*site	0.000000	3	0.00714
J	Month	0.000000	4	0.00952
J	Month*site	0.000000	5	0.0119
MR	Month	0.000001	6	0.01429
PS	Month*site	0.000002	7	0.01667
MR	Month*site	0.000009	8	0.01905
OB	Month	0.000057	9	0.02143
C	Month	0.000088	10	0.02381
MS	Month	0.000156	11	0.02619
MS	Month*site	0.000325	12	0.02857
PS	Site	0.000863	13	0.03095
PR	Month	0.002810	14	0.03333
PS	Month	0.003098	15	0.03571
J	Site	0.025759	16	0.0381
MR	Site	0.031938	17	0.04048
OB	Site	0.033459	18	0.04286
MS	**Site**	**0.039857**	**19**	**0.04524**
OB	Month*site	0.180285	20	0.04762
C	Site	0.404047	21	0.05

3.3.1 Adult mussels and barnacles

The results of the one-way ANOVAs for distribution of adult mussels revealed a significant effect of site for both species (Tables 3.2 & 3.3). Results from the Student Newman-Keuls post-hoc test on the differences in adult mussel abundances among sites, revealed Kenton on Sea as the site that had the highest percent cover of adult mussels for both *P. perna* and *M. galloprovincialis*, whilst Cape St Francis had the lowest percentage cover for both mussel species (Figures 3.2 & 3.3). The result of the one-way ANOVA on the abundance of adult barnacles revealed a significant effect of site (Table 4), where Kenton on Sea had the lowest percent cover whilst Schoenmakerskop had the highest adult barnacle percent cover (Figure 3.4).

Table 3.2: Results of the one-way Analysis of Variance (ANOVA) examining the effect of site on the abundance of *Perna perna* adult mussel percent cover at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis). SS - Sum of Squares; Df - degrees of freedom; MS - mean squares; F - F-ratio and p – p – values: * = < 0.04.

Effects	SS	Df	MS	F	p
Site	5451.40	3	1817.13	3.13	*
Error	67404.07	116	581.07		

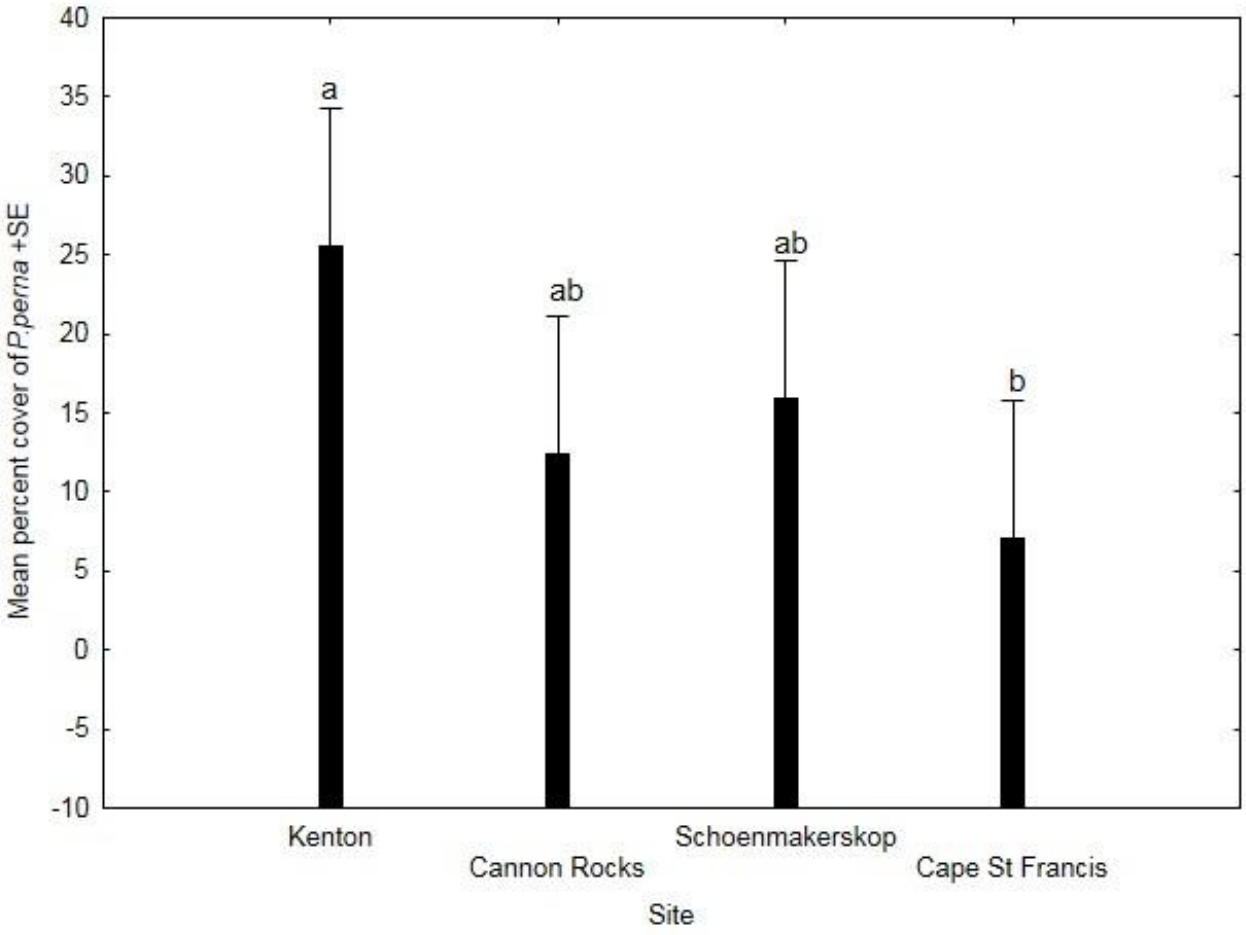

Figure 3.2: Mean abundance of adult *Perna perna* (percentage cover) at the four study sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by the Student Newman-Keuls post hoc test.

Table 3.3: Results of the one-way Analysis of Variance (ANOVA) examining the effect of site on the abundance of *Mytilus galloprovincialis* adult mussel percent cover at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis). SS - Sum of Squares; Df - degrees of freedom; MS - mean squares; F - F-ratio and p – p – values: ** = < 0.01.

Effects	SS	Df	MS	F	p
Site	11796.4	3	3932.12	4.23	**
Error	107887.6	116	930.07		

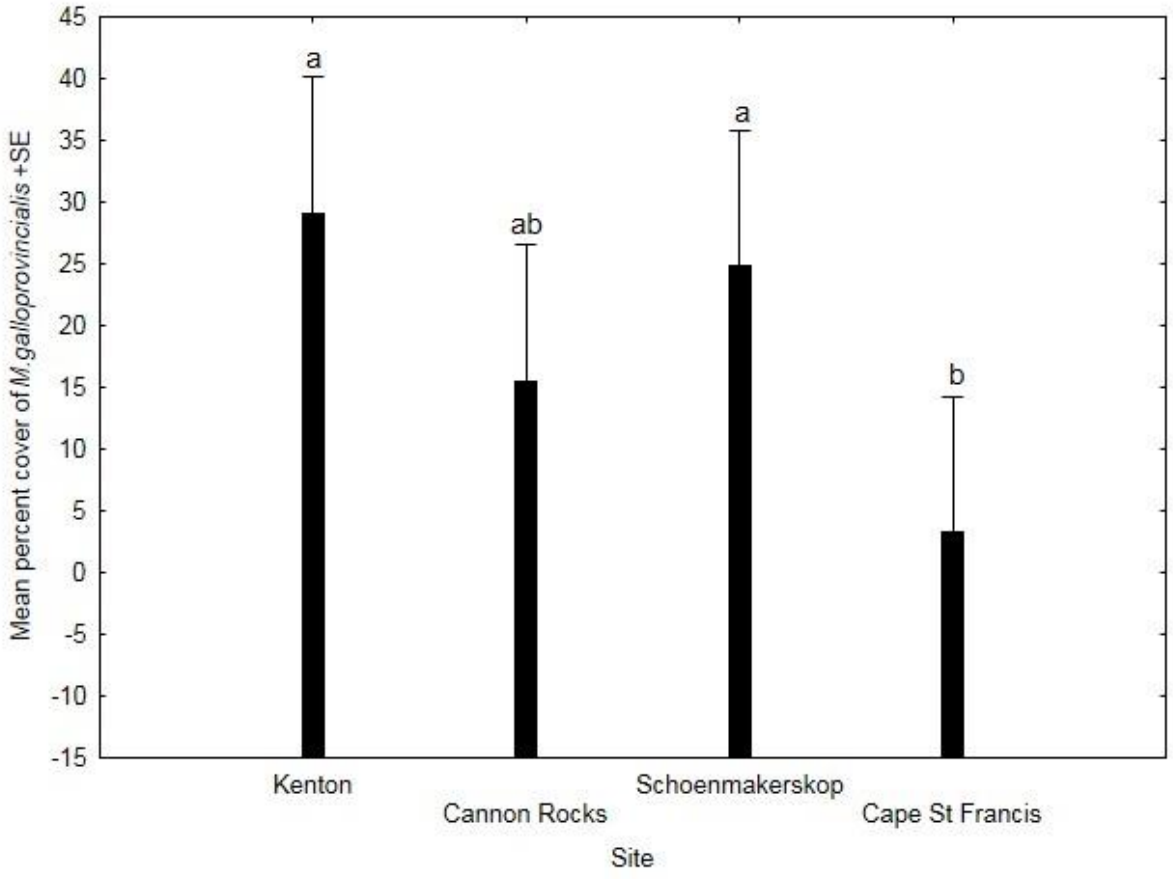

Figure 3.3: Mean abundance of adult *Mytilus galloprovincialis* (percentage cover) at the four study sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by the Student Newman-Keuls post hoc test.

Table 3.4: Results of the one-way Analysis of Variance (ANOVA) examining the effect of site on the abundance of adult barnacle percent cover at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis). SS - Sum of Squares; Df - degrees of freedom; MS - mean squares; F - F-ratio and p – p – values: ** = < 0.01.

Effects	SS	Df	MS	F	p
Site	10752.13	3	3584.04	5.43	**
Error	76576.67	116	660.14		

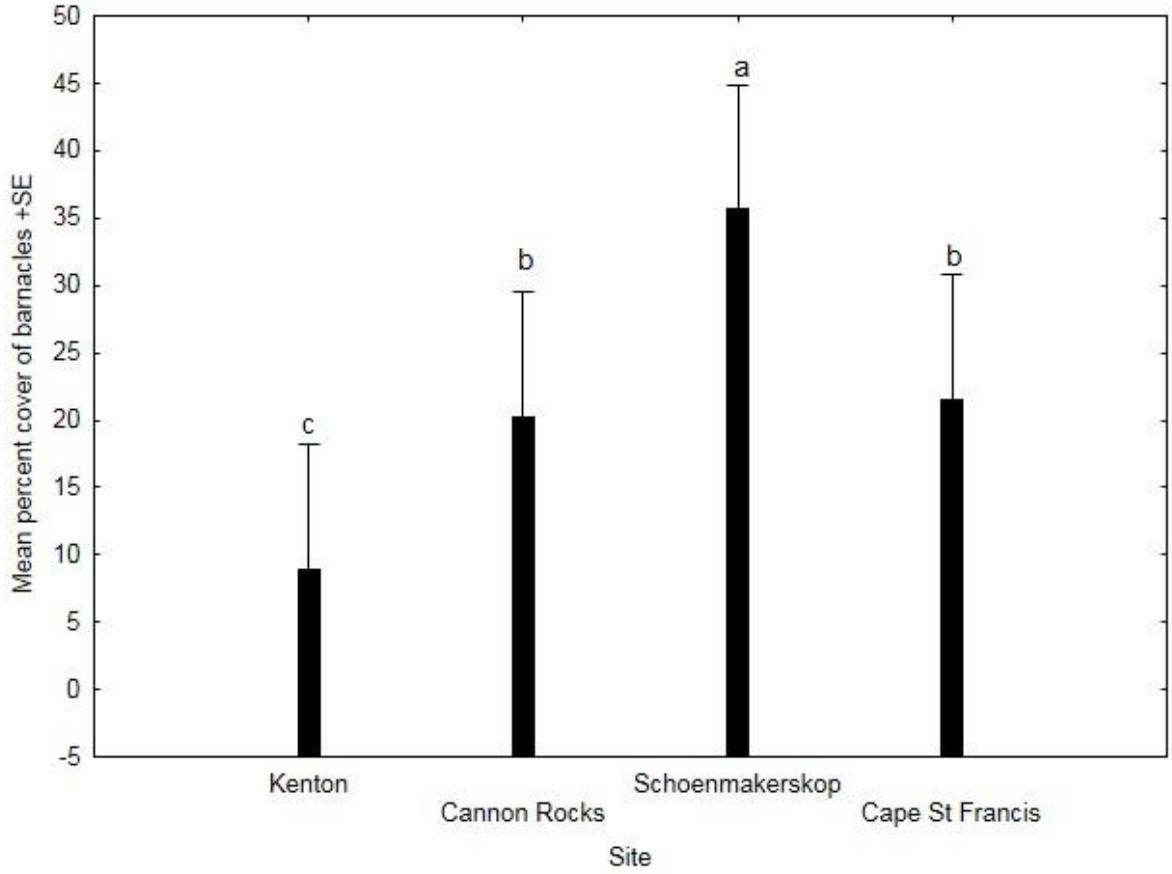

Figure 3.4: Mean abundance of adult barnacles (percentage cover) at four sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by the Student Newman-Keuls post hoc test.

3.3.2 *Perna perna* settlers

The abundance of *Perna perna* settlers followed a clear seasonal trend (Figure 3.5) which was confirmed by the two-way ANOVA, with a significant effect of month (Table 3.5). More *P. perna* settled during summer, i.e. February 2016 – May 2016 and October 2016 – February 2017, than in winter, i.e. June 2016 – September 2016 (Figure 3.5). Generally, *P. perna* settlers were significantly more abundant at Cannon Rocks than the other sites (Figure 3.6). Overall the abundance of *P. perna* settlers varied over the months at the four sites. This was confirmed by the two-way ANOVA (Table 3.5), which yielded a significant effect of the interaction between month and site. The Student Newman-Keuls post hoc test showed several homogenous groups which were difficult to interpret and partly outside the scope of this study. Nonetheless, the grouping confirmed Cannon Rocks as the site with most settlers during March 2016.

Table 3.5: Results of the two-way Analysis of Variance (ANOVA) examining the effects of month and site on the abundance of (log_{10}[X+1] transformed) *Perna perna* setttlers collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis). SS - Sum of Squares; Df - degrees of freedom; MS - mean squares; F - F-ratio and p - p – values: ** = < 0.01; *** = <0.001.

Effects	SS	Df	MS	F	p
Month	13.929	12	1.161	2.915	**
Site	7.701	3	2.567	6.447	**
Month*Site	14.333	36	0.398	5.910	***
Error	7.006	104	0.067		

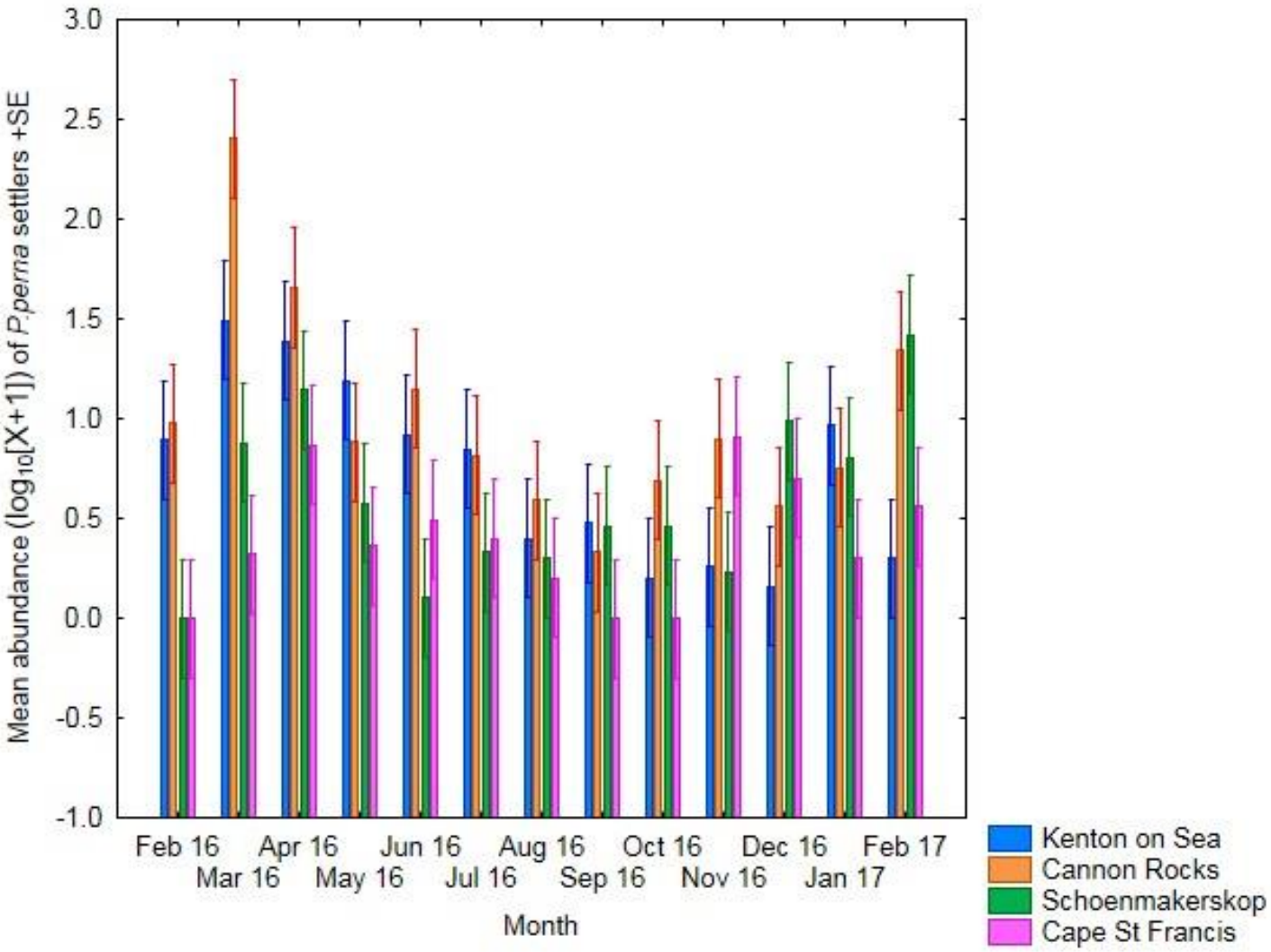

Figure 3.5: 2016-2017 mean monthly abundance (log_{10}[X+1] transformed) of *Perna perna* settlers collected at the four study sites, error bars indicate standard errors.

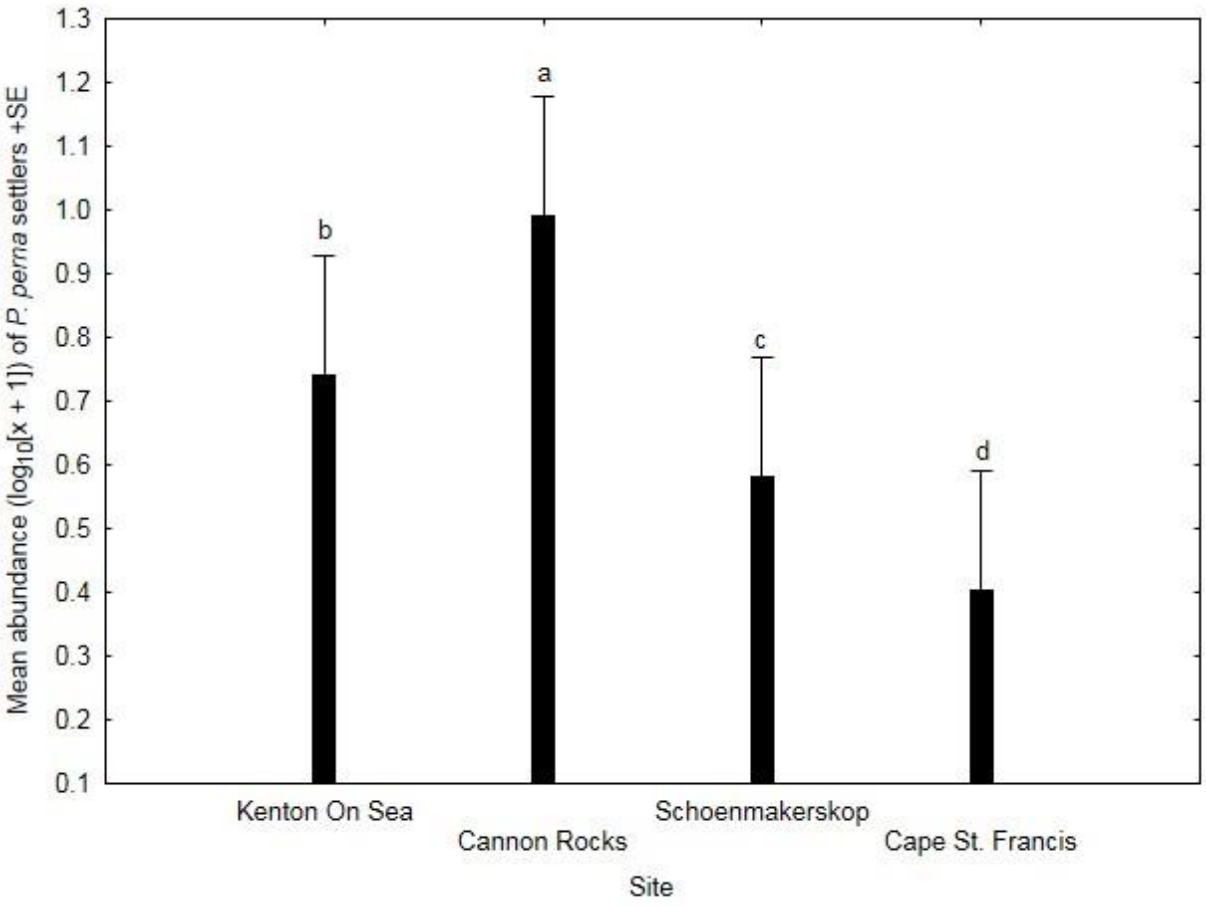

Figure 3.6: 2016-2017 mean abundance (log_{10}[X+1] transformed) of *Perna perna* settlers collected at four sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by the Student Newman-Keuls test post hoc test on the effect of site.

3.3.3 *Perna perna* recruits

As for recruitment, there was seasonal variation in recruitment, with *Perna perna* being more abundant during the summer months, i.e. February 2016 – April 2016 and November 2016 – February 2017 when compared to the winter months, i.e. May 2016 – October 2016 of the sampling period (Figure 3.7). There were significantly more *P. perna* recruits at Cannon Rocks than the other sites (Figure 3.8; Table 3.6). Generally, numbers of *P. perna* recruits varied differently over time at the various sites during the study and this was confirmed by the two-way ANOVA (Table 3.6) on this taxon, which showed a significant effect of the interaction between month and site. The results of the Student Newman-Keuls post hoc test for this interaction showed complicated groupings which were difficult to interpret or beyond the scope of the broad aim of this study. Post-hoc grouping did however highlight that Cannon Rocks had the highest abundance of recruits in the study in February 2016. The post-hoc test also revealed that Kenton on Sea and Cannon Rocks (both east of Algoa Bay) had higher numbers of recruits than Schoenmakerskop and Cape St Francis, which are both located west of Algoa Bay.

Table 3.6: Results of the two-way Analysis of Variance (ANOVA) examining the effects of month and site on the abundance of (log_{10}[X+1] transformed) *Perna perna* recruits collected at the four study sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis). SS - Sum of Squares; Df - degrees of freedom; MS - mean squares; F- ratio and p - p – values.: ** = < 0.01; *** = <0.001.

Effects	SS	Df	MS	F	p
Month	14.236	12	1.186	3.260	**
Site	21.492	3	7.164	19.687	***
Month*Site	13.100	36	0.364	4.562	***
Error	8.295	104	0.080		

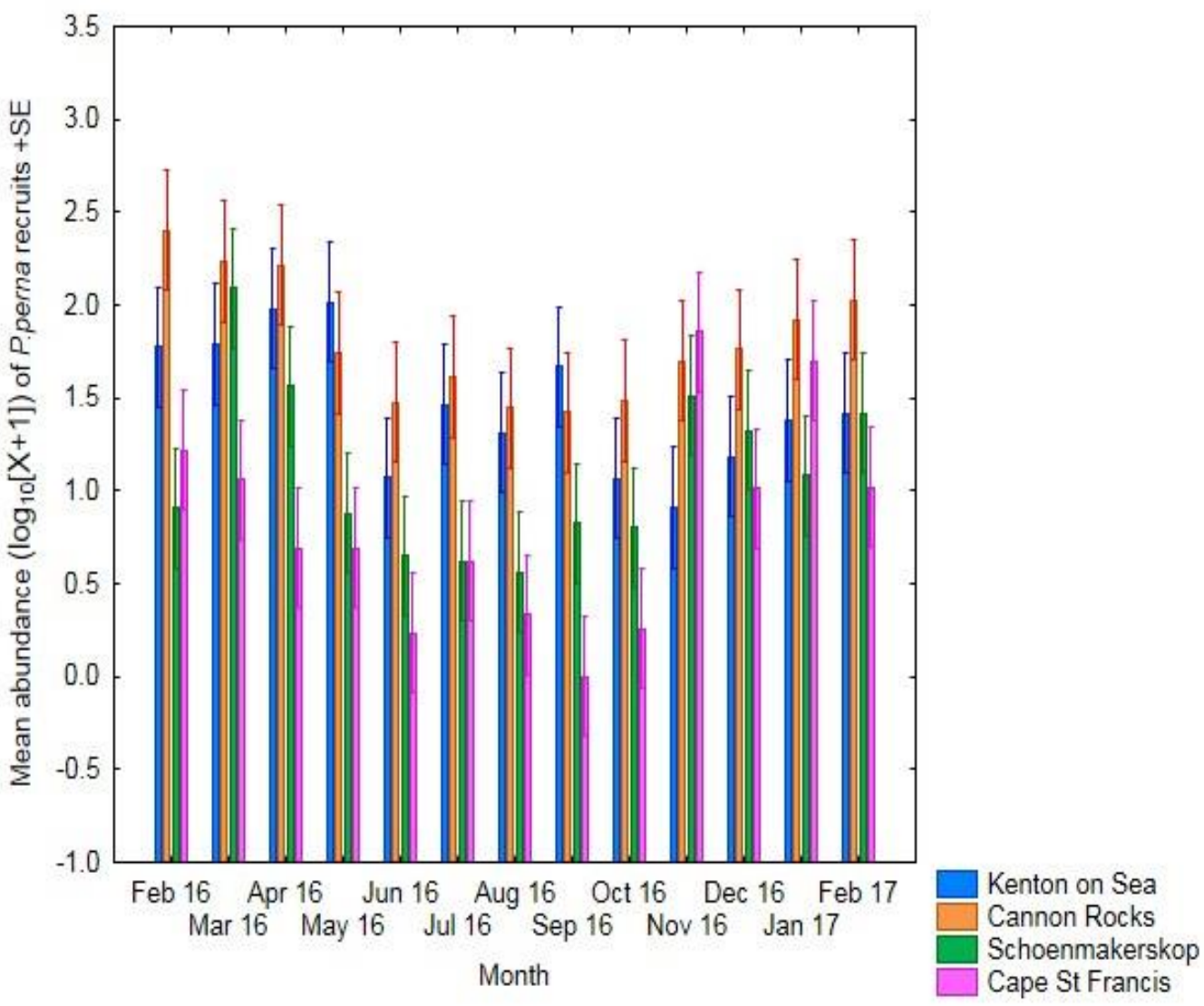

Figure 3.7: 2016-2017 mean monthly abundance (log_{10}[X+1] transformed) of *Perna perna* recruits collected at four sites, error bars indicate standard errors.

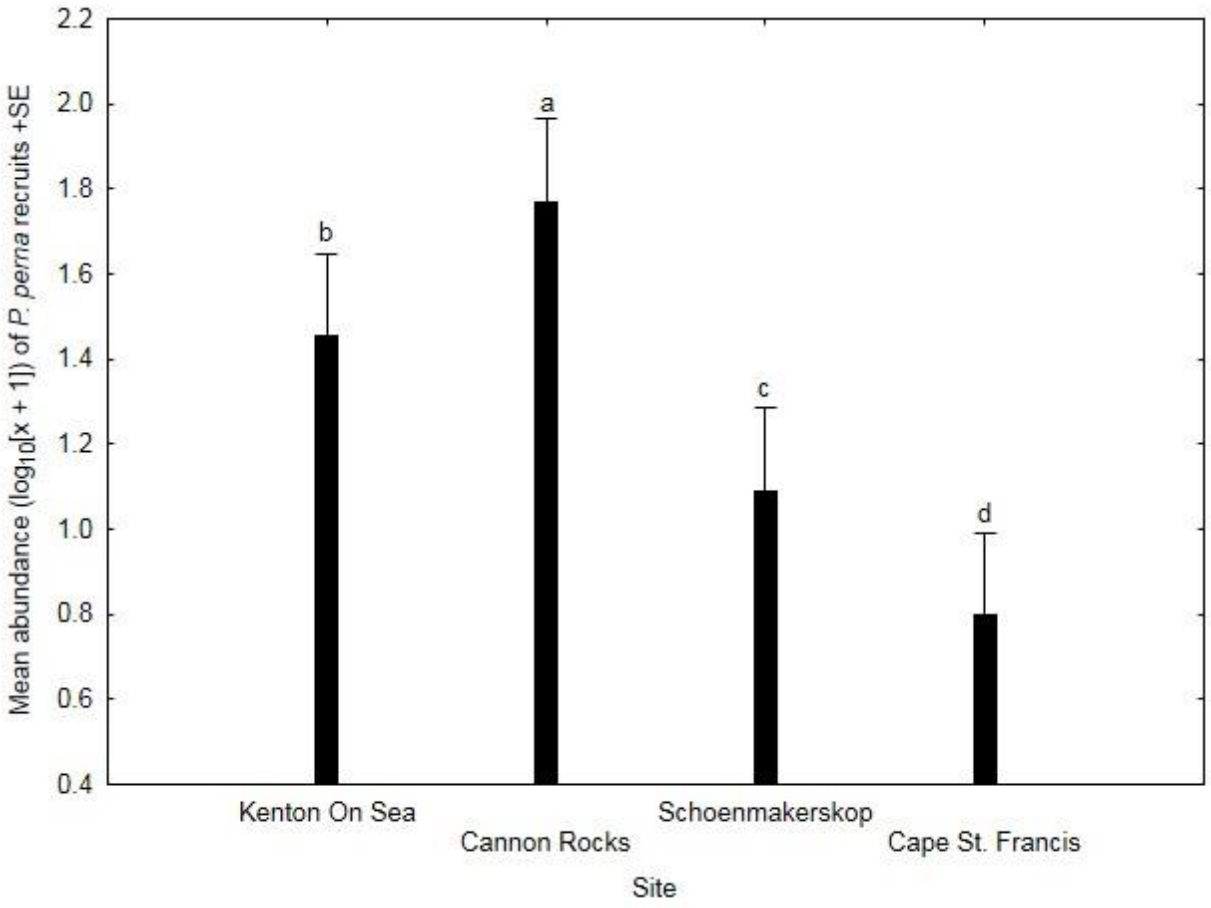

Figure 3.8: 2016-2017 mean abundance (log_{10}[X+1] transformed) of *Perna perna* settlers collected at four sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by the Student Newman-Keuls post hoc test on the effect of site.

3.3.4 *Mytilus galloprovincialis* settlers

Noticeably, the abundance of *Mytilus galloprovincialis* settlers was particularly variable during certain months of the sampling period, i.e. March, June – July and December 2016 (Figure 3.9). *M. galloprovincialis* settlers were significantly more abundant at Cape St Francis and Schoenmakerskop than the rest of the sites (Figure 3.10; Table 3.7). The abundance of *M. galloprovincialis* settlers varied differently throughout the sampling period of the study, at the different sites (Figure 3.9) and this was confirmed by the significant interaction of month and site in the two-way ANOVA (Table 3.7) which showed a. The homogenous groups that resulted from the Student Newman-Keuls post-hoc test for this interaction were complicated to interpret, however, one group stood out from the rest and that was Schoenmakerskop in June 2016, with the highest abundance of *M. galloprovincialis* settlers (Figure 3.9).

Table 3.7: Results of the two-way Analysis of Variance (ANOVA) examining the effects of month and site on the abundance of (log_{10}[X+1] transformed) *Mytilus galloprovincialis* settlers collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis). SS - Sum of Squares; Df - degrees of freedom; MS - mean squares; F- ratio and p – p – values.: * = < 0.04; *** = <0.001.

Effects	SS	Df	MS	F	p
Month	12.807	12	1.067	4.907	***
Site	1.892	3	0.631	2.899	*
Month*Site	7.829	36	0.217	2.868	***
Error	7.886	104	0.076		

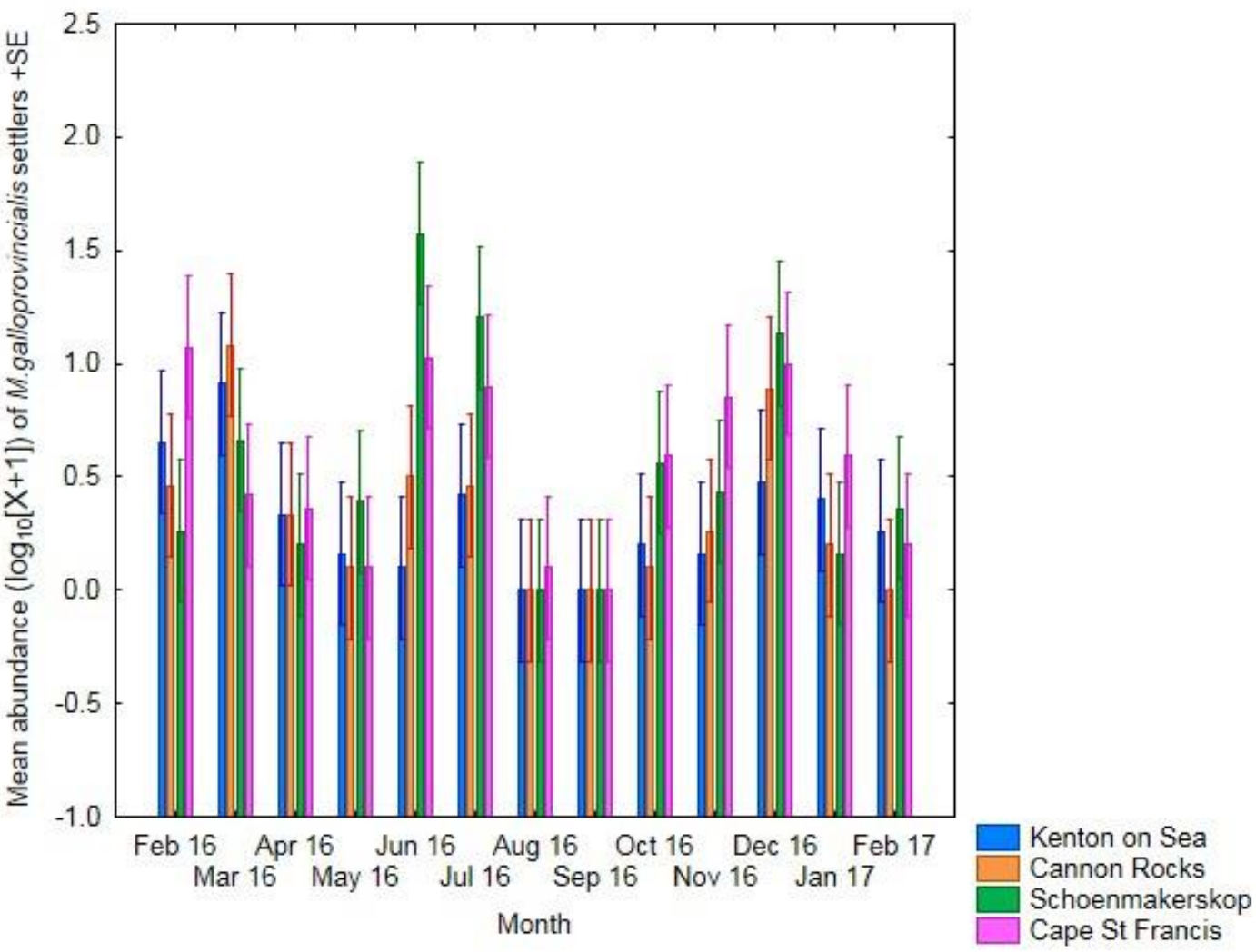

Figure 3.9: 2016-2017 mean monthly abundance of (log_{10}[X+1] transformed) *Mytilus galloprovincialis* settlers collected at four sites, error bars indicate standard errors.

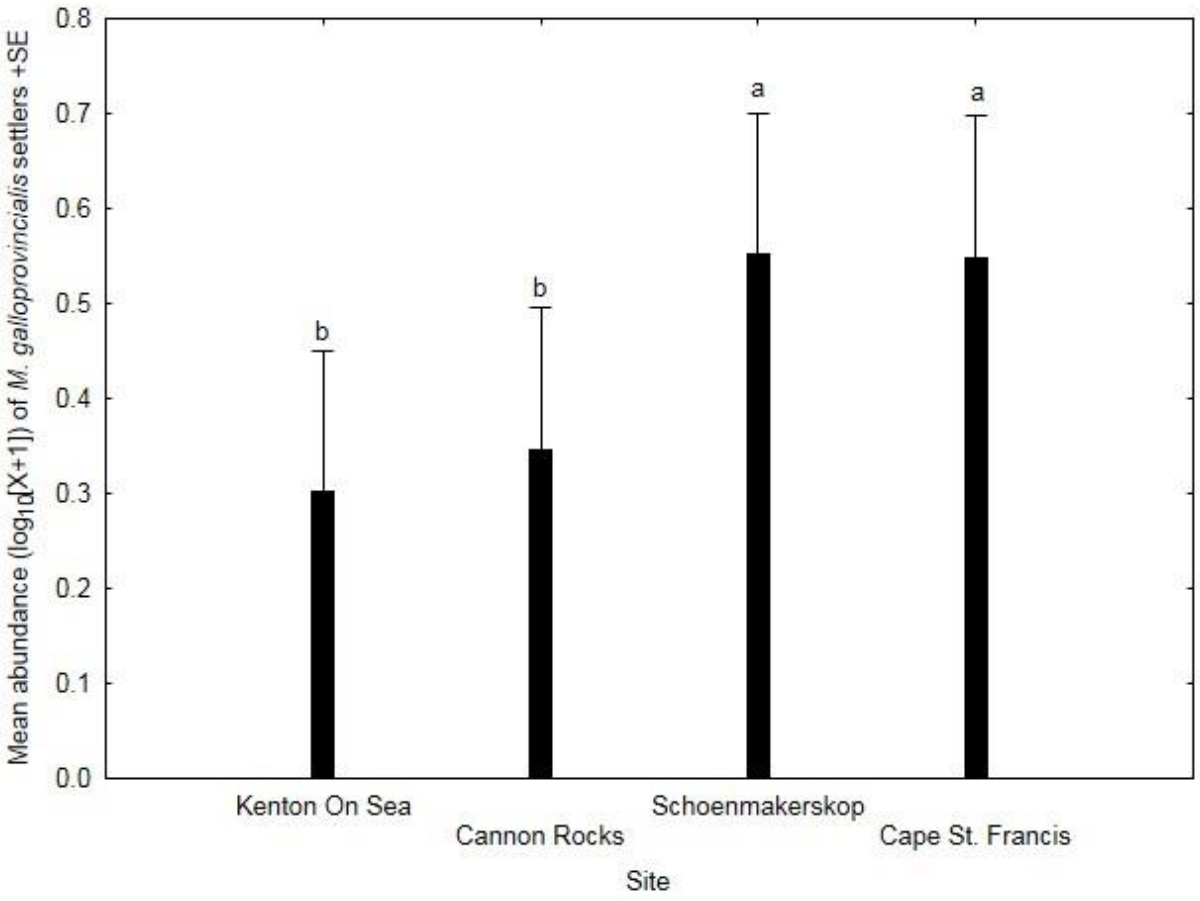

Figure 3.10: 2016-2017 mean abundance (log_{10}[X+1] transformed) of *Mytilus galloprovincialis* settlers collected at four sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by the Student Newman-Keuls post hoc test on the effect of site.

3.3.5 *Mytilus galloprovincialis* recruits

Two-way ANOVA (Table 3.8) of recruit abundances for *Mytilus galloprovincialis* showed a significant interaction between month and site which was confirmed by the overall varying pattern of the *M. galloprovincialis* recruits during the sampling season at the four sites (Figure 3.11). Although there was no significant effect of site (Table 3.8) there were variable peaks in abundance, visually, at Cape St Francis and Schoenmakerskop (Figure 3.11). There was also significant seasonal variation in the abundance of *M. galloprovincialis* recruits which were significantly more abundant in summer, i.e. February 2016 – April 2016 and November 2016 – January 2017 and in a few months of winter i.e. June 2016 – August 2016 (Figure 3.11). One noticeable group resulting from the Student Newman-Keuls post-hoc test indicated the highest abundance of recruits in Cape St Francis for November 2016, corresponding to the overall highest abundances of *M. galloprovincialis* recruits.

Table 3.8: Results of the two-way Analysis of Variance (ANOVA) examining the effects of month and site on the abundance of (log_{10}[X+1] transformed) *Mytilus galloprovincialis* recruits collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis). SS - Sum of Squares; Df - degrees of freedom; MS - mean squares; F - F-ratio and p – p – values; n.s - not significant; *** = <0.001.

Effects	SS	Df	MS	F	p
Month	31.13	12	2.595	6.910	***
Site	2.521	3	0.841	2.238	n.s
Month*Site	13.518	36	0.376	3.710	***
Error	10.527	104	0.101		

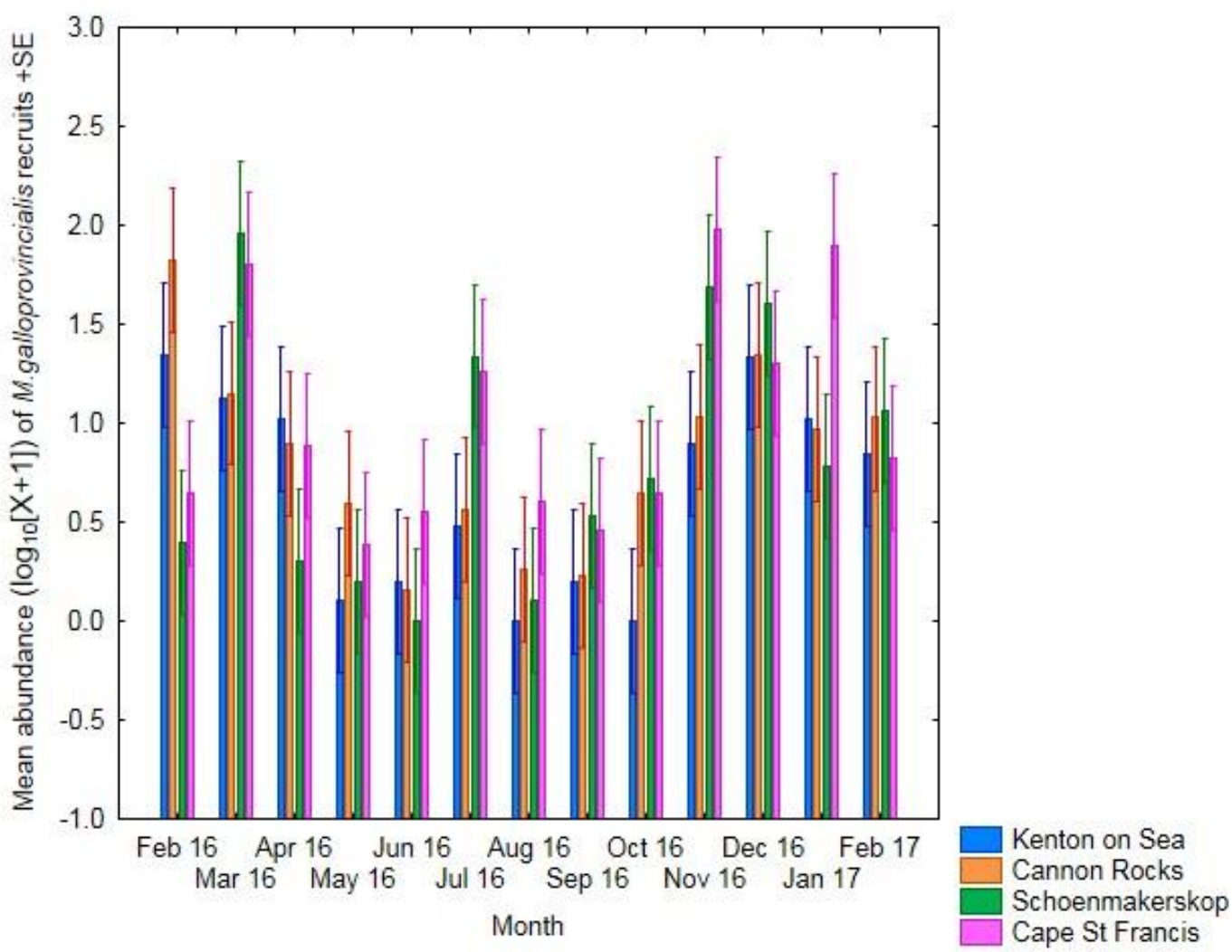

Figure 3.11: 2016-2017 mean monthly abundance (log_{10}[X+1] transformed) of *Mytilus galloprovincialis* recruits collected at four sites, error bars indicate standard errors.

3.3.6 Other Bivalves

The statistical analysis on the abundance of recruitment of 'Other Bivalves' included all bivalves that could not be identified taxonomically. 'Other bivalves' comprises a mixture of most likely several bivalve taxa and there was not enough information on settlement and recruitment and the sizes at settlement for 'Other Bivalves', therefore it was safe to conservatively consider them as recruits since scouring pads were collected on a monthly basis on the rocky shore. This was the only group, out of all seven taxa, for which the statistical test was not significant for the month and site interaction (Table 3.9). There was seasonal variation in recruitment of this group of bivalves, with more bivalves occurring during February 2016 – April 2016 and October 2016 – January 2017 (summer) and fewer occurring during May 2016 – September 2016 (winter), hence the significant effect of month (Figure 3.12; Table 6). These bivalves were more abundant at Cannon Rocks than the other sites and the pattern was confirmed by the results of the two-way ANOVA (Figure 3.13; Table 3.9). The outcome of the Student Newman-Keuls post hoc test for the month effect revealed that the summer months of March and December 2016 yielded the highest abundances of bivalve recruits (Figure 3.12).

Table 3.9: Results of the two-way Analysis of Variance (ANOVA) examining the effects of month and site on the abundance of (log_{10}[X+1] transformed) other bivalves collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis). SS - Sum of Squares; Df - degree of freedom; MS - mean squares; F - F-ratio and p – p – values: n.s - not significant; * = < 0.04; *** = <0.001

Effects	SS	Df	MS	F	p
Month	7.476	12	0.623	4.855	***
Site	1.458	3	0.486	3.787	*
Month*Site	4.619	36	0.128	1.407	n.s
Error	9.483	104	0.091		

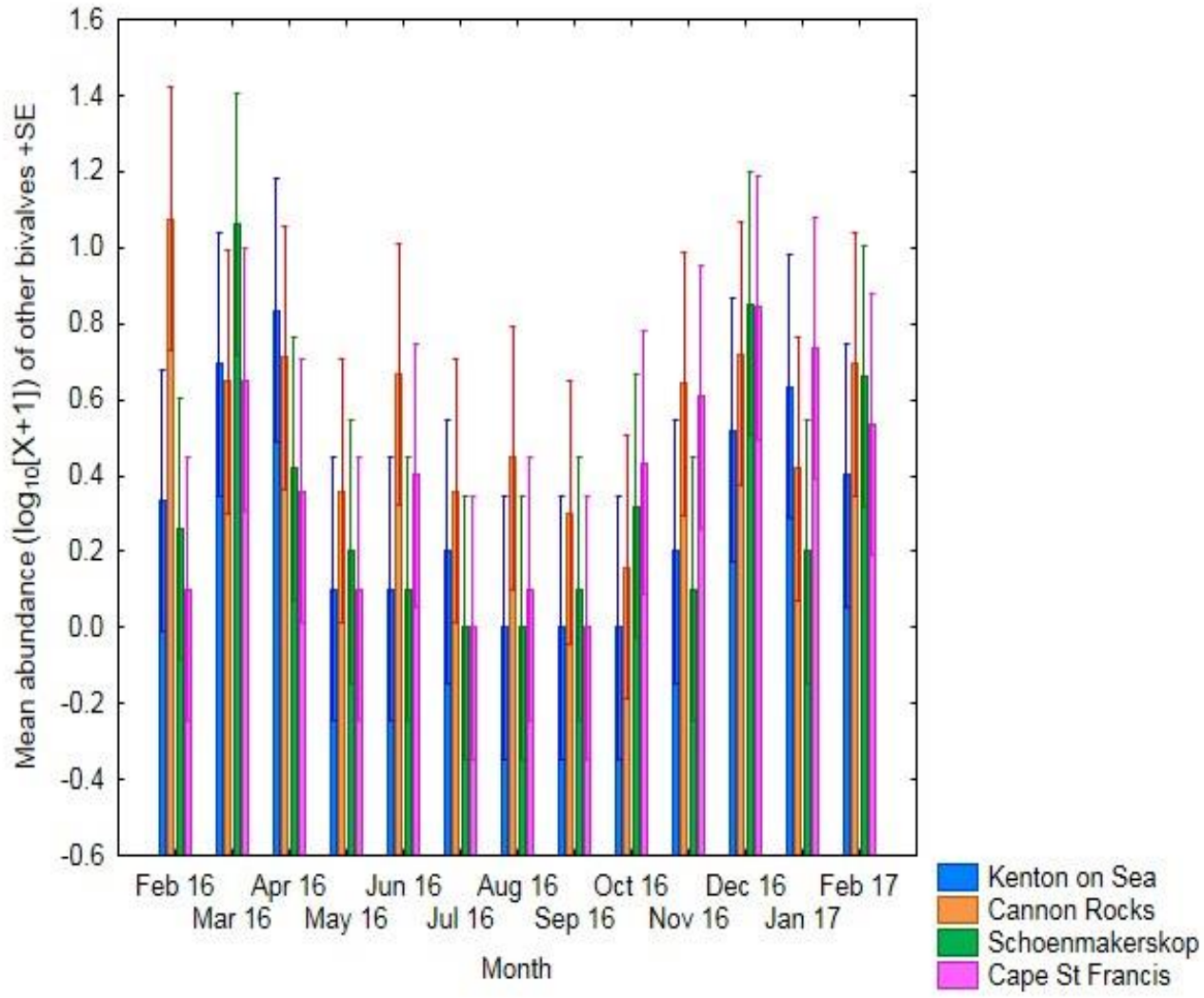

Figure 3.12: 2016-2017 mean monthly abundance (log_{10}[X+1] transformed) of other bivalves collected at four sites, error bars indicate standard errors.

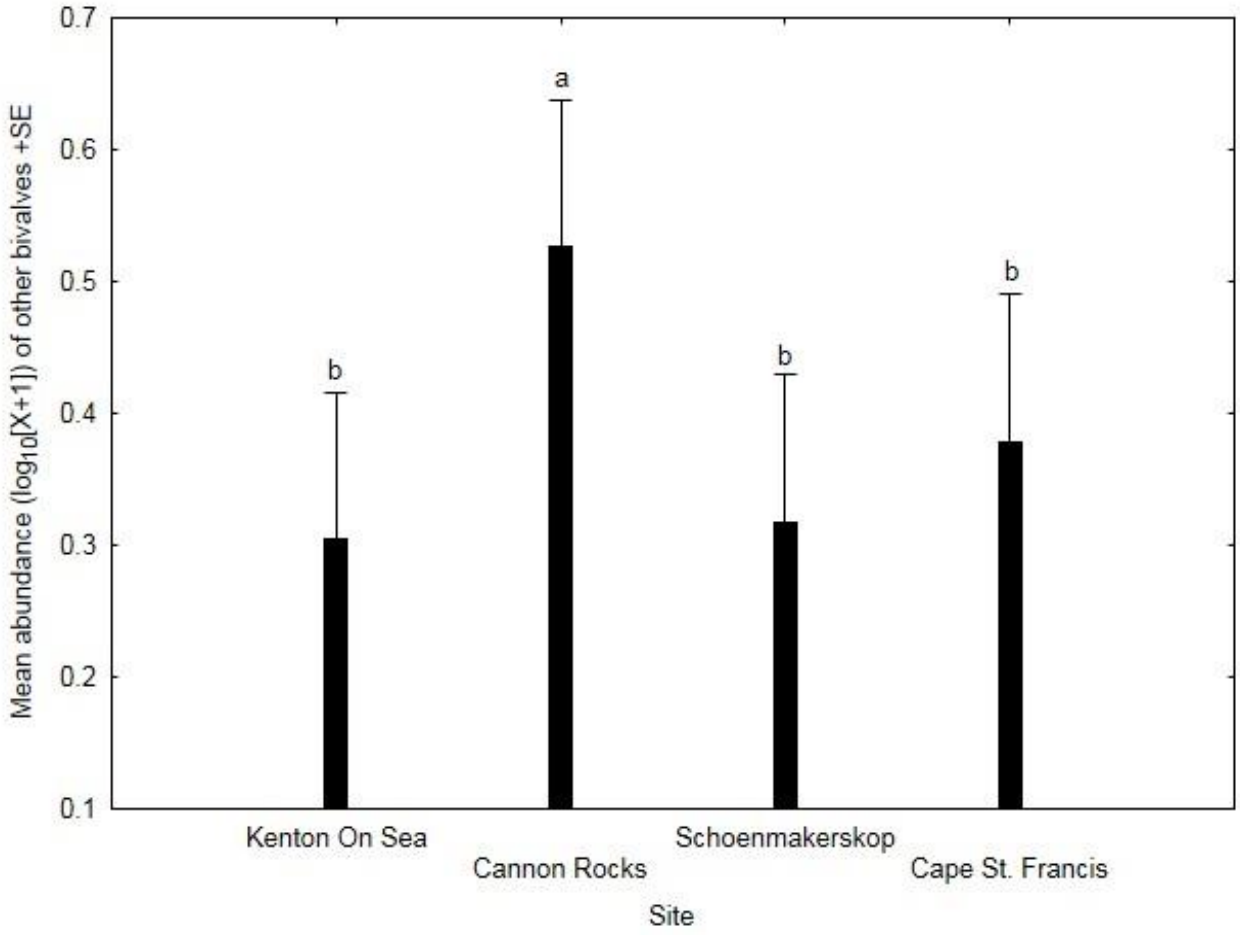

Figure 3.13: 2016-2017 mean abundance (log_{10}[X+1] transformed) of other bivalves collected at four sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by the Student Newman-Keuls post hoc test on the effect of site.

3.3.7 Cyprids

The abundance of cyprids varied according to season, with increased numbers during summer, i.e. March – April 2016 and October 2016 - February 2017 and decreased numbers during the winter months, i.e. May 2016 – September 2016 (Figure 3.14). This seasonal pattern was confirmed by the results of the two-way ANOVA which showed a significant effect of the factor month (Table 3.10). Though there was some variation in cyprid recruitment at each site visually (Figure 3.14), there was no significant effect of site on the abundance of cyprids (Table 3.10). Generally, cyprids varied in abundance from site to site during the sampling period (Figure 3.14) and this was confirmed by the results of the two-way ANOVA which yielded to a significant effect of the interaction between month and site (Table 3.10). The results for the Student Newman-Keuls post-hoc test for season identified Schoenmakerskop, Cannon Rocks and Cape St Francis for November, March and December 2016 respectively as the site/month combination that had the highest abundance of cyprids during the study.

Table 3.10: Results of the two-way Analysis of Variance (ANOVA) examining the effects of month and site on the abundance of (log_{10}[X+1] transformed) cyprids collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis). SS - Sum of Squares; Df - degrees of freedom; MS - mean squares; F - F-ratio and p – p – values: n.s – not siginificant; *** = <0.001.

Effects	SS	Df	MS	F	p
Month	8.234	11	0.749	5.313	***
Site	0.423	3	0.141	1.002	n.s
Month*Site	4.661	11	0.141	7.843	***
Error	7.4021	411	0.018		

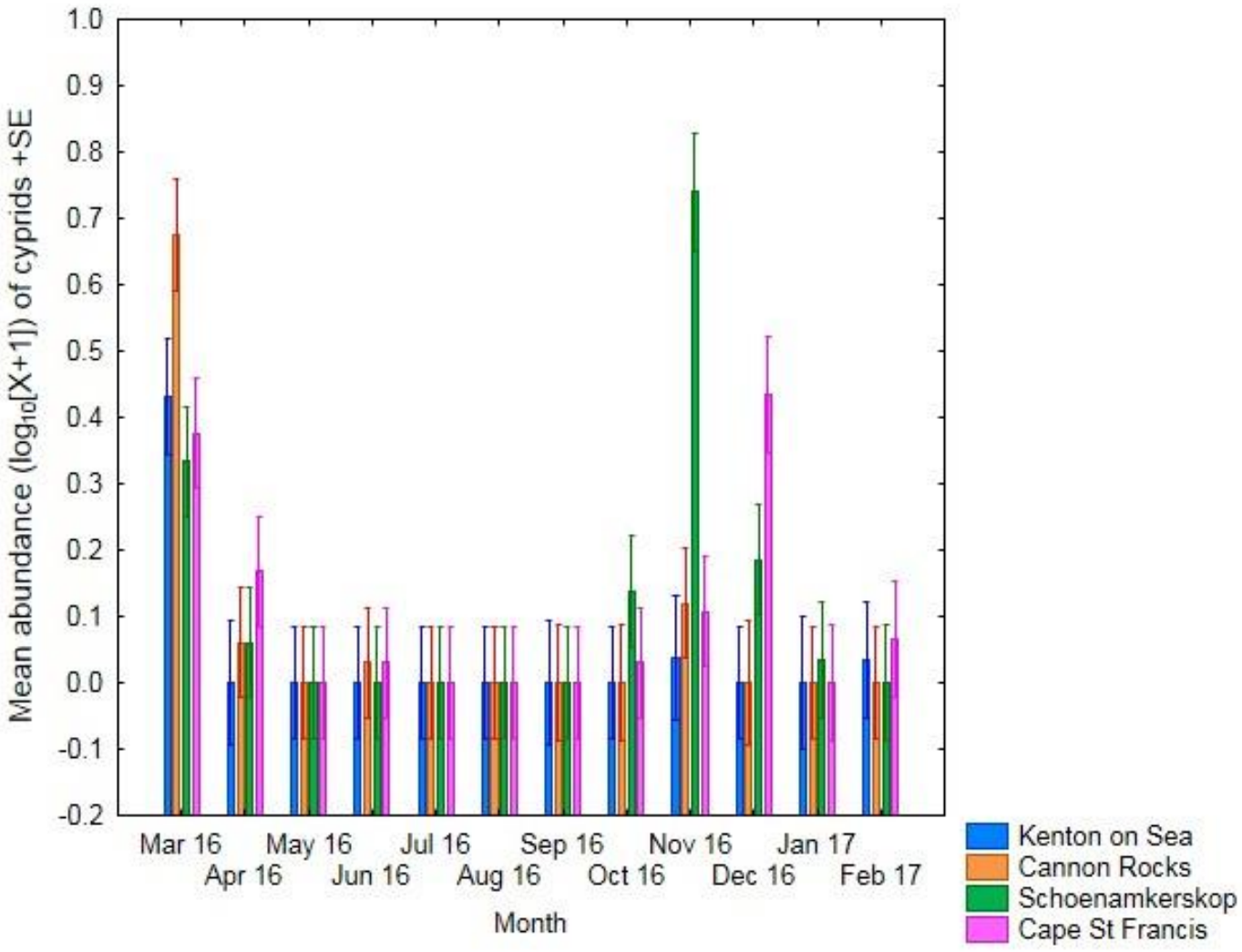

Figure 3.14: 2016-2017 mean monthly abundance (log_{10}[X+1] of transformed) cyprids collected at four sites, error bars indicate standard errors.

3.3.8 Juvenile Barnacles

Consistent with the patterns for most of the other taxa discussed above, there was seasonal variation in recruitment, with juveniles being significantly more abundant during the summer months (March – April 2016 and October 2016 – February 2017) than in the winter months (May – September 2016 Figure 3.15; Table 3.11). The results of the two–way Analysis Of Variance (ANOVA) on the abundance of juvenile barnacles showed a significant effect of site (Table 3.11), with juveniles being more abundant at Schoenmakerskop than the other sites (Figure 3.16). Overall, however, the abundance of juvenile barnacles significantly varied over the months of the sampling period (Figure 3.15), with juveniles being more abundant during particular months at different sites (significant effect of month site interaction; Table 3.11). The results of the Student Newman-Keuls post-hoc test highlighted a set of complex homogenous groups, but identified one group, Schoenmakerskop and Cannon Rocks, in March 2016, and Schoenmakerskop, in April 2016, as site/month combinations with significantly higher numbers of juvenile barnacles.

Table 3.11: Results of the two-way Analysis of Variance (ANOVA) examining the effects of month and site on the abundance of (log_{10}[X+1] transformed) juvenile barnacles collected at four sites (Kenton on Sea, Cannon Rocks, Schoenmakerskop and Cape St Francis). SS - Sum of Squares; Df - degrees of freedom; MS - mean squares; F - F-ratio and p – p – values: * = < 0.04; *** = <0.001.

Effects	SS	Df	MS	F	p
Month	72.35880	11	6.57807	10.79452	***
Site	6.41736	3	2.13912	3.51399	*
Month*Site	20.16466	33	0.61105	10.53084	***
Error	23.84821	411	0.05802		

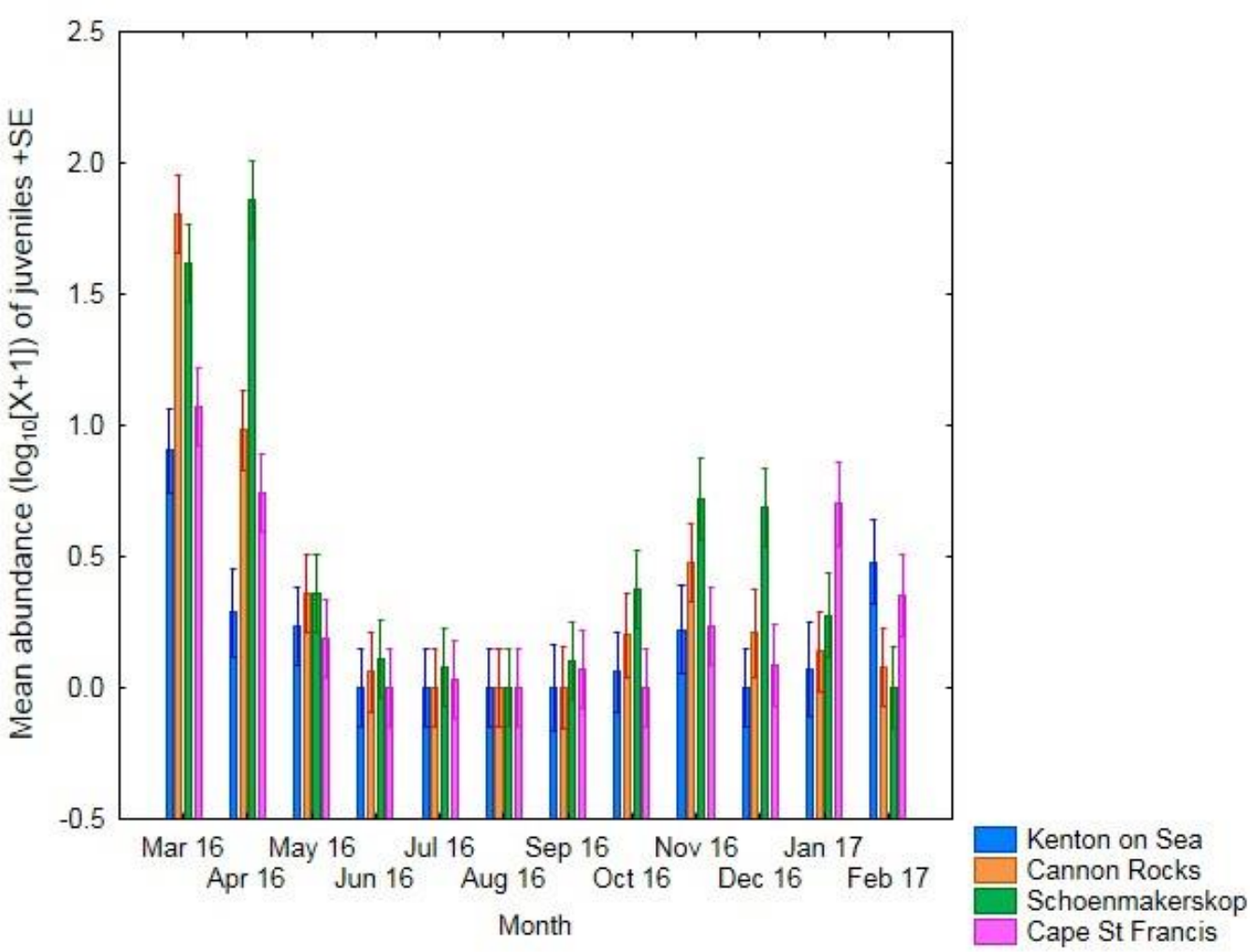

Figure 3.15: 2016-2017 mean monthly abundance (log_{10}[X+1] transformed) of juvenile barnacles collected at four sites, error bars indicate standard errors.

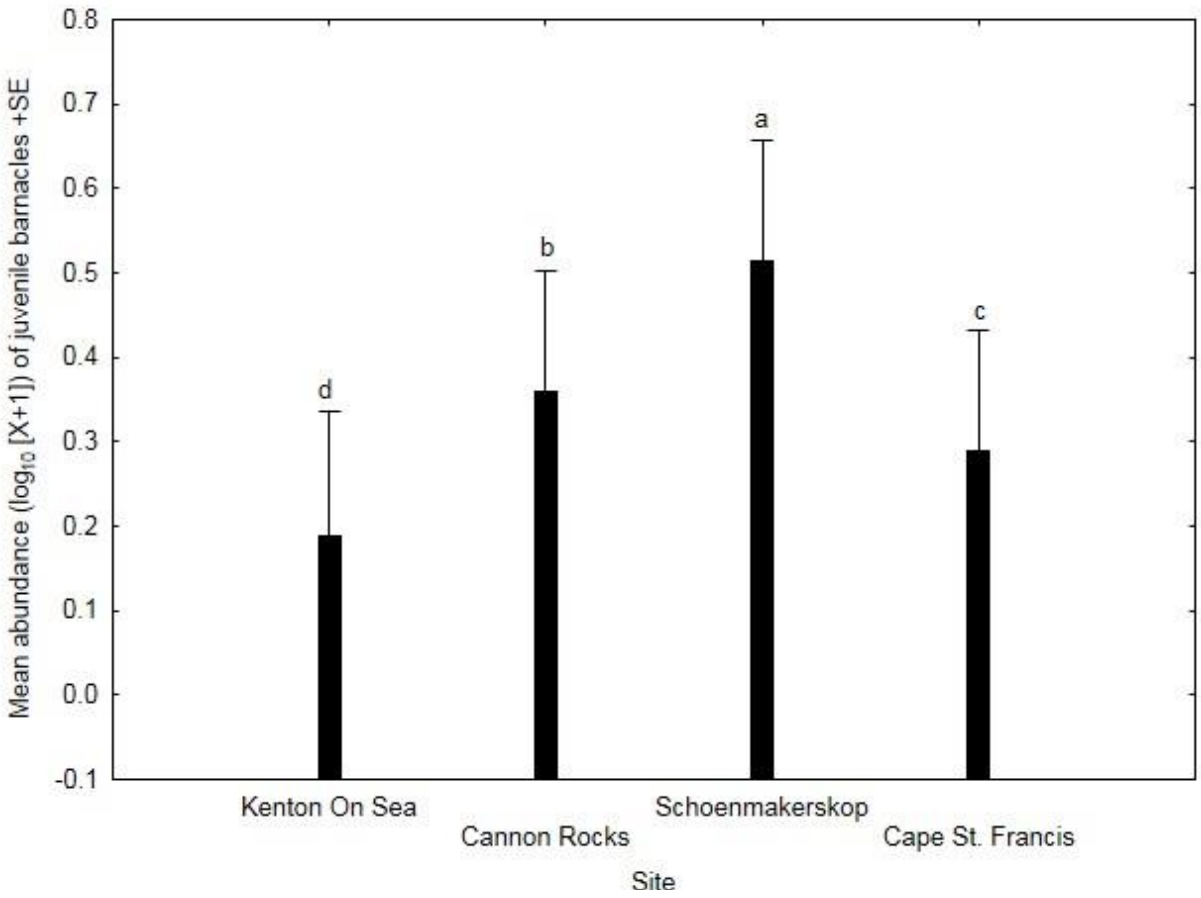

Figure 3.16: 2016-2017 mean abundance (log_{10}[X+1] transformed) of juvenile barnacles collected at four sites. Error bars indicate standard errors and letters above the bar plots indicate homogenous groups identified by the Student Newman-Keuls post hoc test on the effect of site.

From the two-way ANOVAs that were performed, all taxa showed a significant month and site interaction except for the 'other bivalve' taxon. Although most taxa showed a clear seasonal trend, where the highest abundance of larvae settled on the artificial collectors during the summer months (February – April 2016 and October 2016 – February 2017) of the sampling period, cyprids on the contrary showed a more confined recruitment period (Figure 3.14), with peaks of high abundances for short periods. There was however a difference among taxa, with *M. galloprovincialis* (settlers and recruits) having high recruitment in some of the winter months i.e. June – July 2016, during the study. The sites which had the highest numbers of larvae were Cannon Rocks followed by Schoenmakerskop and Cape St Francis. This also differed among taxa, where settlers and recruits of *M. galloprovincialis* and juvenile barnacles had high abundances in Schoenmakerskop and Cape St Francis and the rest of the taxa had high numbers in Cannon Rocks.

3.4 Discussion

Among bivalves, there was an overall seasonal trend with regards to settlement and recruitment. Generally, all of the bivalves had high settlement and recruitment during the summer months and low recruitment during the winter months of the sampled year. There was, however variation in recruitment with regards to one taxon: *Mytilus galloprovincialis*. *M. galloprovincialis* showed high recruitment during the summer, but also and during specific months of the winter season, June – August 2016. A study done west of the current research, has showed that *Perna perna* and *M. galloprovincialis* present different spawning periods at different temperatures (Zardi *et al.,* 2007). *M. galloprovincialis* spawned between 16.4 and 19.5°C whilst *P. perna* spawned at a highest temperature of 22°C and a lowest temperature of 15.5°C. In addition, Bownes and McQuaid (2009) found that the recruitment period of *M. galloprovincialis* in the western region was extended through autumn and winter. Furthermore in other regions such as New Zealand, *M. galloprovincialis* has exhibited high recruitment rates in autumn and winter seasons (Demello and Phillips, 2011). This could explain the additional reproductive winter period in Capes St Francis and Schoenmakerskop. *M. galloprovincialis* is an invasive cool water species, dominating on the west coast, but also occurring on the south coast of South Africa (van Erkom Schurink and Griffiths, 1991). *M. galloprovincialis* has been a successful invasive species in South Africa, with several factors such as high fecundity, fast growth, high recruitment rate, resistance to desiccation, multiple spawning seasons and a wide temperature range for spawning that gives it a competitive advantage over the indigenous *P. perna* (Griffiths *et al*., 1992; Branch and Steffani, 2004; Zardi *et al*., 2006; McQuaid *et al*., 2015).

The results for most of the analysed taxa showed a significant effect of site, which indicated site variability across the 180 km targeted stretch of coast. In most bivalve taxa however, Cannon Rocks received the highest abundances of settlers and recruits throughout the whole sampling period. Although this is speculative this pattern could be explained by the settlement intensification theory where arrival and settlement of benthic larvae to substrata is intensified when there is a decrease in available suitable habitat (Pineda and Caswell, 1997). von der Meden and co-authors (2012a) also found a negative correlation between mussel settlement rate and availability of suitable substrata in South Africa (between Kenton on Sea and Mossel Bay, ~500km stretch of coast), specifically during the summer months, when settlement is expected to be at its maximum (Porri *et al*., 2006), settlement habitat was however not measured for this study. Cannon Rocks an isolated rocky outcrop, with the exception of Cape

Padrone which is west of Cannon Rocks (~7km) and Kenton on Sea which is to the east of Cannon Rocks (~14km). There is a strong possibility of coupling of mechanisms that were at play during the sampling period in Cannon Rocks such as local hydrodynamics, which can cause differential delivery to sites (Porri *et al*., 2006). Wind is one of the main factors in the Algoa Bay region (where most sites are found) that causes upwelling (Goschen and Schumann, 1988), which plays a role in larval transport and delivery (Morgan and Fisher, 2010; Shanks and Morgan, 2018). Another possible explanation for the localised high patterns of settlement and recruitment at Cannon Rocks is that larvae potentially disperse over large distances, but in reality dispersal is spatially more limited than classically thought (Olson, 1985; Porri *et al*., 2014). For example, mussel larvae on the south coast of South Africa have been shown to be poorly dispersed, with most larvae dispersing on scales of 10 km or less (McQuaid and Phillips, 2000). Consistent delivery of larvae at even finer scales (100s of meters) has also been documented locally (Porri *et al*., 2006) and in other regions (Rilov *et al*., 2008).

While factors operating at the local scales may have influenced the rates of settlement and recruitment at the site level along the 180km stretch of coast, there was, in addition, an east – west separation according to species. *P. perna* settlers and recruits were more abundant on the east side of Algoa Bay. In contrast, *M. galloprovincialis* settlers and recruits were more abundant on the west side of Algoa Bay. The epicentre of abundance for *M. galloprovincialis* on the south east coast is around Plettenberg Bay (von der Meden *et al*., 2008), which lies about 134 km to the west of the study region, and this could explain the high abundances of *M. galloprovincialis* settlers and recruits towards the west of the study area at Cape St Francis and Schoenmakerskop (west of Algoa Bay). Cape St Francis is the closest site to Plettenberg Bay (the epicentre), yet presented the lowest adult percent cover (i.e. hypothetically, Cape St Francis should receive the largest number of larvae as it is closer than the other sites to the epicentre of *M. galloprovincialis* distribution). This could be attributed to the distribution of *M. galloprovincialis* mussels along the south east coast being patchy, however, being site specific with well-established populations in some places, but not in others (Bownes and McQuaid, 2006). This could explain the differences in adult distribution, and also influence the supply of propagules among adjacent sites. Another possible explanation is that there are not enough chemical cues being received by settlers/recruits in order to exhibit gregarious behaviour (in response to threats such as predation) as they arrive on shore (Nicastro *et al*., 2007) which may illustrate the patchy distribution The west and south coasts of South Africa experience a sea temperature range of 8 - 18°C and 15 - 22°C respectively (Field and Griffiths,

1991) and, although *M. galloprovincialis* is a cool water species dominating on the west coast of South Africa, it coexists with *P. perna* on the south coast, because of its wide optimal temperature range for growth and survival, which is between 10°C and 20°C (van Erkom Schurink and Griffiths, 1991, 1992).

There was strong seasonal variation in recruitment of cyprids and juvenile barnacles as was observed for the mussels. The abundances of cyprids and juveniles were, however, very different. Very few cyprids were generally found on the PVC plates across all sites throughout the whole sampling period. This can be explained by the short time taken by cyprids to metamorphose. Pyefinch (1948) found that it took about 48 hours for the cyprids of *Semibalanus balanoides* to metamorphose, whilst Connell (1961) recorded 1.5 days for metamorphosis to occur for the same species. As stated in the methodology, the plates at each site were replaced monthly, which provides plenty of time for cyprids to undergo metamorphosis, hence the greater abundance of juvenile barnacles over cyprid barnacles. Consideration of the annual pattern of settlement by cyprids showed a few peak abundances of cyprids in particular months. This temporally confined trend seems to be a characteristic of temperate regions, as seasonality is strong and well defined for barnacle settlement and recruitment, with the reproductive period restricted to summer (see Jenkins *et al*., 2000; Lagos *et al*., 2005).

Spatially, there was a higher abundance of juveniles at Schoenmakerskop than the other sites. This pattern can be linked to the high percent cover of adult barnacles at Schoenmakerskop when compared to other sites (Figure 3.4). Hills and Thomason (2003) found a positive correlation between density of adult barnacles and recruitment density of juvenile barnacles. The surface of Schoenmakerskop is jagged and presents long narrow depressed pits (pers. obs.), which can act as favourable, micro architectured sites for cyprid settlement as this type of complexity increases the chance of survival and thus enhances the success of recruitment within the adult population (Crisp, 1955; Crisp 1961;Wethey 1986).

Spatio-temporal studies of larval supply and recruitment are important to understand the role of early life processes on the structure of coastal benthic populations (Keough and Downes, 1982; Underwood and Fairweather, 1989; Harris *et al*., 1998; Jonsson *et al*., 2004; Porri *et al*., 2006; Adams *et al*., 2014), but this study highlights that other factors can influence the distribution, settlement and recruitment in the benthic habitat and uncouple the spatial structure of adult and early stage abundances. These factors could include (but are not limited to)

settlement intensification, post-settlement mortality, wave exposure, competition and biofilms. For example, *P. perna* mussels from wave exposed areas (open coasts) tend to grow faster as compared to those located in sheltered areas (bays), but at the same time, mortality due to wave action is higher on open coasts than in bays (McQuaid and Lindsay, 2000). Barnacle cyprids can reject high flow environments in order to select suitable surfaces that will ensure a short term juvenile phase because of its vulnerability to starvation during the early stage, thus reducing mortality (Larsson and Jonsson 2006). Bertness (1989) found that high density of the barnacle *S. balanoides* can cause mortality by inducing intraspecific competition for space on the substratum between individuals (Connell, 1961; Gordon and Knights, 2018). Biofilms are composed of unicellular organisms such as diatoms and bacteria that develop on inundated surfaces in the intertidal zone and these can enhance the settlement and recruitment of mussel larvae (von der Meden *et al*, 2010), while inhibiting settlement and recruitment of barnacle larvae (Olivier *et al*, 2000). The presence of biofilm could have had an effect on the overall settler and recruit abundances of all taxa as each artificial larval collector was replaced monthly, which is more than enough time for biofilms to develop (Maki *et al*., 1988). Nevertheless the above mentioned additional factors were not measured in this study.

Even though there was spatial variability among the sites, broadly, temporal variability remained similar for all taxa from all sites. To further and better understand the delivery of larvae to intertidal rocky shores for this region, more factors and processes, such as food availability, behavioural mechanisms operating on delivery and the effects of early post settlement processes need to be incorporated in such studies.

CHAPTER 4

SYNTHESIS

4.1 Overall Summary

Overall, larval abundance was greatest at the thermocline, but this differed among taxa. 'Oysters' and 'Late nauplii' larvae were positioned between the thermocline and the bottom, while cyprids consistently remained at the bottom depths. Furthermore, larval abundance was largely greatest at offshore stations (2400m), but, again, this was highly variable especially for 'season one', with some taxa being located inshore. There were also site specific effects, with high abundances of larvae generally being located at Cannon Rocks and Kenton on Sea, but again, depending on taxon. 'Oysters' and '*Mytilus galloprovincialis*' larvae were found at Cape St Francis for 'season one', but were located at Cannon Rocks during the second sampling season.

For recruitment and settlement, there was, overall, clear temporal (seasonal) variability with the delivery of most larvae to the benthos of both bivalves and barnacles during the summer months of the sampling period. Throughout the 13 months of sampling, there were consistent and very strong site specific effects, with most bivalve settlers and recruits being found at Cannon Rocks. In contrast, unexpectedly this seemed to not hold true for *M. galloprovincialis*, as settlers and recruits were mostly located at Cape St Francis and Schoenmakerskop. For barnacles, cyprid settlers had variable peaks amongst all sites, with no obvious geographic pattern, while juvenile barnacles generally had high abundances at Schoenmakerskop.

4.2 Implications for degree of coupling and/or uncoupling of benthic populations

Mytilus galloprovincialis and oyster larvae were found in the west of Algoa Bay for the first season and were then located in the east of Algoa Bay for the second season. Considering the dispersive phase, with *M. galloprovincialis* and oyster larvae found alternatively to the west and east of the bay, this suggests uniformity in the system among the four study sites in terms of larval distribution as abundances can be higher in east or west at different times. Even though there were relatively few sampling dates, at the site level most larvae were generally located at and around Cannon Rocks with the exception of a few taxa such as *M. galloprovincialis* and cyprids. This brought a suggestion that local hydrodynamics may influence larval distribution and that larvae were possibly largely confined within a single site. Another possible explanation is that sampling was always done closest to the minimum low spring tides for settlement/recruitment. But the state of tide could have changed during the larval sampling as good weather windows are scarce and so sampling was done opportunistically, making the state of the tide possibly influencing the distribution of larvae. The nearshore distribution of cyprids seems to

suggest that cyprids need to be close to adult substrata as they have an evolutionary pressure to settle close to conspecifics (Larsson and Jonsson, 2006) because during both sampling seasons these competent larvae were consistently restricted to the inshore. Depth also seemed to play a role in the alongshore distribution of larvae depending on taxon and ontogenetic stage, together with the hydrography of the region. Most oyster and *M. galloprovincialis* larvae were located at the thermocline, with a prevailing south-west flow during the first sampling season, and north-east flow, during the second. A possible explanation of high larval numbers in the thermocline is the influence of the tidal cycles during sampling. Sampling could have been done during ebb tides which makes larvae to be mostly distributed between mid and bottom depths (Knights *et al*., 2006). However this was not tested for this study. Additionally logistics of good weather windows did not enable me to sample during the dame tidal cycle Given the west-east alongshore orientation of the coastline where the study was carried out, a south-west to north-east shift in direction of the flow of currents would most likely ensure flow along the four sites within the c. 180km stretch of coast. Depth can also indirectly influence cross-shore (i.e. onshore-offshore) transport since larvae can adjust their position in the water column through diel migration, which enables them to be carried by horizontal currents either onshore or offshore (Weidberg *et al*., 2018). Most larvae, besides cyprids, were located in the offshore of the sampled stations, where the currents were flowing alongshore in a north-east direction, hence again supporting an 'open system' scenario. Potentially, larvae can be moved offshore as they get transported by fast flowing currents such as the Agulhas current in this region (Porri *et al*., 2014; Weidberg *et al*., 2015). Cyprids were found at inshore stations during 'season one (though the effect was not significant), with an onshore northerly current flow, which would potentially have favoured onshore retention. During 'season two' however, current direction for inshore bottom depths, where most cyprids were found, was to the south east, suggesting alongshore transport towards Schoenmakersop, which seem to be a favourable site for cyprids to settle. Cyprids are competent lecithotrophic larvae and as such have an evolutionary pressure to settle and recruit within adult populations (Larsson and Jonsson, 2006), hence their prevalence close to shore (Hagerty *et al*., 2018), especially during 'season one, yet an alongshore and inshore distribution during 'season two'.

For settlement and recruitment, a strong site-specific effect was detected, as highlighted by the high abundances of *Perna perna* settlers and recruits (and 'other bivalves') at Cannon Rocks, and of juvenile barnacles and *M. galloprovincialis* settlers and recruits at Schoenmakerskop and Cape St Francis respectively. Such site-specific effects could be linked to local

hydrography overriding other mechanisms such as larval behaviour (diel migration) and other biophysical factors such as consistent differential delivery to the shore (Porri *et al*., 2006) and surf zone hydrodynamics (Shanks and Morgan, 2018). It is however possible that larval behaviour could still mediate and synergistically be conducive to these site specific patterns, but this theory was not tested during this study. A notable pattern was the geographical separation of certain taxa among the four sites for larvae from the nearshore, where *P. perna* settlers and recruits were at high abundances to the east of Algoa Bay (Kenton on Sea and Cannon Rocks) whilst *M. galloprovincialis* settlers and recruits had high numbers of larvae to the west (Schoenmakerskop and Cape St Francis). This was surprising as Kenton on Sea and Cannon Rocks showed the highest abundance of adult percent cover with the lowest at Cape St Francis, in contrast to the settlement/recruitment data (i.e. a degree of uncoupling between the two species amongst the four sites). There was an overall a time integrated structure of adult populations (Smith *et al*., 2006) and this study highlighted a hotspot of abundance for both *P. perna* and *M. galloprovincialis* at Kenton on Sea. Although settlers and recruits of *M. galloprovincialis* and *P. perna* were geographically separated (west and east respectively), ultimately the final structure of the adults on the shore appears most likely driven by post settlement factors (e.g. desiccation, disturbance, mortality, inter and intraspecific competition: Keough and Downes, 1982; Bertness, 1989; Connolly and Roughgarden, 1999; Erlandsson *et al*., 2008). Similarly, the highest abundances of adult barnacles occurred in Schoenmakerskop, which correlates with the cyprid abundance around the west region of Cape St Francis and Schoenmakerskop.

Overall, the results from this study have revealed some degree of coupling and uncoupling among larval distribution, settlement, recruitment and adults of mussels for the 180km stretch of coast, with the results being influenced by taxon, ontogenetic stage and spatial, temporal scales operating in the water column and on the shore. At broad (regional – 100s of km) scales, larval supply can be influenced by hydrography at nearshore stations while season affects the different abundances of larvae at the different sites. At finer scales (local) of about 10s of km, certain sites (e.g. Cannon Rocks) suggest local retention of larvae which matched patterns of settlement, recruitment and adult abundances. Future studies should focus on the very nearshore local hydrography of sites to possibly untangle the mechanisms that characterise regional-to-local differential delivery.

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