MESOSCALE MECHANISMS OF LARVAL TRANSPORT AND SETTLEMENT IN RELATION TO PHYSICAL FACTORS OFF THE SOUTH COAST OF SOUTH AFRICA: A TOPOGRAPHIC APPROACH

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By

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Abstract

The majority of benthic marine invertebrate life cycles include a meroplanktonic phase. Most marine biologists recognise that this stage could play an important role in dispersal, especially for sedentary or sessile organisms. Recent studies on larval dispersal have found that dispersal does not occur to the extent that was previously believed. Some larvae instead remain close to their natal populations through larval nearshore retention mechanisms, both active and passive. This study attempted to a) describe nearshore distribution patterns of several intertidal larvae in relation to nearshore hydrodynamics, b) infer whether larvae are active or passive in the water column and whether this differs among taxa and c) compare pelagic mussel larval abundance with settlement rates, at 2 bay and 2 open coast sites on the south coast of South Africa to note any topographical effects. At each of the four sites, pelagic samples were collected along 2 transects. Larvae and current speed data were collected at various depths (surface, mid-depth and bottom) at distances of 200, 400, 900 and 2400m offshore of the coast. Settlement samples were collected at sites that were onshore of the pelagic transects using plastic souring pads following previous studies.

Pelagic larval distribution showed no effect of topography. Instead larval abundance was highly variable among sample periods and among different taxa. Slow swimming D-stage mussel larvae were found to be positively correlated with both upwelling and turbulence indices suggesting that they behave as passive particles in the water column. The abundances of larval taxa with faster swimming speeds than the D-larvae were negatively correlated with upwelling and did not correlate with turbulence. This suggests that these larvae are more active within the water column than the D-larvae which would theoretically allow them to maintain their position in the water column. Further analysis revealed that mean larval depth correlated with mean depth of shoreward moving water masses regardless of the state of upwelling. These results suggest that larvae were actively selecting the depth at which they were found presumably in order to associate themselves with shoreward moving currents. This interpretation was supported by ontogenetic patterns in the behaviour of barnacle larvae, the nauplii of which were found further offshore as they aged, and closer onshore again once they reach the faster swimming cyprid stage.

Although there was no detectable effect of topography on the abundances of planktonic larvae, the settlement section of this study revealed an effect of topography, with higher settlement and recruitment rates at bay sites than at the open coast sites. Settlement rates were seen to be negatively correlated with turbulence at bay sites but not open coast sites. Recruitment rates for each sample event were positively correlated with upwelling at each site.

This study found pelagic larvae to be generally active within the water column which allowed them to remain close to the shore regardless of topography and upwelling/turbulence regimes. Although meaningful correlation analyses between pelagic larval supply and settlement rates could not be conducted due to loss of settlement collectors, settlement rates were affected by local topography with higher settlement and recruitment in bay sites.

Contents

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I am grateful for you all.

Declaration

I hereby declare that this thesis submitted for the degree of Master of Science at Rhodes University has not previously been submitted for a degree at another university and is my own work.

Mian

Shana Iva Mian

Date

Chapter 1:
General Introduction

> *"To know the history of science is to recognize the mortality of any claim to universal truth."*
>
> \- Evelyn Fox Keller

Most benthic marine invertebrate life cycles include a meroplanktonic phase, the evolution of which is still under debate. Many scientists question the advantages of a planktonic phase as there are many disadvantages associated with it. Despite the gaps in knowledge of the significance of the planktonic larval stage, most marine biologists recognise that this stage plays an important role in dispersal and affects population dynamics (Pechenik 1999; Metaxas & Saunders 2009). For the management and conservation of species, especially those with high socioeconomic value, the mechanisms that determine larval retention and supply, such as scales of larval transport, need to be understood. Unfortunately, the mechanisms that regulate larval transport have not yet been entirely untangled, making a holistic understanding of these invertebrate life cycles still challenging.

WHAT ARE LARVAE?

At first glance, the simple question “What are larvae?” appears straight forward and likely to have a simple definition. Surprisingly though, scientists have yet to settle on a definition that is accepted by all branches of natural sciences. The lack of consensus as to what a larva is becomes even more urgent when one considers that, of the 31 phyla in the animal kingdom, 23 are said to contain approximately 170 000 marine species which undergo indirect development or “biphasic” life-cycles (Young 2002).

Defining larvae is centred on two main problems. The first challenge is to define boundaries between the embryonic and juvenile stages (Hall & Wake 1999). Strathmann (1993) stated that said boundaries are “at some point arbitrary”. The second problem with the definitions of larva thus far is that those that are based on either structural, ecological and/or morphological characteristics do not always coincide with one another (Hall & Wake 1999). To further complicate larval definitions, there are different types of larvae generally related to their feeding strategies.

Structural definitions describe larvae as the form that occurs at the onset of the divergent morphogenesis, following embryonic development (after cleavage and the blastula and grastula stages) and before metamorphosis into the adult form (Giese & Pearse 1974; McEdward & Janies 1993; Nielsen 1998). As the larvae are between the embryonic and adult forms, they possess a mixture of transitory features that will allow them to reach final development (Hall & Wake 1999). Identification of these transitory features allows us to identify species and larval developmental stages. This definition contains some very "arbitrary" boundaries as discussed by Strathmann (1993), which become particularly apparent when one is studying organisms that develop in egg masses or capsules, which are normally considered to be embryos, despite having the structural features of a larva (Hall & Wake 1999).

Ecological definitions of larvae on the other hand, possess their own set of limitations. These definitions describe larvae to be dichotomically distinguished as: a) the free living life-history stage that b) hatches and passes through a pelagic phase (Hall & Wake 1999), as either planktotrophic or lecithotrophic larvae. The loop hole in this definition is that it does not consider larvae that undergo larval morphogenesis while still remaining benthic (Hall & Wake 1999). The lack of distinction between larvae that go through morphogenesis, but remain benthic (i.e. the larvae are "aplanktonic", sensu Pechenik 1999) and organisms that do not exhibit morphogenesis (direct development from the embryo to the adult form) results in the exclusion of a large number of organisms with biphasic life cycles.

For the purposes of this study, larvae were defined as the "developmental stage, occupying the period of post embryonic stage to metamorphosis, and differs from the adult in morphology, nutrition and/or habitat" following Chia (1974, pp 122).

Types of Pelagic Larvae

Pelagic larvae can be divided into two main categories, planktotrophic and lecithotrophic, based on their feeding modes during the larval phase. Larvae that are planktotrophic feed on plankton (Martinsson 1975), whereas lecithotrophic larvae are referred to as non-feeding larvae and rely on the endogenous energy reserves of a yolk sac (Thorson 1950; 1961).

Because planktotrophic larvae do not rely on food reserved supplied by their parent (although they do initially have a small yolk reserve that is quickly used up), their life strategy is an R-selected one (Sterns 1977), with organisms producing large volumes of juveniles at relatively little expense per unit to the parent. Although parental investment per larva is low when compared to lecithotrophic larvae, overall reproductive investment is often high, due to the sheer volume of larvae produced (Chia *et al.* 1984; Grahame 1977).

Lecithotrophic larvae require an increased investment from the parent for larval production, as larvae contain a high energy reserve in the form of a yolk sac. Species that reproduce through lecithotrophic larvae have a K- reproduction strategy (Sterns 1976).

The R-selected strategy is most common in organisms that are located in dynamic, unstable systems including the nearshore region (Jackson 1974; Jablonski & Valentine 1981; Rex & Warén 1982). It is important to note that there are exceptions as in the case of gastropods (Bouchet & Wáren 1980), which exhibit K-selected life strategies.

Pelagic larvae include a third larval feeding type, although it is rare, referred to as facultative planktotrophs (Vance 1973; Perron 1981; Alatado *et al.* 1984; Emlet 1986; McEdward 1997). These larvae develop with endogenous energy reserves, but are also able to feed (Vance 1973; Perron 1981; Alatado *et al.* 1984; Emlet 1986; McEdward 1997). This larval type is thought to be the intermediate evolutionary phase of non-feeding larvae to obligate feeding larvae strategies (Wray & Raff 1991; Hart 1996).

PLANKTONIC LARVAE, WHY?

Evolution: What came first?

For centuries scientists have looked to the adult form of organisms to discern evolutionary pathways in an attempt to construct accurate phylogenies. It was not until the 1900's that Garstang (1922) drew attention to the importance of organisms' larvae with regard to their phylogeny. He stated that, when investigating ancestry, larvae would be the most informative stage as "ontogeny does not recapitulate phylogeny, it creates it" (Garstang 1922 p 81). In fact, the presence of a larval form presents both evolutionary biologists and ecologists with a complex and intriguing question as to the purpose of a larval stage. In chapter 12 of "The origin and evolution of larval forms", Wake & Hall (1999) elegantly stated that "an 'ancient and honourable' question that is not fully answered, nor even fully grasped, is why larvae have evolved at all" (p 412) . Before this question can be addressed one needs to examine when and how the larval form evolved.

Although there is no consensus as to when or why the evolution of a larval stage occurred, or why it persists today, some general themes can be identified in the literature. The evolution of the larval phase is said to have occurred due to the presence of antagonistic selection between an organisms' juvenile and adult stages (Strathmann 1993; Johnson & Shanks 2003). If strong antagonistic selection exists between the adult and its young for more than one trait, then there would be substantial selection pressure to separate the early and later developmental stages, resulting in the evolution of metamorphosis (Havenhand 1995). In fact, there are two dominant views on the evolutionary pathway of biphasic life cycles.

The first view is that larvae evolved as an addition to the original holobenthic adult form (Salvini-Plawen 1980; Ivanova- Kazas & Ivanov 1988; Rouse 1999, Sly *et al*. 2003; Raff 2008; Degnan & Degnan 2010), commonly referred to as the "intercalated" theory. This hypothesis states that the holobenthic adult stage, which completes its entire life cycle in the benthos, appeared first, with the larval stage evolving independently and convergently later on, in response to an increase in predation on the adults during the early Paleozoic (Ivanova-Kazas & Ivanova 1988; Sly *et al*. 2003; Peterson *et al.* 2005). Support for this theory is based on fossil records from early Paleozoic marine communities which were dominated by benthic organisms that did not have a pelagic phase and the correlation between the occurrence of larvae and increased predation pressures during the early Paleozoic (Peterson *et al.* 2005). This theory was put forth by Strathmann (1987, 1993) and mirrored by Peterson *et al.* (2005) who state that the function of the larval form "is not dispersal, but growth". As juvenile sizes fell within the range of the particle size ingested by benthic suspension feeders (Young & Chia 1987), juveniles were unable to escape predation until they had grown larger. The evolution of metamorphosis, and therefore the larval form, provided a mechanism for juveniles to evolve rapid growth rates (Peterson *et al.* 2005), which could be accomplished by the evolution of 'set-aside" cells that allow for the adult body plan to be constructed awhile the larvae are still in the planktonic phase (Davidson *et al.* 1995; Peterson *et al*. 1997). The predation pressure is thought to have selected for the fast growing larval form rather than larval forms with high dispersal potential.

An opposing hypothesis has been argued by Berrill (1931), Jágersten (1972), Nielsen (1979), Nielsen & Nørrevang (1987), Hoagland (1986), Jackson (1986), Strathmann (1987), Emlet *et al.* (1987), Raff (1987), Reid (1989), Mooi & David (1993), Giangrande *et al*. (1994), Page (1994), Rawlings (1994), Rieger (1994), Strathmann & Eernisse (1994), Havenhand (1995), Wray (1995), Bhaud & Duchene (1996), Raff (1996), Byrne & Cerra (1996), Hart *et al.* (1997), Ponder & Lindberg (1997), Nielson (1995, 2009, 2013) who rather sustain the "terminal addition" theory, according to which the adult phase is the addition and the larval stage is the primitive form from which the extant adult evolved (Nielsen & Nørrevang 1985; Nielsen 2009). This theory has received a lot of attention in recent discussions on larval evolution as it claims that the intercalated theory is based on speculation and assumptions rather than direct observation (review by Nielsen 2013).

The assumption that the evolution of the larval stage was driven by predator avoidance via dispersal into the plankton was put forward by the likes of Pechenik (1979), Strathmann (1985) and Lindquist & Hay (1996). This theory was, however, short lived, as it has since been pointed out that any escape from predation, using this mechanism, would be temporary as larvae would have to eventually descend to the benthos to settle (Pechenik 1979; Pechenik 1999). It has been stated numerous times in the literature, but most forcefully in the review by Pechenik (1999 p 272) that "there is no convincing or logical argument that larvae have been or are selected for as dispersal agents" (Pechenik 1980; Hedgecock 1986; Emlet *et al.* 1987; Strathmann 1993). While dispersal may not be a driver of the evolution of the larval form, it is an important by-product or secondary adaptation (Pechenik 1999) and it certainly has a central ecological role in the dynamics of populations of sedentary or sessile species in particular.

Advantages and disadvantages of having a larval stage

Despite the lack of consensus as to the origins of the meroplanktonic stages in marine invertebrates, it is clear that there are various advantages and disadvantages that can be associated with the presence of a larval stage (reviewed by Pechenik 1999) such as dispersal, predation and parental energetic costs against survival of juveniles (Pechenik 1999).

Dispersal is perhaps the most widely published topic in the literature on larval ecology and evolution. An organism that has a planktonic larval phase is thought to have an increased dispersal potential compared to benthic species which use brooding strategies (Pechenick 1999). This greater dispersal potential brings with it various long term to short term benefits. Short term benefits of a pelagic larval stage include: a reduction in competition for resources among siblings (Economou 1991), and between juveniles and their parents (Havenhand 1995), and a reduction in the likelihood of inbreeding (Jackson 1986; Husband & Schemske 1997). Dispersed larvae may also be better able to avoid benthic predation (Pechenik 1979; Strathmann 1985; Lindquist & Hay 1996), although only temporarily (Pechenik 1999). The predator release benefit also requires that mortality due to predation in the pelagic be less than that in the benthic (Pechenik 1979). This may not be the case, however, as, although predation rates have not been widely studied, nor realistically measured, predation rates observed in the field have revealed extremely high levels of predation in the pelagic (Olson & M^{c}Pherson 1987). This, coupled with evidence that pelagic larvae have developed behavioural (Young & Chia 1987; Forward & Hettler 1992), physical (Morgan 1995) and chemical (Linquist & Hay 1995; review by Morgan 1995) defences against pelagic predators, suggests that predation in the pelagic environment is high, though it may be overestimated in some studies (Johnson and Shanks 1997).

The advantage of dispersal has however been said to be overestimated, as further studies have indicated that intertidal populations do not need a high degree of genetic exchange to maintain their current structure (Pineda *et al*. 2007; Slatkin 1993; Cowen & Sponaugle 2009). Larvae of some sessile organisms, such as barnacles, have even shown selection for a reduction in dispersal potential (Newman & Ross 1977; Anderson 1994). Consequently, it has been argued that dispersal may be a result and not a selective driver of planktonic larvae (Pechenik 1980; Emlet *et al.* 1987). Dispersal may also be disadvantageous as it potentially increases the risk of larvae being displaced from suitable environments (Caley *et al.* 1996) and/or swept too far offshore, with no chance for final settlement (Thorson 1946; Strathmann 1986).

High dispersal potential may also bring with it various post-metamorphic consequences. Many studies have found that larvae that delay their metamorphosis have decreased juvenile growth rates or even smaller average sizes at metamorphosis (Woollacott *et al*. 1989; Pechenik *et al.* 1993; Wendt 1996; Qian & Pechenik 1998) even if metamorphosis is delayed for even a short period of time (Woollacott *et al*. 1989; Wendt 1996; Qian & Pechenik 1998).

The various advantages and disadvantages discussed above affect larval types quite differently. Feeding larvae cost less to produce per unit than non-feeding larvae but they also have a higher dispersal potential (Pechenik 1999). This higher dispersal potential would mean that in the short term they would run a greater risk of extreme offshore transport (Strathmann 1986), which could see them never returning to a potential settlement site (Thorson 1946; Strathmann 1986), but it would also result in them having a greater chance of persisting over a geological time period (Verrneij 1978; Jablonski & Lutz 1983; Gili & Martinell 1994; Ridley 1996). This persistence is likely made possible as long distance dispersal would allow them to escape local extinctions, colonise new habitats or recolonize disturbed habitats (Crisp 1974; Jablonski & Lutz 1983; Valentine & Jablonski 1983; Bryan *et al*. 1988; Ridley 1996).

Studies focussing on the fossil record have mirrored these intuitive speculations with species having planktonic larvae surviving mass extinction whereas species having non-feeding are less likely to survive (Vermeij 1978; Jabolanski & Lutz 1983; Gili & Martinell 1994; Ridley 1996). On the other hand, non-feeding larvae would likely be observed as settling closer to their natal population which would result in them being less persistent over geological times (Young *et al*. 1988; Stoner 1990).

Habitat type, specifically topography, may partly (and indirectly) influence the evolutionary benefit, or lack of, the larval stage. As topography affects nearshore hydrodynamics, it can create areas of high larval retention (Graham & Largier 1997; Wing *et al.* 1998a, 1998b; Roughan *et al.* 2005; Mace & Morgan 2006) or exportation. Typically, bays are suggested as areas of high larval retention and capes or open coasts are areas of higher larval export (Graham & Largier 1997; Wing *et al.* 1998a, 1998b; Roughan *et al.* 2005; Mace & Morgan 2006). As lecithotrophic larvae have limited dispersal and are likely only able to successfully settle near natal populations, a higher amount of lecithotrophic larvae, compared to planktotrophic larvae, may be exported too far offshore at open coast or cape habitats, where they would be unable to return to suitable settlement sites. This is not always the case, as lecithotrophic larvae may be exported far from their natal site and still settle successfully if current speeds are high and unidirectional (Dirnberger 1993). Lecithotrophic larvae are thought to conform to the "Desperate Larvae Hypothesis" (DLH) (Knight-Jones 1953; Toonen & Pawlik 2001; Marshall & Keough 2003), which states that, as lecithotrophic resources diminish, larvae become more sensitive to settlement cues (Knight-Jones 1953; Toonen & Pawlik 2001; Marshall & Keough 2003). This would prevent lecithotrophic larvae from being exported too far offshore as they would attempt to settle more rapidly than planktotrophic larvae. This however has obvious draw backs as larvae become more willing to accept suboptimal settlement sites in order to lower the risk of not settling at all.

Planktotrophic larvae have an increased potential for dispersal which makes hydrodynamics, and therefore topography, an important variable to consider as it would greatly affect whether larvae settle near to or far from their natal site (Pechenik 1999). This, in turn, would affect gene flow between populations to a greater extent when compared to lecithotrophic larvae. Planktotrophic larvae are not considered to be affected by the DLH, but are at greater risk of larval "pig-headedness" (Stoner 1996; Pechenik 1999) than lecithotrophic larvae. This term refers to the phenomenon of larvae failing to settle in an environment because the habitat does not produce a small set of predetermined settlement cues (Pechenik 1999), but in doing so they risk the chance of not encountering further suitable substrata. It is clear that habitat site and larval type are important factors when determining the hierarchy of advantages and disadvantages of a particular larval type.

TOPOGRAPHIC DIFFERENCES IN ADULT POPULATIONS: DOES LARVAL SUPPLY HAVE THE ANSWERS?

Previous studies have noted differences in adult population structure of intertidal species between bay and open coast sites (Crisp & Southward 1958; Helson & Gardner 2004; Lagos *et al.* 2005; McQuaid & Phillips 2006; von der Meden 2009; Pfaff *et al.* 2011; von der Meden *et al*. 2012). Despite this being a widespread trend, the difference in population densities between these topographic features is not yet fully understood. Some studies have named factors such as differential wave action and thus differential abiotic pressure over adults, the presence of “upwelling shadows” in bays and not capes, as well as other bathymetrically modified nearshore hydrodynamics, as possible drivers for a topographic trend (Graham & Largier 1997; Wing *et al.* 1998a, 1998b; Roughan *et al.* 2005; Mace & Morgan 2006).

In the present study region, von der Meden and co-authors (2012) found that, although adult populations of mussels were different between bay and open coast sites, neither settlement nor post-settlement processes could entirely explain the structure of adult populations. These findings justify further investigation into the pelagic distributions of larvae and those physical factors that may affect their distribution, as possible factors contributing to the topographical differences in adult populations within the region. Other studies conducted in this region focussing on pelagic larval distributions have also found that, although larval abundances are generally high in bays, there are sporadic isolated incidences when mesoscale hydrodynamic features may export larvae from bay sites to the offshore environment (Porri *et al.* 2014). This highlights the importance of considering regional hydrodynamic features.

STUDY OBJECTIVES

The main objective of this study was to characterise the very nearshore distribution patterns of the larvae of several intertidal taxa and identify whether their distributions could be linked to various small scale oceanographic variables and ultimately determine the active or passive role of pelagic larval behaviour in relation to local hydrodynamics (Chapter 2). A multiple-taxon approach was used to determine if patterns and behaviours were dependent on larval type/taxon. To further understand the ecological links between the larval phase and adult population, settlement and recruitment rates of the intertidal mussels *Perna perna, Mytilus galloporovincialis* and *Choromytilus meridionalis* were measured to determine if there were differences in settlement and recruitment rates between bay and open coast sites during the sampling periods and how these rates were affected by physical factors such as turbulence and upwelling (Chapter 3). A final chapter (Chapter 4) includes an overall discussion and overall concluding remarks for this research.

CHAPTER 2:

CROSS-SHORE DISTRIBUTION OF INTERTIDAL LARVAE IN RELATION TO MESOSCALE OCEANOGRAPHIC FEATURES AND TOPOGRAPHY: ARE LARVAE ACTIVE OR PASSIVE?

> *"Somewhere, something incredible is waiting to be known."*
>
> — Carl Sagan

INTRODUCTION

Ecologists often associate the presence of a pelagic larval phase in many marine invertebrates as a mechanism for dispersal. This was thought to be of significant importance for sedentary and sessile species, as the increase in dispersal potential, would greatly affect population dynamics and be the main (if not the only) means of increasing the connectivity between populations, that would otherwise be isolated (Thorson 1950; Thorson 1961, Scheltema 1971; Roughgarden *et al.* 1985). Through dispersal, larvae would not only facilitate higher genetic exchange between populations, but also enable organisms to effectively exploit new habitats or re-colonise newly available surfaces. Because of the potential relevance of a dispersive life stage, an important factor to consider when examining the early dynamics of intertidal populations of biphasic species is to determine the level of dispersal occurring.

Recent molecular-based research has revealed that very little exchange is needed to maintain the observed genetic structure of intertidal populations (Slatkin 1993; Cowen *et al.* 2000; Cowen & Sponaugle 2009). This may indicate that the realised dispersal of biphasic species has often been overestimated and that larvae may settle closer to their parent population than previously thought (Weersing & Toonen 2009). Studies focussing on pelagic larval distribution have also called the estimation of larval dispersal into question. Traditionally, larvae were thought to be passively exported offshore via upwelling and onshore via downwelling (Gaines & Roughgarden 1985; Farrell *et al*. 1991; Roughgarden *et al*. 1992; Grantham 1997). Studies such as Poulin *et al*. (2002), Shanks & Brink (2005), Genin *et al*. (2005), and Morgan *et al.* (2009) have however shown that many larvae are not exported far offshore, but instead remain close to the coast. Such nearshore retention has been observed for larvae of various shallow water bivalves (Shanks & Brink 2005) and crabs (Morgan *et al.* 2009) along the Californian coast, as well as for gastropods (Poulin *et al*. 2002) off the Chilean coast. Both these coastlines experience distinct periods of upwelling and downwelling events making them ideal locations for investigating how larvae are affected by upwelling and mesoscale oceanographic features that may move larvae offshore. The results of such investigations (Shanks & Brink 2005; Morgan *et al*. 2009; Poulin *et al.* 2002) are in contradiction to those of Roughgarden and co-authors (1988) in which barnacle larvae were reported to move offshore during upwelling and onshore during downwelling events. The differences between the two groups of studies could, however, be partially explained by the very different offshore distances sampled: approximately 9km offshore (Roughgarden *et al.*

1988) and 1 km from the shore (Shanks & Brink 2005; Poulin *et al.* 2002; Morgan *et al.* 2009).

The next challenge to understanding larval transport is questioning how these relatively slow swimming organisms are able to resist offshore transport by fast moving offshore currents. The answer lies in the dichotomy of passive and active mechanisms. A passive mechanism associated with the nearshore retention of larvae was first discussed by Csandy (1972) who described how the Coastal Boundary Layer (CBL hereafter), the layer of slow moving water close to the coastline, increases viscosity and turbulence in the water. The water would later be called “sticky water” by Wolanski (1994) who noted this water mass has lower dynamism and permeability than the more offshore waters, and is thought to trap larvae close to the shore.

Studies focussing on nearshore distributions of larvae have observed nearshore distributions to be more cross-shore limited than if the CBL was the only mechanism at work (Genin *et al*. 2005). This high level of nearshore larval retention suggests that additional mechanisms must be present. Similar spatial scale studies began to note that distribution profiles of larvae in the nearshore region appear to have various depth preferences (Shanks *et al.* 2000; Genin *et al.* 2005; Mace & Morgan 2006; Knights *et al*. 2006; Landeira *et al*. 2012). This observation of depth stratification of larval distributions gave rise to a possible additional mechanism of nearshore larval retention. The horizontal currents in the nearshore are fast moving when compared to larval swimming speeds, suggesting that larvae are not able to actively orientate themselves by swimming against these currents. The vertical currents are however comparable to larval swimming speeds and some larvae are in fact able to swim faster than average vertical current speeds (Mileikovsky 1973, Chia *et al.* 1983). This potential ability for larvae to select their depth would also enable them to actively associate themselves with water masses that are moving onshore and therefore promote nearshore retention.

Nearshore physical hydrodynamics are important to larval distribution regardless of whether nearshore larval retention mechanisms are active or passive and these nearshore hydrodynamics are greatly influenced by the presence of bay, headlands and bathymetric features (Wolanski & Hamner 1988; Geyer & Signell 1992; Largier 2003; Narváez *et al.* 2006). It is therefore not surprising that these topographic features also need to be considered when investigating nearshore larval distribution patterns. These features become particularly interesting to look at when one considers that previous research has found differences between adult populations in bays and at open coast sites both globally (Helson & Gardner 2004, Roughan *et al.* 2005; Mace & Morgan 2006) and also specifically in the region of this study for mussel populations (McQuaid & Phillips 2006; von der Meden 2009). Researches such as von der Meden *et al.* (2012) have ruled out post-settlement mortality as the sole driver of this pattern which suggests that answers lay in supply-side ecology factors.

This study aims to a) determine the nearshore distribution of several larval taxa along the vertical and across-shore axis to see if observations of nearshore retention made at scales of kilometres in the literature remain true at finer spatial scales; b) note possible temporal and topographical effects on the distribution of larvae; c) investigate how mesoscale hydrodynamics may affect larval distribution and d) infer whether larvae are active or passive with regard to these mesoscale hydrodynamics.

MATERIALS AND METHODS

This study took place during 2013 over two sampling periods. The first set of samples was collected between the end of February and mid- May 2013, and will be referred to as the "March" samples. The second set of samples was collected over the September and October months of 2013, and will be referred to as the "September" samples. In this region March is considered to be autumn and September is spring however this study was not concerned with seasonality and therefore seasonal replicates were not collected. Sample periods instead are two replicates of time that would likely have different larval abundances due to seasonality (Porri *et al.* 2006). During each of the sampling periods, nearshore samples were collected from two bay and two adjacent open coast sites. The corresponding bay and open coast sites were no further than 20 km from each other. These sites are located in the Eastern Cape of South Africa (Figs 2.1a&b) and were Algoa Bay, Skoenmakerskop, St Francis Bay and Cape St Francis (Fig 2.1b). At each of the sites, a plankton pump (2.2 KC Denmark 23.580) was used to collect meroplankton samples along two parallel transects (A & B) perpendicular to the coast (Fig 2.1c). Samples were collected at different stations along the transects at offshore distances of 200 m, 400 m, 900 m and 2400 m (Fig 2.1c). At each of the sample stations, meroplankton were sampled from three depths. For the inshore stations (200 m and 400 m), these depth were surface (1 m below the surface of the water), mid depth and bottom. Here the bottom was considered to be the water mass 1 m above the sea floor. The mid shore station (900 m) was shared with another ongoing study. Here four depths were sampled at equal depths apart. In order to avoid an unbalanced design, the samples analysed for this study were taken at surface, mid depth (considered the sample which corresponded with inshore mid depth) and bottom depth. At the most offshore station (2400 m), samples were collected at surface, mid depth or at the depth of the thermocline, if present, and bottom depth.

Physical Data

There were two weather stations located within the study region, one in Algoa Bay and the other at Cape St Francis (Fig 2.1b). The data from these stations were provided by the South African Weather Service for each of the sample events. The anemometer in Algoa Bay was located 60m above sea level and in Cape St Francis it was at 9m above sea level. This discrepancy in height between the weather stations was corrected according to the methodology used in Weidberg *et al.* (2015) by adjusting the Algoa Bay height to be the same at the Cape St Francis weather station:

$$V_{9m} = V_h * ({}^{9}/_{h})^{0.11}$$

where V_{9m} is the wind velocity height at 9 meters (altitude of the Cape St Francis weather station). And V_h is the actual wind velocity recorded by the anemometer at the height h it was positioned at.

The wind data were used to calculate turbulence and upwelling indices at the time of sampling. St Francis Bay and Cape St Francis sites were coupled with Cape St Francis wind data and Algoa Bay and Skoenmakerskop were coupled with Algoa Bay wind data. The South African Weather Service provided an hourly average of the wind speed and direction over the entire sample period.

Wind driven turbulence was calculated using the equation in Pringle (2007):

$$\varepsilon = (V_{9m} *)^3 k^{-1} z^{-1}$$

where $V_{9m}*$ is the height-corrected velocity scale of turbulence, k is Von Karmen’s constant (0.41), z is depth (fixed for 1 meter for this study) and ε is kinetic energy dissipation rate in W kg^{-1}. Depth was fixed at one meter as turbulence in both unstratified (assumed to be the case for this shallow nearshore zone) and stratified water columns becomes small and presumably insignificant very quickly (Madsen 1977; Galperin *et al.* 1988; Burchard *et al.*

1999). At approximately 1 m depth there is a steep decrease in turbulent energy regardless of stratification (Pringle *et al.* 2007). Turbulence was averaged over the 12 hours prior to the collection of each sample, following Weidberg *et al.* (2015), which described this time period to be the most informative. Although the exact scale of turbulence appropriate for this study was not yet know, turbulence was averaged over 12 hours as this time period has been reported to be adequate to capture variability in the system, but is also long enough for larval responses to turbulence to occur (Burchard 2002). Anything less than 12 hours would not amount to a significant amount of movement of the water mass (Pringle 2007). Due to time constraints, the 12 hour average in turbulence was tested on a small proportion of the data for various time periods (12 hours, 1 day, 2 day and 4 day) and the 12 hour average was found to be the most informative. In order to make these results comparable to those of laboratory experiments conducted by Fuchs & Di Bacco (2011) and Fuchs *et al.* (2012) on the response of mussel and oyster larvae to turbulence, it has been noted that 1 W.kg^{-1} is equal to 1 x 10^{-2} cm^{2}s^{-3} (the unit the studies used to measure turbulence). Turbulence units used in this thesis are reported in W.kg^{-1} as this aligns with previous work conducted in this region (Weidberg *et al.* 2015).Values were however also converted when discussing results alongside the laboratory based experiments.

Wind driven upwelling was calculated using the formula first described by Bakun (1973) and was clarified further by Lavin *et al.* (1991). The equation was reported as follows by Llope *et al*. (2006):

$$Q_y = \frac{\tau_x}{f.\rho_w} = \frac{\rho_a . C_d . v_x . |v|}{f.\rho_w}$$

Here τ_x represents the wind stress along the x-axis, ρ_a is air density (considered constant at 1.22 kg m^{-3}), C_d is an empirical drag coefficient also considered to be constant (0.0014) according to Hidy (1972), v_x is the east to west directional component of the wind and $|v|$ is the module of wind. These values are then divided by $f.\rho_w$ where f = 2Ω sin ∅ is the Coriolis parameter (9.96 10^{-5} s^{-1}) and ρ_w is seawater density (1025 kg m^{-3}). The resulting value is the mean mass of water displaced off the coast in m^{3} s^{-1} km^{-1}. If the value calculated is positive then mean upwelling occurred and if the value is negative then downwelling occurred. Upwelling indices were averaged over 4 days prior to sample collection following Weidberg *et al*. (2015) who describe this time period to be the most informative.

At each station, current speed and direction data were collected using a boat based Acoustic Doppler Current Profiler (ADCP). The processing of the ADCP data were conducted with the help of Drs Jennifer Jackson and Nicolas Weidberg. Currents were measured every 2-5 seconds and averaged over 7-10 minutes. Data corresponding to depths above 2.25 m were discarded due to side lobbing. Current velocity was filtered using the percentage of good data which considers the quality of each observation. The data collected were not averaged for each station and transects were plotted separately by Dr Jennifer Jackson.

At each station, temperature profiles were established using either a YSI or a generic CTD depending on which was available. On two occasions during the September sampling at St Francis Bay and Cape St Francis, a dive computer had to be used to attain a rough temperature profile due to the malfunctioning of the preferred equipment. All instruments were calibrated to one another to ensure that the data collected were standardised and there were no discrepancies in the data set.

Larval collection

Larvae were collected at each station at each depth using a plankton pump (2.2 KC Denmark 23.580). Mesh size used in the plankton pump was 60µm. The pump was left to run for 7-10 minutes during which 1000-2000 L were filtered at approximately 30 cm/s.

Larval identification

This study attempted to identify bryozoans and species of bivalves, barnacles and decapods. South African identification papers on local species are rare and were used when available. When identification was not possible, species were grouped at a broader taxonomic level.

Bivalves

Bivalve larvae were grouped into the following taxa based on research done by Bownes *et al.* (2008) who focussed on identification of the intertidal species *Perna perna*, *Mytilus galloprovincialis*, *Choromytilus meridionalis* and D-larvae; Booth (1983) for identification of the "*Hiatella* spp." grouping; Waller (1981) for identification of the "oyster" grouping. There were two distinct larval types that remain unidentified. These were grouped as "bivalve type A & B" (Figs 2.2 a&b respectively). Bivalves that were indistinguishable from one another were all grouped as "other bivalves".

Decapods

Decapod larvae were grouped as either: Pinnotherids, *Brachyurans*, Porcellanids, *Paraesarma* spp. or Anomurans based on the work of Lago (1987, 1993), Shakuntala & Sankolli (1992) and Dos Santos & González-Gordillo (2004).

Barnacles

Barnacle larvae were grouped as Balanid early nauplii, Balanid late nauplii, *Chthamalus* early nauplii, *Chthamalus* late nauplii and two distinct, but identifiable cyprid species referred to as Cyprid type A and B. South African papers used to identify these groups were those of Eyvor & Sandison (1951) and Achituv (1986). International papers were also used to supplement this work, being Brown & Roughgarden (1985), Geraci & Romairone (1986) and Kado & Kim (1996).

Statistical Analysis

Physical Data

All analyses on the physical data were run in STATISTICA 12. To determine if there was a difference in the magnitude of the calculated daily upwelling and turbulence indices between the two sampling periods (March and September), a 2-way ANOVA was run with time (2 levels) as a random factor and site (4 levels) as a random factor. As the data were collected from each site on different days (no 2 sites were sampled on the same day), the wind data used for this analysis were not autocorrelated. The data for both upwelling and turbulence did not meet all of the assumptions associated with ANOVA analysis. Although the data presented homogeneity of variance, the data set was not normally distributed according to several normality tests (Kolmogomov-Smimoff, Shapiro-Wilk and the Jarque–Bera test). Despite the skewness of the data set, according to Box (1953), Glass *et al.* (1972), Zar (1984), Neter *et al.* (1985), Winer *et al.* (1991), the use of the ANOVA analysis is reliable if the data set is large. In statistics it is often a challenge to define what makes a data set large or small. With respect to the robustness of the ANOVA analysis to skewness/ non-normality, Khan & Rayner (2003) provided evidence that some sets with more than 30 data points were not affected by non-normality. The current data set met this requirement as each sample period had a total of 48 data points. This pre-screening of data also indicated that transformation of the data were not necessary. Periodicity was also calculated for both upwelling and turbulence during each sampling period. The periodicity of both was calculated in STATISTICA 12 by plotting a periodogram for each and conducting a single series Fourier analysis and setting the period as hourly. The periodicity was selected as being the highest peak produced on the periodogram.

Larval distribution

The main aim of this study was to analyse the distribution and abundance of several taxa in relation to distance from the shore, depth and physical structure of the water column. Due to the high levels of larval diversity, only larval groups that fitted certain criteria were analysed. The criteria included the presence of more than 10 individuals in at least one sample during each sampling with at least 30% of the samples containing at least one individual.

To determine larval distribution for each sampling event and to observe possible patterns in terms of topography, across-shore position and depth, several 3-way Analysis of Variance (ANOVA) were run. The larval abundance data (abundance per m^3) were used and the analysis was set up so that it included site (4 levels), distance (4 levels) and depth (3 levels) as fixed factors. A nested design was not used as this would not allow for comparisons to be made between sites regardless of topography. The larval abundance data did not meet all of the assumptions associated with ANOVA analysis. Although the data presented homogeneity of variance, the data set was not normally distributed according to several normality tests (Kolmogomov-Smimoff, Shapiro-Wilk and the Jarque–Bera test). The data set however was large however that the effects of non-normal distribution on ANOVA analysis could be ignored (Box 1953; Glass *et al.* 1972; Zar 1984; Neter *et al.* 1985; Winer *et al*. 1991; Khan & Rayner 2003)

Mean depth of larvae was calculated for each site during each sampling event according to Tapia *et al.* (2010):

$$MDD = \left(\sum N_i * D_i\right) / \left(\sum N_i\right)$$

where N_i is larval abundance at depth D_i. In this study, there were three depths for each of the four stations for each onshore-to-offshore transect. The mean of both transects was used.

The mean distance offshore for each taxon was also calculated using the mean depth formula and substituting depth with distance. Here the total larval abundance at each station (the sum of three depths) was used (Shanks & Shearman 2009). The mean distance value was used to discuss possible ontogenetic differences in across-shore distribution of barnacles in particular.

Linking biological and physical data

Multiple regression analyses were run to look at possible relationships between larval abundance (per m^3) and several physical variables: upwelling, turbulence, meridional flow, zonal flow and temperature alongside abundance data for each taxon and sampling period. Because there were many models run, the p-values for each season were Bonferroni adjusted (Feise 2002). In March if the p-value was less than 0.002 and in September if it was less than 0.005 it was considered to be significant.

Regressions were also run to determine if the mean depth of highest upwelling, turbulence or meridional flow were correlated with larval abundance. In this study, mean depth of upwelling, turbulence and meridional flow refers to the mean depth at which maximal upwelling, turbulence and meridional flow occurred. This was done by calculating the mean depth according to the above mentioned formula. Meridional flow data had to be corrected to avoid negative values as these provide measurements of magnitude as well as directional information. This particular analysis was more concerned with how magnitude and less concerned with how direction may have effected with larval abundance. This was achieved by adding a positive value to all meridional flow data that was equal to the lowest value in the original data set.

RESULTS

Physical Profiles

Algoa Bay

In both March and September there was no thermocline as ocean temperature only varied by approximately 1 °C over the entire transect. There were differences in the temperature profiles between the two sample periods, in that the March profiles, for both transects A (Fig 2.3a) and B (Fig 2.4a), revealed slightly higher surface water temperatures (22°C) than at nearshore bottom depths (21°C) which matched the cooler offshore temperatures (Fig 2.3a & 2.4a). In September, this surface pattern was reversed with warmer surface temperatures offshore (22°C) and cooler temperatures (21°C) inshore (Fig 2.3b & 2.4b).

During the March and September sampling periods, the zonal flow at transect A was recorded as being easterly at the mid-shore distance offshore (approximately 900 m offshore) and westerly on either side of that mid-shore zone (Fig 2.3b,c). This easterly zonal flow was seen in two patches in the mid-shore of the transect at depths between 4-6 meters and at 8-9 meters (Fig 2.3b,c). Zonal flow at transect B was slower and less patchy than that seen transect A for both sample periods (Fig 2.4b,c).

The meridional flow pattern in March was similar at both transects; slow northerly nearshore surface currents (above 4 m depth) and faster moving southerly currents at the deeper onshore and throughout the entire water column at the offshore distances (Fig 2.3d & 2.4d). The mid-shore zone, during March, was slower moving than either the nearshore or offshore zones (Fig 2.3d & 2.4d). When compared to March, the September meridional flow was generally slower moving for both transects (Fig 2.3e & 2.4e).Transect B however, displayed a slight peak in southerly meridional flow at the mid-shore zone which was not mirrored in transect A (Fig 2.3e & 2.4e).

Skoenmakerskop

The topographic cross-shore profiles at Skoenmakerskop were steeper and deeper than the bay sites. Despite, this there was no thermocline at Skoenmakerskop during either the March or September sampling periods (Fig 2.5a,b & 2.6a,b). The temperatures at transect A and B during March ranged between 8-19°C, but the vertical temperature gradient was gradual (Fig 2.5a & 2.6a). The temperature profile for September were generally warmer than for March and the gradient was extremely slight for both transects with the highest temperature being a high of 18°C and a low of only 17°C (Fig 2.5b & 2.6b). Both March and September temperatures were highest at the surface waters offshore and decreased with both depth and distance to the shore (Fig 2.5- 2.6a,b).

Both zonal and meridional flow were difficult to compare between sampling periods as the March profiles for both sets of current data were erroneous and did not produce a complete plot (Fig 2.5c & 2.6c). The surface data for March however indicated that surface waters were slow moving in terms of zonal flow velocity (Fig 2.5c & 2.6c). Zonal flow in March was neutral to slow easterly in the inshore zone (<500m) and became faster and westerly farther offshore (Fig 2.5c) at transect A and the same was seen at transect B (Fig 2.6c).

The September profiles of zonal flow shared the same slow moving surface current patterns as March, though currents in September were even slower (Figs 2.5d & 2.6d). The more complete September plots reveal a peak in both zonal and meridional flow at depths of 25 meters (Figs 2.5d & 2.6d). Zonal flow at this depth during September was westerly in direction and the current speed was highest offshore at transect A (Figs 2.5d & 2.6d). Zonal flow at transect B at around 25 m depth was westerly however did not show the cross-shore variation in speed as seen at transect A and was slower moving (Fig 2.5d & 2.6d).

The meridional flow in September is similar to March in that the surface waters are very slow moving (Figs 2.5e,f & 2.6e,f). The meridional flow peaks at the same depth as zonal flow (25m) and is southerly in direction (Figs 2.5e,f & 2.6e,f). This peak occurs at approximately 900m offshore for both transects. Transects A however differs from B in that meridional flow is southerly at the mid-shore zone and becomes northerly offshore (Fig 2.5e & 2.6e). At transect B, the opposite is true, with faster southerly current speeds being offshore and decreasing onshore (Fig 2.5f & 2.6f) with bottom depths (35-40 m) having northerly currents (Fig 2.5f & 2.6f).

St Francis Bay

The temperature profiles for both transects and both sample periods differed and at each no thermocline was present. Transect A in March, was generally cooler than transect B (Fig 2.7a & 2.8a). Both transects however shared similar temperature gradients with warmer waters offshore and at the bottom depths, and cooler waters inshore and at the surface (Fig 2.7a & 2.8a). During September, transect A was instead warmer than transect B, but similarly to March, the warmer surface waters were offshore getting cooler more inshore (Fig 2.7b & 2.8b).

The plot for transect A was incomplete for the flow, but zonal flow in the upper waters appears to be slow moving and easterly inshore increasing in speed offshore (Fig 2.7c). The zonal flow at bottom depths is in the opposite direction to the surface waters with a westerly direction (Fig 2.7c). Transect B, in March, also had a slow easterly zonal flow inshore at the surface, becoming faster and westerly at the mid-shore surface but easterly at bottom depths (Fig 2.8c). Transect B at the offshore stations had less extreme zonal flow in a general easterly direction from surface to near bottom depths with a peak in easterly flow at the very bottom depth offshore (Fig 2.8c). The offshore pattern of transect B zonal flow was westerly moving surface waters and becoming more easterly with depth (Fig 2.8c). During September, both transects A and B showed fast moving westerly zonal flow that was only slightly slower inshore (Fig 2.7d & 2.8d). At mid depths (6-8m), zonal flow was easterly and at bottom depths it was neutral to very slow westerly (Fig 2.7e & 2.8d).

Meridional flow during March was different at each transect. At transect A, inshore surface waters meridional flow was southerly becoming northerly with depth (Fig 2.7e & 2.8e). Around the mid-shore (±900m), at around 6 m depth, flow was southerly becoming northerly at around the 10 m depth (Fig 2.7e). Transect B differed as meridional flow in the surface waters was not captured. At depth between 4 to 5 meters current direction was northerly at all distances with increasing in speed further offshore (Fig 2.8e). Mid-depths were dominated by southerly meridional flow that became weaker offshore and bottom depth showed a peak in strong northerly flow from the mid-shore to offshore (2.7e & 2.8e). During September, both transects had similar patterns with surface waters having southerly meridional flow (Fig 2.7f & 2.8f). Inshore mid-depths (6-8 m) were southerly becoming northerly further offshore. At 8-10 m offshore, the meridional flow direction changed to southerly (Fig 2.7f & 2.8f). The meridional flow at bottom depths offshore were northerly offshore (Fig 2.7f & 2.8f).

Cape St Francis

Although the temperature plots for Cape St Francis could not be completed as the YSI malfunctioned during this sampling event, the raw data indicated that a thermocline present during the March sampling. The thermocline was present between 12 – 20 m with a drop in temperature of 5 °C within this section of the water column. There was no thermocline during the September sampling.

The transects A and B during March had neutral to slow westerly zonal flow that became faster further offshore (Fig 2.9c,d & 2.10c,d). The bottom depth for the two transects was also similar with neutral to slow westerly zonal flow (Fig 2.9c & 2.10c). The transects differed in zonal flow patterns at mid depths, with transect A having westerly inshore to easterly flow offshore (Fig 2.9c) and transect B having constant easterly flow across the shore profile (Fig 2.10c). Zonal flow in September was generally slow and easterly in direction (Fig 2.9d & 2.10d). There was a peak in flow at around 20m depth in a westerly direction at transect A (Fig 2.9d) and at transect B, at the same depth, the easterly zonal flow increased in speed (Fig 2.10d). Transect A had another peak in zonal flow at around 50 m and this was in the easterly direction (Fig 2.9d). The zonal flow of bottom waters of transect B on the other hand was in a westerly direction (Fig 2.10d).

The meridional flow during the March sampling differed at transects A and B, with transect A having slow inshore northerly meridional flow to faster northerly flow further offshore (especially at mid-depths; Fig 2.9e); and transect B having slow inshore to fast offshore southerly flow, especially in the upper layers (Fig 2.10e). Both transects had a peak in flow at 20-30 m depth with transect A having northerly flow inshore and southerly flow offshore (Fig 2.9e), and transect B having a peak in northerly to southerly (mid-shore) flow (Fig 2.10e). During September, transect A surface waters were slow moving and southerly and at around 20-30m the meridional flow became northerly, becoming faster offshore (Fig 2.9f). The bottom depths of transect A were dominated by southerly meridional flow (Fig 2.9e). Transect B also had slow moving southerly meridional flow, with stronger southerly meridional flow at mid-depths Inshore, becoming fast northerly flow further offshore (Fig 2.10e). Like transect A, transect B bottom depths were dominated by southerly meridional flow (Fig 2.10e).

To further investigate the characteristics of the physical environment during the two sampling events and among sites, upwelling and turbulence were considered. The periodicity table highlighted differences for upwelling and turbulence between seasons and regions. The sampling done in March presented shorter upwelling cycles of 73.4 hours when compared to September which had cycles of 106.9 hours (Table 2.1). Turbulence periodicity was not different among sampling events, there was however an effect of region. In Algoa Bay, turbulence presented a 24 hour cycle, while in the St Francis region the cycle was close to 90 hours (Table 2.1).

The ANOVAs were used to establish significant patterns in upwelling and turbulence in relation to time and site (Table 2.2). In March, bay sites experienced more neutral upwelling (upwelling indices values were closer to zero indicating very low to zero upwelling) than September, while open coast sites experienced significantly higher downwelling than bays (Fig 2.11b). In September, the St Francis region (including St Francis Bay and Cape St Francis) experienced no to low upwelling, whereas the Algoa Bay region (including Algoa Bay and Skoenmakerskop) experienced high downwelling (Fig 2.11b). There were differences in turbulence among sample periods at different sites, but no clear pattern in relation to time (Fig 2.11c).

General Larval Distribution

Larval abundance data were analysed using several factorial ANOVAs. The results are reported separately for each taxon, according to the significant outcome of the individual ANOVA for each taxon, resulting therefore in possible inconsistent layout of the figures.

Bryozoans

During the March sampling period, the abundance of bryozoan larvae was found to be significantly affected by site, depth and distance offshore, with no consistent pattern yet higher abundance at the surface up to 900m offshore than elsewhere (Table 2.3; Figure 2.12). The bay sites showed some pattern in terms of distance offshore in September (Table 2.3). There was however no effect of topography and instead sites peaked at varying distances offshore regardless of topography. There were definite surface depth preferences at offshore stations (Fig 2.13).

Hiatella spp.

In March, there was a significant effect on the abundance of *Hiatella spp* larvae driven by the interaction of all three factors (site, depth and distance offshore) (Table 2.4, Fig 2.14). This interaction showed no clear topographic, depth or distance pattern.

Hiatella abundances in September displayed an opposite trend of topography and depth than in March. In September, there were high abundances of *Hiatella spp* at bottom depth in bay sites (although not significantly different at St Francis Bay; Fig 2.15). At the open coast sites, there was no clear trend with high abundances at mid to bottom depths. Patterns were difficult to discern as *Hiatella* abundances were generally very low and only just met the criteria for analysis.

Perna perna

Abundances of *Perna perna* peaked in Algoa Bay and at Skoenmakerskop at 900m and 400m offshore respectively during March (Table 2.5, Fig 2.16a). There was no significant pattern in terms of topography. During March, depth had a significant influence on abundance, regardless of site or distance offshore. During this season, *P. perna* abundance was highest at surface to mid depths (Fig 2.16b). The *P. perna* abundance during September was not significantly affected by the factors site, depth or distance offshore.

Mytilus galloprovincialis

Although *Mytilus galloprovincialis* met the criteria for analysis discussed in the methodology section for March, the ANOVA did not produce any significant results (Table 2.6). The abundance of *M. galloprovincialis* was not affected by any of the factors tested (site, depth or distance offshore).

Choromytilus meridionalis

The effects of several predictors on the abundance of *Choromytilus meridionalis* were analysed for the September season only as the March dataset did not meet the predetermined criteria. *Choromytilus meridionalis* abundance was seen to be affected by distance offshore (Table 2.7). The abundance of *C. meridionalis* was highest onshore, between 200 m and the 400 m off the shore, decreased at 900 m and increased slightly again at 2.4 km (Figure 2.17).

D-larvae

Like *C. meridionalis,* D- larvae were only analysed for the September sampling. Site and distance were found to have a significant effect on the abundance of D-larvae (Table 2.8, Fig 2.18), driven by the highest peak at Cape St Francis at the most offshore station . No effect of topography could be identified and the only notable result was a peak in D-larvae abundance at Cape St Francis at 2400 m offshore (Fig 2.18).

Bivalves A

Bivalve type A data were analysed for both the March and September sampling periods. During March, there was no significant effect of each of the factors on the abundance of this group (Table 2.9a).

In September, there was a significant three way interaction of site, depth and distance offshore for bivalve A abundances (Table 2.9b). There seemed to be some effect of topography, with bay sites generally having higher abundances and larvae showing more distinct depth preferences than at open coast sites, although the preferred depth differed between bay sites (Fig 2.19). In Algoa Bay, there was high abundance of larvae at the bottom while in St Francis Bay high abundance was observed at mid depths (Fig 2.19). There was a general onshore pattern of higher bivalve A larval abundances in bays than on open coasts possibly driven by the high numbers of these groups of larvae at 400m offshore in St Francis Bay (Fig 2.19).

Bivalves B

Bivalve type B data were analysed for both March and September. During March, all the factors tested were found to have no significant effect on abundances of the bivalve type B (Table 2.10a).

In September, at the offshore sampling stations (900m and 2400 m), bivalve type B larvae were mostly abundant at the bottom (Fig 2.120a) confirming the significant interaction between distance and depth (Table 2.10b). The onshore stations (200 m and 400m) did not show this depth pattern (400m, not statistically different from other depths).

There was also an interaction between site and distance offshore in September (Table 2.10b); however this did not translate into a topographical effect (Fig 2.20b). There were high abundances of bivalve type B larvae in Algoa Bay in the mid-shore region (900m), high abundances offshore in Skoenmakerskop and St Francis Bay and no distance offshore pattern at Cape St Francis (Fig 2.20b).

Other bivalves

Bivalves that could not be classified were grouped as other bivalves. This group displayed a site pattern in March only, with highest abundance of “other” bivalves at the Skoenmakerskop (open coast) in March (Table 2.11, Fig 2.21).

In September, the abundance of “other” bivalves was significantly affected by site, depth and distance offshore simultaneously (Fig 2.22). There was an effect of topography in terms of depth, with bays presenting the highest abundance at mid to bottom depths and open coasts at surface to mid depths (Fig 2.22). Open coast and bay sites also differed from one another with regard to distance offshore. At open coast sites, abundance was highest at the offshore distance, while at the bay site no clear pattern was visible (Fig 2.22).

Brachyurans

Larval abundance of brachyurans in March were significantly simultaneously affected by site, depth and distance offshore (Table 2.12, Fig 2.23). There was no clear pattern with regard to possible effects of topography, however, the abundance of brachyurans was highest at mid to bottom depths. In September, the abundance of brachyurans displayed an effect of topography in terms of depth preferences. Bay sites had the highest abundances of brachyuran larvae at bottom depths (Fig 2.24). Open coast sites however did not show a depth pattern.

Pinnotherids

In March, abundances of pinnotherid larvae were found to be significantly affected by site, depth and distance offshore (Table 2.13, Fig 2.25). There were however no clear patterns identified with regard to any of these factors. Generally, abundance was high at the bottom; notable exceptions were however Algoa Bay with a high peak at the surface and Cape St Francis, as this site had zero pinnotherids. Abundances in September were found to be high at bottom depth in bay sites (Fig 2.26), but no depth pattern was identified at the open coast sites.

Anomurans

The abundance of anomuran larvae did not show any distinction between bay and open coast sites in March (significant effect driven by the interaction among site, distance and depth; Table 2.14, Fig 2.27). There was an overall trend of high abundance of anomurans at offshore sampling stations and a general high abundances at mid to bottom depths (Fig 2.28), although this was not consistent.

In September, patterns were similar to March, with abundance showing no topographical effect (Fig 2.28a). There was a large peak in anomuran larval abundance in St Francis Bay at 2400 m (significant effect driven by the interaction between site and distance; Fig 2.28a). Unlike March, during September abundance was highest at bottom depths regardless of site or distance offshore (Fig 2.28b).

Porcellanids

Overall, abundances of larvae of porcellanids were very low. Despite this, porcellanid data met the criteria for analysis for the March sampling, but not for September. March abundances of porcellanid larvae were significantly affected by site, depth and distance offshore simultaneously (Table 2.15, Fig 2.29). There was however no pattern seen with regard to topography, depth preferences or distance offshore trends.

BARNACLES

Unlike other taxa, early life stages of barnacles can easily be separated. For this reason, barnacles were sub-divided into early nauplii, late nauplii and cyprid stages.

Early balanid nauplii

During March, abundances of early stage balanid nauplii were significantly affected by depth (Table 2.16a), being mostly found at mid to bottom depths (Fig 2.30a), regardless of site or distance offshore. There was no effect of topography on early balanid nauplii abundances, however the effect of site was significant (Table 2.16a), with a peak in abundance in St Francis Bay (Fig 2.30b). The peak seen in St Francis Bay in March was confirmed in September (significant effect of site, Table 2.16b; Fig 2.30c)

Late Balanid Nauplii

In March, the abundance of late stage balanid nauplii was significantly affected by site, depth and distance offshore simultaneously (Table 2.17a). The triple interaction of factors on balanid abundances indicates an effect of topography on late nauplii abundances in terms of depths (Fig 2.31). In bay sites, nauplii were found at bottom depth (effect mostly driven by high numbers at the bottom in St Francis Bay); while at open coast sites abundances peaked at mid depths (Fig 2.32a makes the pattern clearer although this representation ignores distance offshore). At both bay and open coast sites, there was an effect of distance offshore, although this pattern is weak, with high late stage nauplii abundances at depth at greater distances offshore (Fig 2.32b). The ANOVA run for the September data revealed that during September there was no significant effect of any tested factor (Table 2.17b).

Balanid Cyprid Type A

Abundance of balanid cyprids of type A was significantly affected by the interaction of site and distance offshore during both sampling periods (Table 2.18). There was no clear pattern, however with abundance of cyprids generally higher at the inshore sampling stations, with Algoa Bay in March being the exception (Fig 2.33a, c). During both sampling periods, abundances of cyprid A were highest at bottom depths regardless of site or distance offshore (Fig 2.33b, d).

Balanid Cyprid Type B

During March, abundances of balanid cyprids type B peaked in Algoa Bay (Fig 2.34). There was no effect of distance offshore or depth (Table 2.19a). There was also no topographic pattern. In September, cyprids type B were significantly related to site, depth and distance offshore (Table 2.19), no clear pattern topography, distance offshore or depth preference could however be identified (Fig 2.35). There were peaks in abundance in Algoa Bay at 400 m, Skoenmakerskop at 900m, St Francis Bay and Cape St Francis at 2400m).

Ontogenetic cross-shore movement

Alongside, mean depth, larval mean offshore distance (Table 2.20) was calculated for the different life stages of barnacle larvae, in order to identify any ontogenetic shift across shore movement. There were too few replicates for this data to be the focus of the study, however these results do suggest that early balanid nauplii were closer to the shore than late stage nauplii and most interestingly that cyprids stages were slightly inshore of late stage nauplii.

Linking Larval Abundance with Physical Data

Regression analyses were conducted for each taxon, for each possible model of physical data. The physical data used were wind data, used to calculate turbulence and upwelling indices. zonal flow, meridional flow and temperature. Tests for autocorrelation between physical variables were conducted and resulted in only 19 models tested in March and 10 in September. Significant regression results have been summarised in Table 2.21. There were no clear relationship between a particular physical variable model and any taxon. There were also major differences with regard to sampling period. The only notable result was the occurrence of upwelling and turbulence as possible predictors in March, with the strongest positive (although still quite weak) relation with the abundance of bryozoans and pinnotherids (Table 2.21), but no general pattern.

Mean Depth and Wind data

As there was no clear pattern with taxon abundance and physical variables, mean maximal depth was calculated for each taxon, upwelling, turbulence and meridional flow. Regression analyses were done to determine whether certain physical variables were related to vertical distribution. The results have been summarised in Table 2.22. An immediate difference appears between sampling periods. In March, 8 taxa were found to have a negative relationship with upwelling indices. This translates to high abundances of these taxa being associated with downwelling dynamics. These taxa were *Hiatella*, Type A bivalve, oysters, brachyurans, anomurans, early balanid nauplii, late balanid nauplii and Type B balanid cyprids, (Fig 2.36 a-g respectively). In September, upwelling was only found to be significantly related to the abundance of *Perna perna* and, unlike March, through a positive relationship (i.e. high abundances of *P. perna* associated with upwelling) (Fig 2.36 h).

Mean Depth and Meridional Flow

Mean maximal depth of meridional flow was calculated and regression analyses were run with mean depth data for each taxon (there were no missing data in this data set). Mean depth of meridional flow was found to positively correlate with the mean depth of: *Hiatella,* Other bivalves, brachyurans, early balanid nauplii, late balanid nauplii, balanid cyprid type A and B during March (Table 2.22, Fig 2.37 a-g). In September, mean depth of meridional flow was found to be positively correlated to *P. perna*, *Hiatella*, Bivalve type B, D-larvae, Other bivalves, *Brachyurans,* anomurans, porcelanid, early balanid nauplii, late balanid nauplii, balanid cyprid type A and B larval mean depth (Table 2.22, Fig 2.37 a-l).

DISCUSSION

In this study, larval distribution of several taxa, was highly variable. There was not only variation in distribution patterns between sampling events (which was mostly expected due to the highly patchy nature of larval abundance), but also high variability between taxa. Perhaps, the most interesting result is that the distribution of most taxa did not fit the classical theories based on upwelling-mediated cross shore transport.

Upwelling-mediated cross-shore distributions of meroplankton

Classical models of cross-shore larval transport hypothesise that water movement generated from Ekman transport would carry larvae offshore during upwelling (Roughgarden *et al.* 1988) and back onshore during periods of downwelling (Roughgarden *et al.* 1992) via the formation of fronts and the accumulation of larvae there within. The conditions required for this model are those of regular fluctuations in upwelling and downwelling regimes (Roughgarden *et al.* 1992) at scales appropriate to larval lifetimes. At all study sites in the present study, the formation of upwelling fronts did occur on occasion (Lutjeharms *et al.* 2000, Goschen *et al*. 2015), it was, however often weak when compared to the upwelling regime of the regions sampled in previous studies (Pineda 1994; Pineda 1999; Shanks *et al.* 2000; Poulin *et al.* 2002; Shanks & Brink 2005; Shanks 2005; Shanks 2009; Shanks *et al.* 2010). The classical upwelling mediated transport model would result in larval distribution being higher offshore during periods of upwelling (as larvae are thought to be transported offshore during upwelling events) and requires larval abundances to be positively correlated with upwelling.

General distribution

Previous research done within this study region (Porri *et al.* 2014; Weidberg *et al.* 2015) reported high abundance of bivalve larvae at 2 km off the coast and generally lower abundances further offshore all along the south coast of Southern Africa. An important feature that occurs in this study region is the Natal pulse. This part of the coast in dominated by the Agulhas Current, a major western boundary current and a Natal pulse is a solitary meander in this current that is thought to originate near the KwaZulu-Natal Bight which then propagate to the south-west along the South African coastline towards the study region (Harris *et al.* 1978; Tsugawa & Hasumi 2010). The feature occurs between 1.6 (Rouault & Penven 2011) to 6 (Lutjeharms & Roberts 1988) times a year and is easily identified using sea-surface temperature imaging (Jackson *et al.* 2012). During the presence of a Natal pulse, researchers have noted that larval abundances are higher offshore and have attributed this phenomenon to the Natal pulse having pushed the larvae offshore (Porri *et al.* 2014).

The present study aimed to investigate the nearshore distribution of larvae at a finer scale of 100s of meters rather than kilometres. Bivalve abundances collected in this study were much lower than the ones reported by recent studies in the same geographic area (Porri *et al.* 2014; Weidberg *et al.* 2015). This could indicate that, although nearshore retention is observed at larger spatial scales, very nearshore (< 2 km from the shore) abundances can be low, suggesting that bivalve larvae could be considered passive within this section of the cross-shore profile, with the coastal boundary layer acting as a semi-permeable barrier (Rilov *et al.* 2008). Another possible explanation for the difference between larval abundances reported by Porri *et al.* (2014) and the present study is the very patchy distribution of larval abundances that may result in vast differences in larval abundance (Pineda *et al*. 2010). Some research has been conducted on how the width of the CBL affects the nearshore hydrodynamics (Wolanski 1994; Largier 2003), however, to my knowledge, no research has been conducted on linking very inshore hydrodynamics to larval distributions. Alternatively or additionally, the timing of spawning may have simply differed between this and the earlier study.

Bivalve larvae in this study were also found not to have a clear distributional pattern with regard to depth, distance offshore or topography. Although other studies in other parts of the world have shown a positive association of larvae in relation to depth (Shanks & Brink 2005; Shanks & Shearman 2009), the patterns observed in this study confirm the absence of a general larval depth stratification in this region (Porri *et al.* 2014).

The lack of an effect of topography on larval distribution found in this study leaves an important question unanswered. Adult populations of intertidal bivalves differ between bay and open coast sites along the South African coast, with higher abundance of adult bivalves in bays than on the open coast (von der Meden *et al*. 2008). Such topographic pattern is not determined by post-settlement mortality factors in this region (von der Meden *et al*. 2012). This, along with other studies (Chiba & Noda 2000; Dobretsov & Wahl 2001) suggest that pelagic distributions of bivalve larvae could shed more light on the issue. The abundance of larvae in this study however, was not higher in bays than open coasts and instead peaks in bivalve distribution were seen at all sites (Fig 2.12 – 2.18). A possible explanation for the absence of a topographic pattern could involve the dynamic nature of bivalve spawning. Samples collected in this study were snap shots of larval distribution at one particular time, while the differences in the structure of adult populations in bays and open coasts may derive from retention within bays and recirculation of larvae over much longer and integrated scales (apart from other post-recruitment processes). Such time-integration could be addressed by tracking spawning events, coupled with sampling of nearshore larval abundance as well as settlement. Bay and open coast sites could potentially have similar larval supply, but different conditions for successful settlement. Such de-coupling between larval abundance and delivery has been observed at different spatial scales in the region targeted by the present study (Porri *et al*. 2006 and this study, Chapter 3) and elsewhere (Rilov *et al*. 2008).

Larvae which have the potential to be increasingly active within the water column, such as brachyurans, pinnotherids, anomurans, porcellanids and barnacles, were found to have clear distribution patterns. Depth was often an important factor with regard to the patterns of distribution of decapods. Decapod larvae were generally found at bottom depths, regardless of distance offshore or topography and this was true during both the March and September sampling. Barnacle larvae also displayed a depth preference, though this was more variable in terms of sampling period, topography and distance offshore. The trend of high abundance of larvae at the bottom has been observed in other studies, with regard to brachyurans and pinnotherids suggesting some degree of diel vertical migration (Garrison 1999; Schmelenbach & Buchhots 2010). This could explain the depth preference observed in the current study, as all samples were collected during the day when species that perform diel vertical migration are expected to be at bottom. Diel migration could be a result of adaptations to predation avoidance or a mechanism to increase a species contact with its food source (reviewed in Hays 2003) and some studies have suggested that diel migratory behaviour serves as a mechanism for retention (Peterson *et al.* 1979). The patterns of distribution of the taxa mentioned above could therefore be strongly linked, if not driven, by such anti-predatory larval behaviour but this was not within the scope of this study.

A clear ontogenetic trend was observed in the distribution of barnacle larvae in relation to depth. This ontogenetic trend has been reported in other studies such as Tapia *et al.* (2010). Abundances of early and late nauplii stages were more variable with regard to depth then the later and more active cyprid stage, which was consistently found at the bottom. This is not only true for barnacles, since brachyurans also showed a greater affinity for bottom depths, which correlates to ontogenetic development (Schmelenbach & Buchholz 2010), although this was not specifically tested by the present study. Barnacles have larvae with morphologically distinct stages of development that are easily identified allowing assessment of distribution patterns according to life stages at a finer resolution to that of other larvae identified in this study. Ontogenetic shifts in larval activity with regard to differences in pelagic distributions of barnacles are common, when barnacle larvae undergo ontogenetic migration to deeper water layers during upwelling (Grantham 1997). The present study confirms similar trends with early and late naupliar stages located at high abundances at mid (at deeper open coast stations) to bottom depths (in shallower bay sites) and cyprid stages consistently located at bottom depths.

The advantage of a multi taxon approach (López-Duarte *et al.* 2012), as in this study, is the ability to compare taxa that have different swimming speeds and could therefore potentially fall in different places along a classic “active/passive” gradient (Pineda 1999; Shanks & Shearman 2009; Shanks *et al.* 2000; Shanks *et al.* 2003). Simply put, in this study, larvae that are mostly considered passive, such as bivalves, did not display any depth-associated pattern, while more active taxa, such as decapods and barnacles, were clearly linked to specific depths.

Effects of physical factors on larval distribution

A characteristic of larval distribution determined by the classical model of cross-shore transport, mediated by upwelling, requires some positive correlation of larval abundance and upwelling. This was not observed for all taxa as only D-stage larvae of bivalves were significantly positively correlated with upwelling and turbulence (Table 2.21). This result highlights that most taxa identified in this study do not fit the upwelling mediated model. This is true even for the later stage of bivalve larvae which were previously thought to be on the passive end of the activity spectrum due to their slower swimming speeds when compared to decapods and barnacles (Chia *et al.* 1983). Laboratory based studies such as those conducted by Fuchs and Di Bacco (2011) and Fuchs *et al*. (2012) describe a threshold with regard to turbulence and larval behaviour. They observed a consistent increase in larval velocity with increased turbulence until a threshold of 8.3 x $10^{-2}cm^{2}s^{-3}$ (8.3 $W.kg^{-1}$) is reached. This threshold was not reached during this study with the highest mean turbulence calculated being 7.0 x $10^{-9}cm^{2}s^{-3}$ (7.0 x 10^{-7} $W.kg^{-1}$). The field results from the present study found no correlation between turbulence and larval abundances for most larval taxa. This suggests that larval abundance is not determined by turbulence and perhaps larvae were actively avoiding turbulence as described in Fuchs & Di Bacco (2011) and Fuchs *et al.* (2012).

The depth preference identified in this study, alongside the nearshore association of larvae observed by Porri and co-authors (2014) and the hydrodynamics of the region, indicate that active larval behaviour is therefore the most plausible explanation for the observed distribution of larvae in this study (excluding D-larvae).

Achieving Nearshore Retention

Possibly Passive?

Although this study suggests active larval swimming behaviour as the most plausible explanation for the observed larval distribution patterns, there are passive mechanisms that would favour nearshore larval retention. The presence of the Coastal Boundary Layer (CBL) is perhaps the most significant feature that could enhance nearshore larval retention through the alteration of current speeds and nearshore wind driven factors. The CBL has been defined as the water layer adjacent to the coastline where shallow profiles and slow current speeds (via friction with the sea floor and water viscosity) enhance turbulence (Csanady 1972).

Wolanski (1994) later coined the term “sticky water” to describe this feature for the lower dynamism and permeability than the very offshore waters. The permeability and width of the CBL are related to the width of the shelf, coastline complexity, the water viscosity (Wolanski & Hamner 1988, Wolanski 1994, Wolanski & Spagnol 2000, Lambrechts *et al*. 2008) and current velocities of the region (Becker 1991, Penven *et al*. 2000). Another possible mechanism worth discussing is the effect of the Bottom Boundary Layer. The slowing of bottom waters due to friction with the benthic surface was thought to enhance retention in the nearshore, however studies such as that of Butman (1986) have shown that, although there are significant differences in the velocities of bottom waters compared to surface waters, the velocities are still greater than larval swimming speeds. Butman (1986) suggests that larvae would not be able to orientate on the horizontal plane but instead would be able to maintain their position if they swam vertically against slower vertical currents. Although passive mechanisms are likely to contribute to the nearshore retention in this region, they are likely to apply only at scales larger than those considered in this study, which was conducted within the CBL. However passive models offer a poor explanation for the vertical distributions observed in this and many previous studies (Poulin *et al*. 2002; Shanks & Brink 2005; Pineda *et al*. 2007; Morgan *et al*. 2009; Pineda *et al*. 2009; Shanks & Shearman 2009; Tapia *et al*. 2010). The inability of passive mechanisms to explain entirely the present patterns suggests that, although the CBL may passively retain larvae within a few kilometres of the shore, larvae may still be able to control their depths and proximity to the coast to some degree.

Probably Active

If a larval behavioural component was not present, one would expect no correlation between larval mean depths with mean depth of upwelling. The abundance of several larval taxa were, however, found to be negatively correlated with upwelling indices during the March, though not the September, sampling. To counteract offshore transport, larvae should therefore be able to stay at the surface during downwelling and the bottom during upwelling (Pineda 1999; Shanks & Shearman 2009). Such a pattern could only be maintained through an active behavioural mediation. During March, upwelling was weaker and more variable than in September (Table 2.1). Such more neutral hydrodynamic forcing likely favoured active behaviour. During September, the upwelling indices were stronger and more persistent, which could have limited the behavioural response of these larval taxa by exceeding a theoretical threshold.

Despite the variation between the sampling periods and mean depth with regard to upwelling effects, during both March and September, mean depth of larvae were positively correlated with shoreward (north) flowing meridional currents. This indicates that even when there is high, persistent downwelling, as seen in September (Fig 2.7a), larvae are still associated with shoreward moving water masses (Fig 2.34). Perhaps the lack of correlation between larvae and upwelling during the September season could be due to persistent downwelling in this period obscuring any trend in mean depth. It is also interesting to note that even D-larvae (which are likely the most passive) were still associated with shoreward moving water masses, although the mechanism responsible for achieving this is not clear.

Within this study region, it is likely that active larval swimming behaviour determines larval distribution for most of the studied taxa. This conclusion is based on several taxa displaying clear mean depth preferences, the lack of significant relationships between larval abundance and upwelling indices as well as the presence of significant correlations of larval mean depth with mean depth of maximal upwelling and meridional flow.

One major drawback of this study was the lack of temporal replication, as is the case with most pelagic research due to the logistic challenges associated with this kind of study. This challenge directly limits temporal resolution. It is, however, important to identify the fundamental mechanisms in which nearshore hydrodynamics may affect larval distribution and behaviour at small scale level. Further empirical integration and analysis of long-term physical data (which is, luckily, becoming more increasingly available for the region targeted by this study) will facilitate the characterisation of larval distribution in the region.

Table 2.1: Periodicity of wind driven upwelling and turbulence indices for the Algoa Bay (includes the Algoa Bay and Skoenmakerskop site) and St Francis (includes the St Francis Bay and Cape St Francis site) over the entire sample season March and September.

Region	**Season**	**Variable**	**Mean periodicity peaks (hours)**
Algoa Bay	March	Upwelling	73.4 ; 249.6
St Francis	March	Upwelling	73.4 ; 124.8
Algoa Bay	September	Upwelling	106.9 ; 196.0
St Francis	September	Upwelling	106.9 ; 196.0
Algoa Bay	March	Turbulence	24.0 ; 89.1
St Francis	March	Turbulence	89.1 ; 104.0
Algoa Bay	September	Turbulence	24.0 ; 90.5
St Francis	September	Turbulence	90.5 ; 168.0

Table 2.2: 2-Way ANOVA on the effect of site and season on A) Upwelling and B) Turbulence

A) Upwelling

Effect	**SS**	**DF**	**MS**	**F**	**P-Value**
Season	2.95E+06	1	2.95E+0+066	5994	<0.001*
Site	1.40E+07	3	4.60E+06	9474	<0.001*
Season*site	1.60E+07	3	5.32E+06	10800	<0.001*

B) Turbulence

Effect	**SS**	**DF**	**MS**	**F**	**P-Value**
Season	0	1	0	2.57	0.11
Site	0	3	0	10.30	<0.001*
Season*site	0	3	0	29.72	<0.001*

Table 2.3: 3-Way ANOVA on the effect of site, distance and depth on abundance of bryozoans during A) March and B) September with “site”, “distance” and “depth” as independent factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	4058	3	1353	10.09	<0.001*
distance	5346	3	1782	13.29	<0.001*
depth	9584	2	4792	35.75	<0.001*
site*distance	5131	9	570	4.25	<0.001*
site*depth	4359	6	726	5.42	<0.001*
distance*depth	1.11E+04	6	1851	13.81	<0.001*
site*distance*depth	9859	18	548	4.09	<0.001*

B) September

Effect	SS	DF	MS	F	P-Value
site	13.7	3	4.57	1.374	0.262
distance	27	3	8.99	2.706	0.056
depth	18.3	2	9.15	2.754	0.074
site*distance	92.8	9	10.31	3.101	.005*
site*depth	31.6	6	5.27	1.586	0.172
distance*depth	56.8	6	9.47	2.849	.019*
site*distance*depth	106.3	18	5.91	1.778	0.058

Table 2.4: 3-Way ANOVA on the effect of site, distance and depth on abundance of *Hiatella* during A) March and B) September with “site”, “distance” and “depth” as independent factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	5951	3	1984	14.73	<0.001*
distance	4183	3	1394	10.35	<0.001*
depth	2765	2	1383	10.27	<0.001*
site*distance	1.14E+04	9	1267	9.41	<0.001*
site*depth	3210	6	535	3.97	.003*
distance*depth	1799	6	300	2.23	0.056
site*distance*depth	5875	18	326	2.42	.008*

B) September

Effect	SS	DF	MS	F	P-Value
site	328.7	3	109.6	3.963	0.013*
distance	110.9	3	37	1.337	0.273
depth	240.9	2	120.5	4.357	0.018*
site*distance	510.8	9	56.8	2.053	0.053
site*depth	397.5	6	66.2	2.396	0.042*
distance*depth	92.9	6	15.5	0.56	0.760
site*distance*depth	528.4	18	29.4	1.062	0.416

Table 2.5: 3-Way ANOVA on the effect of site, distance and depth on abundance of *Perna perna* during A) March and B) September with “site”, “distance” and “depth” as independent factors (p<0.05*)

A) March

Effect	SS	DF	MS	F	P-Value
site	220.6	3	73.54	7.628	<0.001*
distance	108.5	3	36.16	3.751	0.017*
depth	67.3	2	33.63	3.489	0.038*
site*distance	480.3	9	53.36	5.535	<0.001*
site*depth	89.6	6	14.93	1.549	0.183
distance*depth	87.4	6	14.56	1.511	0.195
site*distance*depth	262.3	18	14.57	1.512	0.128

B) September

Effect	SS	DF	MS	F	P-Value
site	130.2	3	43.39	1.452	0.239
distance	128.2	3	42.72	1.43	0.246
depth	9.1	2	4.54	0.152	0.859
site*distance	257.7	9	28.63	0.958	0.485
site*depth	120.7	6	20.11	0.673	0.672
distance*depth	178.1	6	29.68	0.994	0.440
site*distance*depth	482.9	18	26.83	0.898	0.584

Table 2.6: The 3-Way ANOVA results for *Mytilus galloprovincialis* during March only (as September abundances did not meet the criteria for analysis) with “site”, “distance” and “depth” as factors (p<0.05*)

Effect	SS	DF	MS	F	P-Value
site	218.9	3	72.98	2.571	0.065
distance	37.7	3	12.58	0.443	0.723
depth	93.3	2	46.67	1.644	0.204
site*distance	205.3	9	22.81	0.804	0.615
site*depth	314.2	6	52.36	1.845	0.110
distance*depth	81.9	6	13.65	0.481	0.819
site*distance*depth	294.2	18	16.34	0.576	0.900

Table 2.7: The 3-Way ANOVA results for *Choromytilus meridionalis* during September only (as March abundances did not meet the criteria for analysis) with “site”, “distance” and “depth” as factors (p<0.05*)

Effect	SS	DF	MS	F	P-Value
site	4.08	3	1.36	0.208	0.890
distance	76.36	3	25.45	3.894	0.014*
depth	11.31	2	5.65	0.865	0.428
site*distance	85.48	9	9.5	1.453	0.193
site*depth	57.6	6	9.6	1.469	0.209
distance*depth	28.87	6	4.81	0.736	0.623
site*distance*depth	92.15	18	5.12	0.783	0.708

Table 2.8: The 3-Way ANOVA results for D-larvae during September only (as March abundances did not meet the criteria for analysis) with “site”, “distance” and “depth” as factors ($p<0.05$*)

Effect	SS	DF	MS	F	P-Value
site	1.30E+05	3	4.34E+04	2.997	0.040*
distance	1.33E+05	3	4.44E+04	3.067	0.037*
depth	2.30E+04	2	1.15E+04	0.796	0.457
site*distance	4.14E+05	9	4.60E+04	3.18	0.004*
site*depth	7.11E+04	6	1.19E+04	0.819	0.561
distance*depth	6.82E+04	6	1.14E+04	0.785	0.586
site*distance*depth	2.11E+05	18	1.17E+04	0.811	0.679

Table 2.9: 3- Way ANOVA on the effect of site, distance and depth on abundance of Bivalve type A during A) March and B) September with “site”, “distance” and “depth” as independent factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	87.1	3	29.03	2.158	0.105
distance	38.9	3	12.98	0.965	0.417
depth	48.5	2	24.23	1.802	0.176
site*distance	138.2	9	15.35	1.142	0.353
site*depth	77.9	6	12.98	0.966	0.459
distance*depth	106.4	6	17.74	1.319	0.267
site*distance*depth	288	18	16	1.19	0.306

B) September

Effect	SS	DF	MS	F	P-Value
site	195.2	3	65.07	4.511	0.007*
distance	282.5	3	94.16	6.527	0.001*
depth	20.4	2	10.22	0.709	0.497
site*distance	608.9	9	67.66	4.69	<0.001*
site*depth	280.2	6	46.7	3.237	0.009*
distance*depth	127	6	21.16	1.467	0.210
site*distance*depth	584.8	18	32.49	2.252	0.013*

Table 2.10: 3-Way ANOVA on the effect of site, distance and depth on abundance of Bivalve type B during A) March and B) September with “site”, “distance” and “depth” as independent factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	670	3	223.4	2.122	0.11
distance	399	3	133.1	1.264	0.297
depth	123	2	61.5	0.584	0.562
site*distance	1216	9	135.1	1.284	0.270
site*depth	437	6	72.9	0.692	0.657
distance*depth	413	6	68.9	0.654	0.686
site*distance*depth	1523	18	84.6	0.804	0.686

B) September

Effect	SS	DF	MS	F	P-Value
site	558	3	185.9	2.94	0.043*
distance	1023	3	341	5.39	0.003*
depth	1825	2	912.7	14.42	<0.001*
site*distance	1256	9	139.5	2.21	0.038*
site*depth	662	6	110.4	1.75	0.131
distance*depth	1037	6	172.9	2.73	0.023*
site*distance*depth	1828	18	101.5	1.6	0.097

Table 2.11: 3-Way ANOVA on the effect of site, distance and depth on abundance of Other Bivalves during A) March and B) September with “site”, “distance” and “depth” as independent factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	181.6	3	60.54	4.116	0.011*
distance	55.5	3	18.51	1.258	0.299
depth	61.7	2	30.83	2.096	0.134
site*distance	63.4	9	7.04	0.479	0.882
site*depth	44.4	6	7.4	0.503	0.803
distance*depth	29.7	6	4.95	0.337	0.914
site*distance*depth	210.5	18	11.69	0.795	0.696

B) September

Effect	SS	DF	MS	F	P-Value
site	1829	3	610	4.146	0.011*
distance	4047	3	1349	9.173	<0.001*
depth	755	2	378	2.568	0.087
site*distance	9117	9	1013	6.889	<0.001*
site*depth	2425	6	404	2.749	0.022*
distance*depth	3431	6	572	3.889	0.003*
site*distance*depth	5886	18	327	2.224	0.014*

Table 2.12: 3-Way ANOVA on the effect of site, distance and depth on abundance of Brachyurans during A) March and B) September with "site", "distance" and "depth" as independent factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	196.4	3	65.47	6.838	0.001*
distance	187.4	3	62.48	6.526	0.001*
depth	178.4	2	89.22	9.319	<0.001*
site*distance	221.2	9	24.58	2.567	0.017*
site*depth	155.5	6	25.91	2.706	0.024*
distance*depth	249.2	6	41.54	4.338	0.001*
site*distance*depth	383.1	18	21.28	2.223	0.014*

B) September

Effect	SS	DF	MS	F	P-Value
site	394	3	131.4	2.513	0.070
distance	402	3	133.9	2.561	0.066
depth	938	2	468.9	8.969	<0.001*
site*distance	973	9	108.1	2.067	0.052
site*depth	798	6	132.9	2.543	0.032*
distance*depth	648	6	108	2.065	0.075
site*distance*depth	1710	18	95	1.817	0.051

Table 2.13: 3-Way ANOVA on the effect of site, distance and depth on abundance of Pinnotherids during A) March and B) September with "site", "distance" and "depth" as independent factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	3412	3	1137	12.21	<0.001*
distance	2052	3	684	7.34	<0.001*
depth	2807	2	1404	15.06	<0.001*
site*distance	4691	9	521	5.59	<0.001*
site*depth	1602	6	267	2.87	0.018*
distance*depth	1324	6	221	2.37	0.044*
site*distance*depth	6272	18	348	3.74	<0.001*

B) September

Effect	SS	DF	MS	F	P-Value
site	5221	3	1740	10.56	<0.001*
distance	391	3	130	0.79	0.505
depth	6094	2	3047	18.49	<0.001*
site*distance	2348	9	261	1.58	0.147
site*depth	7987	6	1331	8.08	<0.001*
distance*depth	1045	6	174	1.06	0.401
site*distance*depth	3649	18	203	1.23	0.277

Table 2.14: 3-Way ANOVA on the effect of site, distance and depth on abundance of Anomurans during A) March and B) September with “site”, “distance” and “depth” as independent factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	100.6	3	33.54	4.683	0.006*
distance	69.9	3	23.31	3.255	0.030*
depth	119.5	2	59.75	8.343	0.001*
site*distance	215.4	9	23.93	3.342	0.003*
site*depth	119.1	6	19.85	2.772	0.021*
distance*depth	99.4	6	16.57	2.314	0.048*
site*distance*depth	269.2	18	14.95	2.088	0.022*

B) September

Effect	SS	DF	MS	F	P-Value
site	1950	3	650	1.837	0.153
distance	3006	3	1002	2.832	0.048*
depth	2703	2	1351	3.819	0.029*
site*distance	6693	9	744	2.102	0.048*
site*depth	2587	6	431	1.218	0.314
distance *depth	2124	6	354	1	0.436
site* distance *depth	8109	18	450	1.273	0.247

Table 2.15: The 3-Way ANOVA results for Porcellanids during September only (as March abundances did not meet the criteria for analysis) with “site”, “distance” and “depth” as factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	30.6	3	10.2	2.926	0.043*
distance	29.4	3	9.8	2.811	0.049*
depth	20	2	10	2.869	0.067
site*distance	123.1	9	13.67	3.923	0.001*
site*depth	46.6	6	7.77	2.229	0.056
distance*depth	48.8	6	8.14	2.336	0.046*
site*distance*depth	159.7	18	8.87	2.545	0.005*

Table 2.16: 3-Way ANOVA on the effect of site, distance and depth on abundance of Early Balanid Nauplii during A) March and B) September with “site”, “distance” and “depth” as independent factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	1.05E+07	3	3.51E+06	8.557	<0.001*
distance	1.14E+06	3	3.80E+05	0.927	0.435
depth	3.04E+06	2	1.52E+06	3.707	0.032*
site*distance	3.99E+06	9	4.44E+05	1.081	0.394
site*depth	4.54E+06	6	7.56E+05	1.842	0.111
distance*depth	5.29E+06	6	8.81E+05	2.147	0.065
site*distance*depth	1.02E+07	18	5.68E+05	1.386	0.182

B) September

Effect	SS	DF	MS	F	P-Value
site	1.39E+06	3	4.63E+05	7.956	<0.001*
distance	4.75E+05	3	1.58E+05	2.722	0.055
depth	3.28E+05	2	1.64E+05	2.817	0.07
site*distance	8.25E+05	9	9.17E+04	1.576	0.15
site*depth	5.12E+05	6	8.54E+04	1.468	0.209
distance*depth	7.61E+05	6	1.27E+05	2.182	0.061
site*distance*depth	1.17E+06	18	6.51E+04	1.118	0.365

Table 2.17: 3-Way ANOVA on the effect of site, distance and depth on abundance of Late Balanid Nauplii during A) March and B) September with “site”, “distance” and “depth” as independent factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	1.43E+05	3	4.78E+04	18.36	<0.001*
distance	3.98E+04	3	1.33E+04	5.1	0.004*
depth	5.38E+04	2	2.69E+04	10.34	<0.001*
site*distance	1.24E+05	9	1.38E+04	5.29	<0.001*
site*depth	1.36E+05	6	2.27E+04	8.73	<0.001*
distance*depth	1.05E+05	6	1.75E+04	6.73	<0.001*
site*distance*depth	3.28E+05	18	1.82E+04	7.01	<0.001*

B) September

Effect	SS	DF	MS	F	P-Value
site	2.43E+04	3	8101	2.442	0.076
distance	1.48E+04	3	4929	1.486	0.230
depth	1.32E+04	2	6595	1.988	0.148
site*distance	6.02E+04	9	6690	2.017	0.058
site*depth	2.98E+04	6	4964	1.497	0.200
distance*depth	2.09E+04	6	3478	1.049	0.406
site*distance*depth	5.71E+04	18	3171	0.956	0.522

Table 2.18: 3-Way ANOVA on the effect of site, distance and depth on abundance of Cyprid type A during A) March and B) September with “site”, “distance” and “depth” as independent factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	1688	3	563	4.41	0.008*
distance	225	3	75	0.589	0.625
depth	2541	2	1271	9.957	<0.001*
site*distance	3659	9	407	3.186	0.004*
site*depth	959	6	160	1.252	0.297
distance*depth	1552	6	259	2.026	0.080
site*distance*depth	3943	18	219	1.717	0.069

B) September

Effect	SS	DF	MS	F	P-Value
site	5.47E+04	3	1.82E+04	7.488	<0.001*
distance	1.00E+04	3	3339	1.372	0.263
depth	1.90E+04	2	9477	3.895	0.027*
site*distance	4.96E+04	9	5517	2.267	0.033*
site*depth	2.26E+04	6	3760	1.545	0.184
distance*depth	7809	6	1302	0.535	0.779
site*distance*depth	2.81E+04	18	1559	0.641	0.848

Table 2.19: 3-Way ANOVA on the effect of site, distance and depth on abundance of Cyprid type B during A) March and B) September with “site”, “distance” and “depth” as independent factors ($p<0.05$*)

A) March

Effect	SS	DF	MS	F	P-Value
site	4032	3	1344	5.249	0.003*
distance	740	3	247	0.963	0.418
depth	757	2	379	1.478	0.238
site*distance	1731	9	192	0.751	0.661
site*depth	2434	6	406	1.584	0.172
distance*depth	1801	6	300	1.172	0.337
site*distance*depth	5705	18	317	1.238	0.271

B) September

Effect	SS	DF	MS	F	P-Value
site	2.37E+04	3	7897	10.03	<0.001*
distance	3.06E+04	3	1.02E+04	12.95	<0.001*
depth	2.97E+04	2	1.48E+04	18.83	<0.001*
site*distance	9.09E+04	9	1.01E+04	12.82	<0.001*
site*depth	1.69E+04	6	2824	3.59	0.005*
distance*depth	1.86E+04	6	3106	3.94	0.003*
site*distance*depth	6.62E+04	18	3678	4.67	<0.001*

Table 2.20: The calculated mean distances offshore (in meters) during both March and September for early nauplii, late nauplii, cyprid A and cyprid B balanid larvae

Season	Site	Early Nauplii	Late Nauplii	Type A Cyprid	Type B Cyprid
March	Algoa Bay	784	1687	1469	1042
March	Skoenmakerskop	314	984	735	870
March	St Francis Bay	928	1634	520	1029
March	Cape St Francis	296	1376	547	709
September	Algoa Bay	256	1205	903	832
September	Skoenmakerskop	477	1159	1069	1626
September	St Francis Bay	473	581	707	2187
September	Cape St Francis	824	1050	934	1839

Table 2.21 Summary of the significant regressions between taxa and physical variables during a) March and b) September season (Bonferroni corrected p values: $p < 0.002$ and $p < 0.005$ were considered significant for each season respectively)

A) March

Taxon	Variable 1	Variable 2	R^2	P-value	Slope
Hiatella	Temperature	N/A	0.145	<0.002	-
Hiatella	Temperature	Upwelling	N/A	<0.002	-
Bryozoans	Turbulence	N/A	0.1874	<0.002	+
Pinnotherids	Upwelling	N/A	0.1328	0.001	+

B) September

Taxon	Variable 1	Variable 2	R^2	P-value	Slope
Hiatella	Turbulence	N/A	0.0709	0.004	-
Hiatella	Upwelling	N/A	0.0715	0.004	-
D-larvae	Zonal flow	N/A	0.1136	<0.005	+
D-larvae	Upwelling	Turbulence	N/A	<0.005	+
Other bivalves	Zonal flow	N/A	0.145	0	+

Table 2.22: Summary of the significant regressions of the mean depth of larval abundances and mean depth versus each physical predictor (Upwelling, turbulence and meridional flow) for the March and September samplings ($p<0.05$*)

Season	Taxa	Variable	R^2	P-value	Slope
March	*Hiatella*	Upwelling	0.425	0.001**	-
March	Type A Bivalve	Upwelling	0.090	0.005**	-
March	Oysters	Upwelling	0.348	0.003**	-
March	Early Balanid Nauplii	Upwelling	0.224	0.001**	-
March	Late Balanid Nauplii	Upwelling	0.089	0.006**	-
March	Type B Cyprid	Upwelling	0.228	0.002**	-
March	Brachyurans spp.	Upwelling	0.175	0.024*	-
March	Anomuran spp.	Upwelling	0.336	0.004**	-
March	Hiatella	Meridional flow	0.396	<0.001***	+
March	Other Bivalves	Meridional flow	0.764	<0.001***	+
March	Brachyurans	Meridional flow	0.342	<0.001***	+
March	Early balanid nauplii	Meridional flow	0.317	<0.001***	+
March	Late Balanid Nauplii	Meridional flow	0.272	0.003*	+
March	Balanid Cyprid A	Meridional flow	0.237	0.006*	+
March	Balanid Cyprid B	Meridional flow	0.383	<0.001***	+
September	*Perna perna*	Upwelling	0.155	0.042*	+
September	*Perna perna*	Meridional flow	0.131	0.040*	+
September	*Hiatella*	Meridional flow	0.365	0.040*	+
September	Bivalve type B	Meridional flow	0.314	<0.001***	+
September	D-larvae	Meridional flow	0.152	0.028*	+
September	Other Bivalves	Meridional flow	0.427	<0.001***	+
September	Brachyurans	Meridional flow	0.295	0.001	+
September	Anomurans	Meridional flow	0.383	<0.001***	+
September	Porcellanids	Meridional flow	0.186	0.014	+
September	Early balanid nauplii	Meridional flow	0.394	<0.001***	+
September	Late Balanid Nauplii	Meridional flow	0.354	<0.001***	+
September	Balanid Cyprid A	Meridional flow	0.481	<0.001***	+
September	Balanid Cyprid B	Meridional flow	0.145	0.032*	+

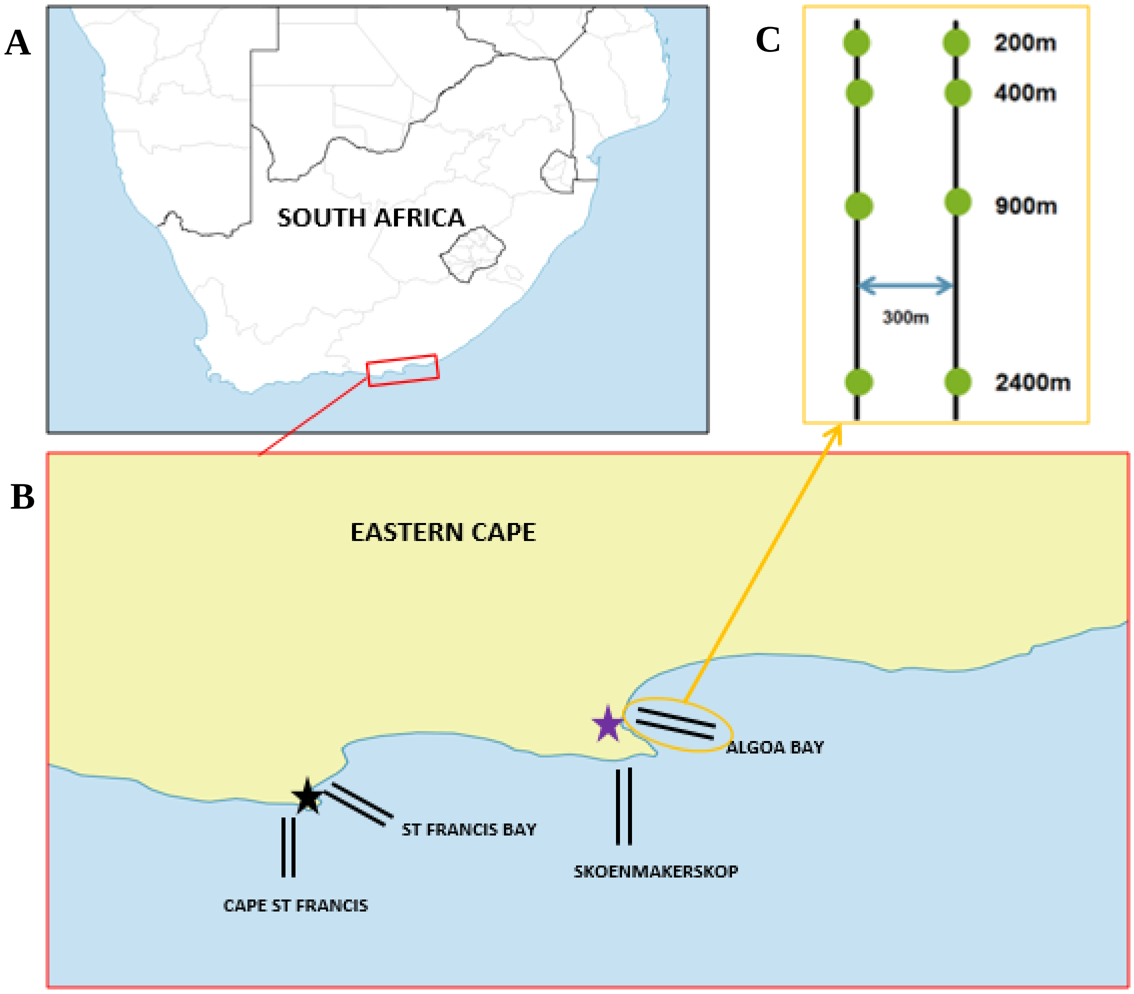


Figure 2.1: Schematic diagram of the study region in the Eastern Cape of South Africa depicting the location of each transect: Algoa Bay, Skoenmakerskop, St Francis Bay and Cape St Francis (‖). Weather stations are represented by black (★) and purple stars (★) for St Francis and Algoa Bay respectively. The stations sampled along the transect is illustrated in C) with stations 200m, 400m,900m and 2400m offshore. Transects were parallel to each other and 300m apart. Three depths were sampled at each station.

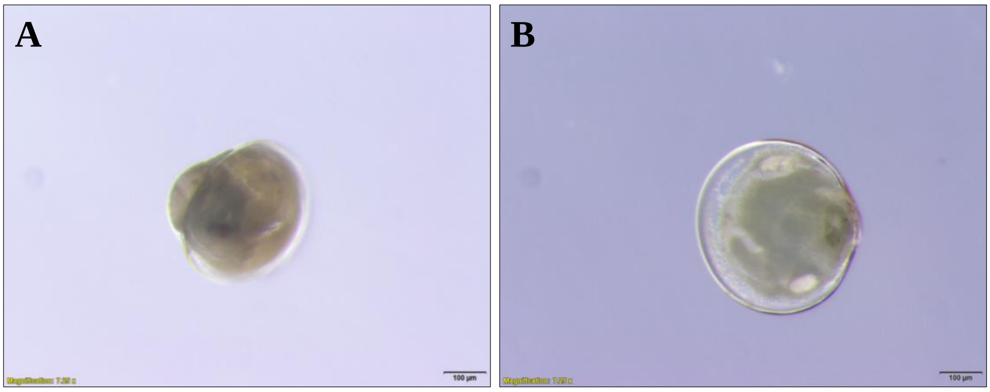


Figure 2.2: Photographs taken at 7.25 x magnification of two common and distinct yet unidentified bivalves referred to in this study as A) Bivalve Type A and B) Bivalve Type B. Bivalve type A have a large protrusion near the ulna and typically grey in colour. Bivalve type A has a thin transparent shell.

ALGOA BAY

TRANSECT A

MARCH **SEPTEMBER**

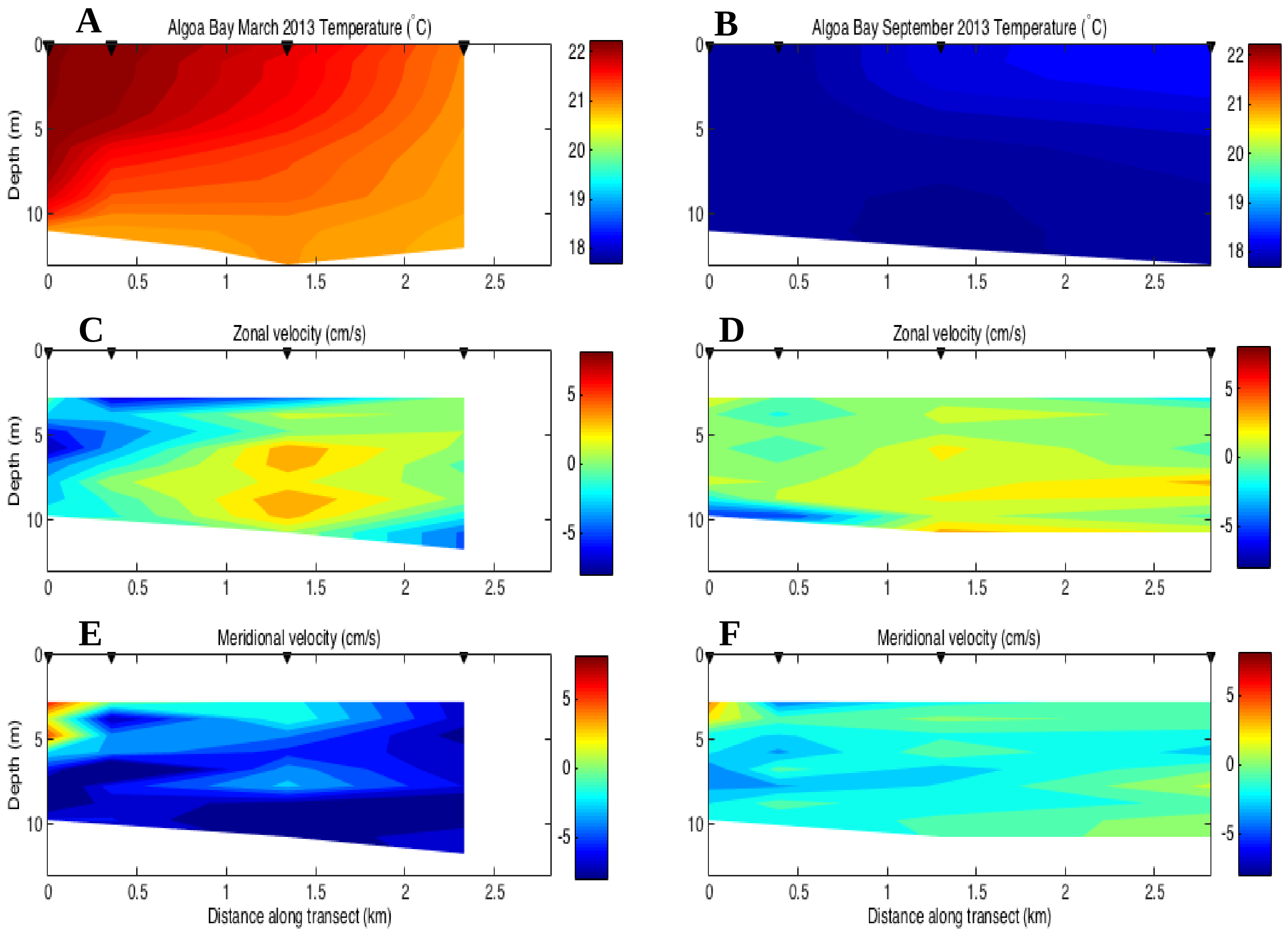


Figure 2.3: Contour plots of A) Temperature in March, B) Temperature in September C) Zonal flow in March, D) Zonal flow in September, E) Meridional flow in March and F) Meridional flow in September along transect A at Algoa Bay

ALGOA BAY

TRANSECT B

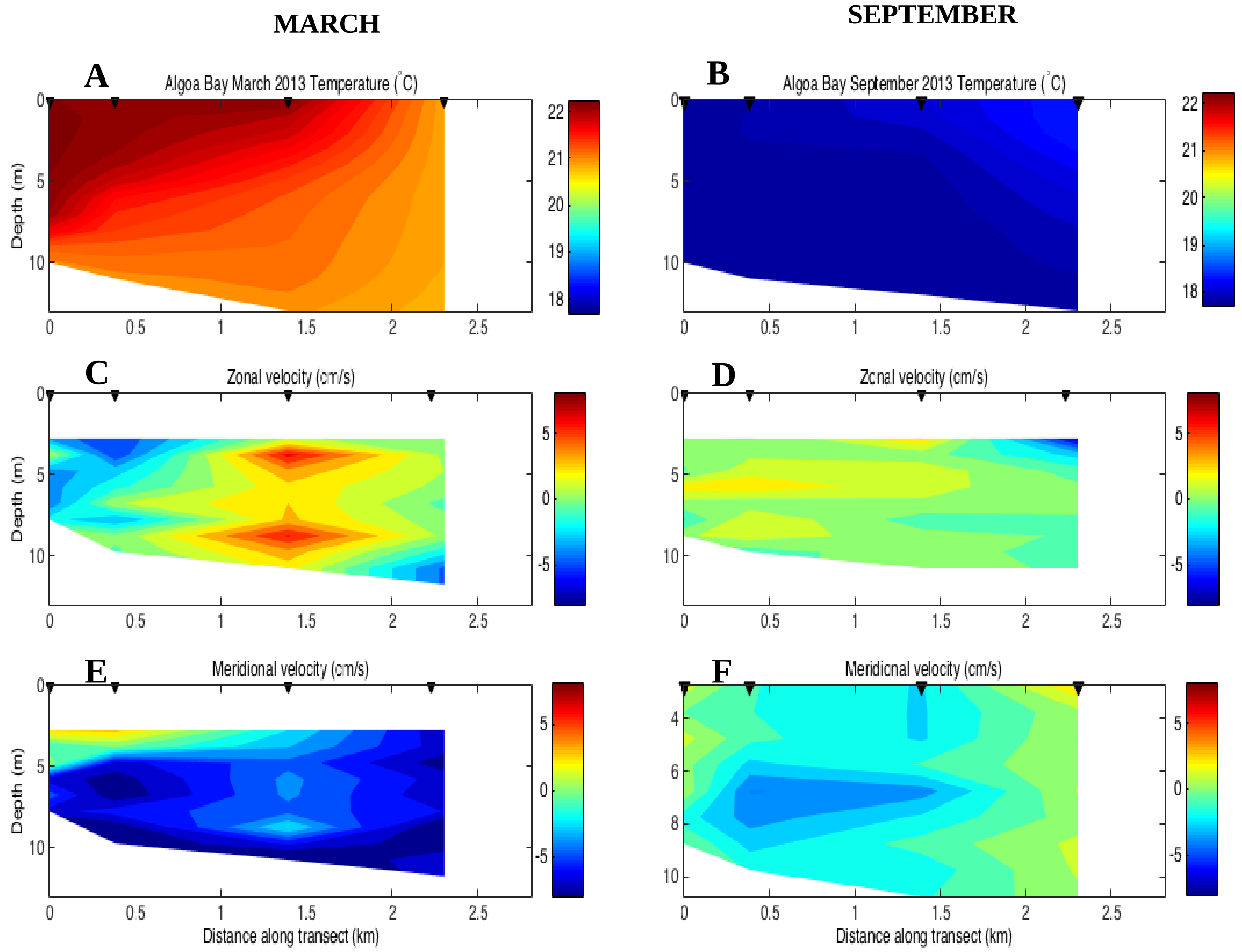


Figure 2.4: Contour plots of A) Temperature in March, B) Temperature in September C) Zonal flow in March, D) Zonal flow in September, E) Meridional flow in March and F) Meridional flow in September along transect B at Algoa Bay

SKOENMAKERSKOP

TRANSECT A

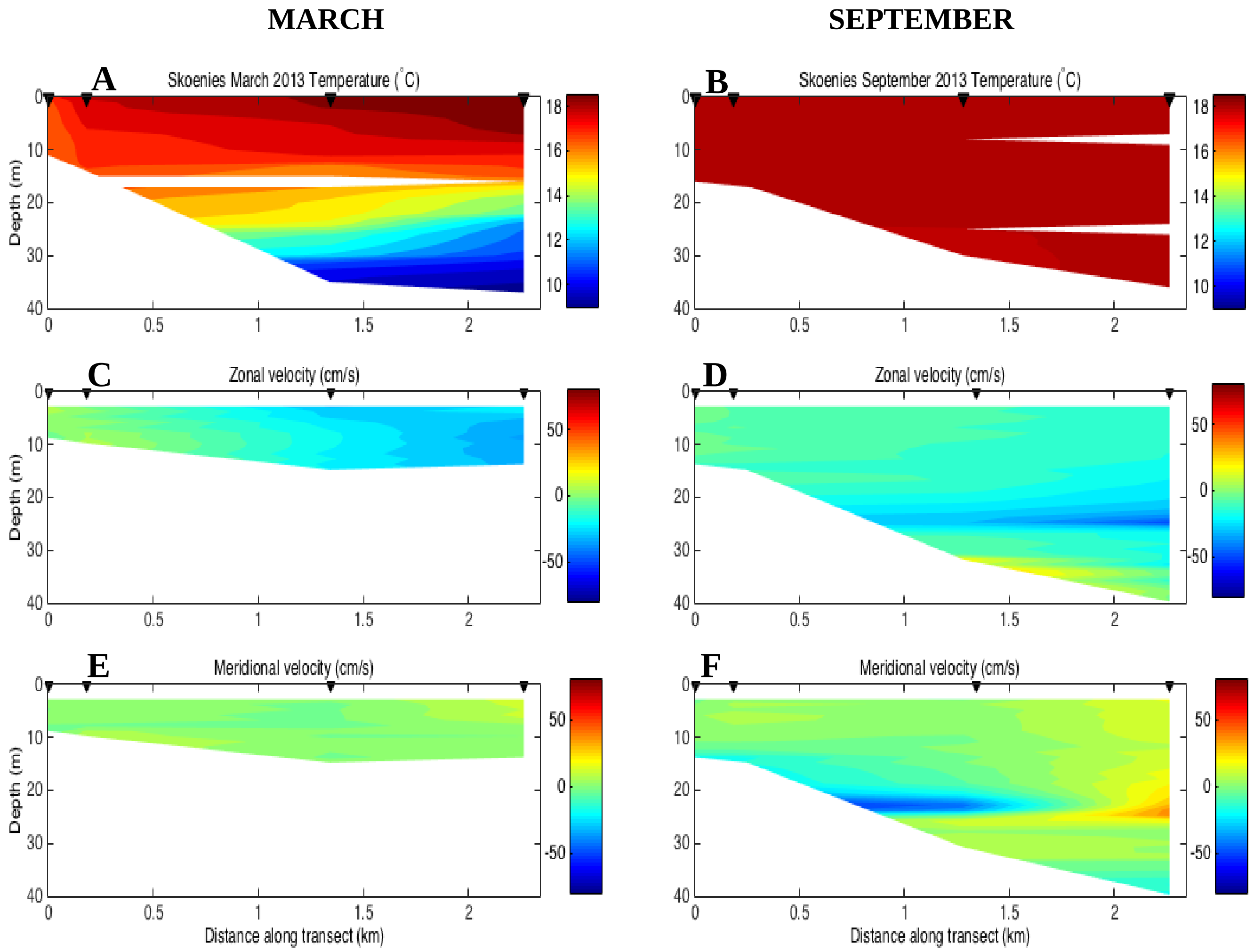


Figure 2.5: Contour plots of A) Temperature in March, B) Temperature in September C) Zonal flow in March, D) Zonal flow in September, E) Meridional flow in March and F) Meridional flow in September along transect A at Skoenmakerskop

SKOENMAKERSKOP

TRANSECT B

MARCH **SEPTEMBER**

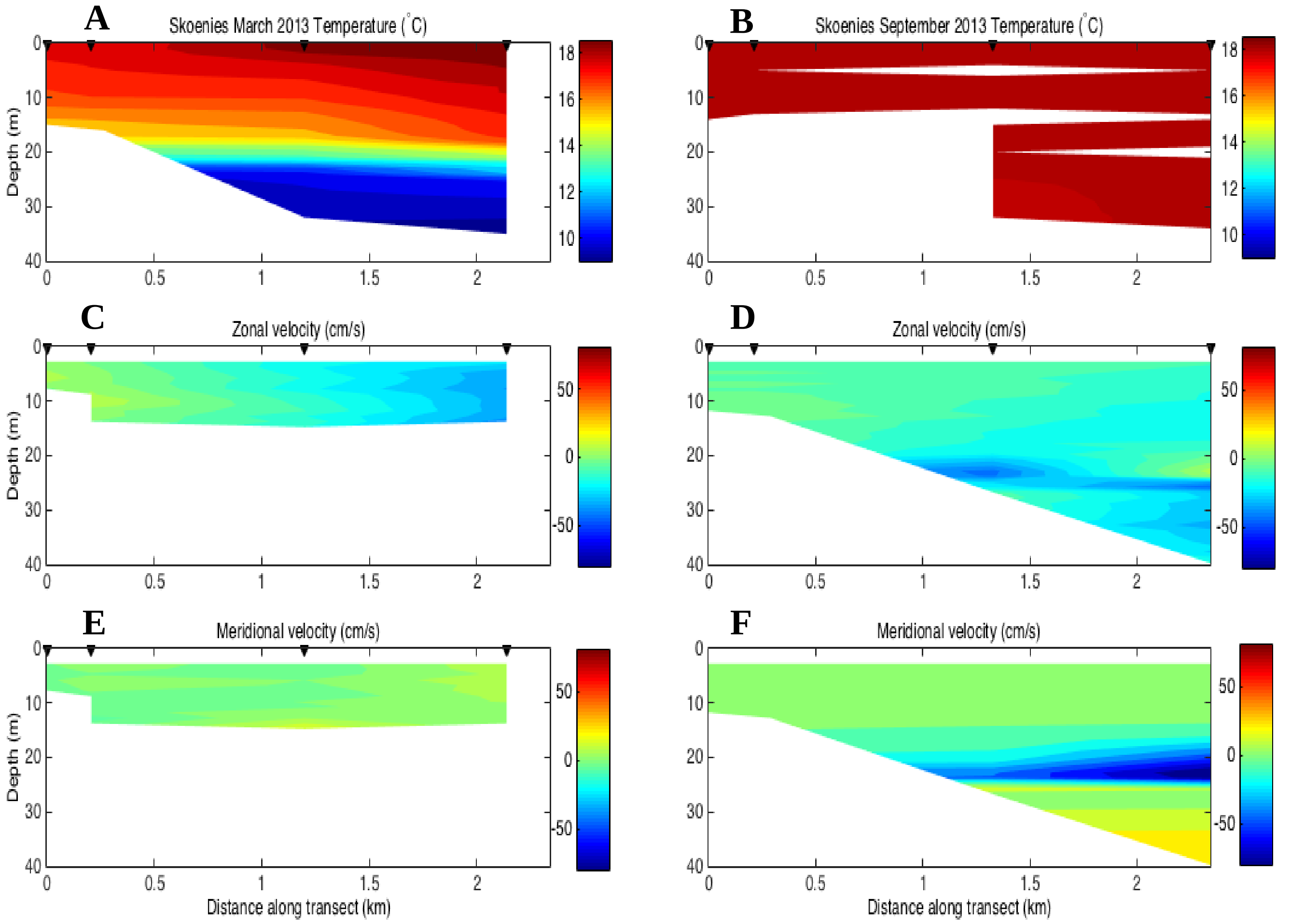


Figure 2.6: Contour plots of A) Temperature in March, B) Temperature in September C) Zonal flow in March, D) Zonal flow in September, E) Meridional flow in March and F) Meridional flow in September along transect B at Skoenmakerskop

ST FRANCIS BAY

TRANSECT A

MARCH

SEPTEMBER

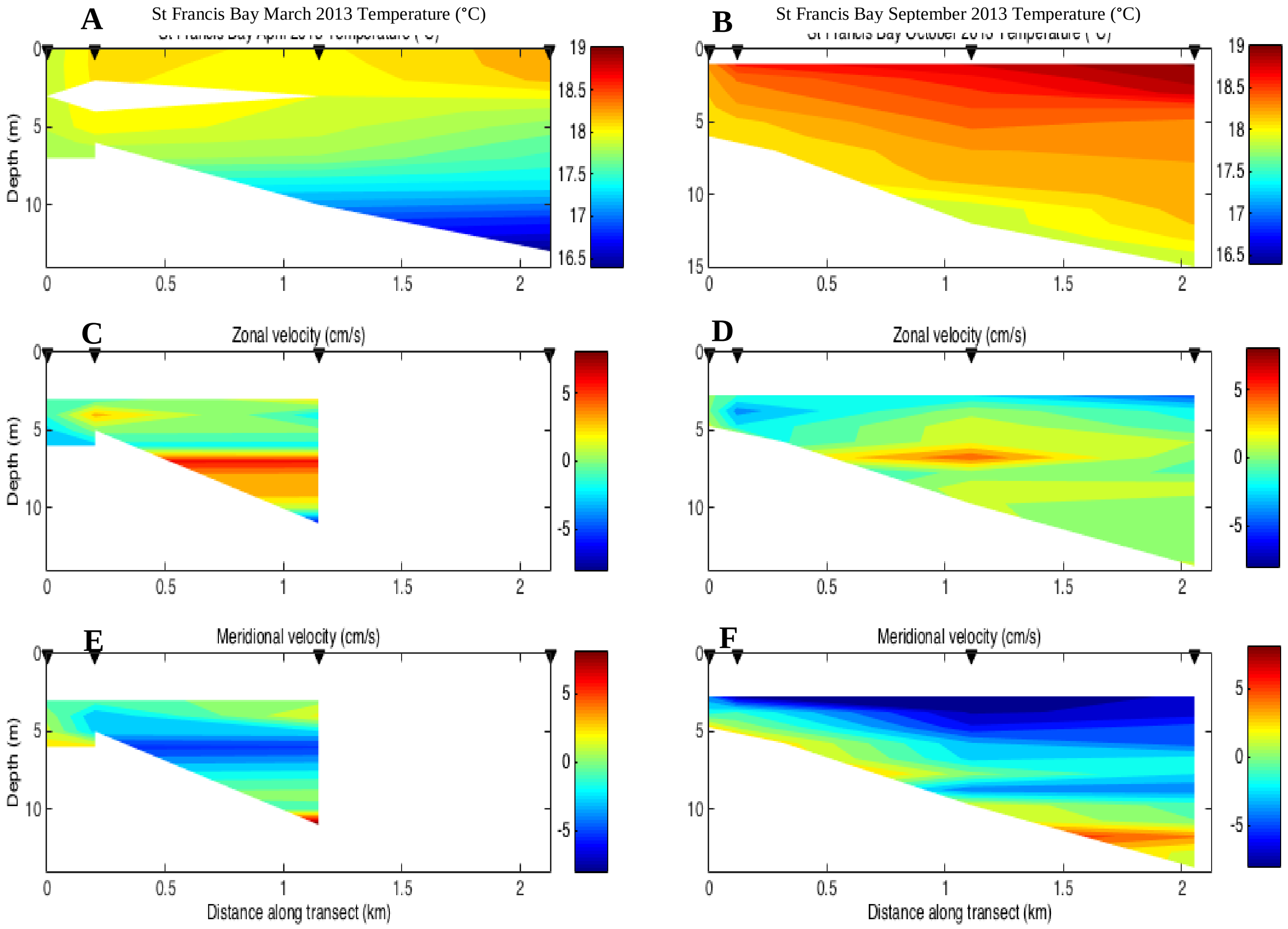


Figure 2.7: Contour plots of A) Temperature in March, B) Temperature in September C) Zonal flow in March, D) Zonal flow in September, E) Meridional flow in March and F) Meridional flow in September along transect A at St Francis Bay

ST FRANCIS BAY

TRANSECT B

MARCH **SEPTEMBER**

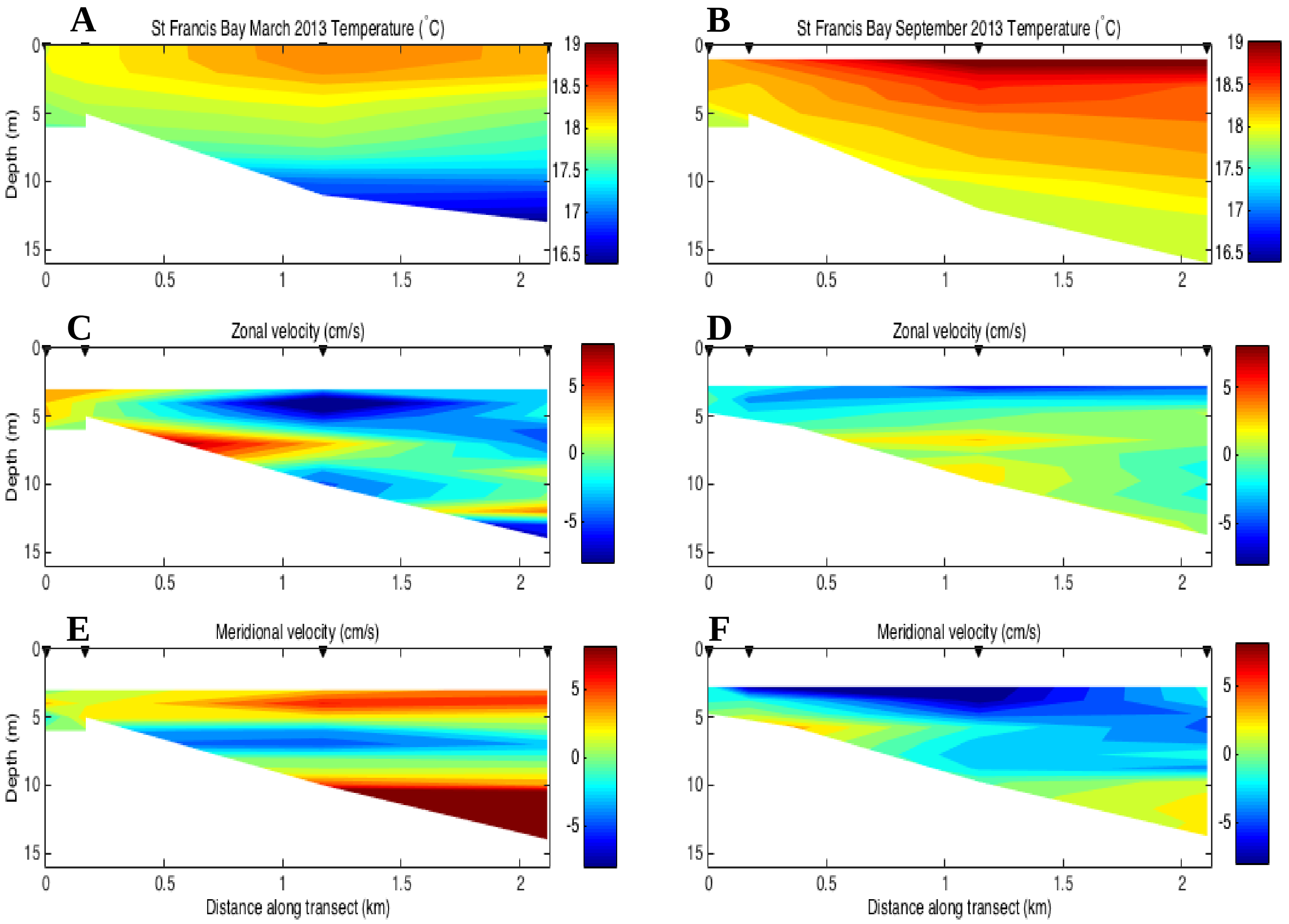


Figure 2.8: Contour plots of A) Temperature in March, B) Temperature in September C) Zonal flow in March, D) Zonal flow in September, E) Meridional flow in March and F) Meridional flow in September along transect B at St Francis Bay

CAPE ST FRANCIS

TRANSECT A

MARCH

SEPTEMBER

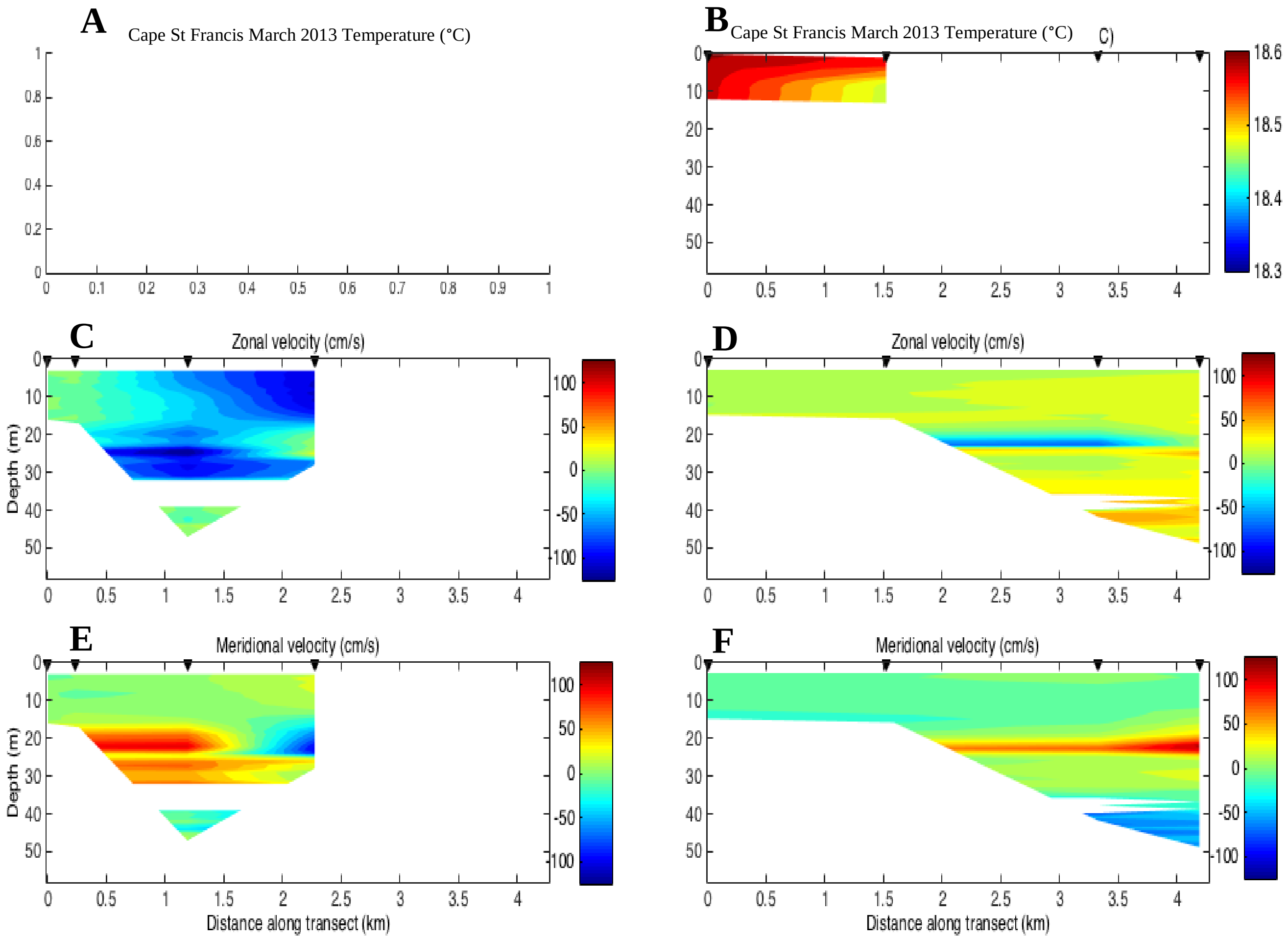


Figure 2.9: Contour plots of A) Temperature in March, B) Temperature in September C) Zonal flow in March, D) Zonal flow in September, E) Meridional flow in March and F) Meridional flow in September along transect A at Cape St Francis

CAPE ST FRANCIS

TRANSECT B

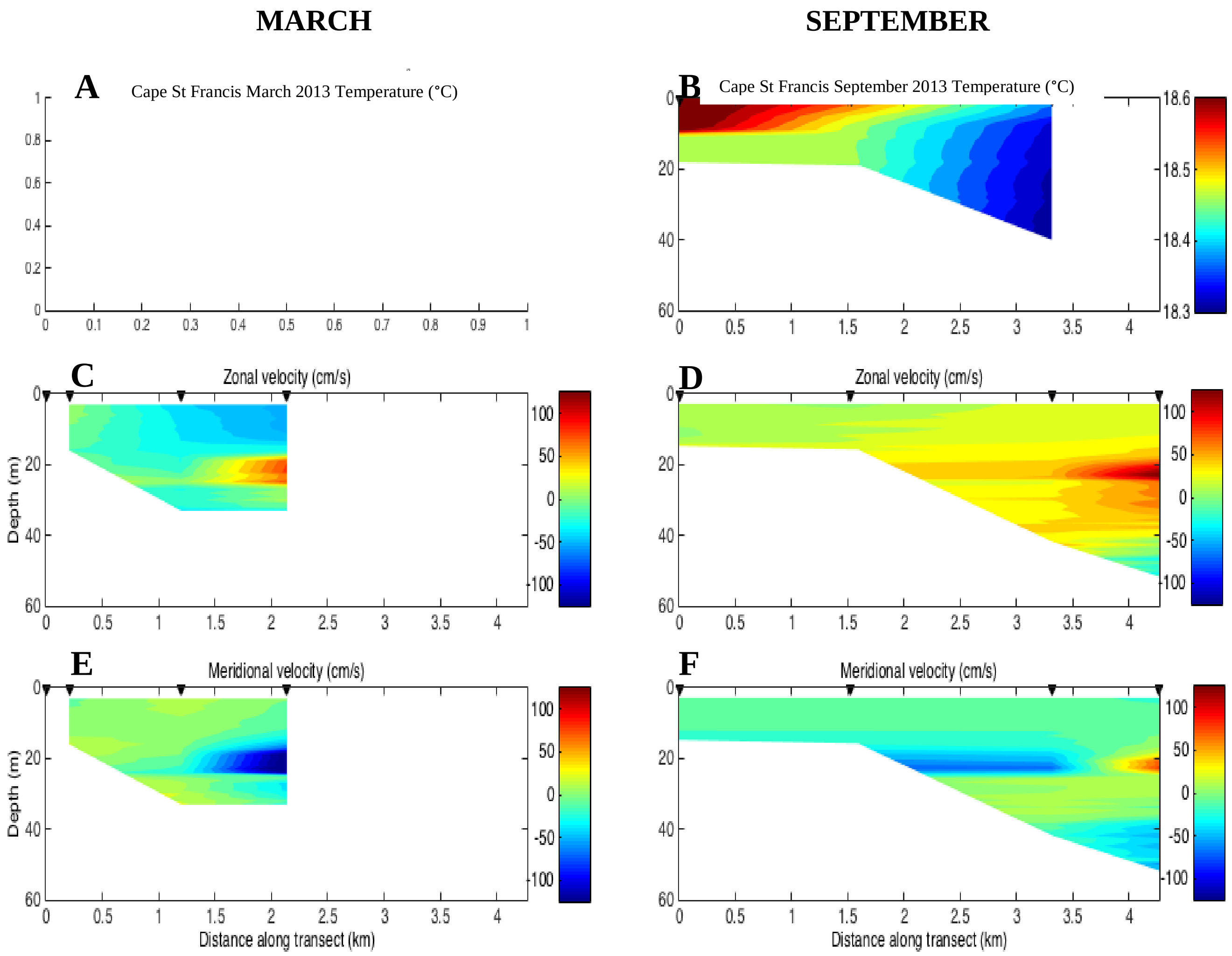


Figure 2.10: Contour plots of A) Temperature in March, B) Temperature in September C) Zonal flow in March, D) Zonal flow in September, E) Meridional flow in March and F) Meridional flow in September along transect B at Cape St Francis

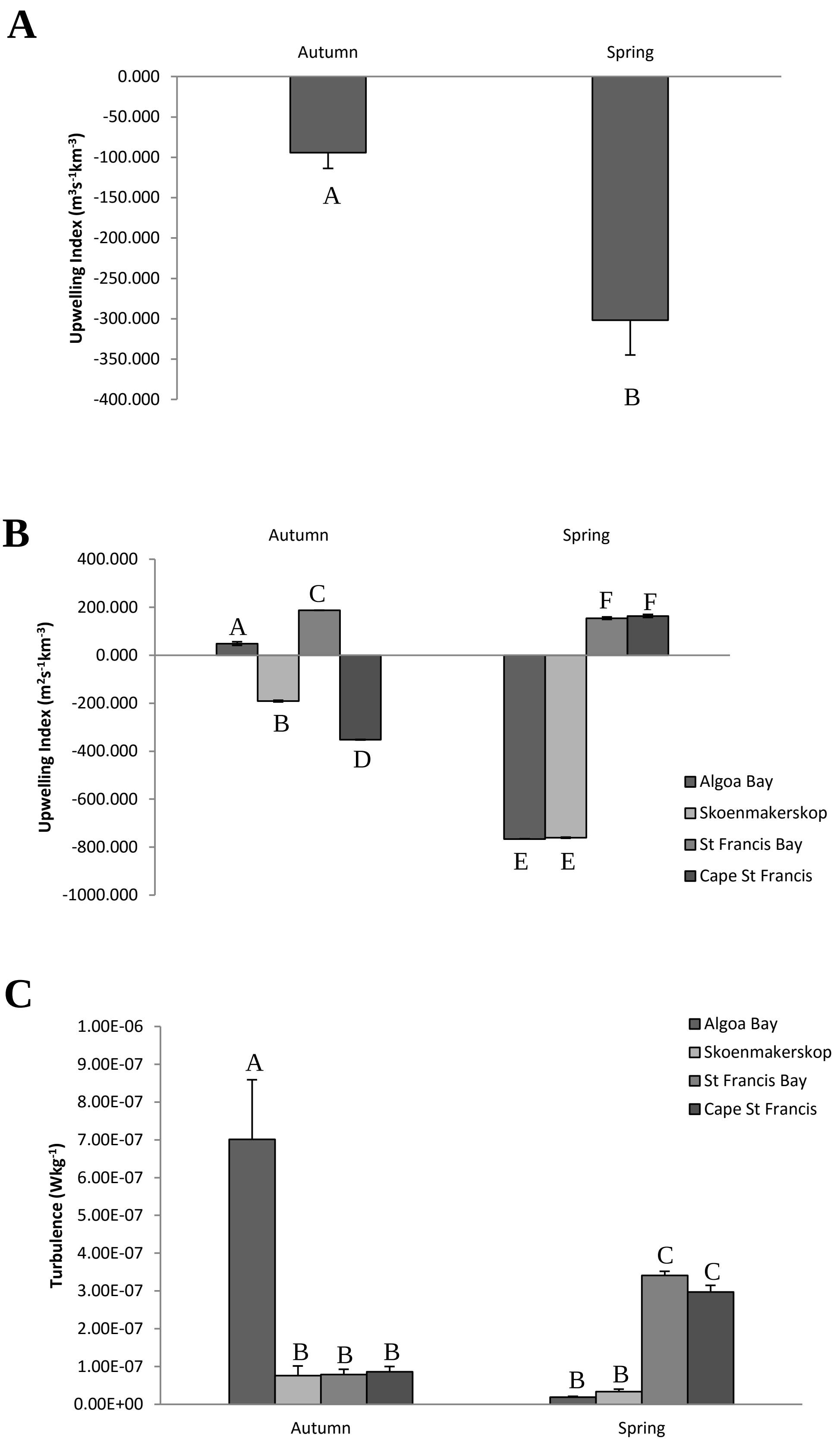


Figure 2.11: Mean **A**) upwelling index for March and September, **B**) upwelling index at each site during each season and **C**) turbulence at each site during each season. Vertical bars denote standard error (SE). Letters on histogram bars denote homogenous groups.

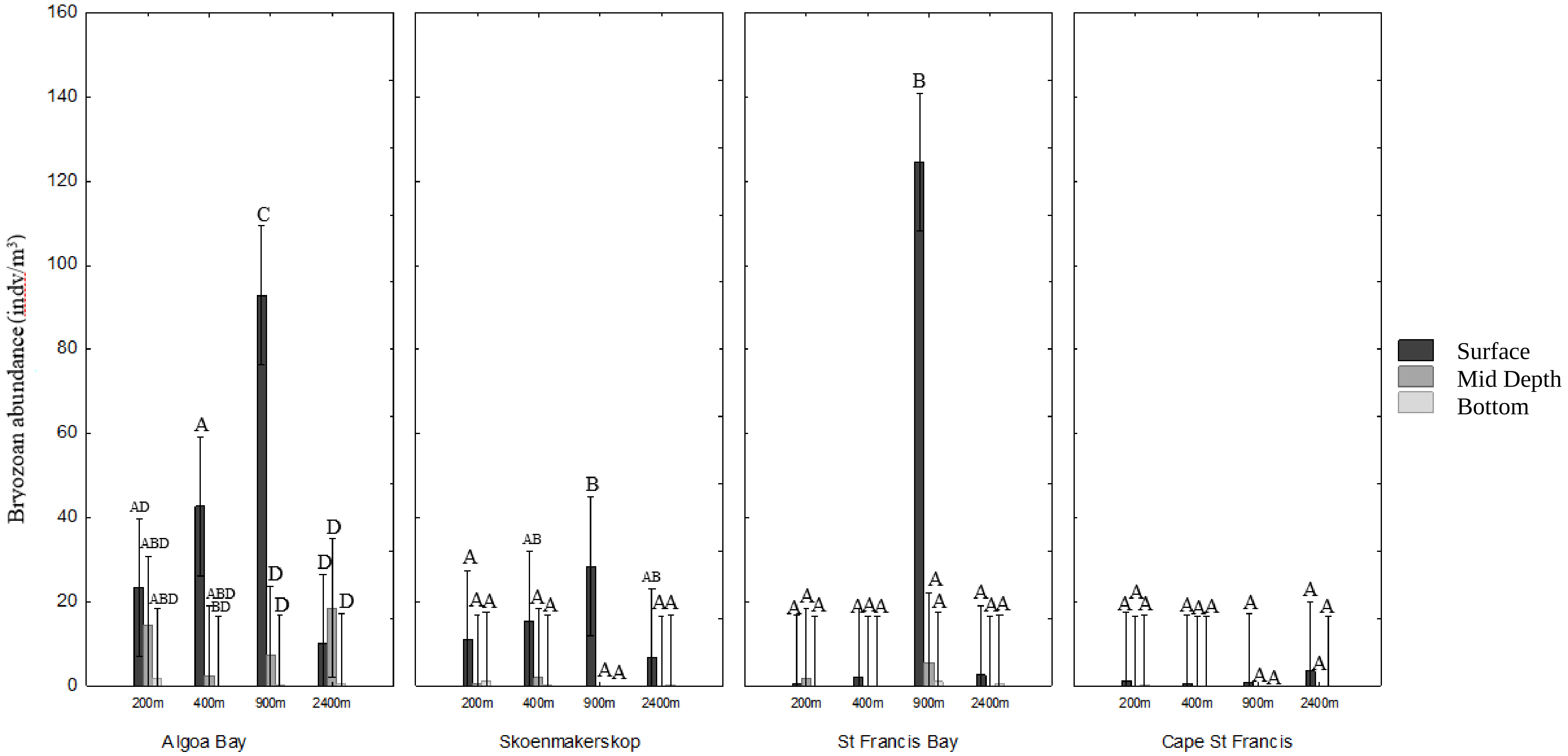


Figure 2.12: Mean bryozoan larval abundances at each site, distance offshore and depth (surface, mid-depth and bottom) during March. The vertical bars denote 95% confidence intervals and letters on histogram denote homogenous groupings at each site

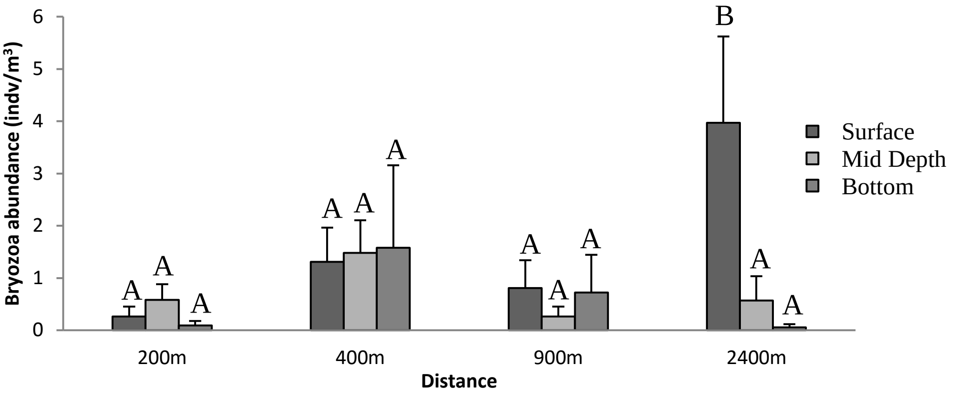
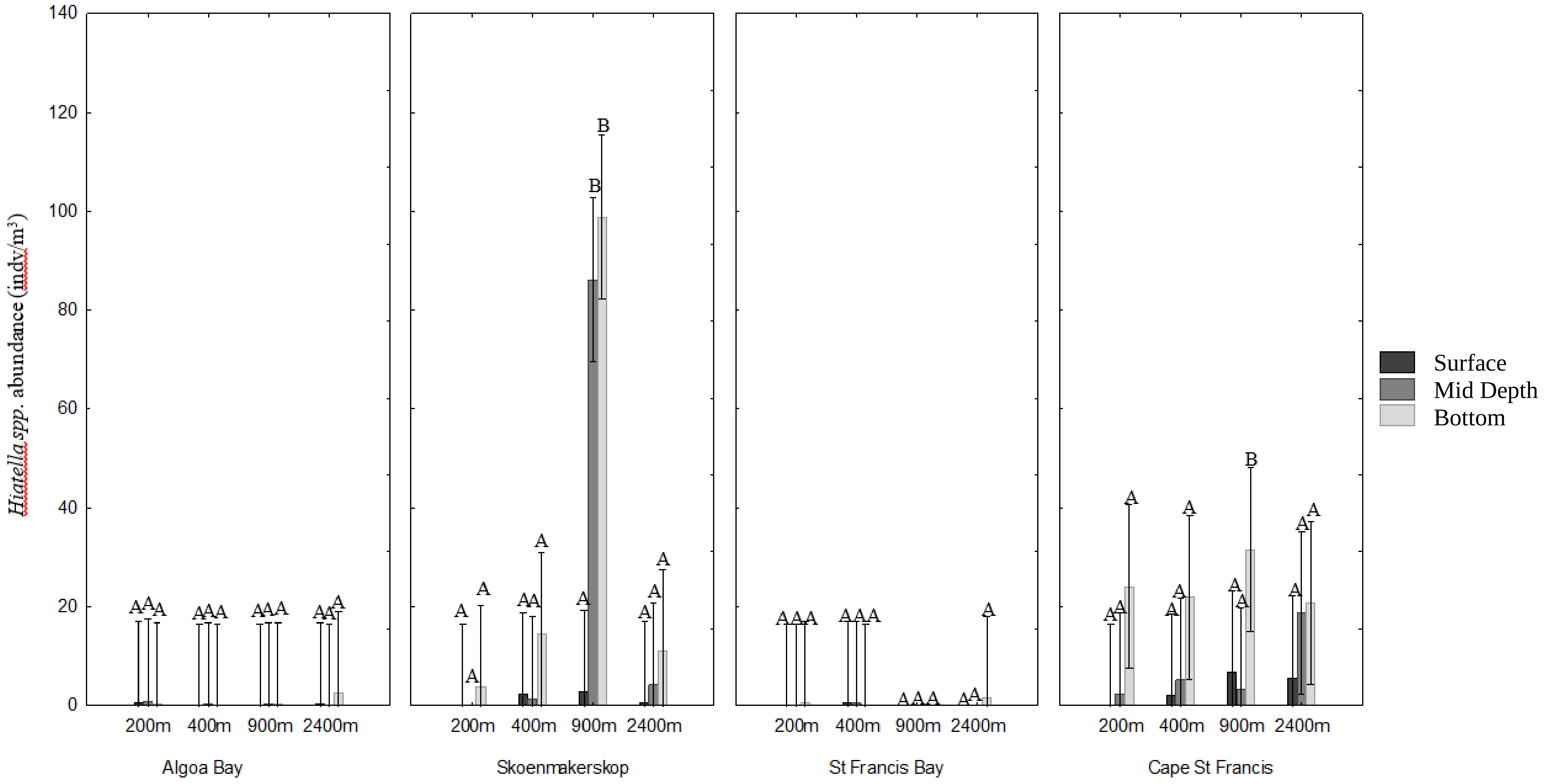


Figure 2.13: Mean bryozoan larvae abundance for all sites (pooled) at each distance offshore and depth during September. The vertical bars are the standard error (SE) of each mean and letters on histogram denote homogenous groupings



<u>Figure 2.14: Mean abundance of *Hiatella* larvae at each site, distance offshore and depth during the March season. The vertical bars denote 95% confidence intervals and letters on histogram denote homogenous groupings within each site</u>

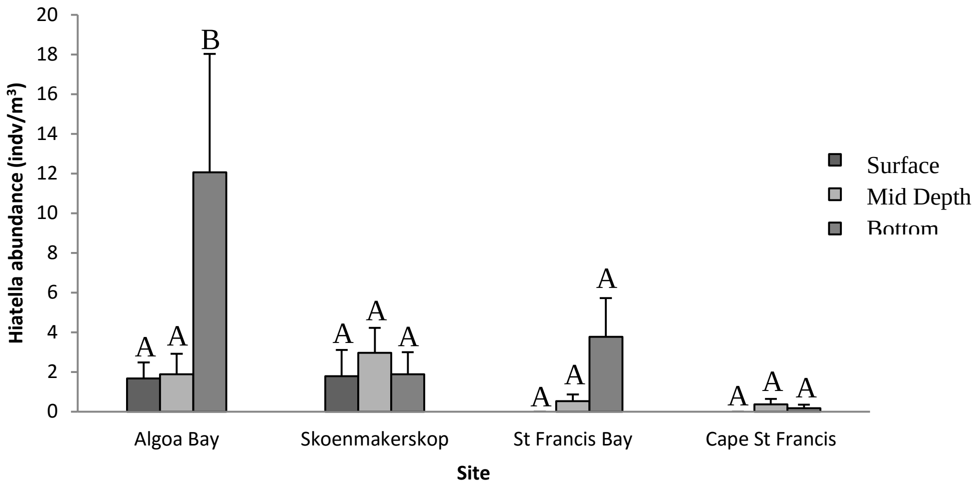


Figure 2.15: Graph represents the mean abundances of *Hiatella* larvae at each site and depth during September. The vertical bars are the standard error (SE) of each mean and letters on histogram denote homogenous groupings

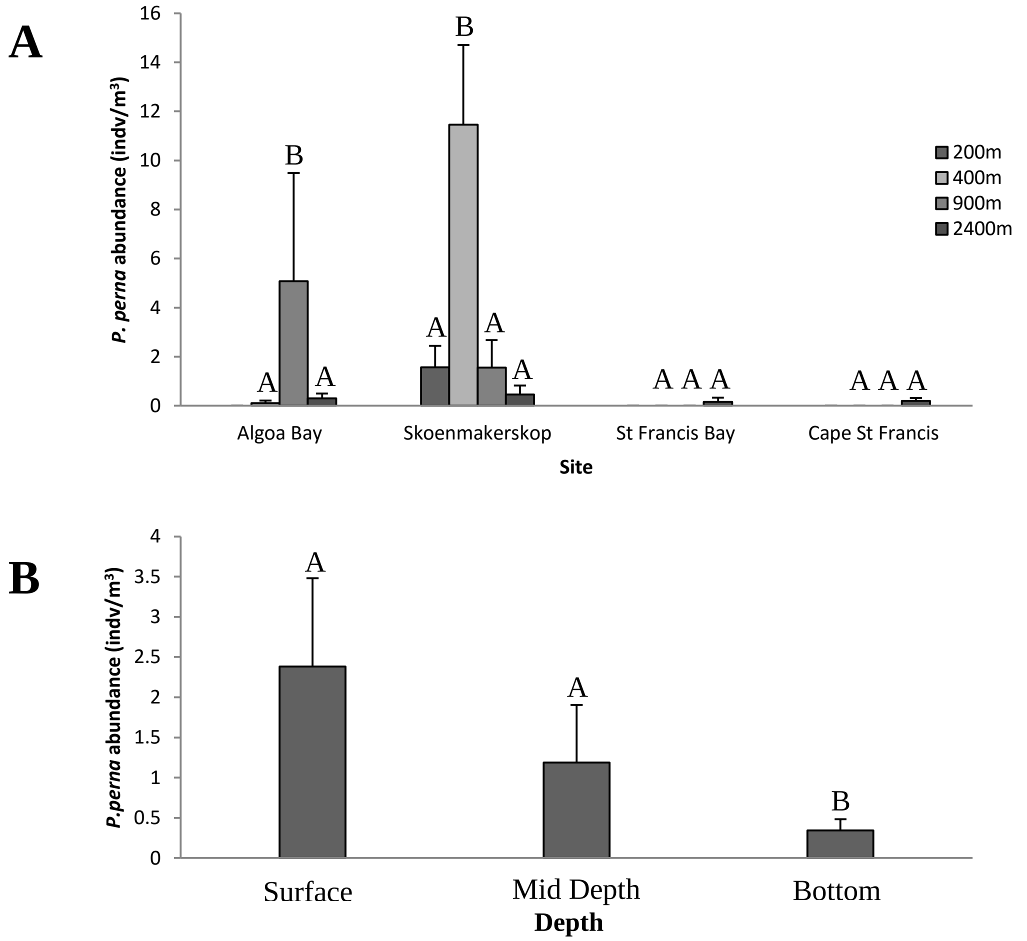
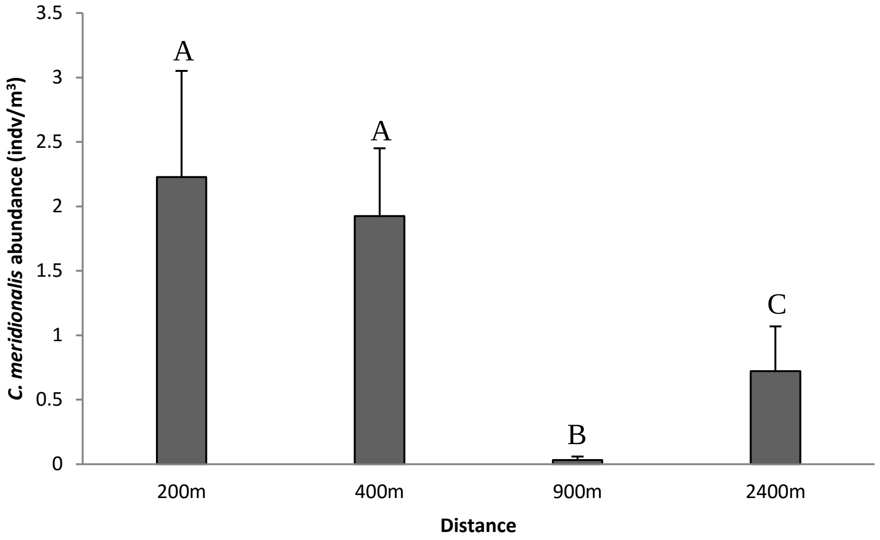
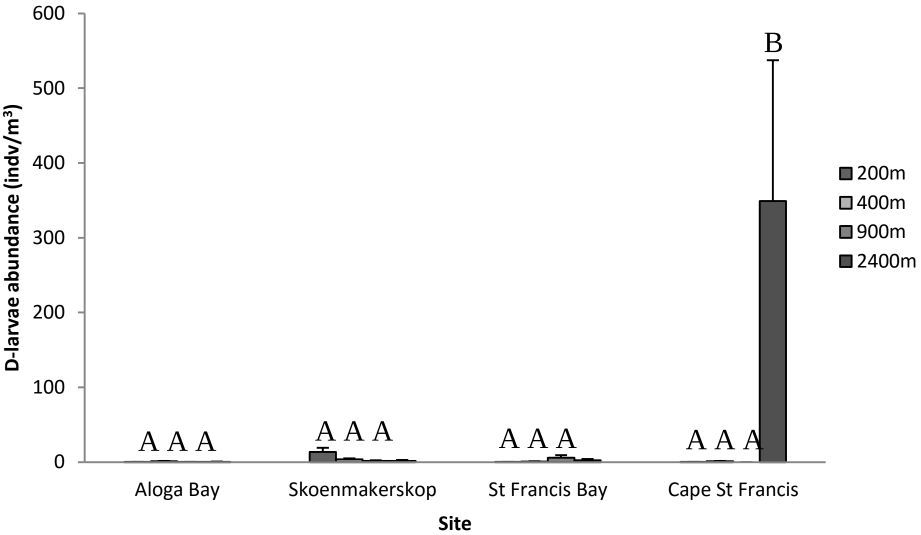


Figure 2.16 Mean abundances of *Perna perna* at **A**) each site and distance offshore and **B**) depths during March. The vertical bars represent the standard error (SE) of each mean and letters on histogram denote homogenous groupings



<u>Figure 2.17: The mean *Choromytilus meridionalis* abundance at each distance offshore during September. The vertical bars represent the standard error of each mean (SE) and letters on histogram denote homogenous groupings</u>



<u>Figure 2.18: The mean D-larval stage bivalves abundance at each site at each distance offshore during September. The vertical bars represent the standard error of each mean (SE) and letters on histogram denote homogenous groupings</u>

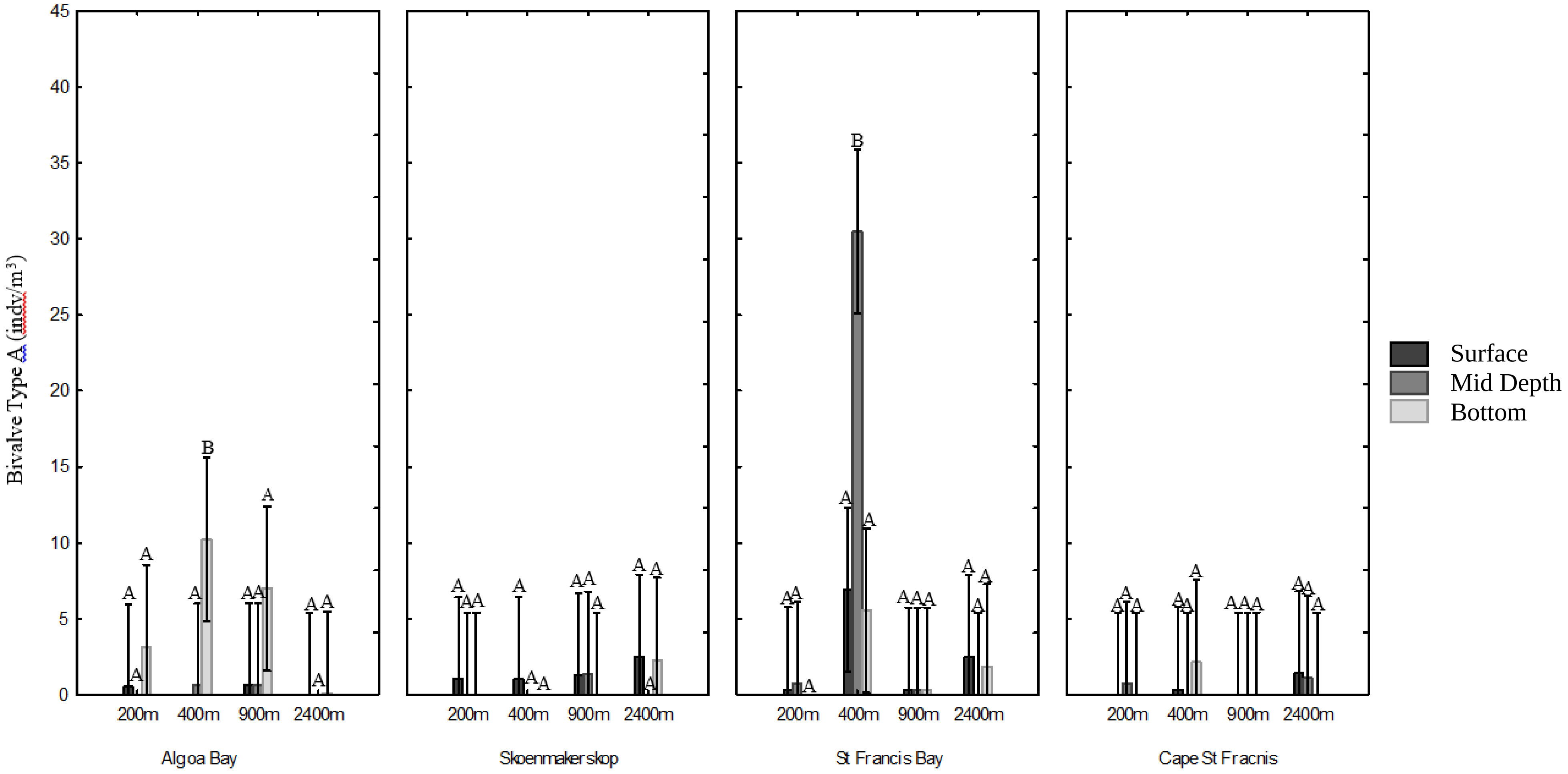


Figure 2.19: The mean Bivalve type A larval abundance at each site, distance offshore and depth during the March period. The vertical bars denote 95% confidence intervals and letters on histogram denote homogenous groupings in each site

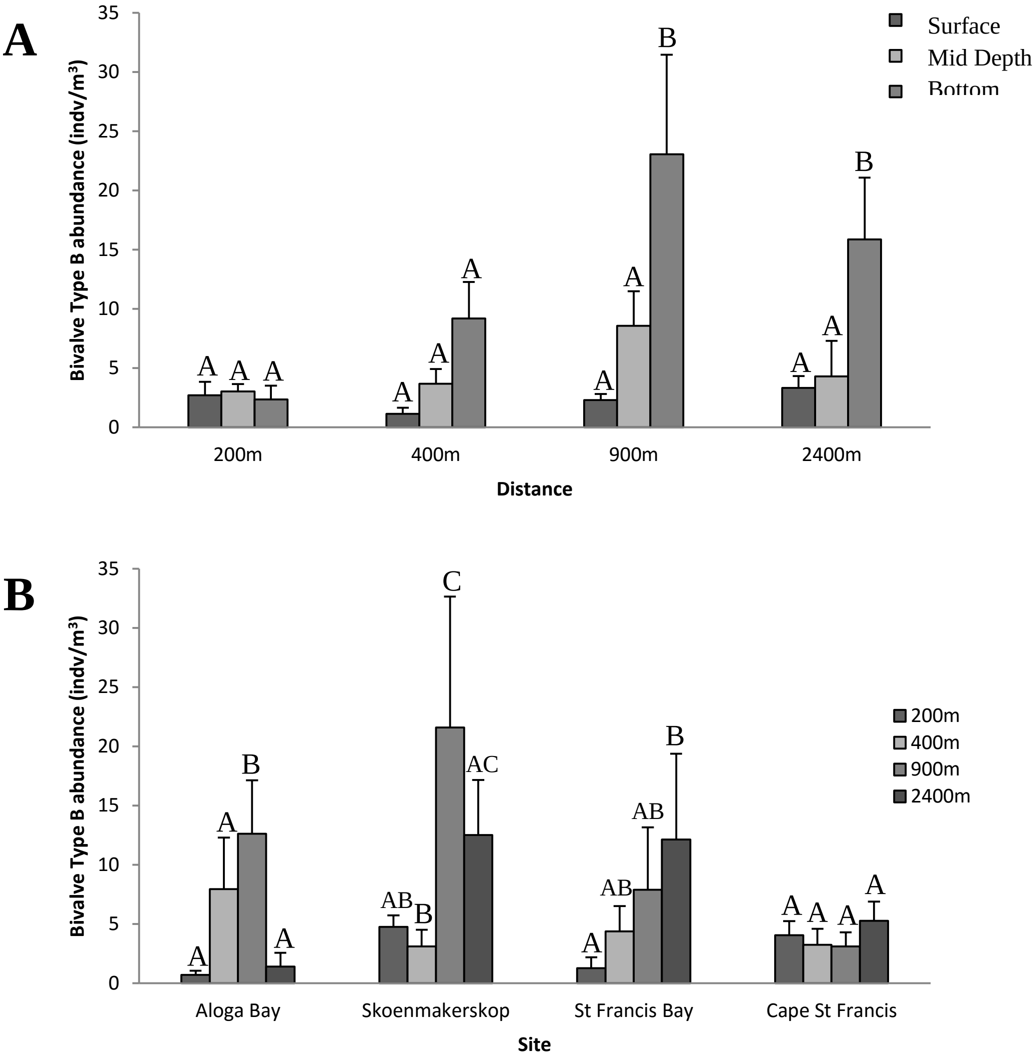


Figure 2.20: The mean abundances of Bivalve type B at **A**) each depth and distance offshore and **B**) each site and distance offshore during September. The vertical bars represent the standard error of each mean (SE) and letters on histogram denote homogenous groupings (in figure **B** groups within sites)

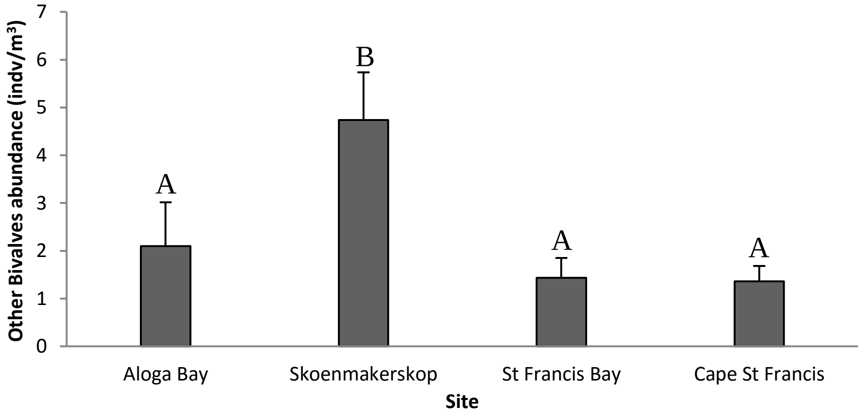


Figure 2.21: The mean abundances of Other Bivalves at each site during March. The vertical bars represent the standard error of each mean (SE) and letters on histogram denote homogenous groupings

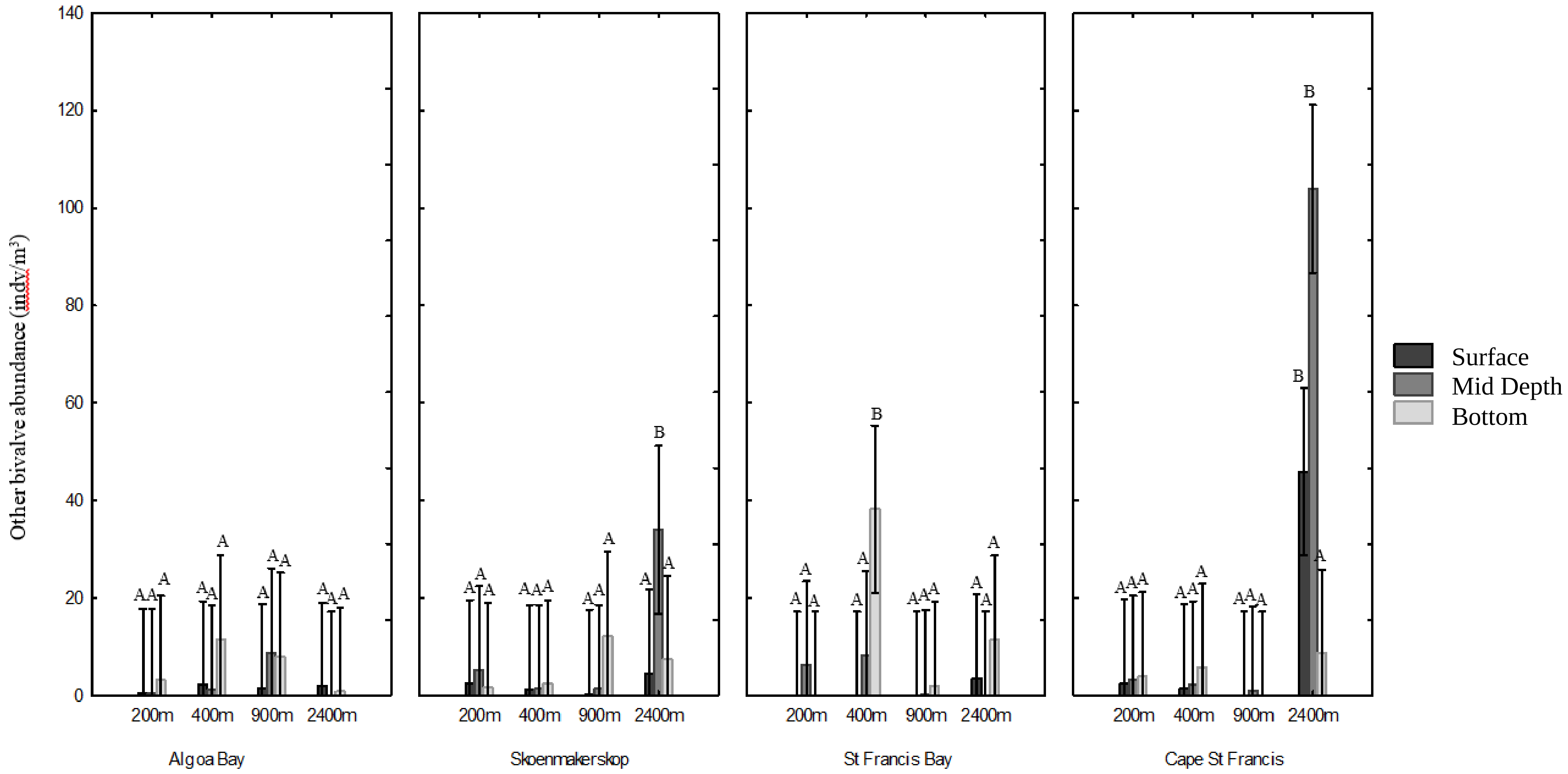


Figure 2.22: The mean Other Bivalves larval abundances at each site, distance offshore and depth during the September season. The vertical bars denote 95% confidence intervals and letters on histogram denote homogenous groupings at each site

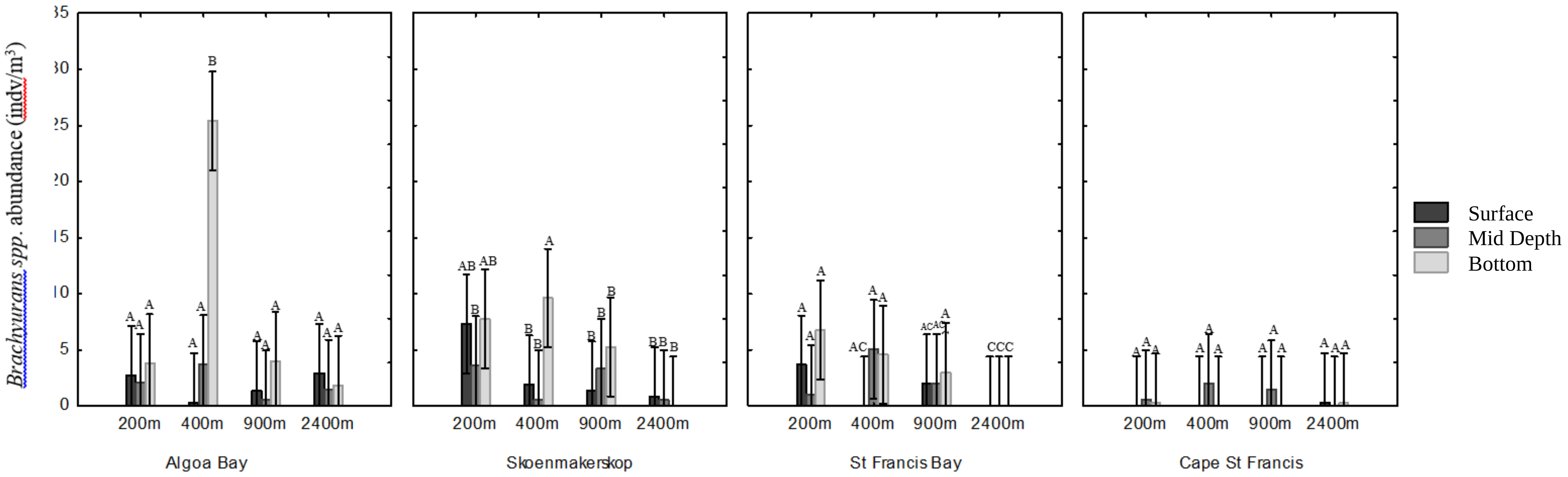


Figure 2.23: The mean brachyurans larval abundances at each site, distance offshore and depth during the March season. The vertical bars denote 95% confidence intervals and letters on histogram denote homogenous groupings

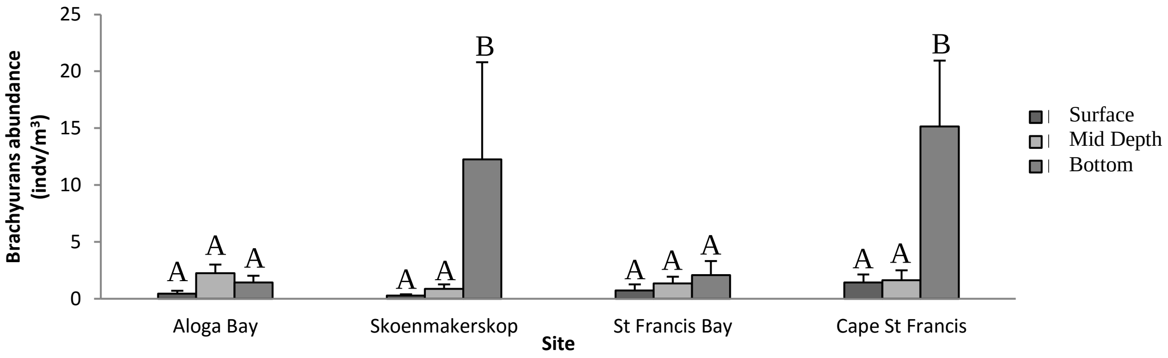


Figure 2.24: The mean abundances of brachyurans at each site and depth during September. The vertical bars represent the standard error of each mean (SE) and letters on histogram denote homogenous groupings

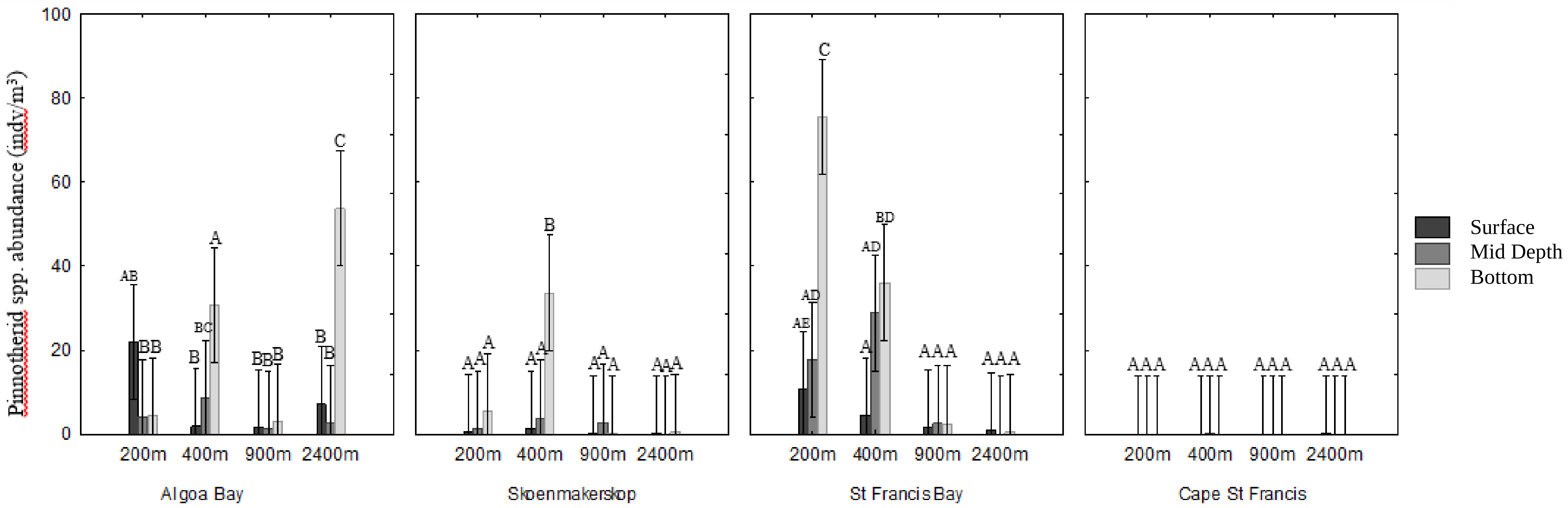


Figure 2.25: The mean pinnotherid spp. larval abundances at each site, distance offshore and depth during the March season. The vertical bars denote 95% confidence intervals and letters on histogram denote homogenous groupings at each site

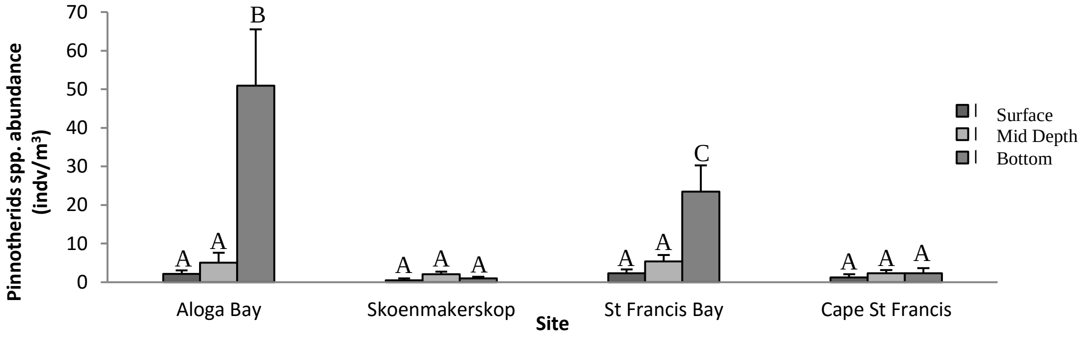


Figure 2.26: The mean abundances of pinnotherid spp. at each site and depth during September. The vertical bars represent the standard error of each mean (SE) and letters on histogram denote homogenous groupings

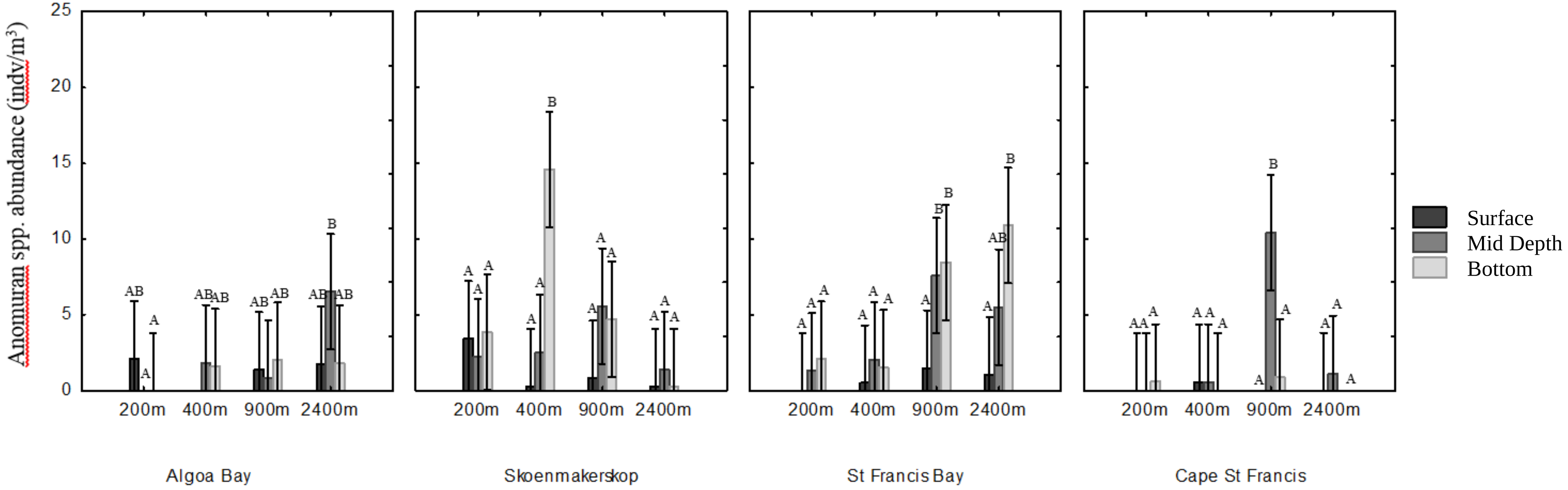


Figure 2.27: The mean anomuran spp. larval abundances at each site, distance offshore and depth during March. The vertical bars denote 95% confidence intervals and letters on histogram denote homogenous groupings at each site

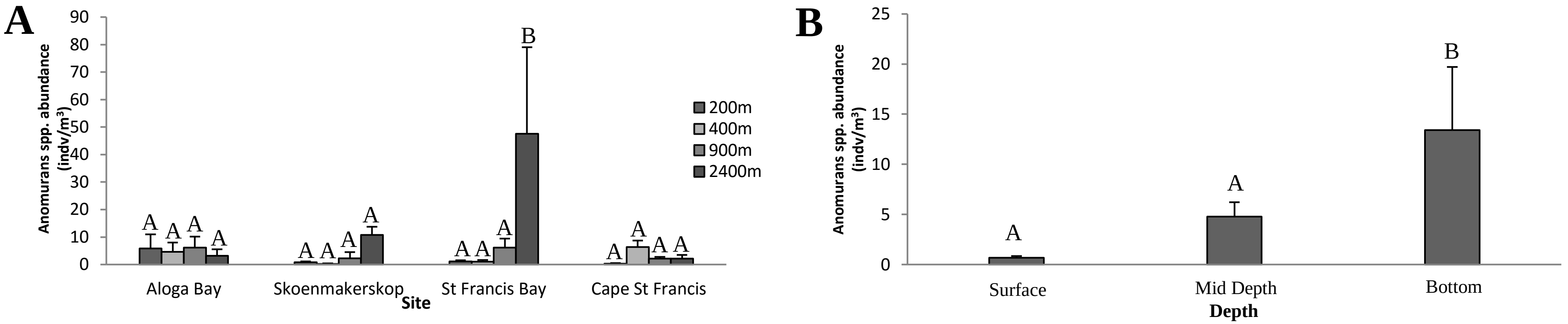


Figure 2.28: The mean abundances of anomuran larvae at **A**) each site and distance offshore and **B**) depth during September. The vertical bars represent the standard error of each mean (SE) and letters on histogram denote homogenous groupings

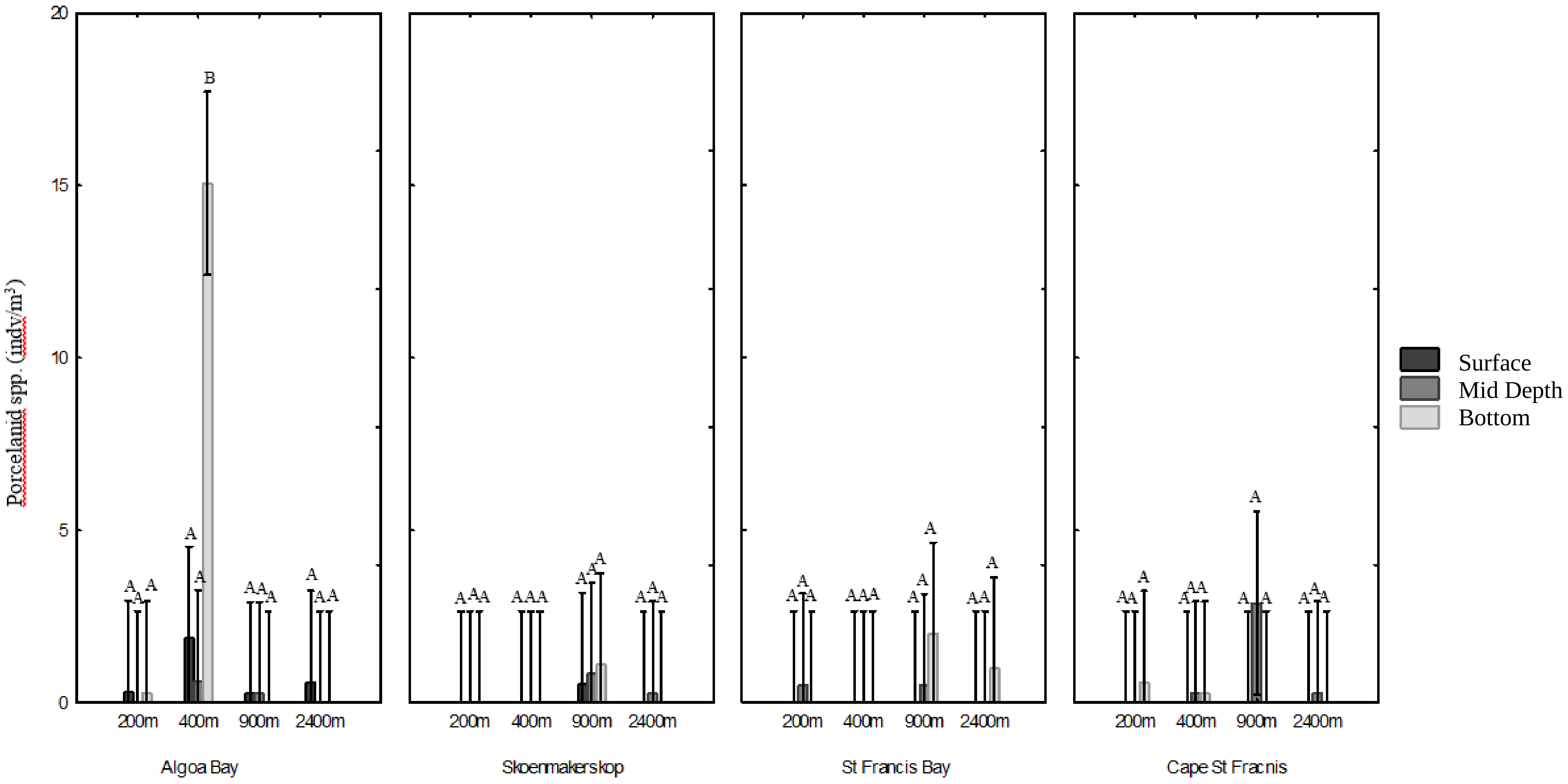


Figure 2.29: The mean porcellanid spp. larval abundances at each site, distance offshore and depth during the March season. The vertical bars denote 95% confidence intervals and letters on histogram denote homogenous groupings

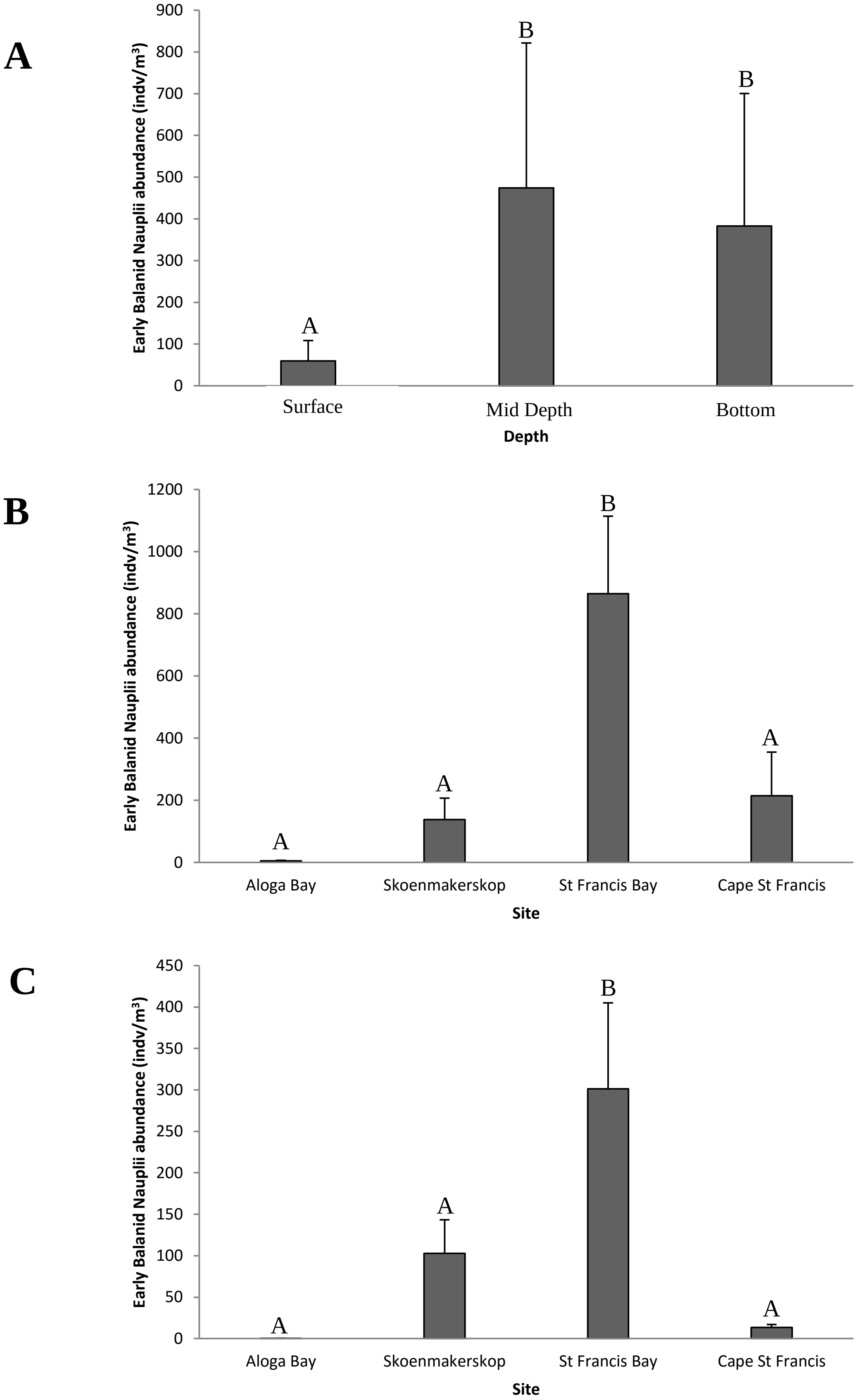


Figure 2.30: The mean abundance of early balanid nauplii at **A**) depth 1-3 during March, **B**) at each site during March and **C**) at each site during September. The vertical bars represent the standard error of each mean (SE) and letters on histogram denote homogenous groups

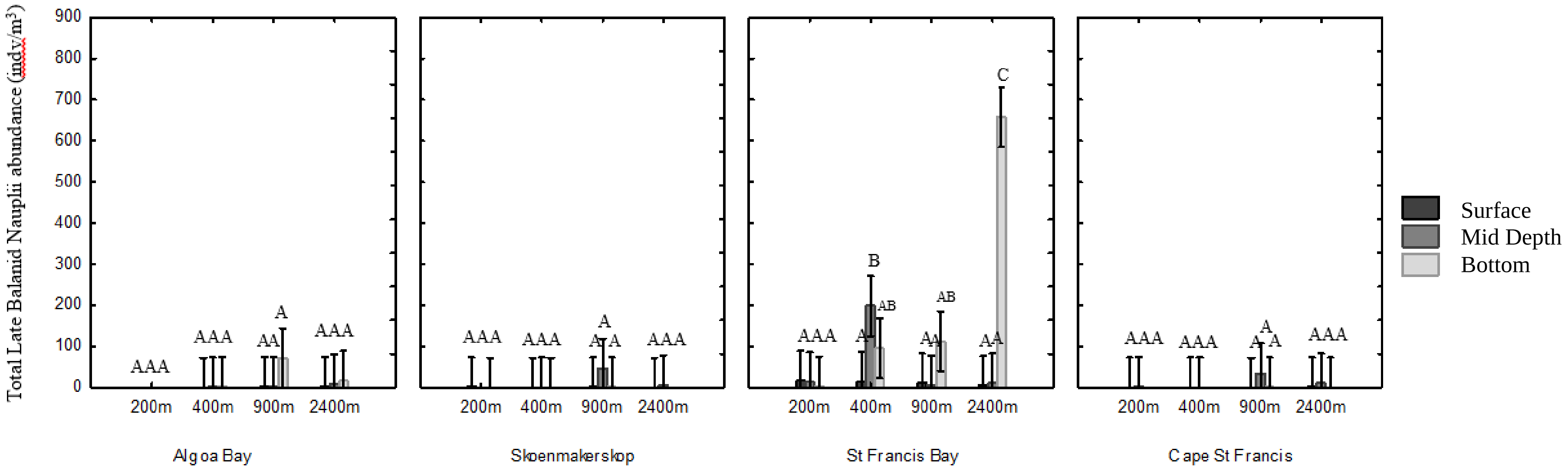


Figure 2.31: The mean abundance of late balanid nauplii at each site, distance offshore and depth during March. The vertical bars denote 95% confidence intervals and letters on histogram denote homogenous groupings at each site

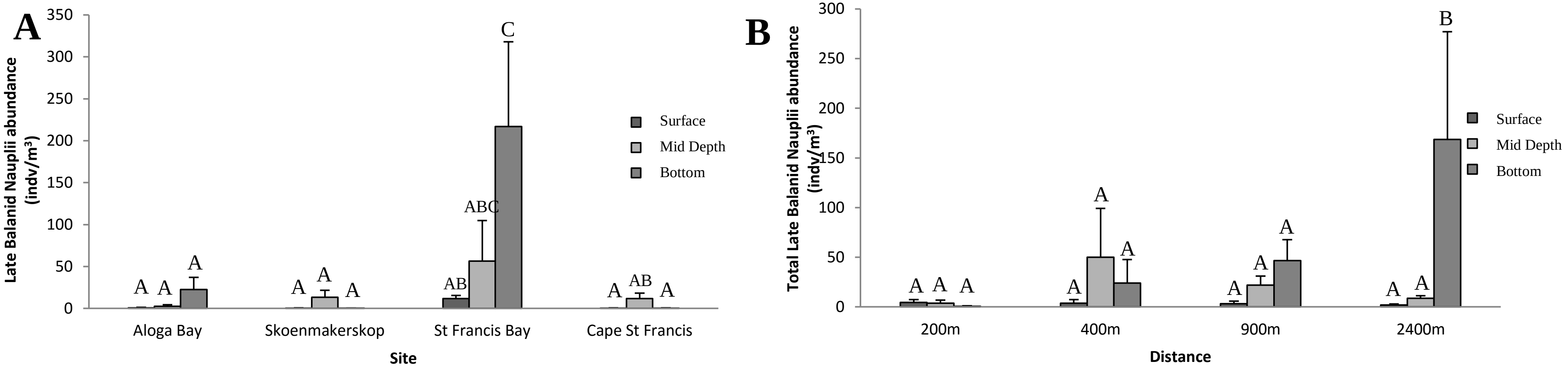


Figure 2.32: The mean abundance of late balanid nauplii during March at **A**) each site and depth and **B**) at each distance offshore and depth. The vertical bars denote standard error (SE) and letters on histogram denote homogenous groupings

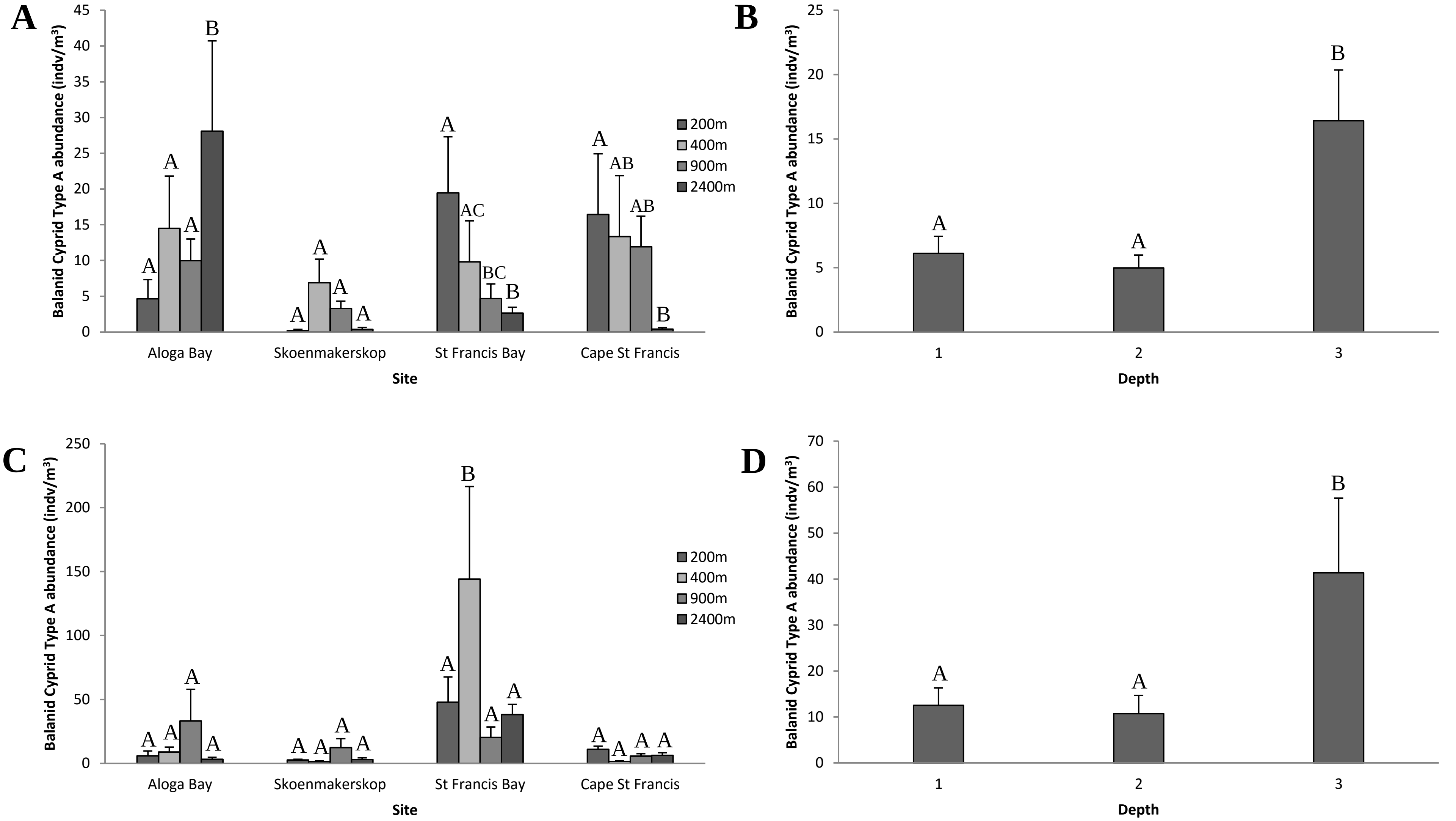


Figure 2.33: The mean abundance of Cyprid type A at **A**) each site and sistance offshore , **B**) each depth duting March and **C**) site and distance offshore and **D**) depth during September. The vertical bars denote standard error (SE) and letters on histogram denote homogenous groupings

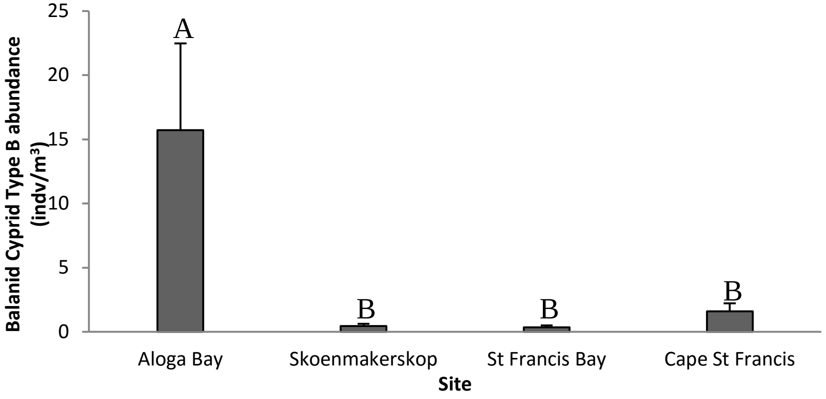


Figure 2.34: The mean abundance of Cyprid type B at each site during March. The vertical bars denote 95% confidence intervals and letters on histogram denote homogenous groupings

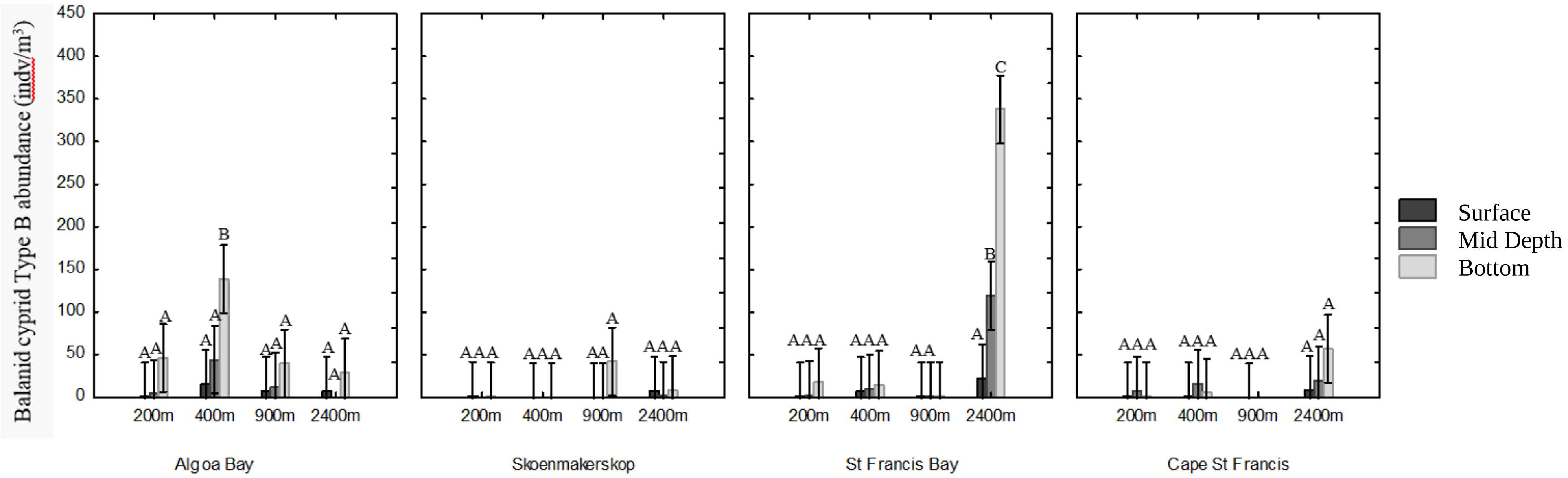


Figure 2.35: The mean abundance of Cyprid type B at each site, distance offshore and depth during September. The vertical bars denote 95% confidence intervals and l homogenous groupings at each site.

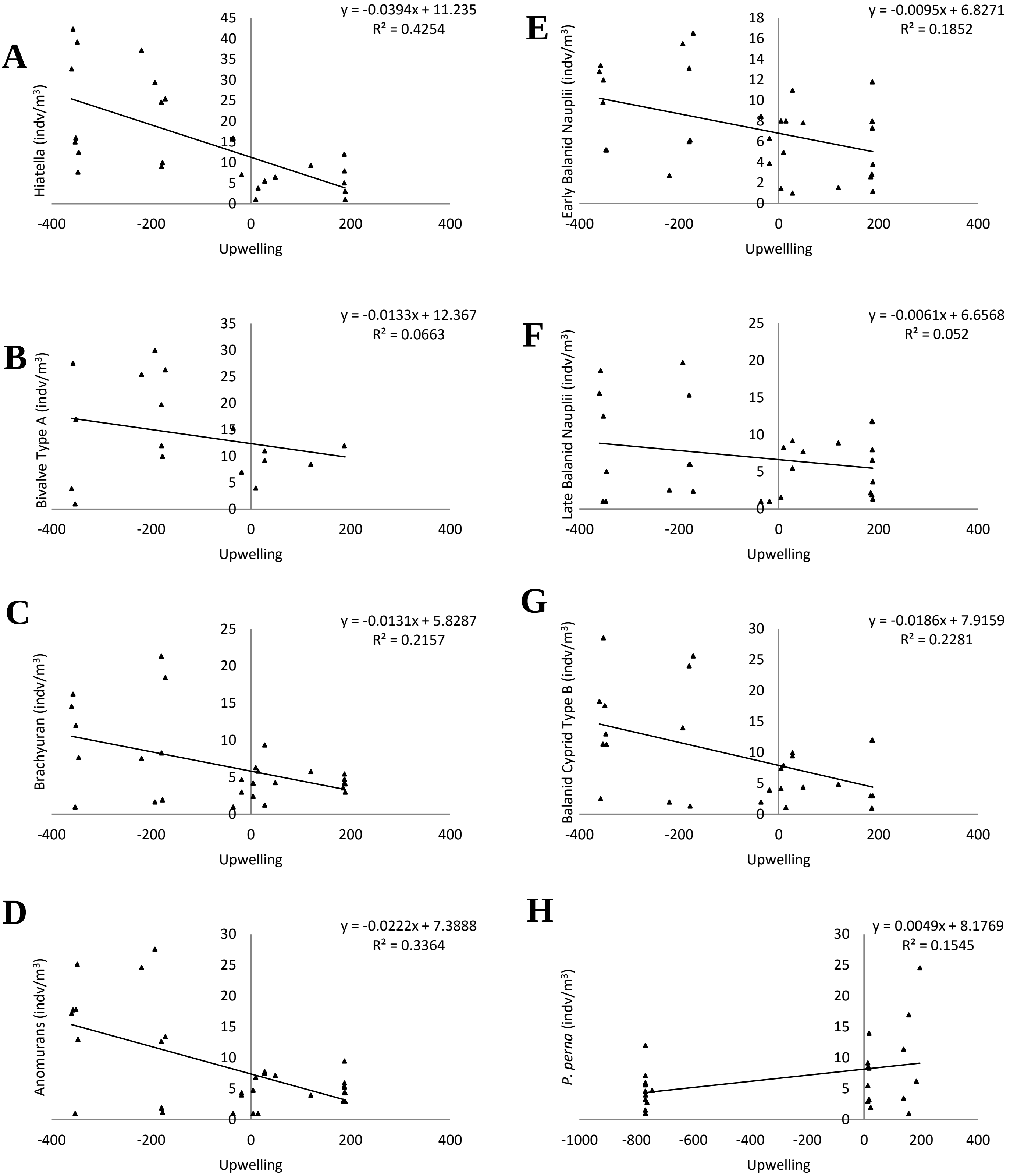


Figure 2.36: Regression plots of abundance of **A**) *Hiatella*, **B**) Bivalve type A, **C**) brachyurans, **D**) anomurans, **E**) Early balanid nauplii, **F**) Late balanid nauplii and **G**) Cyprid type B during March and **H**) *P. perna* during September against 4 day averaged upwelling indices. All regressions are significant ($p<0.05$) and R^2 values are alongside each plot

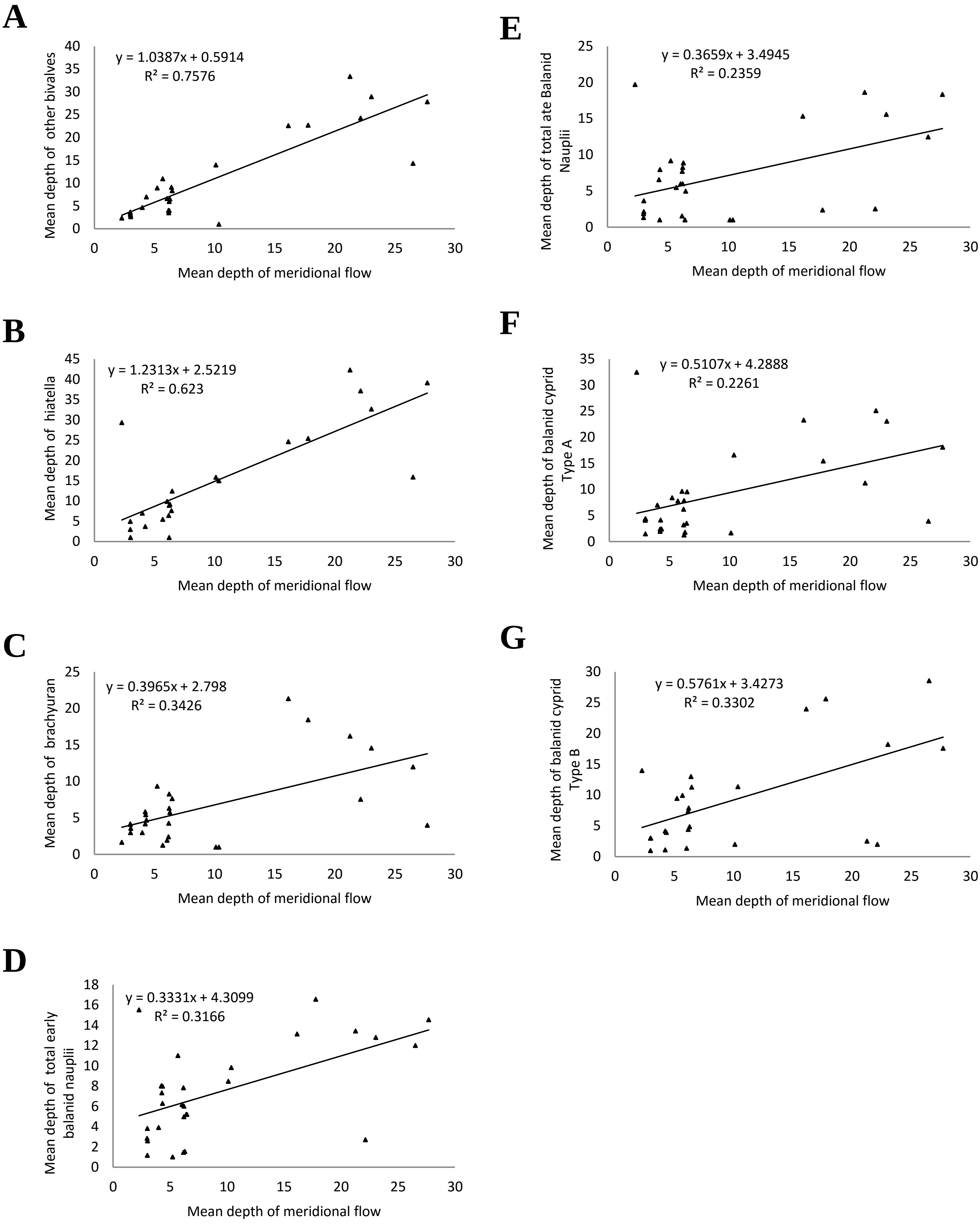


Figure 2.37: Regression plots of mean depth of **A**) Other bivalves**, B**) Hiatella spp., **C**) Brachyuran spp., **D**) Early balanid nauplii, **E**) Late balanid nauplii, **F**) Cyprid type A and **G**) Cyprid type B during autumn against mean depth of meridional flow. The mean abundance of late balanid nauplii at each site, distance offshore and depth during March. All regressions are significant ($p<0.05$) and R^2 values are alongside each plot.

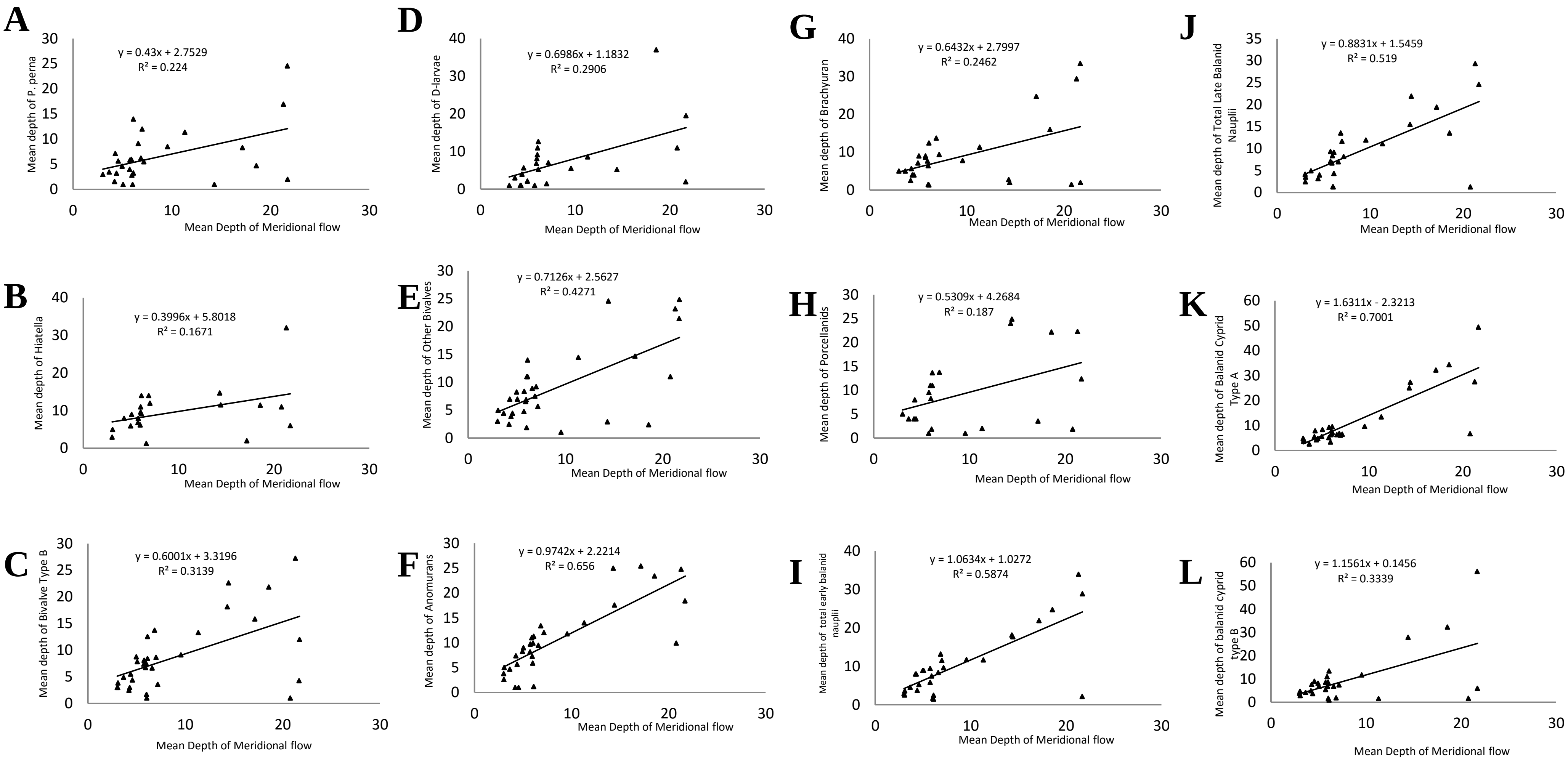


Figure2.38: Regression plots of the mean depth of **A**) *P. perna*, **B**) Hiatella spp., **C**) Bivalve type B, **D**) Bivalve D-larval stage, **E**) Other bivalves **F**) Anomuran spp, **G**) Brachyuran spp., **H**) Porcellanid spp., **I**) Early balanid nauplii,**J**) Late balanid nauplii,**K**) Cyprid type A and **L**) Cyprid type B during September against mean depth of meridional flow. All regressions are significant ($p<0.05$) and R^2 values are alongside each plot.

Chapter 3:

Settlement of mussels in bays and on open coasts in relation to wind driven variables

> *"A thinker sees his own actions as experiments and*
> *questions - as attempts to find out something.*
> *Success and failure are for him answers*
> *above all."*
> — Friedrich Nietzsche

INTRODUCTION

Intertidal mussels are a predominant feature of coastlines all over the world. Not only do the organisms themselves hold high socio-economic value (Branch *et al*. 2002; Robinson *et al*. 2005), they are also considered ecosystem engineers (Bertness & Lenard 1997; Gutiérrez *et al.* 2003). Traditionally, research conducted on mussel populations focussed on physical variables thought to impact on post-settlement mortality such as wave exposure (McQuaid & Branch 1984; Gaines *et al.* 1985; van Erkom Schurink & Griffiths 1993; Dahlhoff & Menge 1996; Hunt & Schiebling 1996; Akester & Martel 2000; Steffani & Branch 2003) and biological factors such as competition and predation (Connell 1961; Menge 1976; Bertness 1989; Minchinton & Scheibling 1993; Leonard *et al* 1998, 1999; Bertness *et al.* 1999; Jenkins *et al*. 2008). Although this research provided important information on post-settlement factors, more recent studies in the last 20 years or so have focused on understanding variables that influence settlement rates. This shift into "supply-side" ecology has led to a greater understanding of the nearshore hydrodynamics and has also improved our understanding of population dynamics of intertidal species that have a pelagic larval phase. The presence of a pelagic larval phase, and the fact that the adult stage is benthic, results in intertidal mussel populations being affected not only by local physical conditions and interactions in the benthos, but also by the pelagic and nearshore environment (Roughgarden *et al.* 1988; Eckman 1996). The complex multi-habitat life cycle of the mussel is further complicated by early benthic processes such as a settlement and recruitment of mussel spat arriving at the shore, into the adult habitat.

Distinguishing between settlement and recruitment

Settlement is often defined as the point at which an individual moves from the pelagic phase and takes up permanent residence on a substratum (Keough & Downes 1982; Connell 1985; Minchinton & Scheibling 1993; Rodriguezl *et al*. 1993; Gosselin & Qian 1997; Balch & Scheibling 2000; Jenkins *et al.* 2000; Porri *et al.* 2006). This definition does not consider the effects of post-settlement processes, which are in fact included in recruitment (Pineda 2000). Many bivalves are also able to initially settle onto filamentous substrata on which they may or may not remain (Bayne 1964; Keough & Downes 1982; Lasiak & Barnard 1995). After an initial settlement, therefore, veligers will then detach and reattach to a suitable substratum (Bayne 1964; Keough & Downes 1982; Lasiak & Barnard 1995). As bivalves undergo primary and secondary settlement as well as recruitment it is essential to define these terms explicitly. Some authors consider a “forced” two-stage process for settlement of mussels, identifying a “primary” and “secondary” phase (Bayne 1964; Keough & Downes 1982). Pelagic larvae would attach to the substratum for a period of time, detach from the initial settlement site and reattaching to a secondary settlement site (Bayne 1964; Keough & Downes 1982; Connell 1985; Lasiak & Barnard 1995; Jenkins *et al*. 2000). While this two-stage process is common, other research has showed that the first-to-secondary settlement is not obligate (McGrath *et al*. 1988; Lasiak *et al.* 1995).

Poulin *et al*. (2002) define settlers as larvae in the “transition phase” from a planktonic to benthic habitats. This definition captures the idea that the settler stage of development is made up of planktonic individuals that have metamorphosed and made initial contact with the substratum. For this reason researchers such as Porri (2003) have further defined settlers as planktonic organisms which are able to either make permanent or reversible contact with the substratum (Bayne 1964; Keough & Downes 1982; Connell 1985; Lasiak & Barnard 1995; Jenkins *et al*. 2000).

Recruits differ from settlers as they have recently attached to the substratum and survived for a certain period of time although they are not yet mature adults (Bayne 1964; Keough & Downes 1982; Connell 1985; Lasiak & Barnard 1995). During this time lapse, some degree of post-settlement mortality has to either have occurred or potentially could have occurred (Bayne 1964; Keough & Downes 1982; Connell 1985; Lasiak & Barnard 1995). Recruitment rate was defined by Pineda (2000) as the rate at which juveniles join the adult population. Both these definitions become problematic when working in the field because, although the definitions satisfy the theoretical understanding of what a recruit is, determining the “period of time” is not only species-specific, but also can pose arbitrary boundaries. Typically, categorising mussel spat into settlers or recruits is based on size classes that represent a certain amount of time on the shore. The size classes of settlers and recruits varies between species and defining size classes of widely studied species has been derived from various laboratory studies (Siddall 1980, Lasiak & Barnard 1995, Garland *et al*. 2002).

Physical factors affecting settlement and recruitment rates

Intertidal mussel population densities have been reported to vary spatially (Shanks & Wright 1987; Harii & Kayanne 2003; McQuaid & Lawrie 2005; von der Meden *et al.* 2008; Zardi *et al*. 2008). This is a result of both passive (nearshore hydrodynamics) and active (behavioural) processes (reviewed in Butman 1987). Perhaps the starkest comparison of spatial variation of mussel population structure is the distinction reported between bay and open coast sites (Pineda 2000; Helson & Gardner 2004; Roughan *et al*. 2005; Mace & Morgan 2006; von der Meden 2009; Zardi *et al*. 2008) and its relationship with settlement and recruitment (McQuaid & Phillips 2006; von der Meden 2009).

In South Africa, post-settlement mortality has been ruled out as the driver behind the observed differences between bay and open coast sites within the present study region (von der Meden et al 2012). This gives reasons to focus on factors that may affect settlement and recruitment rates. The importance of physical factors to the success of settlement and recruitment has been well established (McQuaid & Branch 1984; Steffani & Branch 2003; Helson & Gardner 2004; Roughan *et al.* 2005; Westerbom & Jattu 2006; Mace & Morgan 2006). According to Pineda (2000), among the most important factors to consider are wave exposure and turbulence (McQuaid & Lindsay 2000; Hammond & Griffiths 2004; Dobretsov & Wahl 2008) as well as hydrodynamics driven by local topography (Delafontaine & Flemming 1989; Chiba & Noda 2000). Wind driven coastal processes of upwelling (Guichard *et al*. 2003; Menge *et al*. 2003) and turbulence (Denny 1987; Abelson & Denny 1997) are considered important drivers of settlement and recruitment processes. This is because they act directly on the larval pool, a relatively difficult life stage to study, potentially affecting large numbers of larvae and therefore the supply of larvae to adult habitats (Pineda 2000; Morgan 2001; Underwood & Keough 2001). The link between topography and larval settlement may be attributed to the effect of coastal profiles, in particular the presence of bays, headlands and bathymetric features, on nearshore oceanography (Wolanski & Hamner 1988; Geyer & Signell 1992; Largier 2003; Narváez *et al*. 2006) and therefore larval transport.

As the focus has moved away from post-settlement mortality factors, towards more supply-side studies, two main suggestions as to why bay and open coast sites are distinct are identified in the literature. The first is that bay sites are comparatively demographically closed and have enhanced stock recruitment due to small scale oceanographic recirculation and the potential presence of “shadows” (Graham & Largier 1997; Wing *et al.* 1998a, 1998b; Roughan *et al.* 2005; Mace & Morgan 2006). These “upwelling shadows” were identified by Graham and Largier (1997) as the body of water located in the lee of a large headland characterised by reduced wind forcing and warm surface water temperatures during upwelling periods. The identification of this feature brought up questions as to how this may effect nearshore larval retention (also addressed in this thesis, Chapter 2). In 2006, Mace and

Morgan published the first paper to show that larval accumulation occurred within the "shadow" and ensconce upwelling features into the field of larval dispersal research.

The second suggestion is that bay sites, unlike open coast sites, tend to provide advantageous environmental conditions for settlement and recruitment (Gaines & Bertness 1992). An example of such a condition is the sheltered nature of bay sites in terms of wave intensity (Gaines & Bertness 1992). Although wave action has been shown to be positively correlated with growth rates of mussels (Jones & Demetropoulos 1968; Raubenheimer & Cook 1990; McQuaid & Lindsey 2000), likely due to increased food availability (Seed 1969; Griffiths 1980; Tsuchiya 1980; Newell & Shumway 1993), if wave intensity is too high, adult mussels are in danger of being dislodged from the substratum (Gaines & Bertness 1992). An interesting dynamic to consider is the possibility of both factors (advantageous environmental conditions and higher larval supply) contributing to a positive feedback mechanism in bay sites, but not at open coast sites (Pineda 2000; von der Meden 2009). This may be an explanation for the topographic distinction between mussel populations in bays and on open coasts.

In this chapter, settlement and recruitment rates of intertidal mussels were compared between two prominent topographic features: bays and open coasts. Settlement and recruitment rates were also analysed with reference to the wind driven processes of upwelling and turbulence to determine the potential effect of these factors on the early establishment of mussels onto adult habitats.

MATERIALS AND METHODS

Study Sites

This study took place over two sampling periods in 2013, "March" and "September". Within this region March is considered to be autumn and September is spring however this study was not concerned with seasonality and therefore seasonal replicates were not collected. Sample periods are instead two replicates of time that would likely have different larval abundances due to seasonality (Porri *et al*. 2006) The March samples were collected between the 26th February and the 11th May 2013, while the September samples were collected between the 6th September and the 4th October 2013. During each sample period, samples were collected from two bays (Algoa and St Francis) and two nearby open coast sites interspersed between the bays. The sites were: Algoa Bay (S33°55’46”, E25°36’38”), Skoenmakerskop (S34°02’27”, E25°31’57”), St Francis Bay (S34°10’15”, E24°50’05”) and Cape St Francis (S34°12’36”, E24°49’32”) (Fig 3.1). These sites were selected in order to replicate major topographic features of bay and open coast sites and were also selected due to their proximity to one another, allowing regular sample collection. The location of the intertidal sites was directly onshore of the pelagic plankton transects described in the previous chapter.

Algoa Bay receives moderate wave action, with waves breaking at an average height of 0.7m (McLachlan 1980, cited by Lasiak 1984). St Francis Bay, like Algoa Bay, is relatively protected from the strong wave action (Bruton *et al.* 1991) associated with the south and south-westerly waves generated by storms moving up the coast of South Africa from west to east (Darbyshire & Darbyshire 1964). The open coast sites of Skoenmakerskop and Cape St Francis differ from both bay sites as they are not sheltered from the south and south westerly waves and thus experience a greater degree of wave action (Beckley 1985; von der Meden 2009). Although variability in wave action may be high among sites, in general terms, Algoa Bay and St Francis Bay experience less wave action than the two open coast sites (Bruton *et al.* 1991, Von Der Meden *et al*. 2008).

Meteorological data, including wind speed and direction, were obtained from the weather stations in Algoa Bay (S33°59’02”, E25°36’35”) and St Francis Bay (S34°12’43”, E24°50’06”) (Fig 3.1).

Experimental design

A total of three collectors were analysed at each site for each sampling event (see details below on temporal resolution of sampling). Once collected, the pads were immediately placed into individual containers and covered in 70-100% ethanol. The samples were brought back to the laboratory on the same day of collection for storage and further processing.

Samples for estimates of larval settlement and recruitment were collected fortnightly over each sampling season during consecutive spring tides. Settlement collectors were deployed within the low mussel zone as this area receives the highest number of settlers (Porri *et al*. 2007). There was a total of 5 sampling events during March sampling and 4 events during the September collections. During September, high seas and increased storm activity resulted in a high loss of collectors particularly at the open sites. Due to the loss of collectors (n=1 or 0 at open coast sites throughout the season), data for September were therefore not analysed.

Wind data were provided by the South African Weather Service over the sampling period. Wind speed and direction were used to calculate an upwelling index and wind driven turbulence. The upwelling and wind driven turbulence indices were calculated according to the equations developed by Bakun (1973) and Madsen (1977) respectively and described in detail in chapter 2 of this thesis.

Settlement and recruitment collectors were plastic kitchen scouring pads (Fig 3.2) which have been widely used as an artificial settlement substratum (Farrell *et al.* 1991; Hunt & Scheibling 1996; Gilg & Hilbish 2000; Porri *et al*. 2006). Previous studies have demonstrated that the use of artificial substrata should only be employed for comparative studies where relative abundances are required (Hunt & Scheibling 1996), as settlement rate and size distribution on artificial substrata have been shown to differ significantly from natural substrata (Hunt & Scheibling 1996). The scouring pads were circular and approximately 10 cm in diameter (Fig 3.2). The collectors were attached using two 5 mm cable ties, to eyebolts which had been drilled into the rock surface. At each site, 10 pads were secured approximately 2 m from one another. Due to high losses of the pads and eyebolts, the positions of pads differed by a few meters throughout the study. A total of 3 collectors were analysed at each site for each sampling event (see details below on temporal resolution of sampling) when possible. Once collected, the pads were immediately placed into individual containers and covered in 70-100% ethanol. The samples were brought back to the laboratory on the same day of collection.

Sample processing and settler identification

Once in the laboratory, samples were “washed” to remove bivalves from the artificial substrata. This involved soaking each collector individually in a dilute solution (3.5%) of sodium hypochlorite to insure that bivalves detached from the substratum by dissolving their byssal threads (Davies 1974; Pearce & Bourget 1996; Connolly *et al*. 2001). The collector was then rinsed with fresh water and all debris removed from the surface of the collector. The resulting debris-filled liquid was then filtered through a 75 µm sieve (Porri *et al.* 2007). The sample was then analysed in a petri dish under a dissecting microscope at 25x magnification.

For the purpose of this study, only the three most abundant and conspicuous mussel species in South Africa were considered. These species were: *Perna perna* (indigenous mussel), *Mytilus galloprovincialis* (invasive Mediterranean mussel) and *Choromytilus meridionalis* (indigenous mussel) (Branch *et al.* 2010). Each of these three species was identified from the samples. Although DNA-based identification methods are now available, this is not feasible for large numbers of individuals and instead, larval morphology was used to separate the three different taxa (Porri *et al*. 2006, Porri *et al*. 2007; Bownes *et al*. 2008).

Species were identified and measured using a graduated eyepiece under the dissecting microscope and individuals were placed into one of 5 size classes: a) < 360 µm, b) > 360 µm to 1000 µm, c) 1000µm to 2000µm and d) > 2000µm. Although size classes are able to accommodate larger recruits, the recruits found in this study remained small enough (< 2150 µm) to conclude based on growth rates that they were all likely from the same cohort and not from a cohort of the previous year. Larvae less than 360 µm in size were considered primary settlers, while those that fell into the larger size classes were considered recruits. The categorisation of larvae into “setters” and “recruits” according to these size classes has been used in several studies conducted in the region (Lasiak & Barnard 1995; Porri *et al.* 2006, Porri *et al.* 2007; Bownes *et al.* 2008; Von Der Meden 2009).

Statistical Analysis

This study addressed two main topics: the possible effects of topography on settlement and recruitment, and the influence of physical processes such as upwelling and turbulence on settlement and recruitment of mussels. To investigate the former, 2-way ANOVAs were conducted to compare the effects on both settlement and recruitment of location and sample event for the three species of mussels considered. Site was considered a fixed factor (4 levels) and sample event was selected as random (5 levels). Sites were not nested based on topography as a more conservative approach was favoured whereby all sites were separated regardless of topography to determine whether there were common patterns among the bay sites and among the open coast sites. This conservative approach allows for similarities between topographic types to be identified in the Post Hoc analysis without forcing topographic patterns. A 3-way nested design ANOVA, including Region by grouping sites in the Algoa and the St Francis regions, was also not appropriate as there was no replication of topography (sites or bays) within regions.

The effects of upwelling and turbulence on settlement and recruitment rates were assessed using regression analyses. Upwelling and turbulence were plotted against recruitment and settlement rates for each species separately. Because there were many regression models run, the p-values for each season were Bonferroni adjusted (Feise 2002). Settlement and recruitment rates are presented as abundance per day unit. Previous work on initial settlement size and bivalve growth rates, conducted by Bayne (1965) and Bownes *et al.* (2008), indicate that the settler size class of < 360 µm would not have settled on the collection pads more than 4 days prior to collection, based on their growth rates. The total abundance of bivalves that were smaller than 360 µm was therefore divided by 4 days, instead of averaged over the total days the collection pad was left on the rocks, to achieve a more accurate average daily settlement rate for new settlers. The larger size class abundances were divided by the total number of days the collector spent on the shore (approximately 12-16 days depending on the sampling event).

RESULTS

Settlement

ANOVA results are summarised in Table 3.1. Bivalves that were smaller than 360 µm will hereafter be referred to as "settlers". The settlement rates for this size class were averaged over a 4 day period as described above. Figure 3.3a shows the per day rate for total settlement of all three species together. During event 4, settlement in both Algoa Bay and St Francis Bay was significantly higher than at their corresponding open coast sites ($p < 0.001$ for both sites and events).

Settlement of *M. galloprovincialis* was higher in both Algoa and St Francis Bay when compared to the open coast sites, but similarly to the results for total settlement of all three species together, settlement rates were highly variable between sample events (Fig 3.3b), with sample event 4 having the highest settlement rate for both the bay sites ($p<0.001$). Algoa Bay had a higher settlement rate of *M. galloprovincialis* when compared to St Francis Bay ($p < 0.05$). Apart from sample event 4, all sites presented similar settlement rates for *M. galloprovincialis* ($p > 0.7$).

Settlement of *P. perna* depended on both site and event (Fig 3.3c). *P. perna* followed the general trend of settlement rates being higher is bays than open coast (Fig 3.5a), however this was dependent on only one event (event 3) in Algoa Bay ($p < 0.001$) and was not observed in St Francis Bay for any event. Unlike *P. perna* and *M. galloprovincialisg*, settlement of *C. meridionalis*was only affected by site as a factor and not event (Table 3.2d), with both Algoa and St Francis Bay having higher settlement rates than the two open coast sites of Skoenmakerskop and Cape St Francis (Fig 3.3d).

Recruitment

Mussels that were larger than 360 µm in length were considered to be recruits. This group was made up of recruit size classes B, C and D as described in the methodology. Recruitment rates were significantly related to site, with higher recruitment in bay sites than open coast sites (Table 3.2, Figure 3.4) for all mussel species. As was expected, event (time) had a significant effect on recruitment, but only for the total pooled *P. perna* and *M. galloprovincialis* groups (not for *C. meridionalis*), whereby recruitment rates peaked during different events at different sites for each species (Fig 3.5). Generally, event 1 had the highest recruitment for each species at each site, with Cape St Francis being the exception for *M. galloprovincialis* which was the only peak during event 1 (Fig 3.5b). There was also a general pattern of recruitment rate decreasing from event 1 to event 5 (Fig 3.5). There was a noticeable peak in total recruitment and *P. perna* recruitment rates during event 1 although the results for total recruits would be highly affected by the high *P. perna* abundances (Fig 3.5 a,c).

Upwelling and Turbulence

Wind speeds and direction were used to calculate upwelling indices and turbulence over the whole sample period of March for the Algoa Region (which included the Algoa Bay and Skoenmakerskop sites) and St Francis Region (which included the St Francis Bay and Cape St Francis sites). Figure 3.6 shows the mean daily upwelling indices and turbulence over the March sample period and Figure 3.7 illustrates the mean daily upwelling and turbulence indices for each event separately. Statistically, there was no difference between regions in terms of mean upwelling (1-way ANOVA, $p = 0.926$), but there was a significant difference in mean turbulence ($p < 0.05$), with St Francis Region generally experiencing higher turbulence than the Algoa Bay Region (Table 3.3). The upwelling and turbulence indices were plotted in a simple line graph in order to visualise the degree and periodicity over the entire sampling period but also during each sample event. Turbulence was significantly different during event 4 from the other events in both the Algoa Region and the St Francis Region (Table 3.3 b). This was likely due to a notable spike in wind driven turbulence and downwelling followed by a sudden relaxation of both (Fig 3.7 d & i). To test whether events differed from one another a Kruskal Wallis test was run (an ANOVA was not run as unlike when looking at the entire data set for one site, the number of data point for each event did not meet the criteria for ANOVA analysis discussed in the methodology section). There was a significant difference in mean turbulence between event 4 and events 1 and 2 in the Algoa Region. There was also a significant difference between event 1, 2, 3 and 5 in the St Francis Region (Table 3.4b). Event 4 in the St Francis Region was only statistically different to event 2 in the St Francis Region (Table 3.4b).

The settlement rates of all mussel species were pooled for each sample event in both bay sites and it was found that there was a negative correlation between total settlement rates and mean turbulence for each sample event (n=10), while no significant correlation was found with upwelling (Table 3.5) at both bay sites. When the same correlations were run for each species separately, the pattern was found to be true for every species in Algoa Bay (Fig 3.8), but only true for total species and *M. galloprovincialis* in St Francis Bay (Fig 3.9). In contrast, settlement rates at Cape St Francis (open coast site) for each sample event were positively correlated with both mean upwelling and turbulence, for each sample event (Fig 3.10). There was no significant correlation of settlement rates with either variable at the open coast site of Skoenmakerskop (Table 3.5).

At open coast sites there was no significant correlations of recruitment rates with either upwelling or turbulence (Table 3.6). The results of regression analysis with regard to recruitment rates were inconsistent between bay sites. At the Algoa Bay site, recruitment of *M. galloprovincialis* was negatively correlated with upwelling, while there was no correlation with turbulence (Table 3.6, Fig 3.11). At St Francis Bay, recruitment rates of total, *P. perna* and M. *galloprovincialis* were positively correlated with upwelling (Table 3.6, Fig 3.12a-c) and *P. perna* and total recruits were positively correlated with turbulence (Fig 3.12d,e).

A relative index was calculated to remove any effect of region and allow for insight into effects of topography. This analysis also divided recruits into several scale size classes as described in the methodology in order to gain insight into possible fine-scale ontogenetic effects. The index was calculated by subtracting open coast rates from corresponding bay site rates for each event and region (Algoa Bay - Skoenmakerskop = Relative index; St Francis Bay - Cape St Francis = Relative index). Total settlers and settlers of *M. galloprovincialis* and *C. meridionalis* were more abundant in bay sites and were found to have a negative relationship with turbulence (Table 3.7, Fig 3.13 a-c). The size classes Recruits B and C of *P. perna* species were not affected by turbulence but their recruitment rates were positively correlated with upwelling (Fig 3.13 d & e). Only Recruits B of *C. meridionalis* were correlated with upwelling and this relationship was negative (Fig 3.13 f), unlike *P. perna*. There was not significant correlation of *M. galloprovincialis* recruitment rates with either upwelling or turbulence. Recruits C of *P. perna* were positively correlated with upwelling (Fig 3.13 g). There were no other significant correlations of recruits C. Recruits D of all species were found to be unaffected by either upwelling or turbulence.

DISCUSSION

The results of this study show an interaction between topography and time on settlement and recruitment. Following the general trend of previous literature (McQuaid & Phillips 2006; Nicastro *et al*. 2007; von der Meden 2009), this study highlighted a higher degree of settlement and recruitment in bays than on open coasts (Fig 3.3), but only on one occasion (event 4), when values were markedly elevated in bays. Consequently, this general trend was driven by peaks in settlement during a specific sampling event (Fig 3.3). This high temporal variability in settlement/recruitment in bays and not at open coast sites at small temporal scales has also been reported at a larger seasonal scale by von der Meden (2009). Seasonal peaks in mussel settlement and recruitment linked to pulsed spawning have been observed in bays, but these peaks did not occur at open coast sites (von der Meden 2009).

The differences in topography and bathymetry between bay and open coast sites result in a stark difference in nearshore oceanographic regimes (Wolanski & Hamner 1988; Geyer & Signell 1992; McCulloch 2003; Schmidt *et al.* 2005). In bays, the widening of the continental shelf and concave nature of the coastline often result in nearshore larval retention (Murdoch 1989; Wing *et al.* 1998b; Largier 2004; Reaugh 2006). A possible reason for the higher settlement rates observed in this study in bays could be higher larval retention within bays. In chapter 2 of this thesis pelagic larval abundance in relation to topography have been discussed.

Although wave action was not directly measured during this study, prior research conducted within these areas reported that wave exposure differs between bays and open coasts with open coast sites experiencing increased of wave action (Lasiak 1984; Beckley 1985; Bruton *et al.* 1991). The significance of wave action on settlement rates is a complex issue. Previous studies have discussed the possible benefits of higher flow rates over potential settlement surfaces, as higher flow rates should, in theory, increase the contact rate through more intense turbulence diffusion (Schlichting 1979). In contrast, these higher flow rates would also decrease the time for attachment and increase drag and lift forces that may detach settled larvae from the substratum (Abelson & Denny 1997; Crimaldi *et al.* 2002). The increased wave action at the open coast sites, in this particular study region (Beckley 1985; von der Meden 2009), may have prevented mussels from settling, as the time for larval attachment is reduced and/or perhaps drag and lift forces are excessive, resulting in the removal of settlers and recruits from the substratum. Many prior studies have reported an increase of settlement rates with increased water flow (Judge & Craig 1997), while others have reported the opposite to be true (Crisp 1955; Mullineaux & Butman 1991). Some studies have even shown intermediate flow rates to have the highest settlement rates (Qian *et al.* 2000). The lack of consensus as to the significance of flow rate and wave action on mussel larval settlement rates points to the idea that physical processes may not be the most important factors to consider when developing settlement rate models (Jonsson *et al.* 2004). Larval behaviour, in terms of selective detachment, is not well documented and remains a challenging area, particularly in field studies (Jonsson *et al.* 2004).

The Algoa and St Francis regions did not differ in terms of upwelling and turbulence indices. There appeared, however, to be a significant difference between sampling events with event 4 having the most unique pattern (Fig 3.7 d & i). Event 4 differed in that there was a spike in wind driven turbulence and downwelling followed by a relaxation of both. Because settlers of < 360 µm would not have arrived on the shore more than 4 days prior to sample collection, they could have been associated with this relaxation period. During this sampling event, the number of settlers was significantly higher in bay sites than in open coast sites (Fig 3.3). In contrast to settlement rates, event 4 did not appear to be significantly different to all other sampling events with regard to recruitment rates. There were peaks in recruitment rates during different events at each site and these peaks did not appear in any distinguishable topographic or temporal pattern (Figs 3.5). Although there were few clear patterns in recruitment, there were obvious peaks for both *M. galloprovincialis* and especially *P. perna* in St Francis Bay during event 1 (Fig 3.5). Because wind patterns and settlement rates were found to be different during event 4 to all other sample, but recruitment rates were not, this suggests that wind driven turbulence and upwelling indices may have a relationship with settlement rates, but not recruitment rates specifically in these two bay sites.

Individual regressions were run for each combination of abundance and wind driven process (upwelling and turbulence). In Algoa Bay and St Francis Bay, settlement rates of total settlers increased with decreasing turbulence (Fig 3.8a & 3.9a).

This finding differs from the results of a laboratory simulation of downwelling in which it was found an increase in settlement with increasing turbulence (Pernet *et al.* 2003). In this simulation, mussel larvae did not behave as passive particles, but possible changes in larval behaviour, influenced by the laboratory setting, could explain the differences between the laboratory based study and the present field observations. Another important consideration is that in the study by Pernet *et al.* (2003), turbulence was measured directly, whereas in the present study turbulence indices were calculated using wind data which could potentially be correlated to other processes that influence settlement rates.

Although settlement rates at Skoenmakerskop were found to be uncorrelated to either upwelling or turbulence, at Cape St Francis settlement rates were positively correlated with both upwelling and turbulence (Fig 3.10). The Cape St Francis pattern fits the observation of the Pernet *et al.* (2003) model. Because the open coast site of Skoenmakerskop does not fit the Pernet *et al*. (2003) model, one can assume that broad categories of topography (bay and open coasts) need to be refined further before drawing conclusions. Turbulence was also seen to be higher at Cape St Francis compared to Skoenmakerskop. The difference in turbulence could also have contributed to this difference in results between the 2 open coast sites as settlers would be greatly affected by any changes in turbulence both positively and negatively.

The increased turbulence in the Algoa Region (significantly higher than at the St Francis Region) could perhaps originate from increased wave action at the open coast site of Skoenmakerskop. If wave action was above a theoretical threshold, the chances of detachment of settlers would have increased, resulting in a lack of relationship between these wind driven factors and settlement rates at Skoenmakerskop. This, of course, leaves room for improvement of future studies which could aim to collect not only the settlement and wind data, but also quantify site specific wave action and wind data.

The relationships of upwelling and turbulence with recruitments rates were affected by topography and region. There was no significant correlation between either upwelling or turbulence and recruitment at open coast sites (Table 3.6). Conversely, there were significant correlations of recruitment with turbulence and upwelling in bay sites. These correlations differed between regions, which probably links to the differences in turbulence found between regions, as discussed earlier, although this needs to be tested. What is certain is that the results from the these regressions reinforce the idea that wind driven turbulence and upwelling indices are important predictors of settlement and recruitment rates, at least in bay sites.

Because no significant differences were found between the mean turbulence or upwelling indices, it suggests that recruitment rates were affected by other regional variables. The reason behind the positive correlation between mean upwelling and the relative index of recruits (B & C) rates is unclear. Initially this was thought to be possible associated with increased nutrients having a positive effect on successful recruitment however there is a time lapse between upwelling and phytoplankton blooms (Sakar & Chattopadhayay 2003) that this experimental design would not have been able to account for.

Recruitment of D recruits were not significantly correlated with either upwelling or turbulence, suggesting that post-settlement factors such as competition, predation, or dislodgement become more significant predictors (Keough & Downes 1982; Connell 1985; Minchinton & Scheibling 1993; Rodriguezl *et al.* 1993; Gosselin & Qian 1997; Balch & Scheibling 2000; Jenkins *et al*. 2000). Post-settlement mortality may be the major reason for the decoupling of recruitment rate and wind-driven processes (Ross 2001).

This study found that settlement rates were higher in bay sites and were also commonly negatively correlated with turbulence. These results highlight the need for future studies to attempt to identify a threshold where turbulence becomes excessive (along with the lift and drag forces associated with it) and settlers are either dislodged or unable to settle. Without knowing these thresholds, accurate models of settlement and recruitment rates cannot be designed. Post-settlement mortality variables and how they relate to recruitment rates needs to be incorporated into any model of recruitment.

Table 3.1: ANOVA table of A) Total settlers, B) *M. galloprovincialis* settlers, C) *P. perna* settlers and D) *C. meridionalis* settlers with Site, Event and Site and Event as random factors (p- values < 0.05 were considered significant)

		A				**B**				**C**				**D**			
		Total Settlers				***M. galloprovincialis***				***P. perna***				***C. meridionalis***			
EFFECT	**DF**	**SS**	**MS**	**F**	**P**	**SS**	**MS**	**F**	**P**	**SS**	**MS**	**F**	**P**	**SS**	**MS**	**F**	**P**
SITE	3	11600	3859	4.602	0.007	3785	1262	4187	0.011	2201	733.8	4.614	0.007	9.89	3.298	3.858	0.016
EVENT	4	24700	6185	7.375	<0.001	10400	2612	8.669	<0.001	2744	686	4.314	0.005	9.15	2.288	2.676	0.046
SITE * EVENT	12	37700	3143	3.748	0.001	12000	1002	3.324	0.002	7849	654.1	4.113	<0.001	12.64	1.053	1.232	0.296

Table 3.2: ANOVA table of A) Total Recruits, B) *M. galloprovincialis* recruits, C) *P. perna* recruits and D) *C. meridionalis* recruits with Site, Event and Site and Event as random factors (p- values < 0.05 were considered significant)

		A				**B**				**C**				**D**			
		Total Recruits				***M. galloprovincialis***				***P. perna***				***C. meridionalis***			
EFFECT	**DF**	**SS**	**MS**	**F**	**P**	**SS**	**MS**	**F**	**P**	**SS**	**MS**	**F**	**P**	**SS**	**MS**	**F**	**P**
SITE	3	581	193.7	45.07	<0.001	33.2	11.07	48.2	<0.001	322	107.4	31.81	<0.001	0.3	0.098	5.201	0.004
EVENT	4	554	138.5	32.23	<0.001	1.32	0.33	1.44	0.238	501	125.2	37.1	<0.001	0.14	0.035	1.852	0.138
SITE * EVENT	12	810	67.5	15.7	<0.001	9.42	0.79	3.42	0.002	709	59.1	17.51	<0.001	0.21	0.018	0.941	0.517

Table 3.3: Differences in Upwelling and turbulence between the Algoa Region and St Francis region over the entire March sampling period (Mann-Whitney U test), n = 78 and n = 73 respectively (p- values < 0.05 were considered significant)

		Algoa Region		**St Francis Region**		
EFFECT	**DF**	**Mean**	**SD**	**Mean**	**SD**	**P**
Upwelling	104	-104	166074	-98	668480	0.475
Turbulence	134	1.30E-06	2.41E-12	9.00E-07	1.05E-12	0.03

Table 3.4: Differences in A) upwelling and B) turbulence between the Algoa (AB) and St Francis (SF) regions during each sample event (Kruskal Wallis, Mann-Whitney pairwise) (p- values < 0.05 were considered significant *)

A) Upwelling

	AB 1	AB 2	AB 3	AB 4	AB 5	SF 1	SF 2	SF 3	SF 4	SF 5
AB 1		0.68	0.65	0.91	0.49	0.73	0.74	0.66	0.90	0.33
AB 2			0.36	0.56	0.23	0.89	0.58	0.56	0.74	0.27
AB 3				0.47	0.79	0.47	0.88	0.84	0.51	0.71
AB 4					0.28	0.98	0.44	0.66	0.98	0.20
AB 5						0.35	0.92	0.80	0.28	0.71
SF 1							0.54	0.48	0.98	0.20
SF 2								0.92	0.55	0.63
SF 3									0.59	0.72
SF 4										0.26
SF 5										

B) Turbulence

	AB 1	AB 2	AB 3	AB 4	AB 5	SF 1	SF 2	SF 3	SF 4	SF 5
AB 1		0.51	0.31	0.02*	0.17	0.54	0.68	0.91	0.14	0.88
AB 2			0.14	0.01*	0.06	0.86	0.93	0.69	0.09*	0.72
AB 3				0.23	0.91	0.08	0.19	0.31	0.79	0.28
AB 4					0.28	0.01*	0.00*	0.02*	0.25	0.00*
AB 5						0.06	0.05	0.20	0.98	0.17
SF 1							0.65	0.51	0.05	0.49
SF 2								0.51	0.05	0.60
SF 3									0.17	0.85
SF 4										0.08

Table 3.5: Summary of significant regression analyses of turbulence and upwelling against settlement rates of all mussel species at each site (n = 10, p-values < 0.05 were considered significant)

Site	**x**	**y**	**R^2**	**Slope**	**P-value**
Algoa Bay	TURBULENCE	Total settlers	0.4783	-9E+07	0.004
Algoa Bay	TURBULENCE	*M. galloprovincialis*	0.4566	-5E+07	0.006
Algoa Bay	TURBULENCE	*P. perna*	0.4758	-4E+07	0.004
Algoa Bay	TURBULENCE	*C. meridionalis*	0.4846	-2E+06	0.004
St Francis Bay	TURBULENCE	Total Settlers	0.3207	-2E+07	0.028
St Francis Bay	TURBULENCE	M. galloprovincialis	0.3206	-2E+07	0.028
Cape St Francis	UPWELLING	Total Settlers	0.2881	0.0008	0.039
Cape St Francis	TURBULENCE	Total Settlers	0.3932	752861	0.012
Cape St Francis	UPWELLING	*P. perna*	0.3545	0.0008	0.019
Cape St Francis	TURBULENCE	*P. perna*	0.4115	727827	0.010

Table 3.6: Summary of significant regression analyses of turbulence and upwelling against recruitment rates of all mussel species at each site (p-values < 0.05 were considered significant)

Site	**x**	**y**	**R^2**	**Slope**	**P-value**
Algoa Bay	UPWELLING	*M. galloprovincialis*	0.354	-0.003	0.019
St Francis Bay	UPWELLING	Total Recruits	0.7997	0.047	<0.001
St Francis Bay	UPWELLING	*M. galloprovincialis*	0.416	0.003	0.009
St Francis Bay	UPWELLING	*P. perna*	0.785	0.044	<0.001
St Francis Bay	TURBULENCE	Total Recruits	0.466	3E+07	0.006
St Francis Bay	TURBULENCE	*P. perna*	0.490	3E+07	0.004

Table 3.7: The significant regression analyses of turbulence and upwelling against relative index of settlement and recruitment rates of all mussel species (p-values < 0.05 were considered significant)

x	**y**	**R^2**	**Slope**	**P-value**
TURBULENCE	Total Settlers	0.428	-5E+07	0.040
TURBULENCE	*M. galloprovincialis*	0.493	-3E+07	0.024
TURBULENCE	*C. meridionalis*	0.498	-971965	0.023
UPWELLING	Total Recruits B	0.533	0.019	0.016
UPWELLING	*P. perna*	0.570	0.020	0.012
UPWELLING	*C. meridionalis*	0.452	-0.004	0.033
UPWELLING	*P. perna*	0.529	0.012	0.017

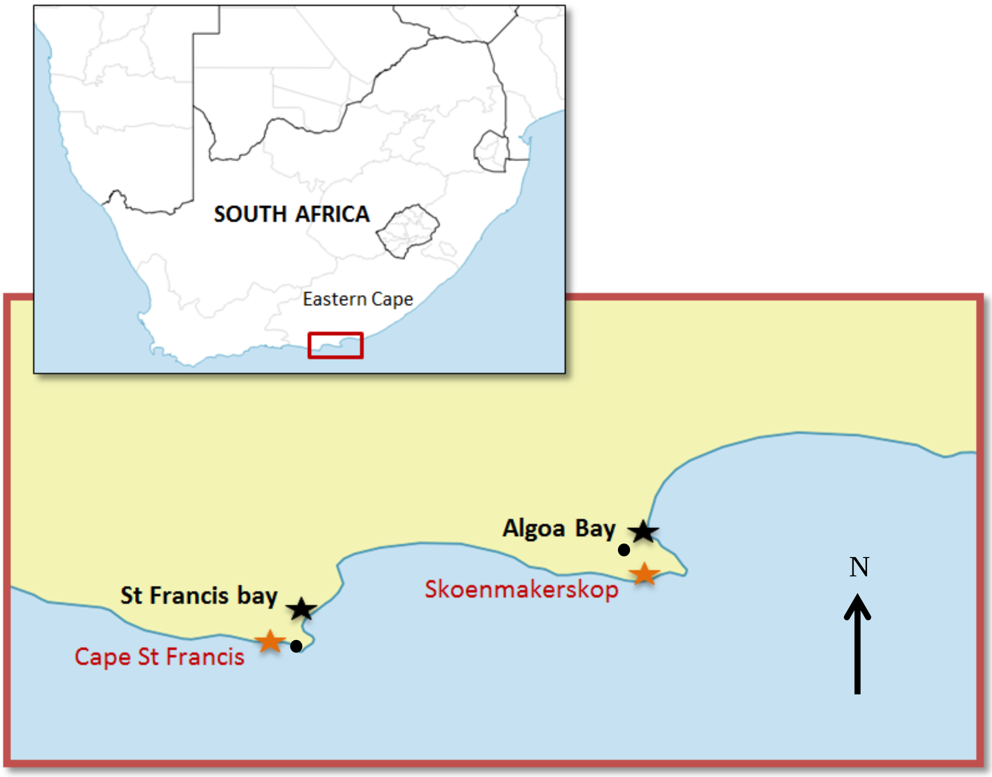


Figure 3.1: The Location of each study site is either denoted by an orange (★) for open coast sites or a or black (★) star for bay sites, Algoa Bay (S33°55’46”, E25°36’38”), Skoenmakerskop (S34°02’27”, E25°31’57”), St Francis Bay (S34°10’15”, E24°50’05”) and Cape st Francis (S34°12’36”, E24°49’32) and weather stations marked by grey dots (●)

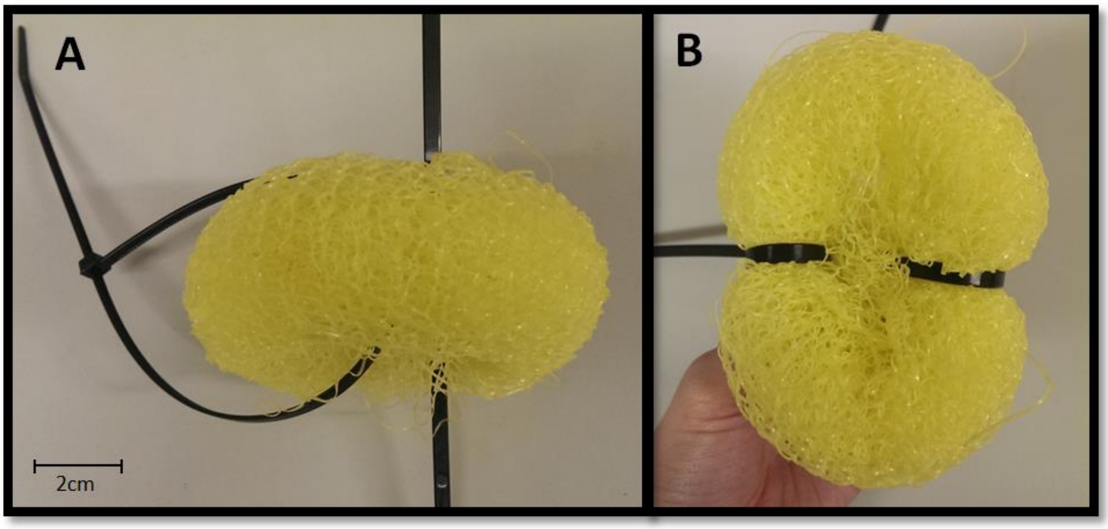


Figure 3.2: Photograph of a settlement collector a) side view with cable ties and b) dorsal view with cable ties tightened

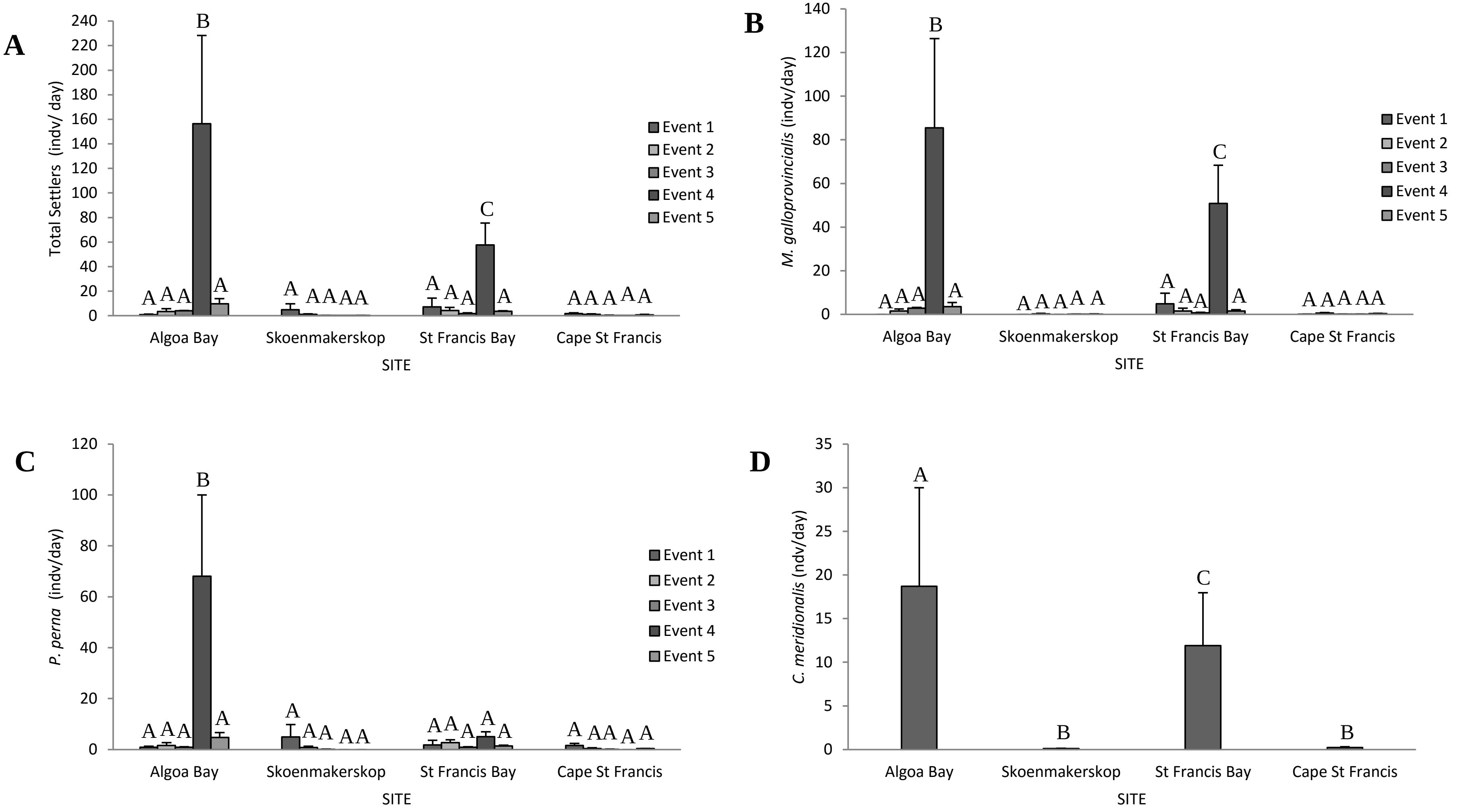


Figure 3.3: The per day settlement rates of A) Total settlers, B) *M. galloprovincialis* and C) *P. perna* at each site during each sample event as well as D) *C. meridionalis* mean settlement rates over the entire March sampling period. Letters A – C above bars differentiate homogenous groups (p- values < 0.05 were considered significant)

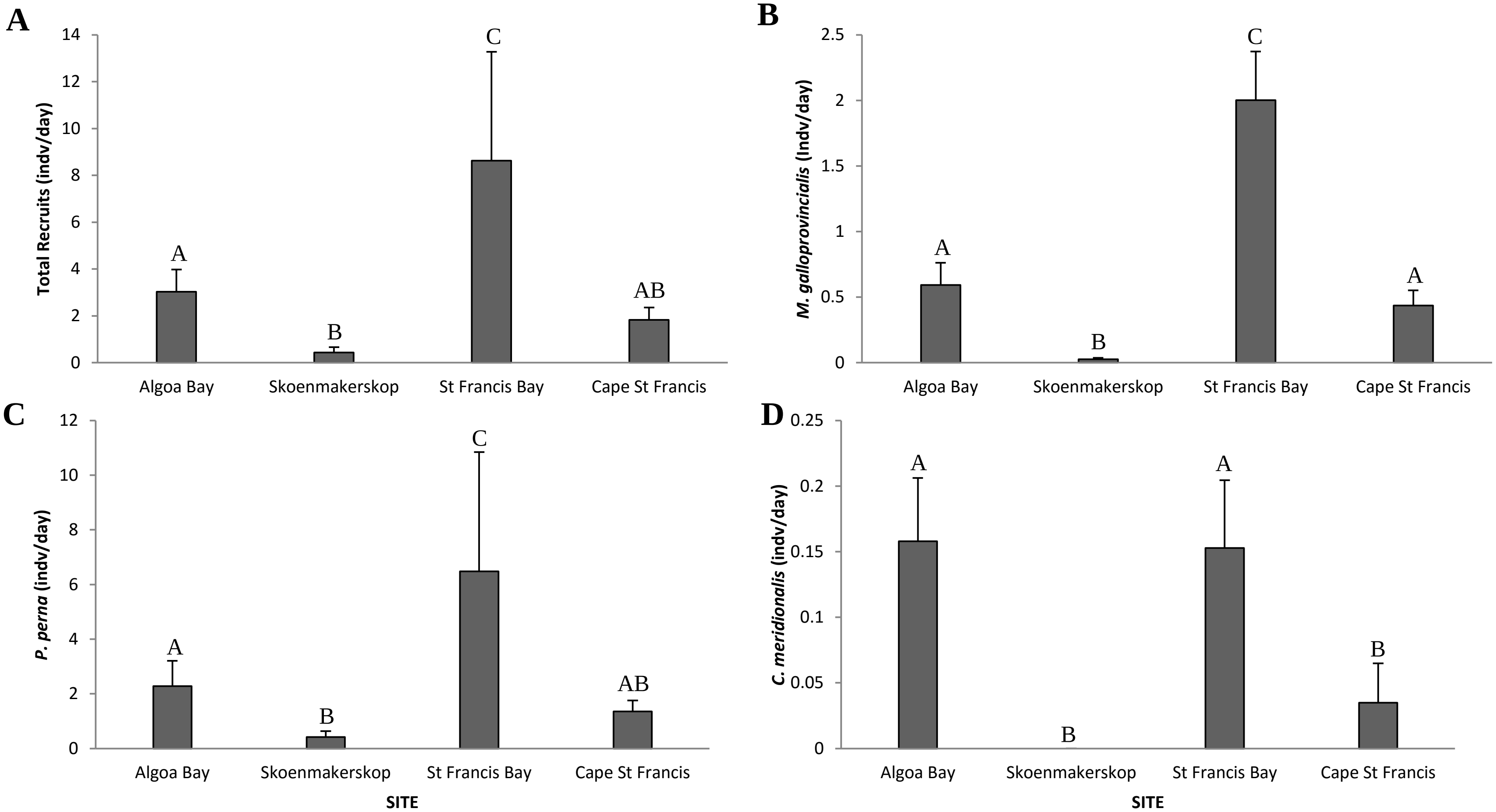


Figure 3.4: Recruits at each site over the entire sample period the per day recruitment rates of A) Total recruits, B) *M. galloprovincialis*, C) *P. perna* and D) *C. meridionalis* averages at each site over the whole season. Letters A – C above bars differentiate homogenous groups (p- values < 0.05 were considered significant)

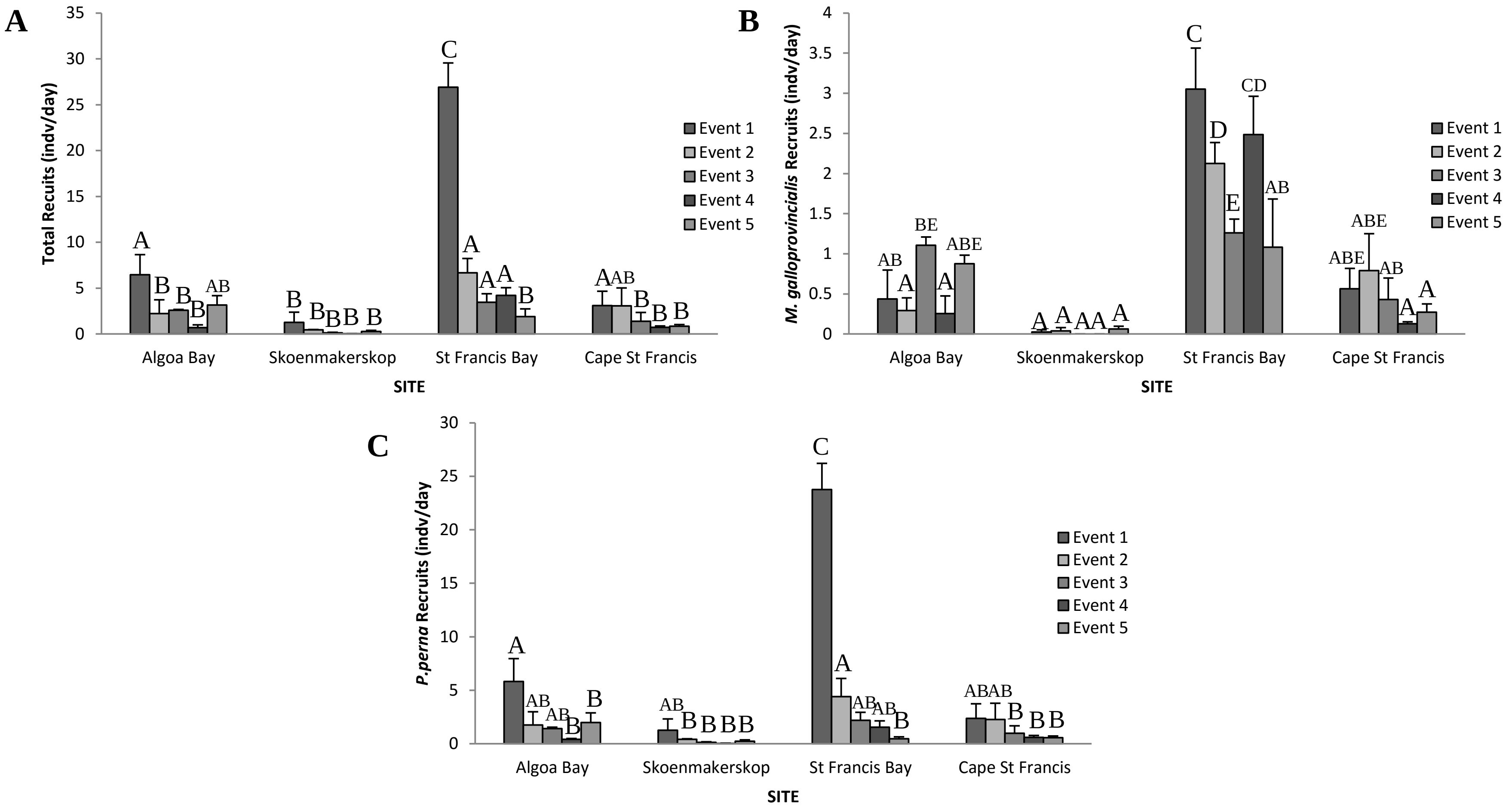


Figure 3.5: The per day recruitment rates of A) Total recruits, B) *M. galloprovincialis* and C) *P. perna* at each site during each event. Letters A – E above bars differentiate homogenous groups (p- values < 0.05 were considered significant)

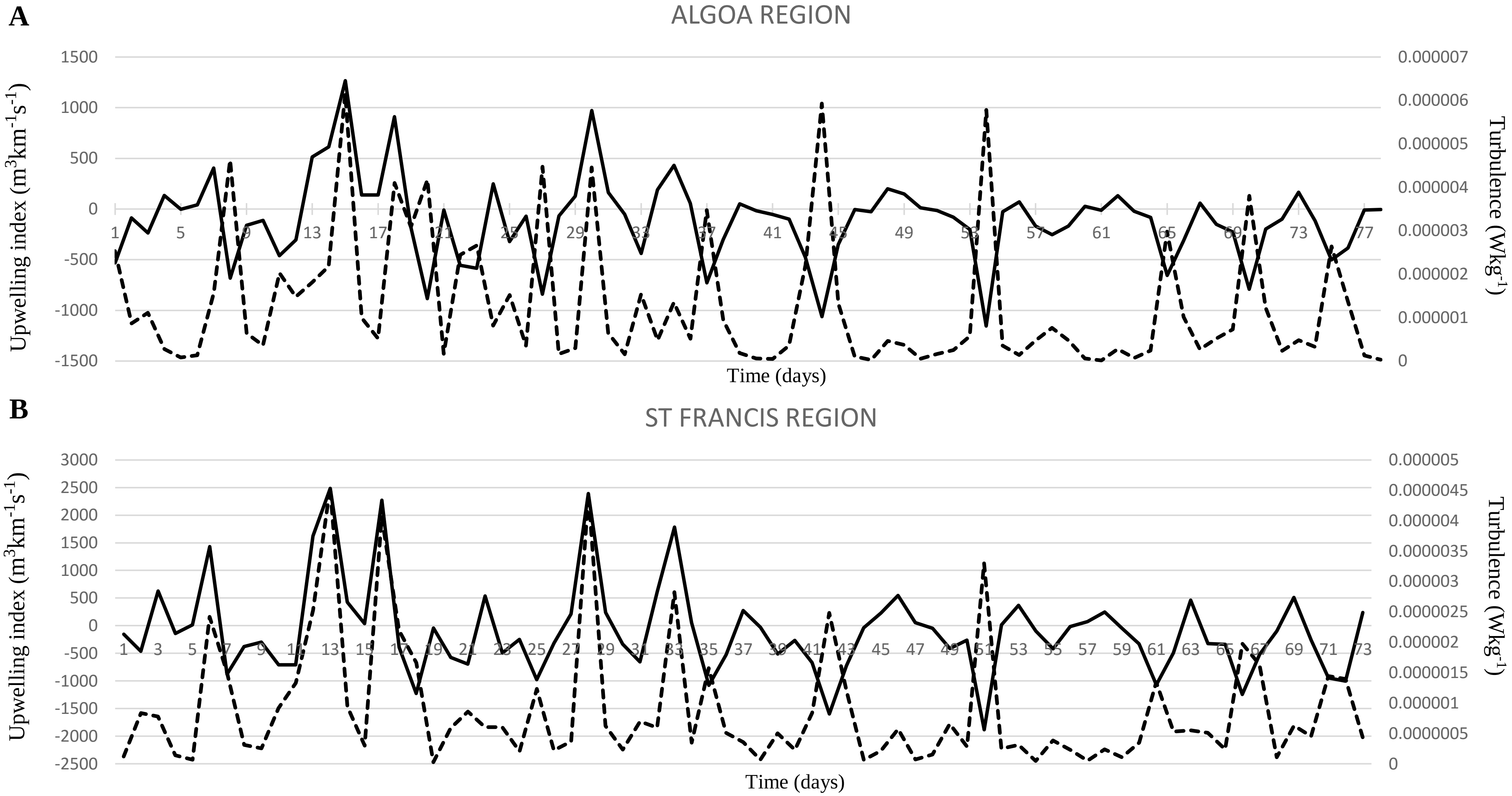


Figure3.6: Daily upwelling ($m^3km^{-1}s^{-1}$) (solid line) and turbulence (Wkg^{-1}) (broken line) over the entire sample season for A) the Algoa Region (Algoa Bay and Skoenmakerskop) and B) the St Francis Region (St Francis Bay and Cape St Francis

ALGOA BAY REGION

ST FRANCIS REGION

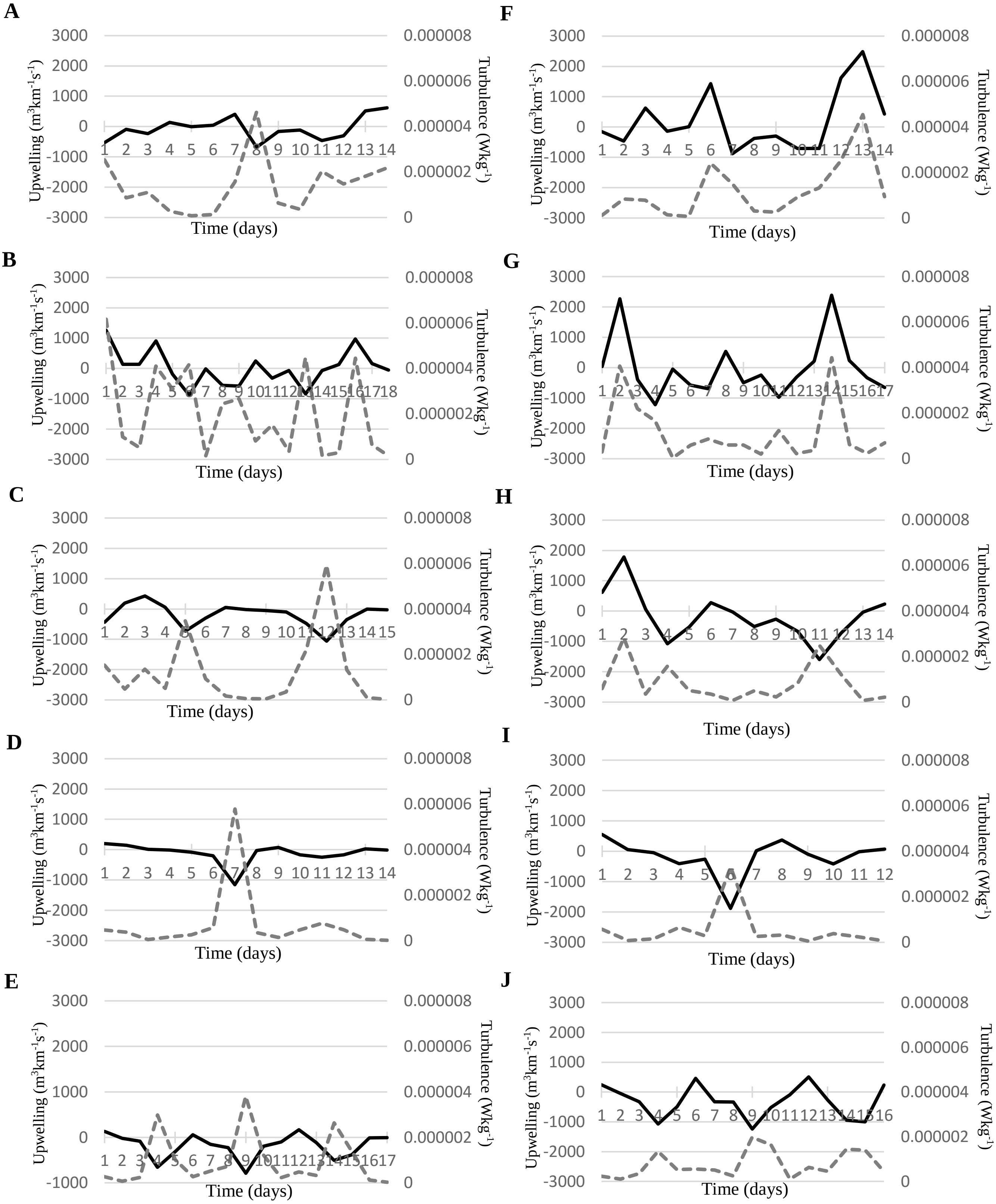


Figure 3.7: Daily upwelling (m^{3}s^{-1}km^{-1}) and turbulence (Wkg^{-1}) for each sample event in the ALGOA BAY region (events 1- 5 are A to E respectively) and the ST FRANCIS region (events 1 - 5 are F to J respectively) NOTE the different Y-axis scales

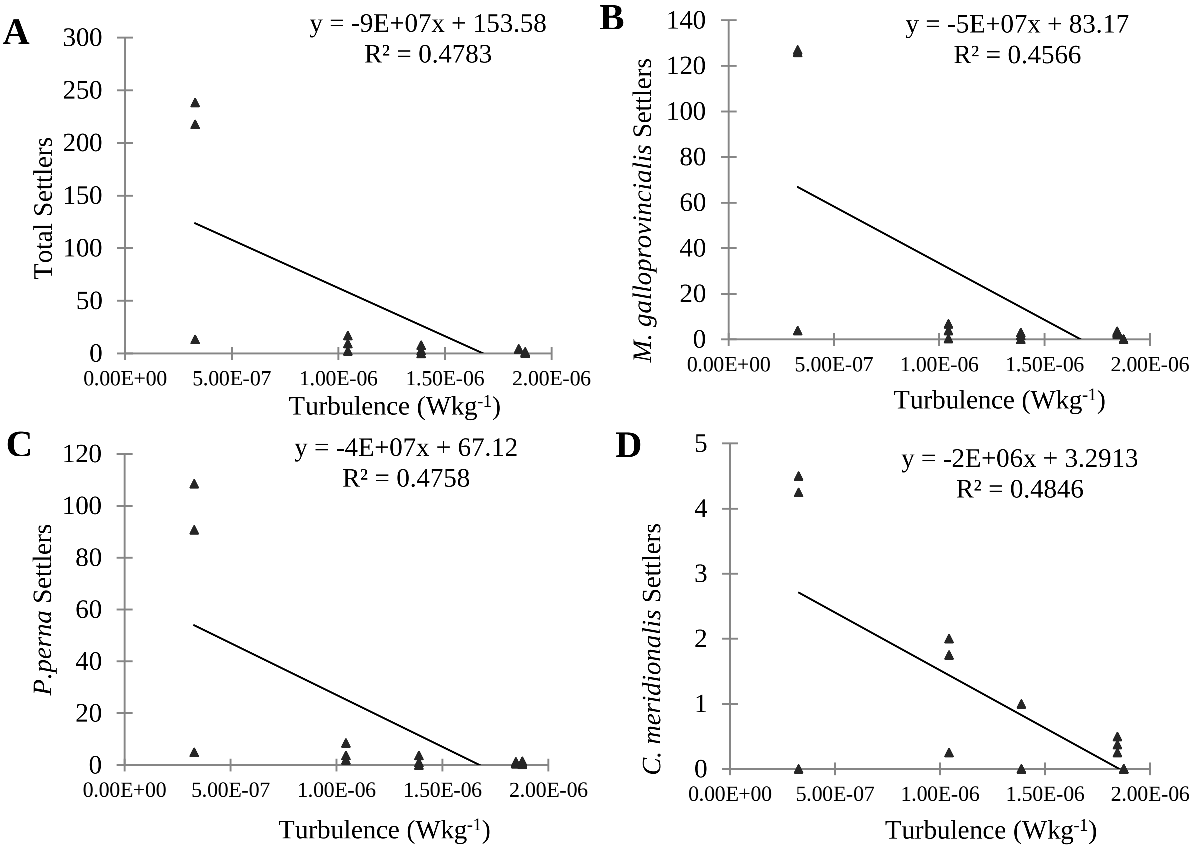


Figure 3.8: Regression graphs of A) Total setters (p = 0,004) B) *M. galloprovincialis* (p = 0.006), C*) P. perna* (p = 0.004) and D) *C. meridionalis* (p = 0.004) against turbulence (Wkg^{-1}) in Algoa Bay

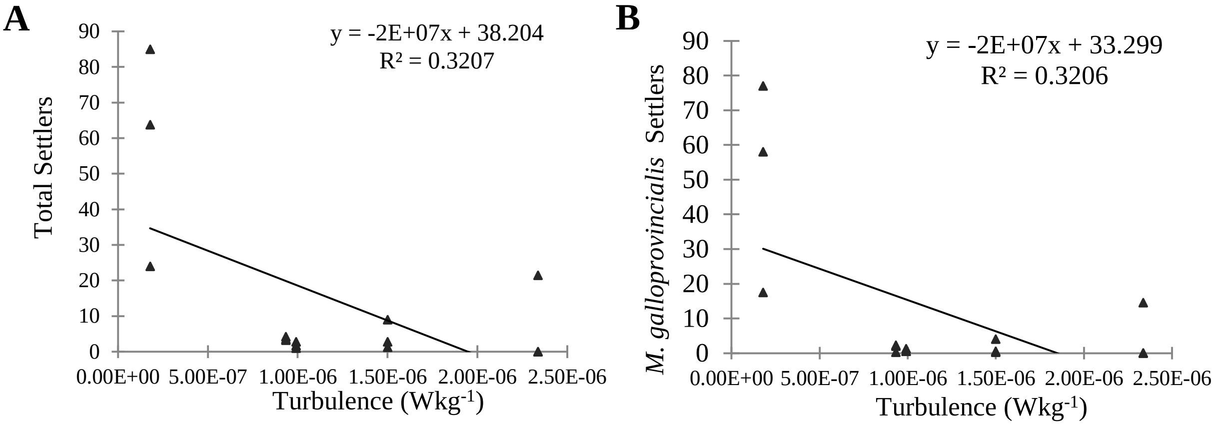
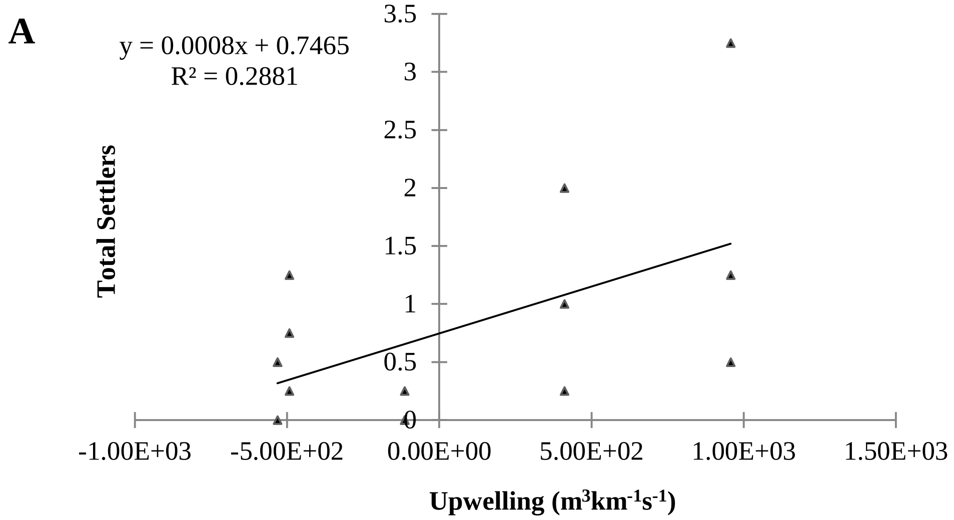


Figure 3.9: Regression graphs of A) Total setters (p = 0.028) and B) *M. galloprovincialis* (p = 0.028) against turbulence (Wkg^{-1}) in St Francis Bay



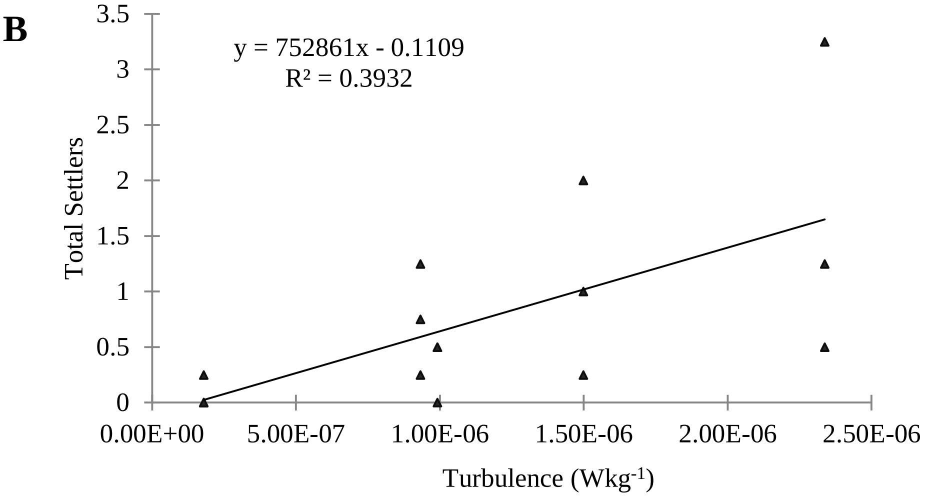


Figure 3.10: Regression graphs of Total setters against A) upwelling ($m^3s^{-1}km^{-1}$) ($p = 0.039$) and B) turbulence (Wkg^{-1}) ($p = 0.012$) in Cape St Francis

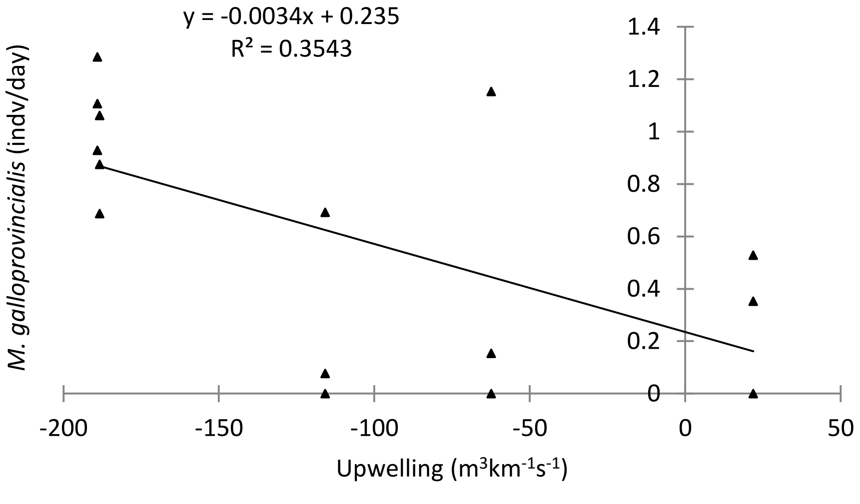


Figure 3.11: Regression graphs of *M. galloprovincialis* against upwelling ($m^3km^{-1}s^{-1}$) in Algoa Bay ($p = 0.019$)

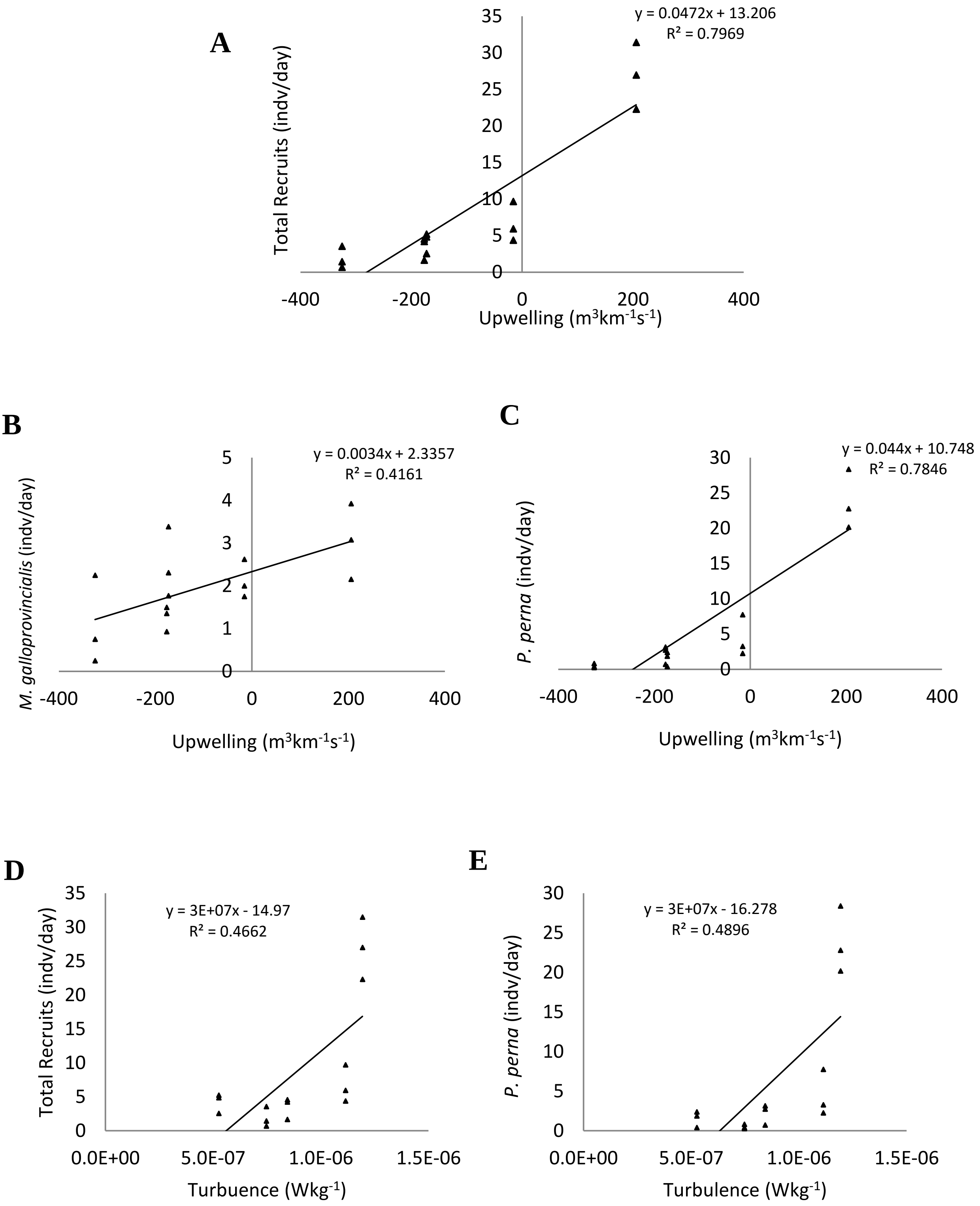


Figure 3.12: Regression graphs of A) Total recruits ($p < 0.001$) B) *P. perna* ($p = 0.009$) and C) *M. galloprovincialis* ($p < 0.001$) recruits against upwelling ($m^3km^{-1}s^{-1}$) and D) Total recruits ($p = 0.006$) and E) *P. perna* ($p = 0.004$) recruits against turbulence (Wkg^{-1}) in Algoa Bay

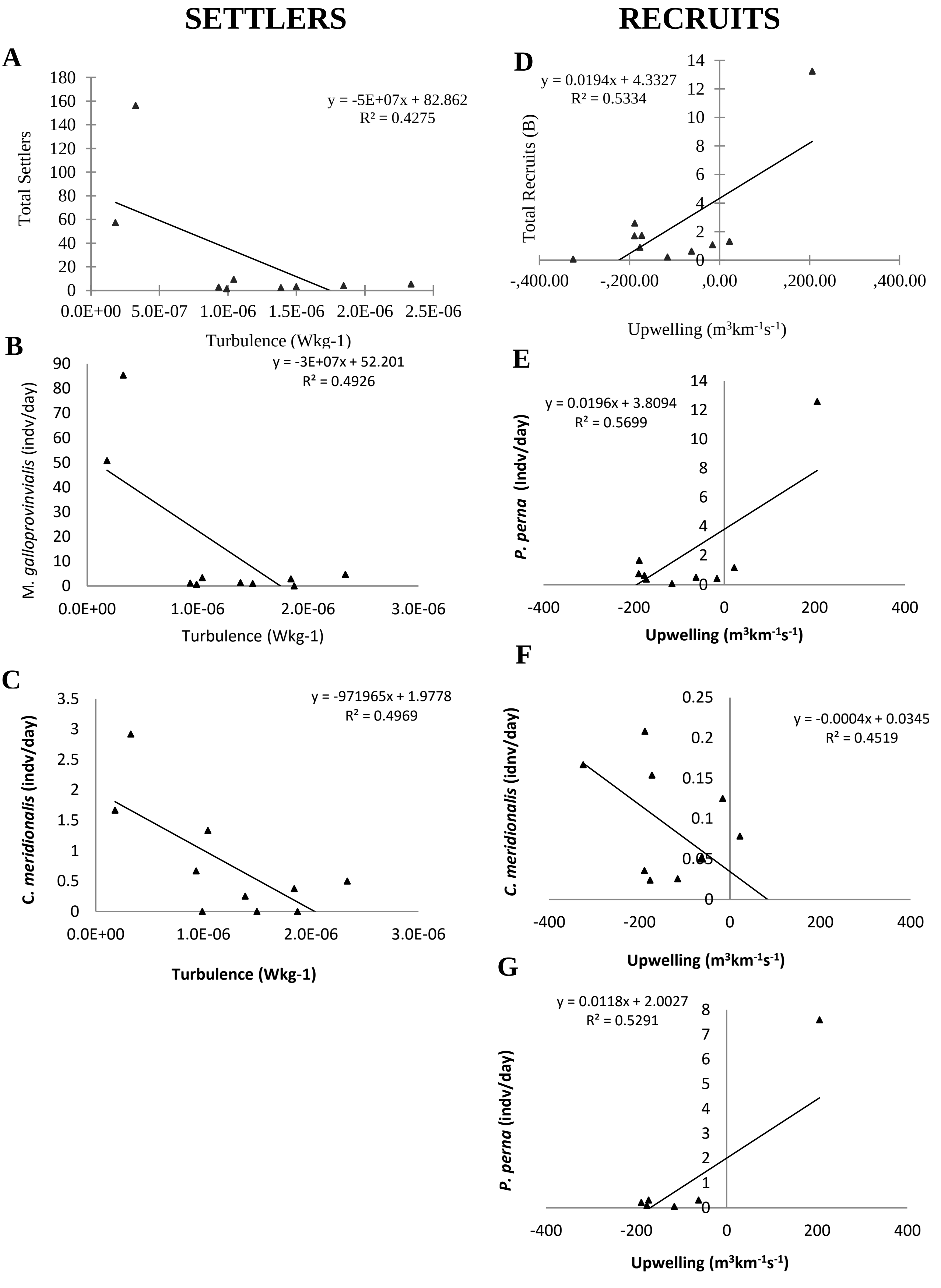


Figure 3.13: Regression graphs of relative abundances of A) Total settlers (p=.04), B) *M. galloprovincialis* settlers (p=0.02) and C) *C. meridionalis* settlers (p=0.02) against turbulence (Wkg^{-1}). Relative abundances of D) Total recruits size class B (0.02), E) *P. perna* size class B (p=0.01), F) *C. meridionalis* recruits size class B (p=0.03) and G) *P. perna* recruits size class C (p=0.02) against upwelling (m^{3}km^{-1}s^{-1})

Chapter 4:

Synthesis

> *“Science is not about control. It is about cultivating a perpetual condition of wonder in the face of something that forever grows one step richer and subtler than our latest theory about it. It is about reverence, not mastery.”*
>
> - Richard Powers

NEARSHORE LARVAL RETENTION

Larval behaviour: a taxonomic and ontogenetic activity gradient

The first aim of the thesis was to determine whether larvae were active or passive in the water column and whether this contributed to nearshore retention. Another aspect was whether larval activity was taxonomically, topographically or ontogenetically driven. The larvae considered in this study were predominantly planktotrophic, however the bryozoan group was likely made up of lecithotrophic larvae (Schopf 1977). Additionally, barnacle larvae made up a mixed model, with an ontogenetic shift from planktotrophy to lecithotrophy (Thiel & Watling 2015).

Larvae were found to be generally active in the water column, however their activity levels fell along a gradient, rather than an active/passive categorisation. Larvae were considered active if their mean depth was negatively correlated with upwelling and if it also correlated with the mean depth of shoreward moving water masses (Grantham 1997; Pineda 2000; Poulin *et al.* 2002; Shanks & Brink 2005; Genin *et al.* 2005; Pineda 2007; Morgan *et al.* 2009; Weildberg *et al.* 2015). The results in chapter 2 of this thesis revealed that mean larval depth was both negatively correlated with upwelling and positively correlated with mean depth of meridional flow (shoreward moving water). The negative correlation with upwelling indicates that, during upwelling, larvae are at lower depths than during downwelling, when they are mostly found closer to the surface. This pattern results in larvae being associated with shoreward moving water. An association with shoreward moving water is a possible mechanism of nearshore retention within the study region.

Larvae with slower swimming speeds, such as the D-stage bivalves and bryozoans were less active when compared to the other larval groups that have faster swimming speeds, such as brachyurans (Queiroga & Bianton 2004; Miller & Morgan 2013) and barnacles (Chia *et al.* 1983).

A clear and general effect of topography on larval abundance was not obvious from this study. Larval abundances instead peaked at various sites (regardless of topography) and distances off shore. The only factor that could be linked to topography was depth, with a clearer bottom to mid-depths shift in larval mean depth from bays to the open coast. This topographic pattern could linked to the shallower depths of the bays in comparison to open coast, making larvae unable to reach bottom depths at the open coast sites.

Larval activity was also linked to ontogeny. Bivalve groups were more active than the early D-stage stages, although it was impossible to resolve the taxonomy of such early stages of bivalves. Older bivalves and decapods were associated with bottoms depth more than the earlier stages, a pattern also observed by previous studies (Brookins & Epifanio 1985; Mann *et al*. 1991; Baker & Mann 2003; Gallager *et al.* 1996; Tamaki *et al*. 2010). Similarly, cyprids were found at mid to bottom depths while nauplii mostly occurred at mid depths. Ontogenetic considerations can certainly further complicate larvae transport models. Studies such as Titelman & Fiksen (2004) noted differences in swimming behaviour of copepods according to ontogenetic development. The same was noted by Guizien *et al.* (2006).

Nearshore hydrodynamics have been suggested as facilitating passive nearshore larval retention. The Coastal Boundary Layer (CBL), for example, with its slow moving and less dynamic water is thought to trap larvae close to the shore (Wolanski 1994; Largier 2003; Siegel *et al.* 2003). This retentive phenomenon would be of significant importance to slow swimming, passive larval taxa, as well as to early stage larvae (D- stage bivalves and early barnacle nauplii), preventing offshore transport (Wolanski 1994; Largier 2003). Larval distributions around the world have, however, demonstrated that larval retention is too nearshore to be solely reliant on passive mechanisms (McQuaid & Phillips 2000; Morgan *et al.* 2009; Poulin *et al*. 2002; Shanks & Brink 2005; Shanks & Shearman 2009). I suggest that larval ontogenetic activity gradients are among the most important factors to consider in fine scale tuning of cross-shore larval distribution. As larvae age, they become more active and capable of orientating themselves in the water column which would allow them to remain closer to the shore than early stage conspecifics.

Passive mechanisms however, may not only have an effect on cross-shore distribution of larvae, but may also greatly affect along-shore transport of larvae (Weidberg 2012). Ontogenetic gradients of activity could further influence the interactions between cross-shore and alongshore transport and explain how nearshore retention does not completely limit along-shore transport.

HOW WOULD THIS RELATE TO SETTLEMENT?

Settlement and topography

Previous studies have noted differences in adult population structure of intertidal species between bay and open coast sites (Crisp & Southward 1958; Helson & Gardner 2004; Lagos *et al.* 2005; McQuaid & Phillips 2006; Von Der Meden 2009; Pfaff *et al.* 2011; von der Meden *et al*. 2012). Despite this being a common trend, the processes that drive the observed differences in population densities between these topographic features are not yet fully understood. Some studies have named factors such as differential wave action, the presence of "upwelling shadows" in bays and not capes as well as other bathymetrically modified nearshore hydrodynamics as possible drivers for a topographic trend.

The present study attempted to build on the work of von der Meden and co-authors (2012) who found that although adult populations of mussels were different, post-settlement mortality was not the driving factor. The data presented in chapter 3 of this thesis found that there were higher settlement rates in bays than open coasts. As discussed by von der Meden *et al.* (2012), this suggests that the topographic trend of adult densities may be driven by supply side factors such as the larval pool. In contrast, the pelagic component of this thesis (chapter 2) did not find the expected topographically driven differences in larval distributions. Pelagic larval abundances were sporadic and peaks were seen at both bay and open coast sites, while negatively affected by turbulence in bays. When turbulence is low it there may also be reduced wave action, allowing settlers to settle without being washed off the new settlement sites by drag forces. Because bay sites, unlike open coast sites, are generally more wave sheltered in this region (Darbyshire & Darbyshire 1964; McQuaid *et al*. 2000, Erlandsson *et al.* 2005, von der Meden *et al*. 2008), a reduction in turbulence would be associated with greatly decreased wave action. It is possible that open coast sites do not experience a reduction in wave action that is low enough to result in a correlation between turbulence and settlement rates. A reduction in turbulence could also result in the reduction in width of the surf zone (Mocke 2001), allowing pelagic larvae to move closer and spend longer periods near potential settlement sites (Shanks *et al.* 2010). This reduction in the width of the surf zone could occur in bays, but not on the open coast as the surf zone dynamics change with regard to shore type (Shanks *et al.* 2010). This possible difference between bay and open coast sites could be an important cue to explain the presence of a topographic pattern for settlement/recruitment, but not for overall pelagic larval abundance.

Coupling supply-side ecology and settlement rates

Unfortunately, the loss of settlement collectors due to rough seas during sampling in September 2013 prevented meaningful correlation analyses to accurately investigate possible relationships between larval supply and settlement. Coupling (Minchinton & Scheibling, 1991; Pineda *et al*. 2002) and/or uncoupling of larval supply and settlement (Miron *et al*. 1995; Olivier *et al.* 2000; Porri *et al*. 2006; Rilov *et al.* 2008) is a current issue in understanding connectivity and overall population dynamics (Pineda *et al*. 2010 for full review). Scaling of the processes involved when trying to compare dispersal and settlement remains one major limitation. Pelagic sampling provides instantaneous measurements (10min – 1hour), whereas settlement rates are determined over longer integrated time scales (1day - 30days) (Bushek 1988; Minchinton & Scheibling 1991; Noda *et al.* 1998; Olivier *et al*. 2000; Satumanatpan & Keough 2001; Palma *et al*. 2006; Porri *et al*. 2006). Because larval abundance is known to be patchy (Barnes & Marshall 1951; Cassie 1957, 1959; Natunewics & Epifanio 2001), the instantaneous sampling of the pelagic environment is likely to miss important peaks in larval abundance or overestimate it at times due to the patchiness of larval distribution in the water column (Pineda *et al.* 2010).

Uncoupling between larval supply and settlement could further be linked to the Desperate Larva Hypothesis (DLH), which originally stated that, as the energy reserves of lecithotrophic larvae deplete, they become “desperate” and less reliant on cues to settle. This would result in larvae accepting suboptimal settlement sites against the risk of mortality (Knight & Jones 1953; Toonen & Pawlik 2001; Marshall & Keough 2003). If larvae remain in the pelagic environment for extended periods of time by delaying settlement they increase their likelihood of larval mortality by nearshore predation and other costs associated with delaying metamorphosis (Woollacott *et al*. 1989; Qian & Pechenik 1998). The DLH has since been revised by Botello & Krug (2006) who drew attention to the risk of strictly categorising larvae as either feeding (Planktotrophic) or non-feeding (Lecithotrophic). Barnacle larvae are particularly interesting in this regard, as they begin as, mostly, feeding (planktotrophic) larvae, but then accumulate fat stores and undergo metamorphogenesis into a non-feeding cyprid stage (Anderson 1994; Chan & Høeg 2015). This stage no longer resembles their naupliar stages in terms of either morphology or feeding behaviour. The cyprid stage relies on lipid energy reserves (Anderson 1994; Chang & Høeg 2015) and its morphology is more streamlined than the naupliar stage, which contributes to the dramatic increase in swimming speeds seen from the naupliar to the cyprid stage (Chia *et al.* 1983). As cyprids rely on energy reserves in much the same way lecithotrophic larvae do, this change in feeding behaviour results in barnacles effectively having a planktotrophic larval stage (as nauplii) and a lecithotrophic phase (as cyprids).

If larval abundance is high within the nearshore, and larvae are young and possess high levels of endogenous energy reserves, they may delay settlement until they perceive positive cues for settling. Conversely, if lower abundances of larvae are present, but larvae are older and energy depleted, settlement rates may be high although pelagic abundances may be low. Coupling or uncoupling of larval supply and settlement could therefore depend on what type of larva is considered as well as its age.

This thesis revealed that larvae are largely active in the water column and this assists with the nearshore retention observed in this region. The topographical differences in settlement rates between bays and open coasts was not seen in the abundances of pelagic larvae and brings into question the uncoupling of larval supply and settlement rates. Perhaps the most urgent area of focus is developing clear categories of larvae based on feeding mechanisms that consider changes in mechanisms according to ontogenetic stages. Ontogenetic shifts in larval activity and how these may affect coupling of supply-side and settlement, as well as larval transport/dispersal is a challenging area, somehow neglected thus far. Future studies should attempt to couple investigating nearshore dispersal processes (in relation to specific physical factors such as storms, turbulence and upwelling) alongside benthic/shore level processes (delivery and settlement) to determine how larval supply and availability of natural substrata may affect the fine delivery of larvae onto the shore.

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